Targets and tools for the maintenance of forest biodiversity

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Targets and tools for the maintenance of forest biodiversity

Edited by
Per Angelstam, Monika Dönz-Breuss and Jean-Michel Roberge

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Foreword

Sustainable development should be a guiding vision for the world's future. The environmental component of sustainable development is the natural base upon which the social and economic components can be built. Forests and woodland represent a particularly clear example of this. Unsustainable use has led to problems such as loss of biodiversity and impoverished ecosystems. It also contributes to catastrophic events such as flooding, land-slides, and avalanches. As a consequence, international, EC and national policies have been formulated for the prudent and sustainable use of forests and woodland.

Two important issues must be at the forefront of our attention. First, results from monitoring of indicators need to be compared with the targets we have set ourselves. Only then can we assess whether we are making progress in the desired direction and at a satisfactory pace. Second, we need tools for integrating the policy messages the indicators send us. We also need to communicate the results of assessments of ecological sustainability to stakeholders. However, such targets and tools are not commonly available.

European and international collaboration widens the perspectives of both scientists and policymakers. It encourages mutual understanding and learning using real world case studies.

This process is of paramount importance to ensure real implementation of the visions behind sustainable development.

I therefore welcome this book which bridges the science of ecology with that of practical conservation planning in forest environments.

Margot Wallström

Targets and tools for the maintenance of forest biodiversity

Per Angelstam, Monika Dönz-Breuss and Jean-Michel Roberge

A summary

Maintaining forest biodiversity by combining protection, management and restoration of forest and woodland landscapes is a central component of sustainable development in northern countries. Succeeding with this can even be viewed as an acid test of sustainability as such. This issue of the Ecological Bulletins is an independent further development of the previous issue entitled "Biodiversity evaluation tools for European forests" (Vol. 50), and focuses on biodiversity maintenance in northern forests at the scale of actual landscapes. The forests dealt with in this volume represent reasonably well-studied systems, a fact that we hope will inspire others to explore ways in which targets and tools for the management of biodiversity in actual landscapes of other ecoregions can be developed.

The readers whom we aim at include not only scientists, but also various actors in the forest sector ranging from the policy level to those dealing with the different elements of forest biodiversity by managing actual landscapes in forests and woodlands globally. To mirror this diversity, the different papers composing this book have been written by a large variety of authors from a range of stakeholder groups. Thus the style varies considerably among the papers, ranging from presentation of original data and reviews synthesising many studies to presentations of ideas and even pleas for transdisciplinary and international collaboration.

The papers in this book are divided into five main sections, each starting with an introducing article. We begin with the views of policy-makers, businesses and managers who all pose questions about the balance between use of renewable forest resources and conservation of biodiversity. Second, the human footprint on northern forests is illustrated. Third, a wide range of animal species are used to test the hypothesis that there are limits to how large the anthropogenic footprint can be without species disappearing locally, regionally or ultimately going extinct. Fourth, different tools for monitoring of the elements of biodiversity within a landscape are presented. Fifth, examples are presented on how biodiversity assessments can be made at multiple spatial scales by combining quantitative targets and measurements of habitat elements.

Finally, a concluding paper proposes how the critical knowledge gaps identified throughout the book could be filled through macroecological research and international co-operation.

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BorNet – a boreal network for sustainable forest management

Without a growing network of scientists and managers interested in and working with the applied ecology of boreal forest this book would never have been written. The name of the boreal network described herein is BorNet (see <www.bornet.org>) and its aim is to promote the dialogue between science and practise on a circumboreal scale.

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A. A wide range of actors pose questions

The new paradigm of sustainable forest management is in the process of being operationally defined. The international and national forest policy level, scientists trying to interpret policies and the whole forest sector, ranging from the buyers of forest products to forest owners and managers, are three major groups of actors involved in defining criteria and indicators, and translating them into operational terms. The papers of this section reflect this process.

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Management for forest biodiversity in Austria – the view of a local forest enterprise	109	M. Dönz-Breuss, B. Maier and H. Malin

B. Understanding the human footprint of forests

As a renewable resource, forests have been traditionally measured using tree growth and volume of produced and harvested timber and pulpwood. From the point of view of biodiversity, however, forests are a diverse group of vegetation types representing different natural and cultural disturbance regimes, but also with different negative impact caused by unsustainable very intensive use. In the first paper of this section the diversity of forest types that this volume focuses on is presented. The other papers report on the effects of the human footprint at different spatial scales on forest structures important for the maintenance of biodiversity.

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C. How much habitat is enough?

To make the principle of sustainable forest management more concrete, a large number of criteria and indicators have been presented. However, to achieve environmental sustainability, it is vital that the monitored indicators are compared with scientifically founded targets to assess both status and, if repeated, trends in the level of sustainability. But forests are different, and there are different components of biodiversity at different spatial scales. In this section, animal species with a wide range of life history traits are used to study relationships between presence and fitness of species' populations and different levels of anthropogenic change in their respective habitats.

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E. Assessing status and trends

With the results from monitoring and relevant targets for a range of indicators it is possible to make assessments of the status of a certain criterion. In this section, examples of practical assessment methods are presented both for strategic and tactic planning of operational management for protection, management and re-creation of the structural and functional aspects of biodiversity. The need to evaluate the policy implementation and the barriers that need to be bridged is discussed and the concept of "two-dimensional gap analysis" is proposed as an hierarchichal assessment tool to improve the mutual communication between policy, science and management needed to achieve active adaptive management.

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F. Research and development towards active adaptive management

The articles in the previous sections provide knowledge, which is relevant to the development of environmentally sustainable forests and woodlands in boreal and mountain ecoregions. However, critical knowledge gaps remain. In the final section it is proposed how these gaps could be filled by international co-operation in the fields of policy, management and science.

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Targets and tools for the maintenance of forest biodiversity – an introduction

Per Angelstam, Monika Dönz-Breuss and Jean-Michel Roberge

Angelstam, P., Dönz-Breuss, M. and Roberge, J.-M. 2004. Targets and tools for the maintenance of forest biodiversity – an introduction. – Ecol. Bull. 51: 11–24.

This volume of Ecological Bulletins with 38 papers is dedicated to the development of targets and tools for the maintenance of forest biodiversity, with special emphasis on boreal and mountain forests. In the first section, a range of actors pose questions and express viewpoints about how to strike the balance between wood production and biodiversity maintenance in the context of sustainable forest management. The second section describes the main forest disturbance regimes and resulting forest vegetation types covered in this volume, and the extent of the human footprint on the structure of northern forests in Europe. Thirdly, with the aim to derive quantitative performance targets for conservation management in actual landscapes, a number of specialised forest dwelling animal species are used to study relationships between presence and fitness of species' populations and different levels of anthropogenic change in their respective habitats. In the fourth section, the main tools available for the monitoring of forest biodiversity elements at multiple spatial scales and for different purposes are presented. The fifth section proposes how performance targets and results from monitoring can be combined to make assessments of the status of different elements of biodiversity, and thus guide strategic and tactical planning of protection, management and restoration for the maintenance of biodiversity. Finally, the sixth section outlines how continued systematic research on performance targets for the maintenance of biodiversity ought to be made by an international network of adaptive management teams using replicated landscape-scale studies in representative ecoregions with different histories and governance systems.

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Trees dominate the natural land cover in most biomes at northern latitudes and higher altitudes (Mayer 1984, Shugart et al. 1992, Burton et al. 2003a). However, clearing of natural forests and cultural woodland, and the introduction of intensive forest management have altered the composition, structure and function of both terrestrial and aquatic ecosystems (Darby 1956, Heywood 1995, Siitonen 2001, Liljaniemi et al. 2002). As a consequence, policies at different levels call for measures to mitigate the negative effects of this human footprint on landscapes domi-

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nated by forest and woodland (Angelstam et al. 2004a).

The biological diversity concept, usually abbreviated to biodiversity, was coined to highlight the undesired consequences of the human footprint on the environment such as the extinction of species (Wilson 1988). The Convention on Biological Diversity (CBD) defines biodiversity as "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems, and the ecological complexes of which they are part; this includes diversity within species, among species and of ecosystems" (Anon. 1992). To maintain the ecological complexes a number of processes (e.g. fire, flooding, browsing, fungal and insect infestations in forest) that affect the composition and structure of ecosystems need to be considered (Noss 1990, Bengtsson et al. 2000, Angelstam and Kuuluvainen 2004). This is stressed by the concept of ecological integrity (Pimentel et al. 2000, Norton 2003). There are, however, many definitions of the biodiversity concept (Kaennel 1998) and some authors, like Gaston (2000), have argued that it should be restricted to the diversity of life forms, excluding processes and functions. Nevertheless, at the policy level and in practical management, the prevailing interpretation is that function should be included (Larsson et al. 2001, Puumalainen et al. 2002, Stokland et al. 2003). In this book the focus is on the three groups of biodiversity elements (i.e. composition, structure and function). As to function, the emphasis is on the processes that maintain ecological complexes within landscapes in the short and medium terms, i.e. over an ecological time perspective.

Maintaining forest biodiversity by combining protection, management and restoration of forest and woodland at the landscape scale is a central component of sustainable development in many of the world's ecoregions (Pierce et al. 2002, Norton 2003, Aldrich et al. 2004, Loucks et al. 2004). This is also reflected in the evolution of the Sustainable Forest Management (SFM) concept (Schlaepfer and Elliott 2000, Angelstam et al. 2004a) from policy (Rametsteiner and Mayer 2004) and research (Mårell and Laroussinie 2003) to management (Raivio et al. 2001, Hebert 2004). SFM should ultimately include ecosystem integrity (Pimentel et al. 2000) and even social-ecological resilience (Berkes et al. 2003), which includes both the ecosystems and the institutions exercising governance (Campbell and Sayer 2003, Lazdinis and Angelstam 2004, Manfredo et al. 2004). Depending on the country and region, this transition process results in concern for how to develop indicators and formulate performance targets for the protection, management and restoration of biodiversity of forests and woodlands at multiple scales (e.g. Duinker 2001). Succeeding with this, and to implement it in actual landscapes, can be viewed as an acid test of the achievement of the ecological dimension of sustainability, or maintaining critical natural capital (Ekins et al. 2003, Ullsten et al. 2004).

To become operational at the level of actual landscapes, a principle such as SFM needs to be broken down into criteria and indicators (C&I), the latter of which can be measured repeatedly to examine whether or not change is taking place in the direction stated by the criteria (Table 1). Repeated measurement of a specific variable is referred to as monitoring. Indicators can be monitored at multiple scales ranging from whole countries (Anon. 2003a) to the different regions of a country (Stokland et al. 2003) and to local forest management units (Angelstam and Dönz-Breuss 2004). Monitoring for sustained yield of wood volume, tree species and age classes form an important starting point for evaluation of the implementation of SFM (e.g. Stokland et al. 2003). At the present time, the amount of dead wood (Fridman and Walheim 2000), as well as the location and state of high conservation value forests, varying in size from small near-natural remnants such as woodland key biotopes (Hansson 2001) to larger intact forest areas (Yaroshenko et al. 2001, Aksenov et al.

Table 1. The practical implementation of Sustainable Forest Management (SFM) is developing in several steps ranging from principles to performance targets (rows), and includes strategic, tactical and operational levels (columns) (Higman et al. 1999, Lazdinis and Angelstam 2004).

Steps in the development	Strategic level	Tactical level	Operationel level
Principles	International and national policy level		
Criteria	Forest policy Company policy	Regional and forest management unit	
Indicators	Coarse biodiversity monitoring tools	Detailed biodiversity monitoring tools	
Performance targets	Long-term targets	Regional targets	Management targets
Examples of evaluation methods regarding biodiversity and ecological integrity	Gap analysis	Habitat modelling	Protection, management and restoration

2002, Kurlavicius et al. 2004), are also gradually being incorporated into monitoring.

As a logic step linked to monitoring, assessment denotes the analysis and synthesis of the monitoring data and observations. To facilitate informed decision-making on forest policy and management related to the level of sustainability in the "strong" sense (Ekins et al. 2003), performance targets should be developed and combined with results from monitoring (Higman et al. 1999, Duinker 2001). However, performance targets and tools for monitoring and assessment are not commonly available. Hence the idea behind compiling the articles in this book.

This volume of Ecological Bulletins focuses on the development of scientifically founded performance targets and management planning tools for the maintenance of forest biodiversity. It is an independent further development of the previous issue of Ecological Bulletins "Biodiversity Evaluation Tools for European Forests" (Larsson et al. 2001). In that volume a general procedure for developing tools for the assessment of biodiversity was outlined for Europe's different ecoregions. In the present volume, this approach is applied and developed with a focus on the boreal and mountain forests in Europe. In particular, this book contributes to the need to expand the knowledge about forest ecosystems, including the role of forests in the landscape as a whole (Führer et al. 2000), and to develop tools for the active maintenance of biodiversity (Mårell and Laroussinie 2003).

The landscape concept is thus a central theme in this book. In the European Landscape Convention adopted by the Council of Europe's Committee of Ministers in 2000 (Anon. 2000) "landscape" is defined as a zone or area as perceived by local people or visitors, whose visual features and characters are the result of the action of natural and/or cultural (that is, human) factors. This definition reflects the idea that landscapes evolve through time, as a result of being acted upon by natural forces and human beings. It also underlines that a landscape forms a whole, whose natural and cultural components are taken together, not separately (Berkes et al. 2003). The landscape concept also reflects the need to expand the spatial scale of management hierarchically from trees and stands (e.g. Berglind 2004, Wikars 2004, Aldrich et al. 2004, Loucks et al. 2004), which is the traditional unit for silviculture, to landscapes and regions. Additionally, social organisational scales from individual, household or family, to community, county, national and global need to be included (Lazdinis and Angelstam 2004, Manfredo et al. 2004).

The conservation of forest biodiversity at the landscape scale is thus closely related to the economic and social dimensions of sustainability, and should therefore be treated concurrently in any attempt to achieve sustainability (Norton 2003). In this book we focus on maintenance to indicate the need for active persistent care using a combination of protection, management and restoration (Aldrich et al. 2004, Loucks et al. 2004). Although this book focuses on the ecological dimension of sustainable development, it gains from, and argues for, integration of socio-economic aspects. This ranges from pressures on elements of biodiversity caused by economic development (Shorohova and Tetioukhin 2004, Angelstam et al. 2004c), to the policy response to undesirable states and trends of institutions and different governance systems (Rametsteiner and Mayer 2004, Dönz-Breuss et al. 2004).

The target readers of this book therefore include both scientists and the different implementing actors, from the international and national policy levels to those dealing with forest biodiversity issues in actual landscapes. To mirror this diversity of professionals, the different papers composing this book have been written by a large variety of authors from different stakeholder groups. Thus, the style varies considerably among the papers, including presentations of original data and methods, reviews, as well as conceptual papers.

The papers in this book are divided into six sections (Fig. 1), each of which beginning with an introductory article. In the first section (A), different actors pose questions about the balance between use of wood and conservation of biodiversity. The second section (B) describes natural dynamics in boreal and mountain forests, and illustrates how the human footprint has affected the structure and function of those ecosystems at multiple spatial scales. In the third section (C), the requirements of specialised animal species operating at different spatial scales including birds, mammals, fish and invertebrates are used to test the hypothesis that there are critical levels of habitat loss for species persistence (Hanski 1999, Fahrig 2001, 2002). The ultimate aim is to use such knowledge as a base for developing quantitative performance targets for cost-efficient forest conservation planning at different spatial scales. In the fourth section (D), different tools for monitoring elements of biodiversity within a landscape or forest management unit are presented. The fifth section (E) presents examples on how biodiversity assessments at multiple spatial scales can be made by combining quantitative performance targets and results from monitoring. In the final section (F) an approach is outlined for how large-scale research can be carried out to improve the empirical knowledge about how much of different structural elements are needed to maintain biodiversity, including ecosystem integrity in the long term.

A. A wide range of actors pose questions

Different actors have different ambitions, perspectives and mandates when formulating performance targets for the maintenance of biodiversity. Using various policy development processes, society then makes a compromise between different interests such as those representing ecological,

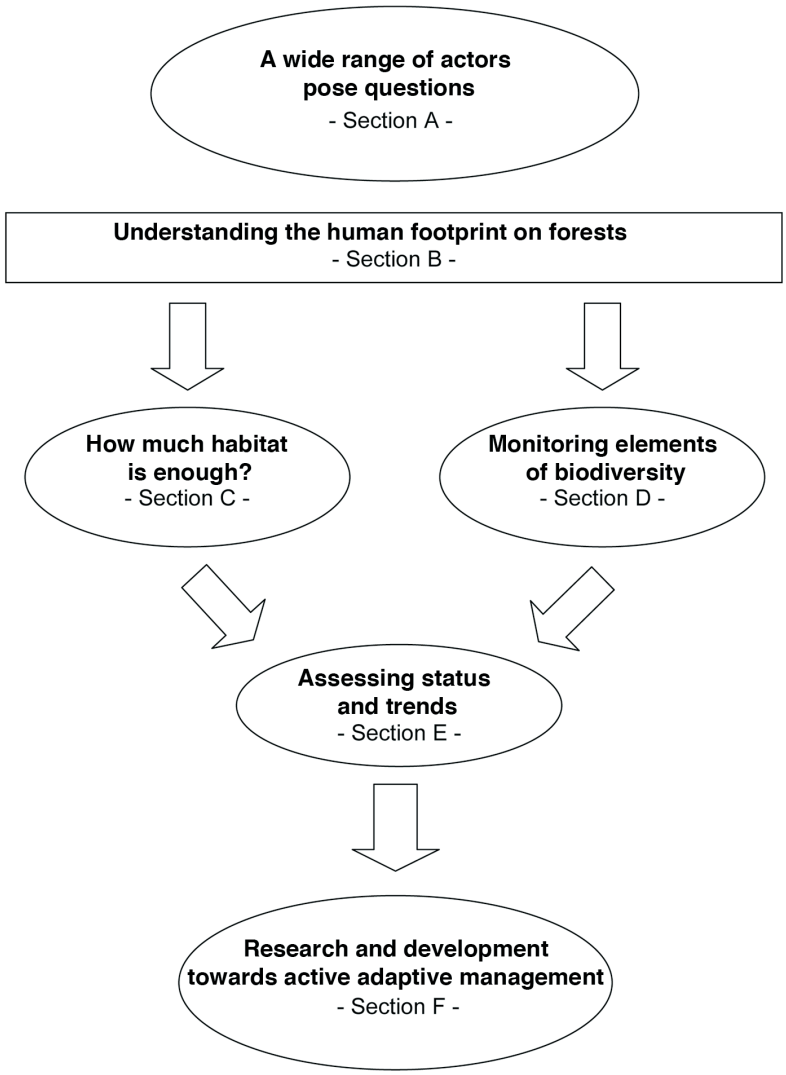


Fig. 1. The general structure of the development of performance targets, monitoring and assessment concerning biodiversity in the context of Sustainable Forest Management (SFM) with reference to the different sections in this issue of Ecological Bulletins.

economic and social interests (Sterner 2003, Campbell and Sayer 2003, Sayer and Campbell 2004). An important role of applied scientists is then to interpret the practical meaning of policies such as those related to forest biodiversity (Mills and Clark 2001).

Performance targets can thus be based both on science and values (Norton 2003). The applied ecological science regarding forest ecosystems presented in this book is done in the context of a long-term vision for the maintenance of forest biodiversity – say a forest rotation or more. This long-term vision can be broken down into targets to be reached within the current paradigm of values represented by, for example, international and national policy life cycles over a decade or more. Finally, operational targets such as environmental quality goals and forest certification standards are usually formulated within a time perspective of 5–10 yr. The extent to which ecological targets can be reached depends on the past human footprint, the quality and quantity of ongoing management efforts and the time that eventual restoration measures require. This section of the book mirrors this diversity of perspectives. Interest groups of particular importance for forest biodiversity maintenance include the international and European policy level, national agencies, municipalities, the forest and forest products sectors, non-industrial private landowners, applied scientists, First Nations and environmental organisations.

At the international policy level in Europe, the new paradigm of sustainable forest management was shaped largely by the European states and non-governmental organisations participating in the Ministerial Conference on the Protection of Forests in Europe (MCPFE). This was achieved through agreeing on a common definition of the SFM principle furthering a set of criteria and indicators

(Rametsteiner and Mayer 2004). Today, long-term sustainability of forests and woodlands is gradually promoted at national, regional and local levels in many countries in Europe, and practical implementation is in progress (Rametsteiner and Mayer 2004, Angelstam et al. 2004a).

Austria and Switzerland, where mountain forests comprise the larger part of the forest area (Neet and Bolliger 2004, Dönz-Breuss et al. 2004), are good examples of that transition. In Switzerland, since 1986 the first Federal Law on Environmental Protection and the subsequent federal regulations on nature conservation have promoted increased environmental concern of official conservation agencies. Today, a national forest biodiversity conservation strategy has been set up, which is based on close-to-nature silviculture, conservation of important ecological objects, and forest reserves (Neet and Bolliger 2004). Austria has been carrying out a nation-wide forest inventories since 1952. With the current inventory (2000–2002), special emphasis was put on the assessment of biodiversity including the genetic, species, and structural levels (Anon. 2002).

However, implementation of SFM faces numerous challenges. For instance, mountain forest owners are expected to produce both market goods (e.g. timber and game) as well as public goods and services (e.g. protection against natural hazards) and to maintain biological diversity (Glück 2002). At present, there is no policy regarding how to cover the costs of supplying public goods. Long-term sustainability requires that the major part of the forest land be managed using methods that take into account the environment and timber yield at the same time. However, due to increased international competition, local forest enterprises are often forced to fulfil short-term goals neglecting long-term sustainability (Dönz-Breuss et al. 2004).

In Canada, the Canadian Council of Forest Ministers (CCFM) produced a national framework of criteria and indicators which includes the criterion "Conservation of Biological Diversity", supported by an indicator statement on the maintenance of ecosystem diversity (Anon. 1995). From the managers' point of view the questions related to these statements include: 1) how an ecosystem should be described with respect to spatial scale, 2) how much of each ecosystem is required for conservation purposes, and 3) what is required regarding the spatial distribution and composition of the retention of trees in stands and stands in landscapes (Hebert 2004). Whittaker et al. (2004) review the central questions for research of the effects of forestry on biodiversity, and stress the need for systematic approaches to acquiring new relevant knowledge. The review reveal that research on the conservation of biodiversity in the boreal forests of Canada has been addressing a small subset of important questions, rather than looking at more general issues associated with landscape-scale biodiversity. As a result, many important conservation issues may have been missed, such as the need to maintain habitat for species dependent on fire successions. According to Whittaker et al. (2004), a major gap is the absence of instruction to forest managers that would aid in improving forest management and meeting biodiversity conservation objectives in the boreal forest.

Stevenson and Webb (2004) examine the traditional roles of Canada's First Nations peoples in maintaining boreal forest biodiversity. They argue that, notwithstanding that Native Americans were not conservationists in the normative use of the term, the traditional land use activities of Canada's boreal forest-dependent First Nations once contributed to create and sustain biodiversity. Based upon the best of western scientific knowledge and practice, the development of biodiversity indicators have been and continue to be based primarily on environmental criteria. Excluded from consideration and analysis is the role of human beings in sustaining the health of ecosystems and maintaining biodiversity (Sardjono and Samsoedin 2001). In many parts of the world, indigenous people once played, and continue to play through the pursuit of a variety of traditional activities, an integral role in maintaining the health and biodiversity of ecosystems (Pierce Colfer and Byron 2001). In this sense, the integrity of a First Nation's traditional uses may be an appropriate indicator of boreal forest biodiversity. On those grounds, Stevenson and Webb (2004) argue that setting aside large tracts of the boreal forest where Canada's Aboriginal peoples can sustain their traditional ecological footprint and exercise their rights makes sense ecologically. Europe also has its First Nations, such as the Sami people in northern Europe, many of whom practising reindeer herding in the northern boreal forest (Borchert 2001). The maintenance of the traditional livelihood is, however, not resolved (Lundmark 1998, Anon. 1999), even if relevant planning tools are at hand (Sandström et al. 2003).

The points-of-view of the different actors are, obviously, not homogenous. Implementation of biodiversity maintenance measures usually has economic consequences to land owners in addition to varying ecological and social benefits. For most forest industries, the mandate of biodiversity managers concerns what can be achieved within the current economic limitations rather than the long-term goal of maintaining viable populations of all naturally occurring species. However, the existence of political economic businesses (sensu Söderbaum 2000) and their effect on management by market pressure is an interesting exception (Djurberg et al. 2004). Setting performance targets that lead to the maintenance of forest biodiversity can thus be argued to promote "green" businesses working with wood products on the global market (Djurberg et al. 2004).

In Europe, European Community Agencies focus on harmonising national monitoring programs based on the concept of a favourable conservation status for species (the Birds Directive) and habitats (the Habitat Directive) within natural and non-administrative borders (the Water Framework Directive). This European biodiversity conservation platform is both underestimated with respect to its

strength, and unclear with respect to its operational application at the level of EU member states and local management units (Anon. 2003b). The spatial scale chosen (e.g. Holarctic, Europe, national, ecoregional, landscape or stand) has major consequences for the efforts required for maintaining viable populations of all naturally occurring species, ecological integrity and social-ecological resilience (Angelstam et al. 2004b). Large forest companies in particular are active in developing and applying management approaches at multiple spatial scales (Raivio et al. 2001, Burton et al. 2003b, Angelstam and Bergman 2004).

B. Understanding the human footprint on forests

Since forests constitute a renewable resource, their performance is traditionally measured using the volume of produced and harvested timber and pulpwood (Anon. 2003a). From the point of view of biodiversity, however, forests and woodlands are a diverse group of vegetation types shaped by different natural and cultural disturbance regimes (Angelstam 2003, Antrop 2004). Although of international scope, this book focuses on European conifer-dominated forests at northern latitudes and high altitudes.

The first paper of this section presents the conifer-dominated forest vegetation types, as well as the different disturbance regimes found in boreal, hemiboreal and mountain forests (Angelstam and Kuuluvainen 2004). Two other papers report on the effects of the human footprint on forest structures important for the maintenance of biodiversity at different spatial scales. Shorohova and Tetioukhin (2004) present an account of the main natural disturbance regimes and amounts of large, deciduous and dead trees in the Novgorod region, western Russia, which has only a 50-yr history of forest management. A comparison of their results with managed boreal forests in Fennoscandia indicates that long and intensive management reduces the amounts of natural forest components such as dead wood by at least one order of magnitude.

In a Swedish study, Angelstam et al. (2004c) show the importance of considering the history of forest management in ecoregional conservation planning. Using the historical development of the timber transport infrastructure, they were able to explain much of the variation in the present amounts of natural forest remnants (dead wood and high conservation value forests) in boreal forest in Sweden. High levels of historic accessibility were linked to lower amounts of dead wood and to smaller areas of protected natural forests. To foresters worldwide, Fennoscandian forestry represents a success story for effective and high sustained yield of wood. However, with the widening of the SFM concept it can also be viewed as an example of what intensive management may lead to in terms of loss of biodiversity. At the European scale, Angelstam and Dönz-Breuss' (2004) evaluation of biodiversity indicators such as dead wood in different forest history gradients supports this conclusion.

With the aim to get an overview of Europe's remaining naturally dynamic forests, Lloyd (1999) and Yaroshenko et al. (2001) located the continent's large intact boreal forest landscapes. This has recently been done also for the whole of Russia (Aksenov et al. 2002) and for Canada (Lee et al. 2003). In Europe, the large intact boreal forest landscapes are confined to the northeastern corner of European Russia (Yaroshenko et al. 2001). However, most of these remnants are not representative of the boreal forest types found naturally on productive sites. In Canada, with few exceptions, most remnants of intact boreal forest landscapes are found at the northern edge of the boreal zone or at high altitude (Lee et al. 2003).

Altogether these studies confirm the recognition that it is important to understand not only the present state of biodiversity, but also how the land-use history and its legacies continue to influence ecosystem structure and function for a very long time (Foster et al. 2003). Knowledge about the economic history, and thus the amount of different forest biotopes in different landscapes is the base for designing studies evaluating dose-response relationships such as between the amount of habitat and the occurrence and fitness of associated species (Angelstam et al. 2004b).

C. How much habitat is enough?

To operationalise the principle of sustainable forest management, a large number of criteria and indicators have been presented. Regarding the biodiversity criterion the indicators include for example dead wood, tree species composition and naturalness. To assess both the level and, if repeated, the trends in ecological sustainability, it is vital that the state of indicators be compared with scientifically based targets. But forest ecosystems are diverse, and there are many elements of biodiversity at different spatial scales (Angelstam and Dönz-Breuss 2004). In this section, forest dwelling animal species with a wide range of life history traits are used to study relationships between presence and fitness of species' populations and different levels of anthropogenic change in their respective habitats. A focal issue is whether or not there are critical levels of habitat loss (Mönkkönen and Reunanen 1999, Fahrig 2001, 2002). This section on "critical loss" of habitat can therefore be viewed as a parallel to the development of the "critical load" concept, which was developed to assess the critical amount of airborne pollution of sulphur and nitrogen that should not be exceeded to maintain ecosystem health (Nilsson and Grennfelt 1988).

There is both theoretical and empirical evidence for the presence of extinction thresholds for the amount of habitat, where the probability of extinction of a population may change sharply from near-zero to near-one following a small loss of habitat (Fahrig 2001, 2002). One avenue in

identifying numerical performance targets for conservation management is to study the response of specialised forest organisms to habitat alteration at different spatial scales. Guénette and Villard (2004) introduce the subject and explore issues related to the detection of threshold responses to habitat alteration. Among others, they discuss the selection of meaningful biological response variables and review statistical tools for the determination of cut-off values, such as ROC-analysis (Manel et al. 2001). The remainder of this section consists of original research papers providing knowledge useful in setting conservation targets for different animal species dependent on a variety of forest habitats at different scales, including insects (Berglind 2004, Fayt 2004, Wikars 2004), fish in forest streams (Degerman et al. 2004), a nationally threatened lizard as an umbrella species (Berglind 2004), various species of birds of high conservation value in Europe (Angelstam 2004, Fayt 2004, Brazaitis and Angelstam 2004, Mikusiński and Angelstam 2004, Bütler et al. 2004, Edenius et al. 2004, Jansson et al. 2004) and mammals (Mikusiński and Angelstam 2004, Reunanen et al. 2004).

From the studies listed above (see summary of the main results in Table 2), and the review by Angelstam et al. (2004f) it is evident that there is large variation in the habitat requirements of different species depending on the scale and level of ambition for their conservation. Focusing on specialised animals of forest and woodland, the landscape-scale thresholds for 17 species (birds, mammals and one insect) ranged from 10 to 50%, with a mean of 19%. This is consistent with Andrén's (1994) review suggesting that 10–30% of habitat is needed to maintain local populations.

The systematic studies of habitat loss thresholds of focal species can subsequently be used for assessing the functionality of habitat networks. The different steps are: 1) carefully select a suite of species representing each land cover type (Berglind 2004, Roberge and Angelstam 2004); 2) use quantitative targets based on the minimum habitat requirements defined by extinction thresholds of the focal species (Angelstam et al. 2004b); 3) make regional gap analysis for the different land cover types (Angelstam and Andersson 2001, Lõhmus et al. 2004); and 4) use habitat modelling based on occurrence thresholds at multiple scales to build spatially explicit maps describing the probability that existing habitat patches really contribute to the functional connectivity of that theme in the landscape (Angelstam et al. 2004f). The latter is important, since quantitative gap analyses alone neglect aspects such as the quality, size, duration and configuration of land cover patches, and therefore overestimate the amount of functional habitat in the sense that it provides sufficient connectivity for specialised species (Angelstam et al. 2003).

But how large is a landscape from the perspective of population viability of species? Using specialised bird species, Angelstam et al. (2004f) estimated the average size of an area hosting 100 females of several specialised bird species over a long time with ideal habitat to be ca 40 000 ha. However, also the dynamics of habitat patches in the landscape has to be estimated. As an example, a species using a 20-yr period in a succession of 100 yr needs an area at least five times as large for its long-term presence compared with being present in the short term. Using the minimum occurrence thresholds at the home-range and landscape scales Angelstam et al. (2004f) estimated that the average minimum area needed for 100 females was ca 250 000 ha for a dynamic managed landscape.

However, we do not know how many such local landscapes are needed within, say, an ecoregion to maintain a viable population. Assuming that viable populations would need to encompass an effective population of 500 females (Meffe and Carroll 1994), the area needed for viable populations would thus exceed 1 000 000 ha for the birds in the example above. With an average size of the local forest companies' ecological landscape plans ranging from 10 000 to 30 000 ha (Raivio et al. 2001), this would mean that ca 50 landscape planning units ought to be included. This size is of the order of magnitude of ecoregions or large administrative regions within a country. For species with large area requirements such as raptors as well as large herbivores and carnivores this means the appropriate management unit would be equivalent to the scales of one large or several smaller European countries.

D. Monitoring elements of biodiversity

A prerequisite for maintaining biodiversity within actual landscapes is the continuous monitoring of relevant indicators covering the different elements of biodiversity. Because it is impossible to measure individually all aspects of biodiversity, there is a need to develop cost-efficient monitoring tools, which can be reported in an understandable way to all relevant parties. The introductory paper to this section (Angelstam et al. 2004d) presents an overview of tools currently available for the monitoring of forest biodiversity, both at the policy level and at the level of the actual forest management unit. Although national-scale forest monitoring has been applied for some time in many countries, several elements of forest biodiversity developed within the MCPFE process (Rametsteiner and Mayer 2004) have been neglected. Likewise, at the level of the forest management unit, real-life application of biodiversity monitoring systems is still rare. Considering SFM as a whole, there are even more gaps in the long-term monitoring of forest landscapes at different spatial and socio-economic scales (Mårell and Laroussinie 2003).

Angelstam and Dönz-Breuss (2004) propose a rapid biodiversity monitoring approach for effective monitoring based on a range of indicators of forest biodiversity covering compositional, structural and functional elements at the stand scale. An evaluation of the method in 5 case stud-

Table 2. Summary of the results of studies about the habitat requirements of forest dwelling animals found in different types of forest dynamics, and for the forest cover of two forest habitat generalists. For a review of habitat area requirements for a pair or social unit and minimum landscape-scale habitat proportion for 17 specialised bird species of forests and woodland, see Angelstam et al. (2004f).

Landscape type		Species	Management target(s) for critical habitat elements	Reference
Type of forest dynamics	Succession	Black grouse *Tetrao tetrix*	More than 90 ha of young forest or open bog for a social unit; 22% of suitable stands at landscape scale for occurrence of leks.	Angelstam (2004)
		Hazel grouse *Bonasa bonasia*	From 10 to 20 ha of unthinned middle-aged or old stands with 5–40% deciduous trees and well developed field layer. Type of landscape matrix type has strong effect on local occurrence.	Jansson et al. (2004)
		Capercaillie *Tetrao urogallus*	About 200–300 ha of old pine forest for a social unit; 34% of suitable stands at landscape scale for occurrence of leks.	Angelstam (2004), Suchant and Braunisch (2004)
		Flying squirrel *Pteromys volans*	From 12 to16% of suitable habitat at the home-range scale, and >10% mature forest cover in the regional landscape; if >60% unsuitable habitat occurrence probability <0.5.	Reunanen et al. (2004)
		Siberian jay *Perisoreus infaustus*	Large patches of old-growth had higher probability of occurrence than managed landscapes.	Edenius et al. (2004)
	Cohort	Sand lizard *Lacerta agilis*	More than 1 ha of pine heath with bare sandy soil at the patch scale; large (>30 km^2) pine heath habitats mosaics needed for metapopulation survival at the landscape scale.	Berglind (2004)
		The pine wood-living beetle *Tragosoma depsarium*	Breeds in bark-free, sun-exposed, large logs from slowly grown Scots pine; the occurrence is clearly less frequent if proportion of mature forest falls <25% at the landscape scale.	Wikars (2004)
	Gap	Red-breasted flycatcher *Ficedula parva*	More than 40 ha large deciduous-dominated forest stands with an average stocking level of >0.8, and a stand shape tending towards that of a circle.	Brazaitis and Angelstam (2004)
		Three-toed woodpecker *Picoides tridactylus*	At the home range scale with a probability of 0.9: 18 $m^3 ha^{-1}$ of standing dead trees in an area of 100 ha.	Bütler et al. (2004), Fayt (2004)
		Brown trout *Salmo trutta*	Increasing trout occurrence if up to 8–16 large woody debris pieces/100 m stream.	Degerman et al. (2004)
Forest cover in general		Brown bear *Ursus arctos*	High probability of occurrence in plots with >50% forest cover.	Mikusiński and Angelstam (2004)
		Lynx *Lynx lynx*	Linear increase of probability of occurrence up to 80% forest cover.	Mikusiński and Angelstam (2004)

ies in hemiboreal, mountain and lowland temperate forest with varying gradients of management intensity in Europe showed clear patterns. Particularly noteworthy was that indicators proposed in the MCPFE process such as dead wood and naturalness were closely linked to both local and regional gradients in the human footprint on forests and woodlands.

Regarding easy-to-use indicators at the landscape scale, Angelstam et al. (2004e) assessed the usefulness of land management data and terrestrial vertebrates as biodiversity indicators in 28 case studies in Europe's forests north of the Mediterranean. They concluded that ordinary forest management data (e.g., area of plantations and of old forest), and knowledge about the occurrence of individual specialised species and ecological groups of bird and mammal species are useful indicators of forest biodiversity at the landscape scale.

Monitoring of forest ecosystems has been facilitated by the recent developments in remote sensing and Geographic Information Systems (GIS). As pointed out by Young and Sanchez-Azofeifa (2004), remote sensing is the best available method for the acquisition of land-cover data over large areas, and is well suited to land-cover change detection. GIS renders possible the integration of different types of spatial data and their analysis. However, these tools present a number of limitations linked to, among others, the spatial and spectral resolution of the data (Angelstam et al. 2004f). Moreover, there is a need for increased application of sensitivity analyses concerning the land cover data, the modelling algorithms and the model parameters (Rönnbäck 2004).

Another important source of land cover information is the forest management data used for strategic and tactical forest management planning (Angelstam and Bergman 2004). Using such data, Kurlavicius et al. (2004) identified in the three Baltic States Estonia, Latvia and Lithuania, large areas of high conservation value forests, which are associated with intact assemblages of specialised and area-demanding species (Angelstam et al. 2004f). Ecologically-based selection criteria adapted to the particularities of each country were applied, and lead to the identification of biologically valuable forests averaging 17% of all forests in the region. Further analyses showed that the vast majority of the selected stands were located outside currently protected areas, and that the estimated rate of final felling was very high, for example 4% yr^{-1} in Estonia.

Finally, sustainable forest management can only be reached if the results of monitoring can be communicated to the managers and decision-makers. Uliczka et al. (2004) evaluated the knowledge of different potential indicator species among non-industrial private forest owners in Sweden. From a list of species presently used by the Swedish National Board of Forestry to identify high conservation value forests, birds and a flowering plant could be recognised by most forest owners in the field. However, lichens, fungi and one cryptogam used as indicator species could only be recognised by a low proportion of the owners. On the basis of those results, the authors propose that indicator species monitoring systems for non-industrial private forest owners should be based on species that have both a high communication value and a well-documented indicator or umbrella function.

E. Assessing status and trends

With the results from monitoring and relevant targets for a range of indicators, it is possible to make assessments of the status of a certain criterion, such as biodiversity and its constituent elements. In this section, examples of practical assessment methods are presented both for strategic and tactical planning of operational management for protection, management and restoration of the structural and functional aspects of biodiversity needed to maintain viable populations of species and ecosystem integrity.

Ideally, given the complexity of the biodiversity concept, detailed data should be collected across all relevant spatial scales. As this is usually not feasible in the real world, there is a need to develop transparent and robust methods for the integration of the more general information that is available (Ullsten et al. 2004). There is also a need for tools allowing rapid and simple assessment, which the managers themselves can carry out (Angelstam and Dönz-Breuss 2004). Angelstam and Bergman (2004) studied the usefulness of the data in forest management plans for ranking forest landscapes with respect to the opportunity for succeeding with the biodiversity maintenance objective of a Swedish forest company. Their analyses indicate that only a few of the studied landscapes have good chances of maintaining viable populations of all species, i.e. including those specialised on forests with a high level of naturalness. The authors argue that landscape restoration management should be concentrated in those landscapes that have been identified as hosting the largest amounts of forest vegetation types that are in limited supply in managed landscapes in a particular ecoregion.

At the strategic level, quantitative gap analysis (Angelstam and Andersson 2001) can be used to identify the present amounts and protection status of different forest types and to compare them with long-term needs for the maintenance of viable populations of naturally occurring species. In a study from Estonia's hemiboreal forests, Lõhmus et al. (2004) estimated the need for protected areas to 10–13%.

For tactical conservation planning, habitat modelling approaches (Angelstam et al. 2004f, Suchant and Braunisch 2004) can be developed to evaluate the extent to which forest landscapes provide functional habitat networks for the species dependent on the main forest types of conservation interest. Angelstam et al. (2004f) propose a general methodology for habitat modelling, while Suchant and Braunisch (2004) introduce a specific model

for the capercaillie *Tetrao urogallus*. By offering the possibility to identify location and size of areas in which habitat improvement measures should be implemented and by defining target values for forest management, the latter model links wildlife research to practical habitat management. The target values are also assumed to offer an operational silvicultural tool to integrate other nature conservation aims (e.g. structural diversity), that are often associated with capercaillie occurrence, into forest management systems.

Lazdinis and Angelstam (2004) stress the need to include assessments not only of the ecosystems' amount and configuration of habitats, but also of the institutions and systems of governance. Using this approach, the barriers can be identified and appropriate bridges for policy implementation can be proposed. This is a major challenge to all actors in society, and requires blending natural and social sciences to evaluate the success of policy implementation in different socio-economic contexts (Sayer and Campbell 2003, 2004, Manfredo et al. 2004). A critical component for the evolution of sustainable forestry through ecosystem or adaptive management is an efficient and open communication between science and practice as well as among different stakeholders. Accordingly, Ullsten et al. (2004) argue for the need to improve the exchange of knowledge about the state of the natural capital of forests and woodlands between natural scientists, managers, the general public, and policy-makers.

F. Research and development towards active adaptive management

The articles in the previous sections contribute to the knowledge base, which is necessary for the development of environmentally sustainable management of forests and woodlands in boreal and mountain ecoregions (Führer et al. 2000). However, critical knowledge gaps remain in terms of limited quantitative knowledge about how ecosystem structure and function affect populations and assemblages of species in different kinds of forest and woodland in different ecoregions (Angelstam et al. 2004f). There are also gaps between the existing knowledge on the one hand, and its application in policy and management on the other (Boutin and Hebert 2001, Clark 2002, Angelstam et al. 2004a, Whittaker et al. 2004).

In the final section it is proposed how such gaps could be filled by international co-operation in the fields of large-scale ecological research, and active adaptive management. Specifically, Angelstam et al. (2004b) present a general approach for identifying multiple thresholds to be used in the determination of performance targets for conservation in forest ecosystems. Performance targets are needed to address different levels of conservation ambition ranging from population viability to ecosystem integrity and ecological resilience.

A six-step procedure is envisaged: 1) stratify the forests into broad cover types based on their natural disturbance regimes; 2) describe the historical spread of different anthropogenic impacts that moved boreal forest ecosystems away from naturalness; 3) identify appropriate response variables (e.g. focal species, functional groups or ecosystem processes) that are affected by habitat loss and fragmentation; 4) for each forest type identified in step 1, combine steps 2 and 3 to look for the presence of non-linear responses and to identify zones of risk and uncertainty; 5) identify the "currencies" (i.e. species, habitats, and processes) which are both relevant and possible to communicate to stakeholders; 6) combine information from different indicators selected. A review of the historical development of forest use in 8 boreal case studies illustrates the need for international collaboration to follow this procedure. Such performance targets should also include 1) mechanisms for consistent application, 2) formulation of short-term goals, and 3) formulation of long-term goals for the maintenance of the elements of biodiversity.

In addition, new knowledge, different policy instruments (Sterner 2003) and the tools for hierarchical planning and operational management (e.g. Fries et al. 1997, 1998, Angelstam 2003) need to be applied in different kinds of arenas for integrated natural resource management (Sayer and Campbell 2003, 2004). Model forests (Besseau et al. 2002, Svensson et al. 2004) and biosphere reserves (Peine 1999) are two promising tools for combining bottom-up and top-down approaches (Lazdinis and Angelstam 2004). Both concepts focus on the development of a systematic procedure for involving the stakeholders in a geographically defined area and identifying key problems and solutions. Likewise, a recently established pan-European network, the European Network for long-term Forest Ecosystem and Landscape Research (ENFORS; see www.enfors.org), has identified and created a network of focal study areas (ENFORS Facilities) that are dedicated to integrated long-term research and monitoring at the ecosystem and landscape scales (Mårell and Leitgeb in press a, b).

Such replicates of "landscape laboratories" (Kohler 2002, Angelstam and Törnblom in press) are potential arenas for multiple case studies linking monitoring, research, management and policy making at local and regional levels. They are as such providers of long-term research and monitoring data, and have good knowledge about past and present management plans, as well as a well-established contact and collaboration network with local and regional decision-makers and stakeholders needed for adaptive ecosystem management (Lee 1993). There are thus good opportunities for macroecological studies to derive performance targets as outlined by Angelstam et al. (2004b, f), and for application of two-dimensional gap analyses assessing the integrity of the social-ecological systems that landscapes form (Lazdinis and Angelstam 2004).

In addition, such studies need to be sufficiently long-term to solve the problem of extrapolation of the traditional short-term and small-scale experiments to longer time and larger spatial scales – i.e. those of whole ecosystems with their processes (Symstad et al. 2003). The US Long Term Ecological Research network (LTER) is an impressive research effort that addresses fundamental and applied ecological issues that can be understood only through a long-term approach (Hobby et al. 2003).

Therefore, to promote ecological sustainability at the level of management units, learning and management at multiple spatial and temporal scales should be integrated with the managing institutions (Lee 1993) into a network of adaptive management experiments including a sufficiently wide range of initial conditions at multiple scales (Angelstam et al. 2004b). To cover the variation among landscapes within regions, and hence be of international interest for answering questions related to habitat loss and biodiversity including ecosystem integrity, it is essential that the experimentation becomes an international endeavour. Only then can the full range from reference areas to altered landscapes be covered.

This approach will resolve the major concern with traditional experiments that even though the "new forestry" with variable retention at the stand scale is certainly positive, in second and third generation forests the quality of this retention will be lower than in first-generation retention (Angelstam et al. 2004c). A long history of intensive management thus provides little room for manoeuvring. Additionally, the direction of change in the amount of habitat also matters. The time lag in species' responses to habitat loss is likely to be shorter than that in response to habitat restoration (Tilman et al. 1994, Hanski and Ovaskainen 2002). Habitat loss studies may hence produce overly optimistic conservation targets for habitat restoration.

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BorNet – a boreal network for sustainable forest management

Per Angelstam, John Innes, Jari Niemelä and John Spence

Angelstam, P., Innes, J., Niemelä, J. and Spence, J. 2004. BorNet – a boreal network for sustainable forest management. – Ecol. Bull. 51: 25–27.

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In September 1998, a Finn (Jari Niemelä), a Canadian (John Spence) and a Swede (Per Angelstam) met in Syktyvkar, Russia at a conference about ecological dynamics in the boreal forest. Much inspired by conversations with our Russian colleagues and students we started thinking of vehicles to bring together people from around the world who work with boreal forest ecology, conservation and management in the same increasingly integrative and rewarding way as we had been working ourselves in our respective countries. In February 1999, the three of us were invited by the Canadian Sustainable Forest Management Network (SFMN) to attend a workshop about "Boreal forest health and dynamics" held at the Univ. of Alberta, Edmonton. At the workshop, led by Vic Adamowicz, there was real enthusiasm for a boreal network of the sort we had imagined in Syktyvkar. During that very meeting Per started to tap on his laptop, writing an outline to provide a rationale for "BorNet" and a basis for applications asking for funding to develop the network. Our earliest focus was on the critical issue of how much forest is enough to maintain the species and ecosystem functions, how the elements of biodiversity could be measured and evaluated, and how an international network of scientists and managers could be built to improve mutual understanding of the boreal forest. Discussions with Jan Nilsson of the Swedish research funding body MISTRA and personnel from the SFMN raised optimism about prospects for funding a network in our respective countries.

During a stay at Hartmut Gossow's Inst. of Wildlife Biology at the Univ. of Agricultural Sciences (BOKU) in Vienna, Austria, in 1999, Per made a visit to the Schwarzenberger forests in Murau with a group of Austrian students. This convinced him that to maximise the variation in the amount of different forest habitats across different spatial scales, it would be wise to include the large but isolated "boreal" forest patches located at high altitudes in the central European mountains. In Vienna, Per met the remote sensing expert Werner Schneider, which eventually led to a common project funded by the EC Joint Research Centre in Ispra about biodiversity assessment (Puumalainen et al. 2002). This was paralleled by similar work in Sweden with a research programme called Remote Sensing for the Environment (RESE) funded by MISTRA (Angelstam et al. 2003a, b). When we three (PA, JN and JS) met again at a conference in Helsinki in 1999 dealing with consequences of habitat loss, we finalised the common theme for our proposals to Swedish, Finnish and Canadian agencies.

Another root for the work in Europe can be found in the EC-funded "BEAR" project titled "Indicators for monitoring and evaluation of forest biodiversity in Europe" (Larsson et al. 2001). Within the BEAR project, two

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of the members (PA and JI) who would later form the BorNet team met. John Innes, a Scot who had been working in Switzerland for seven years, and Per saw the opportunity to develop the BEAR ideas further at the scale of the forest management unit. Soon after John moved to Univ. of British Columbia in 1999, he joined forces to launch the Canadian branch of BorNet with an initial focus on regional issues.

Later in 1999, Per was contacted by WWF representatives, who were interested in supporting their conservation work with a stronger scientific background and in assessing the status and progress of biodiversity conservation work at the landscape scale. The plans were drawn up with the Swedish WWF forest officer Stefan Bleckert in July 1999. About six months later, Stefan and Per met with Per Rosenberg from WWF-International in Geneva and Stockholm and developed the detailed plans for the work to be carried out for three years starting in spring 2000.

Almost a year after the Edmonton meeting, Per visited Jan Nilsson at MISTRA in Stockholm. There he was informed that money was granted to compile, compare, conclude and communicate present knowledge about boreal biodiversity along the lines of the application drafted in Edmonton. So, after a gestation period of ca 18 months the Swedish part of BorNet was started in the autumn of 2000. To assure good communication between the project and the Swedish forest industry, Ragnar Friberg of StoraEnso was contacted to provide insights into the important questions faced by the forest industry in Sweden. Through interesting and stimulating discussions with Ilse Storch, Stan Boutin, Bogumila Jedrzejewska, Grigory Isachenko and Grzegorz Mikusiński at a meeting in Sweden in November 2000, the logical framwork for the work was established. During several seminars in Sweden the project was introduced to major actors working with the forest biodiversity issue.

Meanwhile, in Canada, John Innes and John Spence were working on obtaining funding. John Innes submitted a project to the Sustainable Forest Management Network for funding, based on an extension of the BEAR project. John Spence, who was already closely involved with the SFM Network, realized the potential for collaboration and, in late autumn 2000, John Spence and John Innes received funding for the Canadian part of BorNet. The Canadian BorNet initiative focussed on teasing out regional questions being asked about biodiversity and then looking for common elements to put together in an initial Canadian synthesis (Whittaker and Innes 2001a, b, c). The extent to which forests are managed for biodiversity conservation and renewal varies across Canada. Alberta has a very different context to Ontario, and through work at the national and international scale, BorNet International is helping to inform about the different approaches. BorNet Canada has linked provincial biodiversity research initiatives such as those of the British Columbia Ministry of Water, Land, and Air Protection with national scientific programs such as the Sustainable Forest Management National Centre of Excellence, and has encouraged the better linking of scientists, practitioners and policy makers in western and eastern Canada.

In Finland, BorNet was included in the work and organisation of the Finnish Biodiversity Research Programme (FIBRE). This programme included a special project with the aim to enhance dissemination of research results by encouraging collaboration between researchers and societal stakeholders. This project ("Application of biodiversity research", BITUMI) incorporated and responded to the BorNet needs by organising a series of meetings and workshops in which researchers and stakeholders worked on issues of relevance for the maintenance of boreal biodiversity (Markkanen et al. 2002). In particular, the workshops addressed the main question of BorNet: how much is enough? (Angelstam 2001).

An initial international meeting of the BorNet project was held in Haliburton, Ontario, in March 2001. During two visits to Vancouver in spring 2001, Carolyn Whittaker, who had been hired by John Innes to help coordinate the BorNet project, and Per designed a logo and started to build the web site <www.bornet.org>. In 2001, the participating countries also agreed on some common objectives and a common framework for the project. The group decided that BorNet's primary function would initially be as an internal force, locating biodiversity research collaborators, compiling internal information regarding science and data, finding or building networks and other relevant programs, and summarising these in a form useful to practitioners.

Most of the field work in different parts of Europe, the literature review work, data analyses and communication with colleagues was conducted in the years 2001 and 2002 in close co-operation with Monika Dönz-Breuss in Vienna. Abstracts of the preliminary results were presented as a technical report (Angelstam and Breuss 2001). This was also the first report from the new IUFRO working group 8.02.06 "Benchmarks for biodiversity at the landscape scale". Most of these abstracts, and several other papers, now appear as full papers in this book.

BorNet objectives

The specific objectives of BorNet are to: 1) develop a boreal network of researchers, forest managers, and government policy makers and regulators; 2) develop a synthesis of available information on the conservation of biological diversity; 3) identify gaps in our understanding in order to further develop co-ordinated research efforts among boreal countries; and 4) deliver this information back to a broad set of audiences including scientific communities, industrial communities, as well as other non-governmental and public interest groups.

Key synthesis questions

Three key questions were identified by the BorNet International Steering Committee as a guide for the discussions among boreal countries. These are: 1) How much and where should forests be fully protected in reserves? 2) How can management effectively restore/recreate/maintain important features required to conserve biodiversity? 3) How can we determine the effectiveness of these biodiversity conservation efforts?

BorNet participants have emphasised that we should develop research activities that deal directly with forest management challenges associated with the maintenance of biodiversity. Such challenges involve restoration in some eastern Canadian and European contexts. Moreover, we should not forget that regeneration of habitats suitable for all naturally occurring biotic elements after harvest is an important conservation goal. Further, we should work together with forest companies and other forest-related businesses, as research findings that are not applied in practice will have little impact on conservation. To this end, business, industry and government representatives have attended our regional workshops in Sweden, Canada and Finland, and have participated in our Steering Committee. Developing closer links between research and practice remains an important goal for BorNet.

The first international BorNet symposium was held in Sweden in May 2002 (Leech et al. 2002). Representatives from government agencies from several countries and from the industry (e.g., Weyerhaeuser Canada, Sveaskog, and StoraEnso) participated actively in the discussions. We also developed strong partnerships with environmental non-governmental organisations (e.g., WWF, WRI, and Greenpeace-Russia) and with companies such as IKEA that are supporting the development of sustainable forest management. The meeting was followed by an excursion to Estonia and the WWF Pskov model forest in Russia.

The BorNet programme was favourably evaluated in the context of the FIBRE evaluation by an international expert panel. According to the panel "The BorNet programme appears to be another fruitful collaboration, drawing comparative research and policy insights from a range of nations (Finland, Sweden, Canada and the former USSR) with boreal biodiversity concerns." (Anon. 2003).

BorNet has something to offer all those interested in the quest for understanding the ecology of northern forests, and how to use them in a truly sustainable way. We hope that the papers in this book will stimulate similar kinds of studies and also ultimately encourage team work of scientists, managers and policymakers aiming at perpetual learning (Lee 1993) as a means of addressing problems of uncertainty in forest and land management (Kinzig et al. 2003). The challenge is to sustain momentum to address the work as outlined in the final section in this volume. We are confident that this is just the end of the beginning. We remain convinced that co-operation among nations, disciplines and generations is needed for the maintenance of biodiversity in boreal forest as well as in the other of the Globe's biomes.

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The sustainable forest management vision and biodiversity – barriers and bridges for implementation in actual landscapes

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Sustainable Forest Management (SFM) represents a vision for the use of forests based on satisfying ecological, economic and social values. In response to unsustainable use of products and services we identify three phases in the ongoing development of SFM. The first is based on sustained yield of wood products where humans dominate nature. Second, there is at present in Europe a phase based on multiple use sustaining primarily wood production, but also with attempts to accommodate new issues such as biodiversity and recreation. Third, a future phase is envisioned with sustainable social-ecological systems inspired by and maintaining authentic natural or cultural processes where humans and nature coexist. The current starting point for trajectories towards the SFM vision, however, varies considerably among countries and regions with different socio-economic settings and ecosystems.

Focussing on forest biodiversity, we discuss approaches for making the ecological dimension of the SFM vision operational in practice. International and national policy-makers, the forest and forest products sectors, non-governmental organisations and scientists are major actors trying to interpret international and national policies in this field. So far the main tool has been defining criteria and indicators for SFM. At present different actors also ask for performance targets and tools allowing evaluation of the degree to which ecological sustainability is actually achieved.

Finally, we summarise prerequisites for achieving the SFM vision's ecological dimension including: 1) a societal mindset built on the idea of active adaptive management where land use methods are viewed as experiments designed to test hypotheses about how the amount of habitat affect different elements of biodiversity, which allows 2) formulation of performance targets with which results from monitoring can be compared, and sustainability checked. If necessary, this enables 3) spatially explicit management and zoning at multiple spatial and temporal scales to resolve competing interests. Additionally, 4) there is a need for improved integration of different actors' activities allowing continuous mutual learning among actors and the public, and 5) case studies such as "model forests" where novel approaches are developed and communicated.

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Wood has traditionally been the basic resource for economic development in many countries of the world's Northern Hemisphere. However, the historical use of forests has developed in several more or less distinct steps (Björklund 1984, Angelstam and Arnold 1993, Drushka 2003, Williams 2003, Burton et al. 2003), the timing of which varies among regions. Östlund and Zackrisson (2000) divided the forest history into three phases, viz.: "agricultural", "diverse use" and "industrial". The starting point, and ecological benchmark, could be described as a dynamic forest ecosystem with intact components, structures and processes (Peterken 1996). Humans, first only as hunter-gatherers and later gradually developing low-intensity animal husbandry and agriculture, were probably always a part of forest ecosystems, but did not dominate them (e.g., Balée 1998, Stevenson and Webb 2003, 2004). Then followed a period with a diversified use of wood for products such as charcoal, potash, tar or for selective harvesting of large and valuable trees (Östlund et al. 1997, Björklund 2000, Agnoletti and Anderson 2000, Östlund and Zackrisson 2000). With the advent of the industrial revolution this use eventually evolved into unsustainable exploitation where the wood resources became locally or regionally depleted (Schuler 1998, Drushka 2003, Williams 2003).

The development of sustainability can be divided into three phases. In response to unsustainable use of forests, or even resource liquidation, it is sooner or later realised that such large volumes of wood cannot be extracted any longer. This is sometimes called the "timber fall" (Drushka 2003) and results in calls for regulation aiming at wood production at a lower level than possible during the liquidation phase, and which can be sustained in the long term perspective. This sustained yield paradigm can be viewed as the first step in the development towards sustainability (Schuler 1998) and usually includes effective prescriptions for intensive management for desired wood-products (e.g., Davis and Johnson 1986).

Industrial forest management, increased globalisation of the forest industry and new values regarding the acceptable types and intensity of forest use have made forest resource management an increasingly complex endeavour (Glück 2000, Schlaepfer and Elliott 2000, Davis et al. 2001, Gamborg and Larsen 2003). This second phase towards sustainability is characterised by efforts to balance the intensity of use with other values such as the conservation of biodiversity (Hunter 1999, Lindenmayer and Franklin 2002, 2003). Failure to achieve ecological sustainability goals has encouraged the scientific development of ecologically based forestry with natural disturbance dynamics as a vision (Dengler 1944, Mayer 1992, Lähde et al. 1998, Seymour and Hunter 1999, Angelstam and Kuuluvainen 2004). However, as the practical application lags behind, this step should rather be called sustained yield based on multiple use (Davis et al. 2001) sustaining primarily wood production, game, recreation, and biodiversity in the short term (Raivio et al. 2001, Burton et al. 2003). In order to ensure an ecologically sustainable development in landscapes where forests and woodlands are important elements, criteria and indicators to measure the progress must be combined with performance targets allowing assessment of the degree to which sustainability has been achieved (Davis et al. 2001). We argue that the compositional, structural and functional elements of biodiversity (Noss 1990, Larsson et al. 2001) are useful proxy variables, which could be used to facilitate the evaluation of the ecological dimension of sustainable development. We are thus in favour of sustainability in the strong sense (Goodland and Daly 1996, Angelstam and Lazdinis 2003).

Finally, attempts are emerging to develop a third phase in the introduction and application of the sustainability concept for social-ecological forest and woodland systems including also social criteria (Kennedy et al. 2001, Berkes et al. 2003). This broad evolving vision of satisfying economic, ecological and social values is called Sustainable Forest Management (SFM) (Anon. 1993a, Duinker et al. 1998, Schlaepfer and Elliott 2000, Mills and Clark 2001, Davis et al. 2001, Sverdrup and Stjernquist 2002, Rametsteiner and Mayer 2004).

In spite of considerable progress towards SFM in some countries (Lindenmayer and Franklin 2003), there are many unresolved issues with respect to the gradual implementation of each of these three phases in the development of SFM (Korhonen et al. 1998, Angelstam 2003, Niemelä 2003, Lindenmayer and Franklin 2003, Hebert 2004). A clear indication that we have not achieved SFM is that projections about the evolution of forests in the future within the European Union distinguish between what is euphemistically called "business a usual" and multifunctional SFM (Karjalainen et al. 2003). So, will SFM remain only "business as usual", focusing on economic revenue but with lip service about ecological and social values at the policy level? Is SFM achieved by employing second-party certification and minimal mitigation measures only superficially interpreting ideas such as ecological forestry based on natural disturbance regimes, as the introduction of variable retention at the stand scale only? Or is it a whole new view on resource management based on dealing with both ecosystems and institutions? If so, at what spatial scale should SFM be achieved? Within ecoregions, countries, counties, or in each watershed or forest management unit? How could integration of actors be achieved at multiple spatial and temporal scales?

Focussing on forests and woodland, SFM is paralleled by synonymous but more general terms describing attempts to apply sustainable management of any type of ecosystem. The expression "adaptive management" (Walters 1986) has been advocated for a range of terrestrial and aquatic ecosystems (Lee 1993, Holling 1995, Duinker and Trevisan 2003). According to the adaptive management concept, policies are viewed as hypotheses and management is used as a set of carefully monitored experiments,

the experiences from which are used to correct the course of action. Later "ecosystem management" (Christensen et al. 1996, Meffe et al. 2002), "ecosystem-based management" (Schlaepfer 1997), or "multi-functional forest management" (Buttoud 1998) appeared to capture the contents of SFM. To stress SFM as a means of sustaining ecological, economic and social values in forests, Davis et al. (2001) used the expression "sustainable management of human-forest ecosystems", or simply "forest ecosystem management". Similarly, Berkes et al. (2003) emphasised that not only the ecosystems but also the institutions managing them need to be integrated and used the term "social-ecological systems". More recently, new development within the framework of the Convention on Biological Diversity has lead to the concept of "ecosystem approach" as a strategy for the management of land, water and living resources that promotes conservation and sustainable use (Anon. 2002a, 2003a). Our view is that, by and large, the SFM vision as summarised by Rametsteiner and Mayer (2004) means that at the Pan-Europan policy level the "ecosystem approach" has been defined with criteria and indicators relevant for conservation and sustainable use of forests and woodlands.

The operationalisation of SFM is thus in progress, however, more so in theory than practice (Eckerberg 1998, Sverdrup and Stjernquist 2002, Lindenmayer and Franklin 2003, Burton et al. 2003). In fact, continued unsustainable use of forest resources is economically more profitable (Marchak 1995, Williams 2003). The implementation of SFM and biodiversity in actual landscapes represent a gradual development in several steps. One of the first examples was the management of wildlife on public land in the US (e.g., Thomas 1979), currently also promoted on non-federal land (Anon. 1998a). The experience from the "Interior Columbia River Basin Ecosystem Management Project" in north-western USA is a good illustration of application of a broader set of criteria for sustainable management of natural resources (Lee 1993, Haynes et al. 2001). However, as suggested by Davis et al. (2001), Boutin et al. (2002) and Duinker and Trevisan (2003), there appear to be hardly any examples of large commercial forest companies actually having achieved SFM at the forest management unit level. Some forest companies and businesses, however, make efforts in this direction by formulating explicit and ambitious policies (e.g., Anon. 2002b, Bunnell and Dunsworth 2004, Djurberg et al. 2004). However, to evaluate the degree to which SFM is attained in actual landscapes, the combined efforts of many actors need to be evaluated (Moldan et al. 1997, Angelstam and Bergman 2004, Lazdinis and Angelstam 2004, Ullsten et al. 2004).

In this paper we focus on the ecological dimension of SFM, interpreted as the maintenance of biodiversity and its compositional, structural and functional elements (Larsson et al. 2001). First, we put the maintenance of biodiversity into the context of the ongoing development of the SFM vision by reviewing the international policy development, and especially the Pan-European policy arena (e.g., Holmgren and Persson 2003, Rametsteiner and Mayer 2004, Rametsteiner and Wijewardana 2004). In this context we also present a simple conceptual model showing the range of different trajectories of development towards SFM faced by different countries and regions. Second, we review the issues related to biodiversity maintenance in terms of viable populations and ecosystem integrity put forward by different interest groups of importance for the protection, management and restoration of biodiversity. These actors include the forest and wood processing industry (Korhonen et al. 1998, Raivio et al. 2001, Djurberg et al. 2004), institutions implementing policies on a regional level (Neet and Bolliger 2004), First Nations (Stevenson and Webb 2004), private and communal landowners (Dönz-Breuss et al. 2004), non-governmental organisations (Newton and Kapos 2003) and scientists (Mills and Clark 2001, Hanski 2002). Finally, to highlight the need to adress biodiversity issues at multiple scales, including that of landscapes within ecoregions in the long-term (Andersson et al. 2000, Angelstam et al. 2004c), we propose and discuss bridges towards facilitating the ecological dimension of SFM at the level of actual landscapes.

Defining forest biodiversity

Biological diversity has been defined and re-defined by many actors (Kaennel 1998). According to the Convention on Biological Diversity (CBD) biodiversity is "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems, and the ecological complexes of which they are part; this includes diversity within species, among species and of ecosystems." (Anon. 1992b). Additionally, a number of important processes that affect forest composition and structure should be considered (Noss 1990). Although some argue that the biodiversity concept should be restricted to the diversity of life forms, excluding ecosystem function (Gaston 2000), both at the policy level and in practical management the prevailing interpretation is that function should be included (Larsson et al. 2001, Sverdrup and Stjernquist 2002, Puumalainen et al. 2002). As suggested by Noss (1990) we thus focus on three groups of biodiversity elements: composition, structure and function. The level of ambition may then range from presence of generalised species, population viability of specialised species, and to ecosystem integrity and resilience (see Angelstam et al. 2004c).

The vegetation of a large part of the terrestrial ecosystems in Europe is forest and woodland (Mayer 1984). Forest biodiversity can be maintained within vegetation types hosting species, habitat structures and processes that have co-evolved in forest ecosystems over long time, whether

with minor or major human influence (Angelstam et al. 2001). In other words the maintenance of forest biodiversity encompasses two sets of broad visions, and also management approaches, depending on the history of forests and woodland in the actual landscape (e.g., Agnoletti 2000, Angelstam 2002a). The threats to biodiversity in forests and woodland are usually related to intensive management, which reduces: 1) the number of species (a compositional aspect); 2) the amount of dead wood, large trees, old and structurally diverse stands, large stands and intact areas (structural aspects); and 3) alters important processes such as browsing by deer due to the decline in large carnivores, predation, fire, and the incidence of insects and fungi (functional aspects).

Most policies related to biodiversity of European forests and woodlands make explicit reference to the concept of naturalness (Peterken 1996). In spite of the ambiguity of this concept (Balée 1998, Egan and Howell 2001), it is obvious that forest biodiversity indicators should represent elements found in naturally dynamic forests (Peterken 1996, Prabhu et al. 1996, Angelstam and Dönz-Breuss 2004, Angelstam et al. 2004b). Additionally, both in Europe (Kirby and Watkins 1998, Agnoletti 2000, Angelstam et al. 2003b), and Canada (Stevenson and Webb 2003, 2004) the maintenance of ecological values found in pre-industrial cultural landscapes is highlighted. The latter, although influenced by human land use, traditionally contained structural components such as dead wood, large old trees and old-growth stands that are typically found in naturally dynamic forests (Rackham and Moody 1996, Rackham 1998). Such landscapes may also host cultural and social capitals that promote sustainability (Pierce Colfer and Byron 2001). As a consequence, remnants of the pre-industrial cultural landscape provide a refuge for many species that were adapted to a natural forest environment (Kirby and Watkins 1998). The development of SFM should reflect both of these visions (Anon. 2003c). To sustain these values active management of protected areas is often needed.

Because the cover and types of forests and woodland are dynamic, including both degradation and restoration related to socio-economic changes (Nilsson et al. 1992, Bengtsson et al. 2003), monitoring and assessment of SFM should encompass geographically contiguous units representing actual landscapes, such as grid cells or preferably whole watersheds. Such areas, hereafter called landscapes, have a wide range of implementing actors ranging from the responsible bureaucrats, forest managers, wood processing industry, small private landowners and commons. However, the relative proportion of different categories of managers and owners varies considerably among landscapes, which has strong effects on the ways of and extent to which different policies can be implemented using different planning and management tools (Angelstam and Pettersson 1997, Elliott and Schlaepfer 2001). Additionally a range of other stakeholders including the general public, First Nations, non-governmental organisations and scientists interpret policies from their own perspective.

Existing SFM concepts and multiple trajectories towards its realisation

Definitions of SFM

Internationally, sustainable development in forest and woodland has been promoted in two types of processes (Rametsteiner and Wijewardana 2004). The first is focused entirely on the development of criteria and indicators promoting, facilitating and documenting the status of forests and forest management largely at the national level but also at the forest management unit level. The other route has been the development of forest related indicators in the context of broader sustainable development objectives of different international organisations such as the UN Commission on Sustainable Development (CSD), the UN Convention on Biological Diversity (CBD), the Organisation for Economic Cooperation and Development (OECD), United Nations Environment Programme (UNEP), the World Bank, UN Framework Convention on Climate Change (UNFCCC) and the UN Convention to Combat Desertification (CCD). These processes are briefly summarised below.

When the United Nations was founded in 1945 a special body was established to handle issues related to agriculture and food – the Food and Agriculture Organisation (FAO). Two years later a European timber conference was held to discuss the timber supply in Europe after the Second World War. At this meeting the United Nations Economic Commission for Europe (ECE) timber committee and the FAO European commission were established. In the 1970s acid rain became a problem for forests in many parts of the European continent (Stanners and Bourdeau 1995). This contributed to the establishment of the Ministerial Conference for the Protection of Forests in Europe (MCPFE; see Anon. 1993a, Rametsteiner and Mayer 2004), as well as to the start of long-term monitoring of the condition or environmental health of forests in Europe with respect to air pollution (Strand 1997, Anon. 2003b).

At the Pan-European level the guiding policy process behind SFM is the development of criteria and indicators within the MCPFE (Rametsteiner and Mayer 2004). At the second MCPFE meeting in 1993, the so-called "Helsinki Conference", the European countries agreed on a common definition of SFM reflecting the global discussion on sustainable development. The Helsinki Resolution H1 reads: "Sustainable management means the stewardship and use of forests and forest lands in a way, and at a rate, that maintains their biodiversity, productivity, regeneration capacity, vitality and their potential to fulfil, now

and in the future, relevant ecological, economic and social functions, at local, national, and global levels, and that does not cause damage to other ecosystems." (Anon. 1993a). This definition has also been adopted by FAO.

"Maintenance of biodiversity" is thus a criterion, which is generally accepted in most of the international and national processes for SFM. As an example, the MCPFE has from the beginning considered biodiversity as an essential component, and has accepted in Helsinki the Resolution H2 "General Guidelines for the Conservation of the Biodiversity of European Forests" and at the third MCFE meeting in Vienna in 2003, a resolution "Conserving and Enhancing Forest Biological Diversity in Europe" (Anon. 2003d).

Within the European Union, the European Commission has established several directives, which implicitly have strong bearings on SFM since much of Europe is covered with forests and woodlands (Mayer 1984). This applies to both critical load of pollutants (Nilsson and Grennfelt 1988) and critical loss of habitats (Angelstam et al. 2004c). An example of the former is the "Geneva Convention on Long-range Transboundary Air Pollution" (LRTAP) from 1979 (<http://www.unece.org/env/lrtap/status/lrtap_s.htm>). The history of the Convention can be traced back to the 1960s, when scientists demonstrated the interrelationship between sulphur emissions in continental Europe and the acidification of Scandinavian lakes. The 1972 United Nations Conference on the Human Environment in Stockholm signalled the start for active international cooperation to combat acidification caused by air pollutants that travel several thousands of kilometres before deposition and damage occurs. Examples of policies that deal with habitat-related problems are the Birds Directive (Anon. 1979), the Habitats Directive (Anon. 1992a) and the Water Framework Directive (Anon. 2000). How these habitat-related European biodiversity conservation tools should be applied in practise is under development (Anon. 2003c).

The global debate on sustainability issues has led to other parallel policy-level processes concerning SFM. By early 2002 nine major criteria and indicator processes involving an estimated 150 countries were in operation (Rametsteiner and Wijewardana 2004). For example the Montreal process deals with temperate and boreal forests and encompasses for example Canada and Russia (Oliver et al. 2001). This process resulted in seven criteria, the first six dealing with the same issues as the European MCPFE process. The seventh considers the legal, institutional and economic frameworks. For natural tropical forests criteria for the measurement of sustainable tropical forest management were developed by the International Tropical Timber Organization (ITTO) (Anon. 1992c, Higman et al. 1999). While these focused on the production of timber, ITTO has redirected its attention towards guidelines for the sustainable management of both planted tropical forests and the conservation of biodiversity.

These different international level approaches have basically similar sets of criteria and indicators. In addition scientifically founded interpretations are made. For example, in North America the "ecosystem management" approach was developed (e.g., Christiansen et al. 1996, Meffe et al. 2002, Burton et al. 2003). This concept is based on the idea that forest management should emulate the natural processes in forests (e.g., Bergeron and Harvey 1997, Bergeron et al. 2002, Angelstam and Kuuluvainen 2004) thereby sustaining the structures and processes needed to maintain viable populations of species. In Europe the maintenance of wooded grasslands typical for the pre-industrial cultural landscapes is another management approach explicitly acknowledging the active role of man for maintaining biodiversity (Rackham 1998, Kirby and Watkins 1998, Agnoletti 2000).

The international policy background

At the Rio Earth Summit in 1992, deforestation, biodiversity and sustainable forestry were put on the international agenda (Anon. 1992b, Schlaepfer and Elliott 2000). A Convention on Biological Diversity was established but the negotiations on a Sustainable Forestry Convention stranded and resulted instead in two principle statements, the Forest Principles and Chapter 11 of Agenda 21 (Eckerberg 2000). The Forest Principles (Anon. 1992d), a "…non-legally binding authoritative statement of principles for a global consensus on the management, conservation and sustainable development of all types of forests…", is a so-called "soft law" (Lafferty and Meadowcroft 2000) where the signing states have moral and political obligations toward the treaty. However, this weaker legal status may actually be beneficial for the implementation of SFM, as a forest convention of some kind would have been more vague than "The Forest Principles" in which the guiding objective "…is to contribute to the management, conservation and sustainable development of forests and to provide for their multiple and complementary functions and uses…" (Anon. 1992d).

Chapter 11 of Agenda 21 (Anon. 1992e), a non-binding action program for global co-operation in sustainable development, contains four program areas that deal with combating deforestation: 1) sustaining the multiple roles and functions of all types of forests, 2) enhancing the protection, sustainable development and conservation of all types of forests, 3) promoting efficient utilisation and assessment to recover the full valuation of the goods and services provided by forests and 4) establishing and/or strengthening capacities for the planning, assessment and systematic observations of forests (Anon. 1992e). These program areas reflect the content of the forest principles, and complement the principles by including recommendations on international and national measures. However, unfortunately UNCED had a focus on combating defor-

estation rather than promoting SFM. Another major problem is that the traditional forest sector is not involved with deforestation, but only with what still is forest land. This illustrates the need to deal with forest issues by including the whole land base and thus actors not only in the forest sector but also in agriculture and agro-forestry as well as green space in urban landscapes.

The 1992 Earth Summit triggered further international and national discussions on sustainable development, including biodiversity and sustainable forest management (Lafferty and Meadowcroft 2000). The responsibility to further strengthen the international co-operation related to sustainable forestry was primarily given to the Intergovernmental Panel on Forests (IPF) established in 1995. Under the period of 1995–2000 the IPF and its successor the Intergovernmental Forum on Forests (IFF) developed ca 270 non-legally binding proposals for action. The IPF/IFF action proposals were meant to complement, supplement and elaborate the Forest Principles, the Rio Declaration and Agenda 21. These proposals include measures such as conservation and protection of forests, sustainable forest management and the use of environmentally sound technologies. In order to assess, monitor and facilitate the implementation of these proposals and to further international co-operation, including the prospect of a legal framework, the United Nations Forum on Forests (UNFF) was established in 2000 (Nilsson 2001).

The CBD is a legally binding international convention regarding "…the conservation of biological diversity, the sustainable use of its components and the fair and equitable sharing of the benefits arising out of the utilisation of genetic resources" (Anon. 1992b). According to Hedlund (2002), the CBD is to be seen as a frame document where the convention text is a starting point for further discussions on actual measures. However, with a traditional forestry perspective, the CBD is sometimes viewed as an unwanted intrusion into the traditional forest and forest products sectors.

An interconnected process with a clearer focus on forest biodiversity took place within the CBD. At the fourth meeting of the Conference of Parties (COP) in 1998 the parties decided to endorse a "Work Program for Forest Biodiversity". The focus of the program was on the research, co-operation and development of technologies necessary for the conservation and sustainable use of forest biodiversity (Anon. 1998b). Later the parties endorsed a more action-orientated program. This "Expanded Programme of Work on Forest Biodiversity" included three program elements: 1) conservation, sustainable use and benefit sharing, 2) institutional and socio-economic issues enabling environmental sustainability, and 3) knowledge, assessment and monitoring (Anon. 2002a). The fifth Conference of the Parties to the CBD in Nairobi, in May 2000, endorsed the "ecosystem approach" as a strategy for the management of land, water and living resources that promotes conservation and sustainable use in an equitable way (Smith and Maltby 2003).

The European Community has attempted to adopt a common forest strategy three times. In 1981 the Commission sent the Council a proposal for a resolution on a forestry policy. This was supported by the Parliament, but not endorsed by the Council. In 1988 the Commission adopted a Communication proposing a "Community strategy and action programme for the forestry sector". The Council did not adopt the strategy part of the Communication – which would have implied at least a co-ordination between Member States' forestry policy. With Austria, Finland and Sweden's accession from 1995, the European Union acquired a new dimension in forests. This triggered extensive discussion about forests and forest policy at a European level (Anon. 1997b). In 1997, the European parliament approved a resolution based on a report prepared by the European Deputy David E. Thomas (Anon. 1997c). The European Commission was invited to "…make proposals for instruments and adequate funding for coherent and complementary implementation at Community, national and regional level in order to develop actions dealing with the three main areas of protection, utilisation/development and extension of forestry resources…". The "action plan" was accepted, resulting in different EU funding actions such as aid to Member States for afforestation and aid to develop woodlands in rural areas. The report was can be viewed as an attempt to establish a compromise between the view of the Nordic countries that control over forests should be left to the Member States, and the southern European desire for a more interventionist common forest policy. The result in terms of the development of SFM and biodiversity maintenance can, however, be considered as business as usual.

On the other hand, issues related to forests are to an increasing degree dealt with in many fora outside the control of forestry. For example, a major international political process with clear implications for the forest sector is the Kyoto protocol concerning climate change (Anon. 1997a). These are reasons given for ideas about developing a forest convention (Bergquist pers. comm.). One idea is to couple some of the SFM requirements with legal constraints. Within the EC the Common Agricultural Policy has done so by introducing the standard of "Good Agricultural Practice" as a requirement for financial support. Similarly, the Water Framework Directive introduced "Good Water Status" as the ultimate objective to be achieved in every catchment within a fixed delay. Ideas for what "Good Forestry Practice" represents in terms of biodiversity are certainly at hand (Anon. 2003c, Rametsteiner and Mayer 2004). The challenge is to strike a balance with the complexity of the SFM issue and its long series of related criteria and indicators, and the need to respect the wide range of different conditions that different countries and region in Europe are faced with. The different positions of individual countries is the basis of the failure to come to a global forest agreement or an EU forest policy.

We argue that today's main battlefield for the developement and implementation of SFM in Europe is the boreal area because this is where a contiguous mix of the three stages of the development of sustainability and their supporters currently exist (Angelstam et al. 2004c). If Europe wants to move forward towards a common SFM policy, the battle will have to be fought and won in the North. The resolutions of the 2003 Vienna MCPFE meeting (Rametsteiner and Mayer 2004) form an almost ready to use forest policy charter that could very well be cast into legislation by the EU. The Vienna MCFE resolutions are a very good reflection of what society as a whole expects from the forest and forest products sectors. In this context, it has also to be noted that, if the forest sector does not come to fix a basic charter soon, policy about nature conservation, water, energy, climate, landscape, etc. will continue to erode the forest sector's effectiveness as a self standing centre of governance. The real debate will probably start by the end of 2004 with ten new member states in the European Union, several of which have valuable forest resources regarding all dimensions of SFM.

Different trajectories towards SFM

Depending on the initial conditions there are several possible trajectories towards implementing SFM policies. Using the six criteria of SFM in the MCPFE process, we illustrate that the starting points and challenges towards a balance among ecological, economic and social criteria, i.e. reaching the central part of the triangle in Fig. 1, may vary considerably. As a consequence, different countries and regions focus on different issues, and promote different sets of management tools (e.g., Sheppard and Harshaw 2001, Lindenmayer and Franklin 2003). The range of possible trajectories to the SFM vision is, however, as much dependent on the social and cultural situation as on the forests. This range of regional solutions for bridging barriers towards SFM should be used to share solutions and to facilitate forest management in other areas.

Sweden, Switzerland and remote regions of the European part of Russia provide three contrasting European examples where the current focus is on quite different SFM criteria. In Sweden, where forests have been subject to intensive management for sustained yield of wood for a long time, biodiversity has been a major driving force towards SFM during the past decades (Angelstam 2003), but currently social issues are also appearing (Nordanstig 2003). By contrast, Switzerland's steep terrain has promoted management for protective functions of the conifer-dominated mountain forests and as in Sweden with an increasing focus on biodiversity (Kräuchi et al. 2000, Neet and Bolliger 2004). Finally, in remote parts of Russia such as in the Komi Republic, large-scale logging of forests started only recently, and large intact forest areas still remain (Yaroshenko et al. 2001). Here a major current challenge is to use not previously managed forest landscapes for the development of human welfare in a sustainable manner (Pollard

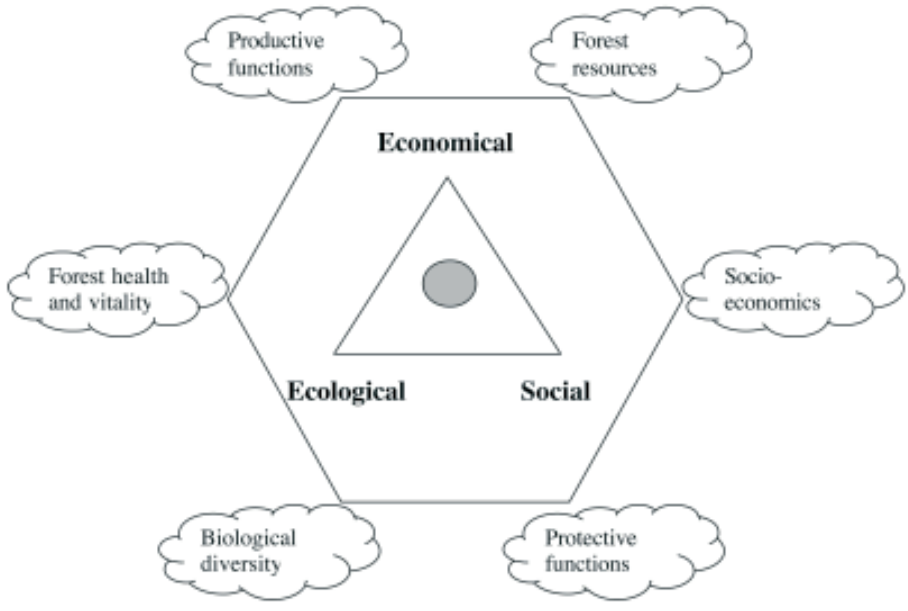


Fig. 1. Sustainable Forest Management (SFM) involves the management of ecological, economical and social values. This can be viewed as a triangle where the challenge is to continuously adapt to changing relative proportion of the three values. The surrounding hexagon summarises the six criteria of SFM accordning to the MCPFE (Rametsteiner and Mayer 2004). Note, however, that the implementation takes place with different trajectories and usually considerable time lags.

2003), and at the same time to maintain the functionality of the last remaining large intact forest areas (Angelstam et al. 2004c). In addition, the problem of illegal logging must be addressed (Lloyd 2000, Lopina et al. 2003).

Similar differences in the emphasis on different SFM criteria can be seen within a country over time. Sweden can be used as an example to illustrate this (Anon. 2001, Enander 2001, 2002, 2003, Ekelund and Hamilton 2001). The very first forest law in this country (from 1647) was a response to swidden agriculture and browsing on trees by domestic herbivores. Similarly, the transition from the liquidation phase in forest in the 19th century led to the first legislation on sustained yield in 1903, but only on the private land. In 1948 a focus on industrial production of wood using intensive management methods was emphasised and practised until the mid-1980s. Recently, however, the public opinion on clear-cuts (Anon. 1974), negative effects of a long history of intensive forest management on a range of specialised species (Berg et al. 1994), led to a new forest legislation in 1993. Additionally there are indications of negative effects by acid rain and nitrogen deposition on the long-term wood production (Sverdrup and Stjernquist 2002). At present the goals for sustained forest production and the maintenance of viable populations of all naturally occurring species are stated to be of equal importance (Anon. 1993b).

The evolution of new forest policies in Sweden includes a wide range of narratives or percieved realities used by different actors to make their point in the public debate. Historically, wood shortage has been the major concern. During the past decade or more it has been conservation of biodiversity, but in practice often narrowly interpreted as the conservation of threatened and red-listed species in the short-term rather than population viability and ecosystem integrity and resilience (Angelstam 2003). Although there has been considerable development in the approaches to landscape planning (Angelstam and Pettersson 1997, Fries et al. 1998), assuring functionality of networks of habitat structures at different spatial scales in the long term (Angelstam et al. 2003a, 2004a) has largely been disregarded. Similarly, the ecosystem processes maintaining not only biodiversity, but also the productive function of forests (Sverdrup and Stjernquist 2002) are neglected. At present a conflict between jobs in the traditional forest sector and the maintenance of biodiversity by establishing protected areas is appearing. This debate includes arguments both about management of biodiversity being too costly for the industry (Anon. 2003e) but also that there is insufficient address to socio-economic problems caused by a narrow perception of what forest products are. Another issue is that biodiversity is viewed as a problem for wood production, while the problem of reduced forest management intensity and expected subsequent reduced wood production caused by deregulation of the forest policy is largely ignored. Finally, because actual landscapes have a wide range of different owner categories, it remains a major challenge to understand what the relative responsibilities of these are.

Narratives are gross simplifications of reality. It is difficult to kill a good narrative with facts. One has to find a new and better alternative. Nevertheless, after a while it is realised that the reality is more complicated than it was first thought. Decision-makers of an old paradigm often have difficulty to take in new knowledge (Anon. 1999). Often there are also actors that would lose if the narratives were corrected. Although such narratives may be efficient in the short term, their communicative power is reduced after some time (Roe 1991). This, we argue, is typical to ongoing paradigm shifts. For example, Davis et al. (2001:524) writes: …"Each interested party wants their values to prevail and are pleased when science, data, and analyses supports their policy positions. If, however, data and analysis does not support strongly held positions and values, a usual first strategy is to discredit the data, the analysis, and the analyst".

We argue that at the national level the need for knowledge transfer is essential when developing policies and strategies, applying them, and monitoring their effects. In the following we therefore examine the role of information in the policy process. We put emphasis on the political process also for the reason that national level information becomes meaningful only if a functioning policy process is in place. Theoretically the policy process should be in place first and information work comes as a second step. In practice the two may usually be developed simultaneously. The policy process should include a number of steps (see Moldan et al. 1997, Janz and Persson 2002) that need to be iterated over and over again: 1) public debate ("political" or "scientific"), 2) identifying problems and potentials, 3) designing options for (political) action, 4) analysing the consequences of such action, 5) decision-making (which option to chose), 6) implementation, and 7) monitoring. In implementing SFM, with biodiversity as a proxy for the ecological dimension, both "hard" sciences ranging from biology and chemistry, and "soft" sciences such as political science and psychology must be included (Andersson 1997, Penn 2003). Finally, the actual management needs time to act so that the land develops and eventually reaches the desired goal of the policy. In reality this policy life cycle is repeated over and over again as values and landscapes change.

It is in this political process that new objectives (the national ambition) and new policies (the way to reach these objectives) can be formed. Various studies are required, in the first place to investigate the current situation and the need for adjusting objectives and secondly, the consequences of alternative policies. Stakeholders should be involved throughout the process, and great emphasis should be placed on consensus building. This has also the very practical implication that the more consensus there is, the easier the implementation will be. Governments change often, but forest management and conservation are long-

term undertakings. It is desirable that there should not be any drastic changes in policy after each election or change of government. However, relevant information is needed throughout all the steps of the process. The general public as well as the stakeholders can only participate meaningfully, if correct information exists and is readily available. It is easiest to build consensus by a series of steps, namely, consensus on: 1) basic facts about the biodiversity, forest resources and their utilisation, 2) the nature of the main political problems, 3) the options that are available to solve the problems, 4) the consequences of different political programmes, and 5) decisions on political action to take.

In this sequence of steps, consensus building becomes progressively more difficult, and the information required becomes increasingly complex. Analysing the consequences of alternative action programmes demands a high standard of information and the ability to interpret it. In real life, even if serious attempts are made, full consensus is hardly ever reached. In cases of disagreement, consensus should at least be sought as to what the issues are that are in dispute. Consensus building is also made difficult by the fact that different participants can view the same information in different ways – they see different sides of reality.

The SFM vision has made forest management dramatically different than it was once (Glück 2000, Mills and Clark 2001, Gamborg and Larsen 2003). There is thus a need for a holistic and cross-sectoral approach for implementing forest policy programs with clear links to rural development and environmental conservation (Nilsson and Gluck 2001, Nilsson 2002). "National Forest Programs (NFPs) for Sustainable Forest Management" proposed by the Intergovernmental Panel on Forests (IPF; Anon. 1997d) is such an approach. NFPs should include the formulation of policies, strategies, and plans of action, as well as their implementation, monitoring, and evaluation. Furthermore the programs should be implemented in the context of a country's socioeconomic, cultural, political, and environmental situation. We emphasise that national policies and programmes for the forest sector must be integrated with other national objectives and policies. Sector policies that are developed considering only sector objectives will lead to conflicting programmes that counteract each other (Janz and Persson 2002).

Questions asked about biodiversity by various stakeholders

The implementing actors

The forest and wood industry

Around 1990 market reactions to intensive management for wood only meant that the forest industry in Sweden, Finland and Canada had to please the consumers, for example by making efforts towards maintaining biodiversity (Elliott and Schlaepfer 2001). As a consequence, the forest industry has developed more nature-friendly approaches at multiple spatial scales (e.g., Angelstam and Pettersson 1997, Raivio et al. 2001, Burton et al. 2003). Within stands, retention of living and dead trees as well groups of trees and riparian corridors is encouraged. At the scale of stands in landscapes a return to a more diverse set of silvicultural practices is advocated (Fries et al. 1997, Angelstam 2002a). Finally at the scale of forest management units (FMUs) or landscapes in regions, tools are developed to aid decisions about the different levels of ambitions to be applied with respect to satisfying biodiversity and production goals, respectively (Fries et al. 1998, Angelstam and Bergman 2004).

Certification is a case in point where the development is governed more by the international market, than by local, regional and national stakeholders (Elliott and Schlaepfer 2001). The area of certified forests is exponentially increasing, mainly in the northern hemisphere (Rametsteiner and Simula 2002). But what will happen to certification in the long term is presently unknown. It has been accepted by large companies in certain regions (Cashore et al. 2003), but appears less so for small owners in most parts of the world – not least developing countries. Many of them still believe that certification involves a cost, but hardly any premium. For this reason the concept of group certification was introduced. The ongoing re-negotiations in Sweden about the first national certification standard for FSC certification will provide an acid test of the sustainability of certification (Angelstam 2003). The risk for the industry of not paying attention to biodiversity issues, because of pressure from some markets (Elliott and Schlaepfer 2001), is currently uncertain. This doubtful benefit of certification employed by all large Swedish companies is indicated by great difficulties to negotiate a revision of the current national certification standard.

SFM can be thus viewed both as a process and a goal. Using the current debate in Sweden as an example, it is evident there is an ongoing shift in paradigm with respect to how the goal is developing. Recent debate articles about SFM in Sweden can be interpreted as an increasing gap between what the SFM vision ultimately entails, and what this is allowed to cost to the industry in terms of reduced areas of old forest available to logging. The forest industry claims that filling the gaps in amount of protected forest areas reduces number of tradition forest jobs (Anon. 2003e), however, without considering jobs in other sectors using forest as a resource without harvesting trees (Nordanstig 2003).

The current economic paradigm assumes that a market-based economy will secure efficient allocation of resources among competing uses, and provide signals (prices, profits, rents) to different actors (firms, households, governments) which subsequently will respond in predictable ways. Markets, however, can also fail badly in this allocation of resources, particularly regarding conservation is-

sues (Hanley 1998). Using the home furnishing company IKEA as case study, Djurberg et al. (2004) discuss the role of non-utilitarian values in promoting environmental responsibility, and how this can promote "green" businesses.

Public owners and planners

In general forests owned by the state have focussed on satisfying a broader set of management objectives than large industrial owners (Thomas 1979). One example is the new Swedish state forest company "Sveaskog" (Anon. 2002b). The recent (2002) policy of the company states that with the company's own set-aside areas, in conjunction with certified forestry practices, the long-term ambition is to achieve nature conservation areas covering 20% of the productive forest land in each forest ecoregion. In contrast, other companies use only FSC certification where 5% set-aside is the national standard in Sweden. Note, however, that in terms of what is set-aside in the short-term the differences in managed landscapes are small between the two compared to the set-aside of larger areas at the scale of ecoregions, which are considerable on state forest land. In Finland, a fairly similar approach to the Swedish model has been developed by the Finnish Forest and Park Service (Metsähallitus) (Korhonen et al. 1998, Karvonen 2000, Raivio et al. 2001, Niemelä 2003). Metsähallitus manages state-owned forests that predominate in the eastern and northern economically more remote parts of the country. The system in Finland is called "landscape ecological planning" and covers all the silviculturally managed forest land. The main goal is to make sure that forests are managed sustainably from economic, ecological and socio-cultural point of view.

Non-industrial small private forest owners, commons and First Nations

While less active in the public debate, Non-Industrial Small Private (NISP) owners manage a high proportion of the forests in most of Europe. In contrast to the forest industries, private forest owners do not usually ask explicit questions about biodiversity. The organisations representing the owners remain more passive than the forest industry and argue that the best way of maintaining forest biodiversity in privately owned land is to encourage the variation in management objectives among different owners (Rolfe 2001). For the maintenance of biodiversity, this hypothesis must, however, to be tested in regions with similar ecosystems but with different socio-economic conditions.

According to Bengston et al. (2001) most studies made in the USA showed that NIPF owners held a positive attitude towards ecosystem management. In a Swedish interview study of private forest owners, Götmark et al. (2000) concluded that NIPF owners were weakly positive to conservation but would dislike having a state reserve on their land without receiving sufficient economic compensation. In Finland a survey study (Kangas and Niemelainen 1996) revealed that from a number of alternative management objectives the health and vitality of the forest was considered as most important. Owners of large woodlots considered conservation less important. Inferences from studies on opinions and attitudes are that demographic factors and place of residence in relation to the forest holding, its size and the time of ownership may indicate different directions of attitudes (Kangas and Niemelainen 1996, Tarrant and Cordell 2002, Uliczka et al. 2004).

Communal ownership is also an important group. Carlsson (2003) analysed the Swedish system of forest commons, and concluded that this type of resource user, being closely connected to a resource system, is in a good position to adapt to signals from the ecosystem. This requires, however, that forest data are continuously available during a long time period. Dönz-Breuss et al. (2004) provide insight to the complexity of forest goods and services that communal managers of mountain forests are faced with in the Austrian Alps. Here the connection between forests and protective as well as social functions are much more obvious than in the boreal forest without steep mountains with hazards as avalanche and flooding and with a very low population density.

While First Nations have become a major stakeholder in Canada in recent years (Stevenson and Webb 2003, 2004) this is not the case in Europe. There are, however, signs of increased considerations in forest management of timber in Fennoscandia for other uses such as reindeer management of Sami people (Borchert 2001, Sandström et al. 2003).

Other stakeholders

The general public

Forest biodiversity in the form of forests and green space in urban areas have documented positive effects on the health and well-being of people (Grahn 1992, 1996). Returning to the Swedish example, a new nature conservation policy from 2001 encouraged the National Board of Forestry to propose how forest could enhance the social dimension of sustainable development (Nordanstig 2003). Four aspects were brought up: 1) to secure the availability of forests and green space in general in urban landscapes, 2) to increase the knowledge about forest in the general public, 3) enhance multiple use such as nature tourism and 4) to market the social values of forests.

An obvious body to funnel the interests of the general public to the forest sector in a broad sense would be the administrations of local municipalities. However, while municipal forests are very important in central Europe, with a few exceptions (Olsson pers. comm.), Swedish municipalities have so far not engaged themselves in forest issues and the functionality of urban green space (Sandström et al. 2004). Nevertheless, being the smallest official

socio-economic unit, municipalities represent an ideal scale for strategic landscape planning, which should be a forum for integrating the efforts of different actors at the landscape scale (parish, village, forest management unit, or even better, related to watersheds). As a consequence, databases describing the existing biodiversity and appropriate planning algorithms should be available at this level.

Non-governmental organisation

Environmental Non-Governmental Organisations (ENGOs) are a very diverse group ranging from activist groups focussing on obvious mismanagement issues to those attempting to build bridges among different interest groups. In a global economy forest certification as advocated by ENGOs is an appearing potential mechanism for negotiating the standpoints of different interest groups.

Wunder (2003) illustrates the role of ENGOs interacting with banks lending money to finance specific investments. As an example, the World Bank and the International Monetary Fund (IMF) often make loans to finance general government spending. To get the loans, poor countries must agree to change their policies. When the World Bank lends money for a specific investment project it always assesses how it will affect the environment. But when it makes loans to support policy reform, called structural adjustment loans, it usually does not. During consultations about the Bank's new forest policy many governments, NGOs, and other groups suggested that the bank should look more responsibly at how structural adjustment loans affect forest development. Often economic changes associated with these loans have a larger impact on forests than forestry projects do. Wunder (2003) studied how societies' spending resulting from oil and mineral exports booms influenced deforestation in tropical forest countries and argues that the World Bank can and should analyse how its structural adjustment loans affect the environment.

Scientists

Decision-making in land management is becoming an increasingly complex task. Research scientists and the information they create can effectively contribute to the development of solutions to management issues. This applies both to the ends (such as use or protection) and to the means (such as choosing silvicultural methods). Mills and Clark (2001) discuss how research scientists can be successful in bringing the skills and knowledge into use when implementing natural resource management policies. For example they argue for making analyses in a broader context than is the norm for research scientists, communicating science findings to diverse audiences, being prepared to respond to harsh critique meant to undermine their work i.e. operating "outside the box" of routine research (Letey 1999, Hanski 2002). Thus, the scientist's credibility needs to be protected by assuring quality control in terms of publishing results and making them available for public review. It is also vital to clearly state the confidence that can be placed in conclusions and to remain independent from the manager's final decision, which is usually based on a broader set of perspectives than science can provide.

Naess (1974) distinguished between the understanding of science within itself and in connection with the development of societies. Traditionally, philosophy of science deals with the former. However, particularly in applied sciences, there is a need to understand the role of science in society. Lee (1993) elaborates further on this and argues that science provides a navigational aid to practise adaptive management or deliberate long-term experimentation with the economic uses of ecological systems to learn what works and what does not. There are, however, many obstacles (Lee 1993, Gunderson et al. 1995, Mills and Clark 2001, Berkes et al. 2003). Kinzig et al. (2003) offer a number of recommendations to improve the science-policy interface, including restructuring of science curricula and establishment of science-policy forums with leaders from both arenas, and specifically constituted to address problems of uncertainty. Finally, as stated by Mills and Clark (2001), "Credibility of science is hard to gain, once lost is even harder to regain".

Bridges towards realising the SFM vision

The implementation of a principle such as sustainable forest management (SFM) can be viewed as a process where an initial step is to satisfy the need for social licence to operate, before starting more complicated scientific, and costly, implementation activities (Bunnell and Johnson 1998). However, the gap between agreed criteria and current practice for forest management in actual landscape is very wide (McDonald and Lane 2004). This means that the development must take place with different small steps each providing an improvement. In the following five sections we discuss five prerequisites for achieving the SFM vision in actual landscapes.

Active adaptive management

Sustainability can be viewed as a direction in which we strive. Using the terms "compass" and "gyroscope" Lee (1993) presents good insight into how science and politics may be integrated for the environment. He argues for adaptive management (Walters 1986), which means treating economic uses of nature as experiments and learning from them. This societal learning process can be called politics, and the combination of the two social learning (Lee 1993). This approach is particularly relevant for answering

the managers' and other stakeholders' questions about how much of different forest and woodland vegetation types that are needed to maintain different elements of biodiversity.

Adaptive management can, however, be both passive and active. Promoting SFM requires management plans and monitoring programs that are informative and provide reliable feedback. The most informative plans are those that are deliberately designed as management experiments, to discriminate between the alternative hypotheses for management. Typically, this involves comparing a range of management actions. This approach is referred to as "active adaptive management". The alternative, referred to as "passive adaptive management", is to assume that the most plausible hypothesis is true, and then implement the action or set of actions that the model forecasts will have the best outcome.

Turning science into practice requires collaboration at all steps, time to build mutual understanding, willingness to change, and a clear presentation of tradeoffs. There is also a need to provide leadership, inspiration, and co-ordination. Active adaptive management teams focused on a particular case study are an efficient approach, because they provide a forum for the involvement of a variety of stakeholders ranging from the land managers, the general public people, and policy makers (Boutin et al. 2002).

By contrast, the situation on the national policy arenas and in actual management units can rather be characterised as reactive and thus passive. Narratives still dominate. As an example, rather than asking how many trees should be left during timber harvest or how much protected areas are needed (Hanski 2002), evaluations of the spatial configuration of what has been agreed in certification standards are requested (Friberg pers. comm.). While forestry with variable retention of trees and small stands during thinning and final felling is certainly positive, it is not enough to fully implement biodiversity policies (Hanski 2002, Hebert 2004). For example, in second-generation forests the quality of retention will be lower than in first-generation retention, and even lower in subsequent thinning operations. There is thus a need to test hypotheses such as: 1) today's nature conservation will maintain the present (i.e. impoverished) species composition at the landscape scale, and 2) the area extent and population size of so far negatively affected species will increase with today's nature conservation efforts. However, the long time and large space needed to test these hypotheses make it difficult to use conventional scientific approaches, which tend to address short-term political goals rather than the long-term goal of achieving SFM approaches (Angelstam et al. 2004c).

To encompass both short-term and long-term goals of SFM, it is necessary that everyday management is viewed and designed as carefully monitored adaptive management experiments including a sufficiently wide range of initial conditions at multiple scales (such as trees, stands and landscapes; Hebert 2004). To cover scales that include the variation among landscapes within regions, and hence be able to answer questions related to what is needed to halt the negative trends in different elements of biodiversity is a major challenge. A long history thus provides little room for manoeuvring. Additionally, the direction of change also matters. The time lag for species' responses to habitat loss is likely to be smaller than to habitat restoration (Hanski and Ovaskainen 2002). Habitat loss studies may hence produce overly optimistic conservation targets for habitat restoration.

In Europe the boreal forest is unique in the sense that its still contains the full range of conditions from intensively managed industrial forests to remnants of naturally dynamic reference areas with no wood use in remote places (Angelstam et al. 1997, Yaroshenko et al. 2001). By comparing regions in different phases of forest ecosystem development, there are unique opportunities for well-informed decisions based on experiences from other regions about how to strike a balance between economic, social and environmental aspects of forest resource management. Finally, the development of adaptive management approaches must be placed in the context of the local socio-economic situation, including institutions and governance systems. Thus, rather than initiating advanced and costly solution in one go one should attempt to gradually add new components in small steps. The question is ultimately a matter of transparency regarding costs and benefits at different scales in time and space to different actors.

Performance targets for sustainability checks

Achieving SFM, i.e. essentially succeeding with sustainable development in forest and woodland landscapes requires a comprehensive framework covering several steps (Gallopin 1997, Higman et al. 1999, Oliver et al. 2001). These include 1) mechanisms for consistent application, 2) a set of relevant variables (i.e. criteria and related indicators), 3) formulation of short-term goals to be reached for each variable within a certain time frame (such as national environmental quality goals and regional certification standards) and 4) formulation of long-term performance targets representing sustainability (derived from thresholds based on reference values characteristic for benchmark conditions).

At the policy level there has been a considerable progress toward such an ideal model over the past two decades. To make the principle of sustainable forest management more concrete, a large number of criteria and indicators have been presented. Still, however, the debate often centres around the type of silvicultural system being used at the stand scale, instead of the amount, location, and intensity of human use, or exploitation at multiple scales (Graham and Jain 1998). Thus, to achieve sustainability, it is of vital importance that results from monitoring of indicators are compared with scientifically approved perform-

ance targets to assess both status, and if repeated, trends in the level of sustainability. Depending on the outcome, evaluation in the form of quantitative gap analyses (Angelstam et al. 2003c) should be used to guide protection, management and if needed restoration of forest structures, species' populations or ecosystem processes.

The development of performance targets need to be encouraged for a range of elements of biodiversity (composition, structure and function; Noss 1990, Larsson et al. 2001), and at multiple spatial scales (Hebert 2004). Such targets can be developed with different levels of ambition. An obvious first level is that the compositional elements of biodiversity are maintained. This is represented by occupancy of one of several species in a given landscape. A second target level is therefore to ensure population viability over long time. The generally occurring increase in the threshold amount of habitat needed for probability of occupancy vs probability of breeding allows estimation of the "cost" of this increased target level. The word "all" in such policies makes it almost imperative to define thresholds for a suite of efficient umbrella species (Lambeck 1997, Mönkkönen and Reunanen 1999, Roberge and Angelstam 2004). Third, as ecosystems are open and dynamic, the total area needed to ensure ecosystem integrity and health in the long term increases further (Pimentel et al. 2000). Minimum dynamic areas (Pickett and White 1985) are necessary to continuously provide habitat for many viable populations over multiple spatial scales, as well as for the interactions among them (Bengtsson et al. 2003). Finally, a fourth target level may be to ensure ecological resilience (Gunderson and Pritchard 2002) thus considering the whole social-ecological system (Berkes et al. 2003). As a consequence there is a suite of targets that can be specified for the maintenance of biodiversity in an area, each target representing an increasing probability of maintaining a functional ecosystem. Designing studies to evaluate relationships between compositional, structural and functional elements of biodiversity as well as with human pressures on the environment is a major challenge, in particular when moving up in spatial scale, dealing with long time perspectives and dynamic systems.

Spatially explicit planning at multiple spatial scales

The chosen spatial scale (such as national, regional, forest management unit, local watershed) has dramatic consequences for the efforts required for implementation of SFM and biodiversity. In fact, it is not easy to define the policy and management arena to a particular country. The large corporate companies are no longer national but global. Processes such as disturbance events affect organisms at different scales differently so there is no single correct scale to use to describe populations or ecosystems. This problem has been examined by Lertzman and Fall (1998), who point out that in forestry, management has concentrated at the stand scale with much less emphasis on the landscape, with the result that bottom-up processes have driven managed landscape dynamics. They refer to this as the "tyranny of small decisions" in one direction. A particular problem is that the cumulative effects of a large number of stand-level interventions have rarely been assessed.

Maintaining Europe's pre-industrial cultural woodland landscapes is partly a different issue. This pastoral type of landscape, which many people generally want to see and would like to conserve, are the result of a million small decisions, but with little planning (Larsson 2004). How can we make the modern cultural landscape acceptable, not only to humans but also to animals and plants? Or should we totally segregate conservation and economic use? That is a fundamental question to be asked, not only by forest managers, farmers and biologists, but also by economists.

Within a country the issues addressed by national agencies mainly relate to satisfying international policies, the European Community and national short-term national goals, usually by designing monitoring programmes and reporting the results by regions such as county administrative units (Angelstam et al. 2004d). The focus is often focus on indicators as point objects such as in national forest inventories, localisation of protected areas, and usually without a perspective that allows evaluation of habitat structures at the landscape scale in a spatially explicit manner (Langaas 1997, Angelstam et al. 2003c). Because landscapes are managed by a number of different owners, there is a need to integrate the efforts towards maintaining natural structures of different actors at different spatial and temporal scales within actual landscapes (Angelstam and Bergman 2004).

Some aspects of SFM can, however, only be solved at the scale of ecoregions. One example is the size of natural intact areas, which is important for the maintenance of ecosystem function and resilience. For example (Skonhoft and Solem 2001) reported a decline in the amount of wilderness areas from almost 50 to <10% in Norway during the 20th century. In Europe, large intact forest areas are now virtually only found in Russia (Yaroshenko et al. 2001). This has clear consequences for biodiversity. For example, while several specialised and area-demanding species have become extirpated for various regions in Fennoscandia, they still have viable populations in the Baltic States (Angelstam et al. 2004a, Kurlavicius et al. 2004).

When striking a balance between different aspects of SFM there are different schools of thought. The main debate is whether there should be multiple use and semi-natural forests, or rather intensive forest management or plantations and protected areas? The solution, we argue, is zoning. As an example, the "triad" approach to landscape conservation (Seymour and Hunter 1999) divides land into

zones of intensive wood production, extensively managed forests, and protected areas. These issues become of paramount importance when the forest history is long: minimising loss of existing forests of high conservation value and emphasising wood production in other areas (Angelstam and Bergman 2004). Maintenance of viable populations of specialised species is most feasible in the former. In the latter, where the landscape is already impoverished, rehabilitation would be costly and success would be uncertain (Tilman and Kareiva 1997, Hanski and Ovaskainen 2002). Arguments for zoning have also been proposed for succesful introduction of intensive forest management (Binkley 1997).

We argue that the use of performance targets for how much habitat is needed to achieve a certain goal representing a given level of ambition at a particular scale would allow more precision in zoning. This means for example determining the size of patches of different forest vegetation types and the spatial arrangement of these patches in order to assure functional connectivity (e.g., Angelstam et al. 2003a, 2004a, Bengtsson et al. 2003). UNESCO established the Biosphere Reserve concept in 1974 as a means of promoting solutions to reconciling the conservation of biodiversity with its sustainable use. It represents one approach that could be used to zone a landscape into different forms of use including core area, the buffer zone and the transition area (see also Seymour and Hunter 1999). Consequently, if considering population viability of specialised and area-demanding species, the SFM vision can probably be attained only at the scale of landscapes in ecoregions (Olson et al. 2002, Mårell et al. 2003).

Integration of actor's activities and tools for assessing SFM

Forests and woodlands are large ecosystems and as such they present some of the most difficult problems in environmental science and policy. The reasons are that they cover large geographical areas, have a mixture of property right systems, concern a multitude of stakeholders and involve a range of management tools (Fig. 2). At an UNFF expert meeting held in Yokohama the key conclusions were that the criteria and indicators' framework is internationally widely accepted and covers most of the world's forested area, and all individual initiatives incorporate the same fundamental elements of SFM (Rametsteiner and Wijewardana 2004). The indicators for each criterion, however, vary from process to process. The meeting also found some limitations, including that the monitoring and assessment of some indicators, in particular those on socio-economic functions, protective functions and biodiversity, have been found to be difficult. Moreover some specific issues such as illegal trade and illegal logging have

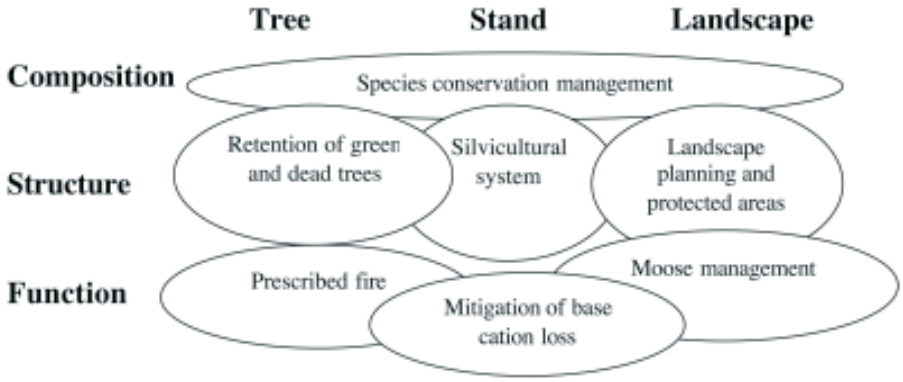


Fig. 2. Maintaining biodiversity within the vision of sustainable forest management (SFM) means considering the elements of biodiversity (rows) across multiple spatial scales (columns) (Noss 1990, Larsson et al. 2001). As an example we summarise the range of current management activities that take place in Europe's northern forests (e.g., Angelstam 2003, Niemelä 2003). Direct species conservation management has focussed on large birds of prey and large carnivores having suffered from persecution for long time. For most species, however, biodiversity conservation is generally indirect, by managing the landscape's structure and function at several spatial scales. Variable retention of live and dead biomass and physical structures, adaptation of silvicultural system to local and regional conditions (Fries et al. 1997, Angelstam 2002a) and landscape planning (Angelstam and Pettersson 1997, Fries et al. 1998) are the main tools affecting structure. Regarding functional elements of biodiversity, prescribed fire is an example of artificial ecosystem resetting, which creates habitat for a range of specialised species. At the stand scale the long-term functionality of forest ecosystems (Sverdrup and Stjernquist 2002) rely on the maintenance of soil physical structures, fertility related nutrient stores (base cations, phosphorus, nitrogen, trace nutrients), chemical conditions (pH, aluminium, heavy metals) and inherent nutrient supply capability (base cation weathering and nitrogen fixation). Moose management is an example of fauna interactions including both vegetation and large carnivores (Angelstam 2002b).

not been explicitly addressed. In particular biodiversity and socio-economic function indicators are fundamental to understanding management of forests, while others reflect "hot topics" that countries or processes can include in their indicator systems.

A critical component for the evolution of SFM through a landscape-scale ecosystem based approach within the framework of active adaptive management is an efficient communication between science and practice as well as among different interest groups (Clark 2002). This requires good understanding of the actors and their views. This in turn requires blending of natural and social sciences to evaluate the success of policy implementation in different socio-economic contexts (Angelstam et al. 2003c, Lazdinis and Angelstam 2004). However, such an ideal course of action and development is often hampered by inappropriate and conflicting policies, compartmentalised knowledge and skills among disciplines as well as insufficient awareness about the solutions and methods available in other regions and countries. Resources, knowledge and attitudes are three groups of factors affecting the implementation of policies (Ostrom 1990). In contrast to the traditional compartmentalisation of different sectors this requires interdisciplinary approaches and a close interaction between management, development and research. This requires the integration of economic, social and environmental aspects, as well as relevant data and tools for analysis and modelling. In particular the harmony between ecological and management dimensions must be evaluated in a spatially and temporally explicit way (Angelstam 2002a). Development and use of geographical information systems and tools for handling complex decisions are therefore needed (Langaas 1997, Young and Sanchez-Azofeifa 2004).

Moreover, there is a need for a suite of simple planning and assessment tools based on indicators representing the management level (Angelstam et al. 2003c, Lazdinis and Angelstam 2004). An obvious starting point is to evaluate the usefulness of existing data used to describe entire landscapes. For example Angelstam et al. (2004b) applied a questionnaire approach to evaluate the extent of presence of basic information about the composition and structure of European landscape-scale case studies. By evaluating species-habitat relationships for specialised birds and mammals, the conclusion was that land management data is useful, but also that the thematic resolution, for example the range of forest stand age classes must be improved (Jansson et al. 2004). To evaluate the chances of different landscapes' ability to maintain biodiversity in the long-term, and to make strategic decisions about different management efforts, Angelstam and Bergman (2004) applied ordination of data from regular forest management databases to rank landscapes within ecoregions. While such compilations are feasible for large contiguous holdings (Kurlavicius et al. 2004), assessment of actual landscapes with many owners is much more complicated. In fact, regarding community forestry in developing countries the Forestry Departments often do not encourage the empowerment of local communities at all (Arnold 1991).

A major problem is the communication among traditional, representing sustained yield of wood, and new stakeholders in forest management. We therefore also need tools for integrating the policy messages conveyed by SFM indicators to a diversity of audiences (Prescott-Allen 2001, Clark 2002). To improve the flow of information to policy makers and the public at large, indices portraying the status and trends in the level of environmental sustainability of forests, such as the natural capital index developed in the Netherlands (Loh et al. 1998), have been proposed (Duelli and Obrist 2003, Ullsten et al. 2004).

The focal area for the implementation of the SFM vision is slowly shifting from the policy level to that of forest management units in actual landscapes. A major barrier to be bridged is the interface between different scientific disciplines (Lee 1993, Penn 2003). In a recent review Jakobsen et al. (2004) stressed that participants in cross-disciplinary projects should not underestimate the influence of different organisation and science cultures. For Sweden, Olsson (2003) summarised how the research community should face the challenges of achieving sustainability in the light of the Johannesburg summit in 2002.

First it was concluded that there are major knowledge gaps related to for example the role of biodiversity for ecosystem function, how integrated management at the level of watersheds can be achieved, how international trade subsidies affect sustainability and relating to the values and behaviour of people. In particular comparative studies among countries were encouraged. The research should also study the social experiment that implementation of sustainability related policies such as SFM forms, and understand what the obstacles for success are. Limited long-term funding is a serious drawback for the implementation of integrated approaches.

Second, the dialogue between policy and science must be improved (Christensen et al. 1996, Kinzig et al. 2003). The current systems for funding and reward are inappropriate, and politically controversial issues are often avoided (Hanski 2002). A major obstacle is the lack of syntheses as a basis for political decisions, as well as of the generalists that have the capacity to carry out such syntheses. Research also needs to be proactive and actively become engaged in promoting sustainable solutions rather than only identifying negative relationships. This has strong bearings on education and training. While continuing specialisation within disciplines, there is also a need for training also generalists being able to work in a transdisciplinary manner (Hammer and Söderqvist 2001, Norton 2003).

Third, the economically more developed part of the world (the north) needs to collaborate with the less developed part (the south). Generally speaking the global problems including biodiversity, as well as water supply and energy systems, are in the south while the research capacity

is in the north. One approach suggested was to encourage civil society research with NGOs and the general public. Without this, the basic knowledge about species diversity in for example Europe would have been very limited.

Fourth, there was consensus that a systems perspective is essential, but that this requires a far more effective collaboration among different scientific disciplines. A major obstacle is to be found within the existing funding and research institutions. The proposed strategy was to establish transdisciplinary facilities where researchers can collaborate, based on continued work within their respective basic disciplines.

An international network of case studies

Many eyes will discover more than one. With this analogy we propose to use the knowledge and experiences gathered in different parts of the European forests to facilitate the development of today's forest management towards the visions of ecosystem management (Christensen et al. 1996) as is endorsed in the Pan-European forest policies. This idea builds on the insight that we cannot perceive what we do not know something about. It is dangerous to assume that we understand our partner, when in fact we have limited knowledge of the context. This can only be overcome by learning about different perspectives.

Researchers and managers traditionally accomplish most of their work in isolation and then present their results to decision-makers. There are hence a number of barriers, in particular when attempting to apply a landscape approach to the conservation of biodiversity (Holling 1995, Christensen et al. 1996, Gutzwiller 2002). One approach towards building bridges is the international model forest network, which forms a partnership between individuals and organisations sharing the common goal of sustainable forest management (Besseau et al. 2002). A network of forest management units consisting of actual landscapes with their characteristic ecosystems, actors and economic activities can be used as the sites for syntheses, development and education. Ideally, in the future adaptive management teams (Boutin et al. 2002, Angelstam et al. 2004c) should be formed whereby researchers, land managers and policy-makers share decisions and responsibilities toward the success or failure of the strategy they jointly adopted. We thus argue in favour of a novel win-win oriented approach to research and development, which is based on exchanging knowledge and experience gathered over long time in different countries and regions. This will be of mutual benefit for both forest science and practice as a whole, and thus for continued sustainable use of forest resources providing a basis for human welfare in a changing world. Ultimately, acknowledging and adopting this perspective requires the gradual development of a new transdisciplinary profession able to facilitate SFM at the landscape scale.

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Sustainable forest management and Pan-European forest policy

Ewald Rametsteiner and Peter Mayer

Rametsteiner, E. and Mayer, P. 2004. Sustainable forest management and Pan-European forest policy. – Ecol. Bull. 51: 51–57.

A new understanding or by some called a new paradigm of sustainable forest management is in the process of being defined. At the international political level in Europe, this new paradigm was shaped largely by the European states and non-governmental organisations participating in the Ministerial Conference on the Protection of Forests in Europe (MCPFE). This was achieved through agreeing on a common definition and operationalising it through a set of criteria and indicators. This concept is now gradually adapted to different national, regional and local conditions in many countries in Europe, and implementation is attempted.

This paper outlines the history of international forest policy, especially of the MCPFE. It outlines the Pan-European understanding of the concept of Sustainable Forest Management (SFM), operationalised through criteria and indicators, and the recent development related to indicators for SFM. It also presents recent political decisions in Pan-European forest policy that are building on and further promote sustainable forest management as their key paradigm. These international forest policy decisions will also guide targets and influence tools for the maintenance of forest biodiversity and cause action on the national and local levels.

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Sustainable forest management as a concept is gradually evolving over the long term. In the last decades of the 20th century it has been re-defined in the wake of the global paradigm shift towards sustainable development. Many institutions have worked towards this end in the context of European forests and forestry, including the International Union of Forest Research Organizations (IUFRO), founded in 1892, the Food and Agriculture Organization (FAO), founded in 1945, the UNECE Timber Committee, set up in 1947 and the European Forest Institute (EFI), founded in 1993.

Since the United Nations Conference on Environment and Development (UNCED) in 1992, several international and regional conferences, as well as initiatives and processes have been initiated in order to encourage countries to accept commitments towards a more sustainable use of natural resources. The follow-up process of UNCED in regard to forests was driven by the Intergovernmental Panel on Forests (IPF) and the Intergovernmental Forum on Forests (IFF) and subsequently by the newly established UN-body, the United Nations Forum on Forests (UNFF). Many other provisions of United Nations Conventions, notably the UN Framework Convention on Climate Change (UN-FCCC), the UN Convention on Biological Diversity (CBD) and the UN Convention on Combating Desertification (CCD) also address aspects of sustainable forest management.

At the international political level in Europe the change to a new approach of a more holistic understanding of sustainable forest management in the context of sustainable

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development was mainly initiated and largely shaped through deliberations, discussions and decisions made by the European states and non-governmental organisations participating in the Ministerial Conference on the Protection of Forests in Europe (MCPFE).

The MCPFE was established in the wake of concerns that mounted during the 1980s about the threats to European forests, resulting in forest degradation and especially forest dieback (MCPFE 2000). International recognition of the presence of these issues played a particularly important role in increasing awareness of the threats to forests in the broader public. The perceived main damaging factors, such as acid rain, could only be addressed through cross-border efforts.

The First Ministerial Conference on the Protection of Forests in Europe, initiated by the governments of France and Finland, was held in Strasbourg in 1990. Cross-border protection of forests in Europe and tackling the problem of forest dieback was at the core of the political decisions in Strasbourg. The Second Ministerial Conference in Helsinki, building on the success of the initiative taken in 1990, was driven by the decisions of UNCED in 1992 with regards to the concept of sustainability. This marks also a slight shift towards a more policy-oriented direction of the MCPFE. At the Helsinki Conference, the European countries agreed on a common definition of Sustainable Forest Management (SFM) reflecting the global sustainable development discussion. The Third Ministerial Conference, held in Lisbon in June 1998, focused on the relationship and interaction between the forest sector and society and socio-economic aspects of sustainable forest management.

The Fourth Ministerial Conference on the Protection of Forests in Europe held in April 2003 emphasised the fact that European forests provide common benefits, and that society as a whole shares responsibilities towards this ecosystem. The Vienna Declaration emphasises the multiple economic, social and ecological benefits, which have to be taken into account for a future-oriented forest policy. In this respect co-ordination and partnerships with other sectors leading to shared responsibilities are highlighted.

The MCPFE is now an established international platform shaping forest policy in Europe. A total of 44 European States and the European Community elaborate common views on forest policy issues and commit themselves to actions at periodic Ministerial Conferences. The outcomes of these meetings are reflected in Resolutions of each conference. In addition 41 observers representing various NGOs, international institutions and scientific organisations contribute significantly to the work of the MCPFE. The Resolutions of the Ministerial Conferences form the basis for forest related policies in European countries and the European Community.

The MCPFE has an important function as a link between the European region and forest policies made in Europe and the forest policy processes on a global level. It has been contributing to the implementation of the forest-related decisions and agreements of the UNCED and its follow-up process within IPF/IFF, as well as the provisions of the United Nations Conventions, notably UN-FCCC, CCD and CBD. For example, the MCPFE has implemented a "Work-Programme on the Conservation and Enhancement of Biological and Landscape Diversity in Forest Ecosystems" in co-operation with the European ministers responsible for environment, which is a Pan-European contribution to the implementation of the Convention on Biological Diversity. This important link to global fora has been emphasised in practically all Resolutions signed at Ministerial Conferences.

As regards the EU, a EU Forestry Strategy was adopted in 1998, which has the application of sustainable forest management as defined by the MCPFE and the multifunctional role of forests as its main principles (EU 2003). Although forests per se are not dealt with in a sectoral policy at the EU level there is an increasingly complex web of EU legislation and policy initiatives within different EU sectoral policies that influence forest policies of EU member states.

Defining and Operationalising Sustainable Forest Management in the Pan-European Forest Policy Context

At the 2nd Ministerial Conference in 1993, the so-called "Helsinki Conference", the European countries agreed on a common view on how to further promote Sustainable Forest Management (SFM) in Europe, reflecting the global sustainable development discussion and implementing the decisions made at UNCED. In the Helsinki Resolutions the signatories committed themselves to a common definition of the concept of sustainable forest management which reads: "Sustainable management means the stewardship and use of forests and forest lands in a way, and at a rate, that maintains their biodiversity, productivity, regeneration capacity, vitality and their potential to fulfil, now and in the future, relevant ecological, economic and social functions, at local, national, and global levels, and that does not cause damage to other ecosystems." (Helsinki Resolution H1, MCPFE, 1993.)

This definition builds the foundation of decisions taken since then with a view to further promote SFM in the form of Resolutions at subsequent Ministerial Conferences. Through Helsinki Resolution 1 Ministers also committed themselves to the implementation of a set of general guidelines that were deemed to be particularly relevant to the achievement of sustainable forest management in Europe.

To operationalise the definition of SFM, a set of Criteria and Indicators (C&I) were elaborated in the follow-up

to the Helsinki Conference, with the involvement of a Scientific Advisory Group. The maintenance and appropriate enhancement of forest biodiversity is one of six criteria (see Table 1). The MCPFE also developed Pan-European Operational Level Guidelines for Sustainable Forest Management (PEOLGs) that are based on the framework of criteria and indicators and that specify, for each indicator, recommendations for forest management planning and practices. The PEOLGs are one instrument to further promote sustainable forest management in Europe by translating the international commitments down to the field level of actual forest management planning and practices. They represent a common framework of recommendations for reference at the field level that can be used on a voluntary basis by e.g. forest managers and forest owners, sub-national and national forest related institutions.

At the 3rd Ministerial conference in Lisbon in 1998, the signatory states adopted the Pan-European criteria for SFM and endorsed the related indicators as well as the PEOLGs, emphasising the need for continuous improvement (Lisbon Resolution L2, MCPFE 1998). The six criteria are listed in Table 1.

At the national and international levels, the criteria and indicators for SFM are increasingly being used in policy formation, implementation and evaluation. Many countries have integrated the definition of SFM and the goals set by the six pan-European criteria into their national legislation. Monitoring and assessment of forests and forestry through national inventories and international data compilations are increasingly taking into account the structure and contents of the C&I for SFM. Likewise, reporting on the status of forests on both national and international levels is rearranged to follow their structure (see e.g. MCPFE 2003a).

On regional and local levels the application of new paradigm of SFM is also promoted by private certification schemes. By and large these are using the C&I for assessment of SFM as well as the Pan-European Operational Level Guidelines developed for voluntary application by the MCPFE as a reference framework for the elaboration of forest management standards to be used in certification, as well as other initiatives (PEFC 1999).

The improved Pan-European Indicators for Sustainable Forest Management

Since the first set of Pan-European Indicators for Sustainable Forest Management (SFM) were developed in the early 1990s, experience has shown that criteria and indicators are a very important tool for European forest policy. In the meantime, knowledge and data collection systems as well as information needs have gradually developed further. Thus, through the work initiated at the Lisbon Conference in 1998, the Ministerial Conference on the Protection of Forests in Europe (MCPFE) decided to review and improve the existing set of Pan-European Indicators for SFM. This work aimed to consider the variety of experiences of European countries in using the instrument of criteria and indicators for facilitation of SFM. Furthermore, topics such as climate change, biodiversity and socio-economic aspects influenced the discussion and the results of the improvement process.

While the old set of indicators was comprised of 27 quantitative and 101 "descriptive" indicators, the new set of indicators comprises 35 quantitative and 17 qualitative indicators (Table 2). The increase in the number of quantitative indicators is mainly due to the fact that indicators of socio-economic conditions have been considerably improved. This improved list of indicators, which had been adopted by the ministers at the 4th Ministerial Conference (see Table 2), will form the basis of SFM-related policies in the foreseeable future.

No further substantial amendments to the set of C&I are expected for some time to come. However, considerable efforts are necessary in some areas to further operationalise and implement the improved indicators, including further specification of definitions, the establishment of data collection systems and routines, their analysis and reporting. This concerns e.g. an indicator related to the cultural aspects of SFM (indicator 6.11). In other areas further operationalisation of concepts used at the international level will be necessary. This concerns e.g. a common understanding of the definition of "forest types" in interna-

Table 1. Pan-European Criteria for Sustainable Forest Management.

Criterion 1	Maintenance and appropriate enhancement of forest resources and their contribution to global carbon cycles.
Criterion 2	Maintenance of forest ecosystem health and vitality.
Criterion 3	Maintenance and encouragement of productive functions of forests (wood and non-wood).
Criterion 4	Maintenance and conservation and appropriate enhancement of biological diversity in forest ecosystems.
Criterion 5	Maintenance and appropriate enhancement of protective functions in forest management (notably soil and water).
Criterion 6	Maintenance of other socio-economic functions and conditions.

Table 2. Improved List of the MCPFE Quantitative Indicators for Sustainable Forest Management.

Criteria	No.	Improved indicator	Improved full text
C 1: Maintenance and appropriate enhancement of forest resources and their contribution to global carbon cycles	1.1	Forest area	Area of forest and other wooded land, classified by forest type and by availability for wood supply, and share of forest and other wooded land in total land area.
	1.2	Growing stock	Growing stock on forest and other wooded land, classified by forest type and by availability for wood supply.
	1.3	Age structure and/or diameter distribution	Age structure and/or diameter distribution of forest and other wooded land, classified by forest type and by availability for wood supply.
	1.4	Carbon stock	Carbon stock of woody biomass and of soils on forest and other wooded land.
C 2: Maintenance of forest ecosystem health and vitality	2.1	Deposition of air pollutants	Deposition of air pollutants on forest and other wooded land, classified by N, S and base cations.
	2.2	Soil condition	Chemical soil properties (pH, CEC, C/N, organic C, base saturation) on forest and other wooded land related to soil acidity and eutrophication, classified by main soil types.
	2.3	Defoliation	Defoliation of one or more main tree species on forest and other wooded land in each of the defoliation classes “moderate”, “severe” and “dead”.
	2.4	Forest damage	Forest and other wooded land with damage, classified by primary damaging agent (abiotic, biotic and human induced) and by forest type.
C 3: Maintenance and encouragement of productive functions of forests (wood and non-wood)	3.1	Increment and fellings	Balance between net annual increment and annual fellings of wood on forest available for wood supply.
	3.2	Roundwood	Value and quantity of marketed roundwood.
	3.3	Non-wood goods	Value and quantity of marketed non-wood goods from forest and other wooded land.
	3.4	Services	Value of marketed services on forest and other wooded land.
	3.5	Forests under management plans	Proportion of forest and other wooded land under a management plan or equivalent.
C 4: Maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems	4.1	Tree species composition	Area of forest and other wooded land, classified by number of tree species occurring and by forest type.
	4.2	Regeneration	Area of regeneration within even-aged stands and uneven-aged stands, classified by regeneration type.
	4.3	Naturalness	Area of forest and other wooded land, classified by “undisturbed by man”, by “semi-natural” or by “plantations”, each by forest type.
	4.4	Introduced tree species	Area of forest and other wooded land dominated by introduced tree species.
	4.5	Deadwood	Volume of standing deadwood and of lying deadwood on forest and other wooded land classified by forest type.
	4.6	Genetic resources	Area managed for conservation and utilisation of forest tree genetic resources (in situ and ex situ gene conservation) and area managed for seed production.
	4.7	Landscape pattern	Landscape-level spatial pattern of forest cover.
	4.8	Threatened forest species	Number of threatened forest species, classified according to IUCN Red List categories in relation to total number of forest species.

Table 2. Continued.

Criteria	No.	Improved indicator	Improved full text
	4.9	Protected forests	Area of forest and other wooded land protected to conserve biodiversity, landscapes and specific natural elements, according to MCPFE protection categories.
C 5: Maintenance and appropriate enhancement of protective functions in forest management (notably soil and water)	5.1	Protective forests – soil, water and other ecosystem functions	Area of forest and other wooded land designated to prevent soil erosion, to preserve water resources, or to maintain other forest ecosystem functions, part of MCPFE protection category "Protective Functions".
	5.2	Protective forests – infrastructure and managed natural resources	Area of forest and other wooded land designated to protect infrastructure and managed natural resources against natural hazards, part of MCPFE protection category "Protective Functions".
C 6: Maintenance of other socio-economic functions and conditions	6.1	Forest holdings	Number of forest holdings, classified by ownership categories and size classes.
	6.2	Contribution of forest sector to GDP	Contribution of forestry and manufacturing of wood and paper products to gross domestic product.
	6.3	Net revenue	Net revenue of forest enterprises.
	6.4	Expenditures for services	Total expenditures for long-term sustainable services from forests.
	6.5	Forest sector workforce	Number of persons employed and labour input in the forest sector, classified by gender and age group, education and job characteristics.
	6.6	Occupational safety and health	Frequency of occupational accidents and occupational diseases in forestry.
	6.7	Wood consumption	Consumption per head of wood and products derived from wood.
	6.8	Trade in wood	Imports and exports of wood and products derived from wood.
	6.9	Energy from wood resources	Share of wood energy in total energy consumption, classified by origin of wood.
	6.10	Accessibility for recreation	Area of forest and other wooded land where public has a right of access for recreational purposes and indication of intensity of use.
	6.11	Cultural and spiritual values	Number of sites within forest and other wooded land designated as having cultural or spiritual values.

tional reporting, data collection on dead wood or landscape-level spatial pattern of forest cover.

The 4th Ministerial Conference on the Protection of Forests in Europe 2003 in Vienna

The 4th Ministerial Conference on the Protection of Forests in Europe re-emphasised the protection and sustainable management of European forests. Forty European states and the European Community signed the Vienna Declaration and five Vienna Resolutions. These political declarations of commitments, the topics addressed and actions outlined will shape the Pan-European policy related to forests for the first decade of the new millennium (MCPFE 2003b).

The "Vienna Living Forest Summit Declaration: European Forests – Common Benefits, Shared Responsibilities" emphasises the fact that forests provide multiple benefits, but co-ordination and partnerships with other sectors and shared responsibilities are crucial for the provision of benefits from forests in the future. The main commitments made through the Vienna Declaration aim at benefiting rural livelihoods and urban societies, building strong partnerships, tackling global challenges, putting commitments of the MCPFE into action, and it contains the Improved Pan-European Indicators for Sustainable Forest Management.

Vienna Resolution 1 "Strengthen Synergies for Sustainable Forest Management in Europe through Cross-sectoral Co-operation and National Forest Programmes" promotes modern policy making, aiming at involving all interested sectors and groups in a dialogue. Through this resolution also the "MCPFE Approach to National Forest Programmes in Europe" as a suitable instrument for optimising this objective has been adopted.

Vienna Resolution 2 "Enhancing Economic Viability of Sustainable Forest Management in Europe" highlights the importance of keeping a balance of all pillars of sustainability as a prerequisite for economic viability. The promotion of the use of wood as an environmentally sound and renewable resource as well as the use of non-wood goods and services are important aspects in this respect. Furthermore the promotion of innovation and entrepreneurship, the enhancement of workforce know-how as well as workforce safety are main commitments of this resolution.

Vienna Resolution 3 "Preserving and Enhancing the Social and Cultural Dimensions of Sustainable Forest Management in Europe" underlines the importance of cultural values for forest policy making. The promotion of the assessment of historical and cultural sites, securing property rights and land tenure arrangements and the promotion and the communication of the social and cultural dimensions are central commitments of this resolution.

Vienna Resolution 4 "Conserving and Enhancing Forest Biological Diversity in Europe" identifies Pan-European issues building on international commitments of CBD, UNFF and WSSD (Convention on Biological Diversity, United Nations Forum on Forests and World Summit on Sustainable Development). Policy planning and implementation in line with the conservation of forest biological diversity, combating illegal harvesting and related trade, further developing protected forest area networks, restoring biological diversity in degraded forests, promoting native tree species and preventing negative impacts of invasive alien species, monitoring the development of forest biological diversity are key commitments of this resolution. In addition, both the "MCPFE Assessment Guidelines for Protected and Protective Forest and Other Wooded Land in Europe" as well as the "Framework for Cooperation between the MCPFE and Environment for Europe/PEBLDS (Pan-European Biological and Landscape Diversity Strategy)" on key issues of forest biodiversity were adopted through this resolution.

Vienna Resolution 5 "Climate Change and Sustainable Forest Management" recognises the need to further promote the concept of sustainable forest management in the context of the continued debate on climate change and forests to ensure the multiple benefits of forests in the long run. It is stressed in the resolution that a lasting improvement to the environmental situation can only be achieved by reducing emissions. Promoting the use of wood as an environmentally sound and renewable resource and as the alternative to non-renewable products can make a significant contribution in this respect.

The Ministerial Conference "Environment for Europe" in 2003 in Kiev

Only one month after the Living Forest Summit in Vienna, the ministers for environment convened the Fifth Ministerial Conference "Environment for Europe" on 21–23 May 2003 in Kiev, Ukraine. At both the Vienna and the Kiev conferences, the ministers responsible for forests as well as the ministers for environment further strengthened the co-operation of the MCPFE and Environment for Europe/Pan-European Biological and Landscape Diversity Strategy (EfE/PEBLDS) by adopting a new framework for co-operation (see Vienna Resolution 4, MCPFE 2003b). This framework aims to further identify and use synergies in the work on forest biological diversity in Europe and sets out priority areas for co-operation between the MCPFE and EfE/PEBLDS.

Issues addressed are, among others, the ecosystem approach, protected forest areas, law enforcement with regards to conservation of forest biological diversity and recommendations for site selection for afforestation. The

framework is scheduled from the year 2003 until 2005 and continues the successful co-operation of the two ministerial processes already initiated through the joint Biodiversity Work-Programme adopted at the previous Ministerial Conferences in Lisbon and Aarhus in 1998.

Concluding remarks

Europe is a diverse continent. Since more than a decade almost all countries on this continent have collaborated in order to shape a common sustainable future for forests and forest management in Europe. Up to now, the MCPFE process has made widely acclaimed progress on the international scale, and it has established a successful conciliation between different interests of society in forests, including the protection of forest biodiversity. Many European countries have adapted their forest laws with reference to the definition of SFM as adopted by the MCPFE and a many of countries has revised their respective reporting structure on SFM to take the six criteria for SFM and the respective indicators into account. However, much remains to be done to put the common international visions and commitments into action on the national and local levels. In respect to forest biological diversity the Vienna Resolution 4 lists 15 actions which ministers committed themselves to implement on regional, national or sub-national level. Finally, it is and still remains the local level that ultimately determines the success of this and other policy initiatives.

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Biodiversity research in the boreal forests of Canada: protection, management and monitoring

C. Whittaker, K. Squires and J. L. Innes

Whittaker, C., Squires, K. and Innes, J. L. 2004. Biodiversity research in the boreal forests of Canada: protection, management and monitoring. – Ecol. Bull. 51: 59–76.

A literature analysis was undertaken to assess the impacts of forest practices on the biological diversity of Canadian boreal forests. The analysis was based on the three key questions identified by the BorNet International Steering Committee: a) How much and where should forests be fully protected in reserves? b) How can management effectively restore/recreate/maintain important features required to conserve biodiversity? c) How can we determine the effectiveness of these biodiversity conservation efforts? The information gathered by this process was supplemented by workshops held in three different locations in Canada. The literature review and workshops revealed that research on the conservation of biodiversity in the boreal forests of Canada has been addressing a small subset of important questions, rather than looking at more general issues associated with landscape-scale biodiversity. As a result, many important conservation issues may have been missed, such as the need to maintain habitat for species dependent on fire successions.

A major gap is the absence of direction to forest managers that would aid in improving forest management and meeting biodiversity conservation objectives in the boreal. Species with limited dispersal ability and specialized habitat requirements have not been the focus of field-based biodiversity research to date, and of those species that have been studied, very few studies have assessed effects of forestry at more than the stand scale. This is despite the emphasis that has been placed on large-scale disturbance patterns in boreal forests. More focussed studies are required, and forest management should move to an active adaptive management model in which every opportunity is taken to link operations to information gathering.

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The boreal forests of the world have been subjected to differing histories (Angelstam et al. 2004a). For example, the boreal forests of Scotland were largely removed, with the land being converted to grazing. During the 20th century, widespread afforestation with exotic species occurred, and it was only towards the end of the 20th century that extensive efforts to restore native forests began. In Scandinavia, the frontier for developed forest gradually moved northwards, with little unmanaged, pristine forest now remaining. It is only in Russia, Canada and Alaska that extensive areas of intact boreal forest remain. These are largely seen as an economic resource, and the development of these forests is progressing.

Across the Canadian boreal, there are concerns regarding the reduction in the average age of the forest and the shrinking area of contiguous pristine forest (Burton et al.

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2003). This paper, which was undertaken as part of the BorNet Canada project (Leech et al. 2002, Angelstam et al. 2004b), outlines a synthesis of information regarding a range of anthropogenic impacts on groups of species and approaches to monitoring the effectiveness of management strategies aimed to limit adverse impacts of forest management on the biodiversity of Canadian boreal forests. This synthesis is based on both a literature review and three regional workshops held across Canada (Whittaker and Innes 2001a, b, c). The objective of the regional workshops was to better define the context for BorNet discussions in Canada, and to identify strengths and gaps in our areas of knowledge. We recognize that there was a diversity of views presented in these regional workshops and that this report is unable to represent all perspectives that were discussed in the workshops. Further, consensus was not reached on many of the issues discussed in this report, particularly in Alberta where workshop participants presented very divergent views on issues such as protection of aboriginal cultural diversity as it relates to biodiversity and the role of social scientists in biodiversity research.

Methodology

Definition of terms and framework

Defining biodiversity is almost as much of a challenge as measuring it. Delong (1996) found 90 different definitions of biodiversity, and many of the problems associated with the definition of the term have been discussed by Kaennel (1998). For the purposes of this paper, we accept that biodiversity is the full variety of life in an area, ranging from the genes to populations within the context of ecological processes and over a range of temporal-spatial scales. This very broad definition needs to be bounded in order for us to be able to tackle this review. Our focus is on forested boreal ecosystems, and does not cover work being done at the genetic level or in aquatic biodiversity; nor does it detail all ecological processes occurring over the complete range of temporal-spatial scales.

A comprehensive documentation of all species occurring in boreal forests has not been completed, and even for those species that have been identified, little is known about the biology of many of them. Processes such as disturbance events affect organisms at different scales differently so, as Levin (1992) suggests, there is no single correct scale to use to describe populations of ecosystems. This problem has been examined by Lertzman and Fall (1998), who point out that in forestry, management has concentrated at the stand scale with much less emphasis on the landscape, with the result that bottom-up processes have driven managed landscape dynamics. They refer to this as the "tyranny of small decisions". A particular problem is that the cumulative effects of a large number of stand-level interventions have rarely been assessed.

The framework in Fig. 1 is useful for illustrating the complexity associated with assessing biodiversity in boreal forest. What does this mean for research? If we cannot actually measure biodiversity, what pieces of the puzzle below biodiversity should we measure? What benchmarks do we measure these against as reference points? What scale, spatial and temporal do we use? What is the relative importance of habitat specialists versus landscape-scale processes? Is active adaptive management the next step to completing our understanding along a gradient of disturbance? This discussion paper attempts to explore many of these issues.

Literature review and workshops

Three key questions were identified by the BorNet International Steering Committee as a guide for our discussions among boreal countries (Leech et al. 2002, Angelstam et al. 2004b). These are: a) How much and where should forests be fully protected in reserves? b) How can management effectively restore/recreate/maintain important features required to conserve biodiversity? c) How can we determine the effectiveness of these biodiversity conservation efforts?

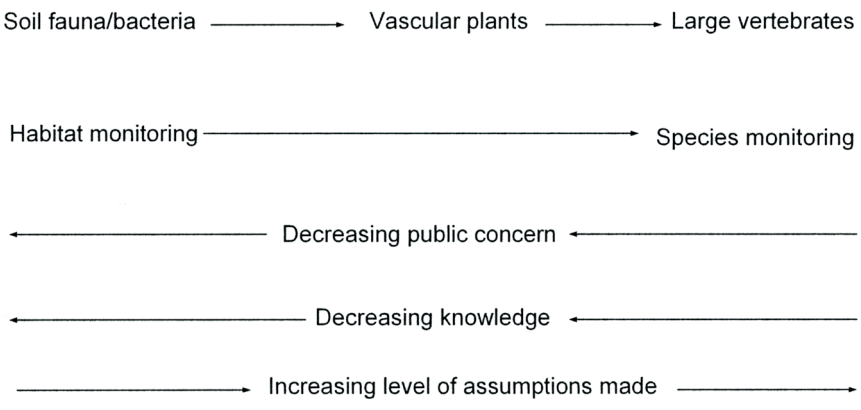


Fig. 1. A framework of integrated continuums (Innes and Gillingham 2001).

The BIOSIS literature database was searched using the following keywords: biodiversity, forest management, Canadian boreal forest, and key taxonomic groups, such as lichens, birds, etc. We did not include papers that addressed the basic biology of the animals and plants; rather, we selected the studies that assessed the effects of forest harvesting on diversity. It should be noted that in Canada, harvesting mostly involves clear-cutting. There are very few, if any, boreal forests in Canada where thinning is practised on any significant scale, although increasing interest is being expressed in alternative harvesting systems (such as variable retention). We focused on Canadian boreal studies with limited reference to key papers from other boreal countries where authors either collaborated with Canadians, or where papers developed key research cited by the Canadian studies. We included both studies that addressed habitat loss resulting from forest harvesting as well as those addressing changes in habitat quality. For those areas where our results found very few papers, we replicated the searches specifically for focal species or taxa. Overall in our literature review, of 121 papers reviewed that assessed the effects of forest harvesting on biodiversity, birds and mammals constituted over 76% of the studies.

This synthesis paper stays within the general bounds of terrestrial ecology and forest management without accessing the important bodies of social science literature regarding policy implications, impacts on forest-dependent communities, etc. We feel that these aspects are important areas for a similar review and for identifying opportunities for future research. Our regional workshops did identify areas within these other disciplines where further research was required. These comments were incorporated into this report. The regional workshop proceedings (Whittaker and Innes 2001a, b, c) were compiled and the composite from those proceedings was used to develop the outline for this synthesis document.

How much and where should forests be fully protected in reserves?

The starting point for such questions was motivated by Arcese and Sinclair (1997) who stated "If we do not manage at least some protected areas as ecological baselines we risk sacrificing our ability to understand natural systems and, as a result, our potential to manage them successfully". By protected areas, we refer to the definition by the IUCN (Anon. 1994) "An area of forest especially dedicated to the protection and maintenance of biological diversity, and of natural and associated cultural resources, and managed through legal or other effective means". Across the boreal, levels of protection differ among types of protected areas (provincial and national designations). Alberta Special Places, Canadian National Parks, BC Provincial Parks, and Ontario Lands for Life all define the management of parks differently. Dudley et al. (1999) outline a categorization system for protected areas (based on the IUCN definition) that identifies the primary management objectives for the area ranging from strict nature reserves managed mainly for science to semi-protected areas that are managed mainly for the sustainable use of natural resources and to allow extractive activities. In some cases, there may be a gradient from a core protected area through different levels of protection in the surrounding areas, to no protection outside of the zone of interest. An example is provided by the Muskwa-Kechika planning area in northern British Columbia, a 6.4 million ha area where different levels of protection have been identified. Core protected areas, totalling > 1 million ha, are surrounded by > 3 million ha of special management zones where some development is permitted as long as it is sensitive to wildlife and environmental values. By recognizing that there are various degrees of protection afforded to the biological diversity found in boreal forests, we will better understand whether the protected areas designated in the boreal in Canada are adequate to ensure the conservation of biodiversity.

There are a myriad of issues underlying the question: How much and where should forests be fully protected in reserves? These range from the values to be protected (special landscape features, unique habitat types or old growth forests), the interaction of these protected areas within the surrounding managed landscape context and finally, the barriers such as land tenure and allocation of timber licences and timber supply that impede further protection. It has been suggested that any deterioration of the landscape surrounding the protected areas will limit their ability to protect biological diversity (Newmark 1987). For example, Dudley et al. (1999) state "The number and area of forest protected areas required, for example, is influenced to a great extent by forest use outside the protected areas. Setting global or even national numerical targets is therefore often simplistic and misleading". At the BorNet regional workshops, participants agreed that 100% of the land base is required for the maintenance of biological diversity but that protected areas serve a key role as ecological benchmarks. By arguing for 100%, they emphasized the need to consider biodiversity in all forests, regardless of the degree of management. Even in intensively managed forests, it is still possible to make provisions for the maintenance of some of the biodiversity, and such forests need to be carefully integrated into landscape level plans that ensure the full maintenance of biodiversity across the landscape.

National parks or protected reserves where legislation excludes extractive activities are the most sensible areas to be managed as ecological references (Dassman 1972, Arcese and Sinclair 1997), although there may be some resistance to their use because of perceived problems associated with the disturbance that research can create. Parks are required to serve as control areas for balancing our biodiversity management objectives with other economic, social and cultural values. Protected reference areas need to be large enough to incorporate natural disturbance events, a

significant problem in the boreal forest, where disturbances can be very large. The protected areas need to be managed within the matrix that surrounds them, ensuring connectivity through time for species with limited ability to disperse and preventing the effects of fragmentation and isolation that can threaten isolated populations.

In Ontario, Alberta and New Brunswick, almost all of the available wood is allocated and there is little room for any other protection initiatives. In Alberta, there were two very different views posed at our regional workshop. The first criticized the emphasis on reserves suggesting that it is an extension of a European idea of land management inappropriate to the Albertan landscape. Scientists countered that preserves are key to sustaining some species, particularly those largely restricted to reserves (e.g., buffalo *Bison bison*). Another opportunity that has not been adequately explored is the potential of increasing protection within the managed forests through the non-harvested land base. There have been no studies assessing the contributions of the NHLB (the non-harvestable land base, usually defined as forest land which is currently uneconomic to harvest) to the maintenance of biological diversity, but again, the protection within the managed forest would need to be only one part of a continuum of protection, as maintenance of the NHLB alone would be inadequate for some species. For example, in Alberta, there is a section map that indicates that 10–15% of the land base constitutes heterogeneous patches and mesic sites that could contribute to the protected areas (Hebert pers. comm.). An examination of the biodiversity conservation values within the managed landscape must also address the issue of whether reserves should be fixed or floating reserves. This issue will become particularly important within the context of climate change.

Theoretical context and modeling approaches

There are two key aspects to the question "How much and where should forests be fully protected in reserves?" The first issue is the effect of habitat loss and the question of how much is enough? The second issue is the interaction of habitat loss with the threshold effects of processes such as fragmentation and connectivity. Fragmentation is not a linear function of habitat loss, thus, habitat abundance may be more important than spatial pattern in most landscapes (With et al. 1997). This has been emphasized by Kolasa and Waltho (1998), who advocate a habitat-based model, in contrast to niche-apportionment models. A review of literature on the differences between species response to habitat loss versus fragmentation in birds (species with high vagility) suggested that disruption of connectivity occurs when 10–30% of the original habitat element remains (Andrén 1994).

Landscape connectivity is a function of the spatial contagion of habitat, the habitat specificity of the species and their dispersal ability or vagility (Andrén 1994). Within heterogeneous landscapes, species with specialized habitat requirements and a limited range of dispersal, connectivity is less important than the absolute abundance of the required habitat available (With and Christ 1995). Further, in boreal landscapes, large-scale industrial forestry has altered the age distribution and, in some cases, species composition of forest without extensive permanent habitat loss. As there is gradual variation between patches and among habitats, matrix and corridors, both temporally and spatially, as processes such as disturbance and regeneration take place, it is difficult to distinguish these features. There has been little study of the application of concepts of island biogeography to the boreal, and it is questionable whether concepts such as corridors are really relevant. There is even greater doubt over the role of corridors in providing an avenue of dispersal for boreal species. Empirical evidence from the boreal is largely missing (Mönkkönen 1999), although it seems likely that corridors will act as differential filters, providing avenues of dispersal for some species but being of little value to others (Whittaker 1998).

Benchmarks

What is the threshold for how much is enough – is there a minimum requirement (temporal and spatial)? What are the targets for no losses of species? Angelstam et al. (2001, 2003) have suggested that in Europe, depending on the regional value systems, both naturally dynamic landscapes and pre-industrial cultural wooded grasslands could serve as a reference benchmark. What benchmarks do we use in Canada? Duinker (1996) questions whether the pre-European settlement state of forests in Canada can be defined adequately. Further, if we can restore some forests to a pre-European state, Duinker (1996) poses the questions: "might we have confidence that survival of the species we have come to expect to inhabit forests will thus be guaranteed? What influences did Aboriginal peoples have on forest biodiversity? How broadly did key forest biodiversity variables fluctuate over time (say, centuries) under purely natural influences such as fire, insects, disease, and windthrow?" These questions illustrate some of the many uncertainties associated not only with defining baseline conditions but also with the use of such baselines. In particular, the idea of comparing current forests with those of pre-European times fails to acknowledge the dynamic nature of most forests. Most forests continue to change in response to, for example, natural climate change, and trying to set a reference condition based on past conditions seems inappropriate.

However, it is essential for any kind of assessment of biodiversity management to have a baseline, or a benchmark reference. The distance from that reference becomes the indicator of increased risk of loss of biodiversity. Without references, the question is raised, "how do we know when we get there if we do not know where we are going?"

Many scientists suggest that the reference in Canada should be the "natural conditions" of the forest (see section below on Natural disturbance based management). However, finding an ecological reference for biodiversity that is considered "natural" is difficult, further confounded by the fact that "because of different growth rates, species mixes, vegetation longevity, shade tolerance, insect disease relationships, species interactions (all possible combinations of plant and animal interactions), and disturbance regimes-fire (stand replacing and low intensity surface fires) and weather, multitudes of different successional pathways naturally occur in boreal forests, creating a multitude of different forest structures and compositions" (Graham and Jain 1998). In light of the complexity related to identifying ecological baselines, it is all the more apparent that parks and protected areas are critical for understanding the impacts of management on landscapes (Arcese and Sinclair 1997). A combination of protected areas (as ecological references) and forest management strategies addressing biodiversity objectives on extensively managed lands will be required to conserve biological diversity. This still leaves us with the question: how much and where should forests be fully protected in reserves?

We propose a combination of approaches to answering this question in Canada. Firstly, we need to understand structure, function and composition as they relate to habitat and landscape elements (Noss 1990). Secondly we need to consider the requirements of habitat specialists (Spence 2001). This approach requires an assessment of different measures at different scales across the boreal and a combination of management objects at these different scales. In our review, we found that the bulk of the studies that have evaluated the effects of forest harvesting on birds and mammals were done at the stand scale; few studies assessed effects at the landscape scale, and some (15) combined regional and stand effects (see Fig. 2). What is the appropriate scale for biodiversity assessment and management? Do we need more studies at the landscape scale?

In relation to the above questions, we need to assess components of biodiversity at the scale appropriate to the component. For example, the stand-level is probably appropriate for assessing the impact of harvesting on soil fauna. However, it is clearly less appropriate when looking at wide-ranging species such as large ungulates or raptors.

Sensitive species in the Canadian boreal

What is a sensitive species and how has sensitivity been measured in the Canadian boreal?

Based on a review of almost one hundred citations relevant to Canadian boreal forests, we were able to identify very few studies that developed population-level thresholds for any species or taxa. We have reviewed the requirements of species identified as sensitive in the boreal, and an annotated bibliography is available from BorNet. We also did a macro-analysis of a subset of these papers to assess the type of data available, the indicators used and the results.

Which species should we choose to manage for as habitat specialists? Probst and Crow (1991) suggest that selected species should have: 1) specialized habitat needs; 2) low densities; 3) large home ranges; 4) poor dispersal and colonizing abilities; or 5) susceptibility to local extinction. Sensitivity to forest harvesting is most commonly quantified

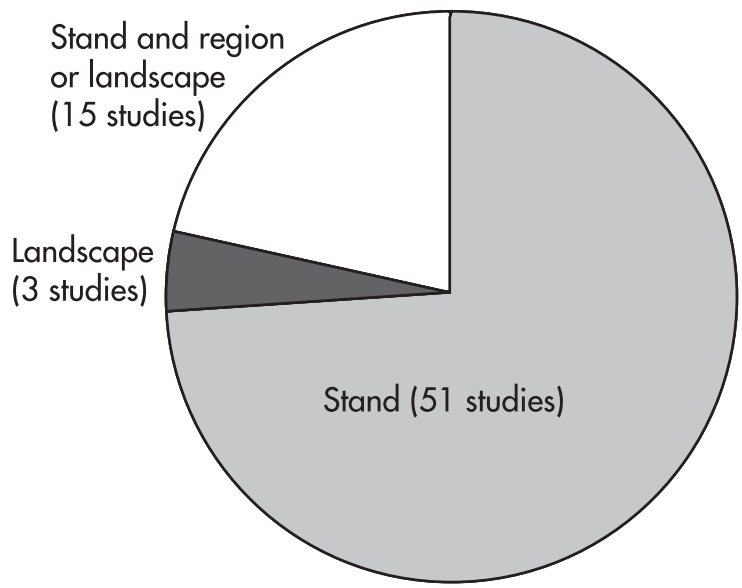


Fig. 2. Forest harvesting effects on birds and mammals: scale of studies in the Canadian boreal (of 69 papers reviewed).

by assessing changes in species abundance and habitat use, though many studies on forest birds also measure species richness, diversity, and indices of nest predation. Reproductive parameters and population responses at the landscape scale are less commonly quantified, yet these may be the most important variables to assess. For example, for migratory birds, while harvesting may affect the abundance of some species (Askins 2000), the abundance of others may have nothing to do with harvesting patterns in their breeding range (Hussell et al. 1992). One problem is the lack of long-term data on population sizes for the Canadian boreal. Sensitivity has also been categorized according to disturbance-adaptability – small-scale adapted species have poorer dispersal ability and are thus more vulnerable to harvesting.

Species differ in their response to forest harvesting. Studies in the Canadian boreal suggest that some habitat generalists, such as red squirrels *Tamiasciurus hudsonicus* (Bayne and Hobson 1998, 2000, Cote and Ferron 2001), deer mice *Peromyscus maniculatus* (Potvin et al. 1999, Moses and Boutin 2001) and other small mammals (Bowman et al. 2000, 2001) can persist in landscapes fragmented by forest harvesting. Similarly, species that prefer open habitat such as the meadow vole *Microtus pennsylvanicus* (Potvin et al. 1999, Darveau et al. 2001), and some forest passerines may benefit from the food resources found in forest clearcuts one to two years after harvesting. However, most species avoid newly clearcut areas and depend on residual forest until the surrounding areas regenerate to provide suitable habitat (Potvin et al. 1999). In general, these species are defined as "sensitive" to forest harvesting. Species preferring early seral stages, such as some passerines, moose *Alces alces* (Rempel et al. 1997), and snowshoe hare *Lepus americanus* (Thompson and Curran 1995, Ferron et al. 1998, de Bellefeuille et al. 2001), while avoiding clearcuts immediately after harvesting, may be found at higher abundances in regenerating harvested areas than in unharvested areas. Species requiring closed canopies and the structure and composition of old forests are usually considered the most sensitive because harvested areas do not provide suitable habitat for at least 80 yr after harvesting. Old-growth dependent species that have been relatively well-investigated for responses to forest harvesting in the boreal forest of Canada include the marten *Martes americana*, some passerine species, and arthropods. However, most species identified as old-growth dependent in other forest types or in the boreal forest of Europe remain poorly studied in the Canadian boreal. These species include the woodland caribou *Rangifer tarandus caribou*, bats, cavity-nesting birds, amphibians and non-vascular plants.

Variations in sensitivity

Sensitivity changes with life history; for example, food for adult moose is favoured by the creation of clearcuts, while cows with calves avoid clearcuts, suggesting that clearcuts are sub-optimal habitat. Similar changes have been identified for some bird species, with studies of temporal variations in the habitat requirements of the capercaillie *Tetrao urogallus* in European forests being a good example (Storch 1993).

Sensitivity also changes by region. For example, prey in Newfoundland tends to be concentrated in old growth and therefore so are marten. This led to an interesting situation: as the volume of old growth was reduced, the endemic subspecies of marten *Martes americana atrata* became increasingly scarce (Thompson and Curran 1995). Consequently, red squirrels were introduced by the Newfoundland Wildlife Service in the early 1960s to provide a food source. However, black spruce *Picea mariana* on Newfoundland had evolved in the absence of squirrels, with the result that the scales that protect cones during winter were significantly different to those on the mainland. An endemic subspecies of the crossbill *Loxia curvirostra percna* had evolved to utilize black spruce seed as a food source throughout the winter (Parchman and Benkman 2002). However, the crossbills were out-competed by the squirrels, precipitating a decline in crossbill populations during the 1970s. The sensitivity to the loss of old growth in Newfoundland was much more apparent than on the mainland because of the presence of endemic sub-species and because of the ecosystem changes caused by the introduction of a non-native species.

Marten

The marten has been identified as a species highly sensitive to forest harvesting (Thompson and Harestad 1994). This sensitivity is typically attributed to their dependence on old, coniferous forest (Thompson 1994, Thompson and Colgan 1994, Thompson and Curran 1995) or more generally, the structures associated with them (Sturtevant et al. 1996, Bowman and Robitaille 1997, Potvin et al. 2000). These structures include cover from aerial predators (Thompson 1994) and a complex understory with abundant CWD for access to small mammal prey during winter and for denning (Sturtevant et al. 1996, Bowman and Robitaille 1997, Bowman et al. 2000). These elements exist concurrently only in forests older than 80 yr (Thompson and Curran 1995, Potvin et al. 2000).

The immediate impact of forest harvesting on marten is the removal of habitat, as is evident in their avoidance of recently clearcut areas (e.g., Thompson 1994, Potvin et al. 2000, Forsey and Baggs 2001). In the short term, most data show that areas regenerating from harvesting are sub-optimal habitat for marten. Indices of density are lower compared to unharvested forest (Thompson and Colgan 1994, Potvin et al. 2000). In Ontario, density indices were 90% less in areas where > 90% of the forest was harvested 45 yr ago (Thompson 1994). Marten using these harvested forests were young, subject to high predation rates and

commercial trapping and did not reproduce (Thompson 1994). Further, marten living in harvested forests encountered and killed less prey than marten in unharvested forests (Thompson and Colgan 1994).

The greatest threat to population viability of marten is the conversion of old growth forests to younger, homogeneous plantations (Thompson and Harestad 1994, Sturtevant et al. 1996). Based on studies in the Canadian boreal and in other forests, some authors have suggested that the amount of clear cutting within a marten home range should not exceed 30% (Potvin et al. 2000) and that at the landscape scale, the amount of old forest needed to maintain a minimum viable population of marten is > 20% (Thompson and Harestad 1994). However, such recommendations are obviously dependent on the relationship between the size of the home range of marten and the proportion of forest that is normally cut within such an area. In summary, the amount and configuration of old, residual forests are important factors for the maintenance of marten in harvested landscape.

Woodland caribou

The threatened woodland caribou of the boreal forests of North America require mature and old coniferous forest and seem sensitive to the disturbance created by ongoing forestry operations. However, while there are proposals for forest management in response to caribou needs (e.g., Euler 1998, Armstrong and Armstrong 1998), there are very few readily available published studies testing the effects of forest harvesting on woodland caribou in the Canadian boreal. Caribou avoid recently clearcut areas by one to two kilometres (Smith et al. 2000) and move away from harvesting operations occurring within 15 km (Chubbs et al. 1993). In the longer term, harvesting can displace the home range of a herd (Chubbs et al. 1993). Much more research is required to quantify the effect of disturbance by forestry operations and particularly of habitat loss and fragmentation in the Canadian boreal. This is especially so given the evidence that the habitat preferences of local populations of woodland caribou differ (Poole et al. 2000).

Snowshoe hare

For snowshoe hares, the habitat structure appears to be more important than species composition (Ferron and Ouellet 1992). In general, snowshoe hare are more abundant in regenerating boreal forests than in old forests (de Bellefeuille et al. 2001). However, despite the presence of adequate forage in regenerating clearcuts, hares avoid them and depend instead on residual forest up to ten years after harvesting. Snowshoe hare generally require > 80% lateral cover and it may take up to 20 yr of regeneration to provide adequate cover in summer and up to 40 yr for winter cover (Ferron et al. 1998, de Bellefeuille et al. 2001). Though snowshoe hare have been observed to double their daily rate of movement for about one week after harvesting, they do not seem to be displaced from harvested areas if residual forest remains. Further, survival does not seem to be adversely affected by forest harvesting (Ferron et al. 1998).

Non-vascular plants

There have been few studies of the effects of forest harvesting on the biodiversity of non-vascular plants in the Canadian boreal. Of those reviewed, all show the highest species richness and diversity and more exclusive species in the oldest stands, which ranged in age from 90 to 280 yr (Johnston and Elliott 1996, Crites and Dale 1998, Boudreault et al. 2000, Lumley et al. 2001). Although older trees generally support greater biodiversity of non-vascular plants, and some species are exclusive to stands with trees older than 100 yr, high biodiversity indices in older stands were independent of the effect of tree age (Boudreault et al. 2000). This suggests that time since disturbance, or "forest continuity", creates unique microhabitats allowing the successful colonization of specialized species (Crites and Dale 1998, Boudreault et al. 2000). In general, some non-vascular plant species are associated with stands of varying ages (Boudreault et al. 2000), disturbance types (Crites and Dale 1998) and substrate decay stage and species indicating that the maintenance of non-vascular plant biodiversity requires not only old stands and old trees but also stands of younger ages and the maintenance of coarse woody debris of varying decay stages and species within harvested landscapes (Boudreault et al. 2000, Nguyen-Xuan et al. 2000). In general, old stands are comprised of a broader range of tree ages and therefore of coarse woody debris of varying sizes, distributions and decay stages, which creates a greater diversity of microhabitats (Crites and Dale 1998).

In some cases, regardless of attempts to maintain biodiversity, harvesting may change the species abundance and composition relative to natural disturbance. For example microfungal species diversity was found to be higher in post-fire sites than post-harvest sites over the same time periods in the mixed-wood of Alberta (Lumley et al. 2001). One microfungal species was isolated almost entirely from post-fire sites. In Quebec, lichens were the dominant ground cover in post-fire sites while feathermoss dominated in post-harvest sites (Nguyen-Xuan et al. 2000).

Results from the Canadian boreal parallel similar studies in the European boreal forest. Sensitivity to forest harvesting has been attributed to the requirement for tree species, old trees (Esseen et al. 1996) (old *Populus tremula* in particular [Kuusinen and Siitonen 1998, Uliczka and Angelstam 1999, Ojala et al. 2000]), changes in microclimate at forest edges (Esseen and Renhorn 1998), complex coarse woody debris found in old-growth (Ohlson et al.

1997), poor dispersing ability of some species, and a requirement for forest continuity (Uliczka and Angelstam 1999). Management recommendations for biodiversity maintenance include a lengthened rotation period, increasing the amount of old, deciduous and standing dead trees at the stand scale and the retention of trees in clearcuts (Hazell and Gustafsson 1999).

Birds

Conserving birds in harvested landscapes requires identifying the forest types and attributes that change with harvesting in order to identify threatened habitats and the species that depend on them (Kirk and Hobson 2001, Schmiegelow and Mönkkönen 2002). There is widespread agreement that in the boreal forest of Canada, forest harvesting and fire suppression results in loss of avian habitat due to a reduction in the amount of old forest and young, post-fire stands (Hobson and Schieck 1999) and the conversion of one forest type to another (Niemi et al. 1998, Drapeau et al. 2000). Since the amount of forest cover may remain constant while the age structure and tree species composition changes, forest cover is not a reliable index of habitat loss (Schmiegelow and Mönkkönen 2002). Bird species have been associated with tree species composition (Willson and Comet 1996, Kirk et al. 1996, Hobson and Bayne 2000a), successional stage (Schieck et al. 1995, Thompson et al. 1999, Hobson et al. 2000, Davis et al. 2001), disturbance type (Hobson and Schieck 1999) and stand-level attributes such as the proportion of coniferous species (Robichaud and Villard 1999) or number of standing dead trees (Imbeau and Desrochers 2002). Some species are found only in pure aspen *Populus tremuloides* or white spruce *Picea glanca* stands (Hobson and Bayne 2000b) while others are more abundant in young stands (Schieck et al. 1995) or disturbed areas (Sodhi et al. 1999). The conservation of bird species diversity will require maintaining amounts and distribution of tree species and ages at the stand and landscape scales relative to that produced by natural disturbance (Schieck et al. 1995, Hobson and Bayne 2000a, b, c).

A number of studies designed to quantify the effects of fragmentation on avian communities in harvested landscapes have found no or only weak correlations between landscape configuration and indices of bird abundance (Schmiegelow et al. 1997, Drapeau et al. 2000, Bayne and Hobson 2001), whereas others report clearer effects (e.g., Mazerolle and Hobson 2002). Some authors have challenged the application of island biogeographic paradigms to harvested landscapes, particularly those in the boreal forest, stating that because forested areas regenerate, remnant patches do not represent isolated islands. Further, some species can compensate for the reduction or loss of one forest type by using another (Norton et al. 2000, Schmiegelow and Mönkkönen 2002). Still, a lack of knowledge on fragmentation effects due to forest harvesting remains an important barrier to our ability to conserve avian species in boreal landscapes (Niemi et al. 1998). In general, the loss of forest is considered more detrimental to species than the configuration of the remnant forest in harvested landscapes (Drolet et al. 1999, Schmiegelow and Mönkkönen 2002). Studies investigating whether fragmentation is associated with increased nest predation have also failed to identify significant impacts (Cotterill and Hannon 1999, Tittler and Hannon 2000, Boulet et al. 2000), probably because the fragmentation caused by forestry is not associated with increases in human habitation (Darveau et al. 1997). Identifying birds threatened by forest harvesting requires identifying habitat types that are declining due to harvesting.

As forest harvesting is changing the forest species composition and reducing the amount of old forests and young, post-fire stands, species reliant on these threatened habitat types have been identified as sensitive to logging. In particular, species that use the dead standing wood in old forests and young post-fire stands for foraging and nesting include the black-backed woodpecker *Picoides arcticus*, three-toed woodpecker *P. tridactylus*, hairy woodpecker *P. villosus*, pileated woodpecker *Dryocopus pileatus*, black-capped chickadee *Poecile atricapillus*, boreal chickadee *Poecile hudsonicus*, boreal owl *Aegolius funereus*, barred owl *Strix varia*, Barrow's goldeneye *Bucephela islandica*, bufflehead *B. albeola* and brown creeper *Certhia americana* (Mazur et al. 1997, Murphy and Lehnhausen 1998, Imbeau et al. 1999, 2001, Bonar 2000, Hobson and Bayne 2000b, Setterington et al. 2000). Habitat loss may be permanent for these species as the rotation period does not allow forests to reach old growth status and because fire suppression reduces the number and area of young post-fire stands (Imbeau et al. 1999). For many species, fire does not emulate clearcuts (e.g., Schulte and Niemi 1998), and clearcuts that were subsequently burnt have been found to have a diminished songbird community in comparison to burned stands (Stuart-Smith et al. 2002). However, some forms of harvesting may emulate other disturbance types (e.g., insect attack), with beneficial (in comparison to large clearcuts) effects on the maintenance of avian diversity (Lance and Phinney 2001).

In our literature review, of 56 papers reviewed that assessed the effects of forest harvesting on birds in the boreal forest of Canada, the bulk of the papers considered forest passerines only. Considering the significance of non-passerine habitat specialists, and the extent to which some of these are reliant on old-growth forests (e.g., Gosse and Montevecchi 2001), this group needs to be better represented in future research (see Fig. 3).

In the central Canadian boreal, the conversion of mature mixedwood to deciduous may cause population declines in species which prefer old mixedwood and coniferous forests, including the ruby-crowned kinglet *Regulus calendula*, yellow-bellied flycatcher *Empidonax flaviventris*, and red-breasted nuthatch *Sitta canadensis* (Drapeau et al.

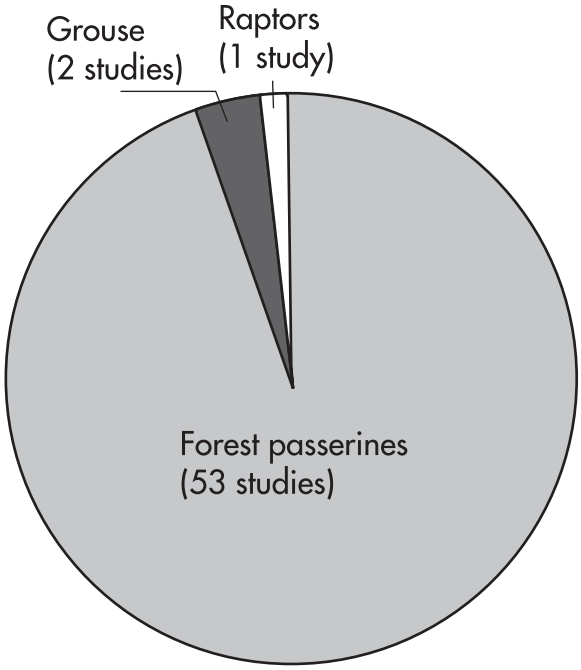


Fig. 3. Forest harvesting effects on birds: studies in the Canadian boreal (56 papers reviewed).

2000). In Saskatchewan, species preferring old mixedwood and coniferous forest may be threatened by harvesting which targets these stands; such species include the mourning warbler *Oporornis philadelphia*, magnolia warbler *Dendroica magnolia*, Blackburnian warbler *D. fusca*, black-throated green warbler *D. virens*, Tennessee warbler *Vermivora peregrina*, bay-breasted warbler *D. castanea*, pine siskin *Carduelis pinis*, winter wren *Troglodytes troglodytes*, white-winged crossbill *Loxia leucoptera*, red-breasted nuthatch, and Swainson's thrush *Catharus ustulatus* (Hobson and Bayne 2000b, c, Hobson et al. 2000). In general, species preferring closed-canopies are unable to use clearcuts until they reach a suitable age; the golden-crowned kinglet *Regulus satrapa*, Swainson's thrush, yellow warbler *Dendroica petechia*, Canada warbler *Wilsonia canadensis*, black-throated green warbler, American redstart *Setophaga ruticilla*, pine siskin, red-breasted nuthatch and rose-breasted grosbeak *Pheucticus ludovicianus* (Norton and Hannon 1997, Schieck and Hobson 2000, Tittler et al. 2001) can all be included in this category. Little is known of the effect of forest harvesting on grouse or raptors, but two studies found that spruce grouse *Falcipennis canadensis* are affected (Turcotte et al. 2000) while ruffed grouse *Bonasa umbellus* are not (Dussault et al. 1998). Management prescriptions to conserve species dependent on closed canopies and old forests include tree retention of 70–80% and the maintenance of unharvested reserves (Norton and Hannon 1997, Tittler and Hannon 2000, Schieck et al. 2000, Simon et al. 2000, Tittler et al. 2001), corridors to facilitate the movement and population persistence of species (Machtans et al. 1996, Desrochers and Hannon 1997, Rail et al. 1997, St. Clair et al. 1998), and riparian buffer strips > 60 m in width (Darveau et al. 1995, Lambert and Hannon 2000).

Invertebrates

Studies by Niemelä et al. (1993, 1994) suggest that carabid beetles are old growth specialists impacted adversely by timber harvesting and a similar pattern has been observed in Europe (Niemelä et al. 1988). These studies suggest that species abundant in the primeval montane pine forests of western Canada have not re-established populations in the oldest available regenerated sites up to thirty years following harvest. Most current forestry practices homogenize the landscape, simplifying forest structure and other attributes such that these forests are unable to support the full compliment of the biodiversity present in unharvested systems (Angelstam 1997, Niemelä 1999). There are some key differences between natural disturbances and the way that forests are managed and, for habitat specialists, we have a poor understanding of the requirements of species reliant on the fire-initiated successional stages (Wikars 2004).

Large-scale patterns of unplanned forest fragmentation and the resulting isolation of species with particular habitat requirements may prevent recolonization of regenerating forest, even when suitable microhabitats develop over time. Spence (2001) argued that landscape-level planning based on the coarse habitat requirements of vertebrates may be insufficient to manage for arthropod species with different dispersal abilities. This notion is supported by Wikars (2004) who found that factors ranging from the scale of logs to landscapes affected the occurrence of the saproxylic beetle *Tragosoma depsarium*.

Forest harvesting effects on biodiversity in Canada

Overall in our literature review, of 121 papers reviewed that assessed the effects of forest harvesting on biodiversity, birds and mammals constituted over 76% of the studies (Fig. 4). This reflects the strong interest in terrestrial vertebrates, and the relative ease with which they can be identified and studied. However, it is likely that further research will identify many other organisms that are sensitive to forest harvesting in the Canadian boreal forest. The importance of invertebrates is gaining increasing recognition, as is the role of non-vascular plants, particularly lichens and fungi, and it seems likely that increased emphasis will be placed on these two groups in the future.

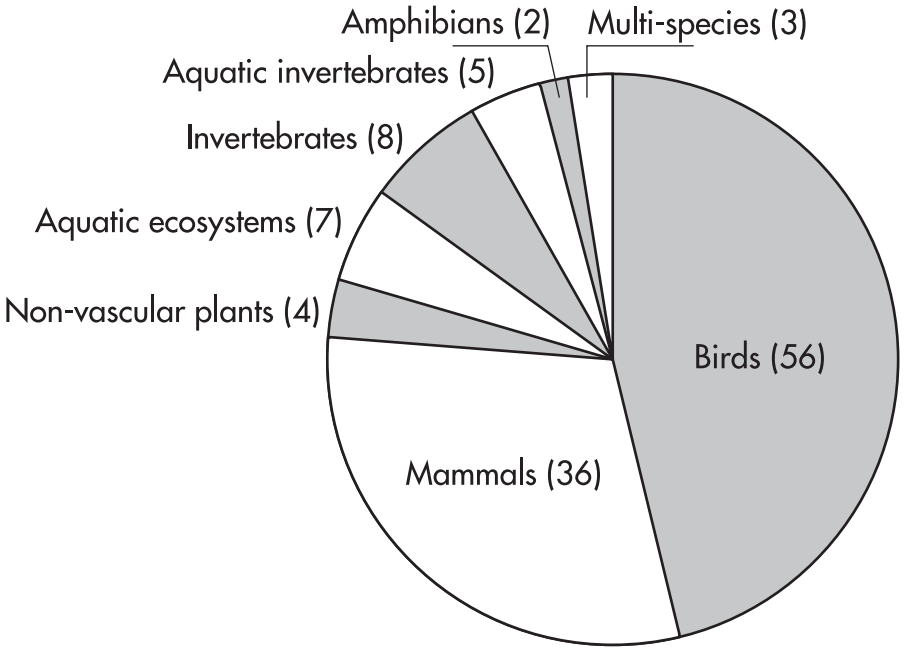


Fig. 4. Forest harvesting effects on biodiversity: studies in the Canadian boreal (121 papers were reviewed).

How can management effectively restore/recreate/maintain important features required to conserve biodiversity?

Until the 1990s, forest management and silviculture planning in commercial forests focused on a traditional sustained yield approach maximizing fibre production at the cost of other forest values. Often the debate centres around the type of silvicultural system being used, instead of the amount, location, and intensity of human use, or exploitation, or both (Graham and Jain 1998). Recently, forest management has begun to move towards ecosystem-based management where forest stands are managed within large management units or over entire landscapes (e.g., Jensen and Bourgeron 1994, Kaufmann et al. 1994, Aley et al. 1998, Haynes et al. 1998). However, the approach has not been so readily taken up in Canada. For example, it was not until late 2003 that the professional magazine of the Association of British Columbia Professional Foresters, Forum, devoted an issue to ecosystem management, despite earlier publications drawing attention to its merits (e.g., Johnson et al. 1998, D'Eon et al. 2000). The new ecological forest management paradigm aims to maintain the naturally occurring species in the landscape while sustaining the timber harvest (Angelstam and Petterson 1993). Assessing the economic and ecological tradeoffs as the new paradigm is implemented is very difficult as our accounting approaches fail to incorporate non-timber values (Mönkkönen 1999). There is also evidence that the ecological implications of the adoption of an ecosystem-based approach have not been adequately considered (Spence et al. 1999). In order to adequately understand the implications of our management decisions for biodiversity, we need to move towards an adaptive management approach (Walters and Holling 1990) that incorporates measures beyond the economic values of fibre production. Such an approach needs to incorporate the active approach to adaptive management – taking it beyond "learning by doing" to incorporate a true experimental approach to management. Such an approach could be complemented by a combination of scenario analyses and planning, incorporating both models of tree cover and seral stage development and habitat supply models (e.g., Calkin et al. 2002, Marzluff et al. 2002).

The variety in structure and composition of boreal forests has been further expanded through human activities. Forests in Canada have been managed for ca 10 000 yr by aboriginal peoples (controlled burning to create browse, berry crops and transportation routes) and more recently through suppression of wildfires, removing individual stems, selective cutting and clear-cutting. The Vikings accessed wood for fuel and construction as early as ca 1000 AD along the eastern seaboard. Although there is a longer history of industrial forestry in eastern Canada, in the western boreal and the northern parts of the eastern boreal the first pass is still underway (it will likely be completed in Alberta, BC, Quebec and Ontario in the next ten years). The southern boreal, particularly in eastern Canada has been continuously high-graded in response to market demands. This repeated high grading has altered the species

composition in many of the boreal forests of eastern Canada as well as altering the genetic stocks (Frelich and Reich 1998). However, despite the relatively recent history of industrial forestry in Canada, detailed information on the rate of exploitation in different parts of the country is surprisingly scarce.

Silviculture (managing forests to meet specific objectives) manipulates forest vegetation in a range of ways according to a prescription. For the purposes of this synthesis and our project, we have not focused on silvicultural systems except as they are relevant to the forest gradient and impacts as the landscape scale. Uneven-aged systems in the boreal will tend to develop shade-tolerant species such as balsam fir *Abies balsamea* and spruce whereas even-aged systems will favor shade-intolerant species such as jack pine *Pinus banksiana* and aspen (Graham and Jain 1998). Ecosystems that are simplified through silviculture focused on production will lose some elements of biodiversity that depend on the natural complexity (Seymour and Hunter 1999). It is also evident that successional pathways following forest harvesting and wildfire cannot be assumed to be equivalent (Timoney et al. 1997, Angelstam and Kuuluvainen 2004). In some landscapes, harvesting tends to favour angiosperm species resulting in the potential decrease in the dominance of conifers (McRae et al. 2001). In others, catastrophic disturbance may completely alter the forest, resulting in the development of different woodland types, such as a change from closed-crown spruce-moss forest to open lichen woodland (Payette et al. 2000).

Using a natural disturbance based management approach

One of the templates used in the new approach to more holistic forestry is a natural disturbance model (Angelstam 1998, Niemelä 1999, Bergeron et al. 1999, 2002). This approach is based on the assumption that organisms in the boreal are adapted to the disturbance regime of the forests that they occupy. Given this assumption, if forest management mimics the pattern and composition of disturbance, the habitat requirements for species occurring in that system will be provided (Hunter 1993). Thus, although disturbance in boreal landscapes varies greatly with different micro and macro-scale topographic, climate and moisture regimes, natural and primordial forests serve as a guideline for the managed forest.

Recent studies have examined the natural disturbance based management approach more closely, and have found that the application of this approach to the boreal can be problematic. For example, Häussler et al. (2002) argued that a switch to natural-dynamics-based silviculture would require the identification of ways to maintain populations of sensitive non-vascular species and forest mycoheterotrophs. In addition, it would be necessary to create regeneration niches for disturbance-dependent indigenous plants in ways that would not accelerate the invasion of non-native species. A review of the comparison between wildfire and forest harvesting and their implications for forest management has been completed by McRae et al. (2001). Among the differences identified in the literature, templates used for clearcuts tend towards a mean disturbance size (for example 60 ha) while natural disturbance, particularly fire, tend to occur as many small disturbances and a few disturbances covering very large areas. The occurrence of fire can be extremely variable, fire history data is not available for many areas, and determining a mean rate of burning may not be possible. Further, the rate of burning differs among stand types and as such is not an adequate predictor for landscape pattern (Cumming 2001). In some systems, such as the boreal mixedwood forest of Alberta, there may be no representative areas at any scale (Cumming et al. 1996). In other systems, differences in disturbance severity between forestry and natural disturbance can result in changes in community composition (Carleton and MacLellan 1994).

The regional differences across the boreal in Canada compound the ecological differences. Although the eastern boreal climate is more affected by insects and the western and central tend to be dominated by fire, as fire protection has improved, insects have taken on a more dominant role (Bergeron and Leduc 1998, Lesieur et al. 2002). Further, our discussions highlighted the key differences between natural disturbance and industrial forestry. Fires kill trees in both young and old stands, but do not take them out of the system whereas forestry removes the trees from older stands. Also, industrial forestry removes trees at a sustained rate that is much higher than that of the irregular disturbance cycles in natural systems. In industrial forestry landscapes, the full spectrum of disturbance is absent; we are practising predominately extensive management replicating the mean size of disturbance. Finally in understanding the impacts of forest harvesting, there is an ecological time lag that will distort the magnitude of any effect. Simplification of the natural disturbance concept to a mean or average leads to simplification of landscapes. If we are to use this template, we must maintain the complexity represented by ranges of variation through time and space, as advocated in natural disturbance-based silviculture.

McRae et al. (2001) provide a detailed summary of the impacts of harvesting on a range of factors including genetics, structural diversity, landscape diversity, nutrient cycling, among others. For a review of the impacts of harvesting on Alberta and British Columbia mixedwoods, see Andison and Kimmins (1999).

Zoning – a continuum of protection and management classes

There are a range of management approaches to timber harvesting and few studies have evaluated the impacts of

these management approaches on biodiversity. New approaches to zoning landscapes to balance forestry objectives with other management objectives are taking hold in New Zealand and more recently eastern Canada. This zoning approach is described by Hunter (1999) as balanced forestry. It is "represented by a triad of production forestry and ecological reserves embedded in a matrix of ecological forestry" (Seymour and Hunter 1999).

Dudley et al. (1999) suggest a typology for management of forest lands that identifies management objectives and associated biodiversity conservation potential. They propose five categories: 1) managed for resource protection; 2) managed for community benefit; 3) reserved for future use; 4) managed for multiple-use; and 5) managed for industrial and intensive forestry. Linked with the IUCN framework for protected areas, these management classes provide a continuum from strict protection to timber production. Although protected areas remain a separate set of categories, some of the forest management units provide strategic and floating reserves (although serving a different function over time). This approach addresses a number of comments raised in our regional workshops regarding the role of the non-timber harvesting land base and the forest management areas reserved but not protected. If such a system were to be implemented as a pilot, the contribution of these land bases could be assessed, and a role for the management zones in biodiversity conservation could be developed and formalized. This provides a potential framework for assessing management treatment differences between timber harvesting land base and non-harvesting.

The importance of strict reserves remains uncertain given the gaps in coverage and representation. For example, in British Columbia, it is the boreal forests of the northeast of the province that are the most under-represented in the province's network of reserves. In Quebec also, the existing network of reserves is far from ideal (Sarakinos et al. 2001).

Several issues require further consideration. Do we understand the differences between natural disturbance and harvesting and the implications for biodiversity, fire obligate species and habitat structure? What are the forest types that we should consider? Do we really want to replicate the full range of natural disturbance across the landscape? What are the implications of the several small and no large disturbances? What are the implications of salvage targets and early successional communities? We require a risk assessment of our management decisions and biodiversity consequences. Further, we need to know what the opportunities for biodiversity management are, for example using road corridors for intensive management, using mixed wood to increase retention, and rotating reserves in plateau landscapes. Are there further opportunities within the Non-Harvested Land Base for biodiversity and should we actively manage it?

How do we monitor the effectiveness of our biodiversity conservation efforts?

The maintenance of biodiversity has increased in importance since the ratification of the Convention on Biological Diversity (Anon. 2001). However, it is clear that many of the requirements that Parties to the Convention agreed to are not being fully implemented by those Parties. These include commitments to the management of biological resources (Article 8c), commitments to indigenous peoples (Article 8j), incorporation of the conservation and sustainable use of biological resources into national decision making (Article 10a) and the protection and encouragement of the customary use of biological resources (Article 10c). In Canada, failure to address these issues led the Heiltsuk and Haida First Nations, together with several environmental groups, to petition the Subsidiary Body on Scientific, Technical, and Technological Advice of the Convention to introduce legislation to prohibit the over-cutting of timber species.

The principle that forest management should be practised in such a way as to maintain biodiversity is one of the criteria used to identify sustainable forest management. Various bodies have adopted such criteria. Canada is a signatory to the Montreal Process, as are the USA and Russia, and the maintenance of biodiversity is the first criterion listed under this agreement. In Canada, the Canadian Council of Forest Ministers has issued its own set of criteria and indicators but, again, maintenance of biodiversity is one of the criteria to be listed. Within Europe, the Interministerial Conference on the Protection of Forests in Europe has also produced a set of criteria and indicators that includes the maintenance of biodiversity (see Rametsteiner and Mayer 2004).

Each list varies, especially amongst the indicators. However, considerable progress has been made in identifying suitable indicators (e.g., Lindenmayer et al. 2000). An important factor to consider is the scale of the indicators. There has been a tendency to develop indicator lists that are appropriate for regions rather than for management units. In addition, there has been inadequate attention given to the importance of developing indicators of biological diversity that are appropriate across a range of scales.

One area where effectiveness monitoring has been applied is in research. Within the context of designed experiments that apply different levels of treatments and maintain proper controls (adaptive management) monitoring is crucial (Walters 1986). There are myriad aspects of biodiversity that we can measure and many that we cannot. Selecting benchmarks and targets for their related criteria and indicators all depends on what it is that you are monitoring for (for whom and for what). Monitoring effectiveness requires that measures or indicators are assessed that

track progress in programs, plans or activities in meeting stated objectives or goals. This is not to be confused with implementation monitoring which relates to the compliance with regulations and resources allocated. Below we summarize both our workshop and review discussions on biodiversity monitoring and those discussions related to monitoring effectiveness.

Monitoring effectiveness

There are a number of strategies to effectiveness monitoring. Effectiveness monitoring is a critical part of sustainable forest management, but one that has been largely ignored. "Monitoring" has often been considered as an expensive and largely worthless activity, despite the huge amount of critical information that it has generated. Effectiveness monitoring requires a benchmark or performance target that is not relative to policies or program objectives, but assesses the actual values and risks to the resource (e.g. Davis et al. 2001). This may be why there has been a reluctance by government and industry to embrace the process. We need both planning and monitoring indicators for effectiveness. We need some measure that says that we expect biological communities to rebound in a certain number of years. Monitoring effectiveness should include assessing progress towards maintaining target age class structure and other habitat objectives under harvesting treatments. The framework, targets/benchmarks and criteria/indicators will differ depending on the objectives that are being managed for. For example, there are specific indicator frameworks for policy makers (Reid et al. 1993). Uncertainties remain over who should be paying for the data collection and who should be leading the effort of collecting specific level measures.

Monitoring biodiversity

From our regional Canadian workshops, there was consensus that producing a long list of indicators would not be very useful (some such lists for local level indicators are available through the Model Forest Network). Rather it was suggested that we should focus on doing research to test the indicators that are currently proposed.

Any approach for monitoring should encompass some measures of the structure, functions or services that ecosystems provide. Although BorNet workshop participants were reluctant to focus on single species management approaches, it was suggested that we should monitor at the species and community level in order to ensure that we are not losing species. It is possible to use population size and abundance of feature species (for those that we current have adequate information).

Noss (1990) suggests a useful framework for the characterization of biodiversity that integrates composition, structure and function with ecological attributes across multiple scales. Further, Noss (1990) suggests that criteria for evaluating potential indicators should include: 1) sufficiently sensitive to provide an early warning of change; 2) distributed over a broad geographic area, or otherwise widely applicable; 3) capable of providing a continuous assessment over a wide range of stress; 4) relatively independent of sample size; 5) easy and cost-effective to measure, collect, assay, and/or calculate; 6) able to differentiate between natural cycles or trends and those induced by anthropogenic stress; and 7) relevant to ecologically significant phenomena. There are existing studies in a range of boreal ecozones that propose indicator species for vertebrates (Kuhnke and Watkins 1999), whereas others have argued for the importance of including all species-rich groups, especially insects, fungi and lichens (Spence 2001).

Extension needs

Bunnell and Johnson (1998) found two key challenges for scientific research approaches that limit the applicability of the findings to forest management. These include the fact that researchers constantly seek novel questions and novel ways to approach them. Even assessing a common phenomenon, scientists will take different approaches to their studies. This approach limits the potential for building on knowledge regarding common variables, replication over large time and spatial scales, and even the potential to build on existing techniques and approaches. Research tends to be conducted at fine scales (see Fig. 1) while managers must make decisions and develop plans for coarse landscape units. In this manner the managers are forced to take the scientific information developed at discrete stand units to coarse scales (problematic particularly in studies that have not been replicated adequately to represent the complexity in the coarse scale).

From our meetings, a number of extension needs were identified. Resource managers do not generally have the time to read books addressing their management problem; they want a three to four page document summarizing the key findings relevant to their operations. The forest companies need a contact that has accessed the scientific information and can delivering it to them in a useful way. It would be useful to develop a list of agencies and people who are active in the area of biodiversity research and practice and make it available to the resource managers. It would be useful to have an annual workshop on themes relevant to biodiversity management. Further it would be useful to develop a central clearinghouse for habitat models with species accounts. Finally there was a request in our BorNet meetings for a clear and agreed upon definition of biodiversity and of natural disturbance.

Conclusion and recommendations for future research

Previous reviews of literature have suggested that Canadian researchers tend to publish research that is less applied than that of scientists from other countries (Bunnell and Dupuis 1994). This trend is changing as pressure on forest resources increases debates about the science underlying management decisions in Canada. There was general agreement within all of the BorNet regional workshops that the science developed within BorNet needs to be applied to current management contexts. It was critically important to involve the resource managers (from communities of NGOs, forest industry, governments and First Nations) to contribute to identifying the key gaps in knowledge and to prioritizing future research areas. This was accomplished through a series of workshops across Canada and through the final international workshop in Sweden. These events were open to representatives from all of the communities mentioned above. Aggregating and synthesizing information from such a diverse set of interests, cultures and values has been very challenging. BorNet was forced to limit its scope to focus primarily on the ecological aspects of biodiversity conservation, but there is recognition of the key importance of other fields of study and social and cultural issues. Generally, if we are to discuss the management of biodiversity, then we must pose the question for whom and for what? We have to find the balance between the socio-economic, cultural and the ecological sides of these questions (Welsh et al. 1996). What is the role of sustainable aboriginal communities and of social science in biodiversity maintenance? Research in western Canada needs to incorporate the impacts of oil and gas extraction and to consider risk management.

There is no single correct scale at which to manage biodiversity. Rather we must constantly consider the implications of management decisions on both generalists and habitat specialists. This must be done while considering the impacts of management decisions today on habitat availability in the future. We must keep in mind the assumptions that are being made as we extrapolate from the fine scale to the coarse, and we must test those assumptions. Bunnell and Dupuis (1994) argue that experiments must extend beyond single species and the small-scale if the science is to be applied in a meaningful way.

A key adage for management is the maintenance of heterogeneity across scales, allowing for the complexity that characterizes the boreal forest (Harvey et al. 2002). Managers must beware of the attempt to do all things in all places as the application of single management strategies across landscapes necessarily leads to homogenization. When science that has been done at the stand scale is extrapolated to coarser scales, experiments should be set up within the adaptive management framework to test the applicability of the results and concepts to that scale (Boutin et al. 2002, Angelstam et al. 2004a).

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Research requirements to achieve sustainable forest management in Canada: an industry perspective

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Timber harvest practices in Canadian boreal forests are currently progressing from concepts surrounding sustained yield of wood to those implicit in sustainable forest management (SFM), including also ecological and social values. This paper discusses the research questions arising from the inclusion of ecological management, which are inextricably linked to the need for management at multiple spatial scales.

The current management challenges thus require the development of a hierarchical SFM framework, including coarse, intermediate and fine filter concepts. First, ecosystems must be identified and represented in the long term at appropriate amounts across the landscapes within ecoregions. Second, forest retention at both landscape and stand scales must include levels of structural elements above thresholds, both spatially and temporally. Third, in order to design adaptive management research questions, both planning and effectiveness indicators are required. Finally, tradeoffs among ecological, economic and social components as well as within and between scales will enhance the ability of practitioners to make intelligent decisions.

In reality, however, traditional sustained yield forest management still dominates.

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The boreal forest covers ca 35% of the Canadian land area, surrounded by grassland, drier coniferous forest and mixed hardwood trees to the south and tundra to the north (Burton et al. 2003). The majority of Canada's forests are publicly owned, with 71% controlled by the 10 provinces and 23% owned by the federal government, in cooperation with the territorial governments. As such, 23 million ha are recognized as "heritage forest" and are to be left in their natural state, while 27.5 million ha are considered "protection forests where timber harvesting is excluded by policy" (Anon. 1998a).

A wide range of actors is involved with the management of boreal forests. These include public managers, the private forest industry, non-industrial small private owners and the public at large. The management of the forest is, however, regulated by provincial governments and conducted by a large forest industry spread across Canada (Burton et al. 2003). While nearly half of Canada's land mass is forested (418 million ha), only about half of it is classified as "commercial" or "timber productive" (Anon. 1998a). Thus, the Canadian boreal forest is managed under a wide variety of legislation, regulation, policy and management regimes.

During < 100 yr, utilization of Canadian forests has proceeded from the drier regions in the south, to the boreal forest in the north (Smith and Lee 2000, Drushka 2003). Similarly, management has progressed from unregulated harvesting toward sustainable forest management in several steps. This process started with regulated harvesting under provincial legislation and regulation in the 1950–

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1960s, and was then influenced by the development of sustained yield (SY) principle for wood production in the 1960s. The transition towards integrated management and multiple use proceeded through constraints on SY (1970s), increased pressure for non timber values (1980s), and to more ecologically based management aiming at sustainable forest management in the 1990s (Drushka 2003, Burton et al. 2003).

The questions arising from the evolution from the SY principle to sustainable forest management (SFM) are inextricably linked to the current management context (Oliver et al. 2001, Burton et al. 2003). Although there is much discussion about SFM and the development of SFM frameworks, SY is still the main influence on rate of harvest, i.e. annual allowable cut (AAC) rather than the retention of ecological, structural and seral stage attributes.

Crown forest tenure evolved into SY management, resulting from agreements between governments and the industry, to allow supply to meet demand, and at the same time generating revenue for both the crown and the industry. Thus, SY management led to short, even-aged rotations, intensive free-to-grow standards, high utilization and enhanced estimates of AAC. Increased constraints on SY principles, such as for non-timber values, altered the system but did not embrace SFM in its entirety (Hebert 2004). Thus, industrial questions emanate from the gradual shift from SY towards SFM. From the point of view of maintaining biodiversity, a major challenge for the implementation of SFM is to embrace the concept of spatial scale (e.g. Peterson and Parker 1998). To deal with the complexity of the biodiversity concept at multiple spatial scales, Anon. (1982) and Noss (1987) used the metaphor of coarse and fine filters. The coarse-filter approach involves maintaining a representative array of ecosystems in a region. Because some species are almost certain to slip through the pores of a coarse filter, a complementary information-intensive fine-filter approach is needed for species of special concern (Hunter 1990, 1999).

Currently, the challenges facing the forest industry include the implementation of spatial representation (coarse filter), seral and structural attributes at a stand and landscape level (medium filter), and species richness (fine filter) management, which recognizes natural disturbance as a potential baseline (e.g. Bergeron et al. 2002, Hebert et al. 2003, Hebert 2004, Angelstam and Kuuluvainen 2004). The aim of this paper is to identify the management challenges when attempting a multi-scale systems approach to SFM in Canada.

Management challenges

Establishing a SFM framework

In order to establish a process to achieve and monitor a desired future forest condition, forest companies should develop a multi-scale SFM framework as a guide for continued improvement (e.g. Oliver et al. 2001). Rempel et al. (2004) suggest that SFM should utilize a logical framework involving five elements: 1) the establishment of a clear set of values, goals, and objectives, 2) planning actions that are most likely to meet desired goals and objectives, 3) implementation of appropriate management activities, 4) monitoring of the outcomes to check on predictions, effectiveness and assumptions, and 5) evaluating and adjusting management depending on the outcome of monitoring. These five elements can be organized into an industrial planning framework (Fig. 1), which uses both planning and effectiveness indicators to relate scale and indicator type (Table 1). To stress that evaluations need to be made both with regard to the implementation of policies in the actual forest management, and of the institutions adjusting management, Angelstam et al. (2003) used the term "two-dimensional gap analysis".

Estimating costs

Ultimately, the costs of harvesting along with the associated costs of measuring ecological benefits are the greatest challenges during the implementation of SFM. In most cases, significant additional costs have been borne by the industry, with no prior assessment of costs or consequences and no assessment of the proposed ecological benefits.

Binkley et al. (1994) estimated the impact of a 10% reduction in AAC in 1989 in British Columbia, Canada, to an employment reduction of 2.2% or 31570 people and a Gross Domestic Product decline of 2.5%, or a $1 billion loss to the provincial GDP. Reinhardt (1999) suggested that managers need to go beyond the question, "Does it pay to be green". The answer is "It depends". With environmental questions the right policy depends on the circumstances confronting the company and the strategy it has chosen (e.g. Djurberg et al. 2004). Environmental problems, ecological management and/or SFM do not automatically create opportunities to make money. In fact, in most cases, the cost is significantly higher but with no proven market premium. Thus managers should begin to look at forest management problems as business issues that require assessment as suggested by Binkley et al. (1994) and Hebert (2004). Fitzsimmons (1996) outlined the confusion that still faces the US industry today by stating, "The ecosystem based aspects of the proposed rule reflect all the uncertainty, confusion and imprecision of the ecosystem concept." Thus, research must outline a multi-scale, systems approach to ecological management that assesses tradeoffs between costs and ecological benefits. Testing hypotheses about the non-linear relationships between organisms and habitats at multiple spatial scales is an important element in research (Angelstam et al. 2004a, Whittaker et al. 2004).

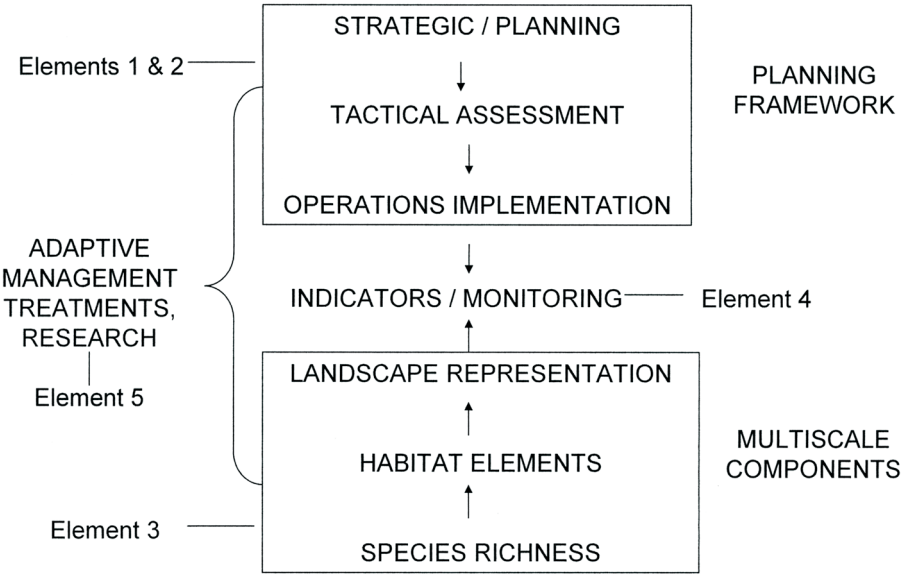


Fig. 1. An SFM framework currently being used by Riverside Forest Products in British Columbia, Canada (Viszlai 2003). For details about the five elements, see text.

Management at multiple spatial scales

Coarse filter: representation of ecosystem diversity

In 1995, the Canadian Council of Forest Ministers (CCFM) produced a national framework of criteria and indicators which includes the criterion "Conservation of Biological Diversity", supported by an indicator statement on the maintenance of ecosystem diversity (Anon. 1995). From the managers' point of view the questions related to these statements include: 1) how an ecosystem should be described with respect to spatial scale, 2) how much of each ecosystem is required for conservation purposes, and 3) the spatial distribution and composition of the retention of trees in stands and stands in landscapes.

At the broadest level, ca 183 million ha (44% of the Canadian forested land base) is classed as the non-harvest land base (NHLB). In addition, a further 50.3 million ha of the forested land base consisting mainly of timber harvest land base (THLB) is protected as heritage forest or as protection forest. This means that for a total of 56% of the Canadian forest land base society has other aims than commercial wood production (Anon. 1998b).

Of the remaining 185 million ha of commercial forest, ca 116 million ha are still to be accessed. Thus, the amount and distribution of this forest matrix (mainly mature to over-mature) contributes significantly to biodiversity and will do so for decades. Harvesting in a newly accessed area is usually made using a "two pass" harvesting system, which involves an initial entry and a second entry following green-up prescriptions during the first entry. Due to the recent Canadian forest history only a few regions in Canada have entered the second rotation. This "two pass" approach distributes the first rotation throughout the whole forest matrix, possibly underestimating the influence of harvest on biodiversity. An alternative approach would be to zone areas of entry at the scale of landscapes within ecoregions (Hunter 1999). However, the influence of the forest matrix on the stand and landscape scales of these two approaches is still unclear at this time (Whittaker et al. 2004).

Within provinces or ecoregions, full, partial and light constraints may restrict, in a variety of ways, up to 50–60% of the forested land base (mainly THLB). This often includes the 12%-rule for protected areas, being advocated by many Canadian provinces (Brundtland 1987). However, the amount and distribution (ecosystem diversity) of NHLB needs to be evaluated prior to the inclusion of constraints on the THLB with respect to: 1) the spatial repre-

Table 1. The relationship between scale and indicator type.

Type	Scale		Indicators
Planning indicators (implementation)	Landscape Stand	Coarse filter Medium filter	Landscape representation Habitat elements
Monitoring indicators (effectiveness)	Biological richness	Fine filter	Species richness

sentation of ecosystems among different geographical regions, 2) costs, and most importantly, 3) for its ability to maintain biodiversity. Recent research (Serrouya and Herbers 2002) has shown that the NHLB may contribute habitat attributes in larger amounts (e.g. riparian areas) than the THLB, as well as lesser amounts of other specific structural attributes (e.g. coarse woody debris). In order to continue developing legislation and regulations to further restrict harvesting on the THLB, the multiscale biodiversity contribution of the NHLB should be more fully evaluated.

At the provincial or company level, mapping programs are often based on a hierarchical system for ecosystem classification ranging from zonal, variant to site series/ecosite scales. In most cases, variant levels describe ecosystems too broadly, while site series/ecosite mapping is too fine scale. For example, an area of 150 000 ha may have only 9 variants but 72 site series. Currently, site series have been grouped (Huggard 2001, Serrouya and Herbers 2002) using vegetation similarity analysis to develop clusters of site series. Clusters appear to be at a scale where ecosystems can describe ecological function, and where structural attributes, species indicators, monitoring programs and forest practices can be implemented effectively. Clusters of site series have been vegetation based, however, moisture/nutrient regimes may also be useful in describing the areas (Kurlavicius et al. 2004). Research is required to determine criteria useful in establishing ecologically effective geographical units. For example, based on the area requirements of local populations of specialized birds and the patch dynamics of their habitat, Angelstam et al. (2004b) estimated that the size of a management unit useful in the long term had an average size of 250 000 ha. However, there was considerable variation among species. Ecosystem representation of set aside areas may range from a landscape scale within ecoregions to stand based variable retention in sites with different return intervals of disturbances. The inclusion of provincial protected area strategies should recognize ecosystem representation as a management goal.

As an example, the concept of variable retention should be based on: 1) ecosystem representation at a range of spatial scales, 2) utilizing landscape retention as protected areas, and 3) natural disturbance return intervals which identify low disturbance sites and expanded stand level retention. To this point research has not clearly identified the amount and distribution of retention required (Whittaker et al. 2004).

Medium filter: habitat attributes

At the medium filter level, i.e. the scale of stands in landscapes, ecosystems appear to function based on the type, amount and quality of the habitat attributes produced by natural disturbance processes and dynamics (Hunter 1993, Stuart-Smith and Hebert 1995, Bunnell et al. 1999).

In the recent past, SY harvesting altered these natural dynamics significantly, altering successional pathways and timing, species composition, seral stage distribution and structural attributes (e.g. Burton et al. 2003). For example Raivio et al. (2001) identified green tree retention, decaying wood and prescribed fire as structural stand-scale consideration for the Fennoscandian industry. Similarly, Bunnell et al. (1999), identified eight stand and landscape habitat elements (cavity sites, downed wood, shrubs (early seral), broadleafed trees, large live trees, riparian, adjacent or continuous canopy and late seral), that appear to accommodate most, if not all the vertebrate species. The relatively equal distribution of vertebrate species, across biogeoclimatic subzones for most habitat elements, suggests the importance of the structural element, rather than the zonal/landscape configuration (Bunnell et al. 1999, Boutin and Hebert 2001).

Important questions involve the amount (threshold), type, quality and both the spatial and temporal distribution of the habitat element. For example, how much green retention is required, throughout the NHLB and THLB, in order to maintain minimum levels of the habitat elements throughout the rotation at both the landscape and stand level? Most research to date has identified stand level requirements, generally with a surrounding mature forest matrix, which may well tend to overestimate the value of the stand retention attributes and which requires further research (Whittaker et al. 2004). The question to be answered is how well does stand or landscape variable retention support species richness in a second rotation forest? Estimates of the requirements for stand level retention are generally done without considering ecosystem representation and broad scale distribution of protected areas, as well as the contribution of the NHLB. Thus, dose-response curves are required for each scalar combination. In addition, threshold levels for each habitat element may vary for different species and by ecosystem and have not been adequately addressed within the SFM framework.

Fine filter: species indicators

The selection and measurement of species indicators in a monitoring program provides an assessment of efficiency of the coarse and medium filters. Such indicators usually consist of species or species groups which are selected to assess the coarse (representation) and medium filter habitat elements, as well as the species groups or guilds they supposedly represent (see Angelstam et al. 2004b for an example). Hannon and McCallum (2002) recently addressed the use of focal species as indicators for management systems. They suggest that studies show that randomly selected species are just as good as "indicators" in representing population trends and biodiversity hotspots of other species. As pointed out by Roberge and Angelstam (2004), single species umbrellas cannot ensure the conservation of all co-occurring species. Moreover, their review also

showed that few studies had attempted thorough testing of the umbrella values. A major problem of choosing the wrong focal species may result in the loss or decline of species in the area that requires different habitat elements (Simberloff 1998).

Discussion

To date, in general, forest management systems have considered a narrow range of parts of multi-scale ecological systems rather than the integrated approach as promoted by the SFM concept (Schlaepfer and Elliott 2000, Gamborg and Larsen 2003, Angelstam et al. 2004c). For example, in Canada both provincial government and industry programs have chosen an exceptionally wide variety of indicator species with little supporting science. As well, the use of rare and endangered species has gained favor, although they may represent only themselves and their particular habitat requirements, rather than a broader range of associated species. It thus appears that our current understanding of biodiversity indicators in Canada cannot adequately assess newly developed forest management system planning or multi-scale integrated planning. By contrast, the development of indicator selection and monitoring programs must reflect the multi-scale, ecological system and its relationship to baseline levels of natural disturbance dynamics (e.g. Larsson et al. 2001).

The development of indicator and monitoring systems must also keep pace with the evolution of forest management systems. Each management system in Canada, which incorporates the distribution of seral stage and patch size at a coarse filter level, as well as a range of habitat elements at a medium filter level, is actually only one treatment on the landscape. Each treatment requires a fine filter assessment before adaptive management and continuous learning can be incorporated effectively. In reality we are thus far from the ideal model presented in Fig. 1.

It is also becoming apparent that decisions must be made among ecological, economic and social jurisdictions, as well as within and among spatial scales. Implementation of biodiversity measures usually has an economic consequence as well as an ecological benefit. To date, the costs in monetary units have been more often and more easily measured than the ecological benefits. Similarly, the ability to meet natural disturbance baseline requirements for biodiversity has most often been measured at the stand level. However, retention of trees and stands at a variety of scales must be assessed in relation to ecological outcomes. Trade-off modeling for both scenarios requires a series of models to address both multi jurisdictional and multi scale options.

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First Nations: measures and monitors of boreal forest biodiversity

Marc G. Stevenson and Jim Webb

Stevenson, M. G. and Webb, J. 2004. First Nations: measures and monitors of boreal forest biodiversity. – Ecol. Bull. 51: 83–92.

With rare exception the roles of indigenous peoples in maintaining the ecological diversity of forest ecosystems have received little serious attention in either scholarly research or the current discourse on biodiversity. This paper examines the traditional roles of Canada's First Nations peoples in maintaining boreal forest biodiversity. It is argued that, notwithstanding that Native Americans were not conservationists (in the normative use of the term), the traditional land use activities of Canada's boreal forest-dependent First Nations once served to create and sustain biodiversity. The ability to maintain these practices and the relationship of Aboriginal peoples with their lands is critical to understanding and sustaining boreal forest biodiversity. In this sense, the integrity of a First Nation's traditional uses, or ecological footprint, may be an excellent "umbrella" indicator of boreal forest biodiversity. Setting aside large tracts of the boreal forest where Canada's Aboriginal peoples can sustain their traditional ecological footprint and exercise their constitutionally protected rights makes sense scientifically (i.e., ecologically), but also morally, ethically, and legally.

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As industrial exploitation expands into the northern forests of Eurasia and North America, the need to assess the impact of such activities on boreal forest biodiversity has grown increasingly urgent (Anon. 1999). In response to this need, the development of measurements of boreal forest biodiversity has attracted the attention of a wide variety of interests from academic institutions to environmental organizations (ENGOs), governments, and forest companies committed to sustainable forest management. Based upon the best of western scientific knowledge and practice, the development of biodiversity indicators have and continue to be based primarily on environmental criteria. Excluded from consideration and analysis is the role of human beings in sustaining the health of ecosystems and maintaining biodiversity (e.g., Sardjono and Samsoedin 2001). In many parts of the world, indigenous peoples once played, and continue to play through the pursuit of a variety of traditional activities, an integral role in maintaining the health and biodiversity of ecosystems (e.g., Pierce Colfer and Byron 2001). This statement may be particularly germane to Canada's boreal forest where many Aboriginal communities still rely on forest resources for sustenance and the attainment of other values (Stevenson and Webb 2003).

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For many of Canada's Aboriginal peoples – the terms First Nations, Native and Aboriginal peoples are used interchangeably in this paper, and are intended to include both Canadians of both Indian and Metis (i.e., mixed) descent – biodiversity and ecological integrity are concepts difficult to separate from notions of identity, culture, subsistence, economy, spirituality, society, polity, rights, etc. Indeed, many of Canada's First Nations peoples traditionally viewed themselves as an integral part of the natural world and vital to the "proper" functioning and health of ecosystems. This paper develops the arguments that: 1) the "traditional ecological footprint" of First Nations, i.e. the constellation of traditional practices and relationships that Aboriginal groups still maintain, and/or wish to maintain, with their lands and resources, may be an excellent indicator of boreal forest health and biodiversity, and 2) Aboriginal peoples may be particularly well-suited to monitoring biodiversity indicators developed by them, as well as those of ecologists and other scientists.

The role of First Nations peoples in maintaining boreal forest biodiversity

The expansion of commercial forestry and other industrial activities into the world's boreal forests has been met increasingly with attempts to identify and measure boreal forest biodiversity. While some of these efforts may have the potential to address key issues surrounding the maintenance of boreal forest health and ecological integrity, they generally do not consider the role of humans, and specifically indigenous peoples, in contributing to biodiversity or sustaining ecosystem function. To the extent that the role of humans is considered at all in contemporary discussions of biodiversity, it is most often in the context of identifying the impacts, usually negative, of human activities on the "natural" ecosystem. In this sense, humans are seen as outlying factors that degrade or detract from the "natural" or "normal" functioning of biological systems and processes. In the academic-state dominated discourse on biodiversity, the dismissal of the role of humans has been a particularly effective tool for marginalizing Aboriginal rights and interests (Langdon 2002).

Yet, northern North America at the time of initial contact with Europeans was not a "natural" environment as biologists and other resource scientists normally use and understand the term, uninfluenced by human activities. First Nations' peoples had played, for thousands of years, a major role in shaping the biological characteristics, especially biodiversity, of the continent's landscape. Sauer (1956) was perhaps among the first to advance and expand the notion of human agency in shaping natural environments. More recently, scholars such as Boyd (1999) continue to challenge the assumptions of North America's "natural" landscapes. Ultimately, these and other works (e.g., Cronon 1983) lead to the conclusion that most, if not all, landscapes, are not "natural" at all, but dynamic cultural expressions related to human uses, perceptions, values, institutions, technologies and social and political interests (Roberts et al. 2003). Cronon (1983) provided one of the first descriptions of the processes by which the "cultural" landscapes of Aboriginal peoples often fall victim to colonial values, institutions, technologies and political interests, thereby dissipating into the mists of history (Roberts et al. 2003).

With regard to Canada's boreal forest, it is only in the last 200 years that the role of Aboriginal peoples in creating and sustaining boreal forest biodiversity has diminished through population displacement, industrial encroachment, cultural assimilation and other factors beyond their ability to control. This, in turn, has created a situation whereby the current composition, structure and function of the North America's boreal forest landscapes are not "natural", in the Aboriginal sense of the term, and the product of only the last few hundred years. No longer do First Nations hunt, gather, fish and trap without restriction, thus undermining their ability to sustain core cultural values and valued ecological relationships (VERs) with their traditional lands and resources. No longer are they permitted to set fires in order to sustain a host of values (sustenance, cultural, spiritual, etc.) critical to their survival and to boreal forest health and ecological integrity. This has resulted not only in a loss of biological diversity, but in the erosion of traditional management approaches and knowledge systems required to sustain such diversity. However, with innovative approaches that consider the role played by human beings in creating and sustaining biodiversity, we can begin to construct a future where ecological diversity, in all its complexity and dimensions, can be sustained for the generations that will follow.

Many of Canada's forest dependent Aboriginal peoples struggle, against almost insurmountable odds, to maintain relationships to lands and resources that are critical to sustaining cultural, social and ecological integrity at local and regional scales. It is these traditional use relationships, or "traditional ecological footprint" of First Nations peoples, that have to date so far not been considered in dialogues about biodiversity indicators for the boreal forest. Yet, there are strong arguments, based in traditional teachings and understandings of ecological relationships, that support and illuminate the role of Aboriginal peoples in maintaining ecological integrity and biodiversity in Canada's boreal forest.

Hunting

For example, Cree, Inuit and other Aboriginal elders believe that the more that animals are hunted, the more there will be. This notion is central to the thinking of many Native cultures and functions to maintain the balance and

reciprocity that the Creator intended for Aboriginal peoples, while upholding their obligations towards animals and all living things. Conversely, not to hunt or to use animals in an appropriate manner is an abrogation of their responsibility. Aboriginal elders will often express the opinion that the reason for a reduction in, or loss of, a species in a particular area is the result of the fact that they were not hunted or used. Non-hunting, rather than overhunting, is often invoked by Inuit elders and hunters as the real cause of the disappearance of animals in certain areas. The lead author has been told repeatedly by Inumarrit (real Inuit) that the best way to restore the number, health and vitality of local animal populations is to hunt them again. In other words, when animals are not hunted, the balance is not maintained and the roles and obligations of each party are not fulfilled. This supports the notion that Aboriginal peoples' traditional use is a fundamental part of maintaining the health and vitality of local animal populations, ecosystems, and their relationships with them.

In the western way of knowing, thinking and acting, termed the "Eurocentric synthesis" by Battiste and Youngblood-Henderson (2000), such notions may challenge existing orthodoxy, at least as it pertains to environmental decision-making. Yet, when practised sustainably (i.e., when a dynamic balance between humans and animals is maintained), hunting functions to promote ecological integrity, biological diversity and the viability of prey species. For example, when a local or regional population of animals is hunted, it is generally healthier and reproduces faster as there is enough food to go around, and the population is kept below the maximum carrying capacity of its environment to sustain it. Moreover, according to the Inuit (Hickey 1984), hunting may also create ecological vacuums in specific areas that attract animals from outlying areas. At the same time, as many animal species traditionally procured by Aboriginal peoples are at the higher end of the food chain, their predation allows greater ecological "elbow room" for creatures at lower levels, which, in turn, serves to benefit animals at higher levels. The same general arguments apply to other traditional Aboriginal resource use practices such as fishing, gathering and trapping.

Fire

Many Native Americans used fire extensively and, at times, intensively. Some anthropologists (Lewis 1982, Cronon 1983) have illuminated the critical role that fire once played in the lives of Native Americans and in shaping the biological composition, abundance and distributions as well as other characteristics of their forested environments. Annually, and often more frequently, Aboriginal peoples would burn selected areas within the boreal forest to maintain and promote access to a variety of plant and animal species. Among many boreal plains groups, fires would be set each spring to increase the take of berries and provide favourable habitat for ungulates (bison, elk, moose, deer, etc.) and other prey species, as well as to facilitate travel. Overall, the effects of controlled burning by First Nations served to encourage new growth, greater habitat diversity, greater species diversity and inter-specific competition, and ultimately biodiversity. In fact, it is almost certain that, prior to the arrival of Europeans, there was far less mature contiguous boreal forest on the boreal plains of northern North America than presently (Lewis and Ferguson 1988). Hence, prior to Europeans uprooting and marginalizing traditional native patterns of land and resource use, the northern plains was characterized by greater and more complex mosaics of parkland and boreal forest. The explosion in the number and diversity of ecotones that these mosaics produced were especially favourable to creating and sustaining biological diversity.

Deconstructing the "Ecological Indian"

The above views are held by very few involved in the current state-academic dominated discourse on biodiversity. That said, it is worthy to note that some anthropologists have argued that indigenous societies have not tended toward equilibrium with their environments. For example Krech (1999) has argued that the spiritually grounded "noble savage" image is a myth, perpetuated, in part, by Aboriginal peoples themselves for political ends. This notion must be challenged if the concepts advanced in this paper are to expand the current discourse on biodiversity.

With the emergence of ecological anthropology in the 1960s and 1970s, the view that pre-industrial indigenous societies tended to reach equilibrium with their ecosystems became popular (e.g., Rappaport 1967). However, recent scholarship (e.g., Brightman 1993, Krupnik 1993, Krech 1999) has argued that traditional use practices have often led to the massive alteration of ecosystems and even to the extinction of species, irrespective of spiritual beliefs and practices (Langdon 2002). This notion has found a receptive audience among both government officials and natural resource scientists, and has been used, in combination with the dismissal of the ecological knowledge of Aboriginal peoples as anecdotal and irrelevant, to assert state control over natural resource management on Aboriginal lands (Langdon 2002). Langdon (2002) for one, singles out the concept of "conservation" as playing a key role in the imposition of state authority over Native resource use in Alaska: "Biologists within governmental (state and federal) organizations have an enormous stake in the hegemonic relationship between the State and natural resource policy with the concept of 'conservation' being the foundation of disciplinary claims to moral superiority and the maintenance of power."

What is not usually appreciated in discourses on natural resource management is that Native peoples traditionally were not "conservationists", at least in the usual sense of the word. Steeped in the puritanical notion that "restraint/sacrifice" will confer future benefits to both resources and resource users (Langdon 2002), the concept of conservation is a product of the Eurocentric synthesis (Battiste and Youngblood-Henderson 2000), and a tool that sustains its existing power relationships (Stevenson and Webb 2003). It is easy, for example, to claim the moral high ground when state authorities witness Aboriginal peoples killing more than they can immediately consume and/or claiming that the "more (of anything) you kill, the more will return" (Langdon 2002). The ethic of conservation based on preservation and "none-use" was developed in social contexts far removed from nature, most notably in degraded or urban environments such as that in which western society and most of its philosophical tenants emerged. We argue that conservation in this sense is an inappropriate concept to describe the relationship that Canada's boreal forest-dependent Aboriginal peoples traditionally maintained with their lands and resources. Rather, conservation should be viewed in the broader context of sustainable use whereby both over-use and none-use undermine this objective.

Interestingly, and perhaps ironically, many Aboriginal peoples have begun to refer to and regard themselves as "conservationists". The marginalizing of traditional Aboriginal forms and philosophies of management and the imposition of state-controlled education on Aboriginal peoples have undoubtedly facilitated the acceptance and adoption of such concepts into Aboriginal parlance. At the same time, in a variety of cross-cultural arenas (land claims/treaty making, environmental assessments arising out of resource development, etc.), Aboriginal peoples are forced into negotiating rights of resource access and use in the language, concepts and terminology of the dominant culture. Aboriginal values, understandings and concepts rarely, if ever, are used as language currency in the negotiation process. Co-optation or forced adoption of the non-Aboriginal language and concepts by Native peoples may ultimately be a "zero-sum game" for First Nations, however, as it plays into the hands of the dominant culture and its hegemonic control over natural resource policy and practice.

We would concede that, to the extent that Aboriginal peoples purposely attempted to "conserve" or "manage" anything, it was/is their relationships with the resources upon which they depended and the ecosystems of which they were apart. Native resource use was not governed by a "conservation ethic", but by the "principle of least effort" and a kinship with "mother earth" whereby use was a profound, maybe the ultimate, form of respect for, and act reciprocity with, other living organisms. To outsiders, the end result of traditional resource uses may look like acts of "conservation". Hunn (Williams and Hunn 1982) has termed this "epiphenomenal conservation". But this was clearly not their intent. Consequently, to apply the term "conservation" to what Aboriginal peoples do, does them (and everyone) a disservice by misconstruing their relationship with nature and by failing to acknowledge the cultural bias inherent in its use, and the hegemonic control that such use implies.

Over-exploitation of natural resources by indigenous peoples, although largely untended, did occur in the past leading to habitat degradation and even species extinction. For example, the adoption of more efficient technologies (e.g., the horse and repeating rifle) and participation in a foreign economic system by North American plains Indians contributed to the massive decimation of plains bison (Krech 1999). But such cases were rare, and more likely to be found in ecosystems where Aboriginal resource use practices continue to be governed by traditional values and beliefs, significant social, ideological, demographic, technological and other changes notwithstanding. Often, under such circumstances, traditional and customary use and management practices are out of sink with contemporary ecological processes and realities, and not enough time has elapsed to serve as a teacher or to allow for successful correction and adaptation.

Closed, or relatively bounded environments where resources are highly accessible/predictable in time and space, and where humans are new arrivals (e.g., the South Pacific Islands) may be particularly susceptible to untended over-exploitation by indigenous peoples leading to species extinction. Such environmental contexts, however, are rare in the boreal forest. Traditional beliefs and values aside, low human population density and high residential mobility, combined with limited technological capacity, and spatially and temporally unpredictable resource distributions, movements and locations served generally to prevent habitat degradation and species over-exploitation. Moreover, resource depletions and imbalances were traditionally met with relocation and enhanced mobility before resources were over-exploited to the extent that they could not recover. "Hitting a hunting or fishing ground hard" until the amount of effort expended was no longer rewarded by the returns, and then leaving it fallow for the animal species or population to recover, was/is a common strategy employed by northern Aboriginal peoples. Langdon (2002) has advanced the notion of "relational sustainability" to better describe the ethic that lay behind Native resource use practices in Alaska, and this term may better fit what most boreal forest dependent Aboriginal peoples practised and may still wish to continue in Canada.

We believe that most of the notions advanced above about the traditional roles of hunting and the use of fire in maintaining biodiversity and ecological integrity are well-established in ecology and related disciplines. Unfortunately, resource use decisions are rarely taken on the basis of "good science" alone or in co-operation with scientists (natural, social, otherwise). Historically, governments have accorded economic considerations and political expedien-

cy priority, and the Canadian public has been left with a legacy of environmental degradation and a loss of cultural and biological diversity (Anon. 1999).

First Nations: not just another stakeholder

From our perspective, the on-going and unjustifiable infringement of Aboriginal and treaty based rights (relating to the resource use) by government and industry remains one of the greatest single barriers to preserving boreal forest biodiversity. This is not to suggest that, under present circumstances, a return to pre-contact conditions is possible or even warranted to conserve boreal forest biodiversity for future generations. Rather, we must develop approaches and means that designate large portions of the boreal forest for Aboriginal peoples so that they can continue to play a major role in creating and maintaining boreal forest biodiversity through the exercise of traditional use practices, which are guaranteed protection as Aboriginal and treaty rights under Section 35 of the Canadian Constitution and treaties with Canada. TRIAD approaches, i.e., partitioning the boreal land base into protected, extensively and intensively managed zones (Anon. 1999, Seymour and Hunter 1999), and/or the establishment of high conservation value forests (HCVFs) are two possible, and not unrelated, ways in which this might be accomplished. At the same time, areas of the boreal forest where Aboriginal peoples are left to pursue their traditional activities may serve as controls for measuring biodiversity and ecological integrity in others areas where industrial and other uses are permitted.

In order to implement such solutions, governments must come to terms with the fact that Canada's boreal forest dependent Aboriginal peoples are not just another stakeholder (Stevenson and Webb 2003). In addition to moral and ethical reasons, there are strong legal and scientific rationales why First Nations must be meaningfully involved in decisions taken in respect to their traditional lands and resource use activities.

Legal basis

Canada's Aboriginal peoples have constitutionally protected rights that most other Canadians do not. These rights stem from the fact that: "When Europeans arrived in North America, Aboriginal peoples were already here, living in communities on the land, and participating in distinctive cultures, as they had done for centuries. It is this fact, and this fact above all others, which separates Aboriginal peoples from all other minority groups in Canadian society and which mandates their special legal and now constitutional status." (Regina vs Van der Peet 1996).

The Supreme Court of Canada (SCC) has defined an Aboriginal right as "an element of a practice, custom or tradition integral to the distinctive culture of the Aboriginal group claiming the right." (Delgamuukw vs Regina 1997). Aboriginal title is a special kind of Aboriginal right that goes beyond those rights directly tied to historic practices before contact. The SCC has found that Aboriginal title is the broad, sometimes exclusive, right to use land for a variety of purposes, whether historically precedented or not. In other words, Aboriginal title flows from traditional use of land by an Aboriginal community, which, in itself, may be sufficient to establish an exclusive right of occupancy, and permits a First Nation to make modern uses of land that may have no direct analogies in historic practice. Recent court decisions also suggest that First Nations do not have to go to court to prove the existence of their Aboriginal rights and title (e.g., Haida vs British Columbia and Weyerhaeuser [2002] and Taku River Tlingit First Nation vs Ringstad et al. [2002]). Rather the Crown's fiduciary obligation is sufficient to trigger meaningful consultation processes designed to accommodate the rights and interests of Aboriginal peoples in decisions taken in respect to their traditional lands. The fiduciary obligation owing Canada's Aboriginal peoples also entitles them to separate and distinct consultation processes if the public process is found wanting (Mikisew Cree First Nation vs Canada 2001).

Many First Nations entered into treaties with Canada. The rights that stem from these historic agreements are called treaty rights. While First Nations view treaties as sacred contracts between sovereign nations to share lands and resources, both federal and provincial governments have traditionally viewed them as "land surrenders". However, the courts view them as neither, but unique agreements that call forth special principles of interpretation, which tend to favour the Aboriginal point of view. Nevertheless, provincial governments, who have the authority for forestry, have not been particularly accommodating of Aboriginal and treaty rights. In fact, most existing provincial forestry policies and legislation, which are based on sustained yield practices, likely violate constitutionally protected treaty rights (e.g., Ross and Sharvit 1998). It follows then that, in any dialogue about industrial and other uses of the boreal forest, including the conservation of its biological diversity, Aboriginal peoples must be included as significant participants.

Scientific basis

Article 8j of The Convention on Biodiversity (Anon. 2002) commits Canada "…to respect, preserve and maintain knowledge, innovations, and practices of indigenous and local communities embodying traditional lifestyles relevant for the conservation and sustainable use of biological diversity…" While such international commitments di-

rects Canada to meaningfully involve Aboriginal peoples and their knowledge in any dialogue about the conservation of biodiversity in the boreal forest, the scientific basis is compelling. Unfortunately, the full contributions of Aboriginal peoples and their knowledge to such discussions are rarely realized; most attempts to incorporate the knowledge of Native Americans into environmental decision-making is characterised by the process described below.

On the face of it, some Aboriginal peoples possess a wealth of knowledge that can serve the interests of biodiversity conservation in Canada's boreal forest. Many elders and traditional land users, for example, have developed extensive knowledge bases about the behaviours, spatial and temporal distributions, health and conditions of specific plants and animals, as well as those factors that influence these phenomena and their inter-relationships. Such knowledge is not readily available to those who do not call the boreal forest home, and decision-makers are often left to rely on practitioners of western science (i.e., biologists and other research scientists) to fill these gaps. Being the product of both personal experience and cumulative knowledge passed down through the generations, the knowledge of Aboriginal peoples, commonly referred to as traditional ecological knowledge (TEK), may reveal much about natural variation over time in valued ecosystems, species and their interrelationships. Many Aboriginal peoples have also been witness to the effects, both individual and combined, of natural (e.g., fires) and human (e.g., logging) disturbances on boreal forest resources, and their relationships with them. It is these types of information and knowledge that forest managers and planners generally do not have access to, but often need, in order to make informed decisions and plans over broad temporal and spatial scales.

In practice, and to date, however, TEK has made very little impact on the ways forests are managed. The reasons for this can be attributed to a number of factors. These range from the lack of power and capacity of First Nations to have their knowledge count in resource use decision-making, to the fact that this knowledge does not easily fit into the western scientific paradigm, or environmental resource management (ERM) for that matter. In order to make TEK fit, those "cultured" in the western scientific tradition often seek out aspects of TEK most palatable to them, such as specific environmental information about resources, which is only a fragment of the knowledge base that most indigenous peoples possess (Fig. 1). In order to inform western science and ERM practice, this knowledge is then subjected to a lengthy process of de-contextualization whereby the knowledge is usually translated from the Aboriginal language to that of the dominant culture and then recorded on maps and/or tapes (Stevenson 1996, 1999). Decisions are then taken using this information, almost always in the absence of its rightful owners and users. Through its systemic and ongoing "dumbing-down" in the context of ERM, specific elements of the knowledge of Aboriginal peoples become sanitized and made more "user-friendly" to the dominant culture. In effect, knowledge becomes information – the main currency accepted in environmental resource management – and TEK assumes the role of "hand-maiden" to western scientific knowledge (Fig. 2). In so doing, alternative ways of seeing, knowing and relating to the natural world are diminished and dismissed, reflecting the authoritative knowledge system of ERM and strengthening the existing power relationships that support it.

If Canada and other nation states are ever going to implement their international commitments to conserve bio-

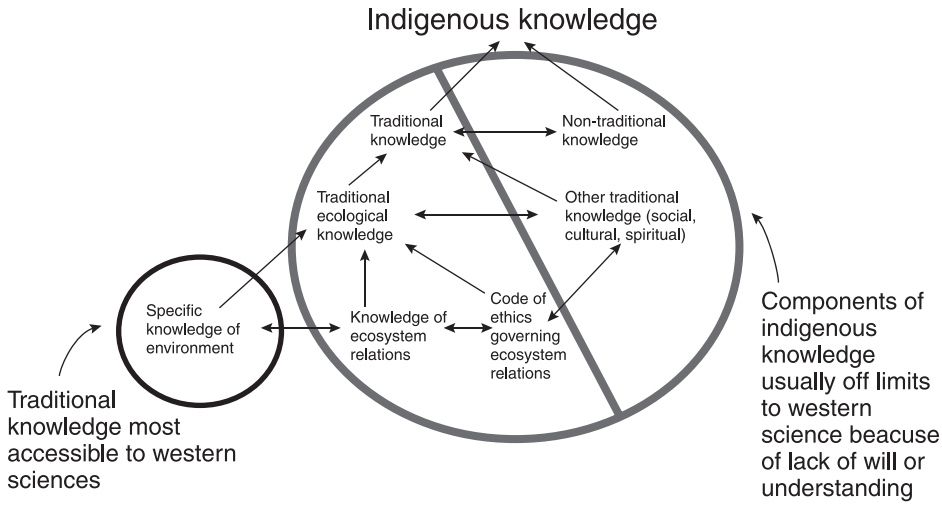


Fig. 1. Related components of Indigenous Knowledge Systems (adapted from Stevenson 1996).

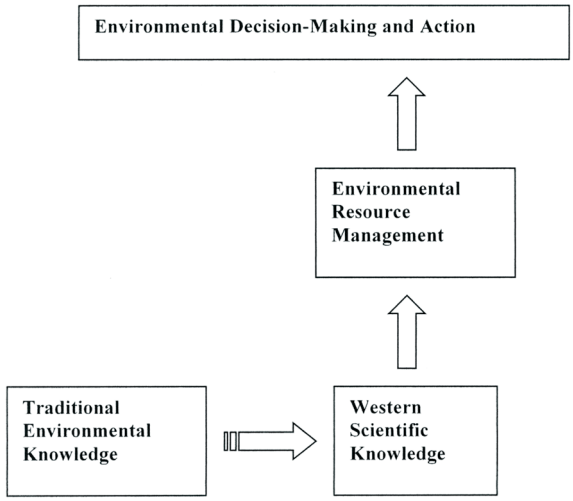


Fig. 2. The incorporation of TEK in western science and environmental resource management: The Status Quo (from Stevenson 1999).

logical diversity, we must consider that the knowledge of indigenous peoples, even their specific environmental knowledge, does not exist to inform western scientific practice or ERM. Indeed, contrary to the claims of many researchers, and even First Nations' peoples, TEK may have little to offer ERM. Rather, it exists to inform ecological understandings and management systems and philosophies that are fundamentally different than those originating in the dominant culture. By acknowledging that the knowledge and management systems of Aboriginal peoples, in all their depth, breadth and complexity, are different from those of western science and ERM, the full contributions of Aboriginal peoples and their knowledge to conserving biological diversity in Canada's boreal forests potentially may be realized.

Perhaps the best way to conceptualize how traditional Aboriginal management approaches, systems and philosophies differ from those of environmental resource managers is to focus on what is being managed. In the latter system, specific resources, spatially defined areas and, more recently, ecosystems as managers attempt to deal with environmental issues of increasing magnitude and complexity, are often arbitrarily designated as management units. The types of information sought for management purposes focus on specific quantitative estimates of species abundance, age, distribution, condition, regeneration rate, removal rate, death rate, etc., often to the exclusion of other types of information and knowledge. The "human factor" is regarded as an outlier, a nuisance that obscures and distorts the "real" data needed for decision-making. In the parlance of environmental impact assessment, the term "valued ecosystem component" (VEC) (Beanlands and Duinker 1984) has emerged as a conceptual tool to manage environmental impacts.

To the extent that Aboriginal peoples manage(d) anything, and as told to the lead author and other researchers (e.g., Spak 2001, Sherry and Myers 2001) it is human activities and their relationships with or connections to the natural world. These they can do something about. Relationships, not specific resources nor spatially bounded areas nor even ecosystems, are conceptually closer to the real "management unit" managed by Aboriginal peoples, and the nexus around which they traditionally constructed their knowledge base. In this context, the concept of "valued ecosystem relationship" (VER) may be a useful way of thinking about what Aboriginal peoples traditionally managed, and how they and their knowledge can be incorporated into management practice (Fig. 3).

If Aboriginal peoples and their knowledge have a significant contribution to make to the conservation of biodiversity in Canada's boreal forests, it is in the area of understanding relationships not only among various non-hu-

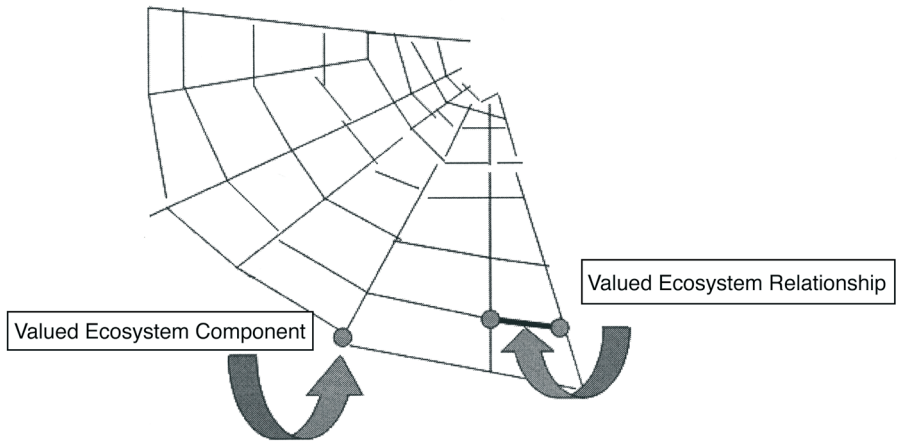


Fig. 3. VEC: the "management unit" of environmental impact assessment management. VER: the "management unit" of indigenous management systems.

man actors (e.g., plants and animals), but all species, and especially between humans and the natural world. Acknowledging the fact that ERM and traditional Aboriginal management systems and philosophies have fundamentally different origins, histories and objectives provides both a challenge and an opportunity for those with a vested interest in maintaining the status quo. On the one hand, it represents a threat to the authoritative knowledge system in power. On the other, it opens to the door to a paradigm shift in co-operative management practice and environmental decision-making, whereby the real contributions of both knowledge and management systems can be realized (Figs 3 and 4).

Aboriginal ecological footprints: an indicator of boreal forest biodiversity

Many researchers have advocated fine-filtered, or focal species indicator, approaches to measure and monitor the conservation of biological diversity in the face industrial development. However, as Hannon and McCallum (2002) have recently pointed out, there are many problems associated with such approaches. Single species indicators may not be sufficient as other species, and even the entire ecosystem, may be compromised by human activities, while the indicator species thrives on new opportunities created by anthropogenic change. For example, while a large ungulate, such as moose, may thrive on the edges of clear-cuts, the habitat requirements for a variety of understory, mid-story and canopy dependent species are destroyed. Problems with focal indicator species approaches range from the selection of criteria based on "charisma" or high public value, to the fact that randomly chosen indicators often prove to be just as effective as purposefully selected species indicators.

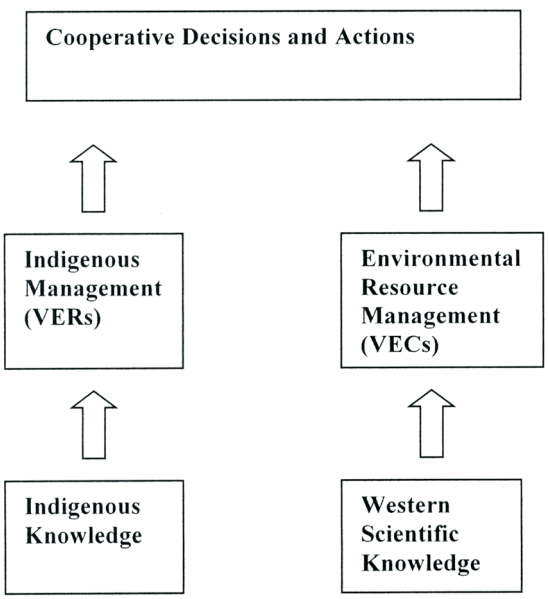


Fig. 4. A model for incorporating indigenous and western scientific knowledge into managing for biological diversity in Canada's boreal forest.

The shortcomings of focal species indicator approaches have, in part, given rise to coarser-filter, ecosystem management approaches based on the emulation of natural disturbance. However, these too have proven to be problematic and difficult to implement. For example, how do we define or know the parameters of the ecosystem processes we wish to conserve or the boundaries in which these processes function? If we focus on ecosystem processes, where does this leave species that are not absolutely necessary to the overall functioning of these processes or systems? In the general absence of comparative or reference habitats, how do we know how effective our efforts are?

Selecting a cohort of specialized, faster-reproducing as opposed to more generalized, slower reproducing species as indicators may have some potential to mitigate a few of the problems associated with focal indicator approaches. Alternatively, "umbrella" indicator species approaches may also offer promise, particularly in the face of limited funding, knowledge and time in which to conserve biodiversity (Roberge and Angelstam 2004). The latter authors define an umbrella species as "a species whose conservation confers protection to a large number of naturally co-occurring species". Roberge and Angelstam (2004) argue against the use of single species umbrellas as they cannot ensure the conservation of all co-occurring species, especially those in different taxa. Although we concur, for the most part with their observation, if there is an exception to the rule it may Aboriginal peoples. We believe that there can be no better single indicator of boreal forest biodiversity than the Aboriginal peoples who still depend on its resources to fulfil a range of traditional sustenance, cultural, social, spiritual, and other needs. Moreover, this umbrella indicator can talk and potentially provide a wealth of knowledge and insight about the ecological health and integrity, not just of individual species with whom it interacts, but of the relationships between and among community members. The junior author, as a way to get biologists to think about the role of humans in maintaining biological diversity in the boreal forest, has suggested to them to think of Indians as "talking squirrels".

It is not the vitality or wellness of Aboriginal peoples per se that is at issue – although highly unlikely, one might possibly imagine a situation whereby an Aboriginal community could be thriving at the expense of the environment on which it depends. Rather, it is the integrity of the "traditional ecological footprint" of First Nations as revealed in the constellation of relationships with the natural world that Aboriginal peoples still struggle to preserve that offers so much promise as an indicator of biodiversity.

The Little Red River Cree and Tallcree (LRRC/TC) Nations of northern Alberta have identified three criteria for establishing their "ecological footprint" and traditional use parameters, with measurable indicators for each. These include cultural resources (cabins, trails, etc.), traditional use commodities (moose meat, berries, fish, medicinal plants, etc.), and traditional use activities (i.e., practices which require a specific ecological setting within a boreal forest landscape). In proposing these concepts, these First Nations and researchers funded by Canada's Sustainable Forest Management Network (e.g., Natcher and Hickey 2002), are undertaking to demonstrate an inseparable relationship among traditional use, cultural sustainability and biological diversity. In turn, these First Nations use the term "ecological footprint" to advocate that these three criteria allow for current traditional use needs, while accommodating demographic projections for their populations to understand how much biodiversity must be conserved within a boreal forest landscape in order to meet current and future traditional use requirements. This research may demonstrate that Aboriginal peoples, in their traditional use of the boreal forest, may be one of the best "umbrella" indicator species for development of biodiversity parameters.

Consideration of the "traditional ecological footprint" of First Nations may require provincial establishment of new resource use management regimes capable of conserving boreal forest biodiversity and respecting the constitutionally protected rights of Aboriginal peoples. In this context, it is easy to understand why professional managers in government and industry, i.e., individuals with substantial investments in the status quo, could well feel threatened by such planning approaches. At the same time, the First Nations are keenly aware that this approach may provide the impetus for solidification of alliances with environmentally conscious stakeholders, who aspire to the establishment of HCVFs. In presenting this approach, the LRRC/TC Nations prefer to reconcile their traditional uses with other uses in a manner that allows for some acceptable balance between ecological and economic sustainability.

Conclusions

While the "traditional ecological footprint" of many First Nations communities may not be what it once was, a surprising number of Aboriginal peoples still depend on boreal forest resources on a daily basis (e.g., Natcher and Hickey 2002). However, the need to use boreal forest resources and to sustain their relationships with them in order to fulfil a range of nutritional, social, cultural, spiritual and other needs and values is far greater than can be currently realized owing to a variety of factors (e.g., wage labour employment, industrial impacts, welfare dependency and the lack of access to capital, etc.). For most boreal forest dependent Aboriginal communities, the maintenance of cultural identity, core values and knowledge is still largely dependent on sustaining their relationship(s) with the forest and its resources.

Even though the "ecological footprint" of most First Nations has changed, many Aboriginal elders and traditional land-users still possess a wealth of knowledge relevant to sustaining their traditional relationships with boreal forest. This knowledge, combined with their access or proximity to the boreal forest, suggest that these Aboriginal peoples are favourably positioned not only to serve as measures, but as monitors of natural and anthropogenic impacts on key VERs, VECs and other biodiversity indicators. Regrettably, Aboriginal peoples are rarely afforded such opportunity.

Models to measure and monitor boreal forest biodiversity using species indicator approaches are being developed on a number of fronts. Boutin (pers. comm.) of the Univ. of Alberta has recently proposed a "multi-metric index" to measure the "human footprint" (i.e., the impacts of oil/gas, forestry and other human uses) on boreal forest ecology using biotic indices representing key indicators of biological diversity. With biotic indicators on one axis and human uses on the other, "dose-response" curves representing multiple and cumulative impacts of human activity on biodiversity are generated (Guénette and Villard 2004). What needs to be considered in such approaches is the placement of Aboriginal peoples, or more precisely, their "traditional ecological footprint", on the indicator axis. Only when we begin to appreciate and understand the fact that, in some parts of the world, indigenous peoples' uses of forest resources are critical to conserving biodiversity, will we ever achieve this lofty objective.

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IKEA's contribution to sustainable forest management

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Monetary thinking, or profit maximisation, in business is challenged by the occurrence of externalities such as loss of biodiversity. Using the production-oriented home furnishing company IKEA as case study we discuss the role of non-utilitarian values in promoting environmental responsibility, and how this can promote "green" businesses. In order to provide society with wooden products while maintaining the values of the forest ecosystems, IKEA believes that it is necessary to: 1) increase forest plantations in order to reduce the pressure on the natural forests, 2) restore ecosystem integrity in areas where the natural ecosystems have been lost and 3) stop unsustainable logging of intact natural forests and high conservation value forests.

It is imperative that wood products from well-managed forests can be produced at competitive costs. Consequently, the process of certification and other means of verifying sustainable forest management need to be cost efficient without loosing performance in the field. The IKEA approach to trace the origin of the wood and to put higher demands on the wood used within the IKEA range, has been successful paths but not without challenges. The biggest challenges so far has been to secure that the wood does not come from intact natural forests, high conservation value forests or from illegal logging.

The development of tools and procedures to identify, map and manage forests with high conservation values is required. Hence, it is important that forest industry, social and environmental stakeholders, in an atmosphere of mutual respect, develop routines for dialogue and agreements with regards to forest management. This is of special importance in areas which are more sensitive or valuable from an ecological or social point of view. IKEA calls on the scientific community and governments to provide credible information pertaining to forest conservation and restoration available to processes where conservation values are evaluated and negotiated.

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The future of the world's forests is determined by the actions of individuals, communities and businesses. Conservation therefore has to address people's needs and attitudes, as well as legal and other policy instruments. The routes society can follow to bring about particular forms of behaviour are education, persuasion, economic and legal instruments (Wynne 1998). Education leads to increased understanding, whereby informed decisions can be made. Persuasion or exhortation is when people or businesses are asked to do some things but not others. Economic instruments include action providing economic incentives, or discouragement through financial penalties. Finally, legal

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instruments mean that regulation and law control behaviour. Globalisation of the market place, however according to some, limits the set of tools (Klein 2000, Söderbaum 2000).

Traditionally, it is assumed that a market-based economy will secure efficient allocation of resources among competing uses, and provide signals (prices, profits, rents) to different actors (firms, households, governments) which then respond in predictable ways. Markets, however, can also fail badly in this allocation of resources, particularly regarding conservation issues (Arrow 1951, Hanley 1998). One example is when property rights are inadequately allocated. For example, no one owns clean air or biodiversity. To use and degrade such aspects of the natural capital represents an external cost. Here it will be argued, however, that businesses may consider the total economic value of utilities including use values and existence values. A good reason is that it is profit maximising to do so because it gives "good-will" and thereby increased demand for the products. Additionally, intrinsic values, which may stem from traditions and cultures with rights-based belief systems (Spash and Simpson 1994) may have importance. Such belief systems and organisations can be discussed as part of business ethics in terms of "politic economic organisations" (sensu Söderbaum 2000).

The differences in the spread of forest certification can be interpreted as the existence of different combinations of monetary value and business ethics. For example, Elliott and Schlaepfer (2001) studied the development of forest certification in different countries and found that some countries are more apt to embark on such voluntary agreements than others.

The home furnishing company IKEA has become an actor in international business, contributing to the development of tools to identify intact natural forests (Aksenov et al. 2002) and high conservation value forests (Jennings 2002) as well as promoting the development of certification and legal compliance (Mooney 2002). The aim of this paper is to present IKEA as a case study disclosing how the company argues and acts to mitigate problems with economic externalities. In particular we deal with forestry issues needed to support IKEA's vision and business idea by meeting the expectations of the customers and other stakeholders to contribute to a more sustainable use of the forest ecosystem resources. The material presented is based on information derived from IKEA's own unpublished studies, for example in the form of deep interviews and customer surveys.

IKEA's business idea

IKEA is a production-oriented home furnishing company. The IKEA business idea is to "offer a wide range of well designed, functional home furnishing products at prices so low that as many people as possible will be able to afford them" (Anon. 1999). The concept of achieving low prices is largely built on applying resource efficiency in the product design and throughout the supply chain. IKEA has a vision "to create a better everyday life for the many people". The vision was originally meant for customers only, but has been extended to include all IKEA's stakeholders, i.e. customers, co-workers, suppliers and the society at large. This vision carries obligations, not least when it comes to the impact of the company's activities on the environment.

IKEA buys its products from ca 1600 suppliers in 55 countries. Swedwood, an international group belonging to the IKEA Group of Companies, produces ca 8% of the products. Many of the suppliers are situated in countries where environmental work has come a long way. But IKEA also works in countries where the environmental agenda is not so well developed or simply not enforced. The trading organisation consists of 42 locally situated trading offices. The local representation makes it possible for purchasers, technicians, quality and environmental coordinators and other co-workers to work closely with their suppliers for continuous development. This creates positive opportunities to work on areas such as outside environment, social and working conditions and forestry. IKEA believes that focus on improvements where the development has not yet come very far will have the greatest overall impact. Many times IKEA considers continuous improvements as being more important than the actual starting point. Consistent with this approach, IKEA now concentrates on raising the lowest level of performance by securing a set of minimum requirements, a code of conduct. This code, known as "The IKEA way on purchasing home furnishing products", outlines the minimum requirements on IKEA suppliers within the areas of social and working conditions, outside environment, i.e. emissions to ground, water and air, child labour and forestry. As of fiscal year 2003, all suppliers have been subject to an on-site audit, and all new suppliers are audited before their first delivery to IKEA. IKEA's own staff at the trading service offices around the world works closely with suppliers to implement IKEA's code of conduct and to correct violations. Some 80 trained auditors make audits and establish action-plans based on non-compliance. The auditors take active part in the corrective actions at the factories of the suppliers. Complex issues can take months or even years to solve, while other corrective measures can be put in place within days (e.g. to equip workers with protection gear) or even within hours (e.g. to unlock emergency exits and to clear blocked escape-ways). Numerous re-audits follow each action-plan. So far, > 20 000 corrective actions have taken place at IKEA's suppliers. More than 50 000 corrective actions are in progress. If a supplier does not implement and adhere to the IKEA requirements within stipulated time frames, IKEA may at its sole discretion and without any compensation to the supplier, immediately terminate all existing agreements with the supplier and cancel any existing order.

IKEA's position on forest ecosystem resources

IKEA recognises wood as an excellent material from a functional as well as an environmental point of view. Approximately 70% of the material used in IKEA products is wood or wood based. In fiscal year 2002, the total wood usage in IKEA was ca 10 million m^3 of roundwood equivalents (Vollbrecht 2002). The inherent properties of wood makes it the principal material in the majority of IKEA home furnishing products. In addition, it is renewable, recyclable and biodegradable. However, for wood to be a good environmental choice, it should originate from forests that are managed in a sustainable way; therefore, forestry is one of IKEA's six prioritised environmental areas. These are: 1) products and materials, 2) forestry, 3) suppliers, 4) goods transports and warehousing, 5) stores, and 6) employee offices.

What does IKEA mean by sustainable forestry?

The term "sustainable forestry" is hard to define and represents a "moving target" since one's perception of what is sustainable is changing over time. Within IKEA, it is believed that the sustainability concept should be based on scientific evidence, and furthermore, that the definition of what is "sustainable management" either should be defined in an open and transparent democratic process or defined in a consensus oriented stakeholder process encompassing ecological, economic and social aspects of forestry. Consequently, IKEA believes that it is important that all relevant stakeholders actively contribute with input to the process when forest management standards and principles and criteria for sustainable forestry are defined. The active participation from all relevant stakeholders gives an element of assurance that nothing important is overseen in the process of defining sustainable forestry. However, while sustainable forestry is the ultimate goal, a more appropriate term would be responsible forestry, used to describe a forest management on its way towards sustainability.

Intact natural forests

Today, just one fifth of the world's original forest cover remains in large tracts of relatively undisturbed forests (Bryant et al. 1997). Russia, Canada and Brazil hold the majority of the remaining intact natural forest. In Europe, large areas of intact natural forest have been converted into other use. In western Europe, few forest areas can be referred to as intact natural forests.

Global Forest Watch, of which IKEA is a co-funder, is producing maps of intact natural forests. One example is the atlas of Russia's intact forest landscapes (Aksenov et al. 2002). An intact forest landscape is a landscape in the forest zone where most natural processes prevail, undivided by infrastructure and almost entirely unaffected by human activities. It is large enough to support viable populations of large vertebrates and keep most of the territory free of edge effects. In the Russian atlas, a minimum block size of 50 000 ha is used. It may, and typically does, contain a mosaic of ecosystems (Aksenov et al. 2002). The atlas provides a valuable tool in IKEA's trading organisation for implementing IKEA's forest policy.

Identifying high conservation value forests

In order for IKEA's demands to be implemented in their supply chains, it is necessary to provide the suppliers and IKEA's co-workers with tools showing how to avoid wood from unsustainable and controversial sources. This is especially important and challenging when it comes to High Conservation Value Forest (HCVF). The concept of HCVF was developed by the Forest Stewardship Council (FSC). The identification and management of HCVFs is covered under Principle 9 of the FSC Principles and Criteria (Anon. 2000). The HCVF concept has moved the debate away from definitions of particular forest types, e.g. primary forests and old growth forests, to focus instead on the values that make a forest important. By identifying these key values and ensuring that they are maintained or enhanced, it is possible to make rational management decisions that are consistent with the maintenance of important environmental and social values (Jennings 2002).

High Conservation Values (HCV) have one or more of the following attributes (Jennings 2002): 1) HCV1 Forest areas containing globally, regionally or nationally significant concentrations of biodiversity values (e.g., endemism, endangered species, refugia). 2) HCV2 Forest areas containing globally, regionally or nationally significant large landscape level forests, contained within, or containing the management unit, where viable populations of most if not all naturally occurring species exist in natural patterns of distribution and abundance. 3) HCV3 Forest areas that are in or contain rare, threatened or endangered ecosystems. 4) HCV4 Forest areas that provide basic services of nature in critical situations (e.g. watershed protection, erosion control). 5) HCV5 Forest areas fundamental to meeting basic needs of local communities (e.g. subsistence, health). 6) HCV6 Forest areas critical to local communities' traditional cultural identity (areas of cultural, ecological, economic or religious significance identified in co-operation with such local communities) (Anon. 2001a). Having identified HCVs, the FSC approach then requires the forest manager to plan management in such a way as to maintain or enhance the identified HCVs and to put in place a monitoring programme to check that this is being achieved.

The HCVF concept is new and still under development. IKEA needs an internationally agreed, robust system for identification and management of HCVFs. Therefore, in a co-operation between WWF (World Wide Fund for Nature) and IKEA, a toolkit for identification and management of HCVFs is under development. The objective of the HCVF toolkit is to provide a practical methodology to be used at a national (or regional) level for defining HCVFs. The generic definition of HCVs contains terms, such as "significant" or "critical", which requires national or regional interpretation in order to define clearly local HCVFs. The toolkit guides this process by providing direction to utilising existing information pertaining to conservation values, and how to handle a lack of such information (Jennings 2002). In this context, the scientific community and governments should take the crucial challenge of further developing credible information and make it available to these processes.

For each of the six types of HCV (see above), the toolkit identifies a series of elements to be considered. For each element, the process is steered to decide what constitutes a HCV in a country or region. Once such national or regional HCVs have been defined, it is possible to evaluate a specific forest area for the presence of HCVs and to delineate these values. The toolkit also provides guidance for managing forests with HCVs to ensure that these values are maintained or enhanced.

In addition to guiding the implementation of IKEA's purchasing policy, the information on national HCVs and the process of evaluating forest areas can also be applied by forest managers looking to meet HCVF standards, certifiers assessing HCVFs and landscape planners prioritising various land uses. The toolkit was finalised in the autumn of 2003.

A four level staircase model

IKEA's long-term goal is to source all wood in the IKEA range from verified well-managed forests, i.e. forests that have been certified according to a forest management standard recognised by IKEA. To achieve its long-term goal, IKEA is implementing a four-level staircase model that gradually places higher demands on the wood used (Fig. 1). The four levels in the staircase model are described below and are applicable for solid wood, veneer, plywood and layer glued wood (below referred to as "wood").

Level 1 in the staircase model represents "start-up requirements" that all suppliers of wood to IKEA must fulfil before the start up of business with IKEA. At Level 1 the following demands have to be fulfilled. The origin of the wood has to be known. The supplier must be able to state from which region within a country the wood originates. The wood must not originate from intact natural forests unless independently verified as coming from well managed sources, i.e. forests certified according to a "Level 4 standard" recognised by IKEA (see below). The wood must not originate from regionally/nationally recognised and geographically identified high conservation value forests unless: 1) the wood is certified according to a Level 4 standard recognised by IKEA, 2) forest management prescriptions maintaining or enhancing the high conservation values have been produced in a balanced stakeholder process or 3) the area(s) with high conservation values have been set aside by the holder of the Forest Management Area (FMA).

Level 2 represents the minimum requirements that all suppliers to IKEA must fulfil. New suppliers to IKEA, not fulfilling the minimum requirements must have an action plan showing how compliance will be met within three months. At Level 2 it is stated that the wood must fulfil the following demands. The wood must be produced in compliance with national and regional forest legislation and other applicable laws. The wood must not originate from protected areas (national parks, nature reserves, forest reserves, etc.) unless independently verified as coming from well managed forests, i.e. forests certified according to a "Level 4 standard" recognised by IKEA or felled in accordance with management prescriptions for the protected area. The wood must not originate from plantations in the tropical and sub-tropical regions established after November 1994 by replacing intact natural forests, Forest Stew-

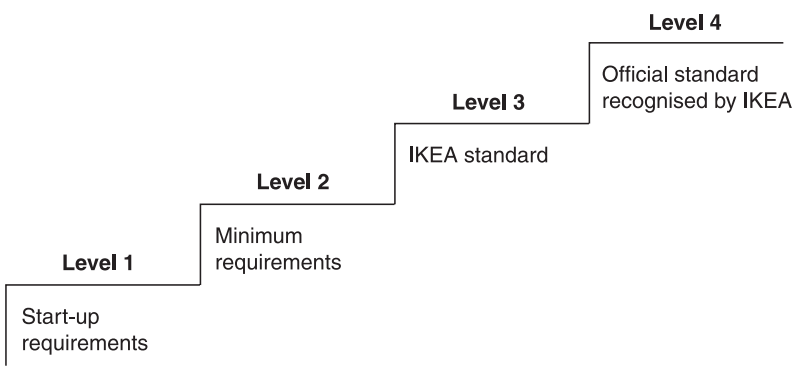


Fig. 1. The IKEA staircase model for wooden merchandise.

ardship Council's (FSC) requirement on plantation forests.

Level 3, called "4Wood", is a standard developed and maintained by IKEA. The forest management is audited against a standard including indicators that describe the transition from level 2 towards level 4. The indicators are adapted to the specific conditions in the different regions where the wood is produced. The standard covers wood procurement requirements for the IKEA supplier and forest management requirements for the forest product supplier i.e. forest owner, concessionaire or management organisation with responsibility for the forest activities within the forest management area. The purpose of "4Wood" is to introduce the concept of forest certification to forest product suppliers that currently are not ready to go for a Level 4 certification. However, when working with "4Wood", the forest product supplier should show continuous improvement towards a Level 4 certification.

Level 4 represents forests that are managed in accordance with an official standard for well-managed forests, such as one developed during the process of implementing of a forest certification scheme of some kind. The standard must include established performance levels co-operatively developed in consensus by a balanced group of environmental, economic and social stakeholders and verified by an independent third party. Currently, FSC is the only Level 4 standard recognised by IKEA. Furthermore, all high value tropical tree species with such a high economic value that they are frequently associated with thefts, smuggling and corruption (e.g., teak, meranti, rosewood, and mahogany) must be certified according to a Level 4 standard.

In order to trace all wood through the wood supply chain, IKEA has developed the Forest Tracing System (FTS). FTS is a questionnaire that all suppliers using wood for IKEA products have to answer. The questionnaire is a supplier assurance used to classify wood sources used by the supplier according to the staircase model. The information given by the suppliers through FTS is verified by audits of the wood supply chains. IKEA's own forest experts and third party auditors appointed by IKEA perform these audits.

Discussion

The customers expectations

Generally, there are very few questions from customers regarding the origin of the wood in IKEA products. Moreover, there is almost no demand or request for certification or wood from sustainable managed forests. It is easy to interpret this as a lack of customer care and awareness. This is however in most cases a questionable assumption. Customers expect international companies such as IKEA to handle forestry issues in a responsible way. It is expected that IKEA should know where the wood originates from, that their business should not contribute to further loss of intact natural forests, and that sustainable forestry methods should be promoted. If the customers perceive IKEA as not acting as a responsible corporate citizen, they may choose another home furnishing retailer. Furthermore, to attract and inspire co-workers it is important to act and be perceived as a responsible company.

Can you do good business while being good business?

An often-asked question is if it is possible to make traditional business objectives and social and environmental responsibility work together for the benefit of all stakeholders. The occurrence of measures to counteract the dominance of monetary thinking in relation to environmental issues suggest that the answer is no. On the other hand, the IKEA case study presented here suggests that monetary performance and business ethics can work very well together. In fact when done in a sensible way, social and environmental work is good for business. It is good business because the customers will feel that they are buying products from a company that shares their views and values. Moreover, it is good for business because it supports cost efficiency. Using resources and raw material efficiently, shortening the wood supply chains, saving energy, improving working conditions at the suppliers etc. will have a positive effect on the costs as well as product quality and will therefore support IKEA's business objectives. Thus, IKEA believes in close co-operation with its suppliers to develop their environmental and social performance as an investment for the future.

Increasing demand for wood and increasing demand for conservation

Most stakeholders would agree that there is an increasing demand for maintaining and enhancing the conservation values of forest ecosystems. Moreover, most stakeholders would also agree that it from an environmental point of view is good to use renewable resources as opposed to non-renewable. However, if done in the wrong way there is an obvious risk for conflicts between the use of renewable resources such as wood and protection of conservation values in forests. Hence, to provide society with wood products, while maintaining the values of the forest ecosystems, IKEA believes that it is necessary to: 1) increase forest plantations in order to reduce the exploitation pressure on the remaining natural forests and substitute planted trees for trees in natural forests, 2) restore ecosystem integrity in areas where the natural ecosystems have been lost and 3) stop unsustainable logging of intact natural forests and high conservation value forests.

According to McNeely (1994), the best way to maintain biodiversity and forest production in forest ecosystems is through a combination of strictly protected areas, multiple use areas managed by local people, natural forests extensively managed for sustainable yield of logs and other products and services, and forest plantations intensively managed for the wood products needed by society.

There is much debate if plantations will help protect natural forests and provide economic growth or harm the environment and cause social injustice (Cossalter and Pye-Smith 2003). In order to avoid this problem, high yielding plantations should be established in suitable areas while minimising negative social and environmental impact. Large-scale plantations of single tree species without respect to the features and values of the landscape are generally not acceptable from environmental and social points of view. Further research is needed to expand the concept of environmentally and socially adapted plantation forestry. New strategies for high yielding plantation forestry need to be explored. This might include a mixture of tree species on stand and/or forest management area level as well as restoration and conservation of natural forests in suitable areas. Moreover, other values and benefits of forests besides biodiversity and wood production, i.e. cultural values, recreational values and other social values, should also be considered. Furthermore, a focus on individual stands alone is inadequate. Both harvest and non-harvest values depend on interdependencies between stands. However, the forest ecosystem should not be seen as just aggregates of stands. The forest ecosystem functions in a way different from the sum of its parts and should be viewed as an aggregated set of structures embracing the stand, the watershed and the physiographic region (Toman and Ashton 1996). Consequently, when setting up strategies for high yielding plantation forestry, it is necessary to take multiple-scale aspects into account in the planning and evaluation process.

Furthermore, it is very important that the wood products from well-managed forestry can be produced at competitive costs. The average customer expects wooden products to be produced in a responsible way. IKEA wishes to provide all customers with such products, and not only cater to those who are willing and able to pay more. Consequently, the process of certification and other means of verifying sustainable forest management need to be cost efficient without loosing their performance in the field.

The phased approach of implementing sustainable forestry

The IKEA approach to trace the origin of the wood and to put higher demands on the wood used within the IKEA range, has been successful but not without challenges. The biggest challenges encountered so far has been to secure that the wood used within the range does not come from intact natural forests, high conservation value forests and from illegal logging. There are many reports identifying illegal logging as a serious problem (Newell and Lebedev 2000, Anon. 2001b, 2003, Brack et al. 2002). Illegal logging damage the environment, deprives the governments of revenues from taxes and fees and are in some countries strongly associated with violent conflicts (Kaimowitz 2002). Most IKEA suppliers buy wood on the market and thus lack direct control of the forest areas from where the wood is harvested. This in combination with the fact that the wood supply chains many times include sawmills and traders of sawn goods make the transparency and control of the wood flows difficult. By using certified wood, adopting and implementing adequate wood procurement policies, performing wood supply chain audits and by shortening the wood supply chains, i.e. by reducing the number of actors in the wood supply chain, it is possible to counteract these difficulties. Although business has an important role to play to counteract illegal logging it can only thrive on top of responsible government policies. National forest law, international agreements and their implementation are the fundaments on which protected areas, conservation strategies etc. must be built.

The development of credible, performance based, voluntary certification is unevenly distributed in the world. Consultative processes with stakeholders representing social, environmental and economic interests require financial resources, time and competence as well as committed people. Both the development of regional or national standards and certification procedures as such are often lengthy processes. Hence, for IKEA and also many other international buyers of wood products it is not possible to only buy products made of certified wood, i.e. FSC or equivalent. In many parts of the world where IKEA buys wood products there are no or few FSC-certified forests. IKEA's phased approach of implementing sustainable forestry makes it possible to gradually increase the amounts of certified wood and at the same time minimise the risk of using wood from intact natural forests, high conservation value forests and illegal sources. IKEA has found that having in-house competence in forestry and wood procurement is key when addressing and understanding the challenges above. Currently, IKEA has 15 full time professional foresters working on these issues.

Adaptive management and sustainable forest management

The transition from the classic forest sustainability concept focusing on wood as renewable resource, to ecological sustainability based on forest ecosystem management requires additional data collection to monitor status and trends, but also an extended and improved toolbox for analytic planning in several steps (Burton et al. 2003, Angelstam et al. 2004). In particular, a widening of the thematic range

of data and spatially explicit analytic tools are crucial for determining the relative use of protection, management and if necessary also restoration by rehabilitation and even re-creation of forests of different types. Hence, it is important that forest industry, social and environmental stakeholders in an atmosphere of mutual respect develop routines for dialogue and agreements on forest management.

We believe that the general lack of spatially explicit information about conservation values and features is a major obstacle for business to make rational decisions about protecting and maintaining environmental and social values. To provide credible information pertaining to forest conservation and restoration values available to processes where conservation values are addressed, evaluated and negotiated is therefore an important task for the scientific community and their funders.

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Biodiversity management in Swiss mountain forests

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In Switzerland, the forest area has been increasing since the 19th century and is growing at a rate of 0.4% yr^{-1}. Three factors explain this growth: the Federal Forest Law that requires all forest clearings to be counterbalanced by reforestation, the reduction of agricultural activities, and the decreasing demand for timber. From an area perspective, Swiss mountain forests have therefore been widely conserved and have one of the lowest proportions of endangered bird species in comparison with other ecosystems in the country.

Nevertheless, there are threats to biodiversity in mountain forests. Plantation forestry, insufficient timber harvest, free public access to all forests and high forest road densities facilitating recreational activities are some of the factors affecting mountain forest biodiversity. In particular this has had a negative impact on forest dwelling species, e.g. capercaillie *Tetrao urogallus*. In recent years, however, species dependent on old-growth structures have not been declining.

The national forest biodiversity conservation strategy is based on close-to-nature silviculture, conservation of important ecological objects, and forest reserves. The target is to establish forest reserves corresponding to ca 10% of the country's forest cover, including 5% of reserves without active management. Species-specific action plans, forest planning and forest certification are three other tools for forest biodiversity conservation in Swiss mountain forests. Recently, a principle of public consultations to be undertaken during local forest planning has been introduced, which promotes multi-functional forest use. The development of a new national forest policy programme was launched in 1999. The main conservation targets developed through this programme for 2015 are presented.

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While loss of forests and woodland has resulted in extirpation of species and reduced amount of natural forest structures, mountain forests constitute semi-natural remnants of ecosystems of paramount importance for the maintenance of forest biodiversity in central Europe. One example is Switzerland, which has undertaken concrete measures to succeed with its ambitions to sustain biodiversity in its mountain forests.

According to the second national forest survey (1993–1995), forests cover 1.2 millions of ha, i.e. about one third of the territory of Switzerland (Brassel and Brändli 1999). A comparison with the first survey established 10 yr earlier shows an increase of forest cover by 4% or even 7.6% if only the Swiss Alps are considered (Anon. 2002a). Comparing this to the mean annual increase in forest area observed in Europe (0.1% yr^{-1}), this value of 0.4% yr^{-1} is

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quite high, only a few other European countries having much higher rates (Anon. 1998). In Switzerland, increasing the forest area and standing volume, as well as enhancing the protective effect of forests, have been important general objectives from 1850 to ca 1970 (Schönenberger 2001a). The forest area expansion observed since the end of this period is not mostly due to reforestation, but rather to spontaneous growth (Küchli et al. 1999). This growth is the consequence of a reduction of agricultural activities at higher altitudes and of a decreasing demand for timber.

A milestone in the history of biodiversity conservation in Switzerland is the Federal Forest Law, which was first issued in 1876. This law and the revised texts that followed require that the forest area of Switzerland must not diminish and that all forest clearings have to be counterbalanced by reforestation. This principle was introduced in order to maintain the protective ecosystem services against inundations, soil erosion and avalanches, particularly of mountain forests in the Alps (i.e. forests situated above 800 m a.s.l.), and to counterbalance the continuous forest clearings and over-grazing by livestock that occurred until the 19th century. As underlined by McShane and McShane-Caluzi (1996), this Federal Law may be considered as one of the first major conservation regulations, resulting in the preservation of very large areas of mountain forests in Switzerland. As a consequence, since the beginning of the 20th century, Swiss mountain forests have been widely conserved by a very strict legislation and have, to a large extent, escaped one of the major factors affecting biodiversity, namely habitat destruction.

The aim of this paper is to review the status and trends in biodiversity management in the Swiss mountain forests focusing on 1) the factors influencing mountain forest biodiversity, 2) the current tools for biodiversity management in Swiss mountain forests, and 3) the work towards a new biodiversity management strategy.

Factors influencing mountain forest biodiversity

Mountain forest biodiversity is strongly influenced by the biogeographical characteristics of Switzerland. To cope with the complexity of their landscapes, Swiss forests can be divided into five regions: the Jura Mountains, Lower Alps, Alps and Southern Alps, and a lowland region called the Central Plateau, situated between the Jura and the Alps, where several large alpine lakes are found. Characteristic plant communities of these regions have been comprehensively described by Hegg et al. (1993). Globally, Norway spruce (*Picea abies*; 40% of stems), beech (*Fagus sylvatica*; 18%) and silver fir (*Abies alba*; 11%) are the three most frequent tree species in Swiss forests, spruce being the most abundant species in subalpine mountain forests.

Mountain forests comprise ca 80% of the total forest area in Switzerland and are considered to contain up to 50% of all living species identified in the country (Anon. 1998, homepage of the SAEFL 2003). Indeed, in comparison with other ecosystems found in the country, forests have one of the lowest proportions (22%) of endangered bird species, a fact that is nicely illustrated by recent ornithological data (Fig. 1). However, due to an overall low timber harvest over the last decades, nevertheless the species diversity is declining. One proposed mechanism is that denser canopies have lead to a reduction in the amount of light reaching the ground-level communities (Keller and Zbinden 2001, Schütz in press). It should not be overlooked that mountain forests often differ remarkably from lowland forests with respect to structure, dynamics, management and diversity of ecological processes. They also differ quite strongly in terms of impacts on biodiversity. However, the lowland forest biodiversity problems will not be described in this paper.

At high altitudes, forests near the tree line are characterised by an open patchwork of single trees, tree clusters and gaps varying in size (Schönenberger 2001a). Such zones are often poorly accessible, have not been utilised over the past decades and have an excellent conservation status. Brassel and Brändli (1999) indicate that 7.5% of the forest area, mostly mountain forests, are inaccessible or shrub-forest, and 23% have not been utilised over the last 30 yr. About 8.2% of the national forest area consists in mountain forests with a direct protective function. In such zones, forest dynamics are slow and the rate of regeneration declines with altitude (Schönenberger 2001a). Simultaneously, those forests are exposed to disturbances such as snow movements, storms and landslides, resulting in thrown and broken timber that is a source of structural diversity contributing to biodiversity (Duelli and Obrist 1999). Another source of structural diversity is the practice of cluster afforestation that is becoming increasingly common at higher altitudes (Schönenberger 2001b). The factors responsible for biodiversity impoverishment are summarised under the acronym of HIPPO (Primack 2000, Wilson 2002), i.e. Habitat degradation, Invasive species, Pollution, human Population and Overkill. Here, we will briefly consider these categories and how they are affecting mountain forest biodiversity in Switzerland.

Habitat degradation

In spite of the fact that no significant habitat destruction has been occurring in mountain forests, some degree of habitat modification and degradation has been reported as a consequence of forest management. The most commonly discussed issue is the modification of forest age-structure (low amount of old-growth forest), as a consequence of timber exploitation. However, a recent review of the status of all breeding-bird species shows that most species depending on structures of old-growth forests have not been declining over the last two decades, a fact that is most likely

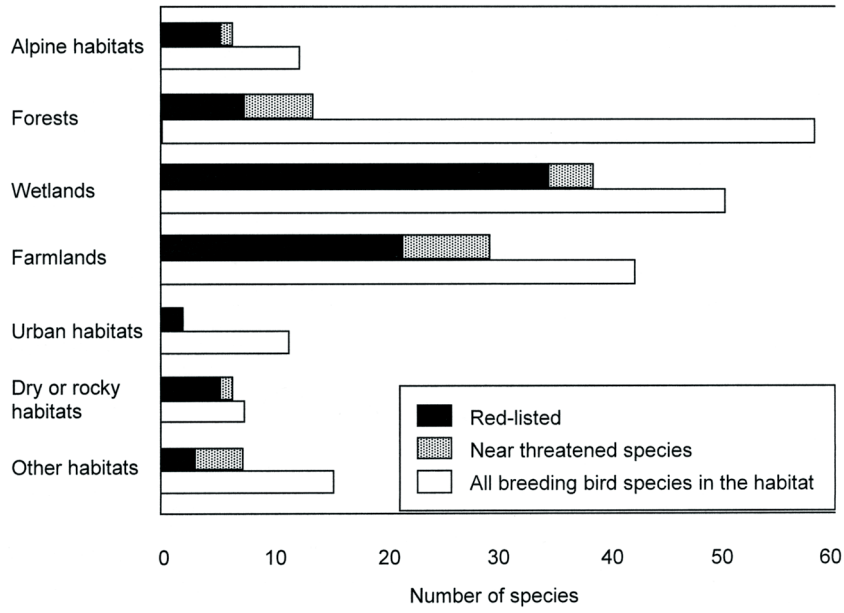


Fig. 1. Numbers of red-listed bird species in relation to the total number of breeding bird species in Switzerland, classified by habitat (after Keller and Zbinden 2001). Red-listed species include the IUCN categories EX (extinct), CR (critically endangered), EN (endangered) and VU (vulnerable). NT (near threatened) is normally included in red-lists but is in the graph indicated separately. This comparative analysis of breeding bird species diversity across habitat-types shows that forests have the lowest proportion of red-listed species in Switzerland.

related to the simultaneous increase of timber volume and absence of forest area reduction (Schmid et al. 1998). Another important factor is the modification of forest species composition (influence of forestry on community structure). Additionally, Swiss forests have to a certain degree been affected by plantations (Hegg et al. 1993). Especially at lower altitudes modifications of the forest community structure is considerable. A third factor is habitat fragmentation, expressed by the number of isolated forest areas, and by the growing density of forest roads. A high forest road density induces increased perturbation as, on one hand, roads contribute to secondary fragmentation effects and, on second hand, they introduce disturbances into the habitats by facilitating human penetration (Soulé et al. 1992, Neet 1995). According to Brassel and Brändli (1999), between 1985 and 1995, 1714 km of forest roads were built in Swiss mountain forests. An example of the effects of habitat fragmentation is given by the work of Estoppey (2001a, b), who suggests that high forest-road densities have contributed indirectly to the decline of the woodcock *Scolopax rusticola*. Another factor is the increasing browsing pressure resulting from high ungulate densities observed in several regions of Switzerland, although the effects of browsing pressure on mountain forest biodiversity remain unclear at present (Anon. 1996a). The latter point is currently gaining attention, especially in the one and only Swiss National Park, where a long-term research programme has been launched to examine this question. So far, even with the extremely high densities of red deer *Cervus elaphus* observed in the Park (> 10 individuals km^{-2}), no significant ecological perturbations could be documented (Haller 2002). Nevertheless, it is beyond controversy that exceeding browsing affects the regeneration and thus the genetical diversity of many tree species, e.g. silver fir and juniper *Juniperus communis*. In addition to these examples, it should be underlined that several forms of direct and indirect impacts of forest management will remain unnoticed until properly investigated. This point is illustrated by the negative impact of forest management on some endangered species, such as the lichen *Lobaria pulmonaria* (Zoller et al. 1999).

Invasive species

Invasive species are a growing problem in Switzerland, as shown by currently available reviews on non-native terrestrial vertebrates (Neet 1999) and invasive plant species (Weber 2000). However, as underlined by Weber (2000), most alien plant species occur on man-made and heavily disturbed sites such as ruderal areas. Nevertheless, at least 55 alien plant species have been found in forests, forest edges and shrub, including some invasive species such as *Heracleum mantegazzianum, Prunus serotina, Reynoutria japonica, Robinia pseudacacia, Solidago altissima* and *S. gigantea.* In mountain forests, this problem remains marginal at present.

Pollution

The impact of air pollution on forests has been a very controversial issue during the 1980s in Switzerland. The number of trees showing a crown thinning level > 25% has increased since 1985 (Anon. 2002b), most probably as a result of accumulating environmental stress factors, which

primarily are man-made. Anthropogenic effects include, among others, excessive nutrient input and acid deposition, which affect forest soil quality and lead to changes in species composition. Between 1986 and 1990, the levels of acid deposition in forest soil exceeded the critical loads at 63% of the sites. In Alpine lakes, the corresponding figure was 100% (Anon. 1994). Between 1993 and 1995, the critical loads for nitrogen were exceeded at ca 70% of the sites in nitrogen-sensitive, near-natural ecosystems and at ca 90% of the forest sites (Anon. 1996b). Further studies are needed to assess the impact of pollution on mountain forest biodiversity.

Population

Another key principle of Swiss forest regulations is the free access to forests that is guaranteed to any citizen. Recreational activities in mountain forests are quite common and are currently growing in intensity and diversity (Bernasconi and Zahnd 1998). The damages these activities may cause to forest ecosystems are currently studied by several research groups in Switzerland. Recreation and tourism affect some forest-dwelling species, e.g. for capercaillie *Tetrao urogallus* (Dändliker et al. 1996, Sachot et al. 2003, Suchant and Braunisch 2004), in particular during the winter and breeding seasons. A priority project was carried out by the Swiss Agency for the Environment, Forests and Landscape (SAEFL) regarding fashionable outdoor sports. A study about the effects by hang-gliders on chamois *Rupicapra rupicapra* showed that disturbance caused chamois to take flight, avoid important grazing areas and, after some time, confine themselves increasingly to woodland areas (Anon. 1996c). Within the framework of the Alpine Convention, the tourism protocol represents the first steps towards international co-operation to handle the impacts of recreation and tourism in mountain ecosystems.

Overkill

Mainly as a consequence of overkill, several species had been completely eliminated by the end of the 19th century. Ungulate species, in particular red deer, ibex *Capra ibex* and roe deer *Capreolus capreolus* (Hausser 1995, Anon. 1996a), large carnivores such as brown bear *Ursus arctos*, wolf *Canis lupus*, Eurasian lynx *Lynx lynx* (Breitenmoser 1998) as well as the lammergeier *Gypaetus barbatus* (Tucker and Heath 1994, Arlettaz 1996) are examples of species that were extirpated. The severe hunting restrictions introduced in 1875, when the first Federal Hunting Law was proclaimed, helped red deer and roe deer to re-colonise during the 20th century. An ibex reintroduction programme started in 1913 and was continued until the 1950s. The reintroduction of lynx and lammergeier started in the 1970s, while the first wolves immigrated in the south-western Alps in the early 1990s. Today, overkill should no longer be considered as an important factor affecting species diversity in Swiss mountain forests. However, in the case of some rare butterfly and plant species, as well as for large predators, several species are still at risk as a consequence of poaching and illegal harvest.

Current tools for biodiversity management in Swiss mountain forests

From 1986 onwards, the first Federal Law on Environmental Protection and the subsequent federal regulations on nature conservation have promoted increased environmental concern of official conservation agencies. Examples of appearing strategies range from land-use planning to various economic activities in almost every domain. For forest biodiversity, a strategy based on three instruments has been adopted by the SAEFL:

1) Close-to-nature silviculture. This hitherto is a set of principles, in the form of a simple list, applicable to forest management in order to emulate a more natural structure. The principles are quite straightforward but unfortunately neither defined as quantitative criteria nor as legal principles. However, most forest managers in Switzerland feel comfortable with this concept and apply the principles, especially in mountain forests. As an element of the coming new "Swiss National Forest Programme", these principles will be substantiated in form of easily applicable criteria and indicators, and anchored in the forest law.

2) Important ecological objects. This concept actually refers to inventories of sharply defined microhabitats or biotopes found within forests. The system of important ecological object inventories has been developed in detail locally, but is still far from being used as a standard tool by a majority of forest managers.

3) Forest reserves. Two types of reserves are distinguished – 1) "Natural reserves" where no management occurs and forests are left to their natural evolution and 2) "Managed reserves", where the forest management plan is designed to focus on conservation goals. The first reserve type is achieved by contracts between forest agencies and forest owners, for a minimum period of 50 yr. In managed reserves, specific action plans are defined and, according to the habitat management goals, may lead to considerable forest management activities. Currently, there are ca 20 reserves > 200 ha in size within a total of ca 330 reserves covering roughly 1.8% of the national territory (homepage of the SAEFL 2003). These figures are expected to grow continuously over the next decade. An example of a forest reserve plan, including a biodiversity monitoring scheme designed to measure the consequences of a local network of forest reserves on plant, insect and bird communities, is described by Neet et al. (2003).

At present time, the Swiss forest biodiversity strategy is characterised by a wide but noncommittal use of the concept of close-to-nature silviculture and a focus on forest reserve projects, which are often controversial issues. The establishment of forest reserves is actually the only tool for which targets have been set at a national scale, i.e. to establish forest reserves over 10% of the country's forest cover, including 5% of nature reserves (Anon. 2002b).

In addition to these instruments, three other biodiversity management tools deserve to be mentioned here: species-specific action plans, forest planning and forest certification. Other federal laws that apply to forest ecosystems, in particular the Federal Law on the Protection of Nature and Cultural Heritage and the Hunting Law, that includes the conservation of most mammals, large carnivores and all bird species, also deserve a mention since they are meant to safeguard the diversity of indigenous species and biotopes. Being committed to the conservation and sustainable use of forest biodiversity as a part of the Convention on Biological Diversity ratified in Rio in 1992, Switzerland is also involved in the implementation of tasks such as the promotion of rare tree species, the establishment of oak forests and in EUROGEN (European Network for Forest Genetics; see homepage of the SAEFL, 2003).

Species-based conservation strategies

For many years and particularly before the rise of the environmental legislation during the 1980s and 1990s, the only significant actions undertaken to preserve mountain forest biodiversity were species-based actions. Some have been carried out as individual initiatives, by conservationists or foresters, while other actions reached a status that may be compared with national action plans.

Among the first initiatives, one may mention the considerable work undertaken by many ornithologists and a fair number of foresters to survey cavities of cavity-nesting birds and to promote the conservation of several species of woodpeckers (Picidae) and owls (Strigiformes). In many cases, ecological field and conservation studies were undertaken in order to improve the understanding of key-features of forest management that may help the conservation of endangered species. Among numerous examples (see Schmid et al. 1998 for a review), the works carried out on mountain forest species such as the black woodpecker *Dryocopus martius* by Blume (1996), the three-toed woodpecker *Picoides tridactylus* by Voser et al. (1992), Derleth et al. (2000), Bütler (2003) and Bütler et al. (2004) and Tengmalm's owl *Aegolius funereus* by Ravussin et al. (1994) illustrate the efforts undertaken in Switzerland.

An example of a national effort is the one undertaken for capercaillie conservation. The Swiss ornithological field station, on behalf of the Swiss Agency for Environment, Forest and Landscape, promoted a nationwide cooperation that included several national surveys and inventories (Marti 1986, Mollet et al. 2003), research programs on the conservation biology of the species (e.g. Dändliker et al. 1996, Sachot et al. 2002, 2003), and also resulted in official guidelines for wildlife managers and foresters (Anon. 2001a, b, c).

Currently, the steering committee that coordinates capercaillie conservation is planning to publish a national capercaillie conservation plan. It is likely that this plan will be based on the quite abundant literature published on the subject of capercaillie in Europe, as several quantitative habitat quality criteria have been proposed by conservation biologists (e.g., Storch 2000, Suchant and Braunisch 2004). Table 1 gives an example of such criteria for the case of the sympatric populations of capercaillie and hazel

Table 1. Forest habitat management criteria for sympatric populations of capercaillie *Tetrao urogallus* and hazel grouse *Bonasa bonasia* in the Jura mountains (after Sachot et al. 2003).

General criteria for sympatric populations	**Target**
Develop a mosaic distribution of habitat types, the hazel grouse habitats being included in a general matrix of capercaillie habitat	A patchy distribution of young regeneration stages within an old successional matrix, created by group-cutting of mature trees
Avoid selective cutting	Reduce the strong and widespread regeneration by beech *Fagus sylvatica*
Capercaillie habitat criteria	
Canopy and undercanopy covers	Maintain ca 30%, with a proportion of fir *Abies alba* exceeding 3% cover
Understorey cover	Keep at a low 20%
Forest structure	0.02–0.1 ha gaps in forest cover
Hazel grouse habitat criteria	
Regeneration stages	High and diversified understorey cover, close to 50%
Species composition	Keep rowan *Sorbus aucuparia* and willow *Salix* sp.
Forest structure	Maintain small groups of spruce *Picea abies*

grouse found in the Jura Mountains, in an area where forestry may play a fundamental role in maintaining habitat structures needed to improve the viability of both species.

Forest planning

Although forest planning has been practiced in Swiss forestry for decades, it has evolved to become a central issue since the Federal Forest legislation introduced the principle of public consultations to be undertaken during local forest planning. In other words, forest planning is widening its scope and will, in the future, also be a tool to help including views and opinions of all stakeholders concerned by forest management issues. Currently, biodiversity conservation is one key-objective included in such consultations and forest planning now clearly appears as an important tool to promote the implementation of biodiversity conservation measures in forestry practices (Huber and Chrétien 1997)

Another key issue in Swiss mountain forest planning is multi-functional forest use. This principle is widely accepted in Swiss forestry and is assumed to be the only effective way to meet the widening demands of society, that include social, recreational, and tourism-related aspects, as well as timber production, protective functions against soil erosion and avalanches and, as mentioned above, biodiversity conservation. These demands are strongly triggering the evolution of forest policy and practical forestry, and explain the considerable attention devoted to forest planning in Switzerland.

An important management component related to forest planning is monitoring. This requires data on the state of forests to interpret forest development as well as ways to assess key risk factors for future planning. The pilot project on biodiversity monitoring in Switzerland tracks the development of natural diversity in Switzerland over the long term, using a set of carefully selected indicators (Hintermann et al. 2002). Data regarding some of the indicators are collected by field workers, but most are calculated on the basis of third-party data from sources such as the Swiss Statistical Agency. At present, 32 indicators are considered for implementation, of which only a subset is currently measured. The planned forest indicators include: 1) change in the proportion of woodland featuring non-indigenous tree species (exotics) or dominated by such species (> 60% exotics), 2) size of young woodland with artificial regeneration, 3) area of woodland used for special purposes, e.g. coppice forest, chestnut *Castanea sativa* forest and unmanaged forest with no human intervention for at least 50 yr.

Forest certification

Since 1993, when the Forest Stewardship Council (FSC) was founded, the two certification labels available in Switzerland, i.e. FSC and Q-Swiss (for Swiss Quality), have been constantly growing in importance. Between 1998 and 2001, ca 65 000 ha of forest have been certified and in some cantons the double certification system is being endorsed by representatives of both public and private forest owners (Anon. 2002a).

The Q-Swiss and FSC labels are both based on criteria that focus on economical viability, environmental friendliness and forest ecosystem functioning, as well as on social responsibility of forest exploitations. However, while the FSC focuses on environmental and social criteria with international references, Q-Swiss also certifies the Swiss origin and is entrusted to the "Q-label Wood" certification agency, itself related to the Pan-European Forest Certification (PEFC), an umbrella organisation responsible for the creation of national certification systems (Anon. 2002b). The aim of PEFC is to offer long-term assurance that the certified wood origins from sustainable managed forests in which sound conservation is practised.

It is now becoming clear that customers are aware of the significance of such labels and start paying attention to certification. Most forest owners also consider certification to be important for their income and appear to be willing to certify their forests or companies. However, some difficulties have arised due to a certain level of confusion regarding the origin of certified timber sold on the market.

Towards a new biodiversity management strategy

In 1999, after the Swiss National Constitution was modified, the Federal forest authorities launched a programme aiming at the definition of a new forest policy, the Swiss National Forest Programme. This programme currently defines objectives and measures in several focus areas. A vision for the forest of 2015 will represent the synthesis of these objectives and this will become the basis for an entirely revised Federal Forest Law. At the time of this writing, this important process is still under way. However, we will report some of the main points of a preliminary report of one of the committees, with recommendations concerning the conservation of forest biodiversity. These points are formulated as targets for 2015 and are largely applicable to mountain forest biodiversity (Table 2). The implementation of these targets will not start before 2007, when the Federal Forest Law is planned to be modified.

Conclusion

From a European perspective, mountain forests belong to the landscape types that still are in a semi-natural condition. Therefore, they are important for biodiversity, natural resource production and ecosystem services. The future of these mountain forests will depend on carefully planned

Table 2. Overview of biodiversity indicators and targets of the Swiss National Forest Programme (adapted from the preliminary report, Swiss National Forest Programme 2003).

Forest ecosystem indicators	**Targets (2015)**
Conifer abundance in young forest stages	No increase (specific criteria need to be defined)
Amount of dead wood	Minimum: 2.5% in all forests situated outside forest reserves
Abundance of standing dead trunks	Minima: Plateau: 1.5% Jura mountains and lower Alps: 2% Alps: 5%
Surface of natural forest reserves	25 000 ha
Surface and distribution of natural forest reserves	Minimum: 15 reserves > 500 ha, evenly distributed over the 5 biogeographical regions
Endangered species indicators	
Increase of formerly abundant species	50% of species are increasing again, the other 50% have stabilized (no more declines)
Number of red-listed species (according to IUCN criteria)	Less than ca 10% of the species
Young mixed forests with > 40% of oak stems	Increase to ca 3000 ha
Abundance of rare and ecologically important tree species	According to regional and specific criteria
Abundance and area of forests actively managed to promote biodiversity	According to regional and specific criteria

multi-functional use, as new priorities such as recreation, conservation of biodiversity and protection against natural hazards grow in importance beside timber production. We believe that some of the models developed in Switzerland and briefly presented in this paper may contribute to a sustainable future of mountain forest management.

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Management for forest biodiversity in Austria – the view of a local forest enterprise

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Compared with most lowland forests, sustainable forest management in Austria's mountain forests involves a wider range of management issues. Using a forest management unit in the Montafon valley, western Austria, as an example, we describe how the maintenance of biodiversity as well as multipurpose functions of the forests under fragile ecological conditions is dealt with.
Long-term sustainability is both formulated by national policies and demanded by the local society. However, due to increased competition foresters are forced to fulfil short-term goals neglecting long-term sustainability. Both market and public goods have to be produced but without any appropriate policy to cover the costs of public goods. Long-term sustainability requires that the major part of the forest land is managed using methods that are accounting for the environment, biodiversity, and timber yield at the same time. For this, specific guidelines and target values are needed. In order to be accepted by practitioners and the general public, these guidelines and target values have to be defined in co-operation with foresters and nature conservationists. Further, maintenance as well as restoration of biodiversity has to become an integral part of forest management planning. To conclude, an applicable and cost-effective forest planning methodology is needed.

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Based on the public concern for biodiversity at the international political level, several processes have led to the development of hierarchical standards for sustainable forest management (SFM) (sensu Rametsteiner and Mayer 2004) as well as for biodiversity (e.g. Spellerberg and Sawyer 1996). A standard is defined as a set of principles, criteria and indicators that serve as tools to promote a desired development. Today, both national and international policies include the maintenance of biodiversity as an objective for land management. However, it is one thing to formulate these policies at the national level and another to implement them at the local level (Rametsteiner and Mayer 2004, Angelstam et al. 2004).

The aim of this paper is to describe the history and present state of forests in Austria and to provide the perspective on forest biodiversity management from a communal forest enterprise with a complex set of management objectives. Ongoing international, national as well as regional processes are outlined and interest conflicts discussed.

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The Austrian forests

Austria is covered by 3.9 million ha of forest, representing 47% of the country's surface area. A total of 169 000 small forest owners (99% of all owners) manage 48% of the forested area in units averaging < 200 ha (Anon. 2000a). The remaining 1% of the forest owners manage 52% of the Austrian forest (Anon. 2000a). The state owned forests cover 16% of the forest area (Anon. 2000a). Because of the complex ownership situation, the forest is managed mostly at a small scale.

In Austria, the concept of sustainability in forestry was defined by G. L. Hartig almost 200 yr ago, stating that future generations have to benefit of at least the same advantages from the forest as the present generation (Bobek et al. 1994). This was later also determined in the Empire's Forest Act of 1852 where the different functions of the forest from fire wood to the protection of human infrastructure had to be guaranteed. Because of the important protective function of the forest, already in that time people used the forest in a wise and sustainable way, not only in the amount of timber taken out but also in the size of the area cut (Bobek et al. 1994).

In the Alps, the term "mountain forest" generally refers to forests between 600 and 800 m a.s.l. and the tree line at 1600–2400 m a.s.l. (Mayer and Ott 1991). The main difference between mountain forests and other forests is the challenge to the forest owner, who is expected to produce both market goods (e.g. timber and game) as well as public goods and services (e.g. protection against natural hazards) and to maintain biological diversity (Glück 2002). Further, mountain forest management and forest utilisation differ from management schemes applied elsewhere mainly with respect to the long temporal sequences of vegetative succession, the remoteness of the forests and their limited accessibility (Kräuchi et al. 2000). People living or staying in mountainous areas primarily expect safety from a mountain forest.

According to the current forest policy the Austrian forest has to fulfil four functions in a sustainable way: 1) Benefit: economically sustainable timber production. 2) Protection: protection of the sites themselves and, at the same time, of the settlements and human infrastructures below these sites against natural forces. 3) Welfare: protection of environmental goods, e.g. drinking water. 4) Recreation. Furthermore, the importance of the forest as a habitat for the fauna and the flora has been introduced into the law (Anon. 2002a). Beside this, the Austrian forest is divided into four management systems: 1) commercial forest, 2) commercial forest with direct protective function (object protection; special regulations because of their purpose to protect villages as well as human infrastructure), 3) commercial forest with indirect protective function (site protection; special regulations because of their ecological sensitivity, protecting the site against erosion) and 4) protective forest (ban forest; Bannwald in German; i.e. forests which have an official status as providing protection against natural hazards). For the ban forest, public interest is considered more important than the disadvantages that the "ban" represents for forest management. The protection function of the forests is mainly linked to natural hazards in mountainous terrain. This is why the amount of protection forests in the mountainous province of Vorarlberg and the forests managed by the enterprise Stand Montafon-Forstfonds, which are located in an alpine valley (Fig. 1), are much higher than in the whole of Austria (see Table 1). Here, the term "protection forest" includes forest with direct and indirect protective function as well as protective forest. In Austria as a whole, there are large amounts of lowland forest, whereas such forests are much less common in the province of Vorarlberg and almost non-existent in the Montafon valley.

Despite the progressive development of sustainability in Austria, mountain forests in the European Alps have been exploited commercially for timber at unsustainable rates and on large spatial scales to fulfil societal needs for resources with deleterious effects including erosion and the disruption of slope stability (Kräuchi et al. 2000). Humans have been using the forest in a variety of ways, from large-scale clearings for mining, to the local collection of firewood and fodder as well as for grazing areas on forest pastures. Approximately 20% of the forested area in Austria consists of forests with direct or indirect protective function. Because of various factors such as over-harvesting, intensive browsing by wild ungulates and long-standing grazing by livestock, three quarters of all the protection

Table 1. Comparison of amount of forest management systems in Austria, the province of Vorarlberg and forest enterprise Stand Montafon-Forstfonds. The term protection forest corresponds to all three classes of protection forest (data sources: Anon. 1998b, 1990b).

	Austria	Vorarlberg	Stand Montafon-Forstfonds
Total forested area (ha)	3 900 000	94 000	6700
Commercial forest (%)	75.7	54.9	7.5
Protection forest (%)	19.3	42.7	89.3
Other forested areas (%)	2.6	2.4	3.2
Coppice forest (%)	2.4	0	0

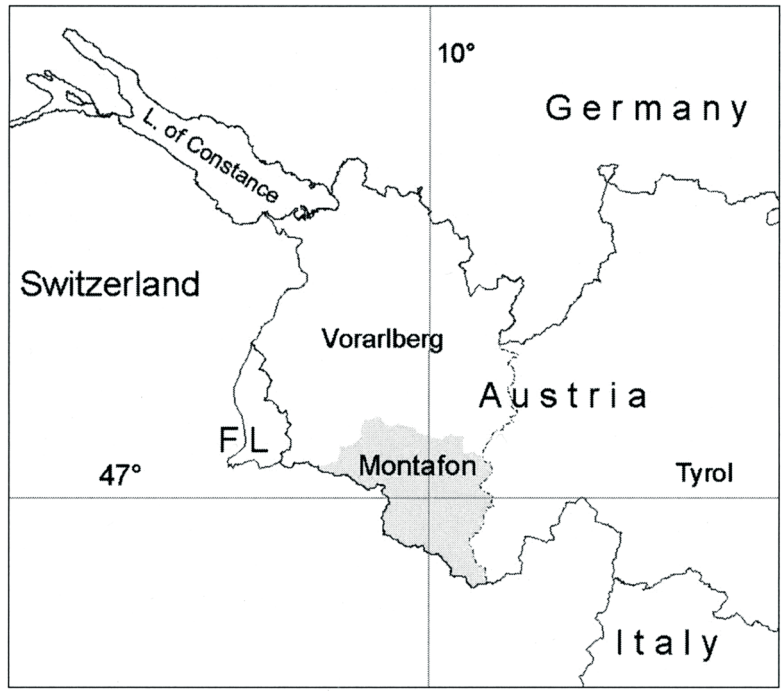


Fig. 1. Map of western Austria showing the location of the province of Vorarlberg and the Montafon valley. FL= principality of Liechtenstein.

forests are in the need of restoration (Anon. 1998b). The plan for the restoration of mountain forests is formally derived from the Forest Act from 1975 and from the forest development plan (Anon. 2002a).

Monitoring of forest biodiversity in Austria

By signing both Resolution S-2 on the "Conservation of forest genetic resources" of the first Ministerial Conference on the Conservation of Forests in Europe in Strasbourg (Anon. 1990a) and Resolution H-2 "General guideline for the conservation of the biodiversity of European forests" on the occasion of the second Ministerial Conference, Helsinki (Anon. 1993), Austria has committed itself to promote measures for the conservation of forest biodiversity. Within the Council of Europe, Austria contributed to establish the "Pan-European Biological and Landscape Diversity Strategy" (Anon. 1996), which was adopted in Sofia in 1995.

To manage a forest in a sustainable way the state has to be measured. The first large-scale, nation-wide forest inventory was carried out in 1952–1956 with the aim to get a representative picture of the Austrian forests regarding age classes, tree species composition, site types, and growing stock (Braun 1983). Because only a limited number of sampling plots can be measured (11 000 permanent plots, evenly distributed over the country), the grid of this inventory is rather coarse and only allows the interpretation of data at a large spatial scale, e.g. for Austria and its provinces. Already a few years later a new, more concrete concept was developed into the Austrian forest inventory 1961–1970 (Anon. 1974a, b). In the beginning (1961–1970, 1971–1980), the emphasis of the inventory was put on the survey of growing stock and increment aiming at sustained yield. With the introduction of remote sensing and field studies a complete cover of all major habitat types has now been collected. Due to the assessment of a systematic grid sample of permanent survey plots from 1981 onwards, the inventory changed to a more complex monitoring system of many aspects of the ecosystem. With the current inventory (2000–2002), special emphasis is put on the assessment of biodiversity including the genetic, species, and structural levels (Anon. 2002c).

Since the early 1990s the terms biodiversity and sustainability have been influencing the contents of forest inventories in Austria. A sign of recent developments in the ecological thinking was the change of the name for the national forest inventory from "Forstinventur" to "Waldinventur" in 1991. Whereas the German term "Forst" is associated rather with a man-made forest, the term "Wald" refers more to the ecosystem as a whole (Anon. 1994). Consequently the inventories are developing further, including new variables such as natural regeneration, near-natural management techniques, volume and structure of dead lying and standing wood, tree and shrub species and the potential and actual natural woodland community (Anon. 1998a).

From 1992 to 1997 the research project "The hemeroby of Austrian forest ecosystems" (Grabherr et al. 1998)

was carried out. In this study the hemeroby (i.e. degree of anthropogenic influence) of the forest ecosystems was determined on the basis of criteria of vegetation science and stand structure on an interdisciplinary basis in co-operation between forest and vegetation scientists. It turned out that the human impact over the past centuries had transformed most of the forests into a cultural landscape. Today, only 3% of the total forest area can be classified as natural (without any human impact), 22% as semi-natural, 41% as moderately altered, 27% as altered, and 7% as artificial (Grabherr et al. 1998). However, the percentages of semi-natural and moderately altered forest areas vary greatly among the Austrian provinces. For example, in the westernmost province Vorarlberg, the long-standing tradition of nature-adjusted wood harvesting on a small area resulted in a large amount of semi-natural forest, while provinces with a high proportion of easily accessible forest areas and mixed forests (e.g. the eastern provinces Styria, Upper and Lower Austria) have a high proportion in forest areas described as unnatural or artificial (Grabherr et al. 1997).

By signing the resolution of Helsinki (Anon. 1993), Austria is bound to establish a representative network of natural forest reserves. The overall objective of the Natural Forest Reserve Programme, launched in 1995, is to establish a network of reserves which is representative of all forest plant communities of the country's forests (Anon. 2002c). In Austria, natural forest reserves have been established since 1965 (Frank 1998). Up to now, 180 reserves covering an area of 8300 ha (0.2% of the forested area) have been established on a voluntary basis by means of contracts between the Government of Austria and forest owners (Anon. 2002b).

Stand Montafon-Forstfonds

Montafon is located in the southern part of Vorarlberg, (47°08′–46°50′N, 09°41′–10°09′E; Fig. 1). The valley consists of 10 municipalities with a total population of 18 000 inhabitants. The main source of income is winter tourism. As an alpine valley its altitude ranges from 600 m in the valley floor up to over 3000 m. The Montafon covers ca 560 km^2 of which 50% are alpine meadows, 23% forests, 20% alpine habitat above the tree-line, and 7% agricultural and urban land. The tree-line is at ca 1800 m a.s.l. and the total forest cover is 15 000 ha. Thirty-three percent of the forested area is steeper than 45°. About 50% of the Montafon forests are managed by the forest enterprise Stand Montafon-Forstfonds. With 8461 ha, Stand Montafon-Forstfonds is the largest forest enterprise in the province.

On the valley bottom and up to 1000 m a.s.l. the forest is dominated by deciduous (beech *Fagus silvatica,* maple *Acer pseudoplatanus,* lime *Tilia cordata,* ash *Fraxinus excelsior*, and others) and mixed forests (Norway spruce *Picea abies*, beech, and silver fir *Abies alba*). Spruce forests predominate above 1000 m, though the mixed forests reach up to 1500 m a.s.l. Larch *Larix decidua* and stone pine *Pinus cembra* can be found only in fragments close to the tree-line. The distribution of forest types is mainly determined by altitude. Because uneven-aged forests predominate, tree distribution, stem density, tree height and basal area vary strongly among forest stands. As is typical for mountain forests such varied forest stands form a patchy mosaic-like structure.

In the Montafon, the forests provide essential protection for villages and infrastructural facilities against avalanches, rockfall, landslides and debris flows but also serve for timber production and play an important role for tourism and recreation as well as landscape and nature conservation. Because forests have always been an important resource for the local inhabitants, the main objectives of Stand Montafon-Forstfonds are 1) the preservation of the forest for protection of the villages and infrastructural facilities under the maintenance of its uniqueness and its ecological variety, 2) the sustainable production of raw wood materials from the area, whether being used to cover commoners rights or for biomass-heating in the valley and 3) the forest management should follow natural processes using only small-scale intervention. By using the local resource timber, transport is minimised and local employment is promoted.

In order to ensure the ability of the forests to fulfil the expected functions, they have to be managed in a multifunctional sustainable way, which is regarded as cost-effective in the long-term. Together with this emphasis on sustainability, Stand Montafon-Forstfonds tries to use the forests in a way which follows natural processes. It is particularly important not to work against the natural stand development but to exploit it for silvicultural objectives. That means e.g. to cut small strips (width from one third up to one tree length) with long edge-lines or group fellings to imitate natural disturbance regimes like wind-throw and snow-breakdown. But at the same time the silvicultural strategy needs to address the economic and technical requirements as well. Cable crane systems are suitable for selective logging in steep terrain. Stand Montafon-Forstfonds is therefore specialised in mountain forest silviculture. Harvesting is carried out by means of cable cranes, in order to protect forest soil and the remaining trees. If one can rely on an existing forest road infrastructure mobile cable crane systems can be set up quickly and thus are economical even when only relatively few trees need to be felled. Only helicopter logging would offer greater flexibility but is in most cases too expensive. According to the principles promoted by Pro Silva (Anon. 2003) this close-to-nature silviculture is thought to reduce ecological and economic risks in the long term.

In the Montafon, a calculation of the costs of close-to-nature silviculture compared with clear-cutting shows increased marginal costs for close-to-nature silviculture of € 10 m^{-3} (Table 2). However, these costs are more than

Table 2. Example for the cost calculation of close-to-nature silviculture compared with clear-cutting. Assumptions: cable crane line with a length of 500 m in an oblique angle to the slope and an intervention width of 40 m (equals 2 ha) in mountainous terrain and an assumed standing crop of 400 m^3 ha^{-1} (source: Anon. 2000b).

	Close to nature silviculture (small-scale intervention)	Area-extensive utilisation (clear cut < 2 ha)
Intervention intensity (harvested volume m^{-1} cable crane line)	0.5 m^3	>1.6 m^3
Corresponding intervention area	0.6 ha	2 ha
Logging costs	€ 35 m^{-3}	€ 25 m^{-3}
Re-forestation costs including tending for minimum of 5 yr	not necessary because natural regeneration is promoted by the measure	re-forestation: 2500 seedlings ha^{-1} á € 2 tending: á € 400 ha^{-1} and yr
Long-term costs (logging costs plus additional costs)	€ 35 m^{-3}	€ 42.5 m^{-3}

compensated if we take into account the additional costs of € 17.5 ha^{-1} for re-forestation and tending after clear-cutting.

However, timber production alone is not enough to secure the various forest functions. As a result the cost-intensive management of mountain forests is in question. The active consumers (e.g. sawmills) are not under pressure from their clients to demand and order timber from sustainably managed forests. The indirect consumers (the society) regard the mountain forests highly but are less willing to pay for them. To overcome these economic difficulties first steps were made to make other beneficiaries, such as the tourism industry, to pay for forest protection services they receive.

Biodiversity and protective function

According to Grabherr et al. (1998), the larger part of the forest in Montafon is natural or near-natural. This is mostly due to the topography and remoteness, and have been set aside from harvesting. There, higher age classes, large amounts of dead wood in different qualities, diverse vertical and horizontal layering as well as ongoing natural disturbance regimes (e.g. bark beetle infestations, wind throws, rock falls, avalanches) are common. Because they usually comprise the last ecologically more or less intact biosphere reserves, mountain forests are highly appreciated by conservationists (Glück 2002). Austria, and especially its mountain areas, is fortunate as a long history of protection forest and the inaccessibility of some areas have helped to maintain biological values. The question is only for how long. The results of the Austrian forest inventory indicate a bad condition of the protection forest. Regarding their function, about one third of the protection forests are extremely unstable due to over-aged stands, missing regeneration or poor tree species diversity and need to be restored (Anon. 1998a). We have to find ways how to manage for forest biodiversity whilst also managing for the other forest functions.

Multifunctional forest inventory

Multifunctional forest management is a challenge for the local forest enterprise. A diverse forest is not only more stable but also less prone to exogenous disturbances. If one aims at a multifunctional forest, one has to set up an adequate tool to monitor functionality. It is the task of the forest planner to coordinate the variety of demands of the forest users in accordance to a long-term fulfilment of the forest functions. Today, it is important not only to measure quantitative (e.g. increment, number of stems etc.) but also qualitative elements (e.g. structural diversity) and to observe changes over time. Permanent survey plots in forest inventories open new possibilities for long-term monitoring (Bobek et al. 1994).

In 2002, Stand Montafon-Forstfonds conducted a multifunctional forest inventory (Maier and Breuss 2002). Using a systematic grid sampling approach, a total of 516 survey points (grid width of 350 m) were surveyed with regard to forest structure (e.g. number of trees, height, diameter at breast height, vertical layering, dead wood of different qualities and quantities) and species composition (e.g. tree species, shrub species, ground vegetation, occurrence of woodpeckers and forest dwelling grouse see Angelstam and Dönz-Breuss 2004). In order to get more accurate information to control sustainable management of uneven-aged natural and semi-natural forests, the former temporary sampling design was changed to permanent plots. This inventory is a monitoring instrument for sustainable management and the results are expected to sup-

port argumentation with nature conservationists. It was funded both by the representatives of the villages in the Montafon as well as the forestry department of the provincial government.

Targets for biodiversity

Although the multifunctional forest inventory is a good tool to measure the states and trends in forest ecosystems, it is not directly possible to derive a management strategy at the local scale. To maintain components of forest biodiversity in managed forests, specific guidelines and target values are needed. To gain acceptance by practitioners and the general public, such guidelines and target values have to be defined in co-operation with foresters and nature conservationists. The guidelines and targets should also consider the technical and economical constraints. Because of topographic and climatic variation, they should further account for regional peculiarities.

Where do we go from here?

Today, it is widely accepted that forests should be managed in an ecologically sustainable way, meaning that wood production, non-timber values as well as biodiversity are included. The 1992 Convention on Biological Diversity has not only focused international attention on the concept of biodiversity but has also set expectations that the signatory nations will establish objectives for local implementation. Along with the ongoing international and national processes for the maintenance and measurement of biodiversity, an additional development is going on in Austria at a smaller scale. Managers of mountain forests have the challenge to fulfil the multipurpose functions, and under fragile ecological conditions (Glück 2002). Although these functions are supported by strong demands from society, the economic context of mountain forest development has completely changed (Buttoud 2002). Due to difficult terrain in mountain forests, timber harvesting cannot be mechanised as high as on flat terrain. Logging by means of cable cranes costs roughly twice as much as highly mechanised logging. Small scale forest ownership inhibits rationalisation and weakens the position in the timber market (Glück 2002). Due to international competition based on low prices, the economy of the forest enterprises is under pressure (Buttoud 2002). As a result, management gets highly mechanised. Small forest enterprises are merged and large-scale forest management is introduced. This is usually followed by a considerable reduction of personnel. Furthermore, these forest enterprises get more and more under the influence of sawmill and paper mill industries. Under these circumstances, increasing competition forces foresters to fulfil short-term economic goals neglecting the long-term sustainability.

In order to make profit, the mountain forest owners may look for additional sources of income from non-wood products and services (Glück 1995). Recreation is one of the four functions that the Austrian forest has to fulfil. According to the current forest policy, forests should generally be open to the public for recreational purposes (Anon. 2002a). Today, the demand for recreation is increasing, both in winter and in summer. Many people consider the forest as their last natural refuge and want to enjoy it as such, and they wish to protect it because they have the impression that it is in danger (Lacaze 2000). But the request to open forest roads for sport activites, especially for horseback-riding and mountain-biking, is still a sensitive forest- and socio-political issue (Anon. 2002c).

In Vorarlberg, free access to forests has started to become a problem especially during winter, because of a conflict of interests. Due to a high increase in off-pist skiing as well as snowboarding, free-riding and snow-shoeing, the forest and the wildlife on higher altitude is under pressure. Tree regeneration gets damaged, and sensitive forest dwelling species (e.g. black grouse *Tetrao tetrix* and capercaillie *Tetrao urogallus*) are disturbed (e.g. Meile 1982, Storch 1999). Furthermore, disturbances in the proximity of winter feeding stations of red deer *Cervus elaphus* provoke an increase in game damage. This conflict of interests among hunters, foresters and the tourism industry has to be resolved. It is of utmost importance that the different interest groups participate in this process. Locals as well as tourists have to be informed and educated regarding their impact on nature. People have to be aware that the forest is not only for recreation but also has to fulfil other functions. Furthermore, wildlife sanctuaries (especially for the sensitive times of the year, e.g. winter or breeding time) have to be established in agreement with the different stakeholders.

Conclusions

There are three major points to be stressed. 1) Increasing competition forces foresters to fulfil short-term economic goals neglecting the long-term sustainability. Both market and public goods have to be produced but without any appropriate policy to cover the costs of public goods. 2) To maintain components of forest biodiversity in managed forests, specific guidelines and target values are needed. In order to have acceptance by practitioners and the general public, such guidelines and target values have to be defined in co-operation with foresters and nature conservationists. 3) Maintenance as well as restoration of biological diversity has to become an integral part of forest management planning. To achieve sustainability of forests will require that the major part of the forest land is managed using methods that are accounting for the environment, biodiversity and timber yield at the same time. Therefore, an applicable and cost-effective forest planning methodology is needed.

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Boreal forest disturbance regimes, successional dynamics and landscape structures – a European perspective

Per Angelstam and Timo Kuuluvainen

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The appearance of the natural disturbance dynamics paradigm in forest ecology has contributed to a more diversified view of forest dynamics. Disturbances in forests range from small to large-scale and from abiotic to biotic, and the mix varies considerably among regions. It is currently acknowledged that boreal forest disturbance and successional features may vary substantially according to the characteristics of the dominant tree species, local site conditions, landscape and regional climate. This has important consequences for how forests ought to be managed by protection, management and restoration to produce renewable resources, maintain biodiversity, and provide ecosystem services. Focussing on Europe's conifer-dominated forests we present different disturbances, disturbance regimes and forest vegetation types found in boreal, hemiboreal and mountain forests. For developing practical approaches to biodiversity conservation it is useful to separate three broadly defined types of forest dynamics 1) succession after severe stand-replacing disturbances, 2) cohort dynamics related to partial disturbances and 3) gap dynamics caused by the death of individual trees or small groups of trees. We use this classification to discuss and define approaches for conservation planning and sustainable forest management. Developing management methods for maintenance of viable populations and important ecosystem processes requires an understanding of how the quality, size, juxtaposition and functional connectivity of the different forest vegetation elements affect species and ecosystem processes at the landscape scale. We emphasise the need for both conservation of networks of forest with different dynamics and studying large intact forest areas which are representative for different ecoregions.

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The boreal forest is the world's largest biome, covering ca 14 million km^2 or 32% of the forest cover of the earth (Burton et al. 2003). Although the boreal forest still encompasses a large proportion of intact forests (Aksenov et al. 2002), it is also an important natural resource from which human welfare is built (e.g. Kuusela 1990, Burton et al. 2003). As such the boreal forest is currently heavily impacted by different kinds of resource extraction. These include both legal and illegal logging (Ovaskainen et al. 1999, Lloyd 2000, Lopina et al. 2003), severe impacts

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caused by the extraction of oil and gas (Schneider 2002), pollution (Sverdrup and Stjernquist 2002), and global climate change (Watson et al. 2000).

It is estimated that the remaining proportion of more or less intact boreal forests is ca 20% (Hannah et al. 1995). The variation is, however, large. In Scotland, the original forest cover has largely been lost, with only ca 1% left and many of the area-demanding or specialised species, such as beaver *Castor fiber* and capercaillie *Tetrao urogallus*, became extirpated several centuries ago (Ritchie 1920). In Fennoscandia the forest cover is still high, but natural remnants are rare. In southern Finland, old-growth forests cover 0.2% of the forest land area (Hanski 2000). If considering all the productive boreal forest in Sweden < 5% can be termed natural forests (Angelstam and Andersson 1997, 2001, Hultgren 2001). Recent studies show that even in European Russia a surprisingly small area (13%) of what could be called large intact natural forest landscapes remains today (e.g. Yaroshenko et al. 2001). So, even if seemingly endless, the boreal forest is continuously changing due to human activity.

These changes do not necessarily threaten the sustained yield of wood for the industry. For example in Sweden, the standing volume has been increasing steadily for > 70 yr (Anon. 2003: 57). It should, however, be noted that in many areas today's volume is only approaching the situation when industrial forestry started in the boreal forest almost 150 yr ago (Linder and Östlund 1998, Björklund 2000). As a consequence, several analyses in regions with a long management history suggest that there are not enough naturally dynamic forests of different kinds required for the maintenance of biodiversity, particularly the viable populations of specialised species (e.g. Angelstam and Andersson 1997, 2001, Lõhmus et al. 2004). Additionally, there is the challenge of maintaining ecological processes in managed landscapes (Sverdrup and Stjernquist 2002). Moreover, there is a need to maintain large intact natural areas that can be used as benchmarks and reference areas for the restoration of highly altered boreal forests (Angelstam et al. 1997, Bryant et al. 1997, Yaroshenko et al. 2001).

In response to the vision of a more ecologically sustainable forest management, forest policies are being redefined (Oliver et al. 2001, Rametsteiner and Mayer 2004), and attempts of practical applications are being made (Angelstam 2003a, b, Angelstam and Bergman 2004). Depending on the country and region, this transition from the sustained yield paradigm results in concern for managing forests to provide a range of conditions and ecosystem services. These include the maintenance of viable populations (Sjögren-Gulve and Ebenhard 2000), biodiversity (Larsson et al. 2001), protective functions (Neet and Bolliger 2004, Dönz-Breuss et al. 2004) as well as socio-economic benefits (e.g. Davis et al. 2001). This trend is particularly pertinent in conifer-dominated forests, which have served as the main source of wood for densely populated regions.

Boreal forests can be defined in several ways (Mayer 1984, Shugart et al. 1992). Being dominated by coniferous trees and adapted to low temperatures and a short growing season, they have large similarities with hemiboreal and mountain forests in southern latitudes (Mayer 1984, Nikolov and Helmisaari 1992). Indeed, a number of typical boreal forest species other than trees, such as grouse (Storch 2000), woodpeckers (Mikusiński and Angelstam 1998), large mammals (Mikusiński and Angelstam 2004) and epiphytic lichens (Brodo et al. 2001) are also found outside the area defined in narrow sense as boreal forest. With this in mind we argue that it is valuable to also include in our wider definition of boreal forest, the transition zones to temperate forests such as the hemiboreal forest found in southern Fennoscandia, the Baltic republics, Belarus and southwestern Russia. Similar forest ecosystems are also found at the southern border of the boreal forest in North American and Asia (Pastor and Mladenoff 1992, Frelich 2002) as well as at higher altitudes in southern latitudes (e.g. Mayer 1984). In this paper we focus on the European boreal forest in this broader sense.

The boreal forest in Fennoscandia is comprised of two conifer tree species and just a few deciduous tree species, which grow tall enough to form a forest (Nikolov and Helmisaari 1992, Pennanen and Kuuluvainen 2001). In Fennoscandia, the main features of forest structure and dynamics and their relationship to site and regional conditions are relatively well studied and understood (e.g. Zackrisson 1977, Arnborg 1990, Esseen et al. 1997, Angelstam 1998, Engelmark 1999, Engelmark and Hytteborn 1999, Niklasson and Granström 2000, Yaroshenko et al. 2001, Gromtsev 2002, Kuuluvainen 2002, Pennanen 2002, Jasinski and Angelstam 2002).

The hemiboreal forests form a transition zone with the broad-leaved temperate forest to the south. In Europe, the southern border can be defined by the southern distribution of Norway spruce *Picea abies* (Mayer 1984). The longer land use history in this ecoregion has made it more difficult to find large intact reference areas and hence to understand natural forest disturbance regimes (Angelstam et al. 1997). The Bialowieza National Park in Poland is an important exception (Falinski 1986).

Finally, mountain forests with an abundance of specialised boreal species are found on the relatively intact slopes of the Scandinavian and Ural Mountains as well as in the central European mountains (Mayer 1974, 1984, Kuusela 1990, Larsson et al. 2001). The boreal tree species are found here, as well as close relatives such as *Larix decidua*, *Abies alba* and *Pinus cembra*.

The aim of this paper is to introduce the boreal ecological theatre to managers of forest biodiversity. We review the most important natural disturbances, successional patterns and the resulting landscape structures of the boreal forest from a European perspective. We thus focus on both the whole and the parts, rather than only the parts (Holling 1995).

Three main forest disturbance regimes

The boreal forest disturbance regimes range from succession following stand-replacing disturbances, such as severe fires and wind-storms, to small-scale dynamics associated with gaps in the canopy created by the loss of individual trees. For simplicity, we distinguish three broad types of forest dynamics for European boreal forests as related to the prevailing disturbance regime: 1) succession, or rather stand development, after stand-replacing disturbances, 2) cohort dynamics related to partial disturbances, and 3) gap dynamics (Table 1). In reality these types are not totally distinct but rather form a continuum in terms of size, severity and repeatability of disturbance (Fig. 1). For example, a site can move from succession after severe disturbance to cohort dynamics caused by partial disturbances and finally, in the absence of external disturbance, reach a stage of gap dynamics (Kuuluvainen 1994).

Succession after stand-replacing disturbances

In succession following severe stand-replacing disturbance a given set of trees of a single age class, or cohort, proceeds from life to death through a series of more or less distinct developmental stages in the stand (Oliver and Larsen 1996). Large-scale stand-replacing disturbances such as fire or wind initiate succession and allow forests to regenerate over large areas simultaneously. In spite of the term stand-replacement, the mortality of trees is rarely complete or even in severe disturbances, especially if the disturbance area is large (Eberhart and Woodard 1987). Consequently, scattered trees and clumps of forest from the original stand often remain alive and form important elements in the developing forest structure in the disturbed area (Östlund et al. 1997, Axelsson and Östlund 2001, Axelsson et al. 2002).

In the boreal forest, examples of different developmental stages following severe disturbances are recent burns, young stands of mixed coniferous and/or deciduous trees, and old-growth forest stands (e.g. Haapanen 1965, Furyaev and Kireev 1979, Furyaev 1996, Angelstam 1998, Yaroshenko et al. 2001). If viewed over longer time spans, such developmental stages are usually ephemeral at a particular locality. To persist in the landscape, species specialising in a particular stage of forest development must be able to disperse from areas with suitable but degrading habitat in order to colonise new sites where the habitat conditions are good or improving. Birds (Haapanen 1965, Swenson and Angelstam 1993, Angelstam and Mikusiński 1994) and insects (Berglind 2004, Wikars 2004) provide good examples of this. A critical requirement of many species is therefore the maintenance of a relatively stable patch dynamics within the landscape but also juxtaposition and functional connectivity (Angelstam et al. 2004a).

Table 1. Summary of the different natural forest disturbance regimes and subtypes found in boreal and temperate forests (based on Dyrenkov 1984, Oliver and Larsen 1996, Angelstam 1998, 2003a).

Disturbance regimes and subtypes	Type of disturbance
Succession	Abiotic: • stand-replacing large-scale external disturbance such as severe high-intensity fire and windthrow
• stand initiation • young • middle-aged • mature • ageing • old-growth	Biotic: • stand-replacing external disturbance caused by: insects, fungal disease, beaver
Cohort dynamics	Abiotic: • low-intensity disturbance with partial loss of trees caused by low-intensity fire or windthrow
• regeneration (mainly young cohorts) • mixed cohorts • digression (mainly old cohorts)	Biotic: • low-intensity disturbance with partial loss of trees caused by large herbivores and insects
Gap dynamics	Abiotic: • local disturbance at the scale of trees or patches by windthrow and self-thinning
• even (gaps created mainly by removal of one or a few trees) • patchy (gaps created mainly by removal of tree groups)	Biotic: • local disturbance at the scale of trees or patches caused by insects, fungal disease

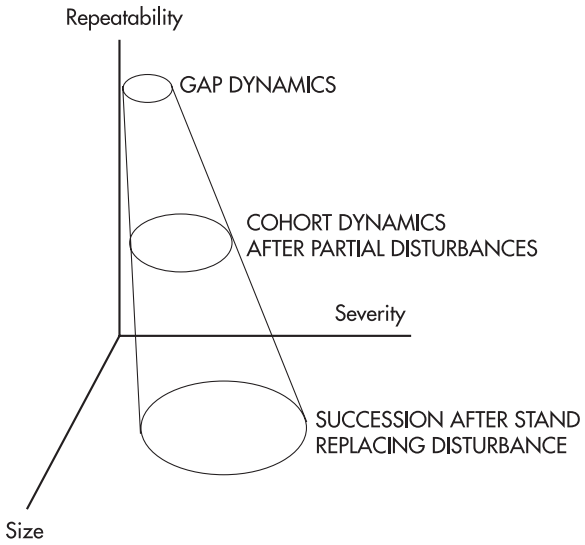


Fig. 1. Illustration of how the three types of natural forest disturbance regimes could take place at landscape level in relation to the size, severity and repeatability of disturbances. Succession is caused by severe disturbances such as fire or strong wind, which often cover large areas, but may occur relatively seldom. Gap disturbances are frequent at the landscape-scale, small in size and often low in severity leaving most of the vegetation alive. Partial disturbances in cohort dynamics represent an intermediate form.

The development of a single cohort of trees following a disturbance event can be divided into several stages. Oliver and Larsen (1996) describe four stages of stand development during succession after stand-replacing disturbance. However, both from a silvicultural and biodiversity point-of-view, more than these four stages are needed to capture the structural and compositional variation among different the different stages of stand development. In managed forest the terms harvested, young, thinning and final felling are useful as they link the development of the stand to the silvicultural operations. However, this division does not include later developmental stages of particular importance for forest biodiversity. Franklin et al. (2002) suggested eight successional stages. In the following section we describe the essential features of six developmental stages after stand-replacing disturbance in boreal forests as a compromise between simplicity and detail (Thomas 1979, Angelstam 1999, 2003a; Table 1, Fig. 2). It is good to bear in mind, however, that forest development is essentially a continuum and therefore all classifications are somewhat subjective.

Stand initiation

The type and severity of disturbance together with pre-disturbance stand structure fundamentally affects the initial conditions for succession. A number of the trees damaged may die during some years after disturbance. Structural legacies from the previous generations, such as standing and down coarse woody debris and living trees strongly affect the density, species composition, growth, survival and spatial pattern of regeneration. Sprouting species such as *Betula* and *Populus* are often abundant on fertile sites as they can rapidly utilise the resources released in disturbance. In natural forests, there is a variable mosaic of forest floor microsites, which often leads to high spatial variation in abundance and species of the tree regeneration.

Immediately following extensive disturbances such as fire, wind-throw, large-scale insect outbreaks, or clear-cutting, the environmental conditions are often unique. As an example, many species of insects have adapted to this by using the burned or sun-exposed dead wood as a substrate (Similä et al. 2002). Similarly, the germination of some plants is enhanced by heat (Granström 1993). The specific conditions of the site and the surrounding matrix determining the subsequent forest forming process are created at this stage.

Young forest

The growth of the trees and gradual closing of the canopy leads to changes in conditions on the forest floor: the amount of light and wind speeds decrease, and humidity increases. In this phase the typical herb, shrub and tree layer vegetation starts recovering, often after a phase of herb-rich pioneer ground vegetation. After natural disturbance, there are often large amounts of coarse woody debris as well as living trees and patches of trees left as legacies from the previous stand. Dead remnants from the previous stand start to decay. It should be noted that even a severe stand-replacing fire usually does not consume more than ca 20% of the standing biomass of the burned stand (e.g. Johnson 1992). Moreover, considerable proportions of the disturbed area are often left intact as groups and stands of trees (e.g. Pyne 1984, Eberhart and Woodard 1987, Johnson 1992, Bergeron et al. 2002).

Middle-aged forest

In this phase of the succession or stand development, or towards the end of the previous stage, severe competition among trees typically leads to stem exclusion (self-thinning), where some trees die from lack of light or soil moisture, a process called competitive suppression. However, this may not happen if the regeneration has been sparse and the trees are widely spaced. Later, the light-demanding species (e.g. *Betula* and *Populus*) may gradually be replaced by shade-tolerant species (e.g. *Picea*) (Haapanen 1965). However, once established as dominants the light demanding species such as *Betula* and *Populus* are able to maintain their position for a long time on sites that are suitable for them. At this phase trees totally dominate the site and many light demanding species disappear from the understorey vegetation.

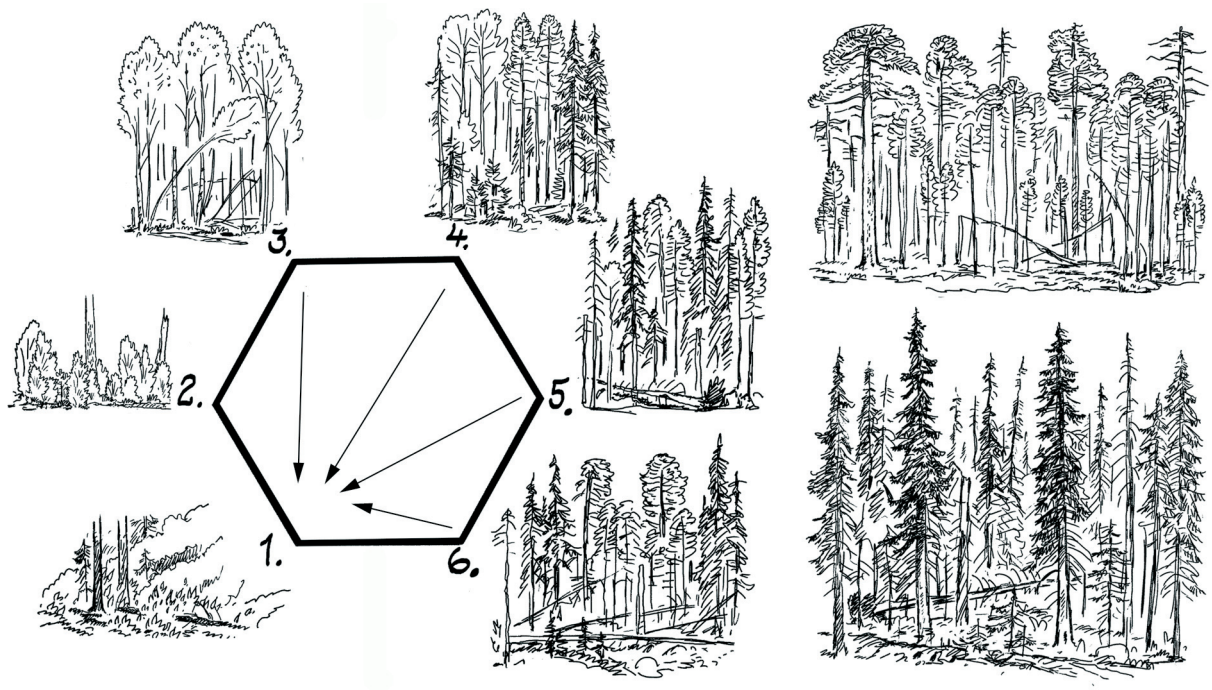


Fig. 2. Drawing illustrating six developmental stages during the succession after stand-replacing disturbances such as fire or strong wind. In Fennoscandia and Russia an early deciduous and a late coniferous phase is typical. Most developmental stages can return to the first stage following disturbance, resulting in a multitude of successional pathways (left). Cohort dynamics in a dry Scots pine forest is shown in the upper right corner, and gap dynamics in a wet Norway spruce stand in the lower right corner (drawing by Martin Holmer).

Mature forest

The trees regenerated after disturbance approach their final height. We use the term mature to denote that it is during this phase that trees are usually mature for final felling within sustained yield forest management. The amount of coarse woody debris is at its lowest, as the dead wood created in the disturbance has largely decayed but significant amounts of new course woody debris has not yet been created (Siitonen 2001). The importance of competition induced mortality decreases, and mortality due to other causes such as fungi and insects starts to increase. At this phase deciduous trees that are present, such as *Betula* and *Populus,* start to show signs of decreased vigour and become important substrates for specialised species. The forest may gradually start to acquire a multi-storey structure and the herb layer vegetation changes towards having more shade-tolerant species.

These four first developmental stages in the succession after severe disturbance have their equivalents in most managed forests. However, due to various silvicultural practices both the tree species composition, the vertical and horizontal vegetation structure as well as the amount and types of dead wood are being manipulated, usually with the aim to reduce unwanted and promote wanted forest components.

Ageing forest

In this stage scattered trees that previously were successful become more and more vulnerable to damage or death due to senescence, insects, fungi, snow-break, wind, falling trees or other factors. Trees from different canopy layers are dying and forming dead wood structures and the amount of coarse woody debris starts to increase. Unless a new disturbance occurs, the ageing and opening stand increasingly differentiates in its vertical and horizontal structure. The gaps in the canopy allow more light and moisture to reach the forest floor. As a result of increasing light the understorey starts to develop and an advanced regeneration of shade-tolerant species emerges (Oliver and Larsen 1996).

In this phase, shade-tolerant tree species are becoming older and start to develop diameters of interest for the largest primary nest excavators, such as the black woodpecker *Dryocopus martius*, bark texture suitable for different specialised lichens (Uliczka and Angelstam 1999), and canopies that can carry the nests of large birds. The vertical and horizontal vegetation structures become more complex. Dead wood also starts to accumulate, but this may not happen if the trunks of dominant trees decompose fast (e.g. Hély et al. 2000).

Old-growth forest

After one to three centuries, depending on tree species and geographic region, in the absence of complete or partial stand-replacing disturbance, most trees that regenerated after the initial stand-replacing disturbance have died. The stand is generally rather open due to the formation of gaps in the canopy as large trees or groups of trees die and fall down. Coarse woody debris is abundant and different types and sizes of dead wood is formed continuously all over the forest. The opening of the canopy creates a diverse horizontal understorey vegetation mosaic. Gap sizes and characteristics vary creating vertical and horizontal structural heterogeneity in the tree layer. The tree age distribution is often multimodal or J-shaped (e.g. Oliver and Larsen 1996, Kuuluvainen et al. 1998), dominated by old trees but with young cohorts appearing both in gaps and as an additional vegetation layer. The relationship between the size and the age of the trees is becoming less and less obvious (Kuuluvainen et al. 2002b). With a shorter time perspective of a few decades or a century the phase in the successional development, the structure of old-growth forest on mesic sites is thus very similar to that of old-growth forest conditions found on wet sites or in moist oceanic or mountain macroclimates. Finally, it must be stressed that an old-growth forest is not a static end-point of stand development, but a dynamic changing system itself (Kneeshaw and Gauthier 2003). Thus, there is great variation in old-growth forest structures depending on the characteristics and duration of the developmental history.

Multiple developmental pathways and their duration

In the natural forest the high variability of the type and severity of disturbances also means high variation in initial stages and developmental pathways. For example, fire and wind disturbance events of equal severity (killing the same amount of trees) create very different conditions and initiate different types of successions. This is because fire usually kills the small trees while some big trees providing seed may survive, whereas in windthrow many of the shade tolerant understorey trees remain alive. Furthermore, even from similar initial conditions successional pathways may diverge (Abrams et al. 1985). All this is important in creating structural and habitat variability typical of the natural boreal forest.

The time that the successional development takes is subject to large variation. Although, as a rule, the development of a full range of successional stages will take > 200 yr, it may take up to 500 yr in some forests in Europe (Falinski 1986, Leibundgut 1993, Wallenius et al. 2002). By contrast succession in riparian forest with willows (*Salix* spp.) and other deciduous trees may enter an old-growth phase in only 60 yr (Oliver and Larsen 1996). Boreal broad-leafed deciduous tree species such as *Populus* and *Betula* may develop old-growth characteristics within similar time frames (e.g. Haapanen 1965).

It is, however, rare that the development after a stand-replacing disturbance in an area is a linear sequence passing through each step in stand development after stand-replacing disturbance described above. Instead there are several pathways through which development may proceed (Fig. 2, left). In principle, disturbances can occur in any of the different stages, albeit with different probabilities. On mesic European boreal forest sites Schimmel (1993) showed that a new fire is unlikely to occur due to low fuel loads and poorly flammable vegetation before a stand age of 20 yr. During the first 3–5 decades after a disturbance episode fire risk increases due to fuel accumulation. Similarly, all other factors being equal, a stand's susceptibility to wind (Quine et al. 2002) as well as insects and fungal disturbance varies with age (Bergeron and Leduc 1999, Lewis and Lindgren 2000).

Cohort dynamics related to partial disturbances

Several tree species show adaptations to low intensity disturbances. Scots pine *Pinus sylvestris* and fire provide a good example in the European boreal zone. Scots pine forests on dry sites are often characterised by frequent low-intensity fires that produce stands with multiple aged cohorts of trees (Sannikov and Goldammer 1996, Angelstam 1998, Gromtsev 2002, Kuuluvainen et al. 2002b; Fig. 2). A Scots pine tree becomes less sensitive to fire damage with increasing age due to its thick bark and to the long distance between the ground and the canopy. As a consequence, Scots pine forests often have several distinct age cohorts of living trees, standing snags, both of which eventually produce a continuous supply of dead wood on the ground in different stages of decay (e.g. Sannikov and Goldammer 1996, Karjalainen and Kuuluvainen 2002, Rouvinen et al. 2002). Such a forest often has a park-like appearance, although in many areas the understorey layer may be quite dense. According to Dyrenkov (1984) this type of disturbance regime may also occur in Norway spruce forests on mesic well-drained sites in association with wind-throw events that remove a portion of the canopy.

Dyrenkov (1984) distinguished three different types of uneven-aged cohort dynamics; 1) regeneration (stands are dominated by younger trees but with an overstorey of old and very old trees as well as snags and coarse woody debris); 2) intermediate (the different age cohorts are evenly distributed within the stand) and 3) digression (cohorts of old and very old trees dominate). In natural Scots pine forests on sediments there are typically 3–5 distinct cohorts that range over at least 200–300 yr of age (e.g. Sannikov and Goldammer 1996). Sometimes, due to the absence of fire for longer time periods, and to the associated accumulation of nutrients, the site type may develop towards a more productive one (Maslov 1998).

Gap dynamics with biotic or autogenic disturbances

While cohort dynamics are driven mostly by external abiotic disturbance often operating on larger areas, gap dynamics is caused mostly by biotic or autogenic disturbances operating at the scale of individual trees and tree groups. Hence, in the absence of large external disturbances, the death of a single tree or groups of trees mainly due to biotic disturbance agents drives forest dynamics by forming gaps in which more or less shade tolerant trees can regenerate. A relatively even, both temporally and spatially, process of mortality and regeneration determines the stand dynamics (Kuuluvainen et al. 1998).

The age/diameter distribution of trees within a forest is the inverse J-type (Kuuluvainen 1994) and a simple mean age conveys no information of the typical age structure. The internal age distribution can be characterised as all-aged or consisting of multiple cohorts (Fig. 2). Note however that the relationship between the size and age of trees is often poor because small trees can become very old when they grow in the shade of older trees (e.g. Oliver and Larsen 1996).

In naturally dynamic landscapes such stands often form corridors, networks or clusters in the wet and moist parts of the landscape. Typically, these forests have a relatively moist and stable microclimate and a continuous supply of dead wood in different stages of decay. This type of dynamics also occurs in large extensive areas where the climate is moist and fire cycles are long enough for this stage to develop (Syrjänen et al. 1994, Angelstam 1998, Ohlson and Tryterud 1999, Gromtsev 2002). The tree species involved include Norway spruce and *Abies* spp. in boreal and mountain forests. Note, however, that even when fire cycles are moderately short, old-growth forests are present because of the random nature of fire events causing considerable parts of the landscape to be skipped by fire (see section about succession).

Dyrenkov (1994) distinguished two sub-types: with even and patchy spatial tree distribution within the stand, respectively. The first type is characterised by an even distribution of different tree ages in the stand. This is associated with smaller gap sizes including one or a few trees. The second type is characterised by a patchy distribution of different tree ages in the stand. This is associated with patch forming processes that create larger gap sizes.

Interaction between different disturbances

In spite of the presented three disturbance regimes, one disturbance factor often affects the probability of occurrence of another. Therefore disturbances may also appear as mixed patterns in different time and space scales. For example, the structure and species composition of pine forests are often determined both by low- or medium-severity fires (abiotic disturbance), regulating regeneration and species composition, and deaths of individual or groups of large overstorey trees (biotic disturbance), releasing growing space and creating coarse woody debris (Kuuluvainen 2002, Rouvinen et al. 2002). These two disturbances, operating in different space and time scales, may interact so that the fires can open up the stand and damage the root systems of the pines making them more susceptible to bark beetle attacks or windthrow (Sarvas 1938). Little is known, however, about the interaction between different disturbance factors in the natural forest.

Estimating stand age distributions under different disturbance regimes

The average stand age distribution of naturally dynamic forest landscapes can basically be estimated using knowledge of the different disturbance regimes, their relative occurrence, interaction and impact on stand structures. In areas with crown fire as a once dominating large-scale disturbance, the age-class distribution of forests has been estimated using simple analytical models of equilibrium dynamics (e.g. Johnson and van Wagner 1985). Another approach is to use simulation models to examine what type of age structures would prevail under historical or natural disturbance regimes (e.g. Pennanen and Kuuluvainen 2001, Pennanen 2002).

In both cases a distinction needs, however, to be made between time since fire and stand age (Kuuluvainen 2002). The reason is that both fire severity and the fire-tolerance of different tree species, and hence site type, strongly affect the resulting stand age distribution of different forest types although the time since disturbance is the same (Pennanen 2002). Not realising this may lead to an underestimation of the internal high structural diversity of the landscape even after a relatively short time since large-scale disturbance.

Finally, it should be noted that disturbances, forest vegetation and site type characteristics interact. For example, repeated intensive fires will shift sites to poorer site, while in the absence of fire the site will develop into more productive ones (Maslov 1998). In some cases the opposite may happen: in the absence of fire the forest is being paludified and transformed to a bog with low probability of fire occurrence (Harper et al. 2002, Pitkänen et al. 2003).

Succession

Stand development after stand-replacing disturbance is a common natural successional pathway in many parts of the boreal forest (Sirén 1955, Yaroshenko et al. 2001, Gromtsev 2002). Particularly forests on mesic sites with multi-layered structure of spruce and mixed coniferous forest with a pine component are susceptible to stand-re-

placing crown fires (Sirén 1955, Niklasson and Granström 2000). The disturbance agent could also be storm winds on moist sites and in certain macroclimates (Syrjänen et al. 1994, Ulanova 2000). On mesic sites shade intolerant species dominate in the early part of the succession and shade tolerant species in the latter part. As a result the deciduous birch and aspen would often have dominated the earlier part of the succession, and the shade tolerant spruce the latter part. However, the empirical knowledge of the quantitative distribution of deciduous trees in natural successions is poor (Axelsson et al. 2002).

If stand-replacing disturbance is dominant, the landscape would obviously be composed of a mosaic of more or less even-aged stands of different sizes and with different times since they last burned or blew over. However, it is important to bear in mind that even in a case of a severe disturbance, some parts of the forest remain untouched as disturbance severity varies over an area (see detailed section about succession). For example, even in severe wildfires parts of the landscape usually remain unburned by chance (Eberhart and Woodard 1987) or because wet sites are skipped by fire (Jasinski and Angelstam 2002, Gandhi et al. 2002). This obviously increases the presence of old forest in the landscape.

Both theoretical and empirical studies provide information about the quantitative distribution of stand characteristics in flammable landscapes following stand-replacing fires. If all stands would burn at a given age (e.g. 100 yr) and if the stands are evenly distributed among the different age classes, just as if they were logged according to the regulated forest paradigm, the result would be a rectangular stand age distribution. Now let us instead assume that a constant proportion of each age class was burned. This would result in a negative exponential distribution (Johnson and van Wagner 1985). Finally, if fires were confined to older stands with a certain fuel load, then a Weibull type distribution (van Wagner 1978) would result. Hence, the conclusion is that the manner in which stands burn under a high-severity fire regime results in a specific age distribution (Fig. 3).

Empirical data from Sweden's middle boreal forest on mesic and dry sites before the appearance of agriculture ca 1650 (Niklasson and Granström 2000) show a distribution of time since disturbance, which was very similar to the mean between the negative exponential and Weibull distributions. For spruce-dominated forests on mesic sites, this empirical information can be used as an estimate of the stand age distribution in the landscape (Niklasson pers. comm.). However, for sites and landscapes dominated by fire-tolerant Scots pine this would not apply (see Cohort dynamics section below).

The formation of the theoretical landscape age structures, such as that proposed by the negative-exponential model, assumes that stand-replacing fires are frequent in relation to the biological age of the dominant tree species. However, due to moist macroclimates, in Europe forests most susceptible to stand replacement after fire, i.e. those dominated with fire-intolerant spruce, appear to be naturally characterised by very long fire rotations, up to several hundred years (e.g. Gromtsev 2002, Wallenius 2002, Pitkänen et al. 2003). Therefore, in most times these forests would be dominated by old-growth stands, in spite of occasional stand-replacing fires (Kuuluvainen et al. 1998, Gromtsev 2002, Wallenius 2002). Thus, the theoretical models, mostly developed in North America, of the stand age structures under stand-replacing disturbance regimes should not be applied uncritically, for example by considering differences in macroclimatic conditions (se Discussion).

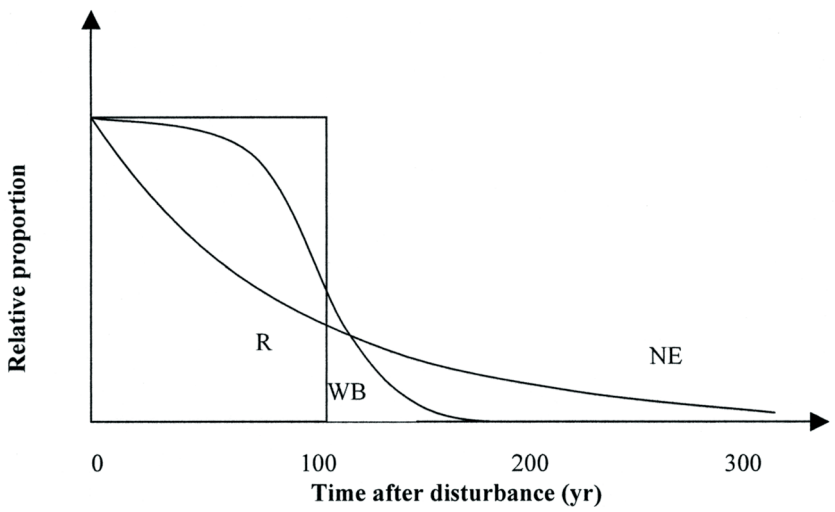


Fig. 3. Different time-since-disturbance distributions during succession after stand-replacing disturbance. The rectangular distribution (R) corresponds to the ideal of sustainable and even timber supply. The negative exponential (NE) and Weibull (WB) distributions correspond to different theoretical stand age distributions in a naturally dynamic landscape driven by stand-replacing disturbance (from Johnson 1992). All distributions have the same average disturbance frequency. The y-axis denotes the relative amount of forest in the landscape.

Cohort dynamics

Partial disturbances such as low- or medium-severity fires often reduce the risk of more intense fires by preventing the accumulation of fuels and formation of multilayered canopy structures susceptible to crown fires, and by favouring the fire resistant Scots pine. When partial disturbances are common, the distribution of time since disturbance cannot directly be used to estimate the stand age distribution of the landscape (Pennanen 2002). This is because the large Scots pine trees often survive the fires (e.g. Kolström and Kellomäki 1993, Kuuluvainen et al. 2002b, Lampainen et al. in press).

Using an empirically evaluated simulation model Pennanen (2002) showed that in landscapes with Norway spruce and mixed Scots pine sites, and assuming stand-replacing fires, the stand age distribution was similar to the previously described theoretical models (i.e. negative exponential). By contrast, pine forests with cohort dynamics had very high mean stand ages due to the almost continuous presence of old fire-resistant trees in the landscape. Empirical and historical data from Scots pine dominated forests with cohort dynamics show the same pattern (e.g. Gromtsev 2002, Kuuluvainen et al. 2002b). Thus, landscapes with partial disturbances would be dominated by forest stands with old-growth characteristics (Pennanen 2002).

Gap dynamics

On wet spruce-dominated sites gap dynamics operating at the scale from single trees to tree groups should dominate (Kuuluvainen et al. 1998, Engelmark and Hytteborn 1999). Such stands have moderate mean stand ages, but with a very high spatial variance due to the presence of regeneration of trees in gaps and old trees. Most stands are consequently old, but due to the shorter life expectancy of Norway spruce compared with Scots pine, the age distribution ought to be narrower. However, although normally dominated by gap dynamics, this forest type can periodically be susceptible to large devastating disturbances such as windthrow or fire during dry periods (Sirén 1955, Syrjänen et al. 1994).

Aggregating distribution of stand age classes at the landscape scale

Actual landscapes have different mixes of site types affecting the occurrence of different disturbance types (Jasinski and Angelstam 2002). Different landscapes are also located in regions with different macroclimates affecting the frequency of occurrence of several types of disturbances, such as fire and strong wind (e.g. Pyne 1984, Agee 1993, 1999, Ulanova 2000). The resulting landscape-scale stand age distribution must therefore be estimated by understanding how different disturbance agents and forest vegetation types interact (e.g. Kuuluvainen 2002, Harvey et al. 2002). Thus, in real landscapes the disturbance types exist as mixed patterns in time and space.

There are principal differences between the distribution of different stand ages in landscapes dominated by combinations of site and macroclimatic conditions favouring the three types of disturbance regimes, respectively (Table 2, Fig. 4). Landscapes characterised by relatively frequent stand-replacing disturbances are dominated by young and middle-aged forests, but also with a long tail of forests that have escaped fire by chance and developed old-growth characteristics. On the other hand, in landscapes where partial disturbances are common, equating time since disturbance and mean stand age only can lead to a very biased

Table 2. Estimated proportions of different age classes measured as time after disturbance in naturally dynamic forests with different natural disturbance regimes in central Fennoscandia (from Angelstam and Andersson 1997, 2001). For succession the theoretical rectangular (RECT), negative exponential (NE), Weibull (WB) and mean of negative exponential and Weibull (NE+WB) and the empirical data for naturally dynamic boreal forests (pre 1650 in Sweden) from Niklasson and Granström (2000: Fig. 14) are presented. For cohort and gap dynamics we use the same estimated distribution as Angelstam and Andersson (1997, 2001). Note that the age classes and relative distribution of different age classes in the landscape vary considerable among different parts of the boreal forest.

Time after disturbance (yr)	Succession					Cohort	Gap
	RECT	NE	WB	NE+WB	Empirical		
1. Stand initiation (0–9)	10	10	9	10	10	5	1
2. Young forest (10–39)	30	25	28	27	29	5	1
3. Middle-aged forest (40–69)	30	19	27	23	23	10	1
4. Mature forest (70–109)	30	17	28	23	17	10	1
5 and 6. Ageing and old-growth forest (110–)	0	28	7	17	22	70	96
Sum	100	100	100	100	100	100	100

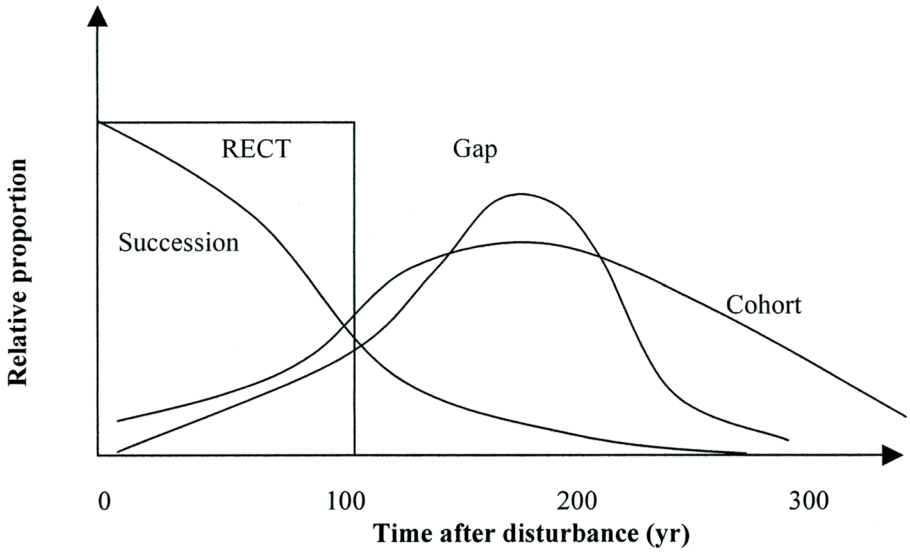


Fig. 4. The expected relative distribution of stands with different mean time since disturbance in the three types of forest disturbance regimes (see Table 1). For succession following stand-replacing disturbances the curve is based on averaging the negative exponential (NE) and Weibull (WB) distributions, as supported by Niklasson and Granström's (2000) empirical data, and for gap dynamics based on Pennanen (2002). Because Scots pine dominated in sites with cohort dynamics and Norway spruce in sites with gap dynamics, and the former has a longer potential life span, the cohort distribution should be slightly skewed to the right. For drawings showing what the forests with the three types of disturbance regimes look like see Fig. 2. The rectangular distribution is shown for comparison (cf. Fig. 3).

view of natural stand and landscape structures (Pennanen 2002). This concept is crucial as living overstorey trees such as Scots pine often largely determine the biological properties and biodiversity carrying capacity of the site even in recently disturbed sites.

A forested landscape dominated by gap dynamics is by definition an old-growth forest. However, at times strong winds or fires kill trees in larger patches of forest and initiate cohort dynamics (e.g. Syrjänen et al. 1994, Ulanova 2000, Wallenius 2002). Consequently, a certain variable proportion of the landscape is made up by early and mid stand-development stages. The same argument can be made for a landscape dominated by conditions favouring cohort dynamics in a Scots pine forest, where fire can sometimes be severe enough to open larger patches of forest (Pitkänen 1991, Gromtsev 2002, Lampainen et al. in press). As a result, the stand age distributions at the landscape level dominated by gap and cohort dynamics are expected to be qualitatively similar (Fig. 4). In both types large trees that live up to their biological age, in the case of Norway spruce ca 200–300 yr and in the case of Scots pine even older, dominate the landscape (Pennanen 2002, Wallenius 2002). Angelstam and Andersson (1997, 2001), Angelstam et al. (2003c) and Lõhmus et al. (2004) used such age distributions for estimating the amount of gaps in different forest vegetation types in today's landscapes. Note that the theoretical estimates used by Angelstam and Andersson (1997), see Table 2, in the Swedish gap analysis (Anon. 1997) for succession on spruce (mesic) sites is very close to the empirical information deduced from Niklasson and Granström (2000) for Swedish northern boreal forests.

The fact that the sustained yield paradigm in traditional forestry results in the absence of biologically old trees and forest stands is one of the main problems when trying to implement policies about the maintenance of biodiversity. As an example, managed forests in Sweden and Finland have usually < 5% of forests older than 120 yr (Stokland et al. 2003). By contrast, both historical and naturally dynamic forest landscapes in Fennoscandia have had amounts of such forest exceeding 40% (Östlund et al. 1997, Axelsson and Östlund 2001, Pennanen 2002).

It is important to understand how managed landscapes differ from landscapes in which species have evolved. Below we exemplify how the average age distribution can be estimated for a naturally dynamic coniferous forest landscape, which consists of a mixture of dry pine forests, wet spruce forests and different stages of succession after fire or other large-scale disturbance on mesic sites (from Angelstam and Anderson (1997)). To estimate how much forest older than the age at which the forest is currently regarded as mature for final harvest there would exist in the naturally dynamic boreal forest landscapes in northern Europe, the area of age classes with high stand ages in the different disturbance regimes must be added up. The first column in Table 3 shows a tentative distribution of different types of forest dynamics for a natural coniferous landscape in lowland Fennoscandia using the average site type distribu-

tion of today's Swedish forest sites (Rülcker et al. 1994). In this example 70% of the area is assumed to be succession after stand-replacing disturbance on mesic sites with forest in different age categories from newly burnt to old forest. The amount of remnant living structural tree legacies from previous tree generations would vary from none to small groups, and even with larger islands of surviving trees in moister spots or just by chance. Further, ca 20% would be on sites with multi-layered pine forest dominated by cohort dynamics, most of which can be considered as old forest because of the large fraction of old trees and different types of dead wood. Finally, ca 10% consists of wet spruce forest sites with internal gap dynamics, which can mainly be counted as old forest.

The second column of Table 3 shows the approximated average proportion of different types of stand dynamics and age classes. Here the definition of biologically old forest corresponds to coniferous forest starting to acquire features of biologically old forest, which is older than the normal management rotation age (i.e. ca 110 yr), as well as younger forest that includes ageing deciduous trees. Both are forest types that normally do not exist in managed Fennoscandian forests. The sum of these age classes not found in managed forest landscapes, which are denoted as B, C, E, F in Table 3 and which, broadly speaking could be counted as biologically old forest, would thus constitute 40–50% of an average coniferous forest landscape with a site type distribution as presented in the example.

Use of models yields further insights into the age distribution under different scenarios. Using an empirically evaluated simulation model Pennanen and Kuuluvainen (2001) and Pennanen (2002) estimated the forest age distributions in unmanaged forest landscapes under mixed-severity fire regimes in conditions typical of eastern Finland. The proportion of old-growth forest (age >150 yr) in the 9 different modelling scenarios for a mean fire interval of 100 yr ranged from ca 20%, corresponding to predominance of extremely severe fires, to 80% corresponding to low-severity fires (Pennanen 2002: 222). Figure 5 illustrates probable stand age distributions of unmanaged forest landscapes in eastern Finland under three fire frequencies, 50, 150 and 240 yr. These fire frequencies correspond to knowledge on historical fire regimes in Finland and Sweden in the 19th and 16th centuries, and ca 1700 yr ago, correspondingly (Pennanen 2002 and references therein). According to these results old pine forests would have dominated the landscape under the short fire rotations that were typical in the 19th century due to human activity (Fig. 5a). Old forests would have been predominant with longer fire rotations and the proportion of old spruce forest would thus increase (Pennanen 2002).

Discussion

Variability of disturbance regimes

It is evident that there are large regional differences in the mixes of different disturbance regimes in Europe's boreal forests (e.g. Angelstam 1998, Yaroshenko et al. 2001, Gromtsev 2002). For example, landscapes on the slopes of the Scandinavian Mountains and the western slopes of the Ural Mountains have more oceanic macroclimates than the lowlands of Sweden, Finland and the Russian plain (Kalesnik 1964, Tuhkanen 1984). There are also clear differences in the mix of local site conditions. Fennoscandia's boreal and hemiboreal forests are characterised by sites on glacial till and shallow soils on a shield of bedrock while the Russian plain is covered by deep deposits of glacio-fluvial sediments (Alayev et al. 1990, Strand 1997).

Table 3. A tentative example of the distribution of forest areas with different disturbance regimes and age classes measured as time after disturbance in a fictive natural coniferous forest landscape. The proportions of the three disturbance regimes correspond to the site type distribution of Sweden (Rülcker et al. 1994).

Type of forest dynamics and distribution in different forest environments in a natural forest landscape	Proportion (%)
Succession (on mesic sites covering 70% of the landscape)	
A. Young and middle-aged trivial stands (ca 2/3)	46
B. Older forest with considerable amount of deciduous trees (ca 1/6)	12
C. Old or almost old forest (ca 1/6)	12
Cohort dynamics (on dry sites covering 20% of the landscape)	
D. <110 yr (ca 4/10)	8
E. >110 yr (ca 6/10)	12
Gap dynamics (on moist and wet sites covering 10% of the landscape)	
F. Almost all stands with old-growth characteristics	10
Sum	100

Consequently, the landscape-scale stand age distribution should be expected to show regional differences. This is also supported by empirical evidence. In west-central Norway gap phase dynamics prevail, but succession after strong winds also occurs, such as in 1837 and 1992 when catastrophic storms blew down large areas of forest in the Trondheim area (Asbjørnsen 1861, Tømmerås 1994). Similarly, Kuuluvainen et al. (1998) showed that the western slopes of the Ural Mountains form large areas with old-growth, sometimes exposed to strong winds (Syrjänen et al. 1994, Lässig and Mochalov 2000). By contrast, on the Russian plain, local site conditions clearly affect the age distribution in local landscapes (Yaroshenko et al. 2001, Gromtsev 2002). This has also been clearly shown in landscapes with similar landforms in Siberia (e.g. Furyaev and Kireev 1979). Finally, in Fennoscandia the clearing of forest for agricultural purposes and the draining of wet forest soils have changed the forest site type distribution from richer wet herb types towards more mesic site types (de Jong 2002). The long-term absence of forest fires (Zackrisson 1977) has also increased the amount of organic matter on poor sandy soils, which consequently have altered the local site and made it more suitable for Norway spruce. These changes need to be taken into account when assessing the representivity of today's forest vegetation types and the degree to which species and ecological processes found in naturally dynamic forest landscapes can be maintained in landscapes that have been intensively managed for a long time.

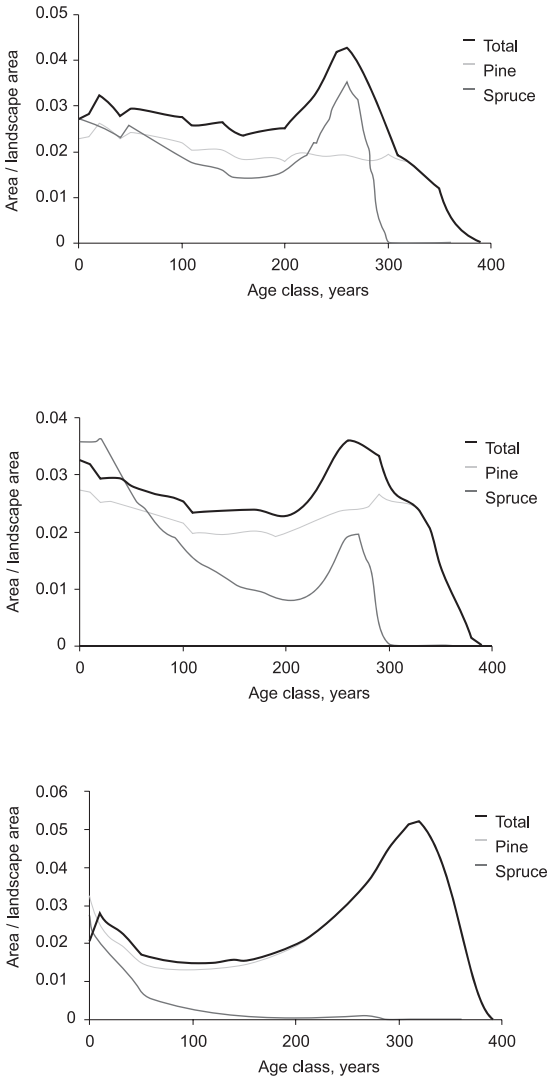


Fig. 5. Simulated stand age distributions under three fire rotations, 50, 150 and 240 yr. Stand age, which is defined according to the oldest cohort, is presented for cohort dynamics (pine) and succession (spruce) separately, and as the sum (total). The area below each graph is not the same because both tree species are not present in all sites (redrawn from Pennanen 2002).

Management approaches based on natural disturbance regimes

For planning management approaches based on natural forest dynamics it is important to recognise that the relative role of local and regional factors determining natural disturbance regimes vary among landscapes (Pyne 1984, Agee 1993, 1999, Angelstam 1998, Yaroshenko et al. 2001). For example, the large regions of moist spruce forests at higher altitudes both in Scandinavia, the Ural Mountains and the Alps are naturally nonpyrogenic. In lowland Fennoscandia in general, there is more and more evidence that partial disturbances of fire and wind were common historically (see Ulanova 2000, Kuuluvainen 1994, 2002). However, severe disturbance dynamics may have prevailed during dryer climatic periods in Scandinavia (Pitkänen 1991) and in dryer sites in more continental Europe (Sannikov and Goldammer 1996). Such differences in natural disturbance dynamics should also be reflected in the variation of management approaches in different ecoregions, aimed at preserving naturally occurring forest structures and biodiversity (Angelstam 2003a).

For the boreal forest we illustrate this by comparing the ASIO-model developed for the management of boreal forest in Fennoscandia (Angelstam et al. 1993, Rülcker et al. 1994, Angelstam 1998) with the multi-cohort model developed by Bergeron et al. (1999, 2001, 2002) for sustainable forest management in Québec, eastern Canada. Both models are based on the hypothesis that if forest management can simulate the composition and structure found in boreal forest landscapes, with naturally dynamic spatial and temporal patterns of forest regeneration after natural disturbances, then ecologically sustainable forest ecosystems will be maintained (Hunter 1999, Lindenmayer and Franklin 2002).

The ASIO-model

The ASIO-model was developed in collaboration with the Swedish State Forest Company in the early 1990s as a conceptual model to guide the maintenance and restoration of ecologically sustainable boreal forest ecosystems (Angelstam et al. 1993, Rülcker et al. 1994). It has been widely used in practical management in both Sweden and Finland to demonstrate that the boreal forest has several types of dynamics, and to stratify landscape sections with respect to the selection of different silvicultural practices (Fries et al. 1997, Korhonen et al. 1998, Heinonen pers. comm.).

The principal relationship between the main disturbance regimes and site conditions in the European lowland boreal forest is described in the ASIO-model (Rülcker et al. 1994, Angelstam 1998). The driving explanatory variable in the model is the occurrence and behaviour of wildfire in sites with different fuel characteristics and macroclimates found in boreal forest stands and landscapes. The four groups of different average fire frequencies that are assigned are inversely related to the average fire intensity (see also Furyaev and Kireev 1979 who made the same classification in central Siberia). These relative fire frequencies range from extremely low in some wet tall herb sites or at high altitude/latitude with a humid climate where fire is Absent, or occurs almost never, to sites where fire occurs Seldom, to mesic sites with Infrequent fire and to dry lichen sites where fire occurs Often. Hence, the name of the model is ASIO. The interaction between fire and local as well as regional site conditions influencing fire behaviour was used to deduce three main disturbance regimes found in the European boreal forest, viz.: 1) succession after severe disturbance, from young to old-growth mixed deciduous/coniferous; 2) cohort Scots pine dynamics; and 3) gap Norway spruce dynamics; (Angelstam 1998, 2003a; see Table 1, Fig. 2). The ASIO-model thus encompasses both the long-term predictability of fire events (e.g. the different mean fire intervals in different site types) and spatially random nature of fire events when they actually take place (e.g. where and when a fire actually takes place).

The differences in natural disturbance regimes have consequences for the desired age structure of the managed landscape to maintain biodiversity. The random occurrence of fires means that parts of even flammable forest types escape fire for prolonged periods and develop into old-growth forests. In forests managed according to the basic ASIO-model assumptions it is important to remember the need to ensure the presence of a long age-class tail for old easily flammable forest types (Rülcker et al. 1994, Fig. 3). Given the long history of forest management in Fennoscandia, the maintenance of such an age-class tail of old forest is a major challenge for forest ecosystem restoration.

The multi-cohort model

Bergeron et al. (1999, 2001, 2002) developed a strategic-level management approach for boreal forests based on natural fire ecology of forests in Quebec, eastern Canada. The idea behind the model is that the features of the fire regime, mainly the frequency, size and severity of fires, can be used to characterise the vegetation structure in a given forest area. According to the resulting management model, the forest area is divided into three (or more) classes for which different cutting methods and rotation periods are applied. In this way the within-landscape structural variation is imitated and the forest age distribution is maintained to resemble one that would exist under natural fire regime (see Fig. 6). For example, a proportion of the area can be regenerated using clear cutting to imitate severe fires occurring with a given frequency (e.g. 100 yr). The other parts of the area are then treated with 200 and 300 yr rotations, during which the stands are treated with partial or gap regeneration cuttings to maintain old-growth characteristics and at the same time to release understorey regen-

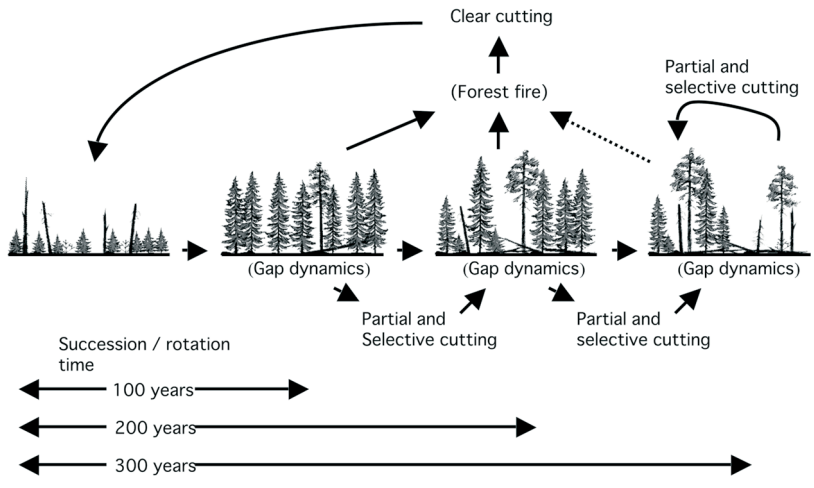


Fig. 6. In the Canadian multicohort model the forest area is divided into three (or more) classes for which different cutting methods and rotation periods are applied. In this way the within-landscape structural variation is imitated and forest age distribution of is maintained resembling one that would exist under natural fire regime. For details and application see Bergeron et al. (2002) and Harvey et al. (2002) (adapted from Kuuluvainen et al. 2004, drawing by Janne Karsisto).

eration. In this way the occurrence of stand structures created with longer fire rotations are ensured (Fig. 6). Clear-felling can be used, or not, at the end of a rotation for each of the cohorts to bring stands back to an initial state. The proportions of stands that are clear-felled are theoretically derived from the negative potential stand age distribution, with silvicultural constraints (see Harvey et al. 2002). Under longer natural fire rotation, the proportion of forests with old-growth characteristics should be greater, and vice versa (Bergeron et al. 2002).

Comparing the models

The multi-cohort model and the ASIO model have in common that both clear cutting and partial cutting methods are advocated to create structural variability similar to that found in natural forests (Bergeron et al. 2002, Angelstam 2003a). The models differ in that the ASIO model assumes that fire frequencies are related mainly to site type quality, whereas in the multi-cohort model, fires are assumed to occur more or less randomly in the landscape and that site type quality is of secondary importance for the frequency of stand replacing fires. This being said, some jack pine *Pinus banksiana* and red pine *Pinus resinosa* stands do have a regime of non-lethal fire.

The natural occurrence of fires is affected both by random factors such as the frequency of lightning strikes and weather, and deterministic factors such as site type, natural fire breaks, successional stage and fuel load (e.g. Pyne 1984). Thus the different emphasis on random vs. deterministic factors in the two models depends on differences in the macroclimatic conditions, but possibly also tree species properties and physical landscape structure affecting the spread of fire. We argue that the differences in the management recommendations of these two models are at least partly based on general differences in the macroecology of Québec vs Fennoscandia. Such regional differences are also found among different parts of Canada (Haeussler and Kneeshaw 2003) and Russia (Yaroshenko et al. 2001).

Thus, both the Canadian and Fennoscandian recommendations for forest management when trying to emulate natural disturbance regimes are similar: 1) a variety of silvicultural practices should be applied, and 2) different management recommendations may be made in different forests depending both on local and regional conditions forests (Mayer 1992, Angelstam and Arnold 1993, Bergeron et al. 1999, Angelstam 2003a).

Benchmarks in time or space?

Research on natural forest benchmarks to understand the historical range of variation can be made using historical studies, by studying natural remnants and by modelling. All approaches have their advantages and disadvantages. An example can be taken from the different efforts to understand the benchmark conditions for the Swedish boreal forest.

According to Östlund et al. (1997) the amount of biologically old forest in Lycksele 1913, in boreal forest in north Sweden, was estimated to be 83%. Without knowing the distribution of the mix of different disturbance regimes and parameters describing frequency and intensity of different natural disturbances, however, such an empirical estimate from a time period when forest fire regimes had already been altered by humans (Zackrisson 1977) is difficult to interpret. In fact, there has been a gradual change in the age distribution of forests within a particular range of site types due to the gradual transition from a naturally dynamic landscape before the advent of industrial use of forests. This includes both altered grazing regimes and human alteration of fire regimes. For the eastern part of Västerbotten county in NE Sweden, i.e. close to Lycksele, such landscape changes began ca 1650 (Niklasson and Granström 2000). Already by the 19th century the age distribution had been considerably skewed compared with what can be assumed to represent naturally dynamic conditions, as well as towards smaller average patch sizes of the forest stands (Niklasson and Granström 2000). Also in Finland an increase in fires has been reported between the 17th and 19th century (Lehtonen 1997, Pennanen 2002). Consequently, it may be that studies based on data from historical maps and descriptions only (e.g. Linder and Östlund 1998, Axelsson and Östlund 2001, Axelsson et al. 2002) do not necessarily represent well the stand age structure of the naturally dynamic forest landscape to which species are adapted (see Figs 5 and 7, Pennanen 2002).

To improve the natural forest benchmarks used for biodiversity conservation both in managed landscapes and protected areas, more needs to be learned from biological archives and contemporary reference landscapes (e.g. Wallenius 2002, Jasinski and Angelstam 2002, Korpilahti and Kuuluvainen 2002, Pitkänen et al. 2003). However, such approaches also have their drawbacks. Natural archives cannot be dated using C14 during the last 200 yr (Hannon pers. comm). In Finland and Sweden remnant forest areas are often left because of their extraordinary properties, or alternatively, because of lower economic interest e.g. due to poor sites, such as the forests on rocky outcrops on the Fennoscandian shield. The site type distribution in more natural remnants is thus different from and not representative of that of today's managed landscapes. Additionally, remnants are often very small and have not for decades been subjected to natural disturbances such as fire (Linder et al. 1997). Finally, forest remnants may be affected by edge-effects such as browsing by large herbivores altering the tree species composition (Boncina 2000, Angelstam et al. 2000, Berger et al. 2001) or generalist predators living in the surrounding matrix (Kurki et al. 2000).

Consequently, a multidisciplinary approach including historical ecology and geography, environmental history

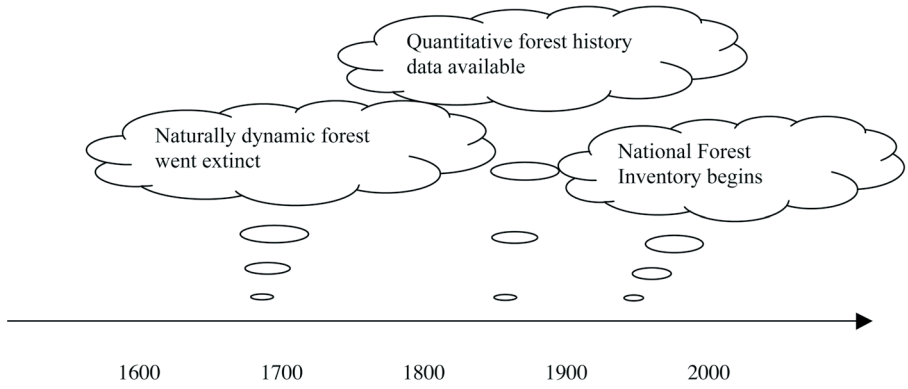


Fig. 7. Generalised description of the phases in land use history and the different points-of-view presented by studies of naturally dynamic forests and the pre-industrial forest landscape as revealed by forest history studies (e.g. Östlund et al. 1997, Axelsson et al. 2002) versus studies based on attempts to understand the natural dynamics of forest (e.g. Pennanen 2002). Note that that the National Forest Inventory in Sweden and Finland did not start until in the 1920s.

and landscape ecology as well as modelling should be employed to set natural forest benchmarks for biodiversity conservation. Practical implementation involves natural sciences such as restoration ecology but also the actual engineering as well as an understanding of the barriers to policy implementation (Angelstam et al. 2003b, Lazdinis and Angelstam 2004). The range of important questions include: 1) which variables are considered important for ecosystem integrity 2) the degree to which parameter values for these variables are different (mean and range) in benchmark and managed areas, 3) what human values and policies define what is a desirable state, such as naturalness (e.g. Peterken 1996) or cultural landscapes (Rackham 2003), and 4) whether or not these changes are relevant to the values. Another complication is climate change. If we use historical knowledge going back many centuries in the past, we face the problem that the macroclimate varies very much along such a time scale, and consequently the distribution of different tree species. For example, Björse and Bradshaw (1998) showed that the climate has been similar in southern Scandinavia only during the past 1000 yr. Moreover, climate is changing much faster now (Watson et al. 2000). This issue should also be taken into account when looking for benchmarks (Dale et al. 2001)

When these issues have been clarified, the set of research tools to be employed can be discussed for a particular ecoregion. Such tools include historical retrospective studies, the use of nature's archives such as found in peat, lake sediments and tree rings, reference areas within the relevant ecoregion, or the unintentional experiments created by politics, as well as modelling (Kuuluvainen et al. 2002a). A range of publications reviews the use of such methods (e.g. Balée 1998, Agnoletti 2000, Agnoletti and Anderson 2000a, b, Östlund and Zackrisson 2000, Egan and Howell 2001, Kuuluvainen 2002).

Sustainable forest management is a discipline that requires quantitative targets to which indicators describing criteria such as biodiversity and forest health can be compared (Angelstam et al. 2004a). This is the essence of systematic conservation planning and is relevant to both its implicit elements, namely analysis for biases in representation and insufficient functional connectivity (e.g. Margules and Pressey 2000, Angelstam and Andersson 2001, Scott et al. 2002, Angelstam et al. 2003c, Lõhmus et al. 2004). The motive for employing such tools is to secure a certain amount (Fahrig 1997, 1998, 2001, 2002), configuration as well as continuous rather than discontinued supplies of different vegetation structures at the landscape scale (Angelstam et al. 2003a). At the landscape scale this requires an understanding of how the quality, size, juxtaposition and functional connectivity of the different forest vegetation types affect species and ecosystem processes. This applies to all spatial scales. For example, for wood-living fungi, the discontinuation of the availability of dead wood for as short as 10 yr may lead to loss of highly specialised species (Heilmann-Clausen and Christensen 2003). Similarly, certain successional stages need to be continuously perpetuated at the landscape scale (Angelstam et al. 2004b)

Finally, we emphasise the need for both functional conservation area networks and large intact forest areas, which are representative for different ecoregions in the boreal forest. The latter are indispensable benchmarks for developing restoration and management methods for forest biodiversity conservation. There is also a need for syntheses of the information available for different forest regions with different mixes of forest disturbance regimes.

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We describe the frequency of occurrence of natural disturbances (fire, snow and wind damage, insects) and the volume of large trees, deciduous trees, snags and coarse woody debris (CWD) in an area with a short (ca 50 yr) forest management history. On average signs of natural disturbance events were observed on 94% of the surveyed field plots. The frequency of occurrence of fire signs (scars, burnt stumps) varied from 8% in the young stands to 32% in the mature and over-mature stands, and 89% of plots had uprooted and broken trees (signs of snow and wind damage). Trees infested with bark beetles were found in 0.6% of the middle-aged stands, 1.0% of the maturing stands, and 3.0% of the mature and over-mature stands. The proportion of deciduous trees in the stands changed during the course of succession after stand-replacing disturbance from 70% in young stands to 50% in mature and over-mature stands. The basal area of trees with a diameter of > 30 cm varied from 0 to 24, reaching a maximum in aspen-dominated stands. The average volume of CWD changed over time from 21 m^3 ha^{-1} in young stands, to 51 m^3 ha^{-1} in mature and over-mature stands. The contribution of snags and stumps to the total amount of CWD was very low compared to that of downed wood. A combination of stand age, dominant tree species, small-scale disturbances and site productivity explained the variation in CWD. Classes of CWD in advanced stages of decay dominated in the forests in earlier successional stages, while CWD in the earlier stages of decay dominated in late successional forests.

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Until recently, most people considered forests to be inexhaustible wood factories. Along with increasing public awareness of the concept of biodiversity and the concomitant development of conservation biology (e.g. Hunter 1996, Hansson and Larsson 1997), forests have gradually come to be seen from a different point of view. The focus of forest management has shifted from a strong emphasis on sustained yield and the production of pulp and timber to a broader perspective, including maintaining the vitality and health of forests, their protective and socio-economic functions, as well as biodiversity and carbon cycle (Parvianen 1996). Sustaining the forest ecosystem and maintaining its biodiversity means ensuring the long-term survival of naturally occurring species in viable populations, and maintaining the important structures and processes which affect the sustainability of the ecosystem (Angelstam 1998a).

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Compared with pristine conditions, changes in land use and forest management in the western European part of the boreal forest region have altered the composition and structure of both the stands and landscapes (Angelstam et al. 1995). The two most important consequences of modern, large-scale forestry are the loss of habitats and the transformation of remaining habitats into homogeneous, productive structures. The regular thinning of stands, clear cut harvesting, efficient forest fire prevention, usage of dead wood for construction and fire-wood, the threat of insect pests, and the practice of salvation logging after natural disturbances such as windthrow, have all contributed to an overall decrease of biodiversity in managed forests (Esseen et al. 1992).

The natural forest landscapes are characterized by a range of disturbance regimes including long continuity of forest cover on sites with frequent low-intensity disturbance, the occurrence of all successional stages after stand-replacing fire, as well as stands with endogenic gap-phase dynamics (for details see Angelstam and Kuuluvainen 2004). The distribution and amount of the natural components of boreal forests have been altered in managed forests. At the stand scale, the presence of old and large trees, burnt wood, snags, downed wood of different decomposition stages is of great importance for the maintenance of biological diversity (Esseen et al. 1992, Samuelsson et al. 1994). An important aspect is the maintenance of the processes that affect habitat renewal. Small-scale disturbances such as insect outbreaks, snow- and wind-caused stem breakage, uprooting, as well as fires, have to be maintained in order to provide for biological diversity (Angelstam and Dönz-Breuss 2004).

This study focuses on quantifying functional and structural elements of biodiversity (Larsson et al. 2001) in boreal forests with a short history of use and management in Russia. Four specific objectives were defined, viz.: 1) to determine the frequency of occurrence of natural disturbances in stands with different successional stages and tree species composition, 2) to estimate the amount of large trees and deciduous trees, 3) to examine the impact of forest age, tree species composition, site productivity level, and disturbances on the CWD volume, and 4) to analyze the CWD distributions by tree species, wood type and decay class. Finally, we discuss some aspects of the biodiversity-oriented management for the region.

Material and methods

Study area

The field data for this study were collected in the Novgorod (58°N, 32°E) region, situated in the northwest of the European part of Russia (Fig. 1). The region occu-

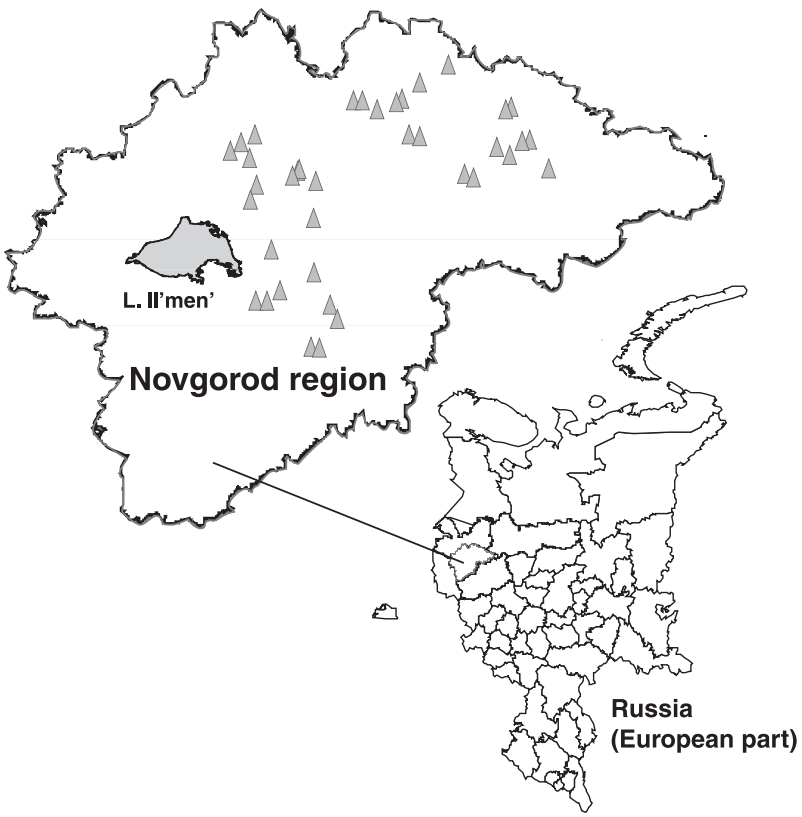


Fig. 1. The Novgorod region, with the location of the studied stands (compartments) shown with triangles.

pies 55 000 km^2 and 63% of this area is currently covered with forests. The climate is mildly continental, with a short and cool summer, warm and long autumn, mild winter and long cool spring. The mean annual temperature is +3.7°C, and the mean length of the growing period is 110–130 d. Annual precipitation varies from 550 to 800 mm depending on the relief. The prevailing wind direction is from the south. Storms occur very rarely. The soils are mostly of the podzol type on deep loamy to sandy sediments. Carbonaceous soils also occur in places.

According to the forest inventory from 2002, the Novgorod region comprises 23 forest management units (leskhozes), the Novoselitskoye Experimental Area, the Valdaisky National Park, and the Rdeisky State Nature Reserve (Chystyakov 2003). The total area under the management of leskhozes is 3.86 million ha including forest lands covering 3.32 million ha, and 2.55 million ha of artificially regenerated stands. In addition, there is also a total of 195 000 ha of protected forests.

Forests of the first category (meaning that harvesting is not allowed) under the management of leskhozes cover 0.88 million ha (23%), including the following types of protected areas: shelterbelts along railways and roads (0.10 million ha); green belts of settlements and industrial areas (0.37 million ha), park belts (0.02 million ha); shelterbelts in forests along river banks, lake shores, water reservoirs and other water bodies (0.38 million ha).

Forests of the second category (exploited forests) cover an area of 2.98 million ha (77%). The dominant species are 41% birch *Betula pendula* Roth., 19% Scots pine *Pinus sylvestris* L., 19% Norway spruce *Picea abies* (L.) Karst., 11% aspen *Populus tremula* L., 9% alder *Alnus incana* L., and 1% other species (Table 1). According to the 2002 statistics, the total area of wetlands in the territory of the forest fund of the leskhozes is 0.41 million ha, or 11% of the total area of the forest fund. The territory of the fourth site index (Moshkalev 1984) and lower comprises a total of 17% of the forest area. The total growing stock of forest stands is 561.9 million m^3, including 208.2 million m^3 of conifers, 236.0 million m^3 of mature and over-mature stands, including 62.78 million m^3 of conifers. The stock of the stands suitable for harvesting totals 487.6 million m^3 (87% of the total stock), including 178.9 million m^3 of conifers (86%), mature and over-mature stands – 206.6 million m^3 (88% of the total stock of mature and over-mature stands), including 54 million m^3 of conifers (86%). The average stock per hectare of forest land is 169 m^3, and in mature and over-mature stands 224 m^3. The average age is 55 yr. Artificially regenerated stands with incomplete crown closure occupy an area of 0.03 million ha.

The forests of the Novgorod region have approximately a 50-yr management history. The volumes of timber cut in main logging operations are equivalent to 2.8–3.0 million m^3. An increase in these figures is expected, owing to the development of rental practices whereby harvesting companies buy logging contracts from the state, to 3.2–3.4 million m^3 per year by 2005. Additionally, it has been estimated that 0.026–0.056 million m^3 of timber are annually cut illegally (Lioubimov pers. comm.). Thinnings in young stands have been planned at the levels recommended on the basis of the forest inventory, and they are performed annually on an area of 0.02 million ha. The program for forest regeneration for the period 2002–2010 envisages forest regeneration activities over an area of 1.00 million ha, including planting on 0.05 million ha. The low level of investments in the forestry sector is the main reason for the current low level of regeneration activities after harvesting in the Novgorod region during the last few years.

Using a combination of surface and aerial inspection of the forest fund during dry seasons wildfire is counteracted. This system is effective in the region, and only conditions such as abnormally hot and dry weather are able to convert small-scale forest fires into uncontrolled conflagrations. The three forest fire peaks in 1992, 1997, and especially in 1999, coincided with abnormally dry and hot summers. The area burnt by these fires was 735, 1884, and 7336 ha, respectively.

General sampling design, field measurements and calculation procedures

The frequency of occurrence of natural disturbances and the estimates of the volume of different tree species, snags and dead wood were determined as a part of the regular forest inventory in the region, the methodology of which has been described by Laasasenaho and Päivinen (1986).

Table 1. Dominant species and age structure of the forests in the Novgorod region 2002.

Age groups	Total area		Scots pine		Norway spruce		Birch		Aspen		Other	
	1000 ha	%	1000 ha	%	1000 ha	%	1000 ha	%	1000 ha	%	1000 ha	%
Young	510.1	15	87.7	13	257.7	40	91.6	6	27.5	7	45.6	12
Middle-aged	1087	31	272.6	41	131.9	20	569.1	40	30.9	8	82.5	22
Maturing	792.2	23	171.5	26	121.4	19	339.6	24	56.7	15	103.0	28
Mature and over-mature	1070.1	31	126.4	19	132.6	21	417.5	29	256.0	69	137.6	37
Total	3459.4	100	658.2	100	643.2	100	1417.8	100	371.1	100	368.7	100

The approach is based on systematic measurement of the basal area of trees using relascope sampling of a randomly selected compartment in a randomly selected block. Basal area measurement means that no fixed plot size is used. However, the approximate size of the plots can be estimated as a circle with a radius of 20–30 m. The diameters of all the trees included in the basal area estimate were also measured. Depending on the area of the compartment (varying from 1 to 3.5 ha), 8–13 relascope sample plots were placed in each compartment. These sample plots were located systematically along survey lines running north–south. The survey line spacing is the same as the sample plot spacing. A total of 1298 plots, 168 compartments, 58 blocks, 22 forest management units (lesnitchestva), in 4 forest enterprises (leskhozes) were inventoried.

The presence of signs of wind and snow damage (uprooted and broken trees), insect outbreaks (signs of bark beetle activity on living trees), fires (fire scars, burnt stumps), were registered on each sample plot. The frequency of occurrence of each kind of disturbance was expressed as the percentage of all the plots on which it occurred.

Line intercept sampling was used in the downed wood inventory (Ståhl et al. 2001). The volume of downed wood was calculated as:

$$V = (\pi^2/8 \sum d_i^2 S) \sum L_j \quad (1)$$

where: V = volume of the downed wood of the i-th decay class, d_i = diameter of the i-th wood unit at the point of interception of the survey line, L_j = length of the survey line (in our case 20 m for each sample plot, or in some cases 10 m), and S = area of the stand. The number of snags (height < 1.3 m) and stumps with a diameter of > 4 cm was counted on the 50 m^2 area which was determined using a 3.99 m long rod. The total number of units with identified species and decay class were determined for each plot. The volume of stumps by tree species and decay class per hectare was calculated as:

$$V = 0.3 * \pi * (D/2)^2 * 200 \quad (2)$$

where D is the diameter of the stump. As we did not measure the stump diameters in the field, this value was assumed to equal the average diameter of the living trees on the plot after taking into account the tapering. Thus, D was calculated:

$$D = 1.1493 * D' + 1.4387 \quad (3)$$

where D' is the average DBH diameter of living trees by tree species on the plot. The standing dead trees (snags) were measured on the relascope sample plots. Their volumes (V) were calculated using the formula:

$$V = k * S * HF \quad (4)$$

where k = a coefficient that takes into account that some snags were broken (equal to 1 for whole snags, and 0.75 for broken ones), S = the snag basal area at breast height (m^2), HF = the species-special height (m). HF was calculated according to the following equations (Moshkalev 1984):

$HF = 1.0781763 * (H - 0.2854016)^{0.7355895}$ – for pine.
$HF = 0.9794946 * (H - 0.3943532)^{0.7784542}$ – for spruce.
$HF = (0.1323202 + 287.31854 * H^{0.9225193})/(475.53904 + H^{0.9225193})$ – for birch.
$HF = 0.1882703 * (H + 6.0838478)^{1.2044838}$ – for aspen and other deciduous species.
H – the average height of a given tree species in the compartment.

In the CWD inventory we used the decay class system described in Shorohova and Shorohov (2001). Briefly, these five decay classes can be characterized as: 1) Volume of decomposed wood is 0–10%. Other wood is sound. Bark may be present or absent due to bark beetle activity. Sporocarps of wood decay fungi are absent. Only epiphytic lichens may be present. 2) Slightly decomposed wood accounts for 10–100%. Other wood is sound. Sporocarps of wood decay fungi and epixylic mosses may be present. 3) Decayed wood (soft rot) accounts for 10–100%. Other wood is slightly decayed or sound. Inclusions of mycelium, small pits and cracks occur. Wood may be crumbled or broken. Sporocarps of wood decay fungi occur. Coverage of mosses, lichens and higher plants can be up to 100%. Tree seedlings may be present. 4) All wood is well decayed. Wood samples of white rot are fragmented into separate fibres. Humification processes have started in the brown rot wood. Some pieces of wood have been lost via fragmentation and complete decomposition. Other features are the same as for decay class 3. 5) Types and borders of rot are difficult to distinguish. Pieces of CWD have significantly changed shape. Humification is continuing. Sporocarps of wood decay fungi are absent or very old. Vegetation on the trunk is similar to the ground vegetation, but with a higher number of tree seedlings and undergrowth.

Data analysis

The plot measurements were grouped by dominant tree species, age of the living trees, site class, development stage, and by observed signs of disturbances. The site class was determined from the forest inventory data. According to Orlov's scale, site class ranges from 1a (best site conditions) to 5b (poorest site conditions). The site class is determined on the basis of the age and height of the dominant tree species using special mensuration tables (Moshkalev 1984). The development after stand-replacing disturbance was divided into four stages. viz.: young (Y), middle-aged (MI), maturing (MA), mature and over-mature (MO). The corresponding age interval for young stands was 0–20

yr. For middle-aged stands the interval depended on tree species and was 41–60 yr for coniferous, 21–50 yr for birch and 21–30 yr for aspen. For maturing stands the corresponding classes were 61–60 yr (coniferous), 51–60 yr (birch) and 31–40 yr (aspen). Finally, maturing and over-mature stands were defined as 81–200 yr for coniferous, 61–100 yr for birch, and 41–80 yr for aspen. ANOVA analyses (Statistica software) were used to estimate the impact of different factors on the CWD variance.

Results

Natural disturbances

Signs of natural disturbance events were observed on 94% of the inventoried relascope plots. The proportion of plots with fire signs (scars, burnt stumps) varied from 8% in the young stands to 32% in the mature and over-mature stands (Table 2). A total of 89% of the plots had uprooted and broken trees (signs of snow and wind damage). Trees with bark beetles were found on 0.6% of the plots in the middle aged stands, 1.0% of the plots in the maturing stands, and 3.0% of the plots in the mature and over-mature stands.

Large trees and deciduous trees

The proportion of deciduous trees in the stands ranged from 0 to 100%, and averaged 50%. The proportion changed over the successional stages: from 70% in young stands up to 49% in mature and over-mature stands (Table 2). The basal area of trees with a diameter of > 30 cm on the relascope plots varied from 0 to 24 $m^2 ha^{-1}$ and was at its maximum in the maturing, mature and over-mature aspen dominated stands (7 $m^2 ha^{-1}$).

Coarse Woody Debris (CWD)

The mean volume of CWD (snags, stumps and downed wood) was 40±1.8 $m^3 ha^{-1}$. The CWD stores differed significantly between the stands with different tree species composition (Fig. 2). Maximum values were observed in the aspen (85±2.1 $m^3 ha^{-1}$) and alder (65±1.9 $m^3 ha^{-1}$) dominated stands. Scots pine dominated stands had the lowest CWD volumes (29±0.6 $m^3 ha^{-1}$). The proportion of snags and stumps out of the total CWD was highest in the Norway spruce dominated stands (6±0.2 $m^3 ha^{-1}$, or 12%). However, the volume of snags and stumps was relatively low in all types of forest. The volumes of these CWD types averaged 3±0.2 $m^3 ha^{-1}$ (range 0–49) for stumps, and 0.5±0.03 $m^3 ha^{-1}$ (range 0–20) for snags.

According to the plot data, the average volume of CWD changed over successional stages from 21±9.6 $m^3 ha^{-1}$ in the young stands, to 51±3.0 $m^3 ha^{-1}$ in the mature and over-mature stands (Fig. 3). The proportion of snags and broken tree (natural) stumps increased with stand age from 4 to 10% of the total CWD. Site conditions also influenced the CWD stores. CWD volume decreased along with reduced site productivity from 57±7.0 $m^3 ha^{-1}$ (site class 1) to only 1±0.9 $m^3 ha^{-1}$ (site class 5a). The CWD volumes in the stands subjected to fires were, on the average, 86% higher than those in the stands without fires. The effect of fires was pronounced in the young and middle aged stands, especially in those dominated by birch and pine. The results of ANOVA show the influence of individual factors on the volumes of total CWD, snags, and downed wood. The effect of the examined factors (development stage, dominant tree species, site index, all disturbances and fires) on all the variables was high and significant. Fires had the strongest impact on the volumes of total CWD and downed wood. The volume of snags was determined chiefly by the dominant tree species (Table 4).

The distribution of CWD by decay class varied with forest development stage (Fig. 4). In the younger stands most of the CWD volume belonged to decay classes 3–5, while in the older stands most of the CWD material was in decay classes 1–3. Most of the CWD in the latter decay classes was derived from the cut stand previously occupying the site. This woody material decomposed during the course of stand development from young stands to middle-aged ones. New CWD began to accumulate in maturing stands. The maximum total volume of CWD and the volume of CWD in decay classes 1–3 were reached in the mature and over-mature stands.

Table 2. Frequency of natural disturbances, large trees and deciduous trees in the stands of different development stage. Values are means ± SE.

Development stage, (n)	Frequency of disturbance, %			Trees with DBH > 30 cm, #	Deciduous trees, %
	Fires	Wind and snow damage	Bark beetles		
Young (25)	8	80	0	0±0.120	70
Middle-aged (183)	16	85	1	1±0.139	54
Maturing (517)	31	90	1	3±0.121	48
Mature and over-mature (573)	32	90	3	6±0.187	49
All plots (1298)	30	89	2	4±0.109	50

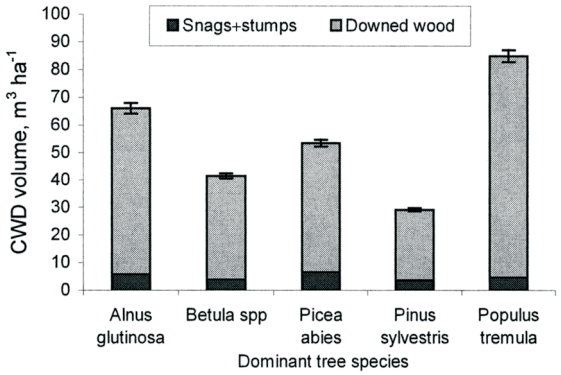


Fig. 2. Differences in CWD volume according to the dominant tree species of the stands on the sample plots. Values are means. Confidence intervals are SE calculated for the total CWD volume (downed wood + snags + stumps).

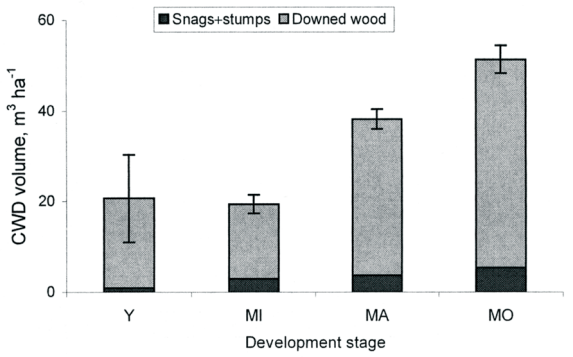


Fig. 3. Differences in CWD volume according to the development stage of the stand on the sample plots. Y = young, MI = middle aged, MA = maturing, MO = mature and over-mature. Values are means. Confidence intervals are SE calculated for the total CWD volume (downed wood + snags + stumps).

Our results showed high spatial variance of all CWD types. The variation coefficient (CV) for the total CWD in the compartments averaged 95±3.0% (range 30–230). When calculated separately, this coefficient was even higher for a number of CWD types, 138±5.0% for snags, 112±4.0% for downed wood, and 127±4.3 for stumps, as these were absent on many of the sample plots. However, when we considered the CWD volume in stands dominated by different tree species, the variation decreased. The CV varied with tree species composition as follows: 57±0.1% for alder, 76±6.4% for aspen, 78±6.2% for spruce, 94±7.0% for birch, and 104±4.2% for pine dominated stands.

According to the compartment data, the volume of living trees increased from the young (mean 165 m^3 ha^{-1}) to maturing and older forests (range 187–301 m^3 ha^{-1}) (Table 3). The volume of CWD was lowest in the young forests (mean 13 m^3 ha^{-1}). The maximum CWD volumes were observed in mature alder forests (mean 93 m^3 ha^{-1}), followed by mature spruce (mean 60 m^3 ha^{-1}) and birch (mean 45 m^3 ha^{-1}) forests. The trend for the downed wood was the same as for the total CWD, while the pattern was different for stumps and snags. The maximum volume of snags and stumps was found in mature spruce forests (mean 7 m^3 ha^{-1}). The proportion of snags and stumps was higher in coniferous forests than in deciduous ones. However, the contribution of snags and stumps to the total CWD stores was very low in comparison with that of downed wood.

The CWD/live wood ratio averaged 0.2±0.02, ranging from 0.0 to 1.1 and increasing from young to maturing and older stands. This ratio was the highest in mature aspen stands (mean 0.4), followed by mature birch (mean 0.3) and spruce (mean 0.2) stands (Table 3). The downed

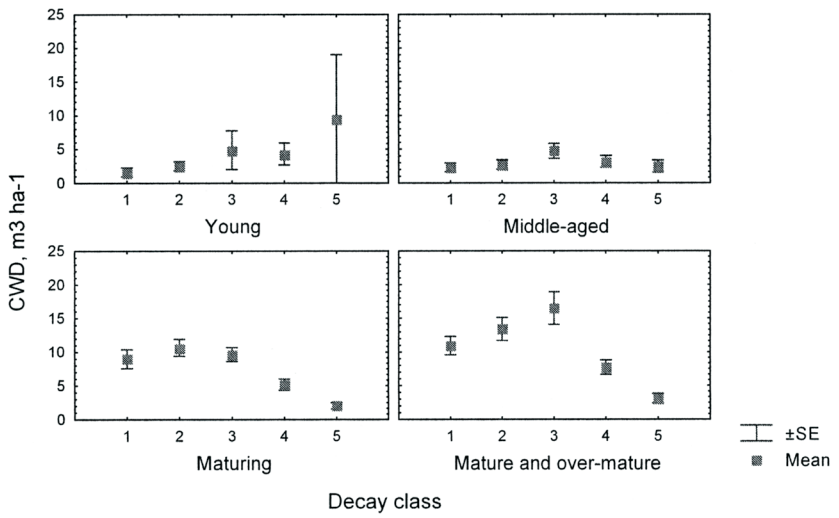


Fig. 4. The distribution of CWD volume in m^3 ha^{-1} on the sample plots by decay class (1–5).

Table 3. CWD stores, m^3 ha^{-1} (SE), and the CWD/live wood volume ratio (SE).

Species group	Age group (number of compartments)	Volume of living trees, m^3 ha^{-1} (SE)	Volume of total CWD, m^3 ha^{-1} (SE)	CWD/live wood ratio (SE)	Downed wood, m^3 ha^{-1} (SE)	Snags and stumps, m^3 ha^{-1} (SE)
All	Young (4)	165.2 (4.60)	12.6 (1.03)	0.03 (0.01)	8.6 (1.51)	4.0 (1.31)
Pine	Middle-aged (21)	171.4 (3.02)	13.9 (2.93)	0.10 (0.02)	10.8 (2.36)	3.1 (1.36)
	Maturing and older (65)	206.6 (4.37)	35.2 (5.08)	0.18 (0.02)	31.2 (3.87)	4.0 (1.40)
Spruce	Middle-aged (4)	227.5 (10.22)	20.4 (0.67)	0.10 (0.02)	16.0 (8.00)	4.4 (1.99)
	Maturing and older (14)	300.7 (12.26)	60.8 (4.19)	0.22 (0.04)	53.4 (14.28)	7.4 (1.67)
Birch	Middle-aged (3)	133.3 (10.17)	17.6 (3.72)	0.16 (0.10)	15.4 (8.91)	2.2 (1.35)
	Maturing and older (27)	187.1 (8.68)	45.1 (4.24)	0.26 (0.03)	41.0 (7.89)	4.1 (1.56)
Aspen	Maturing and older (14)	250.7 (24.73)	92.5 (7.46)	0.42 (0.08)	87.8 (3.47)	4.7 (1.13)

wood/live wood ratio varied correspondingly. The snags and stumps/live wood volume ratio ranged from 0.0 to 0.1. However, only the difference between young stands and middle-aged birch stands and the other groups was statistically significant.

Discussion

Biodiversity components in managed and natural forests

Almost all of our study plots had signs of natural disturbances. Fire scars and burnt wood were observed in 30% of the stands. Wind and snow damage occurred, on the average, on 89% of the plots. Stem breakage and uprooting occurred in stands of all successional stages. The fact that the studied stands had not been thinned probably explains such a high proportion of damaged trees. According to the literature, trees suffering from snow damage are also more prone to subsequent damage though insect or fungal attack (Nykänen et al. 1997). In our study, the proportion of stands with signs of bark beetle activity on living trees was relatively low.

A 93% decline in the basal area of deciduous trees from pristine (Komi Republic, Russia) to intensively managed (Scotland) forest landscapes was reported by Angelstam (1998b). The proportion of deciduous trees in the stands of our plots ranged from 0 to 100%, with an average of 50%. The proportion was high in stands of all successional stages. This means that there was both a high proportion of deciduous dominated stands in the landscape and a high proportion of deciduous trees in the coniferous dominated stands. Almost all the clear-felled and other open areas in the Novgorod region are regenerated naturally. In most cases, the pioneer tree species birch and aspen first occupy the open areas, and, if they are not removed in intermediate harvesting, they are not completely replaced by spruce by the end of the rotation period. In boreal forests developing according to natural dynamics, the proportion of deciduous species strongly depends on the successional stage of the ecosystem. It may be high in the young stands developing in gaps after a windthrow, for example. However, in the late-successional, uneven-aged forests the proportion of deciduous trees does not exceed 30% (Fedorchuk et al. 1998).

The number of large trees decreased by 86% from pristine forest landscapes to landscapes having a long and very long land-use history (Angelstam 1998b). Our data showed a high number of large trees, despite the fact that the studied stands had a relatively low site index. Trees with a DBH above 30 cm occurred even in the young stands; they had either been left during the preceding logging operations, or were remnants of the previously burned or windblown stand. Most of the stands in the studied region have an irregular tree diameter structure that should help to maintain biodiversity.

Table 4. Results of ANOVA on the effect of different factors on the CWD volumes on the sample plots.

		CWD total			Downed wood			Snags		
	DF	Effect, %	F	p-level	Effect, %	F	p-level	Effect, %	F	p-level
Development stage	3	94	15.35	0.000	93	13.25	0.000	96	22.15	0.000
Dominant tree species	4	97	36.86	0.000	97	35.98	0.000	95	19.88	0.000
Dominant + dev. stage	12	61	1.58	0.092	58	1.39	0.162	64	1.76	0.050
Site class	5	93	12.95	0.000	92	11.73	0.000	90	8.70	0.000
All disturbances	3	97	28.89	0.000	97	29.00	0.000	84	5.26	0.001
Fire	1	99	89.56	0.000	99	87.32	0.000	94	15.35	0.000

The volume of CWD in a natural forest stand depends on three factors: 1) the productivity of the site and successional stage of the stand, which affect the input rate of dead wood, 2) the decomposition rate of dead wood, and 3) the disturbances affecting the input rate and stand succession (Harmon et al. 1986). Management regimes therefore determine the amount of CWD in managed forests.

In areas with a long history of forest management the amount of dead wood is low. For example, in southern Finland, the average CWD volumes vary from 1.2 to 2.9 m^3 ha^{-1} depending on the region (Tomppo et al. 1998, 1999a, b, c, cf. Siitonen 2001). The volumes of CWD in the southern boreal zone of Sweden change with forest age: from 2.0 m^3 ha^{-1} in young forests (0–40 yr), to 7.2 m^3 ha^{-1} in mature forests (101–140 yr), to 11.7 m^3 ha^{-1} in forests older than 140 yr. The volume of snags varies from 1.5 to 2.0 m^3 ha^{-1}. The greatest amount of CWD occurs in Norway spruce dominated forests (Fridman and Walheim 2000).

By contrast, where the land use history is shorter, the amount of dead wood is higher. In the St. Petersburg region, the average volume of CWD is high, but varies among successional stages (Krankina et al. 2001). The highest values (186 m^3 ha^{-1}) were observed in recently disturbed forests, and the lowest (2.1 m^3 ha^{-1}) in young forest stands between the ages of 21 and 40 yr. Forests older than 120 yr had 55 m^3 ha^{-1}. The volume of downed dead wood exceeded the snag volume in all stands, except for recently disturbed areas. The CWD ratio is generally higher in coniferous than in deciduous forests, and increases with forest age in both species groups (Treyfeld 2001, Krankina et al. 2001).

Our results also show that the average volume of CWD changes during the successional development: from 21±9.6 m^3 ha^{-1} in young stands, to 51±3.0 m^3 ha^{-1} in mature and over-mature stands. The availability of CWD within early stages of forest development was almost entirely dependent on the history of the individual stand as it was composed of a combination of pre-disturbance debris, disturbance generated debris, and residual standing dead trees. In contrast, CWD within later successional stages must be generated by the present stand, and is therefore dependent on the structure of the standing forest. A "U-shaped" temporal trend for CWD volume after stand-replacing disturbances, including harvesting, has been reported for different, both managed and unmanaged forest ecosystems. Debris levels tend to be high following the initial stand disturbance. Residual CWD then declines over time, with little additional input from the regenerating stand. As the stand matures, tree mortality due to competition and small-scale disturbances contributes to the CWD store. The CWD levels usually peak during the over-mature stage as the even-aged stand senesces into a more uneven-aged structure. We found a "U-shaped" curve of CWD dynamics in all our stands. However, the parameters of the curve varied according to the dominant tree species, which reflects different rates of CWD accumulation and decomposition in these stands. The proportion of snags and broken trees (natural) stumps increased with forest age from 4.2 to 10% of the total CWD. During successional development, a stand produces snags as a result of natural competition. Thus, the volume of snags increases with stand ageing especially in stands that have not been thinned.

One can thus see that the study areas referred to in the above represent a gradient of forest management intensity and, consequently, a gradient of CWD amounts and quality (cf. Angelstam 1998b, Angelstam and Dönz-Breuss 2004). The total CWD volumes increase when moving from Sweden and southern Finland on the one hand, to the St. Petersburg and Novgorod regions on the other. The more intensive the forest management, the less is the impact of other "natural" factors on CWD. For example, Fridman and Walheim (2000) did not find any relationship between forest type and the volume of CWD. Forest age and tree species composition were the only factors influencing the CWD stores. Neither were Treyfeld (2001) nor Krankina et al. (2001) able to find any significant effect of site productivity on CWD volume and on the CWD/live wood ratio. Disturbances affected CWD only at the stand initiation phase and only in restricted areas.

In contrast, according to our data from the Novgorod region, which has a very short history of forest management, several factors such as stand age, dominant tree species, the occurrence of small-scale disturbances, and site productivity, contributed to the variance of CWD. Downed wood was the predominant form of CWD in all the stands studied. CWD of the earlier decay classes was dominant in the forests in the earlier successional stages, while CWD in the advanced decay classes was dominant in the late successional forests.

In pristine, southern and middle boreal mesic spruce-dominated forests without stand or cohort replacing disturbances (Angelstam and Kuuluvainen 2004), the average CWD volumes vary from ca 90 to 120 m^3 ha^{-1} (Kuuluvainen et al. 1998, Jonsson 2000, Siitonen et al. 2000, 2001, Shorohova and Shorohov 2001, Uotila et al. 2001, Storozhenko 2002). The proportion of CWD out of the total stand volume (living + dead) varies from 18 to 40%. The proportion of snags found in spruce dominated forests varies from 9 to 46%. The occurrence of cohort-replacing windthrow disturbances in such forests may increase the volume of CWD up to 206 m^3 ha^{-1} (Shorohova et al. 2002), i.e. consisting of all the trees in the previous stand.

CWD volumes reported for southern and middle boreal pine-dominated old-growth forests vary from ca 60 to 160 m^3 ha^{-1} (Rouvinen and Kuuluvainen 2001, Karjalainen and Kuuluvainen 2002). The proportion of CWD out of the total stand volume varies from 18 to 50%. CWD volumes and proportions in mesic-dry pine-dominated forests do not seem to differ essentially from those in mesic spruce dominated forests. Snags make up 20–40% of the total CWD (Siitonen et al. 2000, Rouvinen and Kuuluvainen 2001, Karjalainen and Kuuluvainen 2002).

Windthrow areas in pristine southern boreal mesic spruce forests contain 132–265 m^3 ha^{-1} of CWD (Linder et al. 1997, Siitonen et al. 2000, Shorohova et al. 2002). The volume of CWD in younger post-fire successional forests dominated by pine or deciduous trees is ca 111–226 m^3 ha^{-1} (Linder et al. 1997, Uotila et al. 2001). Semi-natural, young mesic coniferous forests store 124.9 m^3 ha^{-1} of CWD, while in sub-xeric conditions the volume of CWD in young forests decreases to 25.4 m^3 ha^{-1} (Uotila et al. 2001).

Structural complexity is a characteristic feature of the dead wood of natural forests. Uprooting and stem breakage are typical for spruce, while pines mostly die standing and form long-lasting snags. Deciduous trees, such as birches and aspen, tend to snap after they have died, thus forming broken snags. Because of differences in size and position, the CWD in harvested areas decays more rapidly and persists for a shorter time than the CWD on fire-killed sites. Generally, the CWD distributions by decay class have either a bell-shaped form, or even a maximum in latter decay classes (Jonsson 2000, Shorohova and Shorohov 2001, Storozhenko 2002).

Thus, semi-natural and pristine forests contain more than ten times more CWD than mature managed forests. The effects of management are strongest in young forests when clearcuts are compared with stand replacing disturbances such as fire or windthrow. Timber harvesting especially affects the frequency of snags (the reduction may be even > 90%, Linder and Östlund (1998)) and the amount of CWD of latter decay classes. The disturbance regime related to the successional state of the stand and site conditions determine CWD volume and quality in natural forests. In intensively exploited forests these effects are overlapped by management activities.

Implications for conservation, management and research

In order to ensure the long-term maintenance of biodiversity in boreal forests, forestry practices should imitate natural disturbances such as fire, windthrow and flooding, and avoid management in no fire refugia (Angelstam 1998a). In the Scandinavian countries, where intensive forest management is widely employed, this would require not only protection of the important habitats and leaving trees during final harvest, but also the formation of specific structures and the maintenance of natural processes, including the prescribed burning of stands, the active creation of snags during harvesting (Raivio et al. 2001).

After listing the properties which reflect the composition and structure of naturally dynamic boreal landscapes at different geographical scales, the next step is to determine the critical thresholds regarding the amount of properties, occurring in naturally dynamic landscapes, that is sufficient for maintaining biodiversity in the managed landscape (Angelstam 1998c). In order to determine the management strategy for each biodiversity component, one should first compare the data on this component for the forest landscapes, which have a different land-use history, and then outline the connection between this component and the different groups of species.

Another question is what sort of biodiversity management would be appropriate? The first idea was to develop minimum standards for the amount of each structural element to be retained in harvested units. Esseen et al. (1992) suggested that landowners should leave 5–20 big trees per hectare to mature, die, and decay naturally. This has also been included in the criteria for certification according to the Forest Stewardship Council Working Group in Sweden. They require that at least 10 living trees per hectare should remain after harvest operations, and that all dead wood should be retained. The main forest companies in Sweden have ratified this proposal.

While minimum standards are an improvement in terms of retaining ecological functions, they also have certain problems. This includes the negative effect of homogenizing the properties in space and time, without considering the variability of stands in terms of for example successional stage and forest type (Sippola et al. 1998, Harmon 2001). In view of recent studies focussing on CWD management, the emphasis should be shifted from a static to a dynamic perspective (Harmon 2001, Bengtsson et al. 2003). In practical forest management this means the regulation of mortality, i.e. the process that creates CWD, and choosing the appropriate rotation period. The lack of knowledge on mortality factors and its variation in space and time is a challenge for forest ecologists. Deciding how much CWD is adequate requires knowledge of how various organisms or ecosystem functions vary according to the amount and arrangement of this material (e.g., Bütler et al. 2004). Consequently, which species or processes are to be maintained, restored, or otherwise managed? Perhaps the more complicated question to answer is why other types of structure (for example, old hollow trees) may or may not compensate for CWD? The final element to forming a new paradigm for CWD management involves spatial arrangement. This applies to all spatial scales from that of trees in stands, and to landscapes in regions (Hebert 2004). At the landscape level, the first consideration might be whether the process or habitat provided by CWD is ubiquitous or restricted to certain locations (Angelstam et al. 2003, 2004).

To address the above questions one should compare the temporal and spatial availability of biodiversity components in the landscapes in a gradient of forest management history – from pristine to intensively managed landscapes. Our study provides information for a managed boreal forest region located in the middle of the gradient of this land use intensity. The probability of successful maintenance of the naturally occurring species in this boreal landscape is high, provided that the processes and structures crucial for biodiversity are allowed to occur.

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Natural forest remnants and transport infrastructure – does history matter for biodiversity conservation planning?

Per Angelstam, Grzegorz Mikusiński and Jonas Fridman

Angelstam, P., Mikusiński, G. and Fridman, J. 2004. Natural forest remnants and transport infrastructure – does history matter for biodiversity conservation planning? – Ecol. Bull. 51: 149–162.

To access Sweden's wood resources during the past 150 yr, waterways for timber log driving were prepared and the networks of railroads and roads were developed. We related this human footprint to today's amount of dead wood and protected natural forest remnants.

The accumulated transport infrastructure over time was used as a surrogate measurement of past harvesting intensity in 25 × 25 km grid cells within two study areas in northern boreal forest (Norrbotten and Västerbotten) and one area in southern boreal and hemiboreal forest (central Sweden). The accessibility of the landscape was estimated as the length per grid cell of roads in northern Sweden and railroads in central Sweden, calculated at 50-yr intervals since 1850. Because terrain ruggedness affected the development of log driving on waterways in a given area, we used a 50 × 50 m digital elevation model to calculate the mean slope within grid cells as an estimate of inaccessibility.

We found negative relationships between the amount of dead wood and transport infrastructure (accessibility) in all three study areas. The proportions of variation in dead wood explained by the indices of accessibility and inaccessibility in Norrbotten and Västerbotten were 18 and 28%, respectively. For central Sweden, the total amount of variation explained was only 9%. The average amount of dead wood was lower in central Sweden (2.1 m^3 ha^{-1}) than in Västerbotten (3.7 m^3 ha^{-1}) and Norrbotten (4.0 m^3 ha^{-1}). For the area of natural forest remnants, significant relationships were found in northern but not in central Sweden. A total of 41% (Norrbotten) and 54% (Västerbotten) of the variation in today's amount of protected forest remnants were explained by the indices of accessibility and inaccessibility.

We interpret differences in amount of dead wood and protected forests among regions as a consequence of anthropogenic impacts on local landscapes having occurred before the advent of the modern transport infrastructure. We also stress the need to be aware of the degree of deviation from natural conditions in present landscapes when formulating regional conservation goals.

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An issue of paramount importance in sustainable forest management is how to strike the balance between the use of renewable resources and the maintenance of biological diversity (Hunter 1999, Lindenmayer and Franklin 2002). Analyses of the life-history traits of endangered species show that they require habitat components that are commonly found only in naturally dynamic forests (e.g. Berg et al. 1994). Such components include large trees, old trees, a diverse tree species composition and different types of dead wood, often concentrated in remnants of naturally dynamic forests (e.g. Peterken 1996). Due to a lowered mean age of the forests and more intensive forest management, loss of dead wood is one of the most general consequences of intensified forest management (Siitonen 2001). Similarly, protected or remotely located forests usually represent the last remnants of near-natural forest (Angelstam and Andersson 2001, Yaroshenko et al. 2001, Aksenov et al. 2002, Götmark and Thorell 2003).

Dead wood of different forms constitutes 20–25% of the total number of species in boreal forests (Siitonen 2001). Several studies have documented the amount of dead wood in forests with different histories (Sippola et al. 1998, Fridman and Walheim 2000, Siitonen 2001, Stokland 2001, Jonsson and Kruys 2001, Nilsson et al. 2002, Angelstam and Dönz-Breuss 2004, Shorohova and Tetioukhin 2004). In naturally dynamic old boreal forests the amount of dead wood is 60–90 m^3 ha^{-1} (Siitonen 2001). A general pattern is that ca 30% of the total biomass consists of dead wood of different kinds including standing and lying trees of different size and decay stages (Nilsson et al. 2002). In forests recently subjected to stand scale disturbances, such as fire and wind, the proportion of dead wood is considerably larger.

By contrast, in forests with a long management history, such as in central Sweden and Scotland, the amount of dead wood is considerably lower (ca 2 m^3 ha^{-1}; Fridman and Walheim 2000, Angelstam and Dönz-Breuss 2004). This means that the reduction of dead wood in managed landscapes compared with natural forests can be estimated as being > 95%. Siitonen (2001) argues that such a decline should lead to more than a 50% reduction of species, however, without considering possible effects of fragmentation and lack of temporal continuity. Since dead wood is a complex natural element that consists of many different traits including tree species, size, decay stage and exposition to light and moisture (e.g. Similä et al. 2003), the amount of specific combinations of these traits has declined even more.

Sweden is a good example of an area that has gradually been altered by forest utilisation that started early in the centre of economic development and reached the periphery in relatively recent time. Forests of different types are the dominating natural potential vegetation below the tree line in Scandinavia (Mayer 1984). Clearing of forests started several thousand years ago in southern and coastal Sweden (e.g. Angelstam 1997). The first local industrial use of forest products were for the production of glass (Nordström et al. 1989), potash and tar (Borgegård 1973) as well as iron and steel (Furuskog 1924, Arpi 1951, 1959, Attman 1986). For a long time, from the 17th to the 20th century, this entailed an extensive local exploitation of the forests in Sweden (Wieslander 1936, Arpi 1959, Nordström et al. 1989). Before the middle of the 19th century large areas with near-natural forests subject to only local non-industrial use still existed in the remote upland and northern parts of Sweden (Niklasson and Granström 2000).

In the middle of the 19th century, a fundamental transformation began in society, as well as in the forest landscape (Carlgren 1926, Heckscher 1935–49, Arpi 1959, Schön 2000). Industrialisation received an impetus, agriculture was intensified, and new areas were colonised in northern Sweden (Mörner 1982). Forests acquired a trade value and became a commodity to an extent never previously suspected. Until ca 1830–1840 the timber export from Sweden was modest, but then it increased exponentially (Mattson and Stridsberg 1981). The liberal economy led to a great increase of world trade. Starting in 1849 this resulted in a growth in number of sawmills along the whole Bothnian coast and an exploitation of the primeval forest in the inland areas of northern Sweden (e.g. Carlgren 1926, Bunte et al. 1982). Between 1850 and 1900, Sweden's export of sawn timber had shown a tenfold increase and the annual harvests had reached close to 20 million m^3.

This historical development was clearly dependent on, and associated with, the growth of the transport infrastructure (Nilsson 1990). The first waterways were developed by building canals and by preparing rivers for log driving (Andersson 1907, Nordquist 1959, Törnlund and Östlund 2002). Other types of infrastructure, such as railroads and roads, were then built for long-distance transportation of wood (e.g. Hjelmström 1959, Qviström 2003).

Two types of effects of infrastructure on biodiversity may be distinguished: primary and secondary (Seiler 2003). Primary effects include traffic accidents, noise, and changes in dispersal and movement capabilities of organisms (Forman et al. 2003). Secondary effects of infrastructure include human settlement and resource exploitation, land use changes and intensification, as well as industrial development (Carlgren 1926, Hoppe 1945, Friberg 1951, Lassila 1972, Mörner 1982, Qviström 2003, Williams 2003, Forman et al. 2003). The development of the transport infrastructure thus provides a commonly used surrogate measurement of the impact of economic development on forests worldwide (Yaroshenko et al. 2001, Aksenov et al. 2002, Williams 2003).

The intensification of forest landscape use enabled by infrastructure development has had profound negative effects on forest biodiversity (Gärdenfors 2000). In managed landscapes dead wood and remnants of natural ecosystems provide qualities of high importance for biodiversity, both

of which are negatively affected by macroeconomic factors (e.g. Skontoft and Solem 2001). For example, using National Forest Inventory data Fridman and Walheim (2000) reported at a coarse spatial scale clear dead wood distribution patterns in Sweden being clearly related to the history of forest use. The average amount of dead wood on managed productive forest land was 6 m^3 ha^{-1}, but with considerable variation among different forest regions. Approximately 25% of the total amount of dead wood consisted of snags and 75% of logs. Similarly, natural forest remnants are confined to the periphery of economic development (Yaroshenko et al. 2001). Protected areas devoted to nature protection are usually natural or semi-natural remnants of previously naturally dynamic landscapes. The degree of naturalness of these remnants may vary, but their rescue effect for forest biodiversity has been documented (Uotila et al. 2002). The regional distribution of protected areas in Sweden is clearly linked to the history of economic development. The majority of such areas are found in the northern part of the country, particularly on land being least productive (Nilsson and Götmark 1992, Fridman 2000). On the contrary, highly productive areas have been intensively managed for a long time, and as a result the amount of set-aside areas is low (Angelstam and Andersson 2001, Angelstam et al. 2003a). Such differences in the present amount of dead wood and natural forest remnants need to be considered when formulating regional conservation goals (e.g. Angelstam and Bergman 2004).

The aim of this paper is to explore the idea that relative differences in the development of the transport infrastructure can be used as a measurement of the human footprint on structural elements of forest biodiversity. Specifically, we relate the accumulated transport infrastructure to the amount of dead wood and area of protected land at the landscape scale in three Swedish regions. The underlying hypothesis is that improved land accessibility, which enables forest resource extraction, leads to a decrease in the amount of natural forest remnants at the stand and landscape scale.

Historical background and methods for analysis

During the past 150 yr, Swedish boreal and hemiboreal forests have provided vital raw material for use first in the iron industry, and later the forest industry (e.g. Furuskog 1924, Bladh 1995, Östlund and Zackrisson 2000). To meet the objective of this study, spatially explicit data representing local landscapes within a region were needed. While the amount of dead wood and protected forest areas are monitored for the whole of Sweden (see Fridman and Walheim 2000, Angelstam and Andersson 2001), detailed descriptions of the development of the infrastructure used for industrial forestry are more limited.

Inaccessibility: hindering log driving

Large-scale industrial logging for export was a consequence of the arrival of the industrial revolution to Sweden. This development can be viewed as a "frontier" of logging of forests limited by the contemporary transport infrastructure (Andersson 1960, Mörner 1982, Bunte et al. 1982, Björklund 1984, Bladh 1995). Different means of long-distance transportation were used in different phases throughout the history of industrial forest use (Heckscher 1907, Andersson 1960, Nilsson 1990). Initially log driving on rivers was essential in both northern and upland central Sweden (e.g. Törnlund and Östlund 2002). The use of local log driving was practised during the 17th and 18th centuries in the Swedish mining districts even before the breakthrough of the forest export industry (Winberg 1944, Andersson 1960, Bladh 1995). However, from the middle of the 19th century log driving became a crucial link for the timber industry because natural watercourses allowed for long distance transportation at a low cost (Heckscher 1907, Hellström 1917, Nordquist 1959, Törnlund and Östlund 2002).

We assumed that the early transport infrastructure, consisting mainly of waterways for log driving, was related to the average altitude, altitudinal range and topography. A more "rugged" landscape is relatively more inaccessible for the development of log driving. Using a 50×50 m digital elevation model (DEM), the index of topographic brokenness expressed as mean slope in degrees between each point in the DEM was calculated for each grid cell (Williams and Gallant 2000) and was used as a measure of inaccessibility in the context of log driving.

Accessibility: the development of transport infrastructure

The development of railroads was essential for the transportation of wood products from inland areas to the coast in central Sweden where large rivers are much less common than in northern Sweden (Andersson 1907, Hellstrand 1980). In 1829 Gustaf af Uhr made the first proposal to build railways by connecting the canal systems between lake Vättern and lake Hjälmaren in Sweden (Anon. 1956). The interest for improved communications grew in the 1830s and 1840s. Inspired by the successful establishment of railroads in other parts of Europe, Adolf Eugene von Rosen proposed in 1845 a state railroad network from Stockholm to Göteborg, Ystad and Gävle. The proposal was turned down but meanwhile local narrow-gage railways were built to connect waterways in regions with heavy industry around 1850. However, the first state-supported normal-gage railway was completed from Nora to Ervalla north of Örebro in 1856 and then the railroad network expanded with the advent of the industrial revolution (Jonasson 1950). This railroad network was the main

transport infrastructure for export that enabled intensification of forest use, especially in the eastern part of central Sweden (Hellstrand 1980). Jonasson (1950) summarised the growth of the state railroad network from 1846 to 1946. In addition we used the information from 1990 (Castenson 1992).

The road infrastructure played an increasing role from the mid-20th century (Nilsson 1990, Törnlund and Östlund 2002). For Norrbotten, Hoppe (1945) published maps of the road network expansion in that county up until 1940, and for Västerbotten, Lassila (1972) did the same until 1970. In short, we thus assumed that railroads (in central Sweden) and roads (in Norrbotten and Västerbotten) were factors increasing accessibility to the wood resources.

All spatial analyses on the development of infrastructure were made in ArcView 3.2a (Anon. 2000). The maps published in Hoppe (1945), Jonasson (1950) and Lassila (1972) and were digitised and used in combination with the information from 1990 provided in Castensson (1992). To quantify the accumulated impact of transport infrastructure, the length of public roads and railroads was summed for the four points in time for each 25 × 25 km cell (Table 1). Some 25 × 25 km grid cells had part of their area outside the limits of the areas for which we had information about the transport infrastructure. This was due to the fact that the areas with information about infrastructure were delineated by natural (e.g. coast-line) and administrative (i.e. county and national borders) limits rather than according to the grid network. If the part of a cell located inside those limits was < 500 km^2 (500/625 = 80%), that grid cell was excluded.

Natural forest remnants

As a measurement of a natural forest remnant at the stand scale, we used data about the average volume of dead wood collected 1995–1999 by the Swedish National Forest Inventory (Ranneby et al. 1987) for each 25 × 25 km grid cell. These data cover both standing and lying dead wood. For the landscape scale we used a GIS database from the Swedish Environmental Protection Agency describing protected areas with high conservation value forest in Sweden. The database included the protected areas as of May 2000, i.e. excluding the areas designated in the government decision of 6 July, 2000. For each 25 × 25 km grid cell we estimated the total area of protected areas.

Statistical analyses

To compare the amount of natural forest remnants at different scales (i.e. amounts of dead wood and protected areas) and proxies describing the contemporary transport infrastructure making forests accessible and terrain ruggedness, we expressed all data as mean values for each 25 × 25 km grid cell. The analyses are presented for the counties of Norrbotten (105 grid cells; ca 65 000 km^2) and Västerbotten (76 grid cells; ca 48 000 km^2) in the northern boreal forest, and central Sweden (230 grid cells; ca 144 000 km^2) in the southern boreal and hemiboreal forest (Fig. 1).

First, we used correlation analysis to explore the relationships among all four variables (i.e. dead wood, protected areas, accessibility, and inaccessibility). Then, multiple linear regression analysis was applied to examine the relationships between accessibility and inaccessibility on the one hand, and natural forest remnants on the other.

Results

Accesssibility and inaccessibility

The sums of public roads in Norrbotten and Västerbotten and of railroads in central Sweden for the four points in time are shown in Fig. 1. After a rapid development of railroads during ca 100 yr, which started in the industrial

Table 1. Summary of data sources and year of orgin used to quantify the development of the transport infrastructure concerning roads in northern Sweden (Norrbotten and Västerbotten) and railroads in central Sweden.

Time	ca 1850	ca 1900	ca 1950	ca 2000
Norrbotten (Hoppe 1945, Castenson 1992)	1860	1900	1940	1990
Västerbotten (Lassila 1972, Castenson 1992)	mean of 1810/1910	1910	1950	1990
Central Sweden (Jonasson 1950, Castenson 1992)	1856	1896	1946	1990

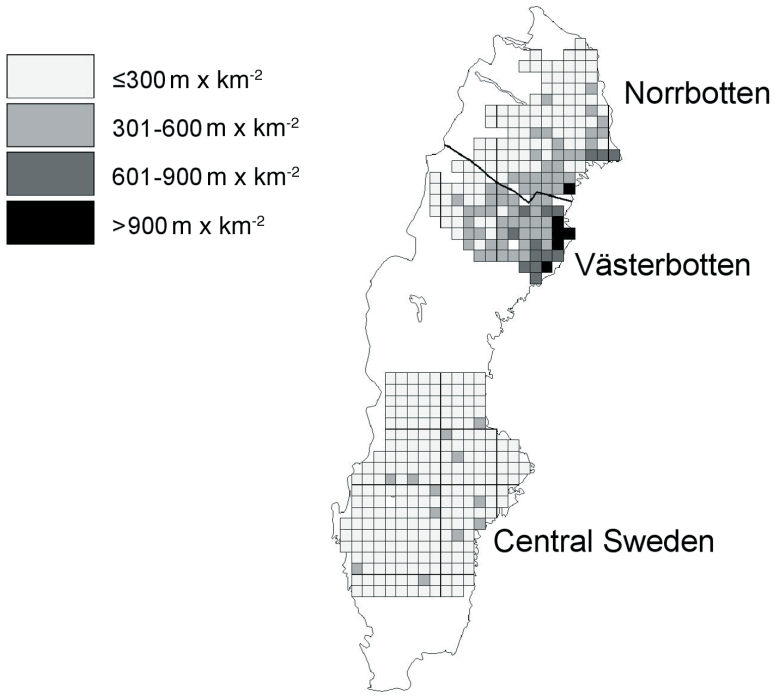


Fig. 1. Map of Sweden showing the accumulated amount of transport infrastructure in 25 × 25 km grid cells. The data refer to the road network from the beginning of the 19th century to 1990 in the counties of Norrbotten and Västerbotten, as well as to the railroad network in central Sweden from 1856 to 1990 (see also Table 1).

centres associated with the iron and wood industry in central Sweden, the expansion halted in the mid 20th century. In fact, the importance of the railroad network has declined in the past 50 yr both in total length (Fig. 2) and spatial extent. By contrast, the development of the road network development in northern Sweden followed a clear pattern of gradual expansion from the coast toward the mountains that covered all time intervals in the study.

The accessibility expressed as the accumulated density of transport infrastructure (Fig. 2) and the inaccessibility of the landscape expressed as the mean slope (Fig. 3) varied considerably among the three regions (Table 2). The accumulated road density in Västerbotten was twice as high as in Norrbotten. The degree of inaccessibility (i.e. topographic ruggedness) was much higher in the two northern regions than in central Sweden.

Amount of dead wood and protected areas

There was considerable variation in the amount of dead wood and protected areas among the three regions in Sweden (Figs 4, 5). In general, today's mean amount of dead wood is lower in central Sweden (2.1 m^3 ha^{-1}) than in Västerbotten (3.7 m^3 ha^{-1}) and Norrbotten (4.0 m^3 ha^{-1}) (Table 2). Similarly the average protected area was 10% in

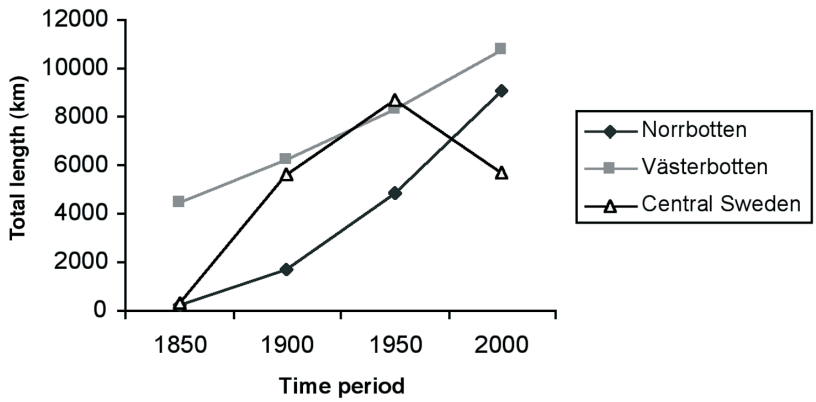


Fig. 2. The historic development of the transport infrastructure in the form of public roads (Norrbotten, Västerbotten) and railroads (central Sweden).

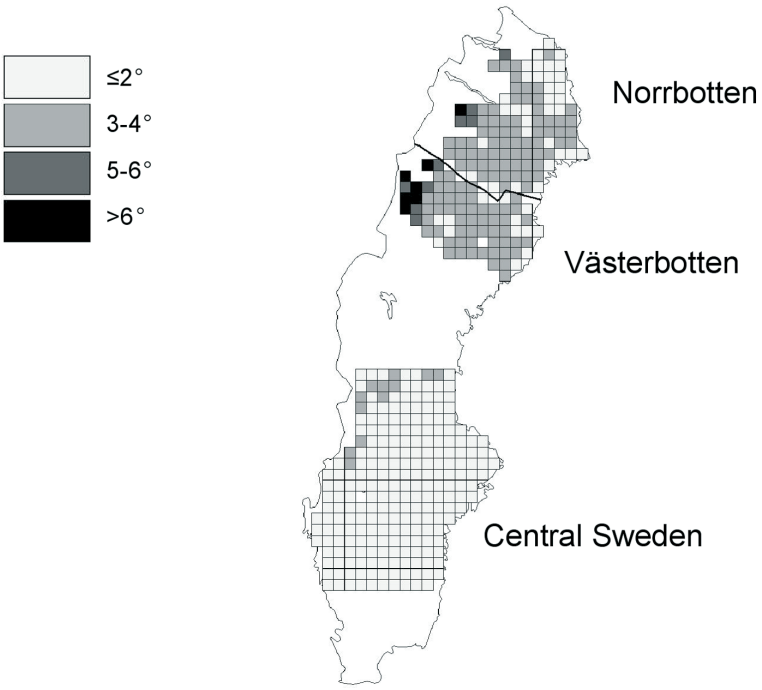


Fig. 3. Mean slope in degrees within 25 × 25 km grid cells in the three study areas in Sweden.

Västerbotten and 14% in Norrbotten, but only 1.2% in central Sweden (Table 2).

Transport infrastructure and natural forest remnants

We found negative correlations between the amount of dead wood in the managed landscape and accessibility due to the development of the transport infrastructure from the middle of the 19th century to present time in all three study areas (Table 3). The relationships were, however, much stronger in Norrbotten and Västerbotten than in central Sweden (Fig. 6). Regarding inaccessibility, Västerbotten showed a clearer relationship than both Norrbotten and central Sweden (Table 3, Fig. 6). For the proportion of protected areas, negative correlations were found in Norrbotten and Västerbotten but no correlation at all was found in central Sweden (Table 3). It should also be noted that the proportion of protected areas in central Sweden was as low as in areas with high accessibility in Norrbotten and Västerbotten (Fig. 7). Note that with increasing accessibility the occurrence of high amounts of dead wood and protected areas declined (Figs 6, 7).

Using multiple regression analysis we found that for the amount of dead wood, accessibility entered first in the models for both Norrbotten and Västerbotten (Table 4). The total variation explained by accessibility and inaccessibility put together was 18 and 28%, respectively. For central Sweden, accessibility entered first but the total amount of variation explained was only 9%. When using both predictor variables to explain the proportion of protected areas, accessibility entered first in Norrbotten and inaccessibility first in Västerbotten (Table 5). Altogether 41% (Norrbotten) and 54% (Västerbotten) of the variation in today's amount of protected areas was explained by these two variables. In central Sweden no significant fit was obtained using those two variables.

Discussion

The impact of macroeconomic development on forests

The aim of this interdisciplinary study was to explore the idea that the development of transport infrastructure can be used as an indicator of the complex macroeconomic history, and be linked to the resulting human footprint on structural elements once found in the naturally dynamic landscape. The negative relationships between the amount of dead wood and proportion of protected area in local landscapes one the one hand, and the development of the transport infrastructure from the middle of the 19th century to present time on the other, supports this idea. Similarly, Skonhoft and Solem (2001) reported a clear relationship between macroeconomic development and the decline in the amount of wilderness areas in Norway from almost 50 to < 10% during the 20th century. Hence, in northern Europe, large intact forest areas are now mainly found in remote parts of Russia (Yaroshenko et al. 2001).

Table 2. Amount of dead wood, proportion of protected areas, accumulated density of transport infrastructure (accessibility) and topographic steepness (inaccessibility) in central Sweden and Västerbotten and Norrbotten (mean ± SE). Transport infrastructure is expressed as roads in Norbotten and Västerbotten, while the corresponding figures for central Sweden refer to railroads.

Variable	Norrbotten (n = 105)	Västerbotten (n = 76)	Central Sweden (n = 230)
Dead wood (m^3 ha^{-1})	4.0 ± 0.2 median = 3.7 range: 0–11.3	3.7 ± 0.3 median = 3.3 range: 0.9–13.3	2.1 ± 0.1 median = 1.8 range: 0–12.4
Protected area (ha km^{-2})	14.2 ± 2.2 median = 2.72 range: 0–88.9	10.3 ± 2.5 median = 0.31 range: 0–91.15	1.2 ± 0.1 median = 0.53 range: 0–13.2
Accessibility – Infrastructure density (m km^{-2})	254 ± 17 median = 229 range: 0–910	428 ± 29 median = 379 range: 38.6–1102	136 ± 6 median = 139 range: 0–445
Inaccessibility – Topographic steepness (degrees)	2.96 ± 0.09 median = 2.90 range: 1.37–7.72	3.53 ± 0.16 median = 3.16 range: 1.38–8.38	1.28 ± 0.05 median = 1.12 range: 0.03–3.48

To validate the general pattern, a closer examination of the regional differences in the amount of different types of dead wood and natural forest remnants is needed. In this study we used the average total volume of dead wood at the stand scale as a response variable. As shown by Fridman and Walheim (2000), the differences in the total amount of dead wood among regions are solely due to differences in the amount of logs on the ground. The amount of snags showed no clear regional pattern, thus indicating that logs on the ground is the relevant indicator of macroeconomic development. There were clear differences in the amount of dead wood between northern Sweden and central Sweden. The average amount of dead wood in central Sweden was half of that found in Västerbotten and Norrbotten in the north. We interpret this difference as a consequence of a longer forest utilisation history in the south with strong effects on forests that occurred before the advent of the modern transport infrastructure. The iron industry in the

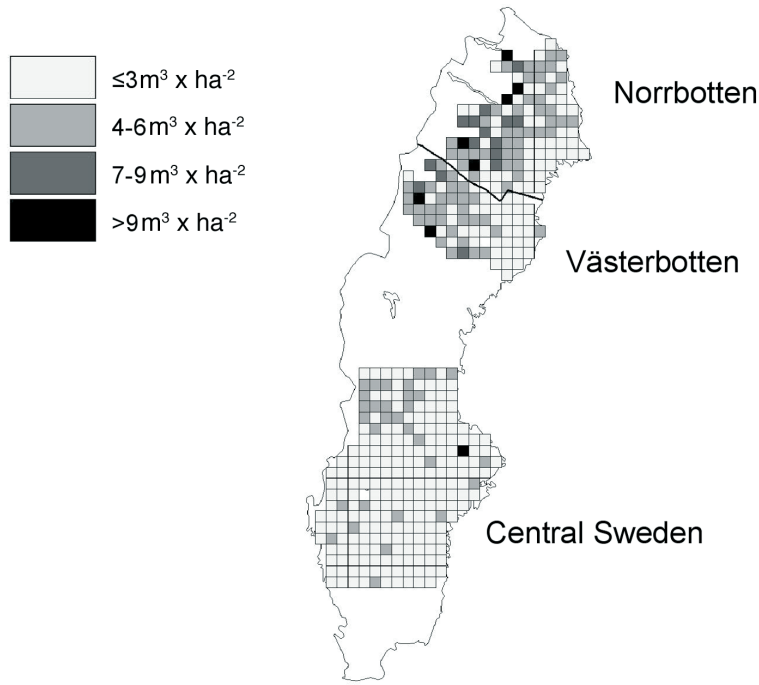


Fig. 4. Amount of dead wood within 25 × 25 km grid cells in the three study areas in Sweden.

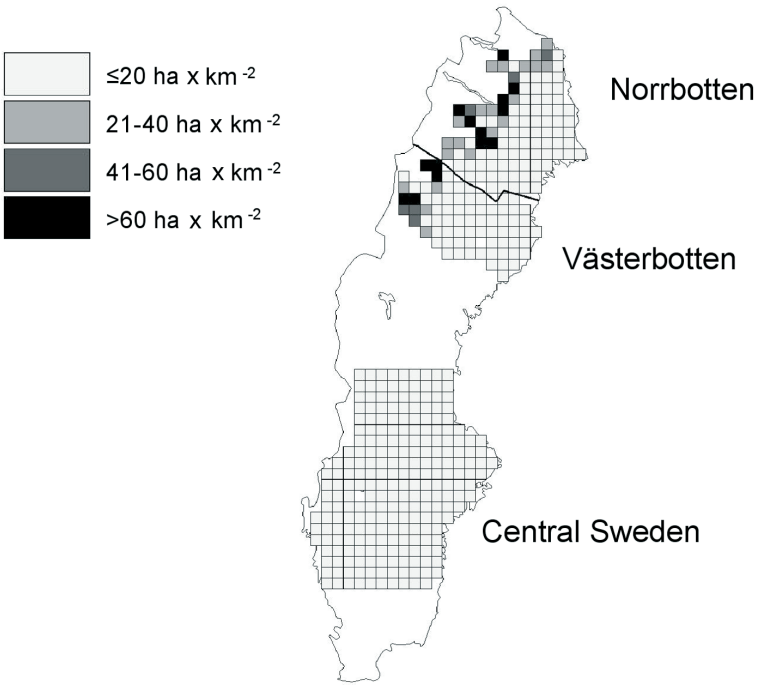


Fig. 5. The amount of protected areas within 25 × 25 km grid cells in the three study areas in Sweden.

Bergslagen area in central Sweden is an important example of a heavier footprint on the forests in the south than in the north. In fact, the shortage of forest had become severe around the mines already by the 18th century (Wieslander 1936). The consumption of charcoal peaked during the end of the 19th century, and in 1885 it was estimated that 20–25% of the cut timber volume was used in making fuel for the iron industry in central Sweden (Arpi 1959).

The spatial difference observed among regions for biodiversity indicators (Rametsteiner and Mayer 2004) such as dead wood (e.g. Siitonen 2001) and near-natural forest areas (e.g. Angelstam and Andersson 2001, Yaroshenko et al. 2001) has a corresponding temporal aspect. This is evident when examining differences in the amount of dead wood and the amount of remaining intact areas within a region over time. For example Linder and Östlund (1998) showed that the amount of dead standing trees declined gradually from ca 12 to < 1 m^3 ha^{-1} during the period ca 1890–1960.

Summarising, the general use of forest resources has developed in several more or less distinct steps linked to the effectiveness of timber extraction (Mattson and Stridsberg 1981, Angelstam and Arnold 1993, Drushka 2003, Williams 2003, Angelstam et al. 2004a). The first steps could be described as a pristine forest with most natural structures and processes being intact. Humans are part of the

Table 3. Correlation matrices for the four variables used in the study (p<0.001 is denoted *** and p<0.05 is denoted *).

Study area	Variable	Dead wood	Protected areas	Accessibility	Inaccessibility
Norrbotten	Dead wood	1	–	–	–
(n = 105)	Protected areas	0.38***	1	–	
	Accessibility	–0.43*	–0.57***	1	–
	Inaccessibility	0.21*	0.39***	–0.19*	1
Västerbotten	Dead wood	1	–	–	–
(n = 76)	Protected areas	0.54***	1	–	–
	Accessibility	–0.48***	–0.55***	1	–
	Inaccessibility	0.45***	0.70***	–0.50***	1
Central Sweden	Dead wood	1	–	–	–
(n = 230)	Protected areas	0.07	1	–	–
	Accessibility	–0.23***	0.04	1	–
	Inaccessibility	0.23***	–0.03	–0.26***	1

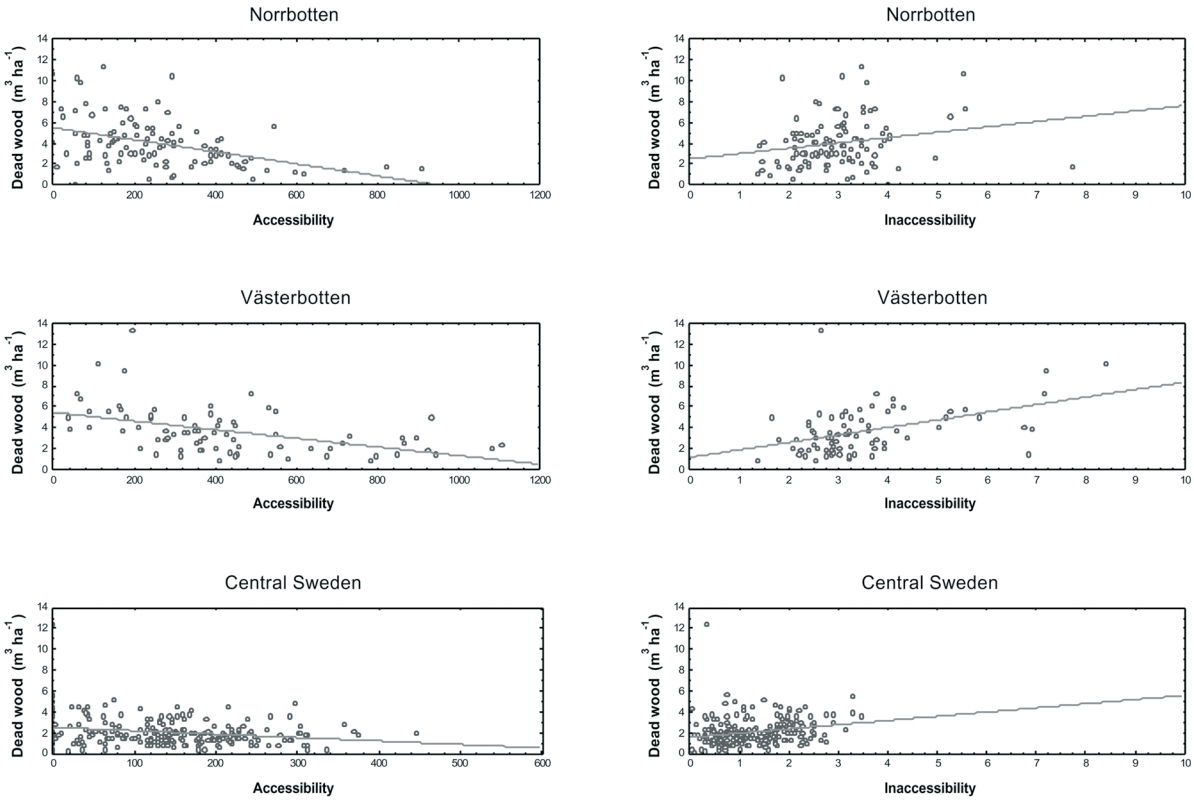


Fig. 6. The amount of dead wood in relation to the indicators of accessibility (transport infrastructure) and inaccessibility (mean slope) in central Sweden, Västerbotten and Norrbotten. Each point represents a 25 × 25 km landscape grid cell (see also Table 3).

ecosystem but do not dominate it (e.g. Balée 1998). The second step entails early use of wood for the production of charcoal, potash, tar and selective harvesting of large and valuable trees (e.g. Östlund and Zackrisson 2000). The third step is the local and regional depletion of timber resources following exploitation (e.g. Drushka 2003). The fourth step is the sustained yield paradigm with intensive management for the desired products that negatively influences other values. Sustainable forest management, including the maintenance of biodiversity and social values can be interpreted as a future vision (Schlaepfer and Elliott 2000).

In spite of a reductionist approach based on coarse data sets, our results show that the gradual development of forest use in Sweden is related to the present amount of dead wood and protected areas, both being indicators of forest naturalness (Peterken 1996). Moreover, this study illustrates the importance of understanding the regional landscape history when managing for biodiversity. The absence of relationships between the transport infrastructure and the proportion of protected areas in central Sweden was expected as local industrial use started here already during the Medieval and was very intense already > 200 yr ago (Wieslander 1936, Attman 1986). However, this study also raises a number of questions. What is the relative importance of different factors affecting accessibility and inaccessibility during different phases in the history of forest use? What are the consequences of this for different structural components? Evaluating these issues requires, however, data with a better spatial, temporal and thematic resolution available for whole regions.

Different times – different kinds of transport infrastructure

The use of bulky natural resources such as forests requires cheap and effective means of transportation (Mörner 1982). According to Nilsson (1990) three different phases in the development of transport infrastructure can be identified: local use only, transportation using waterways and finally road transportation. The conditions were, however, quite different in different parts of Sweden (Andersson 1907).

In central Sweden agriculture had already been developed during the medieval time. The early clearing of forest was, however, restricted to fertile soils at lower altitude (e.g. Angelstam et al. 2003a). Also the history of local use of

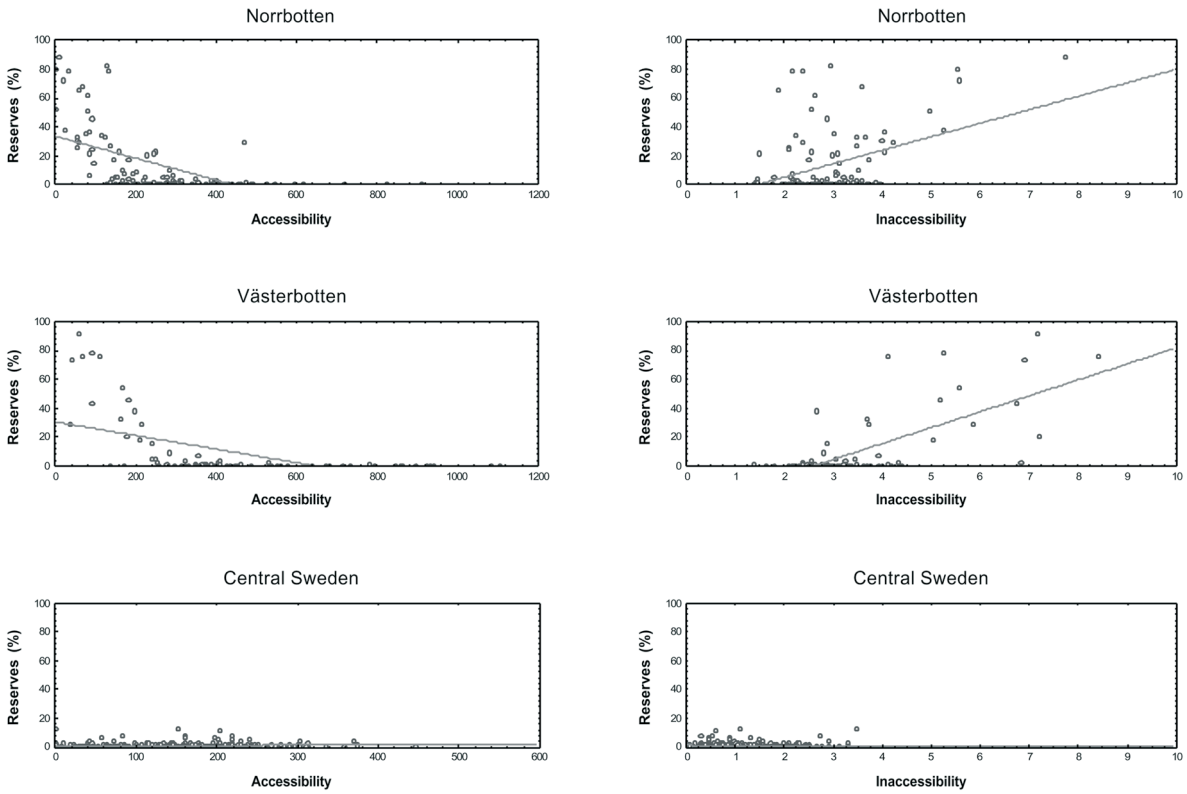


Fig. 7. The proportion of protected areas in relation to the indicators of accessibility (transport infrastructure) and inaccessibility (mean slope) in central Sweden, Västerbotten and Norrbotten. Each point represents a 25 × 25 km landscape grid cell (see also Table 3).

forests is very long. Provision of wood for the local iron industry began in the 8th century and export of timber using waterways in the provinces Dalsland and Värmland in the western part of central Sweden has taken place since the late 17th century (Eklund 1991, Bladh 1995). At the end of the 18th century the international timber frontier reached this region. The waterways to were gradually developed and a canal linking the large river Klarälven to the sea was established. In the late 18th century, the privatisation of forests was discussed as a means of making land use more efficient. That resulted in a major land reform, which had covered most of central Sweden by the end of the 19th century and led to an intensive timber trade (Hellstrand 1980). Large-scale industrial use is restricted to the last 150 yr (Nordquist 1959, Hellstrand 1980).

Until the 1870s, the industrial development in Sweden was largely dependent on events occurring in other countries (Magnusson 1997). Great Britain's removal of customs on timber import in 1849 opened up for the rapid expansion of a Swedish sawmill industry in northern Sweden. The timber frontier thus expanded northwards. Already in 1854 the decision about building a railway connecting Dalälven above major rapids with the seaport at Gävle was taken. This was the starting point for large-scale high-grading of the forests in Dalarna and the first purchases of cutting rights in 1854, as well as the building of Korsnäs' saw mill in 1858. The railway opened in 1859. This stimulated the preparation of rivers for timber mass transportation. Before 1860 log driving was confined to the lower part of river Dalälven. Between 1860 and 1865 there was a rapid expansion including the tributaries in the northeast. Log driving in the northwestern part of the river Dalälven watershed commenced 1870–1875. In 1953, the total length of floatable rivers in the Dalälven river system was 3676 km. The last timber was floated in 1971. In northern Sweden where large rivers are common, log driving was the main way of early long-distance transportation of wood (Andersson 1907, Nordquist 1959). Log driving seized in the 1970s (Törnlund and Östlund 2002). Until the 1950s, virtually all land-transportation in the forests between logging sites and waterways was made with the aid of horses.

Building roads for timber transportation commenced during the severe economic recession in the 1920s, but the growth of the network of forest roads did not really take off before the 1950s (Hjelmström 1959, Nilsson 1990). Today, the forest road network in Sweden encompasses ca 420 000 km of roads, ca 1500 km being built annually (Anon. 2003), resulting in that virtually no productive forest land is located > 500 m from a forest road. This means

Table 4. Results from multiple linear regression analyses of the current volume of dead wood against the accumulated amounts transportation infrastructures in northern Sweden (Norrbotten and Västerbotten, road network) and in central Sweden (railroad network) as a measure of accessibility, and topographic steepness as an indicator of inaccessibility.

Study area	Accessibility	Inaccessibility
Norrbotten n = 105	$\beta = -0.40$ $r^2 = 0.18$ $p = <0.001$, $F = 22.9$	$\beta = 0.13$ $r^2 = 0.02$ $p = 0.15$, $F = 2.1$
Västerbotten n = 76	$\beta = -0.34$ $r^2 = 0.23$ $p = p<0.001$, $F = 21.7$	$\beta = 0.28$ $r^2 = 0.05$ $p = 0.018$, $F = 5.8$
Central Sweden n = 230	$\beta = -0.19$ $r^2 = 0.06$ $p = 0.0003$, $F = 13.3$	$\beta = 0.18$ $r^2 = 0.03$ $p = 0.007$, $F = 7.5$

that almost all productive forests in Sweden are accessible for intensive forest management today, and that remoteness caused by natural conditions that helped to maintain natural structures (e.g. dead wood and naturally dynamic landscapes) are no longer obstacles for modern technology.

Consequences for conservation planning

Most of Sweden's forests have been impacted by a variety of changes and the present landscapes diverge greatly from natural patterns and processes found in the historic forest landscapes (Angelstam 1997, Östlund and Zackrisson 2000, Korpilahti and Kuuluvainen 2002). Natural forest elements such as dead wood and protected areas of importance for the maintenance of forest biodiversity are thus uncommon where the history of modern management is long. However, the human footprint takes a long time to develop. As an example, dead wood decays slowly. Decay has been measured in several ways including time to "disappearance" of the dead wood unit (usually equalling ca 80–90% mass loss), mass loss functions and decay stage transitions. Estimates of the time to disappearance have mostly been conducted in areas where old plots have been revisited (e.g. Hytteborn and Packham 1987, Liu and Hytteborn 1991, Hofgaard 1993). These studies suggest that downed Norway spruce *Picea abies* logs on average disappear from the forest floor within 50–200 yr along a gradient from southern to northern Sweden. A few studies (e.g. Naesset 1999) have reported decay rate constants for boreal Europe corresponding to disappearance in 45–75 yr. Only minor differences were observed between Norway spruce and Scots pine *Pinus sylvestris* while birch *Betula* spp. had significantly faster decay (Krankina and Harmon 1995). Restoration of qualities such as decayed logs thus requires long time.

Dying and dead trees, in particular, have been recognised as being of prime importance as resource and habitat for numerous animal and plant species (e.g. Jonsson and Kruys 2001). The amount of dead wood has also been accepted as a new indicator of forest biodiversity by the Fourth Ministerial Conference on the Protection of Forests in Europe in 2003 (Rametsteiner and Mayer 2004). Dead wood also figures in modern certification standards

Table 5. Results from multiple linear regression analyses of the proportion of protected areas in local landscapes against the accumulated amounts transportation infrastructures in northern Sweden (Norrbotten and Västerbotten, road network) and in central Sweden (railroad network) as a measure of accessibility, and topographic steepness as an indicator of inaccessibility.

Study area	Accessibility	Inaccessibility
Norrbotten n = 105	$\beta = -0.52$ $r^2 = 0.33$ $p = p<0.001$, $F = 50.5$	$\beta = 0.29$ $r^2 = 0.08$ $p = p<0.001$, $F = 14.2$
Västerbotten n = 76	$\beta = -0.27$ $r^2 = 0.05$ $p = 0.005$, $F = 8.5$	$\beta = 0.56$ $r^2 = 0.49$ $p = p<0.001$, $F = 70.3$
Central Sweden n = 230	ns	ns

for best forestry practices, as defined, for example, by the Forest Stewardship Council (FSC). In Sweden a political target for increasing the amount of dead wood by 25% until 2010 has been formulated (Anon. 2002). Attempts are therefore made to increase the amount of dead wood in Sweden. Indeed, the recent changes in forest management are slowly improving the situation (Jonsell and Weslien 2003). But how large should this increase be? Where should it take place? Throughout the whole landscape or only where the probability of succeeding with biodiversity maintenance is reasonably high?

For spruce-dominated forests, Bütler et al. (2004a, b) developed targets for standing dying and dead trees at the scale of habitat patches. This was based on the quantitative habitat requirements of the three-toed woodpecker *Picoides tridactylus*, whose presence is considered an indicator of the properties of naturally dynamic spruce-dominated forests. Both a theoretical model and empirical data resulted in similar estimates (15–20 m^3 of standing dead wood per hectare over a 100-ha area) of the minimum snag quantities for woodpecker occurrence. In hemiboreal forest, Angelstam et al. (2002) studied the relationships between dead wood variables and the presence of different woodpecker species in five different coarse landscape types in northeastern Poland. The mean number of woodpecker species per km^2 varied from 0.6 (plantations) to 4.8 (Białowieża National Park) and was positively correlated with amount of dead wood. The required volume of deciduous dead wood was estimated at ca 20 m^3 of dead wood per hectare over a 100-ha area. Comparisons of the species richness of saproxylic beetles and the amount of dead wood in Norwegian and Finnish forests also indicate a threshold at ca 20 m^3 ha^{-1} (Økland et al. 1996, Martikainen et al. 2000).

These studies suggest that the threshold values for both deciduous and coniferous snags at the scale of habitat patches are 5–10 times higher than the volume found in a managed forest in Fennoscandia, and about a fifth of what is found in naturally dynamic forest (cf. Siitonen 2001). Within the current Swedish management paradigm, nature considerations at the stand scale are dispersed rather evenly over whole landscapes. However, to be cost-effective, based on the evidence from dead wood specialists such as woodpeckers (Bütler et al. 2004a, b) and fungi (Edman et al. in press), we argue that future forest management should rather aim at concentrating dead wood within and among landscapes. Ideally this should be done in the form of a network of functionally connected and sufficiently large forest patches in which the ecological dead wood target is reached (e.g. Angelstam et al. 2003b).

To conclude, our study illustrates the effects of the human footprint on two surrogate measures of the naturalness of forests (sensu Peterken 1996). Both the minimum amount of dead wood in forest stands and the amount of set-aside areas required for the maintenance of biodiversity are discussed in the debate concerning maintenance of forest biodiversity (e.g. Hanski 2002, Angelstam et al. 2004b). The main management implication from our study is that both natural conditions and the regional history of forest use should be considered when formulating regional conservation targets and planning practical conservation measures to attain these targets. The attempts to increase the amount of natural forest components should be made so that the requirements of focal species both at the scale of stands in landscapes and landscapes in ecoregions will be satisfied in the long term.

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Do empirical thresholds truly reflect species tolerance to habitat alteration?

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Guénette, J.-S. and Villard, M.-A. 2004. Do empirical thresholds truly reflect species tolerance to habitat alteration? – Ecol. Bull. 51: 163–171.

The search for thresholds in natural phenomena is not new. Nonetheless, the detection of thresholds in species response to habitat alteration has recently received a lot of attention from conservation biologists and ecosystem managers. Ecological phenomena such as species occurrence and processes exhibiting a step function or threshold in their response to the alteration of habitat structure have obvious implications for conservation. Furthermore, researchers should try to identify a specific cut-off value or at least, a narrow range of values along an alteration gradient for application purposes. Owing to the paucity of objective statistical methods, or to the failure of researchers to apply them in ecology, specific threshold values or ranges are rarely identified. In this paper, we examine issues related to the detection of threshold responses to habitat alteration, specifically 1) the selection of meaningful parameters of biological response and indicators of habitat alteration, and 2) statistical considerations associated with the identification and interpretation of nonlinear responses (focusing on breakpoint regression and ROC analysis). We use theoretical data sets with predefined thresholds to validate threshold values determined by these methods. We also distinguish and interpret different types of thresholds that can be observed empirically. Then, we examine the robustness of threshold values to differences in sample size and in the extent of the habitat alteration gradient sampled and finally, we explore issues concerning data partitioning to control for confounding effects of other factors (e.g., stand composition, geographical variation). The issues discussed here will have direct implications in future research assessing threshold responses to habitat alteration.

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Identifying critical thresholds in species response to habitat alteration is a promising approach to address ecological questions and to provide answers that are meaningful from a management perspective. This approach is not a new one as it is very similar to dose-response curves used in health sciences (e.g., Greiner et al. 2000, O'Meara and Sevin 2001). In ecology, threshold responses have been sought in studies inspired from island biogeography to identify the minimum area of habitat fragments ensuring the presence of species (e.g., Robbins et al. 1989). The threshold concept recently gained momentum in the study of habitat fragmentation effects, where several authors have sought thresholds in habitat loss beyond which these effects become significant (Andrén 1994, Hill and Caswell 1999, Flather and Bevers 2002). Several authors have also examined nonlinear responses of certain species to gradients in habitat alteration or surrogates thereof, either empirically (Jansson and Angelstam 1999, Villard et al. 1999) or

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through simulation modelling (With and King 1999, Fahrig 2001). These approaches have obvious appeal for conservation planning because one can use them to identify threshold values or ranges in habitat alteration beyond which a given biological response changes suddenly. Documenting such thresholds for a wide range of species could then provide specific numerical targets for habitat management over spatial scales relevant to the organisms under study. For example, a target could be identified using species regionally most sensitive to alterations of their habitat (Jansson and Angelstam 1999, Mönkkönen and Reunanen 1999, With and King 1999, Fahrig 2001).

First, it is important to sort through the quickly expanding terminology surrounding the concept of a threshold. Thresholds in species responses are generally examined for nonlinear (or step) functions represented by a logistic curve (Fig. 1). A threshold corresponds to a range of values over which a certain property changes at a fast rate (Fig. 1a). One can also focus on specific values corresponding to the lower or higher portions of a threshold (Fig. 1b–e), or on the inflexion point. Fahrig (2001) defines an ecological threshold as the quantity of habitat at which effects of habitat configuration (fragmentation sensu strictu) are added to those of habitat loss and affect the persistence of populations. This type of threshold is also referred to as a "fragmentation threshold". Muradian (2001) proposed a more inclusive concept of ecological threshold, i.e. the critical values of an independent variable around which the system flips from one stable state to another. Extinction thresholds represent the amount or proportion of habitat in the landscape at which population persistence is ensured (With and King 1999, Fahrig 2002, Ovaskainen et al. 2002). Unfortunately, the concept of critical threshold is too often used loosely to refer either to ecological thresholds or to extinction thresholds. Moreover, the expression "critical threshold" is itself pleonastic; a threshold is, by definition, a critical point where a given property changes from one state to another.

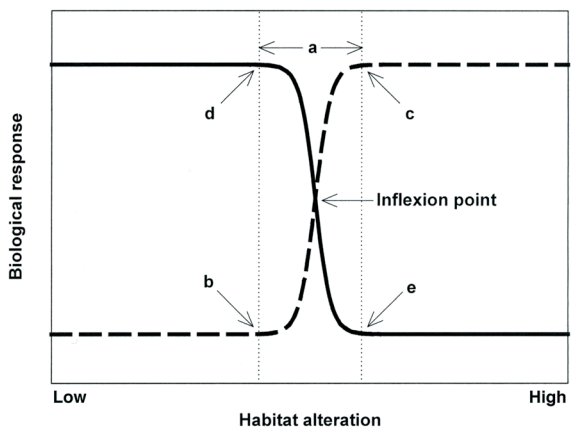


Fig. 1. Hypothetical logistic curves showing the response of species tolerant (solid line) or sensitive (dashed line) to habitat alteration, as well as critical parameters related to threshold ranges. The threshold range corresponds to "a". One may also be interested in the inflexion point, or in the level at which the curves start increasing or level off (b and c or d and e).

In this paper, we will use the terms "occurrence threshold" or "persistence threshold" to refer to a value along a gradient in habitat alteration above which the occurrence or persistence of a species, respectively, become unlikely. Similarly, we will use a variety of other terms to refer to thresholds in other parameters of biological response (e.g. abundance, reproductive activity, etc.).

Several studies examining species/habitat relationships have identified threshold values. For example, Bütler et al. (2004a, b) found thresholds in the occurrence of the three-toed woodpecker *Picoides tridactylus* along a gradient in the density and basal area of dying trees and snags. Hansen et al. (1995) reported abundance thresholds in bird species corresponding to small changes in tree density. At the landscape scale, Jansson and Angelstam (1999) reported an occurrence threshold for the long-tailed tit *Aegithalos caudatus* corresponding to the distance among patches of suitable habitat. Reunanen et al. (2002) found an occurrence threshold in the presence of the Siberian flying squirrel *Pteromys volans* along a gradient in the area of habitat fragments.

If ecological thresholds are to become powerful tools in conservation planning and resource management, researchers must further explore their variability among species, geographical locations, landscape types, etc. Furthermore, numerous statistical issues should be explored 1) to objectively identify thresholds and 2) to understand the sensitivity of such "objective thresholds" to sample size, extent of habitat alteration gradient sampled, etc. Even when focal species or processes exhibit a "step function" (threshold) in their response to habitat alteration, researchers should still identify a specific cut-off value or, at least, a narrow range of values for applications to conservation. Moreover, the fact that thresholds vary among species and study areas can also complicate their application (Mönkkönen and Reunanen 1999, Fahrig 2001, Muradian 2001). To address this issue, Mönkkönen and Reunanen (1999) suggested using the persistence thresholds of the most sensitive species in a given region. In this case, the habitat requirements of those "umbrella-species" should ideally encapsulate those of less sensitive species found in the same guild (Bonn and Schröder 2001, Fleishman et al. 2001, Carignan and Villard 2002, Roberge and Angelstam 2004).

This paper addresses ecological and statistical issues associated with the analysis of nonlinear responses to habitat alteration. More specifically, we will 1) examine issues related to the selection of parameters of biological response and indicators of habitat alteration and 2) review statistical approaches and considerations when examining the shape of species' responses to identify specific threshold values or threshold ranges.

Selection of appropriate variables

Most empirical studies investigating threshold responses to harvesting intensity have focused on single species deemed particularly sensitive to the alteration of their habitat (Jansson and Angelstam 1999, Reunanen et al. 2002, Bütler et al. 2004a, b). Thus, the validity of recommendations based on such single-species studies depends on the quality of the focal species as umbrellas for other, ecologically similar species. However, the mere presence of these putative umbrella species at a site may be a relatively coarse estimate of their actual demographic status such as their probability of persistence. Various options exist to address this concern. First, one may use a fitness parameter (e.g., index of reproductive activity – Vickery et al. 1992, Gunn et al. 2000) as a response variable. For example, we compared threshold values obtained for the probability of presence and the probability of reproductive activity of the blue-headed vireo *Vireo solitarius* (Guénette and Villard unpubl.). As expected, the threshold values were higher for reproductive activity than for the mere presence of the species. Angelstam (2004) found the same pattern in the black grouse *Tetrao tetrix*. Consistent occupancy of a site by a species can also be used to obtain a more sensitive indicator of habitat quality than presence/absence during a single year or season. For example, one could search for a threshold response to habitat alteration using several levels of site occupancy: absent, present 1 yr, present 2 yr, etc. Ordinal logistic regression allows fitting models to this type of response variable (Hosmer and Lemeshow 2000).

Alternatively, one might argue that thresholds should be defined based on variations in species richness or total abundance of indicator taxa or guilds along a gradient in habitat alteration. This more "comprehensive" approach may be problematic, however, given the fact that response to habitat alteration tends to be species-specific (Villard et al. 1999, Hagan and Meehan 2002, Lichstein et al. 2002). We prefer the approach proposed by Mönkkönen and Reunanen (1999), which is to focus on threshold values exhibited by species most sensitive to habitat alteration.

Researchers aiming to provide recommendations concerning the effects of forestry on biodiversity must choose among a variety of indices or measurements of habitat alterations associated with silvicultural treatments. At the stand level, one can use variables such as canopy closure, density or basal area of snags or larger trees, etc. The problem with some of these variables, such as canopy closure, is that they may classify old-growth stands with canopy gaps as being more altered than second-growth stands or older plantations. Furthermore, using a single variable rarely succeeds in capturing the complex changes to stand structure/composition brought about by some forms of intensive silviculture. An alternative is to derive multivariate axes using appropriate statistical techniques (e.g., principal components analysis). This approach facilitates extraction of a linear combination of variables reflecting "harvesting intensity" (Guénette and Villard unpubl.). However, this is not always the case, because the linear combinations obtained may be dominated by variables reflecting both harvesting intensity and stand composition, for example.

Determination of cut-off value

Owing to their multivariate nature, ecological relationships are rarely characterized by sharp thresholds. Hence, an objective method must be used to determine threshold values when species exhibit significant, yet relatively gradual, nonlinear responses. When using a binary response variable (e.g., presence/absence), logistic regression is the most widely used modelling method. Manel et al. (1999b) compared model performance among three methods: logistic regression, multiple discriminant analysis, and artificial neural networks. Based on a series of performance criteria, they found that logistic regression outperformed the two other methods. However, the disadvantage of this method is that it does not directly provide a cut-off value to discriminate between predicted presence and absence. Several authors have simply used the x value corresponding to a predicted probability of 0.5 (e.g., Bisson and Stutchbury 2000, Madden et al. 2000), thus assuming that when $p < 0.5$, the event is unlikely to occur whereas it is likely to occur if $p > 0.5$. In some cases, the cut-off value was subjectively adjusted (0.25 instead of 0.5) to account for the proportion of false negatives (Reunanen et al. 2002). Not only are these criteria subjective, they also fail to account for the effect of species occurrence (or prevalence) on the shape of the logistic curve (Manel et al. 1999a, 2001). Indeed, in the case of rare species, the predicted probability of presence may never reach 0.5. Thus, the model predicts that the species is always absent, irrespective of habitat quality.

Thresholds in a species' binary response can also be identified based on relation optimisation. For example, Collingham et al. (2000) used Cohen's kappa, the proportion of correctly-predicted presences and absences after accounting for chance. This is considered to be one of the most appropriate methods for assessing prediction error for presence/absence data because it makes full use of both presence and absence scores, it measures agreement rather than association, and it varies between 0 and 1 (Fielding and Bell 1997). However, this measure may be sensitive to the sample size and to the distribution of values among classes (Forbes 1995). Another method, commonly used in medicine (see Zweig and Campbell 1993), has recently been applied in ecology: ROC analysis (Manel et al. 2001). ROC (receiver-operating characteristic) analysis makes it possible to determine a cut-off value based on a graph of all sensitivity and specificity pairs resulting from continuously varying the decision threshold over the entire range of data (DeLeo 1993). Sensitivity is the proportion of true positives correctly predicted, and specificity is

the proportion of true negatives correctly predicted (Manel et al. 2001). The area under the corresponding curve (AUC) represents an accurate measure of model performance, with 1.0 representing a perfect model (i.e. perfect discrimination of presence and absence) and 0.5 indicating no significant difference between the two events.

DeLeo (1993) suggested criteria for choosing a cut-off value from a ROC plot: 1) the point where optimum sensitivity is obtained; 2) the point where optimum specificity is obtained; 3) the point at which sensitivity and specificity are equal; and 4) the point where the sum of sensitivity and specificity is maximized. Maximum sensitivity or specificity could always be ensured by declaring all events positive or negative, respectively. Therefore, to choose our cut-off value, we used the point where sensitivity and specificity are maximised, because that point provides the best discrimination between predicted presence and absence.

To illustrate ROC analysis, we used a data set collected in deciduous forests of New Brunswick over a period of three years (n = 197 stations). We visited sampling stations three times each year during the peak of the breeding season of most forest birds. In this paper, we examine the relationship between the probability of presence of the ovenbird *Seiurus aurocapillus* and a gradient in harvesting intensity. This gradient is the second axis of a principal components analysis conducted on 15 local vegetation variables. This principal component explained 19% of the observed variance and was correlated with density and basal area of larger trees (> 20-cm dbh), canopy closure, and snag density, hence we interpreted it as a gradient in harvesting intensity (Guénette and Villard unpubl.).

Logistic regression shows that the probability of ovenbird presence in deciduous stands is negatively related to harvesting intensity (Table 1, Fig. 2, Guénette and Villard unpubl.). According to the area under the ROC curve, the performance of the model is high (AUC = 0.80; $p < 0.001$; Swets 1988). Sensitivity and specificity were maximized when y = 0.89. If we compare the threshold value obtained by this method with an arbitrary cut-off value of 0.5, the former seems more ecologically relevant: below this threshold, the ovenbird was present in almost all stations. The noise apparent above the threshold might reflect the influence of other factors such as landscape structure or the fact that some individuals occupy marginal habitat such as selection cuts (Bourque and Villard 2001).

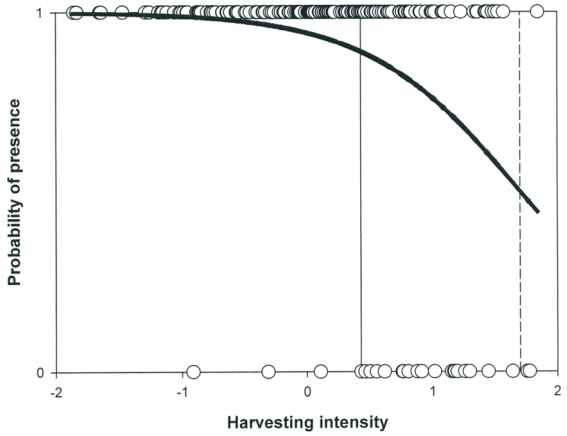


Fig. 2. Probability of presence of the ovenbird as a function of a PCA axis representing a gradient in harvesting intensity (n = 197). The dashed line indicates the threshold corresponding to a cut-off value of 0.5, whereas the solid line represents the value determined by using ROC analysis.

When using continuous dependent variables, there can be more than two stable states. However, it is conceivable that above a certain point, there is a discontinuity in the relationship between the predictor and the response variable. For example, the abundance of a species may increase more quickly when habitat quality reaches a certain threshold. In that case, we can use breakpoint regression (also known as piecewise regression), a nonlinear regression procedure that determines two relationships and a breakpoint that describes the highest proportion of the variance (Dodds et al. 2002). Breakpoint regression could be viewed as an analog to ROC analysis applicable to continuous variables such as species richness or abundance. This technique, like ROC analysis, is increasingly used in ecological research (see Losos and Schluter 2000, Dodds et al. 2002). Lomolino and Weiser (2001) used it to relate species richness to island area. They ran 101 regressions for each data set, incrementing the trial breakpoint by 0.1 at each iteration through the range of 0.0–10.0 (log-transformation of island area [m^2]). They subsequently selected the value yielding the highest r^2 as the optimal breakpoint. They concluded that breakpoint regression can be used to test for the significance, and to explore patterns of variation in nonlinear relationships.

Table 1. Parameters of a logistic regression model predicting the presence/absence of the ovenbird in deciduous stands (n = 197) as a function of harvesting intensity.

Parameter	B	SE	Wald	DI	p
Harvesting intensity	–1.636	0.387	17.912	1	< 0.001

Types of empirical thresholds

Theoretically, three types of thresholds could be expected for a binary response variable. Thresholds are often represented schematically as a perfect relationship, i.e. no false positives or false negatives (Fig. 3a). Hereafter, we will refer to these thresholds as "Type I". Such a perfect relationship implies that the species in question only responds to the variable considered. However, owing to their multivariate nature, ecological relationships rarely if ever exhibit type I thresholds. On the other hand, when it is possible to control other significant variables, some quasi-perfect relationships of this type can be obtained (Guénette and Villard unpubl.). In general, however, we observe two other types of empirical thresholds. A threshold of type II (Fig. 3b) can be defined as the point along a gradient in habitat alteration below which the species is always present. Statistically, the sensitivity is equal to one. Above thresholds of this type, the species is only present in some stands. This implies that other variables come into play. For example, individuals observed in some marginal stands located above the threshold can be transients that do not actually reproduce in those stands. In conservation terms, this threshold is the least risky because species are relatively frequent along the entire gradient, even above the threshold. Therefore, a management plan based on type II thresholds should increase the probability of persistence of the species in some areas, while maintaining at least marginal habitat in portions of the land base falling above the threshold.

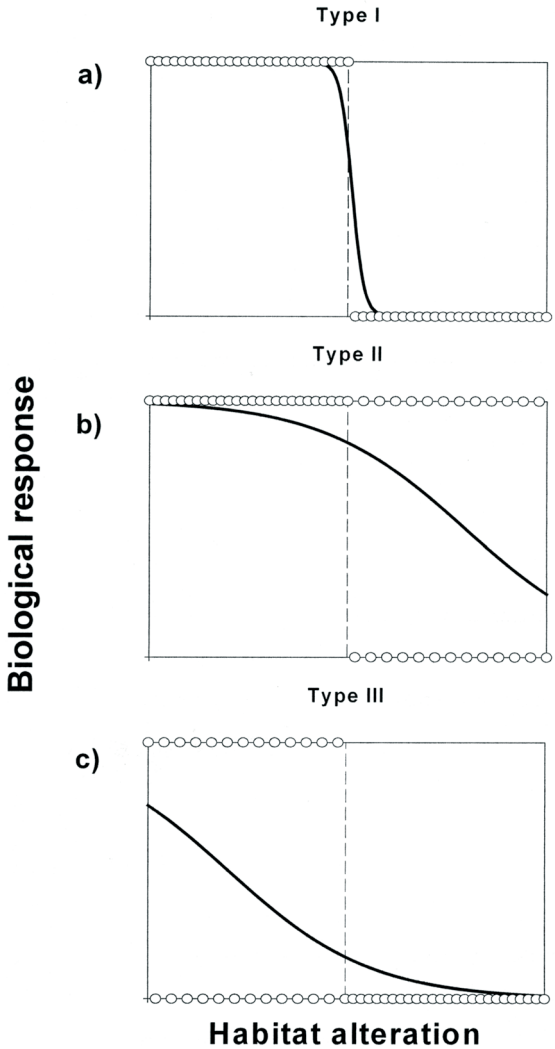


Fig. 3. Three types of thresholds that can be obtained as a function of habitat alteration, or inversely, habitat quality: a) type I, when the discrimination between predicted presence and absence is perfect, b) type II, where the species is always present below the threshold, and c) type III, where the species is always absent above the threshold.

Empirical threshold type III (Fig. 3c) provides the clearest signal with respect to conservation. A species showing this type of threshold is only present in some stations below the threshold and consistently absent above this threshold. This pattern may reflect the fact that the species' presence is influenced by either one or many other variables or that the species does not saturate the suitable habitat. This type of threshold is thus very insightful for conservation. However, thresholds of type III should be applied conservatively by ecosystem managers, for example by adding a safety margin to the observed threshold value.

Validation of ROC-derived thresholds

To validate ROC analysis as a threshold detection method, we built a data set (n = 401 stations) with a pre-defined type III threshold (60.00) above which no stations were occupied by a hypothetical species. Below this threshold, species presence was randomly determined. We used the method previously described to build the logistic regression model. The area under the ROC curve was 0.84, indicating that the model has a high performance (see below). Using logistic regression parameters and the cut-off value obtained from ROC analysis, we calculated the threshold. The ROC procedure provided a cut-off value of 0.22, and an associated threshold of 60.09 (Fig. 4). This suggests that ROC analysis provides very accurate threshold values. The absence of noise in this data set only increased the area under the ROC curve. Swets (1988) pointed out that, to be considered useful, a model should have an area under the curve of at least 0.7. Thus, we recommend that thresholds only be provided to ecosystem managers when models reach such a performance.

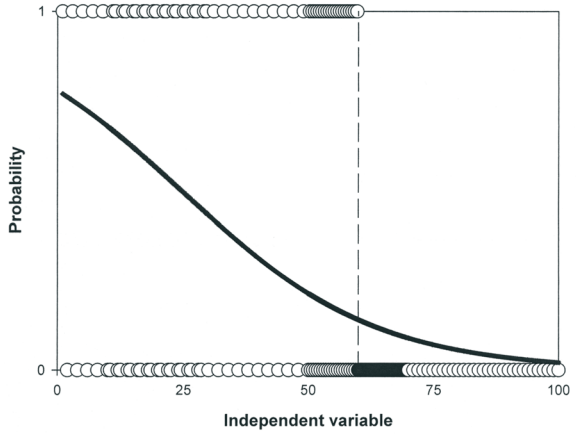


Fig. 4. Detection of extinction threshold for a hypothetical species. The threshold was predefined at 60.00 units, and ROC analysis detected a threshold at 60.09 units (dashed line). Above this threshold, the species is always absent (threshold type III – Fig. 3).

Sample size effect on threshold detection

Although we have found methods that enabled us to objectively identify threshold values in a species' response to the environment, we wanted to examine the robustness of these threshold values to differences in 1) sample size and 2) the extent of an ecological gradient that is sampled in a survey. To address the effect of sample size, we randomly removed data points (5–95% of the actual data points, 5% increments) from the observed relationship previously described for the ovenbird (Fig. 2) and recalculated the threshold value using ROC analysis after each iteration (50 times). We then plotted 1) the area under the ROC curve corresponding to each new model obtained and 2) the corresponding threshold values against sample size. Linear regression was used to assess sample size effect.

Sample size had a significant effect on model performance ($R^2 = 0.247$, $p < 0.001$; Fig. 5a) and on the threshold values found ($R^2 = 0.360$, $p < 0.001$; Fig. 5b). However, these relationships hinged on some influential points falling below a sample size of 145 and 100 respectively. When removing these points, the relationships became nonsignificant. These results are consistent with those of Cumming (2000). He concluded that model reliability increased with sample size. In our case, threshold values remained constant above a certain sample size (n = 100, 51% of the actual data points).

We also hypothesized that the portion(s) of an ecological gradient that are actually sampled influence the threshold values obtained. For example, a data set representing only the extreme values of a gradient might yield a strong threshold when in fact the logistic curve based on a more representative (i.e. continuous) gradient should be more

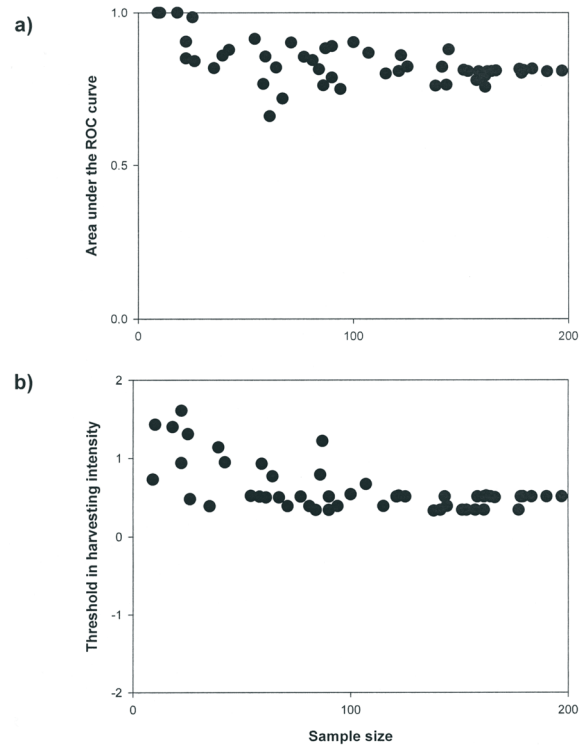


Fig. 5. Variation in a) the area under the ROC curve and in b) thresholds found in probability of presence of the ovenbird as a function of sample size. We randomly removed 5–95% from the original data set at each iteration

shallow, and the relationship possibly nonsignificant. To simulate this scenario, we randomly removed 5–95% of the data points (5% increments), starting from the center of the gradient. The area under the ROC curve increased nearly significantly with sample size ($R^2 = 0.074$, $p = 0.057$; Fig. 6a). The corresponding threshold values were also influenced by the removal of data points ($R^2 = 0.135$, $p = 0.009$; Fig. 6b). However, this is probably due to the high number of outliers appearing below a sample size of 100. Thus, as suggested by Hirzel and Guisan (2002), increasing sample size also increases sampling efficiency. However, the latter simulation also points out that relatively continuous gradients should be obtained when studying nonlinear relationships, because sampling the extremes of a gradient could artificially inflate the predictive power of models and yield misleading threshold values.

Data partitioning

Osborne and Suárez-Seoane (2002) recommended geographical partitioning of data sets when sampling is conducted over a large area. Spatial data partitioning improves distribution models because it better accounts for regional heterogeneity in predictor variables. On the other hand,

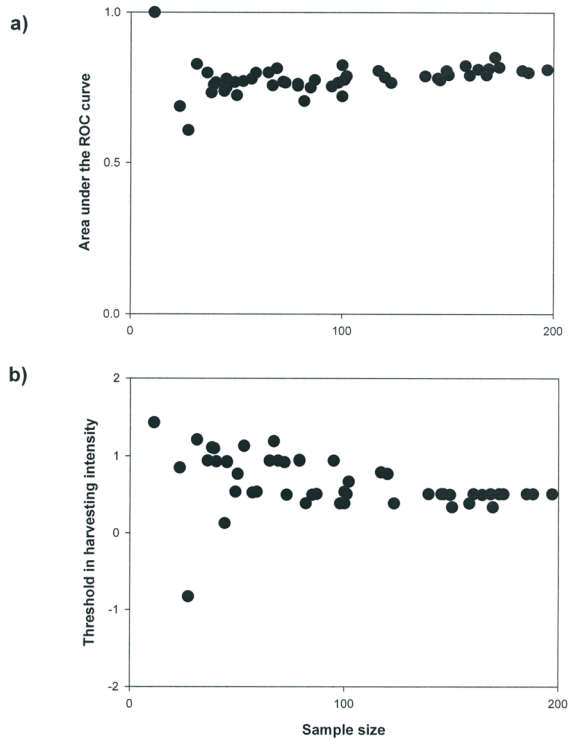


Fig. 6. Variation in a) the area under the ROC curve and in b) thresholds in the probability of presence of the ovenbird as a function of sample size. We randomly removed 5–95% from the actual data set at each iteration, starting from the center of the gradient.

Lichstein et al. (2002) suggested to control for local level effects before investigating landscape level relationships. Most studies assessing the relative influence of these two spatial scales concluded that species distribution is mainly influenced by variables characterizing local stand composition and structure (Drapeau et al. 2000), suggesting that landscape effects can only play a significant role when local conditions are favourable to species (Hagan and Meehan 2002, Lichstein et al. 2002). Therefore, it is wise to control for local-scale habitat relationships before investigating threshold responses to landscape-scale habitat alteration. One way to address this issue is to exclude stations with locally unsuitable habitat from analyses. Measuring vegetation structure and composition can be time-consuming, but the assumption that all habitat patches are equally suitable in terms of microhabitat can confound the interpretation of the actual relevance of landscape effects (Hagan and Meehan 2002).

Even at a relatively fine scale, it can be a good idea to partition data in terms of habitat type because most ecological studies are conducted in heterogeneous landscapes. For example, it is common practice to pool all sampling stations into a single data set, regardless of local habitat types sampled. Let us say a researcher samples forest birds in coniferous, mixed, and deciduous stands, a given species would not be expected to react the same way to harvesting intensity in these three different stand types. Indeed, the probability of presence of the ovenbird in relation to harvesting intensity varied according to local stand type. The ovenbird was much more frequent in mixed and deciduous stands than in coniferous stands. Using the overall data set, the area under the ROC curve was 0.69 (relatively weak discrimination; lots of noise on either side of the threshold). For the three subsets, AUC = 0.69 for coniferous forests (n = 119), 0.93 for mixed woods (n = 103) and 0.80 for deciduous stands (n = 197). These results suggest that in mixed stands, harvesting intensity discriminates almost perfectly the presence/absence of this species.

In the two situations described above, it is necessary to determine this partitioning in an objective manner. The first option is to apply a stepwise logistic regression and to partition the data set according to the most influential variable. However, we can also use classification or regression trees to determine thresholds in species-habitat relationships. These methods are seldom used in ecology (but see De'ath and Fabricius 2000) but widely used to test predicted medical outcomes (e.g. Tafeit et al. 2000, Guzick et al. 2001). Those trees are constructed by repeatedly splitting the data set according to a simple rule based on a single explanatory variable. At each split, the data set is partitioned into two mutually exclusive groups, each of which is as homogeneous as possible (De'ath and Fabricius 2000). For each split, the χ^2 test is used to determine the optimal cut-off value. Selker et al. (1995) compared the performance of logistic regression and classification trees to predict binary outcomes. Based on the area under the ROC curve, they concluded that logistic regression had a slightly higher predictive performance.

Conclusions

As ecological researchers and ecosystem managers are increasingly seeing thresholds in species response to habitat alteration as potentially useful tools for conservation planning, we suggest to use, whenever possible, dependent variables reflecting the relative fitness of individuals rather than mere presence/absence or abundance. Otherwise, management recommendations may underestimate the requirements of certain species and, therefore, fail to provide the resources required for population persistence. Attention should also be paid to the type of empirical threshold obtained. For example, type III thresholds (Fig. 3c) may be the most critical with respect to conservation planning.

To objectively define thresholds in species response, we recommend the use of methods taking into account the frequency of occurrence of target species when determining a cut-off value (e.g., ROC analysis, classification trees). Moreover, researchers conducting studies in relatively large and ecologically diverse areas should consider partitioning

their data a posteriori to control some factors. This procedure ensures that thresholds obtained are not confounded by complex interactions among variables relevant to different spatial scales. Finally, if the objective is to determine thresholds for a guild or a community, we recommend the use of thresholds obtained for the most sensitive species rather than those obtained from species richness or total abundance of these species groups.

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Habitat thresholds and effects of forest landscape change on the distribution and abundance of black grouse and capercaillie

Per Angelstam

Angelstam, P. 2004. Habitat thresholds and effects of forest landscape change on the distribution and abundance of black grouse and capercaillie. – Ecol. Bull. 51: 173–187.

This study reports thresholds for the amount of habitat needed for individuals and local breeding (=lekking) populations of black grouse *Tetrao tetrix* and capercaillie *T. urogallus* in boreal forest. I also examine the effects of the forest age distribution on the abundance of the two species at local and regional scales. Using systematic surveys of displaying males and forest landscape data, the minimum habitat patch size requirements for presence of black grouse and capercaillie was found to be 0.2 and 0.8 km^2 for single males, and 0.9 and 2.2 km^2 for lekking males, respectively. In large patches of suitable habitat the density of lekking males was 5 km^{-2} for black grouse, and 2.5 km^{-2} for capercaillie. The local landscape scale habitat thresholds for presence of displaying black grouse, with a probability of 0.9, were 15% for solitarily displaying males, and 22% for leks, respectively. For lekking capercaillie the threshold was ca 34%. A 97% incidence in habitat patches exceeding the minimum required size, and asymptotic prevalence functions, suggest that available habitat patches were saturated with lekking males, and the grouse populations in equilibrium with their habitat.
On the local landscape scale (16 km^2 plots), 84% of the density of lekking black grouse and 74% for lekking capercaillie were explained by the amount of the preferred habitat patches. Both on short-term (decades) in local landscapes, and on nation-wide long-term (60 yr) scales in Sweden, changes in the relative abundance of black grouse and capercaillie paralleled changes in the forest landscapes' age distribution. The results indicate that grouse species show close environmental tracking in terms of habitat amount, and that regeneration time after stand-replacing disturbance represents a resource axis subdivided by forest-living grouse in boreal Fennoscandia. Differences compared with the situation in the periphery of the distribution of these species are discussed, as well as their role as focal species for conservation.

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Understanding how dynamic habitat mosaics affect populations is a central problem in ecology and conservation (Pickett and White 1985, Wiens 1989, Rochelle et al. 1999, Scott et al. 2002). In most managed forest environments, different stages of succession after harvesting form a mosaic of habitat patches with different ages and sizes. In such landscapes species often inhabit only a certain type of patch (Johnston and Odum 1956, Haapanen 1965, 1966, Ferry and Frochot 1970, Thomas 1979, Swenson and Angelstam 1993, Angelstam et al. 2004). If the habitat preference of a given species is fairly narrow, the number and size of sufficiently large and connected patches of the preferred

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habitat in the landscape should affect population density both on a local and a regional scale. Populations should thus track the amount of their respective preferred habitats (Roughgarden 1974, Wiens 1976, Cody 1981, 1985), which are likely to change as succession proceeds, and also differ among landscapes depending on the management system. As patches become unsuitable, local populations should go extinct, while other local populations should become established as new patches of their preferred habitat arise. The forest landscape composition should thus determine the densities of breeding populations, provided that the dispersal capacity matches the inter-patch distance (Segelbacher et al. 2003).

The naturally dynamic northern boreal forest was characterised by considerable spatial and temporal dynamics caused by fire, wind and other disturbances (Angelstam and Kuuluvainen 2004). These disturbances resulted in a patchy distribution of different successional stages at multiple spatial scales within the landscape (Högbom 1934, Niklasson and Granström 2000). However, due to the development of commercial forestry, more even-aged forests with a reduced range of patch sizes, landscape proportions of different forest types, tree species, and site types, have replaced the variable patch dynamics of natural forest types (Angelstam 1997, Esseen et al. 1997, Mykrä et al. 2000). Because many species had adapted to this dynamic environment, the maintenance of viable populations is dependent on a land management that emulates characteristic habitat structure of a once naturally dynamic landscape. Establishing explicit and quantitative targets for habitat management is consequently an important research task. With knowledge about the duration and rates of disappearance and renewal, and the habitat amount required by different representative habitat specialists, which specialise on certain successional stages, it should be possible to predict both spatial and temporal differences of their distribution and abundance (Angelstam et al. 2004).

The sustainable conservation of species requires that the habitat demands must be satisfied both at the levels of individuals and populations. In forest landscapes where large-scale stand-replacing disturbances dominated, such as in the boreal forest, species can be assumed to have adapted to this shifting mosaic of successional stages. Boreal forest grouse species (Tetraonidae) are highly sedentary birds with a strong potential for population growth. Morphological characters suggest that the grouse family evolved in a boreal environment (Hjorth 1970, Johnsgard 1973). Hence, it can be argued that boreal grouse species ought to have evolved adaptations to a dynamic landscape, such as the ability to colonise newly formed habitat patches. Where all four Fennoscandian forest-living tetraonid birds occur sympatrically, they utilise forest stands of different age (Seiskari 1962, Swenson and Angelstam 1993). The two lekking species black grouse *Tetrao tetrix* and capercaillie *T. urogallus*, using young forest and open woodland habitats such as heaths and bogs (Klaus et al. 1990, Angelstam et al. 2000) and older forest (Cramp and Simmons 1980, Winquist 1983, Klaus et al. 1989), respectively, are the most demanding ones in terms of area requirements.

The aim of this paper is to test Seiskari's (1962) hypothesis quantitatively for black grouse and capercaillie. I focus on evaluating how the abundance and distribution of breeding and non-breeding male individuals is affected by the size of preferred habitat patches at the scale of individuals, and the proportion of the landscape at the scale of local populations. While most studies on forest mosaic structure including fragmentation have employed a patch-centred scheme in which forest patches are studied, I used local landscapes as sampling units (Fahrig 1999). I relate quantitative measurements of size and amount of habitat patches to the abundance of black grouse and capercaillie at different spatial (local and nation-wide) and temporal (short-term and long-term) scales to test the idea that habitat dynamics drive the distribution and abundance of forest-living grouse species (Storch 2002).

Specifically, the following predictions will be tested: 1) There are thresholds in the amount of habitat needed for local occurrence of black grouse and capercaillie both at the scale of the individual (patch scale) and populations (landscape scale). Additionally, because the capercaillie is a much larger bird than the black grouse, one would expect that the area requirements for individual patches should be larger. 2) In species with a complex social organisation like black grouse and capercaillie the area requirements will be larger for a functioning social unit (a lek) than for single individuals. 3) Habitat selection and landscape composition combined determines distribution and abundance. Thus, in boreal forest regional between-area differences as well as trends in black grouse densities should be related to the abundance of young forest, and open raised bogs. Capercaillie densities analogously should be related to the abundance of older forest. 4) Because of changes in forest management practices the age distribution in the Swedish forest landscape has varied during the 20th century. Hence, one would also expect large-scale changes in the relative abundance of black grouse and capercaillie over wide geographic areas.

Study areas

Field work was carried out in the boreal ecoregion in Sweden (Sjörs 1965), viz. 1) in the province Västmanland (the Grimsö area, 59°40′N, 15°25′E), 2) Hälsingland (the Boda and Hälsen areas, 61°30′N, 16°45′E) and 3) Lappland (Vojmsjön, 65°05′N, 16°15′E; Idvattnet, 64°25′N, 17°00′E; Trollforsen, 66°05′N, 19°15′E; see Fig. 1).

In 1979, male black grouse were surveyed within a 576 km^2 (48 × 12 km) south to north transect in Västmanland across the transition from hemiboreal forest in the south with mixed forest and agriculture to tracts of boreal conif-

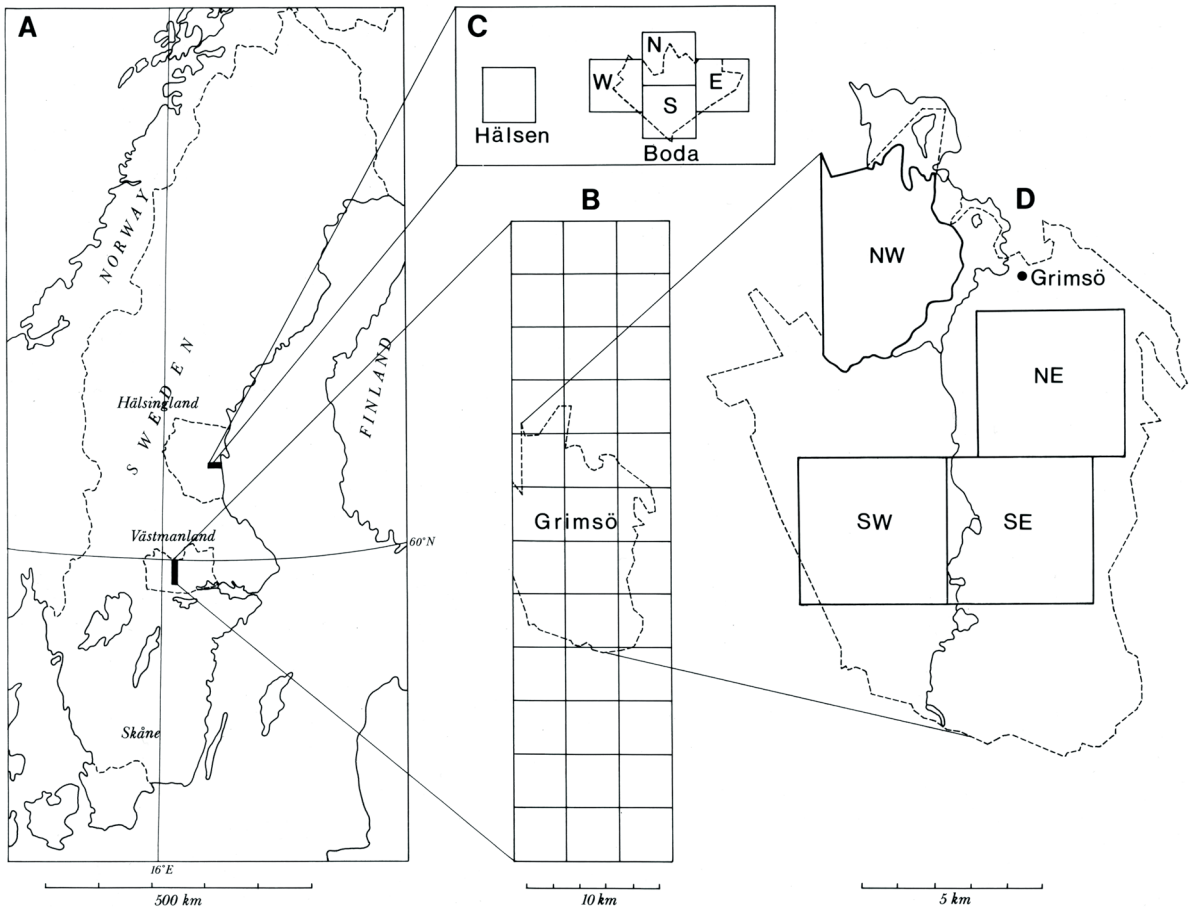


Fig. 1. Location of the study areas where black grouse were surveyed in Sweden (A). Part B of the figure shows the position of the 36 different 16-km^2 survey plots used for the analysis of black grouse density in relation to habitat composition in Västmanland, and the Grimsö area (hatched line). Part C shows the location of the five 16-km^2 survey plots made in Hälsingland. Surveys of capercaillie were made in northern Sweden (see text for co-ordinates) and within four 16-km^2 survey plots in Grimsö (D), and the Hälsen area (C).

erous forest and bogs in the north (see Sjörs 1965). In Hälsingland, birds were surveyed in 1981 within 64 km^2 of the Boda area, and in 16 km^2 of the nearby Hälsen area in 1981 and 1982. The reason for including these areas was to include very large patches containing several leks. To determine annual variations in numbers, birds were also surveyed within the Grimsö area (108 km^2) each year from 1974 to 1984.

Capercaillie densities in Västmanland (four 16-km^2 survey plots within the Grimsö area), Hälsingland (one plot at Hälsen) and Lappland (3 plots at Trollforsen and one each at Vojmsjön and Idvattnet) were estimated over a total area of 160 km^2 in 1983 and 1984. In addition annual variations in numbers of capercaillie cocks on leks were obtained from the Boda area in Hälsingland (31.8 km^2) during the period 1963–1976.

Forests in all areas were totally dominated by Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*. During at least the latest two forest generations these forests have been subjected to commercial logging where clear-felling practices have dominated (Angelstam 1997, Esseen et al. 1997) producing forests that are patchy with respect to their age structure.

Methods

Surveys of black grouse and capercaillie

Black grouse have a lek mating system whereby adult males have communal display grounds (leks), which are attended by females only for mating. One-year old males often display solitarily away from the lekking arenas. Therefore, to estimate the density of black grouse the whole landscape needs to be covered. As units for estimating black grouse density, I used 4 × 4 km quadrates. This area is at least five times the size of a lek group summer home range (ca 3 km^2, Angelstam unpubl.) and twice the size of a male

group winter home range (ca 7 km^2, Angelstam unpubl.). All surveys were made during April and the first half of May between sunrise and 2–3 h after sunrise, i.e. when the display activity is at its peak (Hjorth 1966). Black grouse song may be audible up to 3 km but more often around 2 km (Hjorth 1970). However, taking into account topography and forest features, which sometimes limit the range of detection, I considered 0.8 km as a limit for reliable auditory detection. Thus, when searching for leks and solitary (non-lekking) males, all observation points within a survey plot were not more than about 1.5 km from each other. Usually all displaying birds were seen. Open places identified on maps and aerial photographs and judged to be potential lek sites, were also visited. Surveying a given plot was not considered as complete until it had been covered once by auditory observations during good weather conditions, i.e. no or weak wind and no precipitation (Hjorth 1966).

Density is expressed as the number of displaying males per unit land area, taking into account both communally and solitarily displaying cocks, respectively. The former group in a few cases included some quiet males. I defined a lek as two or more males displaying on the ground within 0.2 km distance. Solitary cocks were usually spaced out >0.5 km. To study within-area population trends, displaying males were surveyed within the Grimsö area three to five times each year. For this purpose the Grimsö area was divided into four sub-areas ranging from 18 to 31 km^2. At least two, but usually all four, sub-areas were surveyed simultaneously by up to 12 people in one morning following the method stated above. For each sub-area the morning survey in which the maximum number of males was observed, was used to calculate a minimum density estimate. Radio-tracking data show that the size of sub-areas was sufficiently large to avoid the problem that birds would move between sub-areas. In this paper trends in density are presented for the eastern (58.1 km^2) and western (49.8 km^2) parts of the Grimsö area by pooling data from sub-areas in each case (Fig. 1).

Since capercaillie males are territorial, population density was estimated by surveying displaying males (Moss and Oswald 1985). Displaying capercaillie males were surveyed within 16-km^2 quadrates from late April to early May and from ca 1.5 h before sunrise until around sunrise, when display activity declined, and listening was hampered by intense bird song. Capercaillie song is audible to the human ear ca 0.30 km but often only 0.15 or 0.20 km (Hjorth 1970). The search for capercaillie males was therefore made by two to four people simultaneously so that all observation points were <0.3 km apart. Leks were visited two to three times. All thinning and final felling forest stands (cutting classes C and D (Svensson 1980)) as well as forested bogs were visited, since capercaillie prefer to lek in such habitats (Hjorth 1982, Winquist 1983, Rolstad and Wegge 1987a, Storch 1997). Summer home range size of capercaillie males (4.9 km^2, Larsen et al. 1982) suggest that a 16 km^2 plot probably was large enough to support several males of capercaillie, at least during the breeding season. The distance between leks in good habitats is usually ca 2 km (Rolstad and Wegge 1987b, Hjeljord et al. 2000).

The number of males on leks only is an obvious underestimate of the total male density (Angelstam 1979, Jones 1982), but even if I attempted total surveys by including also solitarily displaying males, it is obvious that all densities of black grouse and capercaillie obtained are minimum values. But this nonetheless provides a good relative index of abundance for between area and temporal comparisons. Note, that in comparison to other areas of the distribution range the boreal forest terrain is flat, landscapes are sparsely populated and with no disturbing traffic noise.

Minimum area requirements and landscape scale thresholds

To analyse the minimum area requirements and density of black grouse and capercaillie in relation to patch size I defined a patch as an area of preferred vegetation as defined in Table 1, and which was situated >0.2 km from any other areas of the same type. For black grouse no habitat patches <0.02 km^2 and for capercaillie no patches <0.05 km^2 were included because they were judged to be far below the required minimum size of habitat patches for maintenance of one individual bird. Logistic regression was used to determine the thresholds for the occurrence of black grouse and capercaillie regarding the proportion of the local landscape made up of suitable habitat, respectively. All analyses were made using the Statistica software.

Spatial and temporal differences in forest composition and grouse density

In boreal forests the black grouse prefers seedling and young stands while fresh clear-cuts, and older forests are generally avoided. The black grouse is found also on open raised bogs (Johnsson 1979), and was formerly common on anthropogenic heaths and in traditional cultural landscape that are now afforested (Klaus et al. 1990, Kolb 2000, Angelstam et al. 2000). The capercaillie on the other hand prefers later stages in the forest succession throughout its range and throughout the year (Klaus et al. 1989), and in the boreal region with substantial amounts of Scots pine.

The habitat composition of the 16-km^2 survey plots was analysed by using forest company maps with forest stand descriptions made using aerial photographs. I distinguished nine types of habitat (Table 1), and which can be combined to describe the forest land cover types used by forest grouse species (Seiskari 1962, Swenson and Angelstam 1993, Table 1). The size of patches of these nine land cover types was determined by using a planimeter and

Table 1. Definition of variables used to describe the habitat of black grouse and capercaillie. When delineating patches for the threshold analyses, black grouse habitat was defined as the sum of YOFOR and OPBOG, and capercaillie habitat as the sum of OLFOR and FOBOG.

Code	Description
UNFOR	Cutting class A. Unstocked forest. Vertical cover of young tree below 30% or age <3 yr.
YOFOR	Cutting class B. Thicket stage and young forest. Age 3 yr or more. Mean diameter of dominating and co-dominating trees below 10 cm over bark. Subclass B3 (dense young forest where thinning is required) was not included.
THFOR	Cutting class C. Young thinning forest. Mean diameter of dominating and co-dominating trees between 10 and 20 cm over bark. Includes also subclass B3. In the study areas the proportion of Scots pine generally exceeded 70%.
OLFOR	Cutting class D. Old thinning forest and final felling forest. Mean diameter of dominating and co-dominating trees at least 20 cm over bark. In the study areas the proportion of Scots pine generally exceeded 70%.
OPBOG	Open bog. Raised bog with no trees or trees (usually stunted Scots pines) shorter than 2 m.
FOBOG	Forested bog with Scots pine forest on peat.
FEN	Wet mire with sedges (*Carex* spp.) but usually without trees.
AGLAN	Agricultural land. Either land used for crops or grazed or ungrazed meadows.
VILLA	Farms, villages, gardens etc.

1:20 000 or 1:10 000 scale maps to the nearest 0.5 ha, or from stand sizes given in forest stand descriptions to the nearest 0.1 ha. For all grouse survey plots the habitat data concerned the forest situation in the year before the grouse surveys were performed. To analyse which habitat variables (independent variables) affect the local density of displaying black grouse and capercaillie (dependent variables) I used step-wise multiple regression. The means and range of the variable used are listed in Table 2. Only variables significant at the 5% level or better are presented. To validate the regression analyses made on the Västmanland data (n=36), I used these equations to predict the density in the Hälsingland area (n=5).

To study how long-term landscape level changes in the amount of habitat affects the long-term abundance changes of the two grouse species both variables where compared. Surveys of black grouse males made within the Grimsö area (Fig. 1) from 1974 to 1984 in this study, and surveys of capercaillie made within the Boda area (Fig. 1) from 1963 to 1976 published by Sandegren and Nordström (1977) were first compiled. I obtained data on the amount of different cutting classes annually for the Grimsö area, and for four different years (1952, 1966, 1973, 1977) for the Boda area (Wahlgren pers. comm.).

To study the long-term nation-wide changes in the amount of forest in different successional stages I used data from the Swedish Forest Survey (Nilsson and Östlin 1961, Arman 1965, 1969, Eriksson and Janz 1975, Anon. 1981, Toet pers. comm. and Fridman pers. comm.). I defined black grouse habitats as all forest land defined as young forest. Capercaillie habitat was defined as forests older than 60 yr and not classified as spruce forests (Svensson 1980). As abundance indices of black grouse and capercaillie I used the hunters' official bag records (Anon. 1940–2001).

Table 2. Means and standard deviations for variables used in the analyses density in relation to habitat composition (% of land area) with 16-km^2 of male black grouse (n=36) in Västmanland 1979 and capercaillie (n=10) in Västmanland and Hälsingland 1982.

Variable name	Variable code	Black grouse Mean±SD, range		Capercaillie Mean±SD, range	
Total density (males km^{-2})	TOTDEN	0.57±0.66	(0–2.27)	0.81±0.68	(0.11–1.59)
Density of lekking males (males km^{-2})	LEKDEN	0.35±0.56	(0–1.93)	–	–
Clear-felled area (%)	UNFOR	8.4±6.8	(0–24.5)	10.4±7.4	(1.9–20.9)
Young forest (%)	YOFOR	12.1±6.4	(0–32.5)	26.3±27.1	(9.7–73.9)
Young thinning forest (%)	THFOR	13.1±10.4	(0–38.2)	11.4±6.3	(9.5–21.9)
Old thinning and final felling forest (%)	OLFOR	40.5±10.8	(18.6–64.1)	30.8±14.1	(12.3–50.6)
Open bog (%)	OPBOG	2.8±4.3	(0–17.0)	6.2±4.8	(0–13.2)
Forested bog (%)	FOBOG	8.1±5.1	(0–17.0)	10.3±6.8	(1.7–16.1)
Fen (%)	FEN	0.9±1.5	(0–6.7)	1.7±2.9	(0–6.7)
Agricultural land (%)	AGLAN	13.4±15.0	(0–54.1)	2.7±4.8	(0–11.2)
Settlements (%)	VILLA	0.6±2.0	(0–11.0)	0.02±0.05	(0–0.1)

However, bag records per se cannot be used as evidence for long-term trends (Potts 1980). Indeed several difficulties are associated with bag records, such as changes in hunting methods, in the number of hunters, and in length if the open season as well as in the reporting procedures. To minimise these problems, I calculated relative density changes as the ratio of number of capercaillie shot in a given year to number of black grouse shot in the same year. In Sweden capercaillie and black grouse are hunted by similar methods in the autumn only, and there are no restrictions as to the number of birds that can be harvested. I then compared the bag ratios with the ratios of the amounts of forest age and tree species types used by capercaillie and black grouse for nine non-overlapping national forest inventory periods. The bag records used include estimated number of birds shot in all Swedish counties. Due to the habitat selection and present distribution in Sweden of these species (Svensson et al. 1999), this study reflects the situation in the boreal forest, and in upland hemiboreal forests with a boreal character in south Sweden (Sjörs 1965).

Results

Occurrence and density in relation to patch size

Black grouse

In both Västmanland (in 1979) and Hälsingland (in 1981) displaying black grouse males were found only in patches of YOFOR or OPBOG or mixtures thereof. Patches of black grouse habitat could be divided into four types with reference to the occurrence of black grouse (Table 3). In Västmanland 31 patches contained only solitary male, 21 patches two to four solitary males, 16 patches one lek, with or without additional solitary males, and in three patches two to three leks plus additional solitary males were observed. A total of 269 patches contained no black grouse at all. No solitary black grouse males were found in patches <0.20 km^2, and no leks in patches <0.90 km^2 (Table 3). Patches >0.40 km^2 were almost always (98%, n=54) inhabited by black grouse (solitary or lekking) and most patches above 1.00 km^2 (95%, n=19) contained one or more leks. In Hälsingland three patches contained one lek each plus solitary males, and three larger patches contained two to seven leks plus solitary males. All patches in Hälsingland were of the YOFOR type. On average there was one lek 1.5 km^{-2} of YOFOR. The size of both YOFOR and mixed YOFOR/OPBOG patches with two or more solitary males were significantly larger than patches with one solitary male and patches with one or more leks were significantly larger than patches without leks (Table 3).

In Västmanland the density of black grouse per patch was zero at low patch sizes, then increased with patch size until the density per patch levelled off (Table 4). The density per patch was not significantly higher in mixed habitat patches large enough to contain multiple leks, than in patches with only one lek (Table 4). In YOFOR no multi-lek patch was found in Västmanland. In Hälsingland in 1981 the mean density in three such patches was 7.9±1.5 (SD) males km^{-2}, range 6.1–8.8, patch size 7.7±3.7 (SD) km^2, range 3.5–10.5. However, this density was significantly higher than in patches with one lek in Västmanland 1979 ($p<0.01$, cf. Table 4). Note, however, that all data do not originate from the same year. The 1980 reproduction in Hälsingland was good (Carlström pers. comm.), while in Västmanland in 1978 it was bad (Angelstam 1983), producing a larger proportion of one-year-old males displaying solitarily (cf. Angelstam 1979 and 1983) in the three large Hälsingland patches in spring 1981 (71 out of totally 177) compared to the one-lek-patches in Västmanland in spring 1979 (10 out of totally 79) ($\chi^2=17.79$, $p<0.001$). If one omits solitary males from the comparison of density in one and multi-lek patches in Västmanland and Hälsingland, respectively, the density per patch did not differ (4.4±1.0 (SD) vs 5.2±2.2 (SD) males km^{-2}, $t=0.61$, n.s.). To conclude, densities of black grouse per patch in both the YOFOR and mixed YOFOR/OPBOG habitat types thus levelled off asymptotically at large patch sizes.

Table 3. Size (km^2) of patches of the three habitat types in which black grouse were found in Västmanland 1979 (mean±SD, range within brackets and n is the number of patches visited). Small letters denote statistically significant differences.

Habitat	1 solitary male per patch	>1 solitary male per patch	1 lek per patch	>1 lek per patch
Young forest (YOFOR)	0.34±0.08 [a] (0.20–0.47) n=9	0.74±0.14 [a,b] (0.51–0.96) n=7	1.60±0.86 [b] (0.90–3.39) n=10	
Young forest/bog (YOFOR+ OPBOG)	0.39±0.17 [c] (0.22–0.88) n=16	0.82±0.28 [c, d] (0.46–1.39) n=13	1.47±0.25 [d, e] (1.14–1.76) n=6	5.70±1.46 [e] (4.34–7.24) n=3
Open bog (OPBOG)	0.47±0.11 (0.34–0.59) n=6	0.54 0.54 n=1		

Table 4. Density (male km^{-2}) of patches of the three habitat types in which black grouse were found in Västmanland 1979 (mean±SD, range within brackets and n is the number of patches visited). Small letters denote statistically significant differences.

Habitat	1 solitary male per patch	>1 solitary male per patch	1 lek per patch	>1 lek per patch
Young forest (YOFOR)	3.10±0.88 [a] (2.13–5.00) n=9	3.89±1.03 [c] (2.70–5.33) n=7	5.50±0.61 [a, d] (4.07–5.88) n=10	
Young forest/bog (YOFOR+ OPBOG)	2.93±1.03 [b] (1.14–4.55) n=16	3.05±0.87 [c] (1.44–4.57) n=13	4.22±0.52 [b, d] (3.41–5.00) n=6	4.65±0.56 (4.14–5.44) n=3
Open bog (OPBOG)	2.22±0.56 [a] (1.69–2.94) n=6	3.70 3.70 n=1		

In different habitat types within the same area and year, the density per patch was consistently higher in YOFOR than in the mixed type in all categories available for comparison (Table 4). This difference, however, was significant only in patches with one lek. In patches with only solitary males the density per patch was significantly lower in OPBOG (lower primary production) compared to YOFOR (higher primary production) patches. Moreover, the size of habitat patches with only one solitary male was positively correlated to the proportion of the patch which was made up by OPBOG (r=0.44, p<0.02, n=31), i.e. suggesting a compensation for lower habitat quality by increase in patch size.

The distance between patches with only solitarily displaying males and the nearest patch with a lek (1.8±2.0 (SD) km) was not significantly different from the distance between empty patches >0.20 km^2 (i.e. the minimum recorded size if a patch with one black grouse) and a reproducing population (2.6±2.9 (SD) km (t=1.32, DF=81, n.s.)). Empty patches were significantly smaller than even the smallest patch category with single black grouse (0.34±0.08 (SD) km^2, Table 2, t=2.99, DF=81, p<0.01). Still these empty patches were greater than the species minimum area requirement at 0.20 km^2 (mean size 0.25±0.05 (SD)), suggesting that the size of patches is far more important than the isolation of suitable habitats in boreal forest.

Capercaillie

No displaying males were observed in 18 patches of the preferred habitats with a size <0.78 km^2. Among larger patches, all but two (n=10), both 0.95 km^2, were occupied by displaying capercaillie males. The smallest patch with one lek had a size of 2.2 km^2. On average there was one lek 2.9 km^{-2} of OLFOR. Patches with only solitary males were smaller (1.19±0.35 (SD) km^2, n=4) than patches with leks (6.25±5.25 (SD) km^2, n=4), (p=0.014, Mann-Whitney U-test, U=0, n_1=n_2=4). In larger patches density levelled off just below 2.5 males km^{-2} (Fig. 2).

Number and size of habitat patches in relation to density

Black grouse – between area comparisons

Within the 36 survey plots covering 576 km^2 incorporated in the black grouse survey in Västmanland in 1979 a total of 291 male black grouse were observed: 117 males being solitary and 174 males seen on 23 leks. The total black grouse density and the density of lekking cocks, respectively, was positively correlated with the proportion of YOFOR (r=0.61 vs 0.48), OPBOG (r=0.49 vs 0.58), UNFOR (r=0.46 vs 0.34) and FOBOG (r=0.35 vs 0.35), but was negatively correlated to the proportion of AGLAN (r=–0.55 vs –0.46) and OLFOR (r=–0.53 vs –0.48). The positive relationship between the total density in the local landscape of black grouse cocks and the proportion of preferred habitat in Västmanland and Hälsingland (y=0.12x–1.17, t=14.0, n=41, r^2=0.83, p=0) is shown in Fig. 3.

Step-wise multiple regression showed that variables other than those predicted (YOFOR and OPBOG) were unimportant in explaining the observed variation in black grouse density. Without taking the minimum required patch size (0.20 km^2 for solitary males and 0.90 km^2 for

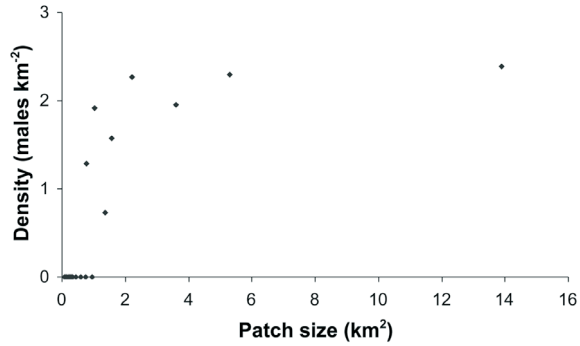


Fig. 2. Density of capercaillie males in patches of preferred habitat (OLFOR, see Table 1) in relation to patch size. Only the 4 points in patches >2 km^2 contained leks.

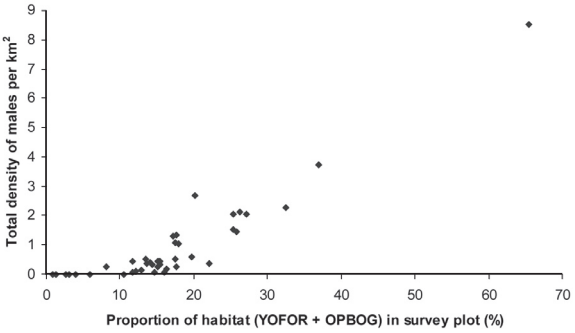


Fig. 3. Relationship between the total density of black grouse cocks and the proportion of suitable habitat in the 16-km² survey plots.

males on leks, Table 3) into account, the variation in density explained was 73% for total density and 70% for the density of cocks on leks. When patches smaller than the minimum required area were excluded the amount of variation explained remained the same regarding total black grouse density (73%), but increased to 84% for lekking males densities.

Using data from five 16-km² plots surveyed in Hälsingland 1981, I tested if the observed relationship between habitat composition and black grouse density in Västmanland had any predictive value in Hälsingland. To minimise differences in spring density between Västmanland and Hälsingland as caused by differences in previous year's reproductive success (Angelstam 1983), I used only the densities of males on leks to predict Hälsingland densities of black grouse. The predicted and observed densities of black grouse were highly correlated (r= 0.99).

Black grouse – density trends within area

With respect to changes over time from 1974 to 1984, the Grimsö area could be divided into two halves. In Grimsö east (Fig. 1) the proportion of young forest increased slowly from 22 to 29%, while in Grimsö west the amount of YOFOR was more than doubled from 18% in 1970 to 44% in 1984 due to clear-fellings made during the early 1970s. The amount of OPBOG remained unchanged. The figures of habitat proportions are not estimates but true figures based on the whole areas. In Grimsö east no significant density trend could be detected (r = –0.27, n = 11, ns), while in the west the density of black grouse almost doubled (r = 0.72, n = 11, p<0.01).

Capercaillie – between area comparison

A total of 71 capercaillie males were observed within the ten 16 km² survey plots. Of these males only one, at a lek, did not display. All but 7 males were found at 8 leks. Total capercaillie density was significantly positively correlated to the proportions of OLFOR (r=0.92), and FOBOG (r=0.89). A step-wise multiple regression included only variable OLFOR (y=0.035 OLFOR –0.36), which was the main preferred habitat. The equation explained 74% of the observed variation in capercaillie density.

Capercaillie – density trend within area

Using a series of spring surveys of capercaillie made within the Boda area from 1963 to 1976, I calculated minimum values of male capercaillie densities. The negative density trend in this local capercaillie population (r = –0.78, p< 0.001) coincided with a reduction of the final felling forests from 1966 to 1977 by 40%.

Landscape scale thresholds

Black grouse and capercaillie

Using the presence and absence of solitarily displaying and lekking black grouse in relation to the amount of habitat in the 16-km² grid cells, I tested whether or not thresholds in the amount of habitats existed. Both logistic regression relationships were highly statistically significant (χ^2=28.8; p<0.0001 for lekking males, and χ^2=21.8; p<0.0001 for solitarily displaying males), see Fig. 4. For a 90% probabil-

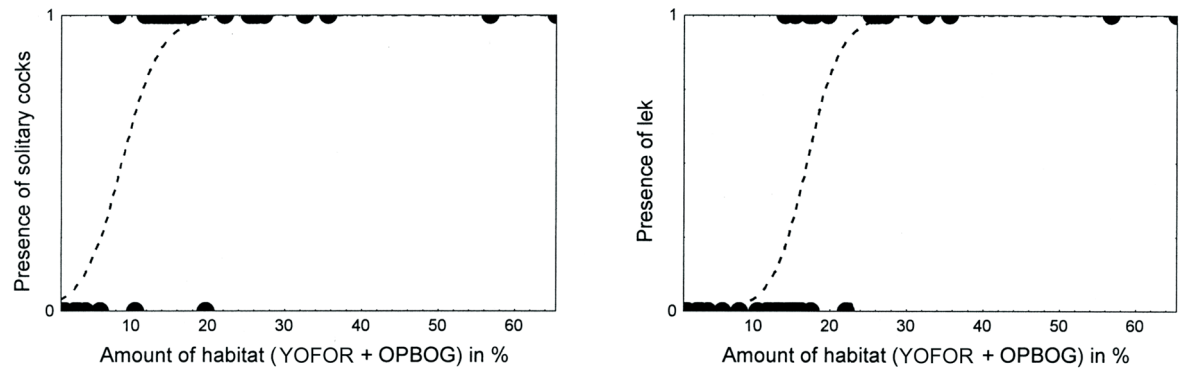


Fig. 4. Logistic regressions showing the occurrence of black grouse displaying solitarily (left) and lekking (right) in relation to the proportion of preferred habitat in the 16-km² survey plots.

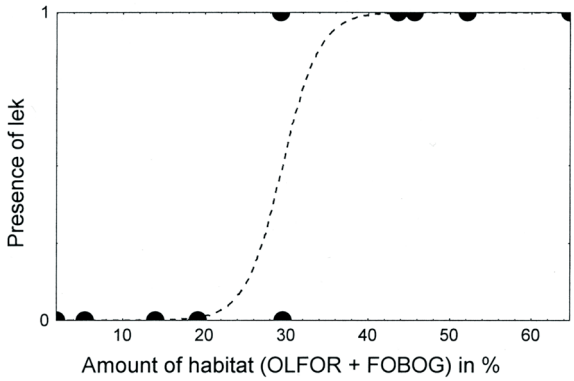


Fig. 5. Logistic regression showing the occurrence of lekking capercaillie in relation to the proportion of preferred habitat in the 16-km^2 survey plots.

ity of presence the amount of habitat needed for solitarily displaying cocks was ca 15% and for lekking males ca 22%.

The presence and absence of lekking capercaillie in relation to the amount of habitat in the 16-km^2 local landscapes was clearly related to the proportion of suitable habitat (χ^2=10.9, p=0.00095, Fig. 5). For a 90% probability of presence the amount of habitat needed for presence of leks was ca 34%.

Nation-wide changes in the relative amount of capercaillie and black grouse and their preferred habitats

During the nine non-overlapping Swedish Forest Inventories from 1938 to 2000, gradual changes in the amount of capercaillie and black grouse habitats have taken place (Fig. 6). The amount of capercaillie habitat increased from 78 000 km^2 to 105 000 km^2 during the first half of the period, and then dropped back to 82 000 km^2 during the later half of period. The amount of black grouse habitat showed inverse changes. The total area of forest land in Sweden is 285 000 km^2 (Anon. 2003). During the same period the ratio of capercaillie to black grouse exhibited long-term fluctuations (Fig. 6), but no statistically significant regression trend (p=0.07). During most of the 1940s the ratio declined gradually, and then increased to a peak in the mid-1960s. As large-scale clear-cutting commenced, the ratio then declined until ca 1980. Since then there has been a small increase in the capercaillie to black grouse ratio. To compare these changes statistically I plotted the annual ratios of the capercaillie bag records to the black grouse bag records against the ratios of the preferred habitats of the two species (Fig. 7). One-way analysis of variance showed that when using the nine different sets of habitat ratios the bag-ratios were not equal (F-ratio=7.67, p<0.001). A Pearson correlation between habitat and bag ratios for the same period was statistically significant (r=0.74, n=9, p<0.02).

Discussion

Factors influencing the abundance of black grouse and capercaillie

Patch and landscape scale thresholds

Local breeding populations (leks) of both black grouse and capercaillie were found only in large patches of their preferred habitats. The minimum patch size was 0.9 km^2 for black grouse and 2.2 km^2 for capercaillie. Moreover, densities were constant at large patch sizes and reached asymptotes of ca 5 and 2.5 lekking cocks km^{-2}, respectively. For capercaillie these requirements are the same as found in southeastern Norway (Rolstad and Wegge 1987b) and in Germany (Storch 1997, Suchant and Braunisch 2004).

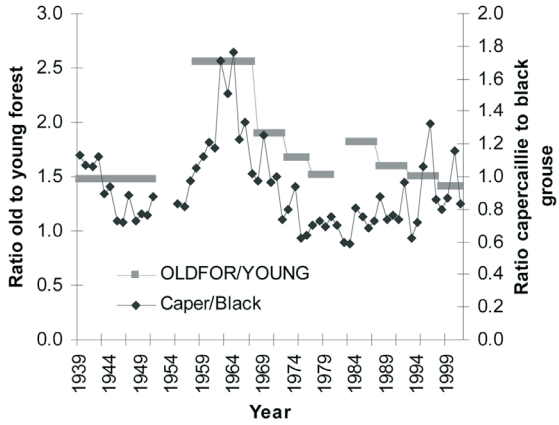


Fig. 6. Variation in the ratio between the hunter's bag of capercaillie to black grouse, and the ratio of capercaillie habitat (final felling forest with Scots pine) and black grouse habitat (young forest and open bog) according to the National Forest Inventory.

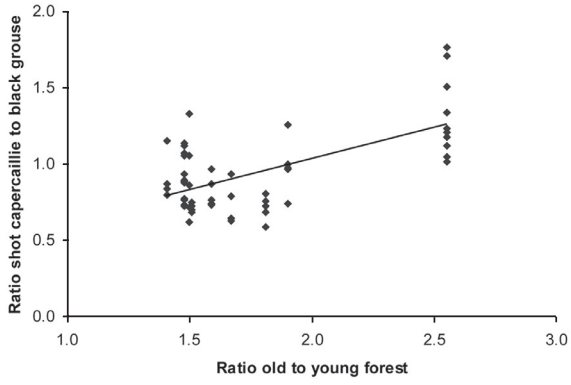


Fig. 7. Relationship between annual ratios of numbers of capercaillie to numbers of black grouse in the hunter's bags, and the ratios of capercaillie habitat to black grouse habitat according to the national forest inventory data.

The presence of both black grouse and capercaillie increased with increasing proportion of habitat in the local landscape in a non-linear fashion. For black grouse it was possible to analyse both solitarily displaying and lekking males independently. The higher threshold value for the lekking males (ca 22%) compared with solitary males (ca 15%), i.e. generally one-year birds (Angelstam 1983), suggests that a local breeding population needs more habitat than just occurrence. The much larger capercaillie (body weight >4 kg) had a higher threshold value (ca 34%) for the occurrence of leks than the black grouse (body weight ca 1 kg).

Such patch and local landscape level thresholds can be viewed as performance targets that can be used to make predictions about the occurrence elsewhere, and can thus be used in landscape conservation planning using relevant land cover data (Angelstam et al. 2004). The threshold values for black grouse and capercaillie fall in the general range reported for specialised species (Andrén 1994). It is, however, important to stress that the amount of physical habitat needed is a necessary but not always sufficient requirement that holds under present conditions regarding macroclimate, predator densities, ground vegetation cover and food availability. These conditions may change as they have done in central Europe without associated change in landscape patterns as revealed by land cover data such as forest maps and remote sensing data. Habitat thresholds thus need to be combined with knowledge about habitat quality if this in not indicated by vegetation cover maps.

The amount habitat determines distribution and abundance

Differences in black grouse densities among areas were strongly correlated with the number and size of patches of preferred habitats, (i.e. amount of young successional stages and open bog). Both locally, and viewed over larger areas, trends in total black grouse densities were closely associated with changes in the amount of preferred habitats. The observed relations between habitat amount and black grouse density also had a strong predictive value, as found for the independent Hälsingland data.

Also for capercaillie temporal and spatial variation in density could be largely attributed to differences in the number and size of patches of the preferred successional stage. Thus, the prediction that capercaillie density trends were strongly related to changes in forest age structure was upheld, in agreement with the result for black grouse, and this confirms Seiskari's (1962) hypothesis that these grouse species utilise forest stands of different age when occurring simultaneously.

The analysis of nation-wide changes in the age structure of forests and in black grouse and capercaillie bags confirms the clear relationship between forest patch dynamics and density trends at the local scale. For capercaillie Moss et al. (1979) attempted a quantitative approach by correlating declining trends in local bags of capercaillie to the removal of pine forest. Nowhere, however, has the possible quantitative relationship between habitat variables and black grouse and capercaillie density been examined in such detail as in this study. To conclude, the quantity of preferred habitats, i.e. number and size of patches of forest of different successional stages, is an important factor explaining between area differences and within area trends in density of black grouse and capercaillie within managed boreal coniferous forest landscapes.

Variation in the quality of habitats

Within the two black grouse habitat types where both the solitary males and lek types of occurrence were represented, the density of males per patch at large patch sizes levelled off at a higher density in the YOFOR type compared to the mixed YOFOR/OPBOG type (Table 4). Hence, the former type seems to be a habitat of higher quality than the latter for the black grouse. The positive correlation between the proportion of single male patches made up by open bog and the larger size of these patches indicates that lower patch quality is compensated for by increased patch size, i.e. lower density per patch. The lower density of black grouse on raised bogs compared with young forest is also evident from Johnsson (1979), who provides data on numbers of lekking black grouse males on raised bogs with leks in the province of Skåne in southernmost Sweden in 1977 and 1978. Using these data I calculated the density per bog area, excluding wet fen complexes in large bogs. To assure that bogs in Skåne are not used only as display sites, but also satisfy most needs of local black grouse groups, I took into account only bogs >3 km^2, i.e. the approximate home range size of a male lek group during the snow-free season (Angelstam unpubl., see also Johnstone 1969, Robel 1969). The density on these bogs was 1.7±1.0 (SD) males km^{-2} (n=9), which thus can be assumed to contain most needs of local black grouse leks, was significantly lower than on patches of young forest ($t=8.89$, $p<0.001$) and on mixed young forest and open patches ($t=6.51$, $p<0.001$) with one lek in Västmanland. This supports the idea of a decreasing trend in mean density of black grouse from the young forest to open bog types of habitats.

For herbivores, such as grouse, higher primary production should imply that more plant food is available. Therefore, their population density, as for many other birds (Newton 1980), should be related to, even if not necessarily limited by, the local production of food (Harestad and Bunnell 1979). Hence, a possible explanation for this difference in population density is a difference in the amount of plant food between the young forest and the open bog habitats. On forest land in Västmanland the site class productivity averages 5.9 m^2 timber per ha and year while on open bogs it is usually below 1.0 (Hägglund and Svensson 1982). Similarly, heather *Calluna vulgaris* growing on both firm land and peat (Lid 1976), produced significantly more shoots and had a significantly higher content of ni-

trogen in the former habitat than in the latter at Grimsö in 1977 (Y. Angelstam unpubl.).

Picozzi (1968) and Moss et al. (1979) have also attempted to correlate the density of grouse species to the amount and/or quality of plant food. Picozzi (1968) found a positive relationship between the average breeding density of red grouse *Lagopus lagopus scoticus* and the density and size of heather burns as well as edaphic factors, both of which affected the quality of heather (main food of red grouse (Moss 1967). Moss et al. (1979) reported that both density and production of young capercaillie in natural Scottish pine forests with a good undergrowth of blueberry *Vaccinium myrtillus* and heather were three times higher than in planted forests, which generally were <50 yr old, had little undergrowth and moreover partly consisted of exotic tree species.

An additional effect on habitat quality may be related to that bogs and wet forest land with low productivity have been drained to a very large extent (see Hånell 1984). Such habitats contain food plants such as cottongrass *Eriophorum* spp., which is an essential food item during the egg-laying period for grouse (Angelstam unpubl.), the destruction of which may influence areas much wider than those directly affected by ditching.

Variations caused by the isolation of habitat patches

According to MacArthur and Wilson's (1967) theory of island biogeography, island size and isolation influence the number of species on islands. Newly created forest habitat patches may remain species-poor because they are too isolated. Furthermore, a given species' ability to colonise a patch of a certain degree of isolation may be too low in relation to the longevity of the patch. Three lines of evidence suggest that isolation of patches within the area studied was unimportant to black grouse and capercaillie in terms of their ability to colonise newly formed patches. First, the fairly sharp limit, in terms of patch size, between patches with and without black grouse and capercaillie suggest that most suitable patches be occupied. Second, this is also indicated by the fact that no patches large enough to contain a reproducing population (lek) were devoid of black grouse and capercaillie, respectively. Finally, the absence of any difference in distance between patches with reproducing black grouse populations (leks) and empty patches with solitary males on the other support the suggestion above.

Grouse and forest succession

This study demonstrates that in boreal forest the local distribution and abundance of black grouse and capercaillie is strongly related to the amount and local distribution of suitable habitat patches. Within patches also habitat quality, possibly related to production of plant food, may influence population density of grouse. On the other hand, isolation of patches appears unimportant for population density, at least in boreal forest. Altogether, the following observations suggest that patches with preferred habitat types of black grouse and capercaillie are saturated with individuals. This represents an example of equilibrium populations whose densities are possible to predict by habitat data: First, the asymptotic densities in large habitat patches and the fact that almost all patches exceeding the minimum patch size required were occupied. Second, both species show close tracking in terms of occurrence and abundance of spatial and temporal variations in boreal forest patch dynamics both on local short-term and regional long-term scales. Work on the hazel grouse *Bonasa bonasia* confirms this (Jansson et al. 2004).

Seiskari's (1962) hypothesis for how the four Fennoscandian grouse species succeed each other at the same site as boreal forest succession proceeds during a century or more was developed for naturally dynamic forest conditions where fire or storm regenerated forests. My results confirm his idea, and show that in a managed forest landscape with a mosaic of patches of different age this simple model describes the main structuring force behind the rise and fall of local black grouse and capercaillie populations over time.

For the other two forest-living grouse species in Fennoscandia circumstantial evidence support Seiskari's (1962) hypothesis. In Sweden the willow grouse *Lagopus lagopus* has expanded its breeding range into boreal forests below the Scandinavian mountains during the last 30 yr (Marcström 1977, Anon. 1978, 2002) in parallel with increased amount of suitable habitats. Also the hazel grouse has expanded its breeding range towards the south (Gärdenfors et al. 1984). This expansion is associated with the gradual appearance of dense middle aged spruce forest with intervening patches with deciduous shrub, i.e. preferred hazel grouse habitat (cf. Pynnönen 1954, Haapanen 1966).

Grouse in the centre and at the edge of the distribution range

During the late 19th century the importance of natural disturbance regimes declined in the boreal forest (Högbom 1934, Niklasson and Granström 2000), and have now almost completely been replaced by intensive forest management including pre-commercial and commercial thinnings followed by clear-felling with variable retention for nature conservation (Angelstam 2003). Unlike many other species (Gärdenfors 2000), capercaillie and black grouse have coped well with this change in the boreal forest ecosystem (Swenson and Angelstam 1993).

However, at the edge of the distribution range, both in Sweden and in continental Europe, the situation is quite different (Lindström et al. 1998, Storch 2000, Angelstam et al. 2000). Decreases in the amount of suitable habitat

have for a long time been a cause of black grouse population declines in western Europe, where heaths have been afforested or turned into agricultural land (Eygenraam 1957, Doencke and Niethammer 1970, Eiberle 1976, Cramp and Simmons 1980, Svensson et al. 1999, Storch 2000). Additionally, predation appears to be an important edge-effect. This applies both were agricultural land with higher density of generalist predators are islands in a forest matrix (Kurki et al. 2000), where forests are islands in a matrix of agricultural land and urban areas (Storch 2000) and in the Alps when tourist provide generalist predators with food (Storch and Leidenberger 2003).

The south Swedish black grouse populations inhabiting heaths have already gone extinct (Marcström 1977). The black grouse is now confined to raised bogs, which however are also deteriorating as habitat due to precipitation of nitrogen altering the vegetation (Angelstam et al. 2000). In the abandoned cultural landscape of the Åland archipelago Haila et al. (1980) reported an 80% decline from the 1940s, which was associated both by an increase of shrubby habitats and of small habitat patches, both factors of which are detrimental for occurrence of black grouse populations. After a steady population decline in Denmark (Degn 1973), the black grouse went extinct in 1998 (Holst-Jorgensen 2000). In several other countries, such as The Netherlands (Niewold and Nijland 1979, TenDen and Niewold 2000) the black grouse accordingly is on the verge of extinction.

For capercaillie the situation is similarly negative at the edge of the distribution range (Storch 2000, 2001). The species' large area requirement makes it particularly sensitive to habitat loss and fragmentation (Klaus et al. 1989, Suchant and Braunisch 2004). Small population size in most remaining forest massifs make local populations vulnerable to stochastic events (Storch 2003), and in addition the cumulative effects of pollution, predation, human disturbance (Storch 2000), and even collisions with deer fences in Scotland (Moss 2001) affects populations negatively.

Thus, when discussing the effects of forest land management on grouse a separation between the boreal forest in the north on the one hand, and the nemoral and hemiboreal ecoregions in the south on the other, should be done. While both black grouse and capercaillie have already gone extinct from the periphery of the distribution of range in Sweden (Svensson et al. 1999), the populations appear to thrive in the boreal forest core of the range.

Grouse as conservation tools

The forest dwelling grouse capercaillie, black grouse and hazel grouse are all included in the EC Birds Directive on the conservation of wild birds (Anon. 1979). In this directive, the species mentioned shall be the subject of special conservation measures concerning their habitat in order to ensure their survival and reproduction in their area of distribution (Anon. 1979, Annex 1).

Having adapted to forest environments of different kinds, and being well known to the public and to managers (Uliczka et al. 2004) grouse species can be viewed as flagship species. There is also evidence that grouse have an umbrella function by indicating the presence of other species with similar habitat use. In an assessment of the potential of the capercaillie as an umbrella species, Suter et al. (2002) examined separately the umbrella effect for all bird species and for mountain species of concern included in the Swiss Red List. The distribution of the capercaillie was related to high species richness in mountain birds of concern, but this was not the case when ubiquitous bird species were included in the analyses. Both capercaillie and mountain birds responded positively to forest structure characterised by intermediate openness, multi-storied tree layer, presence of ecotonal conditions, and abundant cover of ericaceous shrubs. Similarly, Pakkala et al. (2003) surveyed forest birds and capercaillie leks in southern Finland. Several forest birds specialising on old spruce-dominated forest (*Picoides tridactylus*, *Glaucidium passerinum*, *Ficedula parva*) were more abundant near capercaillie leks than in non-lek control sites. These two studies provide one of the few examples of support for the concept of a specialised and area-demanding umbrella species. Management for the conservation of the hazel grouse also appears to favour other bird species in boreal forests (Jansson and Andrén 2003). Similarly, Kolb (2000) used the black grouse as an umbrella for the traditional cultural landscape based on animal husbandry and the associate grazing and mowing. There is thus emerging evidence suggesting that grouse species are potential members in a suite of umbrella species for forest biodiversity conservation (Roberge and Angelstam 2004). However, to cover other forest types and spatial scales of boreal forest environments also other species are also needed.

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Area-sensitivity of the sand lizard and spider wasps in sandy pine heath forests – umbrella species for early successional biodiversity conservation?

Sven-Åke Berglind

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Pine heath forests on sandy sediments occur as "biotope islands" all over Fennoscandia. An important component of the biodiversity within such pine heaths is early successional species restricted to open patches with sparsely vegetated sand. Surveys of the endangered sand lizard *Lacerta agilis* on a regional scale in south-central Sweden showed that populated pine heaths were significantly larger (median area 65 km^2) than those where the species was absent (median area 5 km^2). No effect of pine heath isolation was found. Moreover, on a landscape scale, occupied habitat patches within individual pine heaths were significantly larger than patches where the sand lizard had recently gone extinct. Patch isolation had no significant effect. Furthermore, an analysis of presence/absence of ground-nesting spider wasps (Hymenoptera: Pompilidae) on sandy pine heaths of different size showed that species composition was significantly nested. The highest diversity, of all species and red-listed ones, was found on the largest pine heaths, in sympatry with the sand lizard. It is argued that only the largest sandy pine heaths have provided historical continuity of suitable early successional habitat patches with exposed sand for the most dispersal-limited species. Because of forest fire suppression and afforestation since the beginning of the 20th century, many early successional species in sandy pine heath forests are now threatened due to loss of such patches. To provide habitat for these species, measures to re-create early successional patches must be taken. The sand lizard can be used as a cross-taxonomic umbrella species for red-listed spider wasps and other early successional species. However, to preserve the existing threatened biodiversity within a given pine heath (including the many pine heaths where the sand lizard is absent), a strategy of multiple umbrella species and demarcation of patches with key habitat components is needed.

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Patch dynamics in forest landscapes can be seen as a temporally dynamic process where habitat availability for a given species continuously changes with disturbances and forest regeneration (Pickett and Thompson 1978). Habitat fragmentation, however, may force populations to pass critical lower thresholds in the amount and distribution of preferred habitat required for long-term species survival in a given landscape (e.g. Andrén 1997, Angelstam 1997, Mönkkönen and Reunanen 1999, Fahrig 2001). For many threatened species, critical habitat threshold condi-

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tions are no longer met, and these species are expected to go extinct after some time delay in their response to environmental change. This so called extinction debt can be paid by either "allowing the species to go extinct or by improving the landscape structure sufficiently, before the species have gone extinct, such that the threshold conditions are met again" (Hanski and Ovaskainen 2002).

The conservation of biodiversity in boreal and hemiboreal forests has so far been focused on continuity of habitat for old-growth and/or wood-associated species (see Esseen et al. 1997, Niemelä 1999, Nilsson et al. 2001). Continuity of open habitat for early successional, ground-living species has received little attention. It is evident, however, that the latter group constitutes an important component of the biodiversity in pine forests on dry sites naturally regenerated by fire. In Scots pine *Pinus sylvestris* forests on sandy sediments in Fennoscandia, effective fire suppression and afforestation have caused an accelerating decline of open habitat patches since the beginning of the 20th century (e.g. Cederberg 1982, Väisänen et al. 1994, Berglind 1999). For two endangered species, the blue butterfly *Pseudophilotes baton* and the sand lizard *Lacerta agilis*, the resulting extinction debt has been paid by loss of local populations. However, recent active management measures have been undertaken locally such that habitat threshold conditions can be met again (Väisänen et al. 1994, Berglind 2000, 2004a).

Since dry pine heath forests on sandy sediments occur as islands in an archipelago all over Fennoscandia (Fig. 1), island biogeography theory may be relevant for conservation purposes. The degree of isolation from sources of colonisers would then determine the rate of immigration, while island area would determine the population size and thus the extinction rate. However, extinction is probably the dominant population process for low-vagility organisms in isolated transient landscapes, and the internal disturbance dynamics the critical key to long-term persistence (Pickett and Thompson 1978, Webb and Thomas 1994, Tiebout and Anderson 1997). If so, it is important to define the "minimum dynamic area" with a natural and anthropogenic disturbance regime which maintains internal re-colonisation sources and hence minimises local extinctions (Pickett and Thompson 1978). To identify this area, we would need to have knowledge of the size, frequency of inception and longevity of disturbance-generated patches, as well as of the mobilities of the most extinction-prone species (Angelstam et al. 2004).

Moreover, if the species composition on sandy pine heaths has long been shaped predominantly by local extinctions, a "nested subset" pattern may be expected among differently sized pine heaths, with impoverished species assemblages made up of non-random subsets of more species-rich ones (Patterson 1987, Cutler 1991). Analysis of nestedness may also reveal indicator species for high species richness (Fleishman et al. 2000). Furthermore, if the frequency of occurrence of an indicator is equal to that of sympatric species that share the same habitat or ecoregion and are threatened, it theoretically can confer protection to these and hence be used as an umbrella species (Andelman and Fagan 2000, Fleishman et al. 2001a, b, Roberge and Angelstam 2004).

In this study I compare on a regional and landscape scale (cf. Freemark et al. 2002) the occurrence of a threatened low-vagility vertebrate, the sand lizard, with the occurrence of spider wasps, which are associated with the same type of early successional habitat on sandy pine heaths in central Sweden. On a regional scale, I view sandy pine heaths as "landscapes" in a "matrix" dominated by spruce/mixed forests interspersed with agricultural land and lakes. On a landscape scale, individual pine heaths are composed of habitat patches, where the latter are basically reflections of soil texture, aspect and successional age.

Specifically, the aims are to 1) explore whether the presence of the sand lizard and rare spider wasps is determined by the size of individual pine heaths, 2) evaluate the importance of patch area and isolation within pine heaths for persistence of local sand lizard populations, and 3) identify potential indicator and umbrella species from red-listed taxa for biodiversity conservation on sandy pine heaths.

Methods

Study organisms

The sand lizard is considered primarily a "forest steppe" species and occurs in a variety of semi-open habitats from central Europe to central Asia (Bishoff 1984). It reaches the northern limit of its range in central Sweden with a few isolated populations confined to glaciofluvial sand deposits. These populations are considered to be relicts from the post-glacial warm period (ca 7000–500 B.C.), when the climate was warm enough for this egg-laying ectotherm to disperse northwards from central Europe throughout southern and central parts of Sweden. When the climate subsequently became cooler, the species retreated to southern Sweden but also survived on some sandy pine heaths in the central part of the country (Gislén and Kauri 1959, Andrén and Nilson 1979, Gullberg et al. 1998). It is red-listed as "Vulnerable" in Sweden and included in the EU Habitat Directive (Gärdenfors 2000). A number of early successional insect species are associated with similar habitats in Sweden, and their biogeographic histories may be analogous (Cederberg 1982, Berglind 2004b).

One insect family characteristic of open sandy patches are the spider wasps (Hymenoptera: Pompilidae). About 1/3 of the Swedish fauna of 61 species is red listed (Gärdenfors 2000), and the family is believed to include suitable indicators for threatened early successional habitats (Day 1991). The Fennoscandian species are 4–15 mm long, and all are predators of spiders (e.g. Oehlke and Wolf 1987, Schmid-Egger and Wolf 1992). Many are signifi-

cant components of more or less open, sandy habitats, where they bury their paralysed prey in sand as food for their offspring. Most species have a long flight period, often 2–3 summer months with two generations per year (cf. Schmid-Egger and Wolf 1992), and they are highly attracted to yellow and white water traps. Thus, there is potentially a high probability of catching all or most species in one area during one summer season.

In addition to these focal study organisms, I present local occupancy of other red-listed and local species within the same habitats/patches, including 2 plants, 21 insects, and 3 birds, found on two of the largest and best studied of the sandy pine heaths investigated.

Sand lizard surveys

The sand lizard was surveyed in Värmland and Dalarna (ca 59–62°N), the two northernmost counties in Sweden where the species has been reported during recent decades. Värmland was surveyed mainly in 1984 and 1987 with complimentary surveys in later years/summers including 2002 (Berglind 2004b). The two largest sandy areas in Värmland (area 1 and 2, Brattforsheden and Sörmon, respectively; Fig. 1), have been monitored in most years between 1983 and 2003 (Berglind 2000, 2004b). Dalarna was surveyed mainly in 2001 (Wallgren and Berglind 2002).

Before the start of the surveys it was known that the sand lizard had been found on some of the largest sandy pine heaths with aeolian (wind blown) sand. Therefore all sand deposits > 4 km^2 and some smaller ones with aeolian sand, usually in the form of fossil sand dunes, were surveyed (n = 29). In addition, some other pine heaths > 1.0 km^2 with gravel-mixed sand, and close to dune areas, were surveyed (n = 11). Areas were localised and their size was measured from quaternary sediment maps, scale 1:200 000 (G. Lundqvist 1948, J. Lundqvist 1958). Isolation was measured as the shortest distance across non-sandy soil from one sand deposit to the nearest other with

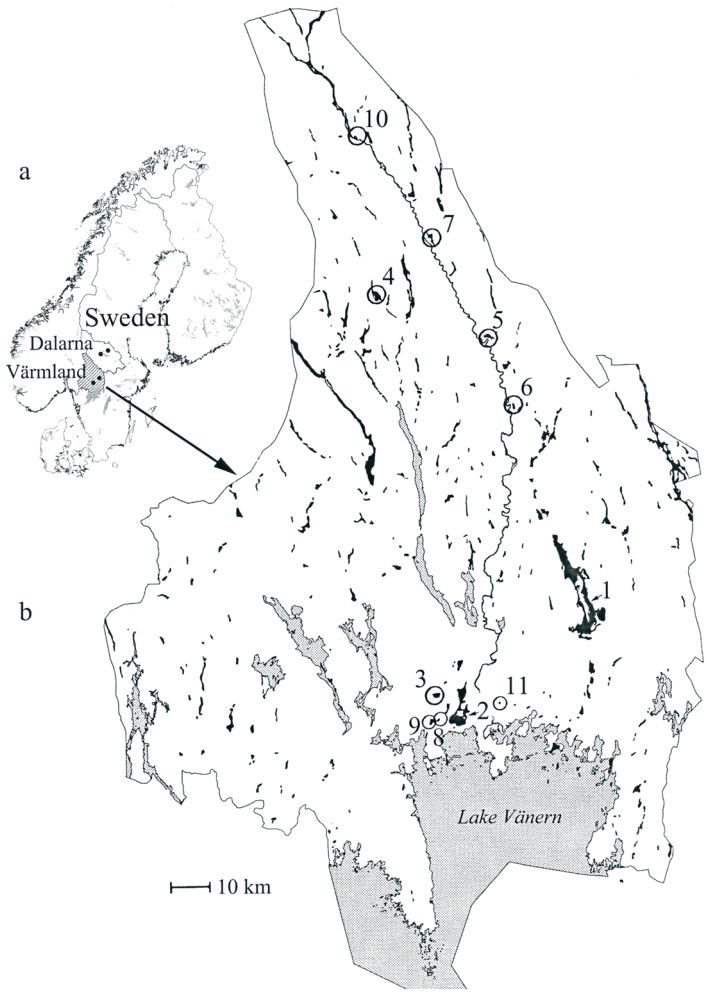


Fig. 1. a) The Värmland and Dalarna counties in central Sweden, which have been surveyed for the sand lizard *Lacerta agilis*. The dots show, from bottom to top, the four sandy areas with records of sand lizards: Sörmon, Brattforsheden, Mora-Bonäsfältet, and Orsa-Skattungbyfältet. b) Glaciofluvial sediments (sand and gravel) (black areas) in Värmland. Areas 1–11 refer to surveyed areas included in the nestedness analysis for spider wasps, and have been numbered in descending order according to their position in the nestedness matrix (see Table 1). Area 1 = Brattforsheden, 2 = Sörmon. Also indicated are larger waters (grey).

aeolian sand. Because the size of individual sand deposits is more or less the same as the size of the pine heath forests covering the same deposits, I use the terms "sand deposit" and "sandy pine heath" interchangeably in this article.

Localised sand deposits were subsequently studied on aerial photographs, and all open patches with or without exposed sand (except for mires) were noted on topographic maps. Thereafter the patches were visited in the field. When patches with suitable habitat, in the form of south-exposed sand patches in combination with a rich field layer of heather *Calluna vulgaris* or grasses/herbs (Berglind 1988, Wallgren and Berglind 2002), were found they were visually inspected for lizards, their egg burrows and/or foot prints in the sand for at least one hour during sunny weather. Patches without signs of sand lizards but with suitable habitat were surveyed on at least two separate days to minimise the risk of not detecting an occupied patch. Empty patches with older records of sand lizards between 1977 and 1992 (Berglind 2000, Wallgren and Berglind 2002) have been visited repeatedly (≥ 5 times) during several years by myself and/or other field workers. I consider the probability of not detecting an occupied sand lizard patch as very low, and on manyt of the empty patches the eurytopic close relative, the common lizard *Lacerta vivipara*, was found (for further details of field surveying techniques, see Taylor and Winder 1997, Moulton and Corbett 1999).

The size of habitat patches with extant or extinct sand lizard populations was estimated by visual inspection of those parts of the patches that contained acceptable habitat for foraging, shelter, dispersal, and/or egg-laying in 1998 (before some patches were subject to major habitat restoration during 1999–2002, which created 5–10 times larger habitat on each). Usually the habitat patches were delimited by closed pine stands and/or lakes. Isolation of habitat patches was measured as the shortest distance of unsuitable habitat (usually closed pine stands) between one patch to the nearest other inhabited patch in 1998.

Surveys of spider wasps and other taxa

In total, 11 sandy pine heaths were surveyed for spider wasps (Fig. 1 and Table 1). Their size was set equivalent to the size of the corresponding sand deposits, shown in Lundqvist (1958). Most of the pine heaths were chosen in connection with nature conservation work by the county administrative board of Värmland. The forest type is similar in all areas, with vegetation dominated by Scots pine forest with a ground and field layer dominated by reindeer lichens (*Cladonia* spp.), pleurocarpous mosses (mostly *Pleurozium schreberi* and *Dicranum* spp.), crow berry *Empetrum nigrum*, cow berry *Vaccinium vitis-idaea*, and sparse stands of *Calluna vulgaris*. Forest-fire suppression and conventional forestry keep most of the areas wooded with pine of various ages. On open, disturbed patches, the acrocarpous moss *Polytrichum piliferum* (< 3 cm high), occurs as a pioneer coloniser of dry, sun-exposed sand. Such patches often also have a mosaic field layer of *Calluna* and/or grasses and herbs. All surveyed pine heaths contain aeolian sand to some degree, except for area 10 and 11, which are dominated by gravel-mixed sand. The matrix in between the pine heaths is dominated by mixed spruce forest on moraine, or agricultural land on clay-dominated soils. Exceptions are the glaciofluvial sand deposits of area 5–7 and 10, which are situated along the eastern side of the Klarälven river valley and interconnected by a narrow strip of post-glacial sand deposits covered by mixed pine forest.

Within each pine heath the majority of existing open patches with a mosaic of south-exposed sand and a rich field layer were localised with the same technique as described for the sand lizard. The patches usually consisted of sand pits, sandy road verges (including S-oriented sand-cuts), power-line corridors, clear-cuts, or glades in younger post-fire pine stands. Water traps were placed on what were considered the most "optimal" patches for each pine heath. Most traps were placed on the ground at sharp interfaces between open sand and a dense field layer of *Calluna* or grasses/herbs, usually at south-oriented forest edges. Patches were considered separate if > 300 m of unsuitable habitat (usually closed pine stands) was situated in between. The majority of patches were separated by > 1 km.

On most surveyed patches one yellow and one white water trap were used, but the number per patch varied somewhat. Also the number of surveyed patches varied between the pine heaths, roughly in proportion to their size and occurrence of suitable patches (Table 1). For pine heaths that were investigated for more than one summer, only new patches were surveyed during the additional years. There was a significant positive correlation between the size of surveyed pine heath and both the number of traps used per pine heath (Spearman rank correlation r_s = 0.68, p = 0.0223) and number of surveyed patches per pine heath (r_s = 0.69, p = 0.0198). However, there was a significant negative correlation between the size of pine heath and the number of surveyed patches per km^2 (r_s = –0.96, p < 0.001). Thus, the absolute sampling effort was higher on larger pine heaths, but the relative sampling effort was higher on smaller ones.

The water traps consisted of plastic, round pans with a diameter of 23 cm and a height of 11 cm. They were 3/4 filled with water, some drops of detergent, and a bottom-layer of coarse salt (to slow down the decay of the caught insects). The traps were inspected and emptied at least once every second week from the end of May to late August. All spider wasps were preserved in 70% alcohol and later identified to species using Oehlke and Wolf (1987) and van der Smissen (1996). In total, ca 5000 specimens were examined. Other caught insect taxa were preserved and identified.

On area 1 (Brattforsheden), 6 surveyed patches were each occupied by a local sand lizard population, two of

Table 1. Presence-absence matrix and sampling effort for ground-nesting spider wasps (Hymenoptera: Pompilidae) on sandy pine heaths of different size (see Fig. 1). The matrix has been maximally packed according to the nestedness analysis (see Results). Also shown, within parenthesis, is presence-absence of the common lizard *Lacerta vivipara* and the sand lizard *Lacerta agilis* (these were not included in the nestedness analysis). Red-listed species are shown in bold. The name and main survey year (within parenthesis) of the areas are: 1 Brattforsheden (1988, 1990, 1997), 2 Sörmon (1989, 1990, 2001), 3 Mellbymon (2003), 4 Kristineforsheden (1990, 1991), 5 Halgådeltat (1989), 6 Säljeheden (1989), 7 Femtåheden (1990), 8 Törnmon (2002), 9 Algustadmon (2002), 10 Klarabro (1989), 11 Gräsås (1997).

	Area											
Species	1	2	3	4	5	6	7	8	9	10	11	No. of areas
Priocnemis perturbator	+	+	+	+	+	+	+	+	+	+	+	11
Priocnemis exaltata	+	+	+	+	+	+	+	+	+	+	+	11
Priocnemis schiödtei	+	+	+	+	+	+	+	+	+	+	+	11
Arachnospila anceps	+	+	+	+	+	+	+	+	+	+	+	11
Arachnospila spissa	+	+	+	+	+	+	+	+	+	+	+	11
Anoplius viaticus	+	+	+	+	+	+	+	+	+	+	+	11
(*Lacerta vivipara*	+	+	+	+	+	+	+	+	+		+	10)
Arachnospila trivialis	+	+	+	+	+	+	+	+	+			9
Evagetes crassicornis	+	+	+	+	+	+	+	+	+			9
Arachnospila fumipennis	+	+	+	+	+		+		+	+		8
Episyron albonotatum	+	+	+	+	+	+	+		+			8
Arachnospila hedickei	+	+	+	+	+	+		+	+			8
Evagetes sahlbergi	+	+	+	+	+	+	+	+				8
Arachnospila sogdiana	+	+		+		+	+	+				6
Pompilus cinereus	+	+	+	+				+				5
Ceropales maculata	+	+	+	+	+							5
Arachnospila wesmaeli	+	+	+					+	+			5
Arachnospila abnormis	+	+			+	+	+					5
Arachnospila opinata	+	+	+	+								4
Priocnemis parvula	+				+	+	+					4
Arachnospila westerlundi	+		+							+		3
Caliadurgus fasciatellus	+		+			+						3
Episyron rufipes	+	+	+									3
Evagetes alamannicus	+	+		+								3
Evagetes dubius	+	+										2
(***Lacerta agilis***	+	+										2)
Evagetes pectinipes		+										1
Priocnemis gracilis	+											1
No. of spider wasp species	25	22	19	17	15	15	14	13	12	8	6	
Size of area (km^2)	80	30	2.4	8	3.8	1.5	3.2	0.7	1.0	0.2	0.05	
No. of surveyed patches	25	10	2	4	2	1	2	3	1	1	2	
No. of surv. patches km^{-2}	0.3	0.3	3.3	0.5	0.5	0.7	0.7	4.3	3.0	5.0	20.0	
No. of traps	35	16	8	6	2	2	3	4	3	2	2	

which have recently gone extinct. In area 2 (Sörmon), 2 surveyed patches were each occupied by a local sand lizard population. Furthermore, insects have been surveyed on both areas by hand netting during several seasons between 1988 and 2003, and on area 1 also with both pitfall traps and UV-light traps in both 1988 and 1990. No additional spider wasp species have been found with these techniques. However, they have revealed many other insect species, making the species composition on these areas unusually well known with respect to sand-associated insects (see Berglind 2004b). Moreover, Brattforsheden has been surveyed with point counts for two pine heath birds, the nightjar *Caprimulgus europaeus* and wood lark *Lullula arborea*, in both 1986 and 1999 (Bengtsson unpubl.). These birds are listed on the EU Bird Directive (Gärdenfors 2000).

Data analyses

Determinants of local extinction

Potential environmental correlates of extinction for local sand lizard populations were analysed using stepwise logistic regression and the statistical software package BMDP

New System (Dixon 1992), ver. 2.0. Logistic regression quantifies how much independent (predictive or explanatory) variables can explain the variation in some dependent (outcome or response) variable. In this study the dependent variable was extinction or persistence of local sand lizard populations in patches known to have been occupied some time between 1977 and 1998, and the explanatory variables were patch area and isolation, as measured in 1998 (see further details under Sand lizard surveys). The effects of the two latter variables are considered as the first-order landscape effects on metapopulation persistence (Hanski 1999). The analysis was done as a forward stepwise logistic regression with 100 iterations, and with $p \leq 0.10$ for the explanatory variables to be entered into (or removed from) the model. A positive coefficient for a significant explanatory variable predicts increased extinction risk with lower values for that variable. I also used the BMDP New System software to conduct univariate nonparametric statistics on the sand lizard and spider wasp survey data.

Nestedness

A nested subset analysis for spider wasps was carried out based on a presence-absence matrix for those sandy pine heaths of different size that are presented in Fig. 1 and Table 1. Only ground-nesting species with known distributional limits in Fennoscandia covering the latitudes for the surveyed region were included. Furthermore, only those species restricted to more or less sandy habitats, and species with wide ecological affinities including sandy habitats, were included. Some species caught in low numbers prefer non-sandy and mesic/moist habitats and were excluded from the analysis (complete species lists for the two richest areas are given in Berglind 2004b).

I used Atmar and Patterson's (1993, 1995) Nestedness Temperature Calculator method and software to establish the extent at which my data were nested. Nestedness values can range from T = 0° for a perfectly ordered system (perfectly nested), to T = 100° for complete randomness. A presence-absence matrix that contains both a degree of nestedness and randomness will register an intermediate T-value between these two end-points (Atmar and Patterson 1995). The nestedness calculator by Atmar and Patterson runs a Monte Carlo simulation to estimate the distribution of nestedness scores expected in a randomly distributed data matrix of the same dimensions as the study data matrix. The actual nestedness score for the study data matrix is then compared against the distribution of randomly generated matrices to determine the probability of observing such a score by chance.

Umbrella index

To evaluate and rank potential umbrella species, the umbrella index developed by Fleishman et al. (2001a, b) was used. Originally, this index takes into account three components: mean co-occurrence of the species, its degree of ubiquity, and its sensitivity to human disturbance. For each species j, mean percentage of co-occurring species (PCS) is defined as

$$\sum_{i=1}^{l}\left[\left(S_i - 1\right) / \left(S_{max} - 1\right)\right] / N_j$$

where l is the number of locations (patches) in the data set, S_i is the number of species present at each location i, S_{max} is the total number of species present at all locations in the data set, and N_j is the number of locations at which species j occurs. PCS is quantified on a scale from 0 (tends to occur with few other species) to 1 (tends to occur with many other species).

The second component of the umbrella index is degree of ubiquity, or median rarity (R). Values for species with an intermediate degree of ubiquity approach 1, for rare or common species the values approach 0. For each species j, this parameter is calculated as

$$1 - 2 * |(N_j/l) - 0.5|$$

The third component of the umbrella index, sensitivity to human disturbance, was omitted in this study. Since life-history-related variables are poorly known for the majority of the analysed insect species, and the greatest threat can be assumed to be common to all species (shading of open habitat patches due to pine canopy formation) this omission was considered a reasonable approach. Thus, the umbrella index (UI) for each species was calculated by summing the scores for the first two components. Species with higher scores (maximum 2.0) are more likely to be effective umbrellas for their ecoregion and taxonomic group or guild.

$$UI = PSC + R$$

I calculated the umbrella index as a cross-taxonomic index for all red-listed and some other local species within the same guild found on the largest and most species-rich pine heath in this study, i.e. Brattforsheden (Fig. 1). This means that also clear differences in mobilities and area requirements between the taxa have to be considered in the evaluation of a species' suitability as an umbrella (see Discussion).

Results

Effects of area and isolation at a regional and landscape scale for occupancy of sand lizard populations

Sandy pine heaths occupied by the sand lizard in the counties of Värmland and Dalarna were significantly larger (range 30–90 km^2, median = 65.0; n = 4) than vacant pine

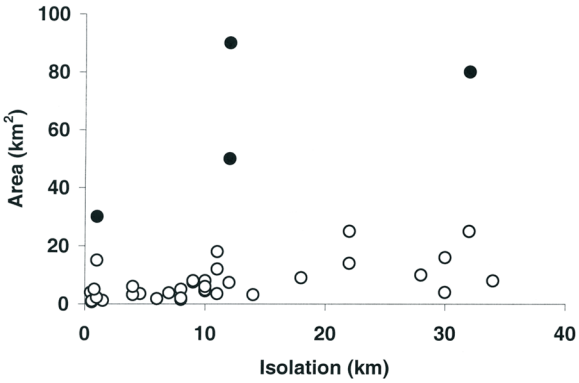


Fig. 2. Area and isolation of sandy pine heaths with (filled circles) and without (open circles) populations of the sand lizard *Lacerta agilis* in Värmland and Dalarna. Aeolian sand, usually with fossil sand dunes, were present at 29 (72%) of the 40 surveyed areas, including the four occupied areas. Isolation = shortest distance of non-sandy soil from one sand deposit to the nearest other with aeolian sand (see Methods for further details).

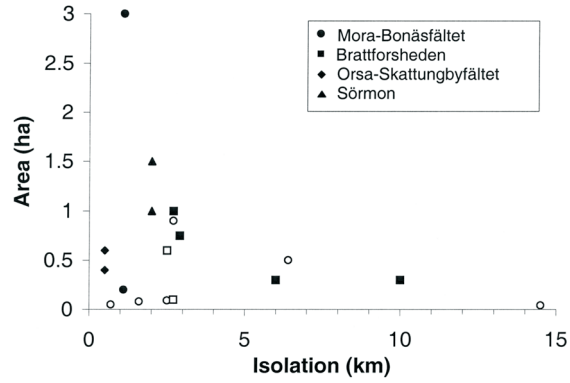


Fig. 3. Area and isolation of patches with extant (filled symbols) and extinct (open symbols) local sand lizard populations on the four occupied sandy pine heaths in Värmland and Dalarna in 1998 (see panel). Isolation = distance to the nearest other occupied sand lizard patch.

heaths (range 0.7–25 km^2, median = 5.0, n = 36) (Mann-Whitney U = 0.0, p = 0.0012) (Fig. 2). There was no significant difference in isolation for occupied pine heaths (range 1.0–32 km, median = 12.0, n = 4) vs vacant pine heaths (range 0.5–34 km, median = 9.0, n = 36) (Mann-Whitney U = 50.5, p = 0.332) (Fig. 2).

Within occupied pine heaths, the number of known local sand lizard populations between 1977 and 1998 was higher on the largest pine heaths. In total, 8 and 6 local populations, respectively, have been found on the two largest areas (Mora-Bonäsfältet and Brattforsheden, 90 and 80 km^2, respectively). Only 2 local populations have been found on each of the two smaller areas (Orsa-Skattungbyfältet and Sörmon, 50 and 30 km^2, respectively) (Fig. 3). In spite of the small sample size, there was an almost significant positive correlation between the number of local sand lizard populations and the size of occupied pine heaths (Spearman rank correlation r_s = 0.949, p = 0.051, n = 4).

Within occupied pine heaths, suitable habitat patches with extant sand lizard populations were significantly larger in 1998 (range 0.2–3.0 ha, median = 0.75, n = 10) than those where the sand lizard had gone extinct (range 0.05–0.75 ha, median = 0.095, n = 8) (Mann-Whitney U = 66.5, p = 0.0183) (Fig. 3). No significant difference in isolation was found between patches with extant populations (range 0.5–10.0 km, median = 2.0, n = 10) vs patches with extinct populations (range 0.7–14.5 km, median = 2.6, n = 8) (Mann-Whitney U = 28.0, p = 0.2843) (Fig. 3). Moreover, a logistic regression model examining extinction or not of local populations supported the notion that extinction risk increased significantly with decreasing patch area, whereas patch isolation had no significant additional effect (Table 2).

Table 2. Effects of area and isolation on extinction probabilities of local sand lizard populations according to a stepwise logistic regression model. Number of patches with extinct populations = 8, number of patches with extant populations = 10. The tabulated χ^2 is the improvement-χ^2 of the variable in the final model, and p the corresponding p-value (at 1 DF). The goodness of fit of the final model (deviance statistic) was χ^2 = 18.46, DF = 16, p = 0.298.

Variable	Coefficient ± SE	χ^2	DF	p
Significant (step 2)				
Area	3.41 ± 1.85	6.27	1	0.012
Constant	–1.42 ± 0.94	2.72	1	0.099
Non-significant (step 1)				
Isolation		1.35	1	0.246

Nestedness and species-area relationship of spider wasps

The spider wasp communities on the surveyed pine heaths were clearly nested (Fig. 4a and Table 1). The matrix nestedness temperature T = 7.19° was highly significantly lower than the mean score for the randomised matrix (T ± SD = 54.1° ± 6.37°; $p = 9.73 \times 10^{-14}$; Monte Carlo runs total = 500). This means that the faunas of low-diversity pine heaths tended to be predictable subsets of the faunas with higher diversity. However, there were eight species and four pine heaths for which the nestedness temperatures were higher than for the matrix as a whole (Fig. 4b–c). This suggests different biogeographic histories for these species and pine heaths compared with those that governed the formation of nestedness in the overall matrix.

Moreover, there was a strong positive correlation between the number of spider wasp species and the size of pine heaths (Spearman rank correlation $r_s = 0.91$, p = 0.0001, n = 11) (Fig. 5), where the two most species-rich pine heaths were occupied also by the sand lizard (area 1 and 2; Table 1). The number of spider wasp species found per pine heath was also significantly correlated with the number of traps used per pine heath ($r_s = 0.77$, p = 0.0059, n = 11) and number of surveyed patches per pine heath ($r_s = 0.66$, p = 0.0266, n = 11). Pine heath size, number of traps and number of surveyed patches per pine heath were also significantly correlated, as mentioned in the methods section.

For the two largest pine heaths (area 1–2; Table 1), significantly more spider wasp species per patch were found on the most species-rich patches that also contained sand lizards (range = 17–22 species, median = 18.5, n = 6) than on the most species-rich patches on the four richest of the smaller pine heaths without sand lizards (area 3–6) (range = 14–17 species, median = 15.0, n = 7) (Mann-Whitney U = 1.00, p = 0.0038). Since there was no significant difference in the number of traps used per patch on the richest patches on the largest pine heaths (range = 2–4 traps, median = 2, n = 6) vs the richest patches on the smaller pine heaths (range = 1–4 traps, median = 2, n = 7) (Mann-Whitney U = 15.00, p = 0.3614), the difference in species number per patch seems not to be an effect of unequal sampling effort.

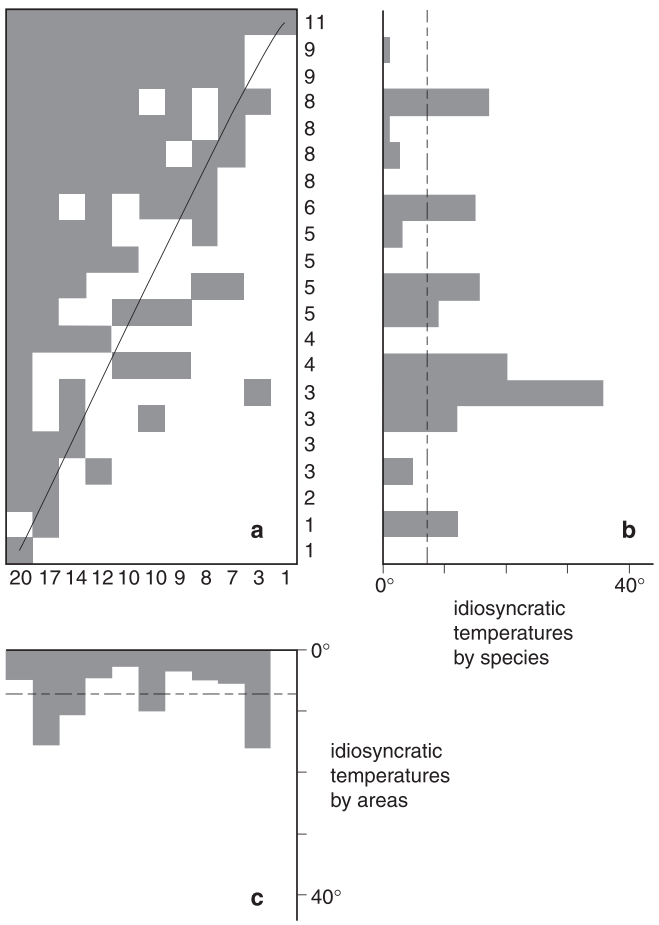


Fig. 4. a) Nestedness matrix of spider wasp faunas on 11 sandy pine heaths in Värmland. Species are listed from top to bottom, and pine heaths from left to right in order of decreasing species richness. The matrix is packed so as to minimize the distance of unexpected presences and absences from the calculated extinction threshold line (diagonal). Note: 5 duplicate "all grey" rows were removed from the top of the matrix; thus all column totals displayed are 5 less than the original data matrix (Table 1). b) Idiosyncratic temperatures by species. c) Idiosyncratic temperatures by pine heaths. Species and pine heaths that generate specifically higher temperatures than the matrix as a whole are above the dashed line.

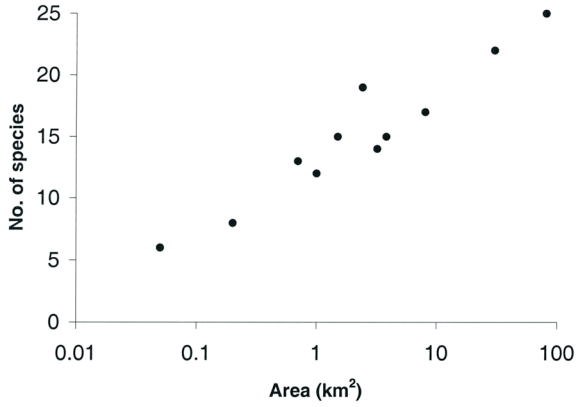


Fig. 5. Correlation between the number of spider wasp species and the size of pine heaths. The investigated pine heaths are presented in Fig. 1 and Table 1. The regression line: number of species = 13.08 + 5.88 × log Area, Pearson's r = 0.96, p = 3.96×10^{-6}, n = 11.

Potential indicator- and umbrella species

Within pine heaths occupied by the sand lizard in areas 1 and 2, i.e. the most species-rich areas with respect to spider wasp diversity (Table 1), significantly more red-listed spider wasp species were found within sand lizard patches (range = 3–5 species, median = 3.5, n = 8) than on patches without the sand lizard (range = 0–5, median = 1.0, n = 27) (Mann-Whitney U = 28.5, p = 0.00137). Furthermore, of a total of 28 red-listed species from all taxa found on areas 1 and 2 (Table 3), significantly more species were found within sand lizard patches (range 5–12 species, median = 11.0, n = 8) than on patches without sand lizards (range = 0–13 species, median = 2.0, n = 27) (Mann-Whitney U = 24.5, p = 0.00094). Thus, pine heaths and patches with sand lizards indicate presence of a disproportionately large number of other red-listed species on, respectively, a regional and landscape scale.

Nevertheless, the sand lizard was also absent from several pine heaths and patches that harboured red-listed spider wasps and other red-listed taxa (Tables 1, 3 and Fig. 6), suggesting that additional indicators would be useful to identify. Although there is a significant correlation between the number of spider wasp species and size of pine heath (see above) as well as between the number of red-listed spider wasp species and size of pine heath (Spearman rank correlation $r_s = 0.72$, p = 0.01, n = 11), the nestedness analysis suggests that few red-listed species are reliable indicators for high regional species richness (Table 1). The most suitable species seem to be *Priocnemis gracilis* and *Evagetes dubius* since they were found exclusively on the two most species-rich pine heaths and lack unexpected absences or "holes" in the nestedness matrix. However, when looking at the local distribution on area 1, these two species failed to indicate the presence of respectively two or three other red-listed spider wasps (*Arachnospila opinata, A. wesmaeli* and *A. westerlundi*), and *E. dubius* co-occurred with the sand lizard on only one patch (Fig. 6).

The cross-taxonomic umbrella index calculated for 25 red-listed and five other local species occurring on area 1 (Brattforsheden) gives further guidance to species that may be useful indicators and umbrellas for biodiversity conservation on a landscape scale (Table 3). The tiger beetle *Cicindela sylvatica* has the highest rank, i.e. it co-occurred with many red-listed species and it had an intermediate degree of ubiquity. Furthermore, the spider wasps *Priocnemis gracilis* and *Episyron albonotatum* and the digger wasp *Ammophila campestris* scored almost as high. The three vertebrates, the wood lark *Lullula arborea*, the nightjar *Caprimulgus europaeus*, and the sand lizard, scored lower but still had among the highest ranks (Table 3).

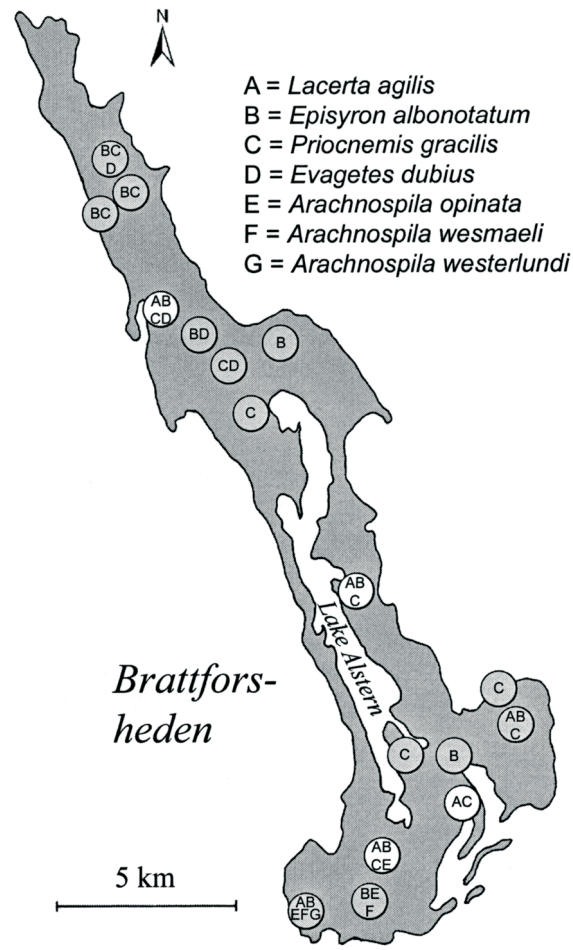


Fig. 6. Patches with known local populations of the sand lizard and red-listed spider wasps on Brattforsheden between 1988 and 2001 (16 out of 25 surveyed patches). In all cases, > 0.5 km of unsuitable habitat (predomintaly closed pine stands) was situated in between the patches. Note the clustering of occurrences of the rarest spider wasps (species D–G). White circles = patches with extant sand lizard populations.

Table 3. Red-listed and some other local species recorded in dry, sandy habitats on the two largest sandy pine heaths in Värmland county: Sörmon (30 km^2) and Brattforsheden (80 km^2). Red-list categories according to Gärdenfors (2000): VU = Vulnerable, NT = Near Threatened, – = not red-listed. The number of patches refers to only those where insects were sampled with water traps. These patches include all red-listed early successional species found on the areas, but some of the species where also found on additional patches, for example *A. vernalis* (3 additional patches on Brattforsheden in 2003), *L. c. chamaecyparissus* (6 additional patches on Sörmon in 2003), and *C. europaeus* (2 additional patches on Sörmon in 2002 and 8 on Brattforsheden in 1999). Numbers within parenthesis refer to the number of patches with co-occurrence of the sand lizard *Lacerta agilis* (2 patches on Sörmon and 6 patches on Brattforsheden). The cross-taxonomic umbrella index is based on those 25 patches on Brattforsheden where insects were sampled with water traps. Note that Diptera and Coleoptera species, except for *C. sylvatica*, have been surveyed less intensively than the other taxa. Umbrella index in bold = the 10 species with the highest rank (for definitions, see Methods).

		Number of patches		Umbrella index (UI) (Brattforsheden)			
Species	Red list category	Sörmon (n=10)	Brattfors-heden (n=25)	PCS	R	UI	Rank
Plants							
Anemone vernalis	VU	Extinct?	1 (1)	0.30	0.24	0.54	14
Lycopodium complanatum ssp. *chamaecyparissus*	VU	1 (1)	0				
Insects							
Hymenoptera							
Pompilidae, spider wasps							
Priocnemis gracilis	VU	0	12 (5)	0.20	0.96	**1.16**	**3**
Arachnospila opinata	NT	1 (1)	3 (2)	0.37	0.24	0.61	12
A. westerlundi	NT	0	1 (1)	0.31	0.08	0.39	20a
A. wesmaeli	NT	4 (2)	2 (1)	0.36	0.16	0.52	15
Evagetes dubius	–	4 (2)	4 (1)	0.26	0.32	0.58	13
Episyron albonotatum	NT	5 (2)	12 (5)	0.22	0.96	**1.18**	**2**
Formicidae, ants							
Formica cinerea	–	0	2 (1)	0.32	0.16	0.48	17
Eumenidae, solitary wasps							
Stenodynerus dentisquama	NT	0	2 (1)	0.26	0.16	0.42	19
Sphecidae, digger wasps							
Ammophila campestris	NT	2 (1)	10 (6)	0.23	0.88	**1.11**	**4**
Lestica subterranea	NT	0	1	0.41	0.08	0.49	16a
Belomicrus borealis	NT	0	1	0.10	0.08	0.18	22a
Crossocerus heydeni	NT	0	1	0.41	0.08	0.49	16b
Andrenidae, sand bees							
Andrena argentata	VU	0	6 (3)	0.26	0.48	**0.74**	**8**
Panurgus banksianus	VU	2 (1)	1	0.41	0.08	0.49	16c
Lepidoptera							
Hesperidae, skippers							
Hesperia comma	NT	0	1	0.41	0.08	0.49	16d
Lycaenidae, blues							
Glaucopsyche alexis	NT	1	1	0.10	0.08	0.18	22b
Noctuidae, noctuid moths							
Spaelotis suecica	NT	1	1	0.41	0.08	0.49	16e
Zygaenidae, burnets							
Adscita statices	NT	0	1	0.41	0.08	0.49	16f
Diptera							
Asilidae, robber flies							
Cyrtopogon luteicornis	NT	2 (1)	4 (2)	0.33	0.32	**0.65**	**9**
Therevidae, stiletto flies							
Psilocephala imberbis	NT	0	2	0.19	0.16	0.35	21
Coleoptera							
Carabidae, ground beetles							
Cicindela sylvatica	–	6 (2)	12 (6)	0.24	0.96	**1.20**	**1**
Bembidion nigricorne	NT	0	5 (2)	0.30	0.32	0.62	11
Amara infima	NT	1 (1)	4 (2)	0.39	0.24	**0.63**	**10**
Cymindis macularis	NT	0	1 (1)	0.38	0.08	0.46	18a

Table 3. Continued.

Species	Red list category	Number of patches		Umbrella index (UI) (Brattforsheden)			
		Sörmon (n=10)	Brattfors-heden (n=25)	PCS	R	UI	Rank
Buprestidae							
Buprestis octoguttata	NT	1 (1)	1 (1)	0.38	0.08	0.46	18b
Curculionidae							
Strophosoma fulvicorne	NT	2 (1)	0				
Neuroptera							
Myrmeleontidae, ant lions							
Myrmeleon bore	VU	5 (2)	0				
Reptiles							
Lacerta agilis	VU	2	6	0.30	0.48	**0.78**	**7**
Birds							
Caprimulgus europaeus	VU	6 (2)	17 (5)	0.19	0.64	**0.83**	**6**
Lullula arborea	–	6 (2)	9 (5)	0.25	0.72	**0.97**	**5**
Riparia riparia	–	0	1 (1)	0.31	0.08	0.39	20b

Discussion

Area sensitivity for focal species at regional and landscape scales

This study has shown that sand lizard populations on the northern periphery of the species' range occurred on only a few, unusually large sandy pine heaths. The occupied areas are four of the largest glaciofluvial sand deposits in the southern half of Sweden, and they also contain four of the largest fields of fossil inland dunes (see Bergqvist 1981). Isolation of pine heaths had no effect on sand lizard occupancy. Generally, if isolation predicts "island" occupancy, a focal species may be present on small islands if they are close enough to a source population for immigration rates to compensate for high extinction rates (Lomolino 1999). In spite of the fact that the distance between several of the surveyed pine heaths were within the dispersal capacity of the sand lizard (≤ 2 km, see Berglind 2000), and the intervening habitat no more inhospitable than closed pine stands, only size of pine heath seemed to influence occupancy. The explanation for this pronounced area effect on a regional scale is probably that sand lizard occupancy has been shaped by selective extinctions since the end of the postglacial warm period (ca 500 B.C. when these sand areas were part of a larger habitat continuum, until climate changed), and that only the largest sand areas have provided continuity of suitable habitat patches for population survival. This hypothesis is also supported by the fact that the two smaller occupied pine heaths in this study contained fewer local populations. Also in other studies of reptiles on islands including habitat fragments, island area was of critical importance for long-term persistence (Foufopoulos and Ives 1999, Diaz et al. 2000).

The same pattern of occupancy was also reflected on a landscape scale, where occupied patches within individual pine heaths were significantly larger than patches where the sand lizard had recently gone extinct. Patch isolation had no significant effect. Thus, there is no support for a classical metapopulation structure, with a balance between distance-dependent re-colonisation and spatially independent extinctions (see Harrison and Taylor 1997). Instead, local extinctions of the sand lizard on these pine heaths seems to occur in accordance with a non-equilibrium, habitat-tracking metapopulation model, i.e. extinction occurs mainly when disturbance or succession cause the loss of suitable habitat. The species' abundance and distribution will remain roughly constant only if the rates of habitat loss and renewal happen to be roughly equal (Thomas 1994) (see also under Disturbance dynamics and population survival). The overall number of potential habitat patches for the sand lizard within occupied sandy pine heaths are very small today, as shown by the number of patches on Brattforsheden that contained a combination of critical habitat components (Fig. 7). Stochastic extinctions do, however, also occur before complete loss of habitat, as indicated in Fig. 3 (see also Berglind 2000).

The strong positive correlation between number of spider wasp species and size of pine heath, in combination with the significantly nested subset pattern, supports the notion that rare species on large sandy pine heaths are less prone to extinction than rare species on smaller ones. Several of the more area-sensitive spider wasp species in this study, seem to have a disjunct or fragmented distribution pattern in NW Europe and are known from few localities in central Sweden (Schmid-Egger and Wolf 1992, van der Smissen 1996). *Priocnemis gracilis* has its main known occurrence in Fennoscandia on Brattforsheden, where it in-

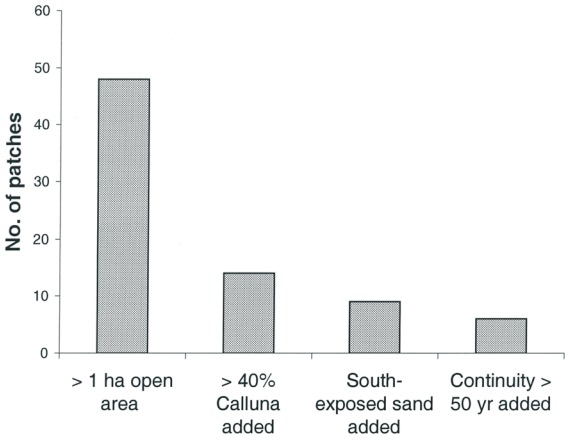


Fig. 7. Schematic illustration of number of patches with four key habitat components for occurrence of the sand lizard in the sandy pine heath forest of Brattforsheden in 1988 (before habitat restorations started). The components have been added from left to next bar to the right. There were 48 open patches > 1 ha (including clear-cuts and some suitable sand road sections; left bar), but only six patches with a combination of all four components (right bar). Only the latter patches were occupied by the sand lizard in 1988. Open area = area with < 20% tree coverage, Calluna = coverage of *Calluna vulgaris* field layer.

habits open sites with a mosaic of exposed sand, heather, grasses, reindeer lichens, and scattered bushes. *Evagetes dubius* is found only on three of the four sandy pine heaths where the sand lizard occurs, but not always on the same patches (Fig. 6). In south Sweden the area of occupancy for both *E. dubius* and the sand lizard is larger and their habitat niches broader (see Berglind 2004b). This type of north-south gradient in ecological range is not unusual in thermophilous ectotherms in NW Europe (Thomas et al. 1999). A third example of a species with a fragmented occurrence is *Arachnospila wesmaeli*, which, however, also occurred on some small pine heaths in this study. This species is more or less strictly confined to coastal and inland dune areas with large patches of open, aeolian sand. On a landscape scale for Brattforsheden, it seems that the two latter species, among others, have a metapopulation structure restricted to two smaller parts of this pine heath, whereas *P. gracilis* is locally distributed over most of the area (Fig. 6).

Disturbance dynamics and population survival

In order for the sand lizard and other early-successional, low-vagility species to survive on the central Swedish sandy pine heaths after the end of the postglacial warm period, there must have been disturbance regimes that continuously created open sand patches. In the past, dry Scots pine forests were probably made up of multi-layered stands strongly shaped by forest fires (Angelstam 1997, 1998, Esseen et al. 1997, Angelstam and Kuuluvainen 2004). Most likely, fire was the dominant disturbance factor until at least the 17th century, after which the influence of human activities in the forests became more prominent (see Angelstam 1997, Niklasson and Drakenberg 2001). There is much evidence that fire recurrently created open patches with exposed sand in boreal and hemiboreal pine heath forests with fossil sand dunes until as late as the beginning of the 20th century (Bergqvist and Lindström 1971, Lindroos 1972, Bergqvist 1981). Since aeolian sand is one of the most well-sorted materials in nature, and lacks finer particles that retain moisture, it has extremely low water-holding capacity (Bergqvist 1981). Thus, burns that consume most of the humus layer on aeolian sand, especially on south-facing slopes, produce vegetation-free patches that remain exposed for a long time (cf. Oksanen 1983, and Fig. 2 in Berglind 2000).

Extensive human activities like forest grazing by cattle, charcoal production, and tree harvesting, also contributed to keeping the central Swedish forests, including the forested inland dune areas, relatively open between at least ca 400–100 yr ago (Cederberg 1982, Angelstam 1997). During recent decades, open patches with exposed sand have been created only at a small, local scale, mainly at sand roads and sand pits. Clear-cuts do not offer open sand habitats, since the humus-layer is left intact after tree harvesting.

The structural components crucial for the sand lizard in sandy pine heath forests include a mosaic of open sand patches for egg-laying, and a rich field-layer of *Calluna vulgaris* and/or grasses for shelter and foraging (Berglind 1999). During recent decades the sand lizard on the central Swedish sandy pine heaths has been found within ca 0.1–3 ha patches of suitable habitat (Fig. 3), including: sand road verges (Fig. 8), sand pits, power-line corridors, old fire fields, and lake shores. Since all these populations have declined and some gone extinct (Berglind 2000, Wallgren and Berglind 2002), such small patches do not seem large enough for long-term persistence. This notion is supported by an age-structured, stochastic population viability analysis for the sand lizard on Brattforsheden. This analysis indicated a quasi-extinction risk (threshold ≤ 10 females, including hatchlings) of ca 60% for 1 ha habitat patches over a 50-yr horizon. In contrast, 5 and 10 ha patches have quasi-extinction risks of only 6 and 1%, respectively, which can be considered acceptably low risks over a 50-yr horizon (Berglind 2004a).

Under a natural fire regime and past human activities, sand lizard colonisations and extinctions probably occurred in a shifting spatiotemporal mosaic, with lizards tracking early successional habitats within their dispersal distance (cf. Thomas 1996, Tiebout and Anderson 1997). It is likely that there was spatiotemporal variation in growth rates within such sand lizard metapopulation networks, due to differences in successional stage, patch size, local topography (affecting microclimate and egg hatching success), catastrophic short-term effects of forest fires etc.



Fig. 8. Example of "key habitat" for biodiversity conservation in sandy pine heath forests. South-oriented sand-cut in a fossil sand dune at a small sand road. The latter was probably created some 300–400 yr ago. The sand-cut has contributed to continuity in open habitat for egg-laying by the sand lizard and several red-listed insect species. Brattforsheden, Djäknetjärn in 1990. Photo: S.-Å. Berglind.

Causes of nestedness

The investigated spider wasp communities were highly significantly nested, with the faunas of low-diversity pine heaths being predictable subsets of the faunas of high-diversity ones. If species richness decreases with declining habitat area, a nested subset structure might allow one to predict future faunal composition in a habitat subjected to reduction or fragmentation (Worthen 1996). Nestedness is frequent in insular habitats and it can principally be explained by: selective extinctions, selective colonisations, habitat nestedness, and passive sampling (e.g. Wright et al. 1998). Future work on nestedness among spider wasp communities should try to tease apart the relative importance of these processes, which are briefly discussed below.

Selective extinction refers to systems where species disappear from habitat patches or islands in a predictable sequence according to their lower threshold area requirements, without replacement by nearby colonists "relaxation" (Wright et al. 1998). In accordance with the suggested extinction dynamics for the sand lizard, selective extinctions may have caused spider wasp species that were formerly widely distributed to survive only on the larger sandy pine heaths. *Evagetes dubius* supports this hypothesis in that it is only found on the same areas as the sand lizard (Table 1).

Selective colonisations may have contributed to the observed nestedness pattern if there are pronounced differences in dispersal abilities among spider wasp species. Then poorer dispersers would tend to be present only on the largest or richest pine heaths, where extinction rates are lower, whereas better dispersers would tend to be present on most pine heaths because local extinctions would be quickly reversed (Cook and Quinn 1995). Haeseler (1988) showed that common species of spider wasps had colonised young dune islands up to 7 km off the North Sea coast. Two of the species encountered, *Episyron rufipes* and *Evagetes pectinipes*, prefer coastal sand habitats. This may explain why they occurred mainly on pine heaths close to the "inland sea" lake Vänern in my study (Fig. 1 and Table 1), where they also inhabit small sandy shores.

A nested distribution of habitats among islands may also result in nestedness of species assemblages (Calmé and Desrochers 1999). Although not obvious to the human eye, it is possible that large sandy pine heaths offer sandy microhabitats (including microclimates and/or species interactions) rarely found on smaller ones, and that this is reflected in the occurrences of rare species. High richness

of sandy microhabitats may explain the surprisingly high species richness of area 3 (Table 1), considering its small size. A large proportion of this area (almost 40%) contained open sand in the form of sand pits (in different successional stages), as opposed to the other areas, where the relative amount of exposed sand was much smaller. The high species richness of this area may also relate to the previous hypothesis, and the one below.

Passive sampling may also cause nestedness, whereby abundant species have a higher probability of being sampled than rare ones (Andrén 1994, Wright et al. 1998). Moreover, the species-area relationship may arise because large areas sample more individuals from a species pool than small areas and therefore have more species (Connor and McCoy 1979). Although the nestedness calculator programme used in this study tends to overestimate the degree of nestedness and its statistical significance (Fischer and Lindenmayer 2002), the low nestedness temperature in my dataset is likely to reflect a genuine signal, rather than being an artefact of passive sampling. This is supported by the fact that the number of spider wasp species per patch was significantly higher on the largest areas than on smaller ones. Furthermore, the potential to find the majority of species in a spider wasp community on individual pine heaths seems to be high. Although the largest studied area, area 1 (Brattforsheden), has been surveyed with varying intensity and local focus for several seasons on a total of 25 patches between 1988 and 2003, it is noteworthy that 23 species out of 25 (92%) of the sand-associated spider wasp fauna known today were caught in water traps from only 7 patches in the first survey season. Two additional species were caught in the second season, on patches not investigated before. However, two species (*Arachnospila wesmaeli* and *A. westerlundi*) have been found with only 3 and 1 specimens, respectively, indicating that the rarest species might be overlooked by chance.

Potential indicator and umbrella species

Pine heaths and patches with the sand lizard had a disproportionately large number of red-listed spider wasps and other early successional species on a regional and landscape scale. Because of the sand lizards' restricted dispersal capacity and association with structurally complex sand habitats (see above), this species indicates historical continuity of such habitats. Since the sand lizard is also conspicuous and rather easy to survey, it can be considered a suitable indicator species for patches of high early successional biodiversity value. Furthermore, potential habitat patches for the sand lizard are fairly easy to identify (Fig. 7), which make surveys for "hot spot" patches straightforward.

In addition, since the sand lizard requires relatively large patches on at least a 50-yr horizon (> 5–10 ha; see above), it makes it a suitable umbrella species for early successional biodiversity conservation on large sandy pine heaths. This was also supported by the relatively high score of the umbrella index calculated for red-listed species on Brattforsheden (Table 3). However, two drawbacks with the sand lizard as an umbrella species for biodiversity conservation in pine heath forests are its restriction to the largest sandy areas, and its rarity within these at present. An ideal umbrella species should be neither too ubiquitous nor too rare but instead strike a balance between these two extremes (Fleishman et al. 2001b). Sites that are identified with an umbrella species should also encompass viable populations of both the umbrella and its beneficiary species (Caro 2003, Roberge and Angelstam 2004). Importantly, this could be achieved after habitat restoration and subsequent population growth.

Although they are less species-rich overall, smaller sandy pine heaths can also be inhabited by red-listed early successional species (Table 1). On such smaller areas, spider wasp species such as *Episyron albonotatum* and *Arachnospila wesmaeli* and the digger wasp *Ammophila campestris*, can be useful umbrellas and/or indicators (Table 3). Moreover, the number of red-listed spider wasp species per patch is significantly positively correlated with the number of other red-listed aculeate Hymenoptera per patch (mostly digger wasps and solitary bees) (data from the areas in Table 3; unpubl.).

Among other insects, the umbrella index suggests that the diurnal, easily observed and identified tiger beetle *Cicindela sylvatica* (for presentation, see Lindroth 1985) is an especially suitable candidate as an umbrella species, since it indicated high red-listed species richness and had an intermediate degree of ubiquity (Table 3). Pearson and Cassola (1992) argued that tiger beetles in general make good indicator taxa for biodiversity conservation because of their conspicuous appearance and often strict association to early successional and threatened habitats.

Among vertebrates, the wood lark and the nightjar scored higher as potential umbrella species than the sand lizard on Brattforsheden; the nightjar mainly because it occurred on relatively many patches, whereas the wood lark better indicated species-rich patches with respect to red-listed early successional taxa (Table 3). However, one disadvantage with these high-vagility species is that they are not dependent on continuity of open habitats, which make them less sensitive than the sand lizard as indicators and umbrellas for threatened, low-vagility species.

Obviously, no one species studied here can be used as an umbrella for all other threatened species on sandy pine heaths, so a strategy of multiple umbrella species (Lambeck 1997), and demarcation of patches with key habitat components (cf. Fig. 7), would be a suitable approach for early successional biodiversity conservation.

Implications for conservation action

I concur with Linder et al. (1997) and Sutherland (1998) that active management of threatened early successional

habitats and species must play a larger role in conservation, as opposed to the passive form of management usually applied in forest reserves. The efficiency of afforestation and fire suppression accelerated during the 20th century, and the Swedish boreal forest is now generally much denser than before (Linder and Östlund 1998). The conservation of the sand lizard and other thermophilous, ground-dwelling, early successional species in sandy pine heath forests requires action to reduce closed canopy formation and subsequent shading, and to re-establish new open habitat patches at suitable locations. On Brattforsheden, ca 20 new 5–15 ha sand lizard habitat patches divided into at least six networks are planned to be restored over the coming years, with the management measures described in Figs 9–10. Since natural colonisation of sand lizards to restored, distant, empty patch networks, is unlikely within the foreseeable future, reintroduction of juveniles is planned to take place (Berglind 2004a).

Several sound, general suggestions for biodiversity restoration in dry pine forests, including use of prescribed burnings, are given by Fries et al. (1997) and Angelstam (1998). It is, however, as Granström (2001) points out, vital to designate selected stands and landscapes with long-term plans for the use of fire. Prescribed burnings may be a suitable long-term way to recreate suitable mosaics of open sand patches and a dense field layer of *Calluna vulgaris* at some distance from sand lizard patches (fire within habitat patches can cause major mortality among sand lizards; e.g. Moulton and Corbett 1999). This more "natural" method of restoration has the advantage of also attracting pyrophilous and thermophilous wood-associated insects (Wikars 1992, Ehnström 1999).

Besides restoration of early successional patches, we must also start focusing on existing habitat patches of conservation importance in sandy pine heath forests. The sand lizard and many other red-listed species often occur in or



Fig. 9. Part of sand lizard habitat patch ten years after habitat restoration (cutting of a 40 yr old pine stand, patch-soil scarification, and excavation of bare sand patches). Note the high coverage of *Calluna vulgaris*, regrown from the existing seed bank, and the excavated sand patches in the fore- and background (on top of fossil sand dunes). Before restoration, the ground was shaded by closed pine canopy, and almost completely covered by a ground layer of reindeer lichens, with only a minute field layer of *Vaccinium vitis-idaea* and *Calluna vulgaris*. The patch is today also habitat for the wood lark, nightjar, and the rare spider wasp *Priocnemis gracilis*. To keep restored patches in such an early successional stage, recurrent management is planned to take place ca every 20th yr, by felling of pine shrubs, mechanical sand disturbance, and/or small-scale burning on a rotational basis. Brattforsheden, site SB (northern part of the southern patch in Fig. 10, view towards NW) in August 2002. Photo: S.-Å. Berglind.



Fig. 10. Aerial photograph of two newly restored habitat patches connected by a dispersal corridor for the sand lizard on Brattforsheden, site SB in 2000. The non-restored area between the patches was less suitable to restore since it has a northerly aspect. Within the patches, pine trees have been cut down, except for groups of ca 5–10 trees. The patches have been subject to patch-soil scarification to allow regrowth of *Calluna vulgaris* from the seed bank, and thus provide shelter and foraging opportunities for the sand lizard. The sand patches have been created on fossil sand dunes with a southerly aspect by an excavator for egg-laying by sand lizards. The unusually broad, open verges (10 m on each side) of the sand road have been created to reduce the amount of shade per day from surrounding tree canopy so as to allow inter-patch dispersal by the lizards. The 12-yr old restoration patches from 1988 were the main ones inhabited by lizards when the photograph was taken in 2000. Photo: Lantmäteriet.

close to sand/gravel pits (Berglind 2004b). These are very important habitats for early successional biodiversity conservation and should in many cases be classified as "key habitats", and kept permanently open, perhaps through subsidies to land-owners. Furthermore, sandy road verges with a southerly aspect often represent high quality habitats for reproduction and dispersal for both the sand lizard (Dent and Spellerberg 1988) and invertebrates (Vermeulen 1993, Eversham and Telfer 1994) (Fig. 8). By clearence of trees at least 5–10 m on each side of the verges along

suitable road sections (cf. Fig. 10), the amount of shade per day can be reduced and habitat offered for many more years than is normally the case (due to tree canopy formation and shading).

Is biodiversity conservation in sandy pine heath forests important?

One might argue that the peripheral populations of red-listed species that occur in the Fennoscandian sandy pine heath forests are on the brink of extinction anyway, the positive effects of increased global warming not withstanding, and that conservation resources should be directed towards, for example, threatened boreal species occurring closer to their centres of range. However, recently Channel and Lomolino (2000) showed that peripheral populations are no more "doomed to extinction" than populations in the centre of a species' range, and in fact often less so. Furthermore, peripheral populations often exhibit unique genetic characteristics that make them especially valuable for biodiversity conservation (Lesica and Allendorf 1995), which has in fact been demonstrated for the central Swedish sand lizard populations (Gullberg et al. 1998). Large sandy pine heath forests may also be viewed as "archives" with regard to early successional species connected to historical ecological processes, including forest fires and associated open sand habitats, which have only relatively recently been suppressed by human activities. Thus, there are strong reasons to direct conservation management priorities towards these heath forests without further delay.

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Influence of edges between old deciduous forest and clearcuts on the abundance of passerine hole-nesting birds in Lithuania

Gediminas Brazaitis and Per Angelstam

Brazaitis, G. and Angelstam, P. 2004. Influence of edges between old deciduous forest and clearcuts on the abundance of passerine hole-nesting birds in Lithuania. – Ecol. Bull. 51: 209–217.

We describe the relationship between the distance to clearcut edge and the relative abundance of hole-nesting passerine birds in old deciduous forest in Lithuania. Bird density data was collected from 358 line transects in mature forest stands adjacent to 50 clearcuts. The red-breasted flycatcher *Ficedula parva* was studied in more detail by counting singing males in 44 additional mature forest stands. The abundance of the great tit *Parus major*, marsh tit *P. palustris*, and blue tit *P. caeruleus* was significantly higher near the clearcut- old forest edges than further inside the forest. The nuthatch *Sitta europea* and the pied flycatcher *Ficedula hypoleuca* showed no significant trend in relation to edge. By contrast, the abundance of the treecreeper *Certhia familiaris*, coal tit *Parus ater*, and red-breasted flycatcher was significantly higher in the mature forest interior of the deciduous stands. For the great tit, blue tit and red-breasted flycatcher the widest edge-influenced zone was observed in medium-aged (4–9 yr) edges, while for the treecreeper and coal tit the widest edge-influenced zone was observed in old (10–20 yr) edges. The red-breasted flycatcher showed the strongest negative edge effect of all species, being absent from the vicinity of clearcuts (<50 m) and confined to the interior of forest stands. The probability of red-breasted flycatcher holding a breeding territory was high if stands were > 40 ha large, had an average stocking level of >0.8, and if the shape of the stand tended towards that of a circle. The reduced availability of large deciduous forest patches caused by current forest management in Lithuania may affect negatively the populations of the forest-interior species identified in this study.

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In forest ecosystems habitat loss appears to be the most important factor causing local and regional extinction of species (Groombridge 1992, Fahrig 1999, 2001, Hunter 1999, Rochelle et al. 1999). Proposed mechanisms include reduction in habitat quality and area, as well as isolation and disturbance from the surrounding matrix (Harris 1984, Wilcove et al. 1986, Rolstad 1991, Saunders et al. 1991, Haila et al. 1993, Hunter 1999, Rochelle et al. 1999).

Where forestry is based on clear-felling practices and a regulated even-aged distribution of trees has been achieved, landscapes form spatial and temporal mosaics of stands with a limited range of ages, shapes, and tree species compositions. In Lithuania and many other European

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countries with traditional central European forestry traditions, long and narrow forest stands are harvested within rectangular forest management units (Dengler 1944, Matthews 1989). The motive for the strip-cutting method was to facilitate the maintenance of an even-aged distribution within the unit, to allow regeneration of the clearcut by seeds from the adjacent mature stands, and to minimise windthrow. Currently, however, because of high variation in tree species composition, in microsite conditions, and because of a high amount of private property borders, clearcuts often tend to be much smaller and irregularly shaped. The resulting reductions in the patch size distribution within a system of a quantitatively and qualitatively stable patch dynamics would be expected to further negatively affect animal species that need large patch sizes, or are confined to forest interior habitats.

Hole-nesting passerine birds form an interesting ecological guild for analysing the effects of habitat loss and alteration, at a spatial scale that is relevant to the issue of how to design the quality as well as size and shape of forest stands in managed landscapes (e.g., Jansson and Angelstam 1999). These species are dependent on natural cavities, nest holes excavated by primary nest excavators (e.g. woodpeckers) as well as natural forest components such as soft snags (Kontrimavičius et al. 1991, Bishnev and Stavrovsky 1998). Several studies show that as a group, hole-nesting species are negatively affected by intensive forest management in boreal environments (Helle and Järvinen 1986, Virkkala 1987, Kurlavičius 1995, Berg 1997, Jansson 1999, Uliczka and Angelstam 2000).

In Lithuania, as is common in many other countries (Lindenmayer and Franklin 2003), improvements in the future forest interior qualities are currently being addressed by variable retention of trees during harvesting of mature stands. However, the design of stand size and shape is not explicitly discussed to the same extent. Changes in managed forest landscapes in Finland have led to fewer large patches with negative consequences to area-demanding species that cannot use the landscape in a fine-grained fashion (Mykrä et al. 2000). Direct and indirect edge effects such as altered microclimate and predation are also important (Angelstam 1992, Kurki et al. 2000). Similarly, European and North American birds have been classified in relation to their occurrence at forest edges (Whitcomb et al. 1981, Hansson 1983, Helle 1983, Helle and Järvinen 1986, Fuller and Whittington 1987, Cieslak 1992, Kurlavičius 1995). A particular concern is that forest interior species are affected negatively by decreasing patch size because the total area consisting of edge habitat will increase (Matlack and Litvaitis 1999).

The aim of this study is to evaluate the effects of edges between clearcut and old forest on the local distribution of hole-nesting birds in a managed forest landscape. We then discuss the effects of forest management on the future availability of sufficiently large patches, and hence of forest interior, for the native bird fauna.

Methods

Study area

The study was conducted in the Marijampole and Kaunas districts in southwestern Lithuania (54°25′–55°10′N, 23°20′–23°80′E). Phytogeographically the study area is located at the border between the temperate lowland forest and the hemiboreal forest (Ahti et al. 1968). Most of the surveyed forests can be categorised as oak-hornbeam forest Quercus-carpinetum. The dominating tree species in the study area are aspen *Populus tremula*, birch *Betula pendula*, black alder *Alnus glutinosa*, hornbeam *Carpinus betulus*, and oak *Quercus robur*. Norway spruce *Picea abies* is not common in the study area and Scots pine *Pinus sylvestris* is totally absent. Mature forest stands with a maximum of 20% of Norway spruce volume were selected for this study. The average age of deciduous trees in the stands was over 60 yr, the stand volume 200–300 $m^3 ha^{-1}$ and the height of trees 20–26 m. All stands selected for this study were mature for final felling. The studied forest stands were dispersed in five large forests (>2000 ha) surrounded by an agricultural landscape. Nearly all stands in the selected forest areas that fulfil the described requirements were investigated. Artificial nest boxes were rare in the study area.

We studied the guild of small passerine hole-nesting birds breeding in forest. In the study area we observed the great tit *Parus major*, blue tit *P. caeruleus*, marsh tit *P. palustris*, coal tit *P. ater*, nuthatch *Sitta europaea*, treecreeper *Certhia familiaris*, pied flycatcher *Ficedula hypoleuca*, and red-breasted flycatcher *F. parva.* The spotted flycatcher *Muscicapa striata* and the willow tit *Parus montanus* were rarely observed in the study area and were therefore excluded from the analyses. Because of the lack of pine forest, the crested tit *Parus cristatus* was absent from the area.

The field study consisted of two parts. First, small hole-nesters were surveyed from 1999 to 2001 using line transects (Pridnieks et al. 1986, Bibby et al. 1992). A total of 358 transects were dispersed in mature forest remnants adjacent to 50 clearcuts. Second, during the last year of the study (2001), the species showing the highest edge avoidance (i.e., the red-breasted flycatcher) was studied in more detail by noting the presence of singing males in 44 mature forest fragments. The two survey methods were applied independently, and to avoid pseudoreplication the studied stands were not the same. All bird surveys were performed in early mornings within four hours after sunrise with clear weather conditions (no strong wind or rain).

Although edges between clearcuts and mature forest are typically sharp, their effects on abundance of birds change with time. The width of the edge influenced zone increases with edge age at least up to 20 yr (Brazaitis 2001). Consequently, we stratified the forest/clearcut edges into three types: 1–3, 4–9, and 10–20 yr old, hereafter referred to as young, medium-aged, and old edges. Due to the forest management regime all clearcuts had a rectangular shape

(>100 m wide and >200 m long). The old forest fragments had a width of at least 400 m. Transects were placed perpendicular to the edge and separated by at least 200 m. Each transect started at the clearcut – forest edge and had a length of 200 m. The walking speed was 1.5 km h^{-1}. The distance from the clearcut to the observer was measured using the length of the footstep. For each bird observation, the distance from the edge was noted in 10-m intervals. Observations further away than 50 m were not used in analysis. Hence, there was no overlap between neighbouring transects. The line transect data was collected during the breeding season from 10 April to 15 June (see also Pridnieks et al. 1986). The line transects was visited twice, before and after 15 May, and then pooled. Transects were distributed in equal proportions in each of the three edge age classes. Following the advice by Järvinen et al. (1977, 1978), bird counts were made by one single observer.

A one-visit survey was used to estimate the presence of the red-breasted flycatcher in 44 old forest remnants having a total area of 1270 ha (for details of the stands see Table 1). All patches were surrounded by young stands up to 20 yr old. Patches that contained immature stands >0.3 ha were not sampled. The presence of singing males in forest fragments was noted by walking through the stand with ca 150 m between routes. This was done during the peak activity period of the red-breasted flycatcher from 20 May to 10 June. The visit lasted at least 10 min in each fragment with a walking speed of 1.5 km h^{-1}. The red-breasted flycatcher has a loud song and therefore is easy to detect.

Evaluation of forest patch structure

The area and shape of fragments was evaluated using forestry stand maps at the scale of 1:10 000. Stocking level of the stands was evaluated according to the Lithuanian forest inventory methodology (Repšys 1994). Depending on the fragment size, the stocking level was measured in 5–13 plots evenly distributed in each stand. The stocking level is closely correlated with the canopy density of the stand. It is defined by "the quotient (ratio) of actual basal area to the maximum attainable for that particular site, or to the basal area of an appropriate yield table" (Loetsch et al. 1973). If stand basal area is at its maximum, stocking level should be 1.0. The stand shape coefficient (M) was calculated according to Thomas (1979), where P is the perimeter (m) and S the area (m^2):

$$M = \frac{P}{2\sqrt{S\pi}}.$$

Statistical analyses

The comparison of hole-nesting birds' responses to clearcut edges was made using the abundance of birds at various distances from edge. The 200-m long zone was divided into 10-m intervals for which the relative abundance of birds was calculated. The relative abundance (A) was calculated using a formula were B is the total number of birds observed in the same 10-m wide interval and N the number of line transects:

$$A = \frac{B}{N} \times 10.$$

For each species, the width of edge effect was defined as the pair-wise distance intervals (i.e. 0–9 vs 10–200 m, 0–19 vs 20–200 m, 0–29 vs 30–200 m, etc.) away from the edge between which the difference in relative abundance was greatest. This was calculated separately for each edge age class using ANOVA. The species were classified as edge or interior species, respectively, if their relative abundance was significantly higher or lower near the clearcut edge compared to the forest interior. Using linear regression we ranked the species according to their sensitivity to edge.

Because of high interdependence among stand and patch measurements of old forest remnants surveyed for red-breasted flycatcher, principal component analysis (PCA) was used for defining the most independent and important factors. We ran PCA and extracted three principal components. Those factors that highly correlated with each of the PCA components were then selected for logistic regression analysis.

Logistic regression was used to assess how factors selected by PCA were related to the occurrence of the red-breasted flycatcher. We analysed each factor separately to find consistent relationships (i.e. little overlap between the range of values for presence vs absence) and assessed good-

Table 1. Summary statistics for the 44 mature forest remnants where the red-breasted flycatcher was surveyed.

Variable	Mean	SD	Max	Min
Area (ha)	28.8	33.5	150	1.8
Maximum width (m)	391	293	1400	90
Average width (m)	292	206	950	16
Length (m)	720	395	1700	220
Perimeter (m)	2213	1277	5500	600
Shape index	273	41	361	180
Stocking level	0.72	0.08	0.90	0.55

ness of fit using Hosmer-Lemeshow statistics. Models that failed the goodness-of-fit criteria ($p<0.1$) were rejected (Hosmer and Lemeshow 1989). The significance of models and the combined effects of measurements were evaluated using Cox and Snell R-square indices.

Results

Abundance of hole-nesters in relation to edge

The total pooled abundance of all eight hole-nesters did not vary along the 200-m zone ($p<0.95$) (Fig. 1). However, the individual species could be grouped according to their degree of edge avoidance. The great tit, marsh tit and blue tit preferred edges, the nuthatch and pied flycatcher were indifferent to edges, while the treecreeper, coal tit and redbreasted flycatcher avoided edges (Fig. 1). The combined effect of species and distance from edge influenced significantly bird distribution ($F=1.67$; $p<0.001$).

The highest significant difference in the abundance of the great tit was detected when grouping the 10-m intervals as 0–89 and 90–200 m from edge ($F=20.42$; $p<0.001$). The blue tit was most abundant at 0–30 m from the edge ($F=9.11$; $p<0.01$) and the marsh tit was most common within 130 m from the edge ($F=5.46$; $p<0.05$). The coal tit was rare in the first 70 m ($F=11.59$; $p<0.005$). The treecreeper avoided the zone within 60 m from the edge ($F=5.00$; $p<0.05$). Finally, the abundance of redbreasted flycatcher differed significantly among the distance intervals of 0–49; 50–79 and 80–200 m from clearcut edge ($F=25.36$; $p<0.00001$).

Temporal dynamics of the edge effect

Judging from the differences among the three different edge age classes, the zone influenced by the edge varied over the 20 yr-period (Table 2). The marsh tit was not included in the analyses because of too few observations. In

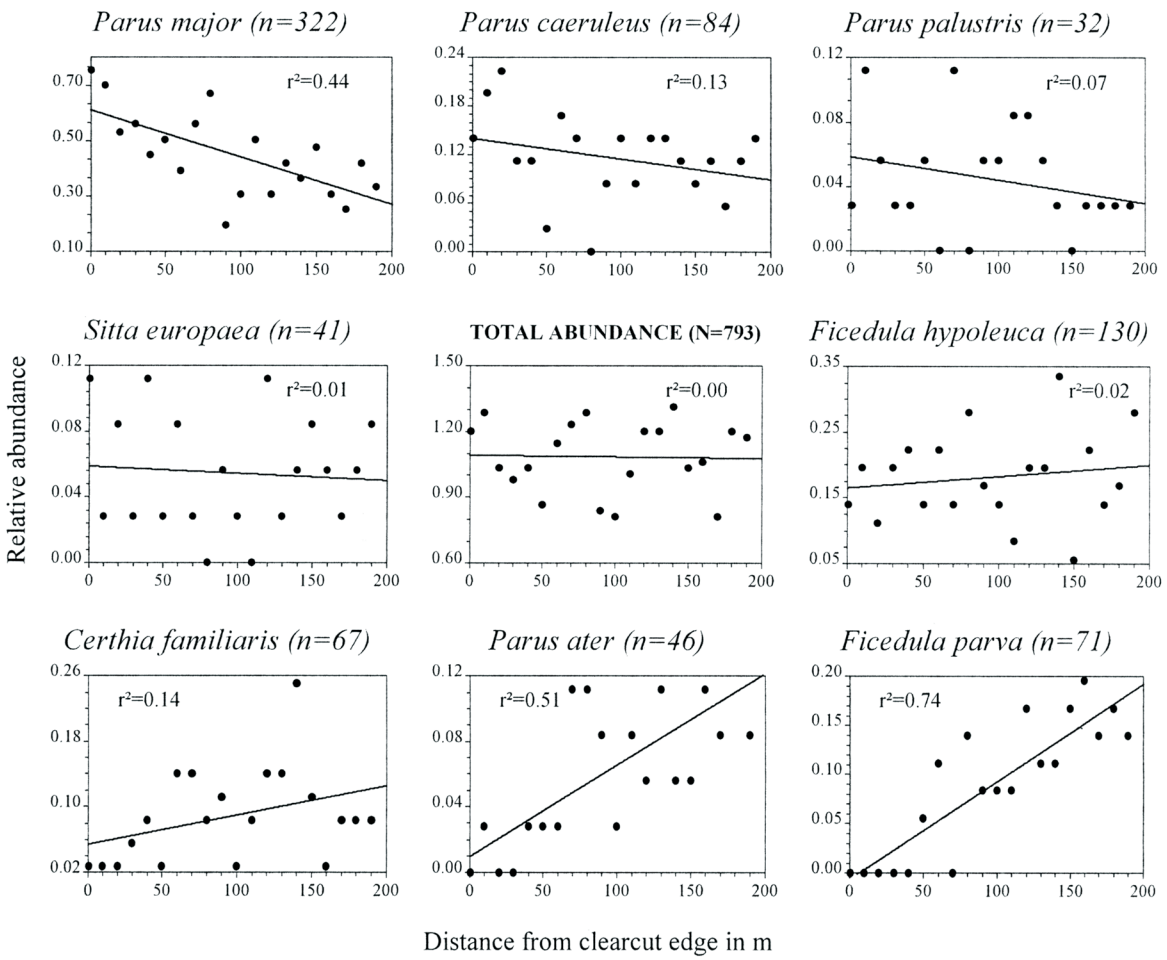


Fig. 1. Linear regression of relative bird abundance on the distance from the clearcut edge for 8 hole-nesting bird species. The total number of birds recorded for each species is given after its scientific name.

newly cut edges only the abundance of the great tit was not significantly different among the various distances from the forest edge. The great tit, blue tit and red-breasted flycatcher showed the widest edge effect in medium-aged edges. In the oldest edge age types, blue tit abundance was not different among various width distance intervals. Treecreeper and coal tit showed the widest edge effect in old edges. The combined effect of distance from edge and type of edge did not have any significant influence on bird abundance ($F=0.37$; $p<0.99$).

Occurrence of red-breasted flycatcher in relation to stand characteristics

Being the most edge-sensitive species, we analysed patterns of occurrence of the red-breasted flycatcher in more detail. As could be expected, area, perimeter, length, maximum and average width were highly significantly intercorrelated. The shape coefficient of the fragments correlated with both width estimates. Finally, the stocking level was significantly correlated with all factors. The strong correlation among factors indicated a need for factor reduction. We extracted three components from the PCA (patch area, patch shape coefficient and stand stocking level), which totally explained 95.8% of the variance in the occurrence of red-breasted flycatchers (Table 3).

The probability of occurrence of red-breasted flycatchers increased with the size of forest stands (Fig. 2). Only fragments > 40 ha always contained red-breasted flycatchers. The average stocking level of forest stands also affected the presence of the red-breasted flycatcher. If the average stand stocking level was 0.8 or more, the probability of red-breasted flycatcher occurrence was high. Finally, the shape of the fragment influenced the occurrence of that species. In narrow fragments with a shape coefficient of 1.65 and more red-breasted flycatchers were absent. The optimum shape coefficient was < 1.15. We also analysed the combined effect of selected factors using logistic regression. Pairs among the factors (area, stocking level and shape coefficient of fragment) significantly affected the effect on the occurrence of red-breasted flycatcher (Table 4), with area and stocking level explaining most of the variation (Fig. 3). The cumulative effect of area and stocking level shows that red-breasted flycatchers are dependent on the interaction of both factors: both smaller stands with higher stocking levels and larger stands with lower stocking levels are acceptable for occurrence.

Table 3. Correlations of characteristics of stands where red-breasted flycatchers were surveyed with the three principal components (PC) obtained from PCA. The variables best correlated with each of the principal components are shown in bold.

Variable	PC 1	PC 2	PC 3
Area (ha)	**0.98**	0.05	0.09
Maximum width (m)	0.96	0.13	0.02
Average width (m)	0.95	0.25	–0.05
Length (m)	0.92	–0.18	0.08
Perimeter (m)	0.97	–0.17	0.04
Shape index	–0.11	**–0.97**	–0.13
Stocking level	0.53	0.24	**0.81**

Discussion

Different responses to edges

This study lends support to previous observations by Whitcomb et al. (1981) that hole-nesting birds show species-specific responses to mature forest edges. The great tit, blue tit, and marsh tit could be classified as edge-preferring species, whereas the treecreeper, coal tit and red-breasted flycatcher were classified as forest interior species. The red-breasted flycatcher stands out as the most edge-sensitive species in this study. It was absent from the vicinity (50–100 m) of clearcuts and was confined to the interior of forest stands. In the mature forest interior the abundance of flycatchers was similar in all the three edge age classes. Also the average stocking level of forest stands significantly affected the abundance of red-breasted flycatchers. If the average stocking level was 0.8 and more, the probability that red-breasted flycatchers would have a nesting territory was high. By contrast, forest stands with stocking levels of < 0.7 were poor habitat for red-breasted flycatchers. In mature stands > 40 ha red-breasted flycatchers were always observed.

Table 2. Differences in bird numbers between the edge-influenced zone and the zone outside of this influence were tested by ANOVA (***p<0.000; **p<0.01; *p<0.05). The marsh tit was not included because of too few observations.

Species	Age of edge (yr)		
	1–3	4–9	10–20
Great tit	NS	70**	40*
Blue tit	40*	80*	NS
Treecreeper	30*	60*	110*
Coal tit	50**	60***	110*
Red-breasted flycatcher	80***	130***	120***

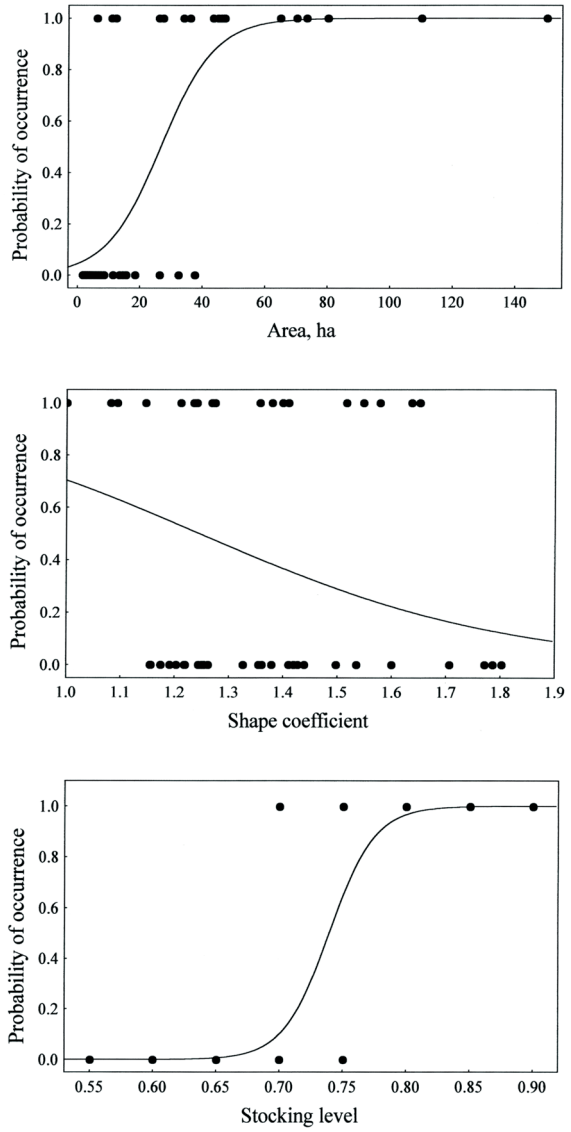


Fig. 2. Influence of area, shape and stocking level of stand on the presence of red-breasted flycather in forest fragments.

In the Białowieza forest in NE Poland, the red-breasted flycatcher was significantly more abundant in closed canopy sites than in tree-fall gaps (Fuller 2000), even though natural gaps were much smaller (<0.2 ha; Runkle 1982, Falinski 1986, Peterken 1996) than the clearcuts in our study (2–6 ha). Hence, clearcuts seem to have the same kind of influence on red-breasted flycatcher distribution, but the influence of clearcuts appears to be stronger compared to natural tree-fall gaps. This suggests that the red-breasted flycatcher is a true interior forest species, which is adapted to the main natural disturbance factors perpetuating rather closed-canopy deciduous or mixed stands such as single blowdowns, insect outbreaks and browsing by wild herbivores. Hence, its presence could be used as an indicator of species being sensitive to reduction in forest stand size.

In boreal forests, the treecreeper and the coal tit have similar requirements, and show a decrease in abundance close to old forest edges (Virkkala 1987, Kuitunen and Helle 1988, Kuitunen and Mäkinen 1993). Such species are described as area demanding old growth forest specialists and are negatively affected by forest fragmentation and reduced habitat quality (Berg 1997, Ulizcka and Angelstam 2000).

However, when considering results from other studies, birds' responses to clearcut edges do not show a consistent pattern. Hansson (1983) reported a significant increase in the abundance of the coal tit and the great tit near edges while Fuller and Whittington (1987) found a near equal distribution. Cieslak (1992) observed an equal distribution or increase of great tit abundance in forest interior. Such differences among regions can be explained by one or more of the following factors: 1) studies may have been performed in forests with different vegetation, structure, or due to annual variation in food production. Conversely 2) there may be regional-scale differences in foraging behaviour of species and this could influence intraspecific interactions in the guild (Nilsson and Alerstam 1976, Wiens 1989). Additionally, 3) bird species composition of the hole-nesters guild differs among regions and habitats. Absence or presence of a species could interact with other species' absence and/or response to edge. This was shown in islands with different species composition (Diamond 1975). Finally, 4) methodological differences may exist among studies.

The great tit, the blue tit and the marsh tit preferred edges and showed a peak in edge-preference in the medium-aged edges. The abundance at old edges was lower than in young edges. Similarly, the abundance of forest interior species (treecreeper, coal tit and red-breasted flycatcher) decreased between the three edge age classes dur-

Table 4. Results of logistic regression models between fragment area, shape and average stand stocking level and the presence of red-breasted flycatchers (Cox and Snell R square (R^2), χ^2 (all three models are significant $p<0.000$), and significance of Hosmer Lemeshow test for goodness of fit).

Factor	R^2	χ^2	Hosmer Lemeshow p
Area and stocking level	0.97	56.26	1.00
Shape and stocking level	0.77	37.15	0.88
Area and shape	0.53	33.40	0.93

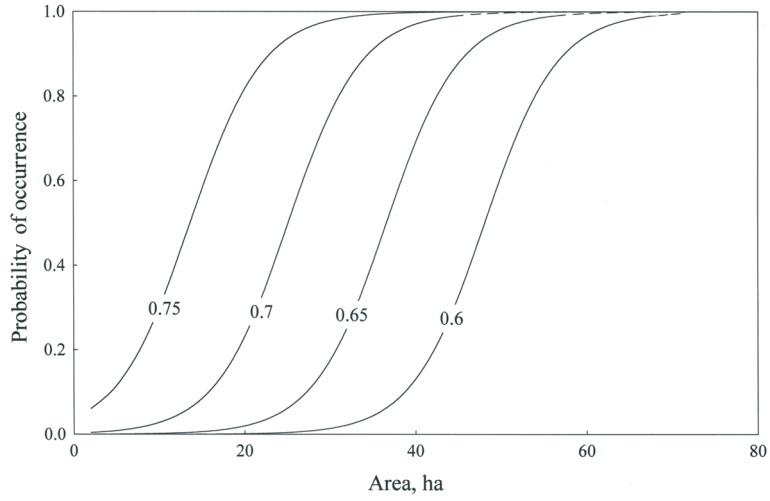


Fig. 3. Influence of the combined effects of area and stand stocking level on red-breasted flycatcher occurrence in forest fragments.

ing the 20-yr chronosequence. For all the studied species the width of the avoided edge zone increased from young to medium-aged and old edges, suggesting a temporal increase of the edge effect.

Causes of edge-effects

Three possible mechanisms behind this apparent limitation of some species to interior forest conditions have been proposed. Firstly, several studies have shown that the risk of nest predation increases near edges (Andrén and Angelstam 1988, Andrén 1995) and consequently some species avoid areas with higher risk of predation (Møller 1989). The abundance of the corvid nest predator jay *Garrulus glandarius* was highest in a 20-m interval from clearcut into the mature stands (Brazaitis 2001). Moreover, the great spotted woodpecker *Dendrocopos major* was a frequently observed nest predator (Aleknonis 1984) and showed an edge preference in medium aged edges (Brazaitis 2001). The relative abundance of these two species was hence highest in those parts of transects, which were rarely utilised by the forest interior species. In a Finnish study, Kuitunen and Helle (1988) observed that a greater proportion of treecreeper nests were destroyed in forest margins than in the interior. The treecreeper and the red-breasted flycatcher have nests in places that are easily reached by generalist predators: bark crevices and decaying trunks. In our study, these species were identified as forest interior species. Additionally, edge-avoidance may be linked to mammalian nest predators, which prefer habitats with high prey densities (e.g. small mammals), such as clearcuts (Hansson 1979, Angelstam 1992).

Secondly, interspecific competition for food and hollows among birds could be a factor of importance (Wiens 1989). Many food competitors prefer forest edges: e.g., dunnock *Prunella modularis*, blackcap *Sylvia atricapilla*, chiffchaff *Phylloscopus collybita*, marsh tit, great tit and others (Tomiałojc and Wesołowski 1990). Most *Parus* spp. species are prominent nest site competitors and showed higher relative abundances near edges, which thus may negatively influence the occurrence of red-breasted flycatcher and treecreeper. The number of bird species that prefer forest edges was up to 3 times higher than those adapted to old forest interior in the same region (Brazaitis 2001, 2003). The great, blue and marsh tits were common visitors in clearcut areas but forest interior birds were scarce (Brazaitis 2003). A possible mechanism supported by Imbeau et al. (2003) is that bird species that feed on neighbouring clearcuts increase in abundance near edges and appear as edge species. This means that other hole-nesting species may be negatively affected by edge-affiliated species, and select territories located further away from the edge. This hypothesis is supported by the equal distribution of all hole-nesters at all distances from edges (Fig. 1, centre).

Thirdly, the occurrence of red-breasted flycatchers was well explained by the stand stocking level implying a high canopy cover or high foliage height diversity. Trees in natural woodland edges are adapted to disturbance from outside and show similar amounts of dead trees and rates/amount of fallen limbs at edges and interior (Hansson 2000). Conversely, the avoidance of small stands by the red-breasted flycatcher may be due to the absence of suitable vegetation structure as these stands were under stronger wind influence, causing higher tree fall rates (Esseen 1994). Similarly, in sharp forest edges trees near edges suffer higher wind and insect damage (Franklin and Forman 1987). In young anthropogenic edges higher wind influence extends up to 40 m into the stand and up to 40% of the trees are windthrown (Juodvalkis and Jakas 1996). The negative correlation between the stocking level and patch shape parameters supports the notion that edges have lower stocking levels.

Management implications

In Lithuania, as in most of central and eastern Europe, managed forest landscapes are divided into rectangular blocks (25–100 ha each). Within these blocks clear-felling is made as rectangular units, which are 100 m wide and with a length equal to the block length, i.e. 500 or 1000 m. Traditionally one aimed at an even distribution of stands of different age classes within each block (Dengler 1944). However, because of more rapid exploitation of large mature forest areas this system has been modified. Today, each third or fourth 100-m wide strip is felled perpendicular to the prevailing wind direction (usually east-west). Stands with a homogeneous age and/or tree species composition and smaller than the strip can be felled separately. In both cases, clearcuts in forests are approximately evenly dispersed.

As a result, the managed forest landscape is becoming an even more fine-grained mosaic of relatively small stands with different age-classes and a large amount of edges. This type of landscape change is particularly critical for the remaining forest interior species. The results of this study suggest that the forest interior species red-breasted flycatcher, treecreeper and coal tit will be negatively affected by the disruption and fragmentation of the remaining larger contiguous areas with mature forest. A wide application of the current forestry practice to cut each third strip therefore appears critical to the existence of forest interior species in such managed landscapes.

Conclusion

Our main management recommendation for the subsistence of hole-nesting birds is to concentrate clear-felled areas so that large forest stands will always be present in the landscape, and to maintain a stable age distribution allowing for mature forest stands. This would decrease the amount of edges and increase the area of functional mature stands. As a result, a stable patch dynamic with an appropriate grain size and habitat quality for forest interior species would be ensured. Finally, due to the listing in the EC Bird Directive and the specialised habitat requirements the red-breasted flycatcher can play a possible role as a focal species for forests of high conservation value in the hemiboreal and nemoral forest zones.

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Quantitative snag targets for the three-toed woodpecker *Picoides tridactylus*

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Bütler, R., Angelstam, P. and Schlaepfer, R. 2004. Quantitative snag targets for the three-toed woodpecker *Picoides tridactylus*. – Ecol. Bull. 51: 219–232.

Sustainable forest management goals include the conservation of biological diversity and its constituent elements. Dying and dead trees, in particular, have been recognised as being of prime importance as resource and habitat for numerous animal and plant species. Nevertheless, few quantitative target values have been defined for dead wood management purposes, and they often lack well-founded scientific bases.
In this study we developed such quantitative targets for standing dying and dead trees (defined as snags), based on the habitat requirements of the three-toed woodpecker *Picoides tridactylus*, a keystone species whose presence is considered an indicator of the properties of naturally dynamic forests. First we developed a theoretical model based on energy requirements and with predictions for woodpecker breeding probabilities as a function of available snag quantities. Then an empirical field study was conducted in Switzerland with the aim of verifying the model predictions. For this purpose, 12 pairs of sites of 1 km^2 in size and comprising one site with and one without a breeding woodpecker, were sampled for snags. We compared these sites using logistic regression. Finally, the comparison of the theoretical model with the field approach enabled the derivation of quantitative snag targets for spruce forests.
Both our theoretical model and the logistic regression analyses resulted in similar snag quantities for predicted woodpecker occurrence. For management purposes, we recommend the observation of the precautionary principle by striving for target values of 1.6 m^2 ha^{-1} (basal area) or 18 m^3 ha^{-1} (volume) or 14 (dbh ≥ 21 cm) snags per hectare in an area of 100 ha, corresponding to a probability of ≥ 0.9 for woodpecker occurrence in both approaches. Maintaining or achieving such optimal snag levels allows the local persistence of three-toed woodpeckers in forest patches and may serve to define strategies for the maintenance of local populations.

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The conservation of biodiversity has become one of the key goals of sustainable forest management (Lindenmayer et al. 2000). At a certain level of forest management intensity, the lack of habitat components causes once naturally occurring species to decline to the level where they risk extinction. Habitat destruction and degradation is currently considered as the major cause of species extinction (e.g., Tilman et al. 1994, Dobson et al. 1997, Fahrig

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2001). In Switzerland, for example, in addition to selective logging of large trees, diseased and dead trees are often systematically removed for sanitary reasons by means of salvage cutting (Guby and Dobbertin 1996) causing a lack of habitats and resources for species that depend on dead wood. Quantitative target values may be derived from reference systems, such as naturally dynamic forests, with the aim of restoring dead wood and other important habitat components in managed forests. However, none or very few natural forests remain in most parts of Europe. Also, the amount of dead wood in natural forests may be so extensive – up to 30% of dead stems (Linder et al. 1997) or 25% of above ground biomass (Siitonen 2001, Nilsson et al. 2002, Bobiec in press) – that such targets would be incompatible with the economic objectives of multifunctional forestry. Another approach involves the quantification of the ecological preferences of species of special interest and derivation of quantitative target values for use in management (Simberloff 1995, With and Crist 1995, Fahrig 2001). One difficulty here, however, is the definition of species of special interest and justification of their role as biodiversity surrogates (Thompson and Angelstam 1999). The use of the keystone, indicator, focal and umbrella species concepts (Pearson 1994, Lambeck 1997, Simberloff 1998, Fleishman et al. 2000) for management considerations is currently increasing, in spite of many remaining scientific uncertainties in relation to certain species being appropriate proxies for others (Lindenmayer et al. 2000).

Among vertebrates, woodpeckers are of special importance due to their key role in supplying forests with tree-cavities, serving secondary users as nesting or roosting holes (Saari and Mikusiński 1996). In terms of their ecological requirements, woodpeckers are considered as being the most demanding guild among resident bird species (Angelstam 1990, Mikusiński and Angelstam 1997). The occurrence of several species of woodpeckers is indicative of the properties of naturally dynamic forests (e.g. old trees, dead wood, structural diversity) (Mikusiński and Angelstam 1997). The three-toed woodpecker *Picoides tridactylus*, in particular, has recently been proposed as a keystone species (Imbeau 2001) and a possible indicator of high biodiversity, i.e. old trees and large dead trees (Mikusiński et al. 2001, Nilsson et al. 2001).

One of the most important habitat features for three-toed woodpeckers are large, standing dying and recently dead trees (Hogstad 1970, Hess 1983, Pechacek 1995, Murphy and Lehnhausen 1998, Ruge et al. 1999b). Such dead wood pieces are the rarest of the diverse dead wood substrata, especially in managed forests (Green and Peterken 1997, Fridman and Walheim 2000). They still have a certain economic value and may, therefore, be cut when timber is harvested. Ecological studies on dead wood have demonstrated the prime importance of large diameters and standing compared to lying dead trees (Samuelsson et al. 1994). They provide habitats and resources for numerous threatened animal, plant and fungal species (Thomas 1979, Utschick 1991, Morrison and Raphael 1993, Samuelsson et al. 1994, Smith 1997, Jonsson and Kruys 2001). Recently, dead wood has been proposed as a new indicator of forest biodiversity to be approved by the Fourth Ministerial Conference on the Protection of Forests in Europe in 2003 (<www.minconf-forests.net> 29 April 2002). Dead wood also figures in modern certification standards for best forestry practices, as defined, for example, by the Forest Stewardship Council (FSC). With its requirement of forests with relatively high dead wood amounts (Derleth et al. 2000) and demonstration of threshold responses related to dead wood (Bütler et al. unpubl.), the three-toed woodpecker is directly linked with the structure-based biodiversity indicator "dead wood".

In spite of the growing agreement between conservation biologists, forest managers and political circles on the importance of dying and dead trees, the few existing quantitative dead wood management targets for European forests often lack well-founded scientific bases. Without sound quantitative targets, however, the achievement of management goals and progress towards sustainable forestry cannot be assessed. Due to its specific requirements for standing dying and dead trees (defined as snags), and due to its qualities as a keystone species and biodiversity indicator, the three-toed woodpecker was used in this study to define quantitative snag target values for sustainable management of spruce forests. The aims of this paper are: 1) to develop and validate a theoretical model based on the energy budgets of the three-toed woodpecker, thus predicting the spatial densities of snags required to meet this woodpecker's energy requirements; 2) to test these predictions by carrying out a subsequent field study and 3) to derive quantitative management recommendations through the definition of snag target values.

Methods

The probability of presence of the three-toed woodpecker *Picoides tridactylus* was predicted as a function of the snag density (SNAG) by developing a simple model based on the energy requirements of the three-toed woodpecker, and on different assumptions with respect to food selection and prey availability. After a sensitivity analysis, this theoretical model was validated on ten study sites in Switzerland. In order to verify the model predictions concerning snags, a field study, aimed at measuring the quantities of snags actually available in sites where three-toed woodpeckers do and do not breed, was subsequently carried out at 24 sites. A logistic regression analysis on the "presence – absence" data in these sites also resulted in a prediction of the probability of woodpecker presence as a function of the snag density. Through comparison of both probability predictions, quantitative snag target values were then derived for this woodpecker species.

The bioenergetic model

The basic idea behind our model is that a three-toed woodpecker breeding pair has to find sufficient energy sources within its home-range so as to fuel all its activities over the course of one year (reproduction, moulting, overwintering etc). According to Glutz von Blotzheim (1994), the mean reproduction of a successfully breeding pair is 1.8 young birds. Such a bird group (2 adults and 1.8 young) is defined as a family. Thus, we included in our model the energy needs of the young birds over 14 weeks, after which they are supposed to leave the home-range definitely. Following Hess (1983) we defined the number per area unit of foraging trees as the most important habitat feature, while regarding the availability of trees for nesting, drumming etc as not being limiting factors. For practical management considerations, the density of all snags, and not only potential foraging trees, was defined as key variable in the model (Fig. 1). As an insectivorous bird, the three-toed woodpecker gains its energy through insect predation. According to the literature, bark beetles (above all *Ips typographus*) were considered as the most important energy source (Hutchinson 1951 in Baldwin 1968, Hogstad 1970, Sevastjanow 1959 in Scherzinger 1982, Hess 1983, Pechacek and Kristin 1993, Formosow et al. 1950 in Glutz von Blotzheim 1994). Bark beetles occur only in a certain phase in the gradual change in the properties of a dying and dead tree. Hence, only a given proportion (b) of snags, trees which have still some bark left, are potential foraging trees. Koplin (1972) estimated the daily energy requirements of free-living three-toed woodpeckers by measuring gross energy intake and energy in excrement. In his model, the energetic requirement is a function of air temperature, considered as the most important metabolic factor. This model served as basis for the estimation of the yearly energy requirements of woodpeckers in our model, defined as the number of consumed prey during one year (CPR). As a substitute for lacking data on movements and energy expenditure by woodpeckers, we used the potential home-range size (PHR), defined as a home-range within a minimum and maximum size, facilitating the viability of the woodpecker family. The size range was based on home-range sizes reported in the literature.

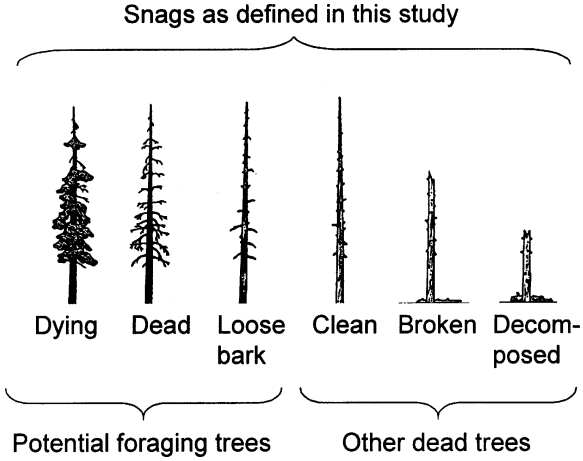


Fig. 1. Definition of snags and potential foraging trees for the three-toed woodpecker, as used in this study. Modified from Thomas (1979).

The available prey number (APR) of the most important energy source, i.e. bark beetles, was estimated on the basis of reproduction and mortality rates from the literature (cf. variable estimation). Since bark beetles live beneath the tree bark, the mean bark area infested by beetles (MIA) was a further variable included in the model. Finally, we defined the woodpecker's foraging efficiency (FEF) as a variable that takes into account a certain loss of prey during foraging. Indeed, even when virtually scaling the bark of a foraging tree, the woodpecker will not capture all available prey items, since bark chips that fall to the ground may contain undetected items. In addition, other insectivores may consume bark-living insects.

Based on the above considerations, the snag density needed to meet the woodpecker's energy requirements can be estimated by calculating:

$$SNAG_{21} = \frac{CPR}{b \times PHR \times APR \times MIA \times FEF} \quad (1)$$

where: $SNAG_{21}$ = density of snags with a diameter at 1.3 m (dbh) ≥ 21 cm (cf. validation of the bioenergetic model) required to meet the annual energy requirements of a woodpecker family [snags × ha^{-1}], CPR = bark beetle prey consumed in the course of one year by a woodpecker family [consumed beetles × yr^{-1}], PHR = potential home-range size of a woodpecker breeding pair [ha], APR = available prey over one year per square meter of bark on potential foraging trees in the woodpecker's home-range area [available beetles × m^{-2} × yr^{-1}], MIA = mean infested bark area of a potential foraging tree [m^2 × foraging $tree^{-1}$], FEF = foraging efficiency of an adult woodpecker [consumed beetles × available $beetles^{-1}$], b = proportion of potential foraging trees to all snags [foraging trees × $snags^{-1}$].

Since a woodpecker breeding pair consists of two adult birds and is supposed to produce 1.8 young birds annually, CPR is further defined by

$$CPR = 2 \times CPR_a + 1.8 \times CPR_y \quad (2)$$

where: CPR_a = bark beetle prey consumed over one year by 1 adult woodpecker, CPR_y = bark beetle prey consumed over 14 weeks by 1 young bird.

CPR_a is further defined by

$$CPR_a = \sum_{i=1}^{12} 30 \times \frac{GEI(T_i)}{e} \times p_a \quad (3)$$

where: GEI = gross energy intake in Joule per day = (51.46 – 0.67 × T_i) × 4185 J, according to Koplin (1972), T_i = mean monthly temperature in °C, e = energy content in

Joule of 1 bark beetle item, p_a = proportion of bark beetles in the diet of an adult woodpecker.

CPR_y is further defined by

$$CPR_y = \sum_{j=1}^{14} 7 \times \frac{BW(j) \times p_y(j) \times p(BW)}{w_f} \quad (4)$$

where: BW(j) = body weight in week j (g), p_y (j) = proportion of bark beetles in the diet of a young bird in week j, p(BW) = proportion of body weight a young bird is eating per day, w_f = fresh weight of a bark beetle larva or adult (g).

APR is further defined by

$$APR = \frac{1}{52} \times a \times n_a \times \sum_{j=1}^{52} 1 - m(j) \quad (5)$$

where: a = bark beetle attack density, i.e. the number of nuptial chambers per square meter of bark (m^{-2}), n_a = mean number of eggs per nuptial chamber, m(j) = cumulative mortality rate of eggs, larvae, pupae, imagos, immature and adult beetles in week j.

Variable estimation

CPR

In order to estimate the consumed prey CPR we assumed a moisture content of 70% for *Ips typographus* larvae or adults (Bell 1990), a mean caloric content of 83.7 J for one item (Koplin 1972, Barbault 1997) and a dry weight w_d of 0.0041 g (Wermelinger pers. comm.) and, thus, fresh weight $w_f = w_d/0.3$. Following Koplin's GEI-model, at 0°C an adult woodpecker was supposed to consume prey whose fresh weight represents ca 0.5 times the woodpecker's body weight. Based on the consideration of the data available on bird digestion (Karasov 1990) and energy requirements for different bird sizes (Kendeigh 1970), this appeared to be a realistic winter daily diet for an insectivorous bird. The proportion of bark beetles in the diet of an adult woodpecker p_a was assumed to be 0.75 (Hutchinson 1951 in Baldwin 1968, Hogstad 1970, Sevastjanow 1959 in Scherzinger 1982, Hess 1983, Pechacek and Kristin 1993, Formosow et al. 1950 in Glutz von Blotzheim 1994).

The body weight in week j BW(j) of young woodpeckers was estimated according to the growth curve of Pechacek and Kristin (1996), in which the body weight is 20 g in the first week, 50 g in the second week and 65 g from the third week on. Since the nestlings' growth is fast and the energy cost of growth is high, and considering data for other bird species (Westerterp 1973), we assumed that a young bird consumes 0.7 times its body weight per day. The proportion of bark beetles in the diet of a young bird in week j p_y(j) was defined as 5.8% during weeks 1–3 (Pechacek and Kristin 1996), 10% in week 4, 20% in week 5, 30% in week 6, 50% in week 7 and 75% from week 8 on.

Based on the above assumptions and on mean monthly temperatures T_i between –6 and +12°C, the estimated CPR varied between 1.605×10^6 and 1.623×10^6 bark beetle items per year (Table 1). Its probability distribution was assumed to be uniform (cf. Monte Carlo simulation).

PHR

The potential home-range size PHR was assumed to vary uniformly between 44 and 176 ha, corresponding to the maximum and minimum home-range size reported in the literature for *Picoides tridactylus alpinus* (Bürkli et al. 1975, Scherzinger 1982, Hess 1983, Pechacek 1995, Dorka 1996, Pechacek et al. 1999, Ruge et al. 1999b).

APR

The breeding density of *Ips typographus* is highly variable within a tree, among trees and at different bark beetle population levels (endemic to epidemic). Our estimation was based on data for endemic (no outbreak) population levels in natural sub-Alpine spruce forests. Only one beetle generation per season was expected and the egg laying was set to the second week of June (Nierhaus-Wunderwald 1995). With an attack density (a) of 150 nuptial chambers m^{-2} (Weslien and Regnander 1990) we expected an average n_a of 27 eggs per nuptial chamber (Thalenhorst 1958). The duration of the development cycle was defined as 3 weeks for eggs, 3 weeks for larval stage and 6 weeks for pupal and imago stage. The mortality rate m(j) in week j was expected to be linear during each development stage and to reach

Table 1. Probability distribution functions defined for the variables in the bioenergetic model used to estimate the density of dying and dead trees required to meet the three-toed woodpecker's energy needs.

Variable [unit]	Type of distribution	x_{min}/x_{max}	μ/σ [1)]	x_a/x_b [2)]
PHR [ha]	uniform	44/176		
APR [m^{-2}]	normal		657/±216	234/1080
FEF [percent]	normal		0.50/±0.13	0.25/0.75
MIA [m^2]	normal		12.5/±3.8	5/20
CPR [number]	uniform	$1.605 \times 10^6/1.623 \times 10^6$		

[1)] μ = mean; σ = standard deviation.
[2)] $P(x_a < Z < x_b) = 0.95$.

25% of the initial population in week 3, 70% in week 6 and 85% in week 12 (Thalenhorst 1958, Balazy 1968). During the 40 weeks of maturate feeding, hibernating, flight and invasion on new trees, another linear mortality of 50% of the individuals that reached full development was expected.

Based on the above assumptions, we estimated the APR as 657 ± 216 (mean ± SD) and normally distributed within x_a = 234 and x_b = 1080 ($Pr(x_a < Z < x_b) = 0.95$); cf. Monte Carlo simulation.

MIA

Very little data exists on the proportion of spruce tree bark area, MIA, infested by *Ips typographus*. Gonzalez et al. (1996) reported a MIA of 21 m^2 for spruce trees with a mean dbh of 46 cm for an endemic population level. Weslien (1990) indicated attacks of 50% of the tree height for spruce trees with a mean dbh of 30 cm.

Based on Gonzalez et al. (1996) and Weslien and Regnander (1990) and our own data on the diameter frequency distributions of spruce trees (Bütler unpubl.), we estimated the MIA as 12.5 ± 3.8 m^2 (mean ± SD) and normally distributed within x_a = 5 and x_b = 20 ($Pr(x_a < Z < x_b) = 0.95$); cf. Monte Carlo simulation.

FEF

Capture rates of insect prey vary seasonally, mainly in relation to weather (Wolda 1990). No data was found on the foraging efficiency of bark beetle predation by woodpeckers. Bark chips removed by the woodpecker fall to the ground and may contain bark beetle items that are not consumed. Based on Baldwin (1968), we estimated the FEF as normally distributed with 0.50 ± 0.13 (mean ± SD) within x_a = 0.25 and x_b = 0.75 ($Pr(x_a < Z < x_b) = 0.95$); cf. Monte Carlo simulation.

b

The proportion of potential foraging trees to all snags (b) was determined by field measurements of randomly selected snags (N = 1392) at six study sites (Bütler unpubl.). The decomposition stage of each tree was determined using the method described in Thomas (1979). Only trees with the decomposition stages "dying", "dead" and "loose bark" were considered as potential foraging trees (Fig. 1). As we observed small variations of b between the six study sites, we defined it as a constant (b = 0.8).

Monte Carlo simulation and sensitivity analysis

The input variables (CPR, PHR, APR, MIA and FEF) do not have one determined value, but are defined as independent random variables. In order to calculate the outcome variable $SNAG_{21}$, we undertook a random experiment by means of ten Monte Carlo simulations, based on a sample size of N = 10 000 for each input variable. The variables PHR and CPR were supposed to have a uniform probability distribution. The largest and smallest home-range sizes reported in the literature for European three-toed woodpeckers were used to define the upper and lower limits x_{max} and x_{min} for PHR (Bürkli et al. 1975, Scherzinger 1982, Hess 1983, Pechacek 1995, Dorka 1996, Pechacek et al. 1999, Ruge et al. 1999a). For *CPR*, the definition of x_{max}/x_{min} was based on lowest/highest monthly mean temperatures within the range of the three-toed woodpecker's geographic distribution. We assumed a normal distribution for the variables APR, MIA and FEF. The mean values of the variables related to bark beetle infestation (APR, MIA) corresponded to an endemic bark beetle population level (cf. Table 1). Ecologically relevant limits x_a and x_b were chosen in such a way as to obtain 95% of the values within those limits, and the corresponding standard deviations were then calculated. Finally, we plotted the probability density function of the simulated output random variable $SNAG_{21}$ and its cumulative distribution function.

The parameter estimation of the input variables (x_{min}, x_{max}, x_a, x_b, mean and standard deviation) for the model variables is subject to uncertainties. A sensitivity analysis changing each variable in turn by ± 20% revealed the extent of changes of the predicted SNAG-value. A simultaneous change of ± 20% for all variables was undertaken to demonstrate an extreme situation.

Validation of the bioenergetic model

The bioenergetic model was validated at 10 study sites in Switzerland, where the three-toed woodpecker was present (n = 6) and absent (n = 4), respectively. Woodpecker presence was determined by visual and aural detection and fresh foraging signs. All of the study sites were dominated by sub-Alpine spruce forests and the surveyed areas varied between 0.6 and 3.0 km^2. The snags were measured at each site using a recently developed method that is further described elsewhere (Bütler and Schlaepfer unpubl.). This method quantifies snags by coupling remote sensing techniques with a Geographic Information System. The dbh of snags that can be quantified by this method is ≥ 21 cm. With the model eq. (1), and with the defined probability distribution functions as input values (Table 1), the p-value (probability of woodpecker presence) associated to each measured $SNAG_{21}$-value was then calculated and compared with information on the presence/absence of the woodpecker.

Study sites and design for the empirical model

The field study was conducted between 1998 and 2001 at 24 sites located in Switzerland in the eastern/central and

western Pre-Alps and in the Jura Mountains. Regional pairs of field plots of 1 km^2 in size were selected (2 × 12 units). Each pair of plots consisted of one plot where the three-toed woodpecker was present during the breeding season of the study years (referred to as "presence") and one where it has never been observed (referred to as "absence"). Breeding was proven for three plots, whereas it was probable for the others, according to the definition in the International Ornithological Atlases (Sharrock 1973). The selection of presence/absence field plots was based on data provided by the Swiss ornithological station of Sempach (cf. Schmid et al. 1998) and local bird watchers in Switzerland, and was subject to the following criteria: a) spruce tree dominated forests; b) the majority of the forest stands > 100 yr old, i.e. mature to over-mature, the stand age preferred by three-toed woodpeckers; c) between 1200 and 1700 m a.s.l., where the probability of three-toed woodpecker occurrence is highest (cf. Schmid et al. 1998).

In each field plot, a 4 × 4 sampling grid was established, with sampling points 250 m apart.

Data gathering and statistical analysis

Data was collected by fieldwork at the sampling points using angle relascope, clinometer and compass. The minimal inventory diameter for snags was 10 cm dbh ($SNAG_{10}$) and their minimum height 6 m. The number of trees being wider than the gap in the relascope at each point represented the basal area (i.e. the area of the cross section of a tree stem at 1.3 m inclusive of bark; m^2 ha^{-1}) of the forest at the sampling point.

For statistical analyses we used the STATISTICA 6.0 software package. The mean basal area of $SNAG_{10}$ at the sampling points was calculated for each field plot. The plots were then separated into two groups ("presence" and "absence") and group means and ranges were calculated. We checked for between-group differences by calculating t-statistics. Logistic regression (Hosmer and Lemeshow 1989) was chosen as the appropriate method to predict the probability of the presence or absence (coded as 1 and 0) of three-toed woodpeckers as a function of the $SNAG_{10}$-densities.

Results

The bioenergetic model and its validation

The simulated model solution predicted a probability of <50% for presence of the three-toed woodpecker, if the density of standing $SNAG_{21}$ (dbh ≥ 21 cm) is less than five trees per hectare (Fig. 2). For densities rising from five to fourteen trees, the expected probability increased from 50 to 90%.

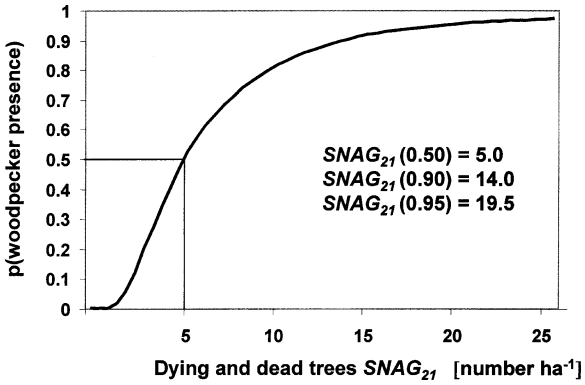


Fig. 2. Simulated solution of the bioenergetic model predicting the probability of three-toed woodpecker presence as a function of the density of dying and dead trees with a dbh ≥ 21 cm.

The results of the sensitivity analysis (Table 2) show the deviation of the $SNAG_{21}$-values (for p(woodpecker presence) = 0.5) due to changes of ± 20%, in turn, of each input variable. The original $SNAG_{21}$-value (p = 0.5) was 5.0. Deviations of the output $SNAG_{21}$-value varied between –0.9 and +1.5. For example, changing the number of consumed prey CPR by + 20% (i.e. assuming lower air temperatures), increased the required $SNAG_{21}$-density from 5.0 to 6.2 trees ha^{-1}. Positive shifts in $SNAG_{21}$-values were always larger than negative shifts.

The validation of the model resulted in predicted probabilities of three-toed woodpecker presence ≥ 0.2 for sites where the species was actually present and $p < 0.05$ for those where it was absent (Table 3).

Results of the empirical model

The mean basal area of $SNAG_{10}$ showed significant differences between the one km^2 field plots with and without woodpeckers. For "presence" plots we obtained 2.3 (0.6–6.0) m^2 ha^{-1} (mean; range) and for "absence" plots 0.4 (0.0–0.8) m^2 ha^{-1} (DF = 22, t = 4.37, p = 0.0002).

Indeed, the probability of woodpecker presence increased significantly with $SNAG_{10}$ (Fig. 3; $\chi^2 = 25.04$, $p < 0.000$, DF = 1). In this empirical model the probability of three-toed woodpecker presence increased from 0.10 to 0.95 when the basal area of $SNAG_{10}$ rose from 0.6 to 1.3 m^2 ha^{-1}.

Comparison of the bioenergetic with the empirical model

In order to compare the results of the bioenergetic model with those of the field study, a data transformation was necessary, since both the measurement units and minimum dbh for snags differed. For this transformation we

Table 2. Sensitivity analysis for the output value of the bioenergetic model: changes in predicted $SNAG_{21}$-values for p(woodpecker presence) = 0.5 after 20% changes of input variables.

Changed variable	New $SNAG_{21}$ [*)] (+Δ)	New $SNAG_{21}$ (–Δ)	Deviation [x)]
CPR	6.2	4.1	–0.9 to +1.2
PHR	4.3	6.5	–0.7 to +1.5
APR	4.2	6.4	–0.8 to +1.4
MIA	4.3	6.5	–0.7 to +1.5
FEF	4.2	6.5	–0.8 to +1.5
CPR, PHR, APR, MIA, FEF	2.9	10.3	–2.1 to +5.3

[*)] Original $SNAG_{21}$-value for p(woodpecker presence) = 0.5 was 5.0.
[x)] Deviation is the change in predicted upper and lower limits for the $SNAG_{21}$-value.

used an experimental curve of tree diameter distributions from field data from six study sites (Bütler unpubl.; Fig. 4). The predicted $SNAG_{21}$-value, given as tree density ($n\ ha^{-1}_{\geq 21\ cm}$), was translated into stand basal area ($m^2\ ha^{-1}_{\geq 10\ cm}$) in two steps:

$$1)\quad \left[n\ ha^{-1}{}_{\geq 21\ cm}\right] \times TBA_{\overline{dbh}} = \left[m^2\ ha^{-1}{}_{\geq 21\ cm}\right]$$

with: TBA = tree basal area [m^2] = $(0.5\ dbh)^2 \times \pi$, $TBA_{\overline{dbh}}$ = tree basal area of the mean-sized tree with a dbh ≥ 21 cm.

$$2)\quad \left[m^2\ ha^{-1}{}_{\geq 21\ cm}\right] \times \frac{1}{p_{\geq 21\ cm}} = \left[m^2\ ha^{-1}{}_{\geq 10\ cm}\right]$$

with: $p_{\geq 21}$ = proportion of total basal area of trees with a dbh ≥ 21 cm. The mean-sized tree with a dbh ≥ 21 cm was 33.5 ± 12.1 cm (mean ± standard deviation; N = 485), corresponding to a $TBA_{\overline{dbh}}$ of 0.09 m^2. The resulting $p_{\geq 21}$ was 0.77.

Figure 5 and Table 4 show the direct comparison between the solution of the bioenergetic model and the results of the logistic regression. Both probability functions lie close together, in particular for p(woodpecker presence) between 0.7 and 0.8. A $SNAG_{10}$-density of < 0.6 $m^2\ ha^{-1}$, i.e. p(woodpecker presence) < 0.5 in both, theoretical modelling and empirical field approaches, is considered as unfavourable for the woodpecker, whereas a density in excess of 0.9 $m^2\ ha^{-1}$, i.e. p(woodpecker presence) > 0.5 in both approaches, is considered as favourable.

Discussion

In North America, some land-management agencies have defined standards requiring the retention of specified numbers and kinds of snags to provide habitats for wildlife. For ponderosa pine *Pinus ponderosa* and mixed-conifer

Table 3. Validation of the bioenergetic model for 10 study sites. The $SNAG_{21}$-value was measured for each study site and the associated p-value calculated with the bioenergetic model equation and the defined probability distribution functions (Table 1) as input values.

	$SNAG_{21}$ [$n\ ha^{-1}$] [*)]	P(woodpecker) [x)]
Site with three-toed woodpecker		
Hobacher	7.1	0.7
Hinteregg	11.2	0.8
Bärenegg	10.7	0.8
Hinterberg	2.9	0.2
Bois des Fayes	4.5	0.4
Bödmeren	3.4	0.3
Site without three-toed woodpecker		
Langenegg	1.5	< 0.02
Mont Pelé	1.9	< 0.05
Schraewald	1.2	< 0.01
Les Arses	0.8	< 0.01

[*)] measured $SNAG_{21}$-value.
[x)] predicted probability of three-toed woodpecker presence by the bioenergetic model.

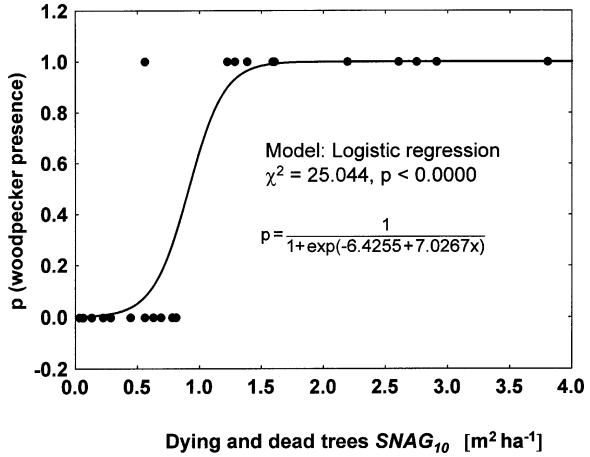


Fig. 3. Logistic regression model showing a significant relationship between the stand basal area of dying and dead trees and the probability of three-toed woodpecker presence.

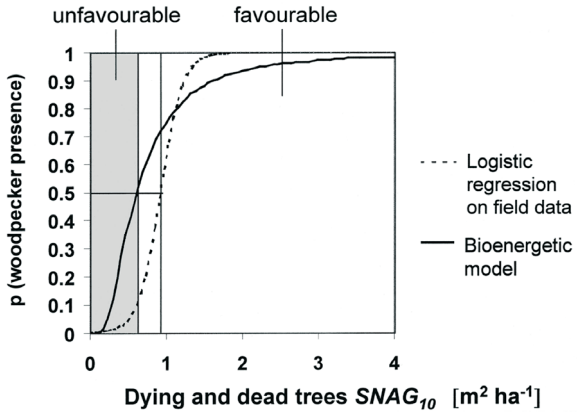


Fig. 5. Comparison of the solution of the bioenergetic model and the regression results of the empirical model. Predicted probability of woodpecker presence as a function of the stand basal area (m^2 ha^{-1}) of dying and dead trees with a dbh ≥ 10 cm.

forests, for example, US Forest Service recommendations call for retention of 4.9 and 7.4 snags ha^{-1} with a minimum dbh of 46 cm and minimum height of 9 m (Ganey 1999). This author demonstrated, however, that these snag standards were seldom met even in unlogged forests and concluded that current standards may be unrealistic and should be reconsidered. One reason is that no solid scientific basis was provided for the recommended snag densities, thus highlighting the great need for additional work in these areas. The lack of scientific bases would also appear evident for European forest standards, as illustrated for example by the English national initiative of the Forest Stewardship Council (FSC): "Due to lack of scientific evidence it is not possible at present to give precise guidance on the amount, distribution and composition of dead wood that is appropriate to the individual site" (Anon. 1999). Several national FSC initiatives (e.g. Sweden, Germany, Switzerland) therefore provide only vague qualitative dead wood recommendations, such as "standing dead wood should be created" or "in general, forest owners should maintain some dead trees in a stand". The conclusions of numerous scientific papers emphasising the ecological importance of dead wood only seldom suggest quantitative recommendations (Table 5). Being careful, they remain generally qualitative: "There is a need to increase the input of large dead trees" (Kruys et al. 1999); "It is important to maintain standing dead trees, wherever possible, during harvesting and renewal operations" (Greif and Archibold 2000); "Leave as many large standing dead trees at harvest as possible" (Mccarthy and Bailey 1994).

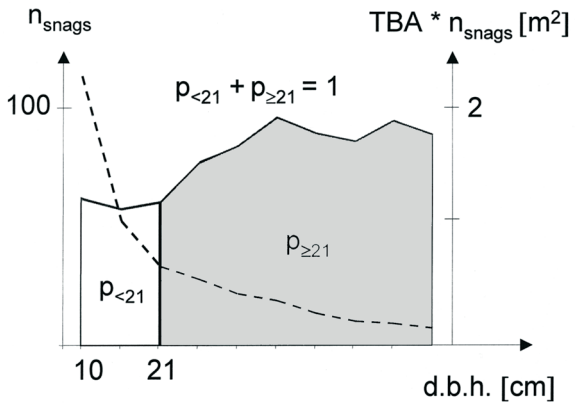


Fig. 4. Experimental determination of the proportion of the total tree basal area for snags with a dbh ≥ 21 cm and < 21 cm, respectively. Number of snags (n_{snags}) – the broken line – on the left axis and tree basal area multiplied with n_{snags} (TBA × n_{snags}) on the right axis. See text for details.

Quantitative recommendations, however, are essential as operational management goals. Without quantitative targets neither the verification of the progress towards sustainable forest management nor a sound adaptive management is possible. Sippola et al. (1998) argue that quantitative recommendations are too rigid to imitate the variation occurring in natural forests. For example, whereas 5 m^3 ha^{-1} of dead wood may be enough for some species, it would, however, always be too little for other species. The patchy distribution of snags observed in numerous studies argues against the application of uniform targets for snag retention across the landscape (Ganey 1999, Meyer 1999). Thus, in accordance with Sippola et al. (1998) and Ganey (1999), we suggest that a more reasonable goal might be to maintain high snag densities across portions of the landscape, while allowing a smaller than average investment in other areas. Hence quantitative recommendations should be associated with a distribution of the values representing species with different quantitative requirements. In this way the specialised species' requirement regarding the local resource density within the home-range size of a breeding pair could be satisfied even if the recommended mean is considerably lower. Mikusiński et al. (2001) showed that the presence of three-toed woodpeckers was strongly asso-

Table 4. Necessary amounts of standing dying and dead trees required for predicted probabilities of the three-toed woodpecker presence. Comparison between the bioenergetic model results and the results of the logistic regression on field data.

p(woodpecker presence)	Results	$SNAG_{10}$ •) [m^2 ha^{-1}]	$SNAG_{10}$ [m^3 ha^{-1}] *)	$SNAG_{21}$ +) [n ha^{-1}]
0.50	SNAG-model	0.6	7	5.0
	Logistic regr.	0.9	10	
0.75	SNAG-model	1.0	12	8.5
	Logistic regr.	1.0	12	
0.90	SNAG-model	1.6	18	14.0
	Logistic regr.	1.2	14	
0.95	SNAG-model	2.2	25	19.5
	Logistic regr.	1.3	16	

•) $SNAG_{10}$: standing dying and dead trees with a dbh ≥ 10 cm.
*) approximate volume calculated with (stand basal area × tree height × shape index) according to Lindroth (1995).
+) $SNAG_{21}$: standing dying and dead trees with a dbh ≥ 21 cm.

ciated with the presence of other forest bird species. Consequently, in spite of remaining uncertainties and an awareness that quantitative targets will never obtain the full endorsement of the various scientific, political and practical management viewpoints, in this paper we still propose provisional snag target values for the maintenance of biodiversity in spruce forests at the stand scale.

Limitations and further development of the bioenergetic model

The model presented in this paper was based on literature data for bark beetle breeding density, infested tree bark area and woodpecker home-range sizes. Our assumption about the preferred diet of the woodpecker as consisting mainly of bark beetles, i.e. *Ips typographus*, is a simplified view of a real diet that might be much more diverse, especially in the case of endemic bark beetle population levels. Since most studies on woodpecker diets have been conducted during bark beetle outbreak conditions, however, only very little data is currently available on diet components other than bark beetles.

Another point to discuss is the validity of Koplin's (1972) model for the gross energy intake that served as the input for our bioenergetic model. According to Blem (2000), the metabolised energy and the consequent food requirements of birds vary in relation to a complex number of factors, including body size, level of reproductive, digestive and physical activity, phase of moult cycle, radiation, air temperature, wind etc. Koplin's model, considering only air temperature as the most important metabolic factor, is hence a simplified way to calculate energetic requirements. In addition, Koplin developed it for American three-toed woodpeckers and not for European populations. Different energy requirements between woodpecker subspecies cannot be excluded, even if no data is available on this question.

Our model is based on the assumption that three-toed woodpeckers are completely resident in winter and do not leave their breeding home-range during a whole year. While this hypothesis is true for the Alpine subspecies *Picoides tridactylus alpinus* (Glutz von Blotzheim 1994), the nominate subspecies *Picoides tridactylus tridactylus* may undertake a partial migration to winter territories (Hogstad 1970). However, the size of measured winter feeding territories (5.5–8 ha in Hogstad 1970) is so much smaller than breeding home-ranges that the assumption of "all energy sources within the home-range" seems to be acceptable for the nominate subspecies also.

Our model exhibits an asymptotic curve (Figs 2 and 5), suggesting an increase, even if diminishing, of the probability of woodpecker presence with increasing availability of snags. Raphael and White (1984) found that the density of all cavity nesting birds in the Sierra Nevada increased with the density of large snags (> 38 cm dbh) until reaching a snag density of ca 7.5 ha^{-1}. Above this snag density level, bird densities were evidently limited by other factors. Considering these findings, we believe that there is an upper limit of snag density favouring woodpecker presence. Therefore, our model should not be over-interpreted at the upper end. We suggest that it should not be used where the p-value for occurrence is >> 0.95.

Snag targets for the three-toed woodpecker

Our two approaches, undertaken in order to define quantitative snag target values based on three-toed woodpecker habitat preferences, were different. The bioenergetic model was mainly based on theoretical considerations, and its validation performed by a method using remote sensing techniques, i.e. aerial photo interpretation and Geographic Information System (Bütler and Schlaepfer unpubl.). Because of the limitations of these techniques, the results produced involved densities of snags with a minimum dbh of

Table 5. Amounts of dead trees in European sub-Alpine spruce forests a) and recommended quantitative values for standing dead trees in North American and European forests b).

a)	Stand age [yr]	Standing dead trees [m^3 ha^{-1}] Mean (range)	Total lying and standing dead trees [m^3 ha^{-1}] Mean (range)	Authors
Managed forests				
Switzerland		0.0–4.2	3.9–25.8	Guby and Dobbertin (1996)
Switzerland	> 100	12	19	Derleth et al. (2000)
Switzerland	all age classes	9	16	Brassel and Brändli (1999)
Unmanaged forests				
Germany	140–260	28	84 (10–180)	Rauh and Schmitt (1991)
Germany	old		20–60	Utschick (1991)
Poland	all age classes	59	131	Holeksa (2001)
Slovakia	all age classes		80–273	Korpel (1995)
Slovakia	all age classes		42	Korpel (1995)
Slovakia	all age classes		80–220	Korpel (1995)
Switzerland	> 100	32	63	Derleth et al. (2000)

b)	Recommendation	Managed organism	Authors
North America			
California	1 clump per 2 ha of 15 snags > 23 cm dbh	Cavity-nesting birds	Raphael and White (1984)
Oregon	0.35 sound snags > 51 cm dbh ha^{-1}	Pileated woodpecker	Bull and Meslow (1977)
Oregon	≥ 8 snags ha^{-1}	Pileated woodpecker	Bull and Holthausen (1993)
Oregon	≥ 14 snags ha^{-1}	Cavity-nesting birds	Schreiber and Decalesta (1992)
Washington	6 hard and 3 soft snags ha^{-1}	Cavity-nesting birds	Zarnowitz and Manuwal (1985)
Europe			
Germany	≥ 2.5–5 m^3 ha^{-1} (medium term) ≥ 7.5–15 m^3 ha^{-1} (long term)		Ammer (1991)
Germany	5–10 m^3 ha^{-1}, i.e. 1–2% of stems (target value); 20–60 m^3 ha^{-1}, i.e. 5–10% of stems (optimal value)	Birds	Utschick (1991)
Sweden	> 10 snags ha^{-1}	Lesser spotted woodp.	Olsson et al. (1992)
United Kingdom	11–50 snags ha^{-1}, all dbh (medium target); > 50 snags ha^{-1}, all dbh (high target)		Kirby et al. (1998)

21 cm (i.e. numbers of trees ha^{-1}). In contrast, the empirical model started from field measurements executed with the angle relascope technique and resulted in stand basal areas of snags with a minimum dbh of 10 cm (i.e. m^2 ha^{-1}). Due to the different measurement units and a different minimum dbh obtained by each approach, a transformation from n ha^{-1} to m^2 ha^{-1} was necessary for comparison purposes (Fig. 4). In spite of the different approaches, the predicted amounts of required snags were similar at a 70–80% probability of woodpecker presence (Fig. 5, Table 4). This fact allows us to strengthen the reliability of the derived snag targets.

We considered a basal area higher than 0.9 m^2 ha^{-1} (p(woodpecker presence) > 0.5 in both approaches) as favourable for the woodpecker. However, in order to maximise the probability of local woodpecker presence and following the precautionary principle, for management purposes we suggest a higher snag target value. For the last ten years, Swiss three-toed woodpecker populations have been stable or even increasing (Schmid et al. 1998). Among the possible reasons for population growth figures the underexploitation of marginal mountain forests since the Second World War (Derleth et al. 2000), which is related to a rapid increase in timber harvesting costs (Brassel and Brändli 1999). In such conditions, the amount of dying and dead trees and the available food resources are likely to increase. A possible economic recovery of the timber market, leading to a harvesting intensification of marginal forests, however, could rapidly cause a reversal of the currently positive trend for the woodpecker population. Such considerations emphasise the usefulness of the precautionary principle. Spruce forests favourable to three-toed woodpecker breed-

ing must contain, among other features, sufficient amounts of dying and dead trees. We recommend the following target values for dying and dead trees: ca 1.6 m^2 ha^{-1} (basal area) or 18 m^3 ha^{-1} (volume) of trees with a dbh ≥ 10 cm, corresponding to 14 standing trees per hectare with a dbh of ≥ 21 cm within an area with a size of an average home-range size (44–176 ha); i.e. corresponding to our sampling area of 100 ha. For such levels, the probability of three-toed woodpecker presence in our study was ≥ 0.9. As demonstrated in Fig. 4, large snags are generally rare in managed forests (main mortality of small trees by stem exclusion processes), whereas their contribution to the total basal area is substantial. Considering the prime importance of large snags, we would argue that management recommendations either be given as basal area, or, if expressed in n ha^{-1}, should specify the minimum tree diameter, and the area in ha for which this recommendation applies. Density targets without diameter precision and area of application may fail to fulfil the ecological objective they aimed for (Table 5).

Our targets are higher than the dead wood amounts that have been measured in managed Swiss sub-Alpine forests, while they do not reach amounts measured in unmanaged forests (Table 5). Considering mean values for living trees in Swiss forests of 32.3 m^2 ha^{-1} and 354 m^3 ha^{-1} (Brassel and Brändli 1999), the suggested snag target values represent not more than 5% of the living wood stock. We argue that, even in production forests, such a loss in favour of biodiversity should be acceptable.

Our values are of the same order of magnitude as the snag retention recommendations for North American and European forests that are based on cavity-nesting birds or other woodpecker species (Table 5). They are higher than Ammer's (1991) recommendations, which were not, however, based on ecological preferences of birds. Many snag requirements for different woodpecker species are based only on their use of snags as nesting trees (Imbeau and Desrochers 2002). They implicitly assume that snags required for nesting are an important limiting factor to woodpecker populations. Imbeau and Desrochers (2002) argued that such models are highly unlikely to be successful in predicting long-term habitat needs, considering the extensive use of snags for foraging. Unlike these models, our snag retention prescriptions are designed to ensure a continuous supply of foraging trees and go beyond the aim of maintaining a supply of potential nesting trees.

So far quantitative recommendations for forest management have been made mainly for the scales of trees and stands, but rarely for forest management units and landscapes. However, maintenance of viable populations involves the provision of targets at multiple spatial and temporal scales (Larsson 2001, Angelstam et al. 2004). Using area-demanding birds as modelling tools stresses the need for formulating targets at the levels of individuals, populations as well as metapopulations. For Alpine and boreal forests, bird groups such as woodpeckers (e.g., Pechacek and d'Oleire-Oltmanns in press), grouse (e.g., Angelstam et al. 2001) and resident tits (e.g., Jansson and Angelstam 1999) are important focal species to begin with.

Hence, for a species as the three-toed woodpecker, which is dependent on a continuous supply in space and time of snags of a particular quality, there still remains work to be able to formulate targets within the framework of sustainable forestry for the following issues: 1) How far apart can home-range sized areas exceeding the stand scale target be? 2) What proportion of a landscape needs to be in what phase of successional development of snags to maintain a local viable population? 3) Finally, in regions with other forest dynamics than the gap-phase dominated one prevailing in Alpine forests, the large-scale succession after stand-replacing disturbances need to be accounted for.

Conclusion

In this study we presented a model based on energetic needs of three-toed woodpeckers. Although simple, it enabled the quantification of snag requirements for this woodpecker species, which has been corroborated by a field study approach. The results made it possible to identify the snag quantities of local forest patches that are necessary to maximise the probability of local three-toed woodpecker presence. Forest patches presenting optimal quantities may be mapped and integrated into management planning concepts in order to define strategies for the maintenance of local populations of this bird species. Since the three-toed woodpecker is an indicator of forest biodiversity, management aimed at the maintenance of this species will also enable the fulfilment of other biodiversity goals.

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Large woody debris and brown trout in small forest streams – towards targets for assessment and management of riparian landscapes

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Degerman, E., Sers, B., Törnblom, J. and Angelstam, P. 2004. Large woody debris and brown trout in small forest streams – towards targets for assessment and management of riparian landscapes. – Ecol. Bull. 51: 233–239.

Large woody debris (LWD) was quantified in 4382 forest stream sites in Sweden. LWD was present at 73% of the sites, but the amount was low with a median number of 1 piece of LWD 100 m^{-2}. Brown trout was the most frequently occurring fish species and occurred in 82% of the sites. Brown trout occurred more frequently in sites with LWD, and the abundance of trout increased with the amount of LWD up to 8–16 wood pieces 100 m^{-2}. By using quantity of LWD and stream width, brown trout abundance could be partly predicted. The largest trout caught were significantly larger at sites with LWD present, with an average of 188 mm in sites without LWD and 200 mm in sites with LWD. The average size of juvenile fish <1 yr old was 6% lower at sites with >4 pieces of LWD then at sites without LWD. This is suggested to be caused by higher trout densities with increasing amount of LWD, i.e. implying a density-dependent effect on growth.

The relationships between LWD and brown trout suggest that both are useful indicators of intactness and functionality of streams. However, we neither know what the absolute amount of dead wood and trout would be in naturally dynamic riparian landscapes, nor the extent to which brown trout indicates other elements of biodiversity in streams. Our study supports the growing insight that there are complex interactions between terrestrial and aquatic systems. We discuss the need for transdisciplinary landscape scale approaches, such as developing assessment tools for aquatic landscapes in parallel to for example terrestrial gap analyses of habitat structures that maintain biodiversity.

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Lotic and lentic systems are closely connected to the terrestrial environment, which provides resources that are essential to their integrity (Karr and Chu 1999). The aquatic-terrestrial interface itself is a porous filter that allows a flow of organisms, water, and matter in both directions. This interface is often a special habitat with its own unique flora and fauna that contributes significantly to the function of the surrounding landscape. Despite their highly dynamic

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nature, intact riparian landscapes provide predictable ecological conditions at local and landscape scales (Karr 2000). A challenge for the future is to more rigorously quantify links between pattern and process, as well as to investigate the mechanistic relationships between landscape diversity and species diversity (Ward et al. 2002).

The production of fish and invertebrates in forest streams is naturally based on the riparian forest supply of organic matter and nutrients, and dimensioned by the riparian forest regulation of stream flow, temperature, insolation and sediment load. The riparian forest also supplies large woody debris (LWD) to forest streams. Several studies, especially in the U.S. coastal Pacific Northwest, have demonstrated the effect of large woody debris on the habitat and hydrodynamics of forest streams. LWD can affect channel morphology by flow deflection sometimes creating scour pools, decreasing distance between pools (Beechie and Sibley 1997), increasing total pool area (Roni and Quinn 2001) and in some instances by reducing flow and thus increasing the deposition of fine sediments and debris (Wallace et al. 1995). This leads to increased nutrient retention in the streams (Valett et al. 2002). Further, the stream banks and channel are stabilized (Tschaplinski and Hartman 1983) and the habitat diversity increases (Naiman et al. 1992).

Large woody debris is important for salmonid production, mainly due to increased habitat diversity (Fausch and Northcote 1992, Flebbe and Dolloff 1995). Studies have shown that artificial addition of LWD will increase salmonid density and biomass (Flebbe 1999, Roni and Quinn 2001, Lehane et al. 2002), as well as individual growth (Sundbaum and Näslund 1998). According to Murphy and Koski (1989), 90% of the large woody debris in the water is associated with the nearest 30 m of the riparian zone. This indicates that the riparian zone even in small streams is of essential importance not only to fish densities but also to retention capacity and stream morphology.

Historically, the amount and quality of LWD in streams has not been studied as well as in terrestrial forest systems. Few studies on LWD exist for Scandinavian streams (Bergquist 1999, Siitonen 2001). However, some evidence suggests large declines of LWD compared with the natural range of variability as in terrestrial environments. Many streams have been cleaned of LWD prior to log driving and for pure drainage reasons, but these actions do not alone explain the last 40 yr situation with a continuing low supply of LWD to Scandinavian streams. Lazdinis and Angelstam (in press) quantified the amount of riparian forest in Sweden and the former Soviet Union having different policies for the management of forests along streams. They found that old forest did not exist along the selected Swedish streams, whereas due to policies in the former Soviet Union demanding riparian corridors an average of 20% the forests along streams was old-growth with continuous production of dead wood. Enetjärn and Birkö (1998) and Liljaniemi et al. (2002) found that the abundance of coarse woody debris (CWD) was 10- to 100-fold higher in reference streams in boreal forest in Russia compared with Swedish and Finnish streams, respectively, in managed boreal forests. It has been suggested that LWD could be a factor limiting trout populations on a large scale in Sweden (Näslund 1999). Indeed, Inoue and Nakano (1998) noted that density of Masu salmon *Oncorhychus masou* was directly correlated with the amount of woody debris.

The purpose of the present study is to test the hypothesis that there exists a positive correlation between occurrence and abundance of brown trout *Salmo trutta* and quantity of LWD in Swedish streams. Should this be the case, it would be possible to relate the level of human disturbance in the terrestrial environment to the amount of different elements of biodiversity in the aquatic environment. This could also encourage the development of tools analogous to the gap analyses for assessment of the amount of different vegetation types needed to maintain biodiversity (e.g. Angelstam and Andersson 2001, Lõhmus et al. 2004). Similarly, it would allow the use of habitat models for proactive planning of representative and functional habitat networks being based on focal species representing vegetation types with gaps (Scott et al. 2002, Angelstam et al. 2004). Hence, using quantitative knowledge about specialised aquatic focal species, such as trout, assessment and planning tools based on quantitative targets for habitat structures like LWD could be developed.

Material and methods

Data on LWD and fish were compiled from the Swedish Electrofishing RegiSter (SERS), a database with over 10 000 studied sites in Swedish streams. To date, LWD has been quantified at 4382 forest stream sites. Only sites in forest, i.e., with riparian zones (15 m wide zone adjoining the stream according to Swedish Electrofishing Field Manual (Degerman and Sers 1999)) classified as coniferous, deciduous or mixed forest, were included. The sites were located at altitudes of 1–895 m a.s.l. (average 175 m a.s.l).

LWD was defined as having a diameter of 10 cm or more and a length of at least 50 cm. The number of pieces of LWD was counted in the site and presented as pieces of LWD 100 m^{-2}.

The sampling sites were normally selected in areas of the streams with a habitat suitable for spawning and the first years of growth of brown trout (i.e. riffle-run habitats). Electrofishing was carried out in August–September by wading, using dead or pulsed dead electric current. The average length of stream sampled was 46.8 m (SD=25), the average width was 6.8 m (SD=10) and the average sampled stream area was 238 m^2 (SD=208 m^2).

Fish were measured (total length), and determined to species, but not sexed or aged. Underyearlings, 0+, were separated from older trout using length frequencies and

treated separately in density estimates. Population densities were estimated according to Bohlin et al. (1979) if consecutive runs had been carried out. Otherwise densities were estimated from average catch efficiencies for the species and age group (Degerman and Sers 1999).

Environmental variables registered were: width, mean depth, maximum depth, dominating and sub-dominating substrate. The substrate was classified in five categories (1–5) based on the dominant particle size: <0.0002 m (fine=1), 0.0002–0.002 m (sand=2), 0.002–0.02 m (gravel=3), 0.02–0.2 m (stone=4) and >0.2 m (boulder=5). Water velocity was classified into three classes: <0.2 m s^{-1} (1), 0.2–0.7 m s^{-1} (2), >0.7 m s^{-1} (3) at sampling, i.e. late summer flow situation. From maps the size of the catchments and the proportion (%) of lakes within the catchment were measured. Due to skewed distributions, fish abundance and stream width were transformed using $\log_{10}$ to avoid significant deviation from a normal distribution when performing statistical analysis. The amount of LWD was divided into three groups in most analyses: 0 pieces 100 m^{-2}, >0–4 pieces 100 m^{-2} and >4 pieces 100 m^{-2}. Also, stream width was in some analyses used as a grouped variable: <4 m, 4–8 m and >8 m.

Results

Trout occurrence

Brown trout was the most frequently occurring fish species in the investigated sites and occurred in 82% of the sites. Along with trout, seven fish taxa occurred at >10% of fishing occasions: bullheads (*Cottus gobio* and *C. poecilopus*), minnow *Phoxinus phoxinus*, burbot *Lota lota*, pike *Esox lucius*, brook lamprey *Lampetra planeri*, Atlantic salmon *Salmo salar* and perch *Perca fluviatilis* (Table 1).

LWD was present at 73% of sites. Brown trout occurred more frequently at sites with than at sites without LWD (Fig. 1, Anova with absence/presence of LWD and three stream width classes, p<0.001, n=4109, the interaction of LWD and width not significant).

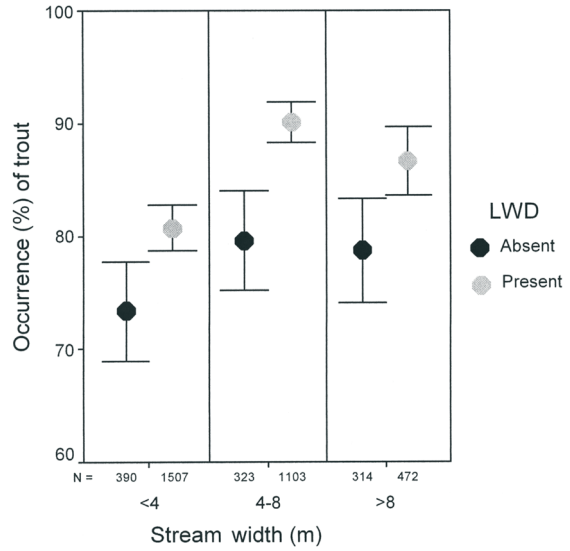


Fig. 1. Proportion (%) of sites with brown trout versus stream width class and presence/absence of Large Woody Debris (LWD). Bars indicate 95% confidence intervals.

Abundance

The abundance of trout increased with LWD (Fig. 2). This was especially pronounced in sites with > 4 pieces of LWD 100 m^{-2} and in larger streams (Anova, $\log_{10}$ abundance 100 m^{-2} with LWD-class (n=3) and width class (n=3) as fixed factors, p<0.001, r^2=0.190, n=3409). In fact, the abundance of trout increased with increasing amount of LWD up to 8–16 pieces 100 m^{-2} (Fig. 3). Using quantity of LWD and stream width, brown trout abundance could be predicted (linear regression, all variables transformed using $\log_{10}$, r^2=0.21, p<0.001).

Size of trout

Maximum size of the trout caught at each site was correlated with LWD. The largest trout caught averaged 188 mm

Table 1. The most frequently occurring taxa at the investigated sites (n=4382). The estimated abundance was calculated only for occasions when the species was caught (i.e. 0 is not included).

Species and taxa	Frequency		Abundance 100 m^{-2}	
	(%)	(n)	Average (SD)	Median
Brown trout	82.4	3609	32.0 (50.5)	15.3
Bullheads	33.3	1461	24.4 (38.4)	11.6
Minnow	30.1	1318	23.9 (63.4)	5.8
Burbot	22.3	1007	2.9 (5.4)	1.3
Pike	18.2	796	1.4 (1.8)	0.9
Brook lamprey	12.0	527	3.9 (9.6)	1.6
Salmon	11.2	492	26.5 (35.1)	13.1
Perch	10.1	441	4.1 (7.5)	1.7

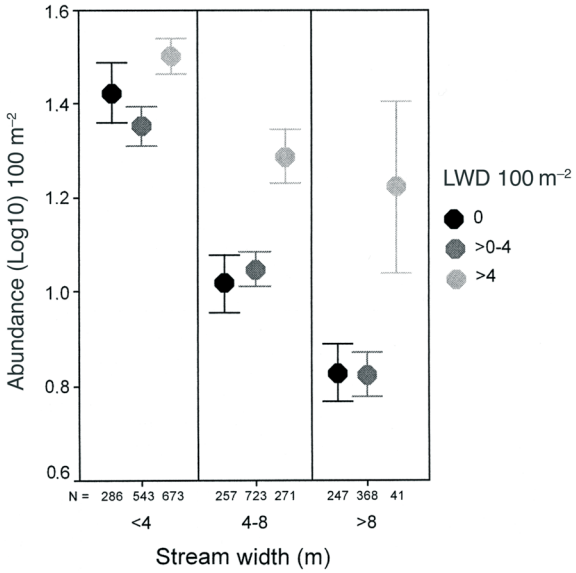


Fig. 2. Abundance (log_{10} no. 100 m^{-2}) of brown trout versus stream width class and LWD-class. Bars indicate 95% confidence intervals.

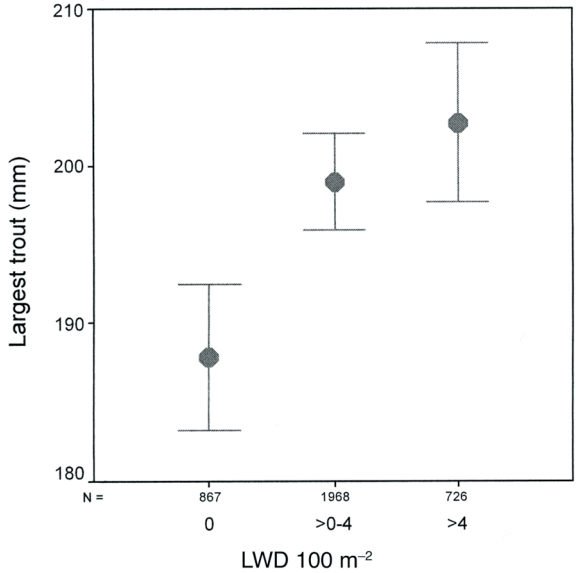


Fig. 4. Length of largest caught brown trout (mm) at each fishing occasion versus the amount of LWD present (expressed as no. 100 m^{-2}). Bars indicate 95% confidence intervals.

(SD=68 mm) at sites without LWD (n=861) and 200 mm (SD=69 mm) at sites with LWD (n=2661). This difference was significant even after the effects of latitude, maximum depth and log_{10}-density of trout >0+ were compensated for (Ancova with three covariates and LWD-class, presence/absence, as fixed factor, p<0.001 model, p=0.046 LWD, r^2=0.14). There was no significant difference between sites with low quantity of LWD as opposed to sites with more LWD (Fig. 4).

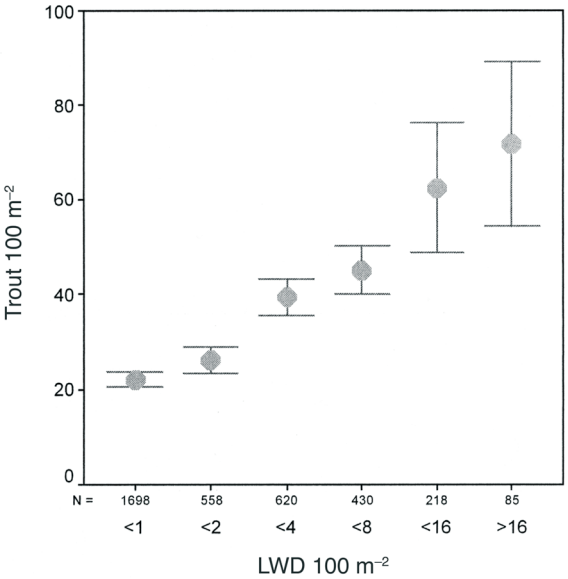


Fig. 3. Abundance (no. 100 m^{-2}) of brown trout versus quantity of LWD. Bars indicate 95% confidence intervals.

Size of trout of the age class 0+ is an indirect measure of growth during the first season, but the size is heavily dependent on sampling date and comparisons must be done with this in consideration e.g., by using Julian date (1–366) as covariate. The largest 0+ averaged 72.7 mm with no LWD, 70.9 mm when LWD >0–4, and 71.1 mm when LWD >4 pieces 100 m^{-2}. This decrease in underyearling size was significant (Ancova with LWD-class as fixed factor and latitude, altitude, Julian date and log_{10} abundance of 0+ as significant covariates, p<0.001 model, p<0.001 LWD, r^2=0.474). When the effects of the covariates were taken into account, new averages for the three LWD-classes could be calculated: 73.3, 71.5 and 68.7 mm, respectively. This means that average size of the largest underyearling was 6% lower when comparing sites without LWD to sites with >4 pieces of LWD.

Discussion

Trout and dead wood

Brown trout was the most common fish species in the investigated forest streams. Whereas occurrence increased with stream width, abundance was highest in the smallest streams. The occurrence and size of the largest trout were higher at sites with LWD present than at sites without LWD. This indicates that LWD creates a suitable environment for a trout, probably by providing a station sheltered both from predators and water current (Tschaplinski and Hartman 1983, Fausch and Northcote 1992), and possibly by creating pools, a habitat that generally has larger

trout than other habitat types (Heggenes 1988). Increased size, occurrence and abundance of trout with the amount of LWD indicate that suitable sites/stations (for foraging and refuge) may be limiting factors for trout (Bachman 1984). It should be noted that the abundance generally increased three times from sites without LWD to sites with >8 LWD pieces 100 m^{-2}. That the abundance of trout increased up to quantities of >8 pieces of LWD 100 m^{-2}, and that such levels of abundance occurred only at 6% of the sampling sites, indicate that the production can be limited by LWD at the landscape scale.

The effect of LWD on trout was particularly evident in larger streams (Fig. 2). In narrower streams the stream bank, submerged roots and probably the shading per se create suitable microhabitat. It is also plausible that the shelter against water currents created by LWD is more important in larger streams that naturally have higher water velocities. The recorded decline in underyearling size, and indirectly growth, can be an effect of increased trout populations along with increased quantity of LWD. This would indicate a density-dependent effect on growth at higher densities, which has been shown previously for brown trout in small streams (Nordwall et al. 2001).

It is known that the quantity (Andrus et al. 1988, Valett et al. 2002) and diameter (Rot et al. 2000) of LWD increase with forest age. Hence, the introduction of forestry to naturally dynamic landscapes normally decreases the amount of LWD supplied to the streams (Valett et al. 2002). Half of the amount of LWD is lost from forest streams within 20 yr, and virtually all of the wood will have disappeared within 50 yr (Hyatt and Naiman 2001). Hence, salmonid production may be substantially lowered 20–60 yr after a clear-cut (Connolly and Hall 1999). In Sweden, >95% of the forested area is managed, i.e., subjected to clearcutting, for several decades without sound watershed management principles. There is a lack of holistic and multidisciplinary perspectives in management of watersheds that have been drained and are dominated by conifer re-forestation. There are also obvious gaps in the functionality of managed landscapes where processes like fire and flooding do not longer continuously maintain old forest and dead wood (Lazdinis and Angelstam in press). Despite the fact that several recent studies have clearly declared that protection of riparian zones is of essential importance to fish in rivers and streams, the information has rarely been implemented. As a consequence, riparian forests have been harvested and the amount of LWD in the streams has been impoverished. In the present study the median quantity of LWD 100 m^{-2} was 1. This result can be compared to North American studies on streams with pristine conditions where the measured density of LWD m^{-2} varied between 0.3 and 17 (Bilby and Ward 1989, Murphy and Koski 1989, Fausch and Northcote 1992, Ralph et al. 1994, Flebbe and Dolloff 1995).

This study indicates that a substantial loss of salmonid production may be a result of diminished amount of LWD in managed forests compared with naturally dynamic riparian landscapes. In some restoration programmes LWD has been artificially added to create a more diverse aquatic habitat. Larson et al. (2001) studied such projects and found that the effect of a single effort only affected stream physical habitat in 2–10 yr and that the effects on biota were small. Obviously, a naturally dynamic riparian landscape with a mixture of young and old trees, which continue providing LWD to the streams, cannot be replaced by artificial substitutes. Hence, it is essential to study LWD in forest streams to quantify the natural amount of LWD that should be present.

Towards aquatic gap analysis

Habitat loss is known as the major factor affecting directly or indirectly the global decline of biodiversity (Heywood 1995, Wilcove et al. 1998). Hence, with a biodiversity conservation perspective, the evaluation of hypotheses claiming species-specific "extinction thresholds" defined as the minimum amount of habitat required for the persistence of species in the landscape is an urgent task (e.g. Lande 1987, Andrén 1994, Ehrlich 1995, Fahrig 1997, 2001, Sih et al. 2000, Angelstam et al. 2004). Apparently, human-driven landscape changes have resulted in the trespassing of such critical levels of habitat loss, e.g. in the form of LWD or the habitat features created by LWD, for many species (e.g. Harmon et al. 1986). This has then caused the extirpation of species. Consequently, the question "how much habitat is enough" has recently received a lot of attention from policy makers and managers dealing with biodiversity issues (e.g. Higman et al. 1999, Duinker 2001). However, for aquatic ecosystems there is no tradition of systematic analyses for conservation planning and restoration management in Scandinavia.

Gap analysis is a tool for strategic assessment of the extent to which environmental policies succeed in maintaining biodiversity by protection, management and restoration of habitats (Scott et al. 1993, 1996). Originally developed in the USA, gap analyses have been used in terrestrial systems to increase society's awareness about conservation needs and to guide the practical implementation of such policies. The rationale for focusing on habitat (i.e. structural elements of biodiversity) is that it serves as a proxy for the maintenance of viable populations of species, vital ecosystem processes and resilience to external disturbance (e.g. Karr 2000).

Originally gap analyses focused on representation i.e., that the different types of conservation areas should reflect the natural composition of different ecosystems (see Margules and Pressey 2000). Angelstam and Andersson (2001) developed the idea further by combining measurements of the habitat area with information about thresholds for the amount and quality of habitats needed to maintain viable populations within an ecoregion. This approach has also

been applied recently in Estonia (Lõhmus et al. 2004).

There is a growing insight that there are complex interactions between the terrestrial and aquatic systems, which require transdisciplinary landscape approaches such as aquatic gap analysis (Rabeni and Sowa 2002, Schneider et al. 2002). For example, the multimetric index of biological integrity (IBI) was developed as an offshoot of basic research in aquatic ecology (Karr 2000). Effective indices require indicators that are either theoretically or empirically flawed (see Karr and Chu 1999 for a review). They contain elements of biodiversity that are sensitive to a broad range of anthropogenic disturbances such as sedimentation, organic enrichment, toxic chemicals and flow alteration. Common metrics are species composition and habitat structure.

However, we do not know what the quantities of LWD of dead wood are in naturally dynamic benchmark ecosystems, nor the extent to which brown trout indicates other elements of biodiversity in small rivers. Three kinds of studies are therefore needed. First, brown trout should be sampled in a wider range of LWD. Second, the LWD index should be calibrated to quantitative data in riparian zones that can be communicated to forest managers. Third, the degree to which trout presence indicates diversity in other elements of biodiversity (Lambeck 1997, Roberge and Angelstam 2004), should be studied.

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Occurrence of Siberian jay *Perisoreus infaustus* in relation to amount of old forest at landscape and home range scales

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Edenius, L., Brodin, T. and White, N. 2004. Occurrence of Siberian jay *Perisoreus infaustus* in relation to amount of old forest at landscape and home range scales. – Ecol. Bull. 51: 241–247.

We analysed occurrence of the Siberian jay *Perisoreus infaustus*, a site-tenacious resident boreal forest corvid, in relation to the amount of old forest (> 100 yr) at landscape and home range scales. Intensity of use of feeding stations was related to the amount of old forest at 50 and 350 ha scales and at the landscape scale. Breeding success of radio-tagged jays provided additional data on habitat quality. Visiting frequency of jays at feeding stations (over 5 yr) was significantly higher in the pristine forest landscape than in the managed forest landscape (0.63 vs 0.36), and breeding success data indicated a similar pattern. In the managed forest landscape, proportion of years with groups of jays, observation time in years of individually marked jays and the density of jays were significantly related to the proportion of old forest at the 50 and 350 ha scales. Thus, the proportion of years with groups of jays at feeding stations increased more than 4-fold when the proportion of old forest increased from zero to 100%. Breeding success showed no clear pattern with respect to the amount of old forest at nesting sites in the managed forest landscape.

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To promote multi-purpose forestry efficient tools to evaluate different forest management scenarios with respect to impacts on non-timber values such as species conservation would be useful. In Fennoscandian boreal forests this is urgently needed in particular for habitat specialists, because the ecological characteristics of the forests in terms of e.g. disturbance regime, spatial contagion and age distribution have been radically altered (Esseen et al. 1997, Axelsson and Östlund 2001, Löfman and Kouki 2001). Wildlife-habitat models provide a potential powerful tool for managers to incorporate resource requirements of specialised species in planning (Morrison et al. 1992). Because the heterogeneity of habitats is scale dependent and species display different use of space dependent on life requirement, processes that govern habitat selection are also scale dependent (Wiens 1989, Jokimäki and Huhta 1996).

Habitat use models could potentially do a better work by invoking principles of landscape ecology, i.e. assessing impact of amounts of habitat at larger spatial scales on habitat use patterns (Addicott et al. 1987, Angelstam 1992, Dunning et al. 1992). Furthermore, inclusion of habitat use measurements indicative of habitat quality should fa-

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cilitate the development of better habitat models (Beutel and Beeton 1999). Habitat assessment should further attempt to identify relevant functional scales for animal-habitat interactions so as to derive proper management units (Kurki et al. 1998, Orrock et al. 2000). By screening gradients in amounts of suitable habitat non-linearities suggesting threshold levels in habitat resources could be detected and incorporated in the models (McLellan et al. 1986, Gustafson and Parker 1992, Andrén 1994, Fahrig 1997, 2001).

Simple and easily derived habitat variables would serve the formulation and adoption of strategies for conservation and land management planning. Coarse habitat classifications e.g. forest stand data, could potentially be useful for assessing habitat of forest specialists, as these kind of data are practical planning and working tools within the forest industry. Furthermore, they have large areal coverage, are digitised and thus easy to manipulate in a GIS so as to accommodate species-specific traits in space use. Despite their potential advantage, the usefulness of these kinds of data for habitat assessment has seldom been evaluated. One critical question when applying forest stand data is whether the spatial resolution of the data, i.e. the compartment or stand scale, provides sufficient detail for habitat assessment.

We applied a landscape ecology approach to study site occupancy by Siberian jay *Perisoreus infaustus*, a site-tenacious, territorial boreal forest resident, in relation to the amount of old forest at landscape and home range scales. Siberian jay is a habitat specialist with ascribed affinity to closed-canopy mature and old growth coniferous forests (e.g. Helle and Järvinen 1986, Virkkala 1991a, Rogacheva 1992, Cramp et al. 1994). Reports on quantitative habitat requirements of the Siberian jay at home range scale are few and partly anecdotal (Mykrä et al. 2000). Data from Finland suggest a more than three-fold reduction in population density since World War II (Väisänen et al. 1998) coinciding with large-scale introduction of stand replacement forestry. This indicates that performance of Siberian jay is negatively affected by fragmentation of habitat at scales larger than the territory (Järvinen et al. 1977, Väisänen et al. 1986, Virkkala 1991b, Kouki and Väänänen 2000, Uimaniemi et al. 2000). The objectives of this paper are twofold: 1) to analyse the relation between occurrence of Siberian jay and amount of old forest at different spatial scales, and 2) determine suitability of forest stand data in jay habitat assessment.

Material and methods

Study area and feeding stations

We performed our study in the transition between the northern boreal and middle boreal zone (sensu Ahti et al. 1968) in Norrbotten County, northern Sweden (66°30´N, 21°45´E). We selected a pristine forest landscape (Granlandet, 280 km^2 in size) composed of pristine multi-layered Norway spruce *Picea abies* dominated forest (see Edenius and Sjöberg 1997, Edenius and Meyer 2002 for details), and a managed forest landscape, Blåkölen (ca 165 km^2 in size), located 50 km from Granlandet. In the managed forest landscape > 50% of the forested land has been converted to regenerating stands (< 60 yr) following clear-cutting. The forests primarily consist of Scots pine *Pinus sylvestris*, followed by Norway spruce and deciduous trees (predominantly *Betula* spp.). We placed feeding stations systematically 800 m apart along roads in both landscapes. This distance was deduced from home range sizes reported in the literature (Blomgren 1964, Lindgren 1975, Sklepkovych 1997). Stations were thus placed in all types of habitat, including regenerating clear-cuts, however in open-mires stations were moved to the closest forest fringe. Thirteen and 26 stations in Granlandet and Blåkölen, respectively, were baited with pig tallow for about one week in September/October each year from 1997 to 2001 (5 yr). Stations were cleaned from fat at the end of each feeding trial to avoid habituation to these sites. When baited, feeding stations were regularly checked for visits of jays, number and, if possible, identities of visiting jays. Between 1997 and 2001 we individually colour-marked a total of 150 jays in the managed forest landscape.

Home range, habitat and breeding data

We radio-tagged 13 jays during autumn 1999–2000 in the managed forest landscape to derive site-specific data on movement scales and ranging behaviour in home ranges rich and devoid of old forest. In addition, we radio-tagged 10 and 12 mated females in March 1997–1999 in the pristine and managed forest landscape, respectively, to derive data on breeding performance. All 13 jays captured during autumn in the managed forest landscape belonged to separate groups of 3 to 4 birds; group constancy and membership were confirmed by visual observations during the telemetry study period. Home range size assessments were based on at least 20 locations regularly taken during September to December. Home range size was calculated with the kernel home range estimator, as this method explicitly takes the spatial patterning of the locations into consideration, i.e. the intensity of use, in contrast to the convex polygon method. We employed the fixed kernel algorithm with default values for smoothing according to Hooge and Eichenlaub (1997) in ArcView 3.1 software (Anon. 1996).

Mean home range size for the radio-tagged jays was 20, 45 and 150 ha for the 50, 70 and 95% kernel isopleths, respectively, but there was a large individual variation in home range size, particularly for the 95% isopleth (Fig. 1). Sensitivity analyses indicated that home range size reached an asymptote around 25 observations and that 90–95% of the home range size was captured with 20 observations.

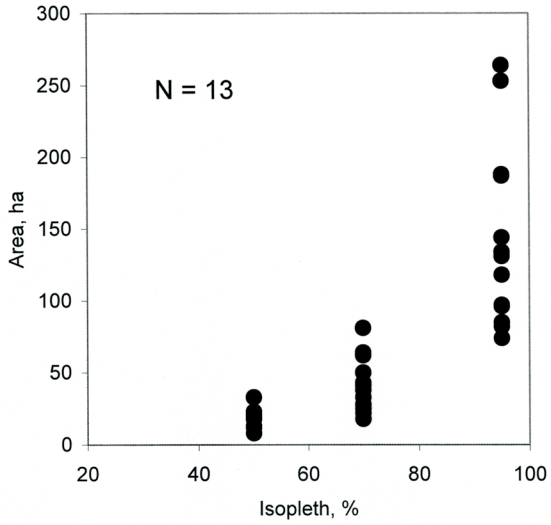


Fig. 1. Fixed kernel estimates of home range area during autumn for radio-tagged Siberian jays in the managed forest landscape.

We therefore used 50 ha as a conservative estimate of the home range core area.

We derived tree volume data and proportion of forest of different age classes using stand records provided by the landowners. This data source contained updated information of cuttings and was available in digital format that facilitated integration of data sources. Mean stand size in the database was 7.1 ha (SD = 11.7 ha, N = 1495) in the managed forest landscape. We adopted an age cut-off of 100 yr to designate "old" forest. Forest older than 60 yr emanated from natural regeneration and stands 60–100 yr of age were labelled "maturing" because of the lack of old trees. Due to selective cuttings in the past "old" forest was devoid of very large standing trees, snags and other legacies characterising old growth forest. Genuine old growth forest was mostly confined to a 6 km^2 large reserve, dominated by Norway spruce, in which we had three feeding stations placed.

A 50 ha hexagon centred on the feeding station was used to extract proportion of old forest for feeding station sites. First order (N = 6, 300 ha) neighbour hexagons were derived to enable analysis at different spatial scales (50 and 350 ha). Because we did not work with identified territories as the observation unit these scales represented different areas of "attraction". Thus the 50 ha scale pertained to a territory centred on the feeding station, i.e. the minimum recruitment area, and the 350 ha scale to the largest recruitment area as determined by the movement distances of the radio-tagged jays. In the managed forest landscape we also derived the proportion of old forest within a 50 ha hexagon at breeding sites, with the hexagon centred on the nesting tree.

Habitat use assessment

We analysed the effect of surrounding habitat on intensity of use of feeding station locations in each landscape. Three different indices of habitat use were employed: a) the proportion of years with visiting groups of jays (at least 3 birds; both landscapes), b) the total number of individually marked birds (managed forest landscape), and c) mean observation time in years of marked birds (managed forest landscape). Siberian jays form winter flocks, that is a social unit composed of mated adults and 1–2 retained and/or immigrant juveniles (Blomgren 1964, Ekman et al. 1994). Recurrent observations of marked birds and social interactions among birds at feeding stations in the managed forest landscape enabled us to establish the existence of such family flocks in many cases. However, as we could not consistently determine group membership over years and stations, we considered groups of jays as indicative of family flocks. The second index reflects population density, whereas the last index should reflect the capacity of the site to sustain jays. The breeding performance data were used as a complementary, and more direct, measure of habitat quality (Van Horne 1983).

Statistical analysis

The habitat use variables consisted of three types of data: count data (density of jays), proportional data (occurrence of groups) and continuous data (observation time of marked jays). The appropriate error structure for these kinds of data is poisson, binominal and normal, respectively. We therefore employed separate regressions models for the different data sets. Poisson regression and binomial regression are sensitive to overdisperson which occurs when the scale factor, i.e. the ratio of residual deviance to degrees of freedom, is significantly > 1. Methods to overcome this include square-root transformation of the response variable (Poisson regression) and adjusting the scale parameter by the Pearson χ^2 statistic (binomial regression) (Crawley 1993). In case of binomial regression such adjustments do not affect the parameter estimates, but increase their standard errors, which in turn reduces the statistical power of the test (Crawley 1993). Separate regressions were applied for the proportions of old forest at each scale. We tested for quadratic relationships by incorporating first order polynomials of the proportion of old forest. Variables were checked for normality by visual inspection of distribution plots and residual regression plots. We evaluated arcsine, log and root-square transformed data when conditions of normality were not fulfilled. These analyses were carried out in the Glim 3.77 statistical software (Royal Statistical Society, London 1985).

Moran's I was used to test for independence of feeding station data with respect to use of jays (Legendre 1993). The Moran's I statistic calculates spatial dependence of ob-

servations at different lag distances according to the formula (Moran 1950):

$$I = \frac{n}{\sum_{i=1}^{i=n}\sum_{j=1}^{j=n} W_{ij}} \bullet \frac{\sum_{i=1}^{i=n}\sum_{j=1}^{j=n} W_{ij}(x_1 - \bar{x})(x_j - \bar{x})}{\sum_{i=1}^{i=n}(x_1 - \bar{x})^2}$$

where W_{ij} is the binary weight matrix such that $W_{ij} = 1$ if sites I and j are adjacent or within the lag distance range otherwise $W_{ij} = 0$. The value at each point is x_i and x_j and the regional mean for the n sample sites is $\bar{x}$. The calculations were performed in the ArcView software using an extension developed by the authors. (This extension is freely available, contact NW). Significance of autocorrelation was examined using 1 km lag distances and the Z statistic under the assumption of normality. Bonferroni adjusted p-values were used in the significance tests. The Moran's I statistic is scaled to take values between +1 and –1, with values around unity indicating strong positive and negative autocorrelation, respectively, whereas values around zero indicate random patterns (Upton and Fingleton 1985). When values approach zero observations can be considered independent, and standard statistical tests applied. Spatial autocorrelation has to be accounted for because it may invalidate standard statistical tests as the true probability of a type I error is unknown (Roxburgh and Chesson 1998).

Results

Landscape scale

Visiting frequency of groups of jays at feeding station sites was significantly higher in pristine than in managed forest ($p < 0.05$; N = 5 yr, Mann-Whitney U-test; only sites dominated by old forest in the managed forest landscape considered, see Table 1). Similarly, breeding success of radio-tagged birds was higher in the pristine forest landscape; due to failure of radio-transmitters and logistic problems we could only document 5 instances of breeding in the pristine forest landscape.

Home range scale (managed forest landscape)

Mean number of years with groups of jays at feeding stations was 1.54 with a range of 0 and 5 (Table 2). Only one station, located in the old growth reserve, were used by groups of jays over all 5 yr. The number of marked jays visiting feeding stations varied between 0 and 19 (Table 2), with the highest number recorded at the old growth site exhibiting use by groups of jays in all years. Of the marked jays seen more than one year at the same feeding station, 27 were seen for two years and 5 for five years. The mean observation time of marked jays at individual feeding stations was 1.26 yr with a maximum of 2.67 yr (Table 2).

Table 1. Forest composition, visiting frequency at feedings stations and breeding success of radio-tagged Siberian jay in the pristine and managed forest landscape.

	Pristine forest landscape	Managed forest landscape
Forest > 100 yr, %	100	21
Frequency of feeding stations with groups of jays (SD; N) [1]. 1997–2001 yr data	0.63 (0.21; 13)	0.36 (0.27; 18)
Successful breeding attempts in landscape, % (N). 1997–1999 yr data	80 (5)	33 (12)

[1] Only stations with > 50% forest > 100 yr within 50 ha hexagon included.

Table 2. Mean, range and standard deviation in occurrence of groups of jays, density and observation time of jays at feeding station sites in the managed forest landscape, N = 26.

	Years with groups	Number of marked birds	Presence in years of marked birds
Mean	1.54	4.81	1.26
Range	0–5	0–19	1–2.67
SD	1.36	4.10	0.61

Forty-three jays (29% of all birds marked) were seen at more than one feeding station, which was not unexpected given the movement distances of the radio-tagged jays.

Use of feeding stations by the jays was not spatially correlated at any lag distance as determined by the Moran's I statistic ($-0.25 < I < 0.2$, $p > 0.05$). This justifies the use of feeding stations locations as independent sampling units.

The binomial regression analysis showed a significant effect of the proportion of old forest on the occurrence of groups of jays at feeding stations at the 50 and 350 ha scales (Table 3, Fig. 2). Also the Poisson regression analysis showed a significant effect of proportion old forest on the density of jays for the 50 and 350 ha scales (Table 4). Mean observation time of jays at feeding stations was significantly correlated with the proportion of old forest at both scales ($r > 0.39$, $p < 0.05$). Most of the variation was accounted for at the 350 ha scale ($R^2 = 22\%$). Inclusion of the quadric term of the proportion of old forest did not increase the explanatory power of any of the models.

Proportion of old forest at nesting sites (50 ha scale) was higher than the landscape average (0.52 vs 0.21, Table 1). Sites with successful breeding (N = 4) did not differ from sites with breeding failure (N = 8) with respect to proportion of old forest [mean 0.59 (SD = 0.34) and 0.48 (SD = 0.30), respectively; $p > 0.05$, Mann-Whitney U-test].

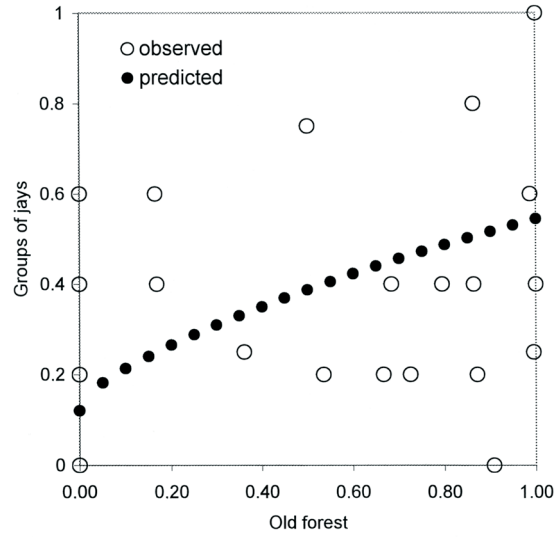


Fig. 2. Predicted and observed proportion of years with groups of Siberian jays at feeding stations in relation to proportion of old forest at the 350 ha scale (managed forest landscape). The predicted relationship was derived by binomial regression using the number of years with groups of jays as the response variable.

Discussion

Determined by visiting frequency of groups at the feeding stations, the density of jays was much higher in the pristine than in the managed forest landscape. Habitat use indexed by visiting frequency may not be directly related to habitat quality, as birds from poor quality sites could be more eager to visit feeding stations than birds from high quality sites. However, there was no auto-correlation in the use of feeding stations, which would have been expected if this was the case. Moreover, albeit sample size was small, the breeding performance data suggest that habitat quality indeed was better in the pristine forest landscape than in the managed forest landscape. In comparison, the breeding

Table 3. Dependence of proportion old forest on occurrence of Siberian jay groups at feeding station sites in the managed forest landscape. Results of binomial regression analysis. Old forest data were root-square transformed before analysis [loge (volume + 0.1)]. The deviance for the full model was 30.717 (DF = 25).

	50 ha scale	350 ha scale
Δ deviance, proportion of old forest (DF, p)	5.605 (1, < 0.05)	6.202 (1, < 0.05)
Parameter estimates		
Constant (SE)	–1.665 (0.507)	–1.987 (0.619)
Old forest (SE)	1.518 (0.678)	2.164 (0.931)

Table 4. Dependence of proportion old forest on density of marked Siberian jay at feeding station sites in the managed forest landscape. Results of poisson regression analysis. Old forest data were root-square transformed before analysis [loge (volume + 0.1)]. The deviance for the full model was 18.680 (DF = 25).

	50 ha scale	350 ha scale
Δ deviance, proportion of old forest (DF, p)	4.922 (1, < 0.05)	4.636 (1, < 0.05)
Parameter estimates		
Constant (SE)	0.190 (0.284)	0.085 (0.333)
Old forest (SE)	0.788 (0.370)	1.020 (0.492)

performance data showed a more complicated pattern with respect to habitat quality at the home range scale.

Habitat fragmentation is often proposed as a causative factor for reductions in realised habitat quality for specialised species. Habitat fragmentation encompasses effects of habitat loss and altered spatial configuration of habitat (Andrén 1994, Schmiegelow and Mönkkönen 2002) but also effects of changed habitat surroundings may be important (Rolstad 1991). Distinguishing between different components of habitat fragmentation is not an easy task, but it is important to try as the management implications may differ, dependent on the mechanism in action (Mönkkönen and Reunanen 1999). Causative mechanisms (sensu Rolstad 1991) potentially applicable to this study are: reduced interior-edge ratio decreasing effective habitat area, reduced habitat heterogeneity within fragments reducing carrying capacity, and increased habitat heterogeneity in surrounding matrix increasing carrying capacity of predators. We did not address effects of landscape structure, but Sklepkovych (1997) found higher breeding success of jays close to forest edge than in interior forest, thus questioning edge-sensitivity in the Siberian jay. Increased abundance of generalist predators resulting from habitat fragmentation at landscape scale has been demonstrated in boreal forests (e.g. Andrén 1992, Kurki et al. 1998). We have no good data on the predator community in the investigated landscapes, but the jay *Garrulus glandarius*, a potential nest predator, was seen only in managed forest. Also reduced structural heterogeneity within remnant old forest patches in managed forest may be influential as selective cuttings have increased visibility and thereby potential predation risk (Edenius and Meyer 2002).

The stronger relationship between occurrence of jays and old forest at landscape scale than home range scale suggests that the amount of old forest at larger spatial scales should be considered in habitat use assessment. In landscapes with low proportions of old forest, as in our managed landscape, a strong "external" pressure can depress realised quality, which would truncate or flatten the response curve. Such response curves sampled over landscapes with different amounts of old forest could potentially be used to detect habitat threshold, i.e. critical amount of resources for population maintenance (Fahrig 2001). We found a positive relationship between the amount of old forest at home range scale and occurrence of jays at feeding stations in the managed forest landscape. Thus the frequency of years with groups of jays at feeding stations increased more than fourfold when the proportion of old forest increased from zero to 100% at the 350-ha scale. However, substantial amounts of the variation in the data were not accounted for in our models. We believe that this could be due to stochastic factors; e.g. home ranges may remain vacant for longer or shorter periods of time after the demise of individual territory holders (Lande 1987). Moreover, occupancy of territories according to simple deterministic density-dependent rules may not apply to Siberian jay which exhibits a complex social system, including queuing for acquisition of territories (Ekman et al. 2001). This will add variation into the models and potentially mask non-linear relationships. Consequently, habitat use models should not be expected to give very precise estimates of dependence of old forest at the home range scale.

We only considered the amount of old forest in our habitat classification and did not take into account, for instance, the spatial configuration of old forest. However, the managed forest landscape was fragmented at a scale smaller than the average home range scale of the jays, i.e. it was fine-grained (sensu Levins 1968) with respect to ranging behaviour. Inclusion of small-scale variation in habitat structure below the stand scale and tree species composition could potentially improve the predictive power of habitat models for the Siberian jay. For example, small-scale (0.01 ha) variation in density of small spruce trees was significantly related to breeding success (Ekman et al. 2001) and spruce was preferred over Scots pine by adult jays in managed forest (Edenius and Meyer 2002). In conclusion, our results suggest that the proportion of old forest derived from forest stand data could be useful as a predictor of habitat suitability for Siberian jay. Because of the many sources of variation affecting local site occupancy we argue that focus in habitat assessment should be on the landscape level. At this scale forest stand data may be useful to predict suitable habitat and potential distribution of Siberian jay, e.g. for evaluation of different management scenarios (Morrison et al. 1992, Mykrä et al. 2000).

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Old-growth boreal forests, three-toed woodpeckers and saproxylic beetles – the importance of landscape management history on local consumer-resource dynamics

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Fayt, P. 2004. Old-growth boreal forests, three-toed woodpeckers and saproxylic beetles – the importance of landscape management history on local consumer-resource dynamics. – Ecol. Bull. 51: 249–258.

I investigated if the distribution of insect prey influencing the breeding success and being the winter diet of three-toed woodpeckers *Picoides tridactylus* changed with edge proximity in old-growth forest patches, and if edge effects depended upon the management history of the surrounding matrix. Measurements of three-toed woodpecker habitat quality during two years included the number of bark beetle species, a variable positively associated with the woodpecker brood size, the relative abundance of wood-boring beetles, whose larvae account for the bulk of nestlings' diet, and the relative abundance of bark beetles overwintering on standing spruces, its winter food. Of eight woodpecker habitat patches, five were surrounded by ditched clear-cuts and three were surrounded by untouched peatlands. Insects were sampled yearly with window-flight traps located at various distances from the nearest edge. Of 17 169 beetles collected, 12 843 were bark beetles (Coleoptera, Scolytidae). Contrasting patterns in woodpecker prey distribution were found in natural vs managed boreal forest landscapes. In habitat patches with natural edges and unditched surrounding, number of bark beetle species did not change and abundance of bark beetles living on standing spruces decreased from the edge into the interior part of the forest. In old-growth remnants embedded in drained managed landscapes, however, bark beetle species richness increased while abundance of spruce bark beetles found on standing trees did not change with the distance from the edge. Looking at the species composition of bark beetle communities living preferentially on logs, roots, stumps and standing trees, only the species assemblage of standing trees showed responses to edge proximity, becoming richer with increasing distance from the edge in stands with managed surrounding. Results on prey distribution suggest the importance of old-growth swamp forests in the boreal landscape to lower the threshold in the proportion of original habitats that is required to ensure the reproduction and secure the winter food supply of a viable three-toed woodpecker population.

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Habitat edges in forest ecosystems have received increasing attention in ecology, conservation biology and land management (Angelstam 1992, Murcia 1995, Matlack and Litvaitis 1999). This mainly stems from the growing awareness of the importance of boundaries or transitions between community types on the outcome of major ecological processes that operate within patches and over the larger landscape (Wiens et al. 1985, 1993, Dunning et al. 1992). Besides abrupt changes in the abiotic conditions such as solar radiation, air temperature, air humidity and wind speed, the proximity to a structurally dissimilar matrix has been stressed to promote directly or indirectly changes in species assemblages and interactions (Murcia 1995, Fagan et al. 1999). As an example, epiphytic lichens, insect, amphibian, bird and mammal species have been shown to respond differently to edge vicinity (e.g., Mills 1995, Peltonen et al. 1997, Demaynadier and Hunter 1998, Kivistö and Kuusinen 2000, Dale et al. 2000). By altering the nature of species interactions, however, habitat edges can also affect critical ecological patterns and processes at a variety of spatial scales such as organic matter decomposition, nutrient cycling, seed dispersal, plant pollination, consumer-resource dynamics, nest parasitism, and interspecific interactions (Chen et al. 1995, Fagan et al. 1999).

Although its structure is relatively homogeneous due to the low tree species diversity (Esseen et al. 1997), the Fennoscandian boreal forest is naturally fragmented. Mires, lakes, forested wetlands and forests form complex landscape mosaics determined by local and regional variations in topography, soil properties, hydrology and climate (Sjöberg and Ericson 1997). In addition, before the 1900s, fire disturbance, including the use of slash-and-burn cultivation, and small-scale gap formation on moister grounds governed most of forest structure and dynamics (Esseen et al. 1997, Kouki et al. 2001). Thus habitat edges, boundaries or transitions are integral parts of the boreal environment. Nevertheless, with the advent of large-scale intensive management of forest landscapes and the development of the forest industry since the early 1900s, fragmentation of the old-growth forest cover and the consequent forest edge/interior ratio of the remaining habitat patches have dramatically increased. Loss, alteration and fragmentation of old-growth stands in the taiga forest have been pointed out as major threats for an increasing number of forest-dwelling species (Rassi et al. 2001).

The three-toed woodpecker *Picoides tridactylus* inhabits old-growth, flooded and recently burnt boreal or montane coniferous forests with a circumpolar distribution closely coinciding with that of spruce tree species (Baldwin 1968, Bock and Bock 1974). In the boreal zone, three-toed woodpeckers have been shown to prey mainly upon bark beetles (Scolytidae) from autumn to spring time, with a marked preference for species living on spruce trees (e.g., Dement'ev 1966, Baldwin 1968, Hogstad 1970, Massey and Wygant 1973, Fayt 1999). During the summer months and/or the reproduction, both adults and offspring rely mostly on longhorn beetle (Cerambycidae) larvae and spiders (Dement'ev 1966, Hogstad 1970, Pechacek and Krištín 1996, pers. comm.). In Finland, its population trend is negative (Virkkala 1991, Väisänen and Solonen 1997); it is now classified as locally- to regionally-threatened species (Rassi 2000). With roughly 30% of its European population breeding in Finland, the three-toed woodpecker is also, together with the Siberian jay *Perisoreus infaustus*, the only forest bird of Finland included in the Wild Birds Directive of the European Union and classified as a Finnish responsibility species of European Conservation Concern (Rajasärkkä 1997).

Recent entomological surveys have emphasised the negative impact that forest edge proximity can have on bark beetle distribution, and in particular on the distribution of species typically found in the diet of the three-toed woodpecker (Peltonen et al. 1997, Peltonen and Heliövaara 1998). This led to the suggestion that three-toed woodpeckers may suffer from a lower winter foraging efficiency in a fragmented mature spruce forest landscape, if the proportion of interior forest decreases (Fayt 1999). On the other hand, poor soil aeration conditions characterising wet forest sites have been noticed to predispose coniferous trees to attack by bark beetles (Lorio 1968, Reeve et al. 1995). In particular, anaerobic soil conditions have been shown to promote pathogen infestations on root tips (Stolzy and Sojka 1984, Fraedrich and Tainter 1989), which, in turn, is an important factor in predisposing trees to beetle colonisation and early mortality (Hertert et al. 1975, Geiszler et al. 1980). In boreal swamp forests, the lack of living trees older than 250–350 yr old is a result of mortality associated with root-rot infections (Hörnberg et al. 1998). Thus, forest drainage, implemented in Finland over an area of 58 000 km^2 mainly since the 1950s to improve soil aeration by lowering the water table and decreasing its water content (Paavilainen and Päivänen 1995, Tomppo and Henttonen 1996), may also contribute to distribution changes of the bird's insect prey. The finding that a ditch significantly lowers the water table up to a distance of 80 m from the ditch (Roy et al. 2000) stresses the potential impact of local ditching practices on processes operating on larger scales.

In this paper, I examine the hypothesis that old-growth forest fragmentation and the consequent decline in the proportion of interior forests affect negatively prey availability for the three-toed woodpecker. This was done by relating in its breeding habitats number of bark beetle species, a major determinant of the bird's brood size (Fayt unpubl.), and abundance of wood-boring beetles, and in particular of longhorn beetles whose larvae account for the bulk of nestlings' diet (Pechacek and Krištín 1996), with the distance to the nearest edge. The availability of bark beetles living on standing dying and dead spruces was also estimated to study effects of edge proximity on the woodpecker's main winter food supply. In order to take into account the potential effect of the management level of the

surrounding matrix on species interactions in the remaining old-growth patches, I studied separately insect distribution in woodpecker habitats surrounded by ditched clear-cuts and untouched peatlands.

Material and methods

Study area

The study was conducted in 1998 and 1999 in North Karelia, easternmost Finland (63°N, 31°E). The study area consisted of a patchwork of eight Norway spruce *Picea abies* dominated old-growth forest stands, distributed over some 3600 km^2. Spatially isolated from the others by a surrounding matrix of younger, managed Scots pine *Pinus sylvestris* dominated stands, each patch (70–162 ha) was inhabited by a single pair of the three-toed woodpecker. During the study period, the different old-growth habitat patches were continuously occupied. Of the eight woodpecker habitats, five were surrounded by 5–15 yr old ditched clear-cuts and three were surrounded by natural peatlands. Within the clear-cuts, few or no standing dead trees were left, making these areas unsuitable for a foraging three-toed woodpecker.

Insect sampling

Insects were sampled yearly with window-flight traps, an efficient sampling device for bark beetles (Martikainen et al. 1996, 1999). Traps were located at various distances from the nearest edge. In this study, "edge" was defined as a boundary line between the clear-cut or peatland and adjacent old-growth forest. Its location corresponded to the point reached by the canopy tree trunks of the old-growth stand. Distances between the traps and the edge were measured with Global Positioning System (GPS). The traps were made of two perpendicular intercepting 20 × 40 cm transparent plastic planes, and a plastic funnel leading into a container attached below the panes. A solution of water, salt and detergent was used in the container to preserve the insects. Woodpecker habitats were divided into 7 ha plots (200 × 350 m) on maps with scales of 1:10 000 to 1:20 000. Within each plot, one living tree was randomly chosen to which one trap was hanged close by the trunk to a solid branch 1.5 m above the ground, measured from the lower margin of the panes. Traps were located after choosing from random number combinations their direction and distance from the centre of each plot. The yearly sampling period was 1 May–20 July. A total of 80 traps were used both in 1998 and in 1999, out of which 49 were located in old-growth patches surrounded by drained clear-cuts. The traps were emptied twice during the summer.

To study whether edge proximity and quality may interfere with habitat use and occurrence of the woodpecker in a remaining old-growth patch, I specifically considered, at various distance from the edge, habitat variables previously found to be of importance for a three-toed woodpecker, both in summer and winter time. On the one hand, as discussed before, estimates of habitat quality for the reproduction included the number of bark beetle species, which affects positively the brood size of the bird, and relative abundance of wood-boring beetles. Together with the total richness, bark beetle species were used as indicators of spatial variation in the distribution of suitable woody microhabitats and categorised according to Lekander et al. (1977) into those living on standing dead trees or on logs, roots and stumps. Among wood-boring beetles, I counted the number of individuals belonging to families known to develop large larvae (i.e., Elateridae, Anobidae, Oedemeridae, Cerambycidae and Curculionidae). On the other hand, based on earlier findings that bark beetles living on spruce trees quantitatively compose most of the bird's winter diet (Hogstad 1970, Fayt 1999), I recorded among the different traps the relative abundance of spruce bark beetles. Scolytids were classified as species living on spruce according to the species assemblage previously found from the bark of spruce trees selected by the woodpecker (Fayt 1999, 2003). Since in the study area snow cover precludes effectively woodpecker foraging on the lower parts of tree trunks, logs and stumps, however, I estimated winter food availability by including only spruce beetle species described to overwinter on standing trees. Additional measurements of food supply were the total number of individual beetles and abundance of the different bark beetle species. All insects were sorted out under a binocular microscope.

Statistical analysis

All statistical analyses were performed using SPSS for windows software. Tested variables were examined for the distribution of the data and standard transformations were used, if necessary. To study the influence of edge proximity on the distribution of the woodpecker insect prey, I used a multivariate analysis of variance (MANCOVA) with distance as covariate, territory as a fixed factor, and beetle richness or abundance as dependent variables. A similar procedure allowed me to test for any edge-mediated effect on the incidence of the different bark beetle species. A sequential Bonferroni correction was performed to control the error rate from multiple comparisons of means (Rice 1989).

Results

Among 17 169 beetles collected, 12 843 were bark beetles (74.8%) from 27 species. A total of 688 wood-boring adult beetles were captured, among which 450 (65.4%)

were Elateridae, 24 (3.5%) Anobidae, 25 (3.6%) Oedemeridae, 100 (14.5%) Cerambycidae and 89 (12.9%) Curculionidae.

Bark beetle species richness did not differ between forest landscapes, with 27 species found in old-growth forest patches surrounded both by untouched peatland and drained clear-cuts. After Bonferroni correction, the number of bark beetle species responded to edge proximity only in habitat patches with managed surroundings, increasing towards the inner part of the forest (Table 1, Fig. 1a, g). Comparing the distribution of the beetle species diversity of standing trees vs logs, roots and stumps in both categories of landscape, significant edge-effect was only found in drained forest landscapes, with an increasing number of species living on standing trees with the distance from the edge (Table 1, Fig. 1b, c, h, i). Edges did not influence the distribution of the bark beetle diversity of logs, roots and stumps.

Relative abundance of bark beetles living on standing spruces decreased significantly from the edge into the interior part in old-growth habitat patches with natural edges and surrounding (Table 1, Fig. 1d). It did not change in patches left over in managed landscapes (Table 1, Fig. 1j). Neither the relative abundance of wood-boring beetles, including the one of longhorn beetles, nor the total number of individual beetles changed with distance from the forest edge (Table 1, Fig. 1e, f, k, l), irrespective of the management history of the landscape. Looking at the influence of edge on distribution of the bark beetle community, none of the 14 beetle species studied showed significant responses to edge proximity, both in managed and natural forest landscapes (Table 2).

Discussion

Studies about the factors underlying patch-level variability in three-toed woodpecker numbers emphasise the importance of bark beetle species richness, a variable positively associated with the woodpecker brood size, the abundance of wood-boring beetles, including longhorn beetles whose larvae account for the bulk of nestlings' diet, and the abundance of bark beetles living on standing dead spruces, its winter food supply. In old-growth stands with natural edg-

Table 1. Results of MANCOVA testing the effect of edge proximity on spatial distribution of the woodpecker insect prey in old-growth patches embedded in natural vs managed forest landscapes. Territory was used as a between subject factor and distance from the edge as a covariate. **Bold** p-values indicate a significant edge effect among patches, after Bonferroni correction ($\alpha = 0.05$). (+) and (–) signs refer to the shape of significant relationships.

Dependent variable	Matrix type	Source of variation	DF	F	Significance	Trend
No. bark beetle species	Natural (N)	Distance (D)	1	4.732	ns	
		Territory (T)	3	1.281	ns	
	Managed (M)	D	1	11.868	**0.012**	**(+)**
		T	4	2.644	ns	
No. bark beetle species living on standing trees	N	D	1	3.337	ns	
		T	3	0.598	ns	
	M	D	1	9.547	**0.044**	**(+)**
		T	4	0.962	ns	
No. bark beetle species living on down logs, roots and stumps	N	D	1	4.167	ns	
		T	3	3.596	ns	
	M	D	1	2.777	ns	
		T	4	2.908	ns	
Relative abundance bark beetles living on standing spruce trees	N	D	1	9.853	**0.044**	**(–)**
		T	3	1.781	ns	
	M	D	1	0.243	ns	
		T	4	2.298	ns	
Relative abundance wood-boring beetles	N	D	1	1.391	ns	
		T	3	0.171	ns	
	M	D	1	0.565	ns	
		T	4	3.831	ns	
Relative abundance longhorn beetles	N	D	1	1.022	ns	
		T	3	3.190	ns	
	M	D	1	0.735	ns	
		T	4	1.140	ns	
Total number of individual beetles	N	D	1	0.000	ns	
		T	3	0.715	ns	
	M	D	1	0.011	ns	
		T	4	1.742	ns	

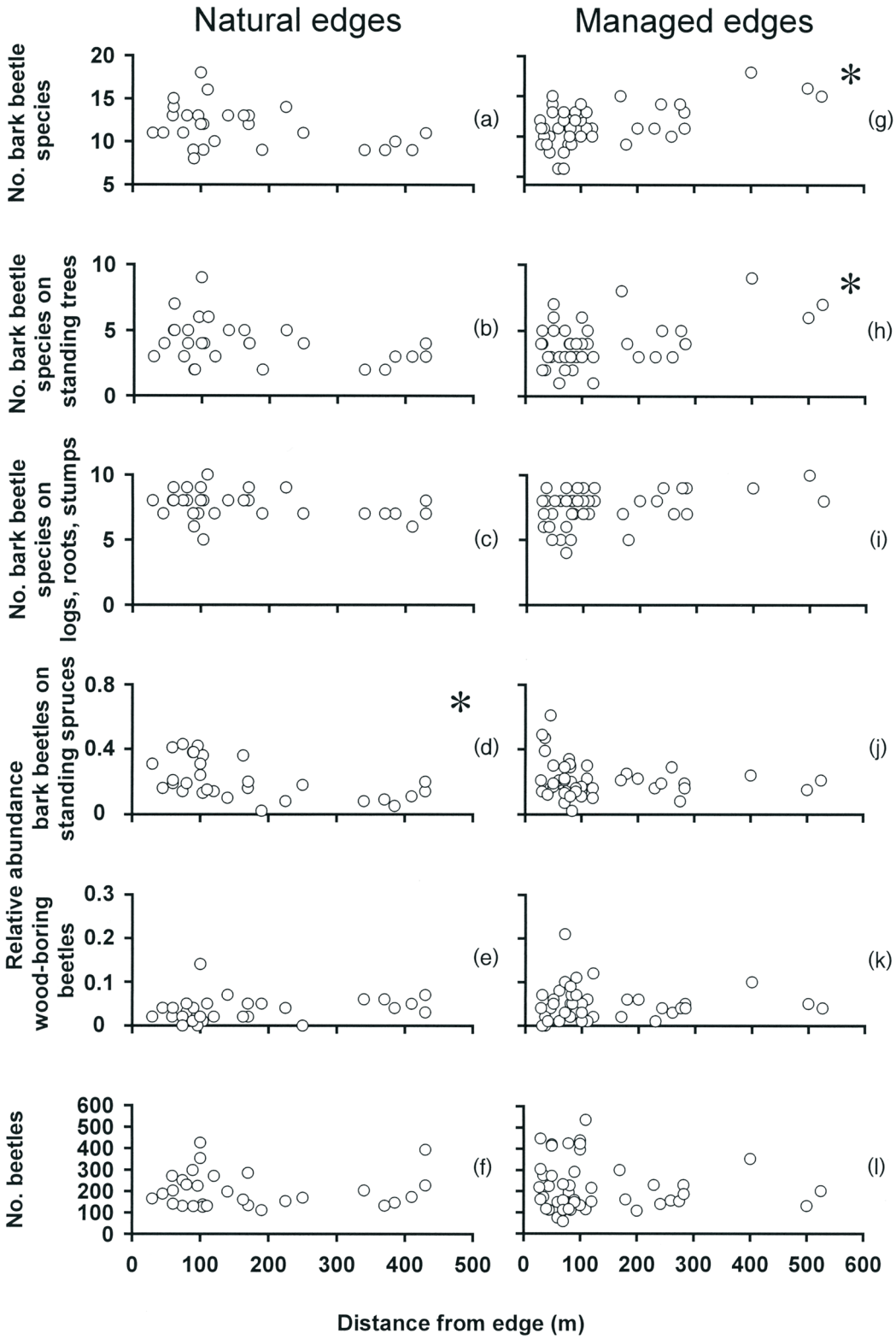


Fig. 1. The effect of edge proximity on species richness and abundance of the saproxylic beetle fauna of old-growth forest patches inhabited by the three-toed woodpecker in natural vs managed forest landscapes. * denote significant ($p<0.05$) results.

Table 2. Results of MANCOVA testing the effect of edge proximity on incidence of the bark beetle species in old-growth patches embedded in natural vs managed forest landscapes. Territory was used as a between subject factor and distance from the edge as a covariate. Only species with > 20 individuals captured were included. Significance levels are added after Bonferroni correction ($\alpha = 0.05$).

Species	Matrix type	n	Source of variation	DF	F	Significance
Xylechinus pilosus	Natural (N)	616	Distance (D)	1	2.488	ns
			Territory (T)	3	0.414	ns
	Managed (M)	971	D	1	0.646	ns
			T	4	1.441	ns
Hylurgops glabratus	N	68	D	1	1.706	ns
			T	3	1.651	ns
	M	86	D	1	1.068	ns
			T	4	5.863	ns
Hylurgops palliatus	N	631	D	1	2.425	ns
			T	3	0.500	ns
	M	1263	D	1	0.005	ns
			T	4	5.741	ns
Hylastes brunneus	N	166	D	1	0.125	ns
			T	3	1.172	ns
	M	299	D	1	0.452	ns
			T	4	7.752	ns
Hylastes cunicularius	N	840	D	1	0.215	ns
			T	3	0.320	ns
	M	1426	D	1	0.249	ns
			T	4	2.280	ns
Polygraphus sp. *(poligraphus-punctifrons-subopacus)*	N	32	D	1	0.087	ns
			T	3	0.394	ns
	M	86	D	1	0.092	ns
			T	4	0.817	ns
Crypturgus subcribrosus	N	18	D	1	0.150	ns
			T	3	0.204	ns
	M	32	D	1	4.579	ns
			T	4	0.572	ns
Cryphalus saltuarius	N	13	D	1	3.736	ns
			T	3	2.125	ns
	M	17	D	1	2.288	ns
			T	4	0.176	ns
Dryocoetes autographus	N	231	D	1	0.031	ns
			T	3	0.601	ns
	M	404	D	1	2.943	ns
			T	4	3.092	ns
Dryocoetes hectographus	N	40	D	1	2.075	ns
			T	3	2.892	ns
	M	94	D	1	0.440	ns
			T	4	3.121	ns
Pityophthorus lichtensteini	N	44	D	1	3.760	ns
			T	3	0.975	ns
	M	45	D	1	0.956	ns
			T	4	5.211	ns
Trypodendron lineatum	N	812	D	1	0.031	ns
			T	3	1.602	ns
	M	1531	D	1	0.016	ns
			T	4	2.624	ns
Trypodendron signatum	N	1020	D	1	3.854	ns
			T	3	0.924	ns
	M	1534	D	1	0.257	ns
			T	4	0.840	ns
Pityogenes chalcographus	N	70	D	1	0.992	ns
			T	3	0.191	ns
	M	92	D	1	2.943	ns
			T	4	0.166	ns

es and swampy environment, number of bark beetle species did not change and abundance of bark beetles living on standing spruces decreased from the edge into the interior part of the forest. In old-growth remnants embedded in drained managed landscapes, however, bark beetle species richness increased while abundance of spruce bark beetles found on standing trees did not change with the distance from the edge. Considering habitat associations of the different bark beetle species, only the species preferentially living on standing trees responded to edge proximity, with a response mediated by the surrounding matrix type. In forest fragments surrounded by ditched clear-cuts, the species assemblage of standing trees became richer with increasing distance from the edge. Thus, my results suggest that fragmentation of the boreal forest may affect differently the reproductive output and winter food intake of three-toed woodpeckers dwelling in old-growth habitat patches, depending on the origin of the process.

A common result from studies dealing with vegetation responses to edge vicinity in managed forest landscapes is that the biomass of coarse woody debris, whether standing trees or windthrows, increase from the interior to the edge of mature-to-old-growth remnants (Chen et al. 1992, Mills 1995, Peltonen 1999). Several factors have been proposed to account for the reduced vigour of standing trees at recently formed edges. Wind, whose influence decreases exponentially from the edge into the forest (Chen et al. 1995), has been found to cause growth decline by inducing crown and fine-root damages during tree sway (Harrington 1986, Rizzo and Harrington 1988). Besides inducing sudden changes in intensity of solar radiation and related microclimatic variables (Chen et al. 1995), harvesting operations may cause stem and root wounds in the remaining fragments. Forest edges can also function as traps for airborne pollutants (Weathers et al. 2001). On the other hand, windthrown trees are known to be an important breeding and overwintering substrate for various saproxylic organisms, including bark beetles (Långström 1984, Peltonen 1999, Göthlin et al. 2000, Siitonen 2001). It justifies the finding that damaged and windthrown trees are the two most important factors determining risk of a spruce bark beetle outbreak (Reynolds and Holsten 1994). Consequently, one would expect edge transitions of old-growth forest remnants to support diverse and abundant saproxylic beetle populations, irrespective of the landscape context. My results do not support this hypothesis. Instead, they suggest that soil properties and hydrology of the matrix surrounding forest patches contribute to explain edge-associated abiotic and biotic conditions of its inclusive old-growth habitat units. This is supported by earlier evidence that local drainage practices lower significantly the water table at several tens of meters from the nearest ditch (Roy et al. 2000), which, in turn, is expected to decrease the suitability of local host trees for colonising beetles and root-rotting fungi (Christiansen et al. 1987, Reeve et al. 1995). In accordance with my suggestion, Imbeau and Desrochers (2002) found foraging three-toed woodpeckers to be insensitive to edge proximity in linear old-growth forest remnants surrounded by unditched clear-cuts.

In contrast to the sharp edges found between clear-cuts and forest remnants, the progressive pine-dominated transition typically found between old-growth swamp forests and surrounding peatland may also buffer effectively extreme abiotic conditions between plant community types. This may contribute to differences in abundance and quality of dead wood material between the natural and clear-cut edges of the forest patches and, in turn, influence responses of saproxylic assemblages to vegetation changes. Accordingly, Peltonen and Heliövaara (1999) found desiccation and subcortical temperatures of woody debris to be significant at forest-clearcut edges, while attack densities of *Hylurgops palliatus* and *H. glabratus*, two bark beetle species living on dead spruces, increased markedly towards the forest interior. Focussing on the reproduction ecology of the former species, they found a parallel increase in its breeding success. That edges could affect differently dispersal behaviour, reproductive success, and population dynamics of the bark beetles' natural enemies, whether predators or parasitoids, according to edge structure and management history of the surrounding matrix is unknown.

Abundance of adult wood-boring beetles and, in particular, of longhorn beetles did not seem to change in relation to edge location and quality. These findings would support the idea that old-growth forest fragmentation and forested land management does not induce variation in the distribution of the bird's nestlings main food supply. An alternative explanation, however, could be that the sampling methodology used in this study (i.e., window-flight traps) was inefficient in trapping those larger beetles with flight abilities and foraging ecology differing from bark beetles. This possibility is supported by recent observations from oak and beech forests, that yellow plastic pan traps filled with water were by far the most effective in capturing longhorn beetles in comparison to white plastic pan, emergence, trunk-window, and window-flight traps (Fayt unpubl.). On the other hand, by showing a positive relationship between bark beetle species richness and distance from the edge in old-growth remnants left in drained forest landscapes, my results would also emphasise the need to maintain forest edge/interior ratio of those remnants as small as possible to maximise the bird reproductive output. For instance, in the managed landscapes of eastern Finland, breeding pairs of three-toed woodpeckers were typically found in spruce-dominated old forest remnants > 70 ha, with their nest located inside or at the periphery of the widest part of the patch (Fayt unpubl.). Hence, present results on spatial distribution of wood-boring beetles should be carefully interpreted when drawing conclusions.

Similarly, none of the 14 most abundant bark beetle species recorded in this study showed significant responses to edge proximity, in both categories of landscape. This result is surprising, since in contradiction with preceding

findings that the species assemblage of suppressed dying and dead spruces avoid luminous forest edges and withdraw into interior shady and moist parts of forest remnants (Peltonen et al. 1997, Peltonen and Heliövaara 1998, 1999). I suggest this discrepancy possibly stem from the inadequacy of the window traps used in my study to sample reliably populations of bark beetles with species-specific microhabitat and -climate requirements, contrarily to the emergence traps and careful hand picking-gallery examination methods used in those other studies. Nevertheless, the fact that the insect sampling carried out with window traps covered distances up to 600 m from the nearest edge, while limited to the first 100 m in the other studies, may account for patterns of insect distribution otherwise overlooked when considering shorter distances.

The main finding of this study, that the abundance of bark beetles living on standing spruces is lower at edges of old-growth remnants in drained managed forest landscapes compared to patches embedded in a swampy environment, has major implications for the woodpecker distribution pattern in modern forest landscapes. Besides immediate consequences on the foraging efficiency of individuals in habitat patches, and so on the effective size a fragment should have to fulfil their daily energetic requirements, a local decrease in autumn–winter food level is expected to affect negatively the number of breeding individuals a patch can support. This is because, in forest birds in general, survival and recruitment of juveniles into populations, a key factor in determining subsequent breeding densities (Perrins 1965, Dhondt and Eyckerman 1980), is regulated by the food supply available outside the breeding season (Gibb 1960, Perrins 1966, Van Balen 1980, Nilsson 1987, Hannon et al. 1987). Accordingly, comparing habitat preferences of the woodpecker species assemblage breeding in Bialowieza primeval forest, eastern Poland, Wesolowski and Tomialojc (1986) documented nests of the three-toed woodpecker to be most numerous in swampy stands. Thus, my results would only confirm an earlier knowledge, that old-growth swamp forests are key elements for the preservation of most of the biological diversity in the boreal environment (Ohlson et al. 1997, Hörnberg et al. 1998).

Management implications and further research

With relationships between the food supply of the three-toed woodpecker and edge location in old forest patches that changed with the management history of the immediate surrounding, my results have several implications for the conservation of the bird and the general management of the boreal forest. First, a small patch of old-growth spruce forest on a wetland would be more valuable for a foraging woodpecker than a similarly-sized patch of old forest with clear-cut edges and ditched surrounding. As a result, the conservation value of old forest patches would be landscape specific for a resident three-toed woodpecker, and thus, as suggested by Mönkkönen and Reunanen (1999), critical thresholds in the proportion of original habitats required for the maintenance of its population would depend on the landscape context. Second, the establishment of corridor-like linear old-growth patches in drained managed forest landscapes would be less beneficial for a foraging woodpecker than in swampy environments. This would make questionable the recent recommendations such as in Finland to create narrow corridors (25–50 m) in order to maintain biodiversity in managed forests (Niemelä 2001). Third, when planning harvesting of drained forest landscapes, and that the setting of logging priorities is considered, existing old forest patches sufficiently large to contain any core habitat (i.e., 70 ha) should be retained over linear patches.

Finally, this study emphasises needs for further research to identify the multi-scale factors associated with population responses of saproxylic organisms to edge proximity in coniferous landscapes, with implications for the predatory three-toed woodpecker. Among major information gaps, it should be assessed whether the prey responses in old-growth remnants vary with drainage history and intensity of the surroundings, after controlling for abundance and quality of dead wood.

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Management targets for the conservation of hazel grouse in boreal landscapes

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Jansson, G., Angelstam, P., Åberg, J. and Swenson, J. E. 2004. Management targets for the conservation of hazel grouse in boreal landscapes. – Ecol. Bull. 51: 259–264.

To emphasise the need for a systematic approach to predict species occurrences, we review studies on the occurrence of hazel grouse *Bonasa bonasia* at forest stand and landscape scales in study areas differing in proportion of suitable habitat and type of matrix. Critical thresholds for patch size and isolation were determined for both scales and models were produced and tested. At the stand scale, hazel grouse habitat described in forestry terms was unthinned middle-aged (20–70 yr) or old (> 90 yr) stands with 5–40% deciduous trees, including *Alnus glutinosa*, and with well developed field layer structures. Such habitats are rare in the managed forest landscapes of Fennoscandia. Minimum habitat patch size in managed forest landscapes was 10 ha for reliable hazel grouse presence, and 20 ha for habitat patches completely surrounded by open fields. Because of its short natal dispersal distances, avoidance of open areas and high degree of site tenaciousness, the hazel grouse is negatively influenced by habitat loss and isolation at the landscape scale. In an agricultural dominated landscape, no hazel grouse occurred in habitat fragments > 200 m from continuous forest, whereas in an intensively managed forest landscape an isolation threshold appeared at ca 2 km. Matrix type thus strongly influenced the occurrence of hazel grouse in forest habitat fragments. However, also within forests the proportion of open land edge contributed to the occupancy rate. Models based on the hazel grouse occurrences in intensively and extensively managed landscapes were tested in a landscape with intermediate intensive management. Models predicted the presence of hazel grouse in the habitat patches well, 84 and 86% correct, respectively. Further, present Swedish stand descriptions used in forestry were rather useful for determination of hazel grouse habitats, but would be improved if measures of ground cover and occurrence of alder were included.

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Even seemingly uniform expanses of forest, such as old-growth viewed from an airplane, are mosaics of different habitats at some level of discrimination. Therefore, to detect a response of habitat fragmentation in living organisms, it is necessary to identify the appropriate spatial and temporal scale at which a particular species is sensitive (Lord and Norton 1990, Wiens 1995, Suchant et al. 2003). Within the rotation time of Scandinavian managed

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forest stands, several thinnings and removal of deciduous trees make the forest structurally one-layered and completely dominated by coniferous trees. This type of management results in checkerboard-patterned landscapes with single cohorts of stands, where old trees, dead wood and deciduous trees are rare (Esseen et al. 1992). For the many organisms that once inhabited such landscapes, the consequences have been severe, because tree and habitat composition and dynamics differ essentially from the pristine forest conditions to which the species are adapted (Franklin and Forman 1987, Gärdenfors 2000).

Species most sensitive to habitat fragmentation and changes in the habitat structure have been suggested to be those that occur at relatively low densities before the alterations occur (Wilcox 1980), are sedentary habitat specialists (Opdam 1990), occupy late successional stages (Gotelli and Graves 1990), and have a low dispersal ability (Pimm et al. 1988, Bolger et al. 1991). The dispersal or mobility of a species may also involve behavioral aspects, such as reluctance to traverse edges or across a matrix of avoided habitat (Gascon et al. 1999, Rodriquez et al. 2001).

Patch size, habitat cover and isolation are classic landscape ecological parameters influencing the distributions of species (Forman 1995). The total habitat cover of a landscape is a significant predictor of species patch occurrences, at least when the total coverage exceeds 20% (Andrén 1994, Fahrig 1997). Below that proportion, a state that applies to the habitats of most threatened species, and where actual connectivity among patches is broken, there are effects of patch size, isolation and position relative to other patches (Verboom et al. 1991, Villard et al. 1999). Besides parameters reflecting habitat configuration, matrix and edge type, with less contrasting edges being more permeable (Wiens 1990, Rodriguez et al. 2001), have been shown to influence individual travel distances and thereby the colonization rates of the habitat patches (e.g. van Dorp and Opdam 1987).

In a world of limited knowledge, a common approach to produce useful tools for conservation management has been to link the habitat use of given species with maps of the vegetation (Verner et al. 1986). A systematic management approach aimed at promoting forest biodiversity requires, however, knowledge of the habitat selection and mobility of a suite of focal species representing the different forest disturbance regimes and forest types of the ecoregion in question (Lambeck 1997, Angelstam et al. 2004). Further, the term "habitat selection" should ideally include a range of spatial scales, e.g. site, local and landscape requirements, as exemplified by Suchant et al. (2003). They (Suchant et al. 2003) developed a species-habitat model for the capercaillie *Tetrao urogallus* where target values for local and landscape parameters were combined into an index for use in management. However, for the successful implementation of such models, correct descriptions of different land cover types are crucial. Possibilities to validate the models by monitoring population changes in the focal species are also important. Predictions from habitat models are often more successful for habitat specialist species (Edwards et al. 1996) and for species adapted to slow changes in habitat structure (Beshkarev et al. 1994). However, multidimensional and relevant knowledge has been obtained for only a few species, while for the majority of the species such is not available, at least not knowledge that is applicable in landscape ecological analyses (Jansson and Angelstam 1999).

Most of the aspects mentioned above as typical for species likely to be negatively affected by habitat fragmentation apply to the hazel grouse *Bonasa bonasia*. The hazel grouse has been studied in a detailed manner regarding ecological and behavioural traits at the home-range scale (e.g. Swenson 1991a), and thereafter in both managed and natural forest landscapes (e.g. Åberg et al. 1995). The aim of this paper is to review a series of systematic studies made to derive quantitative parameters for habitat variables at the scale of stands and landscapes important for the hazel grouse, and to test their validity. We then use this knowledge to discuss the conservation of hazel grouse and its habitat in managed forests.

Hazel grouse ecology

The hazel grouse is a small forest-living grouse, distributed throughout the Palearctic boreal and mountain forests, i.e. from Norway to Siberia and southwards into France and South Korea (Swenson and Danielsen 1991, Bergmann et al. 1996). In natural landscapes, the hazel grouse inhabits old-growth or young spruce dominated forest with a multi-layered structure and deciduous trees on fairly nutrient-rich soils (Eiberle and Koch 1975, Beshkarev et al. 1994, Klaus et al. 1995). In managed forests, such habitats are rare and the hazel grouse face a stronger reduction of available habitat than the other boreal forest grouse species (Swenson and Angelstam 1993). Suitable forest cover, mainly of Norway spruce *Picea abies* and a thick understory of saplings seem to be important habitat features, probably for avoidance of predators, e.g. goshawk *Accipiter gentilis* and marten *Martes martes* (Swenson 1991a, Swenson and Angelstam 1993). The preferred winter food in Fennoscandia is catkins and buds of deciduous trees, preferably alder (*Alnus glutinosa* and *A. incana*) and birch (*Betula pubescens* and *B. pendula*) (Swenson 1993). The hazel grouse is sedentary, very site-tenacious and with a low dispersal ability (Swenson 1991a, b, Swenson and Danielsen 1995). The size of a hazel grouse territory, ranging from 20–40 ha per pair, depends on habitat quality. It is defended through most of the year, but defence is most pronounced in autumn and spring (Pynnönen 1954, Swenson 1991a). The hazel grouse has experienced a general population decline and local extinctions in Europe (Swenson and Danielsen 1991) and in Japan (Fujimaki 2000).

Study areas

Studies on the quantitative habitat requirements of the hazel grouse have been conducted at different spatial scales in Sweden and Finland in landscapes with different management regimes, resulting in varying amounts of suitable habitat (see Table 1). In Sweden the forest landscape in the old mining district Bergslagen has been intensively managed for production of timber and pulp for several centuries (Wieslander 1936), and today only a very small proportion is made up of hazel grouse habitat (Åberg et al. 1995, 2003). Within this region, hazel grouse habitat selection was also studied in a forest reserve with a high proportion of suitable hazel grouse habitat (Åberg et al. 2000a). South of the forested landscape, Åberg et al. (1995) studied hazel grouse in habitat patches in a landscape where agricultural land dominated. There, the matrix consisted of fields, whereas in the forest-dominated landscape the matrix constituted various intensively managed non-suitable forest stands. Finally, a less intensively managed landscape was studied on the island of Aasla in the southwestern Finnish archipelago (Saari et al. 1998). In this study area forestry practices have never been intensive.

Model predictions based on the results from the abovementioned three landscapes were tested in a fourth independent landscape in south-central Sweden close to the city of Sala (Åberg 2000). The forests in Sala differed in management intensity within the study landscape, and the amount of hazel grouse habitat was intermediate compared to the other landscapes.

Methods

Hazel grouse males respond to imitations of the territorial song, being efficiently produced by a hunter's whistle. In all studies reviewed here, such whistles were used to determine the occurrence of hazel grouse males. Surveys were carried out along parallel transects 150 m apart, stopping at 150-m intervals and imitating the territorial song of hazel grouse males. This method discovers ca 82% of all territorial males within a 100 m radius during mid-April to mid-May and between mid-September and mid-October in central Sweden, as determined from radio-marked birds (Swenson 1991c). For details of field procedures and maps used etc in each study, see Åberg (2000).

Results

Stand scale habitat preferences

In all landscapes analysed, the proportion of spruce positively influenced hazel grouse occupancy at the scale of home ranges, and occupancy was negatively affected by the proportion of Scots pine *Pinus sylvestris* (Åberg et al. 2000a, 2003). The proportion of deciduous trees was significantly higher in occupied home ranges, when patches with > 50% deciduous trees were excluded. Stands dominated by deciduous tress were found to be too open to be suitable hazel grouse habitat (Åberg et al. 2003). A positive influence of alder on patch occupancy was found in the intensively managed forests (Åberg et al. 2003), and no hazel grouse was found in patches without alder in Sala (Åberg 2000). Shrub density, a measure of cover above the field layer and below the canopy, was positively related to the occurrence of hazel grouse, also within parts of home ranges (Åberg et al. 2000a). The amount of field layer cover was also an important feature in separating occupied from unoccupied habitats in two intensively managed landscapes (Åberg et al. 2000b, 2003).

However, no clear preferences for specific habitat structures within stands were found within hazel grouse home ranges (< 20 ha) in the forest reserve (Åberg et al. 2000a). These results suggested that the spatial scale of at least one territory size (20–40 ha for hazel grouse, Swenson 1991a) was the proper level to investigate habitat selection and possible effects of density dependence in hazel grouse populations (Åberg et al. 2000a).

No effect of patch size was found for the occurrence of hazel grouse in habitat patches larger than the home range size of hazel grouse (Åberg et al. 1995). However, when the censused habitat patches were smaller (1–30 ha), a threshold where the occupancy rate increased rapidly was apparent at ca 10 ha in the managed forested landscapes (Saari et al. 1998, Åberg et al. 2000b). Similar results, with mean values 11 ha for occupied patches and 3 ha for unoccupied ones, were found in Sala (Åberg 2000). In the two less intensively managed landscapes, Aasla and Sala, patch size was the most important factor influencing hazel grouse occurrence, explaining ca 55 and 25% of the variation, respectively.

The effects of matrix and landscape composition

A distinct matrix effect was found for the occurrence of hazel grouse in an agricultural dominated landscape and in a managed forested landscape (Åberg et al. 1995). The distances between occupied habitat patches differed 10–20-fold, with pronounced isolation effects at 100–200 m across farmland and at ca 2 km within managed forests. In the two less intensively managed forested landscapes, the island Aasla and Sala, no clear effects on hazel grouse patch occupancy due to habitat isolation (distance) were found. That was not surprising, however, because the maximum distance between habitat patches in these landscapes was only about one quarter of the threshold distances found in the intensively managed forest landscape (Åberg et al. 1995). Nevertheless, at Aasla, isolation occurred as a barri-

er effect, with habitat patches surrounded mainly by forest being more often occupied than patches surrounded by open agricultural land. Such a barrier effect, i.e. rather due to matrix type than to true patch isolation, was also evident in Sala, where increased amounts of clear-felled areas within a radius of 800 m significantly reduced the patch occupancy rate.

Accuracy of habitat suitability model predictions

The proportion of correctly predicted presences and absences of hazel grouse in patches in the intensively managed forest in Bergslagen was 73 and 55%, respectively (Åberg et al. 2003), when using the tree age and deciduous component criteria of Swenson and Angelstam (1993) separately. When combining the two habitat criteria, 65% of the patches were correctly predicted. The best model accuracy showed when the criteria for hazel grouse stands contained 5–40% deciduous trees with the age of 20–70 yr or older than 90 yr. In other words the stands should not be heavily thinned and hold developed field layer structures with relatively rich vegetation including herbs and *Vaccinium* species, and moreover, the stands should preferably include alder (Åberg et al. 2003).

The occurrence of hazel grouse in habitat patches in the less intensively managed Sala study area was well predicted by the models based on data from a managed forest landscape in Bergslagen (Åberg et al. 2000b), and from the island Aasla (Saari et al. 1998), with 84 and 86%, respectively, correctly predicted. The fit to the Aasla model was strong, the slope of the regression line was close to 1 and the intercept close to 0, whereas the managed forest model was statistically less precise, with the slope significantly different from 1 and the intercept from 0. The difference between the two model predictions indicates the difficulties to apply knowledge received in a given study to other landscapes or regions.

Discussion

Requirements at multiple scales

The hazel grouse studies reviewed here exemplify a systematic approach that makes it possible to formulate management recommendations. First, habitat selection and behaviour at the home-range scale was studied and described. Then, using that knowledge, the occurrence of the species was analysed from landscape ecological points of view, the response of the hazel grouse to different landscape settings was investigated and finally, the models were tested in an independent landscape.

The preferred habitat of hazel grouse in managed boreal forests consists of unthinned, middle-aged (or older than 90 yr) spruce-dominated stands, with a marked deciduous component including alder and a rich field layer (Åberg et al. 2000b, 2003). Patch size is positively related to occupation rate by hazel grouse, with > 20 ha needed when isolated patches are surrounded by open land and > 10 ha within forests. Within hazel grouse territories, however, few clear patterns relating to its habitat utilization were found, although we used a long-term dataset and detailed vegetation descriptions (Åberg et al. 2000a). This was probably due to the generally high suitability and small variation within that particular study area.

As for many other species habitat preferences, for example expressed as the tree species used, vary for the hazel grouse within its range of distribution (e.g. Fujimaki 2000, Fuller 2002). While in the boreal forest the hazel grouse is a bird of mixed stands, in central Europe the hazel grouse has the highest densities in coppice forests or stands that constitute only deciduous tree species (Suchant 1995). For the hazel grouse, it thus appears as if the vegetation structure of the habitat forms the important cue for selection, rather than which specific tree species it is composed of.

The required patch size varied with the type of surrounding habitats, with larger patches needed when the matrix was open land compared to when it was non-habitat forest. The ecological mechanism behind this pattern has not been studied in the hazel grouse. However, in the former case, patches must include all the year-around needs of individual hazel grouse, whereas within forests movements outside the actual patch to meet changing seasonal needs can more easily be made (Swenson and Danielsen 1995).

Matrix type was an important factor influencing the occurrence of hazel grouse in patches. The effect of isolation was evident over much shorter distances when patch surroundings constituted farmland than managed forest, where the matrix was unsuitable habitat (Åberg et al. 1995). Patch occupancy was strongly affected by habitat type both within and directly surrounding the patch (Saari et al. 1998, Åberg et al. 2000b), as well as by the composition of the entire landscape (Åberg et al. 1995, 2000b, 2003).

Hazel grouse and forest management

Management for the conservation of a focal species based on systematic studies of habitat specialists, such as the hazel grouse, should often also favour other species in boreal forests (Mikusiński et al. 2001, Jansson and Andrén in press, Roberge and Angelstam 2004). Two different analyses showed that the occurrence of hazel grouse was positively correlated with resident bird species richness in managed forests (Jansson and Andrén in press).

Although suitable habitat (see above) is a prerequisite for the existence of hazel grouse, the studies in different landscapes made it possible to determine the importance

Table 1. General criteria for high occupancy rate by hazel grouse in habitat patches. The column Mixed refers to fine-grained forest/farmland landscapes. The numbers refer to the studies defining the criteria, respectively, where [1] Åberg et al. 1995, [2] Åberg et al. 2000b, [3] Saari et al. 1998, and [4] Åberg 2000.

Variable	Matrix dominated by Open land	Mixed	Managed forest
Patch size	>20 ha [1]	>10 ha [3, 4]	>10 ha [1, 2]
Patch isolation	<200 m [1]	<800 m [3, 4]	<2000 m [1, 2]

of some landscape ecological parameters such as patch size and isolation and type of matrix in the landscape. In managed forest landscapes, core areas of habitat patches should be > 10 ha. In landscapes where the habitat is surrounded by open land, patch sizes should exceed the home range size, i.e. at least 20–40 ha must be suitable habitat.

Hazel grouse movements appear to be strongly influenced by the type of matrix. Therefore, to promote hazel grouse populations, habitat patches in agricultural landscapes should not be separated by > 100–200 m of open land, whereas habitat patches in intensively managed forests can be separated by up to 2 km of nonhabitat forest. In addition to the patch criteria showed in Table 1 and regardless of landscape type, however, the higher the proportion of forest immediately surrounding habitat patches, the better.

The planning of forest management aimed to maintain viable hazel grouse populations could be improved if the Swedish forest stand descriptions also included measurements of shrub vegetation cover, field-layer vegetation and the occurrence of alder.

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Occurrence of mammals and birds with different ecological characteristics in relation to forest cover in Europe – do macroecological data make sense?

Grzegorz Mikusiński and Per Angelstam

Mikusiński, G. and Angelstam, P. 2004. Occurrence of mammals and birds with different ecological characteristics in relation to forest cover in Europe – do macroecological data make sense? – Ecol. Bull. 51: 265–275.

We explored the usefulness of large-scale coarse data sets to study relationships between the regional presence of forest-living birds and mammals with different area requirements, and the degree of historical forest loss on the European continent. We used a limited set of vertebrate species that differ in their body size and position in the trophic level, both factors of which affect the area requirements of species. We then tested the prediction that large and/or specialised carnivorous vertebrates are more affected by forest loss at the regional scale than smaller species with an omnivorous or herbivorous diet. The occurrence of birds and mammals in a 50 × 50 km Universal Transverse Mercator (UTM) grid cell system was extracted from two recently published European Atlases of geographic distribution of species. The forest cover was deduced from the Remote Sensing Forest Map of Europe that classifies each square km to three coarse classes: forest, other land and water. Due to very different landscape histories and natural conditions in the Mediterranean region of Europe, we limited our analysis to the temperate and boreal forest zones both in lowlands and mountains.
Six pairs of species predicted to show different sensitivity to forest loss were analysed. Our results suggest that the degree of forest loss in Europe had a much stronger negative effect on the present occurrence of large and/or specialised carnivorous vertebrate species than on smaller and omnivorous/herbivorous species.

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Habitat loss is the major factor affecting directly or indirectly the global decline of biodiversity (Heywood 1995, Wilcove et al. 1998, Fahrig 2001). Being complex to measure directly, biodiversity trends are often monitored as the extent and rate of species extinctions (Groombridge 1992, Reid 1992, Hawksworth 1995, Chapin et al. 2000).

Therefore, species' responses to habitat loss are a central issue of contemporary conservation biology (Ehrlich 1995, Sih et al. 2000, Fahrig 2001). Hence, with a biodiversity conservation perspective, the evaluation of hypotheses claiming species-specific "extinction thresholds" defined as the minimum amount of habitat required for the

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persistence of species in the landscape (Lande 1987, Andrén 1994, Fahrig 1997, 2001, 2002) is an urgent task. Apparently, human-driven landscape changes have resulted in the trespassing of such critical levels of habitat loss for many species. This has then caused local, regional or even global extinction of species. Consequently, the question "how much habitat is enough" has recently received a lot of attention, and policy makers and managers dealing with biodiversity issues urgently require answers (Higman et al. 1999, Fahrig 2001).

The responses to habitat loss vary a lot depending on the species (Andrén 1994, 1997, Fahrig 1997, 2001, 2002, Mönkkönen and Reunanen 1999). A major aspect to consider is the life history of the species in question, such as its reproductive rate, mobility, home range and the degree of specialisation (Melian and Bascompte 2002). The habitat-species relationship may have a linear character where the population decline is proportional to the habitat loss. However, there is growing evidence from empirical and theoretical studies for non-linear relationships (Fahrig 2002), suggesting that populations may react to habitat loss proportionally only up to a certain level (the critical threshold). If habitat loss continues beyond this level, the response is much more rapid, and eventually ends up with extinction (Hanski 1999).

Critical thresholds for habitat loss have been demonstrated in a wide range of studies using theoretical models. Two kinds of thresholds have been addressed: 1) the fragmentation threshold, which is the amount of habitat below which habitat fragmentation (spatial pattern) may affect population persistence and 2) the extinction threshold, which is the minimum amount of habitat below which the population goes extinct. While the former appears for several vertebrate species to occur at ca 20% habitat, there is no common extinction threshold value across species, and such values may range from 1 to 99% habitat, depending on the parameter values (Fahrig 2001). Along with habitat loss and matrix quality, much attention has been drawn to habitat fragmentation, i.e. the spatial arrangement of remaining habitat (Andrén 1994, Bascompte and Solé 1996, Haila 2002). However, the modelling work by Fahrig (2001) showed that a shift from extremely high fragmentation to extremely low fragmentation resulted in only a 6% decrease in the mean extinction threshold. Hence, habitat loss appears generally more important than habitat fragmentation as a predictor of species' existence in landscapes (McGarigal and McComb 1995, Fahrig 2001, 2002).

The need of knowledge concerning species' responses to habitat loss and its practical use is emphasised in the management of forest biodiversity (Duinker 2001, Angelstam et al. 2001, Boutin and Hebert 2002). Because responses to habitat loss vary among species, a solution based on the precautionary principle is to focus on analysing species that are the most sensitive ones to human-caused habitat loss (Angelstam et al. 2003). The adaptation of management practices to the identified critical thresholds of such focal species would possibly ensure the existence of similar, but less sensitive species of the same habitat (e.g., Lambeck 1997, Roberge and Angelstam 2004).

In Europe, the original forest cover under present climatic conditions has been estimated to ca 90% (Huntley and Birks 1983, Perlin 1989). After a very low level in the beginning of the 20th century today's forest cover is presently slightly > 30%. Consequently, the remaining amount of forest and its distribution pattern is closely related to the historic development of human societies on the European continent (McNeely 1994). Large areas of formerly forested land have been converted to agricultural land, urban areas and different types of infrastructures (Darby 1956, Thirgood 1989). According to Hannah et al. (1995) the loss of intact natural forests amounts to 80% for the boreal, 98% for the hemiboreal and 98.8% for the lowland broad-leaf forests. Additionally, due to a very complex and diverse history of forest use in Europe, the forests range qualitatively from artificial plantations of exotic species to large wilderness areas with little human impact (Angelstam et al. 1997). The majority of the remaining forests are highly fragmented, and larger contiguous forest massifs are only found in northern and north-eastern Europe, as well as in mountainous areas in central Europe (Riitters et al. 2000).

Species' responses to the loss and alteration of European forest have been documented at different spatial scales (e.g., Berg et al. 1995, Storch 1997, Tucker and Evans 1997, Breitenmoser 1998, Mikusiński and Angelstam 1998, Kouki and Väänänen 2000, Bengtsson et al. 2000, Martikainen et al. 2000). However, to address regional problems of decreasing biological diversity, macroscopic studies that trade off the precision of small-scale experimental science to seek robust solutions to big problems are required (Brown 1995). The loss of habitat in general is a good example of such a big problem. Unfortunately costs and logistics limit the spatial and temporal range of application of replicated experiments. For example, when analysing the amount of sufficiently large habitat patches for forest specialists Mykrä et al. (2000) found that they are limited for most species, and hence also for experimentation. Consequently, studies that examine the effects of forest loss at the landscape scale within ecoregions are not at hand. At this macroscale, the occurrence of vertebrate species with large area requirements appears to be an appropriate response variable. The recent publication of maps describing the detailed distribution of birds and mammals in Europe (Hagemeijer and Blair 1997, Mitchell-Jones et al. 1999) provides an opportunity to study the impact of coarse-grained forest loss on species throughout the European continent.

In this first exploratory study, we test the idea that forest-living species having different ecological characteristics exhibit different relationships between their present occurrence and the degree of forest loss at the scale of landscapes

among regions in Europe. We begin by using a limited number of mammal and bird species that differ both in their body size and trophic level (i.e. herbivores, omnivores, and carnivores), both factors of which affecting their area requirements. The species chosen are or were widely distributed in Europe in historic times (Glutz von Blotzheim and Bauer 1980, Holloway 1996, Hagenmeijer and Blair 1997, Mitchell-Jones et al. 1999, Boitani 2000, Breitenmoser et al. 2000, Swenson et al. 2000). We predict a stronger negative response of large and/or specialised carnivorous vertebrates to the forest loss measured at regional scale than for smaller species and/or being at lower trophic levels.

Study area

Our study area is the central and western parts of Europe within the boreal and temperate deciduous forest biomes (Jahn 1991). Because the Mediterranean part of Europe is characterised by both very different natural conditions and has had a much longer land use history than the rest of the continent, we excluded this part from our analysis (Fig. 1). Due to limited extent of detailed data on vertebrate distribution in the atlases of vertebrates, the eastern boundary of our study area is delineated by eastern national borders of Bulgaria, Romania, Hungary, Slovakia, Poland, Baltic countries, Finland and Norway (Fig. 1).



Fig. 1. The extent of the study area (marked in dark shade).

Material and methods

The data on the spatial distribution of vertebrate species was extracted from two recently published European atlases describing the occurrence of species of birds and mammals in the 50 × 50 km Universal Transverse Mercator (UTM) grid cell system (Hagemeijer and Blair 1997, Mitchell-Jones et al. 1999). In order to explore variation in species-specific responses to forest loss, 12 species representing carnivores, omnivores and herbivores with different body size and area requirements were selected. The examined species constituted six pairs located along the two gradients, namely body mass difference and the gradient in diet from herbivory to carnivory (Table 1 and Fig. 2).

Paper maps showing the distributions of species were scanned and saved as images. Next, the images were georeferenced in a Geographic Information System (ArcView-ESRI) to fit the digital map with 50 × 50 km UTM grid cell system over Europe. With the images as background, the grid cells were manually assigned to the different cate-

Table 1. The characteristics of species and number of atlas plots with presence and absence of particular species (body mass data from Haftorn 1971, Bjärvall and Ullström 1985).

Pairs of species	Body mass (kg)	Diet	Sample size (absence, presence)
Hazel grouse *Bonasa bonasia*	0.4	herbivorous	785, 730
Capercaillie *Tetrao urogallus*	4.8	herbivorous	854, 662
Roe deer *Capreolus capreolus*	25	herbivorous	190, 1389
Moose *Alces alces*	600	herbivorous	1002, 577
Great spotted woodpecker *Dendrocopos major*	0.1	omnivorous	76, 1488
White-backed woodpecker *Dendrocopos leucotos*	0.1	carnivorous	1223, 295
Red fox *Vulpes vulpes*	8	carnivorous	78, 1501
Wolf *Canis lupus*	55	carnivorous	1120, 459
Pine marten *Martes martes*	1.8	carnivorous	317, 1264
European lynx *Lynx lynx*	30	carnivorous	1009, 570
Badger *Meles meles*	17	omnivorous	224, 1355
Brown bear *Ursus arctos*	230	omnivorous	1134, 445

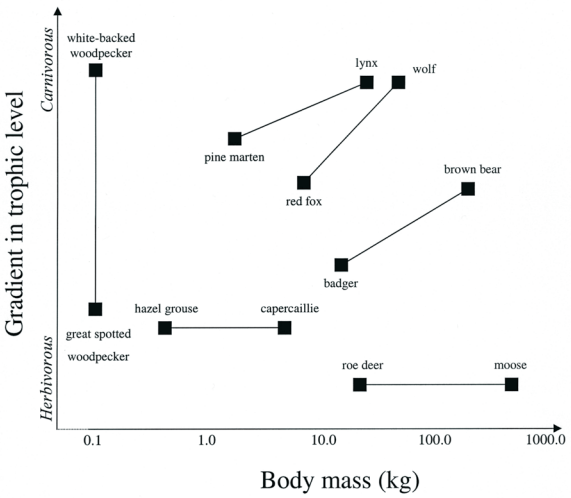


Fig. 2. Pairs of species located along two gradients (trophic level and body size). Larger and/or more carnivorous species from each pair are expected to react more negatively to forest loss. Body mass is shown in logarithmic scale.

gories of species presence. Each cell in the maps of species distribution was originally classified into one of four classes in the case of birds (present, possible, not known, absent) and one of three classes in the case of mammals (present, presumed, absent). More detailed description of original distribution classes for birds and mammals is provided by Hagemeijer and Blair (1997) and Mitchell-Jones et al. (1999), respectively. For the purpose of this study, we pooled the classes "present", "possible" and "presumed" into one new class "present". The classes "absent" remained unchanged in both data sets, while in the case of birds, the class "not known" was excluded from the analysis.

As our source of information about forest cover in Europe we used the Remote Sensing Forest Map of Europe that classifies each square km to three coarse classes: forest, other land and water (Anon. 1992). It is based entirely on the digital classification of National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR) one-kilometre resolution multispectral data, using ca 70 scenes from the summer periods of 1990 to 1992. As such, the European Forest/Non-forest Digital Map is reasonably up-to-date, and most importantly based on a homogeneous data source. The producers of the digital map used only data from AVHRR channels 1, 2 and 3 with "maximal geometric and radiometric resolution" to map European forest areas greater than one square kilometre. Because the AVHRR sensor is not capable of distinguishing among different forest types, all forest classes were grouped together as "forest" in the digital map.

The Remote Sensing Forest Map of Europe was used to calculate the forest cover in 50 × 50 km atlas plots. The presence/absence data for each species was then compared with the proportion of forest in the atlas plots. Since land proportions in plots adjacent to coasts were in some cases quite low we decided to filter out all plots with < 50% land area. After this adjustment, in the case of mammals a total of 1579 atlas plots entered the analysis. Because in the bird atlas the category "not known" was species-specific, the number of atlas plots used in analyses varied among species (from 1515 to 1564) (Table 2).

To enable preliminary exploration of associations between the different degree of forest loss and the occurrence of vertebrates, we calculated proportions of atlas plots with species presence in 10 forest cover classes (< 10%, 10 < 20%, 20 < 30%, 30 < 40%, 40 < 50%, 50 < 60%, 60 < 70%, 70 < 80%, 80 < 90%, 90 < 100%) (Table 2). We interpreted species' incidences in particular forest cover classes as a measure of sensitivity to historical forest loss at the regional level. Classes where presence exceeded absence (> 50% presence) were treated as classes with high probability of species occurrence. Next, we optically compared and discussed pairs of incidence curves that described presence/absence of species in the above classes. The binomial 95% confidence intervals of the mean for each class were used to assess the significance of observed contrasts between species.

Results

In all six examined pairs we found generally lower incidence levels across forest cover classes in larger species and/or more specialised carnivorous species (Figs 3a–f).

Table 2. Number of atlas plots within different forest cover classes used for the analysis at the species level.

Species	Forest cover (%)									
	0 < 10	10 < 20	20 < 30	30 < 40	40 < 50	50 < 60	60 < 70	70 < 80	80 < 90	90 < 100
Mammals	479	227	173	138	121	111	89	93	97	51
Great spotted woodpecker	476	224	172	137	117	110	88	92	97	51
White-backed woodpecker	461	220	161	131	115	104	88	90	97	51
Hazel grouse	460	218	163	132	116	103	85	90	94	51
Capercaillie	460	220	162	131	117	105	86	87	97	51

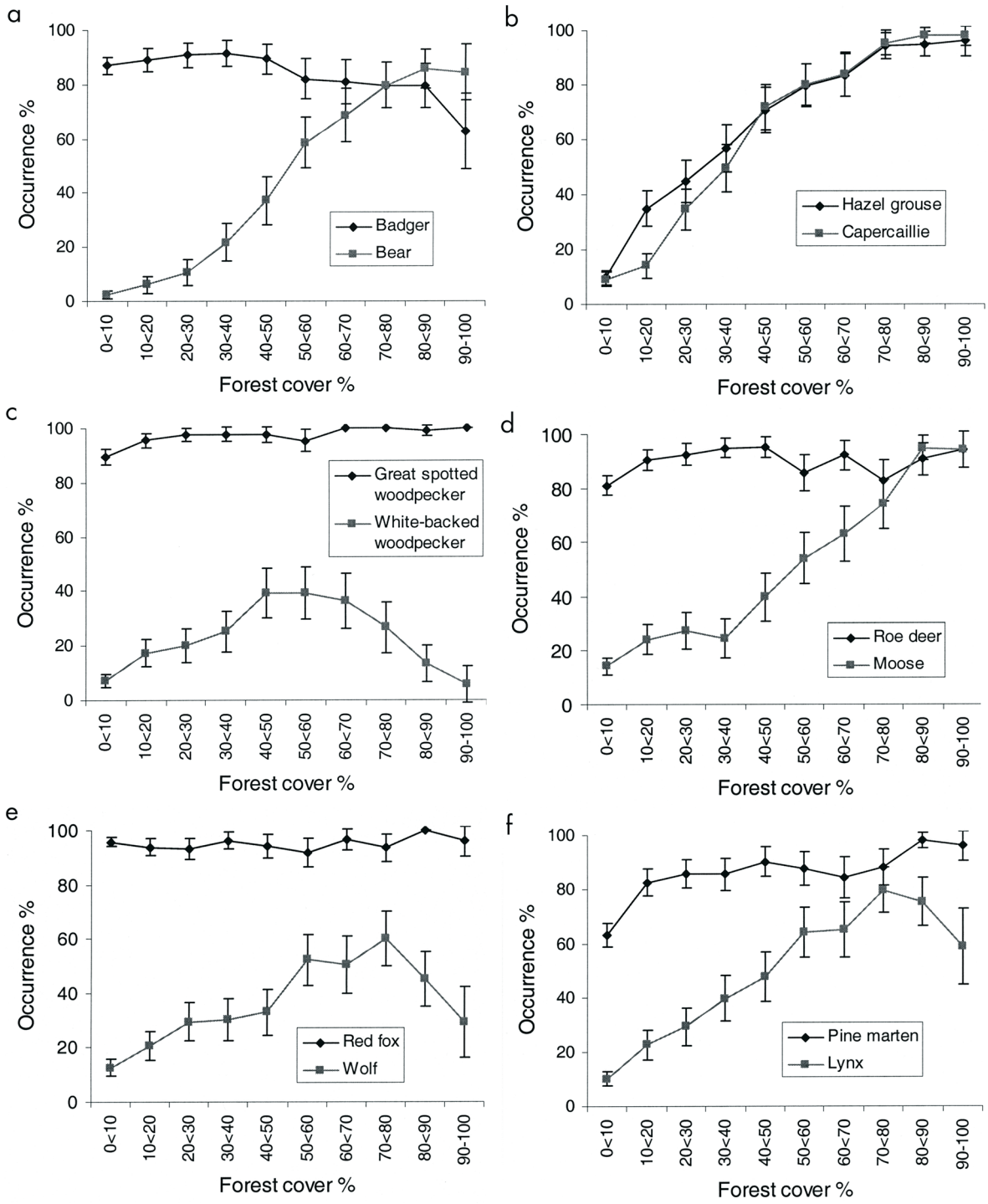


Fig. 3a–f. Occurrence of species in atlas plots with different amounts of forest cover (bars indicate binomial 95% confidence intervals of the mean).

In the first pair (Fig. 3a), the occurrence of badger showed a weak relationship with forest cover, with a tendency for more absences in highly forested landscapes. By contrast, the much larger brown bear had a high probability of occurrence only in plots with > 50% forest cover. In the case of two herbivorous birds (hazel grouse and capercaillie), the probability of occurrence in both species increased steadily with forest cover (Fig. 3b). A forest cover of > 30–35% was sufficient for high probabilities of occurrence.

The two species of woodpeckers considered in this study manifested very different patterns (Fig. 3c). The omnivorous great spotted woodpecker had very high probability of occurrence in atlas plots in all forest cover classes. By contrast, for the white-backed woodpecker both highly forested and open plots were associated with low probability of occurrence. Plots with 40–70% forest cover had the highest probability of species occurrence.

The probabilities of occurrence across different forest classes in a pair of mammalian herbivores with a large difference in body size (moose and roe deer) were quite dissimilar (Fig. 3d). The probability of roe deer occurrence was high everywhere with only marginally lower values in the plots with a very low forest cover. By contrast, moose exhibited continuous increase in incidence level along with increasing forest cover crossing the 50% probability limit at a 55% forest cover.

Red fox and wolf, two related carnivorous mammals with different body size, expressed quite different relationships with forest cover (Fig. 3e). Red fox occurred quite independently of forest cover. The frequency of occurrence of the more area-demanding wolf increased up to 50% with increasing forest cover. A further increase in forest cover was associated with a decline of the probability of occurrence.

The incidence curves for two other mammalian predators with different body size (pine marten and lynx) are shown in Fig. 3f. The smaller pine marten occurred commonly in plots within the entire range of variation in forest cover. However, the probability of occurrence declined slightly in plots with < 10% forest cover. For the lynx, we observed a linear increase of probability of occurrence up to 80% forest cover. The probability reached the 50% threshold at 45% forest cover.

Discussion

Pair wise comparisons

Our results suggest differentiated sensitivity of species with different life-history traits to forest loss at the scale of landscapes in regions in Europe for all the six pairs of species. In general, as predicted large and/or specialised carnivorous vertebrates exhibited stronger relationships with the degree of forest loss expressed by present forest cover. Responses of smaller and/or herbivorous and omnivorous species to forest cover were weaker, if any. The pair-wise comparisons indicate that both body size, as well as trophic position of the species are important traits that matter for the response of species to regional forest loss.

In most of the studied pairs smaller species showed a much higher incidence in highly deforested landscapes. This was found for herbivores (roe deer and moose, Fig. 3d), omnivores (badger and brown bear, Fig. 3a) as well as for both pairs of carnivores (red fox and wolf, Fig. 3e; pine marten and lynx, Fig. 3f). Our comparison of species with similar size but different diet (great spotted and white-backed woodpecker) also confirmed the prediction. In the case of woodpeckers, the omnivorous species being also a generalist in other respects of its life-history (Angelstam and Mikusiński 1994) had a very high probability of occurrence in all classes of forest cover. The highly specialised white-backed woodpecker did never reach a high probability of occurrence in any of the studied forest cover classes. In this case, the deterioration of habitat quality seems to be of greater importance than the pure forest loss measured at this scale (cf. Martikainen et al. 1998).

Species specific responses to forest loss

Among the vertebrates considered in this study, the results suggest three different patterns in species' sensitivity to large-scale forest loss in Europe. The first group consists of species that were able to cope successfully with this process, i. e. their probability of occurrence in all forest cover classes was not < 50%. In this group we found medium sized herbivores (roe deer), smaller and medium sized omnivores (great spotted woodpecker and badger), and finally smaller and medium sized carnivores (pine marten and red fox). In the case of great spotted woodpecker, roe deer and red fox the observed probability of occurrence was very high in all forest cover classes. The great spotted woodpecker, being the least specialised among the European woodpeckers, has been found to be little affected by qualitative and quantitative changes in European landscapes also in other studies (Mikusiński and Angelstam 1997, 1998). As a middle-sized habitat generalist the roe deer has been able to successfully adapt to a whole range of landscapes also including open agricultural land (Mitchell-Jones et al. 1999). The red fox is an opportunistic, mammalian predator with a high reproduction rate and occurs in the whole range of landscape types (Kurki et al. 1998). The negative effects of forest loss and fragmentation on pine marten have been described at a range of spatial scales (Brainerd 1990, Kurki et al. 1998). Our study, which was performed at a very coarse scale, indicated only slightly lower incidence in highly deforested atlas plots. Although the badger did not indicate any sensitivity to forest loss in our study, an other investigation has shown negative effects of forest fragmentation in landscapes with < 20% forest cover (Vir-

gos 2001). On the other hand, a lower probability of occurrence in highly forested regions in our study is in accordance with Kowalczyk et al. (2000).

The second group consists of species that have been negatively affected by large-scale forest loss and its secondary effects. These were herbivores (hazel grouse, capercaillie and moose), the omnivorous brown bear, and the large predator lynx. Both bird species are resident habitat specialists, requiring a mixture of different forest components within their home ranges (Wegge and Rolstad 1986, Swenson and Angelstam 1993, Storch 1997). These qualities can hardly be provided in sufficient amount in managed landscapes with low forest cover. There are several other studies that found negative effects of forest loss and deterioration on these species at different scales (Rolstad and Wegge 1987, Åberg et al. 1995, 2000, Storch 1997, Kurki et al. 2000). Being a habitat generalist with a very large body size, the moose was clearly affected by forest loss in Europe. Being earlier widely distributed across the continent, reduced forest cover along with hunting pressure have apparently made most of the European regions unsuitable for this species (Mitchell-Jones et al. 1999). Also the present distribution of the brown bear in Europe is restricted to highly forested regions. The former distribution range of that species in Europe covered the entire continent including the British Islands (Jakubiec 1993). A clear impact of the amount of forest cover on the regional brown bear distribution was recently found in Slovenia (Kobler and Adamic 2000). Using a spatially explicit model that included forest cover (positive), proximity to human settlements (negative) and altitude (positive) the authors were able to predict the occurrence of the species in the south-western part of Slovenia with an 87% accuracy. Also lynx was in historic times widely distributed in continental Europe (Breitenmoser and Breitenmoser-Würsten 1990). The result of our study shows a clear increase of the probability of occurrence up to 80% forest cover. The relatively lower probability of occurrence above this level is explained by the absence of the species in several highly forested regions in Sweden where lynx is absent due to extirpation in the nineteenth century (Liberg 1997). Interestingly, in southern Sweden where today's hunting is very limited and food availability high, the species is rapidly extending its range (Andrén pers. comm.). Another large-scale investigation on the potential suitability of central European landscapes for an introduction of lynx has recently been presented by Schadt et al. (2002). Also here, only large, intact forest tracts were found to have a high probability of the occurrence of the species.

The third group consists of species that have been affected by forest loss but the pattern of the species response to forest cover indicates a strong influence of other additional factors. To this group belong two very different predators, namely the white-backed woodpecker and the wolf. The white-backed woodpecker is a habitat specialist relying on all year round access to large quantities of dead deciduous wood (Cramp and Simmons 1985, Angelstam et al. 2002a). Due to both forest loss as well as intensive forest management, such habitats are highly fragmented in Europe (Wesołowski 1995, Carlson 2000). Therefore, it is unlikely that any level of forest cover in our study can provide conditions leading to a high probability of occurrence of this species. The highest level is reached in regions with 40–70% forest cover, which coincides with areas with less intensive forest management due to both natural conditions (mountains) or historic development of intensive forest management (eastern Europe) (Mikusiński and Angelstam 1998). Obviously, both highly deforested regions in Western Europe, as well as highly forested but intensively managed regions in e.g. Fennoscandia do not provide enough habitat of sufficient quality for this species. The other species that clearly was influenced by factors other than pure forest loss in our study was the wolf. No class of forest cover provided very high probabilities of occurrence of this species. This pattern may be explained by successful persecution of this formerly widely distributed species in large parts of the continent (Zimen 1978). Therefore, even regions with very high forest cover (Fennoscandia) are only partially inhabited by the species, which explains the decline in the probability of occurrence in forest cover classes >80% observed in our study. The present development of the wolf's conservation status is positive with population and range expansion observed in Scandinavia (Wabakken et al. 2001). In contrast, the situation of the white-backed woodpecker in this region is expected to deteriorate even further (Carlson 2000).

Forest cover, habitat quality and human pressure

Measuring overall forest cover is a very crude method for assessing the effects of habitat loss on biodiversity. Similar forest covers among landscapes in the same ecoregion may in reality provide quite different amounts of suitable habitat for the species (Dudley 1992, Larsson et al. 2001). This is largely due to the fact that forests in landscapes with different management regimes may be very dissimilar. In Europe for instance, forests range from artificial plantations of exotic species to nature reserves or national parks with qualities similar to those found in naturally dynamic forest landscapes (Angelstam et al. 1997, Tucker and Evans 1997). In addition, the spatial distribution of forest patches within a 50×50 km grid cell used in this study may be quite different even if the cover is the same (cf. Trzcinski et al. 1999). Therefore, measuring just the forest cover is necessary but not sufficient to estimate the relationships between habitat loss and forest species. Still, however, the degree of forest loss, forest habitat quality and the degree of human pressure seem to correlate with each other in Europe (Angelstam et al. 1997, Mikusiński and Angelstam 1998). In Europe, larger forest tracts occur in less accessi-

ble areas like the mountains or in eastern Europe, regions that due to the historic development have experienced less massive human impact (Gunst 1989). Similarly, in the peripheral northern parts of the continent where the intensive forest management arrived very late and human population densities never reached high numbers, more natural features can be found today (Korpilahti and Kuuluvainen 2002). Such regions provide forested landscapes with qualities similar to those found in naturally dynamic counterparts, and these may be used as reference areas or benchmarks for forest biodiversity (Angelstam et al. 1997). We argue that at least in the western, central and eastern part of our study area, the higher forest cover is usually associated with a larger amount of natural forest qualities being of importance for the maintenance of forest biodiversity. The situation is somewhat different for Fennoscandia, where intensive forestry operations have been covering very large forest tracts (Larsson and Danell 2001, Korpilahti and Kuuluvalainen 2002).

The future of large and specialised forest vertebrates

The maintenance and restoration of forest biodiversity in Europe is a challenge both for science and management (Angelstam et al. 1997, 2001, Glück 2000, Bengtsson et al. 2000, Larsson et al. 2001). In the case of forest vertebrates being sensitive to forest loss, both theoretical considerations as well as practical measures have been undertaken on continental, national and regional levels. In particular, several action plans at various spatial scales have been established for large carnivores, the group of species that evidently suffers from forest loss in Europe (Corsi et al. 1998, Farmer et al. 1999, Schadt et al. 2002). The potential use of larger vertebrates as indicators for the conservation of forest biodiversity in Europe has been widely discussed (Wallis de Vries 1995, Linnell et al. 2000, Angelstam et al. 2001, Mikusiński et al. 2001).

In this study large or ecologically specialised forest vertebrates at all trophic levels were sensitive to large-scale forest loss and its secondary effects in Europe. The ongoing afforestation of European landscapes thus provides an opportunity to rehabilitate or even re-create components of forest biodiversity lost due to human impact (Nilsson et al. 1992, Rabbinge and Van Diepen 2000, Mikusiński and Angelstam 2001, Angelstam et al. 2002b). It seems that larger vertebrates not being habitat specialists may readily respond to increased forest cover (Mikusiński 1995). In the case of species being Man's competitors or game species, a lowered level of persecution or hunting pressure must accompany this process (Breitenmoser 1998, Wabakken et al. 2001, Schadt et al. 2002).

However, for many habitat specialists, a simple increase of forest cover is often not enough to secure their revival. Here, a restoration of the forest cover with sufficient quality as well as conservation of valuable remnants is necessary. Successful restoration means that forests should have an adequate amount of dead wood in different qualities, different representative successional stages, a untruncated patch size distribution, presence of very big and very old trees and sufficiently connected networks of habitats.

Conclusions

Our exploratory use of macroecological data to describe relationships between the occurrence of species and their principal habitat (forest) gave promising results. Results for the very limited number of species presented here, suggest that large or specialised European forest vertebrates persist mostly in regions with a forest cover of 50% or more in the landscape. However, this investigation ought to be developed further by incorporation of more species, and by inclusion of other factors potentially affecting the occurrence and fitness of species' populations. Such variables could include the presence of predators and competitors in the atlas plots, the spatial arrangement of forest patches within and across atlas plots, the presence of human infrastructure (e.g. roads, railways), regional history of species exploitation and persecution and other factors. Also, life-history traits of the investigated species should be carefully considered.

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Assessing landscape thresholds for the Siberian flying squirrel

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Reunanen, P., Mönkkönen, M., Nikula, A., Hurme, E. and Nivala, V. 2004. Assessing landscape thresholds for the Siberian flying squirrel. – Ecol. Bull. 51: 277–286.

We examined the relationship between the probability of Siberian flying squirrel *Pteromys volans* occurrence and the amount of mature spruce-dominated forest habitat in a boreal forest landscape in northern Finland. We used three different methods for assessing critical landscape thresholds with reference to spatial scale. First, we carried out a broad-scale landscape analysis to estimate the relationship between mature forest cover and the occurrence of the Siberian flying squirrel regionally. Second, we collected data on the presence/absence status of the species in forest patches in four different study areas. We used these data to determine the critical amount of habitat required for the long-term persistence of the species by applying Lande's demographic model. Finally, we introduced a hierarchical moving window analysis to determine landscape thresholds in a landscape where the species was intensively studied.
Our results suggest that there should be 12–16% spruce-dominated forest habitat for the occurrence of the Siberian flying squirrel. In the regional landscape composition analysis there was > 10% of mature forest covering the area where the species was present. Lande's model suggests that critical extinction thresholds in our four study landscapes are at 11.6–15.6% habitat of the total land area. In a moving window analysis, the landscape threshold for the intensively studied area was 12.2%. Additionally, the probability of occupancy in a landscape window dropped < 0.5 when the amount of unsuitable open areas exceeded 60% of the area. However, it is questionable if the amount of habitat alone in a landscape can be used for assessing landscape thresholds. Additionally, structural landscape connectivity and matrix characteristics are likely to affect the distribution patterns of the Siberian flying squirrel in northern Finland.

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The amount of habitat that needs to be sustained for dynamic populations to persist over a predicted time frame has become a central issue in conservation biology. Habitat loss and fragmentation of natural landscapes have been recognised as a severe threat to biodiversity (Saunders et al. 1991). This has recently prompted a discussion about the critical amount of habitat that should be left intact and about landscape thresholds, below which level of habitat availability populations decline and finally run a risk of extinction (see e.g. Fahrig 1998). Viable populations of all organisms require habitat where reproduction is successful and conditions for survival at any part of their life history are favourable. However, species vary conspicuously in their habitat affinities (Andrén et al. 1997) making it difficult to assess landscape thresholds for species in general. This question has to be addressed species-wise by focusing first on the rare and most demanding ones (Mönkkönen and Reunanen 1999), which requires a detailed body of knowledge of the species' ecology, including habitat requirements, movement ecology and distribution patterns.

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Approaches and theories

One possible way to address critical thresholds in landscapes is to simulate landscape patterns using neutral landscape models (Gardner et al. 1987). Neutral models do not include any explanatory factors, such as ecological processes, that influence the emerging spatial pattern (Caswell 1976). Randomly generated landscapes have, nevertheless, revealed that changes in landscape structure may produce critical thresholds where formerly undivided landscapes turn into fragmented ones with increasing habitat loss. For example, percolation theory suggests that a random landscape becomes disconnected when > 40% of the original habitat is lost (Gardner et al. 1987, With et al. 1997). In fractal landscape models, where spacing and aggregation of landscape elements can be simulated, the corresponding threshold level for the proportion of habitat in landscapes settles between 30 and 50% (With and Crist 1995, With and King 1999a). Also, the hierarchical structure of the landscape patterns is likely to affect the percolation threshold and, hence landscape connectivity (O'Neill et al. 1992). Neutral models serve principally as null models for comparisons with real landscapes and for assessment how changes in landscape structure with increasing fragmentation are likely to affect ecological processes (Caswell 1976, With and King 1997).

Lande's (1987) analytical model is one potential way to estimate a critical threshold for territorial animals in fragmented landscapes. His model is based on a modification of Levins' metapopulation model and requires information on the total amount of focal habitat in an area and the proportion of occupied habitat patches. With this information, the "demographic potential", i.e. the maximum proportion of habitat patches that would be occupied at the equilibrium in original stage of the landscape, can be calculated. Lande's model has been applied, for example, to estimate the amount of habitat required for the long-term persistence of the northern spotted owl *Strix occidentalis caurina* in the Pacific Northwest (Lande 1988).

Spatially explicit simulations have also been used to assess landscape thresholds. These models have indicated that the effects of habitat loss alone are far more important for the extinction risk of species than habitat fragmentation (Fahrig 1992, 1997). Fahrig (1998, see also 2001) showed that fragmentation causes population declines only under relatively limited conditions including factors concerning both landscape structure and species life-history characteristics. According to her simulations, species prone to fragmentation 1) have a limited dispersal ability, 2) prefer habitat, which covers < 20% of the area, 3) do not prefer ephemeral habitats, 4) are territorial and show strong site-fidelity and 5) have a clearly higher mortality rate in the landscape matrix than within the preferred habitat. Habitat loss and the emerging fragmentation effect have also been suggested to be dependent on landscape context (Mönkkönen and Reunanen 1999, Lindenmayer et al. 1999) and species' habitat affinities and other life-history characteristics (Andrén et al. 1997, Bender et al. 1998).

Empirical approaches

In real heterogeneous landscapes, habitats are often patchily distributed. Human-induced changes in habitat quantity result in a further subdivision of habitat patches in space and create fragmented landscape patterns. So far, too few empirical studies are available to draw firm conclusions on the critical thresholds for population persistence in such landscapes. Andrén (1994) reviewed empirical studies on birds and mammals and suggested that below certain threshold levels in the availability of the original habitat, population densities declined faster than predicted from pure habitat loss. He proposed that when the fragmentation threshold has been exceeded, the relationship between the amount of suitable habitat and the population size is non-linear. Further, other landscape characteristics, such as the spatial arrangement of habitat patches and their isolation, hasten the decline. For birds and mammals in general, this threshold seems to lie somewhere between 10 and 30% (Andrén 1994), but far-reaching recommendations from such estimates for landscape management has to be drawn carefully because of, for instance, significant changes in habitat patterns and landscape context among regions (Harrison and Bruna 1999, Mönkkönen and Reunanen 1999).

An appropriate way to analyse landscape thresholds empirically for a species within a geographic region is to compare several independent landscapes and quantify population densities and the proportion of focal habitat there. Another way is to use a natural habitat gradient, which extends over a region, and then to quantify trends in the amount of habitat and population size. These methods are likely to be useful for some well known taxa only, because of difficulties in censusing the population numbers accurately at broader scales. Also, the replication of habitat patterns at a landscape scale is seldom possible. With modern remote sensing techniques, it is feasible to quantify the habitat in the area, but in order to accurately and reliably determine the status of the species in a vast area requires more sophisticated sampling schemes.

The species

The Siberian flying squirrel *Pteromys volans* is a threatened boreal forest species in Finland and its population has been declining since the 1950s (Hokkanen et al. 1982). Being a rare forest-dwelling species, the flying squirrel has become a focal species in sustainable forest management in Finland and its persistence in commercial forests is considered important. The species is also listed in EU's habitat directive

as a priority species. Therefore, the assessment of landscape patterns and threshold conditions for the species is needed for maintaining viable flying squirrel populations. The prime habitat for the species is mature spruce and spruce-dominated mixed forests, which is the principal habitat type for breeding. Occupied forest sites are typically characterised by closed canopy cover and the presence of cavity trees (Hanski 1998, Reunanen et al. 2002a). The Siberian flying squirrel forages on leaves in summer and hoards catkins for the wintertime. Therefore, the presence of a number of deciduous trees is also typical of occupied forest sites. However, the Siberian flying squirrel regularly visits other mature and middle-aged forested habitat for foraging and when moving between spruce-dominated forest patches. It only avoids open areas and sapling stands (Reunanen et al. 2000, Selonen et al. 2001). The largest male home ranges are > 100 ha, the annual average being 60 ha for males and 8.3 for females (Hanski et al. 2000, Reunanen et al. 2002a). The female home ranges do not overlap, whereas males tend to share habitat patches, especially the ones occupied by the females (Hanski et al. 2000). The young disperse in autumn on average a distance of 2.5 km, with females moving longer distances than males. The maximum observed dispersal distances are up to 9 km (Selonen 2002).

Study objectives

In this paper, our aim is to assess landscape thresholds for the Siberian flying squirrel in northern Finland with reference to different spatial resolution. We report findings of using different methods to assess critical landscape thresholds and discuss their applicability. First, we have carried out a broad-scale landscape composition analysis to determine landscape characteristics that are linked with the species regional occupancy pattern. Here we use data on regional habitat patterns to estimate the relationship between mature forest cover and the occurrence of the Siberian flying squirrel in a region with a spatial extent of several thousands of square kilometres. Second, we collected data on the presence/absence status of the species in forest patches in four study areas, several hundreds of square kilometres in size. Here, we use these data to determine the critical amount of habitat required for the long-term persistence of the species by applying Lande's (1987) model. Finally, in order to tackle the problems of quantifying and sampling an extensive area, we introduce a hierarchical moving window analysis to assess landscape thresholds in an intensively studied landscape (137 km^2).

Landscape threshold as a concept has several alternative meanings. First, it may refer to the level of habitat availability, below which population density and species presence is no longer a linear function of habitat area. This can be called the fragmentation threshold. A second threshold level in habitat availability lies at the point below which a population is determined to extinction. Because habitat fragmentation can compound the effect of pure habitat loss, populations may go extinct even if suitable habitat still exists. This can be called the extinction threshold. Our approaches are based on qualitative presence/absence status of the species in an area or in a forest patch. Therefore, in this paper, we define a landscape threshold as an estimate of the minimum amount of habitat in a landscape needed for the species to be present there, i.e. extinction threshold.

Methods and results

Regional landscape composition analysis

We compared three different regions in the middle and northern boreal vegetation zones in northern Finland. The total area of this study covered ca 40 000 km^2 (Fig. 1). The regions were delineated by their topographic variation and edaphic conditions. The westernmost region (West) is situated on flat terrain and is characterised by large amounts of peatlands (open fens, bogs). We defined the eastern region (East) to encompass areas east from the westernmost large lakes in the region (see Mönkkönen et al. 1997, Reunanen et al. 2002b). East and West are located on low altitudes (< 50 m a.s.l.), whereas intermediate higher, hilly areas (> 200 m a.s.l.) characterise the central region (Central).

The three regions differ considerably from each other in the estimated population densities of the species. During systematic old-growth forest inventories on public land in Finland in 1993–1996, the Siberian flying squirrel was recorded in 90 old-growth remnants (Rassi et al. 1996). No observations were made in the West, even though 470 km^2 were surveyed. In the Central region, 70 old-growth areas were occupied (820 km^2 surveyed), and in the East the species was recorded in 20 old-growth remnants (1580 km^2 surveyed). We combined the results from the old forest inventories carried out in 1993–1996 (Rassi et al. 1996) with our fieldwork in 1995–1998 (Mönkkönen et al. 1997, Reunanen et al. 2002b) on a map using 10 × 10 km UTM grid cells. In the West, all the 114 10 × 10 km UTM grid squares were unoccupied, but 46 and 9 of the 129 and 119 squares were occupied in the Central region and in the East, respectively. The three regions differed significantly from each other in terms of the occupancy level ($\chi^2 = 67.7$, DF = 4, $p < 0.001$), and the range of densities, from no observations in the West, through moderate in the East, to relatively high in the Central region could be identified.

Correspondingly, the amount of mature forests (total timber volume > 100 m^3 ha^{-1}) vary among these regions from < 10% in the West to 17.2% in the East and 14.2% in the Central region. The proportion of spruce-dominated forests of all mature coniferous forests is highest in the Central region (Fig. 2; Reunanen et al. 2002a, b). In the West, landscapes were generally characterised by open land

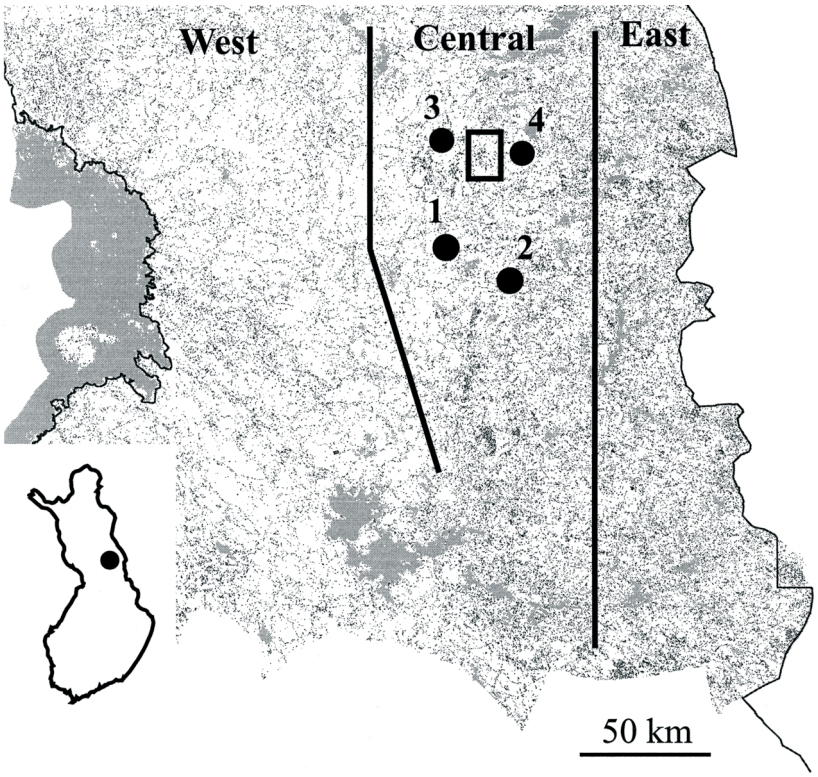


Fig. 1. Our study areas in northern Finland. West, Central and East refer to regional scale studies. Circles denote study areas where independent landscapes were sampled (1 = Puhos, 2 = Metsäkylä, 3 = Syöte and 4 = Salmitunturi). The rectangle shows the location of the intensive study area. Shaded spots in the background indicate mature forest stands.

(wetland areas and bogs, 40% of the land area) and sapling stands (20%). The Central and Eastern regions are principally more forested than the West, but in the Central region spruce-dominated forests cover > 50% of the total area of mature forests (Fig. 2). The regional examination is appropriate to show correspondences between broad-scale landscape patterns and population densities. The above numbers suggest that the overall coverage of mature forests should be above 10% of the total land area for the persistence of the flying squirrel. However, smaller scale examination is needed to more accurately determine critical landscape thresholds.

Comparison of separate landscapes within the Central region

We surveyed four landscapes (spatial extent from 300 to 1260 km^2) to characterise patterns of habitat occupancy by the Siberian flying squirrel in the Central region (Reunanen et al. 2002c). All study areas have been managed by clear-cutting since the 1950s and 1–2% of the forest land is presently harvested annually. The areas were selected to ensure large variation in the amount of spruce-dominated forest habitat (Fig. 1, Table 1). In each area, we first identified forest patches characterised by mature spruce forest. Habitat patches < 1 ha were omitted. Spruce forest habitat was defined by adjusting classification criteria for these specific landscapes (total timber volume > 100 m^3 ha^{-1} and spruce/deciduous tree proportion of the timber volume > 80%) and, therefore, the landscape classification is not exactly the same as in the previous regional scale analyses. In

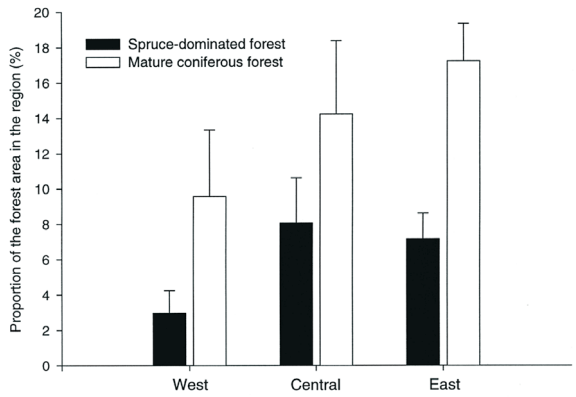


Fig. 2. Proportion of the spruce-dominated forest and the mature coniferous forest (mean and SD) in the regional landscape composition analysis. Note that the bar showing the proportion of the spruce-dominated forest in the regions is included in the bar showing the total amount of mature forest.

Table 1. Study areas in the central region, their size, the amount of preferred habitat for the Siberian flying squirrel and the proportion of occupied patches. Lande's extinction threshold was calculated from the data shown in the table.

Study area	Landscape extent (ha)	Area in patches (ha)	Proportion of the landscape (%)	Number of studied patches	Occupancy (%)	Lande's extinction threshold
1. Puhos	29200	4220	14.5	39	61.5	5.60
2. Metsäkylä	31900	8322	26.0	63	39.7	15.67
3. Syöte	126200	24450	19.3	48	39.6	11.65
4. Salmitunturi	47900	9812	20.5	57	35.1	13.30

these study areas the average patch size ranged from 32 to 56 ha. A stratified random sample of patches was visited in the field and the presence/absence of the species was checked in selected habitat patches. Presence/absence status of the habitat patch was based on faecal droppings that typically accumulate under the spruce and aspen (cavity) trees in occupied forest sites (see Reunanen et al. 2002a). Due to the broad-scale sampling, all inhabited habitat patches were likely to be occupied by different individuals. Our studied landscapes contained 14.5–26.0% of spruce-dominated forest habitat for the Siberian flying squirrel (Table 1). The proportion of occupied habitat patches was fairly constant among the four study areas varying from 35.0 to 39.7% except in Puhos where 61.5% of patches were observed occupied (Table 1).

We applied Lande's model to assess critical extinction thresholds in these study areas. The equilibrium occupancy of habitat patches can be calculated from the equation:

$$p = 1 - (1 - k)/h, \text{ for } h > 1 - k$$
$$p = 0, \text{ for } h \leq 1 - k$$

where h refers to the proportion of target habitat in an area, p is the proportion of currently occupied territories (patches), and k is the proportion of territories that would be occupied by females in a completely suitable area (the demographic potential). Demographic potential can be estimated if p and h are known:

$$k = 1 - (1 - p) \times h$$

Because all the habitat patches are not occupied at one time, it is possible to estimate the proportion of unoccupied habitat patches and how much the remaining patches cover of the area by solving (1–k), which is the critical proportion of habitat necessary for long-term population persistence.

Lande's (1987) model suggests that critical extinction thresholds in the study areas are at 12–16% of the total land area, but for Puhos it is at 6%. Lande's model assumes that populations are in equilibrium, i.e. that the present distribution of individuals reflects the current capacity of the landscape to maintain a flying squirrel population. In our areas, logging is an ongoing process and forests in study areas are harvested annually. Therefore, the landscape is under a continuous change and the equilibrium assumption does not necessarily hold true. In addition, a snapshot of a declining trend can be misleading due to a time-lag in population responses to landscape change and may underestimate the critical extinction thresholds. Therefore, threshold values estimated here have to be carefully considered. Lande's model is simple and easy to interpret, but the accuracy and usefulness of the model depends on how precisely the parameters h and p can be estimated empirically.

Moving landscape window analysis

In the moving window procedure we first delineated a landscape of 370 km^2 (Fig. 1) and determined spruce-dominated forest patches using a similar landscape classification as in the previous landscape comparison. In this study area, we surveyed all patches (n = 136) for the presence of flying squirrels. The study area comprises 17.6% spruce-dominated forest habitat suitable for the Siberian flying squirrel. In the study area, the average size of a habitat patch was 48.5 ha and the mean distance to the nearest neighbouring patch 217 m. The mean distance between the two nearest occupied habitat patches was 395 m and, therefore, it is unlikely that the individuals occupy more than one habitat patch. Forty-eight patches (35%) were observed occupied.

To assess critical landscape thresholds for the species in this area, we used a moving window analysis to determine, first, the appropriate scale at which landscape thresholds should be analysed and, second, how much spruce-dominated forest habitat within a moving window there is at that given scale. To approximate the adequate scale we used landscape windows of different sizes (side lengths 100, 200, 500, 1000, 2000, 4000 m). The spatial arrangement of the habitat patches was not quantified. In the moving window analysis, a landscape window was first superimposed on a corner of the study area and then systematically moved over the entire study area. At each step, the proportion of spruce-dominated habitat was quantified and the status of the species recorded. In the consecutive steps, windows did not overlap each other. A landscape window was assigned occupied if it encompassed an inhabited patch or a part of it.

We plotted the proportion of occupied squares at each scale against the size of the window to assess a relevant scale for our landscape analysis (Fig. 3). The idea was that using too large a window would result in all or most windows being occupied, whereas too small a window size would include too low amount of occupied windows. In either case, the power of the statistical analyses would be inadequate. The proportion of occupied squares evidently increases with an increasing size of the landscape window, exceeding 50% at ca 1000 m side length (Fig. 3). Landscape windows (100–200 m in side length) turned out to be too small and mostly contained either close to 0 or 100% of target habitat. Large windows (2000–4000 m side length), in turn, were too large for the observed patch density (actual landscape resolution) in the study area and, thus, became mostly occupied. Therefore, we selected the 1000 × 1000 m window size for further analyses. At this scale, the amount of habitat in a landscape window varies gradually between zero and 90%. This scale also matches well with the home range size and space use patterns in the Siberian flying squirrel.

We regressed presence/absence data against the amount of spruce-dominated forest habitat in a moving window to see how the probability of a window being occupied depended on the habitat availability. We also ran a similar analysis for the combined proportion of open areas and sapling stands to yield estimates of landscape threshold for this habitat type. We excluded those windows from the analysis that did not contain any habitat for the species and were by definition unoccupied.

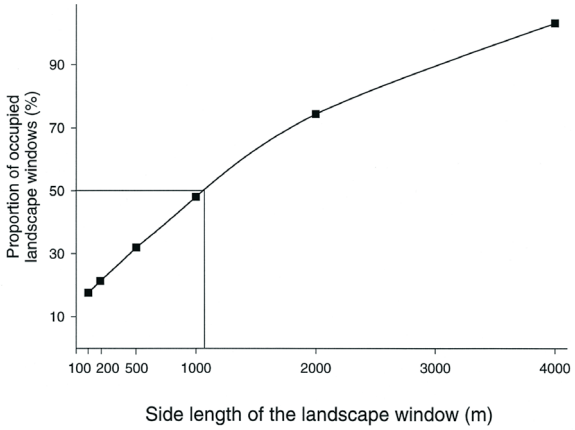


Fig. 3. Proportion of landscape windows that were assigned occupied at different scales. Half of the windows become occupied when the side length of the window was 1063 m.

The results showed that the probability of a moving window to be occupied increases with habitat availability (Table 2, Fig. 4). The probability exceeds 50% when there is 12.2% spruce-dominated habitat in the window (Fig. 4). The relationship was reversed when regressed against the proportion of open areas and sapling stands (Table 2). The probability of finding an occupied patch in a 1 km^2 landscape window falls below 50% when the amount of those habitat types exceeds 60% (Fig. 5). It is notable, however, that the proportion of spruce-dominated forest habitat yields more accurate predictions of the occupancy status than the proportion of open habitat types. Deviances of the models differ significantly ($\chi^2 = 41.9$, DF = 1, $p < 0.001$) and the rate of correct predictions is 76 vs 69% in the models (Table 2). Results of the moving window analysis match surprisingly well with estimates for other study areas in the Central region based on Lande's model (11–16%, Table 1). Lande's extinction threshold for the study area where the moving window analysis was carried out was 11.4%.

Discussion

Population turnover in habitat patches at the broad scale stems from repeated extinction and colonisation events, i.e. classical metapopulation dynamics. At the individual scale, habitat patch turnover reflects birth and death rates in a habitat patch, but also the spatial rearrangement of home ranges. The distinction between the population scale

Table 2. Regression coefficients (B), their significance levels, and the constant term for the variables in the logistic regression models. The deviance indicates the model fit. The models for the proportion of the habitat and open area within the landscape window differ significantly ($\chi^2 = 41.9$, DF = 1, $p < 0.001$). Proportion of correctly predicted cases and the amount of false positive and negative predictions measure the classification accuracy.

Variable in the model	B	DF	Sign.	Deviance	Correctly predicted (%)	False positive (%)	False negative (%)
Habitat within landscape window (%)	8.52	1	0.000	238.68	76.13	17.0	34.0
Constant	–1.08						
Open area (ha)	–0.04	1	0.000	280.61	68.72	27.6	40.6
Constant	2.71						

and the scale of processes that concern individuals is important, because they determine the potential causes leading to true fragmentation effects, i.e. more dramatic population declines than expected by pure habitat loss alone (Andrén 1994). From an individual perspective, a landscape becomes fragmented when habitat patches become too small to contain a home range or the distances between habitat patches are beyond the dispersal capacity of the species. Populations show fragmentation effects when divided into local, relatively independent, sub-populations where survival and reproductive success are dependent on patch size and their recolonisation on isolation. These mechanisms are essential to critical landscape thresholds and the long-term persistence of the populations. In this paper, the regional scale comparison clearly concerns the scale of populations, while the landscape-scale analyses single populations and, hence, habitat patches occupied by individuals.

The regional comparison suggested that at least 14% of the total area should be covered by mature forests for flying squirrel persistence. The species was absent from the western region, where the proportion of mature forests was < 10%. At the broad scale, landscape composition thus seems to account for the species' absence in the West. Spruce-dominated forest habitat for the Siberian flying squirrel is scarce and embedded in unsuitable open areas (ca 60% of the area in the West is covered by open non-forested habitat). The moving window analysis also suggests that if at the local scale, open areas cover > 60% of the area habitat patches are likely to be unoccupied. These results are parallel with the predictions of the percolation theory. However, very broad-scale examination of landscapes can easily generalise habitat patterns too much and underestimate their spatial variation locally. Local habitat patterns vary considerably due to microclimatic and edaphic conditions. The species is regularly distributed throughout the Central region where the proportion of spruce-dominated forests is highest. Landscape level analyses in this region, based on Lande's model and the moving window analysis, suggest that spruce-dominated forests should cover at least 12–16% of the landscape.

In our four study areas in the Central region, the amount of spruce-dominated forest habitat ranged from 14.5 to 26%. However, the occupancy rate of habitat

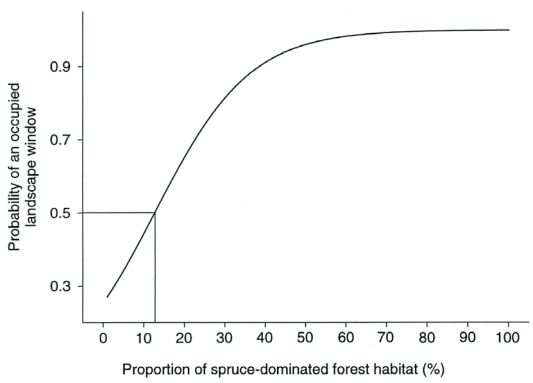


Fig. 4. The proportion of the spruce-dominated forest habitat in a landscape window and the probability of an occupied landscape window. The probability of 0.5 was used as a cut-point in the logistic regression to indicate species occupancy.

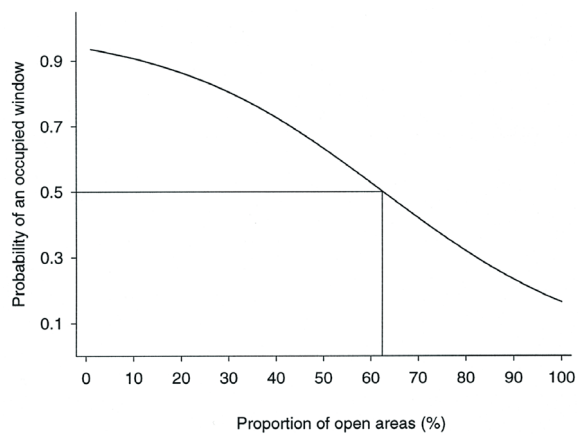


Fig. 5. The proportion of the open areas in a landscape window and the probability of an occupied landscape window. The probability of 0.5 has been used as a cut-point in the logistic regression to indicate species absence.

patches was rather equal among the study areas except in Puhos (35–40%, and 62% respectively). The Puhos area, where the proportion of occupied patches was the highest but the habitat availability the lowest, has the longest history of modern forestry. Large areas were managed already between the 1940s and 1960s, and consequently, young forests comprise a high proportion of the total land area. The young forests are in most cases pine plantations and, therefore, are not likely to be used by the Siberian flying squirrel as a breeding habitat (lack of cavity trees and deciduous trees). The other three areas consist of larger amounts of the spruce-dominated forest habitat and recently harvested stands. The higher amount of young forests (suitable for dispersal) in the Puhos area is likely to increase the landscape connectivity. Our earlier analyses have suggested that landscape connectivity contribute to the spatial pattern of occupied habitat patches (Reunanen et al. 2002c).

Our analyses were based on presence/absence data, which is a potential source of error. Changes in local population densities may take place well before any changes in the patch occupancy emerge. Therefore, presence/absence data may underestimate critical landscape thresholds, i.e. overestimate population viability. However, because two of our analyses were carried out at the scale of individual home ranges, presence/absence data are not likely to cause a major underestimation. Densities are not likely to vary much within smaller habitat patches because particularly females occupy mutually exclusive territories (Hanski et al. 2000). Only in larger patches (several tens of hectares), which may contain several home ranges, changes in density may be difficult to observe in our data. The possibility for underestimation of a landscape threshold must, however, be kept in mind when interpreting the results.

In our study areas, the Siberian flying squirrel does not perfectly fit to the five conditions for a fragmentation prone species as suggested by Fahrig (1998). 1) The average dispersal distance of the Siberian flying squirrel is 2.5 km, which is six times longer than the average distance between two nearest occupied habitat patches (ca 400 m) in our study area, and suggests that the species is a better disperser than a fragmentation-prone species. 2) 17.6% of the study area consists of good quality habitat for the species, which is < 20%. 3) Breeding habitat of the Siberian flying squirrel, i.e. mature spruce-dominated forest, is in principle not ephemeral from the perspective of an individual or a few generations. 4) Females seem to be territorial and occupy the same breeding area annually. 5) Survival probabilities of the Siberian flying squirrel in different habitats are not known precisely, but survival is very likely lower in landscape matrix than in the prime habitat.

Three of these conditions hold for the Siberian flying squirrel, but regarding the dispersal ability and survival in landscape matrix, it seems that the species is not as demanding as species susceptible to fragmentation. Therefore, according to these criteria the Siberian flying squirrel can be considered moderately prone to fragmentation of its prime habitat. The species' ability to disperse relatively long distances and its use of various habitats, indicates that it is not much affected by fragmentation and is adapted to move in landscapes that are to some extent fragmented. Reunanen et al. (2002c) found that not only patch size and quality, but also landscape connectivity are important landscape characteristics increasing the probability of a habitat patch being occupied. This suggests that there might be a threshold distance the species is not likely to cross in non-forested areas. Therefore, successful patch occupancy dynamics may depend on landscape context and sharp contrasts between forested habitat types and open areas, which, in turn, are not directly related to the amount of target habitat in the area.

It is, therefore, likely that the proportion of spruce-dominated forest habitat alone, is not the only determinant of the capacity of a landscape to maintain sustainable populations. The landscape matrix plays an important role in population dynamics and in inter-change of individuals among habitat patches. Quality of the landscape matrix improves connectivity, thus, promoting dispersal of many species (Taylor et al. 1993, Merriam 1995, With and King 1999b). However, the contrast between habitat types in a landscape and the permeability of habitats is dependent on how species perceive them (Lima and Zollner 1996). Therefore, landscape structure in general and the sharpness of landscape boundaries (Wiens et al. 1985) is likely to affect the critical amount of habitat in a landscape. At a regional scale, the amount of open areas i.e. landscape context, rather than spruce-dominated forest habitat tend to account for the absence of the Siberian flying squirrel.

Assessment of critical landscape thresholds normally refers to the habitat availability only, while information on dispersion and spatial arrangement of key habitat patches is not used in analyses. It is somehow paradoxical that only the habitat availability but not the spatial arrangement of the habitat is considered, because the definition of the critical landscape threshold is based on the premise, that below the fragmentation threshold the spatial arrangement of habitat patches becomes an important determinant for population persistence. Ecological conditions, such as landscape context and contrast between two habitat types, may be critical to some species even though there would be much habitat left. Depending on the landscape characteristics and species responses to them, it would be more adequate to speak about a threshold zone. The landscape threshold zone allows the landscape threshold value to vary for a given habitat availability, with the spatial context of that habitat in the landscape. There is a consensus that there are differences in species' habitat affinities and their habitat requirements are likely to affect species' critical landscape thresholds. Therefore, habitat loss effect is always species-specific, but due to variation in landscape patterns, may also be landscape-specific (Mönkkönen and Reunanen 1999).

Our regional scale analysis was carried out at the scale of populations, whereas landscape analyses at habitat patch scale focused on individuals. Regional scale analysis gives an overview of landscape characteristics that are likely to be good candidates to explore in more detail in the landscape threshold analysis. Population viability, however, stems from reproductive success and survival of individuals, and, therefore, local scale information of critical landscape characteristics is more important to apply in forest landscape planning. Our results suggest that home ranges are not established if there is < 12–16 ha of spruce-dominated forest habitat within a one square kilometre block of forest landscape. Our results suggest that it is likely that a landscape threshold for the Siberian flying squirrel exists, but it is unclear to what extent other landscape characteristics, such as landscape matrix, affect landscape threshold estimates. Management recommendations stemming from the current analysis should also include information on temporal changes in population size and environmental stochasticity, which may cause local extinctions even if habitat availability is above the extinction threshold. Therefore, we suggest that the amount of spruce-dominated forest habitat should cover > 12–16% of the total forest area, say, 25–30% (the probability of occurrence is 0.9 when 38% of the landscape window is covered by the focal habitat) to allow the long-term persistence of local populations of the Siberian flying squirrel in northern Finland.

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Ecological Bulletins 51: 287–294, 2004

Habitat requirements of the pine wood-living beetle *Tragosoma depsarium* (Coleoptera: Cerambycidae) at log, stand, and landscape scale

Lars-Ove Wikars

Wikars, L.-O. 2004. Habitat requirements of the pine wood-living beetle *Tragosoma depsarium* (Coleoptera: Cerambycidae) at log, stand, and landscape scale. – Ecol. Bull. 51: 287–294.

The occurrence of the threatened wood-living beetle *Tragosoma depsarium* (Coleoptera: Cerambycidae) was investigated in a 560 km^2 forested area in the mid-boreal zone in west-central Sweden. Twenty 1 km^2 squares of managed forest were searched, together with two 1 km^2 nature reserves and some smaller protected forest areas. The beetle bred in bark-free, sun-exposed, large diameter pine-logs. Several successive generations of beetles had bred in logs formed from old trees (>200 yr), but only one generation in younger trees. Logs formed by younger trees had quickly developed an unsuitable brown-rot, and the type of wood-decay in logs was obviously of importance for the species. Most occurrences were found on clearcuts, especially those with seed-trees left. The species could also be found in pine forests with a naturally sparse tree-layer. It was never registered inside protected forests, but sometimes at their south-facing edges. At the landscape scale the occurrences correlated positively with the amount of mature forest per square. The study area may contain one of the largest populations of the species in Europe outside Russia. However, seemingly suitable pine logs lacked *T. depsarium* in large areas, which indicate that the population suffers from habitat fragmentation. In the last ten years, the amount of old pine forest has decreased by 25% in the study area, so the species may decline rapidly in the near future. To prevent this, there is probably a need for larger forest reserves in which fire is reintroduced. Additionally, in managed forest where this and other threatened species still occur, tree retention of both live and dead pines has to become much more frequent during forest operations than it is today.

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Human impact on boreal forests has substantially decreased the amount of coarse woody debris (Siitonen 2001). A great number of species depend on dead wood and other old-growth characteristics. In Sweden there are ca 1000 wood-living beetle species of which ca 350 are on the national red-list (Gärdenfors et al. 2000). The reason for their decline is the lack of dead wood, both in terms of amount and quality (Jonsell et al. 1998). To reduce the negative impact of forestry on biodiversity a number of measures has been taken. The last ten years of modern forestry has to a varying degree adopted measures for increasing the amount of habitat for threatened species. These include e.g. retention of living trees and dead wood during clearcutting, active creation of dead wood both during thinning and clearcutting, and set-aside areas such as key-biotopes (Larsson and Danell 2001). Also, the amount of protected forest in nature reserves is increasing (Löfgren 1997).

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Although these measures are performed at large scale with considerable costs both to forestry and the community (Larsson and Danell 2001), there is also a possible risk that the measures taken are of too low quality and/or amount to reduce the extinction risks for threatened species. Hanski (2000) suggests that many threatened species in the boreal forest will face delayed extinctions because of their small and fragmented populations. He also emphasises that conservation measures in forestry may be too diluted in time and space to favour specialised species. Therefore, it is probably a great need for improvement of conservation measures in forests. To be able to achieve this we need to know more about the occurrence and habitat needs of threatened species.

This study focuses on the beetle *Tragosoma depsarium* L., whose larvae develop in pine-logs. It has been widely distributed over most of Sweden, but today it has a very fragmented distribution (Gärdenfors et al. 2002). The species is believed to be highly favoured by disturbances such as forest fires. Possibly, felling operations may mimic natural disturbances and create habitats for the species (Ehnström 1999). Here I report a study of the distribution of the species in a large forested area, and relate its distribution to forest characteristics at log, stand, and landscape scale. A major question is how well the present conservation measures, both in managed and protected forest, favour the species.

Methods

Biology of the species

The long-horn beetle *Tragosoma depsarium* (Coleoptera: Cerambycidae) breed in logs of coniferous trees. It is a large species (body length 20–35 mm) that creates easily identified holes through the wood surface when the adult emerges. Also the larval tunnelling inside the wood creates marks that are species characteristic (Ehnström and Axelsson 2002). The development takes four years or more (Palm 1951). It can develop in quite recently killed and fallen trees, but also in very old logs (>100 yr since tree death) (Palm 1951). In Sweden Scots pine *Pinus sylvestris* L., or rarely Norway spruce *Picea abies* Karst., are used for development. The species prefers large diameter, bark-free, and sun-exposed logs (Palm 1951, Löyttyniemi 1967, Gärdenfors et al. 2002), but no quantitative data exist.

The species has a Holarctic distribution. It does not occur close to the Scandinavian mountain range, probably because of too cold climate (Wikars 1997). In most of western Europe it is considered to be very rare. In Sweden, Norway and Finland it is currently classified as a vulnerable species, according to the IUCN-system for red-listed species (Gärdenfors et al. 2002). The main reason for its decline is considered to be the lack of wind-felled pine trees and exclusion of forest fires (Ehnström 1999).

Study area

The study was conducted in a 56 000 ha area in Norra Ny parish, county of Värmland in west-central Sweden (60°N, 13°O), (Fig. 1). The study area is located in the mid-boreal zone (Ahti et al. 1968). The forest is pine-dominated. Bogs and lakes make up ca 10% of the area. From north to south the area is divided by the river Klarälven (Fig. 1). Villages, agricultural land and Norway spruce forests dominate along the river, whereas the surrounding forested hills are very sparsely populated and less intensively managed (Ehrenroth and Schützer 1996). More than 90% of the land is privately owned, and modern forestry has, until recently, to some extent been hampered by complex ownership patterns. According to the forest inventories made on private land by the National Board of Forestry in 1980–1985 >20% of the pine-forest is 120 yr or older. In comparison, the average for the rest of central Sweden is 6% (Ehrenroth, Regional Board of Forestry, Karlstad, pers. comm.).

Species survey

The survey of *T. depsarium* was primarily done in twenty 1 km^2 squares of managed forest in which all pine-logs capable of holding the species were investigated. These 1 km^2 squares were grouped four and four in each of five 25 km^2 squares that were distributed over the study area (Fig. 1). Additionally, two 1 km^2 large nature reserves with old-growth pine-forest were surveyed. Furthermore, 25 key-biotopes, i.e. small forest stands with high conservation value supposed to be set-aside on voluntary basis (Nitare and Norén 1992), were surveyed. This was done to further investigate the value of protected forests as habitat for the species. About one third of the key-biotopes were situated within the 1 km^2 squares and the rest within a 500 m distance.

Prior to the major field work, a detailed study was done in two steps to find out in what kind of logs and stands the species is occurring. Firstly, two known occurrences of the species (information from the Regional County administration) within the study area were visited, and characteristics of logs with and without the species were registered. The result showed that a log being suitable for *T. depsarium* is at least 15 cm in diameter (without bark and at breast-height), bark-free, and not located in total shade.

Secondly, all types of stands were visited in the four 1 km^2 squares in one 25 km^2 square to establish in which type of stands the species is occurring. During this work all logs identified as suitable according to the above definition were surveyed and described in detail regardless of whether they contained the species or not. By using this information, the rest of the survey was to some extent concentrated to those stands that had a higher probability to contain the species. In the other sixteen 1 km^2 squares, only logs with

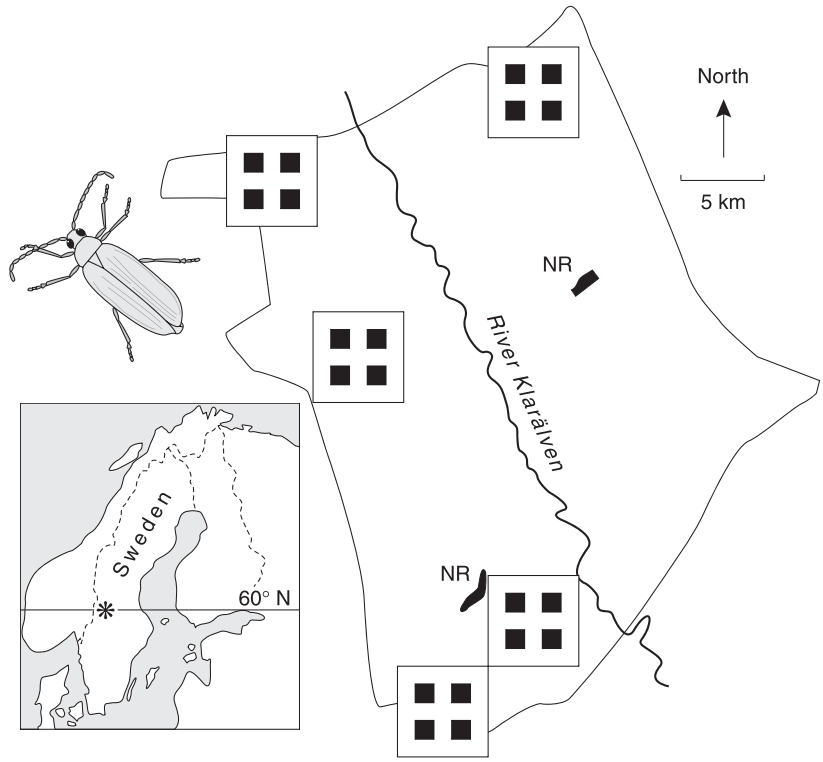


Fig. 1. The study area in Norra Ny parish. Sampling was done in twenty 1 km^2 squares distributed in five 25 km^2 squares, and in two large nature reserves (NR).

the species present were registered, due to time limits. For definition of stands, stand maps based on forest surveys made in 1987–1992 by the Regional Forestry Board, Karlstad, were used. These are in the scale 1:10 000, and they were supplemented with more recent (1995–1998) aerial photographs of the same scale.

The environment immediately surrounding the logs was registered, including stand type, forest vegetation type, and sun-exposure. Forest vegetation types were divided into three classes (modified from Sjörs 1967): dry (dominated by *Vaccinium vitis-idaea* L. and lichens on the ground); mesic (*V. myrtillus* L. and pleurocarpous mosses); and wet (*Sphagnum*-mosses in the bottom layer). Sun-exposure of the logs was subjectively judged into four classes combining information about tree height, crown cover, tree-species, compass direction, and aspect: 1) in shade; 2) some sun-exposure; 3) sun-exposed more than half the day; and 4) completely sun-exposed. Logs at edges between different stand types were specially classified. For instance, logs in forest up to about one tree-length from a clearcut were classified as "forest-clearcut edge", the first stand being the one which the log originated from. For each log the diameter without bark (at breast-height, i.e. 1.30 m from the ground level of the erect tree), length, stage of decomposition, rot-type (brown, white, or other type of rot), amount of sapwood left, ground contact (three classes <20, 20–50, or >50% of the length of the log firmly attached to the ground), and cause of tree death (if possible), were registered. For logs inhabited by the beetle, the number of emergence holes was counted. It could be judged whether these had been made during the summer, or the year before, or if they were older. The absence or presence of larvae in the logs was also registered. Some logs were dissected by saw and axe in 0.5 m sections each at breast-height and 10 m from the root, to investigate larval development stages, and their density. These logs were also cored at breast-height for age-determination, and the proportion of the tree-radius consisting of heartwood was measured. The survey was done in four week-long periods between 1 June and 29 September 1999. The 1 km^2 squares (including the reserves) were each visited between six and twelve hours.

Forest data

To be able to correlate the occurrences of *T. depsarium* with variables describing forests at the landscape scale, stand maps and digital forest survey data were used to summarise the amount of different stand types in the surveyed squares. For the twenty 1 km^2 squares the data were obtained from stand maps that had been updated during the field-study, and from aerial photographs. The area of each stand type was measured by putting a 1 × 1 cm grid over the map and counting the number of cells filled by each stand type. This was not possible for the 25 km^2 squares

due to time limits and insufficient field data, so here the digital data had to be used directly. This work was done with assistance from the Regional Forest Board and County Administration in Karlstad. The age of these data varied by seven years among different stands, but the mean for all five 25 km^2 squares corresponded to the year 1990. The following variables were analysed with respect to their proportion of the area: clearcuts 0–24 yr after final cutting, young forest (25–75 yr), mature forest (>75 yr), proportion over-mature forest (>120 yr) of all mature forest, mires, and the number of stands. The age-classes defined in the forest survey data are not exact but depend on soil-fertility. Data on the proportion of pine-dominated forest (pine ≥50% of cross-sectional stem-area at breast height of all trees) was extracted from the digital data for both 1 km^2 and 25 km^2 squares.

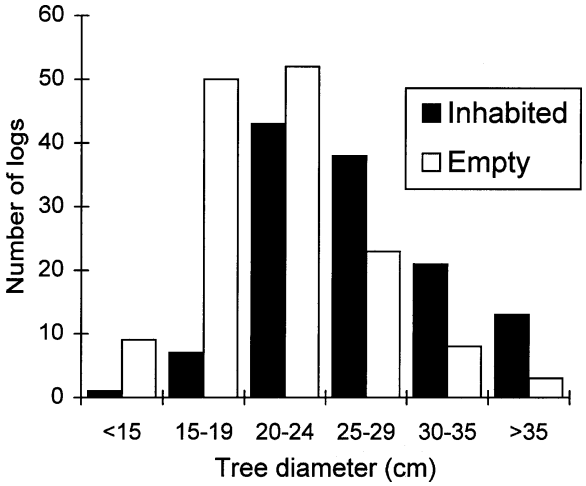


Fig. 2. The majority of logs with *T. depsarium* (60%) had a diameter of 25 cm or more without bark.

Results

Log scale

In the first four 1 km^2 squares (400 ha), 152 apparently suitable logs for *T. depsarium* were found. A total of 145 of these lacked the species, and seven were or had been colonised. In the whole survey, 123 logs with the species were found, including the nature reserves and key-biotopes (total area ca 2200 ha), of which 105 logs were found in the 1 km^2 squares of managed forest. In the analyses the 123 colonised logs are being compared with the 145 logs that lacked the species.

Tragosoma depsarium was significantly over-represented in large-diameter logs (Mann-Whitney, Z = 7.46, p <0.0001), (Fig. 2). The majority of inhabited logs (60%) had a diameter of 25 cm or more (Fig. 2). During the field-study it was also noted that where several logs were clumped, it was clearly the largest logs that contained the species. But sometimes also large-diameter logs lacked the species (Fig. 2).

Sun-exposed logs were clearly preferred (category 3 and 4, see Methods) over logs in semi-shade (category 2), (χ^2 = 26, DF = 2, p <0.0001). Logs in semi-shade constituted 50% of the logs without the species, but only 20% of the logs with the species. However, category 3 and 4 did not differ (χ^2 = 0.33, DF = 1, p = 0.33).

Most occurrences were in logs that rested on mesic vegetation (60%) whereas these logs only constituted 33% among the logs without the species (χ^2 = 7.0, DF = 1, p <0.01). The interaction between the vegetation type under the log and how firmly the log was attached to the ground seemed important. For inhabited logs, logs firmly attached to the ground were over-represented in dry and mesic vegetation (χ^2 = 7.3, DF = 1, p <0.01), whereas inhabited logs with little contact to the ground (e.g. the log was resting on other logs or stones) was over-represented in wet vegetation (χ^2 = 6.5, DF = 1, p <0.05).

The rot-type in the log affected the occurrences. If the log contained many larvae it was always still quite firm, and the wood had a pink colour. This rot-type is probably caused by wood-rotting fungi belonging to Stereaceae (Stenlid pers. comm.). On the contrary, *T. depsarium* seemed to avoid logs with brown- or white-rot. In logs rotted by the common brown-rot fungi *Fomitopsis pinicola* (Swartz:Fr.) Karst., larvae were occasionally found dead, which never happened in logs with other types of rot. The brown-rot seemed more frequent in thinner logs, and more common in shaded than in sun-exposed logs.

Logs with larvae were most often bark-free and had partially decayed sapwood but intact heartwood (between 10 and 15 yr since tree-death). More decayed logs were normally abandoned. However, decayed large-diameter logs stemming from very old trees, with exit-holes and larval tracks more than a decade old, sometimes harboured larvae and/or fresh exit-holes simultaneously (n = 3). Logs formed by younger pine-trees (<200 yr) supported only non-overlapping generations of beetles, i.e. at most 2–3 yearly larval cohorts (n = 62). The larval development had taken place only in the sapwood in logs from young trees, whereas the heartwood was used to a greater extent in logs from old trees.

Up to 30 exit-holes could be found per log. Ninety-two out of 694 exit-holes found were from the study year or the previous year. Few exit-holes were considered to be very old (>50 yr). Up to nine small to middle-sized larvae were found in 0.5 m sections, but never more than two fully grown larvae (n = 16). The number of tree-rings in cored logs with the species present was 208 (range 130–250, n = 6). The mean proportion of the radius in cross-sections being heartwood was 73% (range 65–82%, n = 16).

Stand scale

Tragosoma depsarium occurred primarily in open stands, reflecting its preference for sun-exposed logs. Most occurrences were in older clearcuts or at edges between forest and clearcuts (77%, Table 1). More than 50% of the colonised logs were storm-felled seed-trees on clearcuts. Another 20% were snags that had accidentally been felled by large vehicles during forestry-operations or had fallen naturally. Cutting debris hosted ca 20% of the records. The most important cutting debris was large-diameter logs that had been forgotten, probably due to that the logs had been covered by snow during forestry operations in winter. No pine-wood left or created as a conservation measure could be registered during the study, so there was no possibility to investigate if this could favour *T. depsarium*.

No records of the species were made inside protected forests. The key-biotopes were to a large extent dominated by Norway spruce and hence very shady. In five out of 25 key-biotopes, logs with the species were found at south-facing edges towards clearcuts or younger forest. Also in the two large nature-reserves a few records were made directly at the edges towards south, but none inside the forest. Records were sometimes made in managed mature forest (Table 1), but then in exceptionally open forests, e.g. rocky out-crop forests, forest-mire mosaics, or recently fire-affected forest.

Landscape scale

In total, 105 logs with *T. depsarium* were found in the twenty 1 km^2 squares of managed forest. The number of colonised logs found varied between 0 and 21 in the individual squares. When the number of records was correlated with the forest conditions in each square, the proportion of mature forest and the proportion of pine-dominated forest both had significant positive relations (Table 2). Of these two variables the proportion of mature forest had the highest explanatory power (Table 2, Fig. 3). If all records per 25 km^2 squares were summarised it became even more clear that most records were made where the proportion of mature forest was greatest (Fig. 3). At this larger scale the species was clearly less common when the proportion of mature forest was below 25% based on total area (or 30–35% of the forested area).

By comparing the forest inventory data from 1990 with aerial photographs and field-data from 1999 it was concluded that the proportion of mature forest in the twenty 1 km^2 squares had decreased with 25% during this ten year period. During the field-study it was noted that a large part of the recently cut forests were pine-dominated, earlier affected only by selective cutting, and probably not clearcut before.

Discussion

Clearly *T. depsarium* mainly occurs in clearcut areas in the managed forest. However, its presence also correlates positively with the proportion of mature forest at the landscape scale. One could argue that where there is most mature forest there is also most logging operations going on, creating new habitat for the species. However, then it would have been possible to detect a positive correlation between the number of records and the proportion of clearcuts, but this correlation was clearly non-significant. To explain the pattern of occurrence one need to analyse the occurrence of the species at all three studied scales; log, stand, and landscape.

At the scale of the log this study supports the earlier view that *T. depsarium* prefers large, sun-exposed and bark-free pine logs for its development (Palm 1951, Löyttyniemi 1967, Gärdenfors et al. 2002). That the species prefers logs firmly attached to the ground (Gärdenfors et al. 2002)

Table 1. Proportion of logs with *Tragosoma depsarium* present and absent. A total of 77% of the occurrences were on clearcuts or at forest edges facing clearcuts towards south. Note that logs without the species is only a subsample of all logs searched (see Methods).

Stand type	Present (%)	Absent (%)	Present/Absent
Clearcut [1]	53	27	2.0
Mature forest edge	24	10	2.4
Mature forest [2]	9	26	0.3
Mature forest-mire [3]	4	15	0.3
Clearcut-mire [3]	4	2	2.0
Mire [3]	3	5	0.6
Pre-mature stand [4]	2	3	0.7
Pre-mature stand [4]-mire [3]	1	12	0.1

[1] Including 0–24 yr old clearcuts, normally with planted forest (codes K1, K2, R1 and R2 in forest survey data). [2] Note that only open to half-open forest was included. If closed forest had been included, the proportion without the species would have been much larger. [3] Mire according to forest survey data (including tree-covered bogs, but with lower production than 1 m^3 ha^{-1} yr^{-1}). Investigated logs at edges between mire and other stand types had generally not grown on the mire. [4] Younger plantation forests 25–75 yr (codes G1-2 in forest survey data).

Table 2. Number of occurrences of *Tragosoma depsarium* in twenty 1 km^2 squares tested simultaneously for six different landscape factors (multiple linear regression).

	Range	DF	F	p	Relation
Model		6	5.62	<0.01	
Mature forest [1]	4–28%	1	7.36	<0.05	+
Overmature forest [2]	0–95%	1	1.60	0.23	+
Clearcuts [3]	9–64%	1	1.25	0.28	+
Pine-dominated [4]	15–94%	1	4.70	<0.05	+
Mire [5]	0–43%	1	3.56	0.08	–
Heterogeneity [6]	21–121	1	1.09	0.31	–

[1] Proportion mature forest of total area (including lake and mire). [2] Proportion over-mature forest (codes S2 and S3 in forest survey data) of all mature forest. [3] Proportion clearcuts (0–24 yr after final cutting, codes K1-2, R1-2 in forest survey data) of total area. [4] Proportion forested area dominated (≥50%) by Scots pine *Pinus sylvestris*. [5] Proportion mire of total area. 6) Number of stands (in forest survey data).

holds for dry and mesic vegetation types, but not for wet. This suggests that a certain level of moisture is preferred. I could also establish that the type of wood-rot is crucial for a successful larval development. Decaying wood from trees with an age of normal harvesting of ca 100 yr soon becomes affected by brown-rot fungi, which then make them unsuitable for *T. depsarium*. Older pine-trees have a higher proportion of heartwood, which makes the wood much more resistant to decay (Hillis 1987). The pink rot, which presumably is caused by some fungus belonging to Stereacae, often correlated with ongoing larval activity. This rot was also found in the heartwood. Interestingly, Stereaceae contains fungal species with symbiotic relations with insects (Lawrence and Milner 1996). Many cerambycid beetles can extract fungal enzymes from the wood into their own alimentary system, and use them in cellulose degradation (Martin 1992). If this is also true for *T. depsarium* this could be the ultimate reason for the dependence on a certain type of rot.

Most pine logs in the study area had been formed from younger 100-yr old trees. Such logs seemed to be used by the beetle only for a few years. Additionally, in most of the surveyed squares a majority of the apparently suitable logs had never been successfully colonised, which probably indicates dispersal limitations. This is to be compared with the squares that had most occurrences, where the species actually seemed to occur in the majority of available pine logs. Presumably, the species is not able to track its resource when it is too scarce, or too ephemeral. However, old pine-logs rich in heartwood may be used for many decades by successive generations (Gärdenfors et al. 2002, this study). Such logs may be crucial for buffering the population during periods with low production of pine logs.

At the scale of the stand there was a clear preference for open conditions, providing light. Due to forest management and fire-exclusion, Swedish forests have become increasingly dense over the last 50 yr (de Jong 2002). Also protected forests have become denser and more dominated by the shade-tolerant Norway spruce during the last decades (Linder et al. 1997), which is the reason for the lack of the species inside nature reserves and key-biotopes. During natural conditions pine-forests were much more open due to fire-disturbances (Niklasson and Drakenberg 2001). Presumably *T. depsarium* could exist more or less constantly in the same stand if the fire-return interval was short enough. Fire-return intervals in Swedish boreal pine-forests can be as low as 20–40 yr (Granström 2001, Niklasson and Drakenberg 2001).

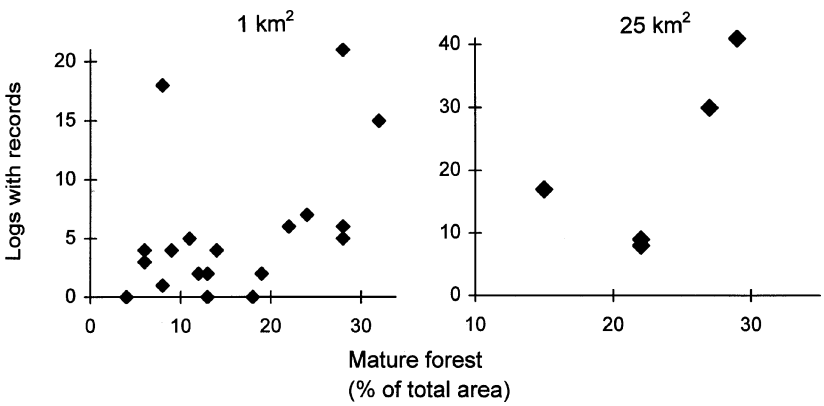


Fig. 3. The number of records of *T. depsarium* in relation to the proportion of mature forest in the 1 km^2 and 25 km^2 squares.

At the landscape scale the species occurred where the proportion of mature forest was greatest. At the same time it only rarely occurred in closed mature forest. This contradiction probably stems from the fact that the proportion of mature forest correlates positively with old-growth characteristics, such as old pine-trees and dead wood. Where the forest has been logged to a larger degree by clearcutting, and successively transformed into plantations, the number of potential breeding logs for the species has been reduced. Logging is normally targeted at the oldest trees (which are potentially most valuable as dead wood for *T. depsarium*), and the old dead wood is to a large degree destroyed accidentally during forestry operations (Fridman and Walheim 2000).

The deterioration of the habitat for *T. depsarium* probably occurs at all three studied scales. Logs are of lower quality today, because they are mainly formed from young trees. Old snags and logs are to a large degree destroyed by large forestry-machines. Stands with mature forest, not least the protected forests, are too shady for *T. depsarium*. At the landscape scale, reduction and fragmentation of older forests makes populations isolated and prone to extinction (Hanski 2000).

Time-lags may strongly affect species dependent on pine-wood. The natural dynamics of pine trees and their decomposition is extremely slow and long-term. To develop a dominance of heartwood often takes 200–300 yr in Scots pine (Hillis 1987). Single trees in this region may live for >500 yr (Ehrenroth and Schützer 1996). Trees often stand as snags for >200 yr (Rouvinen et al. 2002), and the following decomposition of the log may take another 200 yr (Siitonen 2001). Therefore, the present situation will to a large degree depend on the cumulative effects of centuries of human influence.

Most of the big pine-trees were exploited already during the 19th century in most of Sweden, including the study area (Linder and Östlund 1998). However, this exploitation was directed at the largest living trees, and much of the structural complexity of the forest was left intact, in contrast to modern mechanised forestry. It is probable that the widespread occurrence of *T. depsarium* in the studied area can be explained by the fact that mechanised forestry has been hampered by the complex ownership patterns with many small landowners.

The study area probably contains the largest population of the beetle in Europe outside Russia (Wikars 2003). The reason for its relative commonness is probably explained by the fact that the Norra Ny parish still contains an unusually large amount of old pine forest. However, it is plausible that the current rate of habitat degradation for *T. depsarium* nevertheless is strong in the study area. The 25% decrease in the proportion of mature forest the last ten years indicates this.

The protected forests were clearly unsuitable for the species. However, really old pine-trees are mostly found in protected forests (including this study), a pattern that will be accentuated in the future. This calls for active management of the forest reserves to create habitats for those species that needs sun-exposure. On the other hand it may be very difficult to initiate natural disturbances such as fire into the reserves because of technical problems to do so in a safe way (Granström 2001). There is also a great risk of disfavouring late-succession species that need shaded conditions (Niklasson and Drakenberg 2001).

Actual thresholds for the amount of dead wood at the landscape scale to sustain viable populations of *T. depsarium* will depend on the quality of dead wood, quality of stands, and the spatial configuration of wood and stands, i.e. all three studied scales interact. In this study I found that if the proportion of mature forest falls <25% at the landscape scale, *T. depsarium* was clearly less frequent (Fig. 3). This information could probably be used to locate regions or areas where there is a greater probability that the species exists today. Of course this relation needs to be confirmed. However, some support for this is given by the fact that known occurrences in Fennoscandia to a large degree coincide with low-altitude areas with unusually large and old pine-forests (Wikars 2003). It will be important to locate conservation measures specifically to these areas, because only then the species will be able to respond.

Finally, this study reveals the potential to favour *T. depsarium* during forestry operations. Today, clearcuts is without doubt the most important habitat for the species. If more pine-trees were left for conservation, the beetle would probably be able to persist in the managed forest. During final cutting, some trees could actively be felled and left to create favourable logs for the species. Also, by leaving seed-trees as "eternity-trees", logs would continuously be produced over decades due to wind-felling, whereas other seed-trees would survive and become very old. These measures would probably be more efficient if the following regeneration is slow or absent, otherwise the logs will soon become too shaded. Because *T. depsarium* is highly favoured by fire it is also important to include large pine-trees when prescribed fires are made. Before the burning it would be favourable to fell some of the trees actively. However, due to the high economical value of large pine-trees, all these efforts may need some compensation to the forest owners.

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Monitoring forest biodiversity – from the policy level to the management unit

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Angelstam, P., Roberge, J.-M., Dönz-Breuss, M., Burfield, I. J. and Ståhl, G. 2004. Monitoring forest biodiversity – from the policy level to the management unit. – Ecol. Bull. 51: 295–304.

We present an overview of tools to monitor elements of forest biodiversity at multiple spatial scales. At the international and national policy levels, indicators aim at communicating the status and trends of biodiversity to policy-makers and the general public. However, to allow effective operations, indicators should also be developed and applied at the level of forest management units. Such practical indicators need to be adapted to the local conditions and resources available to different end users ranging from corporate companies to the owners of small non-industrial private forests.

Because it is impossible to measure individually all aspects of biodiversity, there is a need for cost-efficient monitoring tools. At the policy level, international reporting is based on individual countries providing data like those collected in national forest inventories. In general, however, such programmes provide neither sufficient data on compositional (e.g., occurrence of specialised species), structural (e.g., quality of habitat networks), or functional (e.g., ecosystem processes) elements of biodiversity to allow effective monitoring. At the management unit level the development of comprehensive biodiversity monitoring systems is still in its infancy, although the testing of indicators system encompassing many major elements of forest biodiversity showed promising results at the scale of both stands and landscapes.

However, real-life applications of such systems are still rare. There is a need for continuous evaluation both of the scientific validity of indicators, and of the degree to which the results from indicator systems can be interpreted and communicated to stakeholders at all relevant levels. Moreover, we argue that the monitoring of forest biodiversity should not only deal with individual areas covered by forest or ancient cultural woodland today, but rather be applied in geographically contiguous units representing actual landscape mosaics or watersheds.

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Monitoring the status and trends of forest ecosystems has a long tradition. Initially the motivation was based on forests as a source of economic revenue (Williams 2003). Mapping and surveying of forest resources like individual oaks in Sweden and large pines in Russia (Redko and Babich 1993) started several hundred years ago. The intensive logging, or even "liquidation" of large trees (Drushka 2003), eventually fostered the sustained yield concept (Schuler 1998). As a consequence, regulated forestry began and long-term forest inventory programmes were developed. Today, a wide range of techniques exist to carefully monitor the tree species and age classes of importance for the forest industry (e.g., Ranneby et al. 1987, Reed and Mroz 1997, Bachmann et al. 1998). However, the guiding principles of forest management as well as the practices derived from them continue to evolve (Davis et al. 2001, Angelstam 2002, Stokland et al. 2003, Rametsteiner and Mayer 2004).

The classic management of forest for sustained yield is currently in transition toward multi-functional ecosystem management (Hunter 1999, Schlaepfer and Elliot 2000, Lindenmayer and Franklin 2002). Ultimately the concept also includes ecological integrity (Pimentel et al. 2000) and even the resilience of social-ecological systems (Gunderson and Pritchard 2002, Berkes et al. 2003). This new evolving management principle for forests is termed sustainable forest management (SFM) (Anon. 1993, Angelstam et al. 2004d). The implementation of SFM necessitates the use of active adaptive management (Lee 1993, Gunderson et al. 1995, Meffe et al. 2002, Duinker and Trevisan 2003), whereby emerging new knowledge about the effects of different practices is continuously fed back into management systems. Adaptive management, in turn, is only achievable if the effects of forest management on biodiversity are monitored in actual landscapes including the whole land base, i.e. both forest and non-forest land (e.g., Duinker 2001, Busch and Trexler 2003a, b). There is also a need to review the level of sustainability by combining monitoring data with performance targets (Linser 2001, Phillis and Andriantiatsaholiniana 2001, Davis et al. 2001). The results should then be communicated, not only to forest managers, but ideally also to a wide range of stakeholders (Busch and Trexler 2003a, b, Angelstam et al. 2003b, Lazdinis and Angelstam 2004, Ullsten et al. 2004).

As it is impossible to monitor individually all aspects of forest biodiversity, the use of indicators has been proposed for a range of criteria related to different elements of SFM. Internationally, several political processes have stimulated the proliferation of criteria and indicators about SFM in particular, and sustainability in general (e.g., Lammerts van Buren and Blom 1997, Moldan et al. 1997, Linser 2001). At the European scale, the need to use biodiversity indicators in European and national forest monitoring programmes has been formalised by the Ministerial Conference for the Protection of Forests in Europe (MCPFE) (Anon. 1993). Hence, a variety of indicators have been developed for monitoring the elements of biodiversity for national scale reporting (Rametsteiner and Mayer 2004).

While the development of international policy-level indicators initiated modifications of monitoring systems at the national level, only data at the landscape scale (or even finer scales) can provide early warning monitoring systems that permit detection of undesired states with a sufficient temporal margin (Puumalainen et al. 2003). Consequently, monitoring must also be undertaken at the local scale, where land management takes place, i.e. at the scale of the Forest Management Unit (FMU). Although the FMU concept lies largely in the eyes of the beholder (Franc et al. 2001), it is widely used to indicate the local level at which operational forest management takes place, i.e. management district or local landscape (Jonsson et al. 1993, Davis et al. 2001, Angelstam and Bergman 2004). The development of monitoring at this operational level has so far been dominated by scientific studies proposing indicators (Ferris and Humphrey 1999, Larsson et al. 2001, Nilsson et al. 2001) and presenting different frameworks for monitoring (Rundlöf and Nilsson 1995, Angelstam 1998a, b). There is thus in principle a three-phased approach to monitoring encompassing implementation monitoring, effectiveness monitoring and validation monitoring, respectively (Busch and Trexler 2003a).

Here, we provide a short overview of the elements of biodiversity in forests and woodland at multiple spatial scales, as well as of tools to monitor them at the policy and FMU levels in Europe. We then summarise the availability of relevant information about the different elements of biodiversity, and describe tools to collect such information at both levels. Finally, we discuss the choice of geographic units in which monitoring should ideally take place.

Indicators of forest biodiversity

Multiple elements and scales

Science develops indicators because they are required for the policy implementation process. Indicators should thus be seen as describing a policy implementation feedback loop that begins with a Pressure leading to a State and resulting in a Response (the PSR model; Linser 2001). Based on the STress Response Environmental Statistic System (STRESS) model by Rapport and Friend (1979), the PSR model was developed to help structure the use of indicators (Linser 2001). Monitoring of biodiversity requires that its different elements are clearly defined, but also that the factors underlying changes can be identified and communicated (Carignan and Villard 2002). In this context we focus on the state indicators.

Biological diversity has been defined and re-defined by many actors and is now one of the most frequently heard ecological buzzwords (Kaennel 1998). In 1992, the Convention on Biological Diversity (CBD) defined biodiversi-

ty as "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems, and the ecological complexes of which they are part; this includes diversity within species, among species and of ecosystems." (Anon. 1992). Similarly, Harper and Hawksworth (1995) proposed the adjectives genetic, organismal (i.e. species) and ecological (i.e. habitats) to describe the three components of biodiversity. Moreover, a number of important processes that affect forest composition and structure (e.g., fire, flooding, browsing, fungal and insect infestation) should be considered by monitoring them directly or indirectly (Noss 1990).

The definition of the biodiversity concept was discussed by Gaston (2000), who argued that it should be restricted to the diversity of life forms, excluding processes and functions. Both at the policy level and in practical management, however, the prevailing interpretation is that function should be included (Larsson et al. 2001, Puumalainen et al. 2002, Stokland et al. 2003). Here we thus focus on the three groups of biodiversity elements composition, structure and function as suggested by Noss (1990). As to function, we focus on the processes that maintain structures at the landscape scale with an ecological time perspective. Further work should also include the evolutionary time perspective including in-depth studies of ecosystem processes affecting forest production (e.g., Sverdrup and Stjernquist 2002) and global change (e.g., Watson et al. 2000).

In this context we focus on the need to build a system for monitoring the state of biodiversity elements including suites of variables representing composition (species and genes), structure (habitats) and function (processes) (cf. Noss 1990, Anon. 1993, Lambeck 1997, Angelstam 1998a, b, Simberloff 1998, Thompson and Angelstam 1999, Larsson et al. 2001, Nilsson et al. 2001, Sverdrup and Stjernquist 2002). This approach is also compatible with the development of the concept of coarse-grained (habitat management) and fine-grained (species management) filters (Seymour and Hunter 1999, Hebert 2004), which includes the management of processes by emulating natural disturbance regimes (Angelstam 2002, Lindenmayer and Franklin 2002).

In forest planning and management, a range of spatial and temporal perspectives are employed (Jonsson et al. 1993, Bachmann et al. 1998, Davis et al. 2001). Similarly, for the maintenance of biodiversity decisions must be made at multiple spatial scales (Angelstam and Bergman 2004, Suchant and Braunisch 2004, Angelstam et al. 2004c). In a broad sense, forest environments can be divided into three scales: 1) trees of different species, age, size and spacing within stands; 2) stands with different tree species composition, tree age structure, etc. within a landscape or FMU; and 3) landscapes with different amounts of forest cover and stand composition within for example an ecoregion. A biodiversity monitoring system at the FMU-level should therefore cover on the one hand the elements of biodiversity and on the other the different spatial scales shown in Table 1. In practice, this requires that more than one monitoring tool be employed.

The international and national policy levels

At the policy level, several international processes have contributed to the development of criteria and indicators for SFM. Given our present European perspective we focus on the Helsinki Process (Anon. 1993), which has mirrored different interests of society at the Pan-European level, including the protection, maintenance and enhancement of forest biodiversity (Rametsteiner and Mayer 2004). Puumalainen (2001) reported the status of different elements of biodiversity for the European countries using the BEAR logic (Larsson et al. 2001; see below) and data from FAO's forest resource assessment (Anon. 2001). Notwithstanding the difficulties of comparing data among countries, clear differences in forest structure among countries were observed. For example, independent of the species groups studied, Puumalainen (2001) found that the extent to which forests hosted specialised forest species increased towards the east in Europe.

In Europe, the MCPFE and the CBD processes have resulted in modifications to traditional monitoring systems and the introduction of new variables in National Forest Inventories (NFIs) (Stokland et al. 2003). At a more

Table 1. Elements of biodiversity (rows) across spatial scales (columns) with MCPFE indicators under the criteria of forest resources, ecosystem health and biodiversity (see Rametsteiner and Mayer 2004 for details).

	Trees	Stands	Landscapes
Composition		threatened forest species (4.8)	
Structure	introduced tree species (4.4) dead wood (4.5)	tree species composition (4.1) regeneration (4.2) naturalness (4.3)	forest area (1.1) age structure and/or diameter distribution (1.3) landscape pattern (4.7) protected forests (4.9)
Function	defoliation (2.3) forest damage (2.4)	carbon stock (1.4) soil condition (2.2)	deposition or air pollutants (2.1)

detailed level, From and Söderman (1997) presented a scheme for the monitoring of terrestrial biodiversity in the Nordic countries which focused on composition (surveys and monitoring of species) and structure (landscapes and biotopes), but excluded processes except for pollination. By contrast, Strand's (1997) report on monitoring of environmental quality of Nordic forests focussed on the process of anthropogenic pollution. An increasing number of NFIs and other monitoring programmes in Europe now monitor elements of biodiversity such as key biotopes, cover of bushes, herbs, lichens, and mosses, as well as vertical layering and other structural elements (Bachmann et al. 1998, Bischoff and Dröschmeister 2000). For example, the Swedish NFI includes regular assessments of standing and lying dead wood since 1994 (Fridman and Walheim 2000).

Stokland et al. (2003) compiled data on a number of MCPFE indicators for Norway, Sweden and Finland and presented them as thematic maps based on interpolation of sampling point data. Using NFI data, they described the proportion of forest, the balance between increment and felling, various forest management practices, natural disturbances, tree species composition, age distribution, dimensions of trees, dead wood, landscape patterns, species diversity, and conservation measures. This approach, however, precludes detailed spatially explicit analyses. In the Baltic States, where the coverage and thematic resolution of land management data is high due to a history of central state planning, Kurlavicius et al. (2004) identified potentially biologically valuable forest areas. Computerised searches of potentially biologically valuable stands were carried out using the national forestry stand level databases on tree species composition and average stand age.

On behalf of the Swedish National Board of Forestry, Angelstam et al. (2003b) reviewed the extent to which different elements of biodiversity, i.e. the cells describing the main elements of biodiversity at three spatial scales in Table 1, are actually monitored at the level of the administrative region. Their conclusion was that the cover, in terms of data collection, was quite uneven. While composition was relatively well represented (except at the landscape scale), ecosystem function was not. A particularly clear example was the lack of knowledge about the functional connectivity of networks of protected or specially managed areas.

BirdLife International and the European Bird Census Council have recently developed an early warning system based on changes in the population levels of common and widespread woodland and farmland birds. The Pan-European Common Bird Monitoring Scheme (PECBMS) unites data from many existing bird monitoring schemes to generate combined annual population trends, which can then be presented as national, regional or Pan-European multi-species indices (van Strien et al. 2001). These indicators are finding increasing acceptance in the European Commission and beyond, and variants based on woodland and farmland birds have already had significant impacts on policy and government action in the United Kingdom (Anon. 2003a).

The forest management unit level

Even though the development of policy-level indicators shows good progress, the success of policy initiatives will ultimately be determined at the local level. To improve the knowledge of biodiversity and awareness of its state of personnel responsible for actual operations at the FMU level, we argue that simple indicators should be used to monitor elements of biodiversity, but also to better inform people about the state and trends in biodiversity.

Several species-based indicator systems have been proposed for forest ecosystems (e.g., Hanley 1993, Jansson 1998, Jonsell et al. 1998, Jonsson and Jonsell 1999, Medellin et al. 2000, Castillo-Villa and Wagner 2002, Busch and Trexler 2003b). However, they often reflect the taxonomic interests of the individual scientists instead of being based on systematic criteria as recommended by Larsson et al. (2001). Thus, most of these indicator species systems are restricted to one or a few of the cells in the matrix of biodiversity elements and spatial scales presented in Table 1. In the Nordic countries, the focus has been on plants and fungi (Norén et al. 2002). In spite of wide application, the appropriate geographical range for the use of certain species-based indicators is not always clearly understood (Rolstad et al. 2001).

While such bottom-up approaches represent a step in the right direction, they are not sufficient for conserving all major elements of forest biodiversity. As a consequence, more comprehensive approaches have been proposed that include several elements of biodiversity at multiple spatial scales (Noss 1990, 1999, Angelstam 1998a, b, McLaren et al. 1998, Ferris and Humphrey 1999, Nilsson et al. 2001, Angelstam et al. 2004b). In Europe, the EC-funded concerted action "Indicators for monitoring and evaluation of forest biodiversity in Europe" with the acronym BEAR (Larsson et al. 2001) was a Pan-European initiative to define principles for developing indicators for the monitoring of forest biodiversity. Based on the forest vegetation types in Europe (Bohn 1994), Larsson et al. (2001) proposed indicators that included compositional, structural and functional elements of biodiversity at multiple spatial scales. The focus was on historic natural vegetation (sensu Peterken 1996), but the same principles can also be applied to the vision of pre-industrial cultural wooded grasslands (Rackham 1998, 2003). At present, regular biodiversity monitoring at the level of FMUs is rarely applied. One exception is the rapid assessment approach used to estimate the conservation value of stands made in landscape planning (Drakenberg and Lindhe 1999).

Angelstam et al. (2004a) evaluated landscape-scale biodiversity indicators, such as 1) the presence of different ec-

ological groups of specialised or area-demanding birds and mammals and 2) existing landscape information about historical forest loss and alteration and age-class specific tree species composition. The diversity of ecological and taxonomic guilds was negatively correlated with measures of human exploitation of the landscapes at the regional scale. Differences in the quality and extent of preferred habitats for the species studied can hence be interpreted as the local human footprint on landscapes. This conclusion was also evaluated using a historical ecology approach where the history of land-use and current biodiversity status were studied in three case studies.

Based on a review of literature and interviews with forest managers, Angelstam and Dönz-Breuss (2004) developed a system for monitoring major biodiversity elements in European forests at the stand scale. The elements (composition, structure, function) to be measured were chosen based on the premise that the development of biodiversity monitoring must proceed from existing forest management data (such as tree species composition, wood volume and site type). New variables can then be added gradually, provided they are typical components in the reference landscapes indicated by the relevant policy. Naturalness (sensu Peterken 1996) and the authenticity of pre-industrial cultural woodland (Rackham 1998, 2003, Agnoletti and Anderson 2000, Angelstam et al. 2003a) were the two visions used to derive indicators. The method was tested in five case studies representing hemiboreal, lowland temperate and mountain forest in Europe. The authors found clear relationships between the amount of different elements of forest biodiversity along both local and regional gradients in all ecoregions and case studies. Indicators such as the sum of dead and lying dead wood showed increasing values towards the locally or regionally remote areas, where naturalness was assumed to be higher.

Young and Sanchez-Azofeifa (2004) provide an overview of how Geographical Information Systems (GIS) and remote sensing (primarily optical sensors) are used as tools to monitor boreal ecosystems. Provided that the thematic resolution is relevant and sufficient, analysis of satellite images through the use of landscape metrics can be a means of determining landscape structure and thereby constitutes an important tool in fragmentation studies (e.g., Brooks et al. 1999, Kurki et al. 2000). Remote sensing offers opportunities for large-scale land-cover mapping and change detection, and methods for investigating the role of the boreal forest in the global carbon budget and impacts on biodiversity from changing disturbance regimes. Further, satellite imagery and GIS are the best way to monitor fire and its effects in the boreal forest (Flannigan and Vonder Haar 1986, Rauste et al. 1997, Fraser et al. 2000a, b, Li et al. 2000a, b, Michalek et al. 2000). Satellites are particularly valuable in remote areas where it would otherwise be impossible to determine fire activity (Flannigan and Vonder Haar 1986). Finally, satellite images can be interpreted visually for rapid assessment of landscape structure found for example in pre-industrial cultural landscapes (Angelstam et al. 2003a).

It should, however, be noted that the thematic resolution regarding biologically relevant qualities such as vertical structure and dead wood component of forest stands needs to be improved (Holmgren and Thuresson 1998, Mikusiński et al. 2003). Moreover, many problems arise in large-scale practical applications of satellite remote sensing, and using satellite imagery for following trends should be carried out with great care, due to the variability introduced by varying sensor properties and atmospheric conditions (Olsson 1993).

The need for scientific validation of indicators

To ensure the usefulness of indicator systems one needs to evaluate their scientific validity in terms of robustness and umbrella value (Noss 1999, Roberge and Angelstam 2004). Several avenues for the scientific dimension can be taken. One way consists in examining how the level or value of a given indicator correlates with other elements of biodiversity. In most cases, one tests the ability of the indicator to predict reliably species richness in a given taxon, or the presence of habitats important for maintaining certain species. Compared with the number of indicators proposed very few of the indicator species used have actually been validated (Setesdal et al. 2003). Those that have been validated include the lichen genus *Lobaria* (Nilsson et al. 1995) and some proposed focal bird species. For example, Mikusiński et al. (2001) used data from the Polish bird atlas and were able to show that the presence of some woodpecker species (three-toed woodpecker *Picoides tridactylus* and white-backed woodpecker *Dendrocopos leucotos*) is strongly correlated with the species richness of other forest birds. Similar results have been found for grouse Tetraonidae (Kolb 2000, Suter et al. 2002). There is thus an urgent need to evaluate the potential of the different focal species proposed for conservation planning by testing hypotheses about their umbrella value (Roberge and Angelstam 2004). The Pan-European Common Bird Monitoring Scheme is currently developing a set of objective criteria for assessing the indicator value of different bird species. This will identify which species may be missing from current indices, possibly due to lack of data, and feed back into the ongoing process of indicator system development. At the regional scale even large mammals can be important indicators (Mikusiński and Angelstam 2004).

Another way to evaluate biodiversity indicators is to compare their level in gradients from intensively managed forests to natural or near-natural forests. If an indicator shows a consistent trend when measured across that gradient of naturalness, then it can be considered a reliable indicator of natural forest conditions. Finally, a historical-eco-

logical approach (Egan and Howell 2001) can be used in which the "naturalness gradient" is provided by the history of land use in a given landscape and the associated changes in the indicator are examined. A structural indicator such as dead wood (Shorohova and Tetioukhin 2004) could thus accurately reflect the chronology of forest use intensification (or of forest restoration). Evidence of clear relationships between compositional (species) and structural (habitat elements and biotopes) aspects (e.g., Bütler et al. 2004) may to some extent make costly monitoring of species redundant.

Endangered or red-listed species are commonly proposed as biodiversity indicators (Reid et al. 1993). However, because red lists contain a mixture of species covering a wide range of life-history traits (Berg et al. 1994), it is unlikely that such species as a group would behave in the same way to a certain type of management. We argue that it can be misleading to use indiscriminately red-listed species without first grouping them according to their ecology or life-history traits. Moreover, the long time intervals between red-list reassessments render such indicators relatively insensitive to change, and there is a risk that species going extinct will simply drop off the list and be forgotten. Thus, focussing on numbers of threatened species, rather than on the composition of species, guilds or communities, means that indicators based on red-listed species alone are unlikely to warn about changes in key ecosystem functions in time for us to react. However, suites of species with demonstrated indicator values, red-listed or not, could be useful. Ideally, groups of species classified according to specific combinations of habitat requirements for reproduction and feeding should be used. This is analogous to Haapanen's (1965) approach with birds in Finland, Thomas' (1979) life form concept, and the functional types concept proposed by Wiens et al. (2002).

From a methodological point of view, it is important to select indicators that can be monitored using methods that generate values that are truly comparable over time. It is also important that indicators representing functional elements of biodiversity be validated. Altered fire frequencies (Niklasson and Granström 2000) and hydrological regimes (Degerman et al. 2004) are important examples of changes in forest ecological processes resulting from human activities. Less obvious examples are disruption of predator-prey relationships, such as factors favouring generalist predators that have reduced the breeding success of species associated with extensively forested landscapes (Kurki et al. 2000), and browsing by superabundant wild herbivores on certain tree species, which changes forest composition (Angelstam et al. 2000). Additionally, air pollution is causing the leaching of nutrients such as nitrogen from sensitive soils, and thereby changing vegetation in some regions (Sverdrup and Stjernquist 2002). Socio-economic changes in rural communities followed by land abandonment constitute another example (Angelstam et al. 2003a).

Integration of monitoring efforts and communication

In addition to the need for scientific validation of indicator systems, the degree to which stakeholders understand indicators used in monitoring must be evaluated. This includes both the communicative efficiency and value systems (Duelli and Obrist 2003). To promote SFM, the results of monitoring data need to be interpreted and communicated to stakeholders at multiple levels, from the international policy arena to the stakeholders in the actual FMU (Niemelä 2000, Franc et al. 2001, Uliczka et al. 2004). Communication plays an essential role in any biodiversity monitoring system for at least two reasons. First, knowledge necessary for the application of the monitoring system must be communicated to the field workers performing the inventories. This is particularly important when aiming at monitoring at the forest management unit level where there is a need to focus on rapid assessment approaches (Busch and Trexler 2003a, b, Angelstam and Dönz-Breuss 2004). Second, the relevance of the indicators and their interpretation must be communicated to all stakeholders who will use the results of the monitoring programme in making policy-related decisions. In association with the review of data collection for different biodiversity indicators at the national level in Sweden, Angelstam et al. (2003b) conducted interviews with officials within the agencies collecting data for regional monitoring programs. The respondents stressed the need for improved integration of different data sets collected by different organisations.

In many parts of Europe, non-industrial private forest (NIPF) owners who carry out their own property management own large proportions of the forested lands. To promote the maintenance of biodiversity in actual landscapes, and not just satisfying the need for monitoring at the policy level, one should encourage monitoring to learn rather than learning to monitor (Gunderson 2003). The target group in this context is thus the land manager who is usually not a biodiversity expert, but who wants a rapid assessment technique that is not too costly, neither in terms of time to learn the approach nor to perform it. Using questionnaire responses from NIPF owners in south-central Sweden, Uliczka et al. (2004) examined their knowledge of species from different taxonomic groups. Their conclusion was that the current level of forestry education among NIPF owners is often insufficient to allow for the practical implementation of monitoring systems based on inconspicuous indicator species such as lichens and fungi. On the other hand, some vertebrates and vascular plants were of more value in communicating the conservation importance of natural forest remnants. One thus needs to balance between communication efficiency and umbrella values for the other, less charismatic ones. We argue that there is a need to evaluate also the extent to which other more

abstract elements of biodiversity, such as functional connectivity of different land cover types and ecosystem functions, are understood by different stakeholders.

Monitoring the whole land base

Depending on the history of forests and woodland in the actual landscape, the maintenance of forest biodiversity encompasses either of two sets of broad visions. First, policies related to the biodiversity of European forests and woodland make explicit reference to the concept of naturalness (Anon. 1993, 2003b). In spite of the ambiguity of this concept (Balée 1998, Egan and Howell 2001), it is obvious that forest biodiversity indicators should represent elements found in naturally dynamic forests (Peterken 1996). Second, in both Europe (Kirby and Watkins 1998, Agnoletti 2000, Rackham 2003, Angelstam et al. 2003a) and North America (Stevenson and Webb 2004), the maintenance of values found in pre-industrial cultural landscapes is highlighted. The latter, although influenced by human land use, contained structural components such as dead wood, large old trees and old-growth stands that are typically found in naturally dynamic forests. As a consequence, remnants of the pre-industrial cultural landscape provide a refuge for many species that were adapted to a pristine or near-natural forest environment (Kirby and Watkins 1998). Ideally, the development of forest biodiversity indicators should reflect both of these visions.

The natural potential vegetation of Europe's terrestrial ecosystems at mid and northern latitudes is forest (Mayer 1984, Bohn 1994). With continuous change in historical land use including habitat loss, forest restoration and global change, the potential for forest biodiversity can be found in at least four types of landscapes: 1) forest; 2) cultural woodland; 3) plantations; and finally 4) land subject to future afforestation. In the first three cases there is a requirement for protection, management and restoration; the fourth case represents opportunities for re-creation of forests. Consequently, we argue that monitoring forest biodiversity should not only deal with what is forest or ancient cultural woodland today, but be applied in geographically contiguous units representing actual landscapes. Monitoring should thus be integrated across biotopes including woodland and non-woodland. This would also alleviate the integration of management of woods in predominantly agricultural landscapes and of management in forests (Mikusiński et al. 2003). There is also a growing insight into the complex interactions between the terrestrial and aquatic systems (Wiens 2002), many of which require transdisciplinary landscape approaches (Rabeni and Sowa 2002). In Europe the EC Water Framework Directive (Anon. 2000) has recently reinforced a drainage basin perspective on biodiversity that sets the stage – and in fact demands – integrated monitoring. The capacity to gather information over large areas and perform spatial analysis greatly enhances our ability to study the large-scale patterns and processes caused by natural and human disturbances, and also to make predictions about the future (Young and Sanchez-Azofeifa 2004). Given the technology now available, the major advances made in ecological research, and the need for integrated management of integral landscapes, piecemeal interventions should be replaced by scientifically-based monitoring at multiple scales.

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Measuring forest biodiversity at the stand scale – an evaluation of indicators in European forest history gradients

Per Angelstam and Monika Dönz-Breuss

Angelstam, P. and Dönz-Breuss, M. 2004. Measuring forest biodiversity at the stand scale – an evaluation of indicators in European forest history gradients. – Ecol. Bull. 51: 305–332.

We present a system for field measurement of compositional, structural and functional forest biodiversity indicators at the scale of stands suitable for use in adaptive management. To evaluate the practical usefulness of the indicators we collected data on 21 groups of basic variables in five European case study landscapes representing hemiboreal, mountain and lowland temperate forests. The stand scale survey sites were stratified with respect to the land use history both within and among case studies. As a measurement of the cost for monitoring all the variables in one management unit we estimated that a total of 23–43 person-days were needed, divided into planning (ca 9%), data collection (ca 70%), data management (ca 15%) and analysis (ca 6%).
We present a sub-set of results focussing on the occurrence of three compositional (specialised pendulous lichen thalli >20 cm, trees with >80 cm DBH, lying and standing dead wood), structural ("special" trees, proportion of deciduous trees and old forest) and functional (uprooted trees, wood-decaying bracket fungi, browsing) indicators of biodiversity. In general the indicators reflected the trends in the history of forest and land use both within and among the five case studies. Two of the indicators stand out as particularly interesting at the Pan-European scale. These are the amount of dead wood and the frequency of occurrence of uprooted trees. "Special" trees, old forest and wood-decaying bracket fungi also performed well, but not always with the same direct relationship to land use history. Trees with >80 cm DBH showed mixed results. Browsing, by contrast, appeared to be related to more subtle changes at the regional scale such as the extirpation of large carnivores and other factors that maintain a high density of large browsing herbivores. Finally, the specialised species indicator and the proportion of deciduous trees appeared to indicate the local, but not the regional situation.
Together with ecologically founded performance targets for different indicators of the elements of biodiversity, monitoring results could be used to evaluate the extent to which biodiversity policies are implemented in actual landscapes.

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The dominant natural vegetation in Europe is forest and woodland (Mayer 1984, Hannah et al. 1995, Ellenberg 1996). For long the major current threat to its biodiversity is the loss and severe alteration of once naturally dynamic forests (Stanners and Bourdeau 1995, Hannah et al. 1995, Peterken 1996, Smith and Gillett 2000, Anon. 2002) and

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of pre-industrial cultural woodland (Kirby and Watkins 1998, Rackham 2003, Angelstam et al. 2003). Additionally, global change is appearing as a new factor, although with less predictable consequences (Watson et al. 2000). Monitoring the status and progress of relevant indicators of biodiversity is hence a basic prerequisite for the development of active adaptive ecosystem management aiming at implementing sustainable development in practise (Davis et al. 2001, Meffe et al. 2002, Berkes et al. 2003). The transition from the classic forest sustainability concept focussing on wood as a renewable resource, to ecological sustainability based on forest ecosystem management requires additional data collection of relevant indicators (Angelstam 1998a, b, Schlaepfer and Elliott 2000, Duinker 2001). Additionally, new tools for assessment and communication of these indicators to different stakeholder groups are needed (Puumalainen et al. 2002, Uliczka et al. 2004, Ullsten et al. 2004).

The Global Biodiversity Assessment (Heywood 1995), a knowledge assessment linked to the convention on biological diversity (Anon. 1992), stressed the need for establishing monitoring systems for biodiversity. Such monitoring systems can be developed for a variety of ecosystems and spatial scales ranging from international to local (Larsson et al. 2001, Angelstam et al. 2004d). In Europe, the need to use biodiversity indicators in forest monitoring programmes has been formalised by the Ministerial Conference on the Protection of Forests in Europe (Rametsteiner and Mayer 2004).

In spite of substantial efforts to derive indicators, many of the broader indicators used at the international, regional and national scale are not operationally useful at the scale of the forest management unit (Puumalainen 2001, Angelstam et al. 2001, Franc et al. 2001, Larsson et al. 2001). Duinker (2001) reviewed the problems and pitfalls related to identification and naming, classification and evaluation, all of which may hamper indicator development and its application in practice. Traditionally, the scientific community has proposed detailed systems for different subsets of biodiversity elements (e.g. Jonsell et al. 1998, Jonsson and Jonsell 1999, Nilsson et al. 2001). However, such detailed systems would be considered very costly to implement in management units, and do not always communicate well to most land managers or to the general public (Uliczka et al. 2004). On the other hand, some rapid assessment systems are currently used in actual forest management. For example, Drakenberg and Lindhe (1999) developed a system originally aimed at education of forest field staff for rapid assessment of the conservation value of forest stands. However, a major drawback with these simple systems is that they are not quantitative, thus often not enabling a comparison of monitoring results with conservation performance targets.

These are some reasons why practical tools to measure elements of biodiversity at the scale of the forest management unit are still not at hand. The challenge of introducing such a system is to bridge the gap between detailed scientific approaches to biodiversity monitoring on the one hand, and the need for a cost-efficient tool that can be applied and communicated without deep expert knowledge on the other (Hambler 2004). We thus see the development of practical biodiversity measurements as a process where an initial step is to satisfy the need for social licence to operate, before starting more complicated and costly scientific approaches (Bunnell and Johnson 1998).

The biodiversity concept is complex, and different ecoregions such as the boreal, temperate and mountain forests of Europe have different natural disturbance regimes with many developmental stages (Mayer 1984, 1992, Ellenberg 1996, Angelstam 2003). For application in practice at the scale of the forest management unit, the measurements used should be relevant, unambiguous, and easy to communicate (Duinker 2001). To manage for forest biodiversity, one needs to stratify forests using the different natural and cultural disturbance regimes to which native species are adapted. Therefore, we propose a top-down approach for selecting several elements of biodiversity representing representative disturbance regimes and forest types (e.g. Angelstam 1998a, b) within different forest regions (e.g. Larsson et al. 2001). Additionally, the data should be simple to collect in the field in a cost-efficient way, the information should be understandable for many stakeholders with a minimum of training, and the method should be applicable throughout the snow-free season. The sample size should be sufficiently large to allow detection of differences in various elements of biodiversity both among stands at a given time and between different points in time when repeated measurements have been made. This would allow the detection of trends over time and the evaluation of progress in policy implementation. To stress these aspects, Higman et al. (1999) argues for a "SMART" selection of indicators that are Specific, Measurable, Action-oriented, Realistic, and Time-framed.

Broadly speaking an increasing anthropogenic footprint on ecosystems eventually results in reduced species richness (e.g. Mikusiński and Angelstam 1998, Trauger et al. 2003). In forest systems intensively managed for sustained wood yield, even-aged stands of single tree species dominate. In addition, the amount and quality of dead wood (Siitonen 2001, Nilsson et al. 2002) and the number of large trees (Nilsson et al. 2002) are reduced to a minimum. Further, the foliage height diversity is often simplified to single layers, therefore altering the vertical structure and thus the suitability of the stand as habitat for a wide range of species (Brokaw and Lent 1999). Additionally, ecosystem processes are altered and ecosystem integrity may be lost (Pimentel et al. 2000). To describe the complex changes, the biodiversity concept and its constituent elements are useful; for details see Larsson et al. (2001:11 et seq.). Here, we follow the same logic by using elements representing the composition, structure and function of

biodiversity as outlined by Noss (1990) and later used by Larsson et al. (2001) and Stokland et al. (2003).

The aim of this paper is two-folded. Firstly, we present a monitoring system (see Appendix) at the scale of stands within a landscape, which aims at communicating the quantity of different elements of biodiversity by selecting robust variables that can be measured in the field with a minimum of training. Secondly, we evaluate this system by testing the idea that management simplifies natural forest ecosystems in a systematic way. This subsequent empirical part of the study was conducted using replicated sampling in land use history gradients in Scotland, W Austria, N Italy, Poland and Russia.

Gradients in land use history among and within case studies

The concept of naturalness

Although with an evolutionary perspective change is the rule, policies such as those related to biodiversity of European forests and woodland make explicit reference to the concept of naturalness (Anon. 2002, Rametsteiner and Mayer 2004). Although we are aware of the ambiguity of this concept (e.g. Balée 1998, Egan and Howell 2001), it is obvious that forest biodiversity indicators should represent elements found in naturally dynamic forests (Peterken 1996), or pre-industrial cultural landscapes with semi-natural woodland components (Kirby and Watkins 1998, Rackham 2003).

The degree of naturalness of forest ecosystems reflects the intensity of human interventions (Peterken 1996). Different levels of utilisation intensity are characterised not only by changed structures, but also by altered composition of species' assemblages. The composition and structure interact with functional diversity and constitute together the biological diversity of an area. Forest and other wooded land where natural processes and species have been retained or restored have a high conservation value that has been recognised at the policy level (Rametsteiner and Mayer 2004). Such forests are also important for understanding basic ecological principles and can be used as reference areas when setting up management priorities and models for sustainable forest management (Lindenmayer and Franklin 2002, Angelstam and Kuuluvainen 2004).

Both regional comparisons of the human footprint on nature (Mikusiński and Angelstam 1998, 2004, Siitonen 2001, Shorohova and Tetioukhin 2004, Angelstam et al. 2004a, c) and local case studies (Östlund et al. 1997, Axelsson and Östlund 2001) provide evidence of declines in different elements of biodiversity following land-use intensification. This suggests that time can to some extent be replaced with space (Angelstam et al. 1995, Egan and Howell 2001). In many regions these gradients in historical impact on landscapes can be steep. In Austria, for example, Grabherr et al. (1998) showed that 3% of the total forest area can be classified as natural (without any human impact), 22% as semi-natural, 41% as moderately altered, 27% as altered and 7% as artificial. These experiences show that forests can be ranked with respect to their degree of naturalness (Peterken 1996).

Description of the case studies

Data were collected in five case studies representing three different European ecoregions north of the Mediterranean, viz. the hemiboreal, mountain, and lowland temperate ecoregions (Larsson et al. 2001). Following the macroeconomic development from the centre to the periphery of economic development in Europe (see Angelstam et al. 2004a) we ranked the case studies from the regionally least to those most impacted by forest management (Table 1). Within each ecoregion we conducted field studies in local landscapes representing the scale of forest management units to cover the range of historical land use types from natural reference areas (Arcese and Sinclair 1997, Angelstam et al. 1997) to altered landscapes. Data collection was made according to the methodology presented in the Appendix.

Hemiboreal forest

The human use of the hemiboreal forest has a long and complex history (Peterken 1996, Kirby and Watkins 1998). The gradual spread of the industrial revolution in Europe (e.g. Williams 2003), and gradual development of intensive forest management practices, have resulted in degradation of the properties of naturally dynamic systems where the land use history is long (Angelstam et al. 1995). Today, intact forest landscapes remain only in the most remote parts of Europe (Faliński 1986, Yaroshenko et al. 2001). Here we report results from case studies in Scotland and westernmost Russia.

Abernethy, Scotland – Abernethy (ca 57.2°N, 3.5°W) is located on the northern slopes of the Cairngorm Mountains in Scotland. In the last 250 yr, the Abernethy forest experienced dramatic changes (Steven and Carlisle 1959, Summers et al. 1999). From ancient times the forest cover was heavily reduced until the 1830s. During the 1840s restoration of timber resources began with plantations and the use of the shelterwood system started. This led to an increase in forest cover until the 1870s. Later, the forest cover remained fairly constant (O'Sullivan 1973). In 1866, the duty on imported timber was removed, which resulted in uneconomic forest management in remote areas (Grant 1994). At that time the landowners started to realise the economic potential of sport hunting, mainly of red deer *Cervus elaphus* and roe deer *Capreolus capreolus*

Table 1. Stratification of the land cover types among (rows), and within (columns) in the five European case studies according to the regional and local forest history from the strata with a long history of use (top/very altered) to the strata with little expected alteration (bottom/natural).

Forest ecoregion	Study area	Very altered	Altered	Near-natural	Natural
Hemiboreal	Abernethy [(1)]	birch woodland, pine centre, Scots pine plantation, exotic plantation	pine savannah, pine remote, pine remote best	–	–
Mountain	Montafon	forest centre, cult. landscape	forest at the periphery	forest in extensive use	–
Mountain	Trudner Horn [(2)]	apple orchard, vineyard, agriculture	coppice forest, larch meadow	private forest, public forest	–
Hemiboreal	Pskov	poor site	cultural landscape	mesic site	rich site
Lowland temperate	NE Poland	plantation	encroaching forest on former cultural land	conif. forest [(3)] decid. forest [(4)]	Białowieża national park

[(1)] See Frid (2001) for details about the strata.
[(2)] See Appendix (Table 1 and Fig. 1) for details.
[(3)] The Knyszyńska forest, see text and Angelstam et al. (2002).
[(4)] The Białowieża forest outside the National Park, see the text and Angelstam et al. (2002).

(Dunlop 1997, Smout 1997). This resulted on the one hand in an increase of forest cover, on the other hand in a simultaneous increase in the number of deer and a strong impact on tree regeneration success by deer. From 1850 to 1900, large areas were considered in need of regeneration. Since some areas were difficult to regenerate naturally, one had to rely on plantations (Dunlop 1997). In the 20th century, forest fellings were mostly done during the two world wars (O'Sullivan 1973) but also in the 1970s and 1980s (Summers 1998). A total of 415 sampling plots subdivided into seven different coarse landscape types were described.

Pskov, W Russia – For very long the forests of the Pskov area were used for agricultural purposes. Forests were cut and burned to gain farmland and meadows. In Russia, the cessation of serfdom in 1861 gradually led to more intensive forest use for local markets. The "farmer and land bank" system, whereby new free farmers acquired land and paid by logging, led to increasing forest harvesting between 1906 and 1914. However, logging was mostly selective. After the revolution in 1917 forests were cut without regulations and logging was generally concentrated to the easily accessible parts of the landscape. Around 1935 all mature stands ready for final-felling as well as older had been cut. During the World War II the forestry activity declined and harvesting was restricted to the vicinity of roads. After the war mechanisation started. The first tractor was used in 1949 and the first "friendship" chainsaw in 1954. In the 1950s central heating became popular in the urban areas and villages, which reduced logging considerably and favoured an increased amount of deciduous trees. Simultaneously the population on the countryside dwindled, and fields and meadows were gradually abandoned. Reforestation after harvesting started only in the 1960s.

During the latter half of the 1990s commercial harvesting increased again. To demonstrate more nature-friendly forest harvesting methods, and to advocate the need for modified forest policies allowing structures to be left for biodiversity conservation, a model forest project was developed in Pskov (<http://www.wwf.ru/pskov/eng/>). The Pskov Model Forest area is located NE of Pskov around the village Mayakovo (ca 50.10°N, 29.15°E). Our data collection was carried out in the actual model forest area (ca 18 000 ha) as well as in its surroundings, totalling an area of ca 45 000 ha. A total of twenty 1-km^2 squares subdivided into four coarse landscape types were sampled using 320 sampling plots. We ranked the survey plots on forest land on wet sites as the most natural ones as they have been traditionally the least accessible ones. Mesic, and in particular dry sites dominated by Scots pine *Pinus sylvestris* forests, were historically the most important sites for forest harvesting because of the value of the wood of this tree species. Abandoned agricultural land was considered as the most altered stratum.

Mountain forest

While variation in the use of the hemiboreal and lowland temperate forests are generally related to differences in accessibility due to longitude and latitude, local gradients in the naturalness of mountain forests are often related to altitude (Grabherr et al. 1998).

Trudner Horn, N Italy – South Tyrol (Alto Adige) is located in the north Italian Etsch river valley south of the Alps. The region has a distinct vegetation zonation from low to high altitude, and an associated variation from higher to lower intensity of past and present land use (Peer 1995). At present, 42% of South Tyrol's land area is forested. Fifty-two percent of the forest area is owned by private landowners with an average size of 10 ha. Private companies own 16% of the forest area, 29% belong to public bodies (e.g. villages), 2% to the church, and 1% is county forest (Ploner pers. comm.). Other important land cover types are orchards and vineyards, fields and meadows, as well as larch meadows and alpine pastures. Norway spruce *Picea abies* (62%), larch *Larix decidua* (18%), Scots pine (11%), stone pine *Pinus cembra* (5%) and silver fir *Abies alba* (3%) are the economically most important tree species (Ploner pers. comm). The proportion of deciduous trees is low (1%).

The nature park Trudner Horn forms the core of the study area and is located ca 20 km south of Bolzano (ca 46.6°N, 11.3°E). Established in 1980 it covers an area of 69 km^2. The park hosts the most diverse and species-rich area in the region, and ranges from sub-mediterranean to alpine vegetation. It includes a wide range of land use forms from vineyards and ancient coppice forest to agriculture, managed forests and larch meadows. To cover the main landscape types of the region additional sampling plots were located outside the nature park. Based on today's characteristic combination of natural and anthropogenic factors we subdivided the study area into 7 different sampling strata excluding tree line forest, which is not reported here (see Appendix for details). We collected data in 21 different km^2 plots, the total number of plots surveyed was 290.

Montafon, W Austria – The Montafon valley is located in the southern part of Vorarlberg, the westernmost province of Austria (ca 47.1°N, 9.9°E). The valley consists of 10 municipalities with an area of 563 km^2 and a total population of 18 000 inhabitants. About 50% of the area is covered by alpine meadows, 23% by forest, 20% is alpine habitat above the tree-line and 7% agricultural and urban land. The forests reach up to ca 1800 m a.s.l., and cover a total area of 16 000 ha. Winter tourism is the main source of income. In historical times, mining was one of the most important local industries. Due to the high demand of timber for mining virtually no naturally dynamic forest is left (Grabherr et al. 1998). However, due to the dramatic topography altered landscapes as settlements at the bottom of the valleys alternate with near-natural areas such as protected forest in steep terrain. Today, >80% of the forest fulfil a protective function for the site itself and for settlements in the valleys. Approximately 33% of the area is in slopes steeper than 45°.

In the Montafon valley, the distribution of forest types is mainly determined by altitude. In the valley floor, and up to 1000 m a.s.l., the forest is dominated by deciduous (beech *Fagus silvatica,* maple *Acer pseudoplatanus,* lime *Tilia cordata,* ash *Fraxinus excelsior*) and mixed forests (Norway spruce, beech and silver fir). Above 1000 m spruce forests predominate. Larch and stone pine can only be found close to the tree-line. The total number of sampling plots was 324 (25 km^2 plots) distributed among four coarse landscape types (of which the stratum tree line has been excluded for the analyses).

Lowland temperate forest

From the Atlantic Ocean to the Ural Mountains, central Europe is a lowland plain. Due to a benign climate for agriculture and easy access only ca 0.2% of the once widespread forest can still be considered intact (Hannah et al. 1995). Reference areas are thus hard to find. An exception can be found in NE Poland, where the Białowieża forest is located (Faliński 1986).

NE Poland – We sampled five different landscape types in NE Poland. These were the Białowieża National Park, managed forest in Białowieża outside the national park, managed coniferous forest in the Knyszyńska forest, pine plantations in the Biebrza valley and the Knyszyńska forest, and encroaching deciduous forest on former agricultural land (for details see Angelstam et al. 2002). The total number of sampling plots was 402.

Due to its remote location, the Białowieża forest (53.1°N, 23.5°E) has undergone much less dramatic changes than other forests of NE Poland. The area has been used as a hunting ground since the 15th century, set aside for Lithuanian dukes, Polish kings, Russian tsars and German nazis (Jędrzejewska and Jędrzejewski 1998). The core area of the Polish section of this 1250 km^2 forest area was declared as a national park in 1921 (Faliński 1986, Vera 2000). The Polish part covers 580 km^2 of which 47 km^2 is strictly protected with tourism and research as the only permitted activities (Jędrzejewska and Jędrzejewski 1998). The forest types range from fresh to wet and from coniferous to mixed and deciduous stands. Riparian forests and alder *Alnus glutinosa* swamps are also present in some parts. The deciduous "grąd" forest (oak-lime-hornbeam *Quercus* spp. – *Tilia* spp. – *Carpinus betulus*) dominates inside Białowieża National Park (Faliński 1986). The old-growth deciduous forest is characterised by a multi-layered structure from small plants and seedlings to trees up to 40 m tall.

Most of the forest outside the National Park has been exploited or partially cleared in historical times. Nevertheless, the forest as a whole has undergone less dramatic

changes than other forests of NE Poland (Faliński 1986, Jędrzejewska and Jędrzejewski 1998, Vera 2000). As early as in the third century, birch *Betula* spp. and hornbeam were used for charcoal production. Forest management started in the 16th century in the forest fringes. At the end of the 17th century the exploitation of the forest increased. Massive timber exploitation occurred during World War I both by Germans and the British European Timber Century Corporation. The intensity of logging has since then slowed down although harvesting is still carried out in most of the forest. The same forest types can be found as in Białowieża National Park, but in different proportions and with structural differences mainly due to past and ongoing logging activities.

The Knyszyńska Forest situated between the Biebrza marshes and Białowieża forms a large continuous forest block (Sokolska and Leniec 1996) north and east of Białystok (53.3°N, 23.2°E). Large parts of the forest grow on acidic sandy soils, which are not favourable to deciduous trees. Scots pine makes up 70% of the standing volume in that forest. Another 10% consist of Norway spruce and ca 20% are deciduous tree species, mostly birch, oak, and alder. The Knyszyńska Forest has been an important timber growing area for a long time. Pine has been exported to the Netherlands and U.K. since the 16th century. The most extensive felling occurred in 1915–1918. Reforestation is mainly done in pure pine stands while natural regeneration is allowed on other sites.

The Biebrza marsh (ca 53.4°N, 22.6°E) is an ancient cultural landscapes gradually being abandoned. Encroaching deciduous forest (*Salix* spp., *Betula* spp., *Alnus* spp.) is common on old formerly mowed and grazed grasslands. The pine plantations in Biebrza were mainly established after World War II. These plantations are characterised by their even age and are in most cases pine monocultures. Natural regeneration is either absent or very poor and undergrowth is missing. The pine plantations in Knyszyńska Forest are generally older than those in Biebrza and contain a higher proportion of other trees species, mainly spruce.

Stratification of regional and local gradients

Incorporating both the regional economic history among, and the local history within the different case studies, we stratified the data into different groups ranging from the centre (very altered landscapes) to the periphery (near-natural landscapes) of economic development (see above and Table 1).

Methodology

Based on a review of literature, interviews with forest managers and field trials we propose a system of measurements of major elements of biodiversity for boreal, hemiboreal and central European coniferous forests (see Appendix). The elements are chosen based on the idea that the development of biodiversity measurements must proceed from existing forest management data (e.g. tree species composition, wood volume and site type), by gradually adding new variables and measurements (Angelstam 1998b) shown to be characteristic of natural reference areas (Mayer 1984, Faliński 1986, Peterken 1996). Such indicators should include elements representing composition, structure and function of forests (Larsson et al. 2001).

The comprehensive system presented in the Appendix is a synthesis of several existing approaches applied in contemporary practical forest management. These include forest taxation (Reed and Mroz 1997), indicator species for high conservation value forests (Thompson and Angelstam 1998, Nilsson et al. 2001, Norén, et al. 2002) and evaluation of high conservation value by careful observation of compositional and structural elements of biodiversity (Drakenberg and Lindhe 1999). Additionally we introduce some new indicators regarding processes affecting the maintenance and renewal of forest habitats. By and large the approach follows that of the EC-funded BEAR project on the development of biodiversity evaluation tools proposed by Larsson et al. (2001). The target user is the manager of the local landscape in the form of the small forest owners in a village, or a management unit of a company that wants to practice adaptive management and thus start collecting information about the status, and if repeated trends, of indicators of different biodiversity elements. To provide an idea of the cost of applying our methodology in a management unit we estimated the total number of working days it took to carry out the five different case studies, respectively. In this paper we report on three indicators for each of the three groups of biodiversity elements (Table 2).

According to the Appendix our method should result in a sample size that is a multiple of the 16 survey plots in each 1 km^2 square. This is, however, not always the case in our data. For example, low forest cover in Abernethy meant that we adjusted the spatial pattern of the survey plots, and in some of the other study areas some sites were simply not accessible. To test for statistical differences among strata in the different case studies we used χ^2-tests for data based on the frequency of occurrence of different elements of biodiversity, and t-tests and ANOVA for comparisons of the basal area of dead wood and the proportion of deciduous trees. In the analyses we consider each plot to be an independent sample. However, given that the plots are clustered and separated by only 250 m within a cluster, there is a risk for spatial pseudoreplication if the forest stands are large. However, because the stands in hemiboreal, mountain and nemoral forest are usually only a few hectares in size, and the main aim of this paper is to present the methodology as such and an overview of the results of a small subset of the data, we do not consider spatial pseudoreplication a problem.

Table 2. List of variables representing different biodiversity indicators analysed in this study.

Biodiversity element	Variable	Description and unit for the survey plot data.
Composition	Lichens >20 cm	Occurrence (%) of pendulous lichen thalli >20 cm
	Trees >80 cm DBH	Occurrence (%) of trees with >80 cm DBH
	Dead wood	Basal area of standing and lying dead wood >10 cm DBH
Structure	Special trees	Occurrence (%) of moss and lichen-covered, bent, damaged, hollow and forked trees
	Deciduous trees >10 cm	Proportion of living deciduous trees of all living trees >10 cm
	Old forest stands	Occurrence (%) of stands with "ageing" or "old-growth" age classes
Function	Uprooting	Occurrence (%) of uprooted trees
	Wood-decaying bracket fungi	Occurrence (%) of wood-decaying bracket fungi
	Browsing	Occurrence (%) of browsing by ungulates

Results

Composition

The frequency of occurrence of long (>20 cm) pendulous lichen thalli varied significantly among the different strata in Trudner Horn, Montafon and Pskov (Table 3, Fig. 1). However, the direction of change differed and was not consistent with respect to the degree of naturalness. In Abernethy there was no significant difference between the two strata, and in NE Poland long lichens were not observed at all. In the two mountain forest case studies (Trudner Horn and Montafon) the frequency of occurrence increased with increasing naturalness. In Pskov there was no clear trend.

Regarding trees with a DBH >80 cm the frequency of occurrence in the plots was generally low (<10%), except for the "altered" strata in Abernethy and the "near-natural" and "natural" strata in NE Poland. The difference among the strata was significantly different in both these case stud-

Table 3. Results regarding compositional elements of biodiversity in five European case studies. Note that in the case studies of Trudner Horn and Montafon there was no natural stratum, and that in Abernethy the near-natural and natural strata did not exist.

	Abernethy (n)	Trudner Horn (n)	Montafon (n)	Pskov (n)	NE Poland (n)
Lichens >20 cm (occurrence, %)					
very altered	1.9 (206)	2.6 (76)	17.4 (161)	14.6 (96)	0.0 (80)
altered	5.3 (209)	11.9 (67)	62.9 (89)	0.0 (80)	0.0 (82)
near-natural	–	19.1 (147)	51.4 (74)	3.1 (64)	0.0 (160)
natural	–	–	–	8.9 (80)	0.0 (80)
	$\chi^2 = 3.3$	$\chi^2 = 12.0$	$\chi^2 = 51.3$	$\chi^2 = 15.9$	–
	$p = 0.07$	$p = 0.003$	$p<0.001$	$p = 0.001$	–
Trees >80 cm DBH (occurrence, %)					
very altered	1.9 (206)	2.6 (76)	5.0 (161)	0 (96)	0.0 (80)
altered	22.5 (209)	7.5 (67)	9.0 (89)	3.8(80)	0.0 (82)
near-natural	–	7.5 (147)	6.8 (74)	4.7 (64)	15.6 (160)
natural	–	–	–	1.3 (80)	57.5 (80)
	$\chi^2 = 40.6$	$\chi^2 = 2.3$	$\chi^2 = 1.5$	$\chi^2 = 5.3$	$\chi^2 = 122.5$
	$p<0.01$	$p = 0.32$	$p = 0.46$	$p = 0.15$	$p<0.001$
Sum dead wood (basal area, $m^2\ ha^{-1}$)					
very altered	0.7 (206)	0.1 (76)	0.8 (161)	2.6 (96)	0.3 (80)
altered	1.9 (209)	0.9 (67)	2.7 (89)	4.6 (80)	1.4 (82)
near-natural	–	1.0 (147)	4.1 (74)	6.0 (64)	2.6 (160)
natural	–	–	–	6.5 (80)	9.7 (80)
	$t = 6.5$	$F = 7.1$	$F = 42.1$	$F = 16.4$	$F = 119$
	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$

studies (Table 3 and Fig. 1). In NE Poland the stratum consisting of the Białowieża National Park was outstanding with a frequency of occurrence of trees with a DBH > 80 cm of 58%

The total basal area of standing and lying dead wood was significantly different among the strata in all five case studies (Table 3). In addition, in all study areas, the basal area increased consistently with increasing naturalness as expected from the local history of each stratum (Fig. 1). The range of basal areas among the strata in the different case studies was 30 to 100-fold, from 0.1 $m^2\,ha^{-1}$ in the very altered strata in Trudner Horn and 0.3 $m^2\,ha^{-1}$ in forest plantations in NE Poland, to 9.7 $m^2\,ha^{-1}$ in the Białowieża National Park.

Structure

The frequency of occurrence of special trees (trees with certain structures such as different microhabitats typical for natural forests) as defined in Table 2 and the Appendix was significantly different among the strata in all five case studies (Table 4). The frequency of occurrence increased consistently with increasing naturalness as expected from the local history of each stratum (Fig. 2). In the "near-natural" and "natural" strata the frequency of occurrence was generally ca 80% or higher.

The proportion of living deciduous trees of all living trees varied significantly among the strata in all five case

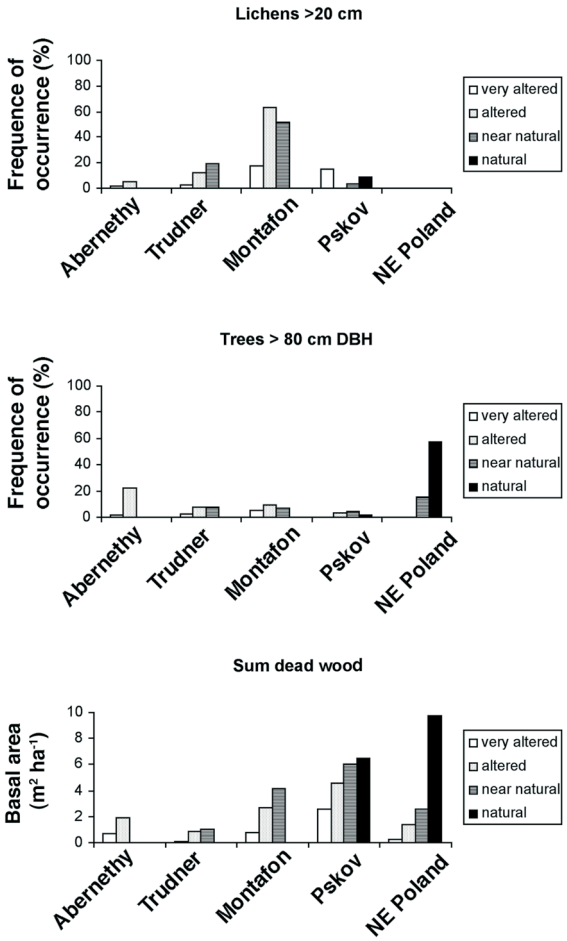


Fig. 1. Differences in the three compositional indicators of biodiversity: frequency of occurrence of pendulous lichen (top), trees with >80 cm DBH (middle) and basal area of standing and lying dead wood (bottom) in the four different strata (see Table 1) in five European case studies. Note that in NE Poland pendulous lichens were not found at all.

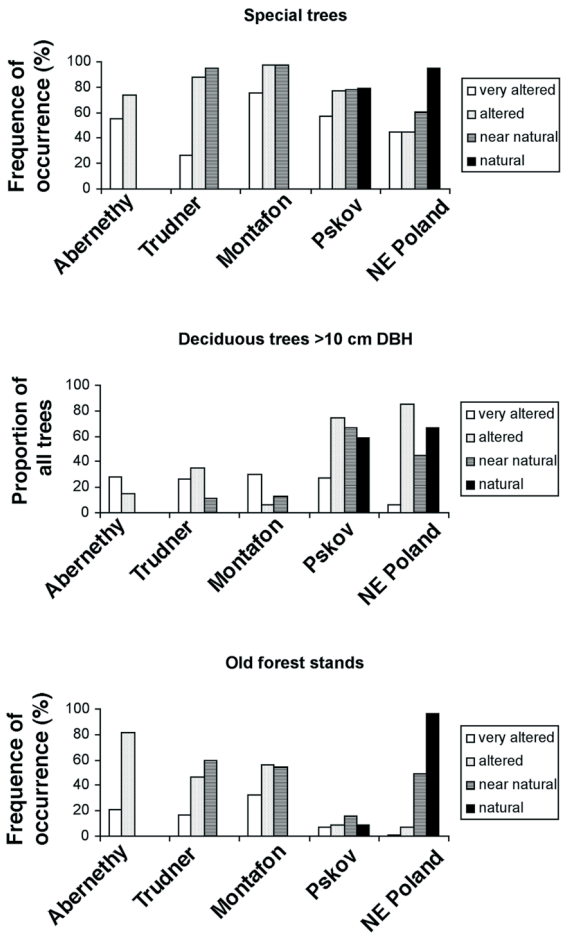


Fig. 2. Differences in the three structural indicators of biodiversity: frequency of occurrence of special trees (top), proportion of living deciduous trees of all living trees with >10 cm DBH (middle) and biologically old stands (ageing and old-growth) (bottom) in the four different strata (see Table 1) in five European case studies.

Table 4. Results regarding structural elements of biodiversity in five European case studies. Note that in the case studies of Trudner Horn and Montafon there was no natural stratum, and that in Abernethy the near-natural and natural strata did not exist. Regarding the n-values see Table 3.

	Abernethy	Trudner Horn	Montafon	Pskov	NE Poland
Special trees (occurrence, %)					
very altered	55.3	26.3	75.8	57.3	45.0
altered	73.7	88.1	97.8	77.5	45.1
near-natural	–	94.5	97.3	78.1	60.6
natural	–	–	–	78.8	95.0
	$\chi^2 = 15.3$ p<0.001	$\chi^2 = 132.8$ p<0.001	$\chi^2 = 33.4$ p<0.001	$\chi^2 = 14.5$ p = 0.002	$\chi^2 = 56.3$ p<0.001
Decid. trees >10 cm DBH (proportion of all living trees, %)					
very altered	27.9	26.3	30.2	27.5	6.2
altered	14.6	34.7	6.0	74.4	84.7
near-natural	–	11.7	13.4	66.7	45.1
natural	–	–	–	58.8	66.5
	F = 9.6 p<0.001	F = 13.7 p<0.001	F = 19 p<0.001	F = 41.1 p<0.001	F = 92.8 p<0.001
Old forest stands (occurrence, %)					
very altered	20.9	17.1	32.3	7.3	1.3
altered	81.3	46.3	56.2	8.8	7.3
near-natural	–	60.0	54.0	15.6	49.4
natural	–	–	–	8.8	96.3
	$\chi^2 = 152$ p<0.001	$\chi^2 = 37.0$ p<0.001	$\chi^2 = 17.4$ p<0.001	$\chi^2 = 3.4$ p = 0.34	$\chi^2 = 197.0$ p<0.001

studies (Table 4). The case studies in regions with a long management history located in hemiboreal (Abernethy) or mountain forest (Trudner Horn and Montafon) had generally lower proportions of deciduous trees than the case study in lowland temperate forest zone (NE Poland), and Pskov where forest management has a short history (Fig. 2). Within the individual case studies the highest proportions of deciduous trees were found in the "very altered" or "altered" strata, which were usually located at lower altitude on richer soils.

The proportion of plots having check-marks indicating the presence of ageing or old-growth stands varied significantly among the strata in Abernethy, Trudner Horn, Montafon and NE Poland, but not in Pskov (Table 4). In Pskov the data indicate that there was generally a low occurrence of older stands. In the other case studies the frequency of occurrence of older stands increased consistently with increasing naturalness as expected from the local history of management of each stratum.

Function

The frequency of occurrence of both uprooted trees and bracket fungi varied significantly among the strata in all five case studies (Table 4, Fig. 3). Except in Abernethy, the values increased consistently with increasing naturalness as expected from the local history of each stratum.

Finally, the incidence of signs of browsing damage by ungulates indicated large differences among the five case studies. In Abernethy the browsing pressure could not be assessed because of the absence of young trees due to a very long history of intensive browsing by red deer and sheep (Watson 1983, Smith 1993). In the two mountain forest case studies the browsing damages increased with increasing naturalness of the stratum (Table 5). While there was a generally low level of browsing (ca 30% or less), and no significant difference among the strata in Pskov, there was a significant difference among strata and a very high level of browsing (>85%) in NE Poland.

Costs

With 5–7 strata within each forest management unit and a large (>50) sample in each stratum, the total number of person-days for applying the complete version of system of biodiversity indicators (as described in the Appendix) was estimated at 23 (flat terrain in Abernethy) to 43 (steep terrain in Montafon) working days. This total effort can be divided into planning (ca 9%), data collection (ca 70%), data handling (ca 15%) and analysis (ca 6%) (Table 6).

Note that in this paper only a small subset of all the indicators described in the Appendix are reported.

Discussion

Patterns in biodiversity indicators within and among case studies

We found large differences in the state of indicators of different elements of biodiversity both within and among the five European case studies. In general the results from analysing a limited subset of 9 different indicators confirm the general pattern of impoverished forest biodiversity with increasing human impact. Broadly speaking, this is related to both clearing of productive sites for agricultural purposes throughout history, and the local and international demand for timber. This has resulted in several frontiers of use, ranging from high-grading to intensive silviculture spreading from the central to peripheral areas of Europe (Angelstam et al. 1995, Yaroshenko et al. 2001). Such historical gradients can be found at several spatial scales. First, with an economic history perspective, western Europe has a longer and more intensive history of land use than eastern Europe (Gunst 1989). Second, in the lowland temperate ecoregion clearing for agricultural purposes has created large variations in forest cover both among and within regions due to a combination of site characteristics and socio-economic changes (Darby 1956). Finally, in mountain forests physical inaccessibility and altitude has governed the intensity of forest use making virtually every valley into a forest history gradient illustrating the complex interaction between nature and man (Grabherr et al. 1998).

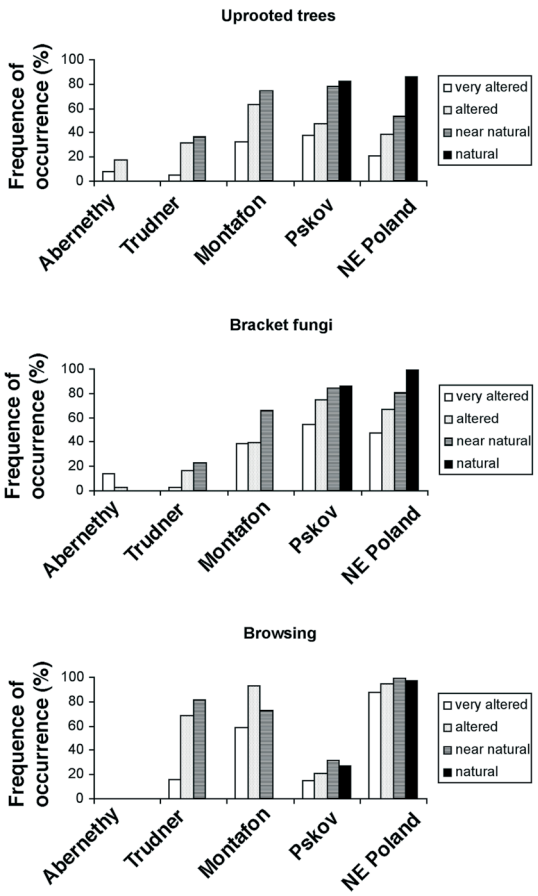


Fig. 3. Differences in the three functional indicators of biodiversity: frequency of occurrence of uprooted trees (top), bracket fungi (middle) and browsing by ungulates (bottom) (y-axis) in the four different strata (see Table 1) in five European case studies. Note that in Abernethy, Scotland there were no shrubs or young trees based on which the browsing pressure could be estimated.

The classification of indicators as compositional, structural and functional (Noss 1990, Larsson et al. 2001) is appealing, but always open for discussion. For example, a certain tree species or "special" trees can be viewed both as a component with the basal area recorded, and as a structural element and the proportion of all trees and frequency of occurrence calculated, respectively. Similarly, bracket fungi can be viewed as a compositional element if individual species are recorded, and as a functional element if their role as wood decaying organisms is stressed. These problems are discussed in detail in the Appendix.

Composition

Species are probably the best known elements of biodiversity. More detailed studies of the occurrence of different species groups such as mosses and lichens have demonstrated clear differences in the frequency of occurrence of specialised species in relation to the naturalness (often approximated as stand age) of forest stands (Gustafsson 2002). Such studies have, however, generally been made in local study areas as regular research projects, and not over large regions including considerable biogeographic variation in the distribution of different species. The highly variable frequency of occurrence of tall pendulous lichen thalli among the five case studies indicates that the use of even such a coarse species indicator is not feasible at the Pan-European scale. Specialised lichen indicator species groups such as pendulous lichens of the genera *Alectoria*, *Bryoria* and *Usnea*, or species with cyanobacteria as photobionts, are adapted to a light and moist microclimate (see Hedenås 2002). Their local occurrence can thus be dependent on presence of microclimatic features such as forest interior old-growth stands and steep shaded ravines, but also on a generally moist macroclimate due to an oceanic climate or high altitude (Rolstad et al. 2001). Thus a high frequency in one landscape may reflect the same degree of naturalness as a low frequency in another.

Analyses of the habitat characteristics of endangered forest species show that they often depend on natural forest components such as large trees and dead wood (Berg et al.

Table 5. Results regarding functional elements of biodiversity in five European case studies. Note that in the case studies of Trudner Horn and Montafon there was no natural stratum, and that in Abernethy the near-natural and natural strata did not exist. Regarding the n-values see Table 3.

	Abernethy	Trudner Horn	Montafon	Pskov	NE Poland
Uprooted trees (occurrence, %)					
very altered	7.8	5.3	32.3	37.5	21.3
altered	17.2	31.3	62.9	47.5	39.0
near-natural	–	36.7	74.3	78.1	53.8
natural	–	–	–	82.5	86.3
	$\chi^2 = 8.5$ p<0.04	$\chi^2 = 25.8$ p<0.001	$\chi^2 = 43.6$ p<0.001	$\chi^2 = 50.8$ p<0.001	$\chi^2 = 73.3$ p<0.001
Bracket fungi (occurrence, %)					
very altered	13.6	2.6	38.5	54.2	47.5
altered	2.9	16.4	39.3	75.0	67.1
near-natural	–	22.5	66.2	84.4	80.7
natural	–	–	–	86.3	98.8
	$\chi^2 = 15.9$ p<0.001	$\chi^2 = 14.8$ p<0.001	$\chi^2 = 17.4$ p<0.001	$\chi^2 = 29.0$ p<0.001	$\chi^2 = 60.6$ p<0.001
Browsing (occurrence, %)					
very altered	–	15.8	58.4	14.6	87.5
altered	–	68.7	93.3	21.3	95.1
near-natural	–	81.6	73.0	31.3	98.8
natural	–	–	–	27.5	97.5
	–	$\chi^2 = 93.6$ p<0.001	$\chi^2 = 34.2$ p<0.001	$\chi^2 = 7.4$ p = 0.06	$\chi^2 = 16.7$ p<0.001

1994). These features are characteristic for old forests and for natural disturbance regimes in a wide range of forest ecosystems (Peterken 1996, Nilsson et al. 2002), but have had to give way to even-aged single-species stands in managed systems (Esseen et al. 1997). The results of this study confirm this. Regarding large trees (>80 cm DBH), Abernethy and NE Poland stand out as being the only two case studies having strata including large nature reserves. Compared to this, the strata in the remaining case studies have a very small proportion of large trees.

The sum of the basal area of standing and lying dead wood appears to be one of the indicators that performs most consistently in relation to both the local stratification within case studies as well as among them. NE Poland is a particularly clear example. The basal area measurements suggest about a 30-fold difference between the forest plantations on the one hand and the Białowieża National Park on the other. A simplified estimate of the total wood volume suggests that the difference is even larger. Using the mean tree height of the forest in the two strata the volume of dead wood in plantation forests can be estimated (volume = basal area × height × trunk form factor; Hamilton 1982) to ca 170 $m^3 ha^{-1}$ in the Białowieża National Park and to ca 3 $m^3 ha^{-1}$ in forest plantations in NE Poland, suggesting a 60-fold difference in the total amount of dead wood. This is consistent with the estimates of Siitonen

Table 6. Number of strata, plots and person-days for application of the collection of data as described in the Appendix in five European case studies. Because this study focuses on strata where the natural vegetation is productive forest, the tree line strata in Trudner Horn (see Appendix) and Montafon were excluded from the analyses. Note also that some of the original strata have been merged (Table 1).

	No. of strata (see Table 1)	Plots per day	Number of person days				
			planning	field work	enter data	analyses	# days total
Abernethy	7	32	3	13	5	2	23
Trudner Horn	7	12	3	24	5	2	34
Montafon	6	10	3	33	5	2	43
Pskov	4	15	3	22	5	2	32
NE Poland	5	14	3	28	5	2	38

(2001) and Nilsson et al. (2002) suggesting a decline of dead wood and large trees by up to two orders of magnitude when comparing the historic range of variation with managed forests.

Structure

The results from the five case studies show that even if the frequency of "special" trees increased with decreasing historic human footprint, they were relatively common in most strata. However, neither of the study areas can be characterised as having intensive forest management, which is the praxis for example in Sweden's and Finland's boreal forests. Therefore, "special" trees have not been removed earlier in the succession during pre-commercial and commercial thinning.

Agriculture creates pressure on the natural forest environment, but also plays an important role in maintaining cultural woodland and semi-natural habitats (Tappeiner et al. 2003). For some forest species depending on early and un-managed stages in the natural succession of deciduous tree species, the abandonment of fields and wooded grasslands may provide increased amount of habitat (Mikusiński et al. 2003). This was evident for example in NE Poland in the altered stratum consisting of abandoned previously managed grasslands in the Biebrza area. Here encroaching deciduous trees maintain several woodpecker species otherwise only found in naturally dynamic forests (Angelstam et al. 2002). In Abernethy, Pskov and NE Poland this was associated with recent abandonment of fields, meadows or pastures. In the case study Trudner Horn the results also reflect the local land-use history where abandoned coppice forests are dominating in the surroundings of settlements. This is also true for the case study Montafon where collection of forest litter was made close to the villages. The strata altered and near-natural were located on higher elevation and deciduous trees are therefore less common in these strata.

Regarding old forest stands, except for Pskov the frequency of occurrence of old forest stands increased with decreased alteration as predicted by the local forest and land use history. The much lower amounts of old forest stands in Pskov is probably also due to the intensive warfare during the World War II that took place in the area in the early 1940s. According to Barraclough (1993) the front line between German and Russian troops was located just NE of the Pskov study area. Still today, the area shows many signs of the war. In the study area Montafon and Trudner Horn, old forest stands are mostly located far away from the settlements on higher elevations. Especially in Montafon, old forest stands remain in locally remote areas, today playing an important role for biodiversity (Dönz-Breuss et al. 2004). In Abernethy, the frequency of occurrence of old forest stands was very high in the altered stratum (80%). This can be explained by the existing Nature Reserve in this stratum.

Function

Uprooting is an important process whereby micro-scale primary succession can take place on the exposed root plates (Read 2000). While strong winds in principle may cause uprooting of trees and create root plates anywhere, the harvesting of trees precludes this. In our case studies, uprooted trees showed a pattern of occurrence that was very similar to the total amount of dead wood with lower frequency in the very altered strata and an increase in the frequency of occurrence in the more natural strata. Still, however, uprooted trees occurred throughout all strata and case studies. In the case studies in the Alps (Trudner Horn and Montafon) avalanches can also cause uprooting.

In general the frequency of occurrence of wood-decaying bracket fungi paralleled both the amount of dead wood and the occurrence of uprooted trees. This is quite natural as all three properties are closely linked. However, Scotland was an exception with a decreasing frequency with less intensive history of management. Note that the overall frequency of occurrence was much lower than in the other case studies.

The browsing level varied more among than within the case studies. Scotland was one extreme with such a long history of browsing on young trees that they were absent and this indicator could not be surveyed. In the two mountain forest case studies high browsing intensity by wild ungulates and livestock was associated with the occurrence of relatively large forest tracts, high densities of ungulates and a low density of human population and transport infrastructure. In the Alps functional populations of large carnivores are absent (Breitenmoser 1998) and hunting regulates ungulate populations. The relatively low browsing level in the Pskov case study is associated with the presence of viable populations of large carnivores, which limits the density of large herbivores (cf. Lindén et al. 2000). In NE Poland the browsing pressure was high in all strata. Studies of the interaction between populations of large mammals thus requires macroecological approaches where landscape-scale studies are replicated (Angelstam et al. 2000, Berger et al. 2001, Ripple and Beschta 2003).

Selection of indicators and monitoring to learn

Monitoring of the state and trends of different elements of biodiversity can be made at several levels ranging from the policy level to the level of forest management units (Angelstam et al. 2004d). In addition, research projects are needed to validate the links between cause and effect. This three-phased approach to monitoring thus encompasses implementation monitoring, effectiveness monitoring and validation monitoring, respectively (Busch and Trexler 2003). This study focuses on effectiveness monitoring, where monitoring is used to learn rather than learning to monitor (Gunderson 2003). The target group for the

present approach is thus the non-expert who wants a rapid assessment technique that is not too costly, neither in terms of time to learn the approach nor to perform it.

Based on the discussion of the subset of 9 indicators of different elements of biodiversity we conclude that most of them did reflect the trends in the history of forest and land use both within and among the five case studies. Two of the indicators stand out as particularly interesting as forest naturalness indicators at the European scale. These were the total amount of dead wood and the frequency of occurrence of uprooted trees. "Special" trees, old forest and wood-decaying bracket fungi also performed well in principle, but not always in the same smooth and gradual way in relation to land use history as the previous two indicators. Very large trees (>80 cm DBH) showed mixed results, probably due to regional differences in factors affecting the size of trees. Similarly, browsing appears to be related to regional scale changes such as the extirpation of large carnivores and other factors that maintain a high density of large wild or domestic herbivores. The specialised lichen species indicator appeared to indicate the local, but not the regional situation. This indicator was thus more restricted at the Pan-European level, even if it has been shown to be very useful locally (e.g. Nilsson et al. 1995). Species are also important from an educational point of view. This, however, does not necessarily require that the species themselves are used as indicator, but knowledge about species, especially those which are valued and well studied, is an effective way of communicating knowledge to different stakeholders (Uliczka et al. 2004). Finally, the proportion of deciduous trees was largely unrelated to the estimated degree of naturalness in all case studies. Nevertheless, the proportion of deciduous trees may be a relevant measurement of the local biodiversity (Mikusiński et al. 2003). This indicator thus suggests a potential conflict between naturalness and cultural landscapes as baselines for conservation. Alternatively, it stresses the need to include processes such as land abandonment as biodiversity indicators of disturbances favouring natural succession without management intervention. Semi-natural forests can thus retain certain characteristics allowing natural dynamics and biodiversity levels close to the natural ecosystems.

At the Pan-European policy level the Ministerial Conference on the Protection of Forests in Europe has gradually developed new indicators of sustainable management. Regarding the criterion biodiversity there are 9 different indicators: tree species composition, regeneration, naturalness, introduced tree species, dead wood, genetic resources, landscape pattern, threatened forest species and protected forests (Rametsteiner and Mayer 2004). The present attempt to evaluate the behaviour of indicators at the stand scale, and particularly dead wood and naturalness, are thus promising. For some other indicators, e.g. tree species and threatened (lichen) species the generality at the Pan-European level was limited. The geographical range of use of indicators should therefore be clearly defined both with respect to regional ecological aspects as well as values (Duelli and Obrist 2003). This requires studies at multiple spatial scales of how biodiversity indicators behave in gradients of land use change, how indicators are related to each other (Roberge and Angelstam 2004), and how different actors perceive them (Uliczka et al. 2004).

The indicators we used were deliberately chosen to be simple to learn and apply. Such indicators need of course to be evaluated in detailed studies where the score of the indicators are compared with the presence, and ideally fitness, of a suite of relevant species (Angelstam et al. 2004b). This is particularly important because forest managers usually assess forest components such as stand age and size rather than the presence of particular focal species. Studies about habitat requirements of declining or endangered lichens and mosses (Berg et al. 1994), insects (Jonsell et al. 1998) and birds (Angelstam et al. 2004b) show that they are closely related to habitat structures such as standing and lying dead wood, large trees and hole trees. However, only for a few of the stand scale indicator species proposed and even used (Norén et al. 2002), it is actually shown what forest components they require at different scales (e.g. Nilsson et al. 1995, Uliczka and Angelstam 1999, 2000). Such studies are urgently needed.

We also stress the need to include processes that maintain different compositional and structural elements of biodiversity. This was pointed out by Norton (2003) who noted the lack of explicit address to all the three main groups of biodiversity elements among institutions working with the implementation of biodiversity policies. We suggest that the least labour-intensive elements should be chosen for practical application in monitoring, and that specific research should aim at elucidating the detailed relationships, and regional variation in the relationships among different elements of biodiversity.

Developing measurements of elements of biodiversity applicable in management is an act of balance. On the one hand the implementation of knowledge and techniques should be affordable, on the other hand it should be a rigorous approach where indicators are used only if their indicator value has been documented, and where indicators are added or revised as new knowledge appears. We argue that the present method approaches this balance. Our experience from interacting with managers while developing this method over several years is that we were able to communicate to local managers that existing forest monitoring schemes need to be revised to address the new paradigm of sustainable forest management. As an example, the managers of the communal forests of Montafon in Austria developed a new forest inventory methodology which addresses the multifunctionality of forests (Maier and Breuss 2002, Dönz-Breuss et al. 2004).

Estimates of monitoring costs

An important factor for the applicability of a study is the financial expenditure. Therefore, one of the goals of developing this methodology was its cost-efficiency. In the five case studies the total amount of person days ranged from 23 (Abernethy) to 43 (Montafon) days. This difference depended on differences in the complexity of the forests, accessibility of sampling plots due to topography and weather conditions. Note, however, that application of the method in the field, and the communication of the results to different stakeholders, also constitutes education efforts in what biodiversity actually is.

Communication of results

Implementing policies concerning the maintenance of forest biodiversity in actual landscapes is a major challenge to a wide range of actors. This requires co-operation among actors with different interests, attitudes and competencies on different levels of society (Lee 1993, Gundersson et al. 1995). As an example, the five case studies included different land owner categories including state (Pskov), non-governmental organisation (Abernethy), communal (Montafon), non-industrial private (Trudner Horn) as well as local, regional and national authorities in the actual landscape as a whole. The process of policy implementation is about goal formulation, mobilisation of resources, organisational solutions and concrete priorities concerning land use (Clark 2002). Considering this complexity, is it at all possible to implement forest biodiversity policies at the scale of forest management units?

This is an urgent research issue, which needs to be addressed for moving towards a more sustainable ecological future (Clark 2002, Angelstam and Törnblom in press). This requires interdisciplinary, but also transdisciplinary (Jakobsen et al. 2004) approaches, bridging the common barrier between natural and social sciences (Berkes and Folke 1998, Hammer and Söderquist 2001, Norton 2003). To understand this complex reality, policy and implementation research is of vital importance (Gunderson et al. 1995, Clark 2002). It can help us in identifying, describing and interpreting troublesome obstacles as well as vital bridges in the actual implementation processes. This empirical knowledge is important for developing and improving different kinds of recommendations (for instance policy formulations, implementation strategies, organisational solutions and decision support systems). Policy and implementation research is a classical field within social sciences with a good potential for fruitful interdisciplinary research (Sabatier 1999). When it comes to implementing ecological sustainability it is essential with a close collaboration between social and natural scientists.

After showing that a biodiversity indicator behaves in the expected way, monitoring results could be compared with performance targets to assess the status of different elements of biodiversity. A next step would then be to evaluate the implementation of biodiversity monitoring, assessment and communication to managers. This includes the mapping of so-called implementation structures, starting from the "bottom" (i.e. from individual owners of land) up to the landscape and its different actors and interest groups (Sabatier 1999). Here, an important aspect to understand are the priorities and strategies in the land-use of the owners and what types of co-operative networks they have (Clark 2002). How do the implementing actors understand policies and directives, and the results from monitoring? Do they have capacity and tools to act, that is resources, competence etc.? Do the implementing actors feel that they have the possibility to influence policies and directives and do they want to act in line with those or are they opposed to them?

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Appendix

Indicators of forest biodiversity at the stand scale – a field guide

The actual landscape managed by a forest company, the private landowners in a village, common land, or combinations thereof, is where policies about maintaining biodiversity and actual management meet. To manage for forest biodiversity one needs to measure its main elements, and if needed, modify management so that the elements develop in the desired direction. A first step in the monitoring process is to stratify forests into different forest vegetation types using the different natural and anthropogenic disturbance regimes to which species are adapted (e.g. Rackham 2003, Angelstam and Kuuluvainen 2004). Then, in order to be cost-effective, one need to identify and select response variables (i.e. indicators) representing different elements of biodiversity that are affected by management directly or indirectly.

Based on a review of literature and experiences from practical application in a number of case studies (Höjer 1999, Drakenberg and Lindhe 1999, Frid 2001, Angelstam et al. 2002a, b) we outline a system for measuring major elements of biodiversity at the scale of stands for European forests and woodland. The elements, or indicators, are chosen based on the idea that the development of biodiversity measurements must proceed from existing management data (e.g. tree species composition, wood volume and site type; e.g. Jonsson et al. 1993), by gradually adding new variables representing elements of biodiversity. As suggested by Larsson et al. (2001) such variables should be derived from the composition, structure and function of reference areas representing both the biodiversity conservation visions of naturally dynamic forest (Mayer 1984, Faliński 1986, Peterken 1996) and pre-industrial cultural landscapes (e.g. Rackham 2003). Such variables should thus include all living and dead tree species, indicator species, the structure of stands and finally the important processes that maintain biodiversity (Noss 1990, Norton 2003). Apart from the indicators' relevance from an ecological perspective, we also stress the need to ensure that the selected indicators communicate well to the stakeholders involved (e.g. Uliczka et al. 2004).

Hierarchical sampling design

When a forest management unit (FMU) has been selected for monitoring, the first step is to make a detailed plan for the work. Before starting with the fieldwork the landscape should be stratified to cover all representative strata or landscape types. In the following section, we describe how field data plots can be clustered to allow multi-scale analyses, and how the collection of data in the plots is made in detail for different elements of biodiversity. This allows statistical analyses based on a stratified sampling procedure (e.g. Quinn and Keough 2002).

Information about the landscape

A landscape as well as a FMU can be defined in many ways (Muir 1999, Davis et al. 2001). However, because current knowledge indicates that very small areas can not maintain local populations of most specialised and area-demanding species (e.g. Angelstam et al. 2004a), we suggest a size of ca 100 km^2. The first step is to collect information about the area to be monitored. If not made before, this can be done by means of a questionnaire consisting of two parts (Angelstam et al. 2004b). The first part concerns the history of presence and breeding status of a selected set of indicator species that represent the actual biodiversity conservation vision for which there is good information. Often that restricts the analyses to vertebrates. The second part refers to the age class and tree species composition of the present landscape, as well as to its history of land use development. In addition to information about the local landscape, the history of land use development at the regional level is compiled by reviewing relevant literature.

Stratification

To stratify a landscape or FMU, both natural abiotic and biotic, as well as anthropogenic factors influencing the pattern of land cover types need to be understood. Therefore, stratification of the study area should be based on knowledge about both the land use history and the present habitat composition. Sampling plots should then be replicated in each stratum. Forest stand maps and land use zones (e.g. different silvicultural and other management regimes both outside and within conservation areas) can also be used to stratify the landscape to be sampled. As an example we describe the coarse landscape types (i.e., strata) identified for the Naturpark Trudner Horn study area (Südtirol/Alto Adige, N Italy), where this methodology was applied (Angelstam et al. 2002a; Table 1, Fig. 1). In this example the stratification was made according to topography, landscape history, and forest management systems.

Clusters of plots

The size of a forest stand can range from <1 ha to hundreds of hectares, depending on the tradition of forest management, and on the other processes affecting landscape patterns. Sampling at the stand scale must therefore be adapted to the structure of the landscape. To cope with this issue, a number of clusters of data collection plots should be placed within each stratum. To allow analyses of the data at

Table 1. Description of the coarse landscape types (strata) of the study area Naturpark Trudner Horn, N Italy as an example for the application of the methodology for measuring elements of biodiversity (see Angelstam et al. 2002a and Fig. 1).

Coarse landscape type	Description of the coarse landscape type
Apple orchards and vineyards	The bottom of the Etsch river valley is completely flat and the main land cover type is apple orchard. The density of transport infrastructure is high with the major highway from northern Italy via Brenner to Austria as well as a north-south connection for railway. On the lower slopes above the Etsch river valley vineyards are found from just over 200 to ca 600 m a.s.l. (Peer 1995). Management is intensive. Several smaller villages with lush gardens are located in this stratum.
Coppice forest	This habitat is the typical historical landscape type of Northern Italy's broad-leafed forest (Puumalainen 2001). The coppice forest is mostly privately owned and today the forest is not managed any longer. Therefore, the forest is gradually getting older, and today most of the forest is ca 50 yr old. The most common tree species are oak (*Quercus* spp.), ash (*Fraxinus* spp.) and hornbeam *Carpinus betulus*.
Agricultural land	This landscape type is located near the villages on intermediate altitude (1000–1800 m) and includes old cultural landscape remnants, farmland that is intensively managed today and litter forest, i.e. forest that has been used for the collection of litter. In some places, the forest is encroaching on the former agricultural landscape. Inside the nature park Trudner Horn, the farmland is managed to maintain the old cultural landscape.
Private forest	The private forest is subdivided into small units of ownership and the management is not very intensive. The forest is dominated by coniferous tree species interspersed with some deciduous components (beech *Fagus sylvatica,* ash and birch *Betula* spp.) and is located at altitudes from 1000 to 1800 m a.s.l.
Public forest	This forest category is owned by the villages in the area and is more intensively managed with distinct age-classes, small clear-cuts and plantation after final harvesting. Norway spruce, fir and Scots pine dominate the forest. In the lower parts, spruce and fir are dominating, whereas in the higher parts, pine is dominating on dryer soils. The altitudinal range is between 1000 and 1800 m.
Larch meadows	The character of open woodland is maintained by grazing and the presence of large trees (e.g. larch). Today, in some areas hazel *Corylus avellana* and spruce are invading the meadows, at some other places the meadows have been afforested. The altitudinal range of meadows is between 1700 and 2100 m.
Tree line	Today the tree line starts at 2100 m. Due to historical land-use (mostly grazing) the tree line has been lowered by 200–300 m compared to its natural level. Above the tree line, dwarf pine *Pinus mugo* can be found. Most of this area is publicly owned but there is also some private land. Some of the sampling plots are close to a ski resort, some near grazing land where people in the villages cut the forest historically to create grassland for their cattle during summer.

multiple spatial scales 1 × 1 km squares with 16 systematically distributed survey plots in each are used (Fig. 2). These 1-km^2 squares are placed in a stratified random manner in the study area, and are evenly distributed among the coarse landscape types. The individual plot can thus be viewed as a local patch, and the aggregation of plots can be seen as clusters that represent stands of different sizes in the landscape. To be able to repeat the survey in the future, with additional types of data if needed, each 1-km^2 square and plot should be marked on a detailed forest map (e.g. 1:10 000) with the plot ID number of the field protocol.

Survey plots

Information about the occurrence of specific species (composition), habitat pattern (structure), as well as natural and anthropogenic processes (function) is collected in each plot. So far data on a total of 21 basic groups of variables

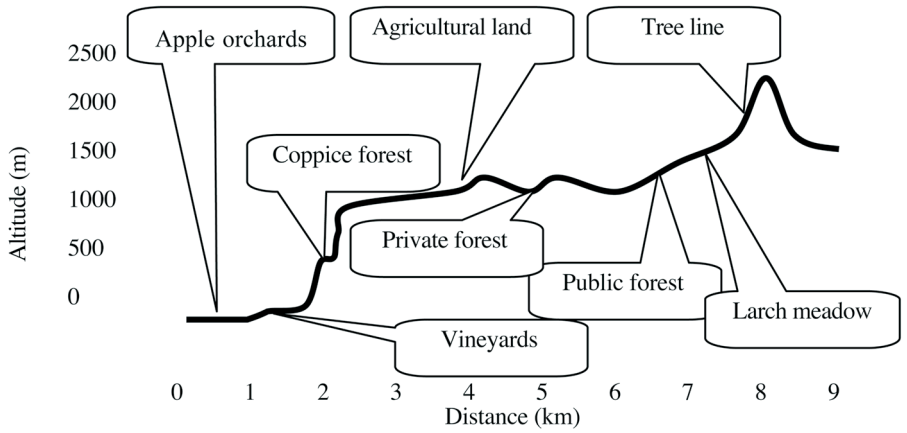


Fig. 1. Schematic illustration of the general sequence of landscape strata (i.e., coarse landscape types) in a case study. This example is for Naturpark Trudner Horn, N Italy (Angelstam et al. 2002a).

(Table 2) has been collected using one field protocol sheet for each plot. The field data is collected in four steps: 1) general information is recorded for the sampling plot; 2) basal areas are measured for the living and dead trees of different kinds; 3) small trees and shrubs are surveyed within a circle with a radius of 4 m; and 4) all other measurements are taken within a circle with a radius of 30 m.

Variables collected

First of all, general information (date, time, observer, location etc.) is noted on the protocol sheet. Since elevation is a potentially important factor for the local distribution of species, the altitude of the sample plots is recorded using an altimeter or information from the topographic map. In addition, slope (in 5° steps), aspect (8 compass directions), and position in the slope (valley, slope, ridge, or hilltop) are recorded.

Composition

For a whole system of forest vegetation types with different disturbance regimes, such as boreal, temperate and mountain forests, it is necessary to build a system that includes several indicator species with different ecologies that represent the different vegetation types (Angelstam 1998a, b, Thompson and Angelstam 1999, Nilsson et al. 2001, Berglind 2004). Trees can be viewed as dominant species in forests and should therefore form the starting point for describing the composition of a forest (Nikolov and Helmisaari 1992). For the boreal forest, analyses of the habitat characteristics of endangered forest species show that most of them require old trees, deciduous trees, or dead wood (Berg et al. 1994). As suggested by Anon. (2002) and Nilsson et al. (2002) the size of trees is an additional attribute of interest.

The key role of trees is not limited to the period when they are living. The legacies that trees leave after they have

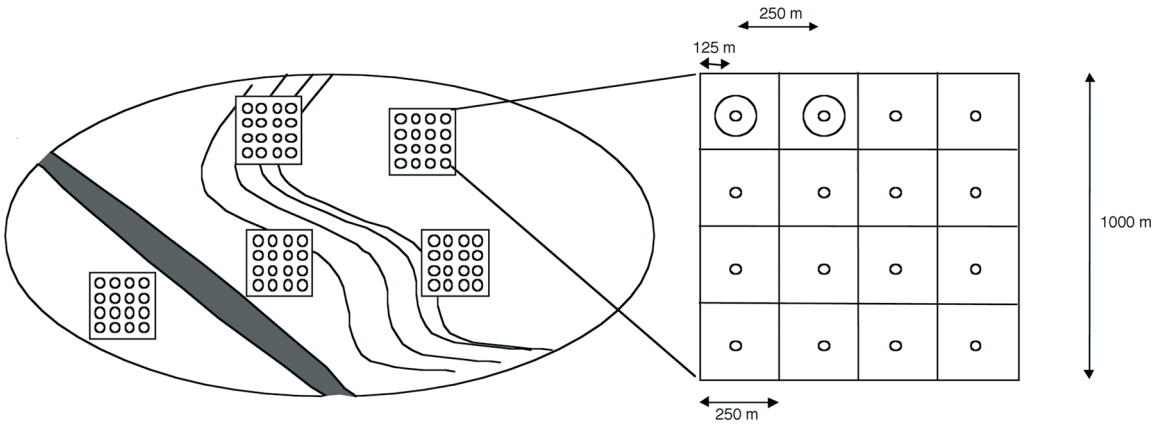


Fig. 2. Principle for the distribution of sample plots in the study area. Every 1-km^2 square includes 16 systematically distributed sampling plots. A number of 1-km^2 plots are distributed within each stratum in the landscape.

Table 2. List of the basic variables collected in the field for the present methodology to measure compositional, structural and functional elements of biodiversity.

	Description of basic variables
Composition	basal area of all living tree species of different diameter classes basal area of standing and lying dead wood of different decay stages and diameter classes specialised pendant lichens (>20 cm) and conspicuous lichen species (e.g. *Lobaria* spp.; *Evernia divaricata*, *Bryoria fremontii*, *Alectoria sarmentosa*) insect specialist signs (exit holes) in standing/lying dead wood without bark direct and indirect signs of specialised vertebrates (e.g. grouse, woodpeckers)
Structure	canopy height site type as determined by ground vegetation and its cover stand structure vertical layering tree age structure tree regeneration shrub species special trees with important microhabitats trees with cavities
Function	land management (fruit trees, pollarded trees) land abandonment (signs of past land use such as harvesting stumps, land abandonment as indicated by dead junipers, ruins, stone walls) abiotic processes (fire, flooding, wind, snow break) biotic processes (wood-living bracket fungi, bark beetle outbreaks, high stumps killed by wood decaying fungi, snow or wind, uprooted trees) damage by large mammal herbivores (browsing, bark peeling and velvet rubbing by ungulates) predation (carnivore scats and corvid observations) human disturbances

died are of great importance for the maintenance of forest biodiversity in both forest and woodland. A large number of studies show that dead wood of different kinds (standing, lying, various diameter classes, decay stages, ground contact, light exposure etc.) is a vital resource for many endangered species and for important ecosystem functions (e.g. Harmon et al. 1986, Siitonen 2001, Stokland 2001, Jonsson and Kruys 2001). In addition, other forest elements at the scale of trees, which are of importance for forest biodiversity (e.g. large old trees, hole-bearing trees, hollow trees) need to be assessed as a complement to traditional forest management planning data (Nilsson et al. 2002). Such elements are characteristic under a range of natural disturbance regimes in a wide variety of forest ecosystems (Peterken 1996), but are uncommon in even-aged, single-species stands created by intensive management (Esseen et al. 1997, Siitonen 2001). To locate remnant stands of the natural boreal forest for conservation, species specialising on these natural forest elements can be used (Norén et al. 2002).

Species with different life-history traits have different levels of specialisation and spatial demands (Angelstam 1996, Mykrä et al. 2000). Restricting management considerations only to species that do not have landscape-scale requirements, such as those used to identify woodland key habitats (Hansson 2001, Norén et al. 2002), is insufficient. Incorporating species with landscape-scale requirements such as grouse (Swenson and Angelstam 1993), woodpeckers (Mikusiński and Angelstam 1998, Mikusiński et al. 2001), overwintering passerine birds (Jansson and Andrén 2003), herptiles (Berglind 2004) as well as different groups of insects (Jonsell et al. 1998, Ehnström and Axelsson 2002, Berglind 2004, Wikars 2004) will increase our understanding of the status and trends of compositional elements of biodiversity in a region. This need for suites of indicator species representing the diversity of forest environments (Angelstam and Kuuluvainen 2004) is generally acknowledged (Angelstam 1998a, b, Thompson and Angelstam 1999, Gustafsson et al. 1999, Nilsson et al. 2001, Berglind 2004). Additionally, genes (provenance) are important in the context of re-introductions of extirpated species and in afforestation.

While the use of vascular plants to indicate forest site type and potential rates of tree growth has a long history (Arnborg 1990), the suggested practical use of vascular plant species to indicate conservation value (e.g. Karström 1992, Norén et al. 2002) has proven impractical in boreal forest (Gustafsson 2001). However, vascular plants have been shown to be useful indicators in other ecoregions (Dumortier et al. 2002). By contrast, at the scale of patches

of trees, the occurrence of wood-living bracket fungi, mosses and epiphytic lichens are important indicators of biodiversity (e.g. Bader et al. 1995, Esseen et al. 1996, Gustafsson 2002). Monitoring of such indicator species has thus been proposed for use both as tools for early detection of environmental changes and in follow-up assessments of management activities (Angelstam 1998a, b, Gustafsson 2002).

So far the lists of indicator species used for assessing the conservation value of forest stands such as those listed by Norén et al. (2002) have generally been compiled by species' experts based on their field experience. However, as a rule the scientific validation of their indicator value (Gustafsson 1999), nor over what geographical area a given species is a relevant indicator, has been done. Nilsson's et al. (1995) study on the of lichen lungwort *Lobaria pulmonaria* and Berglind's (2004) work on the sand lizard *Lacerta agilis* are important exceptions. Both studies indicate that the presence of the focal species was associated with that of several other taxa. Similarly, Mikusiński et al. (2001) showed that with the presence of three-toed woodpecker *Picoides tridactylus* and white-backed woodpecker *Dendrocopus leucotos*, a wide range of other forest birds were also found. Finally, Martikainen et al. (1998) showed that the presence of the latter species was associated with a rich fauna of saproxylic insects. This supports the umbrella species idea, that the presence of area demanding specialist species ensures the presence of other species dependent on a particular habitat (Roberge and Angelstam 2004).

The following requirements should be used for the selection of indicator species: 1) the species should be a well documented specialist of specified stand or landscape properties, 2) the species should be easy to detect and identify in the field. To allow species inventories throughout the snow-free season, the specialised species selected in this study were vascular plants (used only to determine the forest site type and indirectly the potential tree species composition), epiphytic lichens, bracket fungi, insects and resident birds.

Basal area of living trees

To assess the amount of different tree species in the sampling plot, a relascope is used to measure the basal area of all standing living trees with a diameter at breast height (DBH) 10 cm. B ecause large trees have special importance for the fauna and the flora, living trees should be further subdivided into two DBH classes: <40 cm and 40 cm. The occurrence of very large trees (DBH >80 cm) is also noted (cf. Nilsson et al. 2002). Some woody species usually considered as shrubs, such as juniper *Juniperus communis* and hazel *Corylus avellana*, can even grow to the height and DBH of regular trees. In this case the basal area of those species is also noted on the field protocol.

Basal area of dead wood

Coarse woody debris (CWD) is made up of snags and lying trees, and is one of the most important components of the forest ecosystem enhancing biodiversity. Especially CWD of higher DBH classes provides habitat for several animal, plant and fungal species. In addition, large snags are a key component for cavity nesting species. Standing dead wood is measured with the relascope and divided into the same DBH classes as living trees and into coniferous and deciduous trees. To be considered for basal area measurements, a snag must have a height of >1.3 m and a DBH 10 cm.

The basal area of lying dead wood is measured with the relascope at breast-height (i.e., horizontal position corresponding to breast height), measured from the thickest end of the log. Lying dead wood is divided into the same DBH classes as living trees. When possible, lying CWD originating from coniferous and deciduous trees should be noted. For all lying trees different decay stages should be identified (Harmon et al. 1986). We used three stages (hard, soft, and partly decayed logs where the log is no longer straight but follows the local microtopography). According to Stokland (2001) the latter corresponds to a decay level of 50%.

Lichens

The use of epiphytic lichen species as bioindicators has a long tradition. Some species' sensitivity for air pollution (Bates and Farmer 1992) and lack of continuity in microsite conditions of a forest (Tibell 1992) are good examples. Large epiphytic lichen such as lungwort and witch's hair *Alectoria sarmentosa* have been shown to be good indicators of old-growth forest at the stand scale (Esseen et al. 1996). Lichens are used by bird species as food storage and foraging substrate (Pettersson et al. 1995, Esseen et al. 1996). On the protocol sheet, the occurrence of conspicuous species such those mentioned above is noted. The occurrence of hanging lichens (e.g. *Usnea* spp., *Alectoria* spp., *Bryoria* spp.) longer than 20 cm and their frequency of occurrence (single (1–2) trees, several (3–5) trees or abundant (>5)) on trees are also noted.

Insects in dead wood

Wood-living insects are an important component of the forest ecosystem as they are not only parts of the food-web (important food source for e.g. woodpeckers) but also indicators for natural disturbance processes. Dead wood hosts a wide range of insect species. The occurrence of larger insect species depends on dead wood of larger DBH-classes (Zabranski pers. comm.). As insects themselves are not easy to detect in the field, one can look for indirect signs of insects in dead wood such as exit holes (Ehnström and Axelsson 2002). The presence of exit holes of two size categories (>5 or >10 mm) and three general shapes

(round, oval, or half-moon) on barkless snags, logs, and stumps were noted in each survey plot. Although very coarse, this measurement captures some of the diversity in wood-boring species. That such a short-cut can be useful was confirmed by Oliver and Beattie (1993) who estimated the species richness of spiders, ants, polychaetes, and mosses by dividing individuals into recognisable taxonomic units and were able to show that there was little difference between classifications made by a non-expert and taxonomic specialist.

Vertebrate indicators

Forest dwelling grouse (Aves, Tetraonidae) and woodpeckers (Aves, Picidae) are examples of species that are specialised on certain forest types (Swenson and Angelstam 1993, Angelstam and Mikusiński 1994, Storch 1999, Derleth et al. 2000). Woodpeckers for example can be used as indicator species for certain natural forest types (Mikusiński and Angelstam 1998) but also as indicators for the diversity of forest bird species (Mikusiński et al. 2001). Both direct observations (sightings and calls) as well as indirect signs (e.g. feeding signs of woodpeckers; droppings; tracks; cones with feeding signs of red squirrel *Sciurus vulgaris*) are noted during the period of data collection inside the plots. To increase the vertebrate sample size, observations made en route to the next sample plot are noted on the same sheet in a specific field. The number of observations (calls and sightings) of corvid birds (such as raven *Corvus corax*, crow *Corone cornix*, jay *Garrulus glandarius*, and magpie *Pica pica*) are noted. The reason is that a disruption of predator-prey relationships such as increased abundance of generalist predators may affect the breeding success of forest species such as capercaillie *Tetrao urogallus* (Kurki et al. 2000).

Because of their important function as primary cavity nesters, woodpeckers are considered as keystone species. They build cavities used by secondary and weak-primary cavity nesters (Martin and Eadie 1999). Indirect signs of black woodpeckers *Dryocopus martius* noted on the protocol sheet are holes in anthills and deep feeding excavations at the base of spruce trees, in logs, or in stumps. The occurrence of the great spotted woodpecker *Dendrocopos major* is identified by indirect signs such as piles of cones emptied of seeds. Finally, occurrence of the three-toed woodpecker is denoted by horizontal lines of small holes in the bark of trees (Bütler et al. 2004). Fresh signs on spruce show transparent, sticky, and flowing resin, or transparent drops are present in the holes. Fairly fresh signs show a whitish or yellowish resin that does not flow anymore. Old signs show no resin, but only small holes. A sign of long use is when the tree has formed bulges. Finally, indirect signs of woodpeckers that cannot be attributed surely to a specific species are noted on the form as "woodpecker".

Structure

The main components of a forest are the trees. Because species have adapted to different developmental stages of trees from seeds to the decayed wood and to the various tree species, it is essential that the structure of trees at multiple spatial scales is monitored. Compared with dynamic natural forests, managed forests have altered structural variability at all spatial scales. Typical changes are truncated age class distribution (Angelstam et al. 2004b), declines in the amount of large forest areas (Mykrä et al. 2000, Aksenov et al. 2002), altered tree species composition, increased homogeneity in tree spacing, truncated diameter distributions favouring smaller trees (Nilsson et al. 2002), and reduced frequency of occurrence of standing live damaged trees, standing dead trees, and fallen trees in different decay stages (Siitonen 2001). Similarly, but at the landscape scale, there has been a disproportionate loss of forests on rich sites to agriculture and other uses (Angelstam et al. 2003a).

At the stand scale the distribution of different tree species, decay stages of dead wood, basal area, height, as well as horizontal and vertical layering constitute basic structural attributes. Additionally, the variance in tree sizes needs to be included as well as some measurement of horizontal layering. At the landscape scale, the range of age classes including biologically old stands should be estimated. Such structural aspects can be illustrated by combining different compositional elements as described above.

Canopy height

The average canopy height of the trees in the sampling plot is measured with a height-meter to the nearest metre. In the analyses the data is presented in 5-m classes.

Cover of ground vegetation and site type

Vascular plant species indicating abiotic qualities have been used for a long time in agriculture and forestry in many countries (Ellenberg 1996). In most cases the systems have been used to specify soil type or soil productivity, but also for habitat classification. Using the stand classification system of Hägglund and Lundmark (1987), each sample plot is attributed to one of the following site types: tall herb (TH), low herb (LH), ground without field layer (GW), broad-leaved grass (BG), narrow-leaved grass (NG), sedge-horsetail (*Carex* spp./*Equisetum* spp.) (SH), bilberry *Vaccinium myrtillus* (BL), lingonberry *Vaccinium vitis-ideae* (LB), crowberry/heather (*Empetrum nigrum*/*Calluna vulgaris*) (CR), bog (LE), lichen cover 25–50% (WL), lichen cover >50% (LI). In those areas where the classification system of Hägglund and Lundmark (1987) can not be applied, characteristic site indicator plant are noted for the specific stand. For the ground vegetation, cover is recorded in 10% units. For bilberry (BL) and crowberry/heather (CR) the height is noted to the nearest dm.

In various studies, bilberry has been shown to be a key species affecting the suitability of habitat for a variety of species (e.g. Suchant and Braunisch 2004). The flowering part and leaves are used by Lepidoptera larvae (Baines et al. 1993), which in turn are foraged by for example birds (Atlegrim and Sjöberg 1995, Storch 1999). Several herbivores also feed on the berries and stems of bilberry (Breuss 1999, Nordengren et al. 2003). Beside its function as foraging substrate, bilberry (as well as other ericaceous shrubs) also provide cover to forest dwelling species (Storch 1999). Hence, the total cover of the green ground vegetation in general and the cover of bilberry specifically are estimated.

Stand structure

Based on basal area data there are several ways of describing the structure of forest stands. The identity and relative abundance of tree species on different site types and the relative amount of different types of dead wood are two examples (Stokland 2001).

Vertical layering

Vertical structure is the bottom-to-top configuration of above-ground vegetation within a forest stand (Brokaw and Lent 1994). Variation in vertical structure depends on soil, particular climate, tree species and other plant species, but also on temporal aspects (succession). The vertical organisation of forest vegetation has various direct (food, nesting, resting, perching, etc.) and indirect effects (e.g. internal stand microclimate and distribution of animal prey) on animals and plants. Species richness usually increases with succession because species richness increases with vertical complexity, which itself increases with stand age (Brokaw and Lent 1994). The vertical cover of forest vegetation in each plot is estimated in 10% units for three height classes: 1.3–4 m, > 4–10 m, and >10 m. In addition, the relative proportion of deciduous and coniferous foliage is noted for each layer.

Tree age structure

During the succession after natural or anthropogenic disturbance a forest stand goes through a variety of stages that affect the structural diversity (Oliver and Larsen 1996). In a managed forest these age classes can be distinguished into young forest, thicket, middle-aged and final harvest forest. Age classes that are beyond this classification are usually clumped into one "overmature" age class without further distinctions. Yet, for a variety of animal and plant species the older age classes (>>120 yr) constitute suitable habitat. Therefore, a classification of the forest into more age classes (especially including the ageing as well as biological old forest types) is of importance.

Using forest stand databases or field observations all sample plots are classified into six stand age classes with the following age intervals: old-growth (>150 yr), ageing forest (110–150 yr), final felling (70–110 yr), middle-aged forest (30–70 yr), young forest (5–30 yr), and clear-cut (<5 yr) (cf. Angelstam and Kuuluvainen 2004). If the forest is even-aged, the specific age class is noted. If the forest is mixed-aged, all occurring age classes are noted. The specific age-class standards should of course be adapted to local conditions. Indeed, the duration of a natural cycle in a natural forest is ca 350 yr, compared with 60–100 yr in managed forest (Pennanen 2002).

Tree regeneration

The number of small trees with a height 1.3 m and a DBH <10 cm is counted for each species within a 4-m radius. The presence or absence of nurse logs and nurse stumps, defined by the presence of tree seedlings (those species that have been measured for the basal area) on fallen trees or stumps is recorded as a measurement of stand age and occurrence of decay stages in a later developmental phase. Additionally, the type of regeneration (natural or artificial, i.e. planted) is specified.

Shrub species

Shrubs are an important component of forests as they contribute to foliage height diversity, and are used as forage (leaves, stems, fruits) and cover for a variety of animal species. The occurrence of different shrub species is documented. If certain species have been severely browsed by deer or livestock, this is noted in a separate data-field.

Special trees with important microhabitats

The presence/absence of living trees (DBH 10 cm) of special types with certain structures such as different microhabitats typical for natural forests is noted. The types of special trees recorded are: bent tree, naturally damaged trees (broken top), forked trees (only large trees of commercial species), trees with retarded growth (especially at the tree line), very large trees (DBH >80 cm), hollow trees, moss-covered trees, and lichen-covered trees. The presence of such special trees indicates a low intensity in forest use. Indeed, in commercially used forests these trees are generally cut already in the first thinning period due to their low economic value.

Trees with cavities

The presence of different types of trees with woodpecker (or other cavity nesting birds) holes of different sizes are noted: 1) small holes (diameter < 5 cm) mostly used by tits, 2) large holes (diameter 5–10 cm) made by small to medium-sized woodpecker species (e.g. great spotted woodpecker), and 3) very large (oval) holes (longest diameter >10 cm) made by large woodpecker species (e.g. black

woodpecker). Additionally, the occurrence of nest-boxes for cavity nesters is recorded in order to be able to qualify the availability of nesting habitat for cavity nesters.

Function

Species have adapted to certain elements and structures of a landscape in an ecoregion. Most European landscapes have a long history of human land use. As a result, specialised species on certain structures of natural forests and pre-industrial landscapes become vulnerable or even locally or regionally extinct. To maintain viable populations of such species, certain structural elements or vegetation types may have to be continuously maintained or even restored. Maintenance of biodiversity in the long term should therefore include also processes that affect habitat renewal at different spatial scales (Larsson et al. 2001, Norton 2003). Natural biotic and abiotic disturbances maintaining the amount and types of dead wood, different microhabitats and regeneration of tree species are important examples. An example at the scale of patches of trees is the distribution of decay stages of dead wood and uprooted trees (Stokland 2001). Signs of insect or fungal outbreaks and other natural processes as well as signs of land abandonment are useful additional measurements to demonstrate the occurrence of habitat renewal at the stand scale.

Although processes that maintain functions are more subtle elements of biodiversity than species and structures, they are important for the maintenance of different disturbance regimes. Altered fire frequencies (Niklasson and Granström 2000), hydrologic regimes (Bergquist 1999) and air pollution causes leaching of nutrients such as nitrogen from sensitive soils and changes in vegetation in some regions (Ellenberg 1996) are abiotic examples. Past fire events, different forest practices and past agriculture activities may all influence the present situation in a stand. Landscape changes favouring generalist predators that affect breeding success of forest birds (Kurki et al. 2000) and browsing by superabundant wild herbivores on certain deciduous trees species (Angelstam et al. 2000) that modify forest composition are two examples of altered trophic interactions. Socio-economic changes in rural communities followed by land abandonment constitute another example (Angelstam et al. 2003b).

Land management and abandonment

If possible, the silvicultural system of management (e.g. clear-cutting, shelterwood, etc.) and direct signs of timber use such as wood-storage are recorded. Thus the age (fresh/old) and spatial distribution of the stumps in the sampling plot is classified as single, widespread, or clumped and is noted in the field protocol. Similarly, we record evidence of ongoing traditional management of trees by pollarding and coppicing.

The abandonment of woodland pastures and other types of pre-industrial cultural landscapes are other major processes affecting biodiversity. Almost all over Europe the forest area is increasing, either because policies encourage increased forest cover or because forest is encroaching on former agricultural land (Nilsson et al. 1992, Carey et al. 2003). The effects on biodiversity are diverse and complex including both loss of important habitat types in the cultural landscape and initiation of secondary succession of use for other species (Mikusiński and Angelstam 1999, Mikusiński et al. 2003).

Marks and Gardescu (2001) reviewed how site history can be inferred from evidence that can directly be observed from a careful search through a piece of forest or woodland. The presence of signs of local charcoal production, stumps made by ax, chainsaw or a harvester is therefore recorded. In remote areas in northern Scandinavia and Russia, very old and high stumps (0.5–1 m) are signs of logging made during winter very early in the forest history, i.e. during the phase of high-grading. This phenomenon can also be found in the Alps. There, high stumps are left as a natural "hazard control system" to protect against avalanches, land slides and rock falls. Note that the absence of stumps in a plot may have two alternative causes: 1) the stand has never been harvested or has not been harvested for a very long time, or 2) the stand was established on formerly open land, such as abandoned agricultural fields.

Trees that indicate a historically more open landscape such as those having branches close to the ground, dead lateral but living vertical branches, large crowns and old trees (e.g. *Juniperus*, *Sorbus*, *Quercus*) encroached by shade-tolerant tree species (Marks and Gardescu 2001, Rackham 2003) are also recorded. The presence of afforested or overgrown fields, fences of stone walls, trees, or barbed wire, juniper (live or dead), wide-crowned trees, nitrogen-loving species such as elder *Sambucus* spp. and nettle *Urtica* spp. are noted. Damaged or destroyed old farming houses and stables, stone walls and other signs of human use are recorded as well.

Natural abiotic and biotic processes

Both abiotic and biotic processes are important for the maintenance of biodiversity (e.g. Nolet and Rosell 1998, Ulanova 2000). In areas with fire as a natural disturbance regime the presence of fire scars in living trees and in stumps is therefore noted to assess past stand events. Signs of avalanches, trees broken by wind, uprooted trees, erosion, beaver-dams as well as wood-decaying bracket fungi and bark beetle *Ips* spp. (Coleoptera: Scolytidae) infestations in the sampling plots are therefore recorded. Uprooted trees are trees with an exposed root system, an important substrate for several mosses. Finally, trees broken due to fungal attack and top-broken trees as primarily a result of high snow pressure in stands of high altitude or latitude are recorded.

Large mammal herbivory

The effect of large herbivores on the forest at the landscape scale is measurable through the intensity of browsing on preferred shrubs (e.g. Anon. 1988, Angelstam et al. 2000). Droppings of red deer *Cervus elaphus*, moose *Alces alces* and other large herbivores are noted, as well as tracks and game crossings. Note that moose bark peeling on young pine and on middle aged spruce/aspen just above breast height, or even higher made in winter can co-occur with deer damage. Presence/absence of deer damage like browsing, bark peeling, velvet rubbing as well as the presence of livestock in the forest is identified by the observation of livestock dung and recorded in a specific field.

Predation

Sightings and calls of corvids (see above) and large avian predators, scats of red fox *Vulpes vulpes* and marten *Martes* sp. are noted. The relative occurrence of generalist predators indicates the predation pressure (e.g. Andrén et al. 1985).

Human disturbance

Information about the presence of roads, river/brook, ski-slopes (winter tourism), and hiking trails show the accessibility and therefore vulnerability of an area to human disturbance (seasonal or year-around). This information can also be extracted from the maps.

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Land management data and terrestrial vertebrates as indicators of forest biodiversity at the landscape scale

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Angelstam, P., Edman, T., Dönz-Breuss, M. and Wallis DeVries, M. F. 2004. Land management data and terrestrial vertebrates as indicators of forest biodiversity at the landscape scale. – Ecol. Bull. 51: 333–349.

Sustainable land management requires monitoring of the status and trends for elements of biodiversity at the landscape scale. We evaluate the usefulness of two types of data sources as compositional and structural biodiversity proxies, viz.: 1) the presence of different ecological groups of specialised or area-demanding birds and mammals; and 2) existing landscape information about historical forest loss, age-class specific tree species composition by area and transport infrastructures. Data from 28 landscapes (>100 km^2) were collected by means of a questionnaire sent to managers of forest landscapes in Europe's boreal, hemiboreal, mountain and temperate lowland forests, from the Atlantic Ocean to the Ural Mountains.

To facilitate comparisons of landscapes across biogeographic regions, larger birds and mammals were divided into ecological groups based on taxonomy, body size, trophic position, and dependence on different forest structures. The diversity of ecological and taxonomic guilds was negatively correlated with measurements of human exploitation of the landscape at the scale of regions, such as railway advent and position in the European west-east gradient in economic development. The occurrence of species requiring large trees was also negatively correlated with the advent of industrial forestry indicated by railway development in the region. The presence of a set of hole-nesting species was negatively correlated with the proportion of forest plantations on former arable land, and the presence of a natural forest indicator (the three-toed woodpecker *Piciodes tridactylus*) was positively correlated with the amount of coniferous forest with a stand age over 120 yr. The differences in quality and extent of preferred habitat for the species studied can hence be interpreted as the local human footprint on landscapes. This conclusion was also evaluated using an historical ecology approach. A qualitative evaluation of the history of land use and current biodiversity status in three landscapes (South Veluwe in the Netherlands, Säfsen in Sweden, and Yaksha in Russia) confirm the quantitative analyses.

We conclude that both simple forest management data and ecological groups of species can be useful indicators of forest biodiversity at the landscape scale. However, critical evaluation of alternative hypotheses of species distribution in Europe such as those related to biogeography of species must be evaluated more thoroughly for example by using historical ecology approaches.

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Following the policies based on the principle of sustainable development, the need to establish criteria and indicators at international, national and regional scales for assessing the status and trends in biological diversity has been widely recognised (Anon. 1992, 2002). The transition from the classic forest sustainability concept focussing on wood as a renewable resource (Schlaepfer and Elliott 2000), to ecological sustainability based on forest ecosystem management (Anon. 2000) requires operational monitoring of new features that were not traditionally monitored in forest and woodland (Angelstam 1998, 2002a, Duinker 2001, Nilsson et al. 2001, Angelstam et al. in press). In Europe there have been some improvements in monitoring at the national and European Union levels (Higman et al. 1999, Anon. 2001, Puumalainen 2001, Larsson et al. 2001, Puumalainen et al. 2002, Stokland et al. 2003). However, there is only limited experience regarding the practical measurement of forest biodiversity components at the scale of forest management units or landscapes (Bachmann et al. 1998, Angelstam et al. 2001, Franc et al. 2001). Additionally, the availability of relevant, easily accessible, and sufficiently detailed data at this scale is a serious limitation (Angelstam and Bergman 2004, Angelstam et al. in press). Examples of potentially useful landscape-scale data are the composition of communities of specialised and area-demanding species (Mikusiński and Angelstam 2004, Roberge and Angelstam 2004), the size distribution of forest patches and their spatial location (Mykrä et al. 2000), as well as age class and tree species composition and structure (Anon. 2001).

Landscapes can be attributed any size depending on whether the perspective is based on certain species or on stakeholders ranging from private land owners to regional planners (Wiens 1989, Liu and Taylor 2002, Swihart et al. 2003). The size of a landscape thus depends on the beholder and on the objective of the monitoring or assessment. Using focal bird species of importance for conservation according to the EC Birds Directive (Anon. 1979), Angelstam et al. (2004) estimated the area needed for 17 specialised species. The mean minimum size of planning units to support a local population of 100 females where suitable habitat dominates the landscape was 400–2500 km^2. This corresponds to the size of the ecological landscape plans and management units of large forest enterprises in Sweden and Finland today.

A clear definition of the desired benchmark is needed to define management targets. Forest biodiversity is no exception to this rule. Policies related to biodiversity of European forests and woodland make explicit reference to the concept of naturalness (Anon. 2002). Although we are aware of the ambiguity of this concept (e.g. Balée 1998, Egan and Howell 2001), it is obvious that forest biodiversity indicators should represent elements found in naturally dynamic forests (Peterken 1996), or pre-industrial cultural landscapes (Kirby and Watkins 1998, Rackham 2003). The latter, although influenced by human land use, contained structural components such as dead wood, large old trees and old-growth stands that are typically found in naturally dynamic forests. As a consequence, remnants of the pre-industrial cultural landscape provide a refuge for many species that were adapted to a pristine or near-natural forest environment (Kirby and Watkins 1998). Other terms used to describe the conditions in benchmark or reference areas are ecological integrity (Pimentel et al. 2000) and historic range of variation (HRV) (e.g. Egan and Howell 2001). Similarly, cultural authenticity represents a set of values, which is consistent with current policies about biodiversity, sustainable development and cultural heritage in pre-industrial cultural landscapes (Angelstam et al. 2003b). Following the definition of biodiversity (e.g. Larsson et al. 2001) indicators should represent three categories at multiple spatial scales, viz.: 1) species representing naturalness, HRV, or authenticity (i.e. composition), 2) habitats found in naturally dynamic forests and pre-industrial woodland (i.e. structure), and 3) ecosystem processes (i.e. ecological integrity or function).

The structural diversity of the forests is diminished by modern intensive forestry, which often alters or destroys the original dynamic forest habitats (e.g. Hannah et al. 1995). Studies of dead wood (Siitonen 2001), large forest tracts (Mykrä et al. 2000, Yaroshenko et al. 2001) and connected habitats (Angelstam et al. 2003a, b, 2004) imply clear relationships between forest structures and the economic development of a region. Using specialised birds and large mammals as proxies Mikusiński and Angelstam (1998, 2004) and Chamberlain and Fuller (2000) documented the impact of human footprint in landscapes on species sensitive to habitat loss and alteration. Regarding invertebrates, Schiess and Schiess-Bühler (1997) showed that the gradual intensification of both forestry and agriculture resulted in a severe impoverishment of the butterfly fauna. Trauger et al. (2003) provide many other examples.

One of the explanations for this conflict between the intensive use of forests and the maintenance of species is that trees become valuable for the pulp and timber industries at much lower age than they become important for species specialised on natural forest conditions (e.g. Falinski 1986). In the Swedish boreal forest, for example, the preferred age for final felling is 70–100 yr, whereas several species require old-growth components found only in forests older than 150 yr (Eiswerth and Haney 2001). Intensive forestry also modifies the tree species composition towards monocultures of economically valuable species. Similarly, intensification of agricultural practices usually creates extensive monocultures of crops, or pastures on fertilised fields. Trees are unwanted in these systems since they disturb mechanical cultivation and compete with crops for nutrients, water, and light. In contrast, the traditional cultural landscape often contained trees (Peterken 1993), which were managed by coppicing and shredding to supply leaf fodder for sheep and cattle farming (e.g. ash *Fraxinus excelsior*) or for the production of acorns and other

seeds for swine farming (i.e. beech *Fagus sylvatica*, oaks *Quercus robur, Q. petrea*, and hazel *Corylus avellana*.) (e.g. Rackham 2003). Unlike in forestry, the value and output from the trees did not necessarily decrease with their age. As a consequence, human activity supported a certain amount of features characteristic of the natural forest ecosystem in otherwise severely altered landscapes. Finally, both abiotic and biotic processes have been altered more where the land use history is longer, hence affecting the function and resilience of large-scale ecosystems (Pimentel et al. 2000, Gunderson and Pritchard 2002).

For the operational monitoring of forest biodiversity within a management unit in relation to formulated goals, it is vital that landscape-scale trends in the composition, structure and function of biodiversity are measured and communicated (Franc et al. 2001). However, detailed scientific field measurements of different components of biodiversity in landscapes are prohibitively expensive to carry out as a part of regular forest management. Therefore, there is a need to develop cost-efficient methods based on the measurement of a limited number of indicators of the sustainability concept in both forests and woodland.

In this paper we evaluate the usefulness of two basic data sources as forest biodiversity indicators at the scale of landscapes in boreal, hemiboreal, mountain and temperate forests of Europe viz.: 1) the presence of different biodiversity components such as ecological groups of specialised or area-demanding birds and mammals, and 2) information related to biodiversity structures such as historical forest loss, age-class specific tree species composition, and transport infrastructure development. Additionally, we test the hypothesis that the human footprint at regional and landscape scales affects both the ecosystem function and the presence of species with special demands on natural forest components.

Study area

European ecoregions

The study area comprises Europe north of the Mediterranean forests and the Russian steppe (Fig. 1) and includes the boreal, mountain, hemiboreal, Atlantic and lowland broad-leaved deciduous forest regions (Mayer 1984). To cover a wide range of forest and land use histories assumed to affect the selected species, data were collected in the gradient of economic development from Great Britain in the west, to the Ural Mountains in the east.

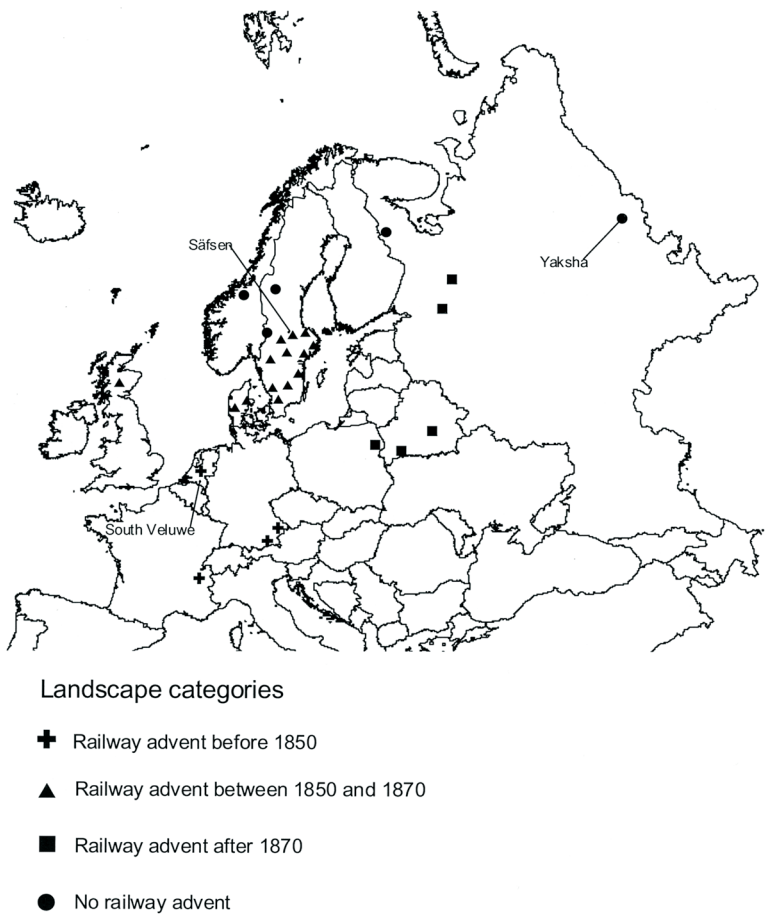


Fig. 1. Map of Europe with the 28 case study landscapes.

Gradients in economic geography

Forests and woodland once dominated Europe (Mayer 1984, Rackham 2003). Most of the continent and especially the Atlantic and lowland broad-leaved deciduous forest regions have been severely altered throughout history (Mayer 1984, Hannah et al. 1995). Even if this transformation has been gradual, the rate of change increased with the advent of the industrial revolution (Thomas 1956, Sylla and Toniolo 1991, Good 1994). The needs of the growing industrialised populations of Europe have resulted in a gradually expanding footprint in more and more remote regions. The demand for timber, grain and other primary products was satisfied by import from the periphery of the spreading industrial revolution (Bladh 1996). The first region to be exploited was the North Sea coast, in the 16–17th century. Eventually the exploitation reached Romania and Ukraine for grain in the 18–19th century (Powelson 1994, Turner et al. 1995), and Russia for timber in the 18–19th century (Bunte et al. 1982). The exploitation of these markets was dependent on the railway development and other facilities for transportation of bulky products (e.g. Williams 2003). As an example the Hungarian export was restricted to live cattle, herded to the destination countries, until the mid-19th century when the development of railways reached Hungary and grain replaced cattle for export (Gunst 1989). Hence, the development of railway systems indicates the level of past large-scale exploitation of important forest habitats and components, which took place during the industrial and agricultural revolutions (Butlin and Dodgshon 1998). Together with the subsequent development of a dense road network for local transports, this eventually resulted in habitat alteration and loss (Darby 1956, Stanners and Bourdeau 1995, Williams 2003, Angelstam et al. 2004b). These changes have affected the viability of populations (e.g., Rolstad 1991, Andrén 1996, Chamberlain and Fuller 2000). Moreover, the development of infrastructures and the associated intensification of human land use resulted in an increase in hunting and persecution of larger vertebrates (Breitenmoser 1998, Mikusiński and Angelstam 2004). Consequently, the parts of Europe that were situated far from the transport infrastructures – such as railroads and rivers draining into the North and Baltic Seas – remained less economically developed than the rest of Europe (Chirot 1989). This pattern is clearly shown in the distribution and growth of cities in the 18th and 19th centuries (Bairoch et al. 1988). The differences in landscape utilisation that are caused by the relation to the centre and the peripheries are affecting the biodiversity in forests throughout Europe (Mikusiński and Angelstam 1998). This means that landscapes having virtually the same local forest structures will be affected differently regarding the loss of species with large area requirements, depending on their location in relation to the centre and periphery of human economic activity (Trauger et al. 2003).

Methods

Encompassing both quantitative data from samples and qualitative analyses of case studies, this study employs a mixed design including a questionnaire, classification of species into ecological groups, statistical analyses of landscape data and literature reviews.

Questionnaire

A questionnaire (Appendix) was sent out to managers of particular landscapes with varying history, forest cover and forest types, and distributed in different parts of Europe (Fig. 1). The ambition was to collect data from a series of landscapes covering the range of variation found in land use intensity and industrial development in Europe. A landscape was defined as an area of >100 km^2. The questionnaire consisted of two parts. The first part concerned the occurrence of a selected set of vertebrate species. The second part referred to the age and tree species composition of the present landscape, as well as to its history of land use development. In addition, the regional history of land use development after the industrial revolution was compiled by literature reviews. Of 70 questionnaires sent out to research and management teams in 15 European countries, a total of 28 were returned (Table 1). All respondents gave information about which vertebrate species were present in the landscape, 13 had information on land use classes and 19 on tree species composition in the forested parts of the landscapes.

Selection of vertebrate species

When species are used as indicators of biodiversity they must scale to the chosen spatial resolution (Swihart et al. 2003). A number of lichens, fungi, insects and vascular plants are being successfully used as indicators of forest naturalness at the stand scale in Sweden (Karström 1997, Nilsson et al. 2001, Norén et al. 2002). Analogously, at the scale of landscapes, species with large area requirements being sensitive to loss of natural forests and to intensive land management should be evaluated (Wallis de Vries 1995, Mikusiński and Angelstam 2004, Angelstam et al. 2004a). Keeping in mind their limitations (Landres et al. 1988) we selected vertebrate species based on two criteria, viz.: 1) that they have area-requirements representing the landscape scale, 2) that they require natural forest habitat.

To satisfy the criterion of representing naturalness at the landscape scale we chose the presence of all species (excluding tundra, steppe and high alpine species) in a number of taxonomic groups with large or predatory species: grouse, woodpeckers, owls, raptors, ungulates and carnivores. Although several passerines do require natural forest compo-

Table 1. List of case study landscapes.

Country	Case study landscape	Latitude °N	Longitude °E
Belarus	Olman bog	52.0	27.0
	Doleby island	53.4	29.4
Denmark	Bjerringbo	56.2	9.4
	Åskov	56.0	8.5
France	Chartreuse	45.1	5.5
Germany	Bayerischer Wald	48.5	13.5
	Chiemgauer	47.5	12.5
Netherlands	South Veluwe	52.0	5.5
Norway	Surnadal	63.0	9.0
Poland	Bialowieza	53.1	23.5
Russia	Gomselga	62.0	34.0
	Kostamuksha	64.4	30.4
	Nizhnesvirsky reserve	60.4	33.2
	Yaksha	62.1	57.4
Sweden	Alken	59.4	12.4
	Bjärka-Säby	58.0	16.0
	Botkyrka	59.1	17.5
	Fröllinge	56.5	12.5
	Grangärde	60.2	15.0
	Hallandsåsen	56.3	13.2
	Höljes	60.5	12.4
	Kvismaren	59.2	15.3
	Njakafjäll	64.5	15.5
	Skillingaryd	57.3	14.1
	Säfsnäs	60.1	14.3
	Tärnan	59.3	18.3
	Vällen	60.0	18.2
United Kingdom	Glenn Affric	57.2	–5.0

nents, we have not included them into our study because of their small area requirements. The presence of all three forest-living grouse (Tetraonidae; black grouse *Tetrao tetrix*, hazel grouse *Bonasa bonasia* and capercaillie *Tetrao urogallus*) indicates a large variation in age classes ranging from recently cleared forest to old forest (but not old growth). The presence of several species of woodpeckers (Picidae) indicates a large variation of habitat components ranging from old-growth coniferous (three-toed woodpecker *Picoides tridactylus*) and deciduous forests (white-backed woodpecker *Dendrocopos leucotos*) to old cultural landscapes (green woodpecker *Picus viridis*) (Mikusiński and Angelstam 1998). As a group the woodpeckers indicate the presence of natural forest components (old large trees and dead wood of several tree species) over a large area (Mikusiński et al. 2001). For biodiversity and ecosystem function it is important that all trophic levels are as intact as possible. Therefore the assessment of biodiversity should include an estimate of the completeness of the trophic levels at the landscape scale. Large avian predators, large herbivores and large carnivores all indicate landscape scale authenticity and function of ecosystems. Avian predators (Strigidae, Accipitridae) depend on a wide variety of prey types found in a variety of habitats. Some species also require old-growth components such as large trees for nesting (Hagemeier and Blair 1997). The presence of viable populations of the largest herbivorous species (Equidae, Suidae, Cervidae, Bovidae) should indicate ecosystem function of a landscape (Wallis De Vries 1995, Vera 2000). Finally, generalists with small area requirements should be the least sensitive species with respect to habitat alteration and loss (Mikusiński and Angelstam 2004). To facilitate comparisons across different biogeographic regions larger birds and mammals were divided into ecological groups. The is analogous to the work on Finnish birds by Haapanen (1965, 1966) and the life form concept used by Thomas (1979) to classify wildlife species into groups based on specific combinations of habitat requirements for reproduction and feeding. Our classification was based on body size, trophic position, and dependence on structural elements such as large trees, nest-holes, and dead wood used for example by woodpeckers (see table in the Appendix).

With many ecological groups and several species per group present in a landscape, the functions of the ecosystems should be better maintained (Pimentel et al. 2000) and the degree of naturalness or integrity of the landscape should be higher. A diversity index that considers the number of ecological groups in a landscape and the number of species within the groups was developed. Based on those premises, we developed a diversity index (DI), wich

results in a high value if many ecological groups (i) are present in the landscape (j) and if each ecological group has high species numbers (a_{ij}) in relation to the mean species number for each ecological group ($\bar{a}_{i\bullet}$) in all studied landscapes.

$$DI = \sum_{i=1}^{n} \left[\frac{a_{ij}}{\bar{a}_{i\bullet}} \right]$$

Landscape data

To estimate the time since large-scale economic development reached a particular case study landscape, we used the spatial expansion of railways in the region as a proxy. We distinguished four stages of railway development in Europe; advent of railways before 1850, between 1850 and 1870, after 1870 and areas where no railways have been built (Parker 1993). We assessed the proportion of plantations on former arable land in the landscapes as a proxy of forest habitat quality. To assess the structure and composition of the presently forested part of the landscape we used questionnaire data on age-class and tree species composition. The data material tree age should at least range over 150 yr (preferably 300 yr) and each age class should be 10–20 yr. Virtually all forest types can have average stand ages of 250 yr or more if they are left unmanaged (Peterken 1996). Old forests are important to a variety of species (Peterken 1996, Hunter 1999, Eiswerth and Haney 2001). The proportion of this forest type is therefore an important indicator of naturalness in forest landscapes.

Relationships between species and landscape data

To test whether the diversity of ecological and taxonomic groups is correlated to the west-east gradient of industrialisation, we used linear regression with longitude as independent variable and the diversity index (di) as dependent variable. We also tested the hypothesis that the advent of industrial revolution as described by railway development is related to species richness of ecological groups and the diversity index (di*)*. We performed Spearman rank correlation tests between railway development and, respectively, the diversity index of ecological groups and the number of species requiring large trees for nesting. Linear regression was used to investigate the relationship between hole-nesters and the proportion of plantations on former arable land in forest dominated landscapes. From the landscape questionnaires we extracted the proportion of forest older than 120 yr and the presence and absence of three-toed woodpecker, which is an interesting candidate for being a natural forest indicator (Mikusiński et al. 2001, Bütler et al. 2004a, b). We then performed logistic regression to test the hypothesis that the occurrence of three-toed woodpecker is related to the proportion of old forest in landscapes.

Results

Quantitative analyses

There was an increasing diversity of ecological groups in the landscapes in the west-east gradient in Europe. This is evident from the relationship between the diversity index and longitude of the landscapes, which was highly significant (n=28, r^2=0.55, F=32.17, p<0.0001; Fig. 2). The regional and local factors indicating species richness were railway development and the recent proportion of plantations in the landscape. The development of railway systems in Europe correlated with the diversity of ecological groups present in the landscapes (n=28, rho=0.77, p<0.0001; Fig. 3) and with the number of species requiring large trees for nesting (n=28, rho=0.61, p=0.002; Fig. 4). The presence of hole-nesting birds in a landscape was negatively related to the proportion of plantations on former arable land in the local landscape (n=13, r^2=0.40, p = 0.02; Fig. 5). However, the presence of hole-nesting birds in a landscape was not correlated with the advent of railway development, which is a good proxy for human land use intensity at a regional scale (n=28, F=2.12 and p=0.16). This suggests that for this group local factors were more important than regional ones. The logistic regression model predicting three-toed woodpecker occurrence based on the amount of coniferous forest older than 120 yr was significant (n=28, χ^2 4.51, p=0.03; Fig. 6). The great spotted woodpecker *Dendrocopos major*, goshawk *Accipiter gentilis*, sparrowhawk *Accipiter nisus*, red fox *Vulpes vulpes* and pine marten *Martes martes*, which could be characterised as generalist predators of medium size, occurred all over the study area and in all landscapes, independent of the land use history and structural composition of the landscapes.

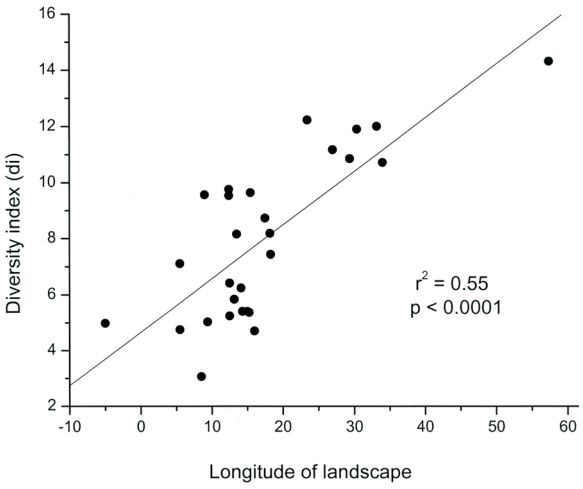


Fig. 2. Diversity of ecological and taxonomic groups in the case study landscapes in relation to longitude.

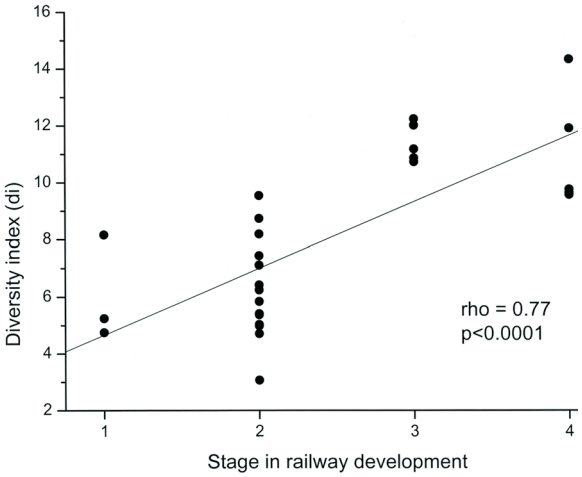


Fig. 3. Diversity of ecological and taxonomic groups in the case study landscapes in relation to the history of railway development.

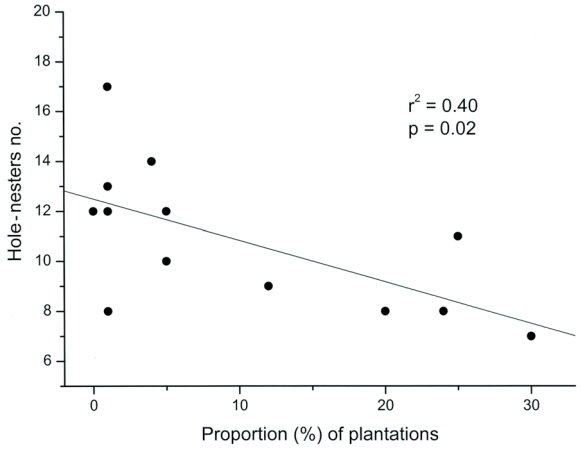


Fig. 5. Relationship between the number of species in the ecological group of hole-nesters and the proportion of plantations on former arable land in the landscape.

Case studies

The questionnaire data illustrate the effect of long and intensive land use on the age class and tree species structure (Fig. 7a–c). Here we present three landscapes (Veluwe in the Netherlands, Säfsen in Sweden, and Yaksha in Russia), discussing their history of land use and their current biodiversity status. These particular landscapes were chosen for two reasons. First, they cover the whole extent of the west-east economic gradient in Europe and thereby constitute a representative sample of the 28 case studies. Second, they provide examples of landscapes where an historical ecology approach can be used to examine patterns of change in biodiversity.

South Veluwe

The South Veluwe (6°E, 52°N, Fig. 1), located in the Netherlands, forms a part of the largest forested area in the lowlands of western Europe (900 km^2). Situated on the southern edge of sandy and loamy Pleistocene glacial deposits, it has a long history of human occupation. By 4000 BP, clearance of the primeval deciduous forest had attained such proportions that open heathlands appeared. Around AD 1400, the forest had almost gone and shifting sands started to spread after overexploitation of heathlands (De Bakker 1979). Only ca 5–10% of the area remained forested, when re-forestation was initiated and large-scale pine plantations appeared between 1850 and 1900, accompanied by the introduction of exotic conifers in the 20th cen-

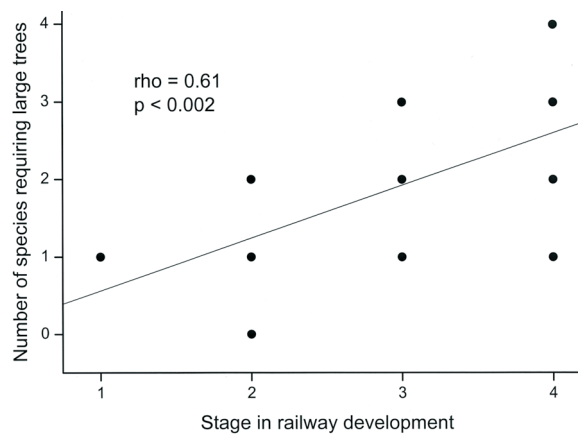


Fig. 4. Relationship between the number of species in the ecological group of species requiring large trees and the history of railway development.

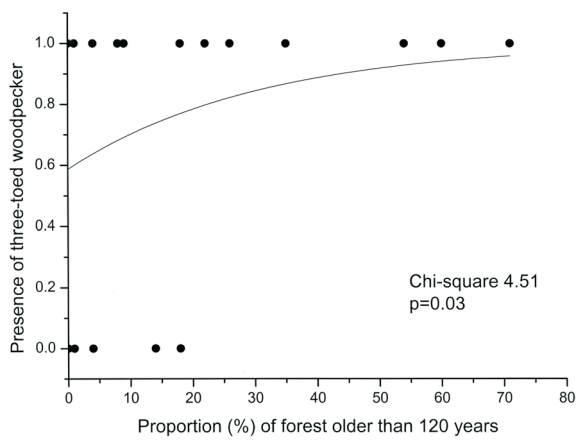


Fig. 6. Relationship between the presence of the three-toed woodpecker and the amount of coniferous forest older than 120 yr.

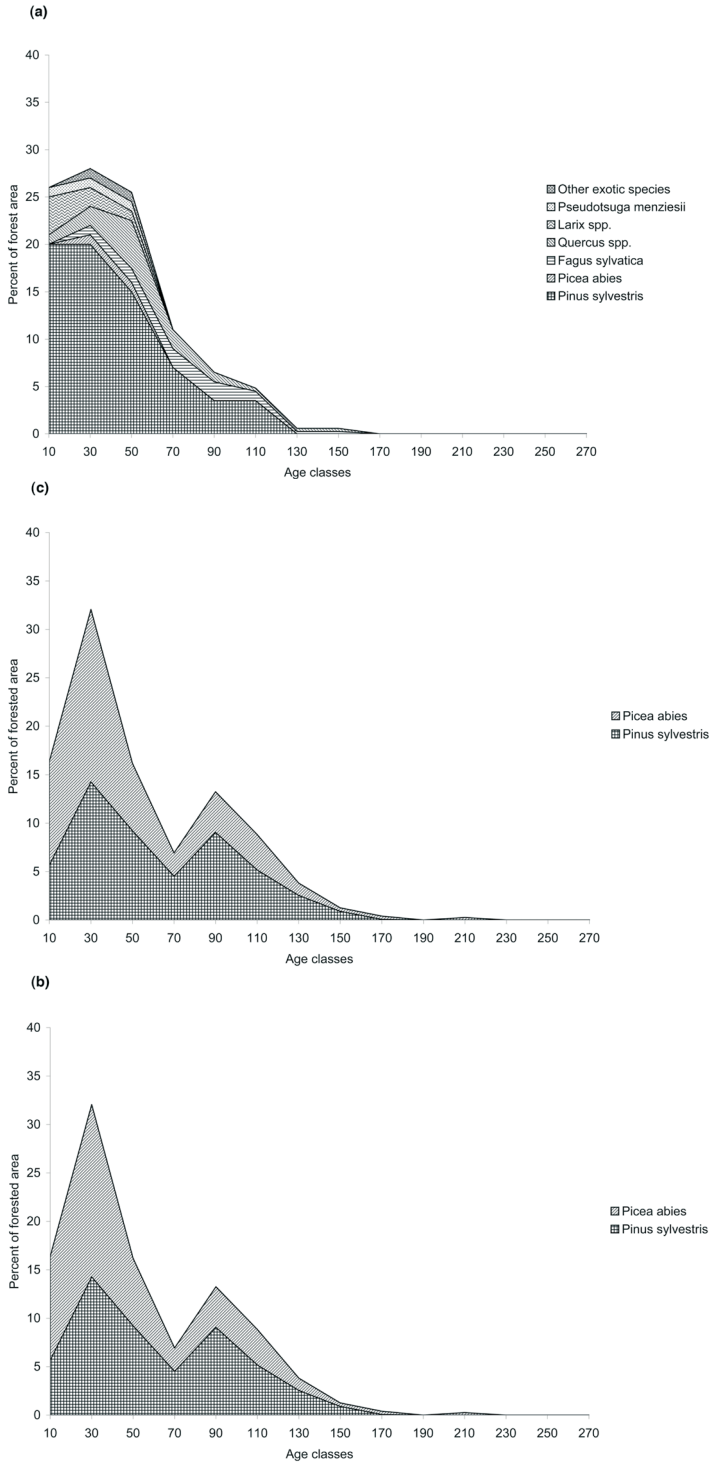


Fig. 7. Diagrams showing the tree species composition and age class distribution in landscapes representing the west-east gradient from fragmented forest with a long and intensive land use history in Western Europe via managed forests in northern Europe to reference areas in the eastern European periphery of economic development. (a) South Veluwe (The Netherlands): plantation reforestation with a mean age of 40 yr and the largest cohort being 30 yr old. There is a large proportion of exotic species (e.g. *Pseudotsuga menziesii* and *Larix kaempferi*) and genotypes (e.g. pine *Pinus sylvestris*) in this young forest. (b) Säfsen (Sweden): forest management aiming at pulp and timber production with a mean age of 55 yr and the largest cohort being 30 yr old. (c) Yaksha (Russia): natural forest regime with a mean age of 140 yr and the largest cohort at ca 180 yr.

tury. Agriculture, pastures and urban areas have remained of minor importance in the area. Heathland has declined dramatically from 67 to 21% during the 20th century. After large-scale damage to the even-aged conifer plantations during severe storms in 1972–1973, a public debate generated support for a more natural forest management. Nature conservation is now the highest priority in most of the area, but multi-functional forest use continues. Tree age increases as well as the proportion of deciduous species, which favours the populations of several animal species (Lensink 1993).

The South Veluwe illustrates well how today's impoverished forest fauna can be explained by human influence causing habitat alteration and loss. Only 18 of the 56 selected forest bird species and 10 of the 25 mammal species are present. However, most losses occurred in a distant past, before AD 1750. For example, the red deer and the wild boar are clearly indigenous but were extirpated. Both species were reintroduced in the period 1850–1950. Most large mammals and many bird species can safely be assumed to be native, and for part of the species this can be substantiated by archaeological or historical evidence. However, for 24 of the bird species and 6 of the mammal species, breeding during the Holocene has never been confirmed (Broekhuizen et al. 1992, Lensink 1993). Generally these species, such as the capercaillie, three-toed woodpecker and wolverine, are considered to have a boreal or continental distribution. Biogeographic reasons would then explain their absence in The Netherlands. Yet, the present study emphasises the possibility that anthropogenic influences may have altered the distribution of species. In this light, it would be of interest to establish whether the apparent westwards re-colonisation of some forest species such as Tengmalm's owl and grey-headed woodpecker (Van den Berg and Bosman 1999) as well as black woodpecker (Mikusiński 1995) constitutes an effect of climatic change, or simply represents a re-colonisation of part of their former range through an increase of suitable habitat in ageing forest stands.

Säfsen

The Swedish case study Säfsen (ca 500 km^2, 60°N, 14°E; Fig. 1) is located in the southernmost part of a narrow corridor of the vast and sparsely settled boreal forest in Sweden (Montelius 1962, Angelstam 2002b). The large Stora Enso Forest Company, whose economic roots in this region named Bergslagen dates 700 yr back, almost exclusively owns the area. The long economic history of mining and forest use in the Bergslagen region has been closely intertwined with the environment and the society and intensive use of forests started in the 16th century (Wieslander 1936). From the 17th century the forest landscape was settled throughout, and the local economy was based on iron, forest products and low intensity agriculture. Concomitantly, domestic grazing animals and extensive managed grasslands were an important part of the economy. As a consequence, the four large predators, brown bear *Ursus arctos*, wolf *Canis lupus*, lynx *Lynx lynx* and wolverine *Gulo gulo* were gradually exterminated (Ekman 1910, Angelstam 2002b). After a long period of forest harvesting for the production of charcoal, the timber itself became an important source of income for these industries and they gradually evolved into large forest industries. The remaining steel industry, which also owned the forestland, was hit by economic problems that peaked between 1975 and 1985. The last iron mines in Bergslagen were closed in 1991. Due to large areas of forests ready for harvesting and to compensate for the reduced incomes of companies owning both industry and forest the logging rates increased (Granqvist pers. comm.). This produced a large cohort of young forest in the landscape, which provided the base for a strong increase of the population of moose *Alces alces*, which now hampers the attempts to restore the amount of deciduous forest (Angelstam et al. 2000).

Yaksha

The largest part of the remaining naturally dynamic boreal forest in Europe is found in the most remote parts of European Russia (Syrjänen et al. 1994, Angelstam et al. 1997, Yaroshenko et al. 2001). In the remote Komi Republic (416 000 km^2) 10.7% of the forest is protected (Taskaev and Timonin 1993). To this should be added the forests in protective zones along water, roads and urban areas as well as buffer zones near reserves which comprise 13% of the forests (Kuusela 1990). In some remote regions, such as the 40 700 km^2 Troitsko-Pechorsk region in the south-eastern part of the Komi Republic, 40% of the forests are protected. The Pechoro-Ilych Strict Nature Reserve with its buffer zone is situated in this region, (62°N, 58°E, Fig. 1). Along with the adjacent National Park Yugyd-Va this is the very last naturally dynamic forest system in Europe and covers an area of > 30 000 km^2. In the reserve all main northern and middle boreal forest landscape types are present, from fire-prone pine plains, to undulating hills with the full range stand types and to mountain forests (Lavrenko et al. 1995). The Pechoro-Ilych reserve, which was proposed in 1915 and founded in 1930, has been used for nature protection, monitoring research and education in Russia for > 50 yr. We chose the well-studied Yaksha area covering ca 200 km^2, located in the westernmost part of this large forest complex. Here no extinction has occurred, but the American mink has colonised the area.

Discussion

Relationships between species and habitats at the landscape scale

This study shows that the diversity of species and ecological guilds in a landscape are related to regional human impact and to the quality and amount of habitat in a landscape. The diversity index of ecological groups correlated well with measurements of human exploitation of the landscape. The most remote landscapes maintained presence of all naturally occurring ecological groups with several species within each ecological group. This is promising for future studies since it shows that our diversity index gives a good indication of naturalness and ecosystem function in the landscapes. The relation between species that need holes for nesting and the proportion of plantations on formerly arable land shows that even simple estimates of habitat quality can help assessing the naturalness of a landscape. The results suggests that both 1) the diversity of ecological groups, the presence of hole-nesters and species requiring dead wood such as many woodpeckers, and 2) landscape structure properties collected by managers could be used as indicators of forest quality with regard to naturalness or authenticity at a landscape scale. Only five small generalist predators were present in all the investigated landscapes. This is in accordance with the hypothesis that generalists with small area requirements are the least sensitive species with respect to habitat alteration and loss (Mikusiński and Angelstam 2004). At a regional scale, the same effects that are caused and indicated by railway development should be expected for the development of the road network aimed at transporting goods among regions (e.g. Corsi et al. 1998).

The aims of this study were to evaluate to what extent available data sources can be used to assess the status and trends in biodiversity in European forest landscapes. The independent variables consist of data describing the human footprint on Europe's forests. For this, several monitoring programs, e.g. EC, UN and national monitoring programs could be used to assess the human footprint on forests at the scale of landscapes within regions. The present distribution of species with different ecological characteristics and scaled to the chosen spatial resolution represent the dependent variable. In Sweden a number of lichens, fungi, insects and vascular plants are being used to indicate the level of naturalness/authenticity at the scales of trees and forest stands (Gustafsson 1999, Norén et al. 2002). However, at the scale of landscapes, forest species with large area requirements, and species that are sensitive to loss of natural forest components and to intensive land use and forest management, are important complements. The presence of species belonging to one taxonomic group is usually not a good indicator of the occurrence of species belonging to other taxa in the same area (Weaver 1995, Flather et al. 1997). Therefore we chose to use several vertebrate groups to indicate forest naturalness (Roberge and Angelstam 2004). Moreover, many vertebrate species are useful in communicating the importance of sufficient connectivity both within and among landscapes (Uliczka et al. 2004). This is supported by the fact that in this study, data concerning species was easier to obtain than forest data. In follow-up studies these taxa could be supplemented by well-studied invertebrate groups, such as butterflies using different canopy cover classes (Schiess and Schiess-Bühler 1997), and beetles exploiting dead wood (Jonsell et al. 1998). However, unless variables related to the fitness of local populations are included the conservation status may be overestimated and the amount of habitats and resources needed underestimated (Pimentel et al. 2000).

This study is limited to compositional and structural elements of biodiversity. However, ecosystem function is also crucial for sustainable forest management (e.g. Sverdrup and Stjernquist 2002). Consequently, the function of the ecosystem should be monitored as well. Large carnivores and herbivores are important for ecosystem functions by controlling prey (Jedrzejewska and Jedrejewski 1998) and maintaining certain habitats (Vera 2000). Similarly beavers are important for the maintenance of aquatic biodiversity (Ray et al. 2001). Additionally, descriptions of ecosystem processes and functions, such as hydrological and fire regimes and storm-felling (Niklasson and Granström 2000, Pringle 2001, Wiens 2002, Sverdrup and Stjernquist 2002), should be added.

This study showed that the number of species present and the diversity of ecological groups can be used as proxy measurements for the degree of human alteration of the landscape. This approach assumes that species requiring natural or authentic components in the landscape have been lost from landscapes with a long land use history. An alternative explanation could be that differences in species distribution patterns reflect biogeographic variation caused by different climate and habitat distribution (e.g. Gaston and Blackburn 2000, Swihart et al. 2003). Unfortunately, our questionnaire data does not provides any information about this. Yet, in many parts of Europe there is clear evidence that parts of the fauna in the pre-industrial conditions have gone extinct (Hagemeijer and Blair 1997, Mikusiński and Angelstam 1998, 2004, Mitchell-Jones et al. 1999). The spatial resolution of such information is, however, not good enough to evaluate alternative hypotheses explaining the reduced naturalness of forests and authenticity of cultural woodland. It is therefore important to improve the knowledge about the past local distribution of species to distinguish between the two alternative explanations.

Several studies have shown that the loss of species in relation to habitat loss is non-linear (Fahrig 2001, 2002, Guenette and Villard 2004). Hence, a landscape that already has suffered great historical loss of species diversity has a low remaining potential of loss. If the history of hu-

man utilisation and the associated species loss is not considered, one may wrongly conclude that total species loss is smaller in areas that are more affected by human activities than in areas that are not as heavily affected. More detailed analyses of the local history of habitats and species in the different case study landscapes are therefore needed. That this is feasible is suggested by the more detailed information about the historic loss of species in three well-studied landscape case studies, ranging from the much altered South Veluwe in the Netherlands to the near-natural Yaksha in Russia.

Management recommendations

For the management of forest biodiversity it is vital to maintain functional habitat structures and balance processes at the scale of forest management units, i.e. landscapes (Franc et al. 2001). It is therefore critical to know which structures and processes affect the maintenance of biodiversity in benchmark landscapes representing naturally dynamic forests and pre-industrial woodland. Understanding the history of forest utilisation is consequently a prerequisite to manage for naturalness of a forest ecosystem (Peterken 1996).

At the stand scale, tree species composition with all species, a high resolution of age classes up to preferably 300 yr, the amount and quality of standing and lying dead wood (Siitonen 2001), and the vertical structure of the stands (Åberg et al. 2003) are some examples of variables that should be included in management plans. Additionally, functionality of habitat networks for populations and communities should be monitored (Scott et al. 2002, Angelstam et al. 2004a) as well as processes such as fire and flooding events, and browsing pressure by large herbivores. By contrast, forest monitoring systems that are used in forestry today are often limited to information vital for production decisions (Jonsson et al. 1993, Angelstam and Bergman 2004). The structures and processes that are important for forest biodiversity are accordingly neglected in these monitoring systems.

Conclusions

Detailed and replicated scientific studies on the effects of land use on components of biodiversity in landscapes are prohibitively expensive to carry out in practise as a means of monitoring different elements of biodiversity. Nevertheless, for the operational monitoring of forest biodiversity within an adaptive management approach in relation to formulated goals (Meffe et al. 2002), it is vital that landscape scale trends in the composition, structure and function of biodiversity are measured and communicated. Our analysis of simple information collected at the landscape scale suggests that this is feasible in principle, but that critical examination of indicators with respect to both their scientific background and communication value to practitioners is crucial. Hence, historical ecology approaches (Balée 1998, Egan and Howell 2001) are needed to critically evaluate alternative hypotheses such as biogeography explaining the differences in species distribution. Using historical data of species composition and landscape structure in case studies where the loss of ecosystem integrity is large would allow this, as well as to explore species-habitat relationships using not only variation among landscapes but within landscapes over time.

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Appendix – The questionnaire

This appendix summarises the contents of the questionnaire sent out to acquire information about the different case study landscapes and to evaluate how measurements of forest biodiversity at the scale of landscapes in regions could be developed. First, we described the three steps in the study:

Step 1. Develop a set of indicators for the criterion of naturalness of forest components in a landscape. These indicators could be found both within pristine or near-natural forests, and in the pre-industrial cultural landscape. The latter is due to that the old cultural landscape contains structural components found in naturally dynamic forests. As a consequence, the cultural landscape is often a refuge for many species that were adapted to a pristine or near-natural forest environment. The indicators that we want to choose from fall into two categories, viz. species and forest structures.

Step 2. Based on the hypothesis that the intensity and duration of the industrial and agricultural revolutions in Europe has negatively affected biological diversity in forests, select landscapes that represent different levels of anthropogenic exploitation.

Step 3. Test the hypothesis that extent of intensive anthropogenic change has negatively impacted biological diversity. Using different statistical analyses we will compare the two groups of factors (i.e. species and forest data with each other) one the one hand with the extent of human impact as indicated for example by regional economic development on the other.

In the questionnaire we asked for information about the following specific items:

1. Name and location of area

2. The species representing naturalness

The selection of vertebrate species (see table on p. 349) was based on two criteria, viz.: that they represent the landscape scale (i.e. large body size and/or high trophic position), and/or that they require natural/authentic forest vegetation types. To satisfy the first criteria we chose the presence of all species (excluding tundra, steppe and high alpine species) in a number of taxonomic groups with large and/or predatory species (grouse, woodpeckers, owls, raptors, ungulates and carnivores). To satisfy the second criteria we added some species from other groups and which require natural forest structures (e.g. large trees, large nest holes, trees near water etc.). Although several passerines do require natural forest components, we have not included them because of their small area requirements.

To increase the resolution somewhat above that given by presence/absence data only, we also asked for indications of the viability of today's populations, and the population trend from before World War 2 to present using the signs +/–/? to denote the situation. The respondents were asked to state the presence or breeding status in the 1990s for each species listed in the tables by using the signs yes/no/? to denote the situation. To describe historical records, the respondent was asked to state the time of last occurrence, last recorded breeding or reintroduction to the nearest 50-yr period (1750–1800, 1800–1850 etc.). Below we explain the arguments for selecting these groups of vertebrates.

Several taxonomic groups have characteristic life history traits. The presence of all three forest-living grouse (Tetraonidae) (black grouse, hazel grouse and capercaillie) ensures a large variation in age classes ranging from recently cleared forest to old forest (but not old-growth). The presence of several species of woodpeckers (Picidae) ensure a large variation of habitat components ranging from old-growth coniferous (three-toed woodpecker) and deciduous (white-backed woodpecker) to old cultural landscape (green woodpecker). As a group they indicate the presence of natural forest components (old large trees and dead wood of several species) over a large area. Avian predators such as owls and raptors (Strigidae, Accipitridae) depend on a wide variety of prey types found in a variety of habitats. Some species also require old-growth components such as large trees for nesting over a large area. The biodiversity of an area is dependent on the number of trophic levels in the system. Hence a diverse avian predator guild should be a good measurement of landscape biological diversity. The presence of viable populations of the largest herbivorous species such as ungulates (Equidae, Suidae, Cervidae, Bovidae) should be an important indicator of landscape authenticity. Because this group shows a large variation in both size and diet ranging from omnivores to grazers and browsers, a high diversity of this group should be a good indicator of landscape authenticity. Finally, several of the large and largely carnivorous predators (Carnivora) have historically shown a negative correlation with an intensified human land use. Because this group shows large variation both in body size and the degree of carnivory, a high biological diversity of this group should be a good indicator of landscape authenticity.

Species from several taxonomic groups require natural forest components such as large trees and nest-holes, trees near water and natural disturbances such as flooding, wind and fire being typical for naturally dynamic forest landscapes. Some birds in other taxonomic groups than those listed above require large trees for breeding (black stork and cormorants). Large hole-nesters (hoopoe, roller, swift, stock dove, goldeneye and mergansers) depend on the accessibility of holes for nesting. That makes these species a good complement to the taxonomic groups.

Finally, together with introduced tree species the number of introduced vertebrates is a measurement of alteration of the ecosystem. Although the introduced species contribute to species richness as a whole, they do indicate that the ecosystem is disturbed, by deviating from the natural/authentic conditions. Their presence may be caused both by the alteration of the ecosystem and be a cause of the alteration. Examples of such introductions are racoon, racoon dog, American mink, white-tailed deer etc.

3. Forest structures

3.1. Landscape history

To assess the structure and composition of the selected landscape it is important to understand both to what extent the natural/authentic forest components have changed as a consequence of forest clearing (decreased cover) or cessation of agricultural activities (increased cover), and how agricultural use of land has replaced forests. Because the vast majority of the European landscapes were originally forested a simple estimate of the total historic loss of forest cover is the present proportion of the landscape not covered by forest.

The respondents were asked to mark important changes in landscape utilisation on a time axis. These could be changes in land ownership due to major land reforms, in agricultural practises with the advent of new techniques, in husbandry practises or even dramatic socio-economic changes including war.

3.2.The historical landscape composition

Due to the complex history of landscape use, we asked the respondents to divide the landscape into five types, viz.; 1) urban areas, settlement etc.; 2) agricultural land on cleared forest land, now in intensive agricultural use; 3) old cultural landscape on cleared forest land but with remnants trees as in the typical old low-intensity agricultural practices with villages or farms surrounded by fenced infield and peripheral outlying land; 4) re-forested agricultural land during less than one tree generation, and 5) the remaining forested land. However, landscapes usually also contain other land cover types (lakes, bogs, wetlands). Therefore, the sum of these 5 selected land cover types will usually not add up to the area of the whole landscape. While detailed information with high resolution would be ideal, we argued that as first step it is sufficient to assess the situation (in % of the whole landscape) today and before the World War 2.

3.3. The history of forest utilisation

Also within the land cover type forest history is very important. We identified four stages in the development of human use, viz.: 1) pristine/near-natural, i.e. never used other than for local hunting, collection firewood and local use for buildings; 2) local use including high-grading of large trees, but no large-scale clear-cutting; 3) large-scale exploitation as a consequence of regional, national and/or international demand of large wood volumes; and 4) intensive forest management aiming at pulpwood and/or timber production. Respondents were asked to mark the important changes in forest utilisation in the actual landscape case study and give a short description of the changes on a time axes.

3.4. Age classes and tree species composition

Data on age-classes were requested to be (10–)20 yr wide and extend from 0 to at least 150 yr, preferably close to 300 yr, the reason being that virtually all forest types can have average stand ages between 250 and 300 yr if they are unmanaged. Ideally the tree species distribution should be given by the individual species. For the purposes of this study, however, we proposed a simpler division into pine, spruce, narrow-leafed deciduous trees (*Betula* and *Populus*), oak, beech and mixed broad-leaved (*Quercus*, *Tilia*, *Acer*, *Fraxinus*). Finally, the respondents were asked to add the identity of the present tree species, which are exotic to their respective areas.

4. Map and human population density

The respondents were asked provide us with a topographic map (1:50 000 or 1:100 000) with the borders of the actual landscape clearly marked, as well as data on the number of inhabitants per square kilometre in your landscape case study.

5. References and comments

The respondents were asked to provide a list of publications or other references and to provide comments and questions to the approach.

Ecological and taxonomic guilds used in analyses.

ducks (Anatidae)	
goldeneye (*Bucephala clangula*)	f, h
smew (*Mergus albellus*)	f, h
red-breasted merganser (*Mergus serrator*)	f, h
goosander (*Mergus merganser*)	f, h
wood duck (*Aix sponsa*)	i
mandarin duck (*Aix galericulata*)	i
storks (Ciconiidae)	
black stork (*Ciconia nigra*)	f, g
hawks and eagles (Accipitriformes)	
honey buzzard (*Pernis apivorus*)	c
black kite (*Milvus migrans*)	
red kite (*Milvus milvus*)	c
white-tailed eagle (*Haliaetus albicilla*)	c
short-toed eagle (*Circaetus gallicus*)	c
marsh harrier (*Circus aeruginosus*)	
hen harrier (*Circus cyaneus*)	
Montagu's harrier (*Circus pygargus*)	
goshawk (*Accipiter gentilis*)	c
sparrowhawk (*Accipiter nisus*)	
buzzard (*Buteo buteo*)	c
rough-legged buzzard (*Buteo lagopus*)	c
lesser spotted eagle (*Aquila pomarina*)	c, g
spotted eagle (*Aquila clanga*)	c, g
imperial eagle (*Aquila heliaca*)	c, g
golden eagle (*Aquila chrysaetos*)	c, g
booted eagle (*Hieraeetus pennatus*)	c
osprey (*Pandion haliaetus*)	c, g
falcons (Falconidae)	
kestrel (*Falco tinnunculus*)	
red-footed falcon (*Falco vespertinus*)	
merlin (*Falco columbarius*)	
hobby (*Falco subbuteo*)	
peregrine falcon (*Falco peregrinus*)	c
grouse (Tetraonidae)	*
hazel grouse (*Bonasa bonasia*)	
black grouse (*Tetrao tetrix*)	
capercaille (*Tetrao urogallus*)	
stock dove (*Columba oenas*)	
barn owls (Tytoide)	
barn owl (*Tyto alba*)	a
typical owls (Strigidae)	*
Scop's owl (*Otus scops*)	
eagle owl (*Bubo bubo*)	
hawk owl (*Surnia ulula*)	
pygmy owl (*Glaucidium passerinum*)	
little owl (*Athene noctua*)	h
tawny owl (*Strix aluco*)	h
ural owl (*Strix uralensis*)	
great grey owl (*Strix nebulosa*)	
long-eared owl (*Asio otus*)	h
short-eared owl (*Asio flammeus*)	
tengmalm's owl (*Aegolius funereus*)	h
rollers (Coraciidae)	
roller (*Coracius garrulus*)	h
hoopoes (Upupidae)	
hoopoe (*Upupa epops*)	h
woodpeckers (Picidae)	*
wryneck (*Jynx torquilla*)	h
grey-headed woodpecker (*Picus canus*)	h
green woodpecker (*Picus viridis*)	h
black woodpecker (*Dryocopus martius*)	h
great spotted woodpecker (*Dendrocopos major*)	h
syrian woodpecker (*Dendrocopos syriacus*)	h
middle spotted woodpecker (*Dendrocopos medius*)	h
white-backed woodpecker (*Dendrocopos leucotos*)	h
lesser spotted woodpecker (*Dendrocopos minor*)	
three-toed woodpecker (*Picoides tridactylus*)	
bears (Ursidae)	
brown bear (*Ursus arctos*)	d
canines (Canidae)	
wolf (*Canis lupus*)	b
red fox (*Vulpes vulpes*)	
racoon dog (*Nyctereutes procyonoides*)	i
cats (Felidae)	
lynx (*Lynx lynx*)	b
wild cat (*Felis silvestris*)	
mustelids (Mustelidae)	
wolverine (*Gulo gulo*)	b
badger (*Meles meles*)	
stoat (*Mustela erminea*)	
weasel (*Mustela nivalis*)	
polecat (*Mustela putorius*)	
European mink (*Mustela lutreola*)	
American mink (*Mustela vison*)	
stone marten (*Martes foina*)	
pine marten (*Martes martes*)	
sable (*Martes zibellina*)	
otter (*Lutra lutra*)	
genet (*Genetta genetta*)	
raccons (Procyonidae)	
racoon (*Procyon lotor*)	i
deer (Cervidae)	
reindeer (*Rangifer tarandus*)	e
red deer (*Cervus elaphus*)	e
roe deer (*Capreolus capreolus*)	
fallow deer (*Cervus dama*)	i
sika deer (*Cervus nippon*)	i
white-tailed deer (*Odocoileus virginianus*)	i
pigs (Suide)	
wild boar (*Sus scrofa*)	d
bovids (Bovidae)	
wild ox (*Bos primigenus*)	e
european bison (*Bison bonasus*)	e
horses (Equidae)	
wild horse (*Equus przewalski*)	e
beavers *(Castoridae)*	
beaver *(Castor fiber)*	f
nutria (Myocastoridae)	
nutria (*Myocastor coypus*)	i

*) Taxonomic groups; used to calculate diversity index (di). a) included in taxonomic group of owls; used to calculate di. b) Large carnivore; used to calculate di. c) Large raptor; used to calculate di. d) Large omnivore; used to calculate di. e) Large herbivore; used to calculate di. f) Riparian forest species; used to calculate di. g) Bird requiring large trees for nesting. h) Bird requiring large nest-holes. i) Exotic species.

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Identifying high conservation value forests in the Baltic States from forest databases

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The Baltic Forest Mapping project (BFM) aimed at identifying high conservation value forest (HCVF) areas for the maintenance of forest biodiversity in Estonia, Latvia and Lithuania. Computerised searches of potential HCVFs were carried out using primarily the national forestry stand level databases on tree species composition and average stand age. Ecologically based selection criteria were elaborated and adapted to the particularities of each forest vegetation type and country.

In Estonia and Lithuania the most common (ca 50%) of BFM-selected potential HCVF stands were of gap dynamics types, primarily wet deciduous and nemoral. In Latvia most BFM-selected stands (40% of total) were pine and oak-pine forests. The most common BFM selection criteria fulfilled were for structural diversity with regard to either advanced tree age or tree species, which together totalled ca 75% of all BFM-selected sites in Estonia, ca 60% in Latvia, and ca 80% in Lithuania.

On average 17% of the forests (Estonia 15%, Latvia 10% and Lithuania 32%) met at least one criteria of the BFM. The vast majority of BFM-selected stands were located outside currently protected areas. In Latvia, only 8% of BFM stands were given some degree of protection, while many forests within the existing forest protected area network did not meet BFM criteria. In Lithuania, as in Latvia, < 1% of BFM stands were strictly protected. High conservation value forests are disappearing rapidly. In Estonia, where logging rates could be estimated, BFM-selected stands were being logged at the rate of > 4% yr^{-1}.

By using information provided about HCVFs in strategic planning, it is possible to identify area gaps for different representative forest vegetation types needed to maintain biodiversity. Moreover, the spatially explicit analyses presented here could be an aid when establishing functional networks of forest protected areas, as well as to developing operational management towards sustainable forest management at all administrative levels.

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Maintenance of forest biodiversity is one of the goals of sustainable forest management (Rametsteiner and Mayer 2004). In practice this is a matter of maintaining representative and functional networks of all naturally occurring forest habitat types at a range of spatial and temporal scales (e.g. Anon. 2000, Margules and Pressey 2000, Angelstam and Andersson 2001, Hanski 2003, Pressey et al. 2003, Lõhmus et al. 2004). Since the amount of protected or specially managed forests is in most cases limited, forest reserves must be complemented by measures favouring natural forest dynamics in commercial forests, in order for the important habitat structures to occur in sufficient amounts (Seymour and Hunter 1999, Lindenmayer and Franklin 2002).

For conservation efficiency, forestry and conservation authorities need to know the type, location, and size of forests that are important for the maintenance of biodiversity (Angelstam et al. 2004a). In the international conservation discussion these are frequently referred to as High Conservation Value Forests, or HCVFs (Anon. 2001a). These may range from woodland key habitats of a few hectares (Nitare and Norén 1992, Norén et al. 2002) to intact landscapes (Aksenov et al. 2002). To optimise conservation values in the long term, one may, depending on the focal species' life history, want to concentrate available conservation resources in landscapes or regions with concentrations of HCVFs. All these issues are dependent on being able to define and identify the amount of high conservation value forest areas, as well as locating them in the field.

The main aim of the Baltic Forest Mapping project (BFM) (Kuuba et al. 2003) was to use existing data sources to map the distribution of HCVFs in the Baltic States (Estonia, Latvia, and Lithuania). The primary data sources were national forestry databases, originally designed and updated for planning logging schedules. However, this data can also yield much useful biological information (Angelstam and Bergman 2004, Jansson et al. 2004). This information is urgently needed in the Baltic States, as commercial logging has greatly intensified since re-independence from the Soviet Union took place in 1991 (Lloyd 2000, Kuuba 2001).

The BFM approach is specifically useful at the landscape level, and provides conservation planning opportunities for species groups with larger area requirements, but also for the maintenance of populations of for example epiphytic plants in the long term (Snäll 2003). Birds are a particularly interesting group to communicate the complex habitat requirements of species at multiple scales within landscapes for the maintenance of viable populations (Angelstam et al. 2004b). Birds represent one of the best studied taxonomic groups of animals (Flade 1994, Tucker and Heath 1994). Many larger birds are also well known by managers and some may even function as flagship species, i.e. species useful for stimulating public interest in conservation (Simberloff 1998, Uliczka et al. 2004). We also draw on the focal species approach proposed by Lambeck (1997), which is consistent with the umbrella species concept (Fleishman et al. 2000). This approach aims to conserve biodiversity by satisfying the requirements of a suite of sensitive species for different attributes of the landscape (Roberge and Angelstam 2004). Several studies of birds support the focal species approach by suggesting that the presence of specialised and area-demanding birds indicates high species richness of other species in the respective forest vegetation types (Martikainen et al. 1998, Mikusiński et al. 2001, Suter et al. 2002).

The BFM approach should thus be seen as a necessary complement to other approaches for locating high conservation value forests in the Baltic States. One is the inventory of woodland key habitats (WKH) (Nitare and Norén 1992, Hansson 2001, Norén et al. 2002). The WKHs are identified based on a combination of field judgements of the naturalness of the stand's structure, presence of indicator species with small area requirements, signs of historical use, and cultural heritage values. As applied in Sweden so far, the WKH concept has been limited to using the occurrence of plants, lichens, and fungi as indicators, i.e. species without landscape scale requirements in the short term. In Latvia also invertebrates have been used as indicators of forests of high conservation value (Mollusca and Insecta) (Andersson et al. 1999, 2003, Auzins et al. 2000). Management of WKH is one of the most important conservation efforts in the Baltic Sea Region, which is an area that lacks large intact forests (Aksenov et al. 2002). Furthermore, in preparation for the membership in the European Union (EU) in 2004, the countries' nature conservation authorities are involved in assigning sites for the EU habitat network Natura 2000 (Anon. 2003).

This report provides an example of how existing forest management data bases can be used for conservation planning. The main findings of the BFM project are presented and ways are suggested in which the results can be applied to maintain functional networks of habitats for the maintenance of forest biodiversity in the Baltic States. The full BFM final report and an interactive BFM map are available at <www.balticforestmapping.net>.

Study area

Ecoregions

The Baltic States are situated in the transition zone between the boreal coniferous and the temperate deciduous forest zones (Laasimer et al. 1993). They no longer harbour much naturally dynamic forest, but there are still relatively large areas of old semi-natural forest ecosystems (Andersson et al. 1999, 2003, Auzins et al. 2000, Viilma et al. 2001). The Baltic States have a dramatic land use history (e.g. Laivins 1997, Dzintara 1999), reflected in the trends in forest cover over the past 300 yr. In Estonia the

forest cover has been estimated to ca 55% around 1700, after which it declined rapidly to a low of ca 20% in the first decades of the 20th century, and then increased to today's 52% (Lõhmus et al. 2004). In Latvia the forest cover 300 yr ago was estimated to 65%, then declined to a low of 25% in the 1930s, followed by an increase to ca 45% in the late 1990s (Prieditis 1999). Finally, in Lithuania, which is more dominated by agricultural land than the other two countries, the forest cover around 1700 was ca 40%, reached a low of 17% before World War II and has today a forest cover of 30% (Tsvetkov 1957, Antanaitis 1981, Anon. 2001b).

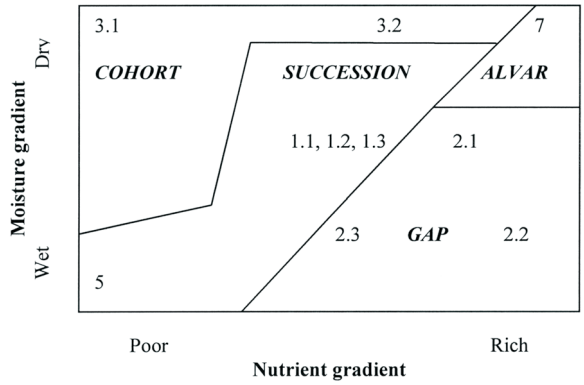


Fig. 1. Moisture-nutrient matrix and the different forest vegetation types used in the Baltic Forest Mapping project; for codes see Table 1.

Forest vegetation types

To expedite their evaluation for biodiversity conservation, forests can be grouped into natural forest disturbance regimes (Angelstam 2002, Bergeron et al. 2002). The starting point is to understand how site conditions, disturbances and macroclimate interact and result in characteristic forest vegetation types. In the Baltic States, forest site type classifications have been developed by Lõhmus (1984) and Paal (1997) for Estonia (see Lõhmus et al. 2004: Fig. 2), by Buss (1981, 1997) and Avis (1997) for Latvia, and by Karazija (1988) for Lithuania. Although they differ in their details, they are all based on a matrix with a moisture gradient and a nutrient gradient (Fig. 1). Three broad types of forest vegetation families with different dynamics can be found, SUCCESSION, COHORT and GAP (Table 1; for details see Angelstam and Kuuluvainen 2004).

Starting in the upper left corner in the moisture/nutrient matrix there are dry Scots pine *Pinus sylvestris* forests with dynamics that usually result in several cohorts of trees with multi-layered open forests. Moving to the right into the central part of the matrix, succession after intensive stand-replacing fire or windfall should be expected. From the point-of-view of biodiversity conservation, three developmental stages in the succession are particularly important, as they are uncommon in forests with intensive management for wood production. These are burned or windfall areas (1.1), pioneer phase birch-aspen forest (1.2), and old-growth spruce dominated forest (1.3). In the lower right-hand part of the matrix, different kinds of gap-phase dynamic should be expected because of the general absence of stand-replacing disturbance by fire. On mesic eutrophic soil, lime *Tilia cordata* and elm *Ulmus glabra* dominate and gap-phase dynamic is the typical natural disturbance regime. On wet and rich sites, forests would be dominated by black alder *Alnus glutinosa* and ash *Fraxinus excelsior*. In the upper part of the matrix, semi-open oak

Table 1. Forest vegetation families (numbers from 1 to 7) and their subtypes (e.g. 1.1, 2.1 etc.) defined in the Baltic Forest Mapping database. The classification covers all the main forest types found in the Baltic States' boreal, hemiboreal and nemoral regions. In addition to the above, also protected forests were classified. This allowed analysis of the biological values of the current forest protected area networks in the Baltic region.

Forest family	Code to subtypes (see Fig. 1)	Description
SUCCESSION	1.1	burned and wind fall areas
	1.2	pioneer phase birch-aspen forests
	1.3	old-growth spruce dominated forest
GAP	2.1	broad-leaved or nemoral
	2.2	wet deciduous forest
	2.3	wet spruce dominated forest
COHORT	3.1	dry pine dominated forests
	3.2	dry oak-pine
RIPARIAN	4.1	black alder, ash
	4.2	primary forest along meandering rivers
WOODED PEATLAND	5	pine forest on peatland
CULTURAL FORESTS	6.1	wooded meadows
	6.2	wooded pastures
ALVAR	7	

Quercus spp. forests once developed due to mowing or presence of domestic animals, and there may have been semi-open *Quercus* forests also in pre-human times because of browsing and grazing of now extinct large herbivores (Vera 2000). Today such forests are mostly aspen *Populus tremula* stands. Finally, the upper right corner is characterised by the alvar forests (dry limestone plains with scattered trees) of Estonia. In addition to those found in the matrix, two other forest vegetation types were distinguished. These were riparian and primary forests along meandering rivers and cultural forests such as wooded meadows and pastures.

Methods

Data sources

The BFM database and maps are based on the national forest databases supplemented by additional information (Table 2). These databases contain information down to stand level on every forest stand in the Baltic States, listing at least the stand's primary tree species and average age, usually together with large amounts of additional data. The system has been inherited from Soviet times, when 10% of stands were inventoried each year, so that data was at most a decade old for any particular stand.

Following renewed independence of the Baltic States these inventories have been continued in publicly owned forests, which cover 37% of Estonian, 49% of Latvian, and 50% of Lithuanian forests. Other forests, either privatised or awaiting privatisation, have not been inventoried systematically in Estonia or Latvia since independence. Consequently, data on those forests is less up-to-date. Private forest logging has increased dramatically and many biologically valuable stands have been lost. In contrast, stands still awaiting privatisation remain in principle intact and older inventory data is still useful.

The possibility for spatially explicit visualisation of the BFM database is affected by the degree to which the database entries on forests have been linked to digital maps. The best situation in this regard was in Lithuania, where at the start of the project in 2001 30% of forests were digitally linked to GIS (Geographic Information System) maps at the stand level. Estonia and Latvia still had substantial regions uncovered by digital maps (Table 2), where visualisation of the BFM database was therefore not yet possible. Stand level digital maps showing the exact location of stands are referred to here as LEVEL 1 data. They give the highest level of accuracy and have been used whenever possible.

In the other cases block level digital maps were available, i.e. a coarser unit of digitalisation of a "kvartal", which is a collection of stands in a block of ca 20–50 ha in size. These are referred to as LEVEL 2 data. If only block level maps were available, the exact location of valuable stands could not be shown, and only the percentage of the area of the block that fulfils the BFM criteria can be given. For Lithuania the entire country could be mapped at block level, but in Estonia and Latvia also block level maps were lacking for part of the country (Table 2).

In order to visualise the BFM databases across the entire Baltic region by combining stand and block level information, we transformed the original data from vector to raster presentation. The transformed data is referred to as LEVEL 3 in the BFM database. The transformation generated a network of 25 ha (500 × 500 m) grid cells covering the entire region, and the percentage of BFM stands within each 25 ha grid cell was then calculated (Fig. 2). The pseudo-grid cell size selected (25 ha) was the smallest possible for the available hardware and software, but the cells could be easily combined to produce a coarser resolution. LEVEL 3 grid cells covered the whole project area for which a digital map was available, with the exception of cells containing no forest at all. The attributes of the LEVEL 3 database are the area's share of stands meeting the BFM criteria within the 25 ha grid cell, as well as information on the share of the total forest cover within each cell. Some geographical precision is lost in the transformation, but the best sites still stand out (Fig. 2).

Table 2. Data sources of the Baltic Forest Mapping project by country.

	Estonia	Latvia	Lithuania
National forest database	yes	yes	yes
Woodland key habitats project *	yes	yes	no
BirdLife database on rare birds	yes	yes	yes
National database on other taxa	yes	no	no
Significant studies similar to BFM	yes**	no	no
Stand level digital maps (% of the country)	35%	20%	30%
Block level digital maps (% of the country)	0%	30%	70%
No digital maps (% of the country)	65%	50%	0%

*Woodland key habitats (WKH) are smaller set-aside areas of biological value in otherwise commercial forest zones. Retention of WKHs is required by e.g. forest certification processes ongoing in all the Baltic States.
**EFCAN = Estonian Forest Conservation Area Network project and database (Viilma et al. 2001).

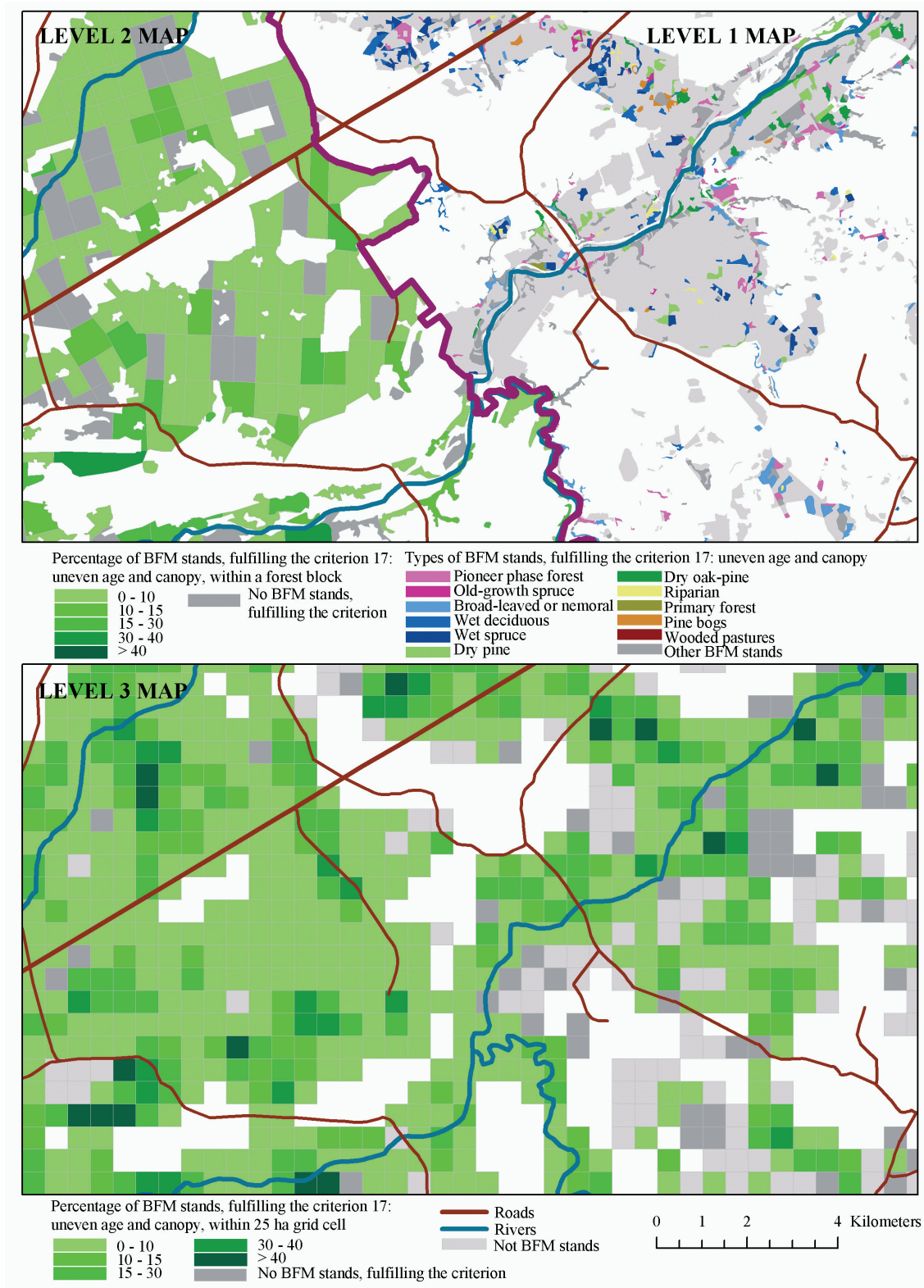


Fig. 2. Examples of the Baltic Forest Mapping database output to LEVEL 1, 2 and 3 scale maps. The precise nature and location of individual stands can be displayed only for LEVEL 1 data (see Methods section for details).

The sources of information on the total forest cover used throughout the project were: the national GIS database with a scale of 1:50 000 in Latvia, the GIS database of forest resources with a scale of 1:50 000 in Lithuania, and the CORINE Land Cover database in Estonia. Digital maps of the entire Baltic region will be completed during the current decade, offering the chance to refine the visualisation of the current BFM analysis for forests where regular inventories continue to be made.

Selection criteria for high conservation value forests

The classification of forest vegetation types used in the present project is given in Table 1. Within these types, the key to using the national forest databases to find HCVFs was relating data on e.g. the composition and age of stands to thresholds for probable high biodiversity value. Apart from the need for sufficient forest cover per se, virtually all threatened forest species in Europe suffer from a lack of natural conditions of various succession stages – i.e. lack forests with little or only moderate signs of human influence. Such conditions typically entail the presence of large volumes of dead wood (Siitonen 2001), old and/or mixed stands, and the presence of old big trees (Nilsson et al. 2002) (Table 3). The criteria in Table 3 were elaborated from expert knowledge (cf. Esseen et al. 1992, Larsson et al. 2001) and represent the link between information available from the databases listed in Table 2 and the possible presence of HCVFs hosting or with the potential to host specialised species (cf. Angelstam et al. 2004b). The criteria in Table 3 were converted into a macro language filter, which was applied to the available forest and species databases of each Baltic country. Typical results of this search are shown in Fig. 3. Available data sources varied somewhat from country to country, so that not all criteria could be applied to all countries, as indicated in Table 3.

Logging rates

Logging rates of BFM stands were sampled in each country using official felling statistics from 2001. In Estonia the

Table 3. Criteria for selection of a forest stand into the Baltic Forest Mapping database. All criteria could not be applied in all the Baltic States because of variation in information in the available databases. Codes in the left column are those used in the BFM database. For further details on all criteria categories see Kuuba et al. 2003, Annex 2.

Code	Description criteria	Country
11	Little or no signs of human influence	Est/Lat/Lit
12	Average age of stand defined for each tree species and country separately [1)]	Est/Lat/Lit
13	Considerable amount or long continuum of dead wood of different types, rich flora of wood rotting fungi [2)]	Est/Lat
14	Largest blocks of unfragmented forest (by human) > 100 ha (no clear-cuts, no draining system, no roads) (regional, non-stand criterion)	Est
16	Forests on steep slopes (> 15°), ravines	Lat/Lit
17	Uneven age/canopy structure, over-mature/big tree generation present (4 or more tree species > 50 yr and age variance > 30 yr + presence of trees fulfilling criterion 12)	Est/Lat/Lit
18	Forests after natural disturbance (fire, storm, flooding)	Est/Lat
21	Nationally classified endangered vegetation types [3)]	Est
22	Population of rare forest-dependent species: spotted eagle *Aquila clanga*, flying squirrel *Pteromys volans*, uncommon woodpeckers [4)]	Est/Lat
23	Presence of capercaillie *Tetrao urogallus* leks	Est/Lat/Lit
24	Very old trees (of previous tree generations) present	Est/Lat/Lit
25	Long living nests of eagles *Aquila* and black stork *Ciconia nigra*	Est/Lat/Lit
26	Broad-leaved species – maple, elms, lime, hornbeam, apple, wild cherry, pear; willows – (*Acer platanoides*, *Ulmus* spp., *Tilia cordata*, *Carpinus betulus*, *Malus sylvestris*, *Prunus avium*, *Pyrus communis*, *Salix* spp.) present in the dominating canopy layer	Est/Lat/Lit
28	Limited access areas (islands, forest "islands" on bogs)	Est

[1)] E.g. oaks *Quercus* 120–160 yr, Scots pine *Pinus sylvestris* 100–160 yr, Norway spruce *Picea abies* 80–120 yr, aspen *Populus tremula* 40–60 yr. The age gradient took account of slower tree maturation in the N of the region, as well as regional differences in soil types.
[2)] Dead wood threshold ca 50 m^3 ha^{-1} (Estonia) or 15 trees ha^{-1} of ø>20 cm (Latvia); data from National Forest Database and Woodland Key Habitat inventories. Fungi data from Woodland Key Habitat inventories – see Auzins et al. 2000, Viilma et al. 2001.
[3)] See Paal (1997).
[4)] Three-toed woodpecker *Picoides tridactylus*, middle spotted woodpecker *Dendrocopos medius*, white-backed woodpecker *D. leucotos*. Data from BirdLife and National Forest/Rare Species Databases.

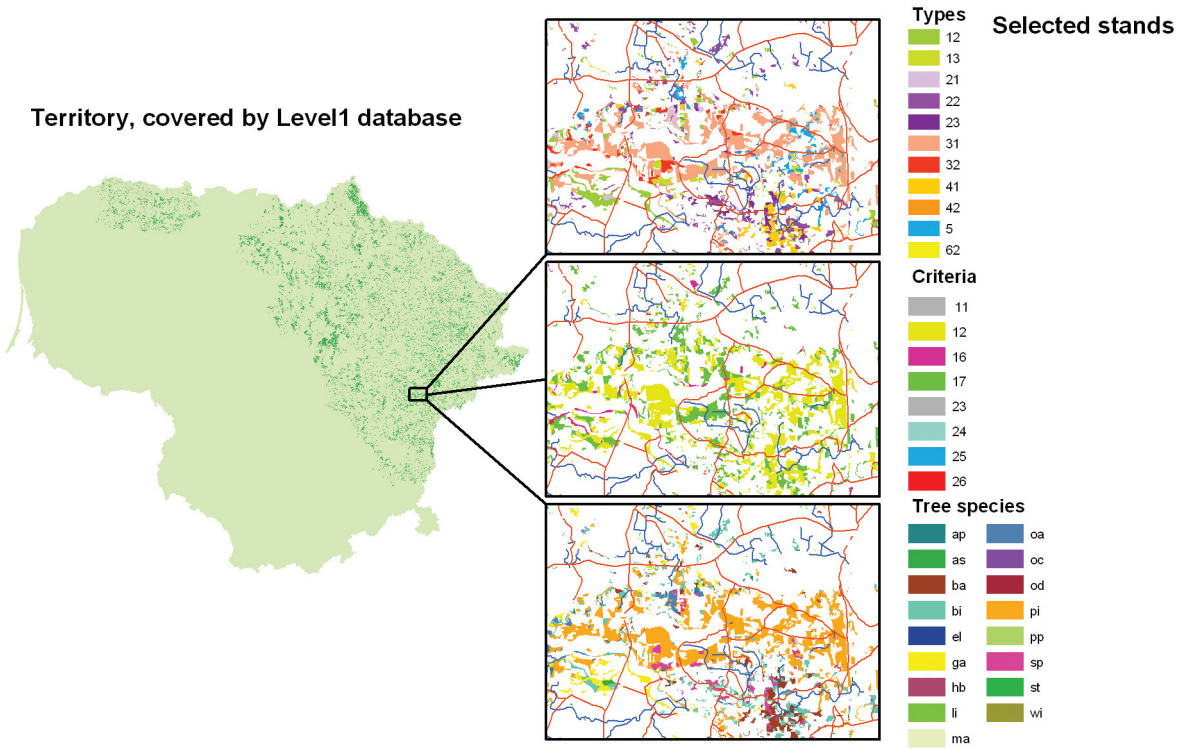


Fig. 3. Examples of BFM results at large (national) and small (individual stand) scale resolutions.

sample covered all state owned forests, where some 177700 ha (17%) fulfilled at least one BFM criterion.

Results

Amount of BFM forests

On average, 17% of the forests of Estonia, Latvia and Lithuania met at least one BFM selection criterion, and were thus included in the BFM database of potential HCVFs (Table 4). Of these, only figures for state forests can be regarded as exact and up-to-date for all countries, with the exception of Lithuania, where records continue to be regularly updated for all ownership categories.

The most common HCVF forest types were broad-leaved or nemoral forests, wet deciduous forests, and dry pine forests (Figs 4–6). Burned and windfall areas, as well as primary forests along rivers were very rare in the entire Baltic region. However, there were also marked differences between Estonia, Latvia and Lithuania in their distribution of HCVF forest types, the most important of which can be characterised as follows:

Estonia

In Estonia (Fig. 4) the forests of the GAP forest family (Table 1) represented the largest area of all BFM-selected forests (53% of all Estonian BFM sites), explained by the prevalence of wet deciduous forests in the country. Of these, the commonest subtypes were broad-leaved or nemoral (30%) and deciduous forests (20%), even though the total amount of the former is not large in Estonia. The forest family SUCCESSION covered 17% of Estonian BFM forests, two thirds of it being old-growth spruce forests. The first stages of the natural succession of these forests, burned and windfall areas, were rare, probably due to current forest management policies.

With regard to fulfilment of BFM selection criteria, the most frequently met criterion was the diversity of stand structure: almost 75% of all BFM forests in Estonia were uneven both with respect to their species composition and age structure. Many stands were also selected by an age criterion (32% of all Estonian BFM stands) or because of the occurrence of very old trees (29%). Sixteen per cent of the Estonian BFM forests fulfilled the criterion of rare forest vegetation types (defined by the main tree species and site type). Over half of Estonian BFM stands met more than one BFM criterion, and ca 20% met three or more.

Latvia

In contrast to Estonia, the most common BFM forest family subtypes in Latvia (Fig. 5) were COHORT dry pine and dry oak-pine forests – making up 19 and 21% of the Latvian BFM area, respectively. Distinguishing between

Table 4. The area and proportion of BFM sites by ownership categories in the Baltic States.

Country	Forest category	Total forest area of country (ha)	Number of sites selected in BFM	Total area selected in BFM (ha)	Proportion total forest selected in BFM (%)
Estonia	State owned forests	831100	84700	163300	19
	Private forests	420000	52900	61400	15
	Other forests *	1140000	55267	116600	10
	Total	2250700	192900	341300	15
Latvia	State owned forests	1434800	87700	168850	12
	Private forests		71200	77980	
	Other forests *	1467400	20820	30670	7
	Total	2902200	183160	283930	10
Lithuania	State owned forests	1001500	139146	331840	33
	Private forests	323900	45951	56330	17
	Other forests *	694600	139448	248600	36
	Total	2020300	324545	636770	32

* Former collective farm forests.

those is difficult, and they could in the future be analysed together. GAP wet deciduous forests made up 22% of the total selected BFM stands, and GAP wet spruce dominated forests 2.2%. Nemoral broad-leaved stands made up only 5.9% of BFM stands. A proportionately large area of old-growth spruce and pioneer phase forests were represented in the Latvian BFM database, 10 and 12% respectively, of all BFM stands.

The three most frequently met criteria in Latvia were "Average age of the stand", fulfilled by 38% of all BFM-selected stands, followed by "Considerable amount and long continuum of dead wood" (24% of stands), and "Uneven age/canopy structure" (21%). A total of 87% of Latvian BFM stands met only one criterion. Two criteria were met in 13% of the BFM area, and three or more were met in < 1%. No stands met five or more criteria.

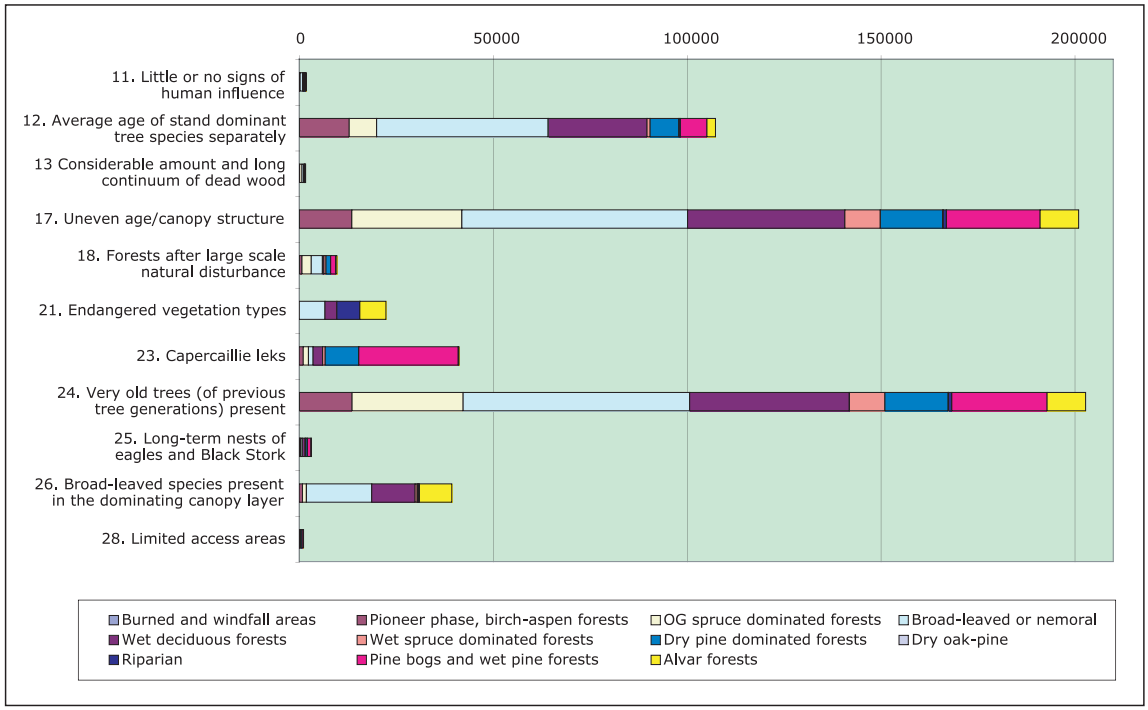


Fig. 4. The total area of Baltic Forest Mapping (BFM) sites by forest types and BFM criteria in Estonia. For types and criteria see Methods. Note that "Broad-leaved" here means hardwoods, not all deciduous tree species.

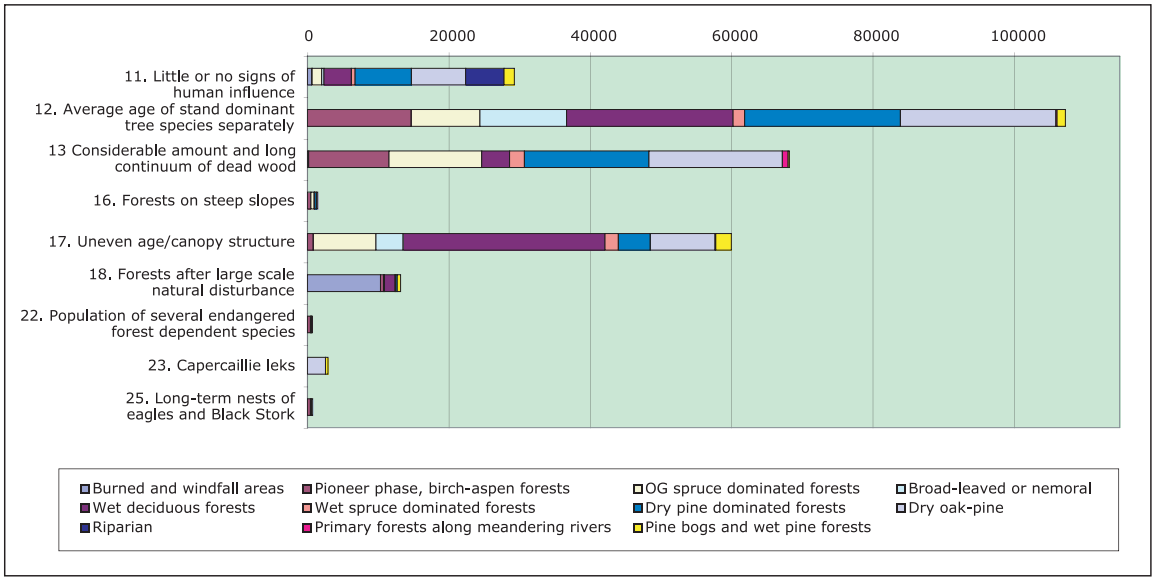


Fig. 5. The total area of Baltic Forest Mapping (BFM) sites by forest types and BFM criteria in Latvia. For types and criteria see Methods. Note that "Broad-leaved" here means hardwoods, not all deciduous tree species.

Lithuania

GAP forests on wet soils and peatlands made up approximately one half of the HCVF area in Lithuania (Fig. 6). Wet deciduous forests prevailed among Lithuanian BFM-selected forest subtypes, with 30% of the total BFM area. Wet spruce dominated forests covered 18% of BFM-selected forests. Wet forests reach potentially higher ages because of restricted access and less economic profit for logging. This is true especially for "wet deciduous forests", 53% of which have reached a mature age (the respective average value for all BFM stands is 42%). Only 14% of the most common forest type in Lithuania, dry pine dominated forests, met BFM criteria. As with Estonia, this probably reflects intensive economic use and management. In general, there was a clear dominance of BFM-selected stands of the GAP group; this group made up almost 59% of all BFM stands in Lithuania.

The three most frequently met criteria in Lithuania were "Average age of the stand", fulfilled by 60% of all BFM-selected stands, followed by "Stand age" (22% of

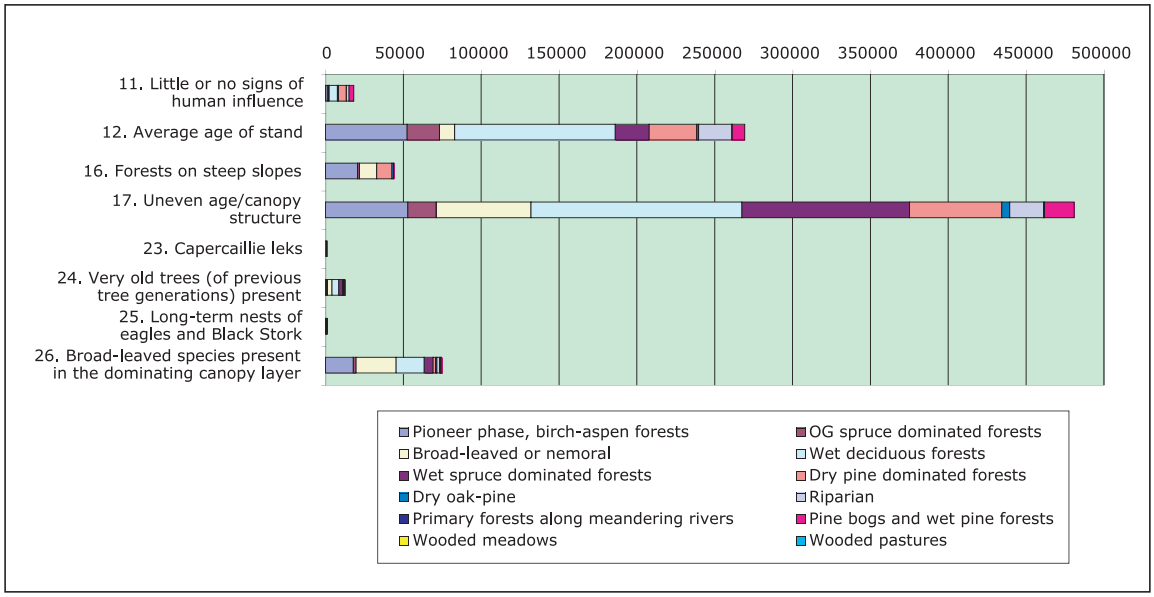


Fig. 6. The total area of Baltic Forest Mapping (BFM) sites by forest types and BFM criteria in Lithuania. For types and criteria see Methods. Note that "Broad-leaved" here means hardwoods, not all deciduous tree species.

stands), and "Broad-leaved species present in dominating canopy layer" (10%). In 65% of the Lithuanian BFM-selected forests one criterion was met. Two criteria were met in 29%, and three or four in 6%. No stands met five or more criteria.

Estimating logging intensity in BFM-selected forests

A comprehensive assessment of the logging intensity in BFM stands could be carried out only in Estonia's state-owned forests. This showed that the current annual rate of logging ranged from 3.0 to 6.9% (Table 6). All forest types were affected, with old stands of uneven canopy structure having the highest logging rate. It was not possible carry out a similar analysis for private and for ownerless forests.

Assessing the reliability of BFM results

BFM results were checked against a variety of earlier field results to evaluate the BFM criteria's success in picking up biologically valuable stands. One such comparison was with a lichen inventory carried out in Estonia by the Estonian Forest Conservation Area Network project (EFCAN; Viilma et al. 2001). The EFCAN study sampled 56 EFCAN sites and found some or high lichen conservation value in 33 of them. Of these 33 sites, 32 (97%) were identified using the BFM criteria. A similar EFCAN study of conservation values for fungi (Korjus and Viilma 1998) had a 95% overlap with BFM (n = 126). On the other hand, the overlap between WKHs and BFM sites in four forest districts in Latvia ranged only from 9 to 30%.

Discussion

High conservation value forest areas of different sizes

The Baltic Forest Mapping (BFM) maps revealed that a considerable amount of biologically potentially valuable forest can be found outside existing protected areas – in fact an average of 17% of Baltic forest fulfils at least one BFM criterion. This means there are excellent opportunities to improve forest protected area networks in the Baltic States in a systematic way, as well as to take the conservation values of forests into account in forestry planning outside protected areas.

The results from the BFM show that the distribution of different types of high conservation value forests varied among the different Baltic States (Table 5). Within SUCCESSION forests, burned and windfall areas were very rare in Estonia and Lithuania, but were quite common in Latvia. Older pioneer phase (birch-aspen) forests where BFM criteria (i.e. stand age, dead wood amount, etc.) were met could be very important for biodiversity conservation in the next decades if management activities remain at current limited levels and natural processes continue to be allowed to operate. Old-growth forests, however, were relatively uncommon in Lithuania, which has the lowest forest cover of the three states, compared to Estonia and Latvia. This is not surprising because the Lithuanian forest cover

Table 5. Relative proportion of different forest vegetation families and subtypes of the forest areas identified in the Baltic States.

Forest family (see Table 1 and Fig. 1)		% of all BFM forests		
		Estonia	Latvia	Lithuania
(1) SUCCESSION	1.1. burned and wind fall areas	0.1	3.9	0
	1.2. pioneer phase birch-aspen forests	6.8	10.1	13.9
	1.3. old-growth spruce dominated forest	10.4	11.9	3.3
(2) GAP	2.1. broad-leaved or nemoral	29.5	5.9	10.4
	2.2. wet deciduous forest	20.2	21.7	30.2
	2.3. wet spruce dominated forest	3.1	2.2	18.3
(3)COHORT	3.1. dry pine dominated forests	8.2	18.5	13.5
	3.2. dry oak-pine	0.1	21.3	0.9
(4) RIPARIAN	4.1. black alder, ash	1.7	1.9	5.8
	4.2. primary forest along meandering rivers	0	0.3	0.1
(5) WOODED PEATLAND	5. pine forest on peatland	15.4	2.1	3.6
(6) CULTURAL FORESTS	6.1. wooded meadows	0	0	0.005
	6.2. wooded pastures	0	0	0.01
(7) ALVAR	7. alvar	4.5	0	0
Total	**% of all BFM forests**	**100**	**100**	**100**
	Proportion (%) of BFM forests of all forests in the country	**15.1**	**9.8**	**31.5**

Table 6. Annual logging rates of BFM stands in State Forests in Estonia.

	Total area of analysed BFM sites in 2002 (ha)	Average annual logging at site (mean period: 7 yr)	
		ha	%
Burned and wind fall areas	45	3	6.9
Pioneer phase birch-aspen forests	12180	560	4.6
Old-growth spruce dominated forests	13830	670	4.8
Broad-leaved or nemoral forests	33390	1780	5.3
Wet deciduous forests	30030	1500	5.0
Wet spruce dominated forests	6060	320	5.2
Dry pine dominated forests	24050	780	3.2
Dry oak-pine forests	93	6	6.5
Riparian forests	3610	130	3.7
Primary forests along meandering rivers	0	0	0.0
Wooded peatlands	48600	1440	3.0
Alvar forests	5240	330	6.4
Total	177120	7520	4.2

has increased by 50% since 1948, largely due to natural and deliberate reforestation of abandoned agricultural land (Anon. 2001b).

Regarding GAP forests (including black alder and ash (forest type 4.1.)), Estonia and Lithuania had a much higher proportion than Latvia. The small proportion in Latvia may be explained by the large-scale drainage that has caused a drastic decline of wet forests in Latvia (Priediti s 1999, 2002). Note that in Estonia GAP forests were mainly deciduous while in Lithuania they were dominated by spruce. Slash and burn agriculture used to be prevalent in such forests (Dzintara 1999) and spruce or birch and aspen have replaced them after clear felling.

The country having the highest proportion of COHORT forests was Latvia. In Estonia, in spite of being common in the country generally, COHORT forests made up only 8% of Estonian BFM forests. Such forests have high economic value and soil conditions that allow effective forestry activities, so that the conservation values of these forest types are often not maintained. Pine forest on peatland was most common in Estonia. Finally, alvar forests were confined to Estonia and wooded pastures were only found in Lithuania. To understand the role of these differences for the conservation of forest biodiversity, it is necessary to understand the relative historic loss of different types of forest vegetation (Dzintara 1999, Margules and Pressey 2000, Angelstam et al. 2003, Pressey et al. 2003). It is also necessary to analyse the size distribution and functional connectivity of the network of patches at the landscape scale.

The results show that in general privately owned and collective farm stands contained less high conservation value forest overall than state forests. This is probably due to the fact that a high proportion of the former are secondary and young stands, since these are largely forests that have been planted or grown on former agricultural lands (Balciauskas and Angelstam 1993). State forests consist mainly of old forest lands, and thus the higher proportion of BFM forests in state forests was expected. Even so, former collective farm forests still awaiting privatisation were well represented in the BFM database, and are likely to have retained or improved their natural values, as legally these stands could normally not have been logged at all since 1991. Agglomerations of BFM stands, i.e. large potentially high conservation value forest entities, stand out well from small-scale maps such as that of Lithuania in Fig. 3.

In regions with long histories of using land primarily to produce tangible products useful to people, identification of high conservation forest usually focuses on small remnants of natural forest. In Sweden (Nitare and Norén 1992, Hansson 2001, Norén et al. 2002) and the Baltic countries (Andersson et al. 1999, 2003, Auzins et al. 2000) small WKHs (usually <10 ha) are mapped. Although often wrongly considered as conceptually homogenous in the public debate, WKHs come in many different kinds having different composition, structure and dynamics (Norén et al. 2002, Angelstam et al. 2004a). Hence, their maintenance may also require specific operational management approaches both at the scale of the actual forest area and its surroundings (Angelstam 2002, Angelstam et al. 2004a).

When evaluating BFM data, it is important to bear in mind that the overall scope of the BFM project is not at stand but at landscape level, in contrast to e.g. the WKH approach commonly used in certification schemes (Anon. 2002). The BFM approach should also be seen as a tool to identify the amount of high conservation value forests in a landscape or region, rather than as a static map showing their location. Regions with high concentrations of BFM stands should be in a better position to conserve forest bio-

diversity because they can be used to plan for the maintenance of populations of not only specialised species but also those with large area requirements (Angelstam et al. 2004b).

Reliability of BFM results

The BFM methodology was developed to work with data of traditional national forest inventories, which makes the system relatively cheap and easy to implement. Because of the general nature of BFM definitions of valuable forests, the biological value of individual BFM stands will vary, but this is not crucial as long as the overall selection criteria are sufficiently stringent. A stand meeting BFM criteria has a high probability of hosting feature of high conservation values than average forests, or high potential to become valuable in a relatively short time.

Data checks in Estonia showed high overlap between BFM results and those of the similar EFCAN study (Viilma et al. 2001) in Estonia. This is encouraging, though perhaps not surprising given that both projects held many data sources in common. However, it should be noted that the overall results of the two projects are not the same: EFCAN declared as HCVFs only slightly > 4% of Estonian forests, whereas BFM found 15%. Estonian law currently requires 4% of forests to be strictly protected.

On the other hand, the overlap between WKHs and BFM sites at four forest districts in Latvia ranged only from 9 to 30%. A probable explanation for this is the different spatial scale: the WKH project is focused on identification of habitats often smaller in scale than individual stands, so that the scale and in some respects also criteria of WKHs differ considerably from the BFM approach. As one might expect, the total area of WKHs in any country is considerably smaller than that of the BFM sites.

Each BFM country adjusted the common set of BFM criteria slightly to meet local conditions. The most significant difference is the age limits of tree species in BFM criterion 12 (Age of the stand) that were defined nationally based on local experts' estimates. This, together with the slight differences in the interpretation of criterion 17 (Uneven age/canopy structure) may have caused most of the differences in the amount of BFM stands e.g. between similar regions of Latvia and Lithuania. This is not, however, a major drawback in the BFM approach, as adjustments of e.g. different age limits of tree species can be done in the BFM database also afterwards as required.

Nevertheless, different national data sources with varying qualities yield different results. For example, there are very probably high conservation value forests on steep slopes along rivers in Estonia, but for technical and manpower limitation reasons these could not be evaluated. Information on stands with a lot of dead wood is in general incomplete because older forest inventories do not have data on dead wood at all, and in some of the more recent inventories the amount of dead wood has been recorded only if it had commercial significance. However, the amount of dead wood in the Baltic States (10–13 $m^3 ha^{-1}$ in Estonia according to Lõhmus et al. (2004)) and Russia (ca 25 $m^3 ha^{-1}$ in the Novgorod region (Shorohova and Tetioukhin 2004)) is generally high compared with managed forests in the same ecoregions in Sweden and Finland (2–5 $m^3 ha^{-1}$ according to Siitonen 2001 and Angelstam et al. 2004e).

Comparison of BFM results and existing amount of protected areas

Only 8% of the BFM area in Latvia is presently strictly protected, with a further 12% under some degree of protection or limitations in the use. A further 15% of BFM forests are situated inside existing protected areas, but are in practice without strict protection. The rest of BFM stands (ca 65% of the total) are situated in commercially managed forests. Using the total area of Latvian forests as a reference, 0.7% of Latvian forests are currently both strictly protected and fulfil at least one BFM criterion; an additional 1.3% of forests are both partly protected and fulfil at least one BFM criterion, while 7.9% of Latvia's forests fulfil at least one BFM criterion but are not protected at all.

The most common BFM forest subtype in Latvia, wet deciduous forests, is not the best protected one. Around 85% of the area of this type is currently not protected at all, and only a minor share (5%) is strictly protected. Dry pine forests are also protected only to a limited extent, and usually need management to maintain their characteristics (Rülcker et al. 1994, Fries et al. 1997). In total, 75% of the total BFM area of dry pine forests is not protected at all. However, the proportion of pine forests under strict protection corresponds to 12% of their total BFM selected area. Another relatively better protected BFM forest type is riparian forests, of which 23% is under strict protection. Around 11% of pine bogs and wet pine BFM forest is strictly protected. The least protected BFM forest types in Latvia are the broad-leaved forests and pioneer phase (birch-aspen) forests. In spite of their presence and abundance in the BFM database, only 1.2 and 0.4% of their total BFM area is strictly protected, respectively.

In Lithuania only 2.9% of the BFM-selected forests are strictly protected, while an additional 28% are afforded some degree of protection or limitations in the use. The rest, 69%, is unprotected. Using the total area of Lithuanian forests as a reference, forests both strictly protected and included in the BFM database amount to 0.9%; the corresponding figure for partly protected BFM forests is 8.8%, while 22% of Lithuanian forest is BFM forest without any protection status. The dominant BFM forest types – wet deciduous and spruce dominated forests – are the least protected ones; 78 and 87% of their area, respectively,

is not protected at all, and only a very small share of these forest types is strictly protected.

The best protected forest types of the Lithuanian BFM database are pine bogs and wet pine forests (13% strictly protected). Approximately 5% of the territory of the dry pine-dominated and riparian forest in the BFM database is strictly protected, and for wooded meadows the figure is 10%. Forest types covering smaller areas are relatively under better protection status than the most common types, e.g. all primary forests along meandering rivers are at least partly protected.

No comparison of protected vs BFM areas was attempted for Estonia. The existing digital data from protected areas was insufficient, as was information on the true level of protection, making assessment difficult. Following the EFCAN project (Viilma 2001), the Estonian government has taken decisions of principle to raise the level of strictly protected forest to 4%, so that at least in the near future the country is likely to attain a somewhat higher percentage of protected stands than Latvia or Lithuania.

The influence of logging intensity on BFM forests

A rapid comprehensive assessment of the logging intensity in BFM stands could be carried out only in Estonia for state-owned forests. All forest types were affected, with old stands of uneven canopy structure suffering most. Only final fellings were accounted for, so in fact the figure of 4.2% annual loss of HCVFs in Estonia is if anything an underestimate. For comparison, one should consider that the annual final felling rate of forests in Finland in recent years has been around 0.8–1.0% (Anon. 2001c). Finland is generally identified as the country of stable forest cover with the most intensive forestry in the world (Harkki 2003). It was not possible to carry out a similar analysis for Estonia's private and ownerless forests. Theoretically no logging should take place in the latter. Nevertheless, the logging intensity in private forests was presumably higher than in state forests, as other analyses (Kuuba 2001) have shown that the average annual harvest rate in private forests in Estonia has been very high (10 m^3 ha^{-1}) in recent years, three times the state forest average of 3.6 m^3 ha^{-1}. Thereby it is probable that BFM stands owned by private persons or companies are disappearing around three times faster than those in state forests.

In Estonia, forests fulfilling the BFM age criteria made up a smaller proportion of BFM stands in state forests (25%) compared with unprivatised (36%) or private forests (41%). This shows that final felling of old forests is a regular activity in state forests, and that private and as yet unprivatised forests potentially hold considerable biological values. Logging pressure in private forests is rapidly increasing, so that many of these forests may be lost in the near future.

Research and management applications of the BFM database

The results of the BFM project, as well as the BFM methodology in general, are aimed at improving forest conservation planning and forest biodiversity management, both being parts of sustainable forest management (SFM) (see Angelstam et al. 2004c). Such an ecosystem management approach for protection and restoration requires planning at multiple scales (Hebert 2004). The approach used in most planning systems for large-scale forestry is hierarchical within a forest management unit (Jonsson et al. 1993, Higman et al. 1999, Davis et al. 2001). The planning process is usually divided into three sub-processes: strategic planning to decide long-term goals covering an entire rotation, tactical planning to select among different alternatives within the strategic goals but on a shorter time horizon, and operational planning to manage actual operations within a year. This same logic can be applied to planning for conservation and restoration of biodiversity (e.g. Angelstam et al. 2003, Lazdinis and Angelstam 2004). Landscape management should be based on ecological targets to which measurements of biodiversity could be compared with increasing detail and at different spatial scales (Higman et al. 1999, Angelstam et al. 2004d). Gap analysis (e.g. Scott et al. 1996) and landscape planning (Fries et al. 1998) are two examples.

Gap analysis aims to identify the most endangered and the most rare but ecologically valuable types of habitats (Perrera et al. 2000). At this strategic level, the focus is on the shortfall in the amount of the different forest types that are needed in the long-term to maintain viable populations of the naturally occurring species that cannot survive in the conventionally managed landscapes within an ecoregion. Questions to ask include what are the long-term needs for protected areas to maintain viable populations of species of concern in different forest types? How much of those forest types exist and how well are they protected? Is there a need for restoration or rehabilitation of habitats?

When a gap analysis has identified the various forest types in short supply within an ecoregion, the spatial distribution of those types must be evaluated as to the extent to which they provide functional networks of habitat for species dependent upon them. Landscape planning can be supported by spatially explicit habitat modelling which combines cover data with the requirements of specialised species to build maps describing the probability that a species is found in a landscape (e.g. Scott et al. 2002, Store and Jokimäki 2003, Suchant and Braunisch 2004). A habitat model for a given species requires data for land cover type(s) constituting habitat, habitat patch size, landscape-scale proportion of suitable habitat, and habitat duration. With adequate habitat models for several carefully selected focal species, a picture can be drawn of landscape functionality. This requires quantitative information on the habitat requirements of the several species at different scales. Ini-

tially, the proportion of sufficiently large patches in a landscape can be used as surrogate for connectivity (Fahrig 2001, 2002, Scott et al. 2002). Patch duration is also important; if patches are ephemeral, the landscape must be large enough to contain a stable proportion of patches of this type (Pickett and White 1985).

Different forest types are variably represented in the current network of protected areas in the Baltic region. When comparing the amount of protected areas with result of for example the Estonian gap analysis (Lõhmus et al. 2004), the BFM results clearly establish that there is need for additional protection of certain forest types in order to attain an ecologically adequate and representative network of forest protected areas. Maintenance of biodiversity in commercial forests can be carried out through management, where the biologically most valuable areas are set aside, or managed as appropriate. BFM is also a useful tool for identifying forest areas where forests restoration is needed.

Finally, the BFM map and methodology can also be used in the forest certification process, particularly in locating High Conservation Value Forest (HCVF) defined by the FSC certification system. All state forests in the Baltic region are certified or becoming so, and the certification of many private forests is underway.

The Baltic States as a biodiversity hotspot in northern Europe

Based on BFM results, and supported by other studies (Tucker and Heath 1994, Puumalainen 2001, Mikusiński and Angelstam 2001, Angelstam et al. 2004b), Baltic forests still host relatively high biodiversity conservation values compared to many other European countries. This is reflected well for birds where the region's forests are important to many specialised focal species, with viable populations of e.g. black stork *Ciconia nigra*, lesser spotted eagle *Aquila pomarina*, capercaillie *Tetrao urogallus*, and a diverse woodpecker Picidae fauna (Mikusiński and Angelstam 1998, Rosenvald and Lõhmus 2003). Many of these species are extinct or declining in other parts of Europe. For example, Lithuania's forests cover < 1% of Europe, but host 7 and 10% of the black stork and lesser spotted eagle world populations, respectively (Raudonikis and Kurlavicius 2000).

On the other hand, the high current logging levels in the region are a major threat to these values. The BFM database is potentially a very helpful tool in establishing new as well as expanding existing forest protected areas, and for developing sustainable forest management in commercial forests. In the case of as yet unprivatised forests, which make up nearly a third of all the forests in the region, the BFM database can be used to identify the most valuable sites and arrange for them to be bought for conservation or exchanged for other forests of similar economic but less biological value. A regularly updated BFM database could form the basis of nation-wide plans for a representative and functional network of protected forest areas as a part of the development of sustainable forest management.

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The role of Geographical Information Systems and Optical Remote Sensing in monitoring boreal ecosystems

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Young, J. E. and Sánchez-Azofeifa, G. A. 2004. The role of Geographical Information Systems and Optical Remote Sensing in monitoring boreal ecosystems. – Ecol. Bull. 51: 367–378.

The boreal forest is being impacted by human activity, primarily forestry and oil and gas exploration. The goal of this review is to provide an overview of the role that Geographical Information Systems (GIS) and satellite remote sensing play in monitoring boreal ecosystems, and to review some of the current issues being studied in the boreal region using these technologies. We find that investigation into the dynamics of land-use and land-cover change is greatly enhanced through the use of GIS and remote sensing. GIS offers the capacity for integrating spatial data of different types, including both raster and vector data models. GIS also allows for the analysis of landscape structure and response to habitat loss and fragmentation. This capacity will be crucial to monitoring the impacts of forestry and other industry in the boreal forests as the degree of disturbance increases, and to planning long-term sustainable use of the forest. Remote sensing is the only feasible method for the acquisition of land-cover data over large areas, and is well suited to regional mapping of land-cover and land-cover change detection. Vegetation indices derived from satellite imagery are useful for characterization of forest biophysical properties. There are certain limitations to these technologies however. Due to the susceptibility of spatial data manipulation to error propagation, there is need for increased focus on sensitivity analysis. The utility of data sets derived from remote sensing is limited by the spatial and spectral resolution of currently available sensors. The capacity to gather information over large areas and perform spatial analysis greatly enhances our ability to study the large-scale patterns and processes of the boreal such as natural and human disturbance, and to make predictions about the future as human impacts on the boreal increase.

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Land-use and land-cover change (LUCC) has a significant impact on global environmental change (Houghton 1994). Patterns and extent of biodiversity, carbon, water, and energy fluxes, erosion rates, and many other such phenomena are directly influenced by LUCC (Ojima et al. 1994, Debinski and Holt 2000). It has been estimated that the effects of land-use changes have contributed as much as 25% to the increase in atmospheric carbon dioxide which in the last 100 yr has risen to over 350 ppm, as well as contributing to the increased emission of other atmospher-

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ically active gasses and particulates (Houghton 1994, Ojima et al. 1994). Long term climatic changes, such as those predicted by the increase of atmospheric greenhouse gasses could be severely disruptive to the boreal forests (Singh and Wheaton 1991). Forestry is the primary agent of LUCC in the boreal, causing changes in age-class structure, loss of specialist habitat, and changing disturbance regime (Schmiegelow and Mönkkönen 2002).

The increased level of forestry is also leading to habitat fragmentation and isolation in the remaining forested areas. Fragmentation can affect ecosystems at many levels, from local population dynamics and successional community development to long-term species depletion (Robinson et al. 1992, Fahrig 1997, Bolger et al. 1997, Stuart-Smith et al. 1997). It has been shown that edge effects including but not limited to invasion by exotic species, extreme abiotic factors such as wind and temperature, and ecological processes such as nutrient cycling can penetrate up to 300 m into remaining patches (Debinski and Holt 2000). This indicates that the quality of the buffer zone surrounding a natural area has a large impact on the ecology within, especially in terms of ecosystem isolation and biodiversity. Information on the forces driving changes is needed in order to set up programs of sustainable management for the boreal forest.

Any program of sustainable management of the earth's natural resources depends on a solid understanding of LUCC and its impact. However, current LUCC studies have been limited by lack of data on natural and anthropogenic variables and problems utilizing empirical data. To fully understand the causes and impacts of LUCC, analysis must cover a range of spatial and temporal scales, bio-physical processes, and human variables such as the socio-economic forces that drive land-use changes (Ojima 1994, Skole et al. 1994). Few comparable studies have been conducted in boreal regions. Studies of land-cover change in boreal ecosystems have mainly focused on the release of carbon dioxide through forest fires and deforestation (Sellers et al. 1995, Li et al. 2000a, Michalek et al. 2000).

Canada and Russia together contain almost half of the world's remaining intact forest, making the boreal forest a highly significant ecosystem on a global scale (Bryant et al. 1997). While deforestation in the tropics has received much media attention, deforestation rates in some parts of the boreal have actually exceeded those in Amazonia, reaching rates of 0.91% yr^{-1} (Anon. 1998). The cumulative impacts of land-cover changes due to human land-use and global climate changes will likely reduce the biodiversity of the boreal forest (Schneider 2002). Cumulative impact is a synergistic phenomenon, in which the total impact on the ecosystem is greater than the sum of the individual disturbances. Schindler (2001) outlines several scenarios in which global warming acted synergistically with other human impacts in Canadian freshwaters. For example, over-fishing and direct habitat destruction combined with habitat degradation due to global warming are causing the decimation of populations of carnivorous fish species such as lake trout *Salvelinus namaycush* in many boreal lakes (Schindler 2001).

The degree of human influence in the boreal is unevenly distributed over the globe. In Scandinavia the amount of remaining intact boreal forest is quite small, making the restoration of habitat the primary issue (Angelstam and Andersson 2001, Angelstam et al. 2004a). In contrast, in Canada and Russia, the cumulative impacts are currently of a lower magnitude, but accelerating, creating a need for conservation of the remaining intact boreal habitat (Yaroshenko et al. 2001, Angelstam et al. 2004b). In the boreal forest, cumulative impacts are a result of the combined impacts of forestry, agriculture, oil and gas exploration and development (cutting lines for seismic exploration, pipelines, heavy oil extraction), climate change, and changes in the fire regime (Schneider 2002).

Forestry is a major economic factor in Canada, and changes in the boreal forest due to climate change could have serious impacts on the industry. Planning is essential for continued boreal forestry (Singh and Wheaton 1991). The forestry industry is beginning to realize that mimicking natural patterns in forest management is essential in maintaining the integrity of the boreal forests (Bondrup-Nielsen 1995, Angelstam 1998, Axelsson and Östlund 2001). Practices such as green-tree retention and fire management are being investigated as possible means of maintaining both biodiversity and long-term forest productivity (Bondrup-Nielsen 1995, Angelstam and Andersson 2001, Axelsson and Östlund 2001). However, it has been shown that forestry, even when carefully planned to mimic fire patterns, cannot fully reproduce the early post-fire seral stage in the boreal (Song 2002). Mechanical forestry causes significant alterations to the post-disturbance soils and plant communities, with the effect of eliminating the early post-fire stage from managed areas (Song 2002). Preservation of the quality of the whole landscape is thus very important (Fahrig 2001).

Because forests are intensively used for commercial purposes, different types of forest inventory systems have been developed to produce information on forest resources, health of forests and biodiversity of forests at national and regional levels. Nowadays, these systems also utilize satellite remote sensing in various countries (Wulder 1998, Gillis 2001, Shvidenko and Nilsson 2002, Reese et al. 2002, Tomppo et al. 2002, Tuominen et al. 2003). As the cumulative impacts of human and natural disturbances alter the boreal region, it is important to be able to monitor the changes in the biophysical land-cover. This includes assessment of current conditions, and quantification of changes in landscape composition and patterns.

The capabilities of Geographical Information Systems (GIS) for landscape structure analysis and remote sensing for obtaining land-cover data over large areas of inaccessible terrain has been, and will continue to be, valuable in studying the boreal biome. While other reviews of GIS and

remote sensing in the context of boreal forest ecosystems already exist, focus had primarily been on applications to the forestry industry (Jaakkola et al. 1988, Næsset 1997, Holmgren and Thuresson 1998, Wing and Bettinger 2003). The goal of this paper is to provide an overview of how GIS and satellite remote sensing are used as tools to monitor land-cover in the boreal biome, and review some of the current issues being studied using these technologies.

The boreal biome

The boreal biome forms a nearly continuous band around the Northern Hemisphere, covering large areas of Alaska, Canada, Fennoscandia, and Russia. It is centered around 60°N, but extends to over 70°N and under 50°N in some areas (Bonan and Shugart 1989). The northern and southern boundaries of the boreal are roughly coincident with the summer and winter front that marks the southern limit of the Arctic air mass (Bonan and Shugart 1989). The boreal is bordered on the north by tundra, and on the south by temperate forest in coastal regions or grasslands in continental areas (Apps et al. 1993). The boreal covers ca 1.3–1.5 10^9 ha (Bonan and Shugart 1989, Apps et al. 1993, Dixon et al. 1994). This represents one third of the global forest area (Dixon et al. 1994), and 11% of the land surface area (Bonan and Shugart 1989, Michalek et al. 2000).

The majority of the boreal region is characterized by extreme summer-winter differences in climate. Summers are generally short, warm and moist, with the long winters being dry and very cold. Mean monthly temperature can vary by as much as 56°C between summer and winter, particularly in the continental climates of interior Alaska and Siberia, and the difference between seasonal extremes can be up to 100°C (Bonan and Shugart 1989). Annual precipitation varies regionally, from as low as 130 mm yr^{-1} in parts of northeastern Siberia too as high as 890 mm yr^{-1} in eastern Canada (Bonan and Shugart 1989).

The boreal has developed its present form since the retreat of the glaciers some 15 000 yr ago (Weber and Stocks 1998). Details of post-glacial species composition have been derived from, e.g., lake-bed pollen records (Davis 1969). These pollen records indicate that species composition changes and migration of eco-zones have occurred on a variety of time scales. Broad changes in vegetation have occurred in the order of thousands of years in response to mean climate variation (Davis 1969). There have also been smaller, faster changes in response to century scale climatic variability such as the little ice age (Apps et al. 1993), and to recent decadal scale changes due to human interference in the fire regime (Kurz and Apps 1993). Boreal species are likely still migrating on a biome level in response to long-term climate change and small-scale climate fluctuations such as the little ice age (Apps et al. 1993).

The boreal forest has been evolving since deglaciation (Weber and Stocks 1998). Analyses of permafrost landforms show that the permafrost region reached its southern (Holocene) maximum during the Little Ice Age (ca AD 1250–1850). It is currently estimated that 22% (5813 km^2) of Canadian permafrost is in disequilibrium with the current climate (Vitt et al. 2000b). Analysis of Canadian boreal peatlands shows that peat began to accumulate 9000 yr ago (following a lag after deglaciation), and peatlands are still accumulating carbon, also indicating that an equilibrium has not yet been reached (Vitt et al. 2000a).

One of the most distinct characteristics of the boreal region is the complex and dynamic nature of its internal spatial arrangement. The boreal region consists of an intricate mosaic of forests and wetlands, driven by factors such as temperature, hydrology, substrate, insect outbreaks and fire (Bonan and Shugart 1989, Lenihan 1993, Fleming et al. 2002). While dominated by just a few tree species, the spatial heterogeneity of the boreal forest provides a wide variety of habitat types (Ustin and Xiao 2001). This mosaic pattern and the boreal forest's location along bird migration routes, allows it to support one of the highest levels of bird species diversity in North America (Schmiegelow et al. 1997). The boreal also hosts a large diversity of fungi, plants, insects, and other animals (Hanski 2000).

Fire is an important factor in boreal forest succession, as fire and insect outbreaks are the primary drivers of the pattern and species composition present (Weber and Stocks 1998, Fleming et al. 2002). An average of 2.4 million ha of boreal forest is burned annually in Canada, 22 million ha globally (Fraser et al. 2000b). Bonan and Shugart (1989) outline the importance of fire in the boreal forest. The fire cycle in the boreal forest ranges from 50 to 270 yr, averaging 110–155 yr. The majority of area is burned in a few large fires. Most (85%) of fires are < 4 ha, but some fires can be > 200 000 ha. Fire has impacts on ground-level thermal characteristics and nutrient cycling. Many species depend on fire for their continued presence in the boreal landscape. Post-fire succession depends on many factors including burn severity and pre-fire species composition. Post-fire colonization in the boreal may occur by several strategies, mainly wind-dispersed seeds, serotinous (fire-opened) cones, fire tolerance (in which individuals are not killed by fire), or vegetative reproduction (root and stump sprouting after a burn). Weber and Stocks (1998) and Angelstam (1998) also highlight the importance of fire in maintaining the complex pattern associated with the boreal forest. Fires burn different areas at different times and at different severity, leaving behind a complex mosaic of vegetation types and age classes. Species-level adaptations to fire were in place by the Pliocene (12 million yr BP), meaning that fire was already established as a dominant process in the boreal biome as the boreal forest re-colonized landscapes exposed by retreating glaciers (Weber and Stocks 1998).

The boreal forest plays a major role in the global climate and carbon budget, and an understanding of this role is crucial to our analysis of global warming. The boreal re-

gion is a significant carbon pool, with the total amount of carbon stored estimated to be between 559 and 709 Pg (1 Pg = 10^{15} g = 1 Gt) (Apps et al. 1993, Dixon et al. 1994). The carbon is stored in above ground biomass, soils, peat, and vegetation (Bonan and Van Kleve 1992, Apps et al. 1993). There is a significant flux of carbon between these pools and the atmosphere through fire, respiration/photosynthesis, and decomposition (Bonan and Van Kleve 1992, Apps et al. 1993). The overall source/sink status depends on the relative impact of changes in forested areas, carbon uptake by trees, carbon storage in soils, decomposition rates, fire regime and peat/permafrost dynamics (Bonan and Van Kleve 1992, Apps et al. 1993, Stocks et al. 1998, Vitt et al. 2000b). The boreal forest may currently be a sink for atmospheric carbon, however, this sink will become saturated over time due to reduced forest area and loss of permafrost (Kurz and Apps 1993, Weber and Stocks 1998).

Global warming is predicted to have an effect on the fire regime in the boreal due to warmer temperatures and increased evapotranspiration leading to drier forests more prone to burning, particularly in the forests of Siberia and Western Canada (Stocks et al. 1998). Examination of Canadian forest fire statistics shows that there has been an increase in both the number of forest fires (from ca 6000 fires yr^{-1} in the 1960s to 10 000 yr^{-1} in the 1980s and 1990s) and the total area burned per year in the last few decades (Weber and Stocks 1998). Increased fire in the southern boreal forest may be the means by which the southern margin of the boreal forest moves northwards, as boreal stands burn and are replaced with temperate grasslands due to the failure of boreal species to re-establish on the site (Weber and Stocks 1998).

On the other hand, fire suppression may also lead to degradation of the boreal forest. Fire is necessary for the maintenance of species and pattern, so its removal is ecologically unsound, and can lead to landscape degradation (Weber and Stocks 1998). Fire has been almost completely eliminated in Scandinavia, resulting in major changes to age-class distribution and virtual elimination of multi-aged stands (Axelsson and Östlund 2001). Fire still plays a major role in Canada and Russia, but fire suppression is altering the age-class structure here as well (Kurz and Apps 1993). The amount of early post-fire habitat (as well as pristine older forest) is drastically reduced in areas of active forest management, leading to reduced available habitat for habitat specialists (Schmiegelow and Mönkkönen 2002).

The boreal biome is particularly sensitive to global warming due to its location and ecology (Singh and Wheaton 1991, Lenihan 1993). In fact the largest changes in mean annual temperature have been recorded in the boreal. Since 1900 the global mean temperature has increased by 0.6±0.2°C (Anon. 2001), whereas western Canada has increased by as much as 1.5°C, primarily manifested as warmer winter lows (Zhang et al. 2000). On a global scale, the largest temperature increases have been in the continental regions of the Northern hemisphere, primarily in northwest Canada and northwest and northeast Russia, with anomalies as high as +4°C (Anon. 1997). This means that large regions of the boreal forest will likely experience much greater warming than the global mean. The responses to global warming will manifest as changing fire regimes, northward migration of the boreal biome, and changes in permafrost distribution (Bonan et al. 1990, Lenihan 1993, Kellomäki and Väisänen 1997, Camill and Clark 1998, Li et al. 2000a, b, Michalek et al. 2000, Vitt et al. 2000a, b, Bielman et al. 2001). Some areas that are currently tundra may become forested at the northern fringe of the boreal, but at the same time in the south forest areas may be lost, becoming grassland (Apps et al. 1993). The response of the boreal forest to global warming is likely to be non-linear (Apps et al. 1993), making precise estimates of the impact difficult.

Land use/land cover change and the boreal forest

The most obvious and direct impact that humans are having on the boreal biome is the conversion of natural habitats to human use, and the fragmentation of the remaining natural habitat (Schmiegelow and Mönkkönen 2002). This is mainly happening through the conversion of natural lands (forest or grasslands) to agriculture or pasture, urban and road network expansion, alteration of forest composition by forestry or other resource extraction, and cutting of seismic lines for oil and gas exploration (Schmiegelow et al. 1997, Stuart-Smith et al. 1997, Wiersma 2001, Axelsson and Östlund 2001).

In the boreal, habitat loss and fragmentation are primarily caused by forestry and oil exploration, with agricultural disturbance generally limited to the southern fringe (Schmiegelow and Mönkkönen 2002). The total forest cover remains relatively constant with forestry, but there are qualitative changes such as alteration of the age class distribution (Schmiegelow and Mönkkönen 2002). Agriculture reduces the amount of forest cover on a more permanent basis, as well as introducing community alterations and higher predation rates at agriculture edges which do not occur at clear cut edges (Bayne and Hobson 1997, Hannon and Cotterill 1998).

Recent studies indicate that habitat loss is the most critical factor in explaining the loss of species, and more specifically that below certain levels of remaining habitat, species begin to go locally extinct. This relationship has been shown both theoretically and in the field (Fahrig 2001, Wiersma 2001, Schmiegelow and Mönkkönen 2002). Fahrig (2001) has modeled theoretical responses to habitat loss, and found that habitat loss is the key factor in extinctions (much more important than fragmentation), often with a distinct threshold around 20% remaining habitat. Schmiegelow et al. (1997) found that fragmentation ef-

fects can be mediated by the total amount of habitat in the area. A further study by Schmiegelow and Mönkkönen (2002) confirm that most species' decline is the result of pure habitat loss.

Once the threshold for remaining habitat is reached, fragmentation begins to play a role in the loss of species. The effects of fragmentation depend on landscape factors such as patch size and shape, connectivity, time since fragmentation, amount of remaining habitat and species-specific biological factors (Schmiegelow et al. 1997, Franklin et al. 2000). As well as the direct impacts of fragmentation on a given species, there are also indirect impacts such as the effects of changing community dynamics as e.g. the increased proportion and/or effectiveness of generalist predators in fragmented landscapes (Schmiegelow et al. 1997, Brooks et al. 1999, Kurki et al. 2000, Schmiegelow and Mönkkönen 2002).

Time since fragmentation has been shown to be important both theoretically and empirically, meaning that multi-temporal remote sensing analysis is critical. Models of habitat fragmentation effects indicate delayed responses to habitat loss (Fahrig 2001). Field studies of boreal birds have also shown sensitivity to the amount of time passed since fragmentation (Schmiegelow et al. 1997). This is related to the concept of extinction lag, the delay between destruction of a species' habitat and its extinction. The length of lag depends on the amount of habitat. The extinction will be slower if the amount of remaining habitat is close to the critical threshold.

Geographical Information Systems (GIS) applied to boreal forests

A Geographical Information System (GIS) is a "…set of tools for collecting, storing, retrieving at will, transforming and displaying spatial data…", with data involving position, attributes, and spatial interrelations (Burrough and McDonnell 1998: 11). Geographical Information Systems are used for a wide variety of applications, including marketing, social studies, archaeology, urban planning, and studying the environment (Burrough and McDonnell 1998). As the ecology of the boreal biome is particularly influenced by spatial and temporal patterns, the utilization of GIS is immensely valuable.

Geographical Information Systems are very flexible in their ability to make use of a wide variety of data. Land-cover information is often derived from remote sensing – either air-photos or satellite images (Flannigan and Vonder Haar 1986, Halsey et al. 1995, Rauste et al. 1997, Brooks et al. 1999, Franklin et al. 2000, Fraser et al. 2000a, b, Li et al. 2000a, b, Michalek et al. 2000, Bielman et al. 2001). Other types of land-cover information (especially past conditions) are often input into the GIS through digitized cadastral or land-cover maps, maps of other spatially-varying phenomena (i.e. peat depth), and digital elevation models (DEMs) (Vitt et al. 2000a, b, Cousins 2001, Axelsson and Östlund 2001, Ustin and Xiao 2001, Angelstam et al. 2003a, 2004a). Data can also be produced through a wide variety of spatially-explicit models, such as General Circulation Models (GCMs), other climate/ecological models, linear programming/forecast modeling, cellular automata, and population dynamics/movement models (D'Arrigo et al. 1987, Lenihan 1993, Bondrup-Nielsen 1995, Bonan et al. 1995, Kellomäki and Väisänen 1997, Stocks et al. 1998, Hanski 2000, Cousins 2001, Fahrig 2001). Other forms of data commonly incorporated into integrated GIS-remote sensing projects include cadastral/geopolitical data such as political boundaries or land-use classes (Luque 2000a, b) or other forms of spatial information such as point data (e.g. from GPS) (Stuart-Smith et al. 1997).

GIS has traditionally been used primarily for the manipulation of vector data (points, lines, and polygons), but the development of integrated systems capable of handling raster data (pixelated images) has been beneficial for the study of the natural environment (Hinton 1996, Wilkinson 1996). For example, incorporation of a digital elevation model (DEM) into an image classification scheme can improve the classification results by accounting for factors such as slope, aspect, and solar radiation in regions of high relief (Giles et al. 1994).

The spatial analysis capabilities of GIS have promoted an explosion of interest in the role that landscape structure plays in ecosystem processes, such as species-level responses to landscape pattern in the boreal forest (Stuart-Smith et al. 1997). GIS offers the capacity to quantify spatial phenomena such as pattern, fragmentation (and other disturbances), and thresholds through the calculation of landscape metrics or indices (Hargis et al. 1998).

One of the ways that landscape structure is quantified is through the calculation of landscape indices – numbers calculated from measurable components of the landscape such as lengths and areas (Hargis et al. 1998). Indices such as diversity, proximity, dominance, contagion, fractal dimension, and shape index attempt to measure independent qualities of landscape structure that can be related to ecosystem function (Turner et al. 1989, Gustafson and Parker 1992, Schumaker 1996, Hargis et al. 1998). New indices are being developed all the time (e.g. Schumaker 1996, Jaeger 2000), some of which could (or might not…) prove to be useful for quantification of the critical spatial elements of the boreal forest. Indices, while attempting to measure spatial quantities, are themselves sensitive to factors such as land-cover proportion and scale (Turner et al. 1989, Turner 1990, Gustafson and Parker 1992, Cain et al. 1997). These indices are generally interrelated, as they are based on a finite number of measurable quantities which can be measured from data sets in a GIS (Hargis et al. 1998).

The study of habitat fragmentation has been particularly active, in order to analyze the negative impact that human activity is having on the boreal forests, and the effect

of landscape patterns on species (Bayne and Hobson 1997, Schmiegelow et al. 1997, Roberts et al. 2000). Recently, research has been shifting to modeling the relative effects of fragmentation vs pure habitat loss (Fahrig 1997, 2001, Schmiegelow and Mönkkönen 2002). GIS and spatial modeling are also being used to examine threshold effects in habitat loss and fragmentation (Fahrig 2001, Angelstam et al. 2003b). This would imply a non-linear response of populations – meaning that while effects of habitat loss and fragmentation are initially low, sudden changes could occur with further degradation (Mönkkönen and Reunanen 1999).

The dependence of species on the amount of habitat should raise some concern, as the amount of remaining intact forest in the boreal is much less than one might suppose. In Russia there remains ca 13%, 5% in Sweden, and 1% in Scotland (Angelstam 2001). A recent study in western Russia by Yaroshenko et al. (2001) found that only 14% of the boreal forest (31.7 million ha) remains in large undisturbed patches. This study utilized GIS coverages of roads (buffered to 100 m) to locate areas without human infrastructure, and then within these areas used satellite imagery to further eliminate areas with signs of human impact such as clear cuts. All of the remaining areas > 50 000 ha were considered intact. A similar GIS analysis was done for Canada by the World Resources Institute (WRI) (Bryant et al. 1997). This study found that there are 321 million ha of forest in Canada in blocks > 50 000 ha including all forests in Canada, not just the boreal. This represents 77% of Canada's 417.6 million ha total forested area (Anon. 2002). This study and a similar one done by Nogueron et al. (2002) did not use satellite imagery to validate land-cover or eliminate areas with signs of human activity, and could represent an overestimation of the amount of forest that is actually intact. A much more detailed study in Alberta, Canada, found that only 9% of the townships (one township equals 6×6 miles, or 93 km^2) in the Boreal Forest Natural Region remain as wilderness, with no wells, linear disturbances, or other human structures (Anon. 1998). Three quarters of the townships contained well sites, and 26% contained logging on public land. The study also found that only 14% of Alberta's boreal remains as "core" habitat, and emphasizes that these figures very likely overestimate the amount of pristine habitat (Anon. 1998).

In fragmentation studies, factors such as time since fragmentation and patch size are frequently determined by the analysis of aerial photographs and satellite images using GIS (Brooks et al. 1999, Kurki et al. 2000). The fragmentation analysis often utilizes data layers such as classifications or change images (Franklin et al. 2000). GIS is very useful for calculating landscape indices, which quantify the landscape structure through metrics based on quantifiable properties such as area, edge, shape, and spatial relationships. These metrics are sensitive to many parameters including scale, raster orientation, pixel size, minimum mapping unit, and number of classes, and the chosen metric must be ecologically relevant (Franklin et al. 2000). Analysis of satellite images through the use of landscape metrics can be a very effective means of determining landscape structure. Landscape structure is the spatial arrangement of those components of the landscape that can be differentiated from one another, and hence mapped (Franklin et al. 2000).

GIS can be used for determining future landscape patterns, so that forestry can be planned to maintain inherent patterns (Bondrup-Nielsen 1995, Kangas et al. 2000). Planning tools such as GIS and modeling with expert knowledge offer much potential for multi-objective optimization (objectives such as ecological integrity and timber supply, for example), but are currently under-utilized (Kangas et al. 2000). Boutin and Hebert (2002) show how GIS can be a vital link between the theories of landscape ecology and the practice of forestry. GIS and spatially explicit landscape projection models allow foresters to predict the outcome of different management practices in terms of the amount of remaining habitat and patch configuration, and choose the most appropriate actions in order to balance commercial value with ecological functioning of the landscape (Boutin and Hebert 2002).

The use of GIS is being explored by the forest industry to analyze the natural patterns in the boreal forest, so that these patterns may be imitated by forest managers (Bondrup-Nielsen 1995, Axelsson and Östlund 2001). In Sweden, historical maps have been analyzed in a GIS to perform a spatio-temporal (gap-analysis) study of forest patterns (Axelsson and Östlund 2001). Where the forests are intensively managed, clear-cutting has entirely replaced fire as the primary pattern-setting regime. Old-growth forest is fragmented and depleted, and mixed-age stands are missing (Axelsson and Östlund 2001). Landscapes where forestry is the principle land-use are highly dynamic. Forestry practices tend to change forest composition, mainly reducing old (over 80 yr) and early post-fire successional stages while not changing the total amount of forest cover (Schmiegelow and Mönkkönen 2002).

GIS and spatial modeling have given insights into the means for conserving biodiversity. For example in Finland a spatially explicit model was used to examine conservation strategies (Hanski 2000). It was shown that concentration of conservation efforts on specific areas is more effective than weaker but more widespread measures, and that the best use of resources is to restore to "near-natural" areas close to remaining high-quality stands, facilitating migration to restored areas (Hanski 2000). In Canada, GIS has been used to analyze the National Parks system. Wiersma (2001) found that the size of a park is the most critical factor in its ability to conserve biodiversity, and that the minimum reserve area required is on the order of 10 000 km^2. Even parks larger than this threshold have been found to have lost biodiversity, however, due to the effects of human infrastructure in and around the parks.

One of the major limitations to the use of GIS is the issue of error and error propagation. As well as introducing new errors, the handling and manipulation of spatial data will tend to compound errors already existing in the data set, making it desirable to incorporate error estimates and sensitivity analysis (Næsset 1997).

Remote sensing applied to boreal forests

Remote sensing includes any method for deducing the properties of an object without physical contact (Nieke et al. 1997). This is normally done through the collection and recording of emitted or reflected electromagnetic radiation (Slonecker et al. 1998). Air-photos and satellite images are the principle forms of remote sensing utilized in studying boreal ecosystems (Table 1).

Aerial photography is still cheaper than satellite imagery, and offers higher spatial resolution and more flexibility in repeat coverage. However, air photos typically cover a much smaller area than satellite images, and raise the problem of dealing with a large number of images if a large area is being studied. Aerial photos have been extensively used by the lumber industry for forest inventory purposes (Bolduc et al. 1999). Land-cover inventories such as the Alberta Vegetation Inventory (AVI) use air photo interpretation.

Satellite images of the earth have only been widely available since the 1970s with the launch of the first Landsat satellite in 1972 (Nieke et al. 1997), but have quickly become one of the most influential tools for monitoring global ecosystems due to the capacity for imaging large areas (Kasischke and French 1996). Multi-spectral satellite systems make use of reflected electromagnetic (EM) radiation from the earth, in the visible (VIS) to infrared (IR) portions of the spectrum (0.4 to 12 mm) (Nieke et al. 1997). Three satellite series have dominated the remote sensing market through the last few decades – the Landsat MSS (Multi-Spectral Scanner, 80 m resolution, 4 spectral bands) and TM (Thematic Mapper, 30 m resolution, 7 spectral bands) series and the National Oceanic and Atmospheric Administration's Advanced Very High Resolution Radiometer (NOAA's AVHRR, 1.1 km resolution, 2 spectral bands) (Sader et al. 1990, Kasischke and French 1996, Nieke et al. 1997). Applications of radar imagery for ground-cover characterization in boreal forests are covered in Rees et al. (2002), and will not be discussed in this paper.

One of the primary uses of multi-spectral imagery is for mapping land-cover and land-cover changes. Land-cover classification is a form of data generalization, in which an image is subdivided into classes or categories (Martínez-Casasnovas 2000). The two most common methods of classification are supervised and unsupervised classification (Martínez-Casasnovas 2000). In unsupervised classification a computer algorithm sorts the pixels into classes of similar spectral composition (Tou and Gonzalez 1974). Supervised classification introduces user knowledge into this process, by choosing "training sites" whose spectral signature is used to define a specific class (Martínez-Casasnovas 2000). Examples of the use of image classification from the boreal are the mapping of vegetation classes for the purpose of identifying human-induced landscape changes, and identifying distribution and carbon release through fire (Rees and Williams 1997, Rauste et al. 1997, Luque 2000a, b, Li et al. 2000a, b, Michalek et al. 2000).

Change detection plays a key role in ecosystem monitoring and many techniques for detecting differences between images taken at different times have been developed, many of which build upon more basic GIS and remote sensing techniques (Singh 1989, Mas 1999). The simplest change detection techniques are image differencing and

Table 1. Common remote sensing platforms used for boreal research. Reference list is not exhaustive.

Sensor	Resolution	Uses	References
Air Photos	variable	Land-cover mapping	Beilman et al. 2001, Cousins 2001, Halsey and Vitt 1995, Vitt et al. 2000a, b
LI-COR LAI 2000	–	LAI measurement	Chen 1996, Chen et al. 1997, Deblonde et al. 1994
Landsat ETM+	30 m	LAI mapping	Eklundh et al. 2001
Landsat TM	30 m	Land-cover mapping	Franklin et al. 2001
		Land-cover change	Franklin et al. 2000
		Fire monitoring	Michalek et al. 2000
Landsat MSS	80 m	Land-cover/change	Luque 2000a, Rees and Williams 1997
CASI	2 m	LAI mapping	Fernandes et al. 2002
AVHRR	1.1 km	Fire monitoring	Flannigan and Vonder Haar 1986, Fraser and Cihlar 2000, Li et al. 2000a, b
		Land-cover mapping	Kasischke and French 1996
SPOT	1.1 km	Fire monitoring	Fraser and Landry 2000
		DEM/land-cover mapping	Giles et al. 1994
AVRIS	20 m	Land-cover mapping	Ustin and Xiao 2000

image ratioing, which involve subtraction or division of multi-temporal image pairs (Singh 1989). A similar method is vegetation index differencing, in which a vegetation index image is formed for each date and the results subtracted (a vegetation index is a ratio of spectral bands aimed at enhancing spectral differences between vegetation types). Principal components analysis (PCA) change detection uses two bands of a multi-date image. Common information is mapped to one component while information unique to one band is mapped to another component. Multi-date classification can be done on a composite multi-temporal image directly, assuming that "change" classes will be spectrally different from non-change classes (Singh 1989). Direct comparison of images is improved by atmospheric correction (Song et al. 2001).

Post-classification analysis is becoming the preferred change detection technique (Mas 1999). In this method, sequential images are classified independently, and the resulting classified images are compared (Singh 1989, Mas 1999). The drawback of this method is the compounding of errors created in the image processing, but advances in data accuracy have reduced the significance of this problem (Singh 1989, Mas 1999). The advantage of post-classification analysis is the ability to resolve not only that change occurred, but also the identity of the pre- and post-change class. Image classification can also allow for change detection through landscape metrics, highlighting not only the change in land-cover, but in landscape structure as well (Franklin et al. 2000). Change detection techniques have been used in a large number of change studies in the boreal, including studies on fires and vegetation changes (Rees and Williams 1997, Michalek et al. 2000).

Spectral vegetation indices provide the most direct means of extracting useful data from remotely sensed images (Peddle et al. 2001). In order to highlight specific qualities of the ground cover, a variety of vegetation indices have been developed that utilize the different information contained in different wavelengths. In their simplest form, a spectral vegetation index is just a specific combination of image bands that highlights a particular property of the scene. Ratio-based indices are common as they are good for discriminating vegetation cover, above ground biomass, Leaf Area Index (LAI), and other such biophysical properties (Lawrence and Ripple 1998, Peddle et al. 2001). These indices take advantage of the fact that green plants reflect more strongly in the near infrared (NIR) than in the red (Teillet et al. 1997). This is directly measured by the "simple ratio" (SR), which is calculated by dividing the reflectance in the NIR by that in the red (NIR/RED). There are more complex variations such as the green vegetation index (GVI) which is based on a linear combination of six bands, and orthogonal based indices that are based on soil lines or other pre-known properties of the scene (Lawrence and Ripple 1998). Chen (1996a) and Peddle et al. (2001) have examined common indices and biophysical properties that are estimated from indices.

The most common index is the normalized difference vegetation index (NDVI), which is calculated as (NIR–RED)/(NIR+RED). There is a whole family of related indices that adjust for % ground cover, local soil line, or other parameters (Teillet et al. 1997, Lawrence and Ripple 1998). In the boreal forests the NDVI has been used to detect changes in vegetation quality such as water stress in forest canopies (Carter 1998). Indices have also been used to attempt to estimate biophysical variables for the forest such as LAI, biomass, and net primary productivity (NPP) (Peddle et al. 2001).

Leaf Area Index is a very important variable for models that emulate carbon and hydrological cycles, and directly relates to the exchange of water, carbon and energy in the ecosystem (Gower et al. 1999). It is a measurement of the area of leaf surface per unit of ground surface area. There are optical sensors for estimating LAI (such as the Li-Cor LAI 2000), and it can also be estimated from satellite images allowing for regional LAI mapping (White et al. 1997). There is some difficulty in measuring LAI in conifers by optical methods, which could have consequences for modeling boreal carbon cycles (Gower and Norman 1991, Deblonde et al. 1994, Eklund et al. 2001). Combining optical methods with shoot sample analysis shows promise for increased accuracy (Chen 1996b). Methods for determining LAI of the deciduous component of the boreal forests are also being investigated (Chen et al. 1997).

Although vegetation indices are widely used and they provide important information, the use of vegetation indices also have some limitations. Vegetation indices are not very accurate for separating functionally different vegetation assemblages that might have different response to e.g. climate change. Vegetation indices such as NDVI have proven to be poor indicators for taiga where coniferous trees dominate. Vegetation indices are also strongly phenology dependent, i.e. index values change over the growing season (Rees et al. 2002).

Increased density of fires will have an impact on boreal forest succession and on global carbon budget (Michalek et al. 2000). Satellite imagery and GIS are the best way to monitor fire in the boreal (Flannigan and Vonder Haar 1986, Rauste et al. 1997, Fraser et al. 2000a, b, Li et al. 2000a, b, Michalek et al. 2000). There are a variety of methods for detecting fires and calculating area burned using satellite images and GIS (Rauste et al. 1997, Fraser et al. 2000a, b). These methods utilize a variety of remote sensing data types such as thermal imaging to detect heat from fires, and visible and near-infrared imaging to determine changes in vegetation (Fraser et al. 2000a, b, Michalek et al. 2000). Satellites are particularly valuable in remote areas where it would be otherwise impossible to determine fire activity (Flannigan and Vonder Haar 1986).

The Boreal Ecosystems Atmosphere Study (BOREAS), from 1993 to 1996, was aimed at improving the current understanding of exchanges of energy, water, carbon, and trace gasses between the boreal forest and the atmosphere

(Sellers et al. 1995). Several seasons of data collection using ground and aircraft based measurements and satellite imagery has been the basis for a variety of studies investigating the interactions between climate, carbon sequestration, gas exchange and interactions, and temporal variability in the boreal forest (Frolking et al. 1996, Chen et al. 1999, Potter et al. 2001, Clein et al. 2002). These studies are improving our understanding of the role of the boreal forest in the global carbon budget, and hence its role in global warming.

As Jaakkola et al. (1988) have outlined, satellite remote sensing is well suited for tasks including land-use/land-cover classification, monitoring major changes in forest resources, and estimating forest class distribution. There are, however, limitations to the use of satellite remote sensing, primarily due to limitations of the spatial and spectral resolution of the sensors. The combination of deficiencies in spatial and spectral resolution can lead to problems including edge and mixed pixel effects, limitations in classifying forest structure and canopy species, and inability to produce spatial data products at a scale suitable for local forestry applications (Holmgren and Thuresson 1998). There are also limitations related to the availability of images. Acquiring time series in boreal regions is limited, since clouds often cover large areas of the image. Satellites also do not revisit all the areas every day, but rather in certain intervals. Taken together, constructing e.g. a time series of the same growing season for a given area is often difficult (Holmgren and Thuresson 1998).

Conclusions and future directions

GIS and optical remote sensing are important tools for monitoring the boreal forest. The boreal is highly dynamic, with complex patterns and huge areas. The capacity to gather information over large areas and perform spatial analysis greatly enhances our ability to study the large-scale patterns and processes of the boreal such as natural and human disturbance, and to make predictions about the future as human impacts on the boreal increase. Cihlar (2000) recommended that the priorities for satellite based land-cover classification should be to improve image preprocessing and classification techniques. This will enable us to take full advantage of new sensor developments including improved calibration, resolution, spectral range, and locational accuracy. Development of GIS methodology is also critical, especially in terms of improved spatially explicit modeling (Næsset 1997). These improved techniques will help to meet the increasing demand for information necessitated by our growing awareness of global environmental issues.

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Indicator species and biodiversity monitoring systems for non-industrial private forest owners – is there a communication problem?

H. Uliczka, P. Angelstam and J.-M. Roberge

Uliczka, H., Angelstam, P. and Roberge, J.-M. 2004. Indicator species and biodiversity monitoring systems for non-industrial private forest owners – is there a communication problem? – Ecol. Bull. 51: 379–384.

We evaluated the practical applicability of different types of indicator species used for monitoring and conservation planning in boreal forests. The results of a questionnaire to Swedish non-industrial private forest (NIPF) owners showed that from a list of 12 species, all birds and one well-known flowering plant could be recognised by a majority of the NIPF owners. On the other hand, lichens and fungi, and one cryptogam, i.e. indicator species currently in use by the National Board of Forestry, could be recognised by < 50% of the NIPF owners. Furthermore, these owners had a level of forestry education above average. These results imply that such species are difficult to learn and to recognise, i.e. their usefulness for communicating the conservation value of forests is low. Thus, the possibility that NIPF owners with low or moderate forestry education will use them as monitoring tools in practice is also low. We argue that an indicator system well adapted to NIPF owners and the general public should build on a suite of species with a well-documented indicator and umbrella value for each forest type of conservation interest, and which also have a high communication value.

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The use of indicators has been put forward in the UN's National Forest Programmes as a key element for the sustainable management of forests (Anon. 1997). Among the various types of possible biodiversity indicators at the scale of forest management units, there has been growing interest in using indicator species as a tool for monitoring of forest ecosystems. Since the beginning of the 1990s, much scientific effort has been devoted to finding and evaluating indicator species for identification of woodland habitats and habitat elements of high conservation values (Ferris and Humphrey 1999). Special interest has been attached to identifying species that require forest structures found in naturally dynamic forests (Peterken 1996) or cannot survive flips in the continuity of the ecosystem they are adapt-

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ed to. A flip means that species or processes in an ecosystem are lost from the area when the environmental change exceeds a certain threshold interval (e.g. Berkes et al. 2003). The presence of such forest species, often with low dispersal efficiencies, is thought to indicate an unbroken continuity regarding tree species composition and site conditions for a time period exceeding the life span of the single tree. Examples of such studies are Gauslaa (1994) and Nilsson et al. (1995) who found the lichen lungwort *Lobaria pulmonaria* to be a reliable indicator of both continuity and presence of a large number of red-listed species. Kuusinen (1996) found cyanobacterial lichens to be good indicators of forest continuity regarding tree species composition and site, and Selva (1997), who calculated an index of ecological continuity using a set of 30 lichens, suggested that the total number of *Calicales* species is a good indicator of forest stand continuity. Similarly, Tibell (1992) created an index based on twenty species of crustose lichens, which was highly correlated with forest continuity and with the number of occurring threatened species. In addition to lichens, bracket fungi, bryophytes, and vascular plants have been evaluated as potential indicators of forest qualities at the stand scale (Karström 1992, Gustafsson 1999, Jonsson and Jonsell 1999).

Indicator species have also been used in practical conservation work. For example, the Swedish National Board of Forestry (NBF) in 1993 initiated a project called "The Swedish Woodland Key Habitat Survey" (WKHS) with the objective to identify habitats of high value for biodiversity maintenance (Anon. 1994, 2002). Privately owned forest land was surveyed by thorough inventories for sites with certain habitat elements or presence of any of a set of more or less threatened or vulnerable species, so-called "signal species", among bryophytes, fungi, vascular plants, and lichens (Anon. 1994). The presence of a signal species was supposed to indicate the presence of other species with specific habitat demands (Anon. 2002) or other forest features, such as a high frequency of occurrence of important habitat elements.

In the light of the above-mentioned studies, the concept of indicator species for forest stand structures seems valid. However, when this approach is expanded, with the aim of being used and understood by individual forest owners, it may present limitations. The species which have been proposed are often neither common nor conspicuous, which may result in pedagogic and practical problems. Such limitations would be unfortunate, given that the National Forest Programme of the United Nations and the forest policies of several countries (Anon. 1997, 1998, Ekelund and Dahlin 1997, Hogl 2002, Schanz 2002) explicitly state the need for involvement of the forest owners in the policy making process, as well as in practical conservation work. While state forests and industrial private owners often have the resources to employ conservation specialists, in most European countries a large proportion of the forest land is owned by non-industrial private forest (NIPF) owners (FAO, Anon. 2001) who do not. At present we have little knowledge of how strong the incentives are for such forest owners to retain habitat structures for the maintenance of species that they may have never seen and have no knowledge of, especially if their importance is poorly explained. In many cases, the economical benefits of harvesting could overshadow the considerations for such rather obscure species.

The aim of this study was two-fold. First we investigated the knowledge of species from different taxonomic groups within a group of NIPF owners. Second, because many forest owners have undertaken forestry education in which they were introduced to the species currently used as indicators, we evaluated whether such education programmes result in a better awareness of the concept of indicator species and the implementation of conservation measures in the field.

Methods

A questionnaire on the subject of forestry and biodiversity conservation was sent to 681 NIPF owners in the municipality of Lindesberg, located in south-central Sweden (59°N, 15°E) (for details see Uliczka 2003). In one of the questions the respondents were asked to check-mark all forest species, from a list of twelve, which they were certain to recognise in the field. The species in the list (see Table 1) were selected to range from species that presumably would be well known by the general public, over species that would be known by foresters, to those that would require deeper knowledge, e.g., some of the signal species from the WKHS (Nitare 2000). Since scientific names are very seldom used in practice, all species were listed using their common Swedish names in the questionnaire.

In another question, the NIPF owners were asked to report their level of forestry education. Different levels of education were ranked using a point system. The points for participation in the various educational activities were summed to provide an index, hereafter called forestry education points (FEP), for each respondent. The alternatives were (number of points in brackets): "none" (0), "read about forestry myself" (1), "one-day course" (2), "course of several days" (3), "educational programme held by NBF" (4), and "forestry education on the vocational training/secondary school/university level" (10). If the respondent marked the last alternative, no points were given for additional educational activities. Differences in median FEP among groups of forest owners were tested using a Mann-Whitney test.

Results

The questionnaire was returned by 393 NIPF owners (response rate = 58%), 382 of which answered both of the

Table 1. The list of forest species (bold denotes a signal species according to Nitare (2000)) from the questionnaire, the taxon they belong to, and the proportion of forest owners which reported to be able to identify them in the field. Also the median and the mean number of forestry education points (FEP) of the NIPF owners who could/could not recognise each species is shown. The last column presents the p-values for the tests of the difference between the FEP of owners who could recognise the species and those who could not (Mann-Whitney test).

		Could owner recognise species?			
Species	Taxon	%	Yes FEP median (mean)	No FEP median (mean)	p-value for difference in FEP
Capercaillie *Tetrao urogallus*	Bird	95	3 (3.6)	1 (1.6)	0.05
Liverleaf ***Hepatica nobilis***	Vascular plant	94	3 (3.6)	1 (2.1)	0.07
Lesser spotted woodpecker *Dendrocopos minor*	Bird	81	3 (3.5)	3 (3.5)	0.98
Treecreeper *Certhia familiaris*	Bird	62	4 (3.6)	3 (3.4)	0.21
Long-tailed tit *Aegithalos caudatus*	Bird	51	4 (3.7)	3 (3.4)	0.32
Red ring rot fungus ***Phellinus pini***	Fungus	44	4 (3.9)	3 (3.2)	0.02
Star-tipped reindeer lichen *Cladina stellaris*	Lichen	32	4 (4.3)	3 (3.2)	0.004
Ostrich fern ***Matteuccia struthiopteris***	Vascular plant	23	4 (4.4)	3 (3.2)	0.004
Witch's hair ***Alectoria sarmentosa***	Lichen	14	4 (4.1)	3 (3.4)	0.18
Red belt fungus *Fomitopsis pinicola*	Fungus	13	4.5 (4.5)	3 (3.4)	0.03
Lungwort ***Lobaria pulmonaria***	Lichen	11	4 (4.9)	3 (3.4)	0.01
Bearded jellyskin ***Leptogium saturninum***	Lichen	5	5 (5.4)	3 (3.4)	0.01

above questions. The proportions of forest owners reporting to be able to identify each of the species and their mean and median FEP are presented in Table 1, where species are listed in order of decreasing frequency of recognition. Overall, the median FEP was 3, meaning that the majority of NIPF owners had participated in at least one day of educational activities in forestry. The frequency distribution of FEP is shown in Fig. 1. There was an inverse relationship between the proportion of NIPF owners reporting to be able to recognise a given species and their median FEP index (Table 1). For birds (except the capercaillie *Tetrao urogallus*) and for one vascular plant (liverleaf *Hepatica nobilis*), the education level of those who could recognise the species was not statistically different from that of the owners who could not. This means that the level of education required for being able to identify those species is not higher than the usual education level found among NIPF owners. For all remaining species in Table 1 (i.e. the two fungi, the only cryptogam, and all lichens except witch's hair *Alectoria sarmentosa*), the education level of the forest owners who could recognise them was significantly higher than that of the owners who could not. Recognition of those species thus required rather high levels of education, compared to the present-day level.

Discussion

Even though the concept of indicator species might work well in a scientific sense (e.g. Nilsson et al. 1995), the results from this survey about species knowledge among NIPF owners, imply that a system of indicators based on, for example, inconspicuous lichens and fungi, is mostly suited for experts, such as forest conservation consultants and biologists. That the birds got higher percentages of recognition may hence make them more useful in an indicator system adapted to both the NIPF owners and the public (also suggested by Morrison et al. 1992). Moreover, the fact that those birds were better known enhances their flagship value (sensu Simberloff 1998) for conservation. The same is true for well-known plants, such as the liverleaf, a spring-flower that is deeply rooted in the cultural tradition in Sweden.

The lichen lungwort has been suggested as a valid indicator of forests of high conservation value, and this species has caught much scientific attention. However, the proportion of forest owners who reported to be able to identify this large and conspicuous lichen was only 11%. Since all figures are self-reported, their validity is difficult to assess. It has been observed that respondents to such enquiries may occasionally exaggerate their qualifications (Krosnick 1990) and the figures in Table 1 may hence turn out to be overestimates. It is also disputable whether 14% of the owners really are able to distinguish witch's hair from similar lichen species of the taxa *Bryoria* and *Usnea*. Furthermore, the common bracket fungus red belt fungus *Fomitopsis pinicola* was known by only 13%, while the rarer red ring rot fungus *Phellinus pini* was reported to be known by 44% of the respondents. One possible explanation would be that the signal species *P. pini* may have been

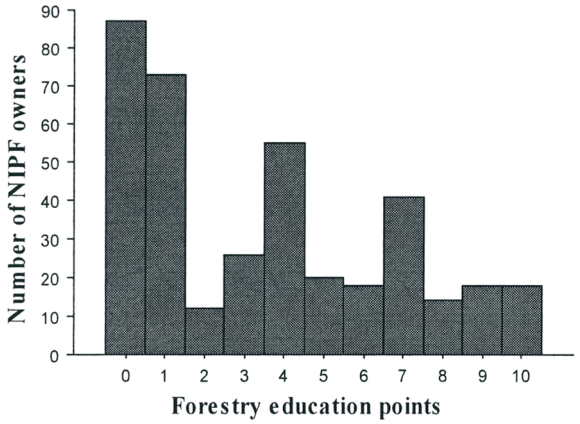


Fig. 1. Distribution of forestry education points among the NIPF owners that responded to the questionnaire (n = 382). See methods for a description of the point system.

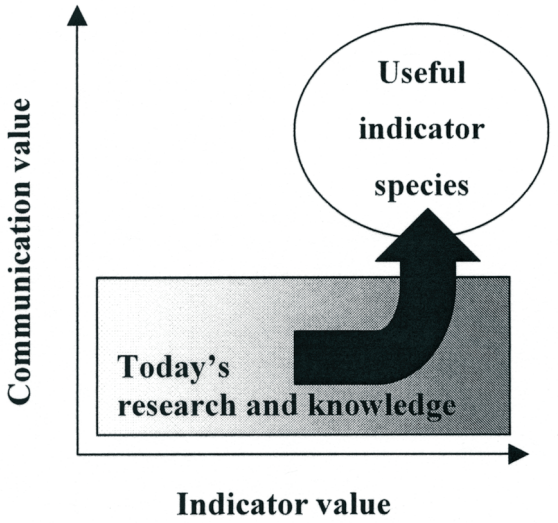


Fig. 2. Two important factors that should be taken into consideration when selecting a suite of indicator species are their indicator value and the possibility to communicate this value to non-experts. Research has so far mostly focused on assessing the indicator value of different species. We argue that a useful indicator species should have both a high indicator value and should be easily communicated to a wide range of stakeholders.

put into focus during recent forestry education activities, such as the NBF educational programmes, while *F. pinicola* did not benefit from so much attention in those programmes. Another explanation may be related to the fact that the Swedish name for *P. pini* is tallticka ("pine-bracket"). This may have led them to believe that this was simply the bracket fungi they had seen most commonly on pine.

Carignan and Villard (2002) argue for the use of many indicator species representing various taxa and life histories. The total WKHS list of signal species (Norén et al. 2000) contains ca 470 species of vascular plants (ca 80), mosses (ca 50), lichens (ca 110), fungi (ca 200), and since 2002 also insects (ca 30). Of these > 380 cryptogam species (mosses, lichens and fungi) are described in detail (Nitare 2000). Few of these species have yet scientifically investigated indicator values. Moreover, very few would be recognised by most of the NIPF forest owners. For use by this fundamentally important target group, we suggest that a monitoring system based on a few species with 1) a high indicator value for each of the main forest type of regional conservation interest, and 2) a likewise high level of recognition (or possibility to reach such a level of recognition by being easily detected or having special characteristics) should be developed (Fig. 2). These species should be communicated to all forest owners and become integrated in forestry education. It might also be the case that some species have an extremely high indicator value, but are generally unknown to the public, e.g. lungwort. In those cases, special efforts should be made to make them better known to the forest owners through special emphasis during, for example, educational programmes or information campaigns. One criterion for a useful indicator species could be, for example, that it is known by at least 50% of the NIPF owners, or has the possibility to become known by so many owners if effective information campaigns are undertaken.

An additional shortcoming with the use of plants and fungi as indicators is that many of those species have small area requirements. They can persist in scattered refuges (such as woodland key habitats) for long time periods, but may not be able to disperse through the hostile matrix of managed forests (e.g. Uliczka and Angelstam 2000, Goodwin and Fahrig 2002, Johansson and Ehrlén 2003). Thus, they do not indicate the conservation value of forests at larger spatial scales and longer time spans needed to ensure population viability. Instead, certain specialised vertebrates with larger spatial requirements (Angelstam et al. 2003, 2004) or insects dependent on habitat features of dynamic forests (Ehnström and Axelsson 2002, Wikars 2004) could be used for monitoring and assessment at larger spatial scales. Additionally, as animals cover a wider range of spatial scales, they have better potential than plants and fungi for addressing the issue of functionality of habitat patches and networks (Angelstam et al. 2003).

Since vertebrates in particular generally are better known by the public (cf. Table 1), they would also constitute more efficient tools in practice. A system of indicators based on such conspicuous species may be possible to develop. The usefulness of vertebrate indicators has, however, been questioned on several grounds (Landres et al. 1988, Niemi et al. 1997). Therefore, we argue for a rigorous evaluation of their indicator value before using them in practice. Such evaluations have been made for some bird species. For example, Mikusiński et al. (2001) found a posi-

tive relationship between the number of woodpecker species and bird species richness in general. Similarly, Jansson (1998) suggested the long-tailed tit *Aegithalos caudatus* as a functional indicator for other birds, partly because it is easily recognisable.

Another species-based approach, the so-called umbrella species concept (Wilcox 1984), could possibly be combined with the indicator concept into a multi-species approach for assessing conservation value of forests. The umbrella species concept consists in using the requirements of demanding species as a tool for setting minimum standards for, e.g., the size of reserves, the amounts of habitat structures, and processes in ecosystems (Roberge and Angelstam in press). This speaks for a translation of habitat needs into quantified recommendations (see, e.g. Bütler et al. 2004). For NIPF owners with a positive attitude towards conservation and a will to preserve biodiversity, but little knowledge of species, the easiest way might be just to retain recommended amounts of habitat structures for the conservation of a list of few and easily communicated umbrella species. Such species lists have already been developed. In Angelstam et al. (2004), a suite of 17 candidate bird species for the boreal, hemiboreal, and nemoral forest zones is proposed to be used for the assessment of the functionality of conservation area networks.

Given the current situation of NIPF owners in Sweden and probably in many other countries, one cannot expect that participation in educational activities would increase drastically in the coming years. Indeed, many are only part-time foresters with small forest holdings and cannot invest much more time in participating in educational activities. Therefore, we stress the need to evaluate the conservation tools that are in use, in the light of present levels of education and species knowledge among forest owners.

Conclusions

This study showed that the current system based on indicator species may be of limited value for practical implementation in small, privately owned forests, because many of the so-called "signal species" were not recognised by most owners. As criteria for an efficient conservation and monitoring tool we suggest that the communication value of a species should be considered together with its indicator value. In that respect, species such as specialised vertebrates should be included – as long as their indicator value is demonstrated – because: 1) they could become well-known by the actors and 2) such species often have large habitat requirements, which may make them potentially good umbrella species for large-scale conservation planning. If less conspicuous species such as non-vascular plants and insects are to remain part of such an indicator system, then special measures should be taken to increase general knowledge about those species among NIPF owners.

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Connecting social and ecological systems: an integrated toolbox for hierarchical evaluation of biodiversity policy implementation

Marius Lazdinis and Per Angelstam

Lazdinis, M. and Angelstam, P. 2004. Connecting social and ecological systems: an integrated toolbox for hierarchical evaluation of biodiversity policy implementation. – Ecol. Bull. 51: 385–400.

Recent policies on Sustainable Forest Management (SFM) include the maintenance of biodiversity. This requires an integrated set of tools for evaluating the status of ecosystems and of the policy implementation process by society's institutions. As a way of integrating analyses of social-ecological systems in these two dimensions of the cycles of policy formation and implementation, we propose to combine methods from natural and social sciences using the term "two-dimensional gap analysis". The ecological dimension involves analyses of the networks of different types of ecosystems in actual landscapes. It includes: 1) estimation of regional gaps in the amount and representation of different ecosystems, 2) analyses of the functionality of the habitat networks in terms of hosting viable populations and ecosystem processes, and 3) understanding of how protection, management, and restoration measures can be combined in practice at different spatial scales. The social dimension concerns the implementing actors and institutions in a selected actual landscape or region and includes: 1) identification of the actors and mapping of policy networks, 2) evaluation of the implementation process to learn about the issues of concern, and 3) evaluation of policy implementation in the defined social-ecological system. We provide examples of methods to carry out all six steps in the context of the policy formation and implementation cycle.
Managers and their institutions must realise that social-ecological systems are complex, self-organising, and adaptive systems with dynamics in multiple spatial and temporal scales across several levels of organisation. Only an explicit recognition of this complexity and application of transdisciplinary approaches will lead to progress in combining the efforts of managers and scientists to implement biodiversity maintenance policies.

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Maintenance of biodiversity in forests and cultural woodlands is one of the new challenges to land managers (Stanners and Bourdeau 1995, Lindenmayer and Franklin 2002). This is consistent with a general trend towards an increased need to satisfy societal goals related to environmental issues (Davis et al. 2001, Lindenmayer and Franklin 2003, Burton et al. 2003). The consideration of such non-timber values, which appeared during the 1950s in

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public management in North America (Anon. 1998) and in central Europe's mountain forests (Dönz-Breuss et al. 2004), has grown quickly during the 1990s in northern Europe's boreal forest (Angelstam et al. 2004a). The maintenance of biodiversity, but also the vitality, health, and protective functions of forest ecosystems, as well as production of non-wood resources and socio-economic development at multiple scales are currently stressed in international and national policies (Oliver et al. 2001, Rametsteiner and Mayer 2004). Hence, only about a decade after the term biodiversity was coined (Wilson 1985), the maintenance of compositional, structural and functional elements of biodiversity (Noss 1990) has become recognised as a central aspect of sustainable development in forest ecosystems (Larsson et al. 2001, Rametsteiner and Mayer 2004). Forest issues are hence no longer non-political ones that can be left to foresters alone (Glück 2000).

To address the biodiversity maintenance goal, research in natural sciences has proliferated (e.g., Hunter 1999, Lindenmayer and Franklin 2002). Models for how management regimes can be inspired by the forests' natural disturbance regimes (Bergeron et al. 2002) have led to new silvicultural practices being proposed (Fries et al. 1997). Similarly, different landscape planning approaches have been put forward (Angelstam and Pettersson 1997, Fries et al. 1998). The trend towards increased efforts to maintain forest biodiversity in managed landscapes is quite similar among different forest ecosystems (Lindenmayer and Franklin 2003).

But how does the implementation of the agreed policies work in practice? To answer that question, the attempts to implement biodiversity policies by forest management efforts in actual landscapes need to be evaluated. This is, however, not just a concern of the natural but also the social sciences (Gutzwiller 2002, Mascia et al. 2003). The issues to be addressed in order to succeed with the implementation of biodiversity policies include both the evaluation of the status of the managed ecosystems and of the institutions responsible for management (Clark 2002, Halahan and May 2003). The geographical area of an ecosystem where land management takes place forms a Forest Management Unit (FMU). Although the FMU concept lies largely in the eyes of the beholder, it is widely used to indicate the local level at which operational forest management takes place, i.e. management district or local landscape (Davis et al. 2001, Angelstam and Bergman 2004). Institutions are humanly devised constraints that shape human interaction (North 1990, Folke et al. 1996), which include, but are not limited to beliefs, norms, relationships, property rights, markets and individual agencies (Anderies 2000, Weisbuch 2000). Following Ostrom (1990:51) an institution can be defined as a set of working rules used to determine who is eligible to make decisions in some area. Institutions can be formal as companies, organisations and agencies managing land, but also be informal cultures characteristic for a particular interest group.

As stressed by Berkes and Folke (1998) and Folke et al. (1998a, b), the delineation of social and ecological systems is artificial. They should be treated as one social-ecological system with critical feedback across temporal and spatial scales. Hence, a set of tools linking on the one side the ecosystems, and on the other the implementing institutions, should be applied (Angelstam et al. 2003a). Unfortunately, due to several fundamental reasons described below the progress so far is limited (Lee 1993, Duinker and Trevisan 2003).

First, the relationship between social and ecological systems is poorly understood (Machlis and Forester 1996). The need for joint action of natural and social fields of science remains unrecognised, or if theoretical frameworks are advocated, they are still not operationalised (Penn 2003). For example, ecologists tend to regard anthropogenic environmental impacts as exogenous (Balée 1998, Holling et al. 1998, Davis et al. 2001, Settle et al. 2002). Social scientists, on the other hand, usually disregard the complexity of the ecological systems (Costanza 1991, Settle et al. 2002). The literature on relations between human action and biodiversity loss is descriptive rather than systematic and analytical, comparative studies are rare and predictive ability is weak (Machlis and Forester 1996).

Second, the natural resource management process until recently was viewed as linear. The conventional reductionist view in science considered that complex phenomena could be studied and controlled by reducing them to the basic building blocks and identifying the mechanisms of interaction (Holling et al. 1998). Now it is becoming accepted that both natural and social systems are non-linear in nature, cross-scale in time and in space, and bear an evolutionary character (Gunderson et al. 1995, Folke et al. 1998a, b, Holling et al. 1998, Gunderson and Pritchard 2002, Berkes et al. 2003). While this is discussed in the scientific literature, implementation in research (Olsson 2003), let alone in reality, lags behind.

Third, the operational link between social and ecological systems is difficult due to fundamental ideological differences in the related scientific fields (Bryman 2001, Penn 2003, Danermark et al. 2003). The natural science process is built on the goal of advancing knowledge, where each advance is built on knowledge acquired earlier. Therefore, the cost of the "incorrect knowledge" is high, affecting not only the current stage, but also the validity of future findings (Kinzig et al. 2003). By contrast, the policy process or the social system is built on the goal of rapidly addressing societal ills or challenges. In this case the timelines are frequently essential and the action may precede the knowledge. The errors that need to be avoided are associated with political and social risks of not taking an action, including possible harm to interested parties, the economy, national security, or the environment (Kinzig et al. 2003).

To implement biodiversity policies barriers such as those listed above need to be addressed. Explicit recogni-

tion of the connectedness, complexity, and ideological differences of ecological and institutional systems would facilitate evaluations of the degree to which ecological values as stated in generally accepted policies are satisfied (Settle et al. 2002). Therefore, a prerequisite for wise and effective management for the maintenance, and if needed even restoration, of biodiversity is to understand both ecosystems and institutions, and the complex interaction between them (Lee 1993, Machlis and Forester 1996). Integration of several disciplines is therefore necessary in order to manage this system composed by humans and nature (Christensen et al. 1996, Holling et al. 1998, Hammer and Söderquist 2001). This means that tools from both the natural and social sciences are needed to evaluate the policy implementation process (Penn 2003, Angelstam et al. 2003a). This requires evaluations of actual landscapes with their distinct ecosystems, land-use types and ownership as well as of the relevant formal and informal institutions. On the basis of such an approach constructive proposals for improvements in land management practices can be made, which will be commensurate with the demands of landowners, land users and society as a whole.

In this paper we make an attempt to combine ecological and social dimensions of biodiversity conservation in proposing a toolbox for iterated evaluations of the process of implementing forest biodiversity policies in actual landscapes. Inspired by Holling (1995), who uses the term "barrier" to describe the policy implementation gaps, and the term "bridge" for the tools to eliminate them, we use the term "two-dimensional gap analysis" (Angelstam et al. 2003a). Bridges include top-down evaluation of regional gaps in the representation (Scott et al. 1996) as well as amount of different types of forest ecosystems (Angelstam and Andersson 1997, 2001, Lõhmus et al. 2004) and functionality of habitat networks (Scott et al. 2002, Angelstam et al. 2003b, c, 2004b). The evaluation of regional gaps of the habitat amount and configuration of patches of different ecosystem elements literally takes place along the surface of the earth and is "horizontal" in nature. The evaluation of institutional aspects of the conservation of landscape elements, which aims at evaluating the implementing institutions, can be considered as "vertical" as it deals with the success of policy implementation in a participatory manner (Forester and McKendry 1996, Scott et al. 1996, Haynes and Quigley 2001). The geographical units for evaluation of horizontal and vertical gaps depend on the issue to be evaluated, but would generally be relevant at the level of forest management units, private forest in villages, municipalities, or the watersheds as envisaged in the European Community water framework directive (Colombo et al. 2001). Landscape is a concept used by a range of disciplines to encompass this complexity (Forman 1995, Angelstam 1997, Muir 1999).

Understanding landscapes as social-ecological systems

Defining a "social-ecological" (Berkes et al. 1998, 2003) or "socio-environmental" (Musters et al. 1998) system is a critical step on the path towards achieving sustainable development of any ecosystem. Following Noss (1990) and Larsson et al. (2001), in this paper we define the ecological dimension of the system as the compositional, structural and functional elements of biodiversity found within an actual landscape (Fig. 1). We consider that the social dimension represents institutional aspects of the system. In order to understand this dimension the following steps are important: 1) identification of the system; 2) delimiting the system in time and space; 3) assessing people involved directly and indirectly, in the past, at present and in the future; 4) describing subsystems, values, constraints, and relations (Machlis and Forester 1996, Berkes et al. 1998, 2003, Folke et al. 1998a, b, Musters et al. 1998). Both the ecosystem and institutional dimensions of "social-ecological" systems are hierarchical regarding the characteristics that can be changed (i.e. be steerable) (Forman 1995, Musters et al. 1998). This means that the landscape concept including abiotic, biotic, social, cultural and administrative dimensions is a very useful common denominator for both the ecosystem and institutional dimensions.

To achieve effective human steering in a defined system, a consensus-building strategy should be used. This means that all the individuals involved in the unit should agree on goals and measures taken to achieve them (Lee 1993, Musters et al. 1998). However, human actors always pursue a spectrum of interests concerned with their viability in a world full of other actors (human or non-human) and organised bodies, each of which is in turn pursuing its own interests in interaction with others (Bossel 2000). The resulting development is thus shaped by conflict and compromise of interests of a variety of concerned actors (Lee 1993, Bossel 2000). Additionally these interests, and consequently expectations, vary throughout the hierarchical and temporal scales (Piussi and Farrell 2000, Mills and Clark 2001).

A social-ecological approach represents an ever-changing dynamic tension between ecological and human change (Peterson 2000). The ecological products and services that are available at a given time and place determine the alternatives that are available for people. This set of alternatives shapes politics, economics, and management of these ecosystems (Peterson 2000). Thus, only a consideration of both ecological and institutional dimensions of biodiversity conservation may lead to fulfilment of the objectives set by the actors of a given social-ecological system. If treated separately, neither of these fields will lead to accomplishment of desired results (Szaro 1996, Brunckhorst 2000). If not successfully integrated into political processes, ecological knowledge and scientific expertise cannot

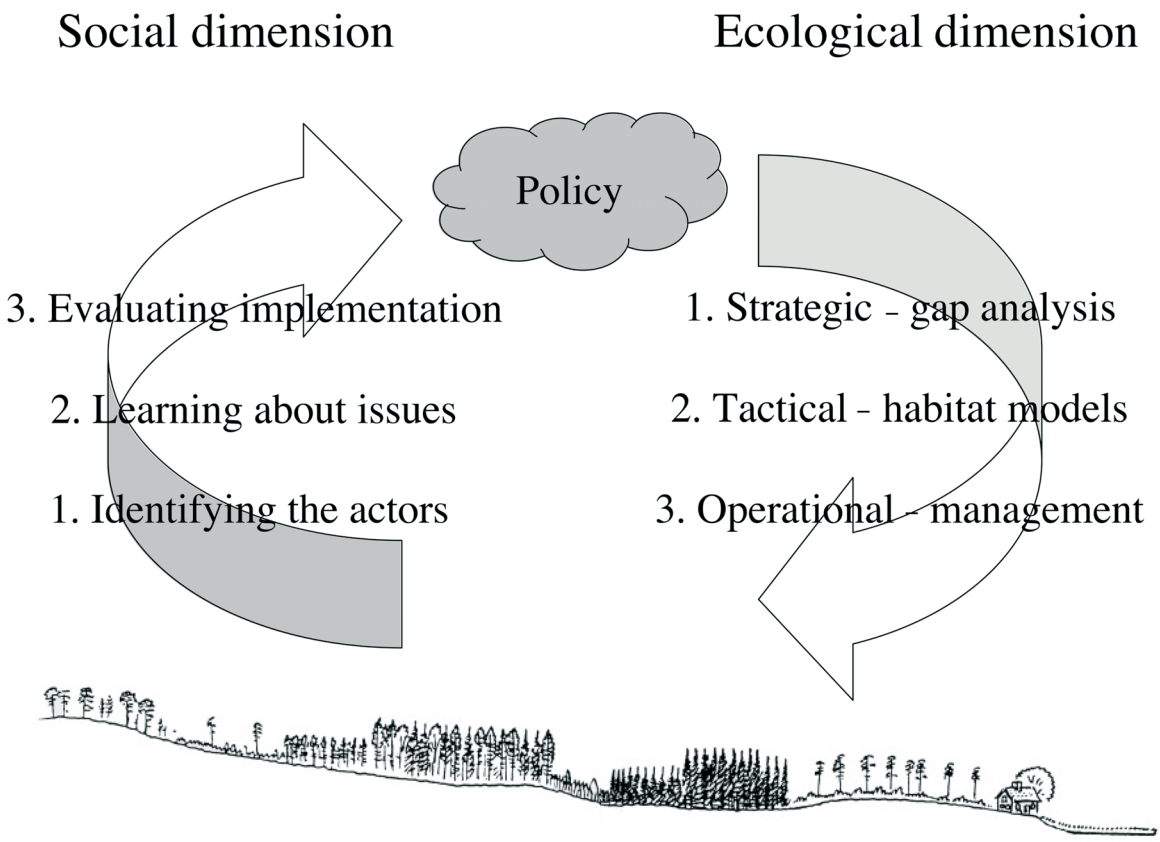


Fig. 1. Illustration of "two-dimensional gap analysis" as a conceptual model for the iterated cycle of evaluation of the functionality of habitat networks and implementation of biodiversity policies, see text. Landscape drawing by Martin Holmer.

become a part of management of natural resources (Bunnell and Johnson 1998). Consequently biodiversity conservation will not take place unless political will is generated and social and economic systems modified (Ehrlich and Wilson 1991). Therefore, in the search for gaps in biodiversity conservation, both ecological and social dimensions must be recognised (Fig. 1).

The ecological dimension

To succeed with the long-term maintenance of biodiversity in forests and woodlands, the combined effects on the maintenance of viable populations and ecosystem integrity of protected areas, management by silviculture, traditional agriculture and pastoralism, as well as re-creation by planting new forests need to be evaluated (Angelstam 2003). Such integrated evaluations should cover actual landscapes and consider historic changes in the cover of different ecosystems (Scott et al. 1996, Margules and Pressey 2000).

Alteration of the elements of biodiversity in forest environments is usually related to long or intensive management (e.g., Stanners and Bourdeau 1995, Mikusiński and Angelstam 1998, Angelstam and Dönz-Breuss 2004). Such changes include: 1) loss of species (a compositional aspect); 2) reduced amounts of dead wood, large trees, old and structurally diverse stands, large stands and intact areas (structural aspects); and 3) altered processes such as browsing by deer due to the decline in large carnivores, fire, incidence of harmful insects and fungi as well as anthropogenic pollution (functional aspects). To ensure the maintenance of ecological dimensions of sustainable forest management (SFM), criteria and indicators to measure the progress in landscapes should be combined with targets allowing evaluation of the degree to which sustainability has been achieved (Davis et al. 2001, Angelstam et al. 2004a).

Planning is used for steering towards agreed goals. As is the case of management for sustainable wood production, management for the maintenance of elements of biodiversity requires planning at multiple scales. The approach used in most planning systems for large-scale forestry is

hierarchical within a forest management unit (FMU) (Weintraub and Cholaky 1991, Jonsson et al. 1993, Davis et al. 2001). In European boreal forests the size of a FMU ranges from 10^4 ha for the ecological landscape plans in Fennoscandia (Angelstam and Pettersson 1997, Angelstam and Bergman 2004), to 10^5–10^6 ha in Russia. FMUs can thus be viewed as replicates of units at coarser scales such as ecoregions. The planning problem is usually divided into three sub-processes. The first level is strategic planning to decide on long-term goals covering an entire rotation. The second level is tactical planning to select among different alternatives based on the strategic goals, but on a shorter time horizon and for a smaller area. Finally, operational planning is made to administrate the actual operations within a year (annual plan of operations). The same logic can be used to build a toolbox of analytic tools for the evaluation of the structural elements of biodiversity such as trees and riparian corridors left during logging, tree species composition and the age class and patch size distribution in the landscape, all of which managers affect by planning and operational management (Angelstam et al. 2004c).

Strategic level – gap analysis

Gap analysis can be defined as the identification of disproportionate scarcity of certain ecological features in a management unit, relative to the representation to a larger region surrounding the management unit (Perrera et al. 2000). Because forest management deliberately affects structural elements at multiple spatial scales, we focus on the gaps in the amount of the different representative forest vegetation types needed to maintain viable populations in the long term. Gap analysis thus aims at identifying the most endangered forest habitats in an ecoregion (Scott et al. 1996), and aims at addressing questions (see Whittaker et al. 2004) such as: what are the long-term needs of protected or specially managed areas to maintain viable populations of the naturally occurring species of different forest types? How much of those forest types exist today? How much of what exists is protected or managed? Is the current status of protection and management appropriate? Is there also a need for rehabilitation, and even re-creation of habitats?

Extending the analyses of representation of different habitats (Scott et al. 1996), Angelstam and Andersson (1997, 2001) developed an approach for quantitative estimation of the area gaps in the present network of protected forest areas for the maintenance of viable populations of specialised species not being able to live in the managed matrix. Based on current policies and using the appearing knowledge about the dynamics of different forest types, forest and land use history, habitat loss thresholds of forest habitat specialists and current management practices, they estimated the need for protected forest areas at different broad ecoregions in Sweden. The procedure included the following steps (Angelstam et al. 2003a, b): A) estimate the amount of different historic forest vegetation types based on the distribution of different soil and site types hosting different natural forest disturbance regimes, and knowledge about the age distribution within them (Angelstam and Andersson 1997, Angelstam and Kuuluvainen 2004). B) estimate today's amount of the naturally occurring forest vegetation types defined in A. A–B) calculate the difference between A and B to describe differences in the representation of different forest vegetation types among different ecoregions. C) estimate the proportion of representative forest types needed to maintain viable populations of the most demanding species based on the appearing knowledge about populations' non-linear responses to habitat loss (e.g., Fahrig 2001, 2002). D) estimate the difference between B and A × C, where a negative value implies a gap in habitat area and a need for habitat rehabilitation and/or re-creation. Note, however, that gap analysis needs to be complemented by spatially explicit analyses to understand the level of functionality of habitat networks at the scale of landscapes and regions, or "green infrastructures", at the scale of forest management units or larger. E) estimate how much of the existing different representative forest types with gaps are protected today in nature reserves (protection gaps), and how much is included in current plans for future protection.

Application of this approach in hemiboreal forest in Sweden (Angelstam and Andersson 1997, 2001) and Estonia (Lõhmus et al. 2004) resulted in very similar long-term goals as to the proportions of protected areas required to maintain forest biodiversity. Although gap analysis is limited by the availability of knowledge regarding the historic range of variability (A), habitat thresholds (C), and by the lack of good descriptions of the current forest vegetation types (B), rather than abstaining from making estimates at all, we argue that gap analyses should be performed and viewed as a part of an iterative, adaptive approach. Indeed, Angelstam and Bergman (2004) indicated that evaluations at the level of strategic planning could be started with the information that is presently available in the forest management plans and then improved as the data availability increases.

Tactical planning – habitat models

When gap analysis has been performed within a particular ecoregion, the forest types for which area gaps have been identified also need to be evaluated as to the extent to which they actually provide functional habitat for the specialised focal species (Angelstam et al. 2003a, b, c). To evaluate the functionality of existing networks of patches of different forest types, there is a need to develop systematic evaluation procedures, the results of which can be used as a basis for the tactical planning of management, conservation, and restoration measures. Such analyses can provide answers to if and where stands should be set aside, managed or restored.

Habitat suitability modelling consists of combining spatially explicit land cover data with quantitative knowledge about the requirements of specialised species and building spatially explicit maps describing the probability that a species is found in a landscape (Scott et al. 2002). Ideally, focal species should be chosen among the most demanding species for a range of landscape attributes (Lambeck 1997, Roberge and Angelstam 2004). Since the most demanding species vary among habitats and scales, the suite of focal species should include representatives from a number of different taxa with different ecologies or functional groups (Angelstam 1998, Karr and Chu 1999, Nilsson et al. 2001). Finally, each model should be validated in order to test how reliably one can predict occurrences of the focal species in real-world landscapes (Scott et al. 2002). With adequate quantitative data on a suite of particular focal species (Lambeck 1997) carefully selected to represent all forest types of concern, a series of predictive models can be built to picture landscape functionality. This requires quantitative information on the habitat requirements of the species at different spatial scales. In general, a habitat model for a given species should build on the following variables: land cover type(s) constituting habitat, habitat patch size, landscape-scale proportion of suitable habitat, and habitat duration (Angelstam et al. 2004b). Using, for example, neighbourhood analysis techniques in Geographic Information Systems, the functionality of the network of each representative habitat (one or several land cover types) can be evaluated (Puumalainen et al. 2002). Because a landscape usually contains a range of types of forest vegetation, a suite of species need to be modelled (Root et al. 2002, Roberge and Angelstam 2004, Angelstam et al. 2004b)

The procedure suggested above provides a general basis for the evaluation and subsequent planning of habitat networks. The development of practical tools using focal species is, however, subject to uncertainty depending on the knowledge about the different parameters included in the models (Fuller 2002). Angelstam et al. (2004b) evaluated the knowledge available for using a suite of specialised forest birds as focal species for conservation planning in northern Europe. While the requirements of individuals at the patch scale are relatively well known for most species, an obvious lack of knowledge was identified regarding the requirements of viable populations at the scale of landscapes and regions. Another factor influencing the development of practical tools is the thematic and spatial resolution of the land cover data available to the planner (cf. Young and Sanchez-Azofeifa 2004). For example, depicting the habitat of species dependent on dead wood (e.g. many species of woodpeckers, beetles, and wood-decay fungi) require spatially explicit data on the occurrence of this resource across the landscape. Such detailed habitat data is not currently available from forest management maps or classified satellite images, and therefore additional ancillary information needs to be collected in the field. Until such data become available, surrogate measures such as vicinity to roads as a proxy for the amount of dead wood found in a landscape could be used (Bütler et al. 2004).

An example of a successful attempt to apply habitat suitability modelling in operational forest management is provided in Suchant and Braunish (2004). Using capercaillie *Tetrao urogallus*, a species of high conservation value and of special concern to major actors in biodiversity conservation in Germany, the authors modelled the habitat conditions for the occurrence of the capercaillie in several analytical steps at different temporal and spatial scales. Based on this, management target values were derived and integrated into an operational habitat management model in order to assess habitat suitability. This study is a good example of how wildlife research can be linked to practical habitat management.

Operational planning – matching silvicultural systems with disturbance regimes

Strategic and tactical planning needs to be complemented with guidance at the FMU and sub-FMU level (Fries et al. 1997). The maintenance of forest biodiversity requires that both the range of natural disturbance regimes and the resulting forest and woodland environments to which species have adapted (the ecological dimension) are understood. Moreover, a corresponding sufficiently wide range of different land management regimes must then be applied in reality (the management dimension) (Angelstam 2003). It also requires that the management regimes chosen for different forest environments harmonise with its ecological past, such as advocated within the natural disturbance regime paradigm for near-to-nature forest management (Hunter 1999, Bergeron et al. 2002).

A forest is far from being one green homogeneous carpet. Broadly speaking the boreal forest disturbance regimes range from succession following large-scale disturbances such as fire and wind to small-scale dynamics associated with gaps in the canopy created by the loss of individual trees (Angelstam 1998, Gromtsev 2002). For the boreal forest three main disturbance regimes are characteristic (Angelstam and Kuuluvainen 2004): 1) succession from young to old-growth mixed deciduous/coniferous after stand-replacing fire or wind, 2) cohort dynamics in dry Scots pine *Pinus sylvestris* forest after low-intensity ground fire, and 3) gap dynamics in moist and wet Norway spruce *Picea abies* forest where fire is a rare event.

Temperate deciduous forests are also characterised by a variety of disturbance regimes. However, the virtual absence of naturally dynamic reference areas makes it difficult to be as specific as for the boreal coniferous forest. In spite of this, gap-phase dynamics is supposed to be dominating in naturally dynamic forests with beech *Fagus sylvatica* and several other shade-tolerant broadleaf tree species (Mayer 1984). This is, however, under debate. For ex-

ample Vera (2000) argues that large herbivores have had major effects on the dynamics of forests dominated by broad-leaved species less tolerant to shade, such as oaks *Quercus* spp. Wind is another important factor determining the dynamics of hemiboreal forests (Ulanova 2000). However, the history of anthropogenic change in temperate Europe is long and complex, and it is therefore not easy to draw firm conclusions about the relative importance of different natural and cultural disturbance regimes. This is a good illustration of where both natural science and social science methods can complement each other (Egan and Howell 2001).

The wide range of different silvicultural systems means that there is in principle good potential for emulating natural disturbance regimes through management both in forest and ancient cultural landscapes with wooded grasslands once commonly found in Europe (Angelstam 2003). Like natural disturbance regimes, management regimes can be divided into three main groups of stand structure: even-aged, multi-aged and uneven-aged. In addition the methods employed in the ancient cultural landscape need to be considered. However, as compared to situations when wood production is the only objective and even-aged management with a narrow range of successional stages is practised, sufficient amount of both recently disturbed as well as old-growth forest need to be added (Esseen et al. 1997). Additionally, as shown by the situation in landscapes with different land use histories, traditional management for sustained yield of wood is poor at maintaining coarse woody debris in all decay classes, very large and old trees, and other components of naturally dynamic forests (Angelstam and Dönz-Breuss 2004). Consequently, conservation areas with both "laissez-faire" and active conservation management strategies will usually be a necessary part of a complete approach to maintain forest biodiversity.

The social dimension

Should analyses of area gaps, functionality of habitat networks or choice of management systems show that the status of ecosystems deviate from the desired according to policies, the next step is to evaluate the institutions involved in implementation of policies. To the dissatisfaction of many natural scientists, in reality the choices regarding what to do about biodiversity problems are seldom based on ecological or even scientific considerations (Willson 1996). Rather these choices are based on decisions by individuals within the social-ecological systems reflecting the goals of formal and informal policy-making bodies, which then determine how biodiversity issues are incorporated into policy (see Clark 2002).

Improving the performance of natural resource management within specific social-ecological systems, or simply landscapes, requires an understanding of temporal and spatial boundaries of the system itself, issues perceived as concerns by the stakeholders in the system, and policy objectives, instruments and organisations addressing these issues. It may be possible to improve the policy implementation and management of ecosystems and hence biodiversity by systematically identifying institutional contexts at play, i.e. people, agencies, and policy processes (Lee 1993, Clark et al. 1996). In order to protect, manage and restore elements of biodiversity it thus becomes necessary to identify the institutional barriers, which also may include major social and economic forces that are currently driving the loss of functional diversity and to create incentives to redirect those forces (Folke et al. 1996). Clark (2002) defined a practical analytic framework to map a policy process by distinquishing three principal groups of variables for different actors. These are 1) the social process and mapping of the context, 2) the decision process and clarification of the common interest, and 3) problem orientation to find solutions. The policy science approach stresses the need for both participants and observers to understand their stand-points in relation to the policy process, to use multiple methods (Bryman 2001) and to be guided by democracy and human rights.

In this section, we review a set of tools that can be used for assessing the institutions dealing with the management for biodiversity. The overall goal of institutional gap analysis is to locate policy and institutional attributes, which commonly have a causal link with resource problems and to communicate this information to decision-makers. As opposed to the top-down approach adopted for the evaluation of ecosystems, we stress the need for evaluating the institutions from the bottom, i.e. in the actual landscape unit or region chosen for the analysis, and upward to the policy level (left part of Fig. 1).

Identifying the actors

The actors, or stakeholders, whether individual or organisational, consumptive or non-consumptive, could be considered as those whose lives due to their work, living environment or leisure activities are affected by some aspect of biodiversity (Clark et al. 1996, Meffe et al. 2002). In a contemporary democratic society many types of actors besides political authorities participate in the processes of policymaking (Carlsson 2000a). Implementation of any program or policy is the product of interaction among the constituencies. Governments are increasingly advised to seek the co-operation and joint resource mobilisation of policy actors outside of their hierarchical control (Glück et al. 2003). Ideally, any biodiversity programme should allow sufficient opportunity for the equitable participation of various actors and interests, but in reality not all perspectives are represented.

Because policy actors pursue distinctive, but interlinked interests and co-ordinate their actions through interdependencies of resources and interests, the rationality

of policies will be ensured by interconnecting representative policy networks rather than by the application of hierarchical governance by the state (Glück et al. 2003). Various studies have demonstrated that the characteristics of policy networks can be helpful starting-points for clarifying the way in which policy instruments and designs work (de Bruijn and Hufen 1998). The concept of "policy networks" generally contains the assumption that there are two main features: links and actors (Carlsson 2000b). The network perspective can be characterised by its 1) non-hierarchical way of perceiving the policymaking process, 2) its focus on functional rather than on organisational features, and 3) its horizontal rather than vertical scope (Carlsson 2000b).

Contemporary decision-making advocates public participation and attempts to ensure that all the relevant actors and stakeholders are involved in the planning and communication process (Nichols 2002). However, this does not necessarily lead to what Lee (1993) calls social learning. The co-ordination of political actors therefore needs to become holistic and inter-sectoral, making sure that all sectors affecting forestry and affected by forestry are considered and externalities are internalised (Glück et al. 2003). Given the assumption that policymaking is performed in networks of actors rather than by formal political units, it is expected that the creation of politics and its outcome will differ depending on how a policymaking arena is organised (Carlsson 2000b).

According to Carlsson (1996), policy analyses studying such networks should concentrate on answering two crucial questions: 1) what is (are) the problem(s) to be solved? and 2) who is participating in the creation of institutional arrangements in order to solve them? To gain a deeper understanding of the processes concerning biodiversity management policy, networks should be mapped. Under the framework of this tool, application of comprehensive theories and methods is necessary. Carlsson (2000b) suggested that if taken within an "Institutional Analysis and Development Framework", different policy network constructs could be understood as instances of collective action emanating from specific contexts. Each context may then be understood in terms of specific incentive structures, norms, rules, and physical attributes that affect particular action arenas. By focusing on individual behaviour we can not only understand how policy networks evolve and are structured, but also how these networks create specific outcomes in particular policy areas. Of a special importance in assessing policy networks for biodiversity management is consideration of current market conditions and forces, which usually have strong effects on progress towards sustainable development. For methods to identifying the actors we refer to Salomon and Engel (1997), Bryman (2001) and Clark (2002).

In the long-term, representatives of implementing institutions may become significant stakeholders and will start influencing the formation of policy goals on their own. Revealing such implicit objectives is difficult and would require qualitative rather than quantitative methods (Bryman 2001). Therefore, at this stage of the evaluation process all institutions and organisations mapped previously as part of the relevant policy networks are to be considered. Human capacities, and more precisely – employment information, and membership where applicable, may be chosen as a proxy measure of the extent to what institutions/organisations can participate and influence forest policy formation and complete their tasks and objectives in policy implementation processes.

Learning about issues

Identifying emerging implementation problems and understanding their magnitude is an important initial step in the forest policy process (Merlo and Paveri 1997, Whiting 2000). This tool in the vertical evaluation of the policy implementation procedure concentrates on answering the first part of the question raised in policy networks (sensu Carlsson 2000a): what is (are) the problem(s) to be solved? Quantitative and qualitative methods can be applied in learning about the problems and needs of stakeholders (Witkin and Altschuld 1995). The quantitative analyses can credibly be based on information provided in a variety of processes on criteria and indicators.

The inquiry approach (Patton 1987, Weiss 1998) is a qualitative method, which can be used in order to characterise the policy networks. Structured deep interviews can be applied to understand how the actors perceive the policies and have knowledge and resources to implement them (Bryman 2001). As an example we use the two-fold research design that was chosen to evaluate the development of forest resources and to learn about the present day issues of concern in forest management of Estonia, Latvia, and Lithuania. The first approach was quantitative, and analysed and compared indicators of sustainable forest development in the context of the three countries (Lazdinis 2002). The second approach was largely qualitative and identified differences between the three countries represented in terms of resource problems, and policy and institutional failures as perceived by the national stakeholders (Lazdinis et al. 2001, 2002a, b). Between 300 and 400 individual problems were identified in each country. The lists of problems provided by survey respondents in all three countries were collapsed into one database table and, using pattern-coding, combined into groups of issues of concern common among all three forest sectors.

Evaluating implementation

After learning about the actors and issues in the system of interest (issues perceived by stakeholders as well as those identified quantitatively) the implementation of biodiversity policy can be assessed. This evaluation may take place in the framework of a participatory programme evaluation

approach. According to the simplified programme theory designed for administration of forest resources, 1) institutions deal directly with forest resources (or those directly managing resources) and do their best to achieve 2) national forest administration objectives through the 3) implementation of policy instruments. A particular political institution (e.g. organisation responsible for administration of forest resources) cannot be extracted from its context and compared to some evaluation criteria without taking into account the whole political system in which that institution is set (Ball and Peters 2000). Therefore, in evaluation we must consider entire policy networks as discussed above, as well as the needs of individual members of these networks.

As a starting point of evaluation according to this program theory it is assumed that a set of national, regional or local forest policy objectives is determined as a result of negotiations and compromising processes. The objectives may be long-term as stipulated in the legislation and other official documents or short-term, as identified by the stakeholders in their current management decisions. Besides changing interests of stakeholders, national or regional objectives may be modified by factors of the physical environment, which directly affect the state of forest structure. They include, among others, insect and disease outbreaks, forest fires, and disastrous storms.

Next, policy instruments (i.e. instruments through which the government can influence society and the economy and can produce changes in the lives of citizens, see Peters 1999) are chosen in order to assess the extent to which SFM is implemented (Merlo and Paveri 1997, Le Master et al. 2002, Lazdinis et al. in press). The general set of tools or instruments for implementing forest sector policies is largely the same whatever the problems to be addressed (Le Master et al. 2002). Mayers and Bass (1998) distinguished five main types of instruments for implementing forest policy: regulatory, market economic, informational, institutional, and contracts/agreements. The types selected and extent of use of particular set of instruments will lead to varying success in biodiversity policy implementation. In order to put the instruments into practice, implementing, both formal and informal, institutions are created or existing ones are charged with such responsibilities.

Combined evaluation of all stages of the program theory for administration of forest resources allows identification of failures in successful implementation of the program. The failures may occur at each stage of implementation process, in this way preventing the achievement of ultimate goal of the program – sustainable development of forest resources.

Discussion

Two-dimensional gap analysis as an integrated toolbox

One stream of science – systems approaches – extends the analysis of populations, ecosystems, landscape structures and dynamics to include the interactions of social and natural systems (Holling et al. 1998). While the traditional natural and social science can be characterised as a science of parts, the systems approach is a science of integration of parts. The main goal of this approach is to reveal the simple causation, which often underlies the complexity of time and space behaviour of complex systems (Holling et al. 1998).

In the context of the systems approach, considering the connectivity, non-linearity, and differences between social and environmental systems we propose a multidisciplinary approach which we term "two-dimensional gap analysis" (Angelstam et al. 2003a; Fig. 1) as a conceptual model and an integrated toolbox for evaluation of biodiversity policy implementation. The ecological dimension is used to identify the gaps in biodiversity maintenance at strategic, tactical and operational levels of planning. If the analyses of gaps are based on empirical knowledge about the actual ecosystems and landscapes it can serve as a basis for analysing gaps in the social dimension including both formal and informal institutions. In an ideal situation, direct satisfaction of the needs or expectations of the different stakeholders would follow the path of issue-objective-instrument-institution-resources stages and lead to elimination of the articulated concerns. However, gaps in biodiversity policy implementation may be found at each six steps of the evaluation (Fig. 1).

Institutional, or "vertical", gap analysis can be viewed as a temporally closed system. In the ideal policy process cycle (Merlo and Paveri 1997) it could be assumed that once a cycle has been completed, none of the related parties will express further concerns and the stakeholders will be satisfied unless new needs and expectations arise. Of course, such a situation will rarely occur in the real world. Here the management for biodiversity is an iterative process, during which the stakeholders prioritise the set of objectives, and commonly produce only the second best, or sometimes even hardly tolerable, outcome for some of the stakeholders. Therefore, the adopted set of biodiversity management objectives is a result of compromises made between various interest groups and reflects their political power. Once a cycle from policy formulation to implementation is completed, actors of the social-ecological system renegotiate the objectives, reselect the set of policy tools, and design new institutional frameworks. The political, economic, social, and cultural objectives of the actors in the system are affected by the results of public interventions as well as by their experiences gained under the previous cycle.

External factors, not directly related to the particular limited system, but rather typical to the whole nation or area of interest, can also strongly affect the choice of political objectives in biodiversity management. These factors may include but are not limited to previous economic development, different patterns of state governance, market forces present at a time, influence of neighbouring nations due to geographical location and differences in religion and culture. The effects of these factors are not easily observable and are typically hidden in the attitudes of stakeholders as they refer to selection of policy objectives, governmental instruments, and structural arrangements of implementing organisations.

Institutional gap analysis also recognises that the management of forest biodiversity in general is only one of the many fields in which stakeholders are involved. Politics and policy setting are in fact framed by many objectives and expected outcomes, and biodiversity management is just one among many fields of activity. Every stage of an evaluation, including evaluation of the resource itself, is affected by cross-sectoral issues. Elements of the other sectoral programmes, such as objectives, instruments, institutions or even resources (e.g., air pollution, nutrient leakage, rural development) may in fact largely influence forest resource development. On the other hand some elements of cross-sectoral policies may be strongly influenced by issues of concern in the biodiversity management.

In spite of the presence of relevant tools from the natural and social sciences, effective use of them in a transdisciplinary fashion to facilitate the implementation of sustainable development policies is rare in the real world (Boutin et al. 2002, Duinker and Trevisan 2003). Working across disciplines in landscape analyses is evidently a major challenge. In a comparison of two case studies, Jakobsen et al. (2004) revealed a set of similar individual-based, group-based and organisation culture-based barriers. However, even if they proposed a number of recommendations to scientists across disciplines, the limited number of case studies and the narrow focus of their study precludes thorough analyses of the effects of ecological, institutional, and cultural contexts on both barriers and facilitators to bridge them. We argue that coining a concept such as "two-dimensional gap analysis" describing a toolbox combining methods from the natural and social sciences is rational. The main reason is that in order to talk about something complex and difficult, it has to have a name.

With the two-dimensional gap analysis approach we argue, as do Kinzig et al. (2003), that natural resource systems should be viewed as self-organising, complex, and adaptive, with dynamics that act on multiple scales of space and time, and across levels of organisation. We also adopt the view of Sanderson et al. (2002) "…that the most effective strategies to conserve biodiversity must account for the complex and diverse needs of wildlife and people…". By developing this toolbox we attempt to match management practices and institutions to the structure and dynamics of ecosystems, as proposed by Folke et al. (1998a, b). Our goal is to make evaluation of biodiversity in a broad sense more flexible and adaptive to changes in social systems and ecosystems. Of course, this requires the capacity of social systems to monitor change and build formal and informal institutions that make it possible to respond to feedback signals of the environment (Folke et al. 1998a, b). However, we believe that the cyclic and iterative manner of two-dimensional gap analysis will allow accounting for the signals both in environmental and social systems.

Connecting social and ecological systems for biodiversity management

All efforts to manage biodiversity require a balance of scientific (including natural and social sciences), social, and regulatory concerns (Clark et al. 1996). The dynamic interplay caused by the interaction of these three concerns in any one conservation effort can lead to conflict and competition. In order for the long-term, sustainable management of biodiversity to become reality, the means to manage their interaction most productively are required. These means can be, but are not limited to a need for careful data collection, rigorous model-testing, and the strengthening of integration and co-operation. Significant advances require expanding and deepening of the communication between the social and biological sciences, individual disciplines, schools of thought, and so called invisible colleges (Machlis and Forester 1996). The term for co-ordinated interaction and integration across multiple disciplines resulting in the restructuring of disciplinary knowledge and the creation of new and shared knowledge is "transdisciplinary" (Rapport et al. 1998, Jakobsen et al. 2004).

Conceptual models of social-ecological interactions have been widely attempted, and these efforts form the basis for developing specific models of biodiversity loss. However, explicit holistic models of the mechanisms behind biodiversity loss are sparse and incomplete. Machlis and Forester (1996) argued that social sciences could potentially contribute to the development and testing of models that attempt to organise the understanding about the causes of biodiversity loss, because purely biological models are limited to investigating intervening variables and proximate causes. The explanatory variables are likely to be socio-economic and political.

A conceptual transdisciplinary model for biodiversity loss requires that 1) socio-economic indicators serve as measures for key social variables, 2) the social variables have specific impacts upon environmental variables, 3) the variables and relationships be derived from biological and social science theory, and 4) biodiversity loss be operationalised for measurement over time (Machlis and Forester 1996). We believe that in the two-dimensional gap analysis approach, the above recommendations would be

accounted for. We envision that in this two-dimensional evaluation scheme the degree to which ecological thresholds are not exceeded could be monitored in order to match their correspondence to set political targets. At the same time, we suggest that political targets should be flexible enough to be timely modified according to the scientific findings regarding what is required for example for maintaining viable populations of species or ecosystem integrity.

We also recognise that the set of variables used in evaluations of both ecosystems and social systems will depend on the scale and locality of socio-environmental system. Socio-economic factors important at one scale may be less significant at another. We adopt that at each different scale, new variables and relations may emerge as critical driving forces (Machlis and Forester 1996). Therefore, we believe that the model resolution and factorial composition will be scale-dependent.

Thresholds in managing for biodiversity

The non-linearity of natural resource management results in unpredictable behaviour of both populations and processes. Small changes can propagate dramatically and shift the system into another development path – just as in a chaos theory (Holling et al. 1998). Individual issues occurring in the management of biodiversity can be compared to the "Butterfly effect", which forms a basis for the chaos theory. This means that small pieces in the system can be responsible for large changes in unpredictable directions (Gleick 1987). The ability to predict the causes of those changes decreases with increasing time and scale. Loss of resilience – capability to absorb changes – can move the system closer to the thresholds, the passing of which may make the system irreversibly shift to another path of development (Holling et al. 1998).

To maintain resilient systems the knowledge on thresholds should be incorporated into functional active adaptive decision-making framework. Berkes and Folke (1998) simplified, and partly made applicable, the definition of sustainable development assuming that sustainability means "not challenging ecological thresholds on temporal and spatial scales that will negatively affect ecological systems and social systems". Therefore, in order to facilitate sustainable development, according to this approach, the delimiting of ecological and social systems and learning about ecological thresholds is critical. Folke et al. (1996) thus argued for a strategy that aims at conserving the capacity of ecosystems to continue to deliver life-support and other ecological services to humanity under the wide range of environmental conditions.

The two-dimensional gap analysis approach provides a possibility to track the causes in shift of biodiversity condition in time and space. However, there can be no definite answer on which factor is the main impediment in conservation and restoration of biodiversity and how close the affect of this factor will move the system to the threshold values. We believe that the approach presented in this paper would facilitate adaptive management of these complex socio-environmental systems as related to the implementation of biodiversity policies, even though this management sometimes seems as trying to manage chaos – the universal behaviour of complexity.

To address the level of functionality of forest landscapes for the maintenance of different elements of biodiversity, the degree of match between the landscape's management and its natural dynamics has to be understood (Angelstam 2003). When making decisions about the management of landscapes, ecologically based performance targets to which measurements of components of biodiversity could be compared with increasing detail and at different spatial scales ought to be formulated (Higman et al. 1999). The knowledge on the ecological thresholds (Muradian 2001), such as non-linear responses of species' populations to habitat loss (Fahrig 2001, 2002) provide a starting point for such true evaluation of different elements of forest biodiversity. With the above information strategic decisions could be made about where environmental sustainability of the forest ecosystem could be achieved at the lowest cost. Ullsten et al. (2004) provides an example of a very general and high-level measure of changes in forest resources over time measured against set targets. This type of index would be a good starting point to communicate the results of regional gap analyses and evaluation of the functionality of habitat networks. However, on the operational level more detailed signals on change and condition are necessary (Angelstam and Bergman 2004). Depending on the level of ambition, evaluation could be made regarding at least four different target levels for the conservation of biodiversity: 1) occupancy of species within conservation areas, 2) ensured population viability over long time 3) ecosystem integrity and health (Pimentel et al. 2000), and 4) ensurance of long-term ecological sustainability, or ecological resilience (Gunderson et al. 1995, Gunderson and Pritchard 2002).

The need for transdisciplinary approaches

Success in sustaining or developing desired ecosystem conditions depends on having scientifically sound, economically feasible, and socially acceptable strategies (Lee 1993, Salwasser et al. 1996). In order to facilitate sustainable development of natural resources, major changes in resource management policy and practice are needed, and the science on which current policy and practice are based should be re-examined (Holling et al. 1998). First of all, it must be accepted that management of natural resources is taking place in a complex co-evolutionary system, with changing functional controls in the ecosystem, in the economy and in the society (Lee 1993, Holling et al. 1998, Duinker and

Trevisan 2003). In short, the complexity and connectedness of social and ecological systems should be understood and addressed by scientists, even though this makes a challenging task (Gleick 1987, Mills and Clark 2001). A critical issue is to find out what works best. We argue in favour of a bottom-up participatory approach where different disciplines come to agreement about common approaches. Working in case studies such as "model forests" alleviates this (Besseau et al. 2002).

We must also acknowledge that failure to maintain biodiversity may not be just gaps in the spatial representation of different ecosystems. Institutional obstacles, usually called political and institutional failures (Mayers and Bass 1998), also play a large role in the maintenance of biodiversity. No ready formula exists for a successful balance of scientific, social, and regulatory concerns in managing biodiversity, and no simple prescription can be given (Clark et al. 1996). The failures in policy process may occur at any of the stages of implementation and be result of multitude of factors, expressed through the attitudes, values, and hidden objectives of those in charge (Mayers and Bass 1998, Larsen et al. 2000). Worrell (1970) and Merlo and Paveri (1997) provide examples for structures of forest policy processes. Therefore, to successfully manage biodiversity in forest landscapes, knowledge produced by natural sciences should be complemented with the expertise representing the social science dimension both in education (Hammer and Söderqvist 2001) and practise (Vogt et al. 2002). In this way, ecological and social disciplines will co-operate to fill the gaps and facilitate implementation of national forest programs, in other words to alleviate the development towards sustainable forest management.

In our approach we support the argument that conservation biologists must use their theories to deliver effective, science-based decision tools for practical use by managers and policy makers (Possingham et al. 2001). Transforming pure science – whether theoretical or empirical – into information that can actually be used by managers and decision-makers to address the conservation problems is the major challenge in conservation biology. To meet this challenge, conservation biologists will need to embrace more economics, management science, decision theory and more of operations research (Possingham et al. 2001, Mascia et al. 2003) but also sociology, psychology and anthropology (Penn 2003). Moreover, scientists must become more effective and compelling communicators of both what is and is not known. Politicians must bolster their ability to make decisions in the face of uncertainty and be clear about the role of ideology and values in interpreting uncertainty (Kinzig et al. 2003). Scientific basis for conservation can successfully be developed by transdisciplinary teams of researchers working hand-in-hand with managers, educators and citizens to address both short and long-term dynamics in the many dimensions of relationships between people and the land (Salwasser et al. 1996, Mascia et al. 2003). Simply recognising the web of interacting scientific, social, and regulatory forces is a first step toward more effective implementation of existing biodiversity policies (Clark et al. 1996).

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Loss of old-growth, and the minimum need for strictly protected forests in Estonia

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Lõhmus, A., Kohv, K., Palo, A. and Viilma, K. 2004. Loss of old-growth, and the minimum need for strictly protected forests in Estonia. – Ecol. Bull. 51: 401–411.

We estimated the minimum area of strictly protected forests, which could maintain species of "management-incompatible forests" (i.e. not surviving in timber production areas), in Estonia. The planned protected area comprised minimum amounts of habitat for the viability of such species, and a "buffer amount", which may be temporarily lost in natural disturbances. The steps were 1) estimation of mean frequency of stand-replacing disturbances for Estonian forest site types; 2) reconstruction of the structure of natural forest area by age classes and forest site types; 3) comparison of the natural age structure with that in managed forests to define the management-incompatible part; 4) estimation of the historical area of different age classes, critical threshold of its loss for specialist species, and the "buffer" area; 5) defining gaps by comparing reserve need with current protected forest area; 6) analysis of the model sensitivity to errors in the estimates of wildfire frequency. Management-incompatible forest (> 100 yr since the last stand-replacing disturbance) covered historically 32–42% of today's forest land. The theoretical minimum need for strictly protected forests was estimated at 8.5–11.3% of current forest land, one-fourth being the "buffer amount". However, if current reserves retain their status, filling the gaps for underrepresented forest site types yields a total coverage of 10.4–13.2%. This difference is mostly due to the high present coverage within the current reserves of heath forests and oligotrophic paludifying forests (low silvicultural interest) and drained peatland forests (not a natural site type). The results were relatively insensitive to variation in the fire frequency data, and close to earlier estimates for Fennoscandia. We suggest that the estimated amount of reserve areas should be taken as approximate minimum targets in forest reserve development in Estonia, even though future studies are likely to increase the accuracy and precision of the estimates.

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In balanced forestry, the first and perhaps most critical step for biodiversity considerations is to leave some of the forest landscape untouched in reserves (Seymour and Hunter 1999). Designing representative reserve systems is a complicated task involving many steps and decisions (Norton 1999). However, the total area of reserves is one of the key issues both politically and economically (e.g. Leppänen et al. 2000) as well as ecologically, given that habitat area

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(combined with the connectivity of patches) has a major effect on the persistence of target populations (Fahrig 1997, 2001, Trzcinski et al. 1999).

Although forest management has a long history in Europe, the first attempts to quantify forest reserve need have been made only recently (Virkkala 1996 for Finland; Angelstam and Andersson 1997, 2001 for Sweden), and after natural forests have almost disappeared. These studies used the concept of critical habitat loss thresholds (e.g. Andrén 1994, Fahrig 2001) but were otherwise different. Virkkala (1996) did not distinguish forest types and added systematic reserve selection to include all species of land birds. Angelstam and Andersson (1997, 2001) reconstructed the area of forest environments with different disturbance dynamics having occurred before major land changes started ca 200 yr ago, calculated critical amounts of habitat loss, and subtracted the extent in which regular forestry mimics the composition, structure and dynamics of the environments. Despite the different approaches, both studies reached similar estimates of how large proportion of forest land should be protected (at least 10% in Finland; depending on ecoregion, 8–16% in Sweden).

In this paper, we estimate the minimum area of forests which should be strictly protected in Estonia to maintain viable populations of the species of "management-incompatible forests" (i.e. not surviving in timber production areas), and calculate gaps compared with the current reserve area. The analysis is based upon critical habitat loss thresholds and forest disturbance dynamics. Our aims are 1) to evaluate the methodology of Angelstam and Andersson (1997, 2001) who made a gap-analysis for the four main Swedish forest ecoregions. We focus the evaluation on the hemiboreal forest, which has a similar composition and history in south Sweden and Estonia. We therefore expect to get an estimate of the same order of magnitude as in Sweden's hemiboreal forest; 2) to draw preliminary conclusions about the applicability of the numerical results obtained so far. Although the tentative nature of the estimates has to be admitted, there is always trade-off between gaining more data and protecting biodiversity values, and politicians should start making decisions before there is little to conserve (e.g. Brunckhorst 2000).

Estonian forests and their biota

Estonia forms a part of the hemiboreal vegetation zone (Ahti et al. 1968). Historically, forests covered probably ca 85% of Estonian land area (Laasimer 1965), a part of which has become deforested by humans, especially since the 18th century (Fig. 1). Forest cover was at its minimum in the first decades of the 20th century (ca 20% of land area) and has been increasing since then, mostly on account of deciduous second-growth in former agricultural lands and drained mires. In 2000, forest land covered 2.25 million ha, i.e. 51.5% of the Estonian land area (Kohava

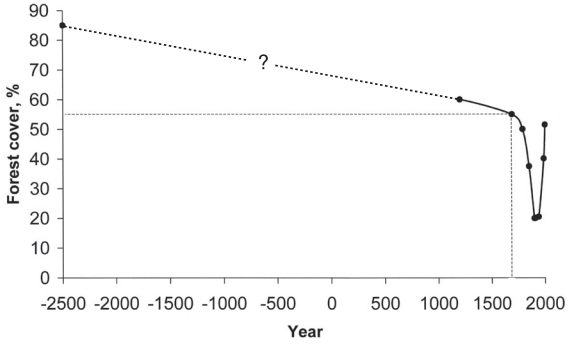


Fig. 1. Forest cover (% of total area) in Estonia in the last 4500 yr. Dots are the actual estimates (Laasimer 1965, Etverk and Sein 1995, Meikar 1998, Meikar and Etverk 2000, Kohava 2001); dashed vertical line denotes the start of rapid deforestation.

2001). Preliminary data (Lõhmus unpubl.) suggest that fragmentation of forest land with other habitats is only a local problem: 1) forest cover is below fragmentation threshold (30%, Andrén 1994) in five isolated regions totalling 19% of land area; 2) in a large reference area in east-central Estonia, 78% of forest land was situated in patches > 10 km^2, 15% in patches of 1–10 km^2, and only 1% of forest land in fragments of up to 10 ha; most patches were separated by narrow roads or rivers.

Based upon climatic, edaphic and hydrological factors, nine natural and one anthropogenic group of forest site types, including a total of 27 forest site types have been routinely distinguished in forest management (Lõhmus 1984); afforested mining areas form an additional anthropogenic forest type. The most common natural site type groups are dry boreal (24% of forest land; usually dominated by Scots pine *Pinus sylvestris*), eutrophic paludifying (21%; mostly birch *Betula* spp.), meso-eutrophic (16%; mostly Norway spruce *Picea abies*) and eutrophic boreonemoral forests (9%; mostly grey alder *Alnus incana* and birch); the dominating anthropogenic forests are drained peatland forests (14%; mostly birch and pine). Today, all the main forest trees are native; 34% of forest area is dominated by Scots pine, 30% by birch, 18% by Norway spruce and 8% by grey alder (Kohava 2001). Stands of exotic trees comprise 0.1% of forest land. Over 25% of the forest land has been drained and over 300 000 ha planted, but there are no intensive plantations and stands usually consist of more than one (most often three) tree species.

In contrast to the increase in forest cover, the area of mature and overmature stands in state forests has dropped from 193 000 ha in 1939 to 123 500 ha (including reserves) in 1999, i.e. by 36% (Liimand and Valgepea 2000; no data about private forests). In a large reference area in east-central Estonia in 1997–2000, only 2.4% (1.2% outside reserves) of forest land was still covered by old unmanaged multi-cohort forests or forests with gap-phase dynamics, in contrast to extensive non-forested clear-cuts (15.8%; Lõhmus 2002). This is in line with the sharp in-

crease in felling volumes after Estonia regained independence (2.4 million m^3 in 1993, 10.8 million m^3 in 2000), whereas in recent years the harvest of coniferous trees exceeds their increment (Kuuba 2001). However, there is still an extensive supply of middle-aged or old unmanaged secondary forests (over 25% of forest land in reserves, over 10% outside; Lõhmus 2002), which will be developing to old-growth if protected.

The average total volumes of coarse woody debris ranges from 98±39 (maximum 227) m^3 ha^{-1} in one primeval forest (Kasesalu 2001) and 25–50 m^3 ha^{-1} in naturally developing protected forests (H. Tukia and P. Lõhmus pers. comm.) to 10–13 m^3 ha^{-1} in other forests, including recently managed ones (Lõhmus unpubl.) of Estonia. The latter values are significantly higher than in managed hemiboreal forests of Fennoscandia, which only have 1–4 m^3 ha^{-1} (Siitonen 2001).

More than 20 000 species are estimated to inhabit the Estonian forests. Forest-dwelling species make up 30.4% (401 species) out of the 1314 nationally threatened species (Lilleleht 1998). Given that the status of only ca 20% of all species was checked, the real number of threatened forest species may reach thousands. Among birds, the populations of old-forest species sensitive to timber cutting (e.g. *Ciconia nigra*, *Accipiter gentilis*, *Tetrao urogallus*, *Dendrocopos leucotos*) have declined during the 1990s, and forest birds are the relatively least represented bird group in current reserves (Lõhmus et al. 1998, 2001).

Estonian forest management regimes follow the classification suggested for balanced forestry (e.g. Seymour and Hunter 1999). According to the national Forest Policy and Forest Act, at least 4% of forest land should be strictly protected for nature conservation (protected forest), 15% should be left for special or restricted harvesting to protect the state of the environment (protection forest) and the rest are commercial forests (Viilma et al. 2001). Key-habitats for threatened species should be protected also in commercial forests, but this has been put into practice mostly in state forests. In 2002, the Estonian state forests (38% of all forests, and containing 84% of protected and most protection forests of the country) were granted a FSC Forest Management certification. Additionally, due to the land reform ca 600 000 ha of not-yet-privatized forest land are temporarily not managed, and a part of these lands could be set aside for new reserves.

General approach and methods

Strategy: to protect disturbance regimes or populations?

In reserve planning there seems to be no consensus about how "untouched" the landscape in strict reserves should be left. Angelstam (1997) viewed this as the difference between conservation biology (protection of species) and landscape ecology (protection of processes), as well as between naturally dynamic forests and ancient cultural landscapes as benchmarks. However, in a real human-dominated world only a fraction of the landscape can be set aside in reserves, and different approaches are needed as they supplement each other. For the Estonian forest land we use natural forest disturbance regimes as the benchmark (Seymour and Hunter 1999, Angelstam 2002).

Process-oriented reserves should have sufficiently large areas to ensure continuous availability of habitat patches for all target species (Baker 1992, White and Harrod 1997). In forest landscapes, "sufficient" means hundreds or thousands of square kilometres (Baker 1989, Angelstam et al. 2001). Given the minimum size of at least 50 times of the area of disturbances (Shugart and West 1981, Baker 1992) and the fact that in the second half of the 20th century at least two forest fires of 20 km^2 have been recorded in Estonia despite fire suppression (Tint 2000), a dynamic forest reserve in Estonia should cover at least 1000 km^2. In practice, the far largest protected area in Estonia (Lahemaa National Park) includes only 326 km^2 of forest. More generally, if only a fraction of landscape is in a natural state but the frequency and area of individual disturbances remain at historical level, it is likely to increase environmental stochasticity and, consequently, decrease the viability of disturbance-sensitive populations in these areas (cf. White and Harrod 1997).

In contrast, conservation biologists selecting representative sites to save populations and their habitats (e.g. Bibby 1998, Possingham et al. 2000) usually do not consider habitat change via disturbances, succession and global processes. If disturbances can destroy habitats of target populations, it should be taken into account whether the magnitude and frequency of disturbances can be suppressed or not. Although the modification of existing disturbance regimes and the introduction of new disturbances should be minimized (Norton 1999), this seems to be inevitable in many cases.

On these grounds, the need for strictly protected forests in Estonia was planned to the conditions of ongoing irregular windthrows but suppressed wildfires, assuming that the availability of young successional stages in the landscape is sufficient. To maintain the biologically valuable fire-created habitats (Esseen et al. 1997, Siitonen 2001), prescribed burns in specially managed areas (protection forest) were considered a better option than stochastic and uncontrolled wildfires in strict reserves.

Tactics: conceptual model and simplifications

Following from the strategy outlined above, strict reserves should include 1) management-incompatible forests in critical amounts for the viability of their biota; 2) a "buffer amount", which is likely to be temporarily lost in disturbances. To identify these areas we first defined the manage-

ment-incompatible part of forest land and then calculated its probable historical and minimum area needed, the latter consisting of the "critical amount" and the "buffer". Before modelling, we made three pragmatic simplifications in the spirit of the "common sense strategies of conservation" for temperate forests (Ehrlich 1996).

1. The current forest land was used as baseline because: a) its total coverage and distribution are close to the 55% before the rapid deforestation started ca 300 yr ago (Fig. 1 and Meikar 1998); b) forest land has not become significantly fragmented by anthropogenic habitats (see above); c) the current forest area is relatively well covered by data.

2. Forest site types were used to address the representativity of reserve network (e.g. Angelstam and Andersson 1997, 2001, Norton 1999). Although detailed biodiversity surveys could give better solutions (e.g. Blamford and Gaston 1999), this is difficult and has never been done in species-rich forests (Norton 1999). The current area under different forest site types was used for calculations, except that afforested mining areas (0.5% of forest land) were completely excluded (original habitats unknown) and the area of drained peatland forests was divided between ombrotrophic and mixotrophic bog forests, and stagnant-water swamp forests according to their current share. Out of the main historical trends in the typological composition, we could not address paludification (peat accumulation) and the loss of forest area to agricultural land. In this study, the essence of forest site types and type groups follows Lõhmus (1984), but the English names have been corrected according to Paal (1997, and pers. comm.).

3. The current reserve network was accepted as such, and only gaps in its typological representativity were analysed (e.g. Bibby 1998). However, we will discuss also the current quality of forest habitats for threatened species in the existing reserves and time lag needed for its improvement.

Estimation of the natural forest age structure

Given the scarcity of data for some key variables, we used a simple and robust deterministic model. The management-incompatible part of the forest landscape was distinguished after 1) estimating the mean frequency of stand-replacing disturbances for different forest site types; 2) using the mean frequencies for reconstruction of the structure of "natural" forest area by age classes and forest site types; 3) comparison of the natural age structure with that in commercial forests and the prescriptions of forest cuttings.

Age structure of natural forests with a successional dynamics was estimated from the negative exponential function $A(x) = p \exp(-px)$, where $A(x)$ = area of age x, and p = annual frequency of stand-replacing disturbances (Van Wagner 1978). Such an age structure has been documented also in nature (Johnson 1992, Niklasson and Granström 2000) but its use has been also criticised due to high temporal and spatial variation, and ignoring that stand-replacing disturbances (e.g. fires) often do not kill whole stands – hence the actual age-distribution is more shifted towards older classes (Anon. 2000). We argue that in large regions and in the long perspective, the random error is likely to diminish, and fires kill a significant part of biota even if large trees stay alive. Estimating the area of forests that were probably never touched by fire in a given period is thus analogous to the complete absence of human disturbance, i.e. strict protection, whereas the forests developing after disturbances that kill a fraction of trees are more similar to partly restricted management regimes.

The model was parameterized with data on mean frequencies (resp. intervals) of wildfires and large windthrows, which were added to the model separately. Fire intervals depend highly on forest site type (e.g. Angelstam 1998), and the type-specific estimates were obtained as expert opinions, based on qualitative data from Estonia (e.g. Sivers 1903, Põder 1941, Laasimer 1965) and extrapolation of quantitative data from Fennoscandia (Zackrisson 1977, Engelmark 1987, Segerström et al. 1994, Hörnberg et al. 1995, Angelstam 1998, Pitkänen 1999). Since lightning ignition rates are probably quite similar in Fennoscandia and Estonia (Granström 1993), the north-Fennoscandian data were re-evaluated in the light of the Estonian landscape structure, which has more fire barriers in the distribution area of most site types, and, hence, lower average fire frequencies. To increase precision, most intervals were given as minima and maxima for different runs of the model (hereafter: minimum and maximum scenarios, respectively).

For large windthrows, we used official monitoring data (Karoles pers. comm). Forests' susceptibility to severe storms was considered independent of site type but dependent on forest age (e.g. Ulanova 2000, Lässig and Mochalov 2000). Young stands up to 30 yr were not considered to be wind-disturbed, while older stands were regarded equally susceptible (cf. Sein 1998, Ruel 2000, Lässig and Mochalov 2000). In these older stands, fires and windthrows were considered to have additive effects (annual disturbance probability was estimated as the sum of fire and windthrow probabilities subtracted by the probability that they occur in the same year).

The minimum threshold of critical habitat loss was set at 20% of original (see Angelstam and Andersson 2001). For calculating "buffers" (i.e. the relative areas that may, on average, be lost due to temporal disturbances), we considered windthrows as described above, and the total suppressed fire frequencies of the 1990s (on the average 0.032% of forest land burning annually; Tint 2000). Suppressed fires were expected to occur in different forest types according to their natural susceptibility and intervals (as used for the reconstruction of natural forest area before), therefore all "natural" frequency values were divided by the magnitude of suppression. The "buffer" was calculated as

maximum area of disturbed stands if the disturbance probability is the same (average) for all years.

Minimum needed area of reserves was calculated both as 1) "theoretical", for which the critical areas and "buffers" were simply summed by forest site types; and 2) "practical gaps", for which the theoretical needs of all forest site types were reduced with their areas currently under strict protection. Finally, in order to explore the model sensitivity to the most probable errors, we repeated the calculations after changing the used values of fire frequencies.

In this paper, the existing protected forests include 1) strict nature reserve or special management zones of protected areas. Most of special management zone forests are not managed, even if some activity is allowed in protection rules. For technical reasons, it was not possible to separate the actually managed part of this zone, but its total area is not likely to exceed 0.2% of forest land; 2) strictly protected zones around the nest sites of black stork *Ciconia nigra*, eagles, osprey *Pandion haliaetus* and flying squirrel *Pteromys volans* as well as in display grounds of the capercaillie *Tetrao urogallus*; 3) forest areas proposed to be strictly protected by the Estonian Forest Conservation Area Network (Viilma et al. 2001); 4) state-owned key habitats of at least 4 ha in size. The minimum size criterion was derived from expert opinions and foreign practice (e.g. Dunwiddie 1991 in Cooper-Ellis 1998) to exclude small patches, which are not likely to be suitable for old-growth species in the long term.

Results

Disturbance frequency and age structure of natural forest

The estimates of prevailing disturbance regimes (sensu Angelstam 1998, 2002) and mean wildfire intervals in Estonian forest site types are presented in Fig. 2. Most forests

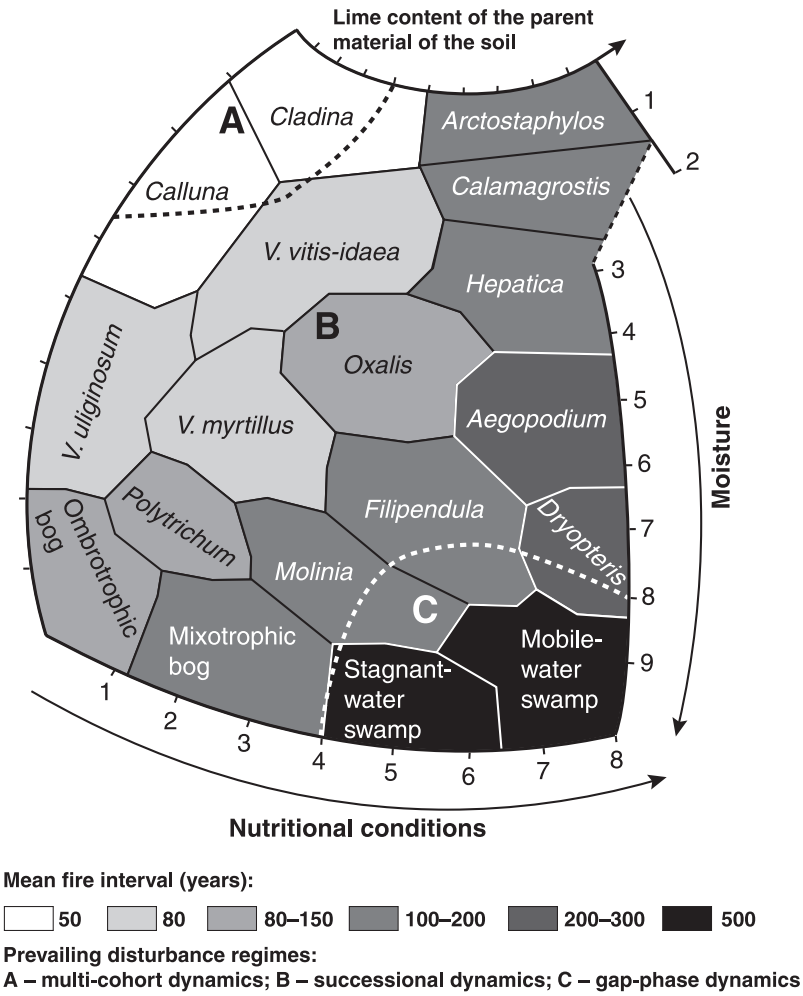


Fig. 2. Prevailing disturbance regimes and mean estimated wildfire intervals in Estonian forest site types. Chart organization (scales and site type pattern) follows Lõhmus (1984), except that *Carex* and *Equisetum* site types have been united into *Molinia* (Paal 1997).

exhibit successional dynamics; only very small areas have more or less pure *Pinus* cohort dynamics (ca 0.5% of forest land) or gap-phase dynamics (ca 5%).

Calibrating the model of age structure with the frequencies of wildfires (Fig. 2) and windthrows, gave the following reconstruction of natural forest dynamics and structure. The average wildfire interval of the whole forest land was estimated at 136–198 yr. The total area of windthrows was 135 000 ha in the second half of the 20th century, i.e. 2700 ha annually (Karoles pers. comm.). Given the 1 077 870 ha average area of stands older than 30 yr, the annual windthrow probability was 0.25% and the average windthrow interval 400 yr in these stands. Joining the wildfire and windthrow submodels gave a total average interval of stand-replacing disturbances of 97–129 yr. Depending on forest site type, the relative frequency of fire of all natural stand-replacing disturbances ranged from 46 to 94%, and was 71–80% for the whole forest land (Table 1).

Compared with the age structure of the Estonian commercial forests, the natural landscape included much more old forests, starting from > 100 yr (Fig. 3). This result was expected, since according to the Forest Act, one hundred years is the official rotation age in commercial forests (for pine and hardwood stands; lower for other tree species). Thus, the age classes over 100 yr were considered management-incompatible in the further analyses. According to the model, natural forest landscapes might have contained 32–42% of such "old-growth" in Estonia (11–64% in different forest site types; Table 1).

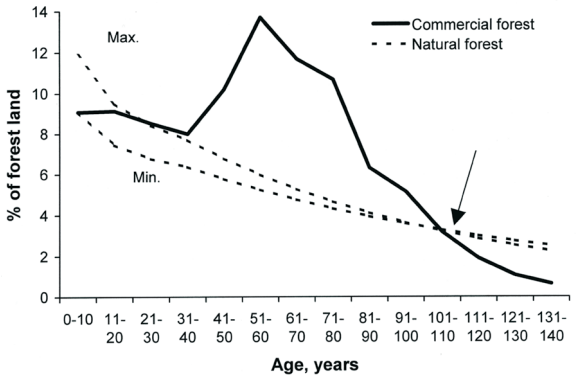


Fig. 3. Comparison of the age structure of the Estonian commercial forests (state forests) with the predicted natural situation (minimum and maximum scenarios shown). The age classes over 100 yr (indicated by arrow) were considered management-incompatible.

Reserve need

Theoretically, the total minimum area of strict reserves was estimated at 8.5–11.3% of the forest land, one-fourth of which was comprised by the "buffer" (Table 2). Current reserves cover 45–60% of the theoretical total need; the largest gaps are for the forests on fertile soils (meso-eutrophic, eutrophic boreo-nemoral and eutrophic paludifying forests) and swamp forests. In contrast, heath, dry boreal and oligotrophic paludifying forests have much higher

Table 1. Predicted mean intervals of stand-replacing disturbances (SR), share of fire in these, and the relative area of "old growth" (forests over 100 yr) by the natural development of Estonian forest site type groups.

Site type group	Site types*	Share of forest land, %	Mean SR interval, yr	Fire-disturbed area of all SR, %	Area of "old-growth", %
Heath	*Cladina, Calluna*	0.7	47	94	11
Dry boreal	*V. vitis-idaea, V. myrtillus*	24.1	85	87	25
Oligotrophic paludifying	*V. uliginosum, Polytrichum*	1.2	80–95	86–88	23–27
Alvar	*Arctostaphylos, Calamagrostis*	3.3	85–140	70–84	29–48
Eutrophic paludifying	*Filipendula, Molinia*	20.9	85–140	70–84	29–48
Meso-eutrophic	*Oxalis, Hepatica*	15.9	92–181	72–86	27–45
Bog	Ombrotrophic bog, mixotrophic bog	16.2	94–186	72–86	28–46
Eutrophic boreo-nemoral	*Aegopodium, Dryopteris*	9.3	140–162	60–70	48–53
Swamp	Stagnant-water swamp, mobile-water swamp	8.3	230	46	64
Total		100.0	97–129	71–80	32–42

* only "pure" types listed (cf. Fig. 2), but also transitional types included in analyses.

protection level than the estimated minimum coverage; and strict reserves include 15 500 ha of drained peatland forests, which are not a natural type. However, "old-growth" forms only 25% of the current reserved state forest (and only 10% in several productive forest types), while 34% are recovering (age 61–100 yr), and the rest are young forests (data absent for private forests).

The model was robust to possible errors in the used values of fire frequency. Changing all used fire intervals by ±10% changed the estimate of long-term aim by only ±4 to ±5%, which means uncertainty about ±0.5% of forest land (Table 3). In different runs of the model, there were no qualitative differences in gaps (no forest site types appeared overrepresented in one scenario and underrepresented in another).

Discussion

Reconstruction of forest structure

If flammability does not depend on forest age, wildfires would result in a negative exponential age distribution of forests (Van Wagner 1978). This is the simplest case of a general model based on the Weibull distribution (Johnson and Van Wagner 1985). We followed the negative exponential model rather than the Weibull distribution, because 1) the age-dependence cannot be formalized at the current stage of knowledge about Estonia's natural forest dynamics. While old stands of some site types may burn relatively more often than young (refs in Angelstam 1998), the opposite may be true for other site types (Van Wagner

Table 2. Theoretical need for strictly protected forest (incl. core, which is 20% of the historical old-growth area, and buffer amount), gaps in the currently protected forest area, and the long-term aim for forest reserves in Estonia. The real values of three last columns are slightly biased because strictly protected forests of indeterminate forest site type cover additional 0.3% of forest land (the total for column D is 7.2% of forest land). The results are rounded to nearest 100 ha.

	Forest land area, ha					
	Theoretical need			Current situation		
Site type group	A Core	B Buffer	C Total (A+B)	D Strictly protected	E Gap (C–D)	F Aim (D+E)
Minimum scenario						
Alvar	4400	1500	5900	4400	1500	5900
Heath	400	100	500	10000	0	10000
Dry boreal	26600	9400	36000	44900	0	44900
Meso-eutrophic	19300	6700	26000	7200	18800	26000
Eutrophic boreo-nemoral	19900	6300	26200	8900	17300	26200
Eutrophic paludifying	27600	9500	37100	20700	16400	37100
Oligotrophic paludifying	1300	400	1700	10800	0	10800
Swamp	19000	5700	24700	7400	17300	24700
Bog	24700	8600	33300	26000	7300	33300
Drained peatland	0	0	0	15500	0	15500
Total	143200	48200	191400	155800	78600	234400
Proportion of forest land	6.4%	2.1%	8.5%	6.9%	3.5%	10.4%
Maximum scenario						
Alvar	7100	2300	9400	4400	5000	9400
Heath	400	200	600	10000	0	10000
Dry boreal	26600	10300	36900	44900	0	44900
Meso-eutrophic	32100	10700	42800	7200	35600	42800
Eutrophic boreo-nemoral	22000	6900	28900	8900	20000	28900
Eutrophic paludifying	44700	14700	59400	20700	38700	59400
Oligotrophic paludifying	1400	600	2000	10800	0	10800
Swamp	21300	6500	27800	7400	20400	27800
Bog	35400	11700	47100	26000	21100	47100
Drained peatland	0	0	0	15500	0	15500
Total	191000	63900	254900	155800	140800	296600
Proportion of forest land	8.5%	2.8%	11.3%	6.9%	6.3%	13.2%

Table 3. Sensitivity of the predicted values of key variables to possible errors in fire intervals. For the analysis, original fire interval estimates (Fig. 2) were changed by 10%.

Variable	Estimates of fire interval		
	–10% of original	original	+10% of original
Share of "old-growth", %	29–40	32–42	34–45
Theoretical need for reserves, %	7.8–10.8	8.5–11.3	9.1–12.0
Gap, %	3.0–5.9	3.5–6.3	4.0–6.7
Long-term aim, %	9.9–12.8	10.4–13.2	10.9–13.7

1978); and 2) preliminary runs of the model with the general Weibull distribution and the age-dependence constants presented in Johnson and Van Wagner (1985) changed our main output value – the total minimum area of "management-incompatible forest" – by < 1% and had very small impact on the reserve need estimate. This was because the minimum age of these forests (100 yr) was close to the average fire interval, and in the Weibull model the values above average account for constant cumulative probability (36.8%; Johnson and Van Wagner 1985).

However, the predicted 32–42%-share of "old-growth" (> 100 yr since the last stand-replacing disturbance) in natural hemiboreal forest landscape is lower than documented in boreal Fennoscandia: 78% of forests over 120 yr old in northern Finland (Virkkala and Toivonen 1999) or the domination of stands > 200 yr old in mid-boreal Sweden (Linder and Östlund 1998). The most probable reasons for the difference are differences in the forest site distribution and the related forest disturbance regimes (Angelstam 2002, Pennanen 2002), and partial burns – for example, in eastern Finland these have formed about half of all burns (Pitkänen 1999). In addition to old-growth reserves, there should be a considerable amount of mature stands in the surrounding landscape matrix managed with selection cuttings to mimic the natural disturbance regimes of (hemi)boreal forest landscapes.

Estimates of forest reserve need in Estonia and Sweden

In several strategic points (e.g. the use of disturbance dynamics and habitat loss thresholds) we followed the Swedish model of estimating forest reserve need (Angelstam and Andersson 1997, 2001). An as objective as possible view of natural forest landscape in the light of current data was constructed, this was compared with the real situation in managed forests to "cut off" the management-incompatible part. This procedure revealed the key role of "old-growth", the scarcity of which is widely recognized in clear-felling forestry systems (e.g. Virkkala 1996, Angelstam 1997, 2002, Esseen et al. 1997, Seymour and Hunter 1999). At the same time, our estimates of reserve need cover also the other targets of forest protection in Estonia: 1) the area of threatened forest communities (Paal 1998) can be included if the gaps in reserve area are filled according to our suggestions; 2) compared with an earlier gap analysis, which was based on conservation status and variability of forest site types (Viilma et al. 2001), only the gaps in protected alvar forests are significantly smaller according to our study. This result suggests that the diversity of alvar forests – secondary forests on ancient pastures (Laasimer 1965) – should be maintained with a not-yet-defined balance between traditional use (or special management) and strict protection.

However, we also made some major modifications to the Swedish model.

First, our model concentrated on strictly protected forests, where no logging is allowed. This excluded some habitats (wooded meadows, recently burnt areas) that should be created or preserved via active management, and which were included in the Swedish model. However, at least in Estonia, active habitat management should not necessarily take place in reserves, and the approach for estimating the minimum needed area of seminatural habitats obviously needs further development. The main biodiversity value of wooded meadows is their small-scale species-richness, but they seem to lack specific "umbrella"-species for which extinction thresholds could be applied (see e.g. Kukk and Kull 1997).

Secondly, we made no estimates using expert opinions about how forest management regimes contribute to the emulation of natural dynamics.

Thirdly, the model was designed for a "moving target", i.e. to be flexible to quantitative changes in commercial forests. For example, if rotation ages are shortened, the management-incompatible part covers more age classes and new (higher) values for reserve need can be estimated at once.

Finally, we added the "buffer amount" to basic reserve need. This amount is expected to consist of different successional stages after stand-replacing disturbances (mostly windthrows), and as such it helps to fill the major gap in recently disturbed habitats in natural state (Lõhmus 2002). However, the buffer does not probably fulfil the need for burnt areas. We also admit that the total area of the "buffer" may be too small, especially in case of catastrophes, because we used the same (average) disturbance

probability for all years. In principle, annual variations in the areas of windthrows and (suppressed) fires could be introduced as stochastic components to the model, but the time frame and the level of acceptable habitat loss depend on public agreement, and were outside the scope of this paper. Despite these differences, theoretical minimum need for strictly protected forest in Estonia (8.5–11.3% of forest land) was strikingly similar to the estimated reserve need in hemiboreal Sweden (12%, out of which 1.9% are seminatural habitats; Angelstam and Andersson 1997, 2001). Therefore, we shall consider the applicability of the numerical results further.

Rule-of-thumb for reserve need?

The landscape-level estimates of needed reserve area depend critically upon three variables: 1) the baseline area; 2) the acceptable extent of original habitat loss; 3) the extent to which timber production creates "natural" habitats. In the simplest case for forest reserves, the existing forest area is taken as baseline and a rough estimate of habitat loss threshold (20% of original in our case) is applied to all units of forest land. Hence, the minimum reserve need equals the threshold if original habitat is completely incompatible with timber production, and less if it is only partly so. All current approaches admit that partial incompatibility is the case in northern Europe, and all numerical estimates of reserve need fall into a comparatively narrow range: 10–15% for "educated guesses" (Liljelund et al. 1992, Esseen et al. 1997) and 9–16% for calculations (Virkkala 1996, Angelstam and Andersson 2001, this study). Therefore, the general 10%-minimum level of strict protection, defined by the IUCN over twenty years ago (Anon. 1980), seems to hold and might be used as "a rule-of-thumb" for boreal forest landscapes if there is no time or data for detailed analyses.

At this stage of knowledge, estimates of acceptable extent of habitat loss (variable 2 above) could change future views on reserve need to the greatest extent. Although the tentative nature of mean threshold values has been admitted (e.g. Angelstam and Andersson 2001) and extinction thresholds can be much higher than fragmentation thresholds (Fahrig 2001), we stress that they are all just economically efficient solutions. What matters more for biodiversity, is the actual probability of survival. At least theoretically, the threshold probabilities may be unacceptably low (for example, < 95% for 100 yr). Hence, a problem for the future is to define the actual survival probabilities of sensitive species at threshold amounts of habitat, and to reach consensus whether the probabilities are ecologically and socially acceptable. However, this gap of knowledge should not prevent enlarging the forest reserve network immediately, because northern Europe has a long way even to the preliminary 10%-target. Moreover, the specific reserve gaps in Estonia can be eliminated very slowly even if the additional reserves were established today, since old forests currently occupy only one fourth of strictly protected forests and even less in potential reserves.

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Assessing actual landscapes for the maintenance of forest biodiversity – a pilot study using forest management data

Per Angelstam and Peter Bergman

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New values and policies related to the maintenance of biodiversity have led to a landscape perspective in Swedish forest management. As a result, data for ecological landscape planning have been compiled. The current challenge is to make strategic decisions about the relative efforts for the two main objectives set out in national and company policies for sustainable forest management: wood production and biodiversity being interpreted as the maintenance of viable populations of species.

We studied the usefulness of the data in forest management plans within Sveaskog Co. for ranking forest landscapes with respect to the opportunity for succeeding with the biodiversity objective. To identify the position of individual landscapes with respect to the policy gradient from nature conservation to production we used ordination techniques to illustrate four variables affecting the maintenance of biodiversity. These were: 1) differences in the fragmentation of the land ownership affecting the property rights of the physical landscape, 2) site type distribution, 3) the proportion of forest with high conservation value both in the landscape as a whole and 4) in the conservation areas already set aside.

The analyses strongly suggest that individual actual landscapes have very different chances of maintaining viable populations of all species, which is the goal of the Swedish forest policy. The ordinations indicate that the landscapes could be grouped into different categories, ranging from just a few with good chances of maintaining viable populations of specialised species (EcoParks), to the vast majority of landscapes having little forest with apparent high conservation value or fragmented ownership. The analyses support the "triad approach" of varying the management ambitions for production and conservation depending on a landscape's chances to maintain biodiversity in the long term. Finally, we discuss the need for improved data collection and active collaboration between scientists and managers to make sustainable forest management operational.

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After a long lasting focus on sustainable wood production the meaning of the concept of sustainable forest management is in the process of being redefined both in policy and practise (von Gadow et al. 2000, Sverdrup and Stjernquist 2002). Ultimately this transition aims at multifunctional ecosystem management (Schlaepfer and Elliott 2000), including a range of products and services ranging from the maintenance of biodiversity (Larsson et al. 2001) and protective functions (Kräuchi et al. 2000) to locally sustainable rural communities (Kennedy et al. 2001). This trend is particularly evident regarding forest management at northern latitudes, where the forests have served mainly as sources of wood for other more densely populated regions (Elliot and Schlaepfer 2001). In Europe, Fennoscandia is a good example of this. Here, according to the present policies, the maintenance of viable populations of all naturally occurring species is an important new aspect (Larsson and Danell 2001, Korpilahti and Kuuluvainen 2002).

In Sweden and Finland, active measures for the maintenance of viable populations of species, which have suffered from a long history of intensive forest management (Gärdenfors 2000), started with variable retention of trees and tree groups during harvesting at the stand scale in the 1980s (Ahlén et al. 1979). Later, especially during the 1990s, this development continued with the addition of a landscape perspective on habitat conservation and restoration (Lämås and Fries 1995, Angelstam and Pettersson 1997, Niemelä 1999, Angelstam 2003). Today, all large forest companies have developed ecological landscape plans with descriptions of their current status and ambitions for biodiversity maintenance (Angelstam and Pettersson 1997, Fries et al. 1998, Heinonen pers. comm.).

The word "ecological" implies both attempts to emulate natural disturbance regimes (Niemelä 1999, Angelstam 2002), and application of landscape ecological principles such as maintaining functional connectivity of habitat patches within landscapes (Angelstam et al. 2003a, b). The size of the landscape ecological planning units range from a few thousand to tens of thousands ha, and the total number of such plans amount to several tens to > 100 for each company. In Sweden, the collection of landscape data is a requirement of the forest certification scheme used by the large forest companies since the late 1990s (Elliott and Schlaepfer 2001), and the collection of the data for the landscape plans has just (2002/2003) been completed. Hence, there is currently a need to set cost-efficient priorities for protection, management, and restoration for different elements of biodiversity at different spatial scales ranging from trees and stands to landscapes and regions. This is consistent with the "triad" approach proposed by Seymour and Hunter (1999), whereby land is divided into zones of intensive forestry, of ecological forestry, and of nature conservation.

At the scale of landscapes and regions, two issues stand out as particularly important. First, given the long history of land use change in Sweden (Angelstam 2003), one should avoid losing existing high conservation value forests where maintenance of viable populations of specialised species is really feasible. Second, it could be efficient to focus on wood production in certain areas because 1) the landscape is already impoverished, and 2) rehabilitation would be costly, with 3) uncertain success of biodiversity conservation due to re-colonisation time-lags (Tilman and Kareiva 1997).

Ideally, given the complexity of the biodiversity concept (Larsson et al. 2001), detailed data ought to be collected across multiple spatial scales (Angelstam 1998a, b, Nilsson et al. 2001). As this is usually not possible in the real world, there is a need to develop transparent, robust, and understandable methods for the integration of the existing more general information with tools for rapid simple assessment, which the managers themselves can carry out (Uliczka et al. 2004). In a first step, such methods must rely on the basic forest management data collected about the forest within companies and organisations. Later, as improved data become available, such methods ought also be applied with increasing thematic and spatial resolution in an adaptive manner. In the long-term, assessment and decision-support systems, which integrate environmental, social, and economical aspects need to be developed (Ullsten et al. 2004).

So far, the ecological landscape plans have focussed on descriptions of the composition of different site types, forest vegetation types and age classes, as well as woodland key habitats (Norén et al. 2002), but without considering population viability of species in general, and species with landscape-scale habitat requirements in particular. Based on these data, plans for different types of management goals have been formulated. Depending on the set of values considered important in the particular region, both natural and cultural dimensions have been advocated (Angelstam and Pettersson 1997, Carlsson et al. 1998, Fries et al. 1998). However, the assessment of functionality in terms of the maintenance of viable populations of habitat set-asides has not been addressed systematically, except for some few demonstration studies where research and development projects have been involved (e.g., Angelstam et al. 2003b). Neither have altered ecosystem functions related to anthropogenic pollution been systematically considered (Sverdrup and Rosén 1998, Sverdrup and Stjernquist 2002).

Intensive use of forests in the past and/or at present poses a problem for the maintenance of viable populations of specialised species (Gärdenfors 2000) and ecosystem integrity (Pimentel et al. 2000). To address the level of functionality of managed forest landscapes for the maintenance of different elements of biodiversity, the degree of match between the landscape's management regimes and its natural dynamics has to be understood (Angelstam 2002). Hence, when making decisions about the future management of actual landscapes, ecologically based targets to which

measurements of components of biodiversity should be compared with increasing detail and at different spatial scales ought to be formulated. The presence of ecological thresholds (Muradian 2001), such as non-linear responses of species' populations to habitat loss (Fahrig 2001, 2002) and of ecosystems' resilience to the level of anthropogenic pollution (Brodin and Kessler 1992, Sverdrup and Rosén 1998, Sverdrup and Stjernquist 2002), provide a starting point for such true assessment of different elements of forest biodiversity (Karr 2000). With this quantitative and qualitative assessment approach, strategic decisions about where conservation of different elements of biodiversity of different forest ecosystems could be achieved with the lowest cost could be made.

In this paper we evaluate the usefulness of the data found in the forest management plans of Sweden's largest forest company Sveaskog Co. for ranking forest landscapes with respect to the opportunity for succeeding with the maintenance of viable populations of all naturally occurring species. We also propose and employ an approach for rapid assessment of the status of compositional and structural elements of forest biodiversity within a particular landscape by aggregating existing basic information on the amount and quality of forestland devoted to nature conservation across spatial scales. The present study is a first report from an ongoing effort encompassing the whole Sveaskog Co. with the aim to determine the relative nature conservation status in different ecoregions for all its ecological landscape plans in Sweden.

Sveaskog Co. and its forest

Sveaskog Co. is Europe's largest forestry company with ca 4.4 million ha of state-owned land throughout Sweden, of which ca 75% is productive forestland. This means that Sveaskog Co.'s land holdings comprise ca 18% of the total forest area in Sweden. The present holding is the result of the merging of two former state-owned companies, the old Sveaskog established in 1992 and AssiDomän, earlier named Domänverket, and buying a third private company named Korsnäs (see Fig. 1).

The holdings of the current Sveaskog Co. are divided into ca 150 ecological landscapes. For the long-term maintenance of forest biodiversity, ecological landscape planning is considered as one of the most important nature conservation measures. For example, the landscape planning process involves an evaluation of the quantity and quality of various environmental qualities such as age distribution of deciduous and coniferous forests within and among stands, landscape grain size and other data found in forest management data bases. Regular species inventories were not made. Based on such strategic analyses, the company can develop tactical forest management plans. These could involve favouring species, which require qualities and quantities that regular management cannot satisfy, or to re-create opportunities for species with poor dispersal abilities by aiming at connecting valuable areas with each other in the long term. Additionally, important ecosystem processes such as fire, creation of dead wood and flooding are actively supported by special management efforts (e.g., Angelstam and Pettersson 1997). Furthermore, landscape planning is a way to live up to the commitment to environmental goals through certification of the forestry practices.

In this paper the focus is on methodological development using 16 landscapes found in the Sveaskog Co. in the two southern ecoregions, the nemoral and hemiboreal zone (Fig. 1).

Swedish forest ecoregions

Sweden forms a latitudinal gradient between the 55th and 69th parallels. Latitude and altitude are two basic abiotic factors affecting organismal and ecological biodiversity. Being latitudinally extended, Sweden has a growing season that varies more than two-fold from the north (< 100 d) to the south (> 200 d). The altitude below which fine sediments rich in nutrients were deposited in the sea then covering parts of today's Sweden, and the distribution of lime-rich soils have a fundamental effect both on the natural potential vegetation and the forest loss due to agricultural development. Further, prevailing southwesterly winds and higher altitudes in the northwest than in the east produce distinct gradients in climate and natural disturbance regimes.

From south to north, the main natural Swedish vegetation types used for wood production are: 1) broad-leaved nemoral deciduous forest with beech *Fagus sylvatica*, oak *Quercus robur,* lime *Tilia cordata,* maple *Acer platanoides,* and ash *Fraxinus excelsior*; 2) a hemiboreal transition zone with mixed deciduous and coniferous forest; 3) a wide belt of boreal forest with Scots pine *Pinus sylvestris*, Norway spruce *Picea abies,* birch *Betula* spp., and aspen *Populus tremula* (see Fig. 1).

Human colonisation closely followed the retreating ice shield. However, the anthropogenic transformation of the landscape was considerably slower. Until the Medieval Period, Sweden was settled up to the border between hemiboreal and boreal forest in the interior, and far north along the coast of the Baltic Sea in the east (Jokipii 1987). Starting ca 150 yr ago, large-scale logging was extended gradually into the interior of north Sweden (Angelstam 1997). Consequently, the deciduous forest in the nemoral zone in southermost Sweden has a very long history of land use (> 5000 yr; Berglund 1991), and thus ecosystem alteration and loss. By contrast, the boreal and subalpine forests in the north have much shorter histories of intensive land use (<200 yr; Angelstam 1997, Esseen et al. 1997).

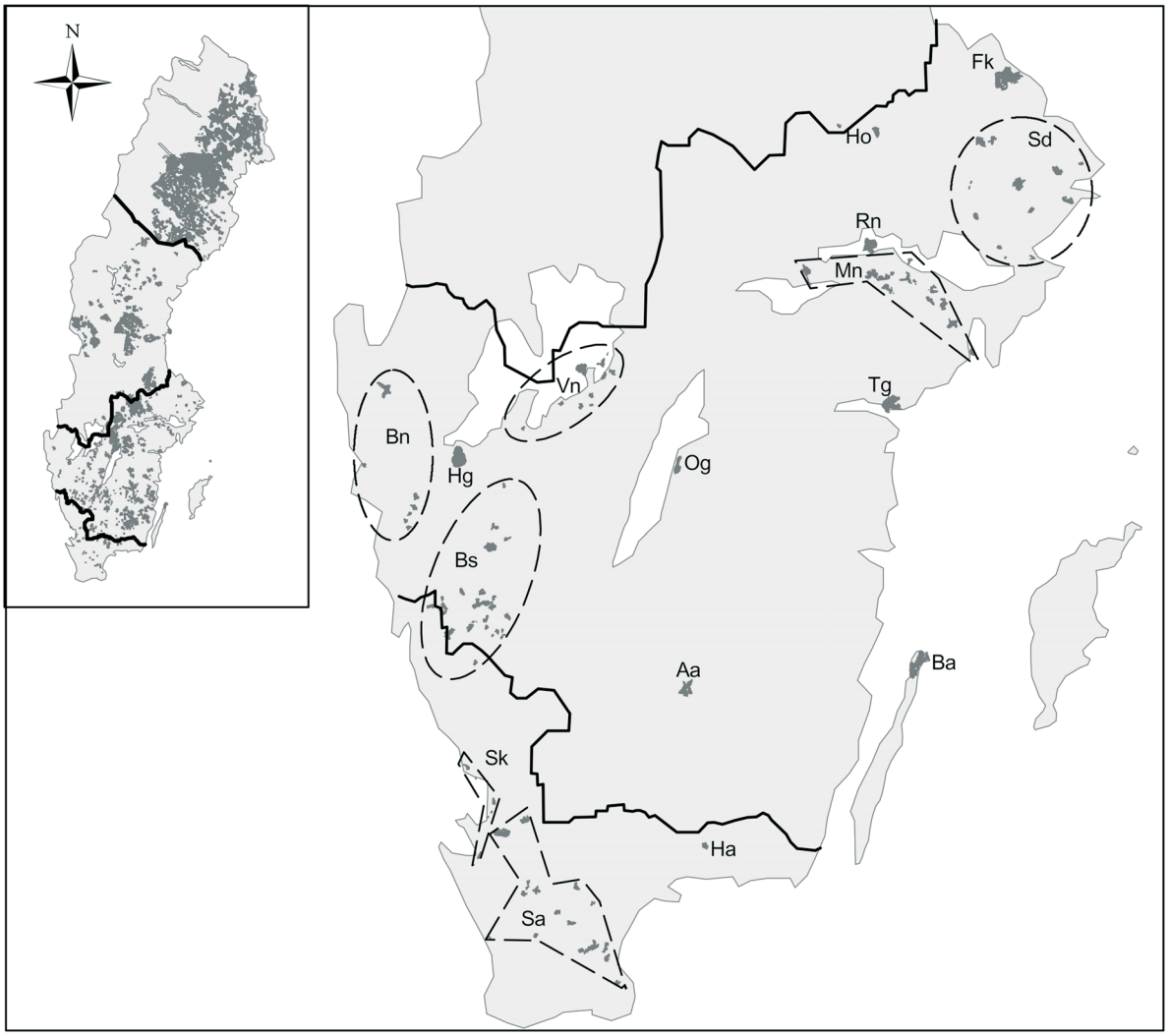


Fig. 1. Map of southern Sweden and the distribution of the holdings in the 16 Sveaskog Co. landscapes analysed in this study. The names of the landscapes are denoted with a two-letter code explained in Table 3. The inset map shows Sweden with the distribution of land owned by Sveaskog Co. after 2002.

Material and methods

Ecological landscape descriptions

The basic quantitative information in the landscape plans is the stand database describing the wood resource based on field inventories about the site conditions and tree species composition in different age classes (Jonsson et al. 1993). In addition, specific inventories have been made of high conservation value forests such as national nature reserves, company reserves, woodland key habitats, and areas set aside in landscape ecological plans as buffer zones and riparian corridors.

To specify the relative objectives in terms of wood production and biodiversity management in forest stands with different site conditions, the National Board of Forestry has developed a system for management ambition attributes to be used along with the traditional wood production information in the forest management plan. Currently four management attributes imply a gradient in the relative importance of wood production and biodiversity management; viz.; PG (production goal with general environmental considerations); PF (production goal with reinforced environmental considerations); NS (nature conservation goal with management); NO (nature conservation goal based on no management).

Based on these data sets, landscapes can be ranked with respect to the potential in terms of habitat structures at multiple spatial scales for maintaining viable populations of species as is stated in both the national and company policies. The landscape plans thus contain one detailed empirical field data set, and one data set encompassing a coarse classification of the stands' relative potential to fulfil the forest production and nature conservation objectives. We assume that a landscape's conservation value for a wide range of species with different specialisations should be considered to be higher if: 1) the land ownership is more contiguous, i.e. less fragmented; 2) the size is large; 3) the area with biologically old forest of different forest vegetation types is high, and 4) the proportion of the areas set aside for nature conservation is high. Additionally, we compiled and analysed shorthand information in the management objective classification using an index method with the highest rank for landscapes with a high proportion of forest stands specially assigned as conservation areas. The variables used in the ordinations and simple assessment are listed in Table 1.

Which landscape plans encompass actual landscapes?

Landscape planning data usually consist of numerical summary data describing the total area of different forest vegetation types and age classes. However, the degree to which these data come from a contiguous actually owned landscape differs among the landscape plans and ecoregions. Usually the archipelago of owned forest land within individual landscape plans is more fragmented in the southern than the northern part of Sweden (Fig. 1). To find out to what extent landscape plans also constitute physically connected landscapes over which Sveaskog Co.

Table 1. Description of the variables available in Sveaskog Co.'s database for the structure of forest landscapes at different scales, and the ones that were used for the PCA ordination and rapid assessment using the threshold index approach, TSL. The numbers following all the PCA variables correspond to the same numbers in Figs 2B–5B.

Variables used for the detailed quantitative analysis (PCA)	Variables used for the rapid assessment (TSL-index)
Used in the first PCA (Fig. 2):	Proportion of general and reinforced stand scale variable retention of trees and clumps
Area of forestland (1)	
Proportion of the actual landscape owned by the company (2)	Proportion of forest land with nature conservation goals, NO and NS
Number of fragments of ownership (3)	
Used in the second PCA (Fig. 3):	Woodland key habitats
Proportion of forest on shallow soils (4) and other poor sites (5)	Nature reserves
Proportion of bog (6) and infield (7)	
Proportion of dry (8), mesic (9), moist (10) and wet (11) forest land	
Proportion of vegetation type herbs (12), grass (13), *Vaccinium myrtillus* (14), *Vaccinium vitis-idaea* (15), *Empetrum nigrum* (16), lichens (17) and *Carex* (18)	
Used in the third PCA (Fig. 4):	
Proportion deciduous (19), *Betula* (20) and broadleaved tree species (21)	
Proportion of pine (22), spruce (23) and pine/spruce (24) forests older than 120 yr	
Proportion of pine (25), spruce (26) and pine/spruce (27) forests mixed with deciduous and older than 80 yr	
Proportion of forest dominated by deciduous older than 80 yr (28)	
Proportion of deciduous forest older than 80 yr (29)	
Used in the fourth PCA (Fig. 5):	
Nature reserves (30)	
Woodland Key Habitats of two types (31 and 32)	
Proportion of forest land with nature conservation goals, NO and NS (33)	

has jurisdiction, we calculated the number of fragments and area proportion of all the owned patches within the polygon containing all the forest ownership patches of a particular landscape plan (i.e., variables 2 and 3, Table 1). A value of 1 means complete control of the actual landscape and lower values less control of the management of the actual landscape.

Ordination

Principal component analysis (PCA) is a multivariate projection method used to extract and display variation in data in order to recognize patterns concealed in a matrix of many tabular variables (Eriksson et al. 2001). The PCA was done using the SIMCA-P 10.0 software (Umetrics). Prior to PCA the variables were scaled using unit variance scaling followed by mean-centering (Eriksson et al. 2001). In a PCA two kind of graphical plots are considered: 1) the score plots visualizing the similarities of the observations (in our case the 16 ecological landscapes) and 2) the loading plot showing the relationships of all variables used and their impact on the two principal components (Table 1).

The principle of a habitat threshold index – the TSL model

Maintenance of viable populations requires a minimum proportion of habitat exceeding a certain threshold (e.g., Fahrig 2001, 2002). Hence, the amount of habitat, and whether it forms functional habitat networks or not, needs to be assessed at the landscape scale (Puumalainen et al. 2002). Of course this can only be done with accuracy for one species or possibly guild at a time (Angelstam et al. 2003b, 2004). However, in land use management there is considerable variation in the range of spatial domains of different actors. For example non-industrial small private forest owners focus on the stand scale, while companies have the potential to manage actual landscapes. Indeed, traditional forest management is focussed on timber production and operates almost exclusively at the stand level (Jonsson et al. 1993, Holmgren 1995). By contrast, the maintenance of biodiversity requires that all spatial scales be considered (Larsson et al. 2001). From the perspective of maintaining well-connected representative networks of the naturally occurring forest vegetation types one therefore needs to understand what the total outcome of protected areas, stand-scale management and variable retention will be in a landscape. Because the forests within a particular actual landscape usually have many owners, it is necessary to quantify how each different owner category uses different combinations of different management methods.

Hence, ideally, the efforts of different actors to emulate natural and anthropogenic disturbance regimes of pre-industrial natural and cultural landscapes in terms of maintaining structural elements of importance for the maintenance of viable populations, should be aggregated across all spatial scales. This includes trees/patches in a stand, stands in a landscape and landscapes within an ecoregion. Such an evaluation should be made for each main forest vegetation type separately. Moreover, to understand the total consequences of management for biodiversity, the efforts of all actors across spatial scales need to be aggregated for each forest vegetation type by providing quantitative answers to the questions in Table 2. Given the large amounts of spatially explicit data needed this is not even feasible within case studies such as large research projects (e.g., Angelstam et al. 2003b). In practical management, therefore, it is necessary to use the existing but coarse data.

We propose that for assessing the status and trends in the proportion of forests of different types in actual landscape, which is devoted to the maintenance of viable populations of species, the aggregated result (i.e., an INDEX) of answers to the questions in Table 2 across the three spatial scales tree, stand and landscape ought to be estimated. Additionally, correction factors describing the efficiency of conservation considerations at each spatial scale in each main forest ecosystem (FOR_X i to j) should be made. Finally, the total proportion of functional habitat could be compared with performance targets based on the habitat

Table 2. Questions that need to be answered to assess the status of forest diversity of a typical Swedish landscape with a mixture of different actors.

	trees in stands (T)	stands in landscapes (S)	landscapes in regions (L)
private owner forest company public owner regional planner	How much of natural stand-scale tree components are left during different silvicultural treatments? (e.g. snags, downed wood, living trees)	How natural are the remaining forests? (e.g. the degree of fit between the ecological and wood production management dimensions)	How much former forested land remains un-cleared for other kinds of land use? How representative and connected is the system of conservation areas?

thresholds for focal species with different degree of specialisation at each spatial scale (e.g., Angelstam et al. 2004). The principal procedure is summarised in the following formula,

$$\text{INDEX for } \sum_{i}^{j} \text{FOR_X} = \left(\frac{aT}{\text{threshold_T}} + \frac{bS}{\text{threshold_S}} + \frac{cL}{\text{threshold_L}} \right),$$

where T is the proportion of structural considerations at the scale of trees in stands such as residual trees and stands within clear-felled areas of particular forest vegetation type, S is the proportion of stands within a landscape, which partly or completely are devoted to nature conservation, and L is the proportion of protected areas. The letter a is a constant describing the quality of the structural consideration within stands, b is a constant describing the functionality of the stands set aside for conservation and the degree of match between the forest ecosystem dynamics and the chosen management regime, and c is a constant describing the functionality (e.g., representation and connectivity) of the network of forest habitats within the actual landscape. The thresholds should represent the proportion of a certain stand structure or forest stand type required to maintain focal species within the landscape or region (e.g. Angelstam et al. 2004). With an appropriate calibration of the formula, the INDEX would be <1 if below the thresholds for the maintenance of focal species of conservation concern at each spatial scale and >1 above such thresholds. In this way it would be possible to know in which landscapes the situation requires habitat restoration and where the forest management intensity could be intensified. This approach would also alleviate the evaluation of different combinations of management methods at different spatial scales.

Using the information about the relative proportion of different management objective classes in each landscape, we compiled the existing information, analysed it using the TSL-model, and evaluated the existence of gaps in the data collection for assessing landscape plans. The TSL-index was estimated for each of the 16 landscapes by setting the area of forest in nature reserves as L, area of woodland key habitats and stands with high conservation values (NO and NS) as S, while the proportion of general and reinforced considerations in terms of variable retention of trees and stands were summed as T.

Results

Ordinations using quantitative forest data

Ownership fragmentation

The three variables chosen to illustrate the spatial configuration of the land encompassed by a landscape plan were 1) the total area of forest land, 2) the proportion of the actual landscape owned by the company, and 3) the number of fragments of ownership (see Table 1). The ordination of the 16 landscapes resulted in three groups (Fig. 2A). These are named FRAGMENTED (large landscapes, low cover, many fragments); INTERMEDIATE (middle-sized to small landscapes, small cover, many fragments); and CONTIGUOUS (one fragment with different sizes). The four largest ones were Forsmark (Fk), Halle-Hunneberg

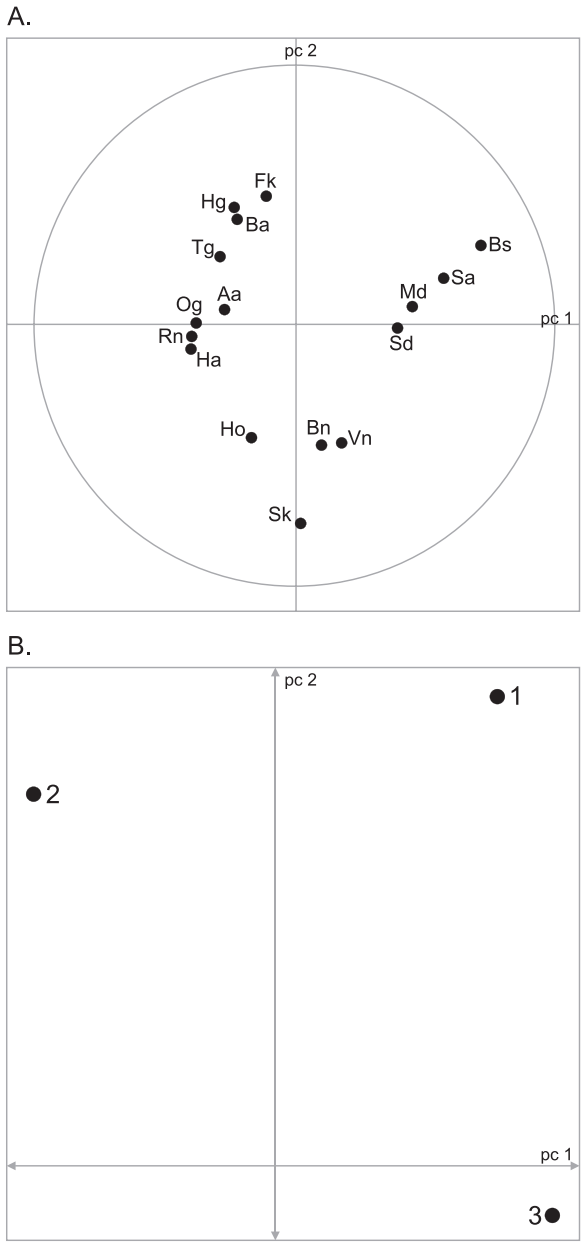


Fig. 2. Principal component analysis using data concerning ownership fragmentation. A. The score scatter plot showing the 16 landscapes (cf. Table 3). B. The loading plot with the variables used (see Table 1) and their contribution to principal component 1 and 2.

(Hg), Böda (Ba) and Tunaberg (Tg). It should be noted that the fragmentation being measured here was entirely fragmentation of ownership. The relationships of the variables and their impact on the landscape ordination are shown in Fig. 2B.

Site type

Using variables describing soil moisture and covering the ground vegetation (see Table 1) the second ordination produced a gradient along the second principal component (PC2) from Böda (Ba) (poor soils) and Bohuslän (Bn) (shallow soils) on the one hand, to the Skåneåsarna (Sa) (wet with herbs) in southernmost Sweden on the other (Fig. 3A). Several of the landscapes were in one cluster along the first principal component and thus did not separate well along the second component. Figure 3B shows the relationships of the 15 variables and their impact on the two principal components.

Landscape quality

Landscapes with high value for biodiversity maintenance were defined as those with more deciduous forest and more old forest. Including the mixed forests we used a total of 11 variables in Table 1 that contained information about proportion of deciduous and broad-leafed species (3 variables) and the age of different forest vegetation types (8 variables). The third PCA resulted in one group with 5 landscapes (Asa (Aa), Hallarsbo (Ho), Hjärtsjömåla (Ha), Vänerkusten (Vn), Tunaberg (Tg)) with low conservation value due to the lack of older forests (Fig. 4A). From this group, a loose cluster with older mixed-deciduous forest stands extends down to the left, ending with Halle-Hunneberg (Hg). Finally, Skåneåsarna (Sa) and Ridön (Rn) stand out as having a very large proportion of deciduous trees, which strongly affect the separation among the other landscapes. However, when removing the two latter landscapes from the analyses, Böda (Ba) with a high proportion of old pine forest, and Skyddsskogarna (Sk) with the highest proportion of deciduous trees in general stand out as being special. The relationships of the variables and their impact on the principal components are shown in Fig. 4B.

Protected areas

To describe the proportional area of a given ecological landscape plan that has been allocated to conservation we used four variables (stands with high conservation value; i.e. NS and NO, woodland key habitats and protected areas; Table 1) in a fourth principal analysis. In the ordination of the 16 landscapes, Böda (Ba), Ridön (Rn) and Halle-Hunneberg (Hg) were the most extreme examples due to their high proportion of protected areas (Fig. 5A). Additionally there was a gradient along the second principal component ranging from landscapes with a higher proportion of smaller conservation areas (Borås, Bs) to a low proportion (such as Hallarsbo, Ho and Asa, Aa). Figure 5B shows the relationships of the variables and their impact on the two principal components in the ordination.

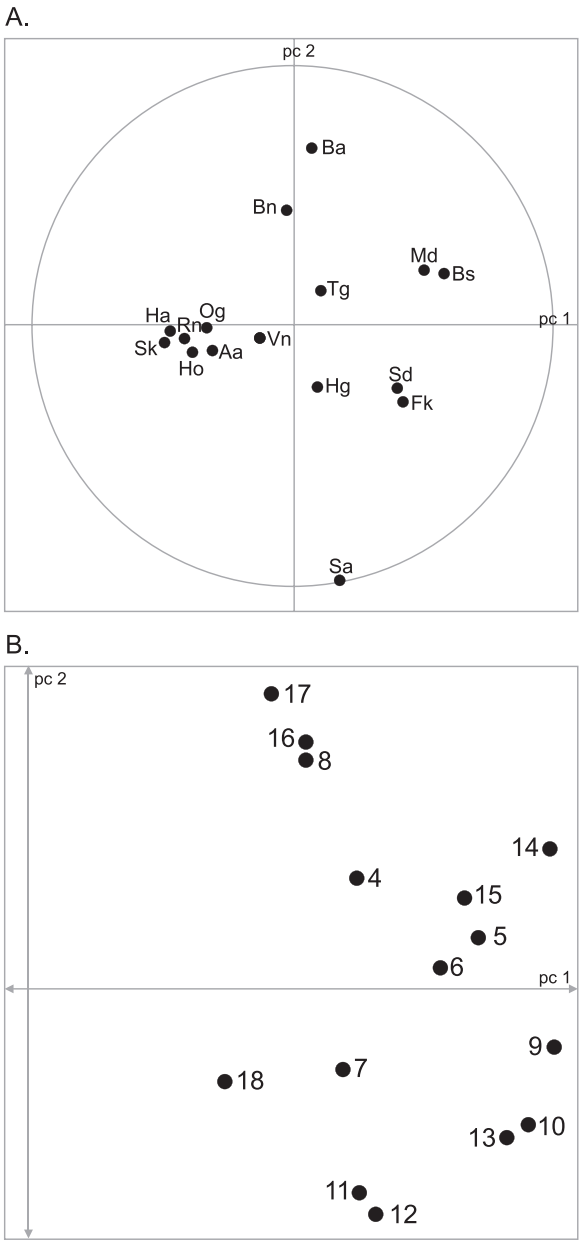


Fig. 3. Principal component analysis of site type. A. The score scatter plot showing the 16 landscapes (cf. Table 3). B. The loading plot with the variables used (see Table 1) and their contribution to principal component 1 and 2.

Relative importance of different factors

Using the four ordination diagrams in Figs 2–5 we ranked the landscapes according to their importance for conservation (Table 3). Landscapes labelled medium in the first ordination concerning fragmentation were given the value 0, while those labelled contiguous and fragmented were given +1 and –1, respectively. The second ordination (site type) did not contribute much due to little separation of the landscapes along the two principal component axes, and thus all landscapes but one were assigned the value 0. This was Skåneåsarna (Sa) with a very nutrient rich site type given the value +1. In the third (landscape quality) and fourth (protected areas) ordinations, the values –1, 0 and +1 were given for the landscapes ranked as low, medium and high, respectively. By doing this qualitative analy-

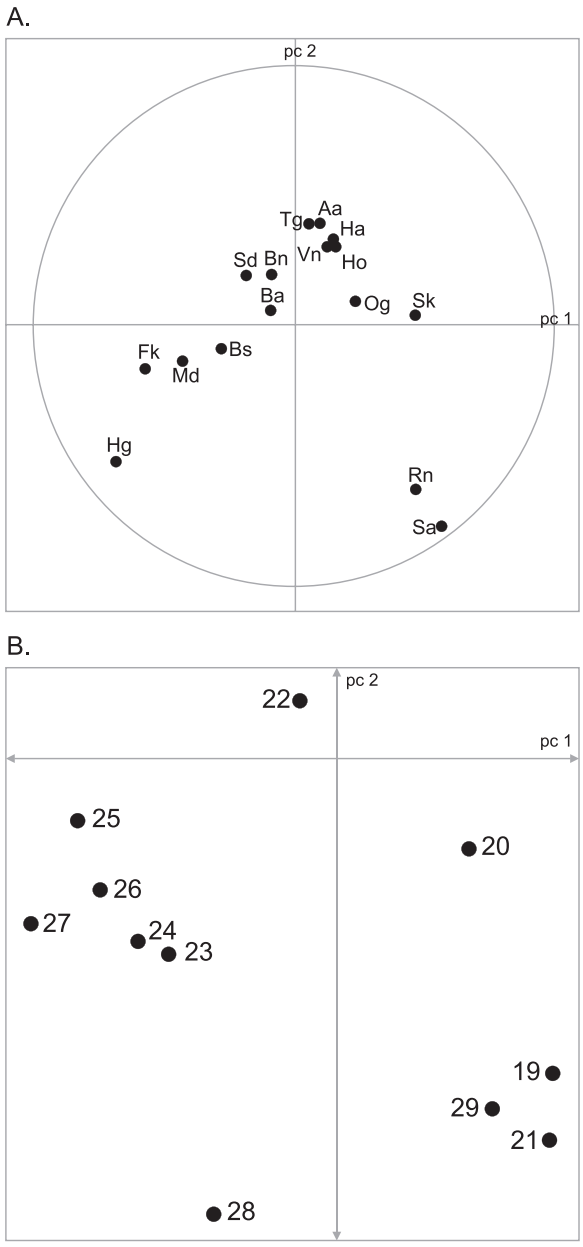


Fig. 4. Principal component analysis with respect to landscape quality. A. The score scatter plot showing the 16 landscapes (cf. Table 3). B. The loading plot with the variables used (see Table 1) and their contribution to principal component 1 and 2.

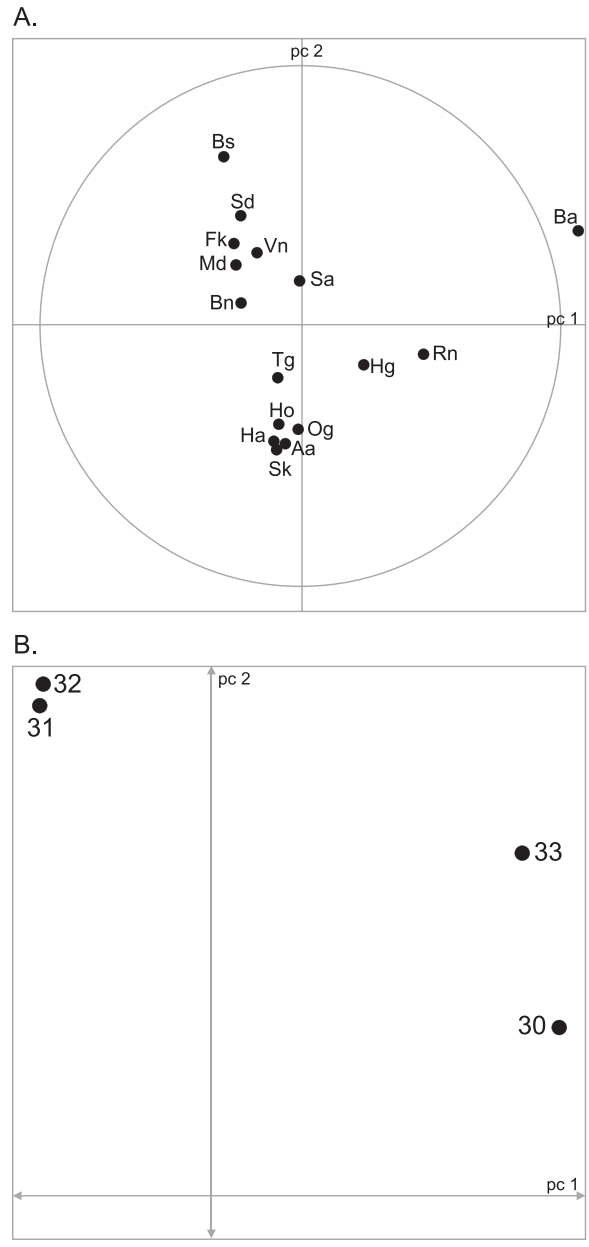


Fig. 5. Principal component analysis of with respect to proportion protected forest. A. The score scatter plot showing the 16 landscapes (cf. Table 3). B. The loading plot with the variables used (see Table 1) and their contribution to principal component 1 and 2.

Table 3. Summary of the results from the ranking of actual landscapes with respect to the forest policy goals for wood production and nature conservation. The final classification is made by summing the ranking for the level of fragmentation measured as the proportion of the actual landscape owned by the company (Fig. 2), site type (Fig. 3), landscape quality (Fig. 4) and proportion of protected areas (Fig. 5). Based on the total rank we tentatively assigned landscapes as most suitable for wood production (WoodProd) or nature conservation (EcoPark), or of intermediate nature (Intermed). ID refers to landscapes in Fig. 1.

Landscape	ID	Ownership fragmentation	Site type	Landscape quality	Protected areas	Tentative classification
Asa	Aa	Medium	Mesic	Low	Low	WoodProd
Böda	Ba	Contiguous	Dry	High	High	EcoPark
Bohuslän	Bn	Medium	Dry	Medium	Medium	Intermed
Borås	Bs	Fragmented	Mesic	Medium	Medium	WoodProd
Forsmark	Fk	Contiguous	Mesic	High	Medium	EcoPark
Hallarsbo	Ho	Medium	Mesic	Low	Low	WoodProd
Halle-Hunneberg	Hg	Contiguous	Mesic	High	High	EcoPark
Hjärtsjömåla	Ha	Medium	Mesic	Low	Low	WoodProd
Mälardalen	Mn	Fragmented	Mesic	High	Medium	Intermed
Omberg	Og	Medium	Mesic	Medium	Medium	Intermed
Ridön	Rn	Medium	Mesic	High	High	EcoPark
Skåneåsarna	Sa	Fragmented	Rich	High	Medium	EcoPark
Skyddsskogarna	Sk	Medium	Mesic	High	Low	Intermed
South Uppland	Sd	Fragmented	Mesic	Medium	Medium	WoodProd
Tunaberg	Tg	Contiguous	Mesic	Low	Low	WoodProd
Vänerkusten	Vn	Medium	Mesic	Low	Medium	WoodProd

sis with a nature conservation perspective, numeric values were given to a landscape resulting in a positive or negative sum. This sum was then used for a tentative classification, which could be used for ranking the landscapes with respect to their relative suitability for management in the gradient from wood production to nature conservation (Table 3). Thus, landscapes with a positive sum were landscapes with high nature conservation values, and denoted as EcoParks. These are Böda (Ba), Forsmark (Fk) and Halle-Hunneberg (Hg) all of which stand out as being contiguous landscapes with high quality, mainly due to high age. For the landscapes Ridön (Rn) and Skåneåsarna (Sa) the fragmentation was larger but still with high landscape quality due to higher age and larger proportion of deciduous tree species. At the other extreme, there was a group with seven landscapes with a negative ranking sum. These are denoted with WoodProd in the tentative classification in Table 3. These landscapes have low qualities with the respect to nature conservation but, of course, high values in the respect of producing wood. Finally, 4 of the 16 landscapes summed up to 0, which gave them the tentative classification term "Intermed".

Rapid assessment using the threshold index

The average index value was 0.18, but ranged from 0.09 to 0.87. However, most landscape were remarkably uniform, except Böda (Ba) and Ridön (Rn) with large areas of protected forest (Fig. 6).

Discussion

Ranking landscapes for applying the "triad" approach

Using the data available in the landscape plans our analysis in southern Sweden clearly suggests that different landscapes have different chances of maintaining viable populations of all species, i.e. including those specialised on forests with a high level of naturalness (sensu Peterken 1996) as stated by the forest policy. The ordinations indicate that the landscapes can be grouped into different categories, ranging from those that have higher chances of maintaining viable populations requiring forests with a higher level of naturalness, to those that have little near-natural forest vegetation types of apparent conservation value and that are fragmented. The best examples of the former were characterised by either having an unusually large proportion of old pine forest such as Böda (Ba), contiguous deciduous forest as Forsmark (Fk) and old forest as Halle-Hunneberg (Hg). Two other interesting landscapes from a conservation point of view were those with considerable proportions of old broad-leaved forest, namely Ridön (Rn) and Skåneåsarna (Sa). Using the TSL-index, a similar pattern was observed with Böda (Ba) and Ridön (Rn) standing out as the ones with the highest proportion of protected forest. These results provide support for the usefulness of the approach for rapid assessment of the current conservation values, but also illustrates that the human footprint on the south Swedish forest is heavy. The tentative use of

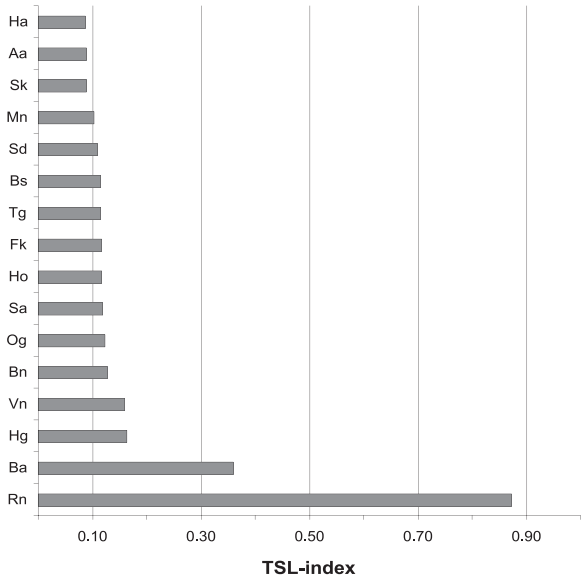


Fig. 6. Ranking of the 16 landscapes using a simplified version of the TSL-index approach.

the threshold index approach shows 1) that the actual status of the structural diversity in the landscapes was highly variable, and 2) that there are both data and knowledge gaps meaning that the index can still not be applied with sufficient resolution. Nevertheless, we feel encouraged to pursue the development of the TSL-model as we believe that attempts to sum up the nature conservation efforts made at multiples scales, whether or not these efforts are called forest and conservation management or nature protection, is a big advantage. In particular the TSL-index approach provides opportunity for showing that biodiversity maintenance can be achieved by using a variety of combinations of conservation management and nature protection efforts at different spatial scales. Even if most of Sweden for historic reasons by and large is restricted to efforts at the scale trees and stands, i.e. the Swedish model (Ekelund and Liedholm 2000, Angelstam 2003), regions and countries with other conditions could choose other combinations.

Ecosystem restoration is also needed

In 2002, according to a new environmental policy, Sveaskog Co. decided that 20% of the productive forest land is to primarily focus on nature conservation. This aim applies to each forest ecoregion (e.g. boreal, nemiboreal, nemoral), but not to each landscape within each ecoregion. The fifth ecoregion, the subalpine forest in northwestern Sweden, is excluded from the new environmental policy, and is treated in a separate policy.

An analysis of gaps in the proportion of forest available to meet the long-term environmental goals of the national forest policy (Angelstam and Andersson 2001) suggested large gaps in the proportion of forest required for the maintenance of viable populations in the nemoral and hemiboreal zones. This is a challenge requiring strategic decisions for rehabilitation, restoration and even re-creation, which ought to be balanced with the chances of succeeding with such efforts in the long term. The state of the landscapes studied suggest that it would not be optimal to set the same goal for all landscapes, but rather that strategic decisions should be based on how successful the national and company production and production policy objectives, respectively, in the policy can be within the individual landscape. We argue that restoration management should be concentrated in those landscapes that have been identified as hosting forest vegetation types that are in limited supply in managed landscapes. The clear difference among the ecological landscape plans with respect to the level of fragmentation of the holding is an additional factor to bear in mind.

At the tactical level we argue that more stands than today in landscapes such as Forsmark (Fk), Halle-Hunneberg (Hg) and Skåneåsarna (Sa) should be allocated for appropriate management to increase the proportion of natural forest structures in the actual landscape (sensu Peterken 1996). At the operational level the management advice should reflect both the local site type and associated forest vegetation type as well as the regional connectivity of the particular habitat today, and in the future. Inventories of specialised species could be used to assess the success of habitat restoration and subsequent improvement in population viability of representative groups of species as well as individual focal species.

Our analysis hence support Sveaskog Co.'s environmental policy of identifying the landscapes with the highest conservation values, thus avoiding the loss of remaining high conservation value forests, as well as identifying those with the lowest values and designating them as production landscapes. In this way also a third group will be identified, the landscapes with intermediate conditions. We suggest the implementation of the policy should be performed so that the quantitative target is met as an average for an ecoregion, thereby allowing for variation among the landscapes within a region. To address the multi-functionality of landscapes the availability to urban people is another criterion that could merit a particular landscape as being subject to conservation management for public educational purposes. Omberg and Halle-Hunneberg, which have together received ca 800 000 visits per year, are good examples of such landscapes.

Improving data and analyses

Using existing forest management data we attempted to integrate them using the TSL-index approach. Our analysis showed that the information in the management plans does provide useful information. To some extent this index

summarises today's situation regarding protected areas. However, to assess the future development in forest structure, improvements in the collection of forest data at the scale of trees, stands and landscapes are needed. This is consistent with a general need to know more about the quality of the matrix around conservation areas and complement the legacy of age class definitions being based on production (< 120 yr) rather than ecological aspects (usually > 150 yr). This includes an improved resolution regarding what is actually achieved within each of the management objective classes PF, PG, NS and NO. Additionally, data on dead wood of different kinds (Siitonen 2001), vertical vegetation structure (Åberg et al. 2003) and a better resolution of tree species and age classes ought to be collected (Angelstam et al. 2003b). Similarly, the traditional forest stand data are not ideally suited for estimating the future conservation value as indicated by an abundance of young broad-leaved trees in the shrub layer of an old planted spruce forest, as is the case for the landscape plan for Omberg.

Sustainable forest management is at a crossroads internationally (e.g, Schlaepfer and Elliott 2000). In Sweden, the issue of how to maintain biodiversity is a major issue (Angelstam 2003), while in other regions the problems are much more complex (Neet and Bolliger 2004, Dönz-Breuss et al. 2004). Having identified which landscapes have the highest probability of succeeding with the implementation of the nature conservation policy, the next issue to address it the functionality of habitat networks aimed at maintaining biodiversity in those landscapes. This means that spatially explicit analyses need to be done for each main forest vegetation type (Angelstam et al. 2003b, 2004). Similarly, the traditional hierarchical planning procedure for wood production used among Swedish forest companies (Jonsson et al. 1993) is now being challenged with the need for spatially explicit planning (Bettinger et al. 1996, Nalli et al. 1996, Carlsson et al. 1998, Öhman 2001).

Succeeding with an extended collection of data and use of new analytical tools requires an openness of the company to adapt and modify management continuously with the aim of promoting institutional learning. The concept of Adaptive Management Experiment Teams (Boutin et al. 2002), which includes active long-term collaboration between scientists and managers representing different elements of sustainability and the comparison of multiple management alternatives using experiments and simulation tools, is an essential approach. We argue that national and international twinning with several proactive companies in regions with different conditions and solution would be an effective approach to promote sustainable forest management in practice.

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Habitat modelling as a tool for landscape-scale conservation – a review of parameters for focal forest birds

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We propose how quantitative knowledge about specialised birds and spatially explicit land cover data describing the terrestrial vegetation can be used to build Habitat Suitability Index models for the assessment and planning of representative habitat networks at the scale of landscapes and regions. Using specialised forest-dwelling species listed in the EC Birds directive, we review the quantitative knowledge, and identify knowledge gaps, about the requirements of species at different spatial scales from individuals to local populations. We also assess to what extent the selected species cover different forest types and ecoregions associated with the drainage basin of the Baltic Sea. We then use this information to estimate the tentative size of planning units for the assessment of habitat networks aimed at maintaining biodiversity.

The estimated mean minimum size of planning units where suitable habitat dominate the landscape was ca 40 000 ha, while in managed landscapes with minimum amount of habitat the unit size averaged 250 000 ha. By contrast, the size of individual conservation areas such as woodland key biotopes and protected reserves from which habitat network can be built in a managed matrix was ca 1–1000 ha. We conclude that when managing for the maintenance of forest biodiversity there is a need to extend the spatial and temporal scale from the stand scale to that of landscapes within large management units. Finally, we discuss perspectives and limitations in using ecological knowledge about birds, landcover information and GIS-modelling as an integrated tool for tactical conservation planning.

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In response to society's concern about the world's forests, considerable attention has recently been drawn to the need for sustainable forest management (e.g., Salem and Ullsten 1999, Kennedy et al. 2001) including the maintenance of representative networks of conservation areas (e.g., Margules and Pressey 2000, Angelstam and Andersson 2001). Consequently, there has been an increased focus on trying to understand the ecology of forest ecosystems (e.g., Barnes et al. 1998, Hunter 1999, Angelstam 2002). The emerging knowledge about the patterns and processes of natural forests and woodlands has resulted in a "natural disturbance paradigm" for forest ecosystem management (Peterken 1996, Angelstam 1998, Hunter 1999, Bergeron et al. 2002), based on the key assumption that native species have evolved under natural disturbance conditions.

The potential vegetation in most of temperate and boreal Europe is forest (Mayer 1984, Larsson et al. 2001). There are, however, different kinds of forest environments to which species have adapted. Consequently, viable populations require the presence of all naturally occurring forest environments in appropriate quality and in sufficient amounts (e.g., Jonsson and Kruys 2001, Larsson and Danell 2001, Korpilahti and Kuuluvainen 2002). The alteration, fragmentation and ultimately loss of one or several of these forest environments may threaten many of these species (e.g., Tucker and Heath 1994, Stanners and Bourdeau 1995, Anon. 2000). Such threats apply to both natural forest types per se (e.g., Larsson et al. 2001), and to anthropogenically maintained woodlands and other ancient cultural landscapes with trees (Kirby and Watkins 1998).

The maintenance of viable populations of all naturally occurring species can not be achieved with a fine-grained filter strategy only, i.e. by working on a species-by-species level (Hunter 1999). Additionally, coarse-grained approaches to management are needed, whereby representative disturbance regimes and forest types in the managed landscape are maintained in the form of functional networks (Perrera et al. 2000, Lindenmayer and Franklin 2002, Scott et al. 2002). To maintain and build such habitat networks in a landscape or a region, three aspects should be sufficiently well known: 1) the dynamics of natural disturbance regimes and resulting forest environments to which species have adapted (Angelstam 1998, 2002, Kuuluvainen 2002); 2) the quantitative requirements of specialised species at the level of individuals and populations (Verner et al. 1986, Scott et al. 2002); 3) the present amount and spatial distribution of the different naturally representative forest types in the landscape. With this information it would be possible to assess the quality of today's habitat networks, and to identify possible gaps to be considered for habitat restoration or re-creation in whole landscapes (Angelstam and Andersson 1997, 2001, Pressey and Olson in press, Lõhmus et al. 2004).

Communication with managers on the complex and often abstract criteria for selection of individual areas to be parts of a functional habitat network would be alleviated if the principles were dressed in simple words, for example by using a set of specialised species and their habitat requirements as a tool. Plants and fungi have been successfully used as indicators of stands of high conservation value (Nitare and Norén 1992, Hansson 2001). However, to communicate the complex habitat requirements at multiple scales for the maintenance of viable populations, animals are more suitable than plants and fungi. For example, many animals range over spatial scales compatible with those of forest management. In particular, birds represent one of the best studied taxonomic groups of animals (Flade 1994, Tucker and Heath 1994). Many larger birds are also well known by managers and some may even function as flagship species, i.e. species useful for stimulating public interest in conservation (Simberloff 1998). More specifically, we are inspired by the focal species approach proposed by Lambeck (1997), which is consistent with the umbrella species concept (Fleishman et al. 2000). This approach aims to protect biodiversity by satisfying the needs of a suite of sensitive species for different attributes of the landscape.

The aim of this paper is to propose how quantitative knowledge about specialised birds and spatially explicit land cover data describing the terrestrial vegetation can be used to build systematic suites of landscape-scale Habitat Suitability Index models (e.g., Verner et al. 1986, Scott et al. 2002) for the assessment and planning of representative habitat networks at the scale of landscapes and regions (see Angelstam et al. 2003, unpubl.). Using the species listed in the Annex 1 of the European Community Council Directive on the Conservation of Wild Birds (Anon. 1979; hereafter termed "EC Birds Directive") and a few additional species of concern, we review the quantitative knowledge, and identify knowledge gaps, about the requirements of forest-dwelling specialised species at different spatial scales from that of the individual to that of local populations. We also assess to what extent the species of the EC Birds Directive cover different forest types and ecoregions. Finally, we use this information to estimate the tentative size of planning units for the assessment of habitat networks aimed at maintaining biodiversity.

Methods

A general methodology for habitat suitability index modelling applicable to management

With new objectives such as the maintenance of biodiversity, land managers are faced with the challenge of using their data for partly new purposes. For example, in forestry the development of landscape ecological plans (e.g., Angelstam and Pettersson 1997), means that forest management data are being used to assess the conservation value of forests based on tree species composition, age classes and

patch sizes of forest stands in the landscape. To evaluate the extent to which existing habitat networks also are functional, there is a need to develop procedures for asssessing networks of conservation areas, and subsequently use that as a basis for planning of conservation and restoration measures.

There are a multitude of factors that affect the distribution and abundance of a species. For operational planning purposes, however, one needs to simplify. Habitat suitability index (HSI) modelling consists of combining spatially explicit land cover data with quantitative knowledge about the requirements of specialised species and building spatially explicit maps describing the probability that a species is found in a landscape (Verner et al. 1986, Brooks 1997, Scott et al. 2002). With adequate data on a suite of particular focal species, a series of predictive landscape models for the different vegetation types can be built. This requires quantitative information on the habitat requirements of the species for at least three spatial scales: 1) the habitat of each species during its yearly activities (i.e. LANDCOVTYPE in GIS/modelling vocabulary), 2) the patch size requirement for a pair/social unit (HAB_PATCH), 3) the threshold for the minimum proportion of habitat on a landscape scale (HAB_PROP). In addition, patch duration (HAB_DUR) must be considered in dynamic landscapes.

First, the landcover of vegetation for a particular focal species (LANDCOVTYPE) must be mapped with sufficient detail to match the operational scale of individuals. The habitat for a given species is often composed of a combination of such landcover types. Secondly, the necessary amount of patches of suitable landcover types must be defined for an individual (HAB_PATCH). To define the patches clearly, the species chosen for HSI modelling should have a high degree of specialisation on certain types of vegetation cover. The species' occurrence is influenced mainly by the extent and spatial distribution of natural or anthropogenic disturbances, which either create or destroy the habitat. In managed forest landscapes, such disturbances are mostly a result of silvicultural systems, ownership pattern (large/small) and the socio-economic situation. Thirdly, species have requirements at the population level. The number of patches and their spatial distribution make up connectivity (Forman 1995). Several studies have investigated the relative importance of habitat amount and configuration for animal populations. Simulation studies have predicted varying effects of habitat fragmentation on extinction thresholds, depending on the life history traits assumed by the different models (Fahrig 1997, 2002). Simulations by Fahrig (1997, 2001) have predicted that habitat loss is more important than habitat configuration. Additionally, almost all empirical studies from North America have shown that the amount of forest cover had a main effect on the distribution and abundance of breeding birds, while configuration did not explain much more (McGarigal and McComb 1995, Drolet et al. 1999, Trzcinski et al. 1999; but see Villard et al. 1999). This suggests that the total proportion of sufficiently large habitat patches in a landscape (HAB_PROP) could be used as a single measurement of landscape suitability, and thus as a surrogate for connectivity, at the population scale (Fahrig 2001, Scott et al. 2002). Moreover, if patches are ephemeral, for example a certain successional stage lasting only a few years or decades (HAB_DUR), the landscape must be large enough to contain a stable patch dynamic of this particular stage (Pickett and White 1985). In summary, a HSI model for a given species (HSI_SP) is made up of all the variables described above and pictures the relative suitability for the species across a given landscape.

HSI_SP = f[(LANDCOVTYPE); (HAB_PATCH); (HAB_PROP); (HAB_DUR)]

Note that this is not a mathematical expression, but rather a summarised description of the information needed for assessing the suitability of the landscape using neighbourhood analysis techniques in Geographic Information Systems (GIS) (Scott et al. 2002). With this approach the maintenance of viable populations of all "focal" species, and their associated species, will require the integration (i.e. not the sum) of the habitats of all focal species' HSI_SP. In other words, the network of each representative habitat (one or several land cover types) as a rule must be analysed and managed as a separate infrastructure. Here we would like to emphasise that HSI models do not attempt to provide estimates of habitat carrying capacity. Rather, they are planning tools intended to be used to evaluate different conservation strategies and forest management scenarios (Verner et al. 1986). In this paper, we do not apply the GIS neighbourhood analysis to data from actual landscapes, but rather present a systematic framework for its application. Field-application of the procedure is presently under way in two Swedish counties, where remote sensing data is used for the planning of conservation networks (e.g. Angelstam et al. 2003).

Land cover types of importance for forest biodiversity in the Baltic Sea region

In this paper we focus on the forest and woodland ecosystems in the countries that are most associated with the drainage basin of the Baltic Sea. This area includes three main European biogeographical regions (see Larsson et al. 2001). The largest ones are the boreal and hemiboreal regions covering most of Sweden, Finland, Estonia and Latvia. The other regions are the alpine region in nortwestern Sweden and the nemoral or temperate region in eastern Denmark, southern Sweden, Lithuania and Poland.

Developing approaches for systematic conservation planning requires an understanding of the necessary thematic resolution of different land cover types and other

factors defining the habitat for a given focal species (Hall et al. 1997). Altogether, different forest types, mires and cultural woodland provide a range of habitats of importance for forest biodiversity in the Baltic Sea region, which also are mapped, for example in forest management plans and by remote sensing (Table 1).

The diversity of forest types in a landscape is determined by the interaction between non-biotic and biotic factors. Soil, topography, climate, and access to nutrients and water are landscape characteristics that largely determine the range of possible compositions of tree species (Arnborg 1990, Ellenberg 1996). Finally, the composition and structure of forests is modified by different kinds of interactions and disturbances. These range from non-biotic (e.g., fire, wind, water) to biotic (e.g., grazing, browsing, seed predation) and anthropogenic (e.g., clearing, livestock grazing) (Pickett and White 1985, Ellenberg 1996, Peterken 1996, Esseen et al. 1997, Angelstam 1998, Kirby and Watkins 1998, Engelmark 1999, Engelmark and Hytteborn 1999). As a consequence, different combinations of these landscape trait layers create characteristic disturbance regimes (Pickett and White 1985) to which different species have adapted (Kohm and Franklin 1997, Hunter 1999). Disturbance regimes vary along a continuum from large-scale disturbances, such as fire, wind, floods, and insect outbreaks to small-scale or localized disturbances such as gap formation caused by fungi, insects and single tree fall.

Here, we use a system with three groups of disturbance regimes in an attempt to simplify, but yet acknowledge the enormous variation of the role of interacting biotic and non-biotic forces in boreal and temperate vegetation. We follow the logic presented by Dyrenkov (1984), who distinguished the following main types of stand age structures: even-aged, uneven-aged, and all-aged. To stress the dynamic characteristics of each type, we use the words succession, cohort, and gap dynamics to describe the three types of forest dynamics (Angelstam 2002). The three types are related to the relative frequency of occurrence of disturbances with different intensities and/or return intervals (Table 1).

Clearing and cultivation of forested land, a major impact on forests for millennia, has caused a dramatic reduction and fragmentation of the once naturally dynamic primeval forests (Hannah et al. 1995). Nevertheless, in some regions, forest biodiversity has to some extent been rescued by management methods practiced in the old cultural landscape (Tucker and Evans 1997, Kirby and Watkins 1998, Fuller 2002). To maintain summer and winter fodder for cows, sheep and other domestic animals, land was managed using fire, mowing, clearing, as well as tree and water management. This range of cultural disturbances often resulted in forest biodiversity being maintained because of the presence of large and special trees in a landscape dominated by grazing and/or agriculture. Today such environments usually remain as small isolated patches in a managed matrix. In some parts of Europe, however, the old management regimes are still in use.

Unless cleared for agriculture or mined for peat, mires are prominent features of the landscapes in many parts of the Baltic Sea region. Several mire types provide habitat for open forest species, in particular because of their low levels of anthropogenic transformation and because of their usually large size.

Potential focal forest bird species

Since the Baltic Sea region includes countries that are members of the European Community or countries in transition, an EC legislation such as the EC Birds Directive (Anon. 1979) would represent a first basis for selecting prospective focal species for assessment of habitat networks. The species mentioned in the Annex I of the Directive shall be the subject of special conservation measures concerning their habitat in order to ensure their survival and reproduction in their area of distribution (Anon. 1979). The first step in the selection process was made by excluding from the 175 species listed: 1) species that are dependent on other landscapes than forest or cultural woodland (Cramp 1977–1994), and 2) forest raptors and owls, which have very large area requirements and use complex mosaic landscapes that are difficult to describe using simple land cover data.

Secondly, we checked whether the 15 species selected from the EC Birds Directive provide good coverage for the different forest types (Table 2) and broad ecoregions in the Baltic Sea region. We found that some ecoregions and forest types could not be covered with the species listed in the EC Birds Directive. These cells in Table 2 were then filled with three additional specialised bird species, all resident: the long-tailed tit *Aegithalos caudatus*, the lesser spotted woodpecker *Dendrocopos minor* and the Siberian jay *Perisoreus infaustus*. These species are also well studied with respect to their quantitative requirements and have been shown to be associated to forest types that tend to be underrepresented in managed forests (Jansson and Angelstam 1999, Wiktander et al. 1992, Edenius et al. 2004).

As a preliminary check of the extent to which the selected 18 species are vulnerable to landscape change, we reviewed the information about the recent population trends in the Baltic Sea region by consulting Tucker and Heath (1994), Anon. (2000), and other sources for the countries concerned (Table 3). This analysis showed that the collared flycatcher *Ficedula albicollis* was absent from five of the seven countries and its populations did not show any negative trend. Therefore we do not consider it as a potential focal forest bird species.

The most relevant biological traits of the 17 remaining species are summarised in the Appendix, where we also discuss each species with respect to how their habitat requirements differ among different biogeographic and socio-eco-

Table 1. Summary of the different natural forest disturbance regimes and subtypes found in boreal and temperate forests (based on Dyrenkov 1984, Malanson 1993, Angelstam 2002).

Disturbance regimes and subtypes	Type of non-biotic disturbance	Type of biotic disturbance
Successional dynamic (single-cohort or "even-aged" stands) stand initiation young middle-aged harvestable ageing old-growth	stand-replacing large-scale external disturbance such as severe: high-intensity fire windthrow	stand-replacing external disturbance caused by: insects fungal disease beaver
Gap dynamic (all-aged or multiple-cohort stands with a wide range of tree diameters/ages) even (gaps created mainly by removal of one or a few trees) patchy (gaps created mainly removal of by tree groups)	local disturbance at the scale of trees or patches: windthrow self-thinning	local disturbance at the scale of trees or patches: insects fungal disease large herbivores
Cohort dynamic (uneven-aged stands with different relative amounts of two or more cohorts of younger and older trees) regeneration (mainly young cohorts) mixed cohorts digression (mainly old cohorts)	low-intensity disturbance with partial loss of trees: low-intensity fire windthrow	low-intensity disturbance with partial loss of trees: large herbivores insects
Cultural woodland (grazed and/or mowed woodland with different amounts of younger and older trees)		large herbivores mowing clearing
Riparian forest (forest affected by water)	flooding erosion high groundwater	beaver
Raised bogs and mire complexes	flooding, physiologic drought	beaver (fens)

Table 2. Forest bird species in the Baltic Sea region listed in the EC Birds Directive Annex I and additional specialised species not included in the Directive (bold). The species are sorted into a matrix of mappable land cover types deduced from both natural and cultural disturbance regimes (Table 1). Note that the species may be linked with more than one habitat type (elaborated from Angelstam 2002).

Disturbance regimes	Subtypes (LANDCOVTYPE)	Gradient between conifer-dominated (left) and deciduous-dominated forests (right)	
Succession (even-aged forest stands)	Stand initiation	Red-backed shrike* Wood lark	Red-backed shrike*
	Young	Black grouse Black woodpecker**	Black woodpecker**
	Middle-aged	Hazel grouse	**Long-tailed tit**
	Harvestable	Capercaillie Black woodpecker	**Long-tailed tit**
	Ageing	Grey-headed woodpecker Hazel grouse Black stork** **Siberian jay**	White-backed woodpecker Lesser spotted woodpecker Black stork** **Long-tailed tit**
	Old-growth	Three-toed woodpecker Hazel grouse Black stork **Siberian jay** Red-breasted flycatcher	White-backed woodpecker Lesser spotted woodpecker Middle spotted woodpecker Grey-headed woodpecker Black stork Red-breasted flycatcher Collared flycatcher
Gap dynamics (all-aged forests) spruce in boreal; otherwise broad-leaved deciduous		Three-toed woodpecker Hazel grouse Black stork **Siberian jay**	White-backed woodpecker Lesser spotted woodpecker Grey-headed woodpecker Black stork Red-breasted flycatcher Collared flycatcher
Cohort dynamics (uneven-aged forest) *Pinus* in boreal; otherwise *Quercus*	Dominated by younger cohort	Nightjar Roller** Wood lark	Roller** Wood lark
	Dominated by older cohorts	Capercaillie	Middle spotted woodpecker
Cultural woodland		Red-backed shrike Black grouse Wood lark	Roller** Wood lark
Riparian forest		Three-toed woodpecker	White-backed woodpecker Lesser spotted woodpecker Middle spotted woodpecker Black stork** **Long-tailed tit**
Raised bogs and mire complexes		Black grouse	Black grouse

* mainly in the boreal forest; normally a bird of open cultural woodland
** provided that large trees are available

nomic regions, whenever such data are available. Information is provided on the migratory status, food and habitat, spatial requirements for individuals and local populations of each bird species, as well the dynamic of the land cover types that provide habitat.

The empirical knowledge about 1) the habitat of each species during its yearly activities (LANDCOVTYPE), 2) the patch size requirement for a pair/social unit (HAB_PATCH), 3) the threshold for the minimum proportion of habitat on a landscape scale (HAB_PROP), and 4) patch duration (HAB_DUR) is presented in the Appendix and quantitative figures are summarised in Table 4. Using the information from columns 1–3 (Table 4) we estimate the approximate size of landscape planning units for the conservation of the different bird species. This, however, requires information about the minimum viable population size. Although figures have been proposed for the minimum size of viable populations (e.g. the "50/500-individuals-rule"; Meffe and Carroll 1994: 171), we do not find sufficient support for using these proposals here.

Table 3. Summary of the breeding status and population trends of the 18 selected species in the seven countries of the Baltic Sea region.

	Included in Annex I of the EC Birds Directive?†	Breeding status and population trends in the Baltic Sea region‡						
		Denmark	Sweden	Finland	Estonia	Latvia	Lithuania	Poland
Black stork	Yes	N	X	NB	↓↓	↑	↓	↑
Black grouse	Yes	↓	↑	↓	↓	↓↓	↓	↓↓
Hazel grouse	Yes	NB	○	○	↓	↓↓	○	○
Capercaillie	Yes	NB	↑	↓	↓	↓	↓	↓↓
Nightjar	Yes	↓	○	↓	○	↓	○	○
Roller	Yes	X	X	X	↓↓	↓↓	↓	↓↓
Lesser spotted woodpecker	No	↑	↓	↓↓	○	↓	○	○
Middle spotted woodpecker	Yes	X	X	NB	NB	N	↓	○
White-backed woodpecker	Yes	NB	↓↓	↓↓	↓	○	↓	↓
Grey-headed woodpecker	Yes	NB	○	○	↑	↑	↓	↑
Three-toed woodpecker	Yes	NB	↓	↓	↑	○	↓	↓
Black woodpecker	Yes	↑	○	↓	↑	○	↓	○
Woodlark	Yes	↓	○	↓↓	↓↓	↓	○	○
Red-breasted flycatcher	Yes	○	○	↓	○	○	↓	○
Collared flycatcher	Yes	NB	○	NB	NB	NB	NB	↑
Long-tailed tit	No	↑	↓	↓↓	○	○	○	○
Red-backed shrike	Yes	↓	↓↓	↓	↓	○	↓	↓
Siberian jay	No	NB	○	↓	NB	NB	NB	NB

† EC Birds Directive (EC 1979).
‡ Breeding status: X = extinct, NB = not regular breeder, and N = new breeder. Population trend (period 1970–1990; for Estonia 1971–1997): ↑↑ large increase of ≥ 50%, ↑ increase of 20–49%, ○ stable with overall changes < 20%, ↓ decrease of 20–49%, ↓↓ large decrease of ≥ 50%. Data from Cramp (1977–1994), Tucker and Heath (1994), Anon. (2000) and Lõhmus (2001).

In spite of this, for the sake of being able to compare the necessary spatial and temporal planning domain of different species, we arbitrarily chose 100 breeding pairs as reference population size. The estimated area requirement for a population of 100 breeding females with minimum landscape-scale habitat proportion was calculated as:

$$[HAB_PATCH/(HAB_PROP \times HAB_DUR)] \times 100$$

Here we would like to stress that the aim is to get an order of magnitude for the area requirements of populations, because the data currently available does not allow for precise calculations. Therefore, for the sake of being able to providing an estimate, we rounded the HAB_PROP to the nearest 5% and HAB_PATCH to the nearest 5 ha.

Results

Population trends

The compilation of breeding status and population trends in the seven countries of the Baltic Sea region (Table 3) was analysed for the 17 bird species listed in the Appendix. In 59 known cases the trend was negative (including 6 extinctions) and in 13 cases it was positive. This distribution differs significantly from the expectation that declines should be as common as increases ($\chi^2 = 29.4$, DF = 1, $p < 0.001$). In 34 cases there was no trend. Although the risk of pseudoreplication should not be neglected, this does not contradict the notion implied in the EC Birds Directive that the general conservation status of these species is problematic. A comparison of the distribution among the categories extinct, declining, no trend, and increase was skewed towards a more negative situation for this suite of bird species in the three western countries (Denmark, Sweden, and Finland) with more intensive forest management (14, 49, 26 and 11%, for the four threat categories, respectively; n = 43) compared with the four eastern countries (Estonia, Latvia, Lithuania, Poland) (0, 51, 36, 13%, respectively; n = 63) ($\chi^2 = 11.2$, DF = 3, $p = 0.011$). All 6 extinctions were confined to the three western countries.

Size of conservation planning units

As shown in Table 4 (column 5) and Fig. 1 the estimated maximum planning unit (Bird_Plan_max) for the species included in the analyses ranged from ca 10 000 to 1 250 000 ha, with a mean of 250 000 ha. To get an idea of

Table 4. Parameters for habitat suitability modelling of potential focal bird species, and estimates of the minimum area hosting a local breeding population of 100 females in a landscape with pure habitat (column 4) and ditto a minimum acceptable amount of habitat (column 5). The figures have been rounded to the nearest thousand. See Appendix for references to quantitative information. Unpublished expert knowledge provided by ornithologists is denoted with the symbol ≈, and no available information is denoted with NA.

Species	1. Habitat area requirements for one pair or social unit† (ha) (HAB_PATCH)	2. Required minimum landscape-scale proportion % (HAB_PROP)	3. Approximate proportion of a 120-yr rotation that provides suitable habitat (HAB_DUR)	4. Area requirement (ha) of a "population" of 100 breeding females in "pure-habitat" landscapes	5. Area requirement (ha) of a "population" of 100 breeding females with minimum HAB_PROP
Black stork	≈1000	≈0.2	0.4	≈250000	≈1250000
Black grouse [1]	100	0.25	0.2	7000	28000
Hazel grouse	25	0.2	0.4	6000	31000
Capercaillie [2]	300	0.25	0.5	12000	48000
Nightjar	≈50	≈0.3	0.1	≈50000	≈170000
Roller	300	≈0.1	0.4	75000	≈750000
Lesser spotted woodpecker	40	0.2	0.5	8000	40000
Middle spotted woodpecker	20	0.15	0.1	20000	130000
White-backed woodpecker	100	0.1	0.2	50000	500000
Grey-headed woodpecker	200	NA	0.4	50000	NA
Three-toed woodpecker	100	≈0.1	0.3	30000	≈330000
Black woodpecker	300	≈0.2	0.5	60000	≈300000
Wood lark	≈5	≈0.1	0.1	≈5000	50000
Red-breasted flycatcher	40	NA	0.3	13000	NA
Red-backed shrike	≈5	≈0.1	0.1	≈5000	≈50000
Long-tailed tit	10	0.15	0.6	2000	11000
Siberian jay	50	0.5	0.5	10000	20000

† Note that this area need not be a single patch but may rather include a network of interconnected patches within the home range.
[1] Assuming a 50/50 sex ratio, 7 cocks/lek and 14 leks.
[2] Assuming a 50/50 sex ratio, 5 cocks/lek and 20 leks.

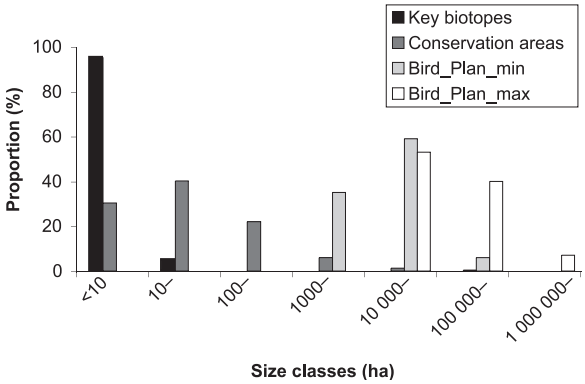


Fig. 1. Distribution of the size of conservation areas (40 071 key-biotopes and 3407 protected areas) in Sweden, and distribution of estimated sizes of planning units required for the maintenance of 17 forest bird species for the minimum estimate and 15 species for the maximum estimate (from Table 4). Data on the size distribution of conservation areas were calculated from Norén et al. (1999) and Anon. (2002).

the range of possible sizes for planning units we also calculated the estimated area requirements under the assumption of a landscape composed solely of the species' habitat, i.e. HAB_PROP = 1. As shown in Table 4 (column 4) and Fig. 1, the minimum size of planning units under this assumption (Bird_Plan_min) was ca 40 000 ha and ranged over of three orders of magnitude.

Discussion

Gaps in knowledge about model parameters for birds

In this paper we suggest a procedure for assessing the quality of habitat networks for the maintenance of forest biodiversity in different environments at the scale of landscapes within regions. The procedure is based on empirical knowledge in forest ecology and emerging quantitative avian biology. Although we feel that the logic for habitat modelling as a conservation tool is clear in principle, the development of a practical tool using a suite of species is subject to some uncertainty depending on the level of quantitative knowledge about the parameters introduced in the different steps.

The knowledge available on the requirements of the focal bird species varies among the different habitat parameters (Appendix, Table 4). At the level of individuals, the requirements regarding the utilisable land cover types, the minimum patch size, and the window of utilisable forest ages are relatively well known for most species. However, there may be differences for a given species in different biogeographic and socio-economic settings. As an example, a species may use different tree species found in different contexts, but may still eat similar kinds of food. For example, the three-toed woodpecker is generally considered as an old spruce forest specialist in Fennoscandia (Amcoff and Eriksson 1996). The older age of the preferred stands procures dead and dying trees used for foraging on bark beetles, for nesting, and for roosting (Hågvar et al. 1990). In Estonia and Latvia, however, the three-toed woodpecker is also known as a species typical of flooded riparian deciduous stands and unlogged burned stands, where it finds large quantities of dead wood (Lõhmus et al. 2000, Peterhofs pers. comm.). Moreover the location within the distribution range (centre vs periphery) may influence habitat selection in a particular species (Fuller 2002).

Few studies have so far been designed to address parameters at the landscape level, such as the minimum proportion of suitable patches necessary for the presence of a species, let alone its persistence (Table 4). To reduce this uncertainty, replicated landscape-scale studies for each species are needed. In particular, we support the view of Fahrig (1999) that documentation of fragmentation thresholds requires that each data point be an individual landscape. Additionally, the regional amount of forest cover is an important factor for the maintenance of viable populations. For example Austen et al. (2001) have recently shown that the regional forest cover has a strong influence on the local distribution of passerines. Therefore, it is necessary to get more data on the incidence and fitness of the focal species in relation to general forest cover at the regional scale in addition to their requirements for the relevant forest types at finer scales.

The need to extend the spatial scale of nature conservation

Our estimates of planning units based on potential bird focal species range from 10^4 to 10^5 ha, depending on the assumptions regarding landscape composition (cf. Table 4; column 4 vs column 5). In managed landscapes, the landscape-scale amount of suitable habitat for many of those specialist species will be close to or lower than the minimum threshold for persistence. This is particularly likely to be the case in western countries (Angelstam et al. 1997). Therefore, we argue that the maximum estimates are more realistic than the minimum estimates (Fig. 1) for most species included in Table 4, given the impoverished composition, the simplified structure, and the greater dispersion of rare resources in today's landscapes.

Clearly such estimates are dependent on the life-history of different groups of species. To exemplify the differences in the amount of a particular habitat that different species need at the scale of populations in today's managed landscapes we use the lichen *Lobaria pulmonaria*, the white-backed woodpecker and the wolf *Canis lupus*. *Lobaria* is found in mixed deciduous/coniferous forest containing deciduous trees with a high pH on the bark and a light and moist microclimate. We first assume a 100-m buffer of old

forest to allow for blow-down of trees at the edge and the maintenance of a moist local climate in a 1-ha area including 500 trees. This corresponds to a stand size of ca 5 ha. Assuming that such stands cover 2% of the landscape as Swedish key biotopes do (Hansson 2001), and that the suitable window in time in the succession is 20% of the rotation of 100 yr, the area needed for a population is ((5/0.02)/0.2) = 1250 ha = 12.5 km^2. For the white-backed woodpecker we estimated the area for a population of 100 units to 5000 km^2 (Table 4). Finally, wolves use forest-dominated landscapes with sufficiently large prey populations and have pack home-ranges of from 100 km^2 in south Poland (Nowak pers. comm.) to 1000 km^2 in Scandinavia (Aronson et al. 2001). Assuming that 33% of the forest cover is suitable due to low human population density, 100 packs would need ca (100(500)/0.33) = 150 000 km^2. Although very crude indeed, these estimates illustrate that the area to be considered for the maintenance of populations of these species differ by two orders of magnitude between the lichen and the woodpecker, and by four orders of magnitude between the lichen and the wolf.

Practical conservation work in the Baltic Sea region has so far focussed on establishing protected areas (Nilsson and Götmark 1992, Angelstam and Andersson 2001) and key biotopes (Hansson 2001), with plants and fungi as focal species (Nitare and Norén 1994, Viilma et al. 2001). However, to stress the need for considering larger spatial scales one additionally needs to use animals with requirements covering a broader range of spatial and temporal scales than plants and fungi. We argue that there is a strong discrepancy between the conservation tools usually applied and those actually needed to maintain viable populations of species being representative for the range of forest types in the Baltic Sea region. To illustrate this we compared the distribution of the sizes of Swedish key biotopes (Norén et al. 1999), nature reserves and national parks (Anon. 2002) and the estimates of the area needed for a reference population of 100 bird pairs. As can be seen in Fig. 1, there is a 2–3 order of magnitude difference between the mean size of individual protected areas and that of the necessary planning units.

Is the land cover information complete and with sufficient thematic resolution?

A range of factors including ownership pattern, silvicultural traditions of landowners, the degree of nature consideration in forest management, and the types of conservation planning affect the way in which viable populations can be maintained. Yet, in spite of these constraints, the assessment of habitat networks must be based on whole landscapes (Perrera et al. 2000).

Land cover maps are produced for a multitude of applications and are therefore not necessarily appropriate for mapping the forest environments in a way that represents the different disturbance regimes and developmental stages. Therefore their usefulness for HSI modelling is highly variable (Hunsaker et al. 2001, Townsend 2002). While the habitat of herbivores such as grouse can be depicted reasonably well using simple land cover maps (Swenson and Angelstam 1993, Jansson et al. 2004), the modelling of several other species also requires some knowledge about habitat quality within the relevant land cover type. For some woodpeckers both old forest stands, forest recently disturbed by fire and storm but also clearcuts with large amounts of suitable dying and dead trees need to be taken into account (Angelstam et al. 2002, Bütler et al. 2004). Similarly, the black stork requires not only large forest tracts, but also old trees for nesting and water networks inside the forest for foraging (see Appendix). Consequently, to be useful, spatially explicit land cover maps should provide a specification of the quality of land cover data (thematic and spatial resolution and accuracy, completeness, temporal relevance etc.). Within our study area, land cover maps are becoming available, for example, from inventories of key biotopes (Viilma et al. 2001), remote sensing (Angelstam et al. 2003) and the Baltic Forest Mapping Project (Walsh pers. comm.).

Validation of the models for the focal species

Validation of HSI models involves testing how reliably one can predict occurrences of the focal species in real-world landscapes (Brooks 1997). However, because of a long and intensive land use history, landscapes in the western part of the Baltic Sea region contain a "narrowed" range of forest environments compared to pre-industrial conditions. Mykrä et al. (2000) showed that in Finnish boreal forest, a long history of forest management has resulted in a very truncated range of patch sizes compared with naturally dynamic landscapes. Consequently some focal species have become extirpated from those regions (Aulén 1988, Kouki and Väänänen 2000). This makes it virtually impossible to find study areas with large patches and high proportions of different important land cover types such as old-growth forest in most managed West-European forest landscapes. We therefore need to find reference landscapes representing less affected forest ecosystems where plenty of suitable habitats are still present (Angelstam et al. 1997). Such areas may be found in the eastern part of the Baltic Sea region, although many of these are already threatened by the intensification of forestry.

The validation of HSI models should be made in areas other than the ones where model parameters were obtained and requires several conditions to be satisfied: 1) digital forest maps or satellite based habitat information in a form, which is relevant for HSI models for particular focal species must be made available; 2) GIS based HSI modelling for different well-studied species that provides probability maps of potential distribution should be carried out; 3) field censuses of the focal species should be made at

relevant spatial and temporal scales and for parts of the population indicating high fitness; 4) comparison of HSI models with actual occurrence of species should be made. If the results are satisfying, the models can then be used to design management guidelines for these species.

Evaluation of the umbrella effect for other species

Habitat suitability modelling does not provide a general tool for forest biodiversity conservation unless one also tests the indicator- and umbrella value of the selected species, i.e. whether or not a large number of other species are associated with the presence of the focal species. Many authors have recently made a plea for the empirical validation of the umbrella species concept (Simberloff 1999, Caro and O'Doherty 1999, Fleishman et al. 2001).

For the suite of focal species discussed here there is appearing evidence supporting the umbrella species hypothesis. Suter et al. (2002) tested the usefulness of capercaillie as an umbrella species in the Swiss Prealps by analyzing relationships between capercaillie occurrence and avian species diversity and examined whether both were associated with the same habitat-structure parameters. Study plots with capercaillie did not hold significantly higher bird diversity than plots without the grouse. However, the species richness and abundance of birds that are more or less restricted to subalpine forests (mountain birds) and that at the same time are red listed was considerably higher in capercaillie plots than in those without capercaillie. Both capercaillie and mountain birds responded positively to forest structure characterized by intermediate openness, multistoried tree layer, presence of ecotonal conditions, and abundant cover of ericaceous shrubs. Capercaillie may therefore be a useful umbrella species, at least for that part of avian biodiversity of conservation interest. Additionally, Jansson and Andrén (in press) showed that the occurrence of hazel grouse was positively correlated to resident bird species richness in managed boreal forests. Similar results were obtained for the white-backed woodpecker, the black grouse and the three-toed woodpecker by Martikainen et al. (1998), Kolb (2000) and Mikusiński et al. (2001), respectively. These results suggest that some species could indeed be useful tools for conservation both in forests and cultural landscapes. However, we do not believe that a single species would suffice for ensuring the protection of all co-occurring species, even within a given forest type. Therefore, combinations of species with complementary requirements should be used. For example, the three-toed woodpecker (highly dependent on dead wood) could be combined to the capercaillie (dependent on large patches of older forest) for old forests, and with the black grouse for young successional forests.

Some authors have criticised the practical value of the focal-species approach on the grounds that an incredibly high number of species would be required in order to cover all relevant landscape attributes (Lindenmayer et al. 2002). Another stated shortcoming of the approach is that the current level of knowledge does not allow for identifying the very most sensitive species for each ecosystem attribute (Lindenmayer et al. 2002, Lindenmayer and Fischer in press). We do not believe that using solely the bird species covered in this paper would be sufficient in order to conserve whole biotas in the Baltic Sea region. However, we think that management aimed at the conservation of this limited suite of focal species, particularly if used in combination with general ecological principles (e.g. promotion of the occurrence of natural disturbance regimes and of connectivity for all major forest types at various scales) and finer-grained strategies aimed at some threatened species, would result in the protection of many important attributes of forest ecosystems.

Multiple taxa for landscape-scale conservation

Assessment and planning at several spatial and temporal scales using HSI modelling requires the use of focal species with different ecological traits. Due to the limited quantitative knowledge needed for HSI modelling we restricted the review to bird species. Although the bird species discussed are probably among the most demanding for their respective forest types, we acknowledge that the selected species may not be the absolute most demanding. Indeed knowledge on the requirements of some organism groups such as insects is still imperfect, and in the future it may turn out that many other species than the birds we propose in this paper are more demanding. However, we prefer to adopt an adaptive strategy by which one begins with the currently selected well-known species and revises the suite of species if appearing knowledge shows that the initial choice was not optimal.

We argue that the use of a wise combination of different species with different ecological traits can be useful in biodiversity conservation work (cf. Lambeck 1997, Thompson and Angelstam 1998). For example, even if several principal aspects of boreal forest composition and structure can be covered by the three grouse species, there are other aspects that are not covered. Grouse are not old-growth species, neither being dependent on late deciduous or late successions, moist local climate, nor disturbances as fire and water (Angelstam 1998). The study of Mikusiński et al. (2001) suggests that the woodpecker family Picidae is a good complement towards an indicator system for assessing biodiversity across spatial scales within the landscapes in a region. However, also other species such as mammals and insects could be used for the same purposes (Angelstam 1998, Nilsson et al. 2001; see Wikars 2004, Reunanen et al. 2004). Similarly, habitat for lichens requiring moist local climate found in old-growth interior stands could be modelled using GIS buffering algorithms and

stand maps as well as using Digital Elevation Models to describe the local climate.

Ultimately, a multiple focal species approach is of particular importance to achieve a "favourable conservation status" (sensu Anon. 1992) of conservation areas, and to understand how to integrate and evaluate the results of different management efforts by different landowners at various spatial scales for the maintenance of native biota (Angelstam 2002). Too often, the species and aspects studied are chosen based on the preferences of the individual scientist, or research group, rather than based on the manager's interest of covering all habitats and spatial scale in a landscape.

Ecology and planning

Landscapes are ecological systems relative to the organism in question (Forman 1995), and can hence be viewed with both a biological species-oriented perspective and an anthropocentric perspective (Allen and Hoekstra 1992, Perrera et al. 2000, Angelstam et al. 2001). The assessment and planning of representative habitat networks for the maintenance of biodiversity requires both views. This means that managers need to understand that different species have different habitat preferences as well as different quantitative requirements, and that viable populations need more than what is found in one patch of habitat. Hence, the successful maintenance of all representative habitats can be viewed as a series of partly overlapping and complementary habitat networks in the landscape, each of which having different properties to which species have adapted.

On the other hand ecologists need to know about the planning process (Brunckhorst 2000). This involves both a good understanding of the tools available to planners, their cost and other constraints. While, on the one hand, it is easy to design a theoretical planning algorithm, on the other hand it is a much larger endeavour to acquire appropriate data bases, develop skills to use the algorithms in a management organisation and apply the results in practise. In Europe, the EC Birds (Anon. 1979) and Habitats Directives (Anon. 1992) represent such approaches. At present the different member states of the European Community (Natura 2000) as well as the Countries in Transition (e.g., Kalamees 2000, Raudonikis and Kurlavicius 2000, Yaroshenko et al. 2001) are involved with the mapping of existing areas of high conservation value. Judging from the negative trends of many specialised species (Table 3), we are apparently far away from successful implementation of the policies stating that biodiversity should be maintained in the long term. There are several reasons for this. The step from being able to quantify the habitat requirements of a species at the level of individuals to that of a population is a large one. Moreover, the step from scientific understanding to practical implementation and maintained biodiversity within landscapes in regions must be taken. Even if it is necessary, however, it is still difficult in practice to encompass planning at the scale of regions including interacting local populations (Lindén et al. 2000). This is due to the simple facts that requirements for bird at this scale are largely unknown, and that there is often no inter-regional or international jurisdictional authority at that level. However, with the planned expansion of the European Community, the whole Baltic Sea region will be at least partly "controllable" in a way that has never occurred before. We argue that when evaluating the representativeness of the Natura 2000 network the EU Commission should be encouraged to carry out the kind of analysis proposed here for different suites of potential focal species.

Conclusion

This study proposes a general procedure for HSI modelling and values for the associated parameters. It also provides a state-of-the-art compendium of the existing knowledge on the spatial habitat requirements of specialised North European birds at multiple scales, and illustrates the need to extend the spatial scale for conservation. Biodiversity conservation is a kind of crisis management. Following the precautionary principle, we feel it is our duty to try to implement existing knowledge even if it presents gaps. However, the procedure proposed here should be used with caution. We advocate an adaptive strategy in which the tool is adjusted as additional knowledge becomes available. We encourage our colleagues to gather more data on the requirements of sensitive species at all relevant scales.

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Appendix

Ciconiiformes

Black stork *Ciconia nigra*

The black stork is a long-distance migrant wintering in tropical Africa (Cramp 1977–1994). In general, it forages in rivers and streams of forested landscapes; only in the post-breeding period does it forage in more open habitats (Tryjanowski and Lorek 1995). It feeds chiefly on fish and amphibians, but also on insects, small mammals, reptiles, crustaceans, and passerine nestlings (Dementiev and Gladkov 1968, Glutz von Blotzheim and Bauer 1980, Cramp 1977–1994). The black stork breeds in mature stands and locates its nest in the upper part of well-grown forest trees such as oak (Cramp 1977–1994, Strazds 1999). Nesting trees are usually considerably older than the rest of the stand and older than the maximum stand age in managed forests (Strazds 1999). Lõhmus et al. (unpubl.) studied breeding of the black stork in relation to forest structure in Estonia. The preference for well-forested landscape was related to higher occupancy of sites. The birds preferred old (> 70 yr; Sackl and Strazds 1997) remote stands near rivers and a certain distance away from ecotones, although the preference for old growth was explained simply by the occurrence of potential nest trees of large size. Rosenvald and Lõhmus (unpubl.) reported that although 200-m zones around known nests of the black stork have been strictly protected in Estonia since 1957, the population has recently suffered a large decline, which coincides with the intensification of forestry.

Breeding densities in undisturbed woodlands in Belarus were between 1.3 and 1.8 breeding pairs 100 km^{-2} (Byshnev pers. comm.). Local densities in east Poland were 5–9 pairs 100 km^{-2} (Keller and Profus 1992, Tryjanowski unpubl.). In intensively managed forests of the Czech Republic and Austria, densities between 0.2 and 1.7 breeding pairs 100 km^{-2} occur (Sackl and Strazds 1997). We estimate the required habitat area for a pair to cover ca 1000 ha. None of the regions with stable or increasing populations have proportions of forest cover lower than 20–25%.

Because the black stork often uses a combination of different, juxtaposed habitats for different purposes (undisturbed forest with large trees for breeding and aquatic habitats for foraging) it is difficult to quantify habitat using simple land cover information. Provided that large trees are retained during forestry operations and remain present throughout the succession, the last 50 yr of an assumed 120-yr rotation would provide habitat for this species. In addition to those requirements, the potential nesting stands should be situated away from permanent sources of human disturbance.

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Galliformes

Europe is inhabited by three resident forest-dwelling grouse species, which have specific habitat requirements and respond to both natural disturbance and land management (Seiskari 1962, Swenson and Angelstam 1993). Time after large-scale disturbance can be viewed as a resource axis subdivided among the forest-dwelling grouse (Swenson and Angelstam 1993). The presence of viable populations of all sympatric grouse species in a boreal or hemiboreal landscape over a whole succession cycle from young to old (but not old-growth) indicates the presence of a landscape with a "stable" age distribution – a so-called minimum dynamic area (Pickett and White 1985). As a result of their close tracking of environmental changes, grouse are considered to be indicators for the health of the ecosystems they inhabit (Storch 2000). Boag and Rolstad (1991) identified three important requirements of the forest grouse that make them suitable as complementary indicator species for taiga landscapes, viz. the large spatial requirements of viable grouse populations, their nutritional requirements, and their vulnerability to predation.

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Black grouse *Tetrao tetrix*

The black grouse is a resident herbivorous bird inhabiting areas with a sparse canopy cover and a rich dwarf shrub layer (Klaus et al. 1990, Baines 1995, Angelstam 2001). Adults are herbivorous and are dependent on evergreen dwarf shrubs and deciduous trees (Cramp 1977–1994). Consequently, in the boreal regions, the black grouse is regarded as a bird of the early stage of forest succession (Angelstam 1983 and unpubl.). Outside the boreal forest, the species is found in structurally similar habitats such as moorland and heaths, young coniferous plantations on such habitats (until the dwarf shrubs have disappeared), as well as tree line habitats, alpine pastures, and cultural woodlands (Klaus et al. 1990, Baines 1995, Storch 2000, Baines et al. 2000, Angelstam 2001).

Throughout its range the black grouse requires large patches of suitable habitat. Quantitative studies suggest minimum area requirement of 20 ha for solitary males and 90 ha for leks (Angelstam 1983, 2001). At the landscape scale a non-linear relationship between the proportion of habitat and presence of solitary (10–15%) as well as lekking males (20–25%) has been observed (Angelstam 2001). Consequently, the abundance of black grouse is influenced by the age distribution of the forest, both on local short-term and on nation-wide long-term scales (Angelstam 1983 and unpubl.).

While undrained raised bogs and anthropogenically maintained woodland may host local populations for > 100 yr, in forest the black grouse typically occupies a narrow window of 15–30 yr in the beginning of the forest succession after large-scale disturbance (Baines et al. 2000, Angelstam unpubl.). As a consequence, in most forest landscapes the black grouse requires a continuous re-creation of large patches of habitat. Similarly, in cultural landscapes management must be sustained (Kolb 2000).

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Hazel grouse *Bonasa bonasia*

The hazel grouse is a resident bird whose occurrence is mainly influenced by the within-stand structure of forests. It inhabits mixed forests and favours dense coniferous (particularly Norway spruce *Picea abies*) or deciduous cover below the canopy (Bergmann et al. 1982, Swenson 1995). When snow covers the ground, hazel grouse feed on catkins and buds of deciduous trees such as *Alnus*, *Betula*, *Corylus*, *Sorbus* and *Fagus* (Breuss 1999). Close interspersion of feeding trees and cover is crucial (Swenson 1995). In natural and managed forests, the hazel grouse is found in multi-layered stands of different ages (Swenson and Angelstam 1993, Viht 1999, Åberg et al. 2003). In Estonia, older stands with a canopy closure of 0.7–0.8 were preferred (Viht 1999), while in Finland also young stands (< 10 m in height) were used more than expected by availability (Nieminen et al. 1995).

This species avoids open areas and seems particularly vulnerable to forest fragmentation (Åberg et al. 1995, Nieminen et al. 1995). The minimum area requirements for one pair are ca 25 ha (Åberg et al. 1995). If located in a forest-dominated landscape, there appears to be no landscape-scale threshold for the amount of habitat. In mosaics of forest and agricultural fields, by contrast, isolation appears to be a problem (Åberg et al. 1995) and the minimum proportion of habitat in the landscape should be at least 20%. Suitable hazel grouse habitat patches can to a large extent be detected using stand descriptions in forest management plans, especially if measurements of vertical cover, the presence of alder (*Alnus* spp.) and the type of field layer are added to the descriptions (Åberg et al. 2003).

The habitat requirements of hazel grouse can be satisfied both in middle-aged and old-growth forests (Beshkarev et al. 1994, Nieminen et al. 1995). In intensively managed landscapes, however, the occurrence of hazel grouse is confined to middle-aged forest until thinning takes place (Åberg et al. 2003). In natural successions, wide windows of opportunity are available, both in the succession from young forest to middle-aged forest as well as in old-growth forest with gap dynamic (Swenson and Angelstam 1993).

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Capercaillie *Tetrao urogallus*

The capercaillie is a very large resident herbivorous bird dependent on older coniferous forest with moderate canopy cover and ground vegetation dominated by bilberry *Vaccinium myrtillus* and other ericaceous shrubs (Storch 2000). In the winter, it feeds almost exclusively on conifer needles, while in the summer it feeds on leaves, buds, flowers and fruits of various herbs and shrubs (Jacob 1987). Young birds feed on insects (Atlegrim and Sjöberg 1995). In most areas, old natural or semi-natural pine forests are the capercaillie's strongholds (Sjöberg 1996). However, if the structure of the vegetation is suitable, the species may also use young and commercially managed forests (Storch 2000).

Maintaining large patches of habitat is an important conservation measure for the capercaillie. The minimum patch requirements for the capercaillie are ca 80 ha for single males and 220 ha for leks (Angelstam unpubl.). In landscapes with continuous forest cover, capercaillie leks are usually evenly spaced with an approximate 2-km distance (Wegge and Rolstad 1986, Storch 1997, Hjeljord et al. 2000). In Estonia, 96% of the lekking sites were situated in forests older than 60 yr, and such stands covered 50% of the area within 1 km of the lekking site (Viht and Randla 2001). At the landscape scale, at least 30% suitable habitat in the landscape is required (Rolstad and Wegge 1989). The spatial requirements of grouse are very large, especially if one considers juvenile dispersal distances, separate summer and winter ranges, as well as specific patch types for territorial requirements and for feeding at different times of the year. For the capercaillie, such requirements encompass areas in the order of 40 km^2 (Rolstad and Wegge 1989). Extensive clear-cutting has been the main cause of the disappearance of 185 leks in Estonia during the last 30 yr (Viht and Randla 2001).

The habitat requirements of the capercaillie are satisfied in coarse-grained landscapes with sufficient areas of older, not too closed forest. Such habitats are common in the succession after stand-replacing disturbance on mesic site and may last for ca 50 yr in managed boreal forest, but are of

shorter duration in hemiboreal forests due to a higher canopy cover shading out the ericaceous shrubs. Pine *Pinus sylvestris* dominated forests on poor sites can be used continuously even if repeated low-intensity disturbance by fire is allowed (Beshkarev et al. 1995).

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Caprimulgiformes

Nightjar *Caprimulgus europaeus*

The nightjar is a tropical migrant spending a short breeding season in Europe. It is an aerial food-gatherer feeding at night, mostly on moths, but also on beetles, Diptera, and Hymenoptera (Cramp 1977–1994, Sierro et al. 2001). Nightjars apparently spot potential preys against the sky light from perches close to the ground level and catch them in the air. Consequently this species prefers open habitats with well-spaced conifers, *Betula*, *Populus*, *Quercus*, as well as sunny woodland margins and burned patches (Cramp 1977–1994). In the Baltic Sea region it is an inhabitant of dry, semi-open pine forests and moorlands (Dombrowski and Rzępała 1993, Kolshorn and Klein 1999). The nightjar has a tendency of moving into post-fire and military training areas (Tryjanowski unpubl.). According to Hölzinger (1987) this species occurs mainly in areas with May–July precipitation of < 260 mm and temperatures over 15°C during that period. Lārmanis (1999) studied nightjars in forests managed by traditional even-aged forestry in northern Latvia. The composition of forests within a 200-m radius around each observed singing male was analysed. These areas contained an average of 73% dry pine forests, 10% wet pine forest, 10% drained forest, and 7% raised bogs (n = 91). The majority of the individuals were found in stands younger than 20 yr. Poor growing conditions, relatively large amounts of open bog patches, and a hilly microrelief can maintain small openings that favour the nightjar (Priednieks et al. 1998). Hence, forestry measures promoting a high wood production over whole areas are probably detrimental to that species. In areas managed through clear-felling, nesting of nightjars in the new stands is restricted to a period of ca 8 yr after harvesting (Scott et al. 1998).

The smallest size of a clearing occupied by the nightjar is 2–10 ha and density is greater if the shape of the clearing approaches that of a circle (Ravenscroft 1989). By contrast, the actual area being used for feeding is much larger. Individuals may range up to 6 km from the nest site whilst feeding (Alexander and Creswell 1990). Therefore 50 ha is estimated as the minimum total area required for a pair. In Notecka Forest (Poland), nightjars occurred with a density of 22.3 males 100 km^{-2} (Tryjanowski et al. unpubl.).

Apparently the nightjar has adapted to a variety of natural disturbances (fire, grazing, trampling, wind erosion) that maintain the open woodland structure of dry pine and pine-oak forests. Traditional progressing strip-cutting in eastern Europe often results in new suitable stands being created next to young forests. Lārmanis (1999) analysed forest statistics to understand the long-term trend in the amount of suitable biotopes in Latvia. The area of clearcuts and young stands of pine decreased by 80% during the period 1961–1988. However, at present the area of young pine forests and clearcuts is increasing. Scott et al. (1998) demonstrated that the rotational planting and felling of land under forestry can provide a periodic abundance of habitat for nightjars.

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Coraciiformes

Roller *Coracias garrulus*

The roller is a tropical migrant once widespread in the nemoral and hemiboreal ecoregions. Its most important preys are medium- to large-sized insects, mostly beetles, ants, and crickets (Snow et al. 1998). The roller forages in open areas with vegetation lower than 1 m such as fields, meadows and clear-cuts (Vahi 1963). In the Baltic Sea region, most nests are found in holes excavated by the black woodpecker, the green woodpecker *Picus viridis*, or in nest-boxes (Pugacewicz 1998, Dmoch and Dombrowski 1998, Račinskis 2000, 2001). Nests are most frequently located in large Scots pines, aspens *Populus tremula*, willows *Salix* spp., and sometimes in alders (Vahi 1963, Račinskis 2000, 2001). The nesting trees are often situated near the forest edge (Račinskis 2000, 2001). In the Garkalne area (Latvia), the roller occupied dry, light and sparse Scots pine forests on sandy soil interspersed with various open patches (Račinskis unpubl.). In Poland, the roller occurred in areas with extensive agriculture on sandy soils, on the edges of areas with trees, mainly Scots pine woods and small thickets.

The feeding area varies according to the diversity of biotopes present around the nest. Vahi (1963) reported that foraging usually took place within 300 m from the nest and, rarely, as far as 1.5 km. The area requirement of a pair in Garkalne has been estimated at 200–280 ha (Račinskis unpubl.) and, in Estonia, at 340 ha (Vahi 1963). We used 300 ha as an estimate of the area of suitable habitat for one pair. However, home ranges are partly overlapping as rollers are not strictly territorial and may form loose breeding aggregations (Snow et al. 1998).

Before the large-scale changes in the ancient cultural landscape, the roller was breeding in the whole hemiboreal region in Sweden (Lönnberg 1927). In Latvia and Estonia, the species was rare in the 19th century, expanded its range in the first half of the 20th century, with thousands of pairs in the 1950s, but declined dramatically after that (Leibak et al. 1994, Račinskis 2000), with only one confirmed pair in Estonia in 2002 (Kalamees and Kose pers. comm.). In Poland, the roller has dramatically declined over the last decades and has survived in only a few isolated localities in the east of the country (e.g. Dombrowski et al. 1998, Pugacewicz 1998). Originally, frequent forest fires probably played a major role in shaping the roller's feeding habitats. Therefore, this species is probably adapted to disturbance regimes characteristic of dry pine cohorts with openings and of the old cultural landscape.

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Piciformes

Along with grouse, woodpeckers form a taxonomic group, which apparently has evolved to occupy virtually all kinds of woodland in Europe (Angelstam and Mikusiński 1994). In fact, in one naturally dynamic landscape all sympatric species can be found (Mikusiński and Angelstam 1997).

Angelstam, P. and Mikusiński, G. 1994. Woodpecker assemblages in natural and managed boreal and hemiboreal forest – a review. – Ann. Zool. Fenn. 31: 157–172.
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Lesser spotted woodpecker *Dendrocopos minor*

The lesser spotted woodpecker, a basically resident species, is the smallest European woodpecker. In the summer it forages for surface-living arthropods on foliage and trees, while in the winter it focuses on food items found in dead wood and under bark (Cramp 1977–1994, Olsson 1998). In most of its geographic range, this species prefers rather open woodlands with old deciduous trees and a high

amount of standing dead trees (Cramp 1977–1994, Spitznagel 1990, Olsson et al. 1992). The highest population densities occur in riparian and broad-leaved deciduous forests (Wesolowski and Tomialojc 1986, Spitznagel 1990, Wiktander et al. 1992). In two studies in Sweden, the area of deciduous forest in a landscape was clearly positively affecting the species' occurrence (Wiktander et al. 1992, Mörtberg and Wallentinus 2000). Deciduous trees dominate both as foraging and nesting substrates (Angelstam and Mikusiński 1994, Stenberg 1996, Olsson 1998, Wiktander 1998). Nesting holes are excavated in rotten dead wood.

The home range size exhibits large seasonal variation (Wiktander et al. 2001). Wiktander et al. (1992) studied the occurrence of lesser spotted woodpecker in 200-ha plots in Sweden and found that the probability of occurrence reached 80% when at least 38 ha was made up of suitable deciduous forest. Using radio-telemetry a minimum requirement of 40 ha of forest dominated by deciduous trees over a maximum of 200 ha was documented (Wiktander et al. 2001). Reported population densities for the lesser spotted woodpecker vary from 0.01 breeding pairs 100 ha^{-1} in unmanaged pine-dominated forest in W Norway (Stenberg and Hogstad 1992) to 2–3 breeding pairs 100 ha^{-1} in primeval deciduous forest in Poland (Wesolowski and Tomialojc 1986). Wiktander et al. (2001) suggested that 20% of deciduous forest in the landscape should be regarded as the limit to the level of acceptable fragmentation.

Because of its need for dead wood, older deciduous-dominated forests (> 60 yr) are considered as suitable for the lesser spotted woodpecker (Wiktander pers. comm.). Such conditions were historically found in the later stages of succession after large-scale disturbances such as fire. This means that this species can utilise approximately the second half of a 120-yr forest rotation, provided that there is a sufficiently high deciduous component.

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Middle spotted woodpecker *Dendrocopos medius*

The middle spotted woodpecker, a generally resident species, has a diet consisting almost exclusively of arthropods (Cramp 1977–1994). It forages mainly on the surface of trees, but excavation in soft and rotten wood also occurs (Jenni 1983, Pettersson 1983, Török 1990, Pasinelli and Hegelbach 1997, Pasinelli 1999). In Switzerland, over 70% of trees chosen for foraging in winter were dead, while in breeding season the corresponding figure was 40% (Jenni 1983). Elderly and dead oaks (*Quercus* spp.) are the most important foraging substrate around the year (Jenni 1983, Pettersson 1983, Pasinelli and Hegelbach 1997, Pasinelli 1999). The nesting cavity is usually excavated in an oak, hornbeam *Carpinus betula*, black alder *Alnus glutinosa*, or ash *Fraxinus excelsior* (Wesolowski and Tomialojc 1986, Wesolowski 1989, Jamnický 1994, Angelstam and Mikusiński 1994, Mazgajski 1997, Pasinelli 2000, Kosiński and Winiecki unpubl.). Both dead and living trees are used but hole localisation seems to be restricted to decayed part of the tree (Wesolowski and Tomialojc 1986, Günther 1993, Jamnický 1994, Mazgajski 1997). In many localities, this species have been found dependent on stands dominated by oaks (Pettersson 1985, Wesolowski and Tomialojc 1986, Schmitz 1993, Bühlmann and Pasinelli 1996, Pasinelli 2000), but ash-alder stands, stands containing coarse-barked beeches, riverine forests, orchards, and olive groves may also provide suitable habitat (Cramp 1977–1994, Wesolowski and Tomialojc 1986, Spitznagel 1990, Hochebner 1993, Winkler et al. 1995, Günther and Hellmann 1997, Winiecki and Kosiński 2000). Pavlík (1994) reported that high crown cover in the upper tree layer, high vertical diversity, and high tree species diversity were profitable for the middle spotted woodpecker in a Slovakian oak forest.

Pasinelli (1999) and Pasinelli et al. (2001) found that the mean size of individual home range of the middle spotted woodpecker was ca 18 ha in winter, 11 ha in early spring, 8 ha in late spring, and 20 ha in summer. Based on observation of unmarked individuals in southern Sweden, Pettersson (1984) estimated the average territory in late spring to 25 ha. Large (> 30 ha) and adjacent (< 9 km) patches of habitat are more likely to be colonised by the species (Müller 1982, Pettersson 1985). Negative effects of habitat fragmentation on breeding success have recently been reported from Russia (Kosenko and Kaigorodova 2001). The breeding density in Europe varies between < 2 breeding pairs 100 ha^{-1} in the Cantabrian Mountains (Spain) and 5–24 breeding pairs 100 ha^{-1} in Białowieża National Park (Poland), where the highest densities were observed in riverine forest (Cramp 1977–1994, Purroy et al. 1984, Wesolowski and Tomialojc 1986, Hagemeijer and Blair 1997, Winiecki and Kosiński 2000, Kosiński et al. unpubl.). Taking into account different figures describing home range, population density and overlap between territories, we used 20 ha of suitable habitat as a minimum requirement for a breeding pair (Pettersson 1984, Pasinelli 1999, 2000, Pasinelli et al. 2001). Required minimum proportion of suitable patches in the landscape was estimated at 15%, based on figures provided by Müller (1982), Pettersson (1985), and Kossenko and Kaigorodova (2001).

Qualitatively, the most important habitat variable is the age of trees used for foraging and nesting. Pasinelli and Hegelbach (1997) report that oaks with trunk diameter of 36–72 cm corresponding to > 120 yr in age were highly preferred. The oak stands > 85 yr old were considered as suitable in Switzerland (Bühlmann and Pasinelli 1996). Therefore, the middle spotted woodpecker usually finds its preferred habitat in stands characterised by gap dynamics and in old even-aged stands. We used 110 yr as a minimum forest age suitable for this species. This means that only a small fraction of a normal forest rotation is likely to provide habitat for the middle spotted woodpecker.

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White-backed woodpecker *Dendrocopos leucotos*

The white-backed woodpecker is a resident species dependent on food resources found in dead and decaying deciduous wood. This specialist of naturally dynamic forest avoids spruce and even-aged planted forest (Aulén 1988, Carlson 2000) and can utilise foraging trees at distances 6–10 km (Aulen 1988, Stenberg 1990) preferably in sun-exposed slopes (Hogstad and Stenberg 1994). In a Norwegian study, the proportion of dead (11–15%) and dying (5–8%) trees (average 154 and 78 trees ha^{-1}) was significantly greater in nesting areas compared to random sites (accordingly 9.3 and 3.6%) (Hogstad and Stenberg 1994). In a study by Bergmanis (unpubl.), 43% of the nesting holes were excavated in dead trees and 14% in dying trees. Only 6.7% of the nest trees had a diameter at breast height < 25 cm. The stands contained on average 26% of dead wood, distributed approximately equally among standing and lying dead wood. Most forest compartments in which this species was breeding were 60–95 yr old. Occasionally, they also selected younger stands, but only if there was some older forest in the vicinity (Bergmanis unpubl.). In NE Poland, Angelstam et al. (2002) found a threshold of 10–20 m^3 of downed and standing dead wood in a 1-km^2 area for the presence of territorial white-backed woodpeckers. In Latvia, older stands are used in specific conditions, such as permanently wet alder forests. In these conditions, trees reach dimensions suitable for excavating a hole and spruce never takes over.

Studies in Sweden and Germany suggest area requirements of 50–100 ha for one pair (Aulén 1988, Scherzinger 1990). In outstanding habitat in Latvia, the density reached 1.45 pairs 100 ha^{-1} (Bergmanis and Strazds 1993). In western Europe density can reach 0.7–2.0 (4.0) pairs 100 ha^{-1} (Glutz von Blotzheim and Bauer 1980). When the amount of suitable habitat in forest landscape falls < 10%, modelling suggests that the decline in population size is accelerated (Carlson 2000). Using empirical data, Carlson and Stenberg (1995) suggested habitat thresholds for the persistence of the white-backed woodpecker at 8–20% of suitable habitat in a landscape.

The habitat can be found in a variety of situations ranging from a wet regional climate (Atlantic region) to late successional stages where light-demanding deciduous trees die. Such successions can be initiated by fire, wind, flooding, logging and abandonment of agricultural land due to socio-economic changes. Since the duration of a suitable successional stage is limited, continuous habitat renewal in the landscape is essential. As a rule traditional forest management is not compatible with the requirements of this species.

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Three-toed woodpecker *Picoides tridactylus*

The three-toed woodpecker is generally considered a resident species, although northern populations exhibit irruptive southward and westward movements (Hogstad 1983). The bulk of its diet consists of bark beetle larvae (Scolytidae) from coniferous wood (Pechacek and Kristin 1993). Other prey types include Hymenoptera larvae and spiders (Winkler et al. 1995). This primary-nesting species has a preference for spruce as a nesting tree, although it also uses aspen (Hågvar et al. 1990). In Fennoscandia this species is typically found in spruce forests, but also occurs in pine or birch (*Betula* spp.) forests in the north, as well as in mixed-deciduous forests and wet alder forests in the Baltic States (Koskimies 1989, Strazds unpubl., Brazaitis unpubl.). In a Swedish study the amount of dead wood was strongly correlated with the occurrence of that species (Amcoff and Eriksson 1996). Bütler et al. (2004) found a clear threshold for the occurrence of breeding three-toed woodpeckers of an average volume of spruce snags amounting to 10–15 m^3 ha^{-1} over a 1-km^2 area.

In a Swedish study, Amcoff and Eriksson (1996) showed that the amount of old forest around nesting sites or observed pairs was 100–400 ha. Although this is not a direct measure of home range, we consider that 100 ha can be use as an approximation for minimum home-range size. A comparison between area with and without breeding three-toed woodpeckers in mountain forests in Austria suggests a landscape scale threshold of 10% forest older than 120 yr (Angelstam and Breuss unpubl.).

The three-toed woodpecker is probably adapted to older stages of succession forest subject to bark beetle infestations and fire, as well as to damp or wet forests containing large amounts of dead and dying trees. Even though this species is often characteristic of old-growth forests, it can also use clearcut areas if they contain snags or are surrounded by damaged and dead trees (Ahlén 1975). Putting together the use of recent clearcuts with sufficient tree retention and old stands, we estimate that this species can utilise about one third of the duration of a typical forest rotation of 120 yr.

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Grey-headed woodpecker *Picus canus*

The grey-headed woodpecker is largely non-migratory, although seasonal movements have suggested a migratory strategy in some instances (Edenius et al. 1999). Ants, beetle larvae, spiders, berries and fruits are part of its diet (Winkler et al. 1995). In the summer on the Norway-Sweden border it fed mostly on ant colonies in soil and in stumps, and shifted to bark-dwelling arthropods in the winter when frost and snow impeded ground feeding (Rolstad and Rolstad 1995). In relation to this shift in diet the habitat varied from young conifer plantations in the summer to old coniferous stands in the winter. Other authors describe the preferred habitat of the grey-headed woodpecker as mixed/deciduous forests, where it favours old, open woodlands (Koskimies 1989). The grey-headed woodpecker is a primary cavity nester and has a strong preference for aspen as a nesting tree (Hågvar et al. 1990, Angelstam and Mikusiński 1994). It prefers woodlands with high structural diversity, i.e. a mosaic of patches with varying age and height (Tucker and Heath 1994).

The average home range size of a few pairs on the Norway-Sweden border was 50–100 ha in the summer and 4500–5400 ha in the winter (Rolstad and Rolstad 1995). Note, however, that the large areas utilised in the winter present overlap among neighbouring individuals. Edenius et al. (1999) reported from northern Sweden the winter home range of two studied females to be ca 2000 ha. Taking into account estimations concerning home range, population densities, and overlap in winter home ranges (Cramp 1977–1994, Rolstad and Rolstad 1995, Edenius et al. 1999) we decided to use 200 ha of suitable habitat as a minimum requirement for a breeding pair. We have not found any studies providing information about the minimum required amount of habitat at the landscape scale.

In short, the grey-headed woodpecker is adapted to habitats in which it can find carpenter ants and other arthropods, as well as large nesting trees. These characteristics are mostly found in ageing forests (> 90 yr) and in recently disturbed forests (ca 10–30 yr) (Rolstad and Rolstad 1995).

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Black woodpecker *Dryocopus martius*

The black woodpecker, Europe's largest woodpecker, is usually considered resident, although northern populations are partly migratory (Winkler et al. 1995). It feeds mostly on ants and wood-beetle larvae (Cramp 1977–1994). Carpenter ants (*Camponotus* sp.) constitute the preferred food source in the winter (Mikusiński 1997). In Scandinavia black woodpecker habitat is composed of young Norway spruce plantations for feeding and older spruce stands for roosting and display (Rolstad et al. 1998). The black woodpecker also occurs in mixed and deciduous stands (Winkler et al. 1995). In managed forests the black woodpecker usually finds good food supply by using stumps as a feeding substrate (Mikusiński 1997, Rolstad et al. 1998). In Scandinavia the nest cavity is usually excavated in a live or dead aspen or Scots pine with a diameter larger than ca 35 cm at the height of the cavity (Hågvar et al. 1990, Rolstad et al. 2000). Spruce seems to be avoided for nest excavation. The nest is preferably situated in trees retained on recent clearcuts, while old stands are avoided for nesting.

In highly fragmented agricultural landscapes of southern Sweden, Tjernberg et al. (1993) concluded that at least a total area of 450 ha of forest must be available for a territorial pair. Year-round home range size increased from 150 to 300 ha in Norway when the proportion of young conifer stands decreased from 60 to 20% (Rolstad et al. 1998). In another study winter home range varied from a mean of 449 ha in a snow-rich area to 226 ha in a snow poor area (Rolstad and Rolstad 2000). Mikusiński (unpubl.) obtained winter home ranges varying from ca 100 to 600 ha in central Sweden. Based on those studies, 300 ha was chosen as the area of habitat needed for a pair. The minimum proportion of the habitat in the landscape was set at 20%, based on Tjernberg et al.'s (1993) and own observations (Mikusiński unpubl.).

Along the successional gradient, the black woodpecker utilises both young stands (ca 10–30 yr) and older stands (> 80 yr) (Mikusiński 1997, Rolstad et al. 1998). Therefore approximately one half of the duration of a typical forest rotation is suitable for this species. It can also utilise forests with internal or cohort dynamics, as long as there is abundance of ants and presence of large trees for nesting.

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Passeriformes

Woodlark *Lullula arborea*

The woodlark is a short-distance migratory species wintering in western Europe and in the Mediterranean basin. During the breeding season it feeds mostly on medium-sized insects and spiders (Cramp 1977–1994). In eastern Europe the woodlark is found mostly in dry pinewoods with clearings, early successional stages after fire, windthrow or felling, or young pine plantations (Dementiev and Gladkov 1968, Pätzold 1971). In central Europe the optimal habitat is dry warm open pine-heath with 2–8 yr-old trees such as abandoned fields near woods (Pätzold 1971). In the southern part of the Baltic region, this species usually breeds in sparse coniferous forests on sandy soil (Viksne 1989) and clear-felled areas (Bowden 1990). The woodlark requires a high proportion of bare ground and low field layer vegetation including grass or low shrubs (Bowden 1990, Sitters et al. 1996). Birds usually select the area based on both of these factors (Valkama and Lehikoinen 1994).

The minimum area of suitable habitat for a pair was estimated at 5 ha and the minimum landscape-scale proportion of habitat was estimated at 10% (Kosinski and Tryjanowski unpubl.). The breeding density varies from 0.11 pair 100 ha^{-1} in SW-Finland (Valkama and Lehikoinen 1994) to < 1 pair 100 ha^{-1} in Białowieża forest (Tomialojc and Wesolowski 1990).

Like nightjar and roller, the woodlark appears to have adapted to a variety of natural disturbances (fire, grazing, trampling, wind erosion) that maintain the open woodland structure of dry pine and pine/oak forests as well as old cultural landscapes and abandoned fields.

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Red-breasted flycatcher *Ficedula parva*

The red-breasted flycatcher is a long-distance migrant wintering in Pakistan and India. It feeds mainly on insects and others invertebrates in the middle layer of the canopy and sometimes in the air (Cramp 1977–1994). The typical habitat for the red-breasted flycatcher is mature stands dominated by deciduous trees or mixed stands with some proportion of spruce (Byshnev and Stavrovsky 1998, Brazaitis and Angelstam unpubl.). The average density of birds increases from mixed spruce-pine to pure spruce, spruce-deciduous, and reaches a peak in deciduous stands (Byshnev and Stavrovsky 1998). The red-breasted flycatcher is more abundant in stands with a rather continuous canopy than in stands containing gaps (Fuller 2000).

In a Lithuanian study, the minimum area of fragments where the red-breasted flycatcher was found was 12 ha in fragments with fresh edges (Brazaitis and Angelstam unpubl.). The effect of edge avoidance increased with time. Birds rarely bred in old forest remnants smaller than 40 ha (Brazaitis and Angelstam unpubl.). The average density has been reported to be 5–15 pairs 100 ha^{-1} in Białowieża forest (NE Poland) (Tomialojc and Wesolowski 1990) and 2–10 pairs 100 ha^{-1} in Estonian forests (Leibak et al. 1994). We use 40 ha as the minimum size of habitat required for a pair. We have not found any studies providing information about the minimum required amount of habitat at the landscape scale.

Apparently the red-breasted flycatcher is a true forest-interior species dependent on mature forests. It is adapted to the main natural disturbances typical of deciduous or mixed stands with almost continuous canopy, such as single-tree windthrow and insect attacks. Along the successional gradient, it seems that only older forests (> ca 80 yr) are suitable for this species.

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Long-tailed tit *Aegithalos caudatus*

The long-tailed tit is a resident species with irregular irruptive movements, feeding on small invertebrates (Snow et al. 1998). Pairs defend territories only during the breeding season, that is approximately three months in spring and early summer (Gaston 1973). However, most of the year long-tailed tits roam around in flocks within an area of ca 1 km^2 (Gaston 1973, Bleckert 1991). Preferred habitats are dominated by middle-aged to old deciduous stands composed of *Alnus* spp. and *Betula* spp. (Jansson and Angelstam 1999).

Studies in the southern boreal forest show that the minimum area requirements are 5–15 ha of middle-aged forest with 20–90% deciduous trees (Jansson and Angelstam 1999). If neighbouring stands are located more than about 1 km apart, the probability of occurrence drops rapidly. At the scale of local landscapes the amount of suitable habitat in 1 km^2 ranged from 10 to 28% where long-tailed tits were present to 6–15% where they were not.

The high dependence on larger functionally connected deciduous stands means that the persistence of a local population of long-tailed tit is dependent on a stable patch dynamics in which a deciduous "window" in the succession is always present somewhere in the local landscape. Based on the results from Jansson and Angelstam (1999) the long-tailed tit should, depending on how the deciduous component is managed, at least be able to use a few decades of a full rotation.

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Red-backed shrike *Lanius collurio*

The red-backed shrike is a long-distance migrant, spending the non-reproductive season in the southern part of Africa. It feeds mainly on insects, other invertebrates, small mammals, birds and reptiles (Cramp 1977–1994). Preferred habitats in eastern Europe are open meadow landscapes, typically with scattered bushes, hedgerows, roadside verges and forest edges. In central Europe, this species occurs in open areas including non-intensive cultivation, pastures, shrubs, and young plantations. In farmland areas in Poland it nests in shrubs and trees – mainly thorny – at a height of 0.7–1.8 m. Nest predation by corvids, domestic cats and martens causes very high losses (Kuźniak 1991, Tryjanowski et al. 2000). Dense shrubs, open areas exposed to sun, and perches seem to be the most important factors explaining habitat quality. In the forest, the occurrence of the red-backed shrike is linked to cutting areas, young pine stands, glades, and ecotones (Olsson 1995a). In open forest habitats nests are built mainly in juniper *Juniperus communis* (Olsson 1995b), but in rapidly changing Swedish farmland it nested in sloe *Prunus spinosa*. Mainly due to nest predation the red-backed shrike may shift territorial preferences adaptively as the season progresses, from sloe to juniper (Söderström 2001). In contrast, the main habitats of the red-backed shrike in Poland are strictly limited to small tree islands among arable fields and meadows (Kuźniak and Tryjanowski 2000).

The size of typical red-backed shrike territory is ca 1.5 ha (0.5–3.5 ha) (Tucker and Heath 1994). In the Baltic Sea region the breeding populations of red-backed shrike have declined as a result of habitat degradation due to intensive agriculture (Tucker and Heath 1994). The future of this species is probably dependent on a return to more extensive agriculture technique (Van Niewenhuyse Dries 1999). Density varies widely from 0.1 to 9.4 breeding pairs 100 ha^{-1}. Density was inversely related to plot area but for plots > 15 km^2 it tends to stabilise at 0.5–1.2 pairs 100 ha^{-1}.

The red-backed shrike is a species of the first part of secondary succession and is well adapted to forests with natural- or human-induced open areas (Kuźniak et al. 2001). In boreal forests they are confined to the clearcut phase during 10–20 yr after disturbance.

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Siberian jay *Perisoreus infaustus*

The Siberian jay is a site-tenacious boreal forest corvid associated with closed-canopy mature and old-growth coniferous forest (Helle and Järvinen 1986, Virkkala 1991, Rogacheva 1992). The food is varied and adjusted to seasonal variation in availability; berries, especially bilberry, are important but fungi, invertebrates, and occasionally small mammals and passerine birds (nestlings) can also be found in the diet. Dependence on old forest seems to be strongest during winter when the jays exclusively feed on arboreally stored food. The nest is built in trees, and both Norway spruce and Scots pine are used. In mature stands Norway spruce is preferred over Scots pine; spruce was used disproportionately by adult jays in pine-dominated forest during summer (Edenius and Meyer 2002). In a study in northern Sweden, there was a positive correlation between number of years with groups of jays present at feeding stations and the proportion of forest older than 100 yr in the surroundings (Edenius et al. 2004). In strongly modified forest landscapes, stem density may be an important determinant of habitat quality (Ekman et al. 2001). Although older growth stages are preferred, the Siberian jay regularly uses young forest and open habitats. Forest-mire edges are good feeding habitat and access to such habitat may affect breeding success (Sklepkovych 1997).

Home range size varies with season: it is smallest during the breeding season (April–May) and largest during au-

tumn (Lindgren 1975). There is large variation in reported home range size of the Siberian jay, which stems both from the method used for delineation of the home range and the time period studied: 100–150 ha (Blomgren 1964), 50–100 ha (Lindgren 1975), 45–75 ha (Sklepkovych 1997), 45–57 ha (Kokhanov 1982 in Mykrä et al. 2000), 50–150 ha (Edenius et al. 2004). We use 50 ha as an estimate of the minimum area of habitat required for a pair. Little is known about habitat requirements at larger spatial scales. However, forest cover may be of importance as the proportion of forest land within home ranges of radio-tagged Siberian jays was significantly higher than in similar sized random plots in the landscape (Edenius unpubl.). Edenius et al.'s (2004) findings suggest that 50% could be used as the minimum amount of forest habitat at the landscape scale.

In conclusion, the Siberian jay seems to require certain amounts of structures such as old trees for food storage and closed-canopy forest for hiding cover, but otherwise appears flexible with respect to habitat structures and forest type. It is adapted to boreal coniferous forests in the later successional stages and therefore is probably restricted to the latter half of the normal duration of a typical forest rotation.

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Multidimensional habitat modelling in forest management – a case study using capercaillie in the Black Forest, Germany

Rudi Suchant and Veronika Braunisch

Suchant, R. and Braunisch, V. 2004. Multidimensional habitat modelling in forest management – a case study using capercaillie in the Black Forest, Germany. – Ecol. Bull. 51: 455–469.

A habitat model for capercaillie *Tetrao urogallus* was developed in a modular structure of several analytical steps investigating habitat conditions and the occurrence of capercaillie within the Black Forest (Schwarzwald, Germany) at different temporal and spatial scales. A total of 104 capercaillie leks distributed over 60 000 ha was analysed and compared with the historical occurrence of 156 leks in 1902. Landscape scale variables in areas with and without capercaillie were examined for the whole Black Forest ecoregion covering 700 000 ha, and local scale habitat analysis was done in three representative study areas of ca 7000 ha each. Habitat variables and parameters differentiating between presence and absence were identified and management target values were derived. These were then integrated into an operational habitat management model, which represents a hierarchical top-down evaluation of habitat suitability.

First, the wildlife ecological landscape types (WELT) classify distinct regions with similar landscape ecological habitat conditions for wildlife species within a country or broader administrative unit. Second, the species-specific landscape ecological habitat potential (LEHP) is defined within a WELT unit. It is based on the evaluation of species-relevant landscape variables and provides information about the potential habitat available to a selected species at the landscape scale. Finally, at the scales of forest district and forest stand, respectively, a habitat structure analysis within the LEHP-area allows for the measurement, improvement and control of habitat variables.

By offering the possibility to identify location and size of areas, in which habitat improvement measures should be implemented, and by defining target values for forest management, this model links wildlife research to practical habitat management.

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Habitat suitability modelling is an appealing method for providing better informed spatially explicit plans for operational forest management aiming at maintaining viable populations of species (e.g. Scott et al. 2002, Angelstam et al. 2004). In the intensively cultivated landscape of central Europe only limited areas are suitable habitat for wildlife. Human land use competes severely with the habitat needs of wildlife species. Expanding infrastructure and the influence of tourism result in a fragmentation of the landscape, which causes habitat insularisation (e.g. Kaule 1991, Amler et al. 1999) and leads to a continuous loss of undisturbed wildlife habitat (Suchant 1999).

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These factors are considered to be the main cause of the population decline of most central European capercaillie *Tetrao urogallus* populations during the last century. Shrinking distribution ranges and a shift to the higher zones of the mountain ranges were noticed in many populations (Rolstad and Wegge 1989, Klaus and Bergmann 1994, Storch 2000, Suchant 2002) often resulting in an extinction of several small and fragmented populations (Klaus et al. 1989, Klaus and Bergmann 1994). Due to increasing demands for conservation measures to inhibit or even to reverse this process a conservation action plan has been formulated (Storch 2000). However, neither are areas specified for the implementation of habitat improvement through wildlife management, nor are specific measures defined for the improvement of habitat quality at the scale of individual management units.

Presently, wildlife management mainly concentrates on principles for species protection and management measures, which are often segregated from practical land use management. Consequently, conflicts arise between wildlife management and protection on the one hand, and utilisation of the land for tourism and economic exploitation on the other (Suchant 1999). There are only few management concepts (e.g. Kangas 1992) that integrate species protection into spatial and regional planning with the intent to meet the requirements of both wildlife and human land use.

Furthermore, species protection and management measures are usually addressing the present abundance of endangered species and refer to the requirements of the species' individuals, i.e. the habitat conditions at a local scale. Regional aspects such as the degree of habitat fragmentation, the mosaic of stands with different properties, the influence of landscape ecological variables or the habitat requirements of a minimum viable population (Hovestadt et al. 1992) are often excluded.

Considering the difficulties in assessing a species' population size and population density, habitat availability and habitat quality increasingly become the focus of management plans and landscape ecological investigations (McGarigal and McComb 1995, Hinsley et al. 1995, König and Linsenmair 1996). Detailed information about habitat conditions often allow predictions of population density, exchange between subpopulations, and habitat use of individual animals. Hence, habitat models can be a valuable tool for understanding the factors underlying the habitat use and population dynamics of a species as they describe the relationship between habitat variables or habitat types and the habitat use of a selected species (e.g. Moeur 1986, Hammill and Moran 1986, Laymon and Barret 1986, Schamberger and O'Neil 1986, Brennan et al. 1986, Gray et al. 1992, Askins 1995, Short et al. 1995, Boroski et al. 1996, Doan et al. 1997, Scott et al. 2002, Angelstam et al. 2004). However, only few habitat models deal with differences in species-habitat interrelations with regard to different spatial scales (Hamel et al. 1986, Hagan and Meehan 2002, MacFaden and Capen 2002). Furthermore, the practical application of most models in forest and wildlife management is limited (O'Neil and Carey 1986) as they lack the crucial link between the knowledge of a species' habitat requirements and practical management by defining what measures are needed to fulfil these requirements, where they are to be implemented and how other land use objectives can be met at the same time.

We use the capercaillie as a focal species, which is characterised by a set of attributes that put it into the focus of wildlife managers' and conservationists' activities (Simberloff 1998). Its narrow habitat-affinity (e.g. Sjöberg 1996) makes capercaillie an indicator species for well-structured boreal or montane forests (Schröder 1974, Leclercq 1987, Scherzinger 1989, 1991, Boag and Rolstad 1991, Storch 1993, 1995, Schroth 1995, Cas and Adamic 1998). Capercaillie requires large areas (e.g. Wegge and Rolstadt 1986, Storch 1993), it is highly sensitive to disturbances, and is endangered by habitat degradation and habitat loss (e.g. Klaus et al. 1989, Klaus and Bergmann 1994, Storch 2000). It has also proved to be an umbrella species for several endangered mountain birds (Suter et al. 2002). In addition to these ecological aspects capercaillie is a species that is often associated with historical and ethical values, which makes it suitable to serve as a flagship species with a high communication value (Uliczka et al. 2004).

This study presents a habitat management model that is based on an analysis of the capercaillie population within the Black Forest at different temporal and spatial scales, and which integrates wildlife research with practical habitat management. The objective is to identify areas of successful capercaillie management in isolated populations and to provide target values for important habitat structures that can be directly implemented through forest management planning. These target values are also assumed to offer an operational silvicultural tool to integrate other nature conservation aims (e.g. structural diversity), that are often associated with capercaillie occurrence, into forest management systems.

Study area

Representing a typical landscape of central Europe, the German federal state of Baden-Württemberg (35752 km^2) provides the administrative border to which the habitat management model refers at the broadest landscape scale (Fig. 1). With an average population density of 291 inhabitants km^{-2} it is characterised by intensive anthropogenic utilisation. Settlements and roads cover 13% of the total area, 47% is used agriculturally, and the proportion of forested area is ca 38%.

The landscape ecological analyses of this study were made in the Black Forest ecoregion (Aldinger et al. 1998).

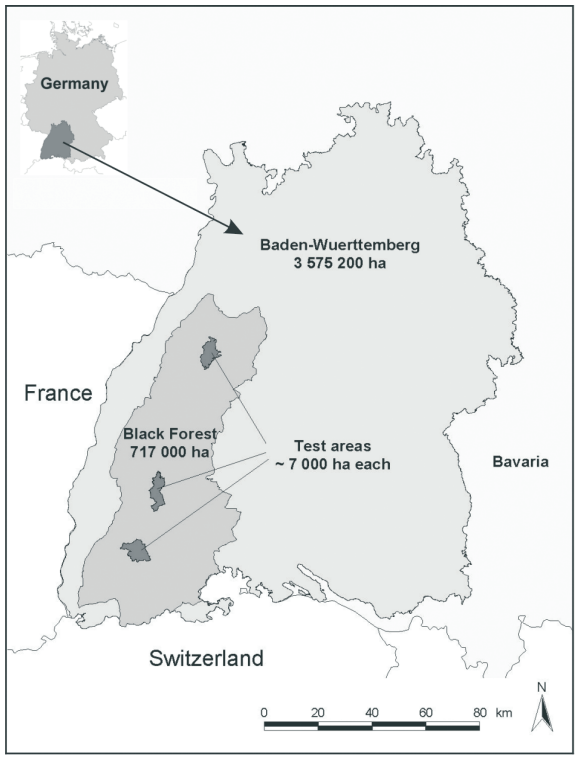


Fig. 1. Baden-Württemberg and the "Black Forest" study area, including the three test areas.

It can be regarded as an ecological unit for wildlife within Baden-Württemberg (Suchant et al. 2003). Two thirds of the total area (ca 7000 km^2) are covered by forests dominated by Norway spruce *Picea abies* (49%) and European silver fir *Abies alba* (19%). Among the broad-leafed species, beech *Fagus sylvatica* is the most common. The macroclimate, as well as the vegetational conditions of the study area, correspond with the extreme differences in elevation, ranging from 120 to 1493 m.

Within the Black Forest three representative test areas were defined, each of them roughly 7000 ha in size, in which habitat variables were studied at the local scale. The northern test area is almost completely forested and covers an area of 7487 ha. The elevation ranges from 500 m in the eastern parts to ca 900 m along the western boundary. In the central test area, 84% of the area is forest, which results in a mapped area of 6509 ha. About 29% of the total area lies above 1000 m (range: 450–1155 m). The southern test area surrounds the Feldberg, which is the highest mountain within the Black Forest (1493 m). The lowest valleys can be found roughly 630 m a.s.l. The peaks of the highest mountains are treeless, so the mapped area covers only 79.5% of the total area, i.e. 6737 ha.

Methods

Distribution and abundance of capercaillie

The distribution of capercaillie in the Black Forest is assessed systematically on the basis of continuous monitoring. Every fifth year starting 1993, all direct and indirect evidence of capercaillie presence (such as faeces, feathers and tracks) within the past five year period is mapped and evaluated using Geographical Information Systems. For the delineation of the inhabited areas, only evidence located within a maximum distance of 1 km to the next piece of evidence was included. Thus, isolated observations in forest patches that are not permanently inhabited but only visited occasionally by capercaillie (e.g. by dispersing birds) were taken into account separately. In addition, the locations of lekking places were mapped and the number of cocks counted annually. Furthermore, within the test areas capercaillie abundance was determined by counting and evaluating direct and indirect evidence of the species' presence at the scale of the forest stands.

The historical capercaillie distribution was based on a complete survey of capercaillie leks made in the eastern part of the Black Forest in 1902, which was created by the gamekeepers of the Fürstenberg principality. Altogether, 156 lekking places were identified. As leks are the centres of the local capercaillie distribution (e.g. Wegge and Rolstad 1986, Storch 1997), the forested area within a circle of a 1-km radius around the lekking place was assumed to be inhabited by capercaillie.

Habitat analysis on different temporal and spatial scales:

To identify habitat variables that are relevant to capercaillie, to derive threshold parameter values for relevant variables and thereby assess habitat quality and availability, the relationship between capercaillie occurrence and habitat conditions was analysed at different spatial and temporal scales (Fig. 2). At the local scale, selected habitat structure variables were recorded from 1996 to 1998 within the three test areas for each forest stand, each representing a habitat patch of between 1 and 50 ha.

The following variables were mapped in the field: forest stand type, canopy closure, age class, species mixture, successional stage, stand height, vertical stratification, ground vegetation, soil type and cover as well as height of blueberry *Vaccinium myrtillus*. The variable "protection on the ground" was recorded by measuring the visibility of an upright black-and-white grid (50 × 50 cm, 100 squares) at a distance of 10 m. The proportion of protection on the ground was derived from the number of squares that were hidden by ground vegetation. In addition to the terrestrial mapping, aerial photographs were used to assess the forest stand mosaic, the occurrence of forest gaps and the linear structures.

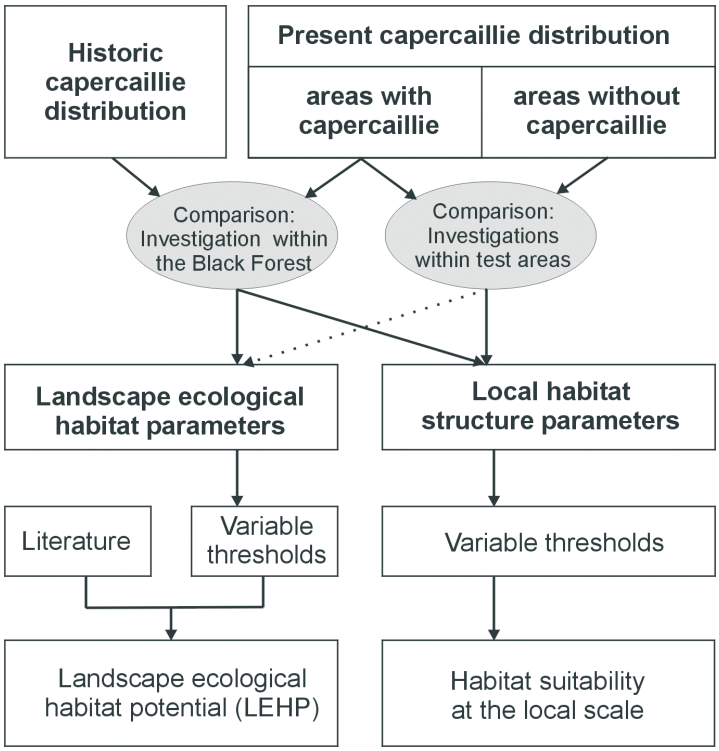


Fig. 2. Delineation of methodological steps and results of the habitat analysis for capercaillie at different spatial and temporal scales.

Comparison between areas with and without capercaillie

Within each test area zones "with capercaillie" and "without capercaillie" were differentiated. Zones "with capercaillie" were defined as areas, in which capercaillie presence was recorded repeatedly from 1991 to 2000, including the 1-km radius of lekking places. In zones "without capercaillie" no or only sporadic and isolated evidence of presence were recorded within the ten year period. The digitalisation and evaluation of the spatial data was conducted with Arc/INFO (Esri), IDRISI, and STATISTICA (Anon. 1999). To examine the differences between habitat with and without capercaillie Mann-Whitney U-Test was used. Associations between the different habitat variables were examined by Pearson's correlation coefficient and logistic regression.

Comparison between current and historical capercaillie distribution

The locations of the 156 lekking places registered in 1902 were compared with the current capercaillie range to distinguish two variants: "permanently inhabited" forest patches, in which capercaillie was present in 1902 and 1998, and "abandoned" forest patches, where capercaillie was only present in 1902. No new lekking sites were found. Leks located within the 100-m border area of the present distribution were excluded. To define the habitat differences between the two variants, local-scale habitat structure variables as well as landscape ecological variables were analysed. Local-scale habitat structure variables were assessed for 100 × 100 m grid cells within an area of 100 ha surrounding each historical lekking place. The procedure for mapping and evaluation was the same as described for the three test areas.

The landscape ecological variables were recorded within an area of 314 ha/lek (i.e based on a radius of 1 km around each of the leks mapped in 1902), which results in a total area of ca 19000 ha for the "permanent" and ca 26000 ha for the "abandoned" patches. Elevation, exposure and slope were taken from the digital elevation model (Anon. 1994). ATKIS data (Official Topographic and Mapping Information System) as well as digital aerial photographs (1:10000) provided information relating to the forest cover. The linear infrastructure was derived from a digital road map 1:200000 (Anon. 1985). The two variants ("permanent" and "abandoned") were compared using the MWU-Test. Pearson's correlation coefficient and logistical regression were employed to test relationships within and among the variable categories.

Thresholds and target values

As wildlife management requires measurable goals for conservation or improvement of habitat structures, quantitative target values were defined. They present threshold values for species-relevant habitat variables in a manner applicable to operational forest management. Based on the comparisons described above, threshold values for habitat structure variables, as well as for landscape ecological variables were derived using logistical regression. To obtain minimum and maximum parameter values for the relevant variables, the variables were correlated with the population density within the forest patch under investigation with the objective to determine at which value capercaillie occurrence is likely. For the analyses of the present capercaillie abundance the amount of capercaillie proof for each forest stand within the test area served as clue about the population density, and for the historical analyses the number of cocks within "permanently inhabited" lekking places was used. For forest management purposes the resulting values for local-scale habitat structure variables of both investigations were combined and related to the total required proportion of suitable habitat.

Habitat suitability at the local scale

To evaluate the habitat suitability for capercaillie, the mapping results for relevant habitat variables were incorporated into a species-specific evaluation matrix (Table 1). This matrix defines various ways of combining the variables, each assessing and evaluating the habitat quality in a specific context: for capercaillie females and males, and for the summer and winter habitat. The transcription of the evaluation matrix (Table 1) was done by employing the STATISTICA-internal programming language STATISTICA BASIC. The results of the evaluation matrix were combined to calculate the total habitat suitability. A forest stand was classified as "suitable" when both the foraging and protection requirements are met and "unsuitable" when both criteria are lacking. "Neutral" conditions apply if only one of the essential habitat properties is fulfilled. The minimum threshold for the proportion of suitable habitat required by capercaillie was derived from the comparison between the proportion of suitable habitat in each of the three test areas and the actual capercaillie abundance.

Landscape ecological requirements

To evaluate the landscape ecological conditions in relation to a species' requirements, the concept of landscape ecological habitat potential (LEHP) was developed (Suchant et al. 2003). It locates that part of a landscape, which provides potentially suitable landscape structures for a capercaillie population within an ecoregion. The LEHP was calculated by evaluating data on topography and land use patterns with regard to species-specific requirements. The variable selection and the definition of threshold values was based on an integration of the investigated thresholds for landscape ecological variables and parameter values derived from literature (for detailed methodological information see Suchant et al. 2003).

The concept is based on the assumption that LEHP identifies the area where the landscape ecological conditions are favourable to "produce" suitable habitat for a certain species. It defines only the potential of the landscape to develop suitable habitat structures, not the actual habitat situation itself. Therefore, the landscape outside LEHP could also be inhabited by individuals, which can be either due to anthropogenic influences overruling natural processes and creating suitable habitat structures at the local scale (e.g. forestry or habitat improvement measures) or to population dynamics (e.g. to colonisation of suboptimal habitat by dispersers from overpopulated areas).

The population – habitat index

The next step was to quantify the percentage of optimal habitat that is required within an area of a given size to maintain a capercaillie population of a certain size. This target population size could be oriented at the minimum viable population size derived from population development models. The relationship between the size of the landscape ecological habitat potential, the target population size and the percentage of optimal habitat is expressed by a so-called "population – habitat" index. The index was derived from the relationship between the proportion of suitable habitat and the capercaillie home range size given in various publications. At 100% optimal habitat the home range size is < 20 ha (Gjerde and Wegge 1989). In the case of home range areas > 100 ha, optimal habitat structures are given on at least 30% of the forest area (Storch 1997). Wegge and Rolstad (1986), Klaus et al. (1989) and Swenson and Angelstam (1993) assume the required proportion of optimal habitat to be inversely proportional to the home range size (within this range 20–100 ha). Based on investigations made by Klaus et al. (1989) and Storch (2000) this relationship was suggested to be an exponential function (Fig. 3). The area requirements of the population was then calculated by multiplying the home range size with the number of individuals of the target population.

Results

Distribution and abundance of capercaillie

In the Black Forest ecoregion, capercaillie is distributed over an area covering ca 56 000 ha. The inhabited areas

Table 1. Example of an evaluation-matrix to assess the habitat suitability in relation to forage and protection for capercaillie males and females in winter (a) and in summer (b). All "AND", and at least one "OR" parameter value needs to be fulfilled.

(a) Indicator variables for protection in winter	Forest stand patches are:	
	suitable	unsuitable
Forest stand type	IF conifer trees	IF broad-leafed trees
Age-class	AND older than thicket	OR younger than pole stage
Cover on the ground	AND good cover	AND poor cover
Indicator variables for forage in winter	suitable	unsuitable
Forest stand type	IF conifer trees or mixed stands	IF broad-leafed trees
Forest stand type of tree regeneration	OR conifer trees or mixed stands	–
Cover of tree regeneration	AND > 20%	AND < 20%
Height of tree regeneration	AND > 0.5 m	AND < 0.5 m
Cover of shrubs	OR > 50%	AND < 10%
Cover of blueberry	OR > 30%	OR <10%
Height of blueberry	AND > 20 cm	OR < 20 cm

(b) Indicator variables for protection in summer	Forest stand patches are:	
	suitable (males/females)	unsuitable (males/females)
Forest stand type	IF conifer trees	–
Age-class	AND thicket or younger	IF older than thicket
Vertical structure of forest stand	OR stocky	AND single storied
Cover of tree regeneration	OR > 20%	–
Height of tree regeneration	AND > 1.3 m	–
Cover on the ground	AND medium cover/ AND good cover	AND no cover/AND few cover
Indicator variables for forage in summer	suitable (males/females)	unsuitable (males/females)
Cover of ground layer – total	IF > 30%	IF < 20%
Cover of shrubs	AND > 10%	OR 0%
Cover of herbaceous vegetation	OR > 10%	AND 0%
Cover of ferns	–	AND < 10%
Cover of blueberry	OR > 30%	AND 0%
Height of blueberry	AND > 20 cm	–

consisted of > 100 patches ranging from 250 to 1000 ha. The capercaillie distribution correlated strongly with the altitudinal zonation. While > 60% of the forest patches in high montane regions were inhabited, capercaillie occurred in only 15% of the montane and in none of the submontane forests. In 1998, 315 cocks were counted on 104 lekking places. The capercaillie population density varied greatly within the Black Forest. In the southern part of the area it was almost twice as high (1 cock/100–150 ha) as in the northern (1 cock/150–200 ha) or eastern part (1 cock/200–250 ha). The lekking place density as well as the population density increased with altitude.

Comparison between areas with and without capercaillie

Twelve areas with capercaillie and 20 areas without capercaillie were delineated within the three test areas. Forest patches inhabited by capercaillie had a higher proportion of open canopy and, corresponding to that, a higher edge length density and less dense vegetation structures (Table 2). They were characterised by a higher percentage of ground vegetation, especially of blueberry and provided better protection on the ground in summer. No differences were found with regard to the forest stand type, canopy

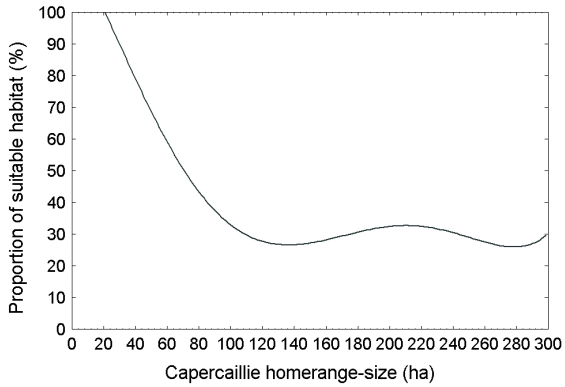


Fig. 3. Relationship between proportion of suitable habitat and home range size of capercaillie that was derived from literature as a basis for the calculation of the "population – habitat" index.

closure, age class, species mixture, successional stage and the vertical stratification.

Comparison between actual and historical capercaillie distribution

Of 156 lekking places mapped within the eastern part of the Black Forest in 1902, 60 were located within the present distribution range (category "permanently inhabited"), 83 were classified as "abandoned" and 13 were excluded because of their location within the 100-m border area of the present distribution range. Table 3 illustrates the differences of the landscape ecological parameter values between "permanently inhabited" and "abandoned" sites. While in 1902 the capercaillie range included small forest patches on steep slopes at lower altitudes, the distribution of capercaillie leks has retreated to large, plane forest areas at higher altitude. Surprisingly, permanently inhabited forest patches show a higher density of linear infrastructure (like roads, trails, railroads etc.). However, the values show great variation for both cases (6–67 m ha^{-1} for abandoned and 9–65 m ha^{-1} for permanently inhabited forest patches). Because of the capercaillies' preference for plane areas, which are often better accessible and therefore better developed with infrastructure than steep slopes, this correlation may be an artefact. No differences were recorded in relation to the persisting preference for eastern exposures.

Differences in local habitat structure parameters are shown in Table 4. The forest patches that have been "permanently inhabited" by capercaillie are mixed coniferous forests with Scots pine *Pinus sylvestris* and an open canopy, they are also characterised by a higher proportion of ground vegetation and provide better protection on the ground than the abandoned patches. The higher percentage of raw humus is correlated with the higher percentage of blueberry cover. Furthermore, the permanently inhabited forest patches have a higher proportion of thickets and single-storied stands. The forest patches abandoned by capercaillie are characterised by a higher percentage of spruce monocultures and closed canopy. No differences were recorded regarding the edge length density.

Thresholds and target values

According to the threshold values for the landscape ecological variables (Table 5) it can be expected with a 75% probability of occurrence that forest patches will be abandoned by capercaillie if they are below 640 m, the forest cover is < 89%, the slope is steeper than 15%, and the linear infrastructure exceeds 52 m ha^{-1} or falls below 32 m ha^{-1}. The resulting target values for the relevant local scale habitat structure variables are shown in Table 6. For example, if

Table 2. Differences between habitat structure parameter values in forest patches "with capercaillie" and "without capercaillie". Parameter values are given in proportion of area (%) resp. m ha^{-1}. Statistical significance: $p < 0.05$ = *, (Mann-Whitney U-test).

Variable	Variant		Statistical significance
	With capercaille	Without capercaille	
Spruce monoculture (%)	21	19	–
Mixed stands with scots pine (*Pinus sylvestris*) (%)	20	15	–
Canopy closure 50–70 (%)	47	39	–
Open habitat structures (%)	21	14	*
Edge length density m ha^{-1}	52	37	*
Dense habitat structures (%)	19	16	–
Old forest	31	33	–
Ground vegetation cover > 40 (%)	76	60	*
Blueberry (> 20 cm) > 10 (%)	36	16	*
Ground cover in summer > 50 (%)	44	32	*
Ground cover in winter > 50 (%)	14	9	–

Table 3. Differences between landscape ecological parameter values for "permanently inhabited" and "abandoned" forest patches. Statistical significance: p < 0.05 = *, p < 0.01 = **, p < 0.001 = ***, (Mann-Whitney U-test).

Variable	Category				Statistical significance
	permanently inhabited		abandoned		
	mean	amplitude	mean	amplitude	
Altitude (m a.s.l.)	900	800–1200	800	400–1200	***
Forest cover %	94	70–100	79	40–100	***
Slope °	11	0–42	19	0–45	*
Linear infrastructure m ha^{-1}	36	9–65	27	6–67	**
Exposition	N	3	–	6	–
	E	42	–	39	–
	S	8	–	4	–
	W	30	–	35	–
	plane	17	–	16	–

suitable habitat on 30% of the total area is aimed for, open structures on 10%, open canopy on 20%, spruce/pine stands on 10%, and sufficient ground vegetation cover (> 40%) on 66% of the area are required. In addition, the proportion of the area with dense structures should not exceed 30% and an edge line density of 50 m ha^{-1} should be given. Here are listed only those variables, which can be easily influenced and measured by forestry. Variables that are found to be relevant to capercaillie but are missing in Table 6 are correlated with at least one of these variables (e.g.; blueberry cover is positively correlated with a canopy closure of 50–70%).

Habitat suitability at the local scale

Variations in habitat quality among the three test areas for capercaillie males and females in summer and for both sexes in winter were observed (Table 7). Considering the sum of suitable forest patches (in both seasons and for both sexes) within an area to be an index for the total habitat suitability, the total proportion of suitable habitat in all three test areas is about 30% (northern test area: 32%, southern test area: 28%, central test area: 23%).

Landscape ecological requirements

At the landscape scale, the LEHP area for capercaillie comprises forest core patches with a minimum size of 100 ha, located in high montane regions with a minimum distance of 100 m to infrastructure and settlement. These variables and target values were defined on the basis of various publications (Koch 1978, Müller 1982, Rolstad 1988, Stuen and Spidsø 1988, Rolstad and Wegge 1989, Picozzi et al. 1992, Storch 1993, Suchant 2002) and the results of this study (Table 3).

The calculation of the LEHP showed that 13% of the forested area of the Black Forest, equivalent to almost 58 000 ha, is potentially suitable for capercaillie with regard to landscape ecological conditions (Suchant et al. 2003). The fragmentation pattern of the LEHP area is also

Table 4. Differences between habitat structure parameter values for "permanently inhabited" and "abandoned" forest patches. Statistical significance: p < 0.05 = *, p < 0.01 = **, p < 0.001 = ***, (Mann-Whitney U-test).

Variable	Category and parameters (%)		Statistical significance
	permanently inhabited	abandoned	
Spruce monoculture	19	32	***
Mixed stands with Scots pine (*Pinus sylvestris*)	56	46	**
Gaps and regeneration	5	2	*
Open structures	38	18	**
Close/dense structures	35/18	49/24	*/*
Single-storied stands	56	48	*
Raw humus	58	39	***
Mull	7	22	*
Visibility < 20%	41	28	**
Cover of blueberry	42	28	***
Blueberry > 20 cm	37	19	***

Table 5. Thresholds for landscape ecological variables critical for the occurrence of capercaillie leks.

Variable	Target value
Forest cover (% of 100 ha)	≥ 89
Altitude (m a.s.l.)	≥ 640
Slope (°)	≤ 15
Linear infrastructure (m ha^{-1})	≤ 52; ≥ 32

reflected by the abundance of capercaillie. However, there is a substantial proportion of LEHP which is not occupied by capercaillie (47% or 27 000 ha). In contrast, ca 25 000 ha of the Black Forest are inhabited by capercaillie, although this area was not mapped as LEHP.

The population/habitat index

The relationship between the potential habitat area, the size of the target population and the proportion of required optimal habitat is presented in Fig. 4. The larger the potential habitat area is, the smaller the percentage of optimal habitat structures can be. Conversely, the higher the target population size is, the higher the percentage of required optimal habitat structures becomes. The population/habitat index can also be used to determine the size of a sustainable target population once a certain landscape ecological habitat potential and a certain proportion of area with suitable habitat structures is given. The threshold of 30% suitable habitat is derived from the habitat structure analysis and is supported by studies conducted by Storch (2000) and Angelstam (2004). Statistically, a landscape ecological habitat potential of 58 000 ha was calculated for the Black Forest, which would result in a population size of almost 600 birds as the mean habitat suitability of 30% is given. This is in agreement with the population size that was estimated by the lek counts.

A multidimensional habitat management model

The scientific literature is often inconsistent with regard to the distinction between the local and the landscape scale. Hence, spatially explicit approaches need to be employed. Consequently, a scaling system was developed that defines four different spatial levels (Fig. 5). On the basis of this a multidimensional habitat management model for capercaillie was developed for use in practical management.

Scaling system

The country level (level 1) represents the broadest landscape scale and refers to administrative borders (the federal

Table 6. Target values (proportion of suitable area) for specific habitat structure variables in a capercaillie habitat.

Target value	Resulting minimum values					Resulting maximum values
required area with suitable habitat-quality (%)	open structures (plantation, forest stands with gaps) (%)	forest stands with canopy closure 50–70% (%)	Norway spruce or Scots pine stands (%)	cover of ground vegetation > 40% (%)	edge line density (m ha^{-1})	dense structures (thickets, dense pre-commercial stands, dense natural regeneration) (%)
30	10	20	10	66	50	30
50	17	33	17	76	83	22
70	23	47	23	86	117	14
100	33	67	33	100	167	0

Table 7. Habitat suitability within the three test areas for capercaillie males/females in summer and for both sexes in winter (proportion of area). u: unsuitable, n: neutral, s: suitable.

Category:	Relative habitat suitability within the test areas								
	Southern			Central			Northern		
Test area:	u	n	s	u	n	s	u	n	s
Males/summer	9	58	33	23	50	27	8	65	27
Females/summer	22	36	42	35	33	32	19	55	26
M/F winter	8	82	10	9	81	10	11	47	42
Average: all categories	13	59	28	22	55	23	13	56	32

state Baden-Württemberg). At this level the general wildlife-related landscape ecological conditions were analysed. At the eco-regional level (level 2, the Black Forest itself) the potential suitability of a given landscape for the survival of a selected species is evaluated. The remaining two levels at the local scale are important for the planning, the implementation and the evaluation of specific wildlife management measures. The district level (level 3, test areas) refers to a management-related area, often represented by forest management districts. The microhabitat or forest stand (compare Hagan and Meehan 2002) is level 4.

Methodological steps

The hierarchical order of the model is represented by six methodological steps, each of them refers to one of the four scale-levels (Fig. 5). At level 1 (the country level), landscape types providing habitat for a viable capercaillie population have to be identified in a first step. Therefore the concept of wildlife ecological landscape types (WELT) has been developed. It is based on the analysis of the landscape structure and divides Baden-Württemberg into twelve structural units: the so-called wildlife ecological landscape types. Details concerning the methods and results of the WELT-concept can be found in Suchant and Baritz (2001b) and in Suchant et al. (2003). The WELT map classifies the complex wildlife habitat system at the broadest scale of a wildlife management system. The Black Forest study area mainly consists of two wildlife ecological landscape types that are characterised by large forested areas and a low density of settlements and industry. They provide the only potentially suitable area for capercaillie within Baden-Württemberg (Suchant et al. 2003).

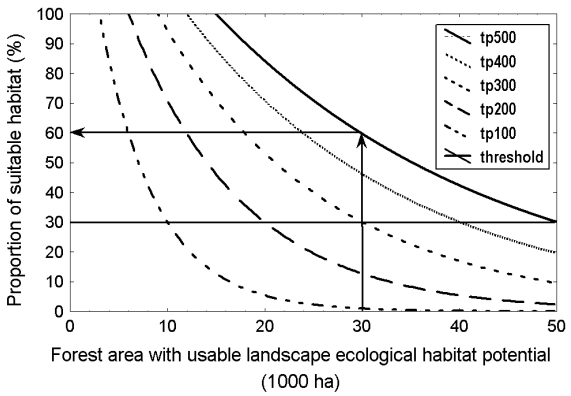


Fig. 4. Relationship between population size, landscape ecological habitat potential (LEHP) (ha) and the required proportion of suitable habitat (tp_{100} = target population size of 100 birds, tp_{200} = 200 birds). As an example, with an area of usable LEHP of 30 000 ha and an aspired population size of 500 birds, a minimum proportion of 60% suitable forest area is required.

At level 2 (the ecoregional level), within the selected WELT types at the eco-regional scale, the landscape ecological habitat potential for capercaillie has to be identified in a second step. For the Black Forest an area of 58 000 ha was determined. In a third step, the accessible habitat potential should be deduced from the landscape ecological habitat potential. This includes those habitat patches that can actually be reached by the individuals of a species. For capercaillie it can be assumed that patches can be colonised or inhabited if the distance between patches of the potential habitat does not exceed 20 km within a mainly forested region (Rolstad 1989, Klaus et al. 1989, Ménoni 1991, Storch 1993). In the Black Forest, an area dominated by woodland, the distance between all LEHP-patches is < 20 km, meaning that the delineated LEHP is identical with the usable potential.

The population size required for species survival must be defined in order to estimate the proportion of required optimal habitat (step 4). The minimum size of a viable population for capercaillie was defined as 500 birds (Grimm and Storch 2000).

The next steps have to be conducted at district and forest stand level. The minimum proportion of optimal habitat required by capercaillie has to be derived from the target population size and the amount of usable LEHP employing the "population/habitat index" (step 5). It must not be less than the minimum of 30% (Andrén 1994, Storch 2000, Angelstam 2004, this study). In the Black Forest with an usable LEHP of 58 000 ha and a target population size of 500 birds a proportion of 30% optimal habitat is sufficient.

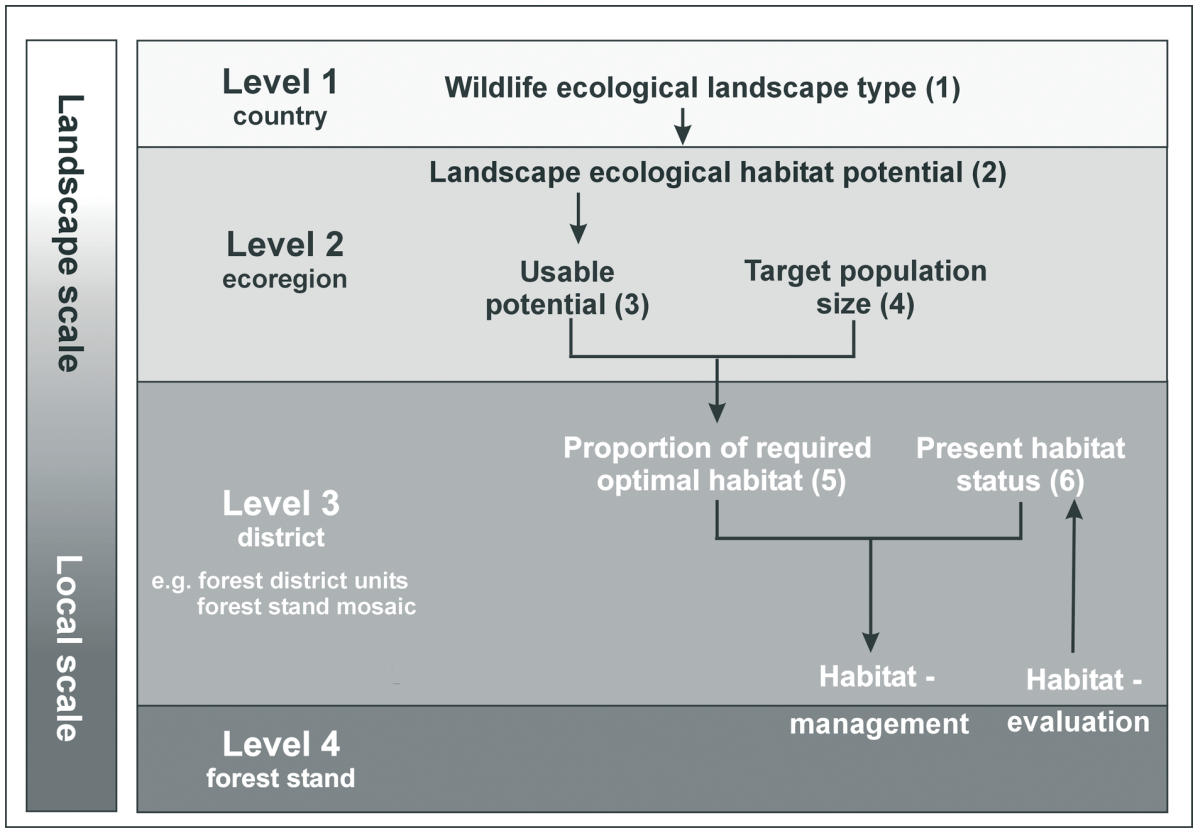


Fig. 5. Scaling system and methodological steps [(1)–(6)] (see text) of the multidimensional habitat management model for the capercaillie.

Step number six is to determine the proportion of the existing suitable habitat area. If it is lower than the required proportion of optimal habitat, habitat improvement measures have to be planned and implemented. Therefore, target values for specific habitat structure variables have to be defined. These target values help to estimate the proportion of suitable habitat and provide a basis for the development of management plans. The target values are to be related to the total proportion of suitable habitat that is required by capercaillie (Table 7).

Discussion

Since habitat availability can be regarded as a key factor for the development of wildlife populations, it is the primary focus of practical wildlife management. Therefore, the direct link between habitat quality and changes to habitats due to forestry has to be considered (Angelstam 1992, Storch 1993, Short et al. 1995, Carlson 2000, Wardell-Johnson and Williams 2000). However, to make use of this linkage for the development of sustainable management concepts, by transforming research results into applicable wildlife-related targets for silviculture, represents one of the major challenges for conservation biologists and wildlife managers. In order to assess and evaluate wildlife habitats in forests, various methods have been introduced (Brennan et al. 1986, Hamel et al. 1986, Doan et al. 1997, Jones et al. 2002). Nevertheless, many approaches lack clear differentiations, whether the habitat of an individual, a subpopulation, or even a metapopulation is addressed, or how the investigated habitat variables are correlated to each other. Furthermore, the habitat analysis is not linked to a practical management system, which should also be applicable at larger scales.

To make up for these deficits, the multidimensional habitat model has been developed. It defines species-specific and scale-specific habitat parameter values and provides thresholds for relevant habitat variables as target values for forest management. The model is based on analyses that include different temporal and spatial scales comparing areas, which were and are inhabited by capercaillie compared with those that are not. The temporal approach takes into account that the present conditions of a landscape represent only a small fraction of all the factors that led to today's situation as a result of a long development process. This process is not only closely linked to changing human land use strategies, but also to indirect anthropogenic impacts or natural processes (Angelstam et al. 2000). It is not always possible to clearly identify or to separate

these impacts and their influence on species abundance. Landscape ecological variables are often overruled by human impacts at the local scale.

The landscape ecological and local scale habitat variables and parameters relevant to capercaillie were deduced from the comparison of habitat conditions in forest sites with historical and present capercaillie distribution. This investigation is based on the assumption that capercaillie has abandoned forest patches where the relevant habitat conditions have deteriorated. Nevertheless, not all parameters that differ from former conditions are necessarily a decisive factor for the disappearance of capercaillie. Moreover, if no differences are shown it does not necessarily mean that a variable is not relevant. By investigating the same variables again with regard to their influence on the present capercaillie distribution within an area, where in theory every place could be reached by capercaillie, the relevance of both variables and parameter values could be verified.

Although species-specific habitat requirements at the local scale have been examined thoroughly and incorporated into habitat models in many cases (Hammill and Moran 1986, Brennan et al. 1986, Carlson 2000, Jones et al. 2002) and habitat analysis at the landscape scale is already fairly widespread (Hagan and Mehan 2002, Martin and McComb 2002), the wildlife manager's basic question of what measures to plan and where to implement them in practical management is often still not sufficiently answered. The concepts of wildlife ecological landscape types (WELT) and the landscape ecological habitat potential (LEHP) provide the framework for the location of management-relevant areas at the landscape scale and as a consequence facilitates the integration of wildlife aspects into regional planning acts (Suchant et al. 2003). The methodological approaches resemble those proposed by MacFaden and Capen (2002). The LEHP model represents a simple method to analyse the species-specific value of landscape ecological variables. The selection of these variables and parameter values is limited and may lack important factors such as soil conditions or climatic data. Particularly, because adequate climatic data were not available, the parameter "altitude" was chosen as an auxiliary variable which represents climatic conditions. These deficiencies may partly be a cause of the deviation between capercaillie abundance and LEHP, and therefore require an enhancement of the LEHP-concept which is currently in progress. Nevertheless, the overlap of the LEHP for capercaillie and the actual and historical abundance of capercaillie confirms that the model does reflect the most dominant landscape variables. In addition, the differences between LEHP and inhabited areas can be explained by local-scale habitat structures to a large extent.

While the LEHP identifies areas, where the landscape ecological conditions are favourable to the development of suitable habitat structures and thus measures for habitat improvement are expected to be successful, the results of the habitat structure analysis provide the basis for locating forest stands with deficient habitat conditions and, thus, the development of specific management strategies at the local scale. Fortunately, most of the habitat structure variables needed to assess habitat suitability correlate highly with variables mapped during the regular forest inventory (see also Åberg et al. 2003). Therefore, the inventory map can be utilised for the habitat assessment with little or no additions and can be directly integrated into forest planning. The evaluation procedure is not restricted to single forest stands but rather considers the habitat structure of a forest stand mosaic, so that the requirements for wildlife management on the population level can be met.

We thus consider the model to be an applicable tool to integrate general nature conservation aims in forest management, which are often associated with capercaillie (Suchant and Baritz 2001a). Many approaches in nature conservation and management concentrate on taxon-based surrogate schemes that assess the abundance of representative species to estimate the condition of ecosystems to quantify biodiversity, to identify threats or to define habitat improvement measures. Umbrella species, indicator species, flagship species as well as the focal species approach (Lambeck 1997) are well-known examples (Lindenmayer et al. 2002). In contrast, concentrating on habitat variables relevant to a focal species rather than on the species themselves is much more easily realised. As variables can be examined and implemented by the regular forest inventory and an elaborate assessment of the species' abundance itself is not the only indicator for success a continuous monitoring of the conservation targets is easy to maintain.

However, management-oriented habitat models are limited as they have to balance between applicability and meeting the requirements of incorporating the complexity of the natural systems they address (Storch 2002). The habitat model presented here does not sufficiently take into account all aspects that are important for the habitat use of capercaillie at the local and the landscape scale. More detailed information about population densities and species-specific movement patterns between habitat patches are required. Thus, the influence of population density on distribution patterns and dispersal rates, source and sink population interactions (Pulliam 1988) as well as metapopulation dynamics (Levins 1969, 1970) could not be incorporated although these aspects are essential for maintaining the long term viability of the population, especially in highly fragmented and disturbed landscapes. Nevertheless, the model provides a valuable framework for further investigations within an adaptive management framework.

Finally, when aiming for sustainable habitat management for capercaillie, the biogeographical scale must not be excluded (Lindén et al. 2000). The capercaillie distribution range with large contiguous populations in the boreal parts and the small, isolated and fragmented populations

in central Europe that are restricted to montane regions and are threatened by human impact and climate change, raises an important question: for how long are these populations viable?

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Towards the assessment of environmental sustainability in forest ecosystems: measuring the natural capital

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The present use of the world's forest resources is not sustainable. Yet over-harvesting and other stresses on forest ecosystems continue to degrade this natural capital on which human welfare is built. To improve information about forest resources to policy makers and the public at large, we propose the formulation of an index for the natural capital of forests that portrays the status and trends in the level of environmental sustainability of forests. The index and the sub-indices on which it will be based should reflect the composition, structure and functions of forests within a landscape perspective. The index should take into account forest ecosystems, ranging from naturally dynamic forests, cultural woodland to previously forest dominated landscapes, which have become highly degraded or transformed to other uses. Comparisons of quantitative and qualitative measurements, or indicators, with ecologically based performance targets, should be used to evaluate resource sustainability. The index could thus serve as a composite measurement of the quality of stewardship of the global forest capital, and signal to the world community its progress, or lack thereof.

A natural capital index for forests is a logical next step after a sequence of international initiatives during the last two decades in support of sustainable management of the world's forest resources. The development of an index should proceed by: 1) selecting indicators measuring the status of forest resources and services in actual landscapes; 2) developing performance targets by systematic research and synthesis; 3) aggregating the chosen indicators and targets into a regularly updated index; 4) applying the chosen methodology in a series of pilot studies in countries with different types of forest ecosystems and phases in the development of the use and management of forests; 5) studying the institutional arrangements needed for gathering, keeping and updating data over time and facilitating its adoption in national forest policies and programmes; and 6) assessing changes in the index over time.

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The world's critical environmental problems usually involve interactions between humans and nature. Hence they are transdisciplinary (Somerville and Rapport 2000) and cover a range of temporal and spatial scales (Mills and Clark 2001). It is clear at the outset that existing aggregate measures fail to adequately account for changes in the world's forested ecosystems and the consequences of these changes for human well being. For example, while GNP provides a basis for assessing economic activity within nations and for making comparisons between nation states, it is a weak indicator of economic development and a completely misleading signal of human welfare or ecosystem wellbeing (Prescott-Allen 2001). To provide a more diversified picture regarding social components of the sustainability concept, the Human Development Index (HDI) and several other approaches have been developed to present indicators of sustainability dimensions (Hardi and Sdan 1997, Moldan et al. 1997, Neumayer 2001, Prescott-Allen 2001, Sayer and Campbell 2003, 2004, Campbell et al. 2003, Ekins et al. 2003a, b). Although there remain some limitations, both GNP and HDI are important tools for measuring aspects of different dimensions of human wellbeing.

Yet these tools fail to capture what is ultimately one of the most critical requirements for human futures – namely the extent to which ecosystem functions – the very basis for our life-support systems, are maintained. This leads us to consider how to track changes in so-called "natural capital" that is changes in the quantity and quality of the earth's ecosystems. Ultimately, it is the viability of the earth's ecosystems that provides the basis for social and economic sustainability (Costanza and Daly 1992, Rapport et al. 1998b, 1999). The development of an index that measures progress towards or away from sustainability of natural capital is seen as a crucial complement to traditional economic measures (Perk and Groot 2000, Prescott-Allen 2001, Campbell et al. 2003, Deutsch et al. 2003, Ekins et al. 2003a, b). To achieve strong sustainability (Angelstam and Lazdinis 2003, Ekins et al. 2003b) each of the individual economic, socio-cultural and environmental dimensions need to be sustainable (Rapport et al. 1999).

In spite of more than a decade of research and development on indicators for an environmentally sustainable development (ESD), there is no agreed upon system for measuring this. While the elements of biodiversity (composition, structure and function) are a commonly proposed proxy for ESD (e.g. Puumalainen 2001, Larsson et al. 2001, Puumalainen et al. 2002), the multitude of indicators needed at multiple spatial scales has so far prevented the development of an operational index capturing concepts such as ecosystem health, ecological integrity or resilience (Fig. 1). Additionally, to make assessments of sustainability in the strong sense, the required performance targets to which indicators should be compared are in limited supply (Linser 2001, Muradian 2001, Angelstam et al. 2003a, Ekins et al. 2003b).

Thanks to a long tradition of describing forest resources and services (FAO 2003), forest and woodland ecosystems represent an opportunity for attempting the development of an index for communicating the status and trends towards sustainability of ecosystems. A beginning would therefore be an index for the natural capital of forests, which is implicit in the Forest Capital Index (FCI) proposed by Salim and Ullsten (1999). The reasons for starting with forest ecosystems are many-fold. Regionally, the world has lost most of its original forested landscape area within the past 8000 yr (Hannah et al. 1995, Matthews et al. 2000, UNEP-WCMC 2000, Woodwell 2002). Beside this loss of forest cover, there has also been a decline in the health or integrity of many remaining forest and woodland regions (Mikusiński and Angelstam 1998, Matthews et al. 2000, Pimentel et al. 2000, Woodwell 2002, Williams 2003, Angelstam et al. 2003b). The vast literature on habitat loss and fragmentation bear witness to these processes.

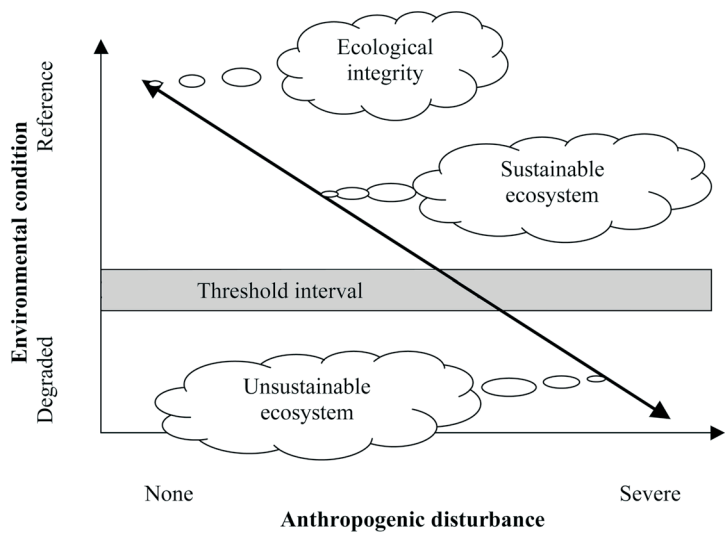


Fig. 1. The environmental condition measured as an indicator that degrades away from ecological integrity found in reference areas. Ecological integrity represents the conditions where the ecosystem has its evolutionary legacy or memory with both parts (e.g. species and structures) and processes (e.g. nutrient cycles, disturbance regimes) intact. With policies aiming at striking a balance between, say, production and biodiversity within different forest types in a forest landscape, conditions well above ecological thresholds would be sustainable (i.e. healthy) and conditions well below thresholds would be unsustainable. Thresholds are rarely distinct, rather they are intervals of change where, for example, a species or function changes from one state to another.

The consequences of these changes are losses in the elements of biodiversity, including species diversity, habitat diversity and ecosystem services such as the capacity to regulate climate, hydrological and nutrient cycles, and reduction of carbon dioxide sequestration capacity (Myers 1997, Alexander et al. 1997). Continued overexploitation in many regions threatens the world's ecological and socio-economic sustainability (Gunderson et al. 1995, Salim and Ullsten 1999, Berkes et al. 2003).

As a result, for many decades, a growing number of experts, policy makers, NGOs and intergovernmental organisations have been calling for the sustainable use of natural resources including forests, and ways to measure the components of sustainability (ITTO 1992, UNCED 1992, MCPFE 1993, 1998, 2003a, Anon. 1995, Salim and Ullsten 1999, Rapport et al. 2003). In 1987, the World Commission on Environment and Development (WCED 1987) highlighted the concept of "sustainable development", which is development that meets the needs of the present without compromising the ability of future generations to meet their own needs. Sustainable development focuses on improving the quality of life for all of the Earth's citizens without increasing the use of natural resources beyond the capacity of the environment to supply them indefinitely. This reflected a milestone in political understanding: rejecting development that is unsustainable.

In 1992, the United Nations Conference on Environment and Development (UNCED, the Earth Summit) called for development of indicators of sustainable development (UNCED 1992). The Intergovernmental Forum on Forests (IFF), established in 1994, and its successor, the UN Forum of Forests (UNFF), recommend such indicators for the systematic evaluation of forests globally.

Many agencies and programs now carry out monitoring of the extent and incremental gain or loss of forests, and publish periodic measures of the extent of the world's forest cover. The Ministerial Conference on the Protection of Forests in Europe (MCPFE) (MCPFE 2003b) and the Montreal Process (Anon. 1995) have now identified a number of indicators of forest condition, based on prior work by UNCED (UNCED 1992) and ITTO (ITTO 1992). A large number of other initiatives related to forests and forestry indicators have arisen (Table 1), notably UNEP's Global Environment Outlook program (UNEP 2003), the Food and Agriculture Organization's State of the World's Forests (FAO 2003), the State of Europe's Forests 2003 (MCPFE 2003c), the Canadian Forest Service's Criteria and Indicators program, the World Resource Institute's Pilot Analysis of Global Ecosystems (PAGE) (Matthews et al. 2000), NASA (2003) and USEPA (2002) forest monitoring programs and State of the Environment reporting in a number of countries. Websites focusing on indicator development include the Compendium of Sustainable Development Indicator Initiatives and Publications (IISD 2003), Development Indicators, Environmental Economics and Indicators, and Convention on Biological Diversity (CBD) recommendations for a Core Set of Indicators of Biological Diversity (CBD 1997). The 2002 Environmental Sustainability Index (World Economic Forum, Yale Center for Environmental Law and Policy, and CIESIN 2002) has attempted to combine environmental and socio-economic indicators into an index of sustainability. Agencies such as the OECD (2000), FAO (2003), NASA (2003), and World Bank (2003) also compile and list hundreds of indicators on forest condition and associated socio-economic variables. A number of initiatives in forest certification have emerged to encourage sustainable use of forest resources, such as the Forest Stewardship Council (<http://www.fscoax.org>) and the Programme for the Endorsement of Forest Certification Schemes (previosly the Pan European Forest Certification) (<http://www.pefc.org>). A number of approaches to developing indices of ecological integrity have been suggested, most notably Karr's Index of Biological Integrity (IBI) for aquatic systems (Karr and Chu 1999). A scientific debate on an index of terrestrial integrity is ongoing (Andreasen et al. 2001). Efforts are also underway to develop integrated indices of biodiversity (e.g. Murray 2003).

An index of the natural capital of forests, such as based on recommendations by the World Commission on Forests and Sustainable Development (Salim and Ullsten 1999), is a logical next step after a sequence of international initiatives during the last two decades in support of sustainable management of the world's forest resources. The index is a way of combining relevant, but complex data related to the condition and trends of forest ecosystems composed of individual indicators that, when considered separately, provide only partial answers to questions regarding sustainable forest management. Large sets of indicators do not answer the question of whether forest management is overall moving towards sustainability from the natural capital perspective or away from it. A properly constructed index of the natural capital of forests ought to be capable of providing this assessment in a straightforward manner. Such an index should thus be able to capture aggregated or overall trends in sustainability understandable to both decision-makers and the public. The need for efficient communication of the status of natural capital is also expressed as a priority at the Global Environmental Facility council in May 2003, and includes strengthening protected area systems, mainstreaming biodiversity, supporting integrated ecosystem management and disseminating best practices. Similarly, the conference of the parties of the CBD has repeatedly emphasised the importance of developing national biodiversity indicators and building capacity for their further development and use and has called for international collaboration on these issues. The policy context for a natural capital index for forests is thus well substantiated.

An important means of measuring trends in forested ecosystems is to combine indicators with scientifically based performance targets (Higman et al. 1999, Duinker

Table 1. A sampling of global environment and forest monitoring programs.

No.	Program	Data type	URL
1.	Convention on Biological Diversity. Recommendations for a Core Set of Indicators of Biological Diversity	Ecological	<http://www.biodiv.org/>
2.	CIESIN Environmental Treaties and Resource Indicators (ENTRI)	Environmental	<http://www.gateway.ciesin.org/>
3.	CIESIN Land and Water Knowledge Management Node (LW-KMN)	Environmental	<http://www.ciesin.org/lw-kmn>
4.	CIFOR Criteria and Indicators for Sustainable Forest Management (C&I)	Forests	<http://www.cifor.cgiar.org/publications/html/ar-98/C_and_I.html>
5.	EEA	Environmental	<http://ims.eionet.eu.int>
6.	FAO Global Terrestrial Observing System (GTOS)	Environmental	<http://www.fao.org/waicent>
7.	FAO Statistics and Sector Analysis Program	Forests	<http://www.fao.org/WAICENT/FAOINFO/FORESTRY/fonprog2.htm>
8.	FAO State of the World's Forests		<http://www.fao.org/DOCREP/005/Y7581E/Y7581E00.HTM>
9.	FAO/ Forest Resources Assessment		<http://www.fao.org/forestry/fo/fra/main/index.jsp>
10.	IBRD (World Bank) Environmental Economics and Indicators Unit (EEI)	Integrated	<http://www.worldbank.org/environmentaleconomics>
11.	IBRD (World Bank) Land Quality Indicators (LQI)	Environmental	<http://www.worldbank.org/environmentaleconomics>
12.	ICP Forests	Forests	<http://www.icp-forests.org/Monitoring.htm>
13.	IGBP Global Land Cover Characterization (GLCC)	Remote sensing	<http://edcwww.cr.usgs.gov/landdaac/glcc/glcc.html>
14.	IISD Measurement and Indicators for Sustainable Development	Clearinghouse	<http://iisd1.iisd.ca/measure/default.htm>
15.	IUFRO Task Force on Sustainable Forest Management	Forests	<http://iufro.boku.ac.at/iufro/taskforce/tfsfm/abtfsfm.htm>
16.	IUFRO, Task Force on Environmental Change	Climate change and forests	<http://iufro.boku.ac.at/iufro/taskforce/hptfec.htm>
17.	MCPFE, The State of Europe's Forests	Forests	<http:/www.mcpfe.org/secure/k-tools/phplib/MedienDatenbankView.inc.php?id=401>
18.	NASA Earth Observing System Data and Information System (EOSDIS)	Remote sensing	<http:/spsosun.gsfc.nasa.gov/New_EOSDIS.html>
19.	OECD, Development indicators	Integrated	<http://www.oecd.org/dac/goals>
20.	State of the Environment Reporting	Clearinghouse	<http://www.ncseonline.org/SciencePolicy/StateOfEnvironment.cfm>
21.	UN CSD Indicators of Sustainable Development	Integrated	<http://www.un.org/esa/sustdev/isd.htm>
22.	UNEP Global Resources Information Database (GRID)	Remote sensing	<http://www.grid.unep.ch>
23.	UNEP State of Environment Reporting (SOER)	Environmental	<http://www.grida.no/enrin/allsoe.cfm>
24.	UNEP, Global Environment Outlook	Integrated, trends	<http://www.grid.unep.ch/geo/geo3>
25.	USGS Earth Resources Observation System (EROS)	Remote sensing	<http://edcwww.cr.usgs.gov/>
26.	UNEP-WCMC Forest Programme	Forests	<http://www.unep-wcmc.org/forest/homepage.htm>
27.	WRI Forest Frontiers Initiative	Forests	<http://forests.wri.org/>
28.	Global Forest Watch	Forests	<http://www.globalforestwatch.org/>
29.	WRI Resource and Environmental Information Program	Environmental	<http://www.wri.org/data>
30.	WWF Forests for Life	Forests	<http://www.panda.org/forests4life/>
31.	European Forestry Institute Databases	Forests, trends	<http://www.efi.fi/information_services/>
32.	European Commission, Environment Portal	Forests	<http://europa.eu.int/comm/environment/index_en.htm>
33.	IUCN Programme	Forests, biodiversity	<http://www.iucn.org/ourwork/programme.htm>

2001). The existence of ecological discontinuities and thresholds has been recognised in ecological economics as a key feature to consider when making operational the concept of sustainable development (Muradian 2001, Wirl 2004, Andriantiatsaholiniana et al. 2004). During the 1980s it was understood that there are critical loads of anthropogenic pollution (Nilsson and Grennfelt 1988), and society acted on a number of such issues, including sulphur and phosphorus, ozone-depleting substances, and some persistent organic pollutants. Similarly, during the 1990s, new results about the causes of extirpation of populations show that there are critical levels of habitat loss that should not be exceeded if we viable populations of species are to be maintained (Andrén 1994, Fahrig 2001, 2002). The same reasoning is behind the concept of critical natural capital (Ekins et al. 2003b). By contrast, forest certification and government policies often focus on criteria and indicators from political processes rather than objective assessment using measurements and performance targets (Lammerts van Buren and Blom 1997, Puumalainen et al. 2002).

The landscape concept used by ecologists and geographers can be linked to the socio-economic landscape perspective of managers and owners on the one hand, and to the policy makers on the other (Lazdinis and Angelstam 2004). Landscapes can thus be viewed as social-ecological geographical units with several layers of properties ranging from tangible ones such as soils, topography, vegetation and land use systems to intangible ones such as cultural and institutional. For monitoring purposes a forest landscape should be defined as contiguous area where forests and woodland are or were the dominating type of vegetation (Angelstam et al. 2004a). Rather than focusing on what is forest today, one should aim at assessing entire landscapes in ecoregions where forest is the natural vegetation. In doing that we can address natural forest capital in operational terms, consider both natural and human factors as creators of habitat, and acknowledge the contribution of new nature-friendly land management methods (Lindenmayer and Franklin 2002, Puumalainen et al. 2002, Angelstam 2003).

In this paper we outline the components of an index of the natural capital of forests, and discuss how indicators of the status of forested ecosystems could be combined with performance targets. We focus on the natural capital, but also discuss the pros and cons of integrating a critical natural capital index with other elements of sustainability and types of capital (Campbell et al. 2003, Ekins et al. 2003b).

Developing an index of the natural capital of forests

The index concept intends to aggregate and communicate important information on the state of the world's forest ecosystems. It should be developed from the numerical values of selected indicators and sub-indices, which measure a range of functions of forest and woodland landscapes. Measurement of the indicators comprising the index over fixed time periods, and comparison of the results to performance targets and to benchmarks, would go well beyond current trends of indicator reporting and would reveal whether or not the management of a region's forests is moving in the direction of sustainability. Ideally, the index should apply to all forest landscapes, natural and managed, regardless of size and type, and go beyond giving guidance for forestry practices alone.

Andreasen et al. (2001) discussed the criteria for a useful index of terrestrial ecosystem integrity: it must be multi-scaled, grounded in natural history, relevant and helpful, flexible, measurable, and comprehensive (i.e., incorporate components of ecosystem composition, structure, and function) of the natural capital of forests (Box 1). The development of an index should proceed by: 1) selecting a limited number of ecological indicators measuring the status of forest resources and ecosystem services of forest dominated ecosystems; 2) developing performance targets by systematic research and synthesis; 3) aggregating the chosen indicators and performance targets; 4) applying the chosen methodology in a series of pilot studies in countries with different types of forest dominated landscapes and phases in the development of the use and exploitation of forests, using the same measurement protocol at all sites; 5) studying the institutional arrangements needed for gathering, keeping and updating data over time and facilitating its adoption in national forest policies and programmes; and 6) assessing changes in the natural forest capital index over time.

Box 1. Characteristics of an index of the natural capital of forests.

- Provides information about a broad range of variables for a forest ecosystem.
- Encapsulates several variables in a single statement, allowing easy comparison across nations.
- Includes ecological indicators at multiple spatial scales.
- Shows the ability of landscapes to function and to support human needs over time.
- Shows trends over time.
- Defines thresholds that indicate the range of indicator values, which represent sustainability.
- Compares levels in the indicators with critical thresholds. This allows decision-makers to ascertain whether policies are effective in preserving the services of forest ecosystems, and whether these services are sufficient to meet current demands.
- Can be applied to and compared among clearly defined regions, such as countries.
- Transparent and easily understandable.
- Includes ability to reveal changes in single or aggregated indicators.
- Should be adaptive and will be improved as better data and information become available.

Selecting indicators

The development of a natural forest capital index would build upon a range of existing monitoring systems of sustainable forest management and make use of indicators that have been developed from processes such as the Criteria and Indicators (C&I) for Sustainable Forest Management developed by the Montreal process and the MCPFE (Anon. 1995, MCPFE 2003b). At the Convention on Biodiversity's (CBD) sixth meeting, the conference of the parties adopted a strategic plan, including the target to achieve by 2010, a significant reduction in the rate of biodiversity loss at the global, regional, and national level. This target was endorsed at the World Summit on Sustainable Development, Johannesburg, 2002. The strategic plan specified that better methods should be developed to objectively evaluate progress in the implementation of the CBD. The convention's scientific advisory body identified five indicators for immediate use. These include extent of natural habitats, abundance and distribution of species, change in status of threatened species, genetic diversity of species of major socio-economic importance, and coverage of protected areas. It is, however, important to critically evaluate the extent to which underlying data are available. For regional and local comparisons more detailed sets of indicators need to be used (Angelstam and Dönz-Breuss 2004, Angelstam et al. 2004a).

Indicators selected for a natural forest capital index, must, of necessity, be relatively few in number to avoid formulation of an index that is overly complicated and ultimately meaningless. The indicators must also satisfy several conditions: they must be sensitive to change, respond to stress in a predictable and unambiguous manner, be supported by precise, accurate, reliable, and, if possible, readily available data for all nations, be verifiable and reproducible, and be understood and accepted by intended users (Landres et al. 1988, Noss 1990, 1999, Kelly and Harwell 1990, Rapport 1992, Cairns et al. 1993, Lorenz et al. 1999, Dale and Beyeler 2001, Andreasen et al. 2001, Schiller et al. 2001). A good indicator will have a direct link from environmental measurement to practical policy options and decision-making (Gallopin 1997, Dale and Beyeler 2001). The indicator data must also be objectively collected, and representative of a wide range of forest ecosystems. In Tables 2 and 3, we provide a list of existing and desirable indicators that might be used in an index for the natural capital at the national level. To describe the natural capital, the focus should be on indicators that describe the state of the forest environment (Angelstam et al. 2004a).

Developing ecological performance targets

The two most obvious drivers of forest loss are the alteration of naturally dynamic systems through intensive forest management, and the clearing of forest for other kinds of land use. These activities involve large-scale habitat destruction, which at different spatial scales may lead to non-linear responses of species and ecosystem services (Muradian 2001, Wirl 2004). We agree with Ekins et al. (2003b) that it should be possible to compare the state of the environment with target values of key parameters for sustaining the health of forest ecosystems. For example, the existence of thresholds for habitat loss has been demonstrated in a wide range of studies (Andrén 1994, Fahrig 2001, 2002). Several kinds of thresholds have been addressed, i.e., the fragmentation threshold, which is the amount of forest habitat below which habitat fragmentation (i.e., the spatial pattern) may affect population persistence of species, and the extinction threshold, which is the minimum amount of forest habitat below which a population goes extinct. While the fragmentation threshold appears to occur at about 20% suitable habitat remaining, there is no common extinction threshold value across species, and such values may range from 1 to 99% habitat depending on the parameter values for species with different life-history traits (Fahrig 2001). This means that evaluation of the forest environment should include spatially explicit analyses such as of: 1) the functional connectivity of habitat networks for different suites of species representing different types of forest and woodland (Angelstam et al. 2004d), 2) landscape configuration (Angelstam 2003), and 3) the occurrence of large intact forest areas (Yaroshenko et al. 2001).

To facilitate comparisons among regions species can be divided into ecological groups. This is analogous to the life form concept used by Thomas (1979) to classify wildlife species into groups based on specific combinations of habitat requirements for reproduction and feeding. Similarly, Angelstam et al. (2004b) used a classification of vertebrate species based on body size, trophic position, and dependence on structural elements such as large trees, nest-holes, and dead wood. This approach allows for inter-regional (or inter-national) comparisons, thus ensuring that variation in habitat will cover the full range from intact reference areas to altered landscapes (Egan and Howell 2001). By combining data on species and habitats at relevant spatial scales it should be possible to look for the occurrence of non-linear responses, and based on such thresholds formulate performance targets (Angelstam et al. 2004c). Using this approach, targets or goals may be set for individual indicators, and eventually for the natural forest capital index overall.

Aggregating indicators and targets into a natural forest capital index

By comparing an indicator with a performance target derived from a threshold relationship, it is possible to evaluate whether or not the status of a particular indicator represents strong sustainability (Rapport et al. 1985, 1998a, b,

Table 2. Examples of existing ecological indicators that could be used for natural capital index for forests at the national level.

No.	Indicator	Unit	Years	Regions available	Data provider/Notes
1.	Naturalness – %	%	1990–2000	World	FAO (classified by "undisturbed by man", "semi-natural" and "plantations") annual change
2.	Protected forest areas – % of total land area	%	1970, 1980, 1990, 2000	World Europe	FAO, IUCN MCPFE
3.	Ratio of forest types protected to forest types available for protection	–			Provides for representativeness in conservation of forests; gap analyses available for some countries; see Joint Research Commission's Global Vegetation Monitoring Unit, IUCN, GFW; could replace indicator #2
4.	Frontier forest, % threatened	%	1996	World	GFW; refers to large, relatively undisturbed forest areas threatened by large-scale disturbances such as logging or mining; low-access forest data to be examined as well; see <www.globalforestwatch.org> for definitions and details
5.	Percent change in forest composition	%	Several	Several	Data can be extracted for some countries; shows change in forest composition over time due to harvesting or other disturbance
5.	Global forest canopy density	0–100	2000	World	GLCC; also NASA EOSDIS (vegetation index)
6.	Number of forest dependent species considered threatened/ endangered/at risk	–		World	Provides for biodiversity protection; WCMC and IUCN; movement within categories will be taken into account; to be separated into categories (e.g. vascular plants/animals)

Table 3. Examples of desirable ecological indicators that could be used for natural capital index for forests at the national level.

No.	Indicator	Data provider/Notes
1.	Patch size distribution of forests with different degree of transformation	Provides data on thresholds of habitat size required for maintaining populations; some data available from World Resources Institute
2.	Fragmentation/connectivity of forested landscapes	Montreal Process indicator; structural component of biodiversity MCPFE indicator 4.7, possible to estimate from remote sensing data.
3.	Age-class distribution of trees	Montreal Process indicator; structural component of biodiversity
4.	Area managed for conservation and utilisation of forest tree genetic resources (in situ and ex situ gene conservation) and area managed for seed production	Montreal Process indicator; conservation of genetic component of biodiversity
5.	Groundwater withdrawal to groundwater recharge ratio	The ratio of water demand to availability provides a picture of groundwater resources available
6.	Soil quality indicators (physical and chemical)	Forest soil resources
7.	Water quality indicators (physical, chemical, biotic)	Forest water resources

1999, 2003, Rapport and Whitford 1999, Karr 2000, Campbell et al. 2003, Ekins et al. 2003b), see Fig. 1. This in turn is essential to alleviate the societal learning process needed for constant iteration between management and assessment (Lee 1993). Aggregation of indicators into an index involves the construction of a mathematical model that defines the relationships of the component indicators (Jesinghaus 1999a, b). Aggregation can be complicated, partly because different indicators are reported in different units of measure on different time and spatial scales. Also, various components may need to have different relative weights (e.g. forest cover having a different weight in the index than forest biodiversity). Non-linear behaviour, where the behaviour of a component indicator may change beyond a threshold, must also be considered.

Phillis and Andriantiatsaholiniana (2001) and Andriantiatsaholiniana et al. (2004) describe a method to integrate measurements and targets for different elements of sustainability using fuzzy logic. Their method rests on the foundation that a reliable measurement of sustainability should be the result of integrating socio-economic and natural resources accounts. However, due both to lack of appropriate data and unsolved methodological problems this has not been done operationally. The use of fuzzy logic in indicator development and aggregation is justified because: 1) it has the ability to deal with complex and polymorphous concepts, 2) it provides a mathematical tool for handling ambiguous concepts and reasoning, and 3) it gives "crisp" answers to problems fraught with subjectivity. Another important aspect of fuzzy logic is that it uses linguistic variables. Hence values and opinions can also be dealt with. To assess sustainability in a "fuzzy logic" manner, the following should be defined, viz. 1) linguistic variables, 2) linguistic rule bases and fuzzy logic operators, which express knowledge qualitatively, for example by using thresholds based on the shape of response curves to the amount of habitat or ecosystem processes, and the position and distance from such thresholds, and 3) a "defuzzification" method to convert fuzzy statements into a single crisp value of overall sustainability. Campbell et al. (2003) explored five other possible approaches to combine indicator to give an integrative assessment. These were: 1) a simple additive index such as used for the Human Development Index, 2) derived variables such as from principal component analysis, 3) two-dimensional plots of indicators to visualise the data, 4) graphical representation of the different capital assets using radar diagrams, and 5) canonical correlation analysis to explore indicators at different scales.

One of the major problems with any method that reduces a range of variables to a single number is eclipsing (Ott 1978). For example, the value of one indicator may decrease significantly, while the value of others may increase slightly, yielding an overall increase in the index value. The only way to avoid eclipsing and the dangers inherent in a single index value would be to conceive and report both the index and the indicators comprising the index simultaneously, as part of the same information system. A diagrammatic approach, such as that used in the 2002 Environmental Sustainability Index (World Economic Forum, Yale Center for Environmental Law and Policy, and CIESIN, 2002), in the Dashboard of Sustainability (<http://www.iisd.org/cgsdi/intro_dashboard.htm>), or as suggested by Andreasen et al. (2001), would render changes in any component of an indicator immediately apparent.

In his study of the wellbeing of nations, Prescott-Allen (2001) combined data answering questions about the well-

being of people and ecosystem, and how they are affecting each other. The results of different elements, based on sub-elements and indicators, were presented in two ways. First graphically as thematic maps for each country, and then also as a barometer of sustainability in the form of two-dimensional graphs where for each country the two dimensions of well-being were illustrated along two axes with five bands, representing bad, poor, medium, fair and good performance. To measure ecosystem wellbeing the focus was on five main pressures people place on ecosystems: conversion and occupation, resource extraction, translocation of species, emissions and waste disposal and soil degradation.

As a disclaimer and an invitation to improvement, Prescott-Allen (2001) noted that it is extremely difficult to take a clear and easily communicated snapshot of something that is so complex and poorly understood as human societies and ecosystems, and their interactions. There is no method that provides a definitive assessment. Rather the approach provides a framework for reflection and debate. It is therefore vital that all data, assumptions, and judgements are made available to allow critical evaluation.

Another example, the Ecological Footprint (EF) (Wackernagel et al. 1999, 2000), combines the quantities of energy and renewable resources a society consumes by converting them into a common unit of area: the area of productive land and sea required to supply the resources and the carbon dioxide from fossil fuels.

Weighting the importance of the indicators in order to calculate a single index is another significant issue. Weighting the index, as well as indicator choice, is ultimately a subjective decision open to criticism (Andreasen et al. 2001). However, if the process of aggregation and weighting of the index is carried out by means of a careful, scientific, and thorough consultation process, the index should be accepted by a reasonable majority of stakeholders. Whatever system is chosen should be constructed such that it can be applied equally across all regions, ensuring the validity of making comparisons between countries.

Applying the index methodology in a series of pilot studies

To evaluate the index methodology it should be applied in a series of pilot studies in countries or regions with different types of forests and land use histories using the same measurement protocol and data sources at all sites. Ideally this should be made in contrasting regions (i.e., regions that are nearly in pristine condition contrasted with regions in which forests have become highly impacted from human activity), or along a series of regions that reflect a steep gradient from pristine to highly degraded (e.g. Good 1994, Angelstam et al. 2004b, c). This will test the effectiveness of the index and reveal its sensitivity to change and the robustness of the aggregation method. The robustness of the index should also be tested through sensitivity analysis to find out how the index responds to excluding/including or changing respective functions and parameters. The purpose of sensitivity analysis will be to identify key variables that affect the index's overall output and examine the consequences of probable adverse changes in key variables on the overall score of the index (modified from ADB 2003). The main possible steps in carrying out a sensitivity analysis include the following: 1) Identify the key input variables, x_{ij} to which the overall value of the index may be sensitive. 2) Calculate the effect of likely changes in these variables on output (i.e. the overall index score) and calculate a sensitivity indicator (S) and/or switching value. 3) Consider possible combinations of variables that may change simultaneously in adverse direction and calculate a sensitivity indicator (S) and/or switching value. 4) Analyse the direction and scale of likely changes for the key variables identified, involving identification of the sources of change.

A number of techniques have been developed for sensitivity analysis and these are normally classified into either global sensitivity analysis (GSA) or local sensitivity analysis (LSA) depending on the problem under consideration. GSA concentrates "on the output uncertainty over the entire range of values of the input parameters" (Helton 1993, Homma and Saltelli 1996). Consideration will be given to a range of applicable techniques to select the one most suited to the case of the natural forest capital index.

Studying institutional arrangements for collection and upkeep of data

An important prerequisite for implementing a natural forest capital index is an understanding of the institutional arrangements needed for gathering, keeping and updating data over time and thus making the index operational for the adoption of appropriate policies and as a tool for informing the public. A clear understanding is required of who will produce the index, and how, and who will use it. Governmental, business, NGO and community audiences have different needs, capacities and perspectives that may need to be considered. They may also be wedded to particular performance measurement tools and systems into which a natural capital index might need to be integrated. Should independent parties in various parts of the world calculate the index, it would need to conform to certain criteria. One would need to understand the type of capacities needed, capacity gaps, and offer strategies for addressing them. A key purpose for a natural capital index is to improve forest ecosystem related decision-making. Use of the index under different institutional conditions must be demonstrated so that actual benefits can occur.

Calculating the index will be computation intensive and require specialised software (Jesinghaus 1999a, b, Anon. 2000). The software will be needed to perform the

required calculations, to serve as a data storage facility, and to present the results of the index in a visually attractive format. Because a natural capital index requires the use of spatially referenced data, a platform with Geographic Information System capabilities should be used.

Assessing changes in the natural forest capital index over time

A key function of the index would be to assess changes over time in the sustainable use of forest resources. Changes in forest ecosystem conditions and use will be measured against benchmarks. Ideally, the benchmark should be the state of the forest prior to significant stress from human activity (Woodwell 2002). Given that this is usually not feasible (Matthews et al. 2000), or would take far too long to ascertain, the year of first publication of the Index may be taken as the benchmark year.

Discussion

Challenges for implementation

The creation of a natural capital index poses many challenges, and one may say that the "devil is in the details". The situation that we are facing with respect to understanding the changing state of the forests may equally be described as "paralysis by overanalysis". Currently there are myriad indicators relating to the conditions of forests, at times motivated more by what can be measured, than by the utility of the measurements in informing decision-makers and the public about the sustainability of forested ecosystems. A major challenge is to present simplified information providing a link between the environment and decision-makers in a world of short sound bites (Kinzig et al. 2003). This link should use the state of the art in scientific knowledge, be made without endless academic discussion, and give decision-makers at different levels direction for action.

A natural capital index for forest might be viewed as a "top down" approach to management of the forest. However, it should equally serve "bottom-up" processes, that is community driven processes to change the management of local forests which are the ecosystem in which that community thrives. The main goal of the index is to provide information as to the changes in the condition of forest landscapes. That information should be of equal value to local communities, as it is to the various levels of governance.

We recognise both the dangers of oversimplifying, and those of having a bewildering number of indicators from which no clear picture emerges. In effect a natural forest capital index seeks middle ground between the two extremes: complexity which fails to communicate, and simplicity which devolves into being overly simplistic. At the end of the day what is sought is a measure with a solid footing in our understanding of the complex dynamics of the forest/human interactions, and with a strong capacity to communicate that understanding to decision-makers and the public.

A major challenge is how this index might be implemented. One may anticipate several kinds of barriers. It is likely that there will be political resistance to an index that allows comparisons of forest quantity and quality to be made equitable across nations. One may also foresee a political challenge in developing a consensus of how the index should be calculated. There is thus a built-in conflict between the different competing interests of different stakeholders, and between short-term and long-term perspectives on natural capital. For example, while the conservationist is keen on presenting data about the negative effects of intensive forest use, interests representing the macroeconomics of global businesses may not. Basically the information about the forest situation needs to reflect the livelihoods for the local people in actual landscapes. Thus the indicators and the index need to make sense locally, and then be aggregated at larger scales for decision-makers at different levels. We therefore advocate a bottom-up process based on local case studies. When different index prototypes have been evaluated recommendations for broader application could be made. This, however, may be hampered in regions and countries where data availability is limited. At the international level it is important to involve FAO in index development.

Our reason for focusing on a natural forest capital index is the important role forests have for the livelihood of people locally and globally. Therefore, natural capital assessments need to be integrative, across scales, but also across land that is no longer forested. Just focusing on what is forest today, would for example not allow studies of the role of historical forest loss at the scale of landscapes and regions.

Audiences and users of the index

There is a wide range of important audiences that need an improved interface regarding the status of the natural capital of forests. These include governments, corporations, non-government organisations, academe, think tanks and research organisations, intergovernmental organisations (including the UN system), financial institutions from national to global, and the news media. It is also vital to reach the public – the benefactors of services provided by healthy forest ecosystems. Public support is essential to build political will and to encourage business to use the index. The development of an index of the natural forest capital will take into consideration that different actors have different needs in terms of level of detail of information. An index should be seen as an information system and the components it builds on should be published simultaneously, so

that both the larger picture and the details are available to index users with full transparency.

The development of an index of the natural forest capital is likely to provide benefits to society in many different ways, especially in the long term. It will permit evaluation of progress in sustaining forest capital in a country, for assessing whether forest capital is increasing or declining. The introduction and use of a natural capital index would make available a kind of "score card" that attributes a numerical value to various forest functions, including a "GNP like" one-dimensional index of the total (Salim and Ullsten 1999).

Human activities have eroded the natural capital of forests and other natural resources over many centuries, and are undermining the ability of future generations to meet their own needs from the natural resource base (Dasgupta 1982, Pearse 1990). Current indices such as the GDP do not take into account the necessity for sustainability, or intergenerational allocation of resources (Dasgupta 1982, Pearse 1990, Tietenberg 1992). By expressing the ecological non-market values of forest outside of routine economic calculus but essential for long term viability, an index of the natural capital would increase awareness about intergenerational equity in forest ecosystems.

Information gaps concerning the natural capital of forests

The very process of formulating a natural capital index for forests would identify gaps in our knowledge of forest ecosystems and would encourage additional research focused on filling those gaps. Data gaps should be analysed with regard to their significance for creating a robust and reliable index. Other data gaps may become apparent in the course of development of the index. Data availability for indicators such as those listed in Table 2 and 3 would enhance the value of a natural capital index for forests. The program of activities to formulate such an index will necessitate a pooling of resources, expertise, resources and outputs from established monitoring activities that could lead to far more incremental value than if they were to continue to operate independently of and sometimes at cross purposes with one another. Building an index of the natural capital would thus foster collaboration.

One gap is related to the need for defining different types of forest, which are representative for a particular region. Within the MCPFE there is an agreement to use only four forest types (broadleaved woodland, coniferous woodland, mixed broadleaved and coniferous woodland, and other wooded land) and to work towards a more detailed classification. There is also a need to define different steps in the alteration of landscapes (Angelstam et al 2004c). For example, FAO (2003) includes only three categories of naturalness: undisturbed by man, semi-natural and plantations. Most managed landscapes are thus classified as semi-natural, but without considering the functionality of the different kinds of habitat networks for species and ecosystem processes. Spatially explicit evaluations are thus needed (Scott et al. 2002). Another obstacle is lack of knowledge regarding what defines ecosystem integrity (Pimentel et al. 2000) and related performance targets for this. As stated in CBD's biodiversity targets for 2010, species are proposed as indicators. Alternatively, with good knowledge of species' habitat requirements combined with relevant land cover data, one can improve the thematic resolution of evaluation of natural capital (Angelstam 2004d).

A natural capital index at multiple scales

An important consideration for construction of a natural capital index is the spatial scale to which it applies. Are we thinking of the global picture, a country level perspective, a particular region, or some other defined area? In principle, an index could be applied to any defined region, provided the data obtained relate to that particular spatial domain. The concept of biomes, ecozones, ecoregions, ecodistricts, and ecosites as well as basins, watersheds and sub-watersheds have found various applications in reporting on the changing state of environments (Bird and Rapport 1986). We envision a nested hierarchy of such regions for purposes of constructing a natural capital index for forest. Ideally there will be ways of aggregating such ecologically based constructs to merge with political boundaries at state and federal levels. Within the European Community the EC Water Framework Directive provides strong support for such an approach.

Linking the natural forest capital index to economic and social indices?

During the last decades of the 20th century environmental issues have gained terrain. Sustainable development has become one of the core organising concepts of policy and can be defined as the maintenance of important environmental, socio-economic and cultural functions into the indefinite future (Ekins and Simon 2001). However, sustainability is also an inherently vague concept whose scientific definition and measurement still lacks wide acceptance. Nevertheless it is a useful concept, and if measurement methods and short-term and long-term performance targets could be developed with a continued scientific credibility (Mills and Clark 2001), it could become possible to assess sustainability gaps at different spatial scales that are also locally meaningful.

In this paper we promote the idea of a natural forest capital index developed by and derived from ecological indicators and thus with a focus on natural capital, simply because of the large body of information available about

this. Ultimately, however, it would be desirable to apply the same approach also to all kinds of capital assets including natural, human, physical, social and financial (Campbell et al. 2003). There are examples of "sustainability indices" that afford both lessons in design, and additional sources of data. One notable example is the "Dashboard of sustainability" (<http://www.iisd.org/cgsdi/intro_dashboard.htm>). Developed by the International Institute of Sustainable Development, the dashboard provides an easy way of interpreting indicators that enable a user to monitor changes across various resource sectors and issues over time. However, the extent to which different capital assets should be integrated needs to be discussed (Moldan et al. 1997, Andriantiatsaholiniana et al. 2004). For example, to achieve sustainability in the strong sense, it will have to be achieved in each of the different domains.

A critical natural capital index combining indicators with performance targets (Ekins et al. 2003b) has potential of being linked to existing and planned broader indicators for sustainable development at the national and international level. Two prominent examples of forest-based criteria and indicator sets are the Montreal Process (Anon. 1995) and the use of the Pan-European Indicators for sustainable forest management, which was endorsed by 40 European countries at the Fourth Ministerial Conference on the Protection of Forests in Europe in April 2003 (MCPFE 2003b). These sets of criteria and indicators allow for standardised measurements of agreed-upon variables including biodiversity, productive capacity of forests, protection of soil and water, contributions to the global carbon cycles, economic factors and contributions, and legal and institutional issues pertinent to forest management (Rametsteiner and Mayer 2004). These well-established systems offer us two helpful assets. First, the inclusion of all relevant criteria of sustainable forest management give us a starting point for the selection of indicators and its assessment provide also regularly useful data to populate them. Second, because these sets of indicators have already been agreed upon by large constituencies, we can capitalise on the investment of time, money and other resources that have moved diverse stakeholder sets from dispute to dialogue to data. This will be important, as a natural capital index will be subject to scrutiny by many groups.

Conclusion

The need for a natural capital index for forest has arisen to improve communication about the state of forest ecosystems. With hundreds of indicators being reported by intergovernmental agencies and scientists, decision-makers and the public are hard pressed to answer the simple question: what are the trends in the natural forest capital, for a particular region or the country as a whole? A natural capital index based on comparisons of indicators and performance targets is essential to address this question, and to provide an overall picture of whether the condition of the forest in a certain region is declining or improving. The reason for developing a natural forest capital index is thus to make complex information more easily available and understood for decision-makers and the public at large.

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Targets for boreal forest biodiversity conservation – a rationale for macroecological research and adaptive management

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The maintenance of biodiversity is one of several internationally recognised objectives of forest management. Empirical evidence from Europe suggests that forest management is responsible for the loss of biodiversity and that the extent of the loss is a function of the amount, duration, and intensity of resource extraction. The pattern of biodiversity impoverishment as a function of habitat alteration is not always linear, but rather it is likely to exhibit thresholds beyond which the long-term maintenance of the elements of biodiversity is threatened. Such thresholds could be used for establishing conservation targets in forest management.

We present a general procedure for identifying multiple thresholds to be used in the determination of conservation targets in forests. We suggest a six-step procedure: 1) Stratify the forests into broad cover types as a function of their natural disturbance regimes. 2) Describe the historical spread of different anthropogenic impacts in the boreal forest that moved the system away from naturalness. 3) Identify appropriate response variables (e.g. focal species, functional groups or ecosystem processes) that are affected by habitat loss and fragmentation. 4) For each forest type identified in step 1, combine steps 2 and 3 to look for the presence of non-linear responses and to identify zones of risk and uncertainty. 5) Identify the "currencies" (i.e. species, habitats, and processes) which are both relevant and possible to communicate to stakeholders. 6) Combine information from different indicators selected. A review of the historical development of forest use in eight boreal case studies illustrates the need for international collaboration to follow this procedure.

To put this procedure into action and to design management applications, we suggest the development of an international network of adaptive management teams consisting of managers, policy-makers, and scientists. This network should be charged with testing different approaches to the management of forests that will ensure that biodiversity is restored in areas where it has been lost and maintained where forestry intensification has yet to occur.

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The concept of sustainable development was created as a strategy to deal with human activities jeopardising the meeting of future needs. The concept has ancient roots (e.g. Hunter 1996, Williams 2003) and the term "sustainable forestry" dates back to 1713 when Hans Carl von Carlowitz in Germany in the very first forestry textbook addressed the problem of sustainable wood production in the context of the local industry's needs (Schuler 1998). In its modern sense, however, sustainable development as defined by the Brundtland Commission in 1987 can rather be viewed as a three-legged stool supported by economic, social, and environmental components or "legs" (e.g. Goodland and Daly 1996). The elements of biodiversity can be considered as being a part of the environmental "leg", although it may be argued that some components of biodiversity should be considered under the auspices of the social and economic "legs". The fact that biodiversity is sometimes defined, or perceived, as being limited to species richness has triggered the development of concepts such as ecosystem health (Rapport et al. 1998) and ecological integrity (Pimentel et al. 2000). The multitude and ambiguity of concepts is thus a continuous source of confusion for practitioners (Kaennel 1998, Franc et al. 2001), despite a clear definition being provided under the Convention on Biological Diversity (Anon. 1992). Following Noss (1990) and Larsson et al. (2001), we define biodiversity as having three main elements: ecosystem composition, structure, and function.

In spite of ubiquitous policies to promote the sustainable use of renewable resources, the clearing of forests for agriculture and human infrastructures together with the intensive management of forests for fibre production continues to challenge the long-term maintenance of forest sustainability globally (Williams 2003). In response to this, concepts such as sustainable forest management (Schlaepfer and Elliott 2000, Franc et al. 2001, Lindenmayer and Franklin 2002, Sverdrup and Stjernquist 2002, 2003, Rametsteiner and Mayer 2004) and ecosystem management (e.g. Meffe et al. 2002) have been advocated over the past 20 yr.

To determine the relative efficacy of biodiversity management tools such as protected areas on the one hand and different kinds of forest management and ecosystem restoration practices on the other, we need to assess the status and trends of biodiversity elements over multiple spatial scales. However, the efficacy of different strategies may vary among ecoregions as a function of the biophysical or geographic conditions and management history, resulting in different kinds of landscape mosaics (Lindenmayer and Franklin 2003, Angelstam and Kuuluvainen 2004). This requires monitoring in the form of repeated measurements of a range of biodiversity elements (e.g. Larsson et al. 2001), as well as mutual learning about experiences conducted under different conditions (Angelstam et al. 1997).

Principles such as sustainable forest management are made more explicit by breaking down the issues into different criteria, such as biodiversity, social issues, and economics. Each criterion is then accompanied by a number of indicators representing measurable variables (Higman et al. 1999). There have been a number of attempts to develop criteria and indicators for the sustainable management of forests (e.g. Duinker 2001, Rametsteiner and Mayer 2004). These include the Montreal Process, the Helsinki Process now termed the Ministerial Conference on the

Protection of Forests in Europe (MCPFE), and a variety of other regional initiatives. A common characteristic for all of these schemes is that the maintenance of biodiversity is identified as an important criterion of sustainable forest management.

According to Loyn and McAlpine (2001), the purpose of indicators is to assess and monitor whether forests are being managed in a sustainable fashion, and to provide information about processes in the forest and their management. Although a substantial number of indicators have been developed to monitor elements of biodiversity, it is important to recognise that most sets of indicators have been designed for regional or national scale reporting and not for use at an operational scale (but see Kneeshaw et al. 2000, Angelstam and Dönz-Breuss 2004). Consequently, the indicators may have relatively little value at the scale of the management unit, i.e. the actual landscape (Loyn and McAlpine 2001, Finegan et al. 2001, Kanowski et al. 2001). Furthermore, many indicators fail to provide a clear link between a given measurement and its relationship to the maintenance of biodiversity.

Ultimately an indicator is useful only if it can be compared with a target based on some kind of benchmark or reference (Higman et al. 1999, Puumalainen et al. 2002). Ecosystems often exhibit non-linearities, thresholds or "flips" corresponding to sudden changes in their properties (Muradian 2001, Gunderson and Pritchard 2002). Thus, a desired range of variation in these properties must be defined so that management goals can be set. For example, a small decrease in the area of forest in a region may result in little immediate concern. However, if that change involves the crossing of a critical threshold, then it may have serious implications for biodiversity. The formulation of targets is implicitly encouraged by the fact the long-term visions such as the conservation of native biodiversity have been incorporated into policy and international treaties (Duinker 2001). As an example, politically-negotiated, short-term targets based on long-term visions are an important part of the Swedish environmental policy (Anon. 2000). Some forms of forest certification, a kind of third-party market-driven mechanism aimed at sustainable forest management, can also be included within this context (Elliott and Schlaepfer 2001). Certification standards hence represent a set of targets at the scale of the forest management unit, and several certification schemes take into account the possibility of continuous improvement. It should, however, be noted that certification tends to focus on short-term political and economic goals, which are locally relevant and viewed as realistic to achieve within a short time frame, generally just a few years. The extent to which certification will prove effective in the long term will depend on the degree to which the resulting targets will actually evolve continuously to promote different aspects of sustainability in actual landscapes (Angelstam 2003).

Policy targets are thus not equivalent to ecologically based targets emerging from theoretical and empirical studies showing that environmental nonlinearities or thresholds exist (e.g. Angelstam et al. 2003a). Even though research on thresholds remain in its infancy, ecologically-based targets inspired from such thresholds could be used to postulate management and conservation strategies. The concept of critical load provides an example of such an approach (see Sverdrup and Stjernquist 2002). It was coined to define the amount of acidic deposition that the most sensitive elements in an ecosystem could tolerate without significant damage. For the maintenance of biodiversity, critical loss of, for example, habitat structures in relation to the range of natural variation, would be an analogous concept. We stress, however, the need for explicitly recognising uncertainty and, rather than proposing target numbers, there should be a focus on probabilistic targets defined using a variety of indicators, and on the associated "zones of risk" (e.g. Muradian 2001, Phillis and Andriantiatsaholiniana 2001, Angelstam et al. 2003a).

There is evidence for non-linear responses of species and ecosystem processes to gradients of habitat alteration (e.g. Andrén 1994, Jansson and Angelstam 1999, Muradian 2001, Cooper and Walters 2002, Benton 2003, Bütler et al. 2004a, b). Such non-linear responses may indicate thresholds, i.e. relatively narrow ranges in forest degradation (at local or landscape scales) over which the biological response changes abruptly. In spite of this, the practical application of objective quantitative targets at appropriate spatial scales has largely been neglected in the development of sustainable forest management (Lammerts van Buren and Blom 1997, Duinker 2001). There are several reasons for this. One is that research is usually restricted to a limited combination of temporal and spatial scales (Vogt et al. 2002). Another is that, until recently, little thought had been given to the theoretical and methodological aspects of threshold detection (Toms and Lesperance 2003, Guénette and Villard 2004). We need to address not only what we do within the framework of what is considered economically possible or socially acceptable at present, but also within a window encompassing the long-term ambition of policies advocating the maintenance of biodiversity. This can be challenging to scientists as it may be considered risky for their own funding and career (Mills and Clark 2001, Hanski 2002). Moreover, even though a considerable amount of knowledge exists, it is often poorly synthesised and communicated to policy-makers and managers (Lee 1993, Kinzig et al. 2003).

Ecological research is seldom designed to provide answers directly applicable to management issues, and planning tools are often not designed to incorporate ecological knowledge as such. In addition, there is insufficient understanding about how policies could be implemented within a given social-ecological system or type of institutions (Angelstam et al. 2003b, Berkes et al. 2003, Lazdinis and Angelstam 2004, Sandström et al. 2004). In other words the active adaptive ecosystem management feed-back loop from research to policy and management and back again

often does not take place (Lee 1993, Ludwig et al. 1993). Finally, due to logistic and economic constraints as well as the scientific challenges involved in measuring high-quality biological response variables such as fitness parameters, the traditional ways of doing natural science often do not lend themselves to studies at the scale of landscapes and regions (e.g. Balée 1998, Egan and Howell 2001, Boutin et al. 2001, Kohler 2002, Kinzig et al. 2003). Addressing the issue of landscape-scale conservation targets can be seen as big holistic science, or macroecology (Brown 1995), and, while there has been some progress (e.g. Gunderson et al. 1995, Gunderson and Pritchard 2002), it remains an area in which little work has been done.

Our experiences come from the World's boreal forests, commonly used as the woodshed of regions of economic growth. The boreal forests are relatively simple ecosystems compared to, for example, tropical forests. For this very reason they are also relatively well known (e.g. Shugart et al. 1992, Hansson 1997, Burton et al. 2003). BorNet (<www.bornet.org>), a network of scientists and managers interested in promoting research on conservation targets (Angelstam et al. 2004a), has organised a number of workshops to identify knowledge gaps (Whittaker and Innes 2001a, b, c, Leech et al. 2002). The project identified knowledge gaps associated with the following questions (Leech et al. 2002, Whittaker et al. 2004): How much and where should forests be fully protected in reserves? How can management effectively re-create, restore, or maintain important features required to conserve biodiversity? How can we determine the effectiveness of these biodiversity conservation efforts? The workshops identified a surprising number of knowledge gaps, and revealed just how scanty our knowledge of biodiversity in boreal forests really is.

The questions posed by BorNet reflect the typical questions asked by managers: How much forest do we need to set aside in reserves to meet biodiversity goals? How much unharvested woodland do we need to leave in the matrix surrounding the forest reserves? How many trees should be left when a stand is cut? What are the important forest features to restore and how much is required? Hence, there are clear indications from forest managers but also policy-makers (Rametsteiner and Mayer 2004), the industry (Hebert 2004) and forest-product retailers (Djurberg et al. 2004) that there is a need for landscape-scale research to address the question "How much habitat is enough?".

The aim of this paper is two-folded. First we suggest a scientific approach that would contribute to filling the knowledge gaps identified in order to develop concrete quantitative targets for conservation at the scale of forest management units. Second, we propose strategies for the efficient international co-operation amongst scientists, managers, and policy-makers that is needed to apply approaches for the implementation of ecologically-based targets for the sustainable use of boreal forest resources. Although the focus is on the boreal forest, we also include hemiboreal and mountain forests because they share similar components, structures and processes (e.g. Mayer 1984, Shugart et al. 1992).

Targets and levels of ambition

The deceptively simple question "How much forest is enough?" does not have a straightforward answer. Forest ecosystems constitute a gradient from "natural" forests, which maintain all components, structures and functions of forests (e.g. Peterken 1996), to fibre crops such as poplar plantations on former agricultural land. All human activities, at least with an historical perspective, probably move forest landscapes along such gradients (Williams 2003), even when the management aims are designed to maintain "natural forests", as in British Columbia, Canada. In fact, all forests on Earth have, to some extent, been affected by various human activities for many centuries, often without apparent negative effects on biodiversity (e.g. Balée 1998). In remote areas, these activities take the form of hunting, reindeer herding, local floodplain clearance, and harvesting of hay along small streams. In North America, aboriginal populations have cleared forests and used fire as a management tool for thousands of years (e.g. Pyne 1984, Williams 1989). The period of industrial exploitation of the majority of European forests has lasted several centuries, starting with high-grading and the removal of large trees and followed by large-scale clear-felling and the gradual development of silvicultural systems aimed at sustainable timber production (Angelstam et al. 1995).

Currently, however, the concept of sustainable forest management is in the process of being redefined both in policy and practice. Hence, from a long-lasting focus on classic sustainable timber management (Schlaepfer and Elliot 2000), there is an ongoing transition toward multifunctional ecosystem management (Meffe et al. 2002), ecological sustainability (Goodland and Daly 1996) and, ultimately, sustainable resilient social-ecological systems (e.g. Berkes et al. 2003). Depending on the country and region this transition results in the consideration of new ecological products and processes such as the maintenance of viable populations, biodiversity, or protective functions (Kräuchi et al. 2000, Larsson et al. 2001, Lindenmayer and Franklin 2003, Angelstam et al. 2004b).

As a consequence, one can formulate at least four different target levels for the conservation of biodiversity (Table 1). An obvious first level is that the compositional elements of biodiversity are maintained. This is represented by occupancy of one of several species in a given landscape. Occupancy is often the only information available for conservation areas such as the Swedish Woodland Key Habitats (Hansson 2001) and other protected areas. However, many national and regional policies (e.g. Boyce 1992,

Table 1. The focal spatial scale of management increases with the level of ambition of conservation targets.

Level of ambition	0.01 km^2	1 km^2	100 km^2	10000 km^2	1000000 km^2
occupancy	vascular plants	small birds	most mammals		
population viability		a plant population	a songbird population		
ecosystem integrity				minimum dynamic area in boreal forest	wolf/caribou interaction
ecological resilience					movements of ecoregions under climatic change

Schmiegelow and Hannon 1993, Mönkkönen 1999, Angelstam and Andersson 2001) are explicit about the fact that occupancy is insufficient, and indicate that "all naturally occurring species should maintain viable populations". A second target level is therefore to ensure population viability over long time (e.g. Sjögren-Gulve and Ebenhard 2000). An increase in the threshold amount of habitat needed for probability of occupancy vs probability of breeding (Angelstam 2004) suggests higher conservation costs of this increased target level. The word "all" in such policies makes it almost imperative to define thresholds for a suite of efficient focal or umbrella species (Lambeck 1997, Mönkkönen and Reunanen 1999, Roberge and Angelstam 2004). As ecosystems are open and dynamic, the total area needed to ensure the persistence of species increases with the time period associated with the term "viability". Hence, a third level is to ensure ecosystem integrity and health (e.g. Pimentel et al. 2000). To achieve this, minimum dynamic areas (Pickett and White 1985) are needed that continuously provide habitat for many viable populations over multiple spatial scales, as well as for the interactions among them (e.g. Bengtsson et al. 2003, Angelstam et al. 2004c). Finally, a fourth target level may be to ensure long-term ecological sustainability, or ecological resilience (Gunderson et al. 1995, Gunderson and Pritchard 2002). Resilience is measured as the magnitude of disturbance that can be absorbed before the system is unable to recover to its previous state, resulting in a restructuring of the ecosystem with different controlling variables and processes. For each of these target levels for the maintenance of biodiversity, there is a continuous gradient with increasing spatial dimensions including specific thresholds for the composition, structure and function of biodiversity. There is thus a suite of targets that can be specified for the maintenance of biodiversity in an area, each target representing an increasing probability of maintaining a functional ecosystem.

A procedure for establishing and communicating conservation targets

Here we present an approach for formulating scientifically-based conservation targets at different spatial scales. We elaborate six basic steps for formulating occupancy targets for conservation, as suggested by Angelstam (2001), which aim at combining management regimes with biodiversity requirements into assessment systems.

Step 1. Stratifying forests based on their natural dynamics

The presence of different disturbance regimes in a forest implies different selection pressures on species, different habitats and a diversity of processes. It is therefore necessary to stratify the broad cover types of the boreal forest into different baseline disturbance regimes such as succession after large-scale disturbance, gap-phase dynamics in the absence of large-scale disturbance and cohort dynamics with frequent, low-intensity fires (e.g. Angelstam 1998), but also the different characteristic developmental stages after disturbance (e.g. Haapanen 1965, Thomas 1979, Angelstam 2002, Angelstam and Kuuluvainen 2004). Disturbance regimes vary according to the complex and regionally varying interaction between biogeophysical and macroclimatic conditions (Pyne 1984, Agee 1993, Angelstam 1998, Haeussler and Kneeshaw 2003) and result in forests with different structure in terms of tree species and age class distributions, both within stands and among stands in landscapes. This step provides insight into the selection of species and functional groups of species as response variables. As a consequence this may also be very relevant to determining the scale upon which the indicator should be maintained as large disturbance events means maintenance is only possible over large regions.

Step 2. Understanding a landscape's historical position (position on x-axis)

Different kinds of sociopolitical and economic systems in particular regional contexts often result in different effects on the biosphere (Balée 1998). The second step is therefore to understand the relationship between economic development and the degree of deviation from the benchmark provided by natural dynamics. This requires an understanding of the historical spread of different waves of anthropogenic impacts on the forest (e.g. Williams 2003). Several studies have identified characteristic steps in the historic development of forest use (see Angelstam et al. 2004b). A common division of phases of forest use is 1) large intact areas with benchmark conditions, not necessarily without people (Balée 1998, Stevenson and Webb 2004), but essentially without any major changes in the composition, structure or function of the forests; 2) high-grading or selective harvesting of the most desirable timber species; 3) large-scale unsustainable exploitation, in the form of "tree-mining", typical for most remote parts of the boreal forest today; 4) economically sustainable sustained timber yield being typical for parts of northern Europe; and 5) the current efforts to include new values such as the maintenance of biodiversity (e.g. Raivio et al. 2001). Active adaptive management of forest ecosystems in the form of sustainable ecosystem management (e.g. Duinker and Trevisan 2003, Burton et al. 2003) can be viewed as a future aim, and thus a sixth phase. This means that a wider array of forest values besides timber must be maintained including biodiversity and ecosystem services, which is beginning to be introduced in some jurisdictions, such as some National Forests within the USA (e.g. Lee 1993). When drawn on a series of maps, the gradual expansion of these historical phases form isolines (e.g. Angelstam 1998, Imbeau et al. 2001) facilitating the identification of landscape replicates in regions with different baseline disturbance regimes (Isachenko and Reznikov 1996).

From a management perspective, these five stages can be translated into semi-quantitative indicators of degree of human intervention. Examples are time since anthropogenic transformation of a particular forest type began in the area (e.g. Williams 2003), management intensity measured as transport infrastructure (Angelstam et al. 2004d), tenure system, match between silvicultural practices (including harvesting, regeneration, and management methods) and forest disturbance regimes (e.g. Angelstam 2002), number of management rotations (Angelstam and Dönz-Breuss 2004), and length of rotation (Thomas 1979). It is important to have the ability to place stages of human development on a long time continuum because although forest management attempts to maintain wood supply over multiple forest rotations, maintenance of biodiversity tends to be considered over the short-term. This can lead to a "shifting baseline" syndrome whereby local management history affects our perception of what is "natural" or possible. For example, a forest manager in Sweden finds it hard to believe that Swedish forests ever had the proportion of old deciduous trees seen in boreal forests with a short management history such as in Canada and Russia. Similarly, forest managers in Canada and Russia find it hard to believe that their practices could lead to the paucity of downed woody material so evident in Scandinavian managed forests despite the fact that the harvesting practices are similar in the two countries. The difference is one of duration of human activity.

Natural forest components which change in relation to these forest history phases include snags, coarse woody material, certain tree species and large trees at the stand scale (e.g. Angelstam and Dönz-Breuss 2004, Shorohova and Tetioukhin 2004), and the proportion of old-growth forest and large unbroken areas at the landscape scale (Yaroshenko et al. 2001). These components can then be related to the steps in the history of forest use. Siitonen (2001), Yaroshenko et al. (2001) and Angelstam and Dönz-Breuss (2004) show how forest history can determine forest structure at multiple spatial scales. Forest structures closely associated with the meta-species and being the most time- and cost-efficient to measure could be density of large trees with bark (for epiphytic lichens), dead/dying trees with bark (for most woodpeckers and saproxylic insects), decayed logs (for certain bryophytes and the regeneration of certain tree species) and proportion of mature old, closed-canopy forest and the landscape scale (for certain birds, litter invertebrates etc.).

Step 3. Finding representative response variables (y-axis)

In this step, response variables – such as species or ecosys tem processes – that are likely to be affected by loss of natural forest structures should be identified (Table 2). For species, we suggest the use of "metaspecies", i.e. groups of species classified according to specific combinations of habitat requirements for reproduction and feeding. This is analogous to Haapanen's (1965) approach used with birds in Finland, to the life form concept used by Thomas (1979) and Gillingham and Parker (2001), and to the concept of "functional types" (Wiens et al. 2002). We thus agree with Copolillo et al. (2004) who argued for clear justification and that selection criteria should accompany any focal species strategy. Such metaspecies or functional groups thus allow 1) conducting macroecological analyses spanning several biogeographical regions, and 2) ensuring that the range of habitat variation covers the full spectrum from intact benchmark areas to extensively altered landscapes, and not only habitat configuration. We recommend that research on the topic should be conducted at the landscape scale and over several years (Stephens et al. 2003).

Table 2. Examples of elements of biodiversity at different spatial scales.

Biodiversity component:	Tree scale	Stand scale	Landscape scale
Composition (species)	Saproxylic invertebrates and fungi	Cyanolichens, invertebrates and small birds	Large birds and mammals
Structure (habitats)	Dead wood, old large trees	Tree species and age classes	Amount of different stand types and their spatial and size distribution
Function (processes)	Mycorrhizal symbiosis	Fire, nutrient cycling	Dispersal, browsing and predation

The following groups are provided as examples of metaspecies with habitat requirements that include the landscape scale and that have evolved to fill the different patch types of the boreal forest biome: 1) guilds of species with particular physiological adaptations that have evolved to cope with certain environmental conditions (e.g. cyanobacterial epiphytic lichens); 2) guilds of species or circumpolar species or genera that require habitats that are not compatible with intensive forest management (e.g. species requiring coarse woody debris of different decay stages and diameter classes, large or old trees, slowly growing wood, very old interior forest conditions, burned forest, certain tree species, or combinations thereof); 3) guilds of species that are sensitive to the loss of large, relatively unbroken woodland (e.g. species with very large area requirements due to large body size or to a predominantly carnivorous diet).

It is also important that the functional elements of biodiversity are maintained. Thus, one could use certain ecological processes as dependent variables. Altered fire frequencies (Niklasson and Granström 2000) and hydrologic regimes (see Degerman et al. 2004) are examples in boreal forest. Less obvious examples are disruption of predator-prey relationships such as factors favouring generalist predators that have reduced the breeding success of species associated with extensively forested landscapes (Kurki et al. 2000) or introduced predators (Nordström et al. 2003), and browsing by superabundant wild herbivores on certain trees species that changes forest composition (Angelstam et al. 2000, Ripple and Beschta 2003). Additionally, air pollution is causing leaching of nutrients such as nitrogen from sensitive soils and changing vegetation in some regions (Sverdrup and Stjernquist 2002). Socio-economic changes in rural communities followed by land abandonment constitute another example (Angelstam et al. 2003c, Mikusiński et al. 2003).

Step 4. Analysing biological response to gradient in forest degradation

This step involves testing hypotheses about non-linear responses to habitat gradients by establishing relationships between steps 2 and 3 for each forest type defined in step 1 (Fig. 1). This could be done by relating response variables (e.g. abundance, fitness, or population viability) of the selected metaspecies ensemble to the position along historical continuum of forest use, or to a surrogate measure for that position (e.g. proportion of pristine forest area, amount of snags or dead wood). We argue that rather than finding an exact threshold, the idea should be to establish intervals along the resource axis that represent the three zones of risk for the conservation of metaspecies of target ecological processes: clearly inadequate, marginal, or clearly suitable conditions (cf. Phillis and Andriantiatsaholiniaina 2001, Angelstam et al. 2003a).

Such analyses can be made in either of the following two main streams. The first involves the collection and analysis of original data. Analyses can hence be conducted using both traditional empirical approaches and by exploring the effects of different levels of habitat loss on species with certain combinations of life history traits using modelling and simulation. In both cases the x-axis (independent variables) would represent forest structures at spatial scales which are relevant for the hypothesis that these affect species, or ecosystem functions, on the y-axis (dependent variables). This is analogous to the dose-response type relationships commonly used in ecotoxicology (Connell et al. 1999). Special efforts are, however, needed to ensure that the dose varies sufficiently for a response to be expected. Such analyses can be done at several levels of scientific scrutiny. Systematic collection of observations and their analytical description leads to more precise and testable hypotheses, which can then be evaluated using mensurative (comparative) or manipulative experimental approach (see Krebs 1999, Haila 2002). Kohler (2002: 212) uses the concept "practices of place" whereby it is "…the arrangement of spatial elements that provides critical evidence of relations between creatures and their environment…". Places are thus to the field ecologist what experimental setups are to laboratories. "Practices of place" are alleviated by co-ordinated co-operation among case studies made in replicated forest and land use history gradients. This means that studies are designed based on the idea that temporal gradients, such as the decline of dead wood over time with the historic development of forest management (e.g. Linder and Östlund 1998), can be replaced with spatial gradients (e.g. Rouvinen et al. 2002, Angelstam and

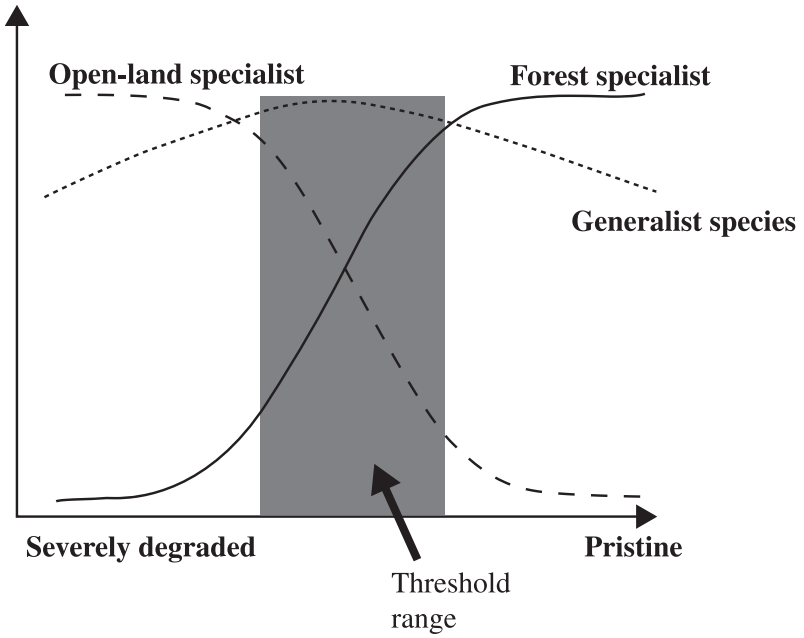


Fig. 1. Responses of three hypothetical species (or metaspecies – see text) to a gradient from intensive harvesting and ecological degradation to pristine forest mosaics. Response curves are dramatically different, but some of these patterns may have been undetected if sampling had been restricted to a short portion of this gradient. Sampling portions where responses change most suddenly (threshold range) is particularly critical to learn from these responses and to make relevant adjustments to management regimes.

Dönz-Breuss 2004). This approach has also been called the ergodic hypothesis.

The second method is to assess a hypothesis by synthesis of the available information, whereby the results of a series of published studies are evaluated in relation to a particular hypothesis. Given that there are a sufficient number of published studies, quantitative syntheses from a series of comparative and experimental studies can be conducted to assess how general the threshold levels are. A quantitative synthesis that analyses a set of analyses is called a meta-analysis (Hunt 1997). Major methodological advances occurred in the 1970s, enabling not only the determination of whether or not an effect was present in a set of studies, but also the estimation of the magnitude of that effect (Rosenberg et al. 2000).

Step 5. Communication between science, practise and policy

Finally, when results from the first four stages are available, there is a need to identify biodiversity "currencies" to communicate the status of biodiversity across different spatial scales. When doing this it is important to consider the wide range of different systems of property rights and management cultures found in the boreal forest. As an example, Uliczka et al. (2004) suggest that sufficiently well-known species should be preferred as "messengers" to communicate the results to managers and other stakeholders. The more managers and other stakeholders can relate to such species, the more effective they are. For example, game species such as the capercaillie *Tetrao urogallus* have widespread appeal in Europe (e.g. Suchant and Braunisch 2004). Hence, at least some of the response variables identified in Step 3 should assess the status of sufficiently charismatic and/or appealing to stakeholders to be used in communicating results to managers and other interest groups. Such an approach was adopted successfully by the Royal Society for the Protection of Birds when the osprey *Pandion heliaetus* was used to communicate the success of their fine-filter conservation strategy to the British public. That being said, such "messengers" must act as umbrellas for less charismatic species to be included in conservation strategies, i.e. their habitat and spatial requirements should be such that their protection should in turn allow maintaining viable populations of many other species (see Roberge and Angelstam 2004).

Step 6. Combining information from different indicators selected

Because several currencies may be relevant to biodiversity conservation in a given area, the final step is to determine how to combine or to choose among these various "currencies" to set conservation targets. This is where ecological data and biodiversity values must be confronted with other, potentially conflicting forest values. No matter how good the science is behind conservation targets, land-owners and land managers determine the ultimate fate of conservation strategies.

Too often, researchers accomplish most of the preceding steps in isolation and then present their results to decision-makers. Another model, which we propose here, is to

form adaptive management teams (Boutin et al. 2002) whereby researchers, land managers and policy-makers share decisions and responsibilities toward the success or failure of the strategy they jointly adopted.

Discussion

The boreal forest as a time machine

The boreal forest provides a unique resource for the gradual development of performance targets to promote sustainable forest ecosystem management as outlined above. It is the only forest biome on the Northern Hemisphere where the full gradient of alteration, from large intact benchmark areas to altered forest in need of restoration exists (Hannah et al. 1995, Angelstam et al. 1997, Yaroshenko et al. 2001, Aksenov et al. 2002, Drushka 2003, Burton et al. 2003, Lee et al. 2003). The reason is the steep gradient in land use history whereby the gradual exploitation and intensive management of boreal forest resources has spread like a tidal wave from areas of high demand to more and more remote regions, and with clear effects on biodiversity (Mikusiński and Angelstam 1998, Angelstam et al. 2004e).

These northern forests hence represent a unique research opportunity (sensu Kohler 2002), enabling retrospective studies that substitute space for time. The boreal forest biome is, however, huge, and within some regions or countries the variation is insufficient to allow for such an approach. Using this natural laboratory as a "time machine" to understand the effects of the human footprint on forests therefore requires international co-operation (Table 3; for a more detailed description of different boreal case studies, see Appendix).

Scientific approaches – methods and pitfalls

Traditional ecological studies are usually reductionist and specialised providing high precision at fine scales but limited value for inference over broader scales such as landscapes and regions (Kohler 2000). Brown (1995) argued that to address regional and global problems of environmental change and decreasing biological diversity, macroscopic studies that trade off the precision of small-scale experimental science to seek robust solutions to big problems are required. The loss of habitat in general and of large forest patches with natural composition, structure and function in particular, is a good example of such a problem. However, the cost and logistical challenges associated with replicated, large-scale experiments limit the spatial and temporal range of application (Carpenter et al. 1995). For example, Boutin et al. (2001) acknowledged that the Achilles heel of the Kluane project (Krebs et al. 2001) was the absence of replication.

Additionally, in regions with a long and intensive history of forest use, or in regions where the history of exploitation is relatively recent, certain parts of the axis representing the gradient from altered landscapes to benchmark areas simply do not exist. For example, when determining the number of habitat patches sufficiently large for forest specialist species in Finnish managed forest landscapes, Mykrä et al. (2000) found that their availability was limited for most species, and hence also for experimentation. The same is true for landscapes with different amounts of dead wood, unless conscious efforts are made to obtain a broad and continuous gradient (Bütler et al. 2004a, b). Given the relatively high number of circumpolar species or genera in the boreal forest, there are major opportunities to compare forest processes along extensive gradients in anthropogenic disturbance.

Table 3. The approximate temporal progression of different forest history phases from the perspective of biodiversity in boreal and hemiboreal forest. Benchmark conditions are defined as a landscape with only local human use of resources (e.g. Yaroshenko 2001). Selective harvest is defined as high-grading of certain species or dimensions of trees and exploitation means that all dimensions are used. Sustainable yield timber production is defined as the use of harvesting, regeneration and stand treatment methods ensuring maximum sustainable yield. For details about the 8 case studies mentioned in the table, see Appendix.

Case study	Benchmark	Selective harvest	Exploitation	Sustained yield	Rehabilitation and re-creation
Scotland	Pre-Roman	Medieval	18th century	20th century	Present
Central Sweden	Pre-Medieval	Medieval	ca 1750	Present	Present
Finnish-Russian border	Present	Late 1800s	Present	Present	Present
Quebec	Variable depending on forest type	19th century	Present	Present	
New Brunswick	Pre-1800s	Early 1900s	Present	Present	
Great Lakes	Pre-1800s	19th century	1850s to present	Present	
Alberta	Pre-1950s	Logging of white spruce in 1950s	Present		
Pechora-Ilych strict reserve	Present				

Sampling suitable response variables along gradients of relevant length can be viewed as establishing dose-response curves (Connell et al. 1999). This means that thresholds are considered as zones of low/high risk, or uncertainty, along the axis describing the independent variable. Rather than showing discrete shifts at a certain value, there is a region on the habitat axis in which the rate of change is accelerated in relation to points away from this threshold interval (Wiens et al. 2002, Angelstam et al. 2003a; Fig. 1). It is the challenge of finding opportunities of sampling the full the gradient in habitat change that requires further attention from researchers, managers, and policy-makers.

A coarse-filter approach to derive management targets would be to use the "historical range of variability" (HRV) (e.g. Egan and Howell 2001: 7, Davis et al. 2001: 30) as determined by natural disturbance regimes. The procedure would be to run a series of forest projections based on a stochastic disturbance regime and tabulate the range of values observed for an attribute of interest, say old forest. We could then establish that our target for old forest is somewhere in that range and companies must show long-term forest projections that meet or exceed this target in order for their forestry activities to be considered sustainable, and a monitoring program should be used to determine if they are meeting the target. Like Davis et al. (2001), we view the HRV approach as a goal to be satisfied on a large regional scale. All local management may not be within HRV but desired future conditions for the region can use HRV as a broad target for management. This notion also applies to fine-filter (i.e. species) targets.

Extinction debts and the direction of change

Nonlinear response to habitat loss is not the only ecological surprise that managers may have to face. The extinction of a local population may not occur immediately following habitat loss or fragmentation, and is also strongly influenced by stochastic processes. The time period during which a species persists after habitat destruction is called the time delay or the extinction timelag. Theoretical models show that this time delay is greatest for species for which the environmental condition is near the threshold for persistence (Hanski 2000). The time delay also depends on species-specific factors. These time delays often result in underestimates of the risk of extinction. Following the deterioration of habitat in a region, there may be a number of species that survive but which will inevitably be extirpated as stochastic processes take effect. The number of species that are expected to become extinct due to past adverse environmental changes is called "extinction debt" (Tilman et al. 1994), although this often reflects extirpation rather than extinction. Before the extinction debt is paid by actual extinction, the relative proportion of rare species in the total number of species will increase.

Thus, after deterioration of a habitat patch network there are a number of species that are likely to go extinct, although they have not yet done so. Within community ecology, this phenomenon was earliest described as faunal collapse or relaxation (Brown 1971), and has been elaborated both theoretically and empirically with respect to loss of species from reserve systems isolated by conversion of surrounding habitats (e.g. Miller 1978, Glenn and Nudds 1989). While a strict island analogy is overly simplistic for most forest management applications, for species reliant on habitats particularly vulnerable to traditional forestry practices, such patterns may still be expected.

On the other hand, boreal forest organisms may be a selected group of species where good dispersal abilities are characteristic of many if not all taxa because of the dynamic nature of the boreal biome. For example, only 20 000 yr ago today's Canada was devoid of boreal forests (Delcourt and Delcourt 1991) and all species that presently occur in the northern forests must have been able to re-colonise their current ranges from glacial refugia further south. This provides some hope that re-colonisation is possible in degraded landscapes if species persist elsewhere.

The critical need for reference areas

Targets need to be defined in relation to a benchmark or reference point. Within the boreal forest there are at least two visions for biodiversity. The naturalness concept (Peterken 1996) represents one. Here, the "natural" state refers to areas without large anthropogenic impacts and this vision is often referred to as the natural disturbance regime paradigm, whereby the nature of the ecosystems in a region are determined by the natural range of variability of disturbances and their consequences (e.g. Angelstam 1998, Bergeron et al. 2001, 2002, Kuuluvainen et al. 2002, Angelstam and Kuuluvainen 2004). The second vision is represented by pre-industrial cultural landscapes (e.g. Kirby and Watkins 1998), and the pre-contact North American landscapes with aboriginal human populations (Stevenson and Webb 2004).

Without benchmarks found in reference areas it is virtually impossible to formulate ecologically based targets. How should a benchmark landscape be selected? Even in the immense boreal forest biome, benchmark areas are not present in each ecoregion (Aksenov et al. 2002, Lee et al. 2003). As each region or country usually represents a narrow range of natural variation, co-operation among regions with different biodiversity status and land use history is needed (Angelstam et al. 1997). Indeed, researchers from extensively altered boreal forest regions need to find appropriate benchmark areas and thus, to collaborate with researchers working in such regions. Finland and Russian Karelia have long established such a relationship. Conversely, regions with a long history of intensive forestry provide an invaluable source of information for researchers

working in less altered regions (e.g. portions of Canada and Russia – Aksenov et al. 2002, Lee et al. 2003).

At first glance, the boreal forest may seem huge and without threats to its biodiversity as a whole. However, it is estimated that the remaining proportion of more or less intact boreal forests is only 20% while for the hemiboreal the figure is 2% and for the nemoral, only 0.2% remains (Hannah et al. 1995). Recent studies (e.g. Yaroshenko et al. 2001) show that even in European Russia a surprisingly small area (13%) of what could be called intact natural forest landscapes remains today. Further west in Europe such intact productive areas no longer exist. Even when considering all the productive boreal forest in Sweden, only ca 5% can be considered to have a high conservation value (Angelstam and Andersson 2001). In southern Finland, the proportion of old-growth forest is 0.5% of the total land area (Hanski 2000). In Scotland, the original forest cover has largely been lost, with only ca 1% left and many of the characteristic species, such as wolf and beaver, extirpated. The maintenance of boreal forest biodiversity is therefore evidently a matter that concerns the European boreal forest as a whole.

Given what has happened in the centres of economic development, such as in western Europe and southern Canada, it is important that people from both the economic centre and the periphery share the biological knowledge gained from these large-scale changes in boreal forest biodiversity (Fig. 2). In the former, the maintenance of biological diversity requires the restoration of habitats to reach the requirement for the full restoration of species in the future. In the latter, forest management should not be intensified to the point that important forest components fall below the threshold and species start to be lost.

A vision for the future – the Boreal Atlas

For the maintenance of boreal forest biodiversity, it is crucial to make sure that what we know is widely communicated. Effective communication and mutual learning can mitigate the frequently occurring gap between policy and practice. Maps are efficient in this respect; they can delineate and describe different properties, allow integration of complex information, show data gaps, are trans-cultural, and have heuristic value. A simple way of communicating biodiversity status and trends is to discuss the fate of particular species, for examples by presenting maps of past and present distributions. Presenting the amount of certain habitat structures in relation to thresholds is another effective tool for communicating biodiversity status in terms that the general public finds easy to understand.

An obvious starting point would be to illustrate indicators suggested by the MCPFE such as dead wood or landscape-level spatial pattern of forest cover (Rametsteiner and Mayer 2004). As an example Stokland et al. (2003) reported the status of a number of MCPFE indicators for Norway, Sweden, and Finland. The recently published data of large intact boreal forest areas based on remote sensing illustrates the potential for beginning to do maps for the whole boreal forest.

Reactive or proactive conservation planning?

With an international perspective, depending on the regional history of land use, it is in principle possible to work with different combinations of forest management, protected areas, and habitat re-creation to maintain forest bio-

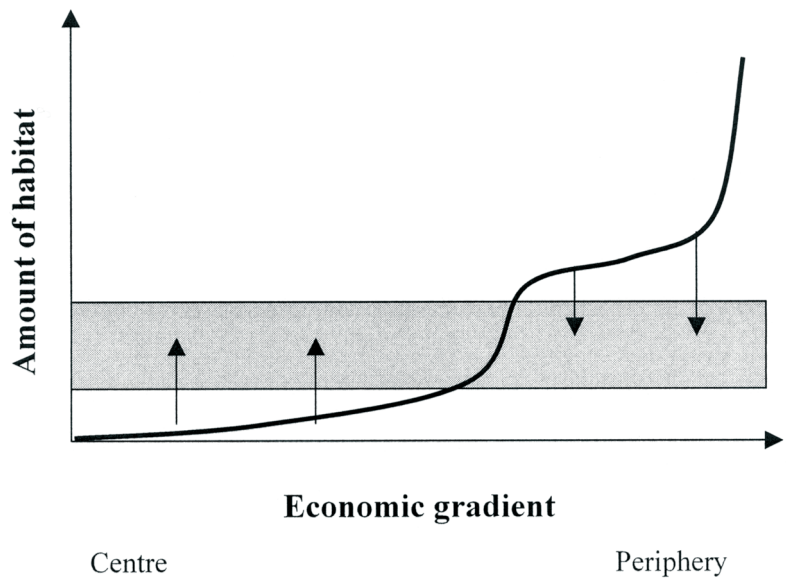


Fig. 2. Illustration of the problem of trying to strike the balance between forest use and nature conservation in boreal forests from the centre to the periphery of economic development. The black line illustrates the range of remaining amounts of authentic habitat along this gradient. The darker interval represents the tentative range of threshold values to be exceeded for the maintenance of viable populations of forest specialists with large area requirements. Finally, the arrows represent the need for restoration in the areas with a long history of intensive land use, and the need for pro-active planning to avoid repeating mistakes as the economic "frontier" spreads to the periphery.

diversity. However, the probability of success, and degree of freedom to choose among different combinations, is considerably higher when the land-use history is short. It is thus vital to realise that some regions may be limited in the range of possible tools for biodiversity conservation due to a long history of land use. This is particularly evident in Europe when contrasting forestry in western and eastern Europe, and should be considered as forestry is rapidly becoming more intensive in the Baltic States and Russia (e.g. Lopina et al. 2003, Kurlavicius et al. 2004). We have to realise that the goals that are discussed in relation to mechanisms, such as in forest certification standards, are political and not ecological. If we do not realise this, there is a considerable risk that even more near-natural forests in eastern Europe will be transformed and biodiversity lost in a very near future, as has happened in Sweden and other countries in western Europe in the past.

The recent mapping of the World's last intact forest areas (e.g. Bryant et al. 1997, Aksenov et al. 2002, Lee et al. 2003) shows that the boreal forest is one of the few ecosystems still having areas of large seemingly intact forests. Unlike the situation in northwestern Europe, where no such forests remain (Yaroshenko et al. 2001), conservation planning could, and should, be undertaken before commencing logging and other forms of resource extraction.

The obvious first step is to ensure ecosystem representation at the landscape scale within a particular ecoregion (e.g. Margules and Pressey 2000). Second, the appropriate structure, species composition and ecological processes with indicators and targets should be formulated at the landscape scale. Finally, at the scale of stands and riparian zones, there is a need to identify the nature and types of forest structures that should be retained. Thresholds for how much retention should take place at multiple scales are thus needed (Hebert 2004), as well information on the spatial configuration of forest that is needed to maintain the functionality of habitat networks.

Adaptive management teams and international co-operation

Active adaptive management can be defined as a systematic approach to adaptive management that involves the deliberate designation of control areas that enable results of management actions to be better interpreted. Ideally, an active adaptive management approach with iterated assessment and corrective action should be applied through continuous mutual learning by scientists, policymakers, managers and other actors until the targets are reached (Gunderson et al. 1995, Meffe et al. 2002). In reality, however, we are usually far away from this ideal situation (Pimentel et al. 2000, Duinker and Trevisan 2003, Trauger et al. 2003). While adaptive management is frequently advocated, it is frustrated by a number of factors. These include insufficient care in the experimental design associated with active adaptive management, and a disconnection in the adaptive management cycle. This may be due to lack of knowledge, resources or will, such that management actions may not be modified, in spite of emerging knowledge (Gunderson et al. 1995). Active adaptive management must take place within the ecosystems of interest for a particular manager or owner. For forest ecosystems, this usually means at the scale of villages actual landscapes, forest management units or river watersheds. Such physical landscape units can be viewed as replicates within an ecoregion. To actually assess the components of biodiversity, one needs to conduct empirical assessments using repeated measurements of relevant indicators, which should link to the management tools and be based on quantitative targets at multiple scales within the forest management unit or landscape.

Where do scientists fit here? Naess (1974) distinguished between the understanding of science within itself and in connection with the development of societies. Traditionally, the philosophy of science deals with the former, discussing theoretical, logical and methodological problems. However, particularly in applied sciences, there is a need to understand the role of science as a part of the ongoing debate in society. Naess (1974: 136) argues that scientists may both "…be a formidable agitator and a responsible and intellectually sound researcher." Lee (1993) elaborates further on this and argues that science provides a navigational aid to practise adaptive management or deliberate long-term experimentation with the economic uses of ecological systems to learn what works and what does not. This aid he calls the "compass" that points in the right direction by applying the rigor of analysis, verification and correction to our public policies. The other is the "gyroscope" of continual democratic debate, or bounded conflict. Together, the "compass" of adaptive management and the "gyroscope" of bounded conflict can bring about social learning in large ecosystems over the decades-long times needed to move towards sustainability. There are, however, many obstacles (e.g. Lee 1993, Gunderson et al. 1995, Mills and Clark 2001, Berkes et al. 2003). Kinzig et al. (2003) offer a number of recommendations, including restructuring of science curricula and establishment of science-policy forums with leaders from both arenas, and specifically constituted to address problems of uncertainty.

Turning science into practice requires collaboration at all steps, time to build mutual understanding, willingness to change, and a clear presentation of tradeoffs. There is also a need to provide leadership, inspiration, and co-ordination. Adaptive management teams focused on a particular case study are an efficient approach, because they provide a forum for the involvement of a variety of stakeholders including ecosystem managers, the public and policy makers.

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Appendix

To illustrate the range of conditions with respect to the maintenance of biodiversity in the boreal forest we review a number of ongoing landscape-scale studies in both the Old and the New World. For each case study we briefly describe the biome, its history, as well as the current management regime and related biodiversity conservation issues. We used this information to illustrate the predictability, in a broad sense, through which landscapes are gradually altered. For detailed analyses of species' responses it is, however, also important to take into account other kinds of gradients such as those related to macroclimatic and biogeographic differences.

The Old World

Scotland

The native forests of northern Scotland form the westernmost boreal forests in the Old World. The boreal forests are typically dominated by Scots pine *Pinus sylvestris*, with small quantities of birch *Betula pubescens* and juniper *Juniperus communis*. The principal boreal forest vegetation type is Scots pine – *Hylocomium splendens* woodland (Rodwell 1991). In warmer humid areas along the west coast, oakwoods predominate, with both sessile and pedunculate oak being present *Quercus petraea*, *Q. robur*, respectively. Alder *Alnus glutinosa* may be locally common, especially on wetter sites. In addition there are far larger areas of plantations of exotic conifers, mainly Sitka spruce *Picea sitchensis*, but including Douglas fir *Pseudotsuga menziesii*, larch *Larix* spp. and lodgepole pine *Pinus contorta*.

The forests of Scotland have had a long history of degradation. The pine-dominated Caledonian forest previously covered > 1.5 million ha of the Scottish Highlands (Anon. undated) but, today, they cover ca 16000 ha, over half of which consists of very open pine woodland. Much of this remaining resource is heavily grazed by deer, preventing any recruitment of young trees. Clearance of the Caledonian forest started in Neolithic times. The broadleaved woodlands of the lowlands were largely gone by the time of Agricola's Roman invasion of 82 BC. It progressed slowly until the 17th century, when large-scale harvesting began (Steven and Carlisle 1959, Aldhous 1995). The timber was used for ship-building, manufacture of wooden pipes and as fuel for iron-smelting and glass making. Replanting sometimes followed harvesting, with records of selected pine seed being used as early as 1613 (Steven and Carlisle 1959). Planting and forest restoration occurred at some of the estates seized after the 1745 uprising – with variable actual success. However, in many cases, the land was converted to sheep range. In the 19th century, the advent of refrigerated transport combined with an increase in sporting interests resulted in many areas being converted to what has become known as "deer forests", where management was focussed on providing trophy stags from open hill habitats. As a result, by the 1913, British-grown timber could only supply 7% of the nation's needs (Wonders 1991). This reliance on overseas (particularly Canadian and Baltic) timber was disrupted by both World Wars, resulting in the heavy exploitation of the remaining forests, primarily by specially recruited Canadian lumbermen (the Canadian Forestry Corps). Following the two World Wars, a major state project to restore timber resources saw many remaining forest areas converted to plantations of exotic species, as well as massive afforestation programme in open unwooded hill areas. This process largely ended in the 1990s, to be replaced with an increasingly biodiversity-focussed effort to restore and expand native and boreal woodlands.

Maintenance of biodiversity in the boreal forests of Scotland must thus pursue a twin approach. Firstly, our relict native forests are too small and fragmented to maintain the boreal biodiversity – indeed our current concerns over capercaillie *Tetrao urogallus* may reflect a fragmentation-induced extinction debt being paid off (Moss 2001). So major efforts are being made to restore and expand the forest area, which paradoxically can bring conflict with open ground biodiversity, also rare in a European context. Understanding the thresholds of species area requirements is vital in planning the balance between functioning woodland and open ground ecosystems.

Secondly, we must find a way of understanding and improving our large plantation areas, which may in time develop large trees, deadwood habitats, structural diversity and transitional edge habitats. The difficulty in terms of the macroecological research proposed in this paper is that the y-axis – the species group response variable – does not use exotic forests in a consistent way. For example deer have readily colonised the plantations, and in the small areas of old plantations bird diversity can be quite high. Lower plants on the other hand can be very poorly represented within plantations, especially where site conditions prevent long term stability of larger trees. Essentially we have a forest which is more boreal-like for some species groups than for others.

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Bergslagen, central Sweden

This region is located in the transition zone between hemiboreal and boreal ecoregions. The forests are dominated by Norway spruce *Picea abies* and Scots pine. The deciduous forest component consists mostly of birches *Betula* spp. and aspen *Populus tremula*. Broad-leaved trees are very rare except near settlements and as remnant of wooded grassland with oak *Quercus robur* and also ash *Fraxinus excelsior* on moist sites.

In Sweden the first local industrial use of the forest was for mining and the production of copper and iron in the

Bergslagen area of central Sweden. Local iron production started > 2000 yr ago, but became a major regional industry during the early Middle Ages. From the 17th to the 20th century, this entailed an extensive exploitation of the forest (Wieslander 1936, Arpi 1951, 1959). At this time the forest landscape was settled throughout, and the local economy was based on iron and charcoal production, as well as low intensity agriculture. Domestic grazing animals and extensive grazing in the forest were an important part of the economy (Angelstam 2002). The consumption of charcoal peaked towards the end of the 19th century, and in 1885 it was estimated that 20–25% of the cut timber volume was used for charcoal production (Arpi 1959). The remaining steel industry, which also owned the forestland, was hit by economic problems that peaked between 1975 and 1985. The last iron mines were closed in 1991. While only minor parts of the forest land have been cleared for agricultural purposes, the composition and structure of forests have been severely altered (Angelstam 1997, Mikusiński et al. 2003).

The long economic history of mining and forest use in the Bergslagen region has affected the environment. The four large predators, brown bear *Ursus arctos*, wolf *Canis lupus*, lynx *Lynx lynx* and wolverine *Gulo gulo* were gradually exterminated during the 19th century (Angelstam 2002). After a long period of forest harvesting for the production of charcoal, the timber itself became an important source of income for these industries and they gradually evolved into large forest industries. Due to large areas of forests ready for harvesting in the middle of the 19th century, and to compensate for the reduced incomes of companies owning both industry and forest, the logging rates increased and forest management became intensive including the use of herbicides and pre-commercial and commercial thinning. As a consequence a number of specialised species have become extirpated (e.g. Angelstam and Mikusiński 1994, Enoksson et al. 1995). From the point of view of sustained timber yield, however, this region is still highly productive. This combined effects of lack of top predators and a large cohort of young forest in the landscape provided the base for a strong increase of the population of moose *Alces alces* (Angelstam et al. 2000). The intensive browsing pressure now hampers the attempts to restore the amount of deciduous forest, which is needed to maintain viable species requiring old deciduous forest (Mikusiński et al. 2003).

During the 1990s the natural disturbance regime concept became a widely accepted approach to argue for applying an increased range of silvicultural methods. Still, however, clear-felling with variable retention is the norm. The current Swedish forest policy defines the biodiversity maintenance objective as that "all naturally occurring species should maintain viable populations". Given the region's very long history of forest use and management, this is an ambitious goal. Consequently, in the absence of a well-developed system of protected areas, the main tool to achieve the biodiversity goal is to attempt proactive forest management and restoration.

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Eastern Finland and Russian Karelia

In the European boreal forest zone one of the most important areas for maintaining forest biodiversity is the border zone between Finland and Russia, stretching 1250 km from the Baltic Sea to the north. This zone still contains large areas of boreal forest in their natural or near-natural state. To protect the uniqueness and biodiversity of the forests along the Finnish-Russian border, an initiative has emerged to form a network of protected areas on both sides of the border – the so-called "Green belt of Fennoscandia". These large unmanaged forest areas are not only important for maintaining forest biodiversity, but also indispensable as natural benchmark areas providing templates of natural variability for developing ecologically sustainable forest management in Fennoscandia (Korpilahti and Kuuluvainen 2002). This is because in areas like southern Finland the often small forest protection areas do not provide useful benchmark areas because their structure and dynamics have been affected by both past utilisation and the surrounding managed forest matrix, where for example fire is excluded.

The "Green Belt" encompasses all three main boreal forest zones: the southern, middle and northern boreal zones, and represents a wide spectrum of variation in ecological conditions. The landscapes are characterised by a

mosaic of peatlands, especially in the north. Although the natural conditions on both sides of the border are similar, the land use history is different. On the Finnish side, intensive forest management has strongly shaped the structure of forests during recent decades, and only relatively small fragments of natural forest are left untouched. Moreover, dense network of forestry roads and efficient fire suppression do not allow any large scale natural disturbances. On the other side of the border, in Russian Karelia, large areas of natural forest still exist, although cuttings are advancing continuously. Forest fires are still rather common in Russian Karelia. This situation has created interesting possibilities for research on how forest utilization at different spatial scales affects forest structure and biodiversity (Kouki and Väänänen 2000, Rouvinen et al. 2002, Brotons et al. 2003).

A fundamental question is what will happen in this area in the future. Protected areas comprise a low proportion of total forest area on both sides of the border, although it increases northward. It is evident that protected areas alone will not be sufficient to maintain the full diversity of the area. The crucial question is what will happen in the managed forests (Burnett et al. 2003). State owned forests in Finland are now being managed with the so-called landscape ecological forest management practices, which aim at ensuring all aspects of sustainability. On private and company owned land, forest certification schemes are used. In spite of more environmentally friendly forestry practices that have been implemented during the past years, the area of old-growth forest will still decrease during the current forestry management plans. On the Russian side, although progress has been made in forest protection, the harvesting of forest will continue and the area of old-growth forests is expected to diminish rapidly (Burnett et al. 2003). The most urgent task is to develop and apply management methods that would allow the maintenance of biodiversity. In Russia the situation is similar to northern Canada where natural forest is being logged. On the other hand, in the intensively managed forests of Finland, the question is more how to restore the biologically impoverished ecosystems (Kuuluvainen et al. 2002).

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Pechora-Ilych strict nature reserve, Russia

In northern Europe, the forests from Scandinavia to the Ural Mountains are similar regarding climate (Tukhanen 1980, 1984) and tree species composition (Kuusela 1990). They differ, however, distinctly from the forests of Siberia in the east (Kuusela 1990). Scots pine and Norway spruce form 98 to 100% of the conifers in the east and the west of Europe, respectively. Birches and aspen dominate in early- and mid-successional stages, which are common features of naturally dynamic boreal forests due to large-scale disturbances. Siberian elements (*Larix sibirica*, *Pinus sibirica*, *Abies sibirica*), occur east of the Fennoscandian shield but constitute only a minor proportion of the timber volume (Kuusela 1990).

The largest remaining tracts of the natural boreal forest in Europe are found in the most remote parts of European Russia (Yaroshenko et al. 2001). In the remote Komi Republic 10.7% of its area of 416000 km^2 is protected (Taskaev and Timonin 1993). To this should be added the forests in protective zones along water, roads and urban areas as well as buffer zones near reserves which comprise 13% of the forests (Kuusela 1990). In some remote regions, such as the 40700 km^2 Troitsko-Pechorsk region in the south-eastern part of the Komi Republic, 40% of the forests are protected. The Pechoro-Ilych Strict Nature Reserve with its buffer zone is situated in this region. Along with the adjacent Yugyd-Va National Park this is the very last naturally dynamic forest system in Europe and covers an area of > 30000 km^2, almost the size of the Netherlands. In the reserve all main northern and middle boreal forest landscape types are present, from fire-prone pine plains, to undulating hills with all stand types and to mountain forests (Lavrenko et al. 1995). The Pechoro-Ilych reserve, which was proposed in 1915, and founded in 1930, has been used for nature protection, monitoring research and education in Russia for > 50 yr.

Although unaffected by logging and exploitation of gas and oil, it has been sparsely settled and exposed to clearing for agriculture along the rivers for centuries (Saveleva 1997). In spite of this, the Pechoro-Ilych reserve and the surrounding buffer zones is one of the very few remaining large intact boreal forest areas in Europe (Kuuluvainen et al. 1998, Yaroshenko et al. 2001, Jasinski and Angelstam 2002, Angelstam et al. 2004).

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The New World

New Brunswick, Canada

New Brunswick has the longest history of intensive forest management among Canadian provinces (Baskerville 1995). Large-scale, industrial harvesting started in the early 1950s but this was preceded by decades of "high-grading" of the forest, during which the best specimens of white pine *Pinus strobus*, red spruce *Picea rubens* and yellow birch *Betula alleghaniensis* were selectively cut.

New Brunswick's forest is dominated by mixed stands with a dominance of conifers (*Picea* spp., *Abies balsamea*). Broad-leaved stands co-dominated by sugar maple *Acer saccharum*, American beech *Fagus grandifolia*, and yellow birch occupy rich, well-drained sites, whereas wet areas and bogs are dominated by black spruce *Picea mariana*. Following the high-grading phase affecting white pine, then yellow birch and red spruce, large-scale clearcutting took place in conifer-dominated stands and spruce plantation started as early as 1957. Since the mid 1980s, large-scale uneven-aged management of broad-leaved stands was undertaken to remove low-quality specimens and gradually increase the quality of sawtimber. Intensive forestry, including spruce budworm *Choristoneura fumiferana* control and fire suppression, has resulted in the virtual disappearance of stands that could be considered as old growth. Forest composition and structure have thus been substantially altered, with unknown effects on forest biodiversity. Among higher vertebrates, however, the only well-documented casualties are the grey wolf and the woodland caribou *Rangifer tarandus*, which were extirpated at the turn of the 20th century. In both cases, however, excessive trapping and hunting rather than habitat loss are probably to blame.

Public lands represent 50% of the forest lands in the province. Conifer-dominated stands are treated through clearcutting with variable retention, replanted with conifers, and treated with herbicides. Deciduous-dominated stands are managed using various uneven-aged systems. The policy for biodiversity conservation on public lands is based on the concept of mobile reserves and targets higher vertebrate species associated with all combinations of stand age classes and tree species composition (Anon. 1995). Companies holding timber licenses must meet quantitative targets expressed as areas of specific wildlife habitat types. Each wildlife habitat type includes specific structural elements defined according to the corresponding list of typical species (e.g. snags of a minimum size, minimum canopy closure). Some of these structural criteria are being reconsidered in the light of recent data on forest birds from Guénette and Villard (unpubl.), which suggest that current threshold values are too low. However, a recent report from a Finnish consulting firm (Anon. 2002) suggests that the province could double its supply of softwood from public lands through an intensification of silviculture while meeting its current biodiversity objectives. This and related proposals are currently being examined through public consultations.

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The Western Great Lakes region, USA

The western Great Lakes region (Minnesota, Michigan and Wisconsin) was settled by Europeans relatively late, and widespread land-clearing did not occur until the mid 1800s in the southern regions and the late 1880s to early 1900s in the more boreal northern areas (Frelich 2002). Historically, the northern regions of Minnesota had high frequency of intense forest fires (Heinselman 1973, Clark 1988). Some large areas (150 000 ha) representing all of the important forest types were even set aside as reserves (Heinselman 1996). Even if affected by native Americans there is a valuable forest history gradient from centres of economic development northward to the US and Canadian border. Pollen studies show that on a century basis the

overall rate of change in the spectrum of forest types during the past 8000 yr was less than half of that during the last century (Jacobson and Grimm 1986).

The northern portions of Minnesota, Michigan, and Wisconsin contain significant representation of the boreal or sub-boreal forests. In presettlement times, these forests were dominated by the spruce-fir-birch, or red *Pinus resinosa* and white pine forest types, with jack pine *Pinus banksiana* on xeric sites and swamp conifers in lowlands (Stearns and Guntenspergen 1987, Host et al. 1996, White and Host 2000). These forests are transitional with the northern hardwood forest type, which includes sugar maple, basswood *Tilia americana*, and yellow birch in the west, and maple-hemlock *Tsuga canadensis* in Michigan's Upper Peninsula and northwestern Wisconsin (Pastor and Mladenoff 1992). The extensive logging at the turn of the century successively removed the pines, hemlocks and hardwoods (Whitney 1987) and led to the widespread development of the seral aspen-birch type, currently the dominant forest type of the Lake States.

Biodiversity management has received considerable attention recently in the Western Great Lakes Region. For example, Minnesota completed a monumental Generic Environmental Impact Statement (GEIS) study on "Timber Harvesting and Forest Management in Minnesota" (Anon. 1994). Among the foci of the study included forest health, plant and animal diversity, and forest wildlife. Major concerns were identified with respect to soil sustainability, landscape patterns, and biological diversity of forest birds (Anon. 1994). The latter is among the most well-known group of animals in the forests and serves as a primary surrogate for overall biodiversity conservation in the region today (Niemi et al. 1998; <http://nrri.umn.edu/mnbirds>). Moreover, society realised that the forest resource is not infinite and a heated debate ensued on sustainable forest cutting levels that continues today. The study resulted in new legislation on forest management practices, policies, and renewed consideration of forest biodiversity values. Most recently, the natural historical disturbance patterns (1870s) and current forest cutting patterns have been examined (Host and White 2003) as well as the potential effects on biodiversity (Manolis 2003).

The northern portions of Minnesota, Wisconsin, and Michigan have a majority of the forests found in the region and a majority of the forest ownership is in the public domain. The Boundary Waters Canoe Area Wilderness (BWCAW) is over 400 000 ha and is off-limits to logging and other human development. The federal Chippewa and Superior National Forests have recently completed forest plans that have explicit consideration of biodiversity values as part of their forest scenario planning. The previously mentioned natural range of variability concepts have been employed by federal, state, and other landowners in the western Great Lakes (Host and White 2001).

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Alberta, Canada

The boreal forests of northern Alberta have only a recent history of large-scale industrial development (Schneider 2002). Whereas harvesting has occurred since the early 1900s, it was essentially restricted to the high-grading of large conifer trees (primarily white spruce *Picea glauca*) by small, localised mills. This pattern began to shift in the 1940s, with a greater demand for timber resources. At this

time, a regulatory and management body was established in the province, with the primary objective of ensuring sustainable timber yields. The most dramatic changes in forest management have occurred in the past few decades, with the advent of technologies and markets for deciduous pulpwood, and the rapid expansion of the forest industry through the granting of huge leases of public land (e.g. Schmiegelow and Hannon 1993). While the forest is now considered fully allocated from a timber standpoint, there nevertheless remain large areas of forest in a relatively pristine state.

Alberta's boreal forest consists primarily of mixed forest. Trembling aspen *Populus tremuloides*, balsam poplar *Populus balsamifera* and white spruce are the most abundant upland species, with lesser amounts of white birch *Betula papyrifera*, balsam and jack pine, whereas black spruce characterises wetter sites. Roughly one third of the forested landbase is considered merchantable with the remainder consisting of treed peatlands, bogs, and fens. Forest tenure systems have resulted in a divided landbase (Cumming and Armstrong 2001), whereby the deciduous and coniferous components of the forest are often allocated to separate companies, and subsequently managed for different objectives. In addition to the rate and extent of forest development activities, this raises further concerns for biodiversity conservation, as older, mixed forests support the highest levels of species richness, and highest abundance of many species. Most harvesting is through clearcutting, with site preparation and re-planting of conifer sites, and natural regeneration of deciduous sites. Efforts at ecologically sustainable forest management by industry leaders have resulted in some retention (ca 5% average) of merchantable material within harvest blocks. However, while commitments have been made to biodiversity conservation, a comprehensive set of management objectives at the provincial level is lacking, and no quantitative targets are specified. Compounding this problem are the often competing interests or other resource sectors on forest land. Continued agricultural expansion and conversion of forest is a serious concern (Hobson et al. 2002), as are the widespread exploration and development activities associated with gas and oil industries. The disturbance rates of the latter approximate that of the forest industry in some areas (Schneider et al. 2003).

In response to the expansion of industrial forestry activities in the early 1990s, substantial research programs have been developed to address sustainable forest management. The focus on biodiversity issues has, however, been largely reactive, rather than proactive to date, and there exists an urgent need to identify and secure benchmark areas for continuing ecological study, and as part of an active adaptive management framework (Boutin et al. 2002). The challenges for biodiversity conservation in this region are somewhat futuristic as the vast majority of species, including large carnivores such as wolves, have large tracts of available habitat remaining. Woodland caribou are an exception. Current industrial activity will lead to a substantial reduction in the habitats and forest structures most affected by forest harvesting (old growth, unsalvaged recent burns, large snags, downed woody material). The challenge is to establish targets for these attributes that must be met in long-term forest projections in a fashion similar to the need to maintain timber supply over the long-term.

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Quebec, Canada

A wide range of forest ecoregions is found in the province of Quebec. The St. Lawrence valley is dominated by temperate hardwood forests and bordered by hemiboreal forest types characterised by admixtures of balsam fir, yellow birch, and associated species. Further to the north and at higher altitudes, the forest is truly boreal. The southern part of the boreal zone is dominated by balsam fir, trembling aspen and paper birch. In the north, black spruce becomes the dominating species, but jack pine, balsam fir, trembling aspen, and paper birch occur in varying proportions depending on site characteristics and stand age. Natural disturbances in Quebec's boreal forests include stand-replacing forest fires (Bergeron et al. 2001, 2002), cyclic epidemics of the spruce budworm (Morin et al. 1993), and windthrow (Ruel 2000). Public lands represent 89% of the productive forest of Quebec. The remaining 11% in private tenure is mostly located in the St. Lawrence valley.

Large-scale forest exploitation in Quebec started in the second half of the 19th century and was concentrated in the St. Lawrence valley, where white pine was selectively harvested for ship construction under the British Empire.

In the boreal forests, however, extensive harvesting by clearcutting started much later, between the 1930s and the early 1950s in its southern parts and later in more remote areas. This northern advance of forestry is still ongoing, virgin forest being harvested further north every year. At the present, an east-west band of untouched forest – varying in width from 100 km to 400 km – is still found between the front of forest operations and the southern edge of non-commercial, open taiga forest. New forest roads are rapidly stretching into this zone, which has almost been totally allocated to forest companies by the provincial government in the form of forest management contracts. Nowadays, almost all harvesting is done through clearcutting, special care being given to the protection of soils and regeneration. Besides final felling, silviculture during stand development is rather minimal, except perhaps the intensive use of pre-commercial thinning in some regions.

Although recent, the intensive use of an even-aged management system throughout this portion of the boreal forest is changing deeply the composition and structure of landscape mosaics, which are considerably more complex under natural disturbance regimes. Studies on fire history regimes of Quebec and north-eastern Ontario's boreal forest show that short fire cycles generally described for boreal ecosystems do not appear to be universal. Rather, important spatial and temporal variations have been observed (Bergeron et al. 2001). Hence, variations in the fire cycle have an important influence on forest composition and structure at both the landscape and regional levels. In northwestern Quebec, Harper et al. (2002) have shown that large proportions of the land base are composed of overmature and old-growth stand types under natural disturbance regimes. The extensive use of even-aged management systems based on clear-cutting practices in these forests is thus likely to truncate their natural age-class distribution, eliminating overmature and old-growth stages (Bergeron et al. 2001, 2002). This will in turn affect the biodiversity that is associated with these stand types (Boudreault et al. 2002, Drapeau et al. 2003). In Quebec's forest act, the only regulation that may refer to the maintenance of biodiversity as a whole refers to the maintenance of 30% of the productive land base into forest cover types of > 7 m height in forest management units. Otherwise regulations concern specific habitats of game and non-game species based on a species by species approach. Such regulations partly address the issue of biodiversity maintenance but do not set management objectives that could address simultaneously all levels biological diversity. Development of forest management planning approaches at the strategic level and diversified use of silvicultural techniques designed to maintain a spectrum of forest compositions and structures at different scales in the land base are coarse-filter avenues that are currently proposed to maintain the variability of stand types and hence, species diversity in such ecosystems (Bergeron et al. 2002). Additionally, the presence of large tracts of untouched natural forests in the North offer opportunities for the development of a functional network of protected areas.

Finally, with the northern expansion of forestry in areas where fire cycles are shorter, it is likely that forestry companies will have to deal more and more with the reality of wildfires in the near future. The salvage logging of burned forests, a practice rarely used in the past, has increased in recent years (Nappi et al. 2004). The Quebec Forest Act of 1986 and its recent modifications have provided several incentives to intensify salvage logging (Quebec Government 2003) with no management guidelines to maintain biodiversity in these habitats. This raises serious concerns given the major contribution of recently burned forests both as a key habitat for wildlife species and as the main source of recruitment for standing dead wood, particularly in the black spruce forest of eastern Canada (Drapeau et al. 2002, Nappi et al. 2003).

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