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Status of wetland forests and their structural richness in Latvia

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Summary

Wetland forest communities are seriously reduced and degraded throughout most of Europe, but significant areas still survive in the east and north-east. Data from 91 forest structures that support biodiversity are analysed in 369 relevés of Latvian wetland forests. These structures include variations in topography, stand composition, water movement and dead wood features occurring in semi-natural conditions undisturbed by management. There is clear structural differentiation between coniferous and deciduous wetlands. The study supports the widely held views on European forest quality: low volume of high-diameter (>50 cm) snags and logs, too few overmature trees, and the threat to pattern heterogeneity caused by traditional forestry and silviculture. Twenty areas (totalling *c.* 3800 ha) are identified as reserves that should be strictly protected in Latvia in order to maintain representative and intact samples of wet forest belonging to Eurosiberian alder swamps (*Alnetea glutinosae*), broad-leaved forests (*Querco-Fagetea*) and boreal forest (*Vaccinio-Piceetea*) communities. Based on habitat features and site ecology, the concept of sustainable forestry must be incorporated widely in utilization of European wetland forests in order to prevent further loss of biodiversity.

Keywords: Baltic region, biodiversity evaluation, boreonemoral wetland, community conservation, site-adapted forestry

Introduction

Wetland forests are amongst the most altered types of potential natural vegetation in Europe and have rapidly decreased due to human habitation and industrial growth (Wenger *et al.* 1990; Döring-Mederake 1991; Eurola *et al.* 1991; Dudley 1992). Europe is the only region in the world with an annual increase in forest cover (Anon. 1996), but there is much dispute over forest quality. This particularly concerns the lack of forest continuity and variation in size of stands (Lähde *et al.* 1991; Linder & Östlund 1992; Haila & Kouki 1994), the absence of coarse woody debris (Samuelsson *et al.* 1994), and sustainable forestry methods (Dudley *et al.* 1993; Mladenoff & Pastor 1993; Angelstam 1996*a*, *b*). Because of the perception that drained forests or cultivated floodplains are more useful to societies, wetland forests are now much reduced and highly fragmented in most of Europe (Wiegers 1990), and large areas with intact peatland and wet mineral forests remain only in the east and north-east.

With its 621 000 ha of forested wetlands corresponding to 22.4% of all forests or 9.6% of the country's area (State Forest Service 1996), Latvia is remarkable in the boreonemoral forest region (Sjörs 1965). This richness is even more obvious if we analyse its composition: both typical nemoral and boreal lowland forests co-occur there as a result of the overlap of two vegetation belts, the low elevation (mostly 40–200 m above sea level), specific hydrology with numerous places of underground water outflow, and historical background (Prieditis 1997*a, b*; Strods 1999). Only a narrow forest strip stretching from eastern Poland across the Baltic countries towards the western provinces of the Commonwealth of Independent States harbours so many well-defined and different communities of wetland forests.

As in most of central and northern Europe, a substantial change in forest cover has taken place in Latvia. Permanent habitation, clearings for crop fields, trade and manufacturing resulted in the destruction of Latvian primaeval forests by the end of the eighteenth century (Sarma 1959). Compared with central Europe, however, the low density of inhabitants (in the 14th–16th centuries the population density was 2–5 times lower than in Britain and Central Europe) and the abundance of springs and associated wetlands supported a relatively low level of exploitation of wetland forests. Nevertheless, all the basic features characterizing heterogeneity and dynamics of contemporary forests (as reviewed by Haila & Kouki 1994) have also changed in Latvian forests. These include increased fragmentation of semi-natural forest areas and decreased abundance of hardwoods; for example, only very small patches of riverine oak forests have been left intact in east Latvia. Because of forestry activities the amount of coarse woody debris (CWD) is low and rotation times of the forest are too rapid to provide a stable niche for organisms demanding forest continuity.

Compared with other forest types, wetland forests bear several essential features. Fire is very rare here, though normally one of the most frequent disturbance agents on a long time-scale (Engelmark 1987; Kangas 1990; Hörnberg 1995; Angelstam 1996*a*). A continuous supply of dead wood in different stages of decay, and subject to frequent disturbance through fluctuations in water level, supports a rich ecosystem with a great number of habitat specialists (Falinski 1978; Kangas 1990; Szczepanski 1990; Hedenäs & Löfroth 1992; Ohlson *et al.* 1997). Furthermore, a hummocky ground topography in certain wetland communities allows the co-

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existence of a wide range of species adapted to different flooding conditions (Ohlson *et al.* 1997; Prieditis 1997*a*, *b*). Wetland forests also facilitate self-purification of water from pollutants (Brinson *et al.* 1980), and the tree canopy can secure aquatic organisms against excessive thermal fluctuations. Large logs that decompose slowly in a stream may serve as a substratum for algae and mosses as well as shelter for invertebrates and fish. Other notable features of the biotope include deposited silt from floods caused by heavy rainfall or melting snow, transport of fertile sediments and nutrients by streams, and water movement close to ground level. All these provide important sources for heterogeneity of the forest.

Successional investigations indicate that the hemiboreal wetland forests belong to stable climax (primary) communities (e.g. with *Alnus glutinosa*, *Picea abies*; Polakowski 1962; Marek 1965) and under suitable conditions can persist for an unlimited time; studies of peat deposits in intact Polish wetlands have indicated thousands of years (Marek 1965). This especially applies to alderwoods, which generally occupy the wettest habitats in the forest.

In order to extend what we already know about moist and wetland forest communities in northern temperate Europe (i.e. the Fennoscandian-Baltic area; Diekmann 1994; Korpela & Reinikainen 1996; Prieditis 1997*a*, *b*), we need to maintain representative community types with their specific site ecology. This must include not only strict conservation but a somewhat broader definition of sustainable forestry (Mladenoff & Pastor 1993; Angelstam & Petterson 1996).

Following the community sociology approach *sensu* Braun-Blanquet (1964), we will consider wetland forests belonging to Eurosiberian alder swamps and carrs (*Alnetea glutinosae: Carici elongatae-Alnetum, Sphagno squarrosi-Alnetum*), European broad-leaved forests (*Querco-Fagetea: Circaeo-Alnetum, Carici remotae-Fraxinetum, Alnetum incanae p.p.*), boreal coniferous forests (*Vaccinio-Piceetea: Sphagno girgensohnii-Piceetum* [spruce mires], *Vaccinio uliginosi-Pinetum* [pine bogs], *Betuletum pubescentis* [birch mires]) and the derived syntaxa from these assemblages (community descriptions in Döring-Mederake [1991] and Prieditis [1997*b*]).

There are two aims. Firstly, to present the established network of wetland forest reserves in Latvia designated to maintain representative areas of intact communities. Secondly, to characterize the heterogeneity of some of these areas by means of a detailed inventory of 91 'forest structures supporting biodiversity'. These structures can enrich the pattern for species to co-exist and include variations in stand composition, ground topography and dead wood features occurring in conditions undisturbed by forestry.

Methods

Sources

Community studies of Latvian wetland forests were undertaken between 1990 and 1995 (625 relevés, each covering 400 m^2; Prieditis 1997*a*, *b*). This covered all uniform wetland forest areas (>100 ha in maps at 1:10 000) in Latvia, and principal structural and ecological features were studied, such as diameter at breast height (DBH), groundwater level and fluctuation, depth of the peat layer and height of vegetation layers (Prieditis 1997*b*). The forest stands had been undisturbed for between 60 and 130 years. In parallel with this study, the World Wide Fund for Nature (WWF) supported two projects on the status and conservation of swamp and wet mineral forests in Latvia (Prieditis 1993), which resulted in the establishment of wetland forest reserves.

Some of the data from a WWF project (Suško 1998) form a background to the analysis of biodiversity structures. The inventory was performed on the basis of the established wetland forest reserves (Prieditis 1993). Within the inventory, forests were split into six groups, namely recently disturbed biotopes (clear-cutting, established monoculture), pioneer phase of deciduous trees, pine forest, spruce forest, wet de-

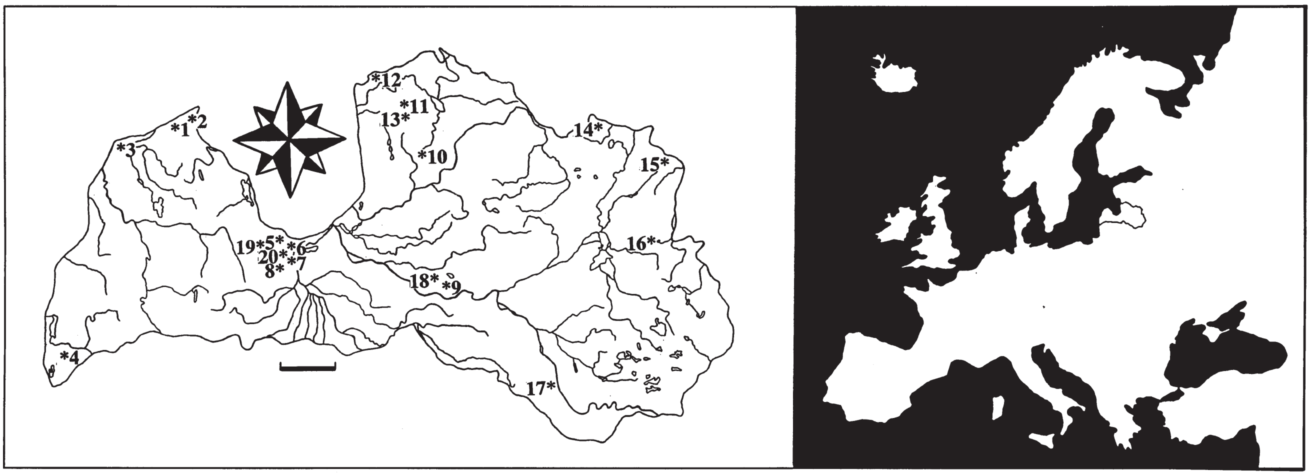

Figure 1 Geographical location of Latvia (right) and map of Latvia indicating the locations of the wetland forest reserves selected by the survey (numbers correspond to those in Table 1). The scale bar represents 40 km.

ciduous forest, and broad-leaved forest (Drakenberg & Lindhe 1994). As well as old-growth stands, heavily managed and transformed forests were included for comparison. Ninety-one different structures that supported biodiversity were recorded and split into nine groups (see Appendix). Their inventory followed the presence and absence approach in *c.* 800 plots in four territories of a size 620–720 ha each (Zilie Kalni, Aizkraukle, Livberze, and Mezole [close to Augstroze]; see Fig. 1 and Table 1). The current analysis of structures in Latvian mature forested wetlands was based on 369 plots rearranged from a total of 800 plots. The plot area for a record corresponded to a uniform forest site according to the forest inventory map (on average, 0.8–15 ha); the structures were recorded per hectare (see also the note to the Appendix).

Community studies and treatment of data

All phytosociological investigations followed the Braun-Blanquet (1964) approach and cover-abundance scale and were recorded separately for trees, shrubs, herbs and the moss layer. The frequency classes represent the following percentage intervals: I (5–20%), II (20.1–40%), III (40.1–60%), IV (60.1–80%), and V (80.1–100%).

Table 1 Summary of the main indicator values in the designated reserves of wetland forests. (1) Intact alder (*Alnion*) wetlands; (2) intact broad-leaved (*Alno-Ulmion*) wetlands; (3) intact spruce (*Vaccinio-Piceion*) wetlands; (4) intact pine (*Dicrano-Pinion*) wetlands; (5) primaeval or virgin-like sites, supported by natural disturbances and successional trends; (6) many over-mature trees and coarse woody debris in various stages of decay; (7) unregulated streams; (8) high diversity in species and communities (including red-listed species); (9) diversity in microhabitats due to topographical relief and soil fertility.

Number of forest location (see Fig. 1) and Latvian name	*Area (ha)*	*Values*									*Remarks*
		1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	
1. Zilie Kalni/Slitere	220	◆	◆	.	◆	◆	◆	◆	◆	◆	High diversity in forest communities, strict reserve (1921), visiting prohibited.
2. Bazkangars/Slitere	70	.	.	.	◆	.	◆	.	◆	◆	Strict reserve since 1970s, visiting restricted.
3. Ovisi	140	◆	.	.	◆	.	.	◆	◆	◆	Specific prolonged coastal dune-mire complex.
4. Liepieni	50	◆	◆	◆	.	.	◆	◆	◆	◆	–
5. Slocene	1320	◆	.	◆	◆	◆	◆	◆	◆	◆	Complex nature reserve (1977), national park (1997).
6. Sloka	58	◆	.	.	◆	.	◆	◆	◆	◆	Typical coastal floodplain.
7. Kalnciems	317	◆	◆	.	.	◆	◆	◆	◆	◆	Probably the largest alderwood subject to natural river floods.
8. Livberze	73	◆	◆	.	.	◆	◆	.	◆	◆	Remnant from what was the formerly largest wet broad-leaved forest in Latvia.
9. Aizkraukle	508	◆	◆	◆	◆	◆	◆	.	◆	◆	Extremely diverse forest-bog complex with deciduous forests on the bog islands.
10. Augstroze	86	◆	◆	.	◆	.	.	◆	◆	◆	Complex nature reserve (1987).
11. Ungurpils	61	.	◆	.	.	.	◆	◆	◆	◆	Well-pronounced area of primarily *Querco-Fagetea* communities.
12. Mernieki	21	◆	.	◆	.	.	◆	.	.	.	Typical forest for north Latvia in remote area.
13. Aloja	23	◆	.	◆	.	.	◆	.	.	◆	–
14. Avoti/Ziemeris	110	◆	.	◆	.	.	.	.	◆	◆	Botanical reserve (1987).
15. Katlesi	110	◆	.	◆	◆	.	◆	.	◆	.	Well defined area of boreal communities.
16. Kugrini	274	◆	.	◆	◆	.	◆	◆	◆	◆	Extremely diverse forest-mire complex with lakes.
17. Dviete	135	◆	.	◆	.	.	◆	◆	◆	◆	River valley carrs with springs.
18. Jumprava	27	.	◆	.	.	.	◆	.	◆	◆	Lies in an area of primarily broad-leaved forests.
19. Lielais Tirelis	38	◆	.	◆	◆	.	◆	.	◆	◆	Bordering to raised bog.
20. Versupite	82	◆	◆	◆	.	◆	◆	◆	◆	◆	Very high diversity of habitats.

TWINSPAN (Hill 1979) analysis was used to classify the data of biodiversity structures. Five pseudospecies cut levels corresponded to the Braun-Blanquet scale (all low-abundance data treated as one level). CANOCO software (ter Braak 1990) was applied to ordinate the plots and biodiversity structures (DCA–Detrended Reciprocal Averaging). The default options of both classification and ordination programmes were selected. One pseudospecies cut level was applied for the TWINSPAN classification of structures in wetland forests. A second TWINSPAN classification and DCA ordination were carried out after including dry forests (another 108 plots) in order to compare the structural richness and to illustrate changes in frequency of particular biodiversity structures under different ecological (wet-dry) gradients.

Selection principles of representative conservation areas

A three-level inventory was completed by 1994 so as to establish a representative network of wetland communities to be strictly protected in Latvia in accordance with the IUCN (World Conservation Union) category 1 (IUCN 1994). Generally, selection principles applied closely follow those recommended by Usher (1986) or Noss (1995).

Firstly, all uniform areas of wetland forests (>100 ha) were investigated throughout the country (a detailed map is given in Prieditis 1997*b*). This included 625 phytosociological relevés and gave a 'rough' evaluation (presence and absence approach) of whether the community harboured only typical species, without naturalized or casual species, and corresponded to the phytosociological standard of the community. At the same time, stands were examined to see if they presented a multi-aged and multi-structured forest, as indicated by the presence of snags, logs, different tree species of different age and diameters, fungi and liverworts on trunks, woodpecker signs (full details in Prieditis 1993). Only high levels of presence of particular structures were noted. This concept was almost identical to that of 'forest structures supporting biodiversity' (Drakenberg & Lindhe 1994). Areas with such features and trees of at least 90–120 years old were marked especially. A note was made of how many communities co-occurred in the forest as a result of the presence of streams, hummocks, gentle slopes or cold springs. An uncommon density of rare and protected species was evaluated. And, finally, the influence of management on the forest was taken into consideration (no drainage, no roads passing the forest, no power transmission lines, no wastes or pits established).

In the second stage, *c.* 10% of the most important forests (selected from previous studies) were re-visited and management details were reconsidered in accordance with data from the forest survey. This included ownership, cutting plans, influence of possible management to the values of the forest, and the compatibility of the proposed activities with the maintenance of a rich biota.

Finally, a network of protected (IUCN category 1) wetland forests was created that ensured that the full range of features that characterize wetland forests in Latvia were represented at least once. These features included, for instance, undisturbed floodplains, habitats with striking hummock-forming processes, areas with outflowing springs, and high cover-abundance of boreal flora, and so on. Thus, every reserve had one or several dominating values to be appreciated within the whole set. The primary values of a semi-natural forest (e.g. virgin sites, evidence of natural disturbances, species demanding forest continuity, presence of coarse woody debris) were shared by all the reserves. Micro-sites of high diversity were also mapped, e.g. spots with vulnerable plants, big trunks with rich fungi and non-vascular flora, solitary overmature trees with holes, and cold springs.

Nomenclature follows Kuusk *et al.* (1993–99) for vascular plants and Prieditis (1997*b*) for wetland forest syntaxa.

Results

Network of conservation areas

From phytosociological features, many of the forests appeared to be mixed and simplified communities with a low number of biodiversity structures. They were especially poor in coarse woody debris and the large-diameter trees that indicate forest continuity. Heavy drainage carried out without ecological expertise in the 1970s and 1980s has resulted in the devastation of internationally important sites, including what was formerly the largest (*c.* 1500 ha) continuous ash-alder wetland forest in central Latvia at Livberze. Twenty areas (*c.* 3800 ha) were selected in order to strictly preserve representative samples of forest communities in wetlands (Fig. 1, Table 1).

It was difficult to identify even small (50–100 ha) areas which adequately represented an intact wetland forest community. There was an unexpected but clear contradiction between the seemingly wide distribution of wetland forests in forestry terms in Latvia and the poor quality of these habitats. Although there is still an abundance of smaller wetland areas (5–20 ha) within larger forest blocks, the decline in intact habitats supported by natural streams and springs now needs both strict conservation and sustainable utilization of wetland forests if it is to be halted. In addition, due to a slight oceanic influence, the eastern Baltic still harbours representative samples of intact wetland hardwoods and alderwoods formerly widespread in central Europe (syntaxonomic details in Prieditis 1997*a, b*). Similar assemblages found eastwards differ, containing more continental species.

The principal features of the forest assemblages recognized are briefly reviewed in Table 2. Of these, the *Circaeo-Alnetum, Carici remotae-Fraxinetum* and *Carici elongatae-Alnetum* associations are rich in subsoil streams and surface run-off and are particularly endangered. The above communities are highly productive forests with an average crown closure of 80–90%, height of tree layer *c.* 22–26 m at

Table 2 Principal characteristics of wetland forest communities commonly found in north-eastern temperate Europe (*– belongs only in part to wetland forests in the sense of the present paper; subassociations of all syntaxa and variants are excluded). Peat layer (cm) groups: a > 30; 31 < b < 100; 101 < c < 200; 201 < d < 400. Groundwater level (cm) groups: a = above surface; b > 30; 31 < c < 100.

Community	*Dominant trees*	*Other high frequency diagnostic species*	*Nutrient status*	*Peat layer groups*	*Groundwater level (extremes excluded) groups*
Carici elongatae–Alnetum Schwick. 1933	*Alnus glutinosa*, *Betula pendula*, *B. pubescens*, *Fraxinus excelsior*	*Calamagrostis canescens*, *Calliergonella cuspidata*, *Carex elongata*, *Iris pseudacorus*, *Lycopus europaeus*, *Ribes nigrum*, *Salix cinerea*, *Solanum dulcamara*	eutrophic, meso-eutrophic	a, b	mostly a or b
Sphagno squarrosi–Alnetum Sol.-Gorn. ex Pried. 1997	*Alnus glutinosa*, *Betula pubescens*	*Calla palustris*, *Carex canescens*, *Comarum palustre*, *Sphagnum squarrosum*, *Sph. palustre*	mesotrophic	b	mostly b
Circaeo–Alnetum Oberd. 1953	*Alnus glutinosa*, *Fraxinus excelsior*	*Chrysosplenium alternifolium*, *Circaea alpina*, *C. lutetiana*, *Eurhynchium angustirete*, *Galeobdolon luteum*, *Impatiens noli-tangere*, *Mercurialis perennis*, *Plagiomnium undulatum*, *Stellaria nemorum*	eutrophic	a	b, c
Carici remotae–Fraxinetum Koch ex Faber 1936	*Fraxinus excelsior*	*Aegopodium podagraria*, *Carex remota*, *C. sylvatica*, *Galeobdolon luteum*, *Lonicera xylosteum*, *Mercurialis perennis*, *Ranunculus cassubicus*	eutrophic	a	b, c
(*) *Alnetum incanae* Lüdi 1921	*Alnus incana*	*Chaerophyllum aromaticum*, *Crepis paludosa*, *Festuca gigantea*, *Humulus lupulus*, *Padus avium*, *Thalictrum aquilegifolium*	eutrophic, meso-eutrophic	no peat	c
Sphagno girgensohnii–Piceetum (Br.-Bl. 1939) Polak. 1962	*Picea abies*, *Betula pubescens*	*Dicranum scoparium*, *Listera cordata*, *Moneses uniflora*, *Oxalis acetosella*, *Sphagnum girgensohnii*, *Trientalis europaea*, *Vaccinium myrtillus*	meso-eutrophic, mesotrophic	a, b, c	mostly c
Betuletum pubescentis (Hueck 1929) Tx. 1937 em. Tx. 1955	*Betula pubescens*	*Filipendula ulmaria*, *Oxycoccus palustris*, *Peucedanum palustre*, *Polytrichum commune*, *Salix cinerea*, *Thelypteris palustris*	mesotrophic	b	c
Vaccinio uliginosi–Pinetum (Hueck 1925) Kleist 1929	*Pinus sylvestris*, *Betula pubescens*	*Eriophorum vaginatum*, *Ledum palustre*, *Polytrichum commune*, *Rubus chamaemorus*, *Sphagnum* spp., *Vaccinium uliginosum*	meso-oligotrophic, oligotrophic	b, c, d	b, c

an age of 100 years and stand volume of 300–350 m^3/ha; they are, therefore, attractive commercially.

Distribution of forest structures supporting biodiversity

The TWINSPAN classification of wetland habitats by biodiversity structures first separated conifers from deciduous trees and then divided each of these into two, giving pine bogs, spruce mires, wet broad-leaved stands and alder carrs, which were further split into eight groups (Fig. 2). This meant that particular structures incorporated in the inventory list (those with a coniferous or deciduous component) determined the dichotomy at the first classification level.

Both pine and spruce wetlands formed two groups. Pine wetlands (phytosociologically *Vaccinio uliginosi-Pinetum s.l.*) with a low number of structures (*c.* 7–15) formed group A, while richer sites (*c.* 14–26 structures) belonged to the group B. The same pattern was seen in the spruce wetlands (phytosociologically *Sphagno girgensohnii-Piceetum s.l.*) which were subdivided into those poorer (<12; group C) and richer (14–29; group D) in structures.

Such a dichotomy is not so obvious in the classification of deciduous wetlands. There was minor overlapping amongst the communities *Circaeo-Alnetum, Carici remotae-Fraxinetum,* and *Carici elongatae-Alnetum*. The phytosociological differentiation of these assemblages was not based precisely on the dominant tree species (in Latvia, *Fraxinus excelsior, Betula pubescens, Betula pendula,* and *Alnus glutinosa*). For instance, *Fraxinus excelsior* (hardwood species) can form *Carici elongatae-Alnetum*, too. Biologically *Carici elongatae-Alnetum* was closer to the group G to which all alderwoods belong, but not to group E, to which hardwood-dominating wetlands were ascribed. Wet forests of a pioneer phase could fall into the broad-leaved forest or the alder carr group depending on the character of the seral stage and development trends. Exceptionally, mixed secondary stands without any obvious dominant could be classified with the conifers (Fig. 2).

Together, the wetland deciduous forests contained on average 14–27 (mean 22) biodiversity structures. Low-value sites were extremely rare, although it should be stressed that the study was performed in priority conservation areas. In strongly altered and recently disturbed sites, which are outside the scope of the present paper, the number of biodiversity structures are reduced to 0–5 (Suško 1998).

Although the full list comprised 91 structures, the maximum number of structures in particular forest groups (spruce, pine, and so on) was almost identical, namely 48–52 structures. Compared with all structures, a seemingly 'low' number was due to many of them being mutually exclusive on the same site. For instance, predominance of conifer species excluded predominance of deciduous species, and the

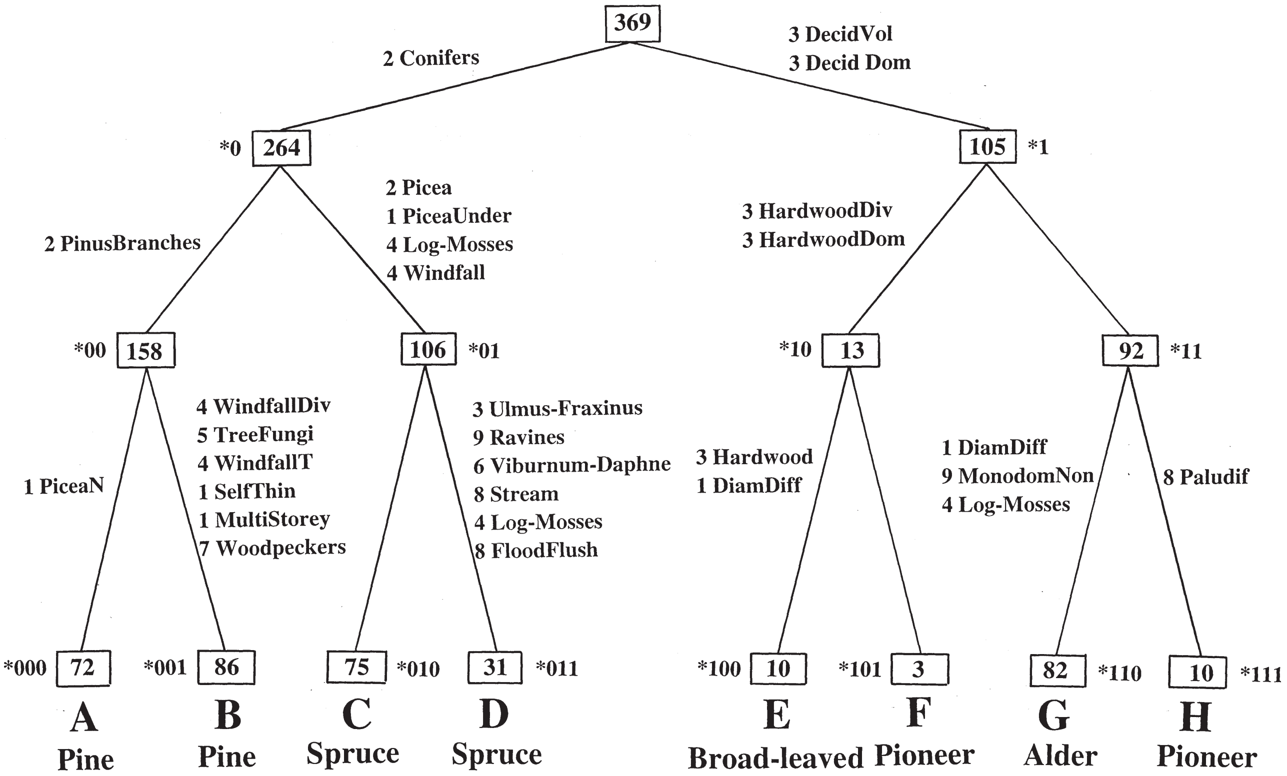

Figure 2 Divisive clustering of forest structures supporting biodiversity in wetland forests for the first levels of TWINSPAN-classification (see Appendix for abbreviations).

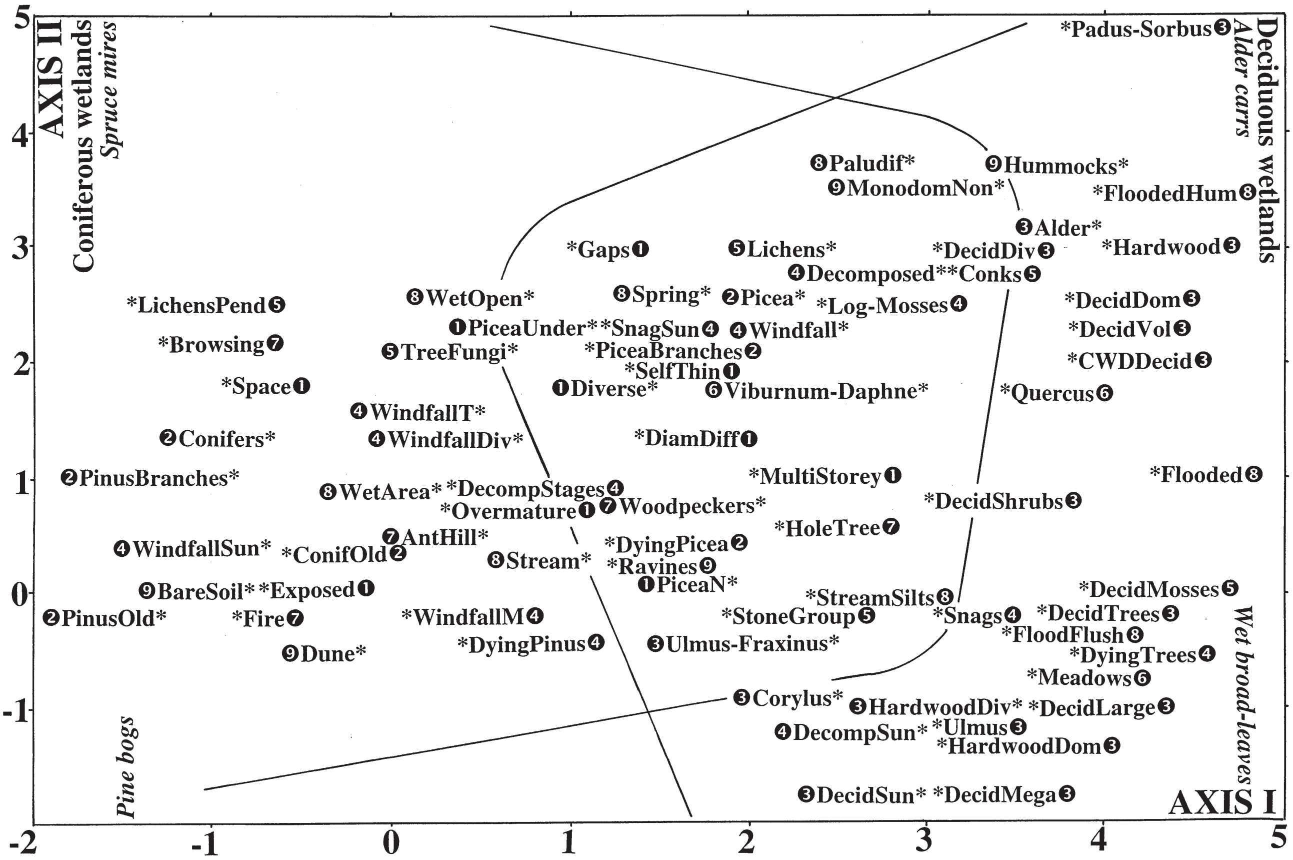

Figure 3 Ordination of forest structures supporting biodiversity along axis I and II by detrended reciprocal averaging in Latvian wetland forests (see Appendix for abbreviations).

presence of dunes or steep slopes excluded intensive paludification. In the richest forests, 25–29 (maximum 34) structures were counted.

Ordination by DCA (Fig. 3) showed that there was quite a broad set of structures common to all forested wetlands. Various forms of CWD and important indices of stand character were well represented in both coniferous and deciduous wetlands, including obvious differences in the stem diameters of the main species, multi-storey tree stands, and a variety of forms of uprooted trees. Nevertheless, the total volume of available CWD was low, especially that of trunks and branches >50 cm in diameter.

For better visual clarity and comparison with the dry forests, an additional TWINSPAN arrangement by frequencies clearly demonstrated that the wetland types were richer than the dry ones (Table 3). Comparison of various broad-leaved forests as well as spruce and pine stands shows that this pattern was clear in all groups. Most structures were more frequent in a wetland community compared with a dry forest of the same species. The data also illustrate some under-represented structures in pine forests, for instance, there was a very low frequency of old, overmature and large-diameter trees (including CWD). This was a direct result of the traditional forest management and clear-cutting practices.

Based on Table 3, ordination by DCA illustrates the spatial association of biodiversity structures in 477 (369 wet and 108 dry) forest sites altogether (Fig. 4). Indices that characterize water and other typical wetland features were grouped in the central lower part and left upper corner of the diagram. Figure 4 shows in detail which structures were likely to occur together (central part) and which are exclusive to particular forest groups. For example, 'DecidSun' indicates sun-exposed broad-leaved trees with DBH >50 cm and belongs to the specific features of broad-leaved forests. The probability of finding it together with, for example, 'PiceaUnder', i.e. in a forest where there is *Picea abies* undergrowth, was very low. In contrast, the feature 'Diverse' was common to all forests, both dry and wet, and coniferous and deciduous; it could be recognized together with any other structure.

Discussion

Concept of biodiversity structures

The use of biodiversity structures was adapted from Drakenberg and Lindhe (1994), who originally developed the concept to evaluate forests in Sweden. The method was developed to serve forest inventory and forestry practice. Combined with an inventory of species, the method provides

Table 3 TWINSPAN-arrangement of forest structures supporting biodiversity in different forests, where I–V are frequency classes. A: wet secondary (pioneer) stands, B: wet broad-leaved forests, C: alder carrs, D: dry broad-leaved forests, E: pine bogs, F: spruce mires, G: dry pine forests, H: dry spruce forests; diagnostic frequencies are shown in bold; the total number of plots in parentheses. Structures (denoted 1–9) belong to the following groups: stand character (1), conifer component (2), deciduous component (3), dead and dying trees (4), non-vascular plants and their substrates (5), shrub component (6), disturbances and animal component (7), water (8), relief and ground cover (9). See Appendix for abbreviations.

Forest habitats/ Biodiversity structures	*A (14)*	*B (12)*	*C (79)*	*D (16)*	*E (157)*	*F (107)*	*G (71)*	*H (21)*
Diagnostic structures of deciduous forests								
3 DecidVol	**V**	**V**	**V**	**V**	–	–	–	–
3 DecidDom	**IV**	**V**	**V**	**V**	–	–	–	–
3 DecidDiv	**IV**	**V**	**V**	**V**	I	–	I	–
3 Hardwood	**II**	**V**	**IV**	**V**	–	–	–	–
4 CWDDecid	**IV**	**IV**	**IV**	**III**	–	–	–	–
6 Viburnum-Daphne	**IV**	**IV**	**III**	**V**	–	III	–	I
5 DecidMosses	–	**V**	**III**	**III**	–	–	–	–
3 DecidTrees	I	**V**	II	**V**	–	–	–	–
3 HardwoodDiv	II	**V**	–	**IV**	–	–	–	–
3 HardwoodDom	–	**V**	–	**V**	–	–	–	–
3 Ulmus-Fraxinus	–	**V**	–	**V**	–	II	–	II
3 Ulmus	–	**III**	–	**IV**	–	–	–	–
3 DecidLarge	–	**IV**	I	–	–	–	–	–
3 Corylus	–	**III**	–	II	–	I	–	–
4 DecompSun	–	**III**	–	I	–	–	–	–
4 DyingTrees	–	**III**	I	–	–	–	–	–
8 FloodFlush	–	**III**	**III**	II	I	I	I	–
3 Alnus	I	–	**IV**	–	–	I	–	–
9 Hummocks	–	–	**III**	–	–	–	–	–
8 Flooded	–	–	**II**	–	–	–	–	–
8 FloodedHum	–	–	**II**	–	–	–	–	–
Diagnostic structures of coniferous forests								
2 Conifers	–	–	–	–	**V**	**V**	**III**	**V**
4 DecompStages	–	II	–	–	**III**	**IV**	II	II
2 PinusBranches	–	–	–	–	**V**	–	II	–
1 Space	–	I	–	–	**IV**	–	I	–
1 PiceaUnder	–	–	–	–	–	**V**	–	**IV**
4 Windfall	–	–	II	–	–	**IV**	–	**III**
2 Picea	–	–	III	–	–	**V**	–	**IV**
4 WindfallT	–	–	–	–	II	**IV**	I	II
Diagnostic structures of all forests								
1 Diverse	V	V	V	V	V	V	V	V
1 SelfThin	IV	IV	IV	III	V	V	II	III
1 DiamDiff	–	V	V	V	V	V	V	V
4 SnagSun	IV	IV	IV	II	V	IV	II	III
1 MultiStorey	–	V	III	V	III	IV	II	IV
7 Woodpeckers	–	V	IV	IV	IV	IV	II	III
4 WindfallDiv	IV	III	–	III	IV	V	II	V
1 PiceaN	–	IV	III	V	IV	–	III	–
1 Gaps	IV	–	II	I	III	III	I	I
5 TreeFungi	IV	III	–	–	II	IV	I	I
4 Log-Mosses	–	–	IV	–	–	IV	–	IV
8 WetArea	–	IV	–	–	V	V	–	–
8 Paludif	V	II	II	–	V	II	–	–
4 Decomposed	III	–	IV	–	II	–	I	–
5 Conks	IV	–	III	–	–	II	–	I
7 HoleTree	–	III	II	III	II	II	I	II
8 WetOpen	IV	–	II	II	II	I	I	–
9 MonodomNon	–	I	IV	II	I	I	I	–
5 Lichens	–	–	II	–	–	III	–	II

Forest habitats/ Biodiversity structures	*A (14)*	*B (12)*	*C (79)*	*D (16)*	*E (157)*	*F (107)*	*G (71)*	*H (21)*
Other structures								
1 Overmature	–	II	–	I	II	II	I	II
4 Snags	–	II	II	II	I	I	I	II
5 StoneGroup	II	II	–	II	I	I	I	–
8 Stream	II	II	–	–	I	I	I	I
1 Exposed	–	II	–	–	II	–	I	–
4 WindfallSun	–	I	–	II	II	–	I	–
9 Ravines	II	–	–	–	I	I	I	I
3 DecidShrubs	–	–	II	–	I	–	I	–
8 StreamSilts	II	I	–	–	–	I	–	–
4 WindfallM	–	I	–	I	I	I	I	I
7 Nest	–	–	–	I	–	–	I	–
6 Meadows	I	II	–	–	–	–	–	–
3 DecidMega	–	II	–	–	–	–	–	–
3 DecidSun	–	II	–	–	–	–	–	–
3 Padus-Sorbus	–	–	I	–	–	–	–	–
6 Quercus	–	–	I	–	–	–	–	–
2 PiceaBranches	–	–	–	–	–	II	–	I
2 ConifOld	–	–	–	–	I	I	–	–
4 DyingPinus	–	–	–	–	I	–	I	–
7 Fire	–	–	–	–	I	–	I	–
7 Browsing	–	–	–	–	I	–	I	–
9 BareSoil	–	–	–	–	I	–	I	–
9 Dune	–	–	–	–	I	–	I	–
4 DyingPicea	–	–	–	–	–	I	–	I
2 PinusOld	–	–	–	–	I	–	–	–
5 LichensPend	–	–	–	–	I	–	–	–
7 AntHill	–	–	–	–	–	I	–	–
8 Spring	–	–	–	–	–	I	–	–

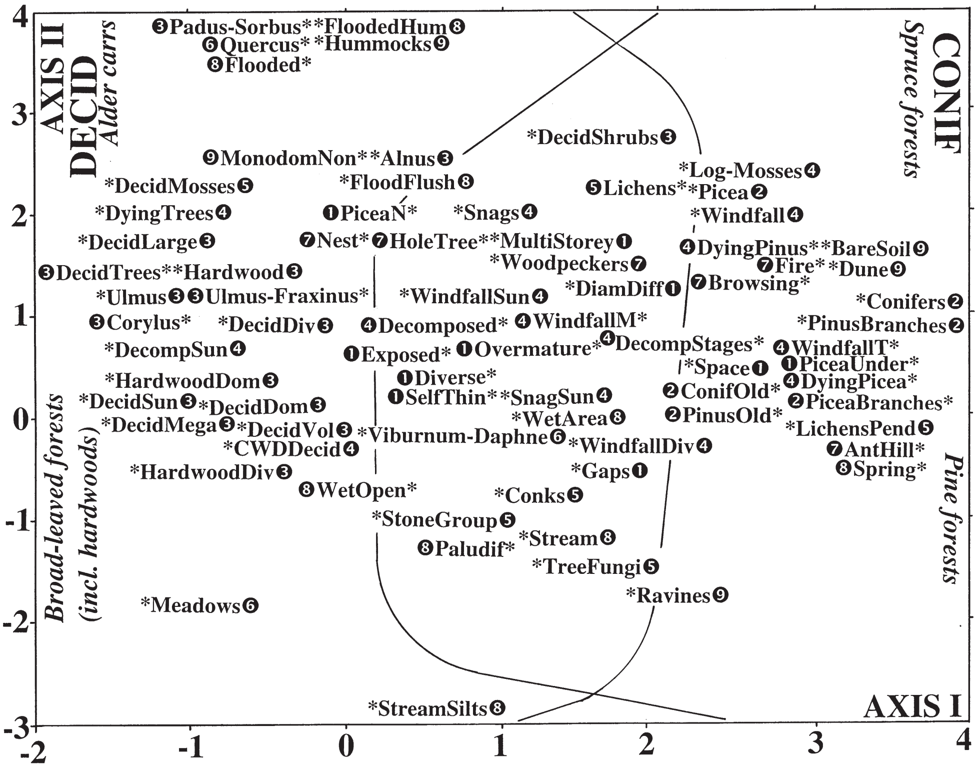

Figure 4 Ordination of forest structures supporting biodiversity along axis I and II by detrended reciprocal averaging in Latvian forests (based on frequencies as given in Table 3; DECID – deciduous forests, CONIF – coniferous forests; see Appendix for abbreviations).

an opportunity to plan forestry activities by taking account of, for example, overmature trees with holes or declining hardwood species, or of specific microhabitats. The method does not consider their relative importance. The structures are taken in a very wide sense and are scored equally, whether ant-hill or forest stream. Although there is direct correlation between the number of structures, their distribution and species (Mannan *et al.* 1980; Andersson 1987; Andersson & Hytteborn 1991; Suško 1998), a forest with 20 structures is not necessarily considered more valuable than one with, for example, 17 structures.

A problem between habitat specialists and seemingly similar, correlated structures obviously is complex; it exists and may prevent the development of a concept of scored relative importance. A particularly rare species usually demands a very specific structure which may have quite a low carrying capacity for other species, as is the case, for example, with bare soil after a windthrow or specific host-plants of insects (Denis & Batson 1974; Ehnström & Waldén 1986; Gustafsson & Hallingbäck 1988; Nilsson & Baranowski 1997; Suško 1998).

Also, the deciduous (especially hardwood) tree component is somewhat overspecified in Drakenberg and Lindhe's (1994) approach. Conifers have expanded at the expense of hardwoods in the boreo-nemoral zone of the Fennoscandian- Baltic region through commercial forestry. Hence, in many parts of the region depicted the composition of trees represents a somewhat more nordic standard than would be expected naturally on the basis of climate, soils, and potential natural vegetation (e.g. Sarma 1959; Strods 1999). Consequently, hardwoods and some other deciduous trees (aspen) are recorded in more detail and are given greater emphasis than spruce in areas where formerly these species were widespread.

Management and its consequences for the biota and structures of wetland forests

Managed wetland forests involve clear-cutting, drainage, artificial fertilization, and establishment of silviculture. Fertilization is not a common practice in Latvia. These practices should be analysed from the standpoint of how the operations have affected the specific site ecology and long-term adaptations of species (i.e. habitats and biodiversity structures).

It is widely assumed that natural disturbances are only small-scale in wetland forests (Kangas 1990; Angelstam 1996*a*). Hence, under normal conditions, large areas have never been opened in a wetland forest to the extent which they have through frequent occurrence of fire in dry forests (Engelmark 1987). Lightning may initiate crown fires in extremely dry years (Kangas 1990), but this is rare over normal timescales, especially in alder carrs. Consequently, the species are adapted to permanent moisture, shade, stable microclimate and short periods of flooding.

Replication of such conditions cannot be achieved by large-scale clear-cutting, which is the most traditional forestry activity. Excessive exposure to light, the drier and warmer microclimate of the site, and changes in the evapotranspiration cycle are the consequences of clear-cutting. This pressure is not felt only by the plant community but also by wood-decaying invertebrates and other decomposers (Ehnström & Waldén 1986; Samuelsson *et al.* 1994).

Minor paludification (i.e. development of bog and mire) takes place after clear-cutting in the *Alnion* wetland, and is a direct response to the changed habitat because of the lower transpiration ability of herbs compared with the tree canopy. Thus, under unfavourable community development (regression), the former forest area can easily move towards a non-woody community from *Phragmition* or *Magnocaricion*, or to the early succession stages of the carr forest where willows (mostly *Salix cinerea, Salix aurita*) predominate (cf. Neuhäusl 1992; Wiegers 1992).

In addition, investigations in Latvia (Suško 1998; Prieditis unpublished data) show that no essential woody structures that originate slowly (i.e. habitats for selective animals and plants) are left during clear-cutting. These include, for example, single overmature trees, trees with holes, snags, and high-diameter logs. Some studies (Prieditis 1999) that overlap in part with the areas where biodiversity structures were recorded, showed that the amount of CWD is variable (minimal dimensions for a record: diameter 10 cm, length 1 m). In semi-natural alder carrs, which are at least 90–100 years old, the CWD reaches 4–20 m^3/ha, in wet to moist broad-leaved (*Alno-Ulmion*) forests it is 12–33 m^3/ha, in pine bogs and mires it is 3–11 m^3/ha, and in spruce mires the CWD is 7–17 m^3/ha. The ratio between snags and logs was about 1:3 (in 60%). In wet spruce forests (*Sphagno girgensohnii-Piceetum*) at Mezole (NE Latvia), Zvagina (1998) has measured CWD volumes of 25 m^3/ha on average, however the fluctuation was considerable, from almost zero in some plots to 136 m^3/ha in intact 130–150 year-old stands.

Our observations show that some wetland species (e.g. *Glyceria lithuanica,* some orchids and sedges) tend to shelter in the ravines of small rivulets or streams passing the forest or in damp depressions inaccessible to heavy forestry machinery. This coincides with the conclusion drawn in Scandinavia that species confined to wetland forests are especially sensitive to traditional forestry and habitat loss (Delin 1992; Berg *et al.* 1994*a*). The presence of old trees, logs and snags is a critical factor for the survival of *c.* 60% of red-listed species in Swedish forests (Berg *et al.* 1994*b*). In contrast to many successful and widespread organisms in urban areas, many forest species are unable to adapt to the changed habitat by finding a new niche.

The common objection made by the silviculture-orientated foresters that dead wood might be a potential and permanent source of the outbreaks of 'harmful' insects (and, thus, the volume loss) is not supported by the recent investigations because strict succession takes place in the invertebrate communities and the primary invaders of the log ('harmful' insects) use dead trees during a relatively short period, not exceeding two years (Samuelsson *et al.* 1994).

Although re-establishment of vegetation structure, similar to that in a mature stand, may span 15–30 years after logging (Zobel *et al.* 1993), the period to reach the formation of a closed tree canopy may be too long for continuity-demanding species, especially if it is accompanied by the absence of structures (e.g. big snags or logs) to shelter in. Only in very specific forested wetlands, such as sparse and species-poor pine forests in sphagnum bogs (*Vaccinio uliginosi-Pinetum*) the differences in the field layer composition between mature forest and the seral stages of succession after a clear-cutting in winter have been found to be small (Zobel 1993).

The forest drainage influences all principal characteristics of a wetland site, including the hydrological cycle, nutrition, and soil properties (both chemical and physical), as well as initiating changes in the species assemblages. Certainly, from the forestry perspective, such an alteration can improve the productive capacity of the site and increase the biomass, but it simultaneously induces a response at the level of biological structures. The drainage for silviculture shifts the forest from wetland to terrestrial conditions.

Numerous studies (e.g. Rozenzweig & Abramsky 1993; Gough *et al.* 1994) report that there is an unambiguous correlation between biomass of plant communities and diversity; first diversity increases, then it rapidly decreases. Although there is still a variety of opinions about the driving mechanism of the process (Rozenzweig & Abramsky 1993), doubt no longer exists that diversity and productivity interact biologically. Hence, there is a low probability that diversity of a wetland forest will remain high after the timber production will be increased by drainage. Long-term observations in various parts of the country show that the vascular plants *Carex remota, C. disperma, C. paupercula, Corallorhiza trifida, Dactylorhiza fuchsii, Hottonia palustris, Listera cordata*, and *Poa remota* rapidly disappear or decline as a consequence of drainage. In contrast, herbs *Aegopodium podagraria, Convallaria majalis, Deschampsia caespitosa, Frangula alnus, Lycopodium annotinum, Oxalis acetosella, Rubus idaeus, Stellaria nemorum, Urtica dioica*, and *Vaccinium myrtillus* appear or spread as a consequence of drainage (Prieditis unpublished data).

Forestry operations in Latvia usually cause changes in the dominant species (*Picea abies* pulpwood plantations instead of *Alnus glutinosa* or *Fraxinus excelsior* stands) after drainage and clear-cutting of the former carr. Even if not changed by silviculture, the drained areas encourage an increase in conifers.

There is evidence, which deserves more attention, that the spruce forests established in areas formerly under deciduous wetlands use are unable both to keep the specific characteristic vegetation of *Alnetea glutinosae*, and to establish the typical vegetation of *Vaccinio-Piceion* (Prieditis unpublished data). Similar observations emerge from the distribution of some non-vascular plants and forest invertebrates (Suško 1998). Thus, this feature might be the tool to distinguish areas with a long continuity of spruce forests from those recently-established.

There is almost no territory left in Europe where natural dynamics still shape the forests. Many authors (Hunter 1990; Haila & Kouki 1994; Kuuluvainen 1994; Angelstam 1996*a*) find that the simulation of natural disturbances could be the best route in practical forestry to taking care of the forest biota and structures. The concept of site-adapted forestry is particularly appreciated in Fennoscandia (The National Board of Forestry 1993; Anon. 1994; Rundlöf & Nilsson 1995).

To evaluate the forests, many concepts have been developed as a direct response to needs in conservation and management (Usher 1986; Dudley *et al.* 1993; Primack 1993; Noss 1995). Valuation is a complex issue and often includes various intrinsic qualities, ecological services (e.g. control of floods and erosion), and the commercial benefits (Groombridge & Jenkins 1996).

Practical forestry and conservation usually demand easily identifiable characteristics, which can be monitored and observed in the forest. The most widely applied concept of indicator species comprises a selection of species which are comparatively easy to observe, which show early warning of change ahead, are able to distinguish human-conditioned changes from the natural ones and are so-called key-species by providing indirect information about possible status of other species depending on a certain (the same) property of the biotope (Noss 1995; Angelstam 1996*b*).

Some forest mosses, liverworts, lichens, fungi, and beetles have been listed amongst the most suitable indicators of ancient forests in the Fennoscandian-Baltic region (Karström 1992; Rundlöf & Nilsson 1995). The best indicators usually are the species which have low dispersal ability and cannot leave the altered site. However, some authors (e.g. Groombridge & Jenkins 1996; Ohlson *et al.* 1997) point out that the concept still needs to be justified by correlative studies between species and the habitats.

Records that were made of fungi, bryophytes, beetles and molluscs and their association with the forest structures and management (Rose 1976; Nilsson & Baranowski 1994; Suško 1998; Thor 1998) have shown that the concept of indicators is a valuable tool in practical forestry and forest inventory for the identification of critical sites that should be left without management or the selection of appropriate sustainable methods. There was good agreement between richness in forest structures and the number of habitat specialists. In Latvia, the most sensitive species appeared amongst non-vascular plants and invertebrates depending on coarse woody debris and large overmature trees (Suško 1998).

To conclude, Latvia is a particularly important country for the conservation of European wooded wetlands, but nevertheless has suffered losses and is threatened with further declines in biodiversity. The present analysis of biodiversity structures has used habitat characteristics as ‘pseudo-species’, which is a relatively new approach developed during the 1990s. Applying the method to large forest areas (>600 ha) has shown that it is a valuable tool for obtaining very detailed descriptions of habitats essential for sustainable forestry and a spatial characterization of forest environment. It is compatible with GIS-based information systems in Latvia (Mezole area, WWF Latvia personal communication 1998). Finally, the diversity hot-spots rich in structures and dependent species can be used as core areas for conservation purposes and for rehabilitation activities in adjacent disturbed forests.

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Appendix[1]

Abbreviations of structures supporting biodiversity used in DCA-ordination and TWINSPAN-classification (listed alphabetically within nine groups of structures)

1. Stand character

DiamDiff, obvious difference of stem diameters of the main species; Diverse, several trees with different stem diameters and ages; Exposed, solitarily growing trees in a sun-exposed place; Gaps, small gaps in the forest; MultiStorey, multistorey tree stand; Overmature, many overmature trees; PiceaN, *Picea abies* less than 10% of the timber volume; PiceaUnder, presence of *Picea abies* undergrowth; SelfThin, self-thinning of the forest stand; Space, open space > 0.01 ha.

2. Conifer component

ConifOld, mainly conifers with DBH > 40 cm; Conifers, conifers with DBH >15 cm dominating; Picea, many natural *Picea abies* with DBH >15 cm; PiceaBranches, *Picea abies* with big, scarce branches at the bottom; PinusBranches, several *Pinus sylvestris* with thick branches; PinusOld, *Pinus sylvestris* with DBH > 40 cm dominating.

3. Deciduous component

Alnus, *Alnus glutinosa* with DBH >15 cm dominating; Corylus, prominent *Corylus avellana* understorey; DecidDiv, several species of deciduous trees with DBH >15 cm; DecidDom, deciduous trees with DBH >15 cm dominating; DecidLarge, several broad-leaved trees with DBH >50 cm; DecidMega, several broad-leaved trees with DBH >80 cm; DecidShrubs, many shrub-like deciduous trees; DecidSun, sun-exposed broad-leaved trees with DBH >50 cm; DecidTrees, deciduous trees with DBH >30 cm dominating; DecidVol, deciduous trees >50% of the timber volume; Hardwood, presence of noble hardwoods, e.g. *Quercus robur, Fraxinus excelsior, Ulmus glabra*; HardwoodDiv, several noble hardwoods with DBH >15 cm; HardwoodDom, noble hardwoods >50% of the timber volume; Padus-Sorbus, several *Padus avium* and *Sorbus aucuparia* with DBH >15 cm; Ulmus, rich *Ulmus glabra, Ulmus laevis, Acer platanoides* and *Tilia cordata* undergrowth; Ulmus-Fraxinus, presence of *Ulmus glabra, Acer platanoides, Tilia cordata* and *Fraxinus excelsior* with DBH >15 cm.

4. Dead and dying trees

CWDDecid, much deciduous coarse woody debris; Decomposed, mainly decomposed soft logs; DecompSun, rotten broad-leaved tree or trees in a sun-exposed place; DecompStages, windfallen trees in various stages of decomposition; DyingPicea, many dying *Picea abies* or recently dead spruce snags; DyingPinus, many dying *Pinus sylvestris* or recently dead pine snags; DyingTrees, many dying or recently dead other species of trees (excl. *Pinus sylvestris, Picea abies*); Log-Mosses, several logs covered with mosses; Snags, many snags and high stumps; SnagSun, several snags in a sun-exposed place; Windfall, several uprooted trees of the main species; WindfallDiv, uprooted trees of the main species in various stages of decomposition; WindfallM, many uprooted trees of the main species with DBH >30 cm; WindfallSun, several uprooted trees with DBH >30 cm in a sun-exposed place; WindfallT, many uprooted trees of the main species.

5. Non-vascular plants and their substrates

Conks, many conks on stems, snags or logs; DecidMosses, mainly alive deciduous trees covered with mosses (incl. liverworts); Lichens, many non-pendulous lichens; LichensPend, many pendulous lichens; StoneGroup, big stone or group of stones; TreeFungi, rich flora of wood-inhabiting fungi.

6. Shrub component

Meadows, ecotone towards a meadow or a sparse shrubland > 0.1 ha; Quercus, several young oaks with diameter >5 cm at the bottom; Viburnum-Daphne, *Daphne mezereum, Euonymus europaea, E. verrucosa, Lonicera xylosteum, Ribes* spp. and *Viburnum opulus* in the shrub layer.

7 Disturbances and animal component

AntHill, ant-hill; Browsing, several alive trees with damages by herbivores; Fire, fire signs on trees and stumps; HoleTree, tree with holes, suitable habitats for mammals and cavity-nesting birds; Nest, nest of *Ciconia nigra* (black stork) or birds-of-prey; Woodpeckers, woodpecker signs on trees.

8. Water

Flooded, temporarily flooded forest area > 0.1 ha; FloodedHum, seasonally or temporarily flooded spaces between hummocks; FloodFlush, intermittently water-exposed area, e.g. during spring floods or after heavy rains; Paludif, paludification, place of intensive accumulation of moss or tree-herbaceous peat; Spring, spring; Stream, stream, brook or rivulet; StreamSilts, stream with deposited silts or windfall debris; WetArea, moist or wet forested depression > 0.1 ha; WetOpen, edge to an open wetland > 0.1 ha, e.g. pond, and so on.

9. Relief and ground cover

BareSoil, bare soil in the forest; Dune, dunes or dune-like formations; Hummocks, hummocky nano-relief; MonodomNon, vegetation of ground layer without any dominant species; Ravines, ravines and steep slopes.

[1]Note to the Appendix

All the structures are recorded per hectare (except moving water, edge formations and dunes or ravines). The specified abundances to be used for each structure mean the following: without any specification which means ‘present’, the structure is present by at least once in the forest; ‘several’, the structure is present at least twice; ‘many’, the structure is present many times here and there; ‘dominating’, ‘mostly’ or ‘rich’, the structure is a diagnostic feature of the forest.