Landscape Ecology **17:** 699–710, 2002.

Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes

Weidong Gu[1,3], Raimo Heikkilä[2] and Ilkka Hanski[1,*]
*[1]Department of Ecology and Systematics, Metapopulation Research Group, University of Helsinki, PO Box 65, Viikinkaari 1, FIN-00014 Helsinki, Finland; [2]Kainuu Regional Environment Centre, Research Centre of Friendship Park, Tönölä, FIN-88900, Kuhmo, Finland; [3]Current address: Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, USA; *Author for correspondence (e-mail: ilkka.hanski@helsinki.fi)*

Received 27 September 2000; accepted in revised form 7 May 2002

Key words: Boreal forest, Connectivity, Habitat loss, Metapopulation dynamics, Regional stochasticity

Abstract

Analyzing the population dynamic consequences of spatio-temporal changes in landscape structure is a formidable challenge for spatial ecology. One key population dynamic process in fragmented landscapes is the influence of isolation on colonization rate and thereby on the occurrence of species in habitat fragments, but it is not obvious how isolation should be measured in landscapes that are affected by on-going habitat loss and fragmentation. We suggest the following procedure for the measurement of spatio-temporal isolation. First, a historical record of habitat loss and fragmentation in the landscape is prepared based on snapshots of the extent of the suitable habitat for the focal species. Second, a metapopulation model is used to simulate the occurrence of the species in this landscape, assuming the empirically observed landscape change. The model-predicted pattern of habitat occupancy at a particular point in time (usually the present time) is then compared with empirical observations on the occurrence of the species. We describe a metapopulation model that has been constructed for this purpose, and we apply it to a changing landscape of boreal forests in eastern Finland. We give an example on the occurrence of four threatened polyporous fungi in 18 small fragments of old-growth forest. In none of the species does the current isolation of the fragments nor the time since their isolation explain the occurrence of the species in the study fragments, but in three species the model-predicted occupancy probability had a significant effect on the observed abundance of the species. The model-predicted occupancy probabilities were also calculated by ignoring past landscape changes, that is, by assuming that the landscape had remained in the present configuration for a long time. These probabilities had a significant effect on the abundance of only one of the four species, suggesting that the occurrence of the species tracks landscapes changes with a noticable time lag.

Introduction

Habitat loss and fragmentation are the primary causes of population, metapopulation and species extinction worldwide (Heywood 1995). Unfortunately, obtaining reliable empirical information about the population dynamic consequences of habitat fragmentation across large spatial scales is difficult. Long-term and large-scale experiments would provide the most conclusive results, but such experiments are expensive and it takes a long time before the results would be available. What experimental results there are typically involve isolated and relatively small habitat fragments (Lovejoy et al. 1984; Robinson et al. 1992; Margules 1996; Debinski and Holt 2000), whereas the most significant questions about habitat fragmentation concern the capacity of entire fragmented landscapes to support viable metapopulations (Hanski and Ovaskainen 2000). ‘Natural experiments’ (non-experimental observations of the occurrence of species) on the effects of habitat fragmentation (e.g., Harris (1984); Heckert (1994) and Settele et al. (1996)) are difficult to interpret for many reasons, including the fact that populations and metapopulations respond with a shorter or longer time lag to changes in the structure of the landscape (Tilman et al. 1994; Hanski (1998, 1999a); Ovaskainen and Hanski 2002). Put in another way, since landscapes are dynamic it is not sufficient to consider just the current area, quality and spatial connectivity of the habitat for the purpose of assessing (meta)population viability. One also has to consider how temporal changes in habitat structure affect population and metapopulation persistence (Hanski 1999b).

A common approach in the ecological study of fragmentation is to survey a range of habitat fragments varying in size and isolation for the presence of focal species. In a static landscape, one may assume that the occurrence of species in the habitat fragments represents a dynamic equilibrium between on-going extinctions and colonizations, and useful inferences can be made about the effects of fragment size and isolation on the observed occurrence of the species in the fragments (Hanski 1994, 1999a). In the case of dynamic landscapes the pattern of occurrence of the species in the habitat fragments is influenced by history as well as by the present landscape structure, and it is not obvious how the results should be analyzed. One approach is to use the species-area relationship to predict the long-term consequences of habitat loss and fragmentation on species persistence (May et al. 1995). With additional data and assumptions, one may roughly estimate the time course of extinctions (MacArthur and Wilson 1967; Brooks et al. 1999). This may be the only feasible approach in the case of very large areas and isolated fragments of suitable habitat, but in the case of metapopulations living within smaller areas of fragmented landscape a more refined approach would be desirable.

In this paper we describe an approach for the study of species persistence in landscapes affected by ongoing habitat loss and fragmentation. Our study was stimulated by a research project on the biodiversity in old-growth boreal forests in eastern Finland, where the area of old-growth has declined rapidly over the past decades and the remaining forests have become increasingly fragmented. We have used results of this project as our focal examples. The first step is to obtain a historical record of the spatial pattern of habitat loss in the study area. The data consist of a series of "snapshots" documenting changes in the extent of suitable habitat for the focal species over time. In our boreal forest example, the observed history goes back 50 years and covers the entire period of industrial forestry in the study area. Secondly, we construct a metapopulation model that can be used to simulate the occurrence of species in changing landscapes. Stochastic model simulations are repeated many times to yield a probability of occupancy in different spatial locations in the landscape, including the habitat fragments that are included in the empirical study. These predictions can then be compared with observed patterns of habitat occupancy in single or multiple species. Sensitivity analyses can be used to examine the sensitivity of model predictions to parameter values. It turns out that while the absolute probabilities of occurrence cannot be reliably predicted, because there is typically insufficient information to parameterize the model, the ranking order of different habitat fragments in terms of the probability of occupancy is insensitive to parameter values. Therefore, the model-predicted occupancy gives a useful measure of spatio-temporal isolation of habitat fragments for further analyses of population dynamics. In the context of an example on four species of polyporous fungi, we also compare the model-predicted probabilities of occupancy derived for the changing landscape with comparable probabilities calculated for the current landscape, thus ignoring the history of habitat fragmentation and its influence on the occurrence of the species. Any difference between the predictions of the two model versions would indicate that the occurrence of the species is tracking changing landscape structure with a time lag as assumed in general metapopulation models (Tilman et al. 1994; Hanski 1998, 1999a; Ovaskainen and Hanski 2002).

Description of the changing landscape

As an example, we consider a forested region in Kuhmo, east central Finland, where commercial harvesting of coniferous trees began in the 1950s. The most threatened habitat is spruce-dominated old-growth forest, which is the habitat for hundreds of specialized taxa (Esseen et al. 1992; Berg et al. 1994), many of which are dependent on decaying wood (Bader et al. 1995; Ohlson et al. 1997) and particular microhabitats, such as bracket fungi (Komonen et al. 2000). In this paper, we will consider only two categories of habitat, old-growth spruce forest versus other habitats. Given sufficient empirical information, the present approach could be extended to situations with spatially varying habitat quality.

Using the information on forest stand structure available in the records of the Finnish Forest and Park Service, we prepared 11 historical maps of forest cover for the period from 1945 to 1995 (Figure 1). Each map represents the extent of old-growth spruce forest in the study area at 5 year intervals. The forest maps were digitized and stored as ArcView® shape files. For our modelling purposes, the ArcView® shape files were discretized into grid-cell format using ArcView® Spatial Analyst®, which provides an option to convert a shape file into a grid-based data set. The grid cells generated were ca 1.6 ha in size. In the final map (1995), we delimited 9 forest fragments consisting of 3–4 contiguous grid cells with dissimilar spatial isolation and isolation history (these fragments were not necessarily isolated from the remaining suitable habitat, just sets of 3–4 contiguous cells with a total area corresponding to the area of forest fragments used in the application of the model to four species of bracket fungi in the Section *An example of threatened species*). The purpose of the modelling is to predict the probability of occupancy of the focal species in these forest fragments in the course of time.

Landscape measures

To characterize the changes that have occurred in the landscape in 1945–1995, we calculated some commonly used measures of landscape structure (Doak and Mills 1994; Gustafson and Gardner 1996). Numerous such measures have been described in the literature and applied to computer-generated and real landscapes (Franklin and Forman 1987; Turner et al. 1989; Riitters et al. 1995; Schumaker 1996). We restricted our landscape description to the basic measures of the amount of habitat, the amount of core habitat, the number of discrete habitat patches, and the perimeter-to-area ratio.

To calculate the above measures we first divided the focal habitat (old-growth spruce forest) in the study landscape into discrete habitat patches. A ‘patch’ was defined as a set of contiguous grid cells of the focal habitat (= suitable cells), separated from other patches by at least one grid cell of unsuitable habitat (= unsuitable cells, representing some other habitat than old-growth spruce forest). The area of a patch is simply the number of suitable cells in the patch. A ‘core’ grid cell is defined as a suitable cell separated by at least one suitable cell from the edge of the patch in all directions, including the diagonals (thus each cell has eight neighbors). The perimeter of a patch is measured as the number of suitable cells touching unsuitable cells. The perimeter-to-area ratio was calculated by dividing perimeter by area.

The above measures characterize a landscape in terms of its geometry without explicitly considering population dynamics. For the latter purpose, Hanski and Ovaskainen (2000) have introduced the concept of metapopulation capacity, which measures the capacity of a fragmented landscape to support a viable metapopulation (Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2001). The metapopulation capacity is derived from a metapopulation model and a description of the landscape in terms of habitat patch areas and connectivities. Mathematically, the metapopulation capacity is defined as the leading eigenvalue of an appropriate matrix (Hanski and Ovaskainen 2000), but a good approximation is provided by the following measure (Ovaskainen and Hanski 2001), called the colonization potential of the landscape (Hanski 1999b), $R_l = \Sigma(A_i\Gamma_i)^2/\Sigma(A_i\Gamma_i)$, where A_i is the area of patch i, Γ_i is a measure of connectivity of patch i, and the sum is calculated across all patches. Habitat connectivity is defined as $\Gamma_i = \Sigma_{j \neq i} exp(-\alpha d_{ij})A_j$, where $1/\alpha$ defines the average dispersal distance of the focal species, and d_{ij} is the distance between patches i and j. We calculated R_l using the suitable cells rather than the discrete patches of habitat as the spatial units, hence A_i in the above formulas is constant (one cell, 1.6 ha). Using suitable cells as spatial units takes into account the shape of the habitat patches, which would be ignored if the patches themselves were used as spatial units.

Modelling of metapopulation dynamics

We modelled the occurrence of the focal species in the set of suitable cells using the Incidence Function Model (IFM; Hanski (1994, 1999a)). In the IFM, only the presence or absence of the species is considered, but note that if the model-predicted occurrence of the species is examined at the level of habitat patches (sets of contiguous grid cells), the model predicts a measure of abundance in the patch, namely the fraction of cells in the patch that are occupied. The IFM assumes temporally constant probabilities of extinction (E_i) and colonization (C_i) of occupied and empty grid cells, respectively, and that only one event (extinction or colonization) may occur per unit time. The

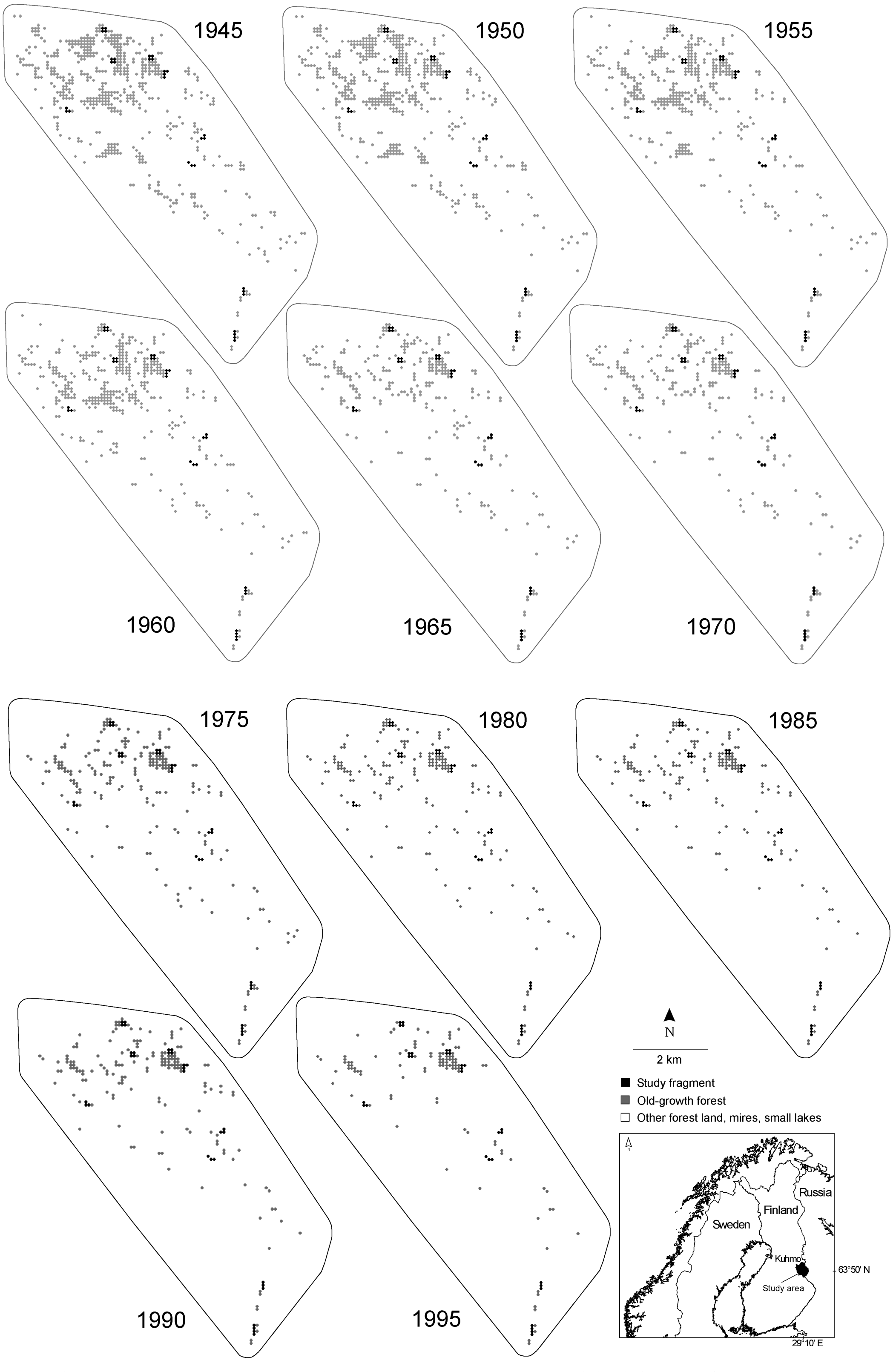

Figure 1. Maps of old-growth spruce forest in a study region in Kuhmo, east central Finland, from 1945 to 1995 at 5-yr intervals. The 9 habitat fragments of ca 5 ha in size are shown by dark color.

long-term probability (J_i) of grid cell i being occupied at quasi-equilibrium is given by

$$J_i = C_i \;/(C_i + E_i). \tag{1}$$

Assuming that the extinction probability is reduced by immigration (the rescue effect), Hanski (1994) modified Equation (1) to the form

$$J_i = C_i \;/(C_i + E_i - C_i E_i). \tag{2}$$

The interpretation of this formula is that the grid cells which are well connected (large C_i) to occupied grid cells have elevated population sizes (though this is not explicitly modelled) and have hence reduced probability of extinction ($E_i - C_i\ E_i$ instead of E_i; Hanski (1999a), pp. 87–88).

The key idea of the IFM is to relate the extinction and colonization probabilities to the structure of the fragmented landscape as described in terms of the size and spatial location of the grid cells (or other spatial units). The extinction probability is assumed to scale by the area A_i as

$$E_i = \min\{1, e/A_i^x\}, \tag{3}$$

where e and x are model parameters. In the present application, all suitable cells have the same size, whereas for all unsuitable cells $A_i = 0$. The colonization probability C_i is assumed to be a sigmoid function of connectivity (Hanski 1994),

$$C_i = S_i^2/(S_i^2 + y^2), \tag{4}$$

where S_i is a measure of the connectivity of grid cell i and y is a constant. Following Hanski (1994), we assume that S_i is given by a sum of contributions from all occupied grid cells,

$$S_i = \Sigma\exp(-\alpha d_{ij})o_j \quad A_j^b, \tag{5}$$

where $o_j = 0$ for empty and 1 for occupied grid cells, d_{ij} is the distance between grid cells i and j, and $1/\alpha$ gives the average dispersal distance. Parameter b scales the rate of emigration by area. Note that, in contrast to the measure of habitat connectivity Γ_i in the previous section, the measure S_i defines connectivity in terms of the distance to occupied grid cells only (because these are the potential sources of colonization of suitable but empty cells).

Given sufficient data, the IFM can be parameterized for real metapopulations living in real fragmented landscapes (Hanski 1999a; Moilanen 1999). In the present application, we do not have sufficient information to estimate model parameters for any particular species, but we use Equations 3 and 4 to simulate metapopulation dynamics in a given landscape using parameter values that are considered to be plausible for the species of interest (for the method of simulation see Hanski (1999a), pp. 238–239).

Modelling regional stochasticity

The IFM is usually applied to discrete patches of habitat. In this case the model assumption that the extinction events are independent in different patches is often an acceptable approximation (Hanski 1999a). However, in the present application the spatial units are small contiguous grid cells, and whatever the biological mechanisms of extinction, they are likely to operate in a correlated manner over short distances, such as separating the adjacent cells in this study. We therefore consider it essential to include the possibility of spatially correlated extinctions in the model. The effect of spatially correlated extinction on metapopulation persistence has previously been investigated in theoretical studies by Harrison and Quinn (1989) and Hanski et al. (1996) and Foley (1997) among others. Unfortunately, these spatially implicit treatments of globally correlated extinction are difficult to relate to real patterns of spatial correlation, which typically display scale dependence.

In this study, a spatially explicit correlation structure was constructed to represent plausible patterns of regional stochasticity (spatially correlated environmental stochasticity; Hanski (1991)) influencing extinction and colonization rates. In real populations, stochasticity influences population sizes which in turn influence extinction and colonization rates. In the IFM and other stochastic patch occupancy models, in which population size is assumed to be a function of patch area, the same effect of stochasticity on extinctions and colonizations can be achieved by assuming temporal variation in patch areas (here the area of grid cells). Therefore, we implement regional stochasticity by assuming spatially correlated changes in the effective areas of grid cells, which leads, by model assumptions (Equations 3 and 4), to spatially correlated extinction and colonization rates. An advantage of this approach is that it allows one to relate the pattern of regional stochasticity to patterns of spatial autocorrelation (correlogram or semivariogram) in relevant environmental variables, such as weather parameters, which often drive regional stochasticity.

We use the following algorithm for a hierarchical representation of regional stochasticity. Consider a square grid that covers the landscape to be modelled. The square is divided into four equal parts, each of which is further divided into four equal parts, and so forth. The divisions are continued until the resultant squares are the size of the grid cells themselves. An example of a five-level spatial hierarchical structure is illustrated in Figure 2a. The effective area $A_{ij}{}^{*}(t)$ of grid cell (i,j) (row i and column j on the lattice) at time t is given by

$$A_{ij}{}^{*}(t) = A \quad \exp(\Sigma c_k R_{ijk}), \tag{6}$$

where A is the actual size of grid cells (constant), k is the level in the spatial hierarchy of increasing squares (scale), and R_{ijk} is a normally distributed random variable with mean zero and variance σ^2. R_{ijk} has the same value in all grid cells (i,j) belonging to the same sub-division at the spatial scale k. c_k is a weight chosen to represent the strength of regional stochasticity at scale k. Note that the sum in Equation (6) has mean zero and variance σ^2. In model simulations, the effective area of each grid cell was recalculated at each time step, hence there is no temporal correlation in regional stochasticity. An important mechanism leading to such correlation structure is spatially correlated weather effects on demographic parameters, which typically have no significant temporal (year-to-year) correlation.

An example of the hierarchical representation of regional stochasticity generated by the above algorithm is given in Figure 2b, which shows the effective areas of the grid cells at one point in time. The weights used in this example are (from small to large spatial scales) {0, 0.6, 0.4, 0, 0}. Thus, in this example regional stochasticity was present at the second and third levels. As no weight is assumed for the level of individual grid cells, the four grid cell at the second level have the same effective area.

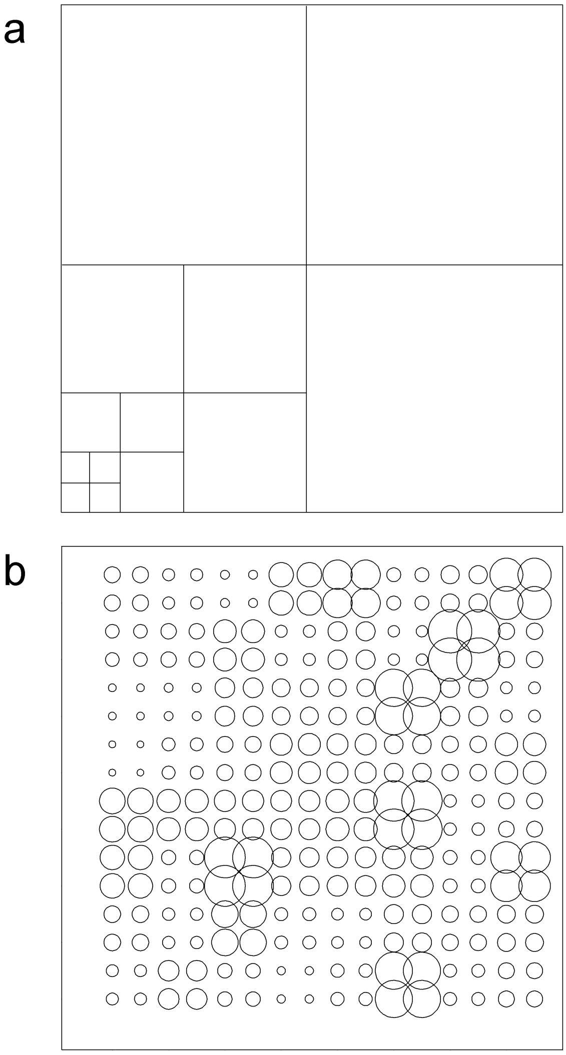

Figure 2. The scheme of implementing regional stochasticity into the metapopulation model. (a) A 5-level nested structure of squares. (b) An example of spatially correlated effective areas of grid cells at one point in time for the correlation scheme {0,0.6,0.4,0,0}. See text for further explanation.

Model application

In the present application of the model we used a hierarchy of eight spatial scales, ranging in size from 1 to 256 grid cells, which was sufficient to cover the entire study area. While simulating metapopulation dynamics using Equations 3 and 4, the spatially correlated effective grid cell areas were substituted for the actual aconstant grid cell area. For each time interval, the pattern of spatial correlation is reshuffled and no temporal correlation is assumed. Simulations were started with an initial condition of 70% occupancy of randomly selected suitable cells representing old-growth in the map for 1945 (Figure 1). Every 5 years, the landscape structure was updated by assuming the next map in the sequence. Populations occupying the suitable cells that turned into unsuitable cells were lost with their habitat. We assumed that the landscape structure would remain unchanged

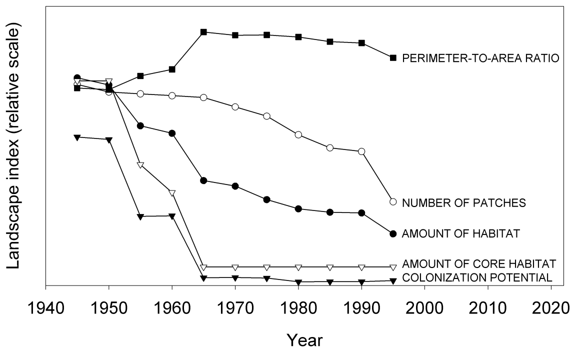

Figure 3. Changes in the values of landscape measures during the 50-yr history of habitat loss and fragmentation shown in Figure 1: the amount of suitable habitat, the amount of core habitat, the number of discrete habitat patches, the perimeter-to-area ratio, and the colonization potential of the landscape (R_l).

from the year 1995 onwards, and the dynamics of the species were simulated for an additional 50 years.

The parameter sets used in the simulations were selected to model species with short and long dispersal distances (α = 0.5 *versus* 0.1) and species with a greater and smaller risk of local extinction (e = 0.5 *versus* 0.1). Large-scale regional stochasticity {0,0,0,0,0,0,1,0} *versus* no regional stochasticity {1,0,0,0,0,0,0,0} were examined in the simulations. Other model parameters had the constant values of b = 0.5, x = 0.5, y = 5.0 and σ = 1.5, which correspond to values commonly estimated with the IFM (Moilanen et al. 1998; Hanski 1999a). Fifty simulations were run for each of the eight parameter combinations.

Results

The amount of habitat loss averaged 6.8% per 5 years in the landscape that we studied (Figure 1), and 75% of the original area of old-growth spruce forest was lost during the 50-yr period (Figure 3). There were two 5-yr intervals during which the loss rate was particularly high, in 1950–55 and in 1960–1965. The number of distinct habitat patches declined gradually and was only halved during the 50-yr interval, hence this measure gives a very rough idea of what was actually happening. The perimeter-to-area ratio increased during the periods of rapid habitat loss, though the change in this measure was not very striking either (Figure 3).

The two measures that changed dramatically during the study period are the number of suitable core cells and the colonization potential R_l: these two measures were halved in 1950–55, and they were reduced to 10–20% of their previous values in the period 1960–1965, when a staggering 31% of the habitat was lost in only 5 years. At this point, both the area of continuous habitat and the connectivity were drastically reduced, even much more than the lost habitat area would suggest, and these changes are reflected in the value of R_l.

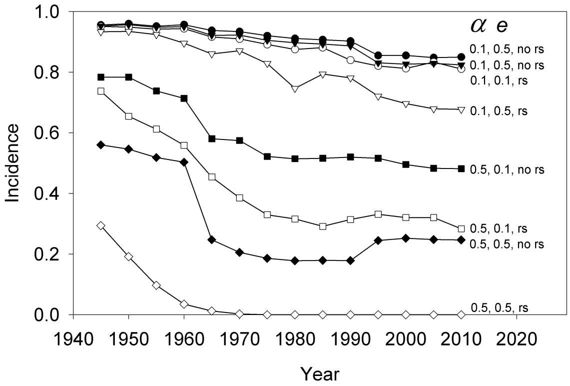

Figure 4. The predicted level of occupancy of suitable habitat in model simulations using 8 different sets of parameter values. We used two levels of α (0.1 and 0.5) and e (0.1 and 0.5), and simulations were performed with no regional stochasticity (no, {1,0,0,0,0,0,0,0}) and with large-scale regional stochasticity (rs, {0,0,0,0,0,0,1,0}). Other model parameters had the constant values of b = 0.5, x = 0.5, y = 5.0 and σ = 1.5. Fifty simulations were run for each combination of parameters, and the average values are shown.

The model-predicted fraction of occupied habitat in the landscape in 1995 varied from ca 90% to nothing depending on the parameter values used (Figure 4). Regional stochasticity did not change qualitatively the pattern of predicted occurrence, but it consistently reduced occupancy level in comparison with the situation without regional stochasticity (Figure 4). The difference was especially great when the predicted level of occupancy was low without regional stochasticity. In the worst scenario for persistence (short dispersal distance and high extinction risk), the metapopulation went rapidly extinct when regional stochasticity was included though it survived with some 20% of the habitat occupied without regional stochasticity (Figure 4).

The 9 habitat fragments (sets of contiguous grid cells) for which the probability of occupancy was calculated included two patches (F2 and F4 in Figure 1) that are still part of a larger stand of forest, two fragments (F5 and F6) that are presently completely iso-

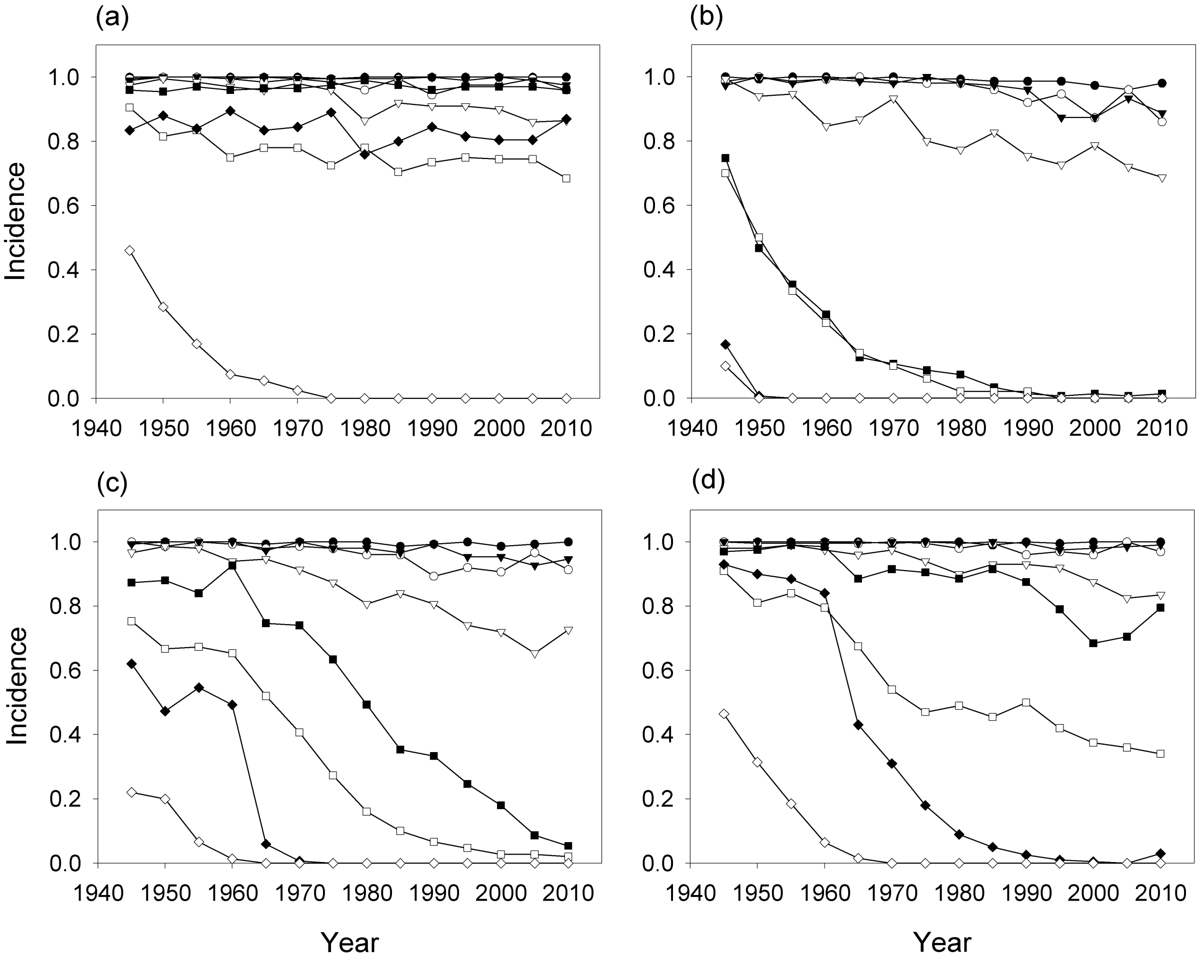

Figure 5. The predicted probability of occupancy in 4 habitat fragments, identified as F2 (panel a), F5 (b), F1 (c) and F9 (d) in Figure 1, during the 50-yr history of forest fragmentation shown in Figure 1 and using the 8 sets of parameter values described in Figure 4.

lated, as well as fragments that have some minor connections to other old-growth spruce forest (Figure 1). The currently least isolated fragments (F2 and F4) showed high predicted probability of occupancy, excepting the worst scenario, short-range dispersal, high local extinction risk and large-scale regional stochasticity (Figure 5a). In the remaining fragments the predicted occupancy varied greatly depending on parameter values used in the simulations (Figure 5b–d). Nonetheless, the predicted occupancy probabilities for different habitat fragments were generally well correlated across different parameter sets: the average value of the Spearman rank correlation coefficient was 0.93 (standard deviation 0.05). The same result was observed for other sets of parameter values (not reported).

An example of threatened species

We describe next an example of how the model-predicted probability of occupancy can be used to analyze the occurrence of species in fragmented landscapes. The example concerns four species of threatened polyporous fungi in the old-growth spruce forests in Kuhmo, eastern Finland, which have been studied in the context of a large-scale study of vertebrates, insects, fungi and lichens in 23 old-growth forest fragments (Varkonyi et al. in preparation). The species are *Amylocystis lapponica*, *Fomitopsis rosea*, *Phlebia centrifuga* and *Cystostereum murraii*. We have recorded the 50-yr history of forest fragmentation within a 5 -km radius around each fragment (Figure 1 includes one of these fragments). Five fragments were controls within an extensive tract of old-

Table 1. Multiple regression models for the occurrence of four species of spruce forest specialist polyporous fungi in 23 forest fragments. The explanatory variables are the model-predicted probability of occupancy (P_{model}), the area of the fragment, its isolation from the nearest other old-growth spruce forest, time since isolation, the amount of decaying spruce downwood in the fragment (D_{wood}), the number of tree stumps (*Stumps*), and a measure of wetness of the forest stand (*Wet*). Variables not shown in the table did not have a significant effect in any of the models. t is the t-test value of the regression coefficient. Results are given for two models, assuming either a dynamic or static landscape structure (in the case of *P. rosea*, P_{model} had an insignificant effect in both cases).

Species	Model	Variables in the model								Model R^2
		P_{model}		D_{wood}		*Stumps*		*Wet*		
		t	p	t	p	t	p	t	p	
A. lapponica	static	4.00	<0.01	5.78	<0.01	2.10	0.05			0.80
	dynamic	4.41	<0.01	5.76	<0.01	2.14	0.04			0.82
F. rosea				4.61	<0.01					0.50
P. centrifuga	static	1.74	0.10	5.05	<0.01			2.36	0.03	0.69
	dynamic	2.04	0.05	5.45	<0.01			2.15	0.04	0.64
C. murraii	static	1.76	0.09							0.12
	dynamic	2.34	0.03							0.19

P_{model} was calculated by running the model with 4 sets of parameter values, $\alpha = 0.3$ and 0.5 and $e = 0.2$ and 0.4. The other parameter values were as in Figure 4 with large-scale regional stochasticity {0,0,0,0,0,0,1,0}. The average value of the four sets of probabilities was used in the analysis (calculated as the first principal component of suitably transformed probabilities).

growth, while the remaining 18 fragments were originally selected to cover a large range of time since isolation. Using the present model we calculated the probability of occupancy in these 23 fragments, and subsequently used these probabilities in regression models to explain the observed occurrence of the four fungi in the fragments. All the four species are specific to old-growth spruce forest. In the regression models, we included the following explanatory variables apart from model-predicted probability of occupancy: the area of the fragment (2.2 to 13.7 ha), the amount of decaying spruce downwood (5.8 to 194 m^3/ha), current isolation (shortest distance to other old-growth spruce forest: 0.2 to 3 km), the number of tree stumps (0 to 23 ha^{-1}), time since isolation (0 to 35 years, excepting three naturally isolated fragments that are surrounded by open mires), and a measure of wetness of the forest stand.

To examine the significance of the history of forest fragmentation for the occurrence of the species in the 23 forest fragments, we calculated another set of model-predicted probabilities of occupancy, but in this case assuming a static landscape, the pattern of old-growth as observed in 1995. The simulations were run exactly in the same manner as in the calculation of the occupancy probabilities for the dynamic landscapes, for instance the simulations were started in the year 1945 with 70% of randomly selected suitable cells initially occupied.

The results are summarized in Table 1. Our first finding was that, not surprisingly, the amount of dead spruce downwood had a highly significant effect on the abundance of three of the four species. Some other variables characterizing the quality of the stand (the number of tree stumps, wetness of the stand) entered the model in one species each (Table 1). Secondly, the current isolation of the forest fragment from the nearest other old-growth spruce forest and the time-since-isolation had no significant effect on the occurrence of any of the species. Therefore, had the influence of habitat loss and fragmentation been assessed with these commonly-used measures of isolation we would have concluded that fragmentation has had no effect on the occurrence of the four threatened species. Thirdly, using the model-predicted probability of occurrence as our measure of spatiotemporal isolation of the study fragment, a radically different result emerges. Assuming the empirically-recorded dynamic landscape, the model-predicted probability of occupancy explains a significant amount of variation in the occurrence of three of the four species (Table 1). Assuming a static landscape, the effect of model-predicted probability of occupancy is significant in one of the four species. Therefore, the model that takes into account the history of fragmentation has more explanatory power than the model that ignores the history of fragmentation, suggesting that the current occurrence of the species is influenced by the history of forest fragmentation.

Discussion

The approach that we have described in this paper provides a practical measure to quantify the consequences of spatio-temporal fragmentation of habitat on the occurrence of species. With increasingly easy access to remotely sensed data and GIS techniques, digitized information on landscape changes is becoming increasingly available to ecologists and conservation biologists. Population modelling that explicitly takes into account the actual change in the study landscapes presents the potential to incorporate more realism into the models, though two problems are likely to occur in many applications. First, though information to characterize current landscape structure is often relatively easy to obtain, it may be difficult to obtain sufficient information to construct an accurate description of landscape changes extending back in time. In the present study, we were able to construct the history of habitat fragmentation for 50 years, which is most likely a sufficiently long period of time to capture the possible influence of history of landscape change on the occurrence of many or even most species living in forested landscapes. This conjecture is supported by the comparison between the results for models assuming static *versus* dynamic landscape (discussed below).

Another problem in the use of the present approach is the general difficulty of obtaining the necessary information to parameterize population and metapopulation models. The Incidence Function Model can be rigorously parameterized with data from metapopulations which occur at stochastic quasi-equilibrium in static highly fragmented landscapes (Hanski 1994, 1999a; ter Braak et al. 1998; Moilanen 1999, 2000), but the amount of data typically available is not sufficient to rigorously parameterize the model for species living in landscapes that change fast in comparison with the rate of metapopulation dynamics of the focal species (e.g., Wahlberg et al. (2002)). Fortunately, for the purpose of investigating the fragmentation effects it is sufficient to have a measure that is well correlated with the 'true' probability of occupancy. In the present study, we found that the rank order of forest fragments in terms of the predicted probability of occupancy was insensitive to the parameter values used in the simulations. Thus, one may expect that any biologically plausible set of parameters produces informative results, or one may average results for several sets of parameters as was done in the example in Table 1. In summary, with the present approach we can rank different habitat fragments for their capacity to retain a local population without having accurate parameter estimates for the metapopulation model. The predictions can be tested with data on single species (as in Table 1) or on many species, in the latter case correlating the empirically observed species number in the habitat fragment with the predicted probability of occupancy.

Comparison of the modelling results for static and dynamic landscapes revealed that the latter made a significant contribution to regression models explaining the occurrence of the polyporous fungi in three of four species, while the model-predicted probabilities assuming static landscape entered the regression model for only one of the four species (Table 1). We draw two conclusion from this result. First, the difference in the results for the two models indicates that the history of fragmentation influences the occurrence of the species in the forest fragments. In other words, as predicted by the theory (Ovaskainen and Hanski 2002), the species track the changing landscape structure with a noticable time lag. Another indication of the time lag is visible in the results shown in Figure 5 for the dynamic landscapes. In these simulations, no further change in the landscape structure occurred after 1995, yet the decline in the predicted probability of occupancy of the habitat fragments often continued for a long time. Similarly, there was a drastic change in the landscape structure in the period 1960–65 (Figure 3), whereas the response in terms of declining occupancy occurred more gradually (Figures 4 and 5). Notice that even in these cases the ranking order of the fragments in terms of the occupancy probability was little affected (Figure 5).

Secondly, though the results in Table 1 and Figure 5 indicate the presence of a time lag in species' responses, the quantitative effect is not very great. Thereby, using the model-predicted probability of occupancy based on the static landscape revealed a strong effect of isolation on the occurrence of *Amylocystis lapponica*, even if the current isolation of the respective forest fragments and time-since-isolation had no significant effect on the occurrence of the species in the study fragments. The practical conclusion from this result is that the model-predicted probabilities of occupancy can often be useful even though there is no data to characterize the history of fragmentation and therefore no opportunity to include the history in the model. Naturally, the strength of the population dynamic influence of the fragmentation history, and thereby the length of the time delay in population response, depend on the properties of the species and the landscape structure (Ovaskainen and Hanski 2002).

Acknowledgements

We thank Otso Ovaskainen for discussions, Pirjo Apelgren for preparing the descriptions of landscape fragmentation, and Kimberly With and two anonymous referees for helpful comments on the manuscript. Financial support was provided by The Finnish Biodiversity Research Programme (6400062), The Academy of Finland (Finnish Centre of Excellence Programme, 44887), and the Ministry of Environment.

References

Bader P., Jansson S. and Jonsson B.G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol. Conserv. 72: 355–362.

Berg Å., Ehnström B., Gustafsson L., Hallinbäck T., Jonsell M. and Weslien J. 1994. Threatened plant, animal, and fungus species in Swedish forests: Distribution and habitat associations. Conserv. Biol. 8: 718–731.

ter Braak J.F., Hanski I. and Verboom J. 1998. The incidence function approach to modeling of metapopulation dynamics. In: Bascompte J. and Solé R.V. (eds), Modeling Spatiotemporal Dynamics in Ecology. Springer-Verlag, New York, New York, USA, pp. 167–188.

Brooks T.M., Pimm S.L. and Oyugi J.O. 1999. Time lag between deforestation and bird extinction in tropical forest fragments. Conserv. Biol. 13: 1140–1150.

Debinski D.M. and Holt R.D. 2000. A survey and overview of habitat fragmentation experiments. Conserv. Biol. 14: 342–355.

Doak D.F. and Mills L.S. 1994. A useful role for theory in conservation. Ecology 75: 615–626.

Esseen P.A., Ehnström B., Ericsson L. and Sjöberg K. 1992. Boreal forests – the focal habitats of Fennoscandia. In: Hansson L. (ed.), Ecological Principles of Nature Conservation. Elsevier, London, UK, pp. 252–325.

Foley P. 1997. Extinction models for local populations. In: Hanski I. and Gilpin M.E. (eds), Metapopulation Biology. Academic Press, San Diego, pp. 215–242.

Forman R.T.T. and Godron M. 1986. Landscape Ecology. John Wiley & Sons, New York, New York, USA.

Franklin J.F. and Forman R.T.T. 1987. Creating landscpe patterns by forest cutting: Ecological consequences and principles. Landscape Ecol. 1: 5–18.

Gustafson E.J. and Gardner R.H. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77: 94–107.

Hanski I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biol. J. Linnean Soc. 42: 17–38.

Hanski I. 1994. A practical model of metapopulation dynamics. J. Anim. Ecol. 63: 151–162.

Hanski I. 1998. Metapopulation dynamics. Nature 396: 41–49.

Hanski I. 1999a. Metapopulation Ecology. Oxford University Press, Oxford, UK.

Hanski I. 1999b. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87: 209–219.

Hanski I., Moilanen A., Pakkala T. and Kuussaari M. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conserv. Biol. 10: 578–590.

Hanski I. and Ovaskainen O. 2000. The metapopulation capacity of a fragmented landscape. Nature 404: 755–758.

Harris L.D. 1984. The Fragmented Forest. The University of Chicago Press, Chicago, Illinois, USA.

Harrison S. and Quinn J.F. 1989. Correlated environments and the persistence of metapopulations. Oikos 56: 1–6.

Heckert J.R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. Ecol. Applic. 4: 461–471.

Heywood V.H. 1995. Global Biodiversity Assessment. Cambridge University Press, Cambridge, UK.

Komonen A., Penttilä R., Lindgren M. and Hanski I. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. Oikos 90: 119–126.

Lovejoy T.E., Rankin J.M., Bierregaard R.O., Brown K.S., Emmons L.H. and van der Voort M.E. 1984. Ecosystem decay of Amazon forest remnants. In: Nitecki M.H. (ed.), Extinctions. The University of Chicago Press, Chicago, Illinois, USA, pp. 295–325.

MacArthur R.H. and Wilson E.O. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersy, USA.

Margules C.R. 1996. Experimental fragmentation. In: Settele J. (ed.), Species Survival in Fragmented Landscapes. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 93–110.

May R.M., Lawton J.H. and Stork N.E. 1995. Assessing extinction rates. In: Lawton J.H. and May R.M. (eds), Extinction Rates. Oxford University Press, Oxford, UK.

Milne B.T. 1991. Lessons from applying fractal geometry of landscape. In: Turner M.G. and Gardner R.H. (eds), Quantitative Methods in Landscape Ecology. Springer-Verlag, New York, New York, USA, pp. 199–235.

Moilanen A. 1999. Patch occupancy models of metapopulation dynamics: efficient parameter estimation using implicit statistical inference. Ecology 80: 1031–1043.

Moilanen A. 2000. The equilibrium assumption in estimating the parameters of metapopulation models. J. Anim. Ecol. 69: 143–153.

Moilanen A., Smith A.T. and Hanski I. 1998. Long-term dynamics in a metapopulation of the American pika. Am. Naturalist 152: 530–542.

Ohlson M., Söderström L., Hörnberg G., Zackrisson O. and Hermansson J. 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. Biol. Conserv. 81: 221–231.

Ovaskainen O. and Hanski I. 2001. Spatially structured metapopulation models: global and local assessment of metapopulation capacity. Theor. Popul. Biol., 60: 281–304.

Ovaskainen O. and Hanski I. 2002. Transient dynamics in metapopulation response to perturbation. Theor. Popul. Biol. 61: 285–295.

Riitters K.H., O'Neill R.V., Hunsaker C.T., Wickham J.D., Yankee D.H. and Timmins S.P. 1995. A factor analysis of landscape pattern and structure metrics. Landscape Ecol. 10: 23–39.

Robinson G.R., Holt R.D., Gaine M.S., Hamburg S.P., Johnson M.L., Fitch H.S. et al. 1992. Diverse and contrasting effects of habitat fragmentation. Science 257: 524–526.

Settele J., Marguyles C.R., Poschlod P. and Henle K. 1996. Species survival in fragmented landscapes. In: Settele J. (ed.). Kluwer Academic Publishers, Dordrecht, The Netherlands.

Schumaker N.H. 1996. Using landscape indices to predict habitat connectivity. Ecology 77: 1210–1225.

Tilman D., May R.M., Lehman C.L. and Nowak M.A. 1994. Habitat destruction and the extinction debt. Nature 371: 65–66.

Turner M.G., O'Neill R.V., Gardner R.H. and Milne B.T. 1989. Effects of changing spatial scale on the analysis of landscape pattern. Landscape Ecol. 3: 153–162.

Wahlberg N., Klemetti T. and Hanski I. 2002. Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. Ecography 25: 224–232.