

Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation

Ilkka Hanski

*Metapopulation Research Group, Department of Ecology and Systematics,
P.O. Box 17 (Arkadiankatu 7), FIN-00014 University of Helsinki, Finland*

Received 29 March 2000, accepted 26 October 2000

Hanski, I. 2000: Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. — *Ann. Zool. Fennici* 37: 271–280.

The extinction debt of boreal forest species is estimated to be of the order of 1 000 species in Finland. Using a spatially explicit metapopulation model, this paper examines the likely consequences for the survival of species of different scenarios of forest management and conservation. The results point to the conclusion that it generally pays to concentrate the efforts of improving forest quality at certain areas rather than to spread the same total effort evenly and therefore thinly throughout the entire forest landscape. The practical conclusion is that in southern Finland an extensive restoration program of managed forests to natural-like successional forests is needed to avert the imminent wave of extinctions of specialist forest species. The greatest positive effect is obtained if forests located close to the existing remnants of biologically diverse forests are restored, which would facilitate the migration of target species to the restored forests.

Introduction

Boreal forests cover some 10% of the land surface on earth and they account for nearly one half of all the forests (Mooney *et al.* 1995). A widespread misconception about boreal forests is that,

in comparison with temperate and especially tropical forests, boreal forests are practically devoid of biodiversity. If by forest we mean the assemblage of tree species, there is substantial truth to this assertion, but in many other forest-inhabiting taxa boreal forests harbour vast num-

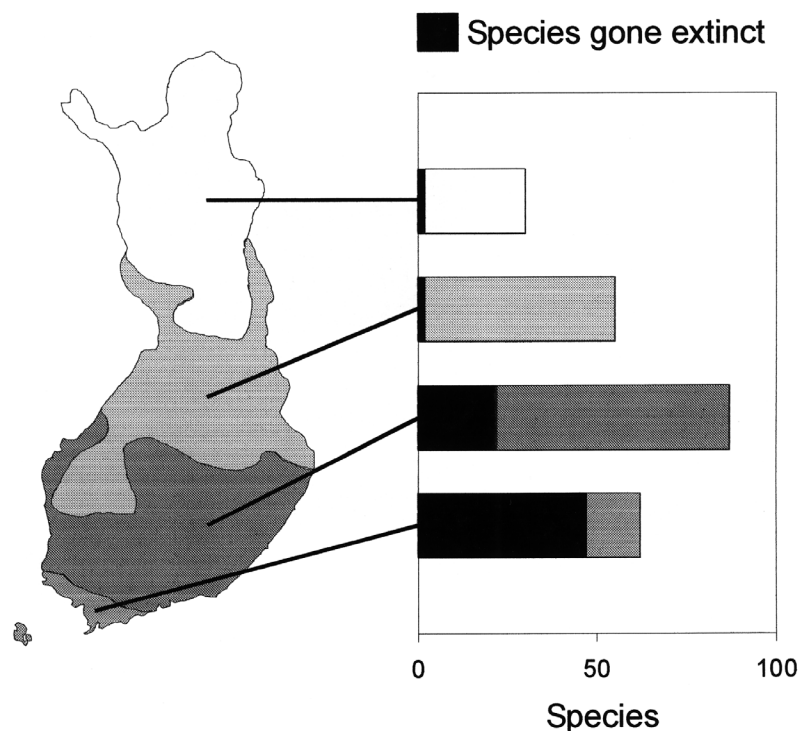


Fig. 1. The past and current occurrence of 100 threatened forest beetle species in the four biogeographical zones of boreal forest in Finland. The bar for each zone gives the number of species (out of the 100 species) that are known to have occurred in that zone; the black part of the bar gives the number of species that are considered to have gone extinct (based on data and analysis by P. Rassi; see also Hanski 1997).

bers of species. For example, there are about 1 000 species of beetles dependent on decaying wood or wood-decomposing fungi in Fennoscandia (Esseen *et al.* 1992).

Roughly 20 000 of the about 45 000 species of fungi, plants and animals living in Finland are forest-inhabiting species. The exact ecological requirements of most species remain unknown, but large numbers of species have become adapted to live under conditions that are rarely found in intensively managed forest landscapes. Currently, 566 forest species are classified as threatened in Finland, out of the ca 20 000 species for which sufficient knowledge is available to allow the classification (Rassi *et al.* 2000). Assuming that the latter species represent an unbiased sample of all the species in Finland, roughly 6% of Finland's forest species are threatened. In certain taxa, the percentage is much higher. For example, there are 115 species of threatened polypores (wood-rotting fungi), which amounts to 17% of the 671 species that could be classified (Rassi *et al.* 2000).

So far, some 60 forest-dwelling species have gone extinct in Finland (Rassi *et al.* 2000). Many

more species have gone extinct from parts of the country, especially from the southern part, which has been most and for the longest period of time influenced by man. Figure 1 gives an example on 100 threatened forest beetle species, for which substantial information is available on their past and present occurrence in the different biogeographical zones of boreal forest in Finland. As expected, the number of species ever recorded declines towards north, with the exception of the narrow hemiboreal zone in SW Finland, explained by the clearly smaller area of this zone than the areas of the other zones (Fig. 1). The number of species considered to have gone extinct from the hemiboreal zone is already staggering 73% of the known species, and it is as high as 25% in the southern boreal zone, which covers the southernmost quarter of Finland (Fig. 1).

The numbers of threatened forest species are large but not surprisingly large when we consider the extent of the changes that have taken place in Finnish forests (Virkkala & Toivonen 1999). Figure 2 shows vividly how little old-growth forest there is left in southern Finland, a mere 0.5%. The ecological requirements of many threat-

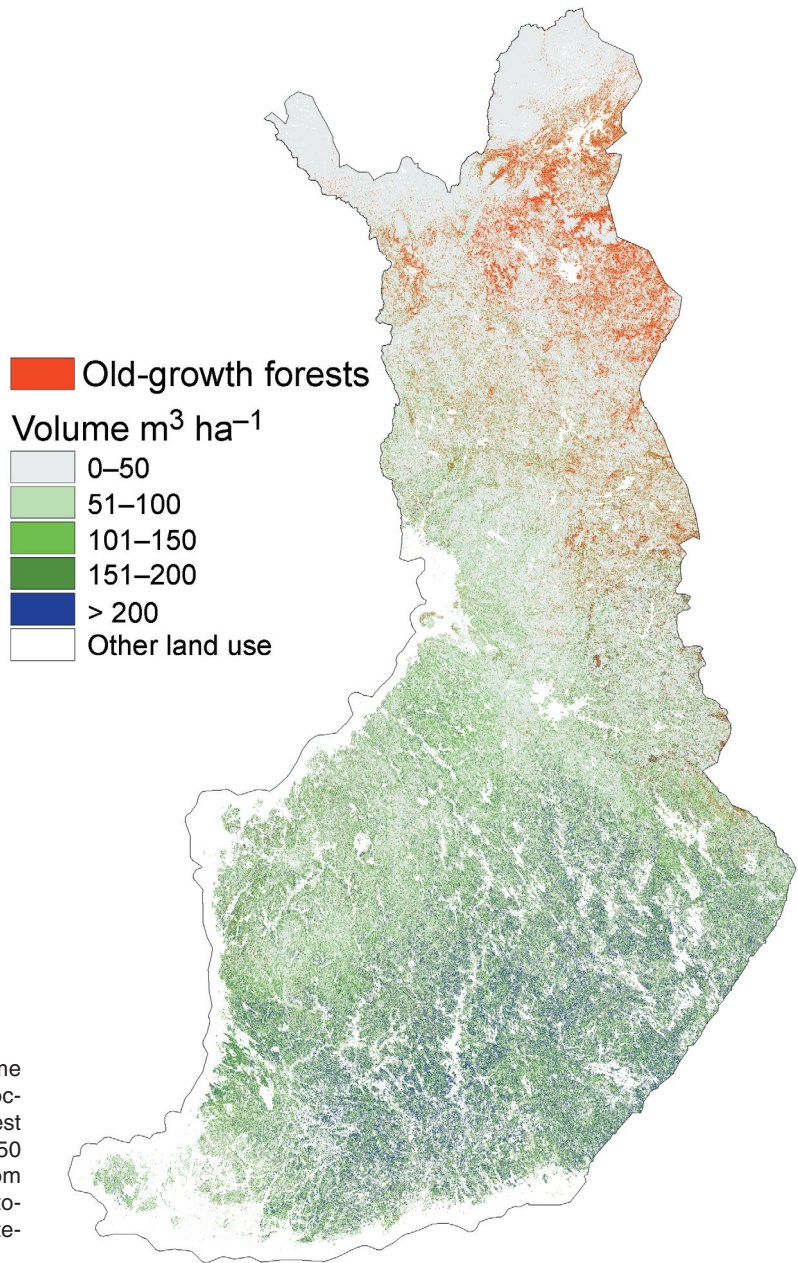


Fig. 2. The standing volume ($\text{m}^3 \text{ha}^{-1}$) of trees and the occurrence of old-growth forest (forest stand older than 150 years) in Finland (data from the National Forest Inventories of Finland; figure courtesy of Prof. E. Tomppo).

ened forest species would be met by natural forests representing young successional stages (Martikainen 2000, Kouki *et al.* 2000), in contrast to old-growth, but such forests are practically non-existent in Finland. As far as the old-growth is concerned, the situation is better in northeastern Finland, but notice that these forests are intrinsically less productive (Fig. 2) and hence have a

clearly lower species diversity (Fig. 1) than forests in southern Finland.

Comparing Figs. 1 and 2 suggests a very bleak view about the coming change in the communities of species associated with natural forests. As such forests are equally sparse in the entire southern part of the country (Fig. 2), one is forced to predict that the fraction of threatened

species that will go extinct in the southern half of the country will gradually increase to a level comparable to that already seen in the southernmost coastal areas (Fig. 1). In other words, the current forest landscape in southern Finland is not expected to support viable populations of these species, and the reason why they have not already gone extinct is simply the time delay that is necessarily involved in the regional extinction of species following habitat loss and fragmentation (Hanski *et al.* 1996; O. Ovaskainen & I. Hanski unpubl.). Intensive forestry has moved from south to north, hence the regional time-delayed extinctions are also expected to spread from south to north. The number of species that is expected to eventually go extinct due to past adverse environmental changes is called the 'extinction debt' (Tilman *et al.* 1994, Hanski 1999a).

The order of magnitude of the extinction debt for southern Finland can be roughly estimated from the species-area relationship (MacArthur & Wilson 1967). Let us assume that 10% of forest species, or roughly 2 000 species, are specialized to live in natural forests, which now cover less than 1% of the forested land in southern Finland. Assuming that 1% of the natural forests remains, and assuming conservatively that the slope of the species-area curve is 0.15 (MacArthur & Wilson 1967), we arrive at the estimate that half of the species will eventually go extinct. This means the order of 1 000 species. This figure agrees with the estimated number of threatened forest species (1275), which by definition have a significant risk of extinction (Rassi *et al.* 2000). (The figure 1 275 is obtained by assuming that the fraction of threatened species is the same among the 20 000 classified species and among the 25 000 species that could not be classified because of inadequate information; $566 \times 45\,000/20\,000 \approx 1\,275$.)

Based on these considerations, it is clear that just preserving the current tiny fragments of old-growth and other natural-like forests in southern Finland will not suffice to avert the imminent wave of extinctions of specialist forest species. The only remedy is to improve the quality of the forested landscape for the threatened species. Given that only less than 1% of the forested land is currently protected in southern Finland, it should not be an unreasonable demand by anybody's standards that more forest should be taken

out of intensive management. The two main methods here are the general improvement of the ecological quality of the managed forests by new practices of forest harvest and regeneration, and the restoration of managed forests to natural-like successional forests. These improvements in forest quality are expected to enhance the capacity of forests to retain biodiversity. But just as in the case of extinction debt, it will take some time before the positive effects become evident. The number of species that will eventually benefit from these measures may be called the species credit.

Species credit consists of three elements. First, species that have already gone regionally extinct may return following the improvement in forest quality, provided that conspecific populations have survived in nearby areas from which they may migrate back to the focal region. These species represent species credit in the narrow sense. Second, a species which is declining towards extinction may recover, in other words, the improved quality of forests may create a positive equilibrium density for species for which the equilibrium was previously regional extinction. In this case species credit (in a broad sense) eliminates extinction debt. And third, a species may become more abundant following the improvement in forest quality, and it may move away from the list of threatened species, meaning that the imminent risk of its extinction has been eliminated.

To explore the likely consequences of different scenarios of forest management and conservation for the occurrence of species I have constructed a spatially explicit simulation model. The impetus for this work was the realization that with the same economic expenditure one may gain a substantially dissimilar benefit in terms of the maintenance of forest biodiversity. It is imperative that this point is fully realized and that the most cost-effective measures of forest conservation are developed.

The model

The model is based on the incidence function model (IFM, Hanski 1994, 1999a), which is here applied to a regular grid of 'habitat patches.' The

model thus assumes a forest landscape that is divided into equally large contiguous forest stands, each one of which may be occupied by a local population of the focal species. The ‘quality’ of the forest stand is denoted by Q , and it may vary from 0 to some maximal value. Q must naturally be defined with respect to the ecological requirements of the focal species. For instance, for beetles living in decaying wood, Q might be the amount of dead wood of certain kind in the forest stand. Q corresponds to patch area in the usual applications of the IFM (Hanski 1999a).

The IFM is a patch occupancy model, meaning that individual forest stands have only two possible states, occupied by the focal species or not occupied (empty). The basic assumptions of the IFM include that the risk of extinction of a local population is inversely related to Q , because forest stands with low quality have small expected population sizes with a high risk of local extinction, while the probability of colonization of an empty stand is a function of its connectivity to existing local populations. The model also assumes the ‘rescue effect’ (Hanski 1999a), reduced probability of population extinction in well-connected forest stands due to increased density of populations in these stands.

The population-dynamic connectivity of stand i is defined as

$$S_i = \sum_{j \neq i} e^{-\alpha d_{ij}} p_j Q_j^b, \quad (1)$$

where $p_j = 0$ for empty and 1 for occupied stands, d_{ij} is the distance between stands i and j , and $1/\alpha$ gives the average migration distance of the focal species. Parameter b scales the rate of emigration by stand quality. The colonization probability C_i is assumed to be a sigmoid function of connectivity,

$$C_i = S_i^2 / (S_i^2 + y^2), \quad (2)$$

where y is a constant. The extinction probability is given by

$$E_i = \min\{1, (e/Q_i^x)(1 - C_i)\}, \quad (3)$$

where e and x are parameters and $(1 - C_i)$ represents the rescue effect. For a more detailed description of the IFM see Hanski (1999a).

The patchwise independence of extinction events assumed in the basic IFM is a reasonable

assumption when modelling discrete habitat patches separated by unsuitable habitat, as is the case in the usual applications of the IFM (Hanski 1999a), but complete independence is a bad assumption while modelling spatial dynamics on a grid, like in the present study, with many small ‘patches’ located next to each other. I included spatially correlated extinctions in the model in the manner described by Gu, W., Heikkilä, R. and Hanski, I. (unpubl.). Briefly, regional stochasticity (spatially correlated environmental stochasticity) was implemented by assuming spatially correlated temporal changes in habitat quality Q , which leads to spatially correlated extinctions (Eq. 3) and to spatially correlated colonizations (Eqs. 1 and 2).

Consider a square grid that covers the entire landscape to be modelled. The square is divided into four equal squares, each of which is further divided into four equal squares, and so forth. The divisions are continued until the resultant squares correspond to the original grid cells themselves. The effective quality $Q_{ij}^c(t)$ of patch i, j (row i , column j) at time t is given by

$$Q_{ij}^c(t) = Q_{ij} e^{\sum c(k) R_{ijk}}, \quad (4)$$

where Q_{ij} is the intrinsic stand quality, k is the level in the spatial hierarchy of increasing squares (scale), R_{ijk} is a normally distributed random variable with zero mean and with the same value in all grid cells belonging to the same square at scale k , and $c(k)$ is the weight of the random variable at scale k (for further details see Gu, W., Heikkilä, R. & Hanski, I. unpubl.). In simulations, a new set of effective areas is calculated for each time step, hence there is no temporal correlation in regional stochasticity.

Results

There are several parameters in the model and hence a vast range of situations that could be analysed. In this paper, I will compare a few selected scenarios that seem to be of the greatest relevance for forest management and conservation. All the simulations were run on a 32 by 32 lattice, the edges of which were wrapped around to eliminate any edge effect, and the following parameters of the IFM were used throughout: $e =$

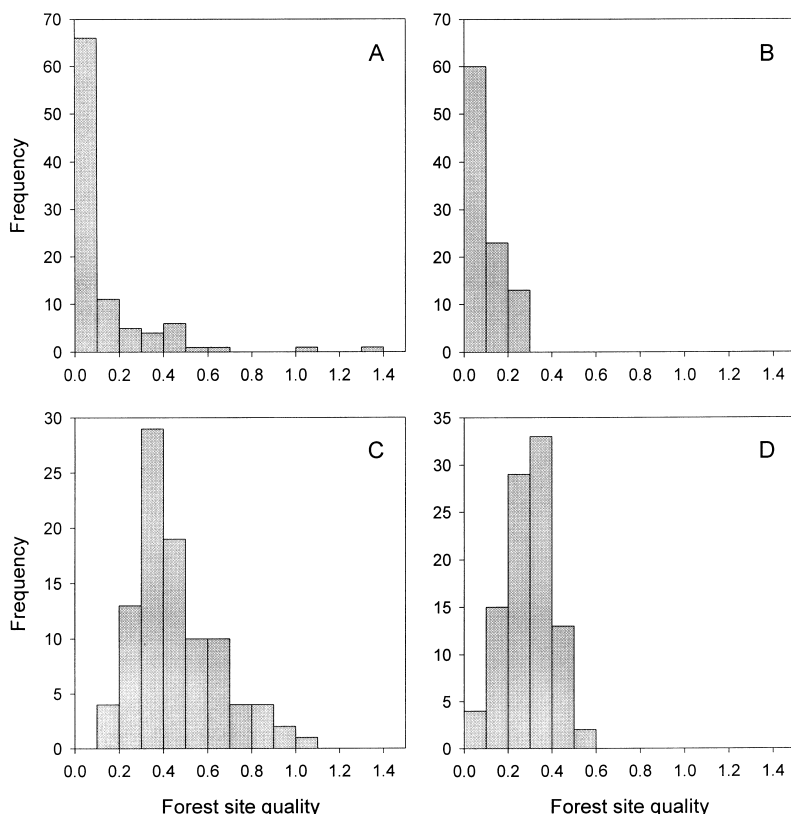


Fig. 3. Distribution of forest stand quality in the four scenarios analysed in the text.

0.015, $y = 4$, $x = 2$ and $\alpha = 0.5$. The parameters of regional stochasticity were $s = 0.9$ (the standard deviation of the normally distributed random variable R_{ijk} with zero mean) and $c(k) = \{0.1, 0.2, 0.5, 0.2, 0, \dots\}$ (from small to large levels in the spatial hierarchy).

The initial state for all simulations was the same. Initially, there was some variation in forest stand quality Q , illustrated by Fig. 3A, though the quality of most stands was low. There was no spatial correlation in stand quality, that is, the landscape was initiated by independently drawing a quality value for each stand from the distribution shown in Fig. 3A. This landscape is considered to represent the current intensively managed forest landscape in southern Finland, with a small number of stands with high or relatively high quality (e.g., old spruce stands) sparsely spread amongst stands with very low value for the focal species.

Initially, each stand had a 50% chance of being occupied. The landscape structure and the parameter values used in the simulations howev-

er dictated that the focal species would rapidly decline towards metapopulation extinction (Fig. 4A). The rationale for this scenario is that previously the forest structure had been more favourable for the species, hence in the beginning of the simulation the species was far 'too common' with respect to the current structure of the landscape. Notice that, starting from the beginning of the simulation, there is no further change in forest structure (the thick broken line in Fig. 4A). The presence of the species in the landscape before its eventual extinction, which often occurred within 100 years (Fig. 4A), thus represents extinction debt. With this background, let us now consider three different scenarios of changing landscape.

The first scenario is meant to mimic the new code of forestry as described in e.g. the environmental guidelines of the Forest and Park Service (Anon. 1998), involving retention trees, snags and a certain amount of decaying wood left in harvested areas. In the model, these measures are implemented by assuming that, over a period of 20 years, the quality of each forest stand is

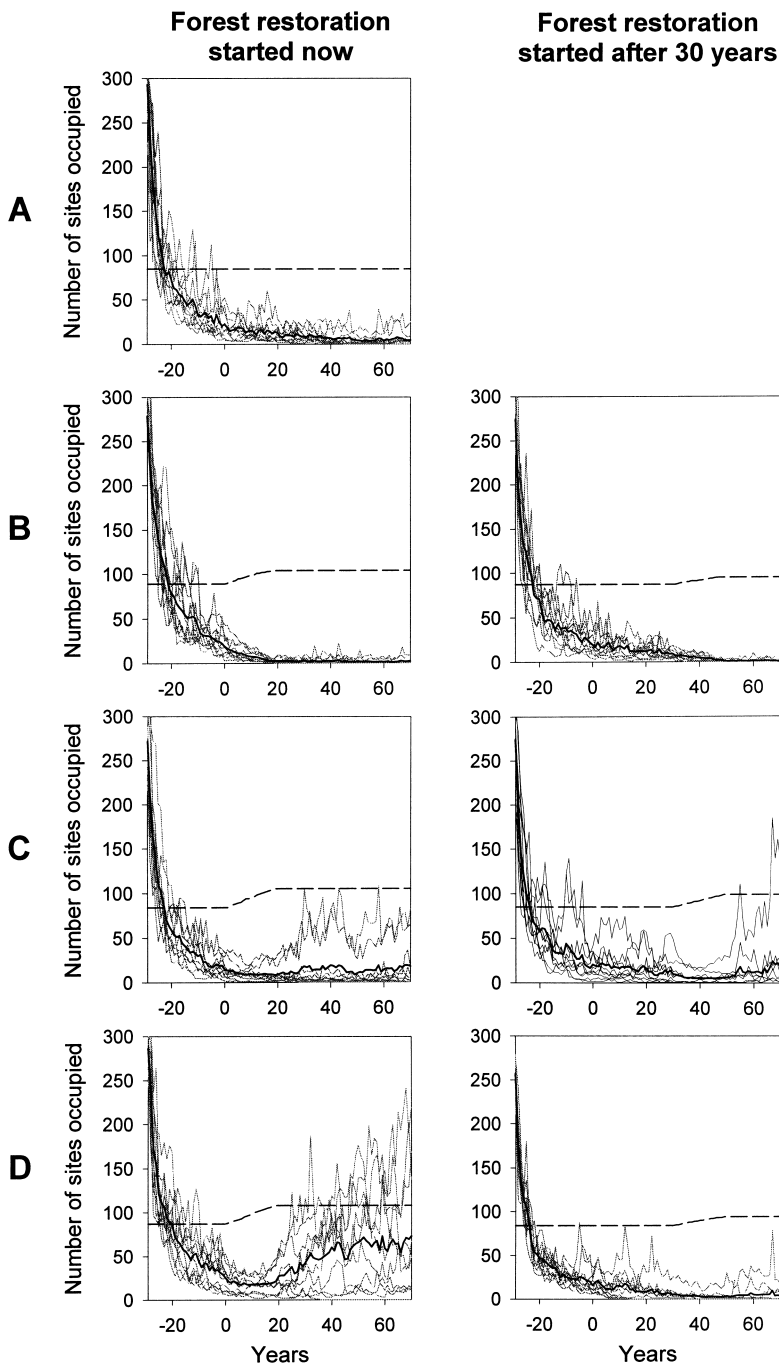


Fig. 4. The model-predicted changes in the distribution (= number of occupied forest stands) of a hypothetical species in the course of simulations of the four scenarios discussed in the text. In each case, the results of 10 independent simulations are shown, with the thick line giving the average distribution. The broken thick line gives the average quality of the forest stands. The uppermost panel gives the prediction for a situation in which the forest structure remains unchanged. The three other rows give the results for three different scenarios of improved forest quality over a 20 year period, starting the improvement of forest quality either now (left-hand panels) or after 30 years (right-hand panels). See text for further explanation and discussion.

changed independently to a new value, which is drawn from the distribution shown in Fig. 3B. There is not a huge difference to the original distribution (Fig. 3A), but the mean of the new values is greater than the mean of the old values, hence the average quality of the entire forest landscape increases by ca. 20% (this figure should not be interpreted as 20% reduction in forest harvest). The lowest values of stand quality are higher than previously, but notice that the new distribution (Fig. 3B) lacks the tail of high values present in the original distribution (Fig. 3A). The reason for this change is that the increasingly extensive forestry is assumed to eliminate these stands, e.g. the few remaining small stands of old spruce forest. Therefore, the overall quality of the forest increases, but at the same time stands with substantially higher quality than the average are cut off.

The model-predicted consequences for population dynamics are shown in Fig. 4B (left-hand panel). Though the average stand quality has increased in comparison with the original situation (Fig. 4A), the extinction rate of species is predicted to increase rather than to decrease. The reason for this at first surprising result is that the small increase in the average stand quality is not sufficient to compensate for the harmful effect that follows from removing the stands that originally had the highest quality.

In the next scenario, the approach to forest management is different. Now the original forest landscape is altered by changing the quality of only 10% of the forest stands, for which a new quality value is drawn from the distribution shown in Fig. 3C. The mean of this distribution is considerably higher than the mean of the previous two distributions (Fig. 3A and B). On the other hand, as only 10% of the forested land is being affected, the overall increase in forest quality is about the same as in the previous scenario (compare the broken lines in Fig. 4B and C, which give the average stand quality). In this case, the predicted consequences for the occurrence of the focal species are positive (Fig. 4C) in comparison with the baseline, the no-change scenario in Fig. 4A.

Finally, in the third scenario the average im-

provement in forest stand quality is again the same as in the two previous scenarios, but now the change in the structure of the forest landscape is achieved via yet another route. I first calculated for each forest stand an index measuring how well that stand was connected to other stands with high quality. Next the quality of those stands with connectivity to high-quality stands greater than a threshold value was changed with probability 0.5, the new quality value being drawn from the distribution shown in Fig. 3D. This approach leads to aggregation of high-quality stands, without however causing a greater overall increase in forest quality than in the previous scenarios.

The population dynamic consequences of this latter change in the structure of the forest landscape are shown in Fig. 4D (left-hand panel). Notice that now the distribution of the focal species substantially increases in many replicate simulations during and following the 20-year period of change in the landscape structure.

The right-hand panels in Fig. 4 show the predicted changes in the occurrence of the focal species following the above-described changes in forest structure, but with the difference that now the 20-year period over which the change in forest structure occurs does not start now (at time 0), but only after 30 years. These simulation results are meant to demonstrate the point that the impact of such delayed measures are to a larger or smaller extent compromised by the continuous decline in the distribution of the focal species in the current landscape (Fig. 4A). In some of the replicates, the focal species actually went extinct during the 30-year period, in which case no improvement of forest quality can do any good for that species, as the model assumes no migration from outside the region that is being simulated. The results in Fig. 4 show no difference between scenarios 2 (panels C) and 3 (panels D) if the restoration measures are postponed by 30 years. Even in this case we would expect scenario 3 to be the preferred option, but in the examples in Fig. 4 the species has declined to such a low level in 30 years that more radical (and more expensive!) measures than considered here would be needed for favourable results.

Discussion

The modelling results described here relate to important issues concerning the maintenance of biodiversity in managed boreal forests. The new and less intensive methods of forest harvest — involving retention trees, a small increase in the amount of decaying wood, and the protection of small-sized ‘key biotopes’ (Anon. 1998) — undoubtedly increase the quality of the forest landscape for many species. However, the species that will benefit (to a yet unknown extent) of these measures represent the less specialized species, those that are able to persist in managed forests. It is doubtful whether these measures will benefit at all the ecologically more specialized species, which are dependent on resources and microhabitats characteristic of natural forests.

If one assumes that there is no cost to the new methods of forest management, the overall effect for biodiversity conservation will clearly be positive. In the real world the situation is more contentious, however. In the scenario shown in Fig. 4B, the old methods of forest harvest, involving infamous clear-cutting practices of the past decades are replaced by the new ‘softer’ methods, but at the cost of extending the management to include practically all forest stands. It is apparent from the modelling results that in this case the cost is prohibitive, as this scenario merely hastens the extinction of many species (Fig. 4A and B), in spite of increase in the average stand quality.

The take-home message of these analyses is that it generally pays to concentrate the efforts to improve forest quality in certain areas rather than to spread the same total effort evenly and therefore thinly throughout the entire forested landscape. Given the current structure of forests in southern Finland, there is hardly any realistic alternative to focusing on restoring some of the existing managed forests into natural-like successional forests, characterized by e.g. a large amount of decaying wood. These measures will be most effective if the restored forests are located close to the existing high-quality forest stands, which facilitates the migration of the target species to the restored forests and thereby reduces the time delay in species credit. The same conclusion was reached by Huxel

and Hastings (1999) in their analysis of different restoration scenarios.

The above conclusions are supported by a very general analysis of metapopulation dynamics. In a general metapopulation model, the capacity of a fragmented landscape to support a viable metapopulation increases with the following measure of ‘colonization potential’ of the landscape (Hanski 1999b; O. Ovaskainen & I. Hanski unpubl.)

$$R_i \equiv \frac{\sum R_i^2}{\sum R_i} = \overline{\Gamma Q} + \frac{\text{Var}(\Gamma Q)}{\overline{\Gamma Q}}.$$

In this formula, Q represents the quality and Γ the connectivity of a forest stand, and the bar denotes the average value in the landscape. Γ_i is defined as

$$\Gamma_i = \sum_{j \neq i} e^{-\alpha d_{ij}} Q_j.$$

where $1/\alpha$ is the average migration range of the focal species and d_{ij} is the distance between stands i and j (this formula is for one specific model, but other reasonable models would lead to qualitatively similar conclusions; note also that Γ_i gives the connectivity of landscape elements, whereas Eq. 1 refers to connectivity to occupied forest stands). Returning to forest management, restoration of managed forests to natural-like forests in the neighbourhood of existing high-quality forests stands gives an especially large increase in R_i , because this will lead to aggregation (large variance in Γ) of the best-quality forest stands, thereby greatly increasing $\text{Var}(\Gamma Q)/\overline{\Gamma Q}$.

To conclude with a hopeful note, the great appeal in forest restoration lies in the fact that with appropriate methods natural-like young successional forests can be created within a relatively short period of time, in contrast to the impossibility of quickly turning, by any means, managed forests into old-growth forests. Many threatened forest species are likely to persist in such natural-like young successional forests, including for example many species dependent on large quantities of decaying wood (Martikainen 2000). Therefore, though the prospects for forest conservation in southern Finland appear discouraging in view

of the current structure of the forests (Fig. 2), this does not need to be the case, and with an aggressive restoration program much remains to be gained. The ideas of focusing conservation efforts in certain areas and preferably close to the ecologically most valuable stands are recognized in the so-called landscape ecological plans recently produced by the Forest and Park Service (Metsähallitus) for state-owned forests (Anon. 1998), and the principles have been discussed by the committee (chaired by Prof. R. Ruuhijärvi) currently examining the means of improving forest conservation in southern Finland. The big challenge is to implement these ideas at a sufficiently large scale to make a real contribution towards forest conservation in southern Finland.

Acknowledgements

I thank Mikko Mönkkönen, Otso Ovaskainen and an anonymous referee for comments on the manuscript. Financial support has been provided by the Academy of Finland (Finnish Biodiversity Research Programme, grant 6400062; and the Finnish Centre of Excellence Programme (2000–2005), grant 44887).

References

- Anon. 1998: *Environmental guidelines to practical forest management*. — Forest and Park Service, Edita, Helsinki.
- Esseen, P. A., Ehnström, B., Ericson, L. & Sjöberg, K. 1992: Boreal forests — the focal habitats of Fennoscandia. — In: Hansson, L. (ed.), *Ecological principles of nature conservation*: 252–325. Elsevier, London.
- Hanski, I. 1994: A practical model of metapopulation dynamics. — *J. Anim. Ecol.* 63: 151–162.
- Hanski, I. 1997: Biodiversiteetin katoaminen. — *Duodecim* 113: 2411–2416.
- Hanski, I. 1999a: *Metapopulation ecology*. — Oxford University Press, Oxford.
- Hanski, I. 1999b: Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. — *Oikos* 87: 209–219.
- Hanski, I., Moilanen, A. & Gyllenberg, M. 1996: Minimum viable metapopulation size. — *American Naturalist* 147: 527–541.
- Huxel, G. R. & Hastings, A. 1999: Habitat loss, fragmentation and restoration. — *Restoration Ecol.* 7: 309–315.
- Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A. 2000: Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. — *Scand. J. Forest Res.* [In press].
- MacArthur, R. H. & Wilson, E. O. 1967: *The theory of island biogeography*. — Princeton Univ. Press, Princeton.
- Martikainen, P. 2000: *Effects of forest management on beetle diversity, with implications for species conservation and forest protection*. — Ph.D. thesis, University of Joensuu, Finland.
- Mooney, H. A., Lubchenco, J., Dirzo, R. & Sala, O. E. 1995: Biodiversity and ecosystem functioning: ecosystem analyses. — In: Heywood, V. H. (ed.), *Global biodiversity assessment*: 327–452. UNEP, Cambridge Univ. Press.
- Rassi, P., Mannerkoski, I., Peltonen, S.-L. & Alanen, A. 2000: *2nd red data book of Finland*. — Report, Ministry of Environment, Helsinki.
- Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. 1994: Habitat destruction and the extinction debt. — *Nature* 371: 65–66.
- Virkkala, R. & Toivonen, H. 1999: Maintaining biological diversity in Finnish forests. — *The Finnish Environment* No. 278, The Finnish Environment Institute, Helsinki.