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Extinction risk of wood-living model species in forest landscapes as related to forest history and conservation strategy

Thomas Ranius* and Oskar Kindvall

Thomas Ranius, Department of Entomology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-750 07 Uppsala, Sweden.

Oskar Kindvall, Swedish Species Information Centre, P.O. Box 7007, SE-750 07 Uppsala, Sweden.

Corresponding author. Tel.: +46-18-67 23 34; fax.: +46-18-67 28 90. E-mail address: thomas.ranius@entom.slu.se (T. Ranius).

Abstract. Dead wood is a critical resource for biodiversity in boreal forests. We analysed the persistence of five model species inhabiting dead wood. By parameterising a metapopulation model (the incidence function model), the model species were all assigned characteristics that makes it likely that they have disappeared from some (20%) forest landscapes with a long history of forest management. In the metapopulation model, a forest stand (5 ha) was regarded as a habitat patch. The amount of habitat in each patch was obtained from models of dead wood dynamics of Norway spruce in central Sweden. Dead wood generated by altered management over the entire landscape was found to be less efficient in reducing extinction risks in comparison to the same amount of dead wood generated by protecting reserves. Because generation of dead wood by altered management is often less expensive than setting aside reserves, it is difficult to determine which conservation measure is most cost-efficient. In a landscape subjected to forestry for the first time, it was better to preserve a few large reserves than many small ones. However, in a managed, highly fragmented forest landscape it was better to set aside many small reserves. The reason for this was that small plots with high habitat quality could be selected, while large reserves originally contained habitats both of high and low quality, and the rate of habitat quality increase was low. A strategy for biodiversity conservation in a managed forest landscape should include information about the history of the landscape, the current amount and spatial distribution of forest habitats, and the potential for rapid restoration of forest habitats, both on managed and unmanaged forest land.

Keywords: coarse woody debris, extinction debt, population viability analysis, restoration, saproxylic, SLOSS

Introduction

Extinction risks of species are determined by their demographic characteristics and the changes in distribution and quality of their habitat. The latter processes generally occur over such large scales in space and time that they cannot be effectively studied experimentally or in the field. Consider, for example, forest structures that take decades to develop after a restoration (e.g. Singer and Lorimer 1997; Ranius and Kindvall 2004). Computer simulations support studies of larger spatial and temporal scales than are possible in empirical studies (Akçakaya *et al*. 2004). Landscape models can be used to predict habitat dynamics in response to natural processes and human activities (e.g. Baker and Mladenoff 1999), while population models, often metapopulation models, can be used to predict the viability of a focal species in a landscape (e.g. Sjögren-Gulve and Hanski 2000).

Due to the extent and history of forestry, threats to forest biodiversity differ widely between regions. For instance, in southern and central Sweden and Finland almost all forest land has been managed for timber production, and this has generated monospecific, even-aged stands with short rotation periods (Esseen *et al*. 1997; Axelsson and Östlund 2001). In other regions with boreal forests, *e.g.* large areas in Russia and Canada, there are still large areas where commercial forestry has been absent or less intensive (Bryant *et al*. 1997). Among species that have decreased and are threatened due to forestry, a large proportion is saproxylic, *i.e*. dependent on dead wood, either directly or by being associated with other saproxylic species. This is because dead wood is a species-rich habitat, and the amount of dead wood is much lower in managed than in unmanaged forests (Siitonen 2001). In Fennoscandia, invertebrates (especially beetles) and cryptogams (especially fungi) comprise the largest groups of red-listed saproxylic organisms (Dahlberg and Stokland 2004). Changes in the population sizes of saproxylic invertebrates and cryptogams and the dynamics of their local colonisations and extinctions are poorly known. Therefore, knowledge about their requirements for long-term persistence is scant.

Protection of forest biodiversity has been attempted through the establishment of protected areas. Particularly during the last decade this approach has been combined with changes of silvicultural methods that also aim at preserving some components of biodiversity in the intervening matrix (*e.g.* Larsson and Danell 2001; Putz *et al*. 2001; Lindenmayer and Franklin 2002). Many threatened saproxylic species require dead wood that can occur both in managed and protected areas. Thus, both forest reserves and silvicultural methods are relevant for the preservation of these organisms (Kouki *et al*. 2001). In Finland and Sweden, the current strategy to preserve biodiversity is, to a greater extent than in many other countries, based on improvement of forest habitats by altered silvicultural methods (Raivio *et al*. 2001). Over the long-term, the combination of silvicultural methods and forest reserves have been predicted to increase the amount of dead wood of Norway spruce considerably (Ranius and Kindvall 2004). It will, however, take more than 100 years until these higher levels have been reached. In Finland, ongoing restoration projects (e.g., Kuuluvainen *et al*. 2002) aim at accelerating the formation of dead wood by damaging trees and creating small gaps in the forests by felling trees (Anonymous 2003).

In this study, we conducted population viability analyses of generalized saproxylic species by combining simulations of dead wood dynamics with a metapopulation model. The model species differed in their colonisation ability and local extinction risk, but were all given characteristics that would made their populations decreasing (but still present) in managed forest landscapes to such an extent that they would be red-listed. We compared two habitat history scenarios. The first emulated the situation in parts of Canada or Russia where forest landscapes are used for commercial forestry for the first time, and at the same time biodiversity preservation is considered (‘with constant conservation effort’). The second emulated the situation in parts of Fennoscandia, where there has been large-scale commercial forestry on almost all forest land for a long period of time, and now the forest landscape may be restored (‘with a bottleneck’). In the second scenario, we also studied the impact on population persistence if active measures are taken to increase the amount of dead wood rapidly, in comparison to generating dead wood at a lower, more natural rate. The study aims at answering the following questions: Do the efforts required for species conservation differ between a forest landscape used for commercial forestry for the first time and a landscape where almost all forests have long been used for commercial forestry? Is the amount of dead wood required for persistence of resident species dependent on whether dead wood is dispersed among all managed stands or concentrated in reserves? What is the most cost-efficient strategy for preservation of species associated with dead wood? Should we expect red-listed species with declining patch occupancy in a managed forest landscape to exhibit particular patterns of occurrence?

Methods

The metapopulation model

We modelled extinction risks of generalized saproxylic species (cryptogams or invertebrates) using the incidence function model (IFM) (Hanski 1994; 1999; 2000). We assumed that a forest landscape is divided into forest stands, and each stand is either occupied or not by a local population. The amount of habitat (denoted by Q) in the forest stand is equal to the volume of dead wood (in m^3) useful for the species.

The probability of colonisation of an empty stand is a function of its connectivity to existing local populations. The connectivity, S, of stand i is defined as:

$$S_i = \Sigma\, e^{-\alpha d_{ij}} p_j Q_j$$

where $p = 0$ for empty and $p = 1$ for occupied stands, Q is the amount of habitat, d is the distance between stands *i* and *j*, and 1/α is the mean dispersal distance. The colonisation probability *C* is assumed to be a function of connectivity and the constant *y*:

$$C_i = S_i^2 / (S_i^2 + y^2).$$

The risk of extinction of a local population is assumed to be inversely related to *Q*, because lower habitat amount gives rise to a smaller expected population size with a higher risk of local extinction. The extinction probability is given by

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

where *u* and *x* are species-specific parameters and (1 – *C*) represents the rescue effect.

We parameterised the IFM for the five model saproxylic species, setting the values of *α*, *u* and *x* for each to obtain a range species characteristics (Table 1). A species with a base-line combination of parameters was compared with species that have a higher and lower turn-over rate (*i.e.* rate of local colonisation and extinction) and species with longer and shorter dispersal distances. The mean dispersal distance has not been estimated for any threatened saproxylic organism in boreal forests, but it seems to vary widely (Jonsson *et al*. 2005). In the primaeval forest landscape, the extinction risk was <0.5% in 100 years for all species. By adjusting the value of *y* (a variable negatively related to the colonisation probability), the extinction rate of all species rose to 20% during the first 150 years in the scenario with a bottleneck. This was done to get a level of population decline that is similar to the level that is required for red-listing species according the IUCN's criteria (Anonymous 2001), which is used for the national red-listing in Sweden (Gärdenfors 2005). We should expect that species with these characteristics still occur in many managed forest landscapes. Furthermore, the adjusted extinction rate facilitated comparison of extinction risks between species during the following 100 years, because all species started with the same proportion of landscape with the species present. For the species with a high or low turn-over rate, the adjustment of y was in agreement with the combination of traits allocated to species in our model, *i.e.* those with a high local extinction risk obtained a lower value of y and thus a higher colonisation probability. Species with long-distance dispersal were assigned a higher value of y than those with short-distance dispersal. Thus, model species with long-distance dispersal are less successful in establishing new populations in comparison to species with short-distance dispersal. This relationship resulted from our desire to obtain the same extinction after 150 years for all species in the bottleneck scenario; for saproxylic organisms the empirical data supporting this relationship are weak (however see Jonsson 2003).

The landscape model

We considered a 13.4 x 13.4 km landscape, which is similar to the scale used by Swedish forest companies in landscape planning (Larsson and Danell 2001). The landscape consisted of 3,600 squares, corresponding to forest stands, each 5 ha, which is near the average for harvested forests in Sweden (Anonymous 2004). Because we assumed this landscape to be adjacent to similar landscapes, the edges of the landscape were wrapped around. Thus, stands situated at the left and upper margin were bounded to those at the right and lower margin, respectively, as if they were located on a spherical surface.

Landscape dynamics were taken into account with respect to the habitat for the model species. Hard dead wood of Norway spruce with most of the bark left (< 10 years after death) was considered to be suitable for the model species. Bark on dead wood is an important microhabitat; of 542 saproxylic red-listed invertebrates, 168 (31%) are directly dependent on bark as a microhabitat (Jonsell *et al*. 1998). In each stand that we modelled, either 0% or

100% of the trees were Norway spruce. The tree species composition of each stand was determined stochastically for each stand, with a 40% probability of being a Norway spruce stand. In Sweden, 43% of the growing stock is Norway spruce (Anonymous 2004). The amount of dead wood changed over time, determined by the management regime of the forest. We assumed that 50% of the volume of dead wood less than ten years old was suitable as a habitat for the model species. The remaining 50% was unsuitable, for instance, because of inappropriate microclimate or absence of appropriate rot types.

We simulated persistence of saproxylic organisms over a period of 250 years under two scenarios, imitating different forestry history. The first scenario ('with constant conservation effort') imitated landscapes where commercial forestry was practiced for the first time, and thus it was possible to avoid a bottleneck in the amount of habitat (which is the case in parts of Canada and Russia). The other scenario ('with a bottleneck') imitated the situation where commercial forestry had long been practiced in the entire landscapes, such as in southern Fennoscandia (Fig. 1), without efforts to conserve dead wood.

In both scenarios, the whole landscape was initially unmanaged, and the model species were present in all spruce stands. During the first 100 years, most forest stands (all except those that were unmanaged 100 – 150 years from the starting point) were cut and randomly given a value between 0 and 100, representing year of cut. Our simulations aimed at comparing different conservation regimes (i.e. a certain amount of large and small reserves and a certain management regime) that prevailed after that (Table 2). In the first scenario this conservation regime took over immediately after the first 100 years of logging (Fig. 1). This conservation regime was held constant 100–250 years from the starting point. In the second scenario, during the first 100 years 2% of the stands were left as small reserves, there were no large reserves, and forests were managed with traditional methods. This level can be compared to the fact that in Sweden about 1% of the productive forests outside the mountains are legally protected, and in most of the regions, less than 2% of the privately owned forests are classified as key habitats (Anonymous 2004). This regime was held constant 100–150 years from the starting point. Year 150 represented the current situation, when it was possible to select a strategy for the future. Thus, in this scenario the new conservation regime (Table 2) prevailed from this year.

To make the three measures to increase the amount of dead wood comparable, in the scenario with constant conservation effort we used the number of small reserves and level of dead wood increase in the managed forest that over the long run generated the same amount of dead wood at the landscape level as setting aside different numbers of large reserves. One 500-ha large nature reserve, for example, would correspond to 100 small reserves (5 ha each) and to an altered management generating a 15.7% increase of dead wood over all managed forest in the landscape.

For the scenario with a bottleneck, we modelled a combination of large and small reserves, and altered forest management, in a manner similar to that done to meet certification requirements and follow the current forestry policy in Sweden. Moreover, we analyzed each of the three measures taken one at a time, at a level that in the long run generates the same amount of dead wood as the combination (Table 2). We also compared a scenario with dead wood accumulated at a natural rate, with active efforts taken to speed up dead wood accumulation (Fig. 1). The details are presented in *Habitat amount*.

Using both scenarios, we predicted the extinction over a 850-year period, i.e., 150-1000 years from the starting point. We found that for all species, conservation measures were ranked in the same way regarding their extinction rates whether extinction rates were modeled over the initial 100 years or the entire period of 850 years. In the majority of the simulations, most of the extinctions took place within the first 100 years. For several scenarios, an extinction risk of 100% were yielded when the entire period was considered. Given these findings, we present only the extinction risk over 100 years, 150–250 years from the starting point.

Unmanaged forest stands are rarely evenly distributed in a forest landscape. We divided the landscape into 36 equally large (500 ha) squares. Each square was randomly assigned a value, representing the probability for each forest stand (5 ha) within the square to be a small reserve. These probability values were evenly distributed between zero and two times the proportion of small reserves in the whole landscape. For each stand, it was randomly determined whether it was managed or a small reserve, based on the probability value for the square where it was situated. When the number of small reserves was increased, we assumed that stands of ages with the highest amount of dead wood were selected. When the number of large reserves was increased, those squares with the largest proportion of unmanaged forest were selected. When the management regime was changed, the same change was imposed on all managed forests in the landscape.

Habitat amount

We modelled habitat amount in managed forests as in Ranius *et al*. (2003), *i.e.* by simulating dead wood dynamics taking into consideration forest growth, tree mortality, dead wood decay, and destruction of dead wood at forestry operations. Site index (*i.e.* tree height at 100 years) was assumed to be 24 m and the rotation period 100 years. We simulated two different management regimes: (*i*) traditional management with no particular care taken to preserve dead wood (dead wood volume = 7.4 m^3/ha), and (*ii*) biodiversity-oriented management, following the FSC's certification regulations (Anonymous 2000) (Table 3) (resulting in a dead wood volume of 16.8 m^3/ha). In managed forests in Sweden the present average is 6.1 m^3/ha (Fridman and Walheim 2000). In the landscape model, we predicted habitat amount in each stand based on a relationship between the amount of dead wood and stand age (Fig. 2) established from simulations. Furthermore, we used two measures of stochastic variability in the predictions: one between stands and one between years within each stand. We estimated the variability from 500 replicate simulation runs.

For unmanaged forests, we modelled long-term equilibrium between dead wood input (calculated from the volume of standing trees multiplied by tree mortality rate) and output (equivalent to decomposition) (Ranius *et al*. 2004). We used parameter values from Ranius *et al*. (2004) for central Sweden (site index = 24 m), which were based on field data from unmanaged forests. Our model found equilibrium at 83 m^3/ha, which is near the amount estimated in field surveys in Fennoscandia (Siitonen 2001). Of these 83 m^3/ha, 14 m^3/ha belonged to the early decay stage, and thus, 7 m^3/ha was assumed to be suitable for the model species (Fig. 2). As for managed forests, we estimated the variability from 500 replicate simulation runs.

In our landscape, management regimes applied to various stands changed over time. When a biodiversity-oriented management regime was adopted, it did not change the amount of dead wood until the forest was cut. After cutting, the amount of dead wood typical for the new management regime was immediately assigned because the largest change in the amount of dead wood takes place immediately after cutting (Ranius and Kindvall 2004). When an unmanaged stand became managed, the amount of dead wood typical for managed forests was assigned after cutting. This is a reasonable assumption because a large proportion of dead wood is usually destroyed at clear-cutting, mainly due to the machinery used for soil scarification (Hautala *et al*. 2004). In transition from a managed to an unmanaged stand, we assumed that it takes 40–140 years (dependent on the age of the managed stand when it was set aside) for dead wood of early decay stages to reach amounts typical for unmanaged forests. When a managed forest is set aside, it has the same amount of dead wood as a forest that was continuously managed until it had reached an age of 60 years. After that age, dead wood was assumed to increase faster in the unmanaged forest, due to higher standing volume and tree mortality. At the age of 140 years, the level of dead wood of early decay stages typical for unmanaged forests was assumed to be reached.

By actively damaging and felling trees in set aside forest stands and in forests where biodiversity-oriented management measures had been adopted, it is possible to increase the amount of dead wood much faster (Anonymous 2003). Levels of dead wood of early decay stages typical for unmanaged forest, or for biodiversity-oriented management, were assumed to be reached immediately after the forest is set aside, or management changed, if active measures were taken. We assumed active measures to be conducted only in forests older than 60 years, because it is difficult to generate dead wood of sufficient size in younger stands. In forests set aside or where biodiversity-oriented management had been adopted when they were younger, the damaging and felling of trees would take place when stands reach the age of 60 years.

In the model, we emulated the effect of weather by including regional stochasticity, which affected the extinction risk and colonisation rate by generating a temporal change in habitat amount, Q. This factor was equal for the entire landscape but varied stochastically between years according to a normal distribution. Arbitrarily, we set the coefficient of variation of this factor to 0.25.

Results

With constant conservation efforts, relatively small efforts were required to avoid extinction of the species (Table 4). For example, to keep the extinction risk below 5% at the landscape level during a 100-year period, one single large reserve (2.8% of the landbase), or small reserves on an area corresponding to two large reserves (*i.e.* 5.6% of the landbase) were sufficient for most species. Almost all species required the same number of reserves. A larger amount of dead wood was needed if it was generated by altered management on all forest land, instead of being generated in reserves. There was a difference in responses of modelled species to altered management methods (Table 4); species with long-distance dispersal or a high turn-over rate responded more strongly and positively to increases in amounts of dead wood due to altered management, in comparison to those with short-distance dispersal and a lower turn-over rate.

In the scenario with a bottleneck, it was difficult to avoid extinction at a landscape level; with the combination of measures that emulated the current forest policy in Sweden, the extinction risk during the following 100 years was 26% for the base-line species (Fig. 3). If these measures (*i.e.* small reserves cover 2% of the land and the remaining forest land is managed with traditional management methods) were not taken, the extinction risk rose to 98% during this period. In contrast to the scenario with constant conservation efforts, setting aside smaller reserves was a more efficient way to decrease the extinction risk under the bottle-neck scenario than was use of larger reserves (Fig. 3). If the amount of dead wood was increased only through altered management, the extinction risk remained high (72–100%) for all species. Active efforts to speed up the accumulation of dead wood considerably improved the effect, especially for altered management. For all species, a combination of efforts always generated an extinction risk in between the most efficient and the least efficient measure.

We divided the forest stands into categories reflecting the density of suitable habitat in the stand and the surrounding area (Fig. 4). The two categories with the lowest amount of dead wood correspond to typical managed forest, while the two categories with the highest amounts correspond to typical old-growth forest. After the first 100-year period of forest cutting, for the base-line species, the frequency of occupancy was only weakly correlated with the amount of dead wood per stand (Fig. 4). Fifty years later, the frequency of occupancy was about three times higher in forest stands with dead wood amounts typical of unmanaged forests in relation to managed forests. The relationship between presence/absence per stand and amount of dead wood was stronger at a larger spatial scale than at the stand level (Fig. 4).

Discussion

Extinction risks when dead wood is generated in large or small reserves

In a landscape with constant conservation efforts, large reserves generated a lower extinction risk than the same protected area divided into smaller reserves. The same pattern has been achieved in many other theoretical studies (*e.g.* Diamond 1975; Wright and Hubbel 1983; Burkey 1995). This may be because the habitat is more fully used when it is more concentrated, as it is easier to colonise dead wood that is situated nearby the dispersal source (Jonsell *et al*. 1999; Edman *et al*. 2004a). However, when we studied a landscape with a habitat bottleneck, we found that setting aside forests in small areas generated the lowest extinction risk. This was because when small areas are set aside, it is possible to select older stands (which are those with the largest amount of dead wood), while large reserves must contain both older and younger forest stands. In the long run, dead wood per hectare in large reserves will reach the same level as in the small ones. Because that process is slow, however, many species will go extinct before sufficient amounts of dead wood have accumulated in the large reserves.

Our results do not suggest that protection of large contiguous areas should not be prioritised in Fennoscandia. On the contrary, it is urgent to protect the remaining few more continuous forest areas with high conservation value, as restoration is time-consuming. This is because large forest areas with high conservation values are rare in relation to such areas of smaller size (for instance, on privately owned land in Sweden the mean size of woodlands classified as key habitats, *i.e.* habitats that may sustain red-listed species, is 3 ha, and the median is 1.4 ha (Anonymous 2004)), and some species are confined to the cores of larger forest areas (Berglund and Jonsson 2003) or forests with long continuity (Siitonen and Saaristo 2000). However, conservation strategies in forest landscapes should not only be based on standard rules regarding the positive effect of habitat patch size and the negative effect of fragmentation. The current spatial structure of the most valuable forests and the potential to increase the habitat amount rapidly by habitat restoration must also be considered.

Cost efficiency of biodiversity conservation: creation of reserves or altered management

Dead wood generated by altered management reduced extinction risks to a lower extent than if the same amount of dead wood was generated in unmanaged forest (Table 4). To evaluate conservation measures information about the species' response is not enough, but estimates of financial costs must also be considered. Jonsson *et al*. (in press) have estimated the cost of setting aside a forest stand typical for different parts of Sweden and compared with biodiversity-oriented management measures that aim at increasing the amount of dead wood (here including 3 artificially created high stumps per hectare at thinnings and harvesting, 5% of the land retained at harvesting, and that 80% of the snags are preserved at harvesting). In northern Sweden, the cost of generating a certain amount of dead wood was highest for biodiversity-oriented management, while in southern and central Sweden setting aside forests was more expensive (Table 5). This means that if our model species are to be preserved in northern Sweden, it is more cost-efficient to set aside forests than to alter management in the harvested area. However, in southern and central Sweden, it is less clear which is the most cost-efficient strategy; to generate a certain amount of dead wood by setting aside a forest is more expensive, but on the other hand the reduction of extinction risks is larger, in comparison to altered management.

There was a large difference between species in their response to altered management. For species with high colonisation ability and no threshold in the amount of dead wood at the stand level (species B and D), the spatial structure is less important, and thus biodiversity-oriented management was more useful for the preservation for these species than for others. Therefore, dependable knowledge about the colonisation ability of saproxylic organisms in boreal forests is critical for a firm evaluation of the cost-efficiency of conservation efforts in managed forests, but today such data are generally absent (see however Jonsson 2003, Edman *et al*. 2004b).

The combination of measures was always less efficient in decreasing the extinction risk than setting aside small reserves, given that the same amount of dead wood was generated. This suggests that for individual species there is no advantage to combining measures. However, for the preservation of a larger assemblage of species it may be an advantage, because species differ in their habitat requirements. In this study, we assumed dead wood in managed and old-growth forest to be of equal quality. For a species that prefers dead wood in large, unmanaged forest areas (for instance, because they require a high local habitat density continuously over time (Siitonen and Saaristo 2000), or dead wood in managed forests (for instance, because they prefer the warmer microclimate on clear-cuts; Lindhe and Lindelöw 2004) the relative efficacy of different conservation efforts would obviously differ from the results in this study.

Efforts to speed up the generation of dead wood

If a managed landscape is to be restored, the result, in terms of population persistence, becomes much better if the accumulation of dead wood is actively enhanced (Fig. 3). This was particularly evident when management was altered. It is mainly at final cutting that biodiversity-oriented management increases the amount of dead wood (Ranius and Kindvall 2004). Thus, it takes a rotation period until altered management generates an increase in dead wood in all stands in a managed landscape. The cases with accelerated accumulation of dead wood meant that in all managed forests older than 60 years the amount of dead wood in earlier decay stages immediately reaches the level typical for biodiversity-oriented management. We simulated the scenario mainly in order to analyse the effect of a delayed increase of dead wood. For economic reasons it is hardly realistic to actively accelerate tree mortality over entire forest landscapes at one single occasion, however, it has been suggested that the accumulation of dead wood should be accelerated by more measures carried out at thinnings (Jonsson *et al*. 2005). Active measures are also a realistic alternative in more restricted areas, such as, nature reserves (Anonymous 2003).

Delayed population changes after a change in amount of dead wood

Under the IUCN's red-listing criteria (Anonymous 2001), annually reproducing species that show a population decline of at least 30% during the last 10 years are classified as vulnerable (VU), while they are near threatened (NT) if the decrease is somewhat lower. With the bottleneck scenario, during the ten-year-period before 'today' (between year 140 and 150), all species went extinct from about 7-16% of the landscapes and their incidence per stand decreased by 7-54%. Thus, the model species we have studied would have been classified as NT, or perhaps VU, in the Swedish red-list. Despite this, the species also occurred frequently in managed forest stands, especially early after the first cutting (Fig. 4). This is probably due to a delay in the population decrease in relation to the habitat decrease, and to migration within the landscape. Thus, even a species occurring relatively frequently in managed forests may become extinct in a landscape because it is sensitive to the consequences of silviculture. For that reason, observations of saproxylic species in managed forest stands with low amounts of suitable substrate do not necessarily indicate that this habitat density is enough for species persistence. This is especially the case if the habitat density has only been studied at a small spatial scale and after a recent decline of habitat.

The extinction risk was much larger in the scenario with a bottleneck, *i.e.* when there had been a period with a low amount of habitat (Table 4; Fig. 3). This is caused by a delay in the formation of dead wood (Ranius and Kindvall 2004), and a restoration lag in the populations, which enhanced the extinction risk even after the amount of habitat has increased (Huxel and Hastings 1999). With a combination of measures in the bottleneck scenario, the extinction risk for our model species during the next 100 years decreased from almost 100% to 9–96%. Most Swedish counties contain 20–200 landscapes similar in extent to those modelled in this study. If the extinction risk per landscape could be decreased below 50%, that would be enough to hold the extinction risk low at the county level, because the species would survive at least in a few forest landscapes. For strong dispersers a rescue effect would also reduce their extinction risk. If the goal is to preserve biodiversity at a county level, the same conservation measures should not be practiced everywhere. Instead, for each forest landscape habitats that occur or recently have occurred in high amounts should be identified, as they consequently are expected to harbour species communities with many threatened species at a relatively high abundances (cf. Axelsson and Östlund 2001; Nilsson and Baranowski 2003). Conservation efforts should be focused on maintaining and restoring these habitats, because it is much easier to preserve species associated with these habitats in landscapes where they have not been exposed to a long bottleneck in habitat availability.

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Table 1. Parameters used in the incidence function model for five model species. 1/α is the mean dispersal distance (in km). Definition of other parameters, see Methods: *The metapopulation model*.

	A. Base-line	B. Long-distance dispersal	C. Short-distance dispersal	D. High turn-over rate	E. Low turn-over rate
u	0.5	0.5	0.5	0.85	0.2
x	0.2	0.2	0.2	0.1	0.4
y	60.5	765	2.05	33.7	300
1/α	0.5	2	0.1	0.5	0.5

Table 2. Four assumed conservation regimes in a forest landscape that is restored after a bottleneck, each in the long run generating the same amount of dead wood as the combination (1.86 m^3/ha).

Conservation regime	Large reserves (numbers/landscape and % of the area)	Small reserves (% of the area)	Altered management. Increase of dead wood of in relation to a forest with traditional management
Only large reserves	5 (13.9%)	0	0
Only small reserves	0	13.9%	0
Only altered management	0	0	79%
All measures	1 (2.78%)	2.23%	53%*

* equal to the situation with biodiversity-oriented management (see Table 3).

Table 3. Assumed differences between traditional forest management and biodiversity-oriented management that influence the amount of dead wood in managed Norway spruce forests. The biodiversity-oriented management of managed stands, in combination with setting aside stands, means that the FSC-regulations are followed.

Management measure	Traditional management	Biodiversity-oriented management
Artificially created high stumps at thinning and final cutting (number/ha)	0	3
Area with retained trees at final cutting (diameter of these trees 85% of the mean)	0%	5%
Dead wood destroyed at final cutting	58%	20%
At occasions of high tree mortality: (*i*) minimum volume of newly dead wood present when it may be removed, and at such a removal (*ii*) the amount of newly dead wood retained.	(*i*) 2 m^3/ha (*ii*) 0 m^3/ha	(*i*) 3 m^3/ha (*ii*) 1 m^3/ha

Table 4. Outcome from simulations in a landscape with constant conservation efforts with one of three possible measures taken to increase the amount of dead wood. (*i*) Extinction risk over 100 years, with the amount of dead wood equal to a landscape with one nature reserve. (*ii*) Amount of dead wood required for maintaining the extinction risk during 100 years below 5%, measured as equivalents of large reserves (*i.e.* the number of 500-ha reserves with unmanaged forests generating the same amount of dead wood in a 18,000 ha managed forest landscape). Model species denoted A-E according to Table 1. n = 500.

Species	Large reserves		Small reserves		Biodiv. management	
	i	*ii*	*i*	*ii*	*i*	*ii*
A. Base-line	1%	1	25%	2	74%	3
B. Long-dist.	7%	2	30%	2	42%	3
C. Short-dist.	1%	1	18%	2	98%	5
D. High turn-over	0%	1	20%	2	43%	3
E. Low turn-over	0%	1	94%	3	100%	9

Table 5. Estimated cost-efficiency of increasing the amount of dead wood by (*i*) biodiversity-oriented management (includes 3 artificially created high stumps per hectare at thinnings and harvesting, 5% of the land retained at harvesting, and that 80% of the snags are preserved at harvesting) and (*ii*) setting aside a forest from Jonsson *et al*. (in press). The cost is an estimate of the present value at the time for final cutting and the amount of dead wood generated in the long run. From data for forest stands dominated by Norway spruce typical for three parts of Sweden (see Jonsson *et al*., in press, for details).

	i) biodiversity-oriented management			*ii*) setting aside a forest		
Part of Sweden	Cost (SEK/ha)	Dead wood (m^3/ha)	Cost / dead wood (SEK/m^3)	Cost (SEK/ha)	Dead wood (m^3/ha)	Cost / dead wood (SEK/m^3)
Southern	2201	7.52	**290**	69528	92	**760**
Central	1261	4.93	**260**	43424	68	**640**
Northern	1000	2.36	**420**	9870	63	**160**

Fig. 1. The two types of landscape scenarios that were analysed: (*i*) landscape with constant conservation efforts, and (*ii*) landscape with a bottleneck, with a natural increase of dead wood without active efforts, and an increase of dead wood speeded up with active efforts. Prop. unman. = proportion of the total forest area that was unmanaged, Dead wood / ha = the amount of dead wood per hectare over the entire landscape, in relation to the initial amount. In all scenarios, the extinction risk was predicted for a 100-year period, 150 to 250 years from the starting point.

Fig. 2. Amount of dead wood of Norway spruce suitable for the model species (equal to half of the total amount of dead wood, because the other half was considered unsuitable for the study species) in relation to stand age of managed forests, used as input in the incidence function model. Output from simulations of dead wood dynamics (taking into account forest growth, tree mortality, dead wood decay, and destruction of dead wood by forestry operations) in Norway spruce forests, managed with traditional or biodiversity-oriented methods (Table 3), or unmanaged.

Fig. 3. Extinction risk (% over 100 years) in a landscape with a bottleneck, with the new management regime in the long run generating an amount of dead wood equal with a landscape with five large reserves (Table 2). With (Fig. 3b) or without (Fig 3a) active efforts taken to speed up the accumulation of dead wood. Model species denoted A–E according to Table 1. $n = 500$.

Fig. 4. Occupancy per stand of species A at three different occasions in relation to the amount of suitable dead wood. The amount of suitable dead wood was measured at three different spatial scales. In the landscape, forestry started during the first 100 years, followed by a

constant conservation regime (small reserves on 2% of the area, traditional management in the managed forests). $n = 500$. Amount of suitable substrate measured (*i*) per stand, (*ii*) within a radius of 500 m, (*iii*) within a radius of 1,000 m.

Fig. 1

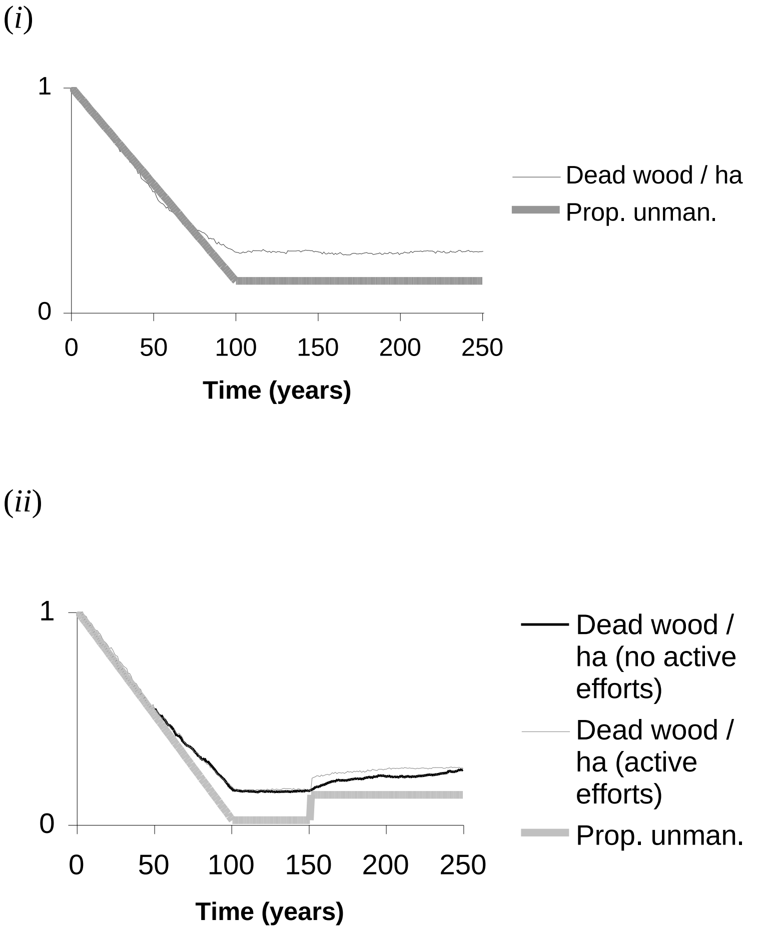

(i)
1
0
0
50
100
150
200
250
Time (years)
Dead wood / ha
Prop. unman.
(ii)
1
0
0
50
100
150
200
250
Time (years)
Dead wood / ha (no active efforts)
Dead wood / ha (active efforts)
Prop. unman.

Fig. 2


8
6
4
2
0
Amount of dead wood
(cubic meter per hectare)
0
20
40
60
80
100
Age (years)
Unmanaged
Biodiversity-oriented
Traditional

Fig. 3a

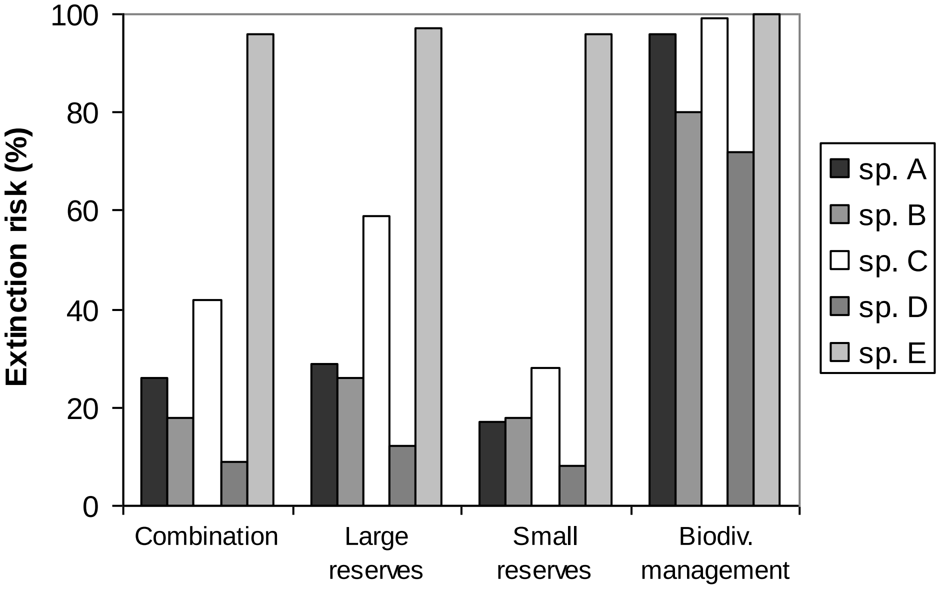

100
80
60
40
20
0
Extinction risk (%)
Combination
Large reserves
Small reserves
Biodiv. management
sp. A
sp. B
sp. C
sp. D
sp. E

Fig. 3b

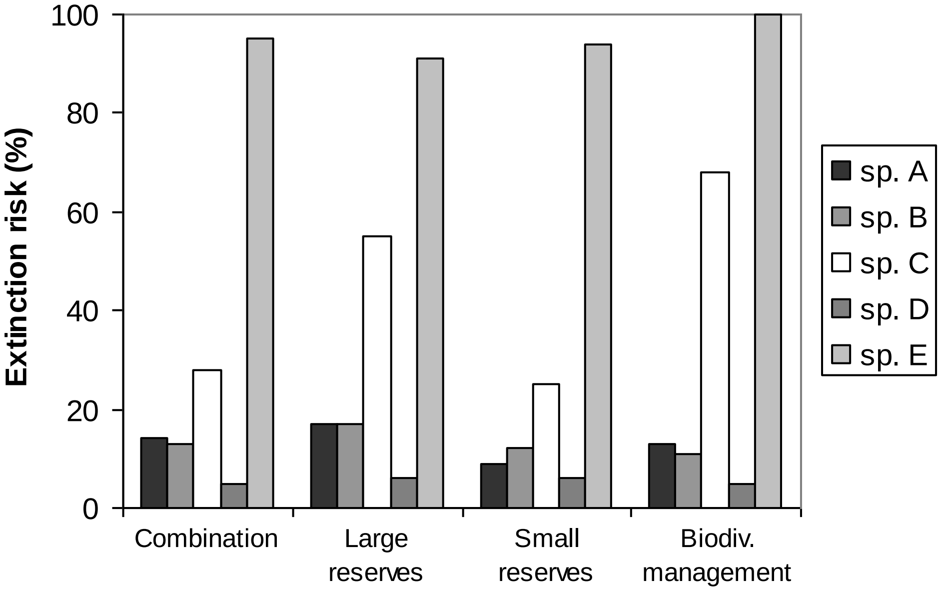
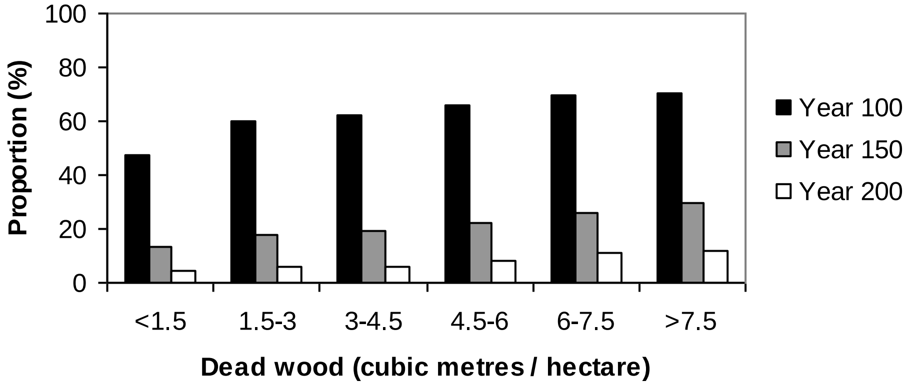
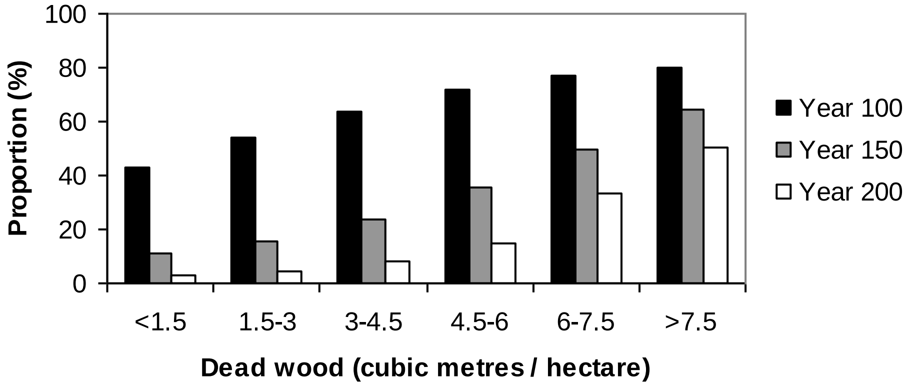

100
80
60
40
20
0
Extinction risk (%)
Combination
Large reserves
Small reserves
Biodiv. management
sp. A
sp. B
sp. C
sp. D
sp. E

Fig. 4

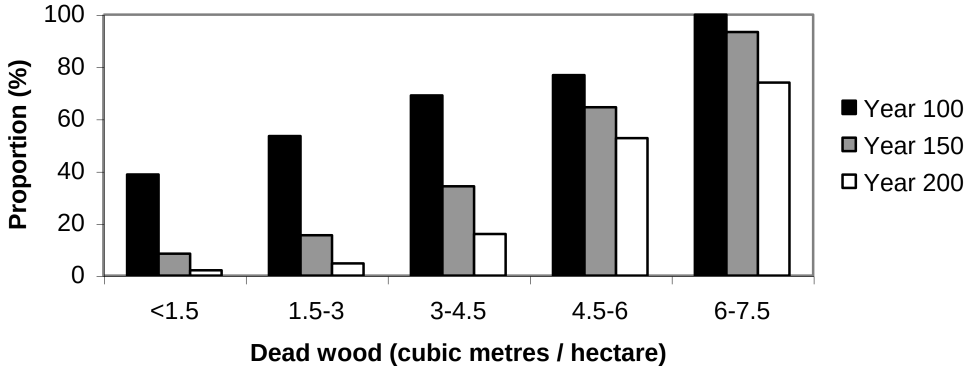
(*i*)



(*ii*)



(*iii*)



for >7.5 m^3/ha: $n = 0$.

References

Akçakaya H.R., Radeloff V-C., Mladenoff, D.J. and He, H.S. 2004. Integrating landscape and metapoulation modeling approaches: viability of the sharp-tailed grouse in a dynamic landscape. Conservation Biology 18: 526-537.

Anonymous 2000. Svensk FSC-standard för certifiering av skogsbruk. 2:a uppl. Svenska FSC-rådet, Uppsala, Sweden (in Swedish).

Anonymous 2001. IUCN red list categories and criteria: ver 3.1. IUCN, Cambridge, UK.

Anonymous 2003. Ennallistaminen suojelualueilla. Ennallistamistypryhmän mietintö. Suomen ympäristö 618. Ympäristöministeriö, Helsinki (in Finnish).

Anonymous 2004. Skogsstatistisk årsbok. Skogsstyrelsen, Jönköping, Sweden (Statistical yearbook of forestry. In Swedish with English summary).

Axelsson A.-L. and Östlund L. 2001. Retrospective gap analysis in a Swedish boreal forest landscape using historical data. Forest Ecology and Management 147: 109-122.

Baker W.L. and Mladenoff D.J. 1999. Progress and future directions in spatial modeling of forest landscapes. *In* Mladenoff D. J. and Baker W.L. (eds.), Spatial modeling of forest landscape change: approaches and applications, pp. 333-349. Cambridge University Press, Cambridge.

Berglund H. and Jonsson B.G. 2003. Nested plant and fungal communities; the importance of area and habitat quality in maximizing species capture in boreal old-growth forests. Biological Conservation 112: 319-328.

Bryant D., Nielsen D. and Tangley L. 1997. The last frontier forests: ecosystems and economies on the edge. World Resources Institute, Washington.

Burkey T.V. 1995. Extinction rates in archipelagos: implications for populations in fragmented habitats. Conservation Biology 9: 527-541.

Dahlberg A. and Stokland J.N. 2004. Vedlevande arters krav på substrat. Rapport No. 7.

Skogsstyrelsen, Jönköping, Sweden (In Swedish).

Diamond J.M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation 7: 129-146.

Edman M., Kruys N. and Jonsson B.G. 2004a. Local dispersal sources strongly affect colonization patterns of wood-decaying fungi on spruce logs. Ecological Applications 14: 893-901.

Edman M., Gustafsson M., Stenlid J. and Ericson L. 2004b. Abundance and viability of fungal spores along a forestry gradient: Responses to habitat loss and isolation? Oikos 104: 35-42.

Esseen P.-A., Ehnström B., Ericson L. and Sjöberg K. 1997. Boreal forests. Ecological Bulletins 46: 16-47.

Fridman J. and Walheim M. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. Forest Ecology and Management 131: 23-36.

Gärdenfors, U. (Ed.) 2005. The 2005 Red List of Swedish species. Artdatabanken, Uppsala.

Hanski I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63: 151-162.

Hanski I. 1999. Metapopulation ecology. Oxford University Press, Oxford.

Hanski I. 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. Annales Zoologici Fennici 37: 271-280.

Hautala H., Jalonen J., Laaka-Lindberg S. and Vanha-Majamaa I., 2004. Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. Biodiversity and Conservation 13: 1541-1554.

Huxel G. R. and Hastings A. 1999. Habitat loss, fragmentation, and restoration. Restoration Ecology 7: 309-315.

Jonsell M., Weslien J. and Ehnström B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7: 749-764.

Jonsell M., Nordlander G. and Jonsson M. 1999. Colonization patterns of insects breeding in wood-decaying fungi. Journal of Insect Conservation 3: 145-161.

Jonsson M. 2003. Colonisation ability of the threatened tenebrionid beetle *Oplocephala haemorrhoidalis* and its common relative *Bolitophagus reticulatus*. Ecological Entomology 28: 159-167.

Jonsson B.G., Kruys N. and Ranius T. 2005. Ecology of species living on dead wood – lessons for dead wood management. Silva Fennica 39: 289-209.

Jonsson M., Ranius T., Ekvall H., Bostedt G., Dahlberg A., Ehnström B., Nordén B. and Stokland J. N. 2006. Cost-efficiency of silvicultural measures to increase substrate availability for red-listed wood-living organisms in Norway spruce forests. Biological Conservation, in press.

Kouki J., Löfman S., Martikainen P., Rouvinen S. and Uotila A. 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. Scandinavian Journal of Forest Research Supplement 3: 27-37.

Kuuluvainen T., Aapala K., Ahlroth P., Kuusinen M., Lindholm T., Sallantaus T., Siitonen J. and Tukia H. 2002. Principles of ecological restoration of boreal forested ecosystems: Finland as an example. Silva Fennica 36: 409-422.

Larsson S. and Danell K. 2001. Science and the management of boreal forest biodiversity. Scandinavian Journal of Forest Research Supplement 3: 5-9.

Lindenmayer D.B. and Franklin J.F. 2002. Conserving forest biodiversity. A comprehensive multiscaled approach. Island Press, Washington.

Lindhe A. and Lindelöw Å. 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. Forest Ecology and Management 203: 1-20.

Nilsson S.G. and Baranowski R. 2003. Biologisk mångfald i Linnés hembygd i Småland 3. Rödlistade vedskalbaggar i centrala Stenbrohults socken. Entomologisk Tidskrift 124: 137-157 (Biodiversity at Linnaeus' birthplace in the parish of Stenbrohult, southern Sweden. 3. Red-listed wood-beetles. In Swedish, English abstract).

Putz F.E., Blate G.M., Redford K.H., Fimbel R. and Robinson, J. 2001. Tropical forest management and conservation of biodiversity: an overview. Conservation Biology 15: 7-20.

Raivio S., Normark E., Pettersson B. and Salpakivi-Salomaa P. 2001. Science and the management of boreal forest biodiversity—a forest industries' view. Scandinavian Journal of Forest Research Supplement 3: 99-104.

Ranius T. and Kindvall O. 2004. Modelling the amount of coarse woody debris produced by the new biodiversity-oriented silvicultural practices in Sweden. Biological Conservation 119: 51-59.

Ranius T., Kindvall O., Kruys N. and Jonsson B.G. 2003. Modelling dead wood in Norway spruce stands subject to different management regimes. Forest Ecology and Management 182: 13-29.

Ranius T., Jonsson B.G. and Kruys N. 2004. Modeling dead wood in Fennoscandian old-growth forests dominated by Norway spruce. Canadian Journal of Forest Research 34: 1025-1034.

Siitonen J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11-41.

Siitonen J. and Saaristo L. 2000. Habitat requirements and conservation of *Pytho kolwensis,* a beetle species of old-growth boreal forest. Biological Conservation 94: 211-220.

Singer M.T. and Lorimer C.G. 1997. Crown release as a potential old-growth restoration approach in northern hardwoods. Canadian Journal of Forest Research 27: 1222-1232.

Sjögren-Gulve P. and Hanski I. 2000. Metapopulation viability analysis using occupancy models. Ecological Bulletins 48: 53-71.

Wright S.J. and Hubbell S.P. 1983. Stochastic extinction and reserve size: a focal species approach. Oikos 41: 466-476.