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Citation for the published paper:
Ranius, Thomas. & Roberge, Jean-Michel. (2011) Effects of intensified forestry on the landscape-scale extinction risk of dead-wood dependent species. *Biodiversity and Conservation*. Volume: 20, Number: 13, pp 2867-2882.
http://dx.doi.org/10.1007/s10531-011-0143-8.

Should be cited as: Ranius, T. & Roberge, J.-M. (2011) Effects of intensified forestry on the landscape-scale extinction risk of dead wood dependent species. Biodiversity and Conservation 20: 2867-2882.

The published article is available at: http://link.springer.com/article/10.1007%2Fs10531-011-0143-8/fulltext.html

Effects of intensified forestry on the landscape-scale extinction risk of dead-wood dependent species

Short title: Effects of intensified forestry on extinction risks

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Abstract

In the future, a significant proportion of northern forests may become intensively managed through the planting of monospecific stands of native or introduced trees, and the use of multiple silvicultural treatments such as forest fertilization. Such an intensification of management in selected parts of the landscape is suggested by different zoning models, for example the Triad approach, which is under evaluation in some regions of North America. In this study, based on Fennoscandian conditions, we predicted landscape-scale extinction risks of five hypothetical model insect species dependent on fresh dead wood from Norway spruce (*Picea abies*), by simulating colonizations and local extinctions in forest stands. Intensified forestry applied to 50 % of the spruce stands led to strongly increased extinction risks of all species during the following 150 years. For one species – the sun-exposure specialist – there were strong effects already after 50 years. The negative effects of intensive plantation forestry could be compensated for by taking greater biodiversity conservation measures in other managed forests or by setting aside more forests. This is consistent with the Triad model, which is according to our analyses an effective way to decrease extinction risks, especially for the short-dispersing species and the species associated with closed forest. A zoning of forest land into intensive forestry, conventional forestry, and set asides may be better at combining increased timber production and maintenance of biodiversity in comparison to landscapes where all production forests are managed in the same way.

Keywords: CWD, functional zoning, metapopulation, plantation forestry, population viability analysis, saproxylic insects, Triad

Introduction

Forest management includes a range of intensities, from management based on close-to-nature principles (e.g., Madsen and Hahn 2008) to plantation forestry involving non-native tree species and multiple silvicultural treatments. Plantation forestry generally implies that tree species (native or introduced) are sown or planted so that evenly spaced and even-aged monocultures are obtained. In 2006 it was estimated that plantation forests covered 3.5 % of the forest area in the world, and the covered area was increasing with 2 % per year (Anonymous 2006).

In Sweden, it has been estimated that 4 million ha could be used for intensified forestry, which may be compared with the country’s 23 million ha of productive forest. The main part of the land potentially dedicated to intensified forestry is currently supporting conventionally managed forests, and a smaller part is abandoned agricultural land (Larsson et al. 2009). Intensive forestry in Sweden involves multiple silvicultural treatments (including fertilization) in monocultures of introduced tree species such as lodgepole pine (*Pinus contorta*), hybrid aspen (*Populus tremula* × *P. tremuloides*), and hybrid larch (*Larix* × *eurolepsis*), or of native tree species, especially Norway spruce (*Picea abies*) (Larsson et al. 2009). In Sweden, forest plantations are increasing, and in 2005 they covered 2.4% of the forest land (Anonymous 2006).

Due to negative effects on the abundance of natural forest structures and processes, intensified forestry has been shown to have negative effects on large numbers of naturally occurring species at the scale of forest stands (e.g., Baguette et al. 1994; Chey et al. 1997; Magura et al. 2000). For example, many saproxylic species (i.e. species dependent on dead wood) may be affected because stands managed intensively for the sole aim of maximizing timber production contain virtually no dead wood of larger diameters, except ephemerally in the case of accidental disturbances, where dead trees are typically salvaged shortly after disturbance. When experts were asked about intensified management in Sweden, they estimated that the effect on all evaluated organism groups (vascular plants, lichens, bryophytes, grasses, shrubs, birds, saproxylic species, and red-listed species) would be strongly negative (Gustafsson et al. 2009). Hence, at the scale of individual forest stands, intensive forestry is not compatible with the conservation of native biodiversity. Consequently, implementing intensive forestry over the entire forest land base would clearly not be compatible with society's commitment to sustainable development. However, little is known about the ecological effects of dedicating various proportions of landscapes and regions to intensive forestry.

A forest management concept which has gained interest in the past decades is the Triad model (Seymour and Hunter 1992), whereby the forest landscape is divided into three types of uses: (1) intensive forestry, (2) ecological forestry and (3) set-asides. In that zoning system, the negative ecological effects of intensive forestry would be compensated by increased biodiversity conservation measures in the rest of the landscape through ecological forestry and forest protection. Such a zoning model is in place in some regions, e.g. southwestern Australia (Stoneman 2007). The Triad has also been proposed for implementation across Canada's boreal forest (Anonymous 1999) and case studies are ongoing in different regions (e.g. Montigny and MacLean 2006; Messier et al. 2009). However, empirical studies of the consequences of such an approach for biodiversity are difficult, because most species extinctions at the landscape level occur with some delay after the management regime has been changed (Ranius and Kindvall 2006).

In this study we use population viability analyses of generalized model species over 250 years to isolate the effect of different landscape zoning scenarios in the long term. We predict the landscape-scale extinction risk for five saproxylic model insect species by combining simulations of habitat dynamics with a metapopulation model. The aims were: (1) to analyse how long time it takes before intensified forestry increases the extinction risk at the landscape level for species with different characteristics, (2) to compare the response of species with different habitat affinities and life-history traits, and (3) to test the efficacy of compensation measures whereby greater biodiversity consideration is made in the rest of the landscape to counteract the potential negative effects of intensified forestry.

Methods

The metapopulation model

For a hypothetical forest landscape divided into forest stands, we used computer simulations to predict the availability of dead wood in every forest stand and the colonization-extinction dynamics of the saproxylic model species in these stands. As response variable we used the extinction risk at the landscape level, estimated from 1,000 replicates for each scenario–species combination. This number of replicates is sufficient to obtain stable outcomes among simulation runs.

We used the incidence function model (IFM) equation to predict colonization-extinction dynamics (Hanski 1994; 2000). Every year each stand could either be 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 suitable for the species.

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

$$S_i = \Sigma\, e^{-\alpha d_{ij}} p_j Q_j \qquad \text{eq (1)}$$

where $p = 0$ for unoccupied and $p = 1$ for occupied stands, Q is the amount of habitat, d is the distance between stands i and j, and $1/\alpha$ is the mean dispersal distance. The yearly colonization probability C of an unoccupied stand is assumed to be a function of connectivity and the constant y:

$$C_i = S_i^2 / (S_i^2 + y^2) \qquad \text{eq (2)}$$

A higher value of y implies that a higher connectivity (i.e. larger populations nearby) is required to obtain a given colonization probability, which may be due to a stronger Allee effect. The yearly extinction probability for an occupied stand is given by

$$E_i = \min\{1, (u / Q_i^x)(1 - C_i)\} \qquad \text{eq (3)}$$

where u and x are species-specific parameters and $(1 - C_i)$ represents the rescue effect. The risk of extinction of a local population is assumed to be inversely related to Q, because population size tends to be smaller when the habitat amount is lower, which generates a higher risk of local extinction. u reflects the level of the local extinction risk and x the difference in extinction risk between stands holding large vs. small dead wood amounts.

Model species

We modeled the metapopulation dynamics of five generalized model species of insects having different characteristics regarding mean dispersal distance and substrate requirements: a "normal" (i.e. average) species, a long-distance disperser, a short-distance disperser, a closed-forest specialist and a sun-exposure specialist (Table 1). Furthermore, due to poor empirical knowledge about local extinction risks and turnover rates, we modeled four additional species to explore the sensitivity to the local extinction risk parameters. All species were dependent on dead wood of Norway spruce being younger than 10 years and having a diameter >10 cm. Young dead wood is an important substrate, especially for saproxylic insects living under bark, because almost a half of Norway spruce dead wood is without bark after 10 years (calculated from data presented in Ranius et al. 2003). The inner bark and subcortical space of dead trees is an important microhabitat; among 542 saproxylic red-listed invertebrates in Sweden, 168 (31 %) are directly dependent on bark as a microhabitat (Jonsell et al. 1998). We assumed that 50 % of the volume of dead wood less than 10 years old and having a diameter > 10 cm was suitable as habitat for the model species. The remaining 50 % was unsuitable, for instance, because of unfavorable microclimate or absence of appropriate rot types. We adjusted the value of y after setting the values for the other parameters in such a way that the extinction risk during the following 250 years became about 50 % for all model species if the current management regime (95% conventionally managed and 5% set-asides) would prevail during the whole period. Hence, all model species represent species which would run a significant risk of extinction given today's management regime.

There are only a few studies of the spatial occurrence patterns of saproxylic insects in boreal forests that indicate at which spatial scale colonizations take place. For the saproxylic beetle *Hadreule elongatula* there was a positive relationship between occupancy and the amount of habitat (clear-cuts with high stumps) within a radius of 1 km (Schroeder et al. 2006), and for *Bellamira scalaris* between larval abundance and the non-coniferous forest cover within a radius of 1.2 km (Saint-Germain and Drapeau 2011). For another saproxylic beetle, *Harminius undulatus*, the strongest relationship between observed occurrence patterns and stand-scale probability of occurrence was predicted by a metapopulation model in which $1/\alpha$ (using eq. 1) was set to 1500 – 2500 m (Schroeder et al. 2007). Furthermore, in a study of beetles (Coleoptera) and bugs (Hemiptera) specialized on fresh aspen (*Populus tremula*) wood, the strongest relationship between species richness and amount of aspen wood in the surrounding was obtained with $1/\alpha$ = 93 m (Ranius et al., subm ms). Consequently, we assumed mean dispersal distances varying between 100 m and 2 km for the model species.

For *u* and *x*, which regulates the local extinction risk, no relevant empirical data are available. We believe that the extinction risk within a smaller area (with the rescue effect excluded) is high for many saproxylic insect species, because their abundance may be very low (for many species, on average a few individuals per managed forest stand; Schroeder et al. 2006) However, in forest landscapes local extinctions may still be rare because they are counteracted by a rescue effect (i.e by immigration from surrounding forest stands). For the normal species, we adjusted the values of *x* and *u* to obtain a yearly extinction risk of 10 % in an average future unmanaged stand, and 50 % at the stand age with the lowest amount of dead wood in a future conventionally managed forest and with the rescue effect excluded. As a sensitivity analysis, we also tested "normal" species with other combinations of local extinction risks (2 % and 50 %; 25 % and 50 %; 10 % and 20 %; and 10% and 80 %, in unmanaged stands and in stands with the lowest amount of dead wood in managed forest, respectively).

For the sun-exposure and closed forest species, we used the same *x*-value as for normal species and adjusted *u* to obtain a local extinction risk of 10 % under the best conditions also for these species. We assumed that in stands with high amounts of dead wood ($Q > 1.15 m^3/ha$, which is the case for all unmanaged forest and some managed forest; Fig. 1) the species with long-distance dispersal had a higher extinction risk than the normal species; *x* and *u* were set so the local extinction risk in a future unmanaged stand was 25 % per year. On the contrary, the species with short-distance dispersal was given values of *x* and *u* that generated a local extinction risk in a future unmanaged stand of only 2 %. This is based on knowledge that strong dispersers may be poorer competitors than weak dispersers (Tilman et al. 1994) and that populations with higher dispersal rates and ranges tend to suffer to a larger extent from dispersal mortality (Fahrig

2007). We believe this makes a difference especially when the density of dead wood is high. Hence, we adjusted *x* and *u* so the extinction risk remains the same as for the normal species (50 %) when Q = 1.15 m^3/ha. Higher levels of dispersal may also lower the actual local extinction risk due to a rescue effect. However, this effect is not included in the *x* and *u* parameters but is a separate factor (eq. 3).

For all species except two (the closed forest and sun-exposure species) the dead wood was of equal quality independent on forest age. We assumed that for the sun-exposure specialist, dead wood was only suitable in managed forests with an age < 20 years, and to some extent (only 0.5 m^3/ha) in unmanaged forest, while the other dead wood (in managed forests > 20 years + all dead wood in unmanaged forest except 0.5 m^3/ha which is assumed to be sun-exposed) was suitable for the closed forest specialist. This is because in unmanaged forest, gaps are created due to small-scale disturbances, while gaps are generally avoided in even-aged forest management (Caron et al. 2009). A large proportion of the saproxylic beetles has indeed a preference either for sun-exposed or shaded conditions (Lindhe et al. 2005), but the preferences are rarely so strong as in the cases of the closed forest and sun-exposure specialists. Thus, we analyzed species at two extremes (closed forest and sun-exposure specialists) and a midpoint (normal species) of the scale, acknowledging that real species are more or less continuously distributed along that scale.

The landscape model

We simulated habitat development in a model landscape of 13.4 km × 13.4 km, which is similar to the scale suggested to be used in landscape planning of Swedish forests (Larsson and Danell 2001). The landscape consisted of 3,600 squares, corresponding to forest stands. Each square was 5 ha, which is near the average size of harvested forest stands in Sweden (Anonymous 2010). 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 donut-shaped surface. Tree species composition of each stand was determined stochastically for each stand, with a 40 % probability of being a Norway spruce stand (in Sweden, 41 % of the growing stock is Norway spruce;

Anonymous 2010). We assumed that the rest of the landscape was entirely unsuitable for the model species.

The extinction risk may be dependent on present occurrence patterns. To obtain realistic occurrence patterns, we started the simulations 100 years before present. We assumed that the landscape had been unaffected by commercial forestry based on clear-cutting until 100 years ago, and that the species were present in every spruce stand at that time. During the following 100 years, 0.95 % of the forest was clear-cut annually. We assumed that today 95 % of the forest has been managed, and that the age distribution is even among managed forest stands. The simulated scenarios we compared all started with the same current landscape situation and covered a period of 250 years from now. The extinction risk was estimated as the proportion of all replicates in which the species had gone extinct at the landscape level every 50 years for 250 years into the future.

We assumed that the unmanaged forest stands are currently unevenly distributed in the landscape. We did this by dividing 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 have been left unmanaged until today. These probability values were distributed between 5×10^{-9} % and 50 %, by using the equation $P = 5 \times 10^{x}$, in which P is the probability value for each square, and x is a stochastic variable, randomly given a value between –9 and 1 according to an even distribution. Each stand was randomly determined as having been managed or not, based on the probability value for the square where it was situated. When the number of set asides was increased from now into the future, we assumed that stands of ages with the highest amount of dead wood were selected.

The habitat amount changed over time, as determined by the management regime of the forest (Fig. 1). We predicted the amount of dead wood in managed forest in relation with stand age 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 during forestry operations. We assumed a site index (i.e. tree height at an age of 100 years) of 24 m and a rotation period of 100 years. Furthermore, we assumed that since about 10 years ago the forestry is biodiversity-oriented, following FSC’s certification regulations (Anonymous 2000), but that no concerns were taken to preserve dead wood before that. In unmanaged forest, we assumed that the average amount of dead wood was constant over time. This is close to reality if forests are dominated by fine-scale disturbances (Jonsson 2000), which at least sometimes is the case in Fennoscandian spruce forests (e.g., Hörnberg et al. 2005; Steijlen and Zackrisson 1987). For both managed and unmanaged forests 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.

We emulated the effect of weather by including regional stochasticity, which affected the extinction risk and colonization 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.

Scenarios

In the simulations, forest stands were managed in three different ways from today and 250 years into the future:

i) free development (i.e. no management)
ii) conventional forestry (following certification standards)
iii) intensive plantation forestry based on Norway spruce or another (native or introduced) tree species

We assumed that at the beginning of the simulations (i.e., 100 years before today), the amount of suitable dead wood corresponds to 50 % of what is found in old-growth forests. Indeed, the amount of dead wood at that time was often considerably lower than in old-growth forest because there was a lower density of living trees due to cattle grazing and selective logging (e.g., Lindbladh 1999; Sippola et al. 2001; Groven et al. 2002). We assumed that the amount of dead wood has further decreased because of increased management during the past 100 years, so forests that have been left for free development until today were assumed to contain 30 % of the dead wood volume that occurs in old-growth forests. This is consistent with survey data of Swedish key habitats with Norway spruce (Jönsson and Jonsson 2007). Setting aside these forests will increase the amount of dead wood in the future; we assumed that after 40 years the volume of suitable dead wood will have increased from the current 30 % to 80 %. However, it will never reach 100 %, because some dead wood is removed also from unmanaged forests, especially in the event of extensive storm felling in order to decrease the risk of damage by the spruce bark beetle *Ips typographus* to nearby managed forest (Schroeder 2007). This means that the amount of suitable dead wood (i.e. younger than 10 years old, with diameter > 10 cm) in forests with free development is first 4.16 m^3/ha today and 11.10 m^3/ha after 40 years. In future conventionally managed forest, the amount of suitable dead wood varies with stand age, with an average of 2.08 m^3/ha. We assumed that intensively managed plantations are totally unsuitable for the model species (i.e. there is no suitable dead wood). This is likely to be the case if intensive forestry is based on the plantation of non-native tree species which are unsuitable for the Norway spruce specialists. As regards Norway spruce plantations, this assumption implies that intensive multiple-entry silviculture minimizes natural tree death and allows salvaging dying trees which may occur accidentally after disturbance.

In all scenarios simulating future conditions, conventional forest management initially takes place in 95 % of the forest stands. Intensive forestry can become implemented only when forest stands are harvested. Furthermore, we assumed that each year only 50 % of the clear-cuts were suitable for implementing intensive forestry, due to e.g. variations in landowners’ interests, transport infrastructure or terrain characteristics. Consequently, the higher the proportion of intensive forestry, the longer time it will take until the new distribution of management types is reached; because about 1 % of the forest is cut annually it takes, for instance, ten years until the new level is reached for the scenario with 5 % intensive forestry, while it takes 100 years to reach 50 % intensive forestry.

In Scenario 1, the proportions of forest subject to intensive forestry and conventional management varied, and no measures were implemented to compensate the landscape-scale loss of dead wood resulting from an intensification of management (Table 2). In the other two sets of scenarios, compensations were implemented to maintain the amount of dead wood constant at the landscape level. Scenario 2 involved compensation by increasing the amount of dead wood in managed forest through changed management (more green tree retention at final logging; Table 3). Scenario 3 involved compensation by setting aside more forest (Table 4). Hence, in sets 2 and 3, the total amount of dead wood in the landscape was the same for all scenarios.

Estimations of changes in annual harvestable volume at the landscape level

For each scenario, we conducted a rough estimation of how the annual harvestable volume differed compared to the scenario with no intensive plantation forestry. The estimations were based on the following assumptions:

i) In intensively managed forests, the volume production over 100 years is expected to be 95 % higher than in conventionally managed forests at the stand scale. This is based on predictions made for 15% of all forest land in Sweden which would be dedicated to intensive production involving fertilization, clone forestry based on Norway spruce and plantation of lodgepole pine (Fahlvik et al. 2009; Larsson et al. 2009).

ii) In set asides, the harvestable volume is equal to 0 m^3/ha.

iii) For conventionally managed forest, we made calculations from the data presented in Jonsson et al. (2006). We assumed a forest situated in central Sweden. All compensation was assumed to be made by green tree retention at final harvest, and it was assumed to result in a decrease in volume production equal to 0.75 times the proportion of area that is retained, which is consistent with assumptions made in Jonsson et al. (2006).

Results

Intensified plantation forestry applied to 50% of the spruce stands had increased the extinction risk relatively strongly compared to the *status quo* scenario (i.e. no intensive plantation forestry) for all species after 150 years (Fig. 2). For four of the five species, most of the expected extinctions took place 50–150 years from the intensification of forestry. The sun-exposure specialist was an exception, as most extinctions took place already during the first 50 years.

The extinction risk increased rather gradually with an increasing proportion of intensive plantation forestry for all species under Scenario 1 (no compensation), but the degree of increase varied much among species (Fig. 3). For the short-dispersing species and the closed-forest specialist, extinction risk increased more slowly with increasing proportion of intensive plantation forestry than for the long-dispersing species and the sun-exposure specialist.

Given that compensations were made to maintain mean dead wood volumes constant at the landscape level, the extinction risk decreased with an increasing area of intensified forestry in many cases (Fig. 3). Compensation by setting aside forest was a very effective way of decreasing the extinction risk for the normal species, the short-distance disperser and the closed-forest species. Compensation through changed management was generally less effective; in most cases it resulted in more similar extinction risks compared to the scenario with no intensive plantation forestry. Moreover, the sensitivity analysis showed that the four additional variants based on different ranges of local extinction risk yielded outcomes which were qualitatively similar to those for the normal species, suggesting that the general pattern is robust to variation in the local extinction parameters (Appendix).

The response of the sun-exposure specialist differed clearly from that of most other model species: its extinction risk increased with the area of intensified forestry, even with compensation efforts made (Fig. 3). Compensation through set-asides was clearly ineffective for that species, whereas compensation through adapted management resulted only in a slightly lower extinction risk than without compensations made, except at 50% intensive plantation forestry, where compensation through management was better at mitigating the negative effects of intensive forestry. Also for the long-distance disperser the compensation measures were less effective than in other species: compensation kept extinction risk at a level rather close to that of *status quo* scenario, no matter the proportion of intensive plantation forestry, i.e. it did not result in strongly decreased extinction risk.

Implementing intensive plantation forestry increased the harvestable timber volume production at the landscape scale in the long term (Tables 2, 3 & 4). This was clearly the case even if the negative effects of intensified forestry on dead wood were compensated for by increased conservation efforts elsewhere in the landscape. The scenarios involving compensation through set-asides (Table 3) yielded smaller increases in harvestable volume compared to those assuming compensation through changed management (Table 2).

Discussion

This study suggests that intensified forestry has negative effects on biodiversity at the landscape level if no compensations are made for nature conservation. Still, negative effects on population persistence were limited when intensive forestry was applied to only 5 – 10 % of the spruce stands. However, it should be emphasized that the amount of suitable habitat required for population persistence differs widely among species (e.g., Baguette et al. 2000; Vance et al. 2003; Holland et al. 2005). Some very demanding forest species are most likely unable to persist in a managed forest landscape independent on whether the forests are managed intensively or conventionally (Ranius and Fahrig 2006), while other species with lesser requirements can be expected to persist even at high proportions of intensive plantation forestry. In this study, we parameterized the models to represent species which are already sensitive to forestry given today’s management regime. Hence, the effects observed on the model species are probably stronger than we should expect for forest species in general. Rather, they reflect the effects expected for species which are currently red-listed. We studied specialized saproxylic insects, but we believe that our results also apply to a much wider range of species, because the mechanisms behind the outcome (specialized species are strongly negatively affected by intensified forestry, and are able to use the habitat more efficiently if it occurs more aggregated in the landscape) are likely to be common to many, if not most, other groups of forest organisms.

In this study we assumed that intensive forestry was applied on forest land of average productivity and conservation value. In Sweden, it has been suggested that intensive forestry will be applied only on land of low conservation value (Larsson et al. 2009). On the contrary, intensive forestry is probably more profitable on the most productive land, which often also is land of high conservation value. Therefore, the negative impacts may become both larger or smaller than suggested by this study, depending on where intensive forestry is being implemented.

The simulation outcome indicates that it takes a long time before species richness at the landscape level is affected. When intensive plantation forestry was applied to 50% of the stands, the extinction risk of the model species did not increase strongly over the first 50 years except for the sun-exposure specialist. However, extinction risks of all species had increased strongly after 150 years compared to the *status quo* scenario (Fig. 2). It has been suggested that intensification of forestry in Sweden should be implemented within an adaptive management framework over a time period of 20 years (Larsson et al. 2009). To some extent it is possible to study effects on biodiversity at the stand level over a 20-year period. However, according to the present study we should not expect any significant effects on biodiversity at the landscape level over such a short period. To gain knowledge about the effects of intensive plantation forestry at the landscape scale without having to wait so long, we must rely on modeling studies like this one, or retrospective studies in landscapes which already have characteristics comparable with future landscapes containing intensively managed forests.

The effects of intensive plantation forestry differed among species with different habitat affinities and life-history traits. In biodiversity conservation, focus has often been on species associated with forests in late successional stages (e.g., Bauhus et al. 2009; Fritz et al. 2008; Siitonen and Saaristo 2000) and species with a limited dispersal (Baguette et al. 2000; Kotiaho et al. 2005). Populations of such species are typically conserved by setting aside forests. Our results show that for such species, an intensification of forestry is more advantageous than the current management regime if intensification in parts of the landscape is compensated by setting aside more forests (Fig. 3). However, this compensation measure was ineffective for the sun-exposure specialist, which was highly sensitive to intensive plantation forestry at the landscape scale, even already after 50 years. Clear-cuts may potentially host a species-rich insect fauna (Sippola et al. 2002), because they harbor species associated with sun-exposed habitat that originally occurred after forest fires. In the light of the trend for an intensification of forestry in northern forests, our results call for an increased interest in species associated with early successional stages.

We found that for three of the five model species (including the “normal” species assumed to represent an average red-listed species), extinction risk actually decreased with an increasing proportion of intensive plantation forestry compared to the *status quo* scenario (i.e. 0 % intensive forestry), given that appropriate compensations were made elsewhere to keep the mean dead wood volumes constant over the whole landscape. This is due to the fact that the compensation measures resulted in a better spatial aggregation of dead wood and hence positive effects on species persistence in stands subjected to these compensation measures, which were stronger than the negative effects of a decreased total area of suitable stands in the landscape. We assumed that all set asides had an area of 5 ha, but in many real landscapes there may be much larger areas of high conservation value that may be set aside. That will generally tend to decrease the extinction risk in comparison to have only 5-ha set asides (Ranius and Kindvall 2006), and consequently the present study probably tends to underestimates the usefulness of setting aside forests as a compensation measure.

Hence, our results provide support to zoning approaches such as the Triad, whereby intensive forestry is implemented on part of the land base and protected area networks are expanded to compensate for negative effects of intensified management. Such an approach would decrease biodiversity locally in intensively managed forest stands, but more species would be likely to persist at the landscape level. In a simulation study based on a boreal landscape in Quebec, Canada, Côté et al. (2010) showed that Triad scenarios resulted in larger areas of forest with old-growth properties than current land use, which suggests that many species sensitive to forest management would benefit. In our analyses, we found that timber volume production would increase with an increasing proportion of intensive plantation management, even when dead wood compensation measures were implemented. In a case study in New Brunswick, Canada, Montigny and MacLean (2006) also found that intensive management resulted in increased timber yields in a Triad zoning context. In Quebec, Côté et al. (2010) found that Triad scenarios with 12 % set-asides yielded higher timber volumes in the long term than both a *status quo* scenario and scenarios involving 20 % set-asides.

To conclude, a combination of intensive plantation forestry, ecological forestry, and set asides seems to allow for a combination of different goals, such as increased timber production and carbon sequestration, and maintenance of biodiversity. However, we stress that species with different life-history traits may respond differently, and hence the implementation of such a system should be accompanied by continuous biodiversity monitoring allowing for early warning and adaptive management. To implement such a zoning approach in Fennoscandia, some changes in forestry laws and certification standards (e.g. Anonymous 2000) would be required. Also, it should be kept in mind that landscape zoning is easier to implement in regions where forests are publicly owned (e.g. Messier et al. 2009) or where one actor owns most of the land base, and may not be a socially viable option in landscape with highly fragmented ownership.

Acknowledgements

This study was financed by the “MINT-project” which was a commission from the Swedish Government (Jo 2008/1885) to SLU, and Future Forests, a multidisciplinary research programme supported by the Foundation for Strategic Environmental Research (MISTRA), the Swedish Forestry Industry, the Swedish University of Agricultural Sciences (SLU), Umeå University, and the Forestry Research Institute of Sweden.

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Table 1. Parameter values for the five different model species. For parameter designations, see *Methods*.

Species	*u*	x	y	1/α (km)	Dead wood exposition
Normal	0.53	0.5	96.5	0.5	All
Long-distance	0.51	0.21	850	2	All
Short-distance	0.56	1	6.8	0.1	All
Sun-exposure	0.39	0.5	6.3	0.5	Sun-exposed
Closed forest	0.51	0.5	88	0.5	Shaded

Table 2. Mean volume of suitable Norway spruce dead wood (diameter > 10 cm, age < 10 years) across the landscape and change in annual growth of harvestable volume compared to the *status quo* (0 % intensive forestry) for scenarios assuming varying proportions of intensive plantation forestry over a period of 100 years. No compensation is made to counterbalance the loss of dead wood due to intensive plantation forestry (Scenario 1).

Plantation forestry (%)	Conventionally managed (%)	Set aside (%)	Dead wood in managed forest (m^3ha^{-1})	Dead wood (m^3ha^{-1})	Change in harvestable volume (%)
0	95	5	2.08	2.32	0
5	90	5	2.08	2.22	+5
10	85	5	2.08	2.12	+10
25	70	5	2.08	1.80	+25
50	45	5	2.08	1.28	+50

Table 3. Mean volume of suitable Norway spruce dead wood (diameter > 10 cm, age < 10 years) across the landscape and change in annual growth of harvestable volume compared to the *status quo* (0 % intensive forestry) for scenarios assuming varying proportions of intensive plantation forestry over a period of 100 years. More dead wood is created in conventionally managed forest to keep mean dead wood volumes constant at the landscape scale with an increasing proportion of intensive plantation forestry (Scenario 2).

Plantation forestry (%)	Conventionally managed (%)	Set aside (%)	Dead wood in managed forest (m^3ha^{-1})	Dead wood (m^3ha^{-1})	Change in harvestable volume (%)
0	95	5	2.08	2.32	-
5	90	5	2.20	2.32	+4.7
10	85	5	2.32	2.32	+9.5
25	70	5	2.82	2.32	+23.7
50	45	5	4.40	2.32	+47.3

Table 4. Mean volume of suitable Norway spruce dead wood (diameter > 10 cm, age < 10 years) across the landscape and change in annual growth of harvestable volume compared to the *status quo* (0% intensive forestry) for scenarios assuming varying proportions of intensive plantation forestry over a period of 100 years. More forest is set aside to keep mean dead wood volumes constant at the landscape scale with an increasing proportion of intensive plantation forestry (Scenario 3).

Plantation forestry (%)	Conventionally managed (%)	Set aside (%)	Dead wood in managed forest (m^3ha^{-1})	Dead wood (m^3ha^{-1})	Change in harvestable volume (%)
0	95	5	2.08	2.32	0
5	87.86	7.14	2.08	2.32	+2.9
10	80.72	9.28	2.08	2.32	+5.7
25	59.3	15.7	2.08	2.32	+14.3
50	23.6	26.4	2.08	2.32	+28.6

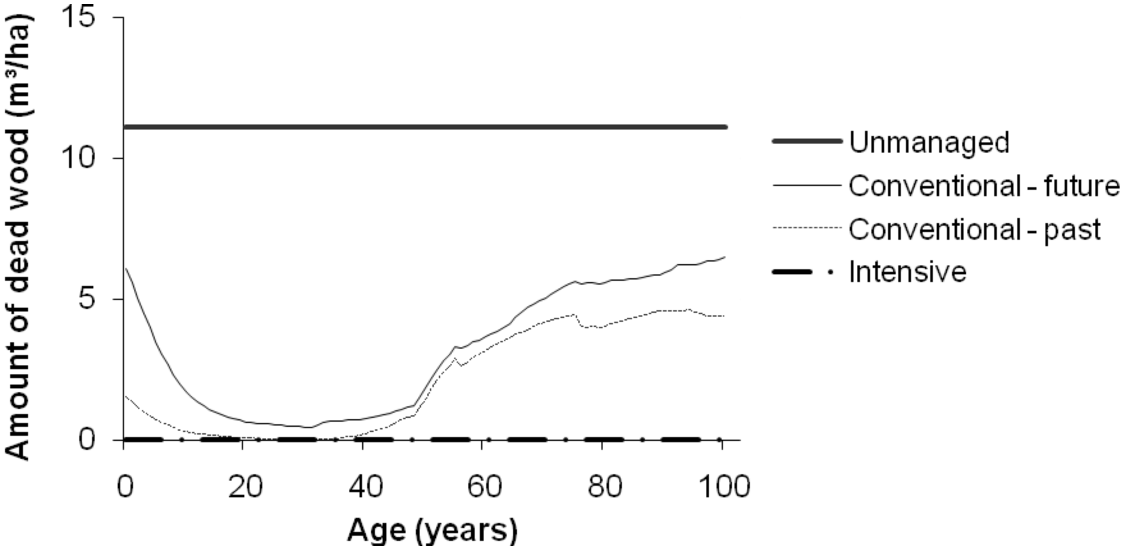


Fig. 1. Amount of dead wood of Norway spruce suitable for the model species (diameter > 10 cm, age < 10 years) over a 100-year rotation. Output from simulations of dead wood dynamics (taking into account forest growth, tree mortality, dead wood decay, and destruction of dead wood by forestry operations) of unmanaged forest in the future, conventionally managed forest in the past (until ten years ago) and future (started ten years ago), and intensively managed Norway spruce forests.

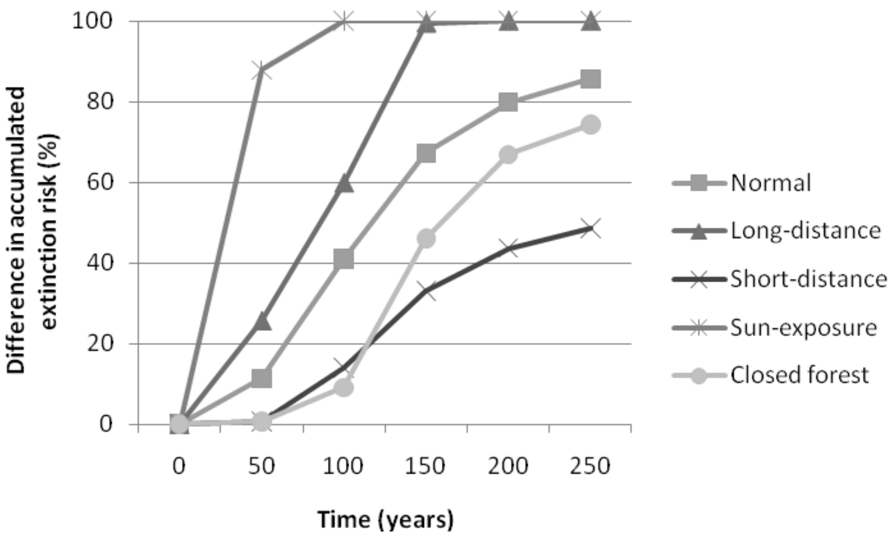
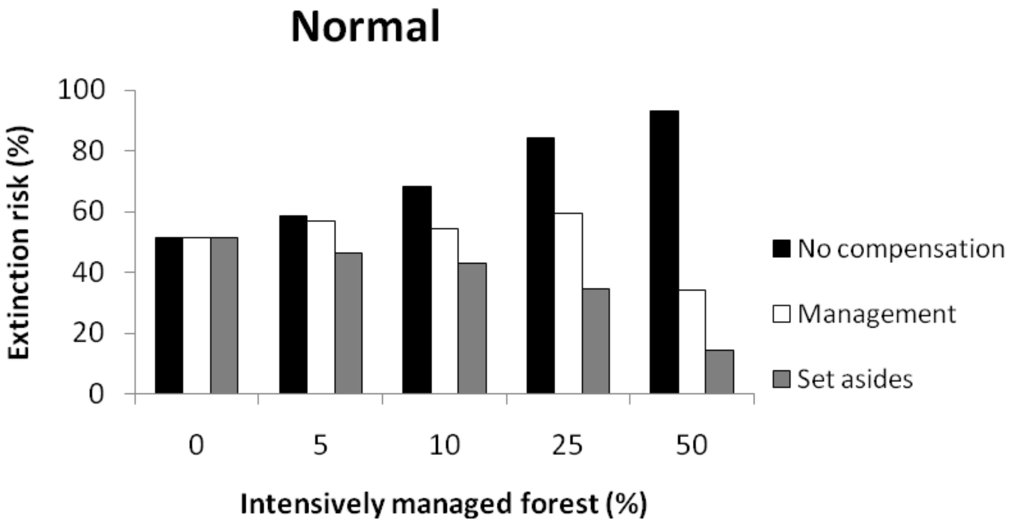
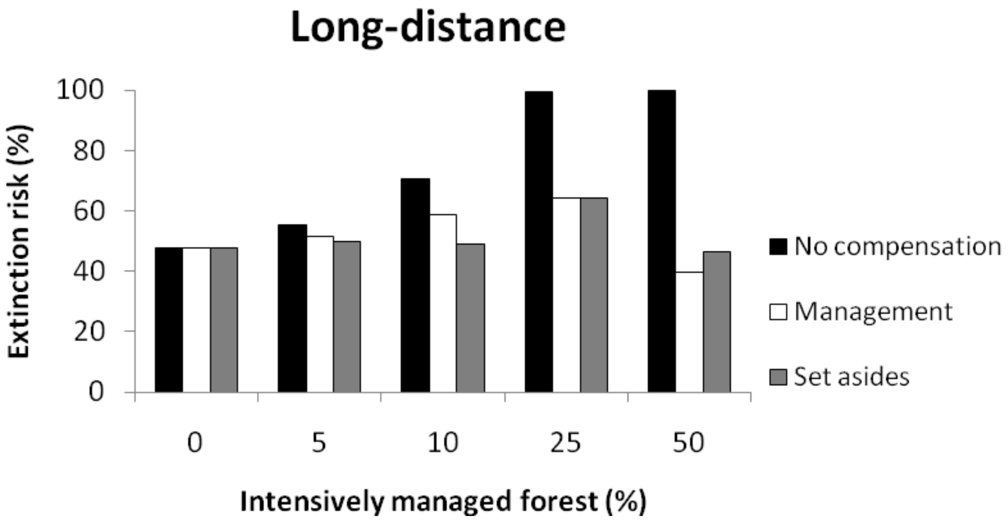
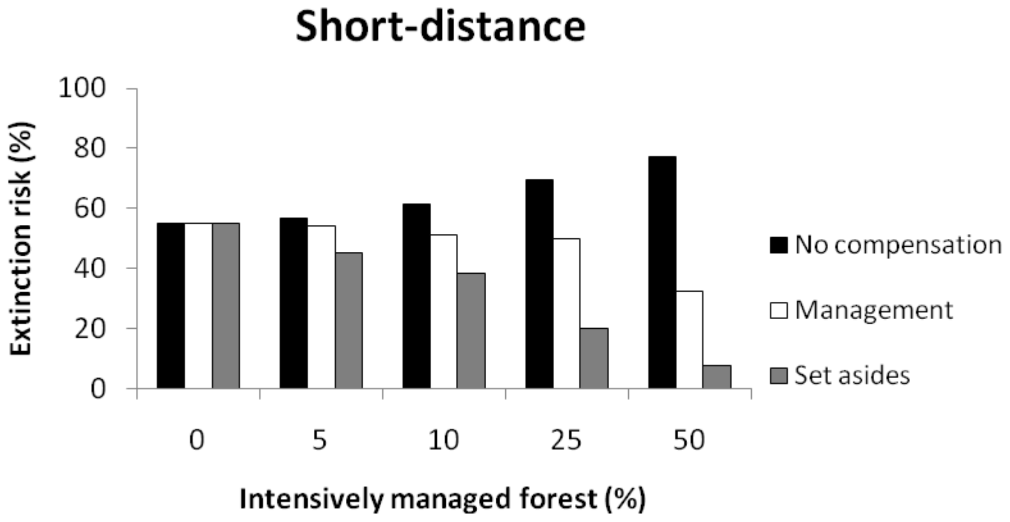
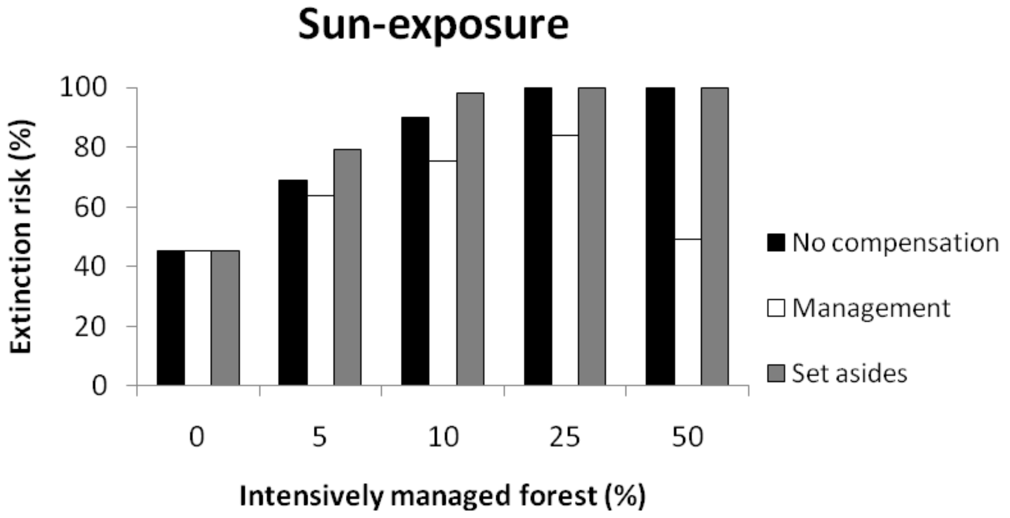


Fig. 2. Difference in accumulated extinction risk if 50% of the current spruce stands are dedicated to intensive plantation management and no compensation measures are taken. The difference is calculated as (Extinction risk with 50% intensive forestry – Extinction risk without intensive forestry) / (1 – Extinction risk without intensive forestry). For species characteristics, see Table 1.


Normal
Extinction risk (%)
100
80
60
40
20
0
0
5
10
25
50
Intensively managed forest (%)
■ No compensation
☐ Management
▨ Set asides


Long-distance
Extinction risk (%)
100
80
60
40
20
0
0
5
10
25
50
Intensively managed forest (%)
■ No compensation
☐ Management
▨ Set asides


Short-distance
Extinction risk (%)
0
20
40
60
80
100
0
5
10
25
50
Intensively managed forest (%)
■ No compensation
☐ Management
▨ Set asides


Sun-exposure
Extinction risk (%)
0
20
40
60
80
100
0
5
10
25
50
Intensively managed forest (%)
■ No compensation
☐ Management
▨ Set asides

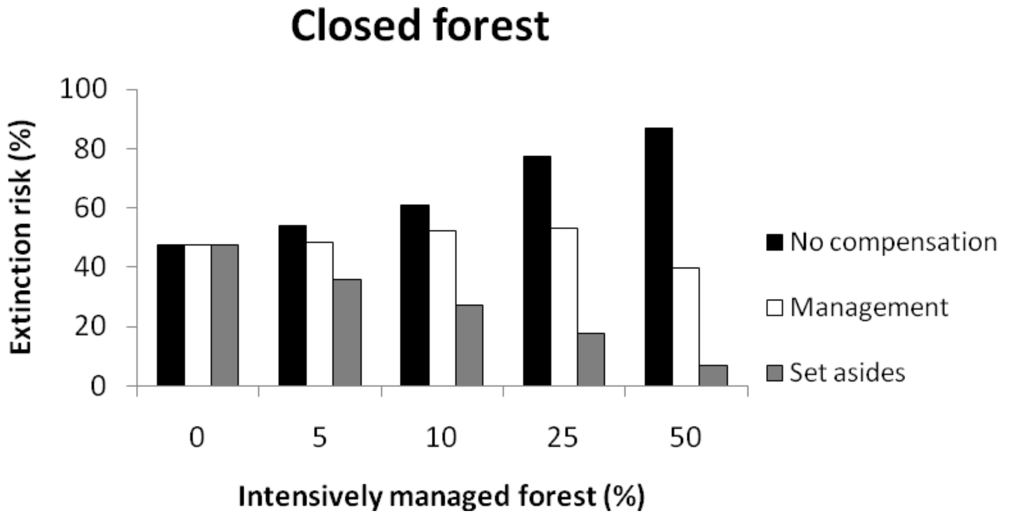
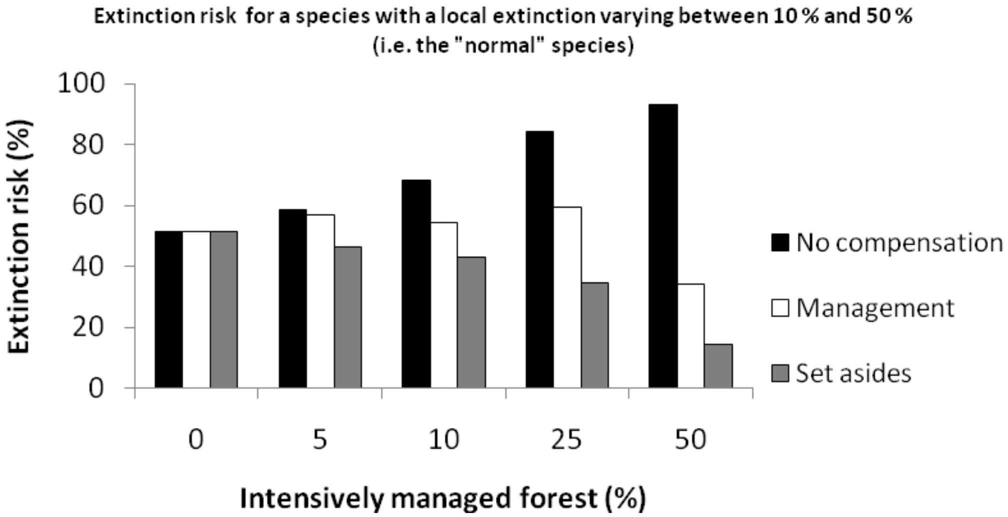
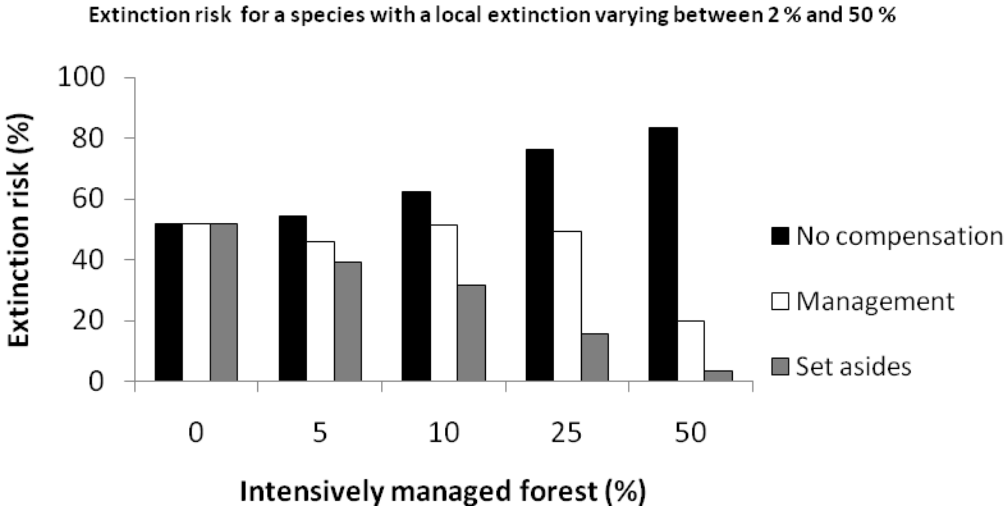
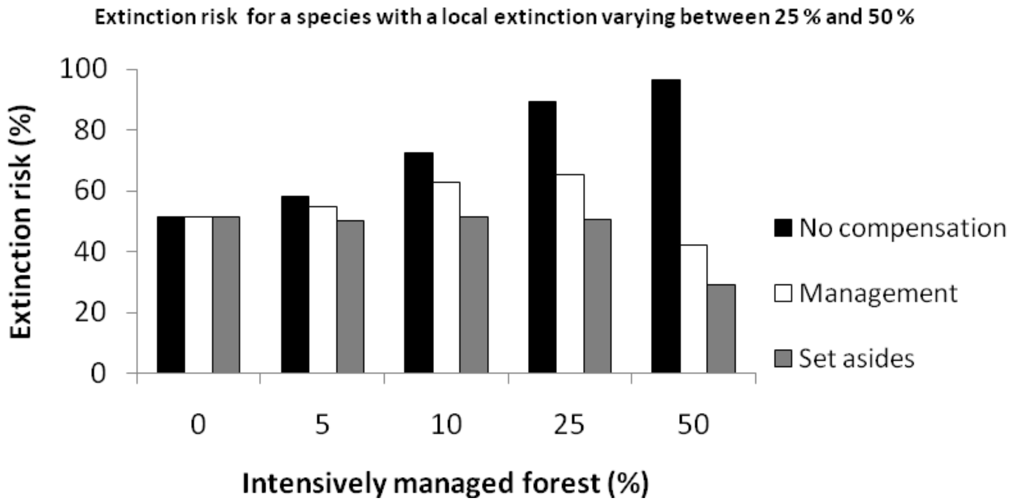

Closed forest
Extinction risk (%)
0
20
40
60
80
100
0
5
10
25
50
Intensively managed forest (%)
■ No compensation
☐ Management
▨ Set asides

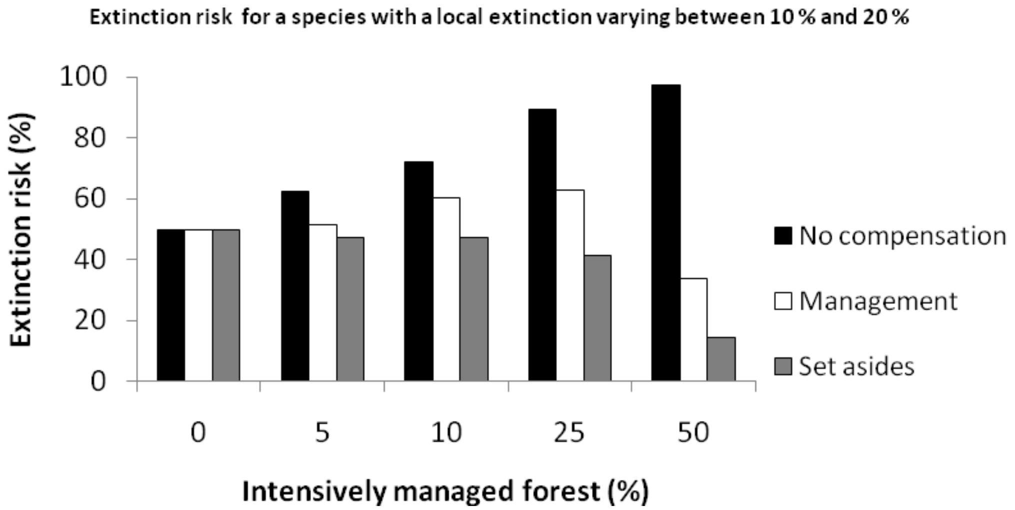
Fig. 3. Predicted extinction risk for the model species at a landscape level 250 years into the future in relation to the proportion of intensively managed stands. “No compensation” implies that no compensation efforts were conducted, and consequently the mean volume of dead wood at the landscape level varies among the scenarios. “Management” implies that a constant dead wood volume was obtained through increased conservation concern in all conventionally managed forest, and “Set asides” implies that a constant landscape-scale dead wood volume was obtained by setting aside a larger proportion of forest for free development.

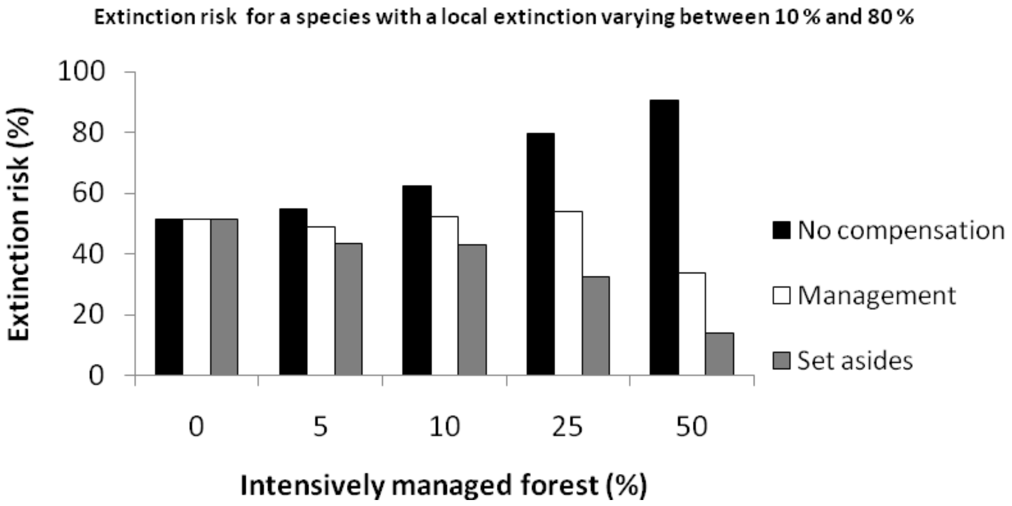
Appendix. Outcome from the sensitivity analyses. Four variants of the normal species (see main text) are modeled, representing different ranges of variation of the local extinction risk according to the local amount of dead wood. The bar diagrams show the predicted extinction risk for species at a landscape level 250 years into the future in relation to the proportion of intensively managed stands. “No compensation” implies that no compensation efforts were conducted, and consequently the mean volume of dead wood at the landscape level varies among the scenarios. “Management” implies that a constant dead wood volume was maintained through increased conservation concern in all conventionally managed forest, and “Set asides” implies that a constant landscape-scale dead wood volume was maintained by setting aside a larger proportion of forest for free development.






Extinction risk for a species with a local extinction varying between 25 % and 50 %
Extinction risk (%)
100
80
60
40
20
0
0
5
10
25
50
Intensively managed forest (%)
■ No compensation
☐ Management
▨ Set asides


Extinction risk for a species with a local extinction varying between 10 % and 20 %
Extinction risk (%)
100
80
60
40
20
0
0
5
10
25
50
Intensively managed forest (%)
■ No compensation
☐ Management
▨ Set asides


Extinction risk for a species with a local extinction varying between 10 % and 80 %
Extinction risk (%)
100
80
60
40
20
0
0
5
10
25
50
Intensively managed forest (%)
No compensation
Management
Set asides