

ORIGINAL ARTICLE

## Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds

THOMAS RANIUS<sup>1</sup> & LENORE FAHRIG<sup>2</sup>

<sup>1</sup>Department of Entomology, Swedish University of Agricultural Sciences, Uppsala, Sweden, and <sup>2</sup>Ottawa-Carleton Institute of Biology, Carleton University, Ottawa, Ontario, Canada

### Abstract

Forestry decreases the amount of dead wood, thereby threatening the persistence of many saproxylic (wood-living) organisms. This article discusses how targets for efforts to maintain and restore dead wood in managed forest landscapes should be defined. Several studies suggest extinction thresholds for saproxylic organisms. However, because the thresholds differ among species, the relationship between species richness and habitat amount at the local scale is probably described by a smoothly increasing curve without any distinct threshold. The most demanding species require amounts of dead wood that are virtually impossible to reach in managed forests. This means that unmanaged protected forests are needed. In managed forests, conservation efforts should focus on the landscape scale and on certain types of dead wood, but it is impossible to come up with any particular amount of dead wood that is desirable at the forest stand level.

**Keywords:** Beetles, ecological thresholds, occurrence patterns, saproxylic, species richness.

### Introduction

Ecological thresholds are important concepts in the conservation and management of natural resources (Muradian, 2001; Huggett, 2005). An ecological threshold can be defined as a critical value of an independent variable at which the ecological response variable changes rapidly from one condition to another. In biodiversity conservation, a particular kind of ecological threshold, the extinction threshold, is an important concept (Lamberson et al., 1992; Angelstam et al., 2003). The extinction threshold implies that at a critical value of habitat density (the extinction threshold), population persistence probability changes rapidly, such that above the threshold the population persists and below the threshold the population becomes extinct. In deterministic models, the relationship between persistence probability and habitat density (i.e. the amount of habitat per unit of area) is a clean step function (e.g. Lande, 1987), while in stochastic models the relationship between persistence probability and habitat density becomes sigmoidal

(Fahrig, 2001) (Figure 1). A sigmoidal function has by definition a non-negative derivative with a single local maximum. The extinction threshold can be defined as the habitat density where the probability of population persistence changes most quickly with changing habitat density, i.e. where the derivative of persistence probability with respect to habitat density reaches a local maximum. Using this definition, the target for biodiversity conservation should be set at a habitat density value that is higher than the threshold (Figure 1). If the model is highly stochastic, the sigmoidal pattern becomes blurred (Ovaskainen & Hanski, 2003), and at some stage it can become impossible to identify any threshold, because it becomes totally hidden by the stochasticity.

Extinction thresholds are very difficult to estimate empirically. Extinction estimates can be made using computer simulations. However, the input data are typically difficult to obtain and the variability in input parameters is extremely difficult to estimate. Since parameter variability has a large effect on persistence estimates, it is generally recognized that

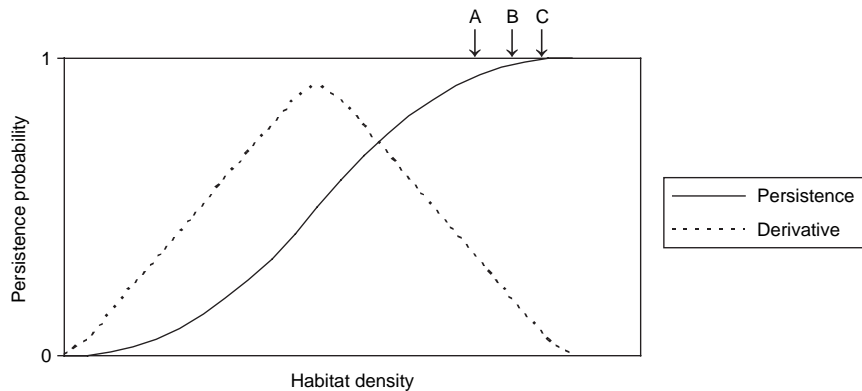


Figure 1. An extinction threshold. The extinction threshold is the level of habitat density (i.e. habitat amount per unit of area) where the derivative of the persistence probability reaches a local maximum. The  $y$ -axis represents either the probability of persistence of an individual species or the sum of such probabilities for all species in a community. In the latter case it is a measure of the expected number of species present. The goal for nature conservation should be to maintain a habitat density that exceeds the extinction threshold. The amount of habitat to be maintained depends on how large an extinction risk is acceptable: A, the appropriate goal if extinction risks up to 5% are acceptable; B, up to 1%; C, up to 0.1%.

simulated predictions of extinction risk of real populations are not reliable (Akçakaya & Sjögren-Gulve, 2000). Therefore, in many cases the per-population extinction risk is estimated by surveying many populations and then using the frequency of occurrence of the species, given a particular habitat level, as the estimate of probability of persistence at that habitat level. The results from such studies are affected by both the current habitat level and the habitat history (Hanski & Ovaskainen, 2002). Habitat history is rarely known in detail, which makes interpretation of such studies difficult. The most reliable estimates would be obtained from long-term studies that run over many decades, but such studies are very rare.

Studies on extinction thresholds typically consider individual species (Fahrig, 2003), although a few recent studies considered assemblages of species (Huggett, 2005; Radford et al., 2005). In most cases, the goal for conservation is not to preserve individual species, but to preserve overall biodiversity including many taxa that are poorly known. One example occurs in forestry where there are competing environmental and production goals (Larsson & Danell, 2001). Forests are species-rich biotas, and deforestation and transformation of forest habitats due to forestry can have a huge impact on biodiversity (Turner, 1996; Hanski, 2000). During the past decade there has been increasing concern in forestry for biodiversity preservation (Thomas, 1997).

A decrease in dead wood is one of the largest changes that takes place when a forest is intensively managed. For instance, the volume of dead wood in Swedish managed forests is about  $6 \text{ m}^3 \text{ ha}^{-1}$  (Fridman & Walheim, 2000), while in Fennoscandian old-growth forests the volume is between 20 and

$130 \text{ m}^3 \text{ ha}^{-1}$  (usually  $>40 \text{ m}^3 \text{ ha}^{-1}$ ; Siitonen, 2001; Gibb et al., 2005). This has strongly affected the density of saproxylic species (Hanski & Hammond, 1995; Siitonen, 2001), i.e. those that depend directly on dead wood or on other saproxylic species during some part of their life cycle (Speight, 1989). Reduced populations and regional extinctions of saproxylic organisms have been reported from western Europe, which has a long history of commercial forestry and transformation of forest to other land types (Grove, 2002a). In Sweden at least 6000–7000 species are saproxylic, of which 1126 are red-listed, representing about 25% of all red-listed species in Sweden (Dahlberg & Stokland, 2004).

The amount of substrate for saproxylic organisms is maintained and increased by setting aside forests as reserves, and by changing silvicultural methods (Ranius & Kindvall, 2004). To avoid further impoverishment of forest biodiversity, the Swedish government has set goals for the forest area that should be set aside, and has specified that the amount of hard (less decayed) dead wood should have increased by 40% from 1995 to 2010. The 40% value was not based on biological knowledge, indicating that this, or any other amount of dead wood, should be “enough” for biodiversity preservation (Anon., 1999). It has been debated how to define goals for nature conservation based on information about extinction thresholds (e.g. recently in Sweden: de Jong et al., 2004; Ranius, 2005). Scientists and policy makers should be aware of the main issues in such debates before they use thresholds to assist conservation goals and management programmes.

This article discusses how to study extinction thresholds to obtain information required for formulating environmental goals, with saproxylic organisms as an example. The empirical evidence for

extinction thresholds in saproxylic organisms in the literature is evaluated, and the implications for environmental targets and future research are discussed.

### Empirical evidence for extinction thresholds in saproxylic organisms

Woodpeckers are the only vertebrate group dependent on dead wood that has been studied in the context of extinction thresholds (Table I). The white-backed woodpecker (*Dendrocopus leucotus*) required 10–20 m<sup>3</sup> ha<sup>-1</sup> dead wood from deciduous trees over 100 ha areas in Poland (Angelstam et al., 2003). Carlsson (2000) compared the occupancy and amount of habitat in Poland and Scandinavia, and suggested that for maintenance of a white-

backed woodpecker population, suitable habitat should cover at least 10–17% of a landscape (in the order of tens of square kilometres). In Switzerland, the probability of the presence of the three-toed woodpecker (*Picoides tridactylus*) increased from 0.10 to 0.95 when the basal area of snags (standing dead wood) increased from 0.6 to 1.3 m<sup>2</sup> ha<sup>-1</sup> over a 100 ha forest area (1.3 m<sup>2</sup> ha<sup>-1</sup> corresponds to a volume of snags of 15 m<sup>3</sup> ha<sup>-1</sup>), while in Sweden a smaller basal area of 0.3–0.5 m<sup>2</sup> ha<sup>-1</sup> was needed (Bütler et al., 2004). These basal area levels, as well as the volume of dead wood for the white-backed woodpecker, are thresholds that are relevant for species presence. Because the territory sizes of these two woodpeckers are in the order of 100 ha (Carlsson, 2000; Pechacek, 2004), these thresholds are not a measure of the amount of habitat required

Table I. Studies on extinction thresholds in saproxylic organisms.

Individual species	Red-listed <sup>a</sup>	Measure of habitat amount	Threshold level	Spatial scale of the measure of habitat amount	Source
White-backed woodpecker ( <i>Dendrocopus leucotus</i> )	Yes	Dead wood of deciduous trees	10–20 m <sup>3</sup> ha <sup>-1</sup>	Contiguous areas of 100 ha	Angelstam et al. (2003)
Three-toed woodpecker ( <i>Picoides tridactylus</i> )	Yes	Snags (standing dead wood)	0.6–1.3 m <sup>2</sup> ha <sup>-1</sup> (Switzerland); 0.3–0.5 m <sup>2</sup> ha <sup>-1</sup> (Sweden)	Contiguous areas of 100 ha	Bütler et al. (2004)
Five beetle species ( <i>Anaspis frontalis</i> , <i>Anoplodera maculicornis</i> , <i>Octotemnus glabriculus</i> , <i>Placusa suecica</i> , <i>Triplax aenea</i> )	No (none)	Total amount of dead wood	8–28 m <sup>3</sup> ha <sup>-1</sup>	Average over either 100 ha or 400 ha	Økland et al. (1996)
Three beetle species ( <i>Ipidia quadriplagiata</i> , <i>Xylophilus corticalis</i> , <i>Dendrophagus crenatus</i> )	Yes (all)	Large logs	3–7 ha <sup>-1</sup>	Average over either 100 ha or 400 ha	Økland et al. (1996)
Three beetle species ( <i>Tenebrio opacus</i> , <i>Elater ferrugineus</i> , <i>Osmoderma eremita</i> )	Yes (all)	Hollow oaks	10 oaks per stand	A stand = all oaks that are <250 m from another oak within the stand	Ranius (2002)
Twelve saproxylic longhorn beetles (Cerambycidae)	No (none)	Area covered with forest	4.8–99% forest cover	0.1–1256 ha	Holland et al. (2005)
Species richness					
Wood-living fungi	–	Total amount of dead wood	All species: no sigmoidal relationship; no threatened species when <20 m <sup>3</sup> ha <sup>-1</sup> , more than two threatened species when >100 m <sup>3</sup> ha <sup>-1</sup>	1 ha	Penttilä et al. (2004)
Wood-living beetle species	–	Total amount of dead wood	No sigmoidal relationship	0.0625 ha	Grove (2002b)
Wood-living beetle species	–	Total amount of dead wood	All species: no sigmoidal relationship; about half of the species considered rare occurred only in old-growth forest (> 50 m <sup>3</sup> ha <sup>-1</sup> )	1 ha	Martikainen et al. (2000)

<sup>a</sup> According to the national red list at the time of publication.

for population persistence, but represent the definition of suitable habitat for the individual.

There are three studies suggesting extinction thresholds in saproxylic insects (Table I). In a study by Økland et al. (1996) with about 190 saproxylic beetle species collected, eight beetle species were absent when the amount of dead wood was below  $8\text{--}28\text{ m}^3\text{ ha}^{-1}$ , or 3–7 large logs per hectare. The pattern was observed at larger scales ( $1\text{ km}^2$  or  $4\text{ km}^2$ ), but not at smaller scales ( $0.16\text{ ha}$  or  $1\text{ ha}$ ). In the second study, Ranius (2002) reported that three threatened beetle species inhabiting hollows of oak trees occur in a larger proportion of trees situated in stands with many hollow trees than in stands with fewer hollow trees. The most pronounced threshold was observed in the beetle *Tenebrio opacus* (Figure 2). For this species, the frequency of presence per tree was much reduced in stands with fewer than 10 suitable trees. Finally, Holland et al. (2005) correlated the occurrence patterns of 12 saproxylic longhorn beetles with forest cover, and found that the minimum forest cover for species presence differed widely among species. They found a strong negative relationship between the reproductive rate of the species and the minimum habitat amount required for species presence.

A shortcoming of most of the empirical studies of saproxylic organisms is that they are typically conducted at a single, relatively small spatial scale. Holland et al. (2004) studied the responses of 12 different saproxylic longhorn beetle species to forest cover at multiple spatial scales. The different beetle species responded most strongly to forest cover measured at very different distances, from 20 to 2000 m from the beetle sampling point. Thus, to characterize accurately a species' response to habitat density, the relationship should be evaluated at many different scales, including larger spatial scales than most researchers consider.

For practical conservation, it is more important to know how to preserve the total saproxylic fauna and

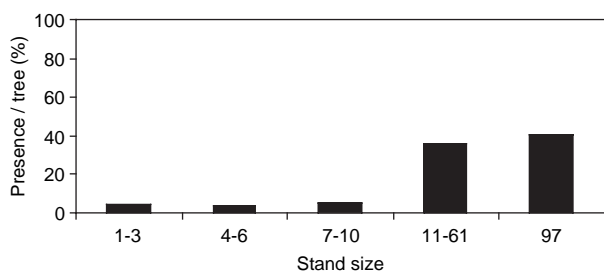


Figure 2. Frequency of occurrence per tree of the beetle *Tenebrio opacus* in relation to stand size. Stand size is defined as the number of hollow oaks within a cluster with a distance of  $<250\text{ m}$  from one hollow oak to another (from Ranius, 2002). The proportion of trees that were occupied increased with stand size (Kendall's tau-b test,  $p < 0.05$ , number of sampled stands = 45).

flora than individual species. By summing the probability of persistence for all species in a community, thresholds for the expected number of species present can be identified. For woodland-dependent birds in Australia, there is evidence for a threshold (defined as a level where the coefficient of the species richness–habitat cover relationship suddenly changes) at a landscape scale (Radford et al., 2005), while in other systems it has been impossible to find any threshold in the relationship between species richness and habitat amount (e.g. Lindenmayer et al., 2005). There is so far no evidence for thresholds in species richness of saproxylic organisms. In southern Finland, Martikainen et al. (2000) found that the relationship between the saproxylic beetle fauna in forests and the amount of dead wood could be described by the following function:

$$N = 18.3 + 31.8 \times \log(V + 1) \quad (1)$$

where  $N$  is the number of species and  $V$  the volume of dead wood per hectare. In a subset of the sites studied by Martikainen et al. (2000), polypores were also surveyed, which resulted in a relationship between species richness and amount of dead wood that was qualitatively similar to the beetle study (Penttilä et al., 2004). Grove (2002b) found a similar relationship in a study of saproxylic beetles in Australia:

$$N = 42.1 + 19.9 \times \log(V) \quad (2)$$

Equation (1) was based on data from 30 forest stands with dead wood amounts varying between 2 and  $200\text{ m}^3\text{ ha}^{-1}$ , while eq. (2) was based on data from nine forest stands with dead wood amounts varying between 4 and  $45\text{ m}^3\text{ ha}^{-1}$ . The derivatives of these equations have their maximum when the amount of dead wood moves towards zero (eq. 1; Figure 3),

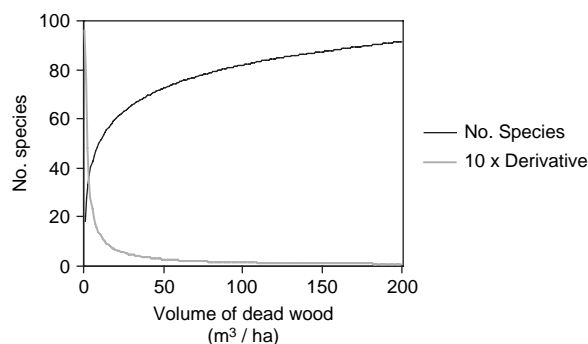


Figure 3. Relationship between the volume of dead wood and the number of saproxylic species collected with window traps in forest stands in a forest landscape in Finland, and its derivative. There is no local maximum in the derivative, and consequently there is no threshold in the relationship. The equation  $y = 18.3 + 31.8 \times \log(x + 1)$ , where  $y$  is the number of species and  $x$  the volume of dead wood, is from Martikainen et al. (2000).

which indicates that there is no sigmoidal relationship and thus no threshold. However, as the sample sizes were small and the deviations from the relationships in individual stands were large, it would have been difficult to detect any thresholds in these studies unless they were very distinct.

Some studies suggest that there are differences between red-listed species and other species (Table I). In the study by Økland et al. (1996), all species showing a relationship with the number of large dead logs were red-listed, but among those showing a relationship with the total amount of dead wood none was red-listed. Martikainen et al. (2000) and Penttillä et al. (2004) observed a rapid increase in the total number of species with increasing dead wood at low levels of dead wood; however, the majority of the rare or threatened species occurred only in old-growth forest with at least 20–100 m<sup>3</sup> ha<sup>-1</sup> (Table I). Because Martikainen et al. (2000) and Penttillä et al. (2004) compared old-growth forests (with large amounts of dead wood) with managed forests (with small amounts of dead wood), the observed pattern could be a result of either rare and threatened species requiring a large amount of dead wood, or the old-growth forests having a certain history, or containing dead wood of certain qualities (e.g. large logs) that are absent in the managed forests.

A possible strategy in conservation work is to focus on the most demanding species. If their requirements are met, the other species will be preserved at the same time (Lambeck, 1997). The red listing of insects and cryptogams is rarely based on any hard data, but rather on expert opinion (Gärdenfors, 2000). If the red listing is correct, species regarded as threatened should generally be more demanding of dead wood. This was indeed found by Penttillä et al. (2004), and for that reason the focus on red-listed species is, at least in that case, justified. Thus, the message for nature conservation from the study by Penttillä et al. (2004) is that a more or less complete assemblage of rare polypore species (i.e. presence of many threatened species) occurs only in old-growth forest with levels of dead wood exceeding 100 m<sup>3</sup> ha<sup>-1</sup>. The fact that the first threatened species (with the lowest demand) arises at around 20 m<sup>3</sup> ha<sup>-1</sup> is less important, because the conservation goal is to preserve all species, including the most demanding.

### How to encounter extinction thresholds in empirical data

The results to date clearly indicate that several saproxylic species are absent or rare when the habitat amount is low (Table I). However, in most of the studies the occurrence of an extinction threshold was

not statistically tested (Økland et al., 1996; Penttillä et al., 2004; Holland et al., 2005; see, however, Ranius, 2002), because the aim of the studies was not to determine whether extinction thresholds exist. Statistical tests are necessary to discriminate between the extinction threshold hypothesis and the proportional habitat hypothesis (Figure 4; terminology according to Fahrig, 2003; see also Andrén, 1994). If organisms were evenly distributed among suitable dead wood objects, and thus presence was independent of habitat density, there would be a linear relationship between species abundance and habitat amount (the proportional habitat hypothesis). In contrast, species showing an extinction threshold should have a lower abundance per unit habitat when the total amount of habitat is low (the extinction threshold hypothesis) (Figure 4a). Note that both hypotheses predict a low abundance, or absence, when the habitat amount is low. Because there are always sampling errors, species may be absent just by chance, especially if the habitat amount is low, even if the relationship between habitat amount and abundance actually is linear. Thus, simply to observe absence of a species at low habitat amounts is not sufficient to conclude that there is an extinction threshold. Statistical tests would be necessary. In such tests, the response

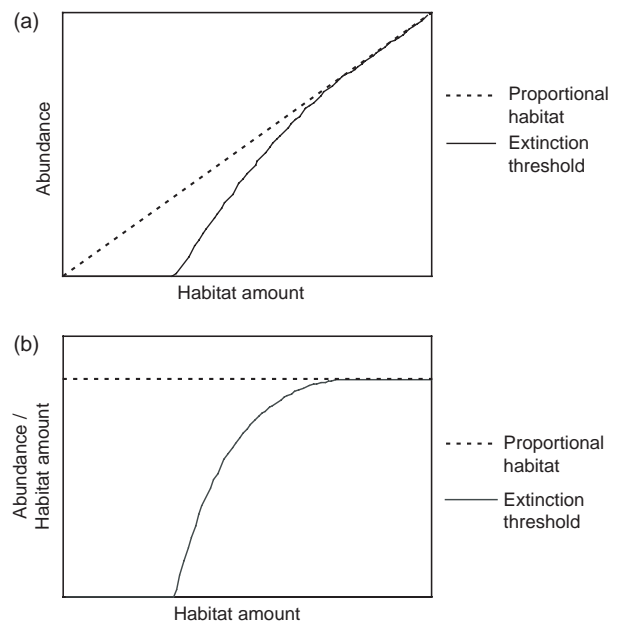


Figure 4. Relationship between species abundance and habitat amount according to two different hypotheses: (i) species abundance is proportional to the habitat amount (“Proportional habitat”), and (ii) species abundance per amount of habitat is lower when the habitat amount is lower, thus indicating an extinction threshold (“Extinction threshold”). Parts (a) and (b) assume the same fictitious data set, but in (a) the y-axis represents simple abundance, whereas in (b) the y-axis represents abundance per habitat amount (i.e. density).

variable should be abundance per unit of habitat (i.e. species density) rather than simple abundance. A significant positive relationship between species density and habitat amount would reject the proportional habitat hypothesis and would be consistent with the extinction threshold hypothesis (Figure 4). In contrast, analyses showing positive relationships between habitat amount and abundance are consistent with both hypotheses.

### Modelling extinction risks

Simulation models may be very useful for understanding extinction thresholds. One reason for this is that in all empirical studies (Table I) the frequency of presence has been measured, which is not the same as the extinction risk. Even though populations are found to be frequently present at localities with a certain habitat amount, one cannot be sure that this habitat amount is enough for population persistence; perhaps the occupancy pattern observed reflects a historical, higher habitat density (Hanski & Ovaskainen, 2002). So far, however, modelling studies on saproxylic organisms are few (Carlsson, 2000; Gu et al., 2002; Fox et al., 2004; Ranius & Hedin, 2004), and none of them aims at suggesting any threshold in the relationship between the amount of dead wood and extinction risk.

### Conclusions for environmental targets

All studies to date suggest that there is no threshold for the number of species overall. This is probably because different saproxylic species depend on different types of dead wood and respond to habitat density at different spatial scales. This would tend to create a smoothly increasing curve of species number versus dead wood volume, rather than a sigmoidal curve. It may be hypothesized that species richness increases with the amount of dead wood, with a decreasing rate of increase, which will be the case if there are more species with low threshold levels in comparison to high (e.g. Figure 4). Any forest with dead wood volume less than needed for all species (which at least in boreal forests is probably equal to the volume in old-growth forest; Martikainen et al., 2000; Penttillä et al., 2004) will be lacking in some species. This means that if all species are to be preserved, there must be areas with old-growth volumes of dead wood. There is a wide natural variability in dead wood amounts over space and time due to, for instance, the productivity of the forest land and fire dynamics (Siitonen, 2001), and it is important that some more productive forests are also left unmanaged. Areas with large amounts of dead wood will preserve species with very high

demands as well as those that require lower levels of dead wood at a stand level. As relevant studies at a larger spatial scale are lacking, it is not known how large a proportion of the area should be covered by such forests for long-term persistence of saproxylic species. A model by Carlsson (2000) suggested that for maintenance of a white-backed woodpecker population, suitable habitat should cover at least 10–17% of landscapes in the order of tens of square kilometres. Woodpeckers probably require generally larger areas than cryptogams and insects. However, because different kinds of forests are suitable for different species, and there are so many saproxylic insect and cryptogam species, the total area of habitat needed for maintenance of all species that are sensitive to forestry is probably quite high.

For practical reasons it is impossible to combine efficient forestry with near-old-growth volumes of dead wood. Furthermore, in managed forest dead wood amounts vary over the rotation period (Fridman & Walheim, 2000), which means that even if it is possible to obtain high levels of dead wood volumes during some parts of the rotation period, it is unlikely that sensitive saproxylic species will be able to occur in the same forest stand continuously over the entire rotation period. Consequently, protected forests are generally more important than managed forests for species that demand high concentrations of dead wood. Still, managed forests are important for the preservation of threatened saproxylic species. This is because managed forests are potentially useful for species that are good dispersers and consequently are affected by the amount of dead wood at a landscape scale, rather than within individual stands. Furthermore, managed forests may contribute certain types of dead wood that are rare in protected areas. One example is given by Wikars and Orrmalm (2005), who found that the beetle *Upis ceramboides* occurred in clear-cuts with large amounts of sun-exposed logs, while the species seemed to be absent in a nature reserve and mature forests in the same forest landscape. Consequently, conservation efforts in managed forests should focus on certain types of dead wood, and should be at a landscape scale, rather than focusing on reaching a certain volume of dead wood in individual forest stands. Økland et al. (1996) found that some red-listed species occurred only when there were at least four to seven large dead logs per hectare over one to several square kilometres, which could be used to formulate targets for the preservation of some species.

Given that within a forest region there are thousands of saproxylic species with different habitat requirements, it will never be possible to summarize the requirements for biodiversity con-

servation in simple rules. Still, this does not mean that it is impossible to use quantitative targets for the amount of dead wood. For example, the Swedish government set a target that the amount of hard (less decayed) dead wood on Swedish forest land should increase by 40% from 1995 to 2010; this was mainly based on what was regarded as practically and economically possible. There were no quantitative estimates of the biological consequences. Given that the relationship between the amount of dead wood and species richness is similar to that in Figure 3, it should be expected that any increase in the amount of dead wood would improve the persistence for some species, and thus the strategy used by the Swedish government is acceptable as a preliminary target. Another strategy, which is better in the long run, is to specify the biodiversity goal by identifying umbrella species that represent different assemblages of saproxylic species that depend on certain kinds of dead wood (examples of possible target species are in Nilsson et al., 2001). The conservation efforts should be tailored to these species, and they would differ among regions according to the species' distribution. With this strategy, the target would be biologically more relevant, because the quality and spatial distribution of dead wood would be taken into consideration.

### Acknowledgements

Stig Larsson and Martin Schroeder made valuable comments on the manuscript. Support for this project came from the project "Predicting extinction risks for threatened wood-living insects in dynamic landscapes", financed by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning, the project "Conservation of biodiversity in managed forests" financed by the Faculty of Forestry at the Swedish University of Agricultural Sciences (SLU), Stiftelsen Lars Hiertas Minne, and a grant from the Natural Sciences and Engineering Research Council of Canada to L. F.

### References

Akçakaya, H. R. & Sjögren-Gulve, P. (2000). Population viability analyses in conservation planning: An overview. *Ecological Bulletins*, 48, 9–21.

Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. *Oikos*, 71, 355–366.

Angelstam, P. K., Büttler, R., Lazdinis, M., Mikusinski, G. & Roberge, J.-M. (2003). Habitat thresholds for focal species at multiple scales and forest biodiversity conservation—Dead wood as an example. *Annales Zoologici Fennici*, 40, 473–482.

Anon. (1999). *Miljö kvalitetsmål 8: Levande skogar*. Jönköping: National Board of Forestry. (In Swedish.)

Büttler, R., Angelstam, P., Ekelund, P. & Schlaepfer, R. (2004). Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. *Biological Conservation*, 119, 305–318.

Carlsson, A. (2000). The effect of habitat loss on a deciduous forest specialist species: The white-backed woodpecker (*Dendrocopos leucotus*). *Forest Ecology and Management*, 131, 215–221.

Dahlberg, A. & Stokland, J. N. (2004). *Vedlevande arters krav på substrat* (Rapport No. 7). Jönköping: Skogsstyrelsen. (In Swedish.)

Fahrig, L. (2001). How much habitat is enough? *Biological Conservation*, 100, 65–74.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*, 34, 487–515.

Fox, J. C., Mesibov, R., McCarthy, M. A. & Burgman, M. A. (2004). Giant velvet worm (*Tasmanipatus barretti*) in Tasmania, Australia. Effects on planned conversion of native forests to plantations. In H. R. Akçakaya, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjögren-Gulve, J. S. Hatfield, & M. A. McCarthy (Eds.), *Species conservation and management. Case studies* (pp. 150–161). Oxford: Oxford University Press.

Fridman, J. & 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*. Uppsala: ArtDatabanken.

Gibb, H., Ball, J. P., Johansson, T., Atlegrim, O., Hjältén, J. & Danell, K. (2005). Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. *Scandinavian Journal of Forest Research*, 20, 213–222.

Grove, S. J. (2002a). Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology, Evolution and Systematics*, 33, 1–23.

Grove, S. J. (2002b). Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: A case study from the Australian lowland tropics. *Ecological Indicators*, 1, 171–188.

Gu, W., Heikkilä, R. & Hanski, I. (2002). Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. *Landscape Ecology*, 17, 699–710.

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.

Hanski, I. & Hammond, P. (1995). Biodiversity in boreal forests. *Trends in Ecology and Evolution*, 10, 5–6.

Hanski, I. & Ovaskainen, O. (2002). Extinction debt at extinction threshold. *Conservation Biology*, 16, 666–673.

Holland, J. D., Bert, D. G. & Fahrig, L. (2004). Determining the spatial scale of species' response to habitat. *BioScience*, 54, 227–233.

Holland, J. D., Fahrig, L. & Cappuccino, N. (2005). Fecundity determined the extinction threshold in Cerambycidae. *Journal of Insect Conservation*, 9, 109–119.

Huggett, A. J. (2005). The concept and utility of "ecological thresholds" in biodiversity conservation. *Biological Conservation*, 124, 301–310.

de Jong, J., Dahlberg, A. & Stokland, J. N. (2004). Dead wood: A critical resource for maintaining forest biodiversity. *Svensk Botanisk Tidskrift*, 98, 278–297. (In Swedish with English abstract.)

Lambeck, R. J. (1997). Focal species: A multi-species umbrella for nature conservation. *Conservation Biology*, 11, 849–856.

- Lamberson, R. H., McKelvey, R., Noon, B. R. & Voss, C. (1992). A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. *Conservation Biology*, 6, 505–512.
- Lande, R. (1987). Extinction thresholds in demographic models of territorial populations. *American Naturalist*, 130, 624–635.
- Larsson, S. & Danell, K. (2001). Science and management of boreal forest biodiversity. *Scandinavian Journal of Forest Research*, 16(Suppl. 3), 5–9.
- Lindenmayer, D. B., Fischer, J. & Cunningham, R. B. (2005). Native vegetation cover thresholds associated with species responses. *Biological Conservation*, 124, 311–316.
- Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation*, 94, 199–209.
- Muradian, R. (2001). Ecological thresholds: A survey. *Ecological Economics*, 38, 7–24.
- Nilsson, S. G., Hedin, J. & Niklasson, M. (2001). Biodiversity and its assessment in boreal and nemoral forests. *Scandinavian Journal of Forest Research*, 16(Suppl. 3), 10–26.
- Økland, B., Bakke, A., Hågvar, S. & Kvamme, T. (1996). What factors influence the diversity of saproxylic beetles? A multi-scaled study from a spruce forest in southern Norway. *Biodiversity and Conservation*, 5, 75–100.
- Ovaskainen, O. & Hanski, I. (2003). Extinction threshold in metapopulation models. *Annales Zoologici Fennici*, 40, 81–97.
- Pechacek, P. (2004). Spacing behavior of Euroasian three-toed woodpeckers (*Picooides tridactylus*) during the breeding season in Germany. *Auk*, 121, 58–67.
- Penttilä, R., Siitonen, J. & Kuusinen, M. (2004). Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. *Biological Conservation*, 117, 271–283.
- Radford, J. Q., Bennett, A. F. & Cheers, G. J. (2005). Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation*, 124, 317–337.
- Ranius, T. (2002). Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. *Biological Conservation*, 103, 85–91.
- Ranius, T. (2005). Hur mycket död ved behövs i skogen? *Svensk Botanisk Tidskrift*, 99, 60–61. (In Swedish.)
- Ranius, T. & Hedin, J. (2004). Hermit beetle (*Osmoderma eremita*) in a fragmented landscape: Predicting occupancy patterns. In H. R. Akçakaya, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjögren-Gulve, J. S. Hatfield, & M. A. McCarthy (Eds.), *Species conservation and management. Case studies* (pp. 162–170). Oxford: Oxford University Press.
- Ranius, T. & 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.
- Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, 49, 11–41.
- Speight, M. C. D. (1989). *Saproxylic invertebrates and their conservation*. Strasbourg: Council of Europe.
- Thomas, J. W. (1997). Foreword. In K. A. Kohm, & J. F. Franklin (Eds.), *Creating a forestry for the 21st century. The science of forest management* (pp. ix–xii). Washington: Island Press.
- Turner, I. M. (1996). Species loss in fragments of tropical rain forest: A review of the evidence. *Journal of Applied Ecology*, 33, 200–209.
- Wikars, L.-O. & Orrmalm, C. (2005). Större svartbaggen (*Upis ceramboides*) i norra Hälsingland: En hotad vedskalbagge som behöver stora mängder aggregerad död ved [The occurrence of the threatened wood-living beetle *Upis ceramboides*: A species dependent on high densities of aggregated dead wood]. *Entomologisk Tidskrift*, 126, 161–170. (In Swedish with English abstract.)