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

Running headline: Targets for biodiversity conservation

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Abstract

Forestry decreases the amount of dead wood, thereby threatening the persistence of many saproxylic (wood-living) organisms. In this article, we discuss how targets for efforts to maintain and restore dead wood in managed forest landscapes should be defined. We found several studies suggesting 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.

Key words: beetles, ecological thresholds, occurrence patterns, saproxylic, species richness

INTRODUCTION

Ecological thresholds are important concepts in conservation and management of natural resources (Huggett 2005, Muradian 2001). 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 (e.g. 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 goes extinct. In deterministic models, the relationship between persistence probability and habitat density 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; Fig. 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 (Fig. 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 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 last 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 last decade there has been increasing concern in forestry for biodiversity preservation (Thomas 1997).

Decrease of 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 usually between 20 and $130 \text{ m}^3 \text{ ha}^{-1}$ (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 6,000–7,000 species are saproxylic, and among these 1,126 are red-listed, which represents 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 programs.

In this article we discuss how to study extinction thresholds in order to obtain information required for formulating environmental goals, with saproxylic organisms as an example. We evaluate the empirical evidence for extinction thresholds in saproxylic organisms in the literature, and discuss the implications for environmental targets and future research.

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 1). The white-backed woodpecker (*Dendrocopus leucotus*) required 10 to 20 m³ ha⁻¹ 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 (on 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 m²ha⁻¹ over a 100-ha forest area (1.3 m²ha⁻¹ corresponds to a volume of snags of 15 m³ha⁻¹), while in Sweden a smaller basal area of 0.3 to 0.5 m²ha⁻¹ 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 obviously are relevant for species presence. Because the territory sizes of these two woodpeckers are on the order of 100 ha (Carlsson 2000; Pechacek 2004), these thresholds are not a measure of the amount of habitat required for population persistence, but represent the definition of suitable habitat for the individual.

There are three studies suggesting extinction thresholds in saproxylic insects (Table 1). In a study by Økland et al. (1996) with about 190 saproxylic beetles collected, eight beetle species were absent when the amount of dead wood was below 8–28 m³ha⁻¹, or 3–7 large logs per hectare. The pattern was only observed at larger scales (1 km² or 4 km²), but not at smaller scales (0.16 ha or 1 ha). Second, 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* (Fig. 2). For this species, the frequency of presence per tree was much reduced in stands with fewer than ten suitable trees. Finally, Holland et al. (2005) correlated the occurrence patterns of twelve 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 twelve 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 m to 2,000 m from the beetle sampling point. Thus, to accurately characterize 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 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:

$$N = 18.3 + 31.8 \times \log (V + 1) \quad \text{eq (1)}$$

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). Also Grove (2002b) found a similar relationship in a study of saproxylic beetles in Australia:

$$N = 42.1 + 19.9 \times \log (V) \quad \text{eq (2)}$$

Eq (1) was based on data from 30 forest stands with dead wood amounts varying between 2 and 200 m³ ha⁻¹, while eq (2) was based on data from 9 forest stands with dead wood amounts varying between 4 and 45 m³ ha⁻¹. The derivatives of these equations have their maximum when the amount of dead wood goes towards zero (eq. 1; Fig. 3), 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 1). 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 were red-listed. Martikainen et al. (2000) and Pentillä 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 m³ ha⁻¹ (Table 1). Because Martikainen et al. (2000) and Pentillä 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 either be because rare and threatened species require a large amount of dead wood, or because

the old-growth forests have a certain history, or contain 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 are 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 take home 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 $100 \text{ m}^3 \text{ ha}^{-1}$. The fact that the first threatened species (with the lowest demand) arises at around $20 \text{ m}^3 \text{ ha}^{-1}$ 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 1). However, in most of the studies the occurrence of an extinction threshold was not statistically tested (Holland et al. 2005, Økland et al. 1996, Penttillä et al. 2004, see however Ranius 2002), because the aim of the studies was not to determine whether extinction thresholds exist. Statistical tests are necessary in order to discriminate between the Extinction Threshold Hypothesis and the Proportional Habitat Hypothesis (Fig. 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) (Fig. 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 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 (Fig 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 1), 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, we can not 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 (see however, Carlsson 2000, Fox et al. 2004, Gu et al. 2002, 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 most likely 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 vs. dead wood volume, rather than a sigmoidal curve. We hypothesize 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., Fig. 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 is lacking, do not know 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 on the order of tens of square kilometres. Probably woodpeckers require generally larger areas than cryptogams and insects. On the other hand, 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 & 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 focussing 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 4–7 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 conservation in simple rules. Still, this does not mean 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 Fig. 3, we should expect that any increase in the amount of dead wood will 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 between 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.

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Table 1. Studies on extinction thresholds in saproxylic organisms.

Individual species	Red-listed*	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 ³ ha ⁻¹	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 ² ha ⁻¹ (in Switzerland) 0.3–0.5 m ² ha ⁻¹ (in 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 ³ ha ⁻¹	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 ⁻¹	average over either 100 ha or 400 ha	Økland et al. (1996)
three beetles (<i>Tenebrio opacus</i> , <i>Elater ferrugineus</i> , and <i>Osmoderma eremita</i>)	yes (all)	hollow oaks	10 oaks per stand	a stand = all oaks that are less than 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	0.1ha to 1256ha	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 ³ ha ⁻¹ , more than two threatened species when >100 m ³ ha ⁻¹	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 ³ ha ⁻¹)	1 ha	Martikainen et al. (2000)

*) according to the national red-list at the time of publication

Fig . 1. An extinction threshold. The extinction threshold is the level of habitat density where the derivative of the persistence probability reaches a local maximum. The y-axis either represents 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) shows the appropriate goal if extinction risks up to 5% are acceptable, (B) up to 1%, and (C) up to 0.1%.

Fig. 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 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).

Fig. 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. (2002).

Fig. 4. The relationship between species abundance and habitat amount according to two different hypotheses, (i) species abundance is proportional to the habitat amount (= "Proportional habitat"), (ii) species abundance per amount of habitat is lower when the habitat amount is lower, thus indicating an extinction threshold (= "Extinction threshold). Fig 4a and

4b assume the same fictitious data set, but in 4a the y-axis represents simple abundance whereas in 4b the y axis represents abundance per habitat amount (i.e., density).

Fig. 1

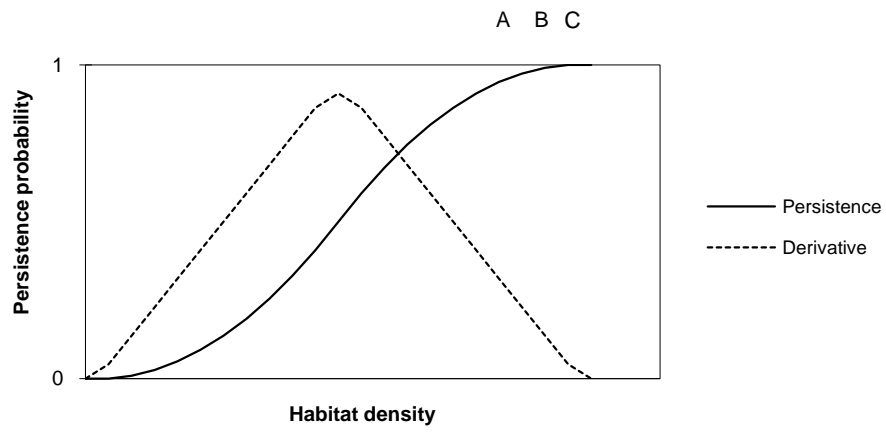


Fig. 2

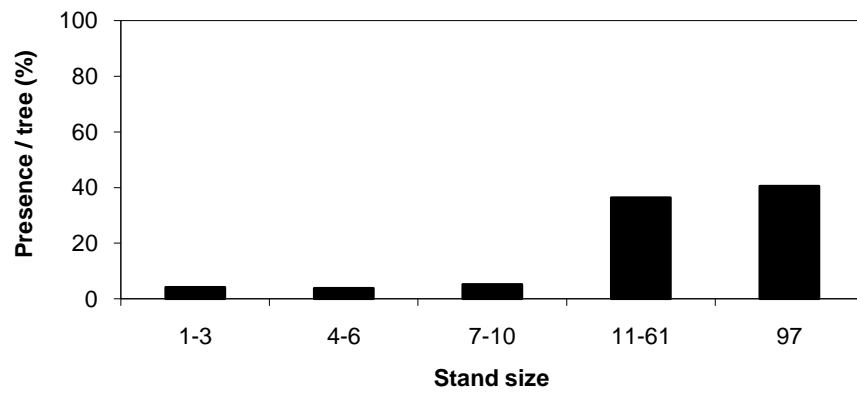


Fig. 3



Fig. 4a

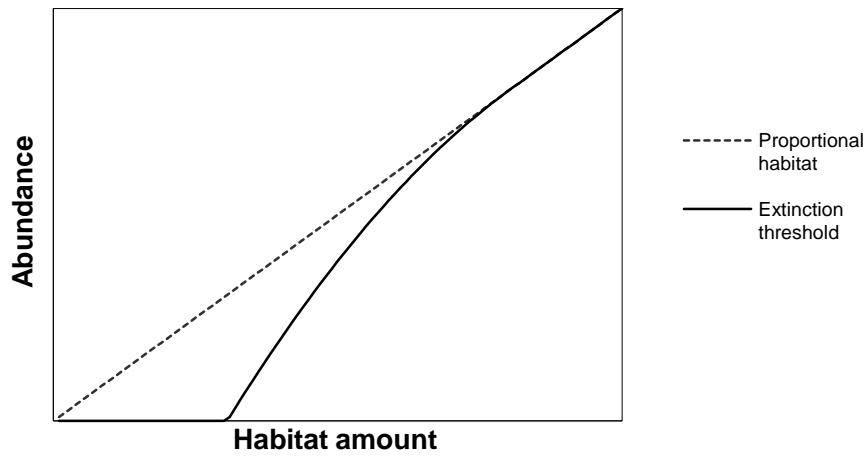


Fig. 4b

