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Density of dispersal sources affects to what extent restored habitat is used: A case study on a red-listed wood-dependent beetle

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ABSTRACT

When restoring habitats, an important question is whether the spatial distribution of habitat affects its contribution to biodiversity conservation. In Sweden, high-cut stumps are routinely created at forestry operations. By counting the number of exit holes of a red-listed beetle, *Peltis grossa*, we assessed occurrence, colonisations and extinctions per high-cut stump and beetle density per clear-cut. We found a threshold, at which the form of the relationship between density of the beetle and density of high-cut stumps per clear-cut changes abruptly. The beetle density was considerably higher where the density of high-cut stumps exceeded 4.5 per hectare. Such thresholds can be explained by colonisation-extinction processes. Observed colonisation-extinction dynamics were consistent with metapopulation theory. For instance, there was a positive relationship between colonisation rate and a connectivity measure that considered beetle abundance and distance for each high-cut stump in the surrounding area. However, the relationship disappeared when using a connectivity measure solely based on the distance of the high-cut stumps. The observed threshold implies that *P. grossa* benefits from aggregating the same total number of created high-cut stumps into fewer clear-cuts. This is because the total area with a density of high-cut stumps exceeding the threshold increases, and this expands the number and size of dispersal sources. Therefore, *P. grossa* and other species that reveal thresholds in their distribution patterns, are favoured when conservation measures are more spatially aggregated than what is resulting from current Swedish policy.

1. Introduction

Habitat loss and deterioration constitute the main threats to biodiversity worldwide. Measures to mitigate biodiversity loss include maintenance and restoration of habitat. When doing this, an important question is whether the spatial distribution of habitat matters, and if so, what is the optimal spatial distribution (e.g., Fahrig, 2013; Hanski, 2011). To understand this, the potential existence of extinction thresholds is important. When there is an extinction threshold, the abundance of species is not proportional to the amount of habitat, but the abundance per amount of habitat decreases when the amount of habitat is below the threshold (Fahrig, 2003). Thus, an increase of the amount of habitat at sites where the threshold is exceeded will result in a larger increase of the species abundance in comparison to an increase at sites where the amount of habitat is lower (Fahrig, 2003). In contrast, if the abundance is proportional with the amount of habitat, it does not matter for the landscape-scale abundance of a species where habitat is maintained or restored. Thus, only with an extinction threshold, aggregated conservation measures (generating some areas with the amount of habitat exceeding the threshold) has a stronger positive effect on species abundance than evenly distributed conservation measures.

The occurrence of extinction thresholds can be explained by colonisation-extinction processes (Lande, 1987). According to metapopulation theory, the colonisation rate increases with increasing connectivity, while the extinction rate decreases with increasing patch size and quality, and connectivity (Hanski, 1998). Metapopulation dynamics are often affected by habitat dynamics; colonisations occur in newly formed habitat patches and local extinction can either result from patch

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destruction, or demographic or stochastic events in small populations (Thomas, 1994). Thus, processes behind threshold patterns can be understood by testing hypothesis about colonisation-extinction dynamics (Sjögren-Gulve and Hanski, 2000). This can be done by assessing the colonisation and extinction rate of habitat patches over time at different spatial locations in relation to potential dispersal sources (e.g., Falaschi et al., 2021). An alternative to follow populations over time is to draw conclusions from species occurrence patterns and abundance measured only at one occasion (see Sverdrup-Thygeson et al., 2014 for a review on dead wood-associated species). That may be more convenient, but involves a risk that conclusions are influenced by unknown historical conditions (Sjögren-Gulve and Hanski, 2000).

"Connectivity" is a term with three distinct origins (Fahrig et al., 2021). One of the origins is metapopulation ecology, where connectivity is a characteristic of local habitat patches reflecting the probability of colonisations from dispersal sources in the surrounding landscape (Hanski, 1998). This type of connectivity measure is based on species occurrence (or abundance) in surrounding habitat patches, where the contribution of each patch is weighted by its distance to the focal patch (usually with a negative exponential function). This has been found to be useful, for instance when predicting colonisation patterns of butterflies (Moilanen and Nieminen, 2002). However, when planning conservation measures, e.g. where to create habitats, information about existing populations is most often not available. One option is then to simplify the calculations by only considering the amount of surrounding habitat patches (Ranius et al., 2010).

A large proportion of forest biodiversity is associated with dead wood; in boreal forests, it has been estimated that 25% of all multicellular species depend on dead wood (Siitonen, 2001). In managed forests, dead wood amount is strongly reduced (Siitonen, 2001), resulting in declining populations of many saproxylic (= dead wood-dependent) species. Therefore, many such species are on national and European Red Lists (e.g., Swedish Information Centre, 2020; Nieto and Alexander, 2010). The negative trend is mitigated by increasing the amount of dead wood, both by area protection and by a more biodiversity-oriented regime in managed forests (Felton et al., 2020).

It has been proposed that for biodiversity associated with dead wood, there are thresholds at which the form of the relationship between species abundance or richness and dead wood amount changes abruptly, and often they are at around 20–50 m^3/ha (Müller and Bütler, 2010). This can be compared to the average amount of dead wood in Swedish production forests, which is around 8 m^3/ha (Kyaschenko et al., 2022). If the proposed threshold level is true and dead wood is evenly distributed among regions and forest stands in Sweden, the amount of dead wood would everywhere be too low for many species. In contrast, if the dead wood is spatially aggregated, there may be enough habitat for all species at least at some sites. Unfortunately, for individual saproxylic species, hypotheses about extinction thresholds have only rarely been tested (Ranius and Fahrig, 2006). Thus, for making informed decisions in forest conservation planning, there is a need for more studies on this.

Active restoration efforts can speed up the increase of dead wood amount. One of the few examples of restoration efforts that have been done at a large scale is the creation of high-cut stumps, which in Sweden is routinely conducted at clear-fellings (Felton et al., 2020). In Sweden, more than a million high-cut stumps are created each year at the time of harvest and thinning of forest (Gustafsson et al., 2016). This is to a high extent due to the requirements in the Swedish forest certification standards that at least 3 high-cut stumps or girdled trees per hectare should be created (FSC, 2019). High-cut stumps are known to be used by a large number of saproxylic species, especially beetles (Schroeder et al., 1999; Lindhe and Lindelöw, 2004; Jonsell et al., 2005; Fossestoel and Sverdrup-Thygeson, 2009). So far, the possible existence of thresholds and the effect of the spatial distribution of high stumps on species' colonisation-extinction dynamics have never been studied.

In this study, we assessed potential threshold levels and the colonisation-extinction dynamics of a specialised, red-listed beetle, *Peltis grossa* (L.) (Trogossitidae), occurring in high-cut stumps. We hypothesised (1) that there is a threshold in the relationship between the clear-cut scale density of high stumps and density of *P. grossa*. Based on metapopulation theory (Hanski, 1998), we tested the following hypotheses: (2) the probability of a high-cut stump to be colonised by *P. grossa* increases with connectivity and stump characteristics reflecting high quality for the species, while extinction probability decreases with the same factors; (3) a connectivity measure considering species abundance and distance of high-cut stumps in the surrounding landscape is more strongly related with colonisation and extinction rates in comparison to a connectivity measure considering only the distance of high-cut stumps in the surrounding landscape.

Based on these analyses, we draw conclusions about how the spatial distribution of created dead wood affects its utilisation by a species of conservation concern. We assessed colonisations and extinctions over a 10 year period, with two inventory occasions (year 2005 and 2012), since the recruitment of saproxylic beetles at disturbed habitats changes over time (Ranius et al., 2014; Jonsell et al., 2019).

2. Material and methods

2.1. Study species

Peltis grossa (L.) (Trogossitidae) (Fig. 1a) breeds in brown-rotten standing dead wood of several tree species such as Norway spruce (*Picea abies* (L.) H. Karst), Scots pine (*Pinus sylvestris* L.) and grey alder (*Alnus incana*) (Palm, 1951; Saalas, 1917). In Germany, *P. grossa* is considered as a primeval forest relict species (Eckelt et al., 2017), while in Sweden it occurs to a high extent in recently cut forests (Djupström et al., 2012). It is described as "dependent on open forests" (Nilsson et al., 2001), or occurring in more or less sunexposed dead wood (Palm, 1951). The species is assessed as near threatened (NT) on the Swedish Red List (Swedish Information Centre, 2020). This is due to a small area of occupancy, indications of decreasing population sizes, a distribution area that probably is strongly fragmented, and population fluctuations that probably are extreme. The total distribution area in Sweden is rather large, and thus not a reason for redlisting the species. Extensive creation of high-cut stumps at clear-cuts is likely to increase the landscape-scale population size of *P. grossa* (Djupström et al., 2012).

2.2. Study area and site selection

We conducted the study in a ca. 10 × 10 km forest area situated in the province of Dalarna in the southern boreal vegetation zone of Sweden (Ahti et al., 1968) (Fig. 1b and 2). The forest region consists mainly of managed boreal forest dominated by Norway spruce Karst) and Scots pine. The forest land was mainly owned by the forest company Bergvik Skog AB and managed by Stora Enso Skog AB. Later Stora Enso Skog AB became also landowner. Fig. 2.

These companies were certified by Forest Stewardship Council (FSC) and according to their standards for management practices, at least 3 high-cut stumps per hectare should be created at the time of final felling (FSC, 2019). The clear-cuts in this area that were felled in 1993–1994 are among the first in Sweden where high-cut stumps were created. Six of these clear-cuts (Fig. 1b) were included in an experiment where many more high-cut stumps were created than was required from the certification standards (Djupström et al., 2012). The average density of high-cut stumps on these clear-cuts was 6.2 ha^{-1} in comparison to 3.0 ha^{-1}, which was the average density in Sweden for the felling period of 1993–2000 (Swedish Forest Agency statistics).

To find all high-cut stumps within the study area we identified all clear-cuts made between the years 1993–2002 from a database provided by Stora Enso Skog AB. Additional clear-cuts on private land were identified using digital maps.

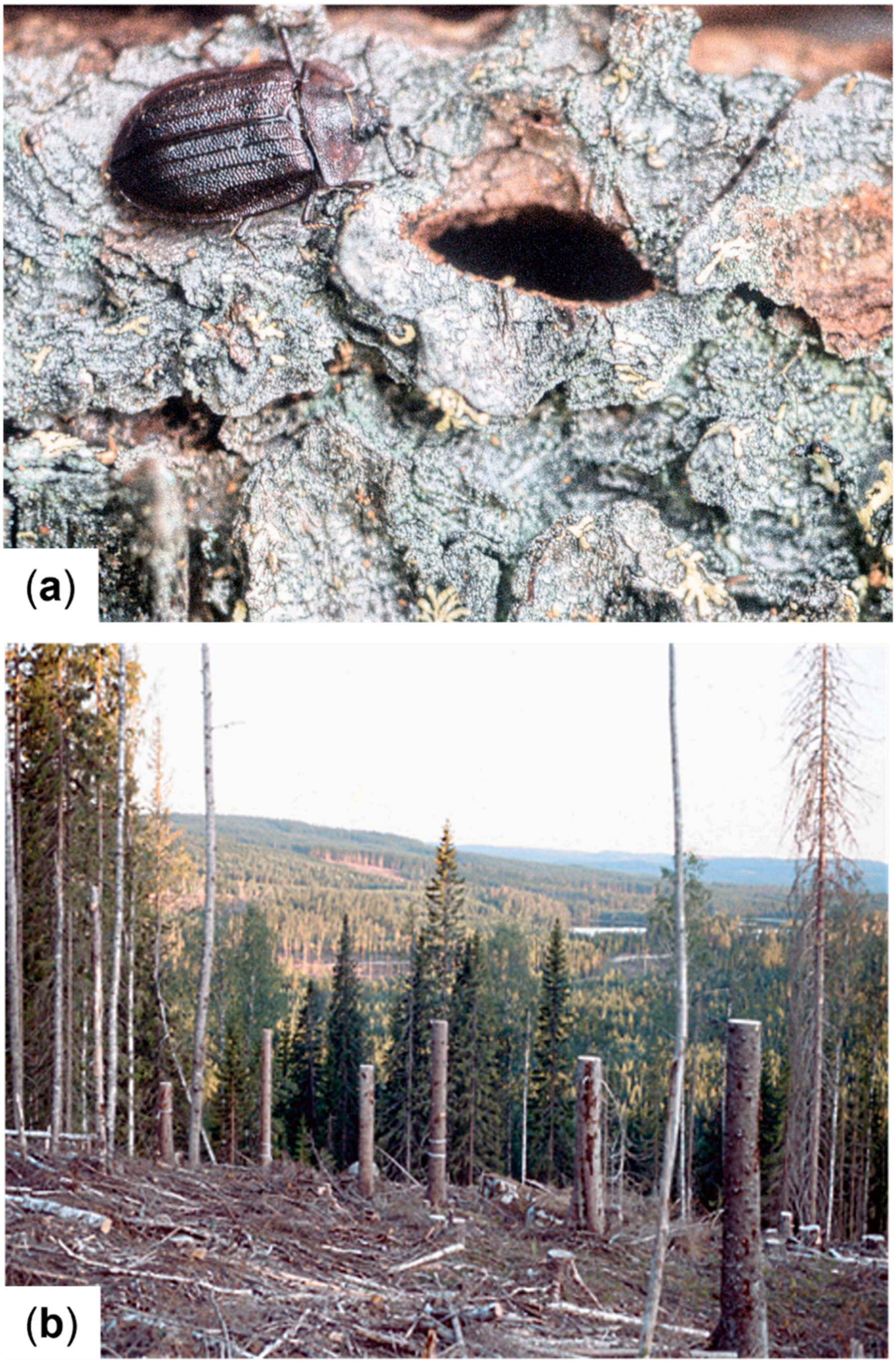

Fig. 1. a) A specimen of the beetle *Peltis grossa* (L.) Trogossitidae next to its emergence hole and b) landscape picture of high-cut stumps at one of the studied clear-cuts Photos: J. Weslien.

2.3. Species survey

In 2005 and in 2012, we visually inspected 2978 high-cut stumps of Norway spruce, distributed over 47 clear-cuts and counted all exit holes from *P. grossa,* adding up to 758 exit holes in 2005 and 4004 exit holes in 2012. The exit holes of adult *P. grossa* have a characteristic oval shape and are easily detectable (Fig. 1a) (Ehnström and Axelsson, 2002). For all high-cut stumps their diameter at breast height (dbh), presence of fruiting bodies of *Fomitopsis pinicola* (Sw.) P. Karst. and time since felling were recorded. These are all qualities that have previously been found to be of importance for the suitability of a stump as a breeding substrate for *P. grossa* (Weslien et al., 2011; Djupström et al., 2012). The position for each high-cut stump was recorded using a GPS.

The estimate of connectivity is dependent on knowledge about relevant habitats in the whole landscape. Therefore, during the 2005 survey, we also searched for exit holes along transects in forests older than 15 years and on clearcuts on other standing dead wood objects than high-cut stumps (Djupström et al., 2012). Two types of transects were used: (i) 42 randomly selected forest transects using a grid net over the study landscape, each 500 m long and 20 m wide (i.e. 1 ha each and altogether 42 ha) and (ii) 6 transects adjacent to the six experimental clear cuts, covering in total 8.2 ha forest area (see Djupström et al., 2012 for details). No exit holes were found on standing dead wood in forest. A comparison between high-cut stumps and other standing dead wood at clear-cuts revealed that despite that high-cut stumps constitute a minor fraction (20.4%) of all standing dead wood objects, they harboured

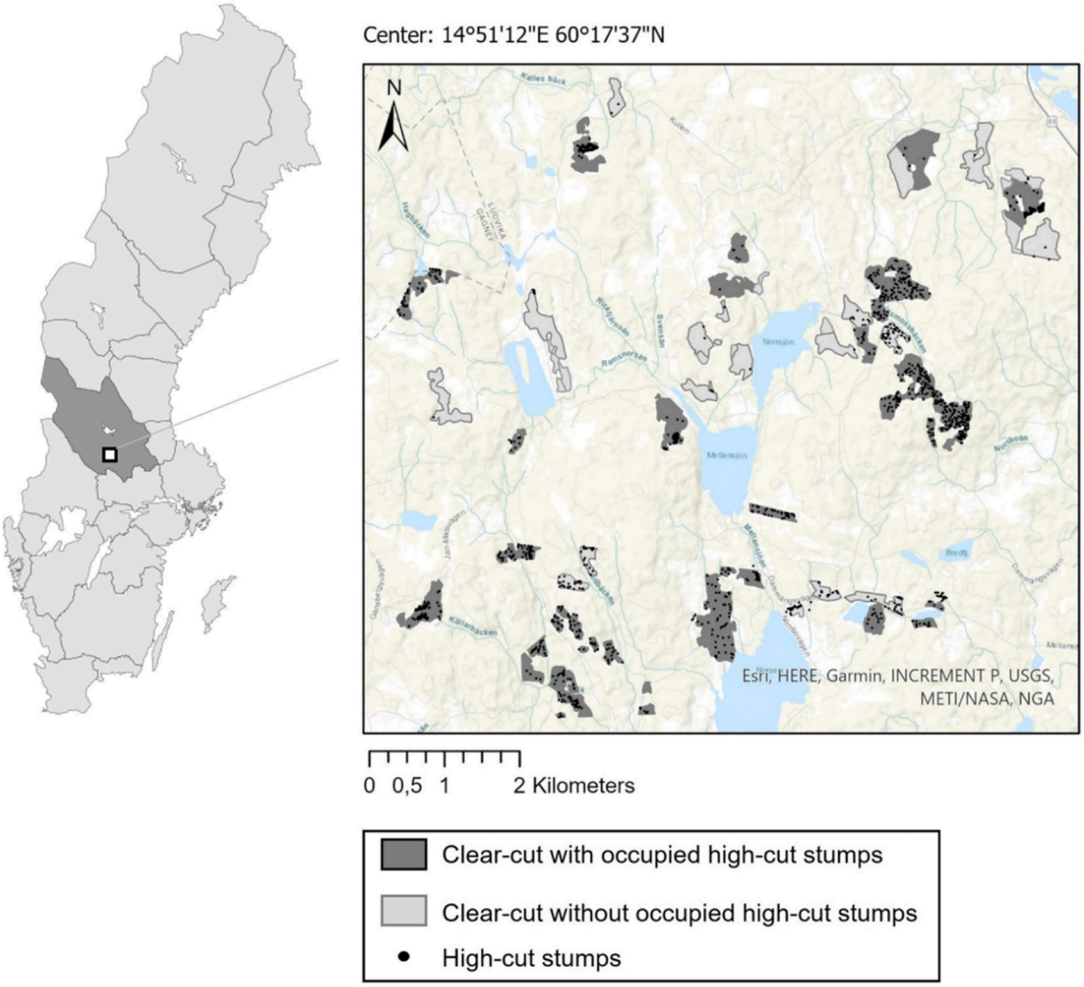

Fig. 2. Study area, in the province of Dalarna in Sweden, with clear-cuts harvested between the years 1993 and 2002 in the southern province of Dalarna, which was inventoried in 2005 and in 2012. 31 of in total 47 inspected clear-cuts were colonised (dark shading) by *Peltis grossa* (L.).

62.4% of all exit holes on clear-cuts older than 10 years. Thus, we have most likely included most of the suitable dead wood items in the landscape in this survey.

2.4. *Statistical analyses*

To assess potential threshold values in the density of *P. grossa* in relation to the density of high-cut stumps within a clear-cut, we used recursive partitioning with maximally selected rank statistics (Müller and Hothorn, 2004; Müller and Bütler, 2010), using the add-on library 'partykit' in R. This method separates two groups of observations with maximal discrepancy of the response values by a simple cut-point defined by the explanatory variable.

We modelled (1) colonisation probability, (2) extinction probability, and (3) occurrence probability of *P. grossa* per high-cut stump in relation to the following explanatory variables: (i) stump diameter (dbh), (ii) stump age, (iii) abundance of *F. pinicola* fruiting bodies, and (iv) connectivity (see below). As an adaptation to our sampling design, colonisation and extinction probability was estimated for 7-year periods. We defined colonisation in 2005 as presence of exit holes at a high-cut stump (since at that time no stumps had been suitable for the beetle 7 years earlier) and in 2012 as presence of exit holes where there were no exit holes in 2005. Extinction was defined as when a high-cut stump had stopped producing *P. grossa,* i.e. there were no additional exit holes in 2012 in comparison to 2005. Occurrence was defined as when a high-cut stump had exit holes in 2005 and when there were additional exit holes in 2012 in comparison to 2005. Age was defined as the time since felling (i.e., high-cut stump creation). We only considered high-cut stumps that were at least 10 years at the time of survey in 2005 (i.e., cut in 1995 or earlier), since it takes about ten years before *P. grossa* starts to emerge (Djupström et al., 2012).

All high stumps of study occurred in the same landscape, but they had different spatial locations within this landscape. Thus, they differed in where they occurred in relation to dispersal sources, and that was considered in the connectivity measure we used. We based the connectivity measure either on the distance to high-cut stumps or on both the distance to high-cut stumps and their abundance of *P. grossa* (i.e. the new holes, estimated as the number of exit holes at present minus the number of exit holes seven years ago) in the surroundings to test the difference in the outcome between these measures. For each high-cut stump we considered all other high-cut stumps within the study area.

We estimated connectivity of high-cut stumps I (S_j) using the following equation:

$$S_i = \sum_{j=1}^{n} \exp(-\alpha d_{ij}) A_j, \mathit{forallj} \neq i \qquad (1)$$

where d_{ij} = distance between the focal high-cut stump i and surrounding high-cut stump j; n = total number of high-cut stumps; A_j = either species abundance in high-cut stump j or equal to 1 in connectivity measures only considering occurrence of high-cut stumps; and α is a parameter that sets the spatial scaling. The α value reflects how the importance of surrounding potential dispersal sources decreases with distance. We parametrised α based on the observed data by searching for the α that resulted in the highest mean explained deviance (= (null deviance – residual deviance)/null deviance) among the six models (three response variables × two connectivity measures) described below. This function has been found to be useful in connectivity measures for animal species (Moilanen and Nieminen, 2002; Prugh, 2009).

Colonisation probability, extinction probability and occurrence probability of *P. grossa* were modelled based on the explanatory variables described above using generalised linear mixed effect models with a binomial distribution and a log-link function (logistic regression), with clear-cut identity as a random factor, as high-cut stumps within the same clear-cut are not independent. Models were built based on AIC, and the final best model was the one with the lowest AIC. For each model we also calculated the explained deviance (in %), i.e. the proportion of the total variation explained by the model (an analogue to R^2).

3. Results

There was a clear threshold of 4.5 high-cut stumps per ha (95% confidence interval = 4.1–6.7) for the density of *Peltis grossa* within a clearcut (Fig. 3). The mean clear-cut density of high-cut stumps in our study area was 3.3 stumps per hectare.

Both the occurrence probability and colonisation probability of *P. grossa* was positively related to stump diameter, stump age, and the presence of *Fomitopsis pinicola,* where the latter had the highest explanatory power (based on ΔAIC, Table 1). The colonisation probability increased with increasing connectivity, and the relationship was clearly stronger when connectivity included also the abundance of *P. grossa* (ΔAIC >20 for both models) rather than only of the distance to high-cut stumps (ΔAIC <2). The extinction probability decreased with increasing connectivity, and no other explanatory variable was included in the final model (Table 1). The scaling of α implies that the probability of occurrence, colonisation and extinction are mainly influenced by dispersal sources within 200 m (Fig. 4).

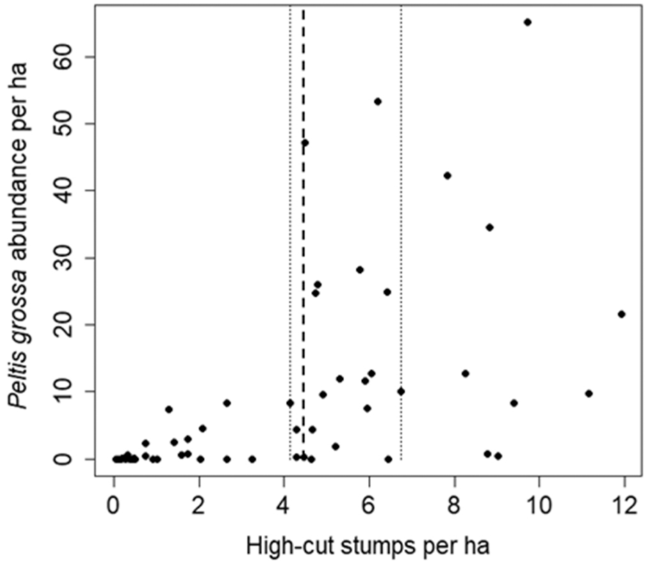

Fig. 3. The density of *Peltis grossa* in relation to density of high-cut stumps within a clear-cut. Vertical broken line signifies a threshold value with associated 95% confidence interval (dotted lines) from a recursive partitioning with maximally selected rank statistics.

4. Discussion

4.1. Threshold in the species density-habitat density relationship

We observed a clear threshold, with densities of *Peltis grossa* increasing much more strongly with high-cut stump density when there were more than 4.5 high-cut stumps per hectare. In Sweden, the practice of creating high-cut stumps during the final felling has been implemented on a large-scale during approximately 25 years. This approach is not only prescribed by the law but also a requirement in certification standards (SFS 1993; FSC, 2019). These stumps are obviously habitat for *P. grossa*, but still, *P. grossa* is red-listed in Sweden. Our result reveals that the prescribed level of 3 high-cut stumps per hectare is below a threshold level, which suggests that the creation of habitat has so far not been efficient for increasing the abundance of the species. To enable *P. grossa* to effectively respond, it would be more beneficial to aggregate the created high-cut stumps within a reduced number of clear-cuts. By doing so, the abundance of *P. grossa* per high-cut stump can be increased, subsequently expanding the areas where the density of high-cut stumps surpasses the required threshold.

Several studies on saproxylic beetles in dead wood resulting from living and dead wood retained at clear-felling reveal that the frequency of occurrence or species richness per dead wood unit increases with the density of habitat (e.g., *Hadraeule elongatula* (Gyllenhall) in high-cut stumps of Norway spruce (Schroeder et al., 2006); beetles in dead wood of aspen (Sahlin and Schroeder, 2010), and *Upis ceramboides* (L.) in logs of birch (Rubene et al., 2014)). This gives support to the existence of thresholds, suggesting that *P. grossa* is not a unique case. However, in these previous studies, the threshold levels have not been estimated. Since saproxylic species have different habitat requirements, also the threshold levels most likely vary widely among species (Ranius and Jonsson, 2007). Therefore, to favour a large number of species, it is desirable with a wide variation in habitat density among sites, to make some sites suitable also for the most demanding species.

Thresholds for saproxylic insects may also manifest in other forest and dead wood types. However, the pattern may often be weakened due to the adaptability of most species to various forest and dead wood types. Instead, it is easier to establish thresholds for a species highly linked to a dead wood type, like high-cut stumps on clearcuts, than for overall species richness in more varied habitats, such as old forests (cf. Ranius and Jonsson, 2007).

4.2. Colonisation and extinction rates in relation to succession and habitat quality

As hypothesised and consistent with metapopulation theory (Hanski, 1998), we observed colonisation and extinction patterns of *P. grossa* being determined by connectivity and habitat characteristics reflecting succession and habitat quality. The colonisation-extinction dynamics have been analysed by repeated surveys for two other saproxylic insect species: *Osmoderma eremita* (inhabiting hollow trees; Lindman et al., 2020) and *Stephanopachys linearis* (inhabiting burned forest areas; Ranius et al., 2014). Also for them, habitat characteristics reflecting succession and habitat quality, and to some extent also connectivity, were important factors. Thus, all these species have features of “habitat-tracking metapopulations”, which means that many of the extinctions from trees take place due to that they become unsuitable for the species (Harrison and Taylor, 1997). Thus, they differ from “classic” metapopulations, in which local extinctions take place stochastically in small populations inhabiting habitat patches that later can be recolonised.

The colonisation rate of *P. grossa* increased with the age of the high-cut stumps, while age did not affect the local extinction risk. This suggests that the studied stumps were at various successional stages and especially among the younger ones, some had not yet developed the right qualities for *P. grossa*. However, there was no evidence that any of

Table 1
Parameter estimates (Est) with standard error (SE) for the final best model (based on AIC) for the colonisation probability, extinction probability, and occurrence probability of *Peltis grossa*. Connectivity is either based on species abundance (A) or the number of available high stumps (HS), with $\alpha = 13.3\ \text{km}^{-1}$ (see Eq. 1). ΔAIC = the change in AIC when removing the variable from the final model.

Response variable	Intercept	Age		*Fomitopsis pinicola*		Diameter		Connectivity	
	Est (SE)	Est (SE)	ΔAIC	Est (SE)	ΔAIC	Est (SE)	ΔAIC	Est (SE)	ΔAIC
Colonisation, HS	-2.09 (0.21)	0.71 (0.08)	87.8	1.15 (0.10)	176.7	0.55 (0.09)	34.4	0.19 (0.14)	0.02
Colonisation, A	-2.03 (0.18)	0.42 (0.10)	16.7	1.13 (0.10)	170.3	0.54 (0.10)	32.7	0.51 (0.11)	21.7
Extinction, HS	-0.56 (0.37)	-		-		-		-1.12 (0.41)	6.6
Extinction, A	0.001 (0.38)	-		-		-		-0.98 (0.28)	12.5
Occurrence, HS	-2.00 (0.22)	0.81 (0.08)	136.0	1.12 (0.09)	181.8	0.57 (0.09)	40.8	0.26 (0.13)	1.9
Occurrence, A	-1.94 (0.18)	0.50 (0.09)	27.8	1.09 (0.09)	171.8	0.57 (0.09)	40.0	0.55 (0.10)	28.8

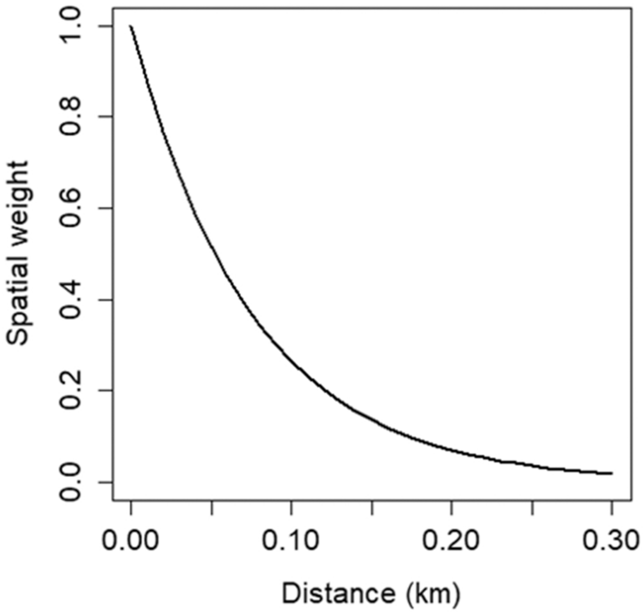

Fig. 4. Weight of the contribution of dispersal source *j* to the connectivity of focal high-cut stump *i*, with the estimated value of α ($13.3\ \text{km}^{-1}$), as a function of distance (*dij*) between *i* and *j* (see Eq. 1).

the stumps had become too old for the species. This differs from *S. linearis*, which often occurs already three years after burning, and for which the frequency of occurrence clearly decreased when the time since burning exceeded 10 years (Ranius et al., 2014). Thus, *P. grossa* both colonises and goes extinct at a later stage of succession after the disturbance compared to *S. linearis*.

As expected, diameter and the presence of fruiting bodies of a fungi (*Fomitopsis pinicola*) were both positively related to the colonisation rate (Weslien et al., 2011; Djupström et al., 2012; Busse et al., 2022). One explanation for the importance of diameter is that it reflects the amount of available resources (i.e. patch size according to metapopulation theory; Hanski, 1998), but the diameter may also reflect quality, since a large diameter narrows the width of temperature fluctuations (Lindman et al., 2022). The strong positive correlation between *P. grossa* and *F. pinicola* supports the view that the species occurs in brown-rotten wood (Palm, 1951; Saalas, 1917), since that is what is generated by decomposition by *F. pinicola.* It has been suggested that the *F. pinicola* mycelia present in the wood serve as a food source for the larvae and the fruiting bodies serve as a food source for the adults (Hågvar, 1999; Ehnström and Axelsson, 2002).

4.3. Colonisation and extinction rates in relation to connectivity

Using a connectivity measure based on species abundance revealed a positive relationship between connectivity and colonisation rates, and a negative relationship between connectivity and extinction rates. This is consistent with metapopulation theory (Hanski, 1998). Positive relationships with colonisation rate have been found also in other colonisation-extinction studies on saproxylic insects (Lindman et al., 2020; Ranius et al., 2014). A positive relationship between colonisation rate and connectivity is due to differences in the rate of immigration causing different colonisation rates among high-cut stumps differing in their spatial location, with larger dispersal sources at shorter distances generating a higher immigration rate. The negative effect of connectivity on extinction can be explained by a rescue effect (Brown and Kodric-Brown, 1977), i.e., that the rate of extinction decreases due to immigration from nearby patches.

The connectivity explained the variation in species occurrence to a relatively high extent when including species abundances of distances of high-cut stumps in the surrounding landscape. However, when based only on distances of high-cut stumps, the goodness-of-fit was clearly much lower. Thus, information about the abundance of high-cut stumps in the surroundings, without any species data, is of low value for predicting the occurrence of *P. grossa*, while abundance data makes such predictions possible.

5. Conclusions

The combining of assessments of thresholds in the shape of the species density – habitat density relationship with analyses of colonisation-extinction dynamics is rare but makes it possible to assess the effect on species of the spatial distribution of habitat patches and thus also conservation efforts. This study shows that there is a threshold in the relationship between the density of *P. grossa* and the density of habitat, and that the probability of colonisation and presence increases with connectivity. This implies that when maintaining or restoring habitats for saproxylic insects, the spatial distribution of these efforts may be important. For our study species, the conservation efforts are more efficient (i.e. it is a higher probability that the created dead wood will indeed be used by the species) when conservation measures are unevenly distributed among forest stands, so the habitat becomes spatially aggregated. This increases the area where the density of habitat exceeds the threshold, which increases the total population size, and thus also the dispersal sources. Both increased size of the populations and of dispersal sources are important for reversing the trends that make *P. grossa* red-listed in Sweden today. Since the threshold levels most likely differ widely among species, conservation strategies should not be adapted to the level for one particular species. To favour a large number of species it is better to have a wide variation in habitat density among sites, to make some sites suitable also for the most demanding species.

There are still large uncertainties about the influence of the spatial distribution of conservation efforts on biodiversity (Hanski, 2011; Fahrig, 2013). Our outcome provides one possible explanation for some of the discrepancies between studies conducted with different approaches. When analysing species occurrences in relation to a connectivity measure considering only the habitat density in the surrounding landscape the effect was weak. However, connectivity measures and buffer metrics only considering habitat but not species occurrences in the surrounding landscape are often applied in studies of landscape-scale effects on biodiversity. Our results indicate that they might often be too poor at reflecting the distribution of dispersal sources, which is an explanation for weak effects. On the other hand, we found that when the connectivity measure was based on detailed knowledge about the abundance of a certain species, there were clear positive effects of connectivity. Thus, using more data of that kind may improve our understanding of the effect of the spatial occurrence of habitats and conservation measures.

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CRediT authorship contribution statement

Ranius Thomas: Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing. **Weslien Jan:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Validation, Writing – review & editing. **Johansson Victor:** Data curation, Formal analysis, Investigation, Validation, Writing – review & editing. **Djupström Line:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Validation, Writing – original draft, Writing – review & editing. **Schroeder Martin:** Conceptualization, Investigation, Methodology, Validation, Writing – review & editing. **Lindman Ly:** Data curation, Formal analysis, Investigation, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Ethics approval

All applicable national guidelines for the care and use of animals were followed.

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