Received: 11 January 2023 | Accepted: 24 April 2023

DOI: 10.1111/1365-2664.14429

Journal of Applied Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Effective management for deadwood-dependent lichen diversity requires landscape-scale habitat protection

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Funding information
Svenska Forskningsrådet Formas, Grant/Award Number: 2015-00904 and 2019-01559

Handling Editor: Yolanda Wiersma

Abstract

1. Habitat loss is considered a major threat for biodiversity. However, the scales on which its effects occur are still insufficiently understood, namely, is the amount of available habitat important for species richness on both local and landscape scales? We studied the effects of local and landscape-scale habitat amount on local-scale species density of deadwood-dependent lichens in Swedish boreal forests. Creation and retention of deadwood are common practices to benefit forest biodiversity, and recognizing the relevant scale is critical for them to be successful.
2. We surveyed deadwood-dependent lichens in 90 unmanaged forest stands that differed in the local and landscape habitat amount. The local habitat amount was measured as the amount of deadwood in the sampled stands (m^2 deadwood ha^{-1}), while six alternative proxies were used to estimate the landscape habitat amount, that is, the amount of deadwood in the surrounding landscapes. Lichen species density (number of species per standardized deadwood area of 3.7 m^2) was modelled as a function of local and landscape habitat amount at multiple scales (300 m–5 km from the stands).
3. Lichen species density increased with the landscape habitat amount. The proportion of old forests (>100 years, including newly clear-cut stands that until recently were old forests) within 5 km from the stands explained species density better than the other proxies of landscape habitat amount. Local deadwood amount did not affect species density, and there was no interaction between the local and landscape habitat amount.
4. *Synthesis and applications*: To promote the conservation of deadwood-dependent lichens, the amount of old forests in managed forest landscapes should be maintained or increased. A certain amount of deadwood hosted more lichen species when situated in a landscape with more old forest, while there was no effect of the local deadwood amount. This suggests that management aimed at increasing the local species density of deadwood-dwelling lichens should focus on creating and maintaining habitat in the surrounding landscape rather than only adding deadwood to that local site. In other words, effective management for deadwood-dependent lichen diversity requires landscape-scale habitat protection.

KEYWORDS
biodiversity, boreal forest, deadwood, forest conservation, habitat amount hypothesis, landscape composition, lichens

1 | INTRODUCTION

Habitat loss is considered to be a major reason for the global decrease of biodiversity. However, there is disagreement about the scales over which habitat loss affects biodiversity (Miller-Rushing et al., 2019). The habitat amount hypothesis (HAH) (Fahrig, 2013, Figure 1) predicts that landscape habitat amount is more important than local habitat amount in determining species richness at a local sample site (species per unit of area, hereafter 'species density'). Species density increases with the amount of habitat in the surrounding landscape due to a higher colonization rate of sample sites that are surrounded by more habitat. A landscape with more habitat is assumed to contain more of the species found in the ecoregion, and the number of species that can colonize the site is, therefore, higher for a site in a landscape with more habitat than for a site in a landscape with less habitat. Furthermore, the HAH predicts that the size of the patch containing the sample site (the local patch) does not affect species density at the sample site, once the effect of habitat amount in the landscape surrounding the sample site is accounted for. Often, the amount of habitat surrounding the sample site is positively related to the size of the habitat patch containing the sample site (i.e. the local habitat amount). Therefore, according to the HAH, the reason why species density at a sample site increases with patch size is that it is related to the amount of habitat in the landscape surrounding the sample site. In other words, the effects of patch size on species density are subsumed in the effect of habitat amount in the landscape. Although local (patch) extinctions decline with local habitat amount, the HAH implicitly assumes that this does not affect species density at a sample site separately from the effect of landscape habitat amount, as long as the landscape is sized appropriately to allow dispersal and colonization. Hence, in a model containing both local patch size and landscape habitat amount, the effect of landscape habitat amount should dominate, and there should be no additional effect of local patch size on species density. This prediction has important implications for conservation prioritizations: support for the HAH would imply that, when the interest is on protecting or increasing species richness at a site, effective conservation action requires landscape-scale habitat protection, not just protection or creation of local habitat.

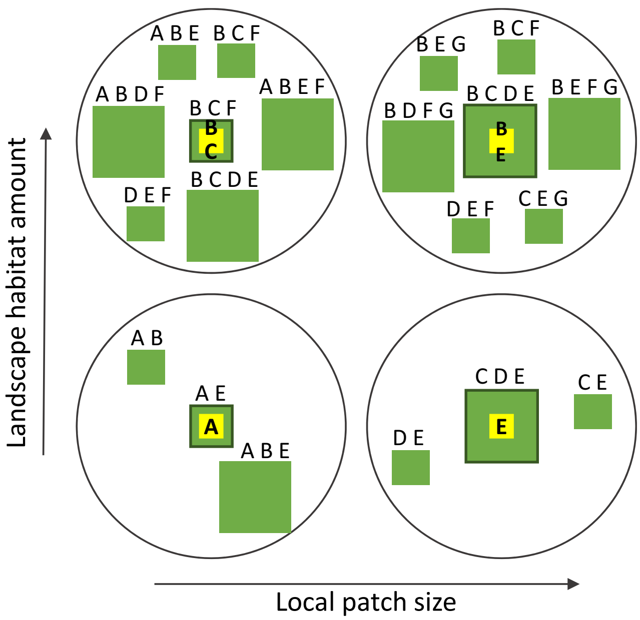

FIGURE 1 Illustration of the habitat amount hypothesis (HAH). Sample sites are small yellow squares. The 'local landscapes' of the sample sites are indicated by the large circles. Green (and yellow) areas are habitat, and the 'local patch' containing each sample site is indicated by a dark border. Letters represent species. The two lower landscapes have fewer species (three species) than the two upper landscapes (six species) due to the species–area relationship, that is, because the upper landscapes contain more habitat area in total than the lower landscapes. Consequently, there are fewer species available to colonize the two lower sample sites than the two upper sample sites. This leads to lower species density in the lower sample sites than in the upper sample sites (bold letters). The local patches of the two left sample sites are smaller than the local patches of the two right sample sites. However, the HAH predicts no effect of this difference in patch size on the number of species in the sample sites because the landscapes on the left contain the same amount of habitat as their respective landscapes on the right.

In this study, we test the HAH for deadwood-dependent lichens in boreal forests by examining how their species density is affected by the local habitat amount (amount of deadwood per area in a forest stand) and landscape habitat amount (amount of deadwood, or a proxy of it, in the landscape). We intentionally selected sites to minimize the correlation between local and landscape habitat amount, allowing us to clearly identify their effects. We use deadwood-dependent lichens as a study group because deadwood is important for forest biodiversity, but has decreased greatly in production forests due to intensive forest management (Cyr et al., 2009; Siitonen, 2001) with negative consequences for deadwood-dwelling species. Therefore, retention and creation of deadwood in production forests are frequently recommended for the conservation of forest biodiversity (Halme et al., 2013; Sandström et al., 2019). For these practices to be successful, it is essential to understand over what spatial scales the amount of deadwood within the landscape affects deadwood-dwelling species.

In support of the HAH, two quantitative reviews (Martin, 2018; Watling et al., 2020) found that the effects of local habitat amount—usually measured as the size of the patch containing the sample site—on species density are generally weak or non-existent in models containing both local and landscape habitat amount (as in Figure 1). The findings may, however, be habitat- or taxon-specific

(Martin, 2018). Results of previous empirical studies on deadwood-dwelling species vary: in certain studies, species richness has been found to increase with landscape habitat amount within 1–10 km of sample sites (saproxylic beetles, e.g. Gibb et al., 2006; Larsson Ekström et al., 2021; Olsson et al., 2012), whereas others have found no effects of habitat amount when assessed at similar scales (lichens, Hämäläinen et al., 2021; saproxylic beetles, Lindbladh et al., 2007). Further studies are, therefore, needed to clarify the scales of effect of habitat amount on the species richness of deadwood-dwelling species. In particular, there is a shortage of studies on passively dispersing species such as lichens or fungi, as well as studies that assess the effects of both local and landscape habitat amount (but see e.g. Seibold et al., 2017).

In this study, we examine the assemblages of deadwood-dependent lichens in unmanaged boreal forests in Sweden. We test the HAH by assessing whether, in models containing both local and landscape habitat amount, the landscape habitat amount affects lichen species density (species richness per a standardized deadwood area) within a forest stand, but the local habitat amount has no additional effect. In addition, we test whether the effect of the local habitat amount depends on the landscape habitat amount (i.e. whether there is an interaction effect between local and landscape habitat amount) because it has been suggested that the effects of local habitat amount only occur below a certain level of landscape habitat amount (Andrén, 1994; Tscharntke et al., 2005). Since habitat for the studied species is deadwood, we measure local habitat amount as the amount of deadwood per area in the sampled forest stands, and the amount of habitat in the surrounding landscapes using either estimated amount of deadwood or a proxy (the amount of old or protected forest) within the landscape. Consistent with the HAH, we predict that, in a model containing both local and landscape habitat amount:

(i) lichen species density (species richness per a standardized deadwood area) is higher in landscapes with more deadwood,
(ii) the local habitat amount (i.e. amount of deadwood within a stand, $m^2 ha^{-1}$) does not affect species density and
(iii) there is no interaction effect between local and landscape habitat amount.

2 | MATERIALS AND METHODS

2.1 | Study design and field survey

We surveyed deadwood-dependent lichens and allied fungi (hereafter 'lichens') in 90 old forest stands in Sweden. We included species defined as deadwood-dependent (i.e. found only on deadwood in the Fennoscandian region) by Spribille et al. (2008). The surveyed stands were located in three different regions, with 30 stands in each (Figure 2). The regions were located in the hemiboreal, middle boreal and northern boreal vegetation zones (Ahti et al., 1968). The stands were arranged in blocks of three (Figure 3),

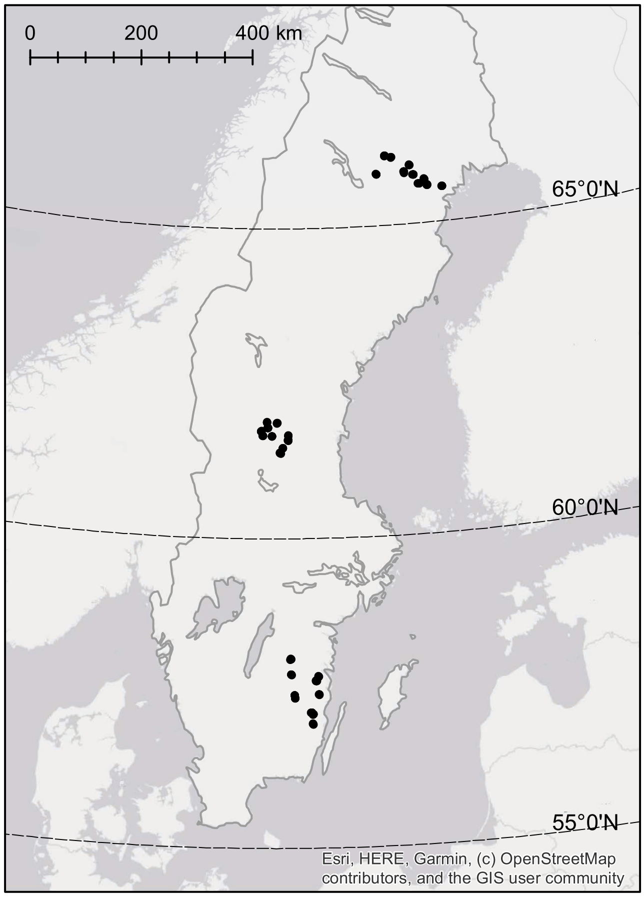

FIGURE 2 Map of the forest stands where lichen surveys were carried out in Sweden.

each block including (i) a stand on productive forest land (annual forest growth >1 $m^3 ha^{-1}$), (ii) a stand on dry, low-productivity land (e.g. rocky outcrops or hilltops) and (iii) a stand on low-productivity mire. We expected that these stand types would have different amounts of deadwood, since in unmanaged boreal forest, the amount of deadwood is typically lower in low-productivity forests (Hämäläinen et al., 2018; Kyaschenko et al., 2022). The stands were all dominated by Scots pine (>60% of the basal area of living trees) and set aside from intensive forestry, although some indications of former human use (e.g. selective harvest) could be seen. The stands were a minimum of 1.5 ha and surrounded by managed forests or open mires. The distance between the three stands within a block was less than 3 km (median 908 m), while the distance between any two blocks was more than 5 km.

The stands were surveyed in the summers of 2017 and 2019. Eight circular study plots with a radius of 20 m were randomly placed in each stand (Figure 3). All bark-free deadwood (fresh deadwood items with bark cover were excluded) of Scots pine with a diameter >10 cm within these plots was surveyed for lichens. This included both fallen and standing deadwood. The deadwood was mainly naturally created, with the exception of a few old, cut stumps. Deadwood of other tree species than pine >10 cm was rare, or absent, in the studied stands and was not sampled. Similarly, deadwood of pine

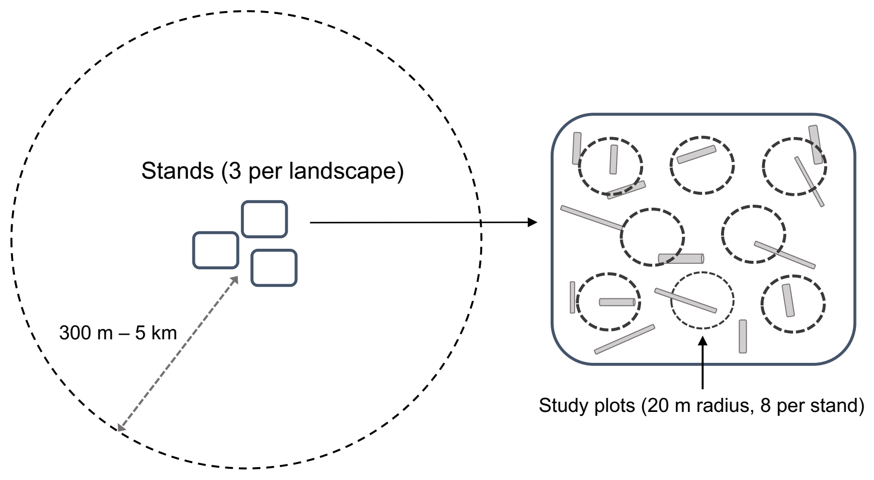

FIGURE 3 Study design. Deadwood-dependent lichens were surveyed in 90 forest stands, located in blocks of three stands each. Within each stand, we randomly placed eight study plots (radius 20 m). All bark-free deadwood items within the plots were surveyed for lichens. The landscape habitat amount was estimated within 300 m–5 km from the center of each stand (i.e. the center of the eight study plots).

<10 cm was rare, even in the stands with lower productivity. For fallen dead trees that were only partly within the plots, every second tree was included. For each deadwood item, a standardized area (0.62 m^2, which corresponds to the area of a tree of 10 cm diameter surveyed to 2 m height) was surveyed for lichens. When necessary, samples of lichen specimens were collected for laboratory identification using microscopy and chemical spot tests. Nomenclature of lichens followed Jääskeläinen et al. (2015). In addition, the length, diameter, decay stage (on a 5-point scale) and amount of bark left (%) were measured for each deadwood item. The field surveys did not require any licences or permits.

2.2 | Statistical analyses

2.2.1 | Lichen species density

To account for the variation in sampling effort among stands (i.e. varying amounts of deadwood sampled), we calculated lichen species density by constructing species accumulation curves for each stand using the package iNEXT (Hsieh et al., 2016) in R version 3.6.2 (R Core Team, 2019). From the species accumulation curves, we obtained the number of lichen species per standardized area of deadwood. The standardized area was set as 2× the smallest sampled area because the species accumulation curves can be reliably extrapolated up to double the sample size (Chao et al., 2014). This resulted in a standardized area of 3.72 m^2 deadwood per stand (i.e. six deadwood items per stand).

2.2.2 | Local habitat amount

The local habitat amount was calculated as the amount of deadwood within the stands. We calculated the total deadwood amount as the area of wood not covered by bark or bryophytes (i.e. available for lichens) per hectare. In addition to the total deadwood amount, we calculated the amount of old deadwood (decay stages 3–5), as this has been suggested to be a better quality habitat for lichens than fresh deadwood (Santaniello et al., 2017). The amount of old deadwood correlated indeed better with stand-scale lichen species density than the total amount of deadwood and was, therefore, used to describe the local habitat amount in the following analyses.

2.2.3 | Landscape habitat amount

We calculated six different variables to assess the amount of habitat on a landscape scale: (a) the proportion of formally protected forests and woodland key habitats (WKHs: not formally protected, but classified as valuable for forest biodiversity and rarely harvested due to forest certification standards); (b) the proportion of forests not under intensive management, including protected forests, WKHs and low-productivity forests (forests with annual tree growth rate <1 m^3 ha^{-1} that according to the Swedish Forestry Act should be left unharvested); (c) the proportion of old forests, including forests over 100 years or under 20 years (rationale below) and (d–f) the amount of deadwood within the landscape, estimated with three different methods (see the next paragraph). The forest types included in (a–c) typically host more deadwood than regular managed stands (Fridman & Walheim, 2000; Gibb et al., 2005) and were, therefore, assumed to function as proxies for the landscape habitat amount for deadwood-dependent species. In (c), proportion of old forests, we included recently clear-cut forests (<20 years) that had been old forests before clear-cutting. As long-lived organisms, lichens can be expected to react to changes in the landscape with a time lag (Johansson et al., 2013). Therefore, current lichen density in the surveyed stands may be a result of the past amount of old forest in the landscape, rather than the current amount. Moreover, as a legacy from the pre-harvest stand, young forests (<20 years) may host more deadwood than 20–50 year-old forests (Ekbom et al., 2006) and certain lichens that occurred in the old forest may persist on this legacy deadwood, providing potential colonists to the sample sites. The summed proportion of >100-year- and <20-year-old forests was found to correlate with lichen species density better than the proportion of >100-year-old forests only. In addition, we included the proportion of total forest area within the landscapes in the models. This is to control for variation in matrix quality, on the assumption that managed forest is of higher quality than open areas. The variables (a–c) were calculated as the proportion of the landscape, whereas (d–f) were calculated as the absolute deadwood amount. Hereafter, we use the term 'proportion' when referring to (a–c) specifically, and 'habitat amount' when referring to (d–f) or when discussing the landscape habitat amount more generally, without defining how it was measured.

The landscape habitat amount variables were calculated using ArcMap 10.6 (Esri Inc., 2018). Data on formally protected forests and WKHs were obtained from the Swedish Environmental Protection Agency, data on forest age were from SLU Forest Maps (Dept. of Forest Resource Management, Swedish University of Agricultural Sciences, 2021), and data on the total forested area and the area of low-productivity forests were from the Swedish National Land Cover Database (Swedish Environmental Protection Agency, 2020). We used three different estimates for the amount of deadwood, based on two datasets: data from the Swedish National Forest Inventory (NFI; unpubl. data, 2021, measured as $m^3 ha^{-1}$ of all deadwood), and data from our earlier surveys from the same regions, in which we measured the amounts of deadwood in managed, protected and low-productivity forests (Hämäläinen, et al., 2020: measured as $m^2 ha^{-1}$ of deadwood not covered by bark or bryophytes). These were then multiplied by the area of each forest type in the landscape to obtain an estimate of the landscape-scale deadwood amount. With this latter dataset, we estimated both the total deadwood amount and the amount of old (decay stage 3–5) deadwood.

All landscape habitat amount variables were estimated within 300 m, 500 m, 1 km, 2 km, 3 km, 4 km, and 5 km of the center of the studied stands, with the exception of deadwood amount based on NFI data which, due to sampling accuracy, could only be calculated within 5 km. We used multi-scale modelling to find the most relevant scale for each habitat amount estimate. Using the package LME4 in R (Bates et al., 2015), we constructed generalized linear mixed models (GLMMs) with a Poisson distribution, with lichen species density as the response variable, the landscape habitat amount variable as the explanatory variable and, to account for potential spatial autocorrelation, the block of stands (three stands in each block) was included as a random variable. We constructed separate models for each landscape habitat amount variable and each scale (i.e. only one explanatory variable was included in the model at a time). For each variable, the scale that yielded the best model according to Akaike's Information Criteria (AIC) was selected and used in the following analyses (Figure S1).

2.3 | Generalized linear mixed models

We used GLMMs with a Poisson distribution to examine whether the local habitat amount affected lichen species density while accounting for landscape habitat amount. The response variable was species density. As explanatory variables, we always included the local habitat amount (the amount of old deadwood ($m^2 ha^{-1}$) within the stand), the amount of habitat in the surrounding landscape (one of the habitat amount variables described above, at the best scale determined for that measure of habitat amount), the interaction between these two, and the total forested area within the landscape (at the same scale as the landscape habitat amount variable). In addition, block was included as a random variable. The variables describing landscape habitat amount were each included in separate models, resulting in six different models (Table S1). The total forested area was not included in models in which landscape habitat amount was measured as deadwood amount because the total forested area was already included in calculations of the landscape-scale deadwood amount. All explanatory variables were standardized prior to modelling to enable comparisons of model coefficients (Gelman, 2008). The best model was selected among the six alternative models based on AIC. The interaction term was kept in the final model if this resulted in lower AIC.

3 | RESULTS

We found 34 species of deadwood-dependent lichens, of which 10 were red-listed (Table S2). The mean species density was 9.7 (range from 2 to 20) per standardized deadwood area (3.7 m^2). Local habitat amount ranged from 1.74 to 131.36 $m^2 ha^{-1}$ (mean 28.89 $m^2 ha^{-1}$). The best model for species density was that in which the proportion of old forest (including young forests <20 years) within 5 km of the studied stands was used as the measure of landscape habitat amount (Table S1, Figure S1). At that scale the mean proportion of old forest was 20.57% and the range was from 6.07% to 30.54%; means and ranges of all landscape habitat amount estimates at all scales are given in Table S3. The correlation between local habitat amount and old forest within 5 km was 0.13 (Pearson correlation). The correlations between local habitat amount and all landscape habitat amount variables are presented in Table S4. The lichen species density increased with the proportion of old forest in the surrounding landscape, whereas there was no evidence for an effect of stand-scale deadwood amount (Figure 4). Neither the total forest area (to account for matrix quality) nor the interaction between landscape-scale habitat amount and stand-scale deadwood amount, improved any of the models.

4 | DISCUSSION

Our results are consistent with the HAH: the species density of deadwood-dependent lichens increased with landscape habitat amount. In models containing both landscape and local habitat amount, we found a positive effect of landscape habitat amount on species density, but no effect of local habitat amount nor evidence for an interaction between local and landscape habitat amount. The

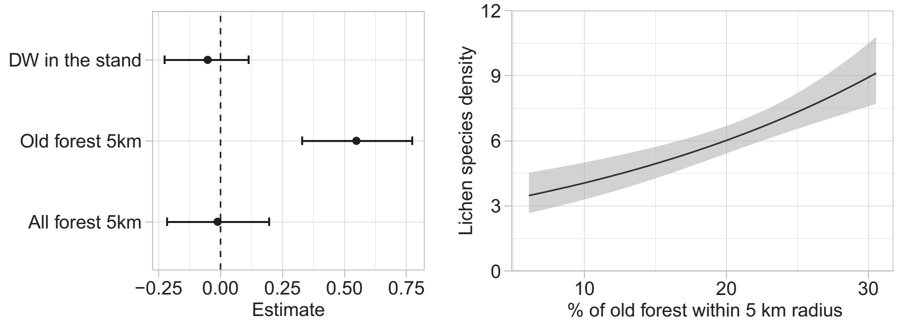

FIGURE 4 Left: estimated model coefficients (±95% CI) for the final generalized linear mixed model testing the effects of local deadwood (DW) amount, and the proportion of old forests and the total forest cover in the landscape on the species density (number of species per surveyed deadwood area within a stand) of DW-dependent lichens. Included model variables are (i) the amount of old DW (decay stages 3–5) in the studied stand, measured as $m^2 ha^{-1}$, (ii) the proportion of old (over 100 years or under 20 years) forests in the landscape and (iii) the total forested area within the landscape. Right: model-predicted lichen species density (±95% CI) as a function of the percentage of old forest in the landscape.

strongest effects of landscape habitat amount on species density occurred at the 5-km scale, that is, habitat amount measured within 5 km of the studied stands. Previous studies of deadwood-dwelling lichens on cut stumps (Svensson et al., 2013) and epiphytic lichens in young aspen stands (Randlane et al., 2017) and on urban trees (Coffey & Fahrig, 2012) have found an effect of landscape habitat amount on lichen diversity at smaller scales (500 m–1 km). However, both in the current study as well as the studies cited above the strongest effect was found on the largest (or only) scale studied. Therefore, we are not able to rule out the possibility that the actual scale of effect is even larger (Jackson & Fahrig, 2015). Such large scales of effect have been observed for other sessile taxa: for example, Nordén et al. (2018) found that deadwood-dwelling fungi which, like lichens, disperse passively by spores, were affected by the amount of habitat within 100 km. Furthermore, we note that the scale of effect observed here is an average for the deadwood-dependent lichen assemblage as a whole. If individual species were analysed separately, the scales of effect would likely differ among them (Bergman et al., 2012; Paltto et al., 2010).

We found no evidence for an effect of local habitat amount on lichen species density. This is consistent with the HAH, and with several previous empirical studies finding that once the effect of landscape habitat amount is accounted for, the local habitat amount does not affect species density (Watling et al., 2020). It has been suggested that the effects of local habitat amount should depend on the landscape habitat amount and should begin to appear when the proportion of habitat within the landscape is less than 20% (Tscharntke et al., 2005) or 30% (Andrén, 1994). In our landscapes, the proportion of old forests was low (<30%), which implies that we should have found an effect of local habitat amount if one were present. Since we did not find an effect of local habitat amount, nor a significant interaction between local and landscape habitat amount, our results do not support the idea that the effects of local habitat amount differ with landscape-scale habitat amount (Andrén, 1994; Tscharntke et al., 2005). However, such an interaction has been observed for other deadwood-dwelling taxa. Larsson Ekström et al. (2021) found that the local deadwood amount affected the density of deadwood-dwelling beetles in managed forest landscapes, but not in 'multifunctional landscapes' where the landscape habitat amount was assumed to be higher. In contrast, Rubene et al. (2017) observed that deadwood creation and retention increased the local deadwood-dwelling beetle diversity only if the landscape habitat amount was sufficiently high, consistent with a lower effect of local habitat amount in landscapes with very low habitat amount (<1%) as suggested by Tscharntke et al. (2005). An interaction between local and landscape habitat amount has also been observed for sessile taxa by Nordén et al. (2018) who found that habitat amount in the surrounding landscape increased indicator species of deadwood-dwelling fungi only above a certain threshold in local deadwood volume. Thus, for other deadwood-dwelling taxa the effects of local habitat amount may depend on landscape habitat amount, and vice versa, even though we did not find support for this for lichens.

The best proxy of landscape habitat amount was the proportion of old forest. Old forests are regarded as an important habitat for various species groups, and the proportion of old forests in the landscape has previously been found to increase the species richness of deadwood-dwelling beetles (e.g. Olsson et al., 2012) and indicator species of lichens, fungi and vascular plants (Kärvemo et al., 2021). The proportion of old forests explained lichen species density better than the proportion of protected forests, which suggests that there are old forests with high biodiversity values that remain outside protected areas in our study regions, or that protected areas include forests with lower biodiversity value, for example, former production stands or forests with lower productivity (cf. Ekbom et al., 2006). Our measure of old forests included forests over 100 years old and young forests (<20 years), which in our study regions originated from clear-cutting. The inclusion of young forests in this measure improved the correlation with lichen species density. A potential explanation for this is a time lag in the response of lichen communities to clearcutting. A time lag can occur because the lichen density at the sample sites reflects the past landscape habitat amount rather than the current one, since they are the result of colonizations that may have taken place decades ago (cf. Johansson et al., 2013). In addition, certain lichens and their deadwood substrates occurring in a young forest might remain from when the stand was an old forest. The fact that many lichens occurring on recent-clear-cuts, especially red-listed and deadwood-dependent species, are associated with old deadwood created before the clear-cutting (Hämäläinen et al., 2015), gives support to the view that they remain at the clear-cut as a legacy from the old forest.

We can only speculate on why the proportion of old forest was a better measure of habitat amount than direct estimates of the amount of deadwood. Perhaps, the simplest explanation is very high uncertainty in direct estimates of deadwood, rendering the amount of old forest a better means of estimating it. It is also possible that the amount of old forest incorporates other aspects of habitat beyond simply the amount of dead wood, which might increase the strength of the relationship between lichen species density and amount of old forest. For example, the quality of deadwood as lichen habitat may be higher in old forests than elsewhere in the landscape. This is supported by a previous study by Kärvemo et al. (2021), who also found that the amount of old forest, but not that of deadwood, in the landscape explained species richness of indicator lichens in WKHs. Deadwood quality in terms of e.g. decay stage, diameter, or position (standing or fallen) is important for many lichen species (e.g. Nascimbene et al., 2008), and deadwood diversity has a positive effect on the species richness of various species groups, including lichens (e.g. Hämäläinen, et al., 2020; Similä et al., 2003). In addition, in the studied regions old forests can harbour specific deadwood types that are especially valuable for lichens and absent or rare in younger forests, such as very old, hard deadwood or charred wood originating from past forest fires (pers. obs.). Moreover, older pine-dominated may have more open canopies, which leads to higher light levels and can thus promote lichen diversity and abundance (Hauck, 2011). One could also imagine that old forests, where the deadwood amount are generally higher than in younger production forests (e.g. Fridman & Walheim, 2000), increase the aggregation of habitat on a landscape level and that this may be beneficial to maintaining a large pool of lichen species in the landscape, available to colonize the sample site. However, the absence of a relationship between local deadwood amount (local habitat aggregation) and local species density seems counter to this suggestion.

4.1 | Applications

We find that the species density (number of species per deadwood area) of deadwood-dependent lichens increases with the amount of old forest in the surrounding landscape. Thus, our result supports the common recommendation that to conserve forest biodiversity we should attempt to maintain or increase the amount of old forest in managed landscapes. For deadwood-dependent lichens, the landscape composition should be examined within 5 km or more from sites of interest, as we found that old forest explained species density best within 5 km of the stand, which was the maximum scale evaluated in our study. We find that a given amount of deadwood holds more lichen species when situated in a landscape with a higher habitat amount.

The local habitat amount did not have an additional influence on the species density of lichens, beyond the effect of landscape habitat amount. This suggests that management actions aimed at increasing the species density of deadwood-dependent lichens, such as creation or maintenance of deadwood, prolonged cut rotations, or setting aside forests, should prioritize creating and maintaining habitat in the surrounding landscape over adding deadwood to a site of interest. We note, however, that this might not be applicable to other species groups or regions if, for example, species traits such as dispersal mode or habitat specificity (e.g. Hedenås & Ericson, 2008) influence the result.

Although the local deadwood amount did not affect local lichen species density, in practical forestry and biodiversity conservation it may still be most efficient to increase the local deadwood amount by setting aside stands with high deadwood amounts or restoring deadwood within certain stands, as this will maintain lichen habitat in the landscapes surrounding other local sites, and thus increase lichen density in them. Therefore, for practical conservation, it is relevant to aim to preserve or restore as much forest containing high-quality lichen habitat as possible.

Given our study aims, we can only make inferences about the effects of local and landscape habitat amount on the local species density of deadwood-dependent lichens. We acknowledge that conservation goals, especially national goals, often consider much larger scales than the local site. Therefore, future studies are needed that examine lichen diversity at larger scales than within local sites. Such studies should sample lichens across multiple whole landscapes that vary in habitat amount and would, therefore, be extremely labor-intensive if landscapes were defined and analysed on the relevant scales documented here (at least a 5-km radius).

AUTHOR CONTRIBUTIONS

All authors (Aino Hämäläinen, Lenore Fahrig, Joachim Strengbom and Thomas Ranius) contributed to planning the study and sampling design. Aino Hämäläinen collected and analysed the data and led the writing of the manuscript. All authors contributed substantially to the writing of the manuscript and gave their approval for its publication.

ACKNOWLEDGEMENTS

This study was funded by the Swedish research council Formas (grant nos. 2015-00904 and 2019-01559). We thank Sveaskog AB for providing access to their stand data to find study sites and Göran Thor for help in identifying some of the collected lichen specimens.

CONFLICT OF INTEREST STATEMENT

The authors do not have any conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.9s4mw6mn8 (Hämäläinen et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Results of multi-scale modelling searching for the most relevant scale for the different estimates of habitat amount. The response variable was the species density of deadwood-dependent lichens. Separate models were constructed for each landscape variable and each scale (300–500 m, 1–5 km from the center of the study plots). The models were compared using Akaike's Information Criteria (AIC) and the scale that yielded the lowest AIC was selected for the following analyses. The landscape-scale variables included were (a) protected forest, that is, the proportion of formally protected forests and woodland key habitats (WKHs); (b) unmanaged forest, that is, the proportion of forests outside intensive management, including protected forests, WKHs, and low-productivity forests (forests with annual tree growth rate $<1\,m^3\,ha^{-1}$); (c) old forest, that is, the proportion of forests over 100 years or under 20 years (see Section 2); (d) amount of deadwood, that is, the amount of deadwood in the landscape, estimated using data from our earlier surveys in the same regions (Hämäläinen, et al., 2019); and (e) the amount of old deadwood based on survey data; that is, the amount of deadwood in decay stages 3–5, estimated using the abovementioned survey data.

Table S1. The generalized linear mixed models for species density of deadwood-dependent lichens with alternative landscape habitat amount variables, ranked according to Akaike's Information Criteria (AIC). Marginal R2 given. The amount of old deadwood (decay stages 3–5) in the studied stands is included in all models as the measure of local habitat amount. The included landscape habitat amount variables were (a) protected forest, that is, the proportion of formally protected forests and woodland key habitats (WKHs); (b) unmanaged forest, that is, the proportion of forests outside intensive management, including protected forests, WKHs, and low-productivity forests (forests with annual tree growth rate $<1\,m^3\,ha^{-1}$); (c) old forest, that is, the proportion of forests over 100 years or under 20 years (see Section 2); (d) amount of deadwood, that is, the amount of deadwood in the landscape, estimated using data from our earlier surveys in the same regions (Hämäläinen, et al., 2019); (e) the amount of old deadwood based on survey data; that is, the amount of deadwood in decay stages 3–5, estimated using the abovementioned survey data, and (f) the amount of deadwood based on NFI data, that is, data from the Swedish National Forest Inventory. In addition, (g) the total forest area in the landscapes was included to control for matrix quality.

Table S2. List of observed species of lichens and allied fungi (nonlichenized, saprotrophic calicioid species, marked with *). Only deadwood-dependent lichens (according to Spribille et al. (2008)) are included. Red list categories are given for nationally red-listed species (Swedish Species Information Centre, 2015).

Table S3. Mean values and ranges of the landscape habitat amount variables used to model lichen species density. See Table S1 for description of the included variables. All variables were examined within 300 m–5 km from the study plots, with the exception of (iv) that due to data accuracy could only be estimated within 5 km. The proportion of old forest (iii) includes forests over 100 years and recent clear-cuts (less than 20 years) that before clear-cutting had been old forests.

Table S4. Pearson correlation coefficients between the local old deadwood amount (decay stages 3–5, calculated as $m^2\,ha^{-1}$) and the landscape habitat amount variables included in the generalized linear mixed models. See Table S1 for descriptions of the included variables.

Appendix S1. Analysis of lichen species composition.

Appendix S2. Variance partitioning of the final GLMM.

How to cite this article: Hämäläinen, A., Fahrig, L., Strengbom, J., & Ranius, T. (2023). Effective management for deadwood-dependent lichen diversity requires landscape-scale habitat protection. *Journal of Applied Ecology*, *60*, 1597–1606. https://doi.org/10.1111/1365-2664.14429