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Research article

Increasing the amount of dead wood by creation of high stumps has limited value for lichen diversity

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ABSTRACT

Artificial creation of dead wood in managed forests can be used to mitigate the negative effects of forestry on biodiversity. For this to be successful, it is essential to understand the conservation value that the created dead wood has in comparison to naturally occurring dead wood, and, furthermore, where in the landscape addition of dead wood is most beneficial, i.e. how landscape composition influences species occurrence on dead wood. We examined these questions by surveying epixylic lichens on artificially created high stumps of Scots pine (*Pinus sylvestris*) in 3–17 years old clear-cuts. We compared lichen assemblages on high stumps to those on other types of pine dead wood in mature forests, and examined how stump age, the amount of dead wood at the clear-cuts, and landscape composition at 500 m - 2.5 km scale influenced the assemblages. In comparison to other dead wood types, high stumps hosted lower lichen richness and less variable assemblages containing mainly common generalist species. Species richness increased with stump age, whereas dead wood amount and landscape composition were not important; only the total amount of forests in the landscape had a minor positive effect. We conclude that at the studied timescale high stumps of Scots pine are not particularly valuable for epixylic lichens and provide a poor substitute for naturally occurring dead wood in mature forests, although their value may increase with age. Furthermore, directing dead wood creation to specific stands or landscapes does not appear beneficial for lichen biodiversity, given the minor effect of landscape composition found at scales below 2.5 km.

Credit author statement

Aino Hämäläinen, Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Thomas Ranius, Conceptualization, Methodology, Writing - review & editing, Funding acquisition. Joachim Strengbom, Conceptualization, Methodology, Writing - review & editing, Funding acquisition

1. Introduction

Intensive forest management leads to changes in the structure and dynamics of forests, including a drastic decrease in the structural richness that is important for maintaining forest biodiversity (Franklin et al., 1997; Gauthier et al., 2015). One of the components of structural richness that has decreased rapidly in managed forests is dead wood (e.g. Cyr et al., 2009; Siitonen, 2001). The decrease of dead wood, in turn, has led to a decline of species dependent of it, estimated to comprise 20–25% of all forest-dwelling species in European boreal forests (Siitonen, 2001). Therefore, restoration forestry, such as artificial creation of dead wood, is often suggested as a practice to compensate for losses and enhance biodiversity (Halme et al., 2013). Dead wood volumes can be increased for example through girdling of living trees to create snags (Walter and Maguire, 2005), or retention of residual dead wood created during harvest (Doerfler et al., 2017). Another widely used method is to create so-called high stumps by cutting living trees at height of 3–5 m (Stokland et al., 2012). They are commonly used for example in Sweden, where the forest certification standards FSC and PEFC that together cover over 60% of the country's managed forests (Swedish Forest Agency, 2019), require creation of high stumps at all clear-cut stands (Anonymous, 2010, 2016).

Assessments of the conservation value of dead wood creation, a majority of which have focused on effects on beetles, show that addition of dead wood has a positive effect on the diversity of deadwood-dependent species (Sandström et al., 2019; Seibold et al., 2015). Studies examining artificially created high stumps on clear-cuts reveal that these can serve as a habitat for a significant number of beetles (e.g. Jonsell et al., 2004; Lindhe and Lindelöw, 2004) and fungi, although for the latter high stumps were found less species-rich than downed dead wood created at the same occasion

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(Lindhe et al., 2004). To our knowledge, the importance of high stumps for other deadwood-dependent taxa has not been studied. Nevertheless, high stumps may be a valuable substrate for example for deadwood-dwelling lichens, for which standing dead wood is often considered more important than downed (Humphrey et al., 2002; Kuusinen and Siitonen, 1998). Previous studies have found that low stumps in clear-cut stands can host many lichen species (e.g. Hämäläinen et al., 2015; Svensson et al., 2013), which suggests that also high stumps could be potentially important.

Besides of evaluating the outcome for conservation, studies addressing colonization and occurrence of species on artificially created dead wood can also give general insights about species ecology. To what extent species utilize rare habitats is influenced by the amount of colonization sources in the surrounding landscape (Hanski, 1999). Although this landscape context has several times been shown to be important (e.g. Rubene et al., 2017), it is rarely studied in deadwood-dependent organisms. It is often difficult to examine the effects of landscape composition in observational studies utilizing naturally occurring dead wood, as dead wood as a habitat is typically very variable in terms of e.g. age or size (Seibold et al., 2015). In comparison, artificially created dead wood, such as high stumps, is discrete and uniform substrate, for which it is possible to minimize the variation in habitat quality and time available for colonization. Thus, it is suitable for studies addressing the effect of landscape composition.

Results of earlier studies on the effect of landscape composition on deadwood-dependent species vary. While some studies have found that the species richness and abundance of saproxylic beetles per sampled item are higher in landscapes with more dead wood, old-growth forests, or other valuable habitats (Abrahamsson et al., 2009; Gibb et al., 2006; Seibold et al., 2017), others have found no effect (Lindbladh et al., 2007) or even a mix of positive and opposite effects, with sometimes lower abundance of beetles in supposedly more valuable landscapes (Hallinger et al., 2017). Furthermore, the response to landscape composition varies among species: habitat specialists, and species with low dispersal capacity are more affected by the landscape composition than habitat generalists or good dispersers (Nordén et al., 2013; Sverdrup-Thygeson et al., 2014). Regarding dispersal capacity, previous studies have mainly focused on actively dispersing insects, particularly beetles (Ranius 2006), while passively dispersing taxa (e.g. lichens or fungi) are less studied (but see e.g. Norros et al., 2012). Further studies on such taxa are therefore particularly important for understanding the effect of landscape composition.

In this study, we examined the assemblages of epixylic lichens on high stumps and assessed whether they are affected by the surrounding forest stand and landscape. We surveyed lichens on high stumps of Scots pine (*Pinus sylvestris* L.) in 3–17 years old clear-cuts in middle boreal Sweden. In addition, lichens were surveyed on naturally occurring pine dead wood in mature forests within the same region; these data were used to obtain baseline information about the lichen species pool occurring on pine dead wood in the study region. Based on these data, we examined the following questions:

1) How valuable are high stumps as a substrate for deadwood-dwelling lichens in comparison to naturally occurring dead wood; i.e. do they host similar lichen assemblages, in terms of species richness and composition, as other types of dead wood, both standing and downed, in the same area?
2) How does habitat amount (amount of dead wood) at the stand and landscape level influence lichen assemblages on high stumps? Furthermore, does this effect differ between lichens with contrasting dispersal modes (asexual or sexual) or between generalist species and deadwood specialists?
3) How does the age of the high stumps (measure of time for colonization) influence species assembly of lichens?

2. Methods

2.1. Study sites and data collection

Lichens and allied non-lichenized fungi (hereafter addressed collectively as lichens) were surveyed in summer 2018 from high stumps of Scots pine in 74 forest stands. The stands, owned by the forest company Sveaskog AB, were located in the middle boreal region of Sweden in the counties of Dalarna, Gävleborg, and Jämtland (Fig. 1). In this region, Scots pine is the dominating tree species (Anonymous, 2019). The stands had been clear-cut 3–17 years ago; clear-cuts older than this rarely contained high stumps, indicating that high stumps were not routinely created in clear-cuts before 2001. To obtain an even distribution of stand ages, we divided the stands into five age classes, 3–5, 6–8, 9–11, 12–14, and 15–17 years, and selected 15 stands of each age class for the survey (except for stands of 12–14 years, which were 14). All stands were dominated by Scots pine (>70% of stand basal area pine), as were the landscapes within a 500 m radius (>70% of all forested land dominated by pine). The minimum distance between the stands was 1 km. The stands were selected so that the surrounding landscapes had a gradient in the amount of protected forests (including formally protected stands and woodland key habitats, i.e. stands that have high conservation value but are not under formal protection) and unmanaged low-productivity forests (potential forest growth < 1 m^3 ha^{-1} year^{-1}, found to have as high richness of epiphytic and epixylic lichens as protected areas; Hämäläinen et al., 2020).

Lichens were surveyed from five high stumps of Scots pine in each stand. All lichen species occurring on bark-free wood were surveyed up to a height of 2 m (presence/absence). Those occurring on bark were excluded, since the bark will typically fall off within a few years after the creation of high stumps, and is thus a very short-lived resource. Lichen specimens that were not possible to identify in the field were collected for later laboratory examination using chemical spot tests and microscopy. The nomenclature of lichen species follows Nordin et al. (2019). The diameter, height, and amount of bark left on the stumps was measured. The average diameter of the surveyed stumps was 19.2 cm and height 3.75 m.

The amount of dead wood was measured by surveying four transects of 75 m in each stand. Two transects were set up in south-north and two in east-west direction. Downed dead wood was sampled using the line intersect method (Marshall et al., 2000), i.e. measuring all dead wood items that crossed the transects. Standing dead wood was sampled within 10 m distance from the transects (i.e. from plots of 20 × 75 m). All coarse dead wood (diameter > 10 cm, length or height > 0.5 m) was included. For each dead wood item, the diameter, length or height, tree species, decay stage, and amount of bark left were measured. The amount of dead wood was calculated as the area of bark-free wood per hectare.

To compare the high stumps with other types of dead wood, we used a dataset collected in the same area in 2017 (Hämäläinen et al., 2020). In this dataset, lichens were surveyed in 28 Scots pine-dominated forest stands, including four different stand types: stands set aside for protection of biodiversity, 60–80 years old managed stands, and low-productivity stands (the potential annual tree growth < 1 m^3 ha^{-1}) in mires or in rocky outcrops, hilltops or bare rocks (hereafter "thin soil"). In each stand, lichens were surveyed from all dead wood of Scots pine with diameter ≥10 cm at eight study plots with a radius of 20 m. See Hämäläinen et al. (2020) for details on the lichen survey and stand selection.

2.2. Statistical analyses

We used sample-based rarefaction curves (Hsieh et al., 2016) to compare the lichen species richness on high stumps with that on other types of dead wood. High stumps were analyzed as one group, while other dead wood items were separated based on 1) whether they were standing or downed, and 2) which stand type they occurred in, resulting in four classes of both standing and downed dead wood. The rarefaction

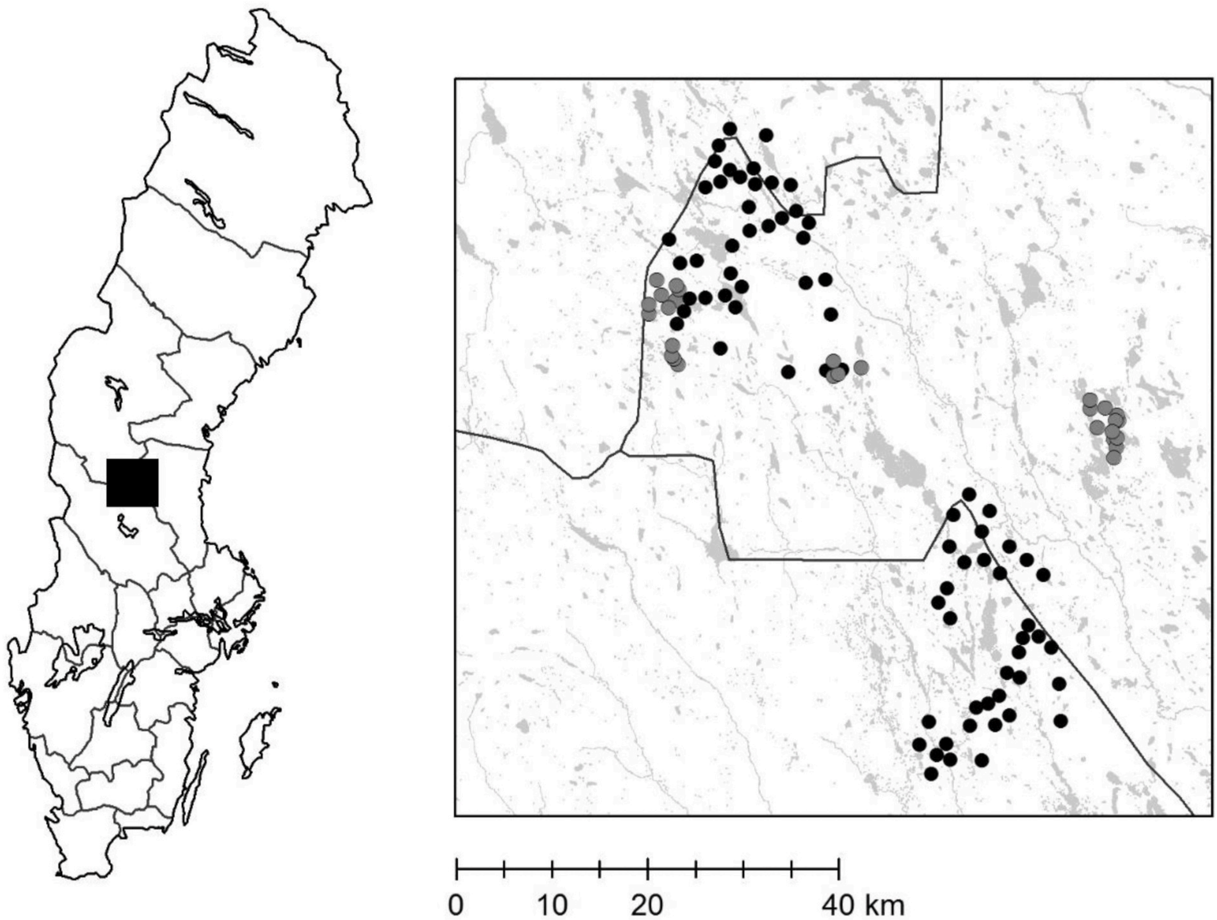

Fig. 1. Location of the study sites. The black circles refer to clear-cut stands with high stumps, and the grey circles to mature stands where other types of dead wood were surveyed.

curves were constructed considering the dead wood items as samples, and x-axes were re-scaled to plot the number of species against the surveyed dead wood area. For high stumps the re-scaling was done using the mean area of surveyed stumps. For all other dead wood items the surveyed area per item was constant, and was thus used for re-scaling.

Secondly, we tested whether the lichen species composition differed among dead wood and stand types using permutational multivariate analysis of variance (permANOVA), run with 5000 permutations and the Bray-Curtis dissimilarity measure. Non-metric multidimensional scaling (NMDS) was used to illustrate the species composition. The NMDS was run with Bray-Curtis dissimilarity measure, searching for 2-dimensional solutions in 500 runs with random starting configurations of real data. Both permANOVA and NMDS were performed considering forest stands as samples and using species abundance data (occurrences per surveyed dead wood area). In addition, we searched for species that were unique to or absent from certain dead wood type, excluding species with <4 observations.

We examined the effects of landscape characteristics on lichen species richness on high stumps using generalized linear models (GLM) with Poisson distribution and a logarithmic link function. We modelled the species richness on stand scale (i.e. on all five high stumps sampled on each stand), and constructed separate models for four groups of species: 1) all lichen species, 2) deadwood-dependent species (according to Spribille et al. (2008)), 3) spore-dispersing species, and 4) asexually dispersed species. In all models, the included explanatory variables were the stand age, the amount of dead wood in the stand, and the following landscape variables reflecting habitat amount: the proportion of protected forest (formally protected stands and woodland key habitats), low-productivity forest, managed forest older than 100 years, and all forested land (in the studied landscapes, area that was not forested consisted mainly of open mires and lakes). We considered also including only Scots pine-dominated forests when calculating the landscape variables, but as this did not improve the models, we included all forested land in the final analyses. For each species group, we constructed three models that assessed the landscape at three scales: 500 m, 1 km, and 2.5 km. There was no collinearity among the included landscape variables at any of these scales (variance inflation factor < 3 (Zuur et al., 2010)). For all GLMs, the explanatory variables were standardized (Gelman, 2008), and sets of all possible models were generated and compared using Akaike's Information Criterion (AICc). In none of the cases a single best model was detected. Therefore we performed model averaging over subsets of models with delta AICc <4 (Grueber et al., 2011).

In addition, we tested the effect of stand and landscape characteristics on lichen species composition on high stumps using permANOVA. The tested variables were again stand age, the amount of dead wood in the stand, and the proportion of protected forest, low-productivity forest, managed forest older than 100 years, and all forested land in the landscape. We run three separate permANOVAs, assessing the landscape at scales 500 m, 1 km and 2.5 km.

The statistical analyses were performed with R 3.5.0 (R Core Team, 2018). Package iNEXT (Hsieh et al., 2016b) was used for the rarefaction, stats (R Core Team, 2018) and MuMIn (Barton, 2016) for the GLMs, and vegan (Oksanen et al., 2016) for the permANOVAs and NMDS. Package ggplot2 (Wickham, 2016) was used to draw the figures.

3. Results

3.1. Comparison among dead wood types

The high stumps hosted 81 species of lichens and non-lichenized fungi (79 and 2 species, respectively), of which 13 were deadwood-dependent (i.e. species that occur exclusively on dead wood). No red-listed species were found (Swedish Species Information Centre, 2015). The other dead wood types hosted, in total, 111 species (106 lichens and 5 non-lichenized fungi), including 27 deadwood-dependent and 8 red-listed species. High stumps had lower species richness per surveyed dead wood area than both standing and downed dead wood in all of the surveyed stand types (Fig. 2). Species composition differed among both dead wood and stand types (Table 1, Fig. 3). Three species were only observed on high stumps, whereas 31 were exclusive for the other types of dead wood (including species with >3 occurrences; Table S1). Of the latter, seven species were red-listed and 12 deadwood-dependent.

3.2. Effects of stand and landscape characteristics

The GLMs included in model averaging are presented in Table S2. The three models assessing landscape composition at different scales did not differ in terms of model fit (AICc) or the proportion of variation explained (Nagelkerke pseudo-R2) for any of the species groups analyzed (Table S2). Therefore, we present results from all three models. Stand age explained most of the variation in lichen species richness on high stumps, and richness increased with increasing stand age for all species groups examined (Fig. 4). Species richness was unaffected by the amount of dead wood in the stands. Similarly, the landscape characteristics were mainly unimportant for species richness. Only the total amount of forested land had a slight positive effect on the richness of deadwood-dependent species at the scale of 500 m (Fig. 4). Stand age affected also lichen species composition, while deadwood amount in the stands or landscape characteristics had no effect (Table 2).

Table 1
Result of permANOVA testing the difference in lichen species composition among deadwood types (high stumps, other standing dead wood, and downed dead wood) and stand types (clear-cuts, set-asides, mature managed forests, and low-productivity forests on mires and on thin soils).

	df	F	R2	P
Deadwood type	2	36.15	0.36	<0.001
Stand type	3	2.45	0.03	<0.001

4. Discussion

4.1. Lichen assemblages on high stumps

High stumps of Scots pine are relatively species-rich habitat, and host several deadwood-dependent lichens, e.g. *Mycocalicium subtile, Calicium trabinellum,* and *Micarea misella*. However, we did not observe any red-listed species, and in comparison to the other types of dead wood, high stumps host a lichen assemblage consisting to a higher extent of common habitat generalists, such as *Hypogymnia physodes*, *Parmeliopsis ambigua* and *P. hyperopta*, or *Lecidea turgidula*. To our knowledge, the lichen assemblages on artificially created high stumps have not been assessed before, but previous studies examining other types of freshly created dead wood on clear-cuts, such as low stumps (e.g. Caruso et al., 2008; Svensson et al., 2013) or dead retention trees (Runnel et al., 2013), report similar results. Thus, on the studied timescale high stumps appear to be less valuable substrate for epixylic lichens than for other taxa, such as saproxylic beetles and fungi, for which they host also rare and red-listed species in addition to common ones (e.g. Lindhe et al., 2004; Lindhe and Lindelöw, 2004). However, the cited studies surveyed high stumps of several tree species, which may have increased the likelihood to observe rare species, in comparison to studying only one dominating tree species, as we have done.

In comparison to other types of dead wood, high stumps host clearly lower species richness and less variable lichen communities, and several lichen species that were observed on naturally occurring dead wood

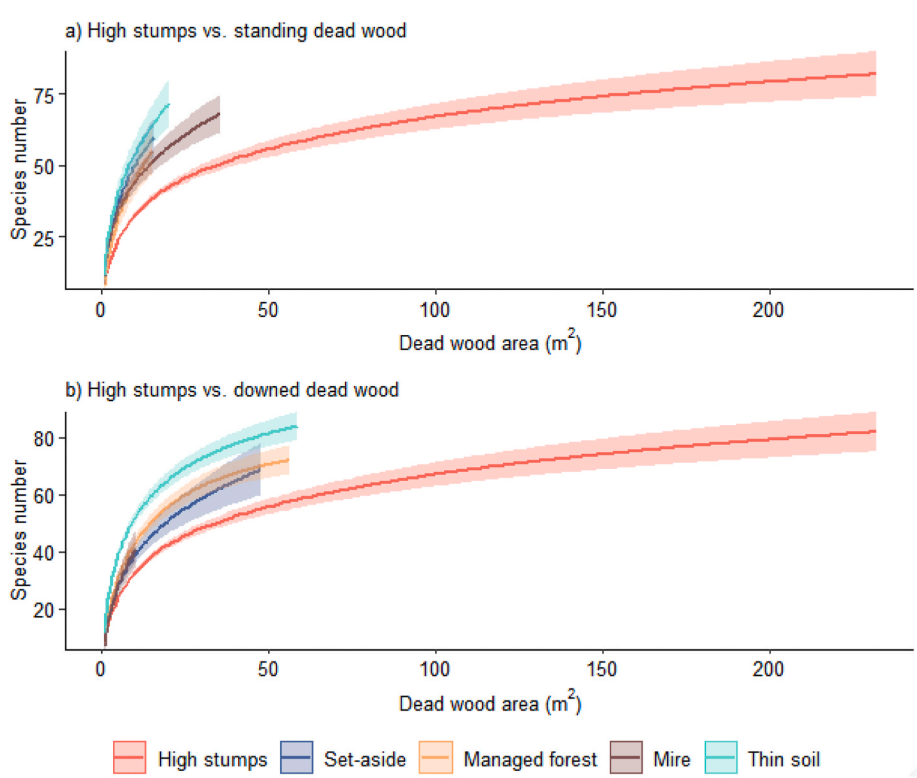

Fig. 2. Rarefaction curves (with 95% CI) comparing lichen species richness among a) high stumps and other standing dead wood, and b) high stumps and downed dead wood in different stand types. The x-axis presents the area of surveyed dead wood.

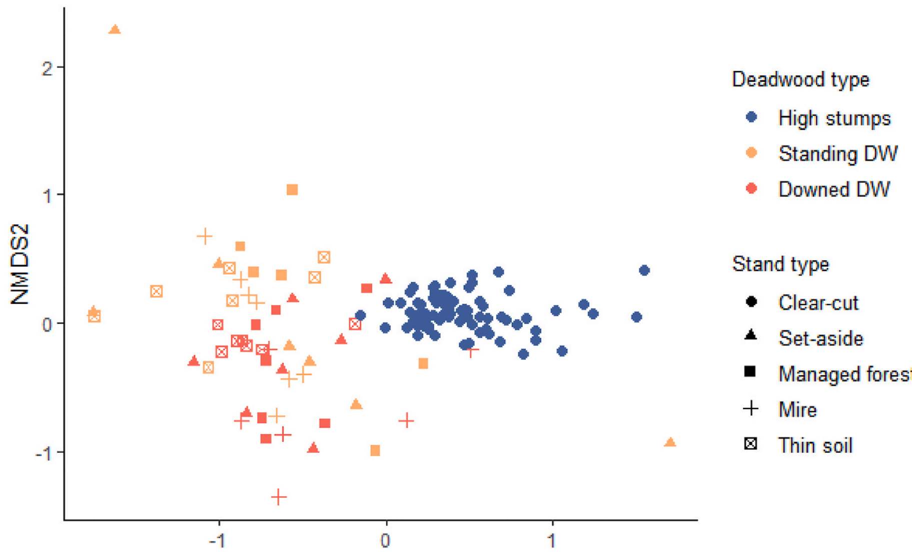

Fig. 3. NMDS comparing the lichen species assemblages among different dead wood and stand types. The final solution was found after 44 tries with a final stress 0.13.

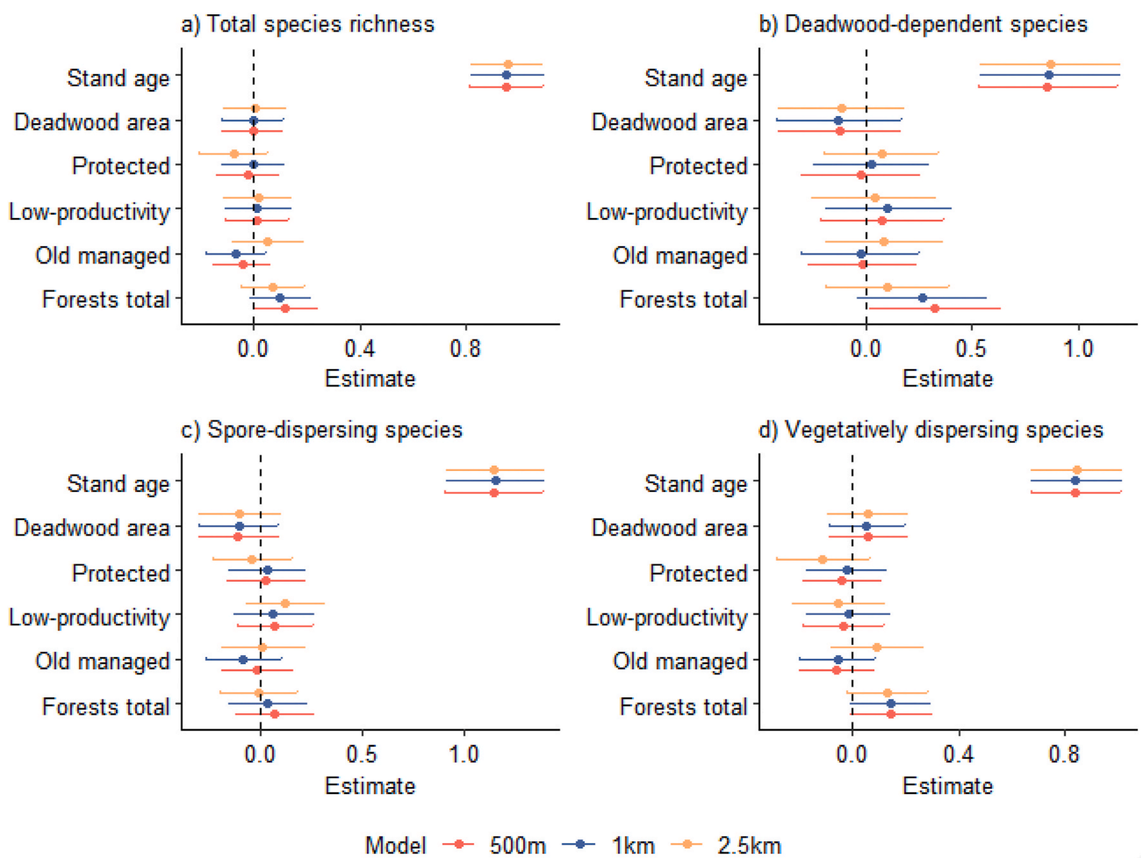

Fig. 4. Model-averaged coefficients (with 95% CI) for GLMs modelling the effect of stand and landscape variables on the richness of a) all lichen species, b) deadwood-dependent lichen species, c) spore-dispersing lichen species, and d) asexually dispersing lichen species on high stumps. Results from three averaged models, assessing the landscape at scales of 500 m, 1 km, and 2.5 km, are presented for each species group.

within the same area were missing from the high stumps. A likely explanation for this is that the high stumps were surveyed on clear-cuts and in young forests originating from clear-cutting, while the other dead wood types were surveyed in mature stands: lichen species richness typically decreases after clear-cutting (e.g. Johansson, 2008), and also the species composition differs between clear-cuts and older stands, as many lichen species require environmental conditions found in denser and older forests. Among the 31 lichen species missing from high stumps (counting species with >3 observations) were indeed many calicioid species, which may prefer mature or old-growth forests (e.g. Holien, 1996), and certain species that prefer downed dead wood to standing (e.g. *Cladonia* and *Xylographa* spp.). Overall, a relatively high proportion of the species missing from high stumps were deadwood-dependent or red-listed species (12 and 7 species, respectively). A further explanation for the lower species richness on high stumps is that the stumps appear to be relatively uniform substrate for lichens, while the other dead wood

Table 2
Result of permANOVA testing the effects of stand age and deadwood amount, as well as landscape compositions, on the species composition of lichens on high stumps. Results of three separate permANOVAs, assessing the landscape on scales of a) 500 m, b) 1 km, and c) 2.5 km are presented.

	Df	F	R2	P
a) Landscape 500 m				
Stand age	1	39.90	0.36	<0.001
Deadwood area	1	0.80	0.007	0.49
Protected forests	1	0.26	0.002	0.97
Low-productivity forests	1	0.39	0.004	0.89
Old managed forests	1	0.54	0.005	0.75
Total forested area	1	1.59	0.01	0.14
b) Landscape 1 km				
Stand age	1	40.29	0.36	<0.001
Deadwood area	1	0.80	0.007	0.46
Protected forests	1	0.46	0.004	0.83
Low-productivity forests	1	0.63	0.006	0.64
Old managed forests	1	0.85	0.007	0.44
Total forested area	1	1.52	0.01	0.16
c) Landscape 2.5 km				
Stand age	1	40.07	0.36	<0.001
Deadwood area	1	0.80	0.007	0.48
Protected forests	1	0.58	0.005	0.69
Low-productivity forests	1	1.06	0.01	0.31
Old managed forests	1	0.58	0.005	0.69
Total forested area	1	0.87	0.008	0.41

types likely are more variable in e.g. age, decay stage, and size, which all can affect lichens as well as other deadwood-dependent taxa (Dahlberg and Stokland, 2004). In the long term also high stumps will occur in older age classes, but such stumps are not available yet.

Lichen richness increased with age of the high stumps, but we did not observe any turnover in species assemblages; the species found in young stumps were also present in the older ones. All high stumps that we surveyed were in the early decay phases (<20 years). Since lichen richness on dead wood generally peaks at middle to late decay stages (e.g. Nascimbene et al., 2008), and many deadwood-dependent lichens prefer several decades old dead wood (Santaniello et al., 2017), species richness of the high stumps will likely continue to increase as the high stumps age. As the surrounding stand matures, the stumps can provide habitat also for species that require closed forests, which might further increase the species richness. With time, the high stumps may therefore become more valuable substrate for lichens, and host species of conservation concern. Studies on timescales >20 years are therefore needed to fully determine the value of high stumps for epixylic lichens, but since high stumps first became a standard practice in Swedish forestry during the late 1990's, such studies are so far impossible.

4.2. *Importance of landscape composition*

Habitat amount in the stand did not influence lichen assemblages on high stumps, while the habitat amount in the landscape had only minor effect. In contrast to our results, lichens have previously been shown to be limited by dispersal at local scale (e.g. Dettki et al., 2000) and the surrounding landscape has been found to affect their occurrence also at spatial scales similar to those covered in our study (Randlane et al., 2017; Svensson et al., 2013). However, there are also indications that lichens have good dispersal capacity, and are able to disperse over long distances: for example, Gjerde et al. (2015) found no evidence of dispersal limitation at 0.2–10 km scale in *Lobarion* communities. Thus, landscape effects on lichens may take place at scales larger than what was possible to assess in this study. In addition, environmental filtering may have played a role: regardless of the landscape, clear-cut stands may not be a suitable habitat for some lichen species, which would result in more similar assemblages among the surveyed stands. The observed species, however, were capable of colonizing high stumps at clear-cut stands, which indicates that they are also adapted to utilize substrates that appear after large-scale natural disturbances, such as fires, as is the case for many lichen species occurring in boreal forests (Johansson, 2008). Species adapted to disturbance-related habitats are expected to be good dispersers (e.g. Travis and Dytham, 1999), which may explain the minor effect of landscape composition. Moreover, many of these species are able to occur on various habitats, including the surrounding managed forests, and therefore protected forests may not be an important colonization source for them.

Lichens response to landscape characteristics may also depend on their functional traits (Hedenås and Ericson, 2008). Due to their larger dispersal propagules, asexually dispersed lichens are sometimes regarded to be poorer dispersers than sexually dispersing (e.g. Bowler and Rundel, 1975; Walser, 2004; however, see also Malíček et al., 2019 for further discussion) and therefore more sensitive to landscape composition. Another potentially important trait is the width of species habitat niche. Species with narrow niche are likely to have more patchy distribution in a landscape than generalist species that are able to occur in various different habitats, and thus they are often more affected by landscape composition (Andrén et al., 1997; Henle et al., 2004). Both dispersal mode (size of dispersal propagules) and niche width have been observed to impact colonization and occurrence patterns of certain lichen species on aspens (Hedenås and Ericson, 2008) and oaks (Johansson et al., 2012). We observed no difference linked to dispersal traits. Niche width appeared to be more important, since landscape composition had a significant impact only on deadwood-dependent lichens, which in comparison with the whole assemblages have a narrower niche. However, even for this group the effect was minor.

4.3. *Implications for conservation*

Creation of standing dead wood, such as high stumps, has been recommended specifically for lichen conservation (Svensson et al., 2016). Nevertheless, high stumps of Scots pine are not particularly valuable substrate for epixylic lichens within 17 years from their creation, and do not appear to function as a substitute for the surveyed other dead wood types. However, it is important to note that the studied timescale, 17 years, is a relatively short time for lichen colonization, and as discussed above, the high stumps may become more valuable for lichens as they age, but this has to be verified by future studies. Nevertheless, certain species will even then require downed dead wood, or conditions that are rare in managed forests even on a longer timescale (e.g. burned wood). Thus, we agree with previous studies on saproxylic beetles and fungi (e.g. Andersson et al., 2015; Lindhe et al., 2004; Schroeder et al., 2006) stating that high stumps alone are not sufficient to maintain species diversity, and that creation of downed dead wood and preservation of naturally generated old dead wood are necessary to preserve the diversity of deadwood-dependent species. Large-diameter dead wood, in particular, can be important for epixylic species (e.g. Hofmeister et al., 2015).

The landscape composition only had a minor effect on lichens on high stumps, which implies that for the observed species, there is no benefit of concentrating dead wood restoration to certain stands or landscapes. This was observed when considering a spatial scale of up to 2500 m, while the potential patterns at larger scales are not known. For other species groups, however, the situation is different; landscape composition has been found to affect the occurrence of saproxylic beetles on high stumps (Abrahamsson et al., 2009; Jonsell et al., 2019), and directing dead wood creation into landscapes with more dead wood is therefore recommended to promote beetle diversity (Rubene et al., 2017). Furthermore, it is important to note that the situation might be different also for lichens if specific groups, e.g. red-listed species, which were not well represented in our study are considered, as for such species the landscape effects could be more pronounced.

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.

Table S1
Lichen species occurrence on high stumps of different age, and on standing and downed dead wood of Scots pine in stands set aside for biodiversity conservation, mature managed stands, and low-productivity stands on mires and thin soils. The numbers refer to the number of stands in which the species was found. The Swedish red-list categories (2015) given in brackets; deadwood-dependent lichen species are marked in bold. Species of non-lichenized fungi are marked with an asterisk (*).

	High stumps					Standing dead wood				Downed dead wood			
Species	3–5 years	6–8 years	9–11 years	12–14 years	15–17 years	Set-aside	Managed	Mire	Thin soil	Set-aside	Managed	Mire	Thin soil
Alectoria sarmentosa (Ach.) Ach. **(NT)**	0	0	0	0	0	0	0	0	0	1	0	0	0
Biatora albohyalina (Nyl.) Bagl. & Carestia	0	0	0	1	0	0	0	0	0	0	0	0	0
Bryoria capillaris (Ach.) Brodo & D. Hawksw.	0	0	1	0	0	0	0	0	0	1	0	0	1
Bryoria furcellata (Fr.) Brodo & D. Hawksw.	0	1	7	7	6	2	3	4	3	1	0	0	3
Bryoria fuscescens (Gyeln.) Brodo & D.Hawksw.	0	1	1	6	6	0	1	1	1	0	0	0	2
Bryoria implexa (Hoffm.) Brodo & D. Hawksw.	0	0	1	0	2	0	0	0	0	0	0	0	0
Bryoria nadvornikiana (Gyeln.) Brodo & D.Hawksw. **(NT)**	0	0	0	0	0	1	0	0	0	0	0	0	0
Buellia arborea Coppins & Tønsberg	0	1	0	2	0	0	0	1	1	0	0	0	0
Buellia arnoldii Servít	0	0	0	0	1	0	0	0	0	0	0	0	0
Buellia griseovirens (Turner & Borrer ex Sm.) Almb.	0	0	0	0	0	1	0	0	0	0	0	0	0
Calicium denigratum (Vain.) Tibell **(NT)**	0	0	0	0	0	3	2	7	4	0	0	2	0
Calicium glaucellum Ach.	0	0	0	1	2	1	0	2	1	0	0	0	0
Calicium trabinellum (Ach.) Ach.	2	9	10	14	15	3	2	5	4	3	2	2	5
Calicium viride Pers.	0	0	0	1	0	0	0	0	0	0	0	0	0
Caloplaca sp.	0	0	0	0	1	0	0	0	0	0	0	0	0
Carbonicola anthracophila (Nyl.) Bendiksby & Timdal **(NT)**	0	0	0	0	0	1	2	0	1	0	0	0	1
Carbonicola myrmecina (Ach.) Bendiksby & Timdal **(NT)**	0	0	0	0	0	3	1	1	4	1	1	0	0
Cetraria islandica (L.) Ach.	0	0	0	0	0	0	0	0	0	1	2	0	1
Cetraria sepincola (Ehrh.) Ach.	3	8	11	14	14	0	0	1	1	1	0	0	3
Chaenotheca brunneola (Ach.) Müll.Arg.	0	0	0	0	0	3	0	2	1	0	0	0	1
Chaenotheca chrysocephala (Turner ex Ach.) Th.Fr.	0	0	0	0	0	2	0	2	2	0	0	0	1
Chaenotheca ferruginea (Turner ex Sm.) Mig.	0	0	0	0	0	2	3	3	5	1	2	0	3
Chaenotheca stemonea (Ach.) Müll. Arg.	0	0	0	0	0	0	0	0	0	0	1	0	0
Chaenotheca trichialis (Ach.) Th.Fr.	0	0	0	0	0	0	1	1	1	1	0	0	0
Chaenotheca xyloxena Nádv.	0	0	0	2	1	0	2	1	2	0	0	0	1
Chaenothecopsis fennica (Laurila) Tibell **(NT)** *	0	0	0	0	0	2	0	2	1	0	0	0	0
Chaenothecopsis pusilla (Ach.) A.F. W.Schmidt *	0	0	0	0	0	1	1	2	1	1	0	0	1
Chaenothecopsis pusiola (Ach.) Vain. *	0	0	0	1	0	0	0	1	0	0	0	0	0
Cladonia arbuscula (Wallr.) Flot.	0	2	4	8	7	0	1	0	1	7	7	2	7
Cladonia bacilliformis (Nyl.) Glück	0	0	0	3	2	0	0	1	0	1	4	1	2
Cladonia botrytes (K.G.Hagen) Willd.	0	1	3	9	7	0	0	1	1	6	7	3	4
Cladonia carneola (Fr.) Fr.	0	0	0	0	0	0	0	0	0	0	0	0	1
Cladonia cenotea (Ach.) Schaer.	0	0	2	10	8	4	2	4	6	6	5	2	7
Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.	0	0	0	2	0	1	0	0	0	2	2	1	5
Cladonia coniocraea (Flörke) Spreng.	0	1	1	2	0	1	0	0	0	2	1	0	3
Cladonia cornuta (L.) Hoffm.	0	0	1	1	5	0	0	0	0	3	2	1	7
Cladonia crispata (Ach.) Flot.	0	0	0	0	0	0	0	0	0	1	1	0	2
Cladonia deformis (L.) Hoffm.	0	1	2	5	8	2	1	6	5	5	5	2	6
Cladonia digitata (L.) Hoffm.	0	3	2	4	3	2	1	4	4	3	3	1	6
Cladonia fimbriata (L.) Fr.	0	0	0	0	0	0	0	1	0	1	4	1	2
Cladonia gracilis (L.) Willd.	0	0	0	0	0	0	0	0	0	1	2	0	4
Cladonia macilenta Hoffm.	0	1	1	0	1	0	0	2	0	4	4	1	5
Cladonia ochrochlora Flörke	0	0	0	0	1	0	0	0	1	5	3	0	3
Cladonia parasitica (Hoffm.) Hoffm. **(NT)**	0	0	0	0	0	0	2	0	1	2	1	1	4
Cladonia pleurota (Flörke) Schaer.	0	0	0	0	0	0	0	0	1	0	2	0	2
Cladonia pyxidata (L.) Hoffm.	0	0	0	0	0	0	0	0	0	0	0	0	1
Cladonia rangiferina (L.) F.H.Wigg.	0	0	4	4	7	0	1	0	0	6	7	2	7
Cladonia sulphurina (Michx.) Fr.	0	0	0	0	0	1	0	1	0	1	1	0	3

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Table S1 (*continued*)

Species	High stumps					Standing dead wood				Downed dead wood			
	3–5 years	6–8 years	9–11 years	12–14 years	15–17 years	Set-aside	Managed	Mire	Thin soil	Set-aside	Managed	Mire	Thin soil
Cladonia uncialis (L.) Weber ex F.H. Wigg.	0	0	0	0	0	0	0	0	0	0	1	0	3
Evernia prunastri (L.) Ach.	0	0	0	0	1	0	0	0	0	0	0	0	0
Frutidella furfuracea (Anzi) M. Westb. & M.Svensson	0	1	1	0	1	0	0	0	0	0	0	0	0
Hertelidea botryosa (Fr.) Printzen & Kantvilas **(NT)**	0	0	0	0	0	1	3	3	5	0	2	1	7
Hypocenomyce scalaris (Ach.) M. Choisy	0	1	3	8	4	3	4	5	6	2	3	0	7
Hypogymnia physodes (L.) Nyl.	14	15	14	15	15	4	6	7	6	7	7	4	7
Hypogymnia tubulosa (Schaer.) Hav.	0	1	2	5	6	2	1	2	4	4	3	1	6
Icmadophila ericetorum (L.) Zahlbr.	0	0	0	0	0	0	0	0	0	1	0	0	2
Imshaugia aleurites (Ach.) S.L.F.Mey	8	13	14	15	15	4	5	7	7	6	5	4	7
Japewia subaurifera Muhr & Tønsberg	1	1	1	0	2	0	1	0	1	0	0	0	1
Japewia tornoënsis (Nyl.) Tønsberg	0	0	0	1	0	0	0	0	0	0	0	0	0
Lecanora aitema (Ach.) Hepp	0	0	1	0	0	0	0	0	1	0	0	0	0
Lecanora albellula (Nyl.) Th.Fr.	1	2	2	5	8	0	0	0	0	0	0	0	0
Lecanora boligera (Norman ex Th. Fr.) Hedl.	0	1	0	0	1	0	0	0	0	0	0	0	0
Lecanora circumborealis Brodo & Vitik.	1	4	2	5	11	2	1	1	2	0	1	0	3
Lecanora expallens Ach.	0	0	2	3	5	0	0	0	0	0	0	0	0
Lecanora fuscescens (Sommerf.) Nyl.	0	0	0	1	0	0	0	0	0	0	0	0	0
Lecanora hypopta (Ach.) Vain.	0	0	1	0	2	1	2	5	7	0	0	0	1
Lecanora hypoptella (Nyl.) Grummann	0	0	0	0	1	0	0	2	1	0	2	0	0
Lecanora norvegica Tønsberg	0	0	0	0	0	0	1	2	2	0	0	0	0
Lecanora pulicaris (Pers.) Ach.	3	7	14	15	14	2	1	1	1	4	3	2	2
Lecanora saligna (Schrad.) Zahlbr.	0	0	1	3	1	0	0	0	0	0	0	0	0
Lecanora subintricata (Nyl.) Th.Fr.	0	1	2	2	1	0	0	0	1	0	1	0	0
Lecanora symmicta (Ach.) Ach.	1	2	5	4	10	0	1	1	2	1	1	0	0
Lecanora varia (Hoffm.) Ach.	0	0	1	0	2	2	0	1	1	0	0	0	0
Lecidea leprarioides Tønsberg	0	1	0	1	2	1	0	0	0	0	0	0	0
Lecidea nylanderi (Anzi) Th.Fr.	1	5	4	12	9	2	1	2	1	1	1	0	2
Lecidea plebeja (Nyl.)	0	0	0	0	1	0	0	0	0	0	0	0	0
Lecidea turgidula Fr.	3	9	13	15	15	3	2	7	5	4	4	2	6
Lepra borealis (Erichsen) I.Schmitt et al.	0	0	0	0	0	0	0	1	0	1	2	1	1
Lepraria sp.	0	0	0	0	0	1	0	1	0	2	0	0	2
Loxospora elatina (Ach.) A.Massal.	0	0	0	0	0	0	1	0	0	0	0	0	0
Melanohalea septentrionalis (Lynge) O.Blanco et al.	0	0	0	0	0	0	0	0	0	1	0	0	0
Micarea contexta Hedl.	0	0	0	0	0	0	1	0	0	0	1	0	0
Micarea denigrata (Fr.) Hedl.	0	1	0	0	0	1	1	2	0	4	4	1	3
Micarea elachista (Körb.) Coppins & R.Sant.	0	0	0	0	0	1	1	0	2	1	1	0	2
Micarea melaena (Nyl.) Hedl.	0	0	0	1	0	2	1	3	3	5	5	0	7
Micarea misella (Nyl.) Hedl.	1	2	4	7	8	1	0	0	0	3	4	4	4
Micarea prasina s.lat. Fr.	0	0	0	0	1	1	0	0	0	2	4	1	3
Microcalicium disseminatum (Ach.) Vain. *	0	0	0	0	0	0	0	0	1	0	0	0	0
Mycoblastus alpinus (Fr.) Th.Fr. ex Hellb.	0	1	1	0	1	1	3	4	3	3	4	1	5
Mycoblastus sanguinarius (L.) Norman	0	0	0	0	0	3	3	4	5	2	4	1	7
Mycocalicium subtile (Pers.) Szatala *	15	15	14	15	15	5	5	5	4	4	2	4	7
Ochrolechia androgyna s.lat. (Hoffm.) Arnold	0	1	2	3	4	4	3	3	6	4	4	1	7
Ochrolechia microstictoides Räsänen	0	1	0	0	2	1	0	1	1	0	3	1	3
Parmelia sulcata Taylor	0	0	0	0	0	0	0	0	0	2	0	0	2
Parmeliopsis ambigua (Wulfen) Nyl.	15	15	14	15	15	5	6	7	7	7	7	6	7
Parmeliopsis hyperopta (Ach.) Arnold	9	15	14	15	15	5	2	5	6	7	7	6	7
Pertusaria pupillaris (Nyl.) Th.Fr.	0	0	0	0	0	1	0	1	1	2	0	0	0
Placynthiella dasaea (Stirt.) Tønsberg	0	0	0	2	2	1	0	1	0	2	0	0	4
Placynthiella icmalea (Ach.) Coppins & P.James	1	4	5	6	6	0	1	0	1	2	2	1	4
Placynthiella oligotropha (J.R. Laundon) Coppins & P.James	0	1	0	1	0	0	0	0	1	1	1	0	1
	0	0	0	0	1	0	0	0	0	0	1	0	1

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Table S1 (*continued*)

Species	High stumps 3–5 years	6–8 years	9–11 years	12–14 years	15–17 years	Standing dead wood Set-aside	Managed	Mire	Thin soil	Downed dead wood Set-aside	Managed	Mire	Thin soil
Placynthiella uliginosa (Schrad.) Coppins & P.James													
Platismatia glauca (L.) W.L.Culb. & C.F.Culb.	0	4	10	8	9	3	2	1	3	6	4	2	7
Pseudevernia furfuracea (L.) Zopf	0	1	4	3	3	2	0	1	1	1	2	0	6
Pycnora sorophora (Vain.) Hafellner	0	2	1	4	4	1	1	7	4	0	1	0	2
Pycnora xanthococca (Sommerf.) Hafellner	0	0	0	0	2	3	2	6	3	0	1	0	2
Ramboldia cinnabarina (Sommerf.) Kalb et al.	0	2	2	4	6	1	1	3	3	0	2	0	0
Ramboldia elabens (Fr.) Kantvilas & Elix **(NT)**	0	0	0	0	0	2	1	2	2	0	1	0	2
Scoliciosporum chlorococcum (Graewe ex Stenh.) Vězda	0	2	2	0	1	0	1	0	1	0	0	0	0
Strangospora moriformis (Ach.) Stein	0	0	0	0	0	0	0	1	0	0	0	0	0
Toensbergia leucococca (R.Sant.) Bendiksby & Timdal	0	0	0	0	0	0	0	0	0	0	0	0	1
Trapeliopsis flexuosa (Fr.) Coppins & P.James	0	0	1	1	2	2	1	2	3	4	3	3	7
Trapeliopsis granulosa (Hoffm.) Lumbsch	0	0	0	2	0	0	1	1	1	4	3	0	6
Tuckermannopsis chlorophylla (Willd.) Hale	3	4	4	6	5	2	0	0	1	4	4	0	6
Usnea dasopoga (Ach.) Nyl.	0	1	0	0	0	3	2	2	2	2	1	0	2
Usnea hirta (L.) Weber ex F.H.Wigg.	0	1	1	5	6	0	2	2	2	1	2	1	0
Usnea subfloridana Stirt.	0	0	0	0	1	1	0	0	0	0	0	0	1
Violella fucata (Stirt.) T.Sprib.	0	0	0	0	0	0	1	4	4	2	4	0	3
Vulpicida pinastri (Scop.) J.-E. Mattsson & M.J.Lai	10	15	14	15	15	4	4	5	5	7	7	5	7
Xylographa pallens (Nyl.) Harm.	0	2	3	0	1	1	0	0	2	2	3	1	5
Xylographa parallela (Ach.Fr) Fr.	1	1	0	7	7	1	0	1	1	6	7	3	7
Xylographa rubescens Räsänen	0	0	0	0	0	0	1	2	1	1	3	2	1
Xylographa soralifera Holien & Tønsberg	0	0	0	0	0	0	0	0	0	0	0	0	1
Xylographa trunciseda (Th.Fr.) Minks ex Redinger	0	0	0	0	0	0	0	0	0	0	2	0	2
Xylographa vitiligo (Ach.) J.R. Laundon	2	0	3	5	6	0	0	1	0	6	7	2	6
Xylopsora caradocensis/X. friesii Bendiksby & Timdal	0	0	0	0	0	2	3	3	6	1	2	1	7

Table S2
List of GLMMs included in the model averaging (deltaAIC$_c$ < 4).

a) All species, landscape at 500 m radius	df	logLik	AICc	deltaAIC$_c$	Weight	R^2
1. Log (stand age) + total forested	3	−222.25	450.8	0.00	0.253	0.96
2. Log (stand age) + old managed + total forested	4	−221.92	452.4	1.58	0.115	0.97
3. Log (stand age)	2	−224.24	452.6	1.80	0.103	0.96
4. Log (stand age) + total forested + protected	4	−222.14	452.8	2.01	0.093	0.96
5. Log (stand age) + low-productivity + total forested	4	−222.19	453.0	2.12	0.088	0.96
6. Log (stand age) + DW area + total forested	4	−222.24	453.1	2.23	0.083	0.96
7. Log (stand age) + old managed	3	−223.90	454.1	3.30	0.049	0.96
8. Log (stand age) + old managed + total forested + protected	5	−221.84	454.6	3.72	0.039	0.97
9. Log (stand age) + low-productivity + old managed + total forested	5	−221.90	454.7	3.85	0.037	0.97
10. Log (stand age) + DW area + old managed + total forested	5	−221.92	454.7	3.88	0.036	0.97
11. Log (stand age) + low-productivity	3	−224.23	454.8	3.97	0.035	0.96
12. Log (stand age) + protected	3	−224.23	454.8	3.97	0.035	0.96
13. Log (stand age) + DW area	3	−224.24	454.8	3.98	0.035	0.96
b) All species, landscape at 1 km radius	**df**	**logLik**	**AICc**	**deltaAIC$_c$**	**Weight**	**R^2**
1. Log (stand age) + total forested	3	−222.73	451.8	0.00	0.180	0.96
2. Log (stand age)	2	−224.24	452.6	0.84	0.118	0.96
3. Log (stand age) + old managed + total forested	4	−222.04	452.7	0.85	0.118	0.96
4. Log (stand age) + old managed	3	−223.53	453.4	1.59	0.081	0.96
5. Log (stand age) + low-productivity + total forested	4	−222.61	453.8	2.00	0.066	0.96
6. Log (stand age) + total forested + protected	4	−222.68	453.9	2.14	0.062	0.96
7. Log (stand age) + DW area + total forested	4	−222.71	454.0	2.19	0.060	0.96
8. Log (stand age) + low-productivity	3	−224.23	454.8	3.01	0.040	0.96
9. Log (stand age) + protected	3	−224.23	454.8	3.01	0.040	0.96
10. Log (stand age) + DW area	3	−224.24	454.8	3.01	0.040	0.96
11. Log (stand age) + low-productivity + old managed + total forested	5	−222.02	454.9	3.11	0.038	0.97
12. Log (stand age) + old managed + total forested + protected	5	−222.03	454.9	3.14	0.037	0.96
13. Log (stand age) + DW area + old managed + total forested	5	−222.04	455.0	3.15	0.037	0.96
14. Log (stand age) + old managed + protected	4	−223.41	455.4	3.60	0.030	0.96
15. Log (stand age) + low-productivity + old managed	4	−223.51	455.6	3.79	0.027	0.96
16. Log (stand age) + DW area + old managed	4	−223.51	455.6	3.79	0.027	0.96
c) All species, landscape at 2.5 km radius	**df**	**logLik**	**AICc**	**deltaAIC$_c$**	**Weight**	**R^2**
1. Log (stand age)	2	−224.24	452.6	0.00	0.174	0.96
2. Log (stand age) + total forested	3	−223.64	453.6	0.97	0.107	0.96
3. Log (stand age) + protected	3	−223.76	453.9	1.22	0.095	0.96
4. Log (stand age) + total forested + protected	4	−222.78	454.1	1.49	0.083	0.96
5. Log (stand age) + old managed	3	−224.12	454.6	1.93	0.066	0.96
6. Log (stand age) + old managed + protected	4	−223.04	454.7	2.02	0.063	0.96
7. Log (stand age) + low-productivity	3	−224.22	454.8	2.13	0.060	0.96
8. Log (stand age) + DW area	3	−224.24	454.8	2.17	0.059	0.96
9. Log (stand age) + old managed + total forested + protected	5	−221.97	454.8	2.18	0.058	0.97
10. Log (stand age) + low-productivity + total forested	4	−223.35	455.3	2.63	0.047	0.96
11. Log (stand age) + old managed + total forested	4	−223.56	455.7	3.07	0.037	0.96
12. Log (stand age) + DW area + total forested	4	−223.62	455.8	3.18	0.035	0.96
13. Log (stand age) + low-productivity + protected	4	−223.72	456.0	3.37	0.032	0.96
14. Log (stand age) + DW area + protected	4	−223.72	456.0	3.39	0.032	0.96
15. Log (stand age) + low-productivity + total forested + protected	5	−222.75	456.4	3.73	0.027	0.96
16. Log (stand age) + DW area + total forested + protected	5	−222.77	456.4	3.77	0.026	0.96
d) Deadwood-dependent species, landscape at 500 m radius	**df**	**logLik**	**AICc**	**deltaAIC$_c$**	**Weight**	**R^2**
1. Log (stand age) + total forested	3	−123.18	252.7	0.00	0.306	0.62
2. Log (stand age) + DW area + total forested	4	−122.82	254.2	1.51	0.144	0.62
3. Log (stand age) + low-productivity + total forested	4	−123.03	254.6	1.93	0.117	0.62
4. Log (stand age) + total forested + protected	4	−123.16	254.9	2.19	0.102	0.62
5. Log (stand age) + old managed + total forested	4	−123.18	254.9	2.22	0.101	0.62
6. Log (stand age)	2	−125.51	255.2	2.47	0.089	0.55
7. Log (stand age) + DW area + low-productivity + total forested	5	−122.72	256.3	3.61	0.050	0.63
8. Log (stand age) + DW area + old managed + total forested	5	−122.82	256.5	3.80	0.046	0.62
9. Log (stand age) + DW area + total forested + protected	5	−122.82	256.5	3.80	0.046	0.62
e) Deadwood-dependent species, landscape at 1 km radius	**df**	**logLik**	**AICc**	**deltaAIC$_c$**	**Weight**	**R^2**
1. Log (stand age) + total forested	3	−123.97	254.3	0.00	0.198	0.60
2. Log (stand age)	2	−125.51	255.2	0.89	0.127	0.55
3. Log (stand age) + DW area + total forested	4	−123.52	255.6	1.34	0.101	0.61
4. Log (stand age) + low-productivity + total forested	4	−123.65	255.9	1.60	0.089	0.60
5. Log (stand age) + old managed + total forested	4	−123.94	256.5	2.17	0.067	0.60
6. Log (stand age) + total forested + protected	4	−123.97	256.5	2.24	0.065	0.60
7. Log (stand age) + DW area	3	−125.24	256.8	2.54	0.056	0.56
8. Log (stand age) + protected	3	−125.44	257.2	2.93	0.046	0.56
9. Log (stand age) + low-productivity	3	−125.44	257.2	2.94	0.045	0.56

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Table S2 (*continued*)

a) All species, landscape at 500 m radius	df	logLik	AICc	deltaAIC$_c$	Weight	R^2
10. Log (stand age) + old managed	3	−125.47	257.3	3.00	0.044	0.56
11. Log (stand age) + DW area + low-productivity + total forested	5	−123.27	257.4	3.13	0.041	0.61
12. Log (stand age) + DW area + total forested + protected	5	−123.51	257.9	3.61	0.032	0.61
13. Log (stand age) + DW area + old managed + total forested	5	−123.52	257.9	3.63	0.032	0.61
14. Log (stand age) + low-productivity + total forested + protected	5	−123.63	258.1	3.85	0.029	0.60
15. Log (stand age) + low-productivity + old managed + total forested	5	−123.65	258.2	3.90	0.028	0.60
f) Deadwood-dependent species, landscape at 2.5 km radius	**df**	**logLik**	**AICc**	**deltaAIC$_c$**	**Weight**	**R^2**
1. Log (stand age)	2	−125.51	255.2	0.00	0.232	0.55
2. Log (stand age) + DW area	3	−125.24	256.8	1.65	0.102	0.56
3. Log (stand age) + total forested	3	−125.27	256.9	1.71	0.099	0.56
4. Log (stand age) + old managed	3	−125.37	257.1	1.90	0.090	0.56
5. Log (stand age) + protected	3	−125.38	257.1	1.93	0.088	0.56
6. Log (stand age) + low-productivity	3	−125.49	257.3	2.14	0.079	0.56
7. Log (stand age) + DW area + old managed	4	−124.86	258.3	3.11	0.049	0.56
8. Log (stand age) + DW area + total forested	4	−124.92	258.4	3.24	0.046	0.57
9. Log (stand age) + DW area + protected	4	−124.99	258.6	3.39	0.043	0.57
10. Log (stand age) + low-productivity + total forested	4	−125.13	258.8	3.66	0.037	0.56
11. Log (stand age) + old managed + total forested	4	−125.17	258.9	3.73	0.036	0.56
12. Log (stand age) + total forested + protected	4	−125.22	259.0	3.84	0.034	0.56
13. Log (stand age) + DW area + low-productivity	4	−125.24	259.1	3.88	0.033	0.56
14. Log (stand age) + low-productivity + protected	4	−125.28	259.1	3.96	0.032	0.56
g) Spore-dispersing species, landscape at 500 m radius	**df**	**logLik**	**AICc**	**deltaAIC$_c$**	**Weight**	**R^2**
1. Log (stand age)	2	−171.77	347.7	0.00	0.206	0.84
2. Log (stand age) + DW area	3	−171.09	348.5	0.81	0.137	0.85
3. Log (stand age) + low-productivity	3	−171.50	349.3	1.62	0.092	0.85
4. Log (stand age) + total forested	3	−171.57	349.5	1.76	0.085	0.84
5. Log (stand age) + old managed	3	−171.74	349.8	2.12	0.072	0.84
6. Log (stand age) + protected	3	−171.76	349.9	2.15	0.070	0.84
7. Log (stand age) + DW area + total forested	4	−170.83	350.2	2.52	0.058	0.85
8. Log (stand age) + DW area + low-productivity	4	−170.91	350.4	2.68	0.054	0.85
9. Log (stand age) + DW area + protected	4	−171.06	350.7	2.98	0.046	0.85
10. Log (stand age) + DW area + old managed	4	−171.07	350.7	3.00	0.046	0.85
11. Log (stand age) + low-productivity + total forested	4	−171.17	350.9	3.20	0.042	0.85
12. Log (stand age) + low-productivity + protected	4	−171.42	351.4	3.70	0.032	0.85
13. Log (stand age) + low-productivity + old managed	4	−171.49	351.6	3.85	0.030	0.85
14. Log (stand age) + old managed + total forested	4	−171.54	351.7	3.95	0.029	0.84
h) Spore-dispersing species, landscape at 1 km radius	**df**	**logLik**	**AICc**	**deltaAIC$_c$**	**Weight**	**R^2**
1. Log (stand age)	2	−171.772	347.7	0.00	0.192	0.84
2. Log (stand age) + DW area	3	−171.091	348.5	0.81	0.128	0.85
3. Log (stand age) + old managed	3	−171.328	349.0	1.29	0.101	0.85
4. Log (stand age) + low-productivity	3	−171.533	349.4	1.70	0.082	0.84
5. Log (stand age) + total forested	3	−171.729	349.8	2.09	0.068	0.84
6. Log (stand age) + protected	3	−171.758	349.9	2.14	0.066	0.84
7. Log (stand age) + DW area + old managed	4	−170.795	350.2	2.46	0.056	0.85
8. Log (stand age) + DW area + low-productivity	4	−170.932	350.4	2.73	0.049	0.85
9. Log (stand age) + DW area + total forested	4	−170.983	350.5	2.83	0.047	0.85
10. Log (stand age) + DW area + protected	4	−171.030	350.6	2.92	0.044	0.85
11. Log (stand age) + old managed + protected	4	−171.204	351.0	3.27	0.037	0.85
12. Log (stand age) + low-productivity + old managed	4	−171.212	351.0	3.29	0.037	0.85
13. Log (stand age) + old managed + total forested	4	−171.288	351.2	3.44	0.034	0.85
14. Log (stand age) + low-productivity + total forested	4	−171.429	351.4	3.72	0.030	0.85
15. Log (stand age) + low-productivity + protected	4	−171.459	351.5	3.78	0.029	0.85
j) Spore-dispersing species, landscape at 2.5 km radius	**df**	**logLik**	**AICc**	**deltaAIC$_c$**	**Weight**	**R^2**
1. Log (stand age)	2	−171.772	347.7	0.00	0.169	0.84
2. Log (stand age) + low-productivity	3	−170.890	348.1	0.41	0.138	0.85
3. Log (stand age) + DW area	3	−171.091	348.5	0.81	0.113	0.85
4. Log (stand age) + protected	3	−171.553	349.4	1.74	0.071	0.84
5. Log (stand age) + DW area + low-productivity	4	−170.482	349.5	1.83	0.068	0.85
6. Log (stand age) + total forested	3	−171.709	349.8	2.05	0.061	0.84
7. Log (stand age) + old managed	3	−171.742	349.8	2.11	0.059	0.84
8. Log (stand age) + low-productivity + total forested	4	−170.860	350.3	2.59	0.046	0.85
9. Log (stand age) + low-productivity + old managed	4	−170.871	350.3	2.61	0.046	0.85
10. Log (stand age) + low-productivity + protected	4	−170.890	350.4	2.65	0.045	0.85
11. Log (stand age) + DW area + protected	4	−171.019	350.6	2.90	0.040	0.85
12. Log (stand age) + DW area + old managed	4	−171.065	350.7	3.00	0.038	0.85

(*continued on next page*)

Table S2 (*continued*)

a) All species, landscape at 500 m radius	df	logLik	AICc	deltaAIC$_c$	Weight	R^2
13. Log (stand age) + DW area + total forested	4	−171.076	350.7	3.02	0.037	0.85
14. Log (stand age) + DW area + low-productivity + old managed	5	−170.331	351.5	3.83	0.025	0.85
15. Log (stand age) + total forested + protected	4	−171.535	351.6	3.94	0.024	0.84
16. Log (stand age) + old managed + protected	4	−171.545	351.7	3.96	0.023	0.84
k) Vegetatively dispersing species, landscape at 500 m radius	**df**	**logLik**	**AICc**	**deltaAIC$_c$**	**Weight**	**R^2**
1. Log (stand age) + total forested	3	−186.285	378.9	0.00	0.207	0.87
2. Log (stand age) + old managed + total forested	4	−185.908	380.4	1.48	0.099	0.87
3. Log (stand age) + DW area + total forested	4	−185.958	380.5	1.58	0.094	0.87
4. Log (stand age)	2	−188.261	380.7	1.78	0.085	0.85
5. Log (stand age) + total forested + protected	4	−186.120	380.8	1.91	0.080	0.87
6. Log (stand age) + low-productivity + total forested	4	−186.231	381.0	2.13	0.072	0.87
7. Log (stand age) + DW area + old managed + total forested	5	−185.568	382.0	3.11	0.044	0.87
8. Log (stand age) + DW area	3	−187.880	382.1	3.19	0.042	0.86
9. Log (stand age) + old managed	3	−187.881	382.1	3.19	0.042	0.86
10. Log (stand age) + low-productivity	3	−187.984	382.3	3.40	0.038	0.86
11. Log (stand age) + DW area + total forested + protected	5	−185.740	382.4	3.45	0.037	0.87
12. Log (stand age) + low-productivity + old managed	5	−185.766	382.4	3.50	0.036	0.86
13. Log (stand age) + old managed + total forested + protected	5	−185.780	382.4	3.53	0.036	0.87
14. Log (stand age) + DW area + low-productivity	5	−185.932	382.7	3.83	0.031	0.86
15. Log (stand age) + total forested + protected	3	−188.245	382.8	3.92	0.029	0.87
16. Log (stand age) + low-productivity + total forested + protected	5	−185.990	382.9	3.95	0.029	0.87
l) Vegetatively dispersing species, landscape at 1 km radius	**df**	**logLik**	**AICc**	**deltaAIC$_c$**	**Weight**	**R^2**
1. Log (stand age) + total forested	3	−186.386	379.1	0.00	0.229	0.87
2. Log (stand age)	2	−188.261	380.7	1.58	0.104	0.85
3. Log (stand age) + old managed + total forested	4	−186.094	380.8	1.65	0.100	0.87
4. Log (stand age) + DW area + total forested	4	−186.163	380.9	1.79	0.093	0.87
5. Log (stand age) + total forested + protected	4	−186.294	381.2	2.05	0.082	0.87
6. Log (stand age) + low-productivity + total forested	4	−186.384	381.3	2.23	0.075	0.87
7. Log (stand age) + DW area	3	−187.880	382.1	2.99	0.051	0.86
8. Log (stand age) + old managed	3	−187.960	382.3	3.15	0.047	0.86
9. Log (stand age) + DW area + old managed + total forested	5	−185.769	382.4	3.30	0.044	0.87
10. Log (stand age) + low-productivity	3	−188.131	382.6	3.49	0.040	0.85
11. Log (stand age) + protected	3	−188.261	382.9	3.75	0.035	0.85
12. Log (stand age) + DW area + total forested + protected	5	−186.023	382.9	3.81	0.034	0.87
13. Log (stand age) + low-productivity + old managed + total forested	5	−186.060	383.0	3.89	0.033	0.87
14. Log (stand age) + old managed + total forested + protected	5	−186.077	383.0	3.92	0.032	0.87
m) Vegetatively dispersing species, landscape at 2.5 km radius	**df**	**logLik**	**AICc**	**deltaAIC$_c$**	**Weight**	**R^2**
1. Log (stand age) + total forested	3	−186.856	380.1	0.00	0.132	0.86
2. Log (stand age)	2	−188.261	380.7	0.64	0.096	0.85
3. Log (stand age) + total forested + protected	4	−186.165	380.9	0.85	0.086	0.87
4. Log (stand age) + old managed + total forested + protected	5	−185.076	381.0	0.98	0.081	0.87
5. Log (stand age) + DW area + total forested	4	−186.651	381.9	1.83	0.053	0.86
6. Log (stand age) + old managed + total forested	4	−186.663	381.9	1.85	0.052	0.86
7. Log (stand age) + DW area	3	−187.880	382.1	2.05	0.047	0.86
8. Log (stand age) + low-productivity	3	−187.914	382.2	2.11	0.046	0.86
9. Log (stand age) + old managed	3	−187.953	382.2	2.19	0.044	0.86
10. Log (stand age) + low-productivity + total forested	4	−186.852	382.3	2.23	0.043	0.86
11. Log (stand age) + DW area + total forested + protected	5	−185.736	382.4	2.30	0.042	0.87
12. Log (stand age) + protected	3	−188.023	382.4	2.33	0.041	0.86
13. Log (stand age) + old managed + protected	4	−187.086	382.8	2.70	0.034	0.86
14. Log (stand age) + low-productivity + total forested + protected	5	−185.964	382.8	2.76	0.033	0.87
15. Log (stand age) + low-productivity + protected	4	−187.176	382.9	2.88	0.031	0.86
16. Log (stand age) + DW area + old managed + total forested + protected	6	−184.951	383.2	3.10	0.028	0.87
17. Log (stand age) + low-productivity + old managed + total forested + protected	6	−184.967	383.2	3.13	0.027	0.87
18. Log (stand age) + DW area + protected	4	−187.437	383.5	3.40	0.024	0.86
19. Log (stand age) + low-productivity + old managed + protected	5	−186.377	383.6	3.58	0.022	0.87
20. Log (stand age) + DW area + low-productivity	4	−187.658	383.9	3.84	0.019	0.86
21. Log (stand age) + DW area + old managed + total forested	5	−186.567	384.0	3.96	0.018	0.86

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