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Low-productivity boreal forests have high conservation value for lichens

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Abstract

1. Land set aside for preservation of biodiversity often has low productivity. As biodiversity generally increases with productivity, due to higher or more diverse availability of resources, this implies that some of the biodiversity may be left unprotected. Due to a lack of knowledge on the species diversity and conservation value of low-productivity habitats, the consequences of the biased allocation of low-productivity land for set-asides are unknown.
2. We examined the conservation value of boreal low-productivity forests (potential tree growth <1 m^3 ha^{-1} $year^{-1}$) by comparing assemblages of tree- and deadwood-dwelling lichens and forest stand structure between productive and low-productivity forest stands. We surveyed 84 Scots pine-dominated stands in three regions in Sweden, each including four stand types: two productive (managed and unmanaged) and two low-productivity stands (on mires and on thin, rocky soils).
3. Lichen species richness was the highest in low-productivity stands on thin soil, which had similar amounts and diversity of resources (living trees and dead wood) to productive unmanaged stands. Stands in low-productivity mires, which had low abundance of living trees and dead wood, hosted the lowest lichen richness. Lichen species composition differed among stand types, but none of them hosted unique species. The differences in both species richness and composition were more pronounced in northern than in southern Sweden, likely due to shorter history of intensive forestry.
4. *Synthesis and applications*. Boreal low-productivity forests can have as high conservation value as productive forests, which should be reflected in conservation strategies. However, their value is far from uniform, and conservation planning should acknowledge this variation and not treat all low-productivity forests as a uniform group. Some types of low-productivity forest (e.g. on rocky soil) are more valuable than others (e.g. on mires), and should thus be prioritized in conservation. It is also important to consider the landscape context: low-productivity forests may have higher value in landscapes where high-productivity forests are highly influenced by forestry. Finally, although low-productivity forests can be valuable for some taxa, productive forests may still be important for other taxa.

KEYWORDS

boreal forests, dead wood, epiphytic, epixylic, mire, productivity-diversity relationship, Scots pine

1 | INTRODUCTION

Land of low productivity is over-represented in areas set aside for biodiversity conservation (Fridman, 2000; Scott et al., 2001). This is partly because it is typically less affected by management and therefore has higher resemblance to natural ecosystems (e.g. Storaunet, Rolstad, Gjerde, & Gundersen, 2005), and partly because it is generally less expensive to set aside than highly productive land. Productivity may affect species composition (e.g. Boudreault, Coxson, Vincent, Bergeron, & Marsh, 2008; Chen, Légaré, & Bergeron, 2004) as well as species richness (e.g. Waide et al., 1999). Diversity typically increases with productivity (e.g. Gillman & Wright, 2006), due to associated increases in resource availability or habitat heterogeneity (Abrams, 1995; Srivastava & Lawton, 1998), or follows a unimodal relationship where the highest diversity is found in habitats with intermediate productivity (e.g. Mittelbach et al., 2001). Therefore, the tendency to protect mainly low-productivity land may affect the representativeness of protected areas, and risk leaving an important part of species unprotected.

In northern Europe, where most forests are intensively managed, a major proportion of protected forestland is of low productivity (Finnish Forest Research Institute, 2014; Swedish Forest Agency, 2014). For example in Sweden, low-productivity forests (defined as forests with potential tree growth <1 m^3 ha^{-1} $year^{-1}$) account for 18% of all forested land, but over 70% of the land exempted from forestry (Swedish Forest Agency, 2014). Nevertheless, their conservation value is largely unknown. However, both the diversity of several forest-dwelling organisms such as birds, vascular plants, bryophytes, and polypores (e.g. Gjerde et al., 2005; Honkanen, Roberge, Rajasärkkä, & Mönkkönen, 2010), and amounts of valuable substrates, such as large trees and dead wood, (Liira & Kohv, 2010; Nilsson et al., 2002) are generally higher in more productive forests. This is consistent with the general hypothesis that diversity increases with productivity due to associated increases in resources (Abrams, 1995), and low-productivity forests are, therefore, considered less valuable for biodiversity preservation (Cederberg, 1997). Accordingly, a recent study concluded that low-productivity forests are not valuable habitats for deadwood-dependent beetles due to low amounts and diversity of dead wood (Hämäläinen, Strengbom, & Ranius, 2018). However, as the study was restricted to beetles, the conservation value of low-productivity forests for other taxa remains unknown.

In addition to diversity, productivity can affect species composition (e.g. Boudreault et al., 2008). Low-productivity forests differ from productive forests in characteristics such as stand structure (Liira & Kohv, 2010) and may therefore provide different habitats for forest-dwelling species. Thus, even though the total species diversity is low, low-productivity forests can still be valuable for species that require such habitats. Among these species may be various lichens (Cederberg, 1997). Typically, low-productivity stands have an open canopy and consequently high light levels, which increases lichen species richness (e.g. Ellis, 2012); for example, *Cladonia* spp. benefit from increased light (Boudreault, Zouaoui, Drapeau, Bergeron, & Stevenson, 2013). Species richness of crustose lichens is also higher on slow-growing trees (Lie, Arup, Grytnes, & Ohlson, 2009), and the lower decay rate of dead wood in low-productivity forests (Shorohova & Kapitsa, 2014) creates old, hard dead wood, which is a valuable substrate for many deadwood-dependent lichens, such as *Carbonicola* spp. (Santaniello et al., 2017). Since low-productivity forests often are less affected by forestry (e.g. Storaunet et al., 2005), they may contribute to maintaining habitat continuity. This is important for maintenance of the diversity of various taxa (Graae & Sunde, 2000), including lichens. For example, the number of red-listed lichens has been found to increase with stand continuity (Marmor, Tõrra, Saag, & Randlane, 2011). However, despite these indications, further knowledge of the importance of low-productivity forests for biodiversity in managed forest landscapes is required.

In this study, we assessed the conservation value of low-productivity forests by examining assemblages of epiphytic (i.e. tree- and deadwood-dwelling) lichens in Scots pine *Pinus sylvestris* (L.)-dominated boreal forests in Sweden, in three biogeographical regions (Ahti, Hämet-Ahti, & Jalas, 1968) with different management histories. Within each region, we compared the lichen assemblages and forest stand structure in four forest types: two types of low-productivity forest (forests on mires and forests on thin, rocky soils), and two types of productive forest (mature managed stands and unmanaged stands set aside for biodiversity conservation). Using the acquired data, we tested the following hypotheses:

1. Following the general positive productivity–diversity relationship, the total species richness of lichens is the highest in the unmanaged productive forests due to high resource availability, that is, high amounts and diversity of living trees and dead wood.
2. The stand types represent different habitats for lichens, and therefore host different species assemblages; both productive and low-productivity forests harbour specialized species that are rare or absent in the other productivity class.
3. The patterns of species assemblages among stand types differ between regions due to regional differences in history of forest use and productivity.

2 | MATERIALS AND METHODS

2.1 | Study sites and data collection

We surveyed lichen assemblages in 84 Scots pine-dominated forest stands in three regions in Sweden (Figure 1): the hemi-, middle, and northern boreal vegetation zones (Ahti et al., 1968). The stands were arranged in blocks of four, each including four types of stands: two types of unmanaged low-productivity stands (forested mires and stands on rocky outcrops, hilltops or bare rocks – hereafter ‘thin soil’) and two types of productive stands (old managed

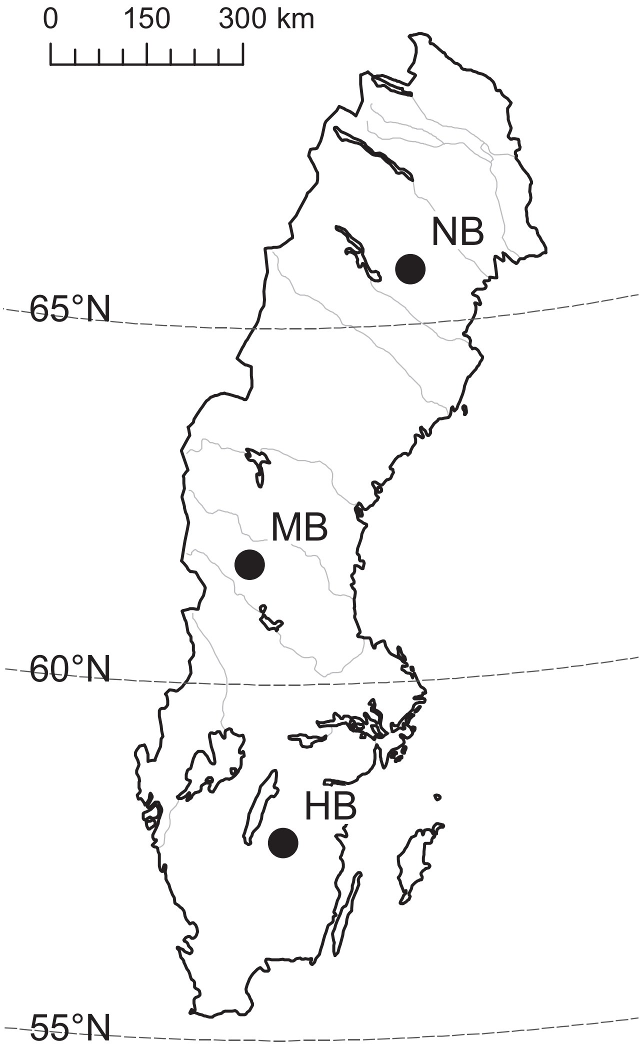


FIGURE 1 Locations of the study regions (HB = hemiboreal, MB = middle boreal, NB = northern boreal)

stands and unmanaged stands voluntarily set aside for biodiversity conservation – hereafter 'set-asides'). Seven blocks (i.e. 28 stands) were surveyed in each region. The stands were selected using information provided by the landowner, the forest company Sveaskog AB. See Hämäläinen et al. (2018) for details of stand selection.

We surveyed lichen assemblages on living and dead Scots pines during summer 2017. In each stand, we surveyed lichens in eight circular plots (radius 5 m for living trees and 20 m for dead wood). Within these plots, we surveyed all living and dead Scots pines with ≥10 cm diameter. We included all downed dead trees that were completely inside the plot, and every second of those downed dead trees that were partly inside the plots. On each tree, we surveyed a surface area of 0.6 m^2 (equivalent to surveying a tree with a diameter of 10 cm to 2 m height). For dead trees only decorticated wood was surveyed; the bark was not included since the bark of Scots pine typically falls off a few years after tree death, and thus provides very short-lived substrate for lichens (e.g. Lõhmus & Lõhmus, 2001). Lichen specimens that could not be identified in the field were collected for laboratory identification (by microscopy, spot tests and thin layer chromatography). *Cladonia arbuscula* and *C. mitis* were treated collectively, as were *Xylopsora caradocensis* and *X. friesii*. All specimens of *Lepraria* were treated together as *Lepraria* spp. Nomenclature of lichen species follows Nordin et al. (2018).

We measured the diameter and height of each surveyed living tree, and the diameter, height or length, decay stage (on a 5-point scale, see Appendix S1), and the proportions covered by bark and bryophytes, of each dead wood item. In addition, in each study plot, we randomly selected a living Scots pine for coring to determine its age and growth rate (in terms of average width of tree rings, mm/year). The basal area and volume of living trees were measured in a previous study in the same stands (Hämäläinen et al., 2018).

2.2 | Statistical analyses

We used the surface area of wood not covered by bark or bryophytes (and thus available for lichen colonization) as a measure of the dead wood amount. For calculation of dead wood diversity, the dead wood items were classified according to four factors: tree type (standing or downed), diameter (10–20 cm, 20–30 cm, or >30 cm), decay stage (5 classes), and presence or absence of charred wood. The diversity of dead wood was calculated as the number of different dead wood types (combinations of the above factors) present in each stand (Siitonen, Martikainen, Punttila, & Rauh, 2000).

We used two-way analysis of variance to test whether stand structure differed among regions or stand types. The tested factors were the total amount of dead wood, amount of standing, downed, new (decay stages 1–2), and old (decay stages 3–5) dead wood, dead wood diversity, mean tree growth rate and age, and stand basal area. If significant differences were detected, Tukey's HSD test was used for pairwise comparisons.

We constructed sample-based rarefaction curves with 95% confidence intervals (Hsieh, Ma, & Chao, 2016a) to compare species richness among stand types. This was done using species presence–absence data and treating the forest stands as samples. We constructed the rarefaction curves for the full lichen assemblages and three subsets: species occurring on living trees, deadwood-dependent species (according to Spribille, Thor, Bunnell, Goward, & Björk, 2008, excepting *Cladonia botrytes*), and red-listed species (Swedish Species Information Centre, 2015). Curves were constructed separately for each of the three study regions, except for red-listed species for which there were too few occurrences for separate analyses.

To assess effects of forest structure and characteristics of trees and dead wood on lichen species richness, we used generalized linear mixed models (GLMMs) with Poisson distribution and logarithmic link function. First, we modelled the species richness on stand scale, constructing separate models for all lichen species, deadwood-dependent species, red-listed species, and species occurring on living trees. The considered explanatory variables were region, stand basal area, mean tree growth rate and age, amount of dead wood, amount of new (decay stages 1–2) and old (decay stages 3–5) dead wood and dead wood diversity. Dead wood variables were not included in the model for species on living trees. Because the total amount of dead wood, amount of old dead wood and dead wood diversity were correlated, we did not include them in the same model. The blocks of stands were included as a random variable in all models.

We also modelled the species richness at tree scale, constructing separate GLMMs for species on living trees and dead wood, and for deadwood-dependent species. For living trees, the considered explanatory variables were tree age, diameter, growth rate, and region. Only trees for which age and growth rate were measured were included (*N* = 354). Tree age, diameter, and growth rate were correlated, and thus were not included in the same model. For dead trees, the explanatory variables were tree type (standing or downed), diameter, decay stage, presence/absence of charred wood and region. Blocks and stands were included as random variables in all models.

For all GLMMs, the explanatory variables were standardized to enable comparisons of effect sizes (Gelman, 2008), and sets of all possible models were generated and compared using Akaike's Information Criterion (AIC_c). Since no single best model was detected in any case, we performed model averaging over subsets of models with delta $AIC_c < 4$ (Grueber, Nakagawa, Laws, & Jamieson, 2011). The relative importance of the explanatory variables (RVI) was calculated by summing the AIC_c weights of all models in which the variables were included.

To test whether the composition of lichen assemblages differed between stand types, we applied permutational multivariate analysis of variance (permANOVA; Anderson, 2001), with 5,000 permutations, using the Bray–Curtis dissimilarity measure. We also used non-metric multidimensional scaling (NMDS) to illustrate the assemblage composition. The NMDS were run with Bray–Curtis dissimilarity measure, searching for two-dimensional solutions in 500 runs with random starting configurations of real data. Environmental variables (stand basal area, mean tree age and growth rate, and deadwood area and diversity) were fitted to the NMDS as vectors. Vectors with significant ($p < .05$) correlation with the ordination axes are presented in the figures. Both permANOVAs and NMDS were performed separately for each study region, using data on species abundances (*N* of dead wood items and living trees hosting species).

Indicator species analysis (ISA, Dufrêne & Legendre, 1997) was used to detect species typical of specific stand types, and species typical of productive or low-productivity stands. The ISA was performed for whole data and separately for each region using species abundance data. We also calculated the numbers of species unique to each stand type as well as productive or low-productivity stands within the whole data and within each region. In this calculation, species with <5 observations were excluded.

All statistical analyses were performed with R 3.5.0 (R Core Team, 2018) using packages STATS (R Core Team, 2018) and CAR (Fox & Weisberg, 2011) for the ANOVAs, INEXT (Hsieh, Ma, & Chao, 2016b) for the rarefaction, LME4 (Bates, Maechler, Bolker, & Walker, 2015) and MUMIN (Barton, 2018) for the GLMMs and model averaging, VEGAN (Oksanen et al., 2016) and RVAIDEMEMOIRE (Hervé, 2016) for the permANOVAs and NMDS, and LABDSV (Roberts, 2016) for ISA.

3 | RESULTS

3.1 | Lichen species richness

In total, we found of 151 lichen species, of which 12 were red-listed and 29 deadwood-dependent (Table S2). Of these species, 84 occurred on living trees and 148 on dead wood. In the hemiboreal and middle boreal regions, the total species richness was the highest in the low-productivity stands on thin soil, while in the northern boreal region stands on thin soil and productive set-asides had similar species richness (Figure 2a). The richness of deadwood-dependent lichens was also generally higher in stands on thin soil and set-asides (Figure 2c), whereas the richness of species on living trees did not display any clear pattern with respect to stand types (Figure 2b). The number of red-listed species was the highest on set-asides, followed by stands on thin soil (Figure 2d).

The sets of GLMMs included in the model averaging are presented in Table S3. At the stand scale, dead wood diversity explained species richness better than dead wood amount, thus the latter was not included in the final models (Figure 3). The total species richness increased with dead wood diversity and mean tree age. Species richness on living trees was positively correlated with the stand basal area, while the richness of both deadwood-dependent and red-listed species was negatively correlated with the basal area (Figure 3). The species richness on dead wood was higher in later than in earlier decay stages and, for deadwood-dependent species, on standing than on downed trees (Figure 4b,c). Although species richness on living trees was the highest in the middle boreal region, and increased slightly with tree diameter (Figure 4a), the amount of variation in species richness explained by the final models was very low (Table S3).

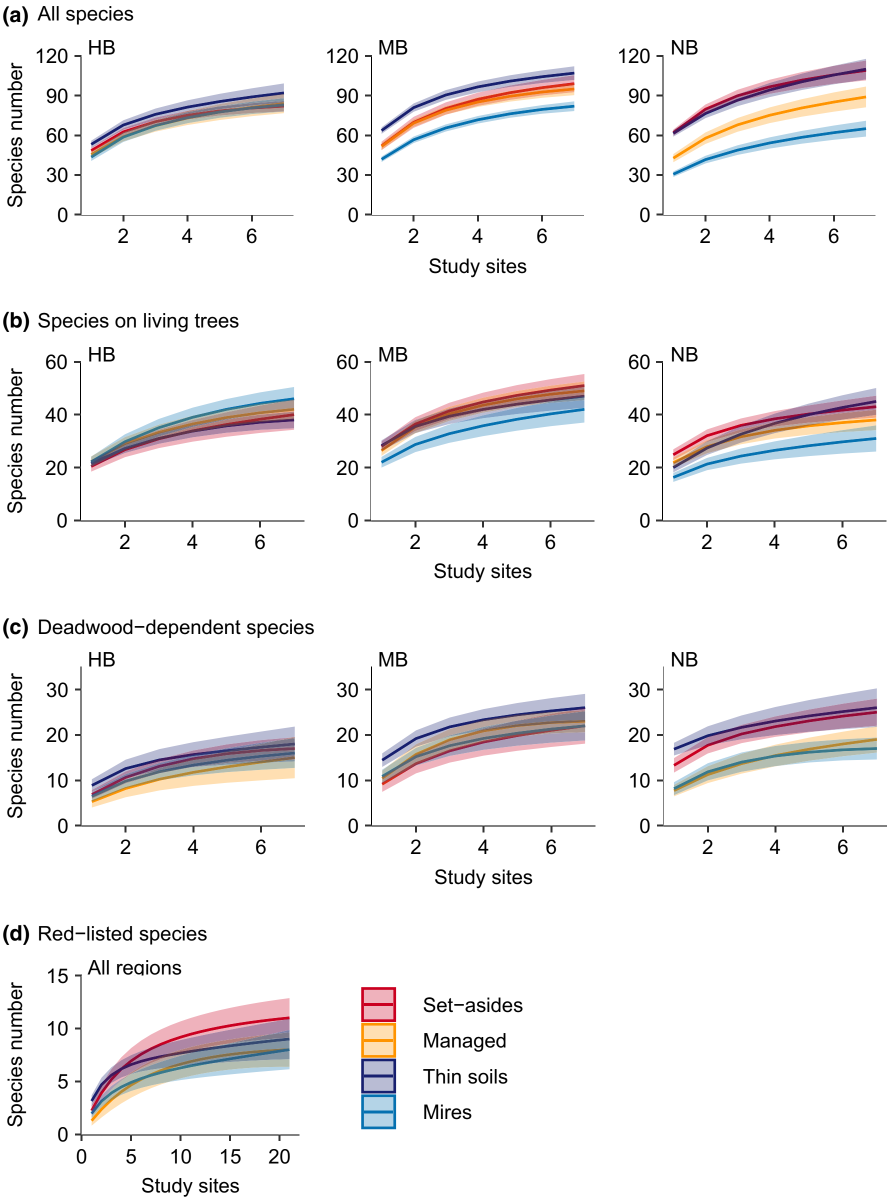
3.2 | Lichen species composition

In all regions, the composition of lichen assemblages differed among stand types (Table 1, Figure 5). The differences were most distinct in the northern boreal region, where only set-asides and stands on thin soil had similar species composition (for all other pairwise comparisons between stand types $p < .05$). In the middle boreal region, stands in mires differed from all other stand types, and in the hemiboreal region stands on thin soil differed from those on mires and managed stands ($p < .05$). Two species were only detected in productive stands and one only in low-productivity stands, but no species were unique to any of the four stand types (Table S2). The productivity classes had similar numbers of indicator species, while the stand types that had most indicator species (in all regions) were stands on thin soil, followed by set-asides (Table S5).

3.3 | Stand structure

The productive stands had a larger basal area than low-productivity stands (Tables 2 and 3), but neither the amount nor diversity of dead wood significantly differed among productivity classes (Figure 6). The

FIGURE 2 Sample-based rarefaction curves (with 95% CI) showing cumulative numbers of the following: (a) all lichen species, (b) lichen species on living trees, (c) deadwood-dependent lichen species, and (d) red-listed lichen species, relative to the number of surveyed stands. Separated between regions (HB = hemiboreal, MB = middle boreal, NB = northern boreal)



amount of dead wood was the lowest in mires, while the differences among the other three stand types depended on the region (Figure 6). Stands on thin soil and set-asides had larger amounts of dead wood in later decay stages, and mires had a larger proportion of standing dead wood than the other stand types (Figure 6, Table 3). The pattern of dead wood diversity varied among regions, but the diversity of dead wood was generally low in mires and higher in stands on thin soil (Figure 6). The differences in dead wood amount and diversity among stand types were most pronounced in the northern region (Figure 6).

4 | DISCUSSION

4.1 | Lichen species richness

Lichen species richness was the highest in the low-productivity forests on thin soil, which contradicts our first hypothesis that the productive forests would be more species-rich because they have more abundant (Srivastava & Lawton, 1998) or diverse resources (Abrams, 1995). It also differs from previous findings in low-productivity forests showing a lower diversity of deadwood-dependent beetles due to a lower dead wood volume (Hämäläinen et al., 2018). More generally, positive relationships between productivity and species diversity in boreal forests has been found for several taxa, such as vascular plants (Chen et al., 2004), bryophytes (Gjerde et al., 2005) and birds (Honkanen et al., 2010). This has been explained by associated correlations in both resources, such as soil nutrients or dead wood (e.g. Gjerde et al., 2005), and habitat heterogeneity (Reich, Frelich, Voldseth, Bakken, & Adair, 2012). However, deviations from the positive productivity–diversity relationship have been reported for several other taxa, including lichens (Gjerde et al., 2005) and spiders (Sætersdal et al., 2004). Thus, although the relationship between stand productivity, resource amount and species diversity may be generally positive, this does apparently not apply to all taxa.

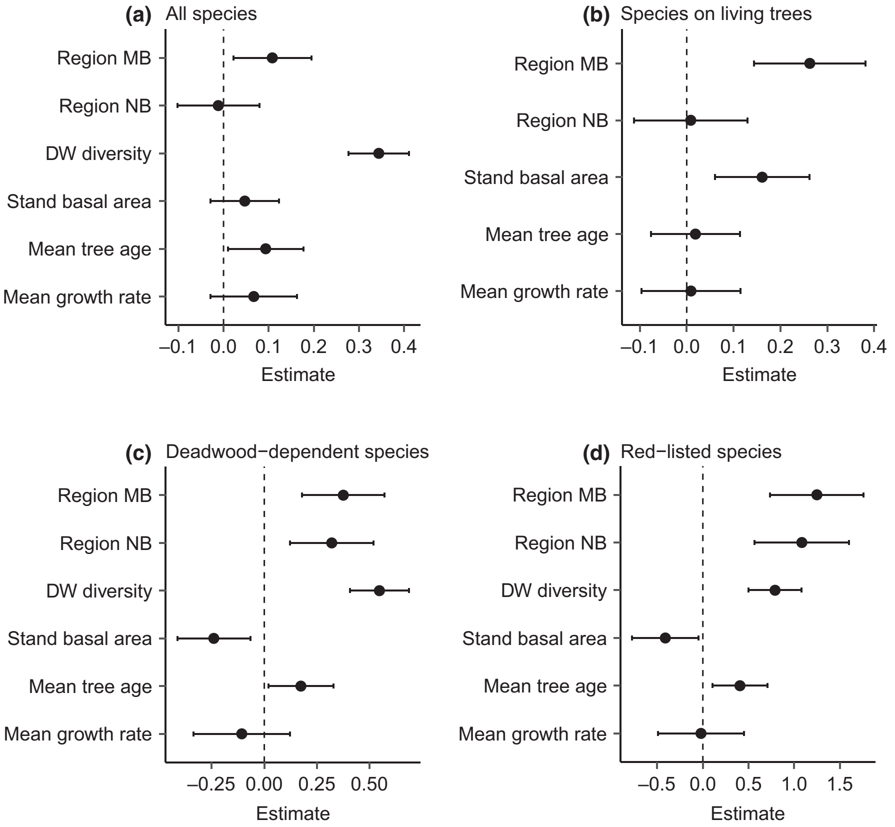


FIGURE 3 Model-averaged parameter estimates (with 95% CI) for the generalized linear mixed models (GLMMs) of stand-scale lichen species richness. Hemiboreal used as a reference level for region. RVI-values for the variables are presented in Table S4

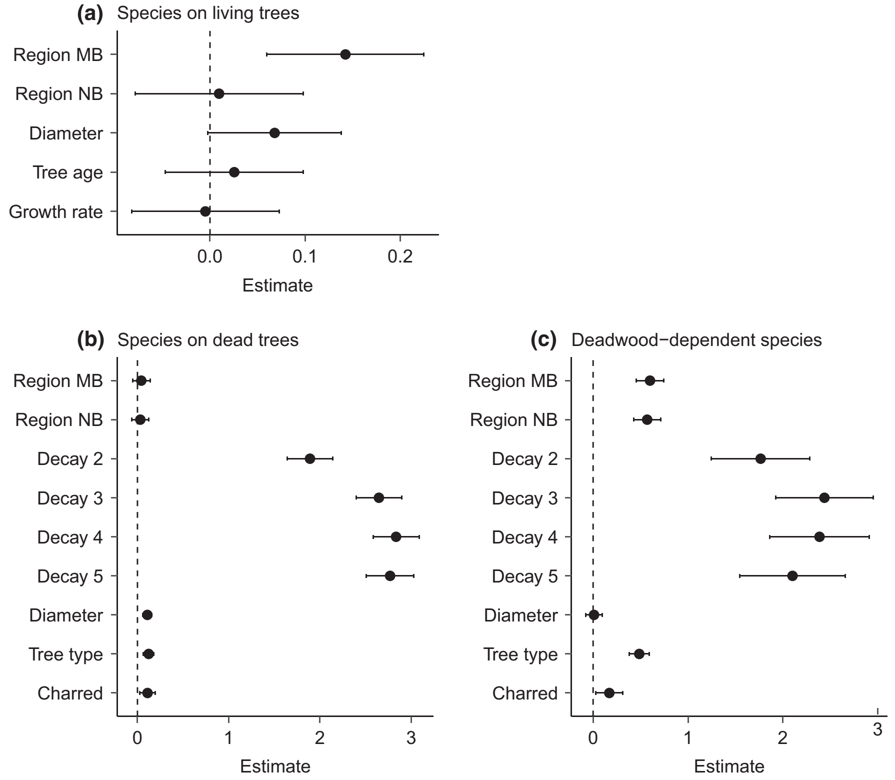


FIGURE 4 Model-averaged parameter estimates (with 95% CI) for the generalized linear mixed models (GLMMs) of tree-scale lichen species richness. Hemiboreal used as a reference level for region, decay stage 1 for decay, downed trees for tree type, and absence of charred wood for charred. RVI-values for the variables are presented in Table S4

For lichens on living trees, the amount of habitat (stand basal area) was higher in the productive stands, and weakly positively correlated with stand-scale species richness. However, the overall species richness did not show any clear patterns in relation to stand type or productivity. Apart from basal area, none of the considered stand- or tree-scale factors notably explained species richness. This

TABLE 1 Results of permutational multivariate analysis of variance comparing lichen species composition among the four stand types in each of the three regions

Region	*F* (*df* = 3)	*p*	R^2
Hemiboreal	1.89	.009	0.19
Middle boreal	2.47	.002	0.24
Northern boreal	5.03	<.001	0.39

was unexpected, as tree age, diameter and growth rate all reportedly affect lichen diversity (Lie et al., 2009; Uliczka & Angelstam, 1999). Possibly the ranges of tree age and growth rates in the surveyed stands were too narrow for detectable differences in lichen richness using our methodology. Moreover, by surveying a standardized area on each tree, we may have diminished the potential effect of tree diameter.

The richness of deadwood-dwelling species was the highest in stands on thin soil, although they differed in neither the amount nor diversity of dead wood from the more productive stand types. However, the quality of dead wood may have differed. In stands on thin soil, the dead wood was older, possibly due to the dry conditions or characteristics of wood from slowly growing trees. This likely increased species richness, since lichen richness on dead

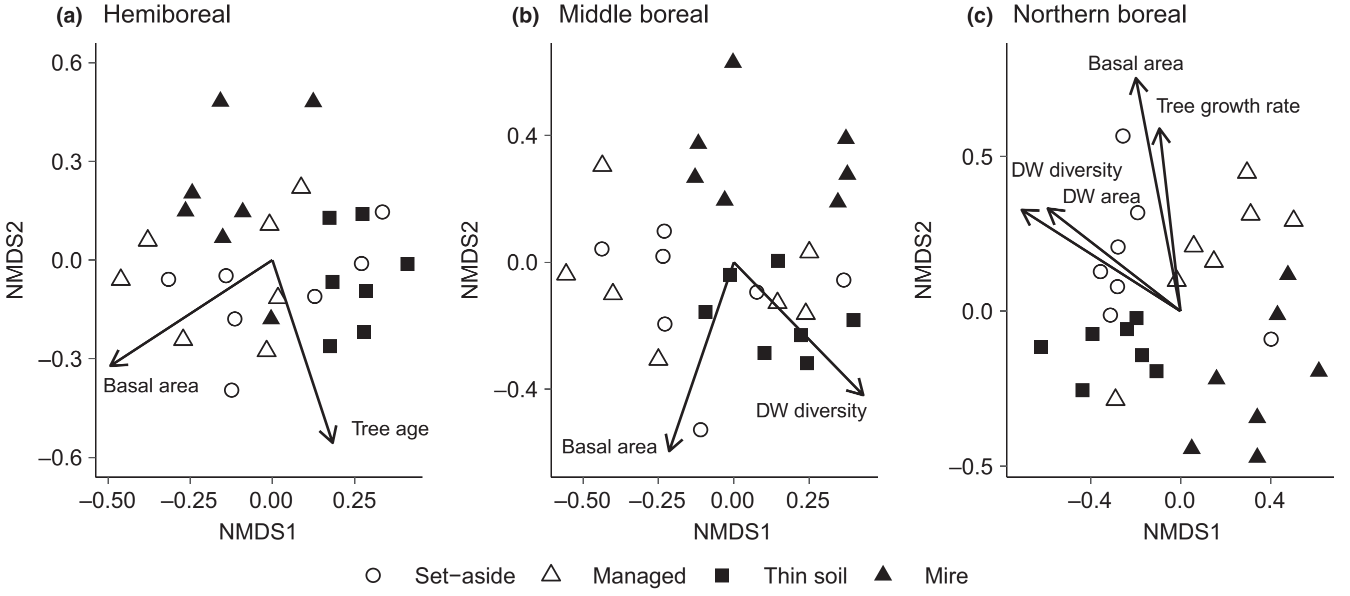


FIGURE 5 Results of non-metric multidimensional scaling (NMDS) ordination comparing the lichen assemblage composition among stand types in the three study regions. The mean final stress values are 23.6, 20.1 and 20.1 for the hemiboreal, middle boreal and northern boreal regions respectively. Environmental variables with statistically significant ($p < .05$) correlation with the ordination axes are shown

TABLE 2 Results of two-way analysis of variance of stand structural variables among stand types and regions. The interaction term is included only when significant ($p < .05$). Results of pairwise comparisons are presented in Table S6

	Stand type		Region		Stand type × Region	
Variable	*F* (*df* = 3)	*p*	*F* (*df* = 2)	*p*	*F* (*df* = 6)	*p*
Amount of dead wood	10.15	**<.001**	0.58	.56	–	–
Amount of old DW	12.44	**<.001**	0.52	.59	–	–
Amount of fresh DW	5.11	**.003**	0.84	.47	–	–
Amount of standing DW	4.59	**.005**	4.30	**.02**	3.39	**.005**
Amount of downed DW	14.90	**<.001**	1.75	.18	–	–
Dead wood diversity	9.76	**<.001**	0.68	.51	5.51	**<.001**
Stand basal area	27.65	**<.001**	14.48	**<.001**	4.12	**.001**
Mean tree age	5.46	**.002**	3.21	.046	–	–
Mean tree growth rate	13.37	**<.001**	12.81	**<.001**	–	–

Significant variables ($p < .05$) are given in bold.

TABLE 3 Mean values (+*SE*) of stand basal area (m^2/ha), age of living trees (years), tree growth rate (mm/year), amount of standing and downed dead wood (m^2/ha of decorticated wood) and dead wood diversity (*N* of dead wood classes present per stand) in indicated regions and stand types

	Stand basal area	Tree age	Tree growth rate	Amount of standing DW	Amount of downed DW	DW diversity
a) Hemiboreal						
Set-aside	19.34 ± 5.14	110.21 ± 28.66	1.12 ± 0.17	23.80 ± 18.48	41.41 ± 18.66	9.43 ± 0.90
Managed	22.77 ± 3.06	74.65 ± 13.16	1.47 ± 0.30	20.08 ± 13.62	32.44 ± 9.60	8.29 ± 0.86
Thin soil	17.80 ± 1.77	104.28 ± 35.47	1.27 ± 0.30	10.81 ± 7.37	41.45 ± 22.31	9.57 ± 0.65
Mire	16.57 ± 4.22	87.84 ± 26.19	1.00 ± 0.23	23.55 ± 20.16	12.21 ± 7.18	8.86 ± 0.86
b) Middle boreal						
Set-aside	17.70 ± 4.79	122.48 ± 35.70	1.13 ± 0.33	14.46 ± 10.90	36.05 ± 27.01	7.29 ± 1.51
Managed	16.00 ± 1.79	84.83 ± 15.14	1.18 ± 0.18	10.64 ± 9.85	36.73 ± 26.28	10.43 ± 1.77
Thin soil	14.91 ± 2.04	108.71 ± 44.33	1.02 ± 0.27	12.03 ± 4.81	41.14 ± 21.32	10.57 ± 1.46
Mire	10.50 ± 2.71	127.34 ± 28.53	0.66 ± 0.20	17.64 ± 15.72	5.38 ± 4.24	5.29 ± 0.61
c) Northern boreal						
Set-aside	22.36 ± 2.22	137.07 ± 35.97	0.92 ± 0.27	50.45 ± 26.28	43.58 ± 26.09	14.00 ± 1.50
Managed	18.96 ± 2.48	92.05 ± 35.46	1.09 ± 0.18	12.56 ± 8.78	11.36 ± 9.00	6.57 ± 0.90
Thin soil	13.14 ± 3.17	115.77 ± 41.56	0.90 ± 0.29	24.12 ± 18.37	35.01 ± 22.88	12.29 ± 1.49
Mire	9.52 ± 0.93	114.71 ± 39.75	0.65 ± 0.16	13.94 ± 6.37	1.89 ± 2.41	4.43 ± 0.69

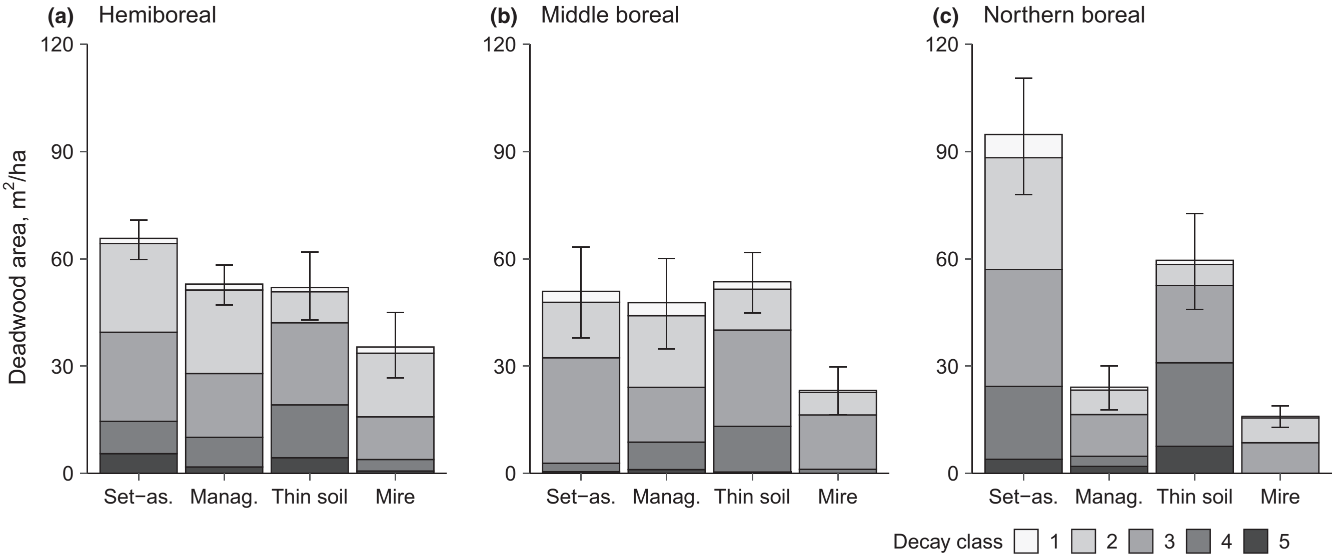


FIGURE 6 Mean dead wood amount (±*SE*, as m^2/ha of decorticated wood), divided into decay stages (scale 1–5), in the studied regions and stand types

wood typically peaks in the middle and late decay stages (e.g. Humphrey, Davey, Peace, Ferris, & Harding, 2002; Kruys, Fries, Jonsson, Lämås, & Ståhl, 1999), and old, hard wood is particularly important for deadwood-dependent lichens (Santaniello et al., 2017). Accordingly, we observed the highest lichen richness per dead wood object in late decay stages. Furthermore, stands on thin soil had the largest number of dead wood items with charred wood, which host specialized lichen species such as *Carbonicola* spp. (Grossmann, 2014). In addition to the difference in dead wood characteristics, the low-productivity stands were more open, which reportedly has positive effects on lichen diversity (e.g. Ellis, 2012). Accordingly, the richness of deadwood-dwelling species was inversely related to the basal area. Low-productivity stands may also be important for lichens because of their generally long habitat continuity (Gjerde et al., 2005; Pykälä, 2004). Although we have no data on the management history of the stands, those on thin soil have probably been less intensively managed than the others. Thus, they have probably had greater habitat continuity, as structures have remained present constantly over time, and thereby have relatively high lichen richness.

Lichen species richness differed between the two types of low-productivity stands. Mires harbored the lowest lichen richness and had a low amount and diversity of dead wood. These findings are consistent with previous studies suggesting that forested mires are insignificant habitats for deadwood-dependent lichens (Svensson et al., 2016) and saproxylic beetles (Hämäläinen et al., 2018) due to their low amounts of dead wood. Mires appeared to have the lowest productivity of the studied stand types, as they had both the lowest stand basal area and mean tree growth rate. Thus, although they likely shared characteristics (older dead wood, high light levels and habitat continuity) that increased habitat quality in stands on thin soil, their productivity (and hence the amount of substrates) was so low that it had stronger negative effects on lichen richness.

4.2 | Lichen assemblage composition

Forest productivity reportedly influences species composition of various taxa, including vascular plants, lichens and bryophytes (Boudreault et al., 2008; Chen et al., 2004). Accordingly, the lichen assemblage composition differed among stand types, and, in the northern boreal region, between productive and low-productivity stands. Assemblages consistently differed between mires and stands on thin soil, but for other pairs of stand types the distinctions differed among regions. Thus, our hypothesis that the assemblage composition would differ between productive and low-productivity stands is to some extent supported. However, none of the stand types hosted unique species, and only three species were confined to a certain productivity class: two to productive stands (*Bryoria nadvornikiana* and *Buellia griseovirens*), and one to low-productivity stands (*Buellia arborea*).

Lichen assemblages were related to stand basal area in all regions, suggesting that canopy openness influenced assemblage composition. Species that occurred more frequently in stands on thin soil, included foliose macrolichens and *Cladonia* spp. that benefit from high light levels (Boudreault et al., 2013), whereas species that were more common in set-asides (e.g. certain calicioid lichens) may require shadier conditions. Differences in light levels along a productivity gradient can affect the species composition of epiphytic lichens and bryophytes (Boudreault et al., 2008), but appear to have little influence on the species composition of vascular plants in the understorey (Chen et al., 2004). In addition to basal area, the diversity and amount of dead wood were related to assemblage composition. Many deadwood-dependent lichens, including the red-listed *Hertelidea botrytes* and *Cladonia parasitica*, were most frequent in stands on thin soil, suggesting that the dead wood may indeed be more suitable for certain lichens in these stands.

4.3 | Regional patterns

In accordance with our third hypothesis, the patterns in species richness and composition varied among regions. In mires, we found lower levels of stand basal area, dead wood amount, and, accordingly, lichen species richness in the northern region, indicating that productivity decreases towards the north. In contrast, in set-asides and stands on thin soil, species richness was lower in southern Sweden, particularly for deadwood-dwelling lichens. A likely reason for this is that stands in the northern region may be less affected by past forest management. Although we do not know the management history of the studied stands, northern Sweden generally has a shorter history of intensive forestry than southern (Angelstam, 1997). Particularly in the set-asides, stand age, amount and diversity of dead wood were higher in the north, which indicates a lower impact of management. Together with the regional productivity pattern, the possible differences in management history likely explain the more pronounced differences in lichen species richness and composition, and both diversity and amount of dead wood, observed in northern than southern Sweden.

4.4 | Implications for nature conservation

Boreal low-productivity forests can be important for preservation of biodiversity, but their conservation value depends on the taxa in question, the type of low-productivity stand, and landscape characteristics. Low-productivity stands on thin soil harbored higher lichen species richness than productive forests. A previous study also found that forests on rocky outcrops (resembling the stands on thin soil we examined) are important for rare macrolichens (Pykälä, 2004). Thus, for lichens, low-productivity forests on thin soil have as high, or even higher, conservation value than productive forests. However, for other taxa, they have lower value. For deadwood-dependent beetles, for example, Hämäläinen et al. (2018) estimated that productive forests had 1.8–3.6 times higher conservation value than low-productivity forests, and hosted several species that were not present in the low-productivity stands. For other taxa, the specific value of low-productivity stands is unknown, but probably low as their richness generally increases with productivity (e.g. Gjerde et al., 2005). Thus, it is not possible to define a general conservational value for low-productivity forests, as it depends on the taxa in question. Moreover, our results are limited to Scots pine-dominated forests; if we had included a wider variety of productive forests, containing a broader range of tree species, the observed value of low-productivity forests might have been different.

The two main types of low-productivity forests in northern Europe have different conservation values. We found that forests on thin soil are more species-rich than mires as they have higher amounts of both living trees and dead wood. A similar pattern was previously observed for deadwood-dependent beetles (Hämäläinen et al., 2018). Thus, different low-productivity forest types should not be lumped together, but rather considered according to their specific values in conservation strategies. Although the stand-scale species diversity in mires is low, so they have low value per unit area, they may still be important as they cover vast areas of the boreal forest. For example, in Sweden and Finland, forested mires cover more than twice the area of forests on thin soil (Finnish Forest Research Institute, 2014; Swedish Forest Agency, 2014).

Furthermore, our results indicate that the conservation value of low-productivity forest, relative to productive, varies across the boreal region depending on landscape characteristics. As low-productivity forests are often less affected by management than productive forests (Storaunet et al., 2005), their conservation value may be particularly high in intensively managed landscapes that have lost most natural forests. In landscapes less influenced by forestry, where productive stands may remain close to natural state, the value of low-productivity forest may be, in relative terms, lower. In addition to management history, other landscape characteristics, such as connectivity to valuable habitats, can affect species richness in low-productivity forests and may be necessary to consider when assessing their conservation value. Although such landscape characteristics are commonly assumed to be important for biodiversity, the empirical support for this is poor. Therefore, further research is needed to clarify the importance of these landscape-level factors.

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AUTHORS' CONTRIBUTIONS

All authors contributed to planning the study and sampling design. A.H. collected and analyzed the data and was responsible for writing the manuscript. All authors substantially contributed to the writing of the manuscript and given approval for its publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.4q1s881 (Hämäläinen, Strengbom, & Ranius, 2019).

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