Received: 21 January 2025 | Accepted: 6 May 2025
DOI: 10.1111/1365-2664.70090

BRITISH ECOLOGICAL SOCIETY Journal of Applied Ecology

RESEARCH ARTICLE

Remnant continuity forests are essential for sustaining epiphytic biodiversity in boreal production forest landscapes

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Funding information
Svenska Forskningsrådet Formas, Grant/Award Number: 2018-00577

Handling Editor: Yolanda Wiersma

Abstract

1. Boreal forest landscapes are rapidly transformed through expanding clearcutting forestry, leading to a decline in forests with long tree continuity and an increase in even-aged production stands. The role of remnant forests in supporting biodiversity within production forest landscapes remains poorly understood. Northern Europe provides an ideal setting for studying mosaics of clearcut and remnant continuity forests, given its long history of clearcutting and the prevalence of even-aged forest stands.
2. New remote-sensing techniques have enabled the identification of forests in boreal Sweden that have maintained permanent tree cover at least since the 1950s ('continuity forest'), meaning that they have likely never been clearcut, with removal of all trees. Using these data (including production forest as well as protected forest), we randomly selected 16 areas, each 225 km^2 in size, with the proportion of continuity forest ranging from 2% to 25%. In each study area, we selected four even-aged production forest stands aged 0–80 years and one selectively harvested (never-clearcut) production stand aged 81–120 years. As model organisms for assessing biodiversity, we used epiphytic lichens on randomly selected Norway spruce *Picea abies* trees.
3. We recorded 164 epiphytic lichen taxa on 926 trees. Species richness (including species of conservation concern) in the even-aged forests <80 years old increased with the proportion continuity forest in the surrounding landscape. In contrast, there was no relationship between the richness of lichens and the proportion continuity forest for the older, selectively harvested production forests.
4. Our results suggest that continuity forests are an important dispersal source for even-aged production forests since almost all of the epiphytic lichen occurrences represent new colonization. Our results also show that continuity production

forests >80 years old are important to epiphytic biodiversity since they host many species of conservation concern.

5. *Synthesis and applications*. Our study has relevance for forestry and conservation across the boreal biome where a continued rapid expansion of clearcutting into primary forest landscapes is likely. Preserving continuity forests for the future would enrich the epiphytic biodiversity of younger, even-aged production forests due to their function as dispersal nuclei. The remnant continuity forests are also conservation targets in their own right due to their rich lichen diversity.

KEYWORDS
biodiversity, continuity forest, epiphyte, forest age, lichen, Norway spruce, species of conservation concern

1 | INTRODUCTION

The forest area used for timber production is increasing globally, with a parallel reduction in the area of forest with low human impact (Potapov et al., 2017), leading to a transformation of forest landscapes towards a mosaic of production forest stands and forests more natural in character. With an allocation of 30% of the world's forest area to wood production and 10% to conservation (FAO, 2020), knowledge on the relative importance of the two types for maintaining biodiversity is essential. The transformation of forests from natural states to production forests caused by industrial forestry affects biodiversity in several ways, not least through reduced habitat availability for species restricted to old-growth forest (Martin et al., 2023), and clearcutting is one of the forestry methods reducing species richness most strongly (Chaudhary et al., 2016). Despite the recent attention to biodiversity in forest landscapes, such as the debate about the relative role of amount and spatial configuration of habitats (Fahrig, 2013), studies targeting possible differences between forests with limited earlier human impact and production forests have been neglected. This is surprising given the projected substantial increase in future timber demand (FAO, 2022), suggesting that industrial forestry will continue to expand into boreal regions with a high share of old-growth forests (Venier et al., 2014). Furthermore, efficient conservation strategies for different types of land-use are increasingly stressed, not least in the newly adopted Kunming-Montreal Global Biodiversity Framework (COP15, 2022).

Due to its long history of clearcutting, Northern Europe is a suitable region to address how landscapes with different shares of production forests and forests in more natural condition influence biodiversity. In Sweden, clearcutting has been practiced large-scale since the mid-1900s, resulting in a dominance of even-aged stands, while forests with less human impact are still present but are rapidly decreasing (Ahlström et al., 2022).

New time-series, remote-sensing data have opened up an unusual opportunity to identify forests with permanent forest cover since the 1950s, before the large-scale introduction of clearcutting forestry (Svensson et al., 2019), in the following referred to as 'continuity forests'. This implies that these forests have had a permanent tree cover for at least six or seven decades but likely considerably longer since they had tall forest already in the 1950s. These data also enable a systematic selection of a large number of study areas varying in proportion of continuity forests in the landscape. Long-term continuous forest cover has been recognized to cater a distinct community of specialized and dispersal-limited species (Nordén et al., 2014).

Epiphytic lichens (growing on living trees) are frequently used as model organisms in forest biodiversity studies due to their distinct habitat specificity, rich species diversity, and sensitivity to anthropogenic disturbance (Ellis, 2012). Experimental and observational studies show that many lichens are dispersal-limited (Ellis, 2012; Johansson et al., 2012), although long-distance dispersal also occurs (e.g. Gjerde et al., 2015). Using species with low dispersal ability as model species is advantageous, as mobile species respond more quickly to landscape transformations (Henle et al., 2004). Studies in Europe, as well as North America, indicate that forests with a long continuity promote lichen diversity (e.g. Dymytrova et al., 2018; Hofmeister et al., 2024; McMullin & Wiersma, 2019; Selva, 1994; Wiersma & McMullin, 2022). Norway spruce *Picea abies* (L.) H.Karst is the tree species in Sweden with the most associated species (Sundberg et al., 2019), and from earlier studies we know that at least 120 epiphytic lichen species may be found on living Norway spruce trees (Ranlund et al., 2018).

A reasonable assumption for production forest landscapes with mixes of continuity forests and clearcut forests is that species diversity will increase with the landscape proportion of continuity forests (Figure 1). This is because dispersal from continuity forests, usually hosting a specialized and species-rich flora and fauna, into production forests has been identified as a key landscape process, that is, spillover effects (Blitzer et al., 2012). A basic ecological assumption is also that the potential for colonization will increase with the longevity of the habitat (McMullin & Wiersma, 2019; Nordén et al., 2014), in our case reflected by the age of the forest (Figure 1). In boreal Sweden, age effects are most probable in stands <80 years old, since production forests >80 years often have longer continuity and many have only been selectively harvested. During the early industrial forestry phase, these older production forests were often high-graded

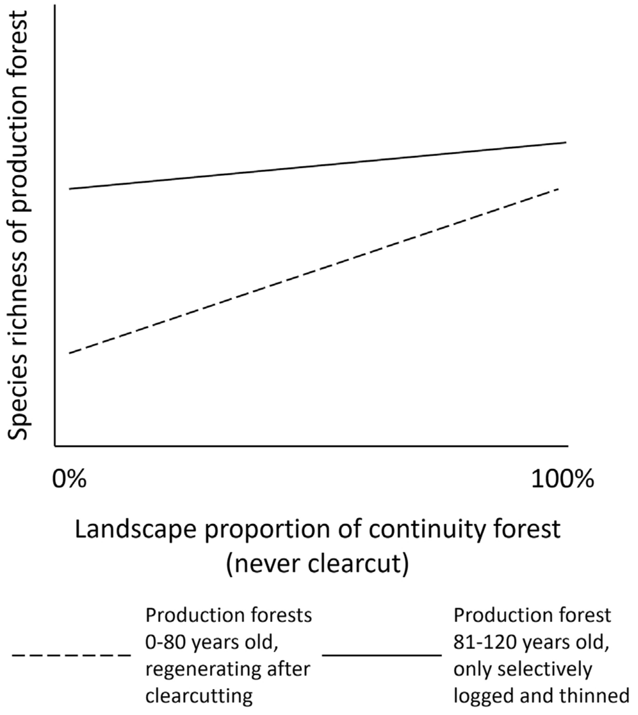

FIGURE 1 Assumptions for the relationship between species richness of production forests and the proportion remnant continuity forests in boreal forest landscapes. We postulate that surrounding continuity forests enrich the young even-aged production forests (0–80 years old) regenerating after clearcutting since all colonization to the trees originates from dispersal from outside sources, of which the continuity forests should be essential. Also, the oldest production forests (81–120 years old) should be enriched through dispersal from the surrounding continuity forests but to a lesser degree since these old forests have likely never been clearcut and thus can be presumed to have a comparatively high lichen diversity.

(with the largest trees removed) and successively thinned over time (Svensson et al., 2019). As a result, they may, despite longer continuity, exhibit structural similarities to forests regenerated from clearcutting. Still, earlier studies have shown that these forests can support a high number of species of conservation concern, likely due to their long continuity (Gustafsson et al., 2004).

Our overall aim is to increase the knowledge of the importance of large-scale habitat patterns for biodiversity in boreal production forests, with special emphasis on remnant continuity forests. We use epiphytic lichens as model organisms, examining all species as a group and specifically targeting species of conservation concern. Our main research question is: What is the importance of remnant continuity forests for the epiphytic biodiversity in boreal production forests? We hypothesize that: (i) species richness in even-aged production forests increases with the amount of continuity forest in the surrounding forest landscape, (ii) the species composition of the old (continuity) production forests is characterized by a high frequency of species of conservation concern and (iii) the influence of the continuity forests is larger in young, even-aged production forests than in older, selectively harvested production forests with longer tree continuity (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Sampling

We conducted our study in Sweden, where clearcutting has been intensively practiced since around the mid 1950s and is today practiced on >85% of the entire productive forestland of 23 million ha (Skogsdata, 2023). The forest landscapes are dominated by even-aged conifer stands <80 years old, with Norway spruce and Scots pine *Pinus sylvestris* L. each constituting about 40% of the total wood volume (Skogsdata, 2023). A limited amount of production forests with long continuity still remains, aged >80 years and initially managed through high-grading and later through thinning operations (Svensson et al., 2019). The remaining small proportion of continuity forest also includes areas set aside for conservation, such as nature reserves protected by the state, as well as forests voluntarily protected by forest owners through their certification. Although detailed studies are lacking, it is reasonable to assume that the human impact in these protected forests is lower than in the old, selectively harvested production forests.

We used a high-resolution mapping of northern Sweden to identify continuity forests through repeated analysis of aerial images and satellite data from the 1950s to 2019, including forests without signs of clearcutting (Svensson et al., 2019). Since our continuity stands had tall forest in the 1950s, they, like the majority of forest land at that time, had very likely never been clear-cut, even though this form of logging was practiced to a small extent already in the early 20th century, and increasing after that (Lundmark et al., 2021). We identified 16 study areas, each covering 15 × 15 km (225 km^2) located in mid-boreal Sweden (12,000 km^2), with a proportion of continuity forest ranging from 2% to 25%; the widest range in the region (Figure 2). These continuity forests comprised all forests, that is, both production forests and protected forests. The study region, situated within the middle and northern boreal Sweden (Ahti et al., 1968), was delimited to enable generalizations to large parts of boreal Sweden. To avoid confounding factors, we restricted the search to areas without calcareous bedrock and a humid, oceanic climate (found in the westernmost regions near the Scandes), since these conditions create deviating tree species composition and lichen flora (Ahlner, 1948; Sjörs, 1965). The size of study areas (225 km^2) was chosen to accommodate a sufficient number of forest stands. Also, this size was deemed relevant for lichen dispersal, since dispersal is considered to be a combination of short-distance via thallus fragments and long-distance through spores (Ellis, 2019), recognizing that the knowledge about lichen dispersal is still limited. Within each study area, we selected one production stand from each of the five age classes 0–20, 21–40, 41–60, 61–80 and 81–120 years based on stand register information from the forestry company SCA. The younger age classes were later merged into the

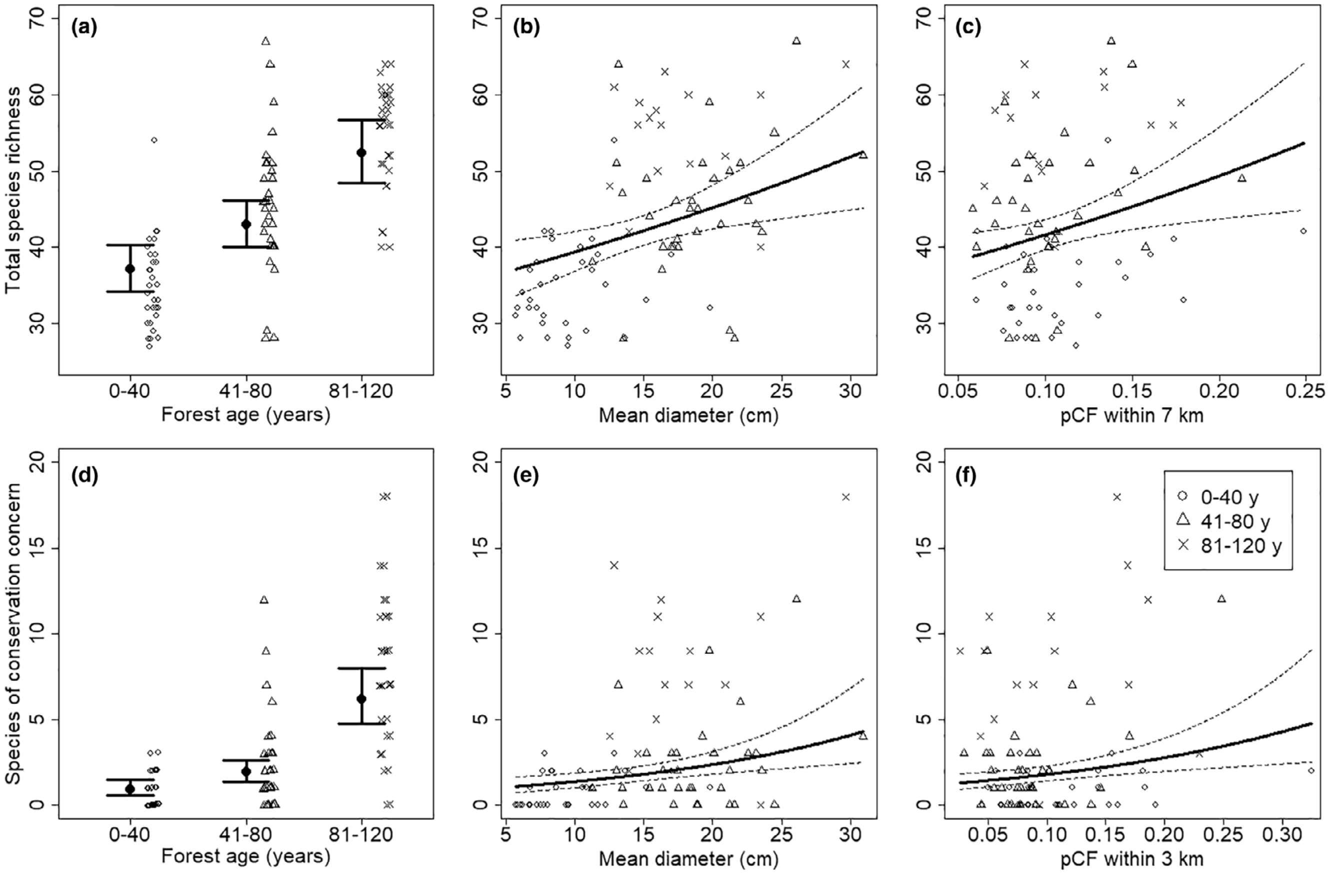

FIGURE 2 Model predictions with 95% confidence intervals from the full model (see Table 1) of the total species richness (a–c) and the richness of species of conservation concern (d–f) in relation to proportion continuity forest in the surrounding landscape. (a, d), forest age (0–40, 41–80, 81–120 = '0–40 years/clearcut', '41–80 years/clearcut', '81–120 years/selective') (b, e), and mean tree diameter (c, f). Raw data are shown with different symbols for the three forest categories (see legend in (d)). To improve visibility of raw data a small scatter has been added in the relation with forest age (b, e).

broader classes 0–40 years old and 41–80 years old, respectively, to ensure statistical power, hereafter referred to as '0–40 years/clearcut', '41–80 years/clearcut', and '0–80 years/clearcut'. By combining the remote-sensing data on continuity forests with the stand register information from SCA, we identified continuity production forests, and these were all >80 years old. In the following, they are denoted as '81–120 years/selective'. Although these forests are far from being 'old' in the ecological sense, we still use this term because they are old in a production forest context.

During the survey, we recorded all lichen species (crustose, foliose, and pendulous) on 12 trees per stand, arranged in 6 pairs. A complete species list was recorded for the first tree in each pair, with additional species recorded on the second tree. This process was repeated for the third tree, with additional species recorded on the fourth tree, and so on, until all 12 trees had been surveyed. To prevent possible overestimation of new (post-harvest) colonization, survey trees in the youngest stands (0–40 years old) were classified as remaining ('legacy trees') or not remaining from before the clearcutting. The restriction to the youngest stands is justified by the fact that the common practice of pre-harvest cleaning (removal of small trees before harvesting to increase the visibility for the operator of the harvester) has been gradually abandoned over the past decades (Appendix SA1: Section S1; Figure S1). No permission was needed for conducting the fieldwork.

2.2 | Statistical analyses

All statistical analyses were performed at the stand level, compiled from the six pairs of trees. First, we analysed total species richness (number of lichen taxa) and richness of species of conservation concern: red-listed species (SLU ArtDatabanken, 2020), indicator species of forests with high conservation value (Nitare, 2019), and species of special conservation concern in the study region (FJ, expert opinion). We used two separate models using generalized linear mixed effect models (GLMMs), with a Poisson distribution and study area identity (16 study areas) as a random factor. The explanatory variables were: (1) stand-age category (0–40 years/clearcut, 41–80 years/clearcut or 81–120 years/selective), (2) mean tree diameter, and (3) proportion of continuity forest in the landscape (including both production forest and protected forest). For the latter, we tested five spatial scales (1, 3, 5, 7 and 10 km radius) and selected the scale with the

TABLE 1 Parameter estimates (with SE and statistical significance) for the final generalized linear mixed effect models (GLMMs) of total species richness and richness of species of conservation concern, and the change in AIC (ΔAIC) when removing the variable from the model.

	Total species richness		Species of conservation concern	
	Estimate	ΔAIC	Estimate	ΔAIC
Intercept	3.61 (0.04)		−0.09 (0.23)	
Stand category[a]		36.4		100.9
41–80 years/clearcut	0.15 (0.06)		0.73 (0.29)	
81–120 years/selective	0.34 (0.06)		1.91 (0.26)	
Mean tree diameter	0.08 (0.03)	6.8	0.32 (0.10)	8.9
Proportion continuity forest within 3 km			0.23 (0.08)	6.7
Proportion continuity forest within 7 km	0.06 (0.02)	4.7		

Note: For model selection see Tables S1 and S2.

[a] Stand category has two parameter estimates as the production forest categories '41–80 years/clearcut' and '81–120 years/selective' are compared to the reference category '0–20 years/clearcut'.

best explanatory power (lowest AIC) for each response variable (Appendix SA1: Tables S1 and S2). We also analysed the Shannon diversity index, based on species abundance (number of occupied tree pairs), using the same model structure as described above but with a normal distribution. Pairwise comparisons between stand-age categories were performed using contrasts implemented through the 'glht function' from the R package multcomp (Bretz et al., 2010).

We used nonmetric multidimensional scaling (NMDS) to describe the general lichen species composition for the three stand-age categories. The analysis was performed on a species by stand matrix, including lichen frequency data (number of occurrences from the six tree pairs). The NMDS was performed with the R package vegan (Oksanen et al., 2013) using the Bray–Curtis dissimilarity measure and default settings (with 2 dimensions, stress = 0.12). Significant relationships between species composition and the explanatory variables (the same as the three described above) were assessed with multivariate ANOVA (function *adonis2* in R package vegan). For pairwise tests between age categories we used the function '*pairwise.adonis*'. We investigated the marginal effect of the variables (instead of the default sequentially test of terms, which is sensitive to the order of added variables). To illustrate relationships between the species composition and significant explanatory variables we used the function *envfit* (Oksanen et al., 2013).

To reveal species that contributed most to the differences in species composition between stands, we also performed an indicator species analysis (Dufrêne & Legendre, 1997) using the 'indval' function in R package labdsv.

3 | RESULTS

In total, we found 164 lichen species on 926 trees with an average number of 43.0 (min = 27, max = 67) per stand (Appendix ST1). Total species richness and richness of species of conservation concern increased with increasing stand age of the production forest (with significant differences between all stand categories; Figure 2). The average species richness per stand was 34.8 (SE = 1.02) for 0–40 year/clearcut, 45.3 (SE = 1.57) for 41–80 year/clearcut, and 54.8 (SE = 1.77) for 81–120 year/selective production forest. The corresponding richness of species of conservation concern was 0.8 (SE = 0.17), 2.4 (SE = 0.49), and 8.0 (SE = 1.17). Both total species richness and richness of species of conservation concern increased with mean tree diameter and the proportion of continuity forest in the surrounding landscape. For total species richness, the 7 km scale showed the best model fit (lowest AIC), even though the 5 and 10 km scales showed similar model fit (Appendix SA1: Table S1). The richness of species of conservation concern was best explained by the 3 km scale (Figure 2; Table 1; Table S2). The Shannon diversity index was explained by the same variables as total species richness (Table S3). A complete list of all recorded species is provided in Appendix ST1. Fifty-four trees were classified as 'legacy trees' with 91% of them found in the youngest age class (0–20 years) and having a mean diameter of 8 cm. There was no correlation between the number of legacy trees and the proportion continuity forest in the landscapes ($p > 0.6$).

When analysing each age category separately, both 0–40 year/clearcut and 41–80 year/clearcut stands showed a significant relationship with increasing proportion of continuity forest in the surrounding landscape ($p_{max} = 0.04$) for all three response variables described above, while 81–120 year/selective stands did not ($p_{min} = 0.38$) (Appendix SA1: Table S4).

The lichen species composition (Appendix SA1: Figure S3) was best explained by stand category, that is, age class, as judged by the highest R^2-value ($R^2 = 0.16$, $F = 9.8$, $p = 0.001$), but it was also explained by mean tree diameter ($R^2 = 0.03$, $F = 3.2$, $p = 0.019$) and the proportion of continuity forest within 7 km ($R^2 = 0.02$, $F = 2.3$, $p = 0.037$). All age classes differed significantly from each other according to the pairwise tests ($p < 0.004$).

According to the indicator species analysis, 18 species were associated with 0–40 year/clearcut stands, with the top three being

Lecanora pulicaris, *L. symmicta*, and *L. fuscescens* (Appendix ST1). Only 10 species were associated with stands 41–80 years/clearcut, with the top three being *Micarea contexta*, *Japewia gyrophorica*, and *Lecanora circumborealis*. A total of 52 species were associated with 81–120 years/selective, with the top three being *Arthothelium scandinavicum*, *Chaenotheca ferruginea* and *Cladonia digitata* (Appendix ST1). For the oldest stand category, 20 species had an Indicator value >0.5, compared to only six species in 0–40 year/clearcut stands and none in 41–80 year/clearcut stands. The legacy trees in age class 0–40 years hosted five species of conservation concern out of a total of 33 in all age classes.

4 | DISCUSSION

Our results show that the epiphytic lichen diversity of even-aged production forests is positively related to the proportion of remnant continuity forests in the landscape. The diversity of all species and species of conservation concern increased, and the species composition varied with the proportion of continuity forest in the landscape. Contrary to our expectations (Figure 1), we found no relationship to continuity forest for the oldest production forests. This indicates that these forests, despite being selectively logged and thinned, have retained species-rich lichen communities with a high number of species of onservation concern. Overall, our study shows that the mosaic of remnant continuity forests and even-aged production forests deserves increased attention in studies of biodiversity within the expanding production forest landscapes of the boreal biome.

We found support for our hypothesis that the species richness of the even-aged production forests (the '<80 years/clearcut' category) increases with the proportion of continuity forest in the landscape. (Figures 1 and 2). We assumed that since spruce trees establish from seeds or planted seedlings after clearcutting, epiphytes on the trees should represent new colonization with the continuity forest as an important propagule source. We found a slight deviation from this pattern as 'legacy trees' (small, slow-growing trees that survived clearcutting) in the youngest stands (0–40 years old) hosted a few species of conservation concern, a possible indication of survival from former stands. However, as this represented a very small proportion of all trees (6%) and of all species of conservation concern (15%), there is strong support for the dominant role of new, post-harvest colonization. Nevertheless, this result points to the importance of not removing small, slow-growing trees before harvest, which used to be the rule. Ideally, direct studies of the dispersal process, such as those based on molecular markers, should be performed to confirm our results. Such improved knowledge would also substantially contribute to a better understanding of the mechanisms behind species colonization, complementing inferences possible from correlative studies such as ours. However, such approaches remain rare (Eaton et al., 2018) and would be exceedingly difficult to apply to entire epiphytic lichen communities, in our case encompassing >160 species.

The species richness of the oldest production forests ('81–120 years/selective') was not associated with the landscape proportion of continuity forest. Although we expected a smaller effect than for the younger, even-aged forests, this result contradicted our hypothesis (Figure 1). A distinct feature of the old age class was also a much higher average number of species of conservation concern per stand compared with the younger forests, supporting the understanding that production forests with a long tree continuity promote lichen diversity (e.g. Allen et al., 2019; Ellis, 2012; Hämäläinen et al., 2020). Although the forestry company classified these forest stands as 81–120 years old, our results indicate that much older trees were present. During the selective harvesting and thinning events, some trees from before the era of large-scale logging were probably retained. A further important study would be to measure the ages of the trees and analyse possible relationships with lichen species diversity.

The assumed dispersal from continuity forest to production forest is consistent with the concept of spillover effects, that is, the impact of remnant habitats on transformed neighbouring areas (Blitzer et al., 2012). Our data also indicate the presence of additional propagule pools beyond spruce trees, as some species are only found on the smooth bark of the youngest trees, for example, *Biatora vacciniicola*, *Cetraria sepincola* and *Rinodina septentrionalis* (Appendix ST1), and have likely dispersed from other habitats, such as *Vaccinium myrtillus*, *Salix* shrubs and twigs of *Betula* spp. Interestingly, the strongest relationship for species of conservation concern with landscape amount of continuity forest was at 3 km, while for all species jointly 7 km was most important, supporting the often-stated claim that rare and declining species have poorer dispersal capability than common species (e.g. Baur, 2014). A shortcoming of our study, and in common with most studies on epiphyte ecology, is that our inventory was limited to the lower 2 m of the tree trunks (Appendix SA1). A distinct species composition further up on the tree stems and in the tree crowns has been manifested in other studies (e.g. Boch et al., 2013). Thus, our results might have differed if the entire trees had been assessed.

The 0–40 years/clearcut category stood out as distinct in species composition, likely explained by the more open character of these young forests compared to their older counterparts. Many species indicative of the youngest age class were common, such as generalist species with broad niches utilizing a variety of substrates, for example, *Biatora pallens*, *Hypogymnia tubolosa*, *Lecanora pulicaris* and *Melanohalea olivacea*. Nevertheless, 27% of all species of conservation concern were also found in this age class, compared to 58% in stands aged 41–80 years and 76% in stands aged 81–120 years. These results indicate that species of conservation concern, often considered to be more or less strictly associated with old-growth forests (SLU Artdatabanken, 2020), can colonize trees in even-aged production forests, especially in landscapes with a high proportion of forests with long tree continuity. Williams and Ellis (2018) found a similar pattern in a study on old-growth lichens, with several species found in a young forest stand adjacent to an ancient woodland. Still, as in our study, the abundance of these species was considerably lower than in the old forests (Appendix ST1).

The indicator species analysis revealed expected patterns regarding the association of red-listed species to the old, continuity production forests. One example is *Alectoria sarmentosa*, a pendulous lichen sensitive to wind disturbance and fragmentation (Esseen, 2019) having 65% of occurrences in the old forest and only 5% in the youngest stands. One exception was *Bryoria nadvornikiana*, a red-listed species which was most common in stands <80 years old (73% of occurrences; Appendix ST1). This finding agrees with another study in the same region (Rudolphi & Gustafsson, 2011) and demonstrates the importance of large-scale inventories that encompass the full range of age classes in production forests, as well as the need for an expanded knowledge base in the red-listing process. For *B. nadvornikiana*, further research is needed to assess its vitality in younger forests and also to investigate the abundance of the species in tree crowns of older production forest, a likely underestimated habitat for this light-demanding species.

Overall, our results highlight the importance of long forest continuity in promoting lichen diversity, which is in line with other studies (e.g. Dymytrova et al., 2018; Fritz et al., 2008; Marmor et al., 2011; Wiersma & McMullin, 2022). Proposed mechanisms include a long time-window for colonization and the development of microhabitats (McMullin & Wiersma, 2019) while microclimatic stability is a likely further important factor. Evidently, despite the impact from selective harvests and thinning, the '81–120 years/selective' category has legacy species from former natural forest landscapes. A way to disentangle the often discussed confounding factors of continuity and habitat availability (Janssen et al., 2019) would be to also record structural diversity in the production forests, and to include protected forests. Based on recent studies demonstrating the importance of structural diversity to biodiversity (e.g. Hekkala et al., 2023) a reasonable assumption would be that protected forests would provide best conditions for a rich biodiversity, due to their combination of long continuity and high structural diversity (Simonsson et al., 2016).

Our study is unusual in being conducted at a large spatial scale with many replicates (16 study areas sized 225 km^2). Observational landscape studies, such as our, commonly only include a few study areas often with one 'treatment' and one 'control', and even the most cited and influential landscape ecology studies lack replication (Wiersma, 2022). It is more common for landscapes to be delimited post-survey, around study sites, as for example has been done for conservation areas (e.g. Kärvemo et al., 2021), and special habitat types (e.g. Herrmann et al., 2005). Our 16 landscapes likely provide a good representation of the situation in boreal north Europe, a region characterized by the most intense and long-lasting clearcutting practices in the boreal biome, including overall homogeneity in forest management (Högberg et al., 2021). The low amount of never-clearcut forest remaining in this region implied that we could not find landscapes with a proportion of continuity forest >25%. Still, our results point to a clear and generalizable pattern for mosaics of even-aged production forests and continuity forests. Importantly, the situation may be different in landscapes in which selective harvest is the dominant harvesting practice, as is often the case in temperate forest regions. This silvicultural system creates continuous-cover forests, shown to have potential to support a rich biodiversity (Schall et al., 2018), although forests with unusually long continuity may still have a special role.

There is an evident scarcity of studies like ours that explore how biodiversity is partitioned across production forests with different ages and degrees of harvest impact. Our findings motivate further studies related to 'The natural forest hypothesis' (Duflot et al., 2022), which proposes that achieving a comprehensive representation of biodiversity at landscape scale in production forestry landscapes, requires interspersed, heterogeneous, unmanaged forests. The specialized habitat requirements, low dispersal capacities and limited recovery abilities of many lichens make them good representatives of biota sensitive to forestry interventions (Lõhmus & Lõhmus, 2019). Thus, although our study focused on a single taxonomic group, our conclusions are likely applicable to a larger array of forest-dependent biodiversity.

4.1 | Implications for forestry and conservation

The most important conclusion for practice is that remnant continuity forests can enrich the epiphytic lichen flora of even-aged coniferous forests of different ages by serving as important dispersal sources, and thus can enhance the epiphytic biodiversity of production forest landscapes. Further, these continuity forests are of interest in view of the newly passed EU Restoration Law (European Union, 2024), as potential nuclei of dispersal for restoration actions. An advantage of continuity forests are their widespread distribution across forest landscapes, in contrast to formally protected forests, which are fewer, much larger and less well connected. The never-clearcut production forests may also be relevant in relation to the EU Biodiversity Strategy for 2030 targeting strict protection of all remaining primary and old-growth forests within the union (European Commission, 2020, 2023). Boreal forest landscapes near Sweden's Scandes mountain range are on the short-list of candidates for this strategy ('the Scandinavian Green Belt'; Svensson et al., 2020). However, our results highlight that the remnant continuity production forests below the mountain range may also qualify for protection from a European perspective, owing to their long continuity and special species communities. Taken together, the last remaining continuity forests have a key role in supporting biodiversity in boreal production forest landscapes shaped by clearcutting.

Our study reflects a transient state of forest landscapes. If current forestry practices continue and if forest protection is not expanded, the remaining old production forests in Sweden will likely be logged within a few decades, confining continuity forests to protected areas (Ahlström et al., 2022). According to our study, this will be a drawback for the ambition to preserve biodiversity in the region. This advanced state of forest landscape transformation may be a template for future developments in other parts of the boreal region. For instance, in Canada, where much of the boreal biome is located, >70% of the productive forestland is already under management, with further expansion likely in the future (Venier et al., 2014).

AUTHOR CONTRIBUTIONS

Lena Gustafsson: Funding acquisition; conceptualization; methodology; project administration; resources and writing original draft. Jon Andersson: Methodology; software; validation; analysis and writing—review and editing. Fredrik Jonsson: Lichen inventory and determination and writing—review and editing. Mari Jönsson: Methodology; statistics and writing—review and editing. Mattias Jonsson: Funding acquisition; conceptualization; methodology and writing—review and editing. Ulrika Nordin: Lichen inventory and determination and writing—review and editing. Joachim Strengbom: Conceptualization; methodology and writing—review and editing. Victor Johansson: Conceptualization; methodology; statistics; data curation and writing original draft.

ACKNOWLEDGEMENTS

The study was supported by the Formas grant 2018-00577 to LG and MattJ. We are grateful to the SCA forestry company for making information on forest stands available for the study.

CONFLICT OF INTEREST STATEMENT

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

DATA AVAILABILITY STATEMENT

Data are available from Figshare https://doi.org/10.6084/m9.figshare.28979498.v1 (Gustafsson et al., 2025).

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SUPPORTING INFORMATION

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

Table S1: Comparison of candidate models explaining lichen species richness in production forests.

Table S2: Comparison of candidate models explaining richness of species of conservation concern in production forests.

Table S3: Parameter estimates (with SE and statistical significance) for the generalized linear mixed effect models (GLMMs) of the Shannon diversity index.

Table S4: Parameter estimates (with SE and statistical significance) for the generalized linear mixed effect models (GLMMs) of total species richness and richness of species of conservation.

Figure S1: Map of study area and sampling design.

Figure S2: The age categories used in the study.

Figure S3: Nonmetric multidimensional scaling (NMDS).

How to cite this article: Gustafsson, L., Andersson, J., Jonsson, F., Jönsson, M., Jonsson, M., Nordin, U., Strengbom, J., & Johansson, V. (2025). Remnant continuity forests are essential for sustaining epiphytic biodiversity in boreal production forest landscapes. *Journal of Applied Ecology*, *00*, 1–10. https://doi.org/10.1111/1365-2664.70090