

## RESEARCH ARTICLE

# Retention forestry can maintain epiphytic lichens on living pine trees, but provides impoverished habitat for deadwood-associated lichens

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## Abstract

1. Managing forests for timber yields reduces the amounts of old trees and deadwood, which has profound effects on species that are dependent on them. Retention forestry, where some trees are permanently left unharvested on clear-cut sites, may enable the formation of deadwood and old trees in managed forests, but it is unresolved how well these practices facilitate the occurrence of species in managed forests, especially in the long term.
2. We studied the capacity of tree retention practices to support the diversity of epiphytic lichens, a key group among threatened forest species. We compared lichen assemblages on retained trees in harvested sites to those on trees in unharvested control sites. The data were collected 21-year post-harvest and included living trees, snags (standing dead trees) and logs (fallen trees) of *Pinus sylvestris* (Scots pine).
3. Living trees, snags and logs each hosted distinct lichen communities. The highest lichen diversity was found on snags.
4. On living trees, species richness was similar in harvested and unharvested sites, but there was slight species turnover. In contrast, deadwood in unharvested sites hosted higher species richness and distinct species assemblages compared to deadwood in harvested sites. These differences were most pronounced on snags. Specifically, unharvested sites contained high-longevity snags (kelo trees), which hosted unique lichen communities with higher lichen richness than any other studied substrate, including the highest numbers of red-listed and deadwood-dependent species.
5. *Synthesis and applications.* Retention forestry can support lichen assemblages associated with living *Pinus sylvestris*. However, maintaining deadwood-associated lichen diversity through retention practices entails significant challenges. Deadwood-associated lichen diversity relies on high-longevity snags and is not sustained by the habitats provided in retention forestry. Biodiversity maintenance in forest management requires comprehensive provision of the habitat

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features of unmanaged forests, such as a qualitatively representative deadwood profile, which can prove difficult.

#### KEYWORDS

boreal forests, coarse woody debris, epixylic lichens, green-tree retention, kelo trees, *Pinus sylvestris*, red-listed species

## 1 | INTRODUCTION

The amount of old trees and deadwood has decreased significantly across managed forest landscapes (Bell et al., 2021; Dieler et al., 2017; Siitonen, 2001). As numerous species are dependent on old or dead trees, the loss of these features has led to a decline in forest biodiversity (Nirhamo, Pykälä, et al., 2023; Siitonen, 2001). During the 1990s, retention forestry was developed to counteract these negative effects on biodiversity (Franklin et al., 1997; Gustafsson et al., 2012). In retention forestry, a variable portion of trees is permanently left unharvested. Retained trees are allowed to grow old and eventually die, and thus can provide habitat to species dependent on old trees or deadwood (Großmann et al., 2023; Nirhamo, Hämäläinen, et al., 2023). Retention forestry has been adopted as a part of forest management in various regions (Gustafsson et al., 2012), which has led to increased structural diversity in managed forests (Kruys et al., 2013; Kvaschenko et al., 2022). It has been identified as a promising approach for combining biodiversity conservation with production forestry (Fedrowitz et al., 2014; Mori & Kitagawa, 2014). However, its long-term effectiveness in maintaining the biodiversity of various taxa remains deficiently known.

In Fennoscandian natural pine forests, *Pinus sylvestris* (Scots pine) trees exceeding hundreds of years in age are common (Kuuluvainen et al., 2002). A notable feature of natural pine forests is the presence of kelo trees: silver-coloured pine snags (standing dead trees) that remain standing for exceptionally long periods after their death (Kuuluvainen et al., 2017; Niemelä et al., 2002). Their longevity commonly exceeds 100 years, with maximal longevity of several centuries (Rouvinen et al., 2002). In natural forests, kelo trees may constitute about 10% of total basal area, and their occurrence is characterized by spatiotemporal continuity (Kuuluvainen et al., 2017). Replicating these structures in production forests is, evidently, a great challenge. Indeed, the snag dynamics of natural pine forests appear not to be replicated in managed forests, where snag longevity is limited to about 50 years (Mäkinen et al., 2006; Nirhamo, Hämäläinen, et al., 2023). Thus, the capacity of retention forestry to maintain the species assemblages of unmanaged pine forests should be scrutinized.

Epiphytic lichens include a high number of threatened species according to the IUCN red list criteria in the Nordic countries (e.g. Pykälä et al., 2019), primarily due to habitat loss and degradation caused by forest management. Similar conservation issues exist also, for example, in North America (Allen et al., 2019). Threatened

epiphytic lichens are associated with specific habitat features (i.e. old trees and dead trees; Nirhamo, Pykälä, et al., 2023) whose formation in managed forests could be enabled with retention forestry. Most epiphytic lichens grow on the bark of living trees, but 11% of epiphytic lichen species in Fennoscandia are restricted to deadwood, and another 31% utilize deadwood to a varying extent (Spribille et al., 2008). In Finland, *Pinus sylvestris* is a host species of minor importance for threatened lichen species on living trees, but it is the most important host species for threatened lichens occurring on deadwood (Nirhamo, Pykälä, et al., 2023). Particularly, kelo trees have been shown to have special importance for lichen diversity (Larsson Ekström et al., 2023; Santaniello et al., 2017).

Timber harvests directly impact epiphytic lichens by removing their substrates, an effect that can be mitigated with tree retention. However, clearcutting causes significant changes in environmental conditions in the surroundings of retained trees by increasing light and lowering humidity (Chen et al., 1993). This can lead to distinct changes in lichen communities on retention trees, such as increased species richness linked to higher light availability (Löhmus & Löhmus, 2010; Lundström et al., 2013; Ranlund et al., 2018). While lichens on living retention trees have been studied extensively in the short to intermediate term, research on lichens on deadwood in the context of retention forestry is scarce. Previous studies have reported rather low lichen diversity on deadwood in retention sites (Hämäläinen et al., 2014, 2021; Runnel et al., 2013). However, longer term studies and especially qualitative comparisons of deadwood originating from retention trees and deadwood in unharvested sites are lacking. Furthermore, the significance of the amount of retained trees has received little attention.

In this study, we assessed epiphytic lichen assemblages on *Pinus sylvestris* trunks that were retained in clear-cuts. We surveyed lichens on the bark of living trees and the exposed wood of dead trees 21 years after harvests in harvested sites and unharvested control sites. The harvested sites represented two retention levels: 10 and 50 m<sup>3</sup>/ha. All studied trees in the harvested sites were alive at the time of harvest, but many died shortly thereafter (Nirhamo, Hämäläinen, et al., 2023). Specifically, we aimed at resolving the following questions: (1) Are habitats provided by retained trees, including living trees and trees that died after their retention, able to support the lichen diversity found on living trees, snags and logs of *P. sylvestris* in unharvested sites? (2) How do different types (living trees, snags and logs) of *P. sylvestris* trunks differ in lichen diversity? (3) What is the role of retention level in maintaining lichen diversity?

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and experimental design

Fieldwork was conducted in eastern Finland. The approximate location of the study sites was 63.2°N 30.7°E, in the transition zone between southern and middle boreal vegetation zones, at the altitude of 150–200 m. The data were collected from nine forest stands, where the following treatments were implemented, each with three replicates: (1) clear-cut sites with a retention level of 10 m<sup>3</sup>/ha (about 3.5% of preharvest volume), designated as 10H; (2) clear-cut sites with a retention level of 50 m<sup>3</sup>/ha (about 17% of preharvest volume), designated as 50H; and (3) unharvested (i.e. control) sites, designated as UH. The 10H and 50H sites are collectively referred to as 'harvested' throughout this study. The harvested sites each constituted a single forest stand of about 3–5 ha. The unharvested sites were located within larger areas of contiguous forest inside a protected area. The harvests were carried out in 2001. Most of the retained trees were aggregated in groups, but about 10% were retained as solitary, dispersed trees. The groups in 10H sites consisted of approximately 15–25 trees (200–300 m<sup>2</sup>), while the groups in 50H sites had around 25–40 trees (300–500 m<sup>2</sup>).

Before the experimental treatments, sites with similar stand structure and management history were sought, and the treatments were randomly assigned to these stands, aside from the unharvested treatments which were represented by sites within a large protected area. By selecting stands with similar structure and history, we minimized between-site variation in tree-level factors that are impactful to epiphytes, such as tree size and tree age. Before the treatments, in all study sites, dominant trees were approximately 150 years old. The sites were sub-xeric and dominated by *Pinus sylvestris*. *Picea abies* was abundant in the understorey, and the stands contained scattered deciduous trees (mainly *Betula* spp.). The study sites had management histories typical for semi-natural stands of the region (Uotila et al., 2002), as they had been subject to selective loggings in the late 19th and early 20th century. Permits to establish the field experiment and to conduct other fieldwork were granted by the landowner, Metsähallitus, that is, the governance body of state-owned forests in Finland.

### 2.2 | Sampling design and tree selection

We surveyed lichens and non-lichenized calicioid fungi on *Pinus sylvestris* trees, including living trees, snags and logs, in 2022 and 2023, that is, 21–22 years after the treatments. We first conducted a standardized survey, followed by additional surveys to achieve a sufficient sample of living trees, snags and logs in all treatments. In the standardized survey, the proportions of living trees, snags and logs among the selected study trees matched their proportions among all trees in each study site. Furthermore, the surveying effort at each site reflected the number of trees remaining there post-treatment.

For a thorough description of the standardized survey, see Nirhamo et al. (2024a), where an identical sampling design was applied.

The standardized survey yielded insufficient sample sizes of some tree types for statistical analyses. Therefore, we increased the sampling effort to include a minimum of 25 study trees of each tree type per treatment. In the harvested sites, we continued the random selection of trees with the same method as in the standardized survey (see Nirhamo et al., 2024a). The 10H sites contained a total of only 19 and 20 snags and logs, respectively, all of which were surveyed. In each of the unharvested sites, we established a transect that was perpendicular to the tangent of the circle (i.e. on the normal to the circle) from which the initial set of study trees was selected (see Nirhamo et al., 2024a). The direction of the transect was selected randomly, but directions where the transect was intercepted by a road, a lake or a peatland within 100 m were excluded. We selected any snags or logs (no additional living trees were required from the unharvested sites) within 10 m on either side of the transect to be study trees. We continued along the transect until the required number of trees was surveyed. An equal number of trees from each study site with a given treatment were included in the additional set of study trees.

The unharvested sites contained, albeit in low densities, old standing deadwood (kelo trees; Niemelä et al., 2002; Kuuluvainen et al., 2017), that are known to host unique lichen communities (Santaniello et al., 2017). With the standardized survey method described above, only very few such trees were included. Thus, we surveyed a complementary sample of kelo trees to gain a more complete view of the lichen assemblages in the unharvested sites. Kelo trees were sought for in the areas where the standardized surveys of the unharvested sites were conducted, as well as in their immediate vicinity in forest areas contiguous to where the unharvested study sites were located. We considered as a kelo tree any standing dead *P. sylvestris* trunk that (1) was fully decorticated, (2) had at least one fire scar and (3) had a worn out, silvery surface. The first 30 trunks that filled these criteria that we encountered were included in the kelo sample, and all trees considered as kelo trees were excluded from the standardized survey.

### 2.3 | Lichen inventory

We recorded the occurrence of all lichens on the lowest 2 m of each sampled tree. On upright trees (living trees and snags), this was because the higher portions of the trees were out of reach. On fallen logs, a similar limitation was applied to maintain comparability between tree types. Living and dead trees are differentiated as substrates for epiphytes especially when dead trees have lost their bark, since bark and exposed wood are inhabited by partially different lichen assemblages (Löhmus & Löhmus, 2001; Spribille et al., 2008). Consequently, on living trees, we recorded only lichens on bark. Similarly, on dead trees, only lichens on exposed wood were recorded. This procedure aimed to eliminate the presence of exposed wood in living trees or remnant bark on dead trees as a confounding

factor. Exposed wood (e.g. in fire scars and other wounds) was very rare on the surveyed living trees. Likewise, remnant bark was very scarce in the surveyed living trees. Likewise, remnant bark was very scarce in the surveyed snags. Remnant bark was more frequent on logs, and thus, on logs, the survey was performed on the lowest 2-m fraction where bark had stripped off. Trees that were dead but had their bark fully or mostly intact were not surveyed. Microscopy and chemical spot tests were used to identify lichen specimens when necessary. Lichen nomenclature followed Pykälä et al. (2023).

There was probably some level of variation in surveyed area per tree due to variation in tree sizes and in the extent of remnant bark on dead trees. Although we did not record surveyed area per tree and are thus not able to exactly quantify this variation, we assume that the variation of surveyed area between trees representing different treatments was low. We consider this assumption justified because the study sites had similar stand structure, including tree size distribution, prior to the treatments, which suggests that the size of the surveyed trees should not differ drastically between the study treatments. In addition, according to our field observations, variation in the amount of remnant bark on dead trees was low: The surveyed dead trees had generally undergone rapid decortication and had very little remnant bark across all treatments, and we excluded all dead trees with high proportion of intact bark.

Red list classifications of lichens followed the Finnish Red List (Pykälä et al., 2019). Species classified as data deficient (DD) were not included in the analyses regarding red-listed species. Classifications of deadwood-dependent species followed Spribille et al. (2008). However, a large share of the occurrences of *Cladonia bacilliformis*, *Cladonia macilenta* and *Xylopsora friesii* were on living trees, and therefore, they were not classified as deadwood dependent as a deviation from Spribille et al. (2008).

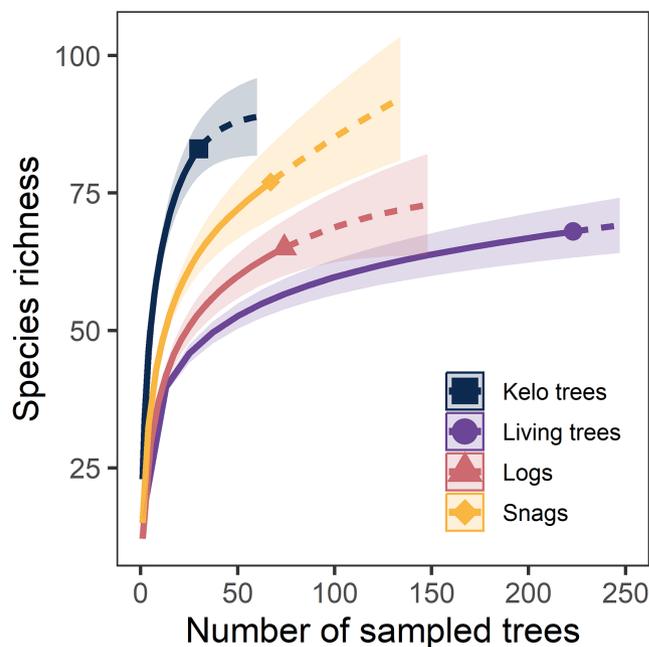
## 2.4 | Statistical analyses

All statistical analyses were performed in R version 4.2.2. We explored patterns in  $\gamma$ -diversity with sample-based rarefaction. We considered individual study trees as samples. The rarefaction analyses, including both interpolated and extrapolated rarefaction, were performed using the function *iNEXT* in the package *iNEXT* (Hsieh et al., 2016). Rarefaction was used to compare  $\gamma$ -diversity on different tree types, and on all trees, living trees, snags and logs in different treatments.

To illustrate the differences in tree-level lichen community composition between tree types and between harvested and unharvested sites, we applied non-metric multidimensional scaling (NMDS) using the Sørensen index. This analysis was done with the function *metaMDS* in the package *vegan* (Oksanen et al., 2022).

## 3 | RESULTS

We surveyed a total of 396 *Pinus sylvestris* trees, consisting of 223 living trees, 99 snags (including 30 kelo trees) and 74 logs. On these trees, we recorded a total of 111 lichen species, including

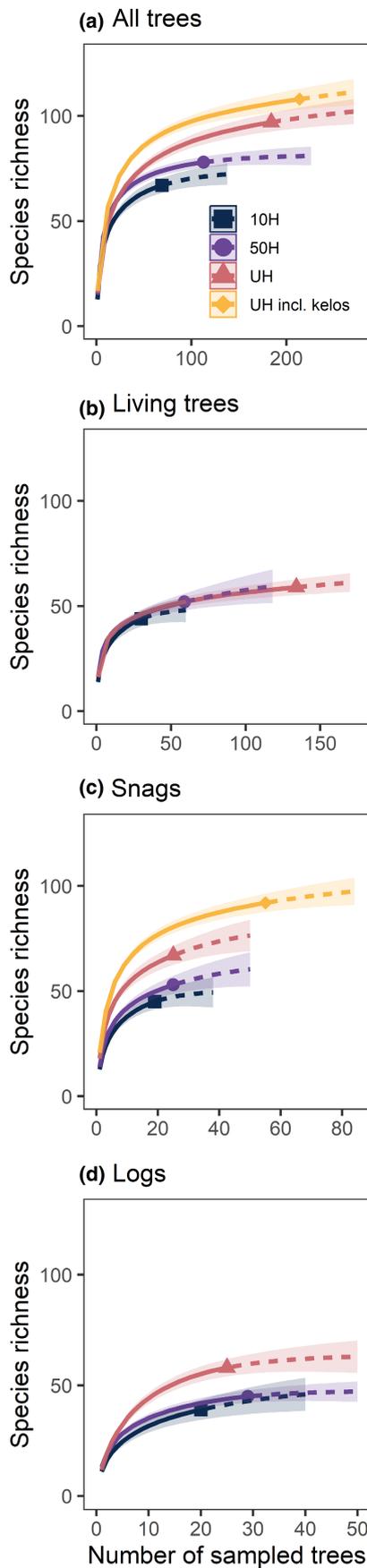


**FIGURE 1** Rarefaction curves (with 90% CI) showing the accumulation of lichen species, that is,  $\gamma$ -diversity, on living trees, snags, kelo trees and logs relative to the number of sampled trees based on our sample. The intact lines indicate interpolated rarefaction, and the dashed lines indicate extrapolated rarefaction.

24 red-listed species (see Appendix S1 in Supporting Information). Nearly all species, 106 in total, were recorded on dead trees: 96 species on snags (including kelo trees) and 63 on logs. In contrast, 67 species were recorded on living trees. As such, even after accounting for differences in sample sizes, snags hosted the highest and living trees the lowest  $\gamma$ -diversity of lichens (Figure 1).

Total lichen species richness ( $\gamma$ -diversity) was higher in the unharvested than in the harvested stands (Figure 2a). Specifically, snags (Figure 2c) and logs (Figure 2d) in the unharvested sites hosted considerably higher  $\gamma$ -diversity than those in harvested sites, while  $\gamma$ -diversity on living trees was similar across treatments (Figure 2b). When the kelo trees of the unharvested stands were included in the sample, the difference in  $\gamma$ -diversity between unharvested and harvested sites was larger (Figure 2a,c). The 10H sites had slightly lower  $\gamma$ -diversity than the 50H sites (Figure 2a). All patterns described above hold true also for red-listed and deadwood-dependent species (see Appendix S2).

Tree-level lichen richness ( $\alpha$ -diversity) on living trees was equal in unharvested and 50H sites, but slightly lower in 10H sites (Figure 3A). For snags,  $\alpha$ -diversity was higher in unharvested sites compared to harvested sites (Figure 3B). In particular, kelo trees in the unharvested sites hosted higher  $\alpha$ -diversity than other types of snags. There were no differences in  $\alpha$ -diversity on logs between treatments (Figure 3C). The  $\alpha$ -diversity of red-listed species on living trees was similar in the unharvested and harvested sites (Figure 3D). The  $\alpha$ -diversity of red-listed and deadwood-dependent species was higher on kelo trees than on the snags in the harvested sites (Figure 3E,G). Additionally, compared to the logs in the



**FIGURE 2** Rarefaction curves (with 90% CI) showing the accumulation of lichen species, that is,  $\gamma$ -diversity, in 10H, 50H and unharvested sites on (a) all trees, (b) living trees, (c) snags and (d) logs relative to the number of sampled trees based on our sample. In unharvested sites, rarefaction curves were generated separately with and without kelo trees being included in the sample. The intact lines indicate interpolated and the dashed lines indicate extrapolated rarefaction.

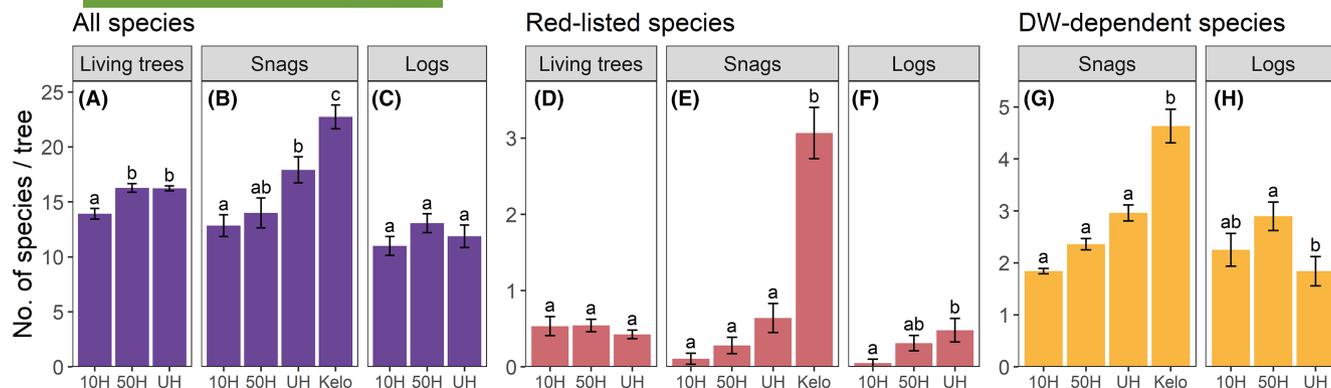
unharvested sites, the logs on the 10H sites hosted fewer red-listed species (Figure 3F), while the logs in the 50H sites hosted more deadwood-dependent species (Figure 3H). When comparing tree types, kelo trees had the highest overall  $\alpha$ -diversity, as well as the highest numbers of red-listed species and deadwood-dependent species (Figure 3B,E,G). Excluding kelo trees,  $\alpha$ -diversity was similar on living trees and snags, but lower on logs.

Lichen communities on living trees, snags and logs each formed distinct clusters in the ordination space (Figure 4). Snags formed two distinct clusters, with one primarily consisting of kelo trees, and the other mainly comprising snags in harvested sites. Non-kelo snags in the unharvested sites occurred in both clusters, but most were located in the cluster dominated by snags in harvested sites. Lichen communities on living trees in harvested and unharvested sites formed their own clusters that partially overlapped, indicating relatively small but consistent differences in lichen community composition. The differences in community composition on logs between harvested and unharvested sites were smaller. However, logs in the unharvested sites had higher  $\beta$ -diversity than those in the harvested sites, while  $\beta$ -diversity on living trees and snags was similar in harvested and unharvested sites (see Appendix S3).  $\beta$ -diversity was low on living trees compared to snags and logs. Additionally, if the kelo trees were taken into consideration,  $\beta$ -diversity was higher on snags than on logs.

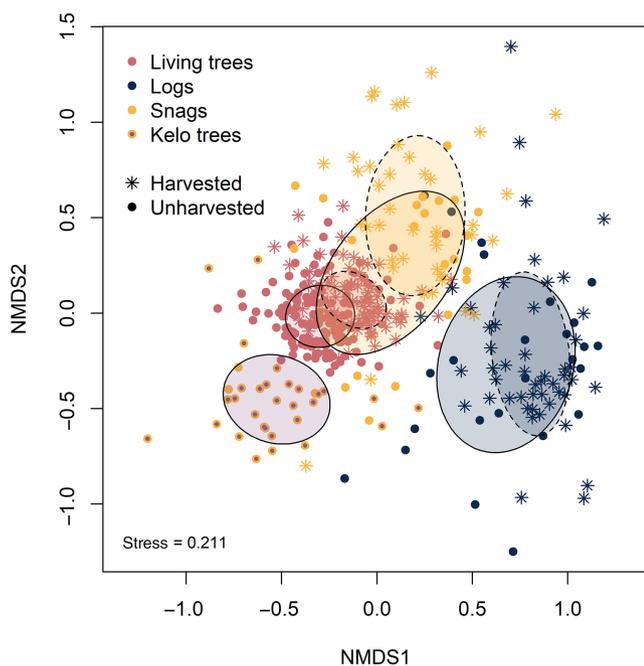
An analysis of species–sites associations revealed that on living trees, harvested and unharvested sites both had eight associated species (see Appendix S4). On snags, 26 species were associated with unharvested sites, with 21 species specifically connected to kelo trees, and none with harvested sites. On logs, there were no species associated with either harvested or unharvested sites.

## 4 | DISCUSSION

The main findings of this study were (1) The deadwood formed from retention trees that were alive at the time of harvest but died soon thereafter does not provide habitat for many deadwood-associated lichens, primarily due to the absence of high-longevity standing deadwood. (2) Lichen communities on living *Pinus sylvestris*, while having relatively low  $\gamma$ -diversity, can be maintained with retention forestry even over longer time scales, although with some changes in community composition. (3) On *P. sylvestris*, lichen diversity, particularly that of species of conservation concern, is mainly associated



**FIGURE 3** Tree-level species richness ( $\alpha$ -diversity)  $\pm$  SE of all lichen species (A–C) red-listed species (D–F) and deadwood-dependent species (G, H) on living trees (A, D), snags (B, E, G) and logs (C, F, H). Tukey's tests, as expressed by the letters, were performed to assess the statistical significance of the differences in species richness between treatment categories within tree types.



**FIGURE 4** The arrangement of the lichen communities on 396 study trees in the ordination space based on the first two dimensions of the nonmetric multidimensional scaling (NMDS). The ellipses illustrate the standard deviation from the centroid of a given group of points, that is, trees of a certain type in a certain treatment. The colours of the ellipses refer to tree types correspondingly as in the legend. The ellipses with intact borders refer to unharvested sites, and the ellipses with dashed borders refer to harvested sites.

with high-longevity snags (kelo trees) rather than with living trees or logs.

#### 4.1 | Comparison of living trees, snags and logs

Living trees, snags and logs each hosted different lichen communities, with snags supporting the highest diversity. The most important

factor in differentiating snags and logs as substrates for lichens is most likely their moisture content, which is higher in logs (Yatskov et al., 2022). The higher moisture of logs causes them to decay at a higher rate (Yatskov et al., 2022), and advancing decay significantly alters substrate properties, which is reflected in changing lichen composition and eventual outcompetition of lichens by bryophytes as decay proceeds (Dittrich et al., 2014; Santaniello et al., 2017). Several previous studies have also noted higher lichen diversity on snags than on logs (Dittrich et al., 2014; Runnel et al., 2013; Santaniello et al., 2017; Wagner et al., 2014). It is possible that the average surveyed area differed between some of the tree types (see Section 2.3), but we are confident that these differences were so small that their influence on the results was negligible.

Overall, deadwood-utilizing species are in the minority among epiphytic lichens (Spribile et al., 2008). Still, we observed higher lichen diversity on deadwood than on living trees. We presume, however, that since *P. sylvestris* has important attributes that are advantageous for the formation of diverse lignicolous lichen communities, namely rapid decortication (Löhmus & Löhmus, 2001) and high snag longevity (Rouvinen et al., 2002; Rouvinen & Kouki, 2002), this pattern is probably seen rarely on other tree species that do not have these attributes. On living *P. sylvestris*, tree-level species richness ( $\alpha$ -diversity) can be comparable to other tree species that occur in boreal Europe (Kuusinen, 1996), but we observed low compositional variance ( $\beta$ -diversity), possibly because of low variation in bark properties between *P. sylvestris* trunks. As such,  $\gamma$ -diversity was low on living *P. sylvestris* compared to snags and logs. We conclude that *P. sylvestris* is a tree species with relatively low lichen diversity on bark, but high lichen diversity on deadwood, especially on standing deadwood.

Only the lowest parts of tree trunks are easily accessible for epiphyte inventory, which causes a common issue of undersampling in epiphyte studies (Marmor et al., 2013). On upright trees, there is a gradient along the length of the trunk in the level of exposure. Notably, this gradient is less prevalent on retention trees in harvested sites. Living trees also contain a vertical gradient in bark age, and consequently, in bark properties. The upper canopy of *P. sylvestris*

may include thick branches that provide horizontal substrates that may host different assemblages than the vertical surfaces on the trunk. On logs, there is likely to be within-tree variation in how far decay has advanced. Thus, surveying only the lowest part of the trunk can lead to a significant underestimation of the  $\alpha$ -diversity of entire trees (Marmor et al., 2013) on living trees, snags, as well as logs. It is difficult to evaluate whether the extent of underestimation varies between the tree types. The underestimation of  $\gamma$ -diversity is probably much lower.

#### 4.2 | Lichens on living retention trees

We found no differences in species richness on living trees between harvested and unharvested sites. Some previous studies have reported increased species richness on retention trees following harvests, linked to increased light availability (Löhmus & Löhmus, 2010; Lundström et al., 2013; Ranlund et al., 2018). These studies represent mesic sites, with assumably denser preharvest stand structures than in the sub-xeric pine-dominated sites of our study. Thus, it is likely that, in our study sites, the microclimatic changes inflicted by clearcutting were smaller and less impactful to epiphytes. Moreover, lichens associated with late-successional tree species (e.g. *Picea abies*) may more often be shade-adapted and thus intolerant of open conditions, making them more sensitive to canopy removal than lichens associated with early-successional tree species such as *P. sylvestris* (Ranlund et al., 2018). The magnitude of the community change of epiphytes on retained trees can be expected to be connected to preharvest site conditions, so that in drier and more open stands, where harvest leads to smaller changes in microclimate, the magnitude of change in epiphyte communities is smaller.

Although there were no differences in species richness on living trees, we observed some degree of species turnover between harvested and unharvested sites. Eight species were less frequent on retention trees (see Appendix S4). Most of these species are probably not sensitive to microclimatic changes, and therefore, the reasons for their poor performance on retention trees are difficult to pinpoint. These species include several species (e.g. *Micarea melanea*, *Xylopsora friesii*, *Chaenotheca ferruginea*) that were recently shown to be sensitive also to prescribed fires (Nirhamo et al., 2024a), which suggests that these species could possibly function as indicators of undisturbed pine forests. Additionally, another eight species were more frequent on retention trees. These were mainly species that are likely to have been favoured by open conditions (e.g. *Imshaugia aleurites*, *Bryoria* spp.).

#### 4.3 | Lichens on dead retention trees

Our results show that the deadwood originated from retained trees that died soon after harvests did not support the deadwood-associated lichen diversity that is found in unharvested forests. The

loss of deadwood-associated biodiversity is often linked to reductions of deadwood quantity (Parajuli & Markwith, 2023). However, our results originate from differences in deadwood quality. Lichen richness on snags has been shown to increase with time since the death of the tree (Saine et al., 2018; Santaniello et al., 2017). The snags in the harvested sites had died 21 years prior at most. Dead stems of *P. sylvestris* may remain standing for at least up to 250 years in the study region (Rouvinen et al., 2002), and although exact data are missing, this range was undoubtedly represented much more comprehensively in the unharvested sites. This was amplified by the kelo trees, which represented the highest snag longevities in this study and hosted the highest lichen diversity. The kelo trees were larger on average than other trees surveyed in this study, which potentially had a positive effect on lichen richness. However, time since tree death has an overwhelmingly strong effect on lichen richness on the exposed wood of snags compared to the effect of their size (A. Nirhamo, unpublished data), and thus, we consider the higher richness on kelo trees to have been caused predominantly by their higher longevity. We conclude that the dead trees in the harvested sites had lower lichen  $\gamma$ -diversity because of lower deadwood heterogeneity and lower  $\alpha$ -diversity on snags because of lower snag longevity.

Lacklustre success in providing habitat for deadwood-associated lichens with management practices that increase deadwood amounts has been previously reported (Hämäläinen et al., 2021; Larsson Ekström et al., 2023; Runnel et al., 2013). Evidently, the reason for this is that many deadwood-associated lichens require standing deadwood with a longevity of several decades, or even over a century (Santaniello et al., 2017). Yet, both the present and the previous studies have studied restored deadwood with longevities of only up to a couple of decades. However, this is unlikely to be resolved merely with longer time frames, since it appears that pine snags do not attain similar longevity in managed forests as they do in natural forests: Only up to about 50 years in managed forests (Mäkinen et al., 2006; Nirhamo, Hämäläinen, et al., 2023), and commonly over 100 years, with a maximum of hundreds of years, in natural forests (Niemi et al., 2002; Rouvinen et al., 2002; Rouvinen & Kouki, 2002). Therefore, it seems that snags in managed forests do not provide habitat to many lichen species because of their limited longevity. A possible cause for the differences in snag longevity is the lower heartwood content of the younger trees in managed forests (as discussed by Mäkinen et al., 2006), while also the role of past forest fires in having built decay resistance in surviving trees has been suggested (Kuuluvainen et al., 2017; Niemelä et al., 2002). Investigating the enablers of high snag longevity would be highly relevant for the development of management practices that promote high-longevity snags.

Deadwood that is present in preharvest forests is recommended to be retained during harvests (Kruys et al., 2013). Our study did not include such deadwood. Retaining preharvest deadwood can increase the heterogeneity of deadwood in post-harvest sites, and thus presumably leads to higher lichen diversity. Lichens on retained

preharvest deadwood seem to be resilient to changes in exposure inflicted by clearcutting, at least in pine forests (Larsson Ekström et al., 2023). Still, the retention of preharvest deadwood does not circumvent the issue of high-longevity snags not being formed in managed forests.

#### 4.4 | The significance of the retention level

Many of our analyses indicated lower lichen species richness on the retained trees in the 10H sites than on those in the 50H sites. This would suggest that the trees in the 50H sites provided habitats of slightly higher quality than in the 10H sites. However, these differences were small and rarely statistically significant, and thus, we do not consider retention level to have affected habitat quality for lichen communities at the scale of individual trees.

Retention level is more clearly connected to habitat quantity. The rarefaction analyses indicated that a rather high number of trees is required before lichen species richness reaches an asymptote. Thus, when trees to be retained are selected randomly, a rather large number of retention trees is required before populations of species with low frequency (e.g. red-listed species) are secured. Second, low numbers of retention trees may be unable to uphold population dynamics of epiphytes over long time frames (e.g. Johansson et al., 2013). Third, due to the mortality rates of living retained trees, and the fall rates of snags (Nirhamo, Hämäläinen, et al., 2023), only a fraction of retention trees fulfil their maximum potential in providing long-lasting substrates that many lichen species require (Nirhamo, Pykälä, et al., 2023; Santaniello et al., 2017). Because of these reasons, low retention levels (such as those applied in Fennoscandia; Kuuluvainen et al., 2019) are very likely to limit the effectiveness of retention forestry in maintaining epiphytic lichen diversity.

#### 4.5 | Implications for management

We showed that snags, especially those of high longevity, are crucial for epiphytic lichen diversity in Fennoscandian sub-xeric pine-dominated forests. This implies that when the conservation value of pine-dominated sites is assessed, the presence of high-longevity snags is a key factor. Such snags are absent from managed forests, and for now, it seems that retention practices do not enable their formation either (Nirhamo, Hämäläinen, et al., 2023). Therefore, lichen diversity associated with snags is not fully sustained in managed forests and its conservation is dependent on strictly protected sites. Our study indicates that lichen assemblages on living *P. sylvestris* can be maintained with retention practices, but since living *P. sylvestris* hosted relatively low lichen diversity, the provision of suitable deadwood habitats should be prioritized in the conservation of Fennoscandian pine forests.

Based on our results, we give the following recommendations to facilitate the maintenance of biodiversity in managed forests:

1. Qualitative variation of deadwood is critical for species diversity and should be upheld. Our study exemplified that the lack of high-longevity snags reduced lichen diversity in managed Fennoscandian pine forests.
2. Retention trees should be selected carefully. In forests represented by our study system, the retention of old deadwood, especially kelo trees, and old living trees with the potential to form kelo trees in the future (e.g. large trees with fire scars) should be prioritized. Other forest biomes may be expected to contain comparable specific habitat features that are highly important for maintaining biodiversity.
3. We encourage to apply higher retention levels, for example, compared to what is currently applied in Fennoscandia. Higher retention levels are more likely to secure infrequently occurring species, maintain larger epiphyte population sizes and facilitate better long-term continuity and higher qualitative variation of deadwood (Nirhamo, Hämäläinen, et al., 2023).

Although studies on lichens on retention trees remain scarce outside of northern Europe, it is likely that the impacts of retention forestry on epiphytic lichens in pine forests and other xeric forests around the world (e.g. Sevgi et al., 2019; Wagner et al., 2014) would resemble what we observed here. This expectation is based on the assumed functional similarity of lichen assemblages and a similar magnitude of change in environmental conditions induced by harvesting across xeric or pine-dominated forests in different regions. However, forests in other regions may have distinctly lower snag longevity compared to Fennoscandian pine forests (Grayson et al., 2019; Onodera & Tokuda, 2015), which is expected to lead to a deviation from the patterns we observed here. Regarding lichens on snags, similar patterns as what we observed could emerge in regions where tree species that produce snags with extended longevity are present (e.g. Daniels et al., 1997; Everett et al., 1999; Goward & Arsenault, 2018). Our study demonstrates that biodiversity maintenance in forest management requires comprehensive provision of the habitat features of unmanaged forest ecosystems such as, for example, a qualitatively representative deadwood profile. Combining commercial management with the provision of critical old-growth habitat features can prove difficult.

#### AUTHOR CONTRIBUTIONS

Jari Kouki designed the field experiment. Aleksi Nirhamo, Aino Hämäläinen and Jari Kouki planned the study and the sampling design. Aleksi Nirhamo collected and analysed the data and led the writing of the manuscript. Karoliina Hämäläinen collected supportive data. All authors contributed to the writing of the manuscript and gave their final approval for publication.

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### CONFLICT OF INTEREST STATEMENT

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

### DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.q2bvq83v0> (Nirhamo et al., 2024b).

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## SUPPORTING INFORMATION

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

**Appendix S1.** A list of the species observed in this study.

**Appendix S2.** Sample-based rarefaction curves for red-listed species and deadwood-dependent species.

**Appendix S3.** Analysis of differences in  $\beta$ -diversity, both between tree types and between treatments within tree types.

**Appendix S4.** Analysis of the associations between species treatments.

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