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Epiphytic lichen diversity in pine-dominated boreal forests: community dynamics in relation to snag dynamics and disturbances

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Academic dissertation

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ABSTRACT

In my thesis I studied the diversity patterns of epiphytic lichens on dead and living Scots pines (*Pinus sylvestris*) in boreal Europe. My main intent was to address how epiphyte diversity is affected by forest dynamics, namely snag dynamics and disturbances. I surveyed lichens in near-natural forests and in experimental sites where forest dynamics had been emulated in forest management. A 275-year chronosequence showed that time since tree death is a primary determinant of alpha and beta diversity patterns of lignicolous lichens on standing deadwood. Snags that have been dead for at least 90 years are crucial for lignicolous lichen diversity. However, modeling snag fall rates in managed forests, specifically snags originating from trees retained during final harvests, revealed that maximal snag longevity in managed forests is 50 years. Thus, deadwood restoration faces two challenges. First, it takes several decades or even a century until restored (standing) deadwood hosts high lichen diversity. Accordingly, I found relatively low lichen diversity on restored deadwood when 20 years had passed since restoration. Second, restoration may fail to facilitate the formation of high-longevity snags. Inventories of lichens on living retained trees showed that residual structures may uphold lichen diversity in post-disturbance sites. High-severity fires changed habitat structure significantly by removing previously available substrates through tree mortality. However, they also produced new substrates in the form of deadwood, and thus the species richness of epiphytic lichens was only slightly reduced. Still, the freshly formed and homogeneous deadwood hosted relatively low lichen diversity. Low-severity fires had similar effects on community composition as high-severity fires, but smaller in magnitude. The emulation of natural dynamics should be effective in improving the epiphyte diversity of managed forests. The availability of heterogeneous substrates, but particularly old trees (or “old” deadwood, i.e., high-longevity snags), should be a focus.

Keywords: ecological restoration, kelo trees, old-growth forests, retention forestry, prescribed burning

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Many other people have also supported me in my career so far. I want to especially thank Jenna Purhonen and Kaisa Junninen for employing me after my MSc graduation.

My collaborators Pemelyn Santos, Mariina Günther and Karoliina Hämäläinen made huge efforts to collect and analyse data and organize field work that made my life so much easier. I am extremely grateful to them.

Lastly, I want to thank my friends and family for supporting and tolerating me. Most of all I want to thank my partner Nenna.

Jyväskylä, May 2025
Aleksi Nirhamo

"*I could not help laughing at this odd little man; for it was not the beautiful blossoms, such as you delight to paint, that drew forth these exclamations, but the queer little plants which he had rummaged for at the roots of old trees, among the moss and long grass. He sat upon a decayed trunk, which lay in our path, I do believe for a long hour, making an oration over some greyish things, spotted with red, that grew upon it, which looked more like mould than plants, declaring himself repaid for all the trouble and expense he had been at, if it were only to obtain a sight of them. I gathered him a beautiful blossom of the lady's slipper, but he pushed it back when I presented it to him, saying "Yes, yes; 'tis very fine. I have seen that often before; but these lichens are splendid."* –Diary of Susanna Moodie (1803–1885)

LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following articles referred to in the text by their Roman numerals I–IV:

I Nirhamo A, Santos P, Günther M, Kouki J, Aakala T (2025) Time since tree death determines the diversity patterns of lignicolous lichens on standing deadwood. Manuscript.

II Nirhamo A, Hämäläinen K, Junninen K, Kouki J (2023) Deadwood on clearcut sites during 20 years after harvests: The effects of tree retention level and prescribed burning. Forest Ecology and Management 545: 121287. https://doi.org/10.1016/j.foreco.2023.121287

III Nirhamo A, Hämäläinen A, Hämäläinen K, Kouki J (2024) Retention forestry can maintain epiphytic lichens on living pine trees, but provides impoverished habitat for deadwood-associated lichens. Journal of Applied Ecology 61: 2717–2726. https://doi.org/10.1111/1365-2664.14772

IV Nirhamo A, Hämäläinen A, Hämäläinen K, Kouki J (2024) The response of epiphytic lichens on living and dead *Pinus sylvestris* to prescribed fires of varying severity. Forest Ecology and Mamagement 551: 121558. https://doi.org/10.1016/j.foreco.2023.121558

Below are the contributions of Aleksi Nirhamo to the studies included in this thesis. Conceptualization and sampling design was always done in cooperation with collaborators. AN was the main writer of the manuscripts, but the texts were reviewed and edited by collaborators. The study in **I** was designed by the co-authors regarding other parts than lichen surveys. PS made a major contribution to **I** by collecting and analyzing tree ring samples. Jari Kouki designed the field experiment utilized in **II**, **III** and **IV**. The monitoring data in **II** was collected by several people, with major contributions by Kaisa Junninen in the previous surveys, and Karoliina Hämäläinen being responsible for the most recent survey.

I Conceptualization, lichen sampling design, lichen data collection, data analysis, writing.

II Conceptualization, data analysis, writing.

III Conceptualization, sampling design, data collection, data analysis, writing.

IV Conceptualization, sampling design, data collection, data analysis, writing.

TABLE OF CONTENTS

1 INTRODUCTION

1.1 Forests, humans and biodiversity

Forest ecosystems of the world are facing many anthropogenic pressures. In many regions, there have been high levels of deforestation, mainly from conversion to agricultural land, either historically (Kaplan et al. 2009) or presently (Curtis et al. 2017). A very low share of the remnant forests in densely populated regions are primary forests (Sabatini et al. 2018). In boreal Europe, the land is poorly suited for agriculture and thus deforestation has been low (Kaplan et al. 2009). Instead, ecosystem productivity has been harnessed for human use in the form of silviculture. Consequently, forest cover in boreal Europe remains high, but in the pursuit of timber yields, boreal European forests have faced large-scale anthropogenic modifications. These include a truncated age distribution of trees and forest stands, reduced quantity and qualitative variation of deadwood, and a near-absence of sites impacted by natural disturbances (Kuuluvainen 2002). In short, European boreal forests have become homogenized from the impacts of human activity.

Natural selection pushes populations to adopt strategies that best ensure their survival and reproduction. To achieve this, they may adopt strategies seldom used by others and thus carve their own specialized niche. Heterogeneous habitats enable the coexistence of species with different niches (MacArthur and MacArthur 1961, Chase and Leibold 2003). Correspondingly, anthropogenic habitat homogenization reduces the number of species that may coexist. Consequently, there is typically less biodiversity in human-modified forests than in natural forests (Swanson et al. 2011, Nirhamo et al. 2025).

The principle of sustainability has been integral to forestry for centuries (von Carlowitz 1713). What precisely “sustainability” entails has changed over time. Nowadays it is widely accepted that ideally forests are managed so that biodiversity in all its forms is maintained. There are three grounds on which biodiversity may, or should, be maintained. First, the preservation of biodiversity is mandated by national and international agreements. Second, biodiversity maintains ecosystem functioning, which maintains human societies. Third, ethics dictate that no life form should be deprived of their ability to live.

1.2 Natural forest dynamics as a management model

During the second half of the 20th century, evidence of conflicts between forestry practices and ecological sustainability began to accumulate. New approaches to forestry started to be formulated, with the aim of finding a better balance between ecosystem preservation and commodity production. An idea was developed that forest management should aim to emulate natural forest dynamics (Franklin 1989, Franklin et al. 2002, Kuuluvainen 2002, Gauthier et al. 2009). In practice, manipulation of forest ecosystems through timber harvests and other forestry operations should, as much as possible, resemble natural patterns of disturbance and succession. An underlying assumption is that ecological attributes such as biodiversity are best maintained when ecosystems are self-organized through ecological and evolutionary processes, and all anthropogenic impacts are external forces that disrupt these processes. It is expected that the better natural forest dynamics are emulated, the better biodiversity is maintained, because that equates to approaching the conditions to which forest biota have adapted. Thus, the principle of natural dynamics emulation is ultimately based on the theory of evolution (Darwin 1859).

Natural forest dynamics are not only a model for management, but also for restoration (Kuuluvainen 2002). In the EU Nature Restoration Law, restoration is defined as "*the process of* [...] *assisting the recovery of an ecosystem*". The words "restoration" and "recovery" both refer to bringing back a previous state, or the original state. That may be interpreted to allude to a reintroduction of natural forest dynamics. The emulation of natural forest dynamics in managed forests may be contextualized as (partial) restoration even if timber harvests are continued.

So that natural forest dynamics may be emulated, an important and obvious prerequisite is detailed knowledge of natural forest dynamics. When the aim is to maintain biodiversity, specifically the aspects of natural forest dynamics that are relevant for biodiversity must be understood. Then, the assumption of the emulation of natural dynamics being a successful method for maintaining biodiversity should be tested. A scientifically rigorous approach is to use field experiments where natural forest dynamics are emulated with a variety of treatments.

1.3 Forest dynamics in boreal Europe

Forest dynamics in boreal Europe depend on the dominant tree species (Kuuluvainen and Aakala 2011). Spruce-dominated forests are mainly driven by gap dynamics. In an absence of major disturbances, forests remain dynamic as individual or small groups of senescent trees die, usually because of the combined effects of pathogens and abiotic factors (Lännenpää et al. 2008). Typically, the shrub layer consists of small but up to at least several decades old spruces which are released when canopy gaps are formed by tree mortality. Over time, gap dynamics lead to a heterogeneous canopy structure and distribution of tree ages and sizes, but may lead to low tree species diversity since tree species other than spruce struggle to regenerate (Lilja et al. 2006, Fraver et al. 2008). In addition, spruce-dominated forests may experience intermediate disturbances (i.e., patch dynamics), most commonly caused by strong winds, or also, for example, by bark beetle outbreaks. The outcome is a larger gap, where spruce may be at an advantage due to advance regeneration, but which potentially also enables the regeneration of other tree species.

Pine-dominated forests are, in turn, characterized by cohort dynamics, which are driven mainly by intermittent surface fires (Kuuluvainen and Aakala 2011). Pines are fire-resistant and typically survive surface fires, whereas spruces and broadleaved trees are vulnerable to fire. Surface fires also eliminate the ground vegetation and thus facilitate the establishment of a new generation of pine saplings (Lampainen et al. 2004). Thus, surface fires both sustain the dominance of pine and lead to a cohort-based age distribution of pines due to waves of regeneration. In an absence of surface fires, pine-dominated forests become driven by gap dynamics, which may eventually lead to dominance by spruce (Aakala 2018).

Both spruce and pine-dominated forests also sporadically face large-scale stand-replacing disturbances, mainly due to crown fires or exceptionally strong wind (Kuuluvainen and Aakala 2011). Stand-replacing disturbances initiate successional dynamics (Angelstam and Kuuluvainen 2004), in which stands are initially dominated by broadleaved trees in mesic sites and pines in drier sites. Spruces regenerate with a delay, and the stand transitions toward spruce dominance after about 100–150 years when the broadleaved trees begin to senesce (Lilja et al. 2006). At first, the initial spruce cohort is fairly even-aged, and gap dynamics begin properly when the initial spruce cohort reaches senescence, which may take up to at least 300 years (Lilja et al. 2006, Aakala et al. 2009).

Natural disturbance dynamics are stochastic with an infinite number of iterations with different combinations of size, severity, return interval and agent of disturbance. However, as a rule, small disturbances are frequent, moderate disturbances are rare, and large disturbances are much rarer still (e.g., Senf and Seidl 2021). The result of natural disturbance dynamics is a heterogeneous landscape, but since the return interval of stand-replacing disturbances is typically several centuries, the majority of natural forest landscapes consists of late-successional forests (gap or cohort dynamics; Berglund and Kuuluvainen 2021).

1.3.1 Snag dynamics

Whether trees die standing or fall down depends on the mortality agent. For example, trees killed by fire or insects remain upright, whereas wind-blown trees, obviously, fall down. In the absence of major disturbances, a common case is that the mechanical strength of tree trunks is weakened by wood-decaying fungi, after which the stem is snapped by wind, leaving both a standing snag or a short stump and a fallen log (Lännenpää et al. 2008). Alternatively, trees may die by succumbing to multiple stressors as their performance decreases due to senescence, often causing them to die standing.

The duration that snags remain standing after their death is significantly affected by geographic location and the focal tree species. Wood decomposition rate increases with temperature, and thus snag longevity is lower in warmer climates (Gärtner et al. 2023, Aakala et al. 2024). In addition, stand-level variables such as basal area and soil fertility may affect snag longevity, probably also due to effects on decomposition rate via temperature and moisture (Aakala et al. 2024). Wood decomposition also varies by species, with clear differences, e.g., between conifers and broadleaved trees (Schreiber et al. 2025), reflected in higher longevity in conifer snags (Gärtner et al. 2023, Aakala et al. 2024). Snag longevity is also likely to be affected by some tree species producing decay-inhibiting chemical compounds in the wood (Venäläinen et al. 2003). Often, snags remain standing for no longer than a few decades (e.g., Onodera and Tokuda 2015, Grayson et al. 2019). However, in appropriate conditions, snag longevity may extend to centuries. One such case are pine snags in boreal Europe, which may remain standing for several centuries (Niemelä et al. 2002, Rouvinen et al. 2002b).

1.3.2 Emulation of natural forest dynamics in management and restoration

The stochasticity of disturbances creates a challenge for emulating natural forest dynamics. Therefore, it is both more practical and representative of natural dynamics to establish the range of natural variability and use that as a model (Aszalós et al. 2022) instead of an exact formula that should be replicated. A further challenge is that there is a history of at least several centuries of human interference in the dynamics of boreal European forests, seen evidently, for example, in the fire history of remnant old-growth forests (Wallenius 2011). Thus, it is difficult to obtain evidence about forest dynamics without any human interference.

The ideas about emulating natural dynamics originated in the northwestern USA (Franklin 1989) and have impacted forest management in many regions. The most frequent application of natural dynamics emulation in boreal Europe is retention forestry, a modification of clearcut-based forestry in which some portion of trees is left permanently unharvested (Gustafsson et al. 2012). Thus, the outcome of harvests is more resemblant of natural disturbances in terms of residual structures. Old trees and dead trees are common or ubiquitous in natural forests, but rare or absent in many human-modified forests (Siitonen et al. 2000, Rouvinen et al. 2002a). Many forest-dwelling species are associated with old or dead trees, and those species are particularly vulnerable to habitat modifications from forestry (Nirhamo et al. 2025). Retained trees may grow old and eventually die. Thus, the adoption of retention practices increases the presence of old trees and dead trees in managed forests. Retention forestry has a strong ecological foundation (Franklin et al. 1997), but its application is often lacklustre due to low proportions of retained trees. Consequently, natural dynamics are, in the end, poorly emulated (Aszalós et al. 2022).

A large proportion of forests that are now protected have previously been subjected to timber harvests and structural modifications to enhance timber production. These forests will recover toward a more natural condition over time, but also restoration methods that emulate natural disturbances have been used to expedite their recovery (Halme et al. 2013). Typical methods are gap creation and prescribed burning, with the latter having been done mainly in pine-dominated forests. These methods diversify the structure of previously managed forests, and increase biodiversity by, for example, inducing tree mortality and thus providing resources for deadwood-associated taxa (Sandström et al. 2019).

1.4 Epiphytic lichens

Vegetation growing on top of other plants are called epiphytes. Epiphytes on wood are lignicolous, as opposed to corticolous epiphytes on bark. Lignicolous communities are mainly found on decorticated dead trees, and corticolous communities on living trees. In temperate and boreal climates, epiphytes consist of bryophytes and lichens, while in the tropics they also include vascular plants. Lichens are the most stress-tolerant epiphytes and thus they dominate the epiphytic communities on the harshest substrates such as acidic bark and standing deadwood.

The assembly of epiphytic communities is a slow process. As trees grow, they offer more space for epiphytes, and often also their bark properties change (Ranius et al. 2008). Thus, it may take decades if not centuries until tree growth diminishes and substrate properties stabilize. In addition, epiphytes may be dispersal-limited due to which the colonization of substrates may be delayed (Dettki et al. 2000, Löbel et al. 2006). Thus, the epiphyte community of each tree undergoes primary succession over the lifespan of the tree. Although there are countless factors that may influence the successional assembly of epiphyte communities, a common pattern is that epiphyte diversity is highest on old trees, and some species occur (almost) exclusively on old trees (Johansson et al. 2007, Lie et al. 2009, Fritz et al. 2009, Marmor et al. 2011).

Metapopulation theory (Hanski 1999), or metacommunity theory (Leibold et al. 2004), when scaled up to the community level, are useful for understanding the spatiotemporal dynamics of epiphytes. For epiphytes, trees are like habitable islands in a sea (i.e., matrix) of uninhabitable space. Trees are discrete habitat patches that are heterogeneously distributed in space and dynamic in time due to tree growth and development of substrate properties, and eventual tree fall. Stochastic extinctions are rare in epiphytes, and instead, after a habitat patch is colonized, epiphytes usually remain there until a deterministic extinction caused by tree fall or changes in substrate properties due to the growth or aging of the tree (Löbel et al. 2006, Johansson et al. 2012). Thus, epiphytes form habitat-tracking metapopulations (and metacommunities), since they follow spatiotemporally dynamic habitats with their movement as spores or other propagules (Snäll et al. 2005). It may be assumed that the adaptations of epiphytes ensure that they succeed in this in natural forest dynamics, but anthropogenic habitat changes may jeopardize the ability of epiphytes to maintain metapopulation dynamics.

Tree species vary in bark properties and thus provide different conditions for epiphytes. This effect is highlighted in the boreal zone where tree species diversity is low, and most tree species are unique epiphyte hosts (Kuusinen 1996). In this perspective, decorticated deadwood functions like another tree species, since it hosts a unique set of epiphyte species (Lõhmus and Lõhmus 2001, Spribille et al. 2008). In boreal forests, standing dead pine trees may remain upright for centuries after their death (Niemelä et al. 2002, Rouvinen et al. 2002b). During this time, the substrate provided by the dead tree undergoes a gradual transformation due to the weathering and decomposition of the wood surface (Fukasawa 2018, Arpaci et al. 2021). Thus, successional patterns similar to those on living trees may be expected in lignicolous communities over the period that standing dead trees remain upright.

1.4.1 Epiphytes and forest dynamics

The tree-level diversity of epiphytes usually increases with tree age (Johansson et al. 2007, Lie et al. 2009, Marmor et al. 2011). This directs toward a view that epiphytes, as a group, are mainly associated with old forests, and that disturbances would affect epiphytes negatively. Indeed, epiphyte diversity generally is higher in older stands (Kuusinen and Siitonen 1998, Marmor et al. 2011, Tullus et al. 2022), and especially fire disturbance has been shown to affect epiphytes negatively (Johansson et al. 2006, Miller et al. 2018). However, a variety of factors lead to complexity in epiphyte responses to disturbance. As photosynthesizing autotrophs, epiphytes benefit from light availability (Gauslaa et al. 2006, Marmor et al. 2012), and thus they may benefit from the canopy being opened by disturbances. Although disturbances kill trees and thus remove the substrates of epiphytes, they also provide new substrates by generating deadwood and enabling the regeneration of new trees, which possibly belong to species not present before disturbance (Lõhmus et al. 2018). Small to moderate disturbances lead to mixtures of young and old trees, open and sheltered conditions, and various tree species. All these factors are significant contributors to the tree-level beta diversity of epiphytes, suggesting that stand-level alpha diversity of epiphytes is, in fact, increased by disturbance. Epiphytes may, however, be unable to survive larger and more severe disturbances such as crown fires. Still, even large disturbances typically have surviving individual trees or unaffected refugial patches (Lampainen et al. 2004), due to which late-successional epiphyte assemblages may be carried over to post-disturbance conditions (Goward and Arsenault 2018).

1.5 Aims of the thesis

In this thesis, I explored the species diversity of epiphytic lichens on Scots pines (*Pinus sylvestris*; henceforth, pines). The main focus is on lignicolous lichens, but corticolous lichens are also addressed. I examined the tree-level succession of lignicolous communities on snags to understand the conjoined dynamics of snags and lignicolous lichens in near-natural forests (**I**). Thereby I reinforced the understanding of lignicolous lichen community dynamics in natural forests. Then, I examined how lignicolous and corticolous lichens are affected by the emulation of natural dynamics and/or restoration of managed forests. I looked into two methods, retention forestry (**II**, **III**) and prescribed burning (**II**, **IV**). This may also be framed as studying the effects of disturbance, namely timber harvests (**II**, **III**) and fire (**II**, **IV**). I looked into the effects on the substrates used by epiphytes (**II**), and the effects on the epiphyte communities themselves (**III**, **IV**).

2 METHODS

The data used in **I** was collected in three landscapes located in the municipalities of Lieksa, Kivijärvi and Kuusamo. The data used in **II**, **III**, **IV** was collected from sites belonging to a field experiment in the municipality of Lieksa (Figure 1). All study sites are in the middle boreal zone or just outside its range as defined by Ahti et al. (1968).

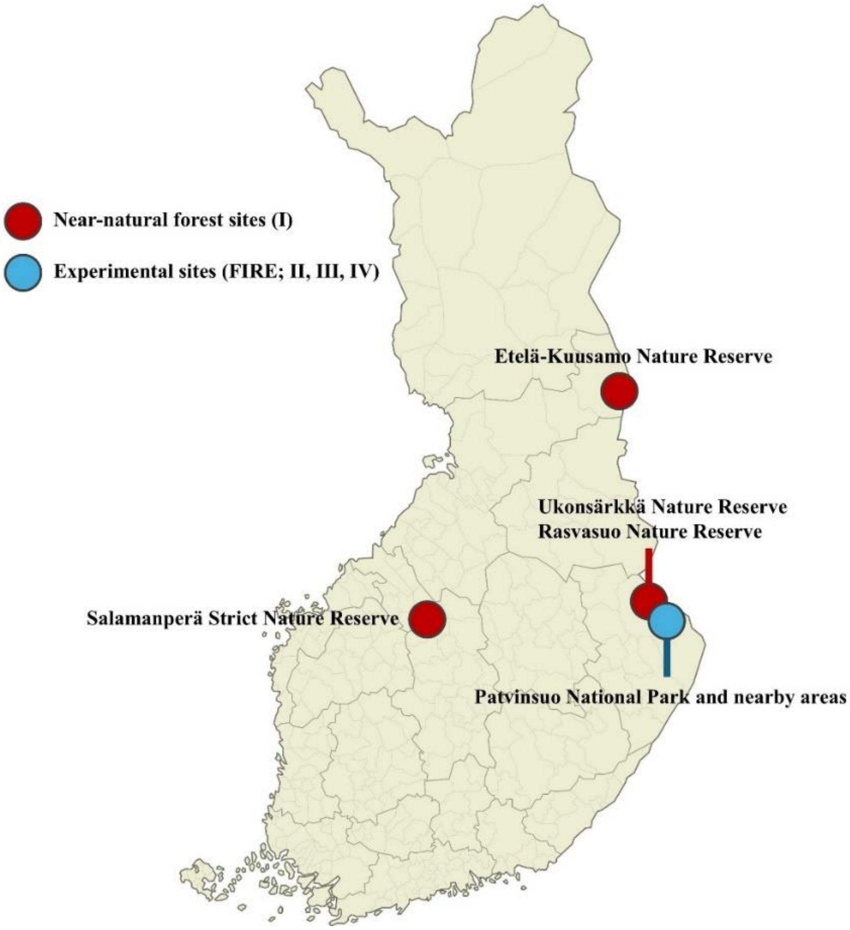

Figure 1. The location of the study sites on a map of Finland.

The experiment conducted in the study sites of **II**, **III** and **IV** included two factors: burning (two levels: burned, not burned) and harvest intensity (four levels: unharvested, harvested with 10 m^3/ha of trees retained, harvested with 50 m^3/ha of trees retained, full harvest with no retained trees). Each combination of the two factors, i.e., treatment, was replicated in three forest stands. Each of **II**, **III** and **IV** used a different set of these treatments (Table 1). Although the experiment includes treatments with full harvests, they were not included in any of the studies of this thesis. The field experiment is known as FIRE (FIre and Retention Experiment), and it has been used in numerous studies prior to this thesis (Kouki 2013).

In **I**, plots were established in randomized locations while ensuring ease of access, i.e., vicinity to roads or trails. First, all snags were mapped from these plots. Then, snags were selected for further study using stratified randomization with three factors: size (four levels), site type (three levels), study landscape (three levels). Thirty trees were selected for each combination of the factor levels. From the selected trees, those with less than 20% of bark remaining on the whole stem and less than 50% of bark remaining on the lowest two meters were included in **I**.

The study sites of **II**, **III** and **IV** were subjected to experimental manipulations in 2001. Before that, the sites were similar in structure. Like the study sites in **I**, they were also impacted by selective logging and elevated fire frequency in the previous centuries. Historical logging intensity had probably been higher than in the study sites of **I**. These sites were sub-xeric and pine-dominated.

II included all retained trees (diameter at breast height > 5 cm) on the study sites. For **III** and **IV**, retained trees were selected randomly so that, in each replicate stand, the share of living trees, snags and logs was similar among the selected trees as they were among all retained trees. **II** included all tree species while **III** and **IV** included only pines. The number of selected trees per replicate stand depended on the number of trees remaining after the treatments: 50 trees in unharvested sites, 30 in sites with 50 m^3/ha retention, 10 in sites with 10 m^3/ha retention. In unharvested sites, coordinates for 50 locations within the sites were selected randomly. In the field, for each coordinate, the closest pine (alive, a snag or a log) was selected.

Table 1. The treatments of FIRE used in the studies of this thesis.

	Burned	Unburned
No harvests	**IV**	**III**, **IV**
50 m^3/ha	**II**, **IV**	**II**, **III**
10 m^3/ha	**II**, **IV**	**II**, **III**
Full harvest	-	-

Table 2. The number of surveyed trees and observed lichen species in the studies that included lichen surveys.

	I	III	IV
Number of surveyed trees	331	396	420
Dead trees	331	173	133
Living trees	0	223	287
Number of observed lichen species	135	111	109

In **I**, **III** and **IV**, all lichens occurring on the lowest two meters of the selected trees were recorded. The surveys were limited to this height because of difficult access to higher parts of the stems. Lichens were surveyed on 331–420 trees in each of the studies (Table 2). Only lignicolous lichens were recorded on dead trees, and only corticolous lichens were recorded on living trees. When necessary, specimens were collected for identification with microscopy and spot tests. The year of death of the standing dead trees surveyed in **I** was determined with dendrochronological methods. The surveyed snags comprised a chronosequence of 275 years in time since tree death.

The data were analyzed with quantitative statistical methods. The studies on lichen communities (**I**, **III**, **IV**) focused mainly on community composition and species richness, but also species-specific responses (**I**, **IV**) and traits (**IV**) were analysed. The statistic methods varied among the studies, and included ordination by nonmetric multidimensional scaling (all studies), rarefaction (**III**, **IV**), analysis of variance (**II**, **III**, **IV**), generalized additive models (**I**), survival analyses (**II**), and indicator species analysis (**IV**).

3 MAIN RESULTS AND DISCUSSION

3.1. High-longevity snags are important for lignicolous lichen diversity (I, III)

A chronosequence of pine snags spanning 275 years in time since tree death showed that the alpha and beta diversity patterns of lignicolous lichens on snags are strongly determined by time since tree death (**I**). The main pattern along the chronosequence was a continuous replacement of species present on the snags, paired with increasing species richness until a high point was reached when 90 years had passed from tree death. This pattern was similar to what has been observed in epiphytes on living trees (Johansson et al. 2007, Lie et al. 2009, Fritz et al. 2009, Marmor et al. 2011). A group of species worth highlighting are those that I called old snag specialists. They are obligate lignicoles (i.e., species that occur only on wood; Spribille et al. 2008) that exhibited a late-successional niche on snags. A threshold analysis indicated that they began to occur in high frequency when time since tree death was 90 years. Eleven species were identified as old snag specialists, but the lichen flora of Fennoscandia undoubtedly includes many more such species that were rare or absent in my data. Ecologically similar species are evidently present also in other regions (Thor et al. 2024).

Over time, after a tree has died and lost its bark but remains upright, the snag surface undergoes a transformation due to the decomposition and weathering of the wood. As lichen species have differentiated niches regarding substrate preferences, the snag surface transformation is assumably a central driver of the observed successional patterns. This process is analogous to succession in fungal communities caused by changing deadwood properties along the decomposition gradient (Renvall 1995, Dawson et al. 2024). Microhabitat heterogeneity is most likely higher on older snags, explaining the increasing species richness. In addition, increasing species richness in early succession is inevitably caused partly by delays in colonization of the newly exposed substrate. Although competition-colonization trade-offs are often used to explain succession in vegetation, they probably played a minor role here (for further discussion, see original article **I**).

Compositional change, i.e., succession, continued for at least the first 150 years of the chronosequence. Beyond that, time since tree death was confounded with extensive wood charring. Only some of the oldest snags were extensively charred as the study sites had not been impacted by fire for a long time. Some species occurred almost exclusively or more commonly on charred wood, while others were less frequent on it. Thus, charring via forest fires appears to induce an alternative successional trajectory for lignicolous lichens. Compositional changes observed in 150–275 years in time since death were at least partially due to time since death being confounded with alternative trajectories rather than succession per se.

High-longevity snags thus are important for lignicolous lichen diversity. In natural (pine-dominated) forests, high-longevity snags have a low recruitment rate but they still are spatiotemporally continuous because of their long persistence (Rouvinen et al. 2002b, Kuuluvainen et al. 2017). An area of two hectares in a near-natural forest contained 27 snags that had been dead for over 90 years (Rouvinen et al. 2002b), which was identified as a threshold for frequent occurrence of old snag specialists (**I**). With such a density, high-longevity snags are about 25–30 meters apart assuming an even spatial distribution (in reality, their occurrence is somewhat clustered; Kuuluvainen et al. 2017). The high availability of the kinds of substrates provided by high-longevity snags explains why several species (i.e., old snag specialists) have specialized in utilizing them. The slow-paced snag dynamics of natural pine forests are the basis of high lignicolous lichen diversity.

The role of high-longevity snags is highlighted not only for lignicolous lichens, but also for overall stand-level epiphyte diversity in pine-dominated forests. The drier the site, the lower the frequency of tree species other than pine. On pines, higher lichen diversity is found on snags than on logs or living trees (**III**). This pattern is probably unique to pine, as far as boreal European tree species are concerned. Pine bark hosts relatively low lichen diversity, which may be specifically due to low beta diversity because of low variation among pine individuals in bark properties. Other tree species have, when living, more variability in bark properties, and, when dead, much lower snag longevity. Standing dead broadleaved trees usually do not lose bark at all (Lõhmus and Lõhmus 2001). A central reason for lignicolous lichen diversity being lower on logs than snags is that bryophytes usually outperform lichens on logs in advanced decay (Kushnevskaya et al. 2007), but also, lower substrate stability on logs because of a higher decomposition rate may be infavorable to lichens. The stand-level diversity of epiphytic lichens in spruce-dominated sites may be noticeably affected by the presence or absence of aspen (Kuusinen and Siitonen 1998). The presence or absence of high-longevity snags is likely to have a similar effect in pine-dominated sites.

3.2 Restoring the habitats of late-successional lignicolous lichens is an ultimate challenge (II, III)

Trees retained in clearcuts have a high mortality rate in the first years after harvesting, but in a few years, it reduces to be relatively close to the background mortality rate (**II**). Thus, tree retention may cause a pulse in deadwood input soon after harvesting, after which the deadwood input from retained trees becomes lower but may continue for long. Obviously, the size of the deadwood input is determined by the number of retained trees. In addition, the mortality of retained trees, and thus the deadwood input, is affected, for example, by the species identity and size of retained trees and their position in relation to topography and other living trees (Hämäläinen et al. 2016). Thus, as many as half of retained trees may die within a couple of decades (Rosenvald et al. 2019), but mortality may also remain much lower (i.e., 12% in pines in Hallinger et al. 2016). In **II**, when 20 years had passed since harvesting, 55% and 31% of retained trees had died in sites with retention levels of 10 m^3/ha and 50 m^3/ha, respectively. This difference was probably because, in the latter, retained trees were in larger groups and thus less exposed to wind. Moreover, applying prescribed fire to retention sites caused almost complete mortality of retained trees. The severity of prescribed fire depends on fuel loads, which can be manipulated.

Whether retained trees die standing or are blown down by wind is also affected by several factors (Hämäläinen et al. 2016). In **II**, a considerable share of retained trees died standing and formed snags. Based on survival modeling, the maximal longevity of snags formed from retained pines was estimated to be about 50 years (**II**). A very similar maximal longevity was found for pine snags in managed forests in another Finnish study (Mäkinen et al. 2006). This is in stark contrast to pine snag longevity in natural forests (Niemelä et al. 2002, Rouvinen et al. 2002b). This indicates that high-longevity snags, on which lichen diversity is the highest and some specialized species are dependent (**I**, **III**), are not formed in managed forests. Retention practices may be an effective pathway toward the restoration of deadwood to managed forests, but the restoration is qualitatively deficient.

Deadwood originating from retained trees hosted relatively low lichen diversity (**III**). Other studies have similarly found low lichen diversity on restored deadwood (Hämäläinen et al. 2021, Larsson Ekström et al. 2023). This is because lichen communities on restored deadwood had still been in early succession, while high diversity occurs in late succession (**I**). I expect that the data in **I** predicts how lichen diversity on restored deadwood develops over the period it remains standing. However, the snags I studied in **III** had died at most 21 years ago, and the mean lichen species richness on them was about 14. In the modeling of the data in **I**, mean species richness on snags that had died 20 years ago was slightly below 10. This difference could be because of faster bark loss in the open clearcut sites in **III**. A higher abundance of subcortical saproxylic beetles may be a reason for faster bark loss in open sites (Jacobsen et al. 2015). This highlights the effect of bark loss rate on lignicolous lichens, which is an important factor particularly when snag longevity remains low.

Most likely none of the methods of deadwood restoration addressed in various studies (Sandström et al. 2019) will produce high-longevity snags. The high longevity of pine snags in natural forests may be assumed to be because of high decay resistance in the wood (Venugopal et al. 2016). Decay resistance may be higher in natural forests because of factors related to slow growth and old age of trees. It has also been suggested that trees experiencing and surviving forest fires during their lifespan builds up decay resistance because of investments by the tree to avoid further damage after injury from fire (Niemelä et al. 2002). Therefore, successful restoration of high-longevity snags probably requires a build-up of decay resistance before tree death. It is currently not known how to facilitate this process. It may be that if trees grow old and die of natural causes, they build up decay resistance sufficiently for high snag longevity, but this is uncertain. Injuries from fire, or other comparable injuries, may be required to build up decay resistance. Passive restoration of high-longevity snags by reintroduction of natural dynamics is assumed to take centuries. There is no knowledge of methods of active restoration that would accelerate this process. Thus, restoring high-longevity snags is difficult. As written by Kuuluvainen et al. (2017), "*managing for [high-longevity snags] and conserving their specialized species can be regarded as an ultimate conservation and restoration challenge in boreal forest landscapes*."

3.3 Forest fires affect epiphytic lichen diversity in several ways (IV)

Given that epiphytic lichen diversity is, to a large extent, associated with habitat structures of late-successional forests (e.g., old trees), it may be expected that disturbances such as fires would affect them negatively. However, low-severity fires (surface fires) did not reduce the species richness of epiphytic lichens on pines, and high-severity fires (crown fires) reduced it only slightly (**IV**). Instead, fires caused large changes in species composition. High-severity fires killed most trees, and thus bark substrates were replaced by wooden substrates. Most dead trees had fallen 21 years after high-severity fires. Low-severity fires killed almost no pines, but the scorching by fire reduced the frequency of some species and apparently changed substrate properties of the bark. In both types of fire, the strongest negative effect was directed to corticolous species associated with mature or old trees. The compositional changes were generally similar in fires of low and high severity, but the magnitude of the changes were higher in high-severity fires.

Epiphyte studies are usually restricted to the lowest two meters of trunks because upper heights are difficult to access. Because of this, a considerable portion of epiphytes occurring on a tree are omitted, as upper heights may host species not present at the base, in part because of differences in abiotic conditions (Marmor et al. 2013). In pines, the bark on the upper trunk scales off at a fast rate, and thus it hosts few species, but pines may have stocky branches that host many lichens (Marmor et al. 2013). In decorticated trees, the surface transformation is likely to proceed similarly in the lower and upper trunk, in which case there would be little species turnover along tree height (except for the base, i.e., the lowest 0.5 meter). In any case, surveying only the lowest part of the trunk may lead to particularly misleading results when studying surface fires. Scorching by fire concerns only the lowest part of the stem, and lichen communities may remain unchanged over most of the length of the tree in surviving stems.

Saproxylic diversity is typically very high following high-severity disturbances because of high amounts of deadwood (Swanson et al. 2011). However, I sampled lichens on 99 dead trees in sites affected by high-severity fires, and on 18 dead trees in unburned sites (the number of sampled dead trees was related to the number of dead trees present in the sites), and found a very similar number of lichen species on these sets of dead trees. This means that the dead trees in the unburned sites were of higher quality from the perspective of lignicolous lichens and/or contained more qualitative variation. Specifically, there was practically no variance in time since tree death in the burned sites, and "old" deadwood such as high-longevity snags were absent. Post-disturbance sites are inhabited by large populations of early-successional lignicolous species (sensu **I**), but overall, they are not particularly diverse in lignicolous lichens despite high quantities of deadwood. The development of lignicolous diversity in post-disturbance sites in longer time scales than addressed in **IV** will be strongly impacted by snag fall rates. In our study sites, snag fall rates were quite high (**II**), suggesting that lignicolous diversity will not reach much higher levels than observed in **IV**.

Dead trees are not rendered unusable for lignicolous lichens when they fall. However, snags and logs host very distinct lignicolous communities (**III**). Although bryophytes were not measured in any way, the practically complete absence of bryophytes on the logs in the open post-disturbance sites could not go unnoticed. In closed forests, bryophytes become dominant in lignicolous communities on logs quite soon after tree fall (Kushnevskaya et al. 2007). Instead, in open sites, lichens appear to remain dominant on logs until their decomposition or disintegration. However, I mainly observed common generalist epiphytes (Parmeliaceae) or terricolous taxa (e.g., *Cladonia*) on logs, and overall lignicolous lichen diversity was low compared to snags. Still, some obligate lignicoles (e.g., *Xylographa*) were observed much more frequently on logs than snags. Some obligate lignicoles occurring mainly on logs may require more humid conditions, and thus were rare or absent in the data collected from pine-dominated forests and open sites. Deadwood decomposition may be faster in open than closed sites (Schreiber et al. 2025), and 21 years after disturbance, many of the logs in the open post-disturbance sites seemed not far from disintegration. This further suggests that lignicolous diversity will not increase much from what was observed here. As snags fall by mid-stem snapping, the remnant stumps probably persist and continue to provide substrates for lignicolous species for longer than logs.

The destructive effect of fire on epiphytic lichens was underestimated because of two factors. First, tree species other than pine were not included in the surveys. Other tree species are vulnerable even to surface fires. Thus, had they been included in the study, the destructive effect of the fire would certainly have been found to be stronger. Second, I would assume fires to have negative effects on late-successional lignicolous lichens (sensu **I**), but this could not be addressed properly because of a low sample size of deadwood in the control sites. Even low-severity fires may consume fallen deadwood and cause premature falling of snags (Eriksson et al. 2013), as well as scorching of the lowest part of the stem also in surviving snags. Thus, destructive effects of fire on late-successional lignicolous species would probably have been observed with more extensive sampling of deadwood in the control sites. Surface fires potentially reduce the formation of high-longevity snags by causing premature snag falls, but on the other hand, may facilitate their formation by causing a build-up of decay resistance in living trees or by partially charring snags which may make them more difficult targets for decomposers. These interactions between fire disturbance and the formation of high-longevity snags are currently poorly understood. Lastly, it should be noted that fires are important in diversifying landscapes and enabling large-scale regeneration of broadleaved trees through which they are important also for epiphyte diversity.

3.4 Surveys of lichens on retained trees showed that residual structures can uphold lichen diversity in post-disturbance sites (III)

After 20 years from clearcutting, the species richness of corticolous lichens was similar on retained pines and pines in uncut control sites, although community composition had changed slightly (**III**). Severe disturbances may kill most trees and thus remove the substrates of epiphytes. However, typically some trees remain alive as residual structures even in severe disturbances. This result shows that residual structures can uphold lichen diversity in post-disturbance sites. Moreover, maintaining the diversity of corticolous lichens on pine seems achievable with retention forestry. However, quite a large share of trees may be needed to be retained to secure infrequent or rare species.

When the trees surrounding retained trees are harvested (or, generally, when trees surrounding residual trees die), microclimate changes substantially. This is likely to cause changes in the lichen communities on retained trees, often including an increase of tree-level species richness, which has been linked to increased light (Lundström et al. 2013, Ranlund et al. 2018). While this has been demonstrated clearly on residual trees of major disturbances (i.e., retention trees in clearcutting), small to moderate disturbances are likely to have a similar but probably more subtle effect. I observed relatively small compositional differences which may be because microclimatic changes from clearcutting are smaller in pine-dominated forests than in spruce-dominated forests in which other studies have been conducted. Corticolous communities on pine include few species that are specialized in a way that would make them sensitive to forestry, which is seen, e.g., in the low number of pine-associated corticolous red-listed species (Nirhamo et al. 2023). Therefore, the results I obtained on pines may not be generalizable to mesic forests and other epiphyte host species.

Retention practices have been in use since the 1990's, and there are several publications about its effects on epiphytes. However, so far, they have focused only on tree-level communities, specifically, the survival of epiphytes on retained trees. Their survival is imperiled by the microclimatic changes caused by clearcutting, and the rather high mortality of retained trees (**II**). Many lichen species may, in fact, be favored by the microclimatic changes, since pre-harvest even-aged managed forests may be dense and light-limited. However, the conditions on clearcut sites are perilous to species adapted to conditions of sheltered habitats (Gauslaa et al. 2006). The mortality of retained trees should be accounted for by retaining a higher number of trees so that the mortality is compensated, or by ensuring that retained trees are not left exposed to wind. What remains poorly known is how stand-level communities are affected by retention practices, e.g., the number and species identity of retained trees. Moreover, data on the long-term colonization-extinction dynamics of epiphytes on retained trees and, for example, the importance of nearby source populations, would be important for understanding the effectiveness of retention practices in maintaining epiphyte diversity. Future studies should focus on these aspects.

4 CONCLUDING REMARKS

My thesis highlights the importance of deadwood quality for lignicolous lichens. Managed forests having low quantities of deadwood, and thus reduced saproxylic diversity, is widely acknowledged. It is important to also recognize the qualitative differences of deadwood between managed and unmanaged forests. High-longevity snags are a type of deadwood that is absent in managed forests and difficult to restore. Even selective logging may disrupt deadwood dynamics for a long time (Sippola et al. 2001). If harvest intensity is low enough, the disruption of deadwood dynamics probably could remain small enough for species diversity to be maintained. However, this would lead to substantially lower timber yields and would require a major revision of silvicultural principles. The time frame of the restoration of high-longevity snags far surpasses the human lifespan and thus is difficult to grasp from a human perspective. The significant challenges related to restoration and "land sharing" highlight the need to conserve the remaining forests with intact snag dynamics. A high frequency of high-longevity snags, indicating intact snag dynamics, is a supreme way of identifying pine-dominated (i.e., xeric or sub-xeric) forests of high conservation value.

In the past decade, increasing research attention has been devoted to so-called kelo trees and associated biota (e.g., Venugopal et al. 2016, Kuuluvainen et al. 2017, Larsson Ekström et al. 2023, Crosier et al. 2025). Kelo trees were popularized in the international scientific context by Niemelä et al. (2002), but the term has been used for long in Finnish literature (e.g., Renvall 1919, Leikola 1969). Authors seem to have had varied interpretations on the definition of a kelo tree. The lack of clear terminology muddles the research on the phenomenon. However, much of the use of the term kelo tree seems to overlap with my use of the term high-longevity snag. I propose to use time since tree death as the basis of defining kelo trees. While it is probably not sensible to have a definite cut-off point, the threshold of 90 years for frequent occurrence of old snag specialists could be helpful in defining kelo trees. The time since the death of snags is laborious to measure, but lignicolous lichens appear to be fairly reliable indicators for it. Also classifying snags on the basis of remnant branches can be a useful proxy for time since death (Storaunet 2004, Aakala et al. 2008). Time since death is a meaningful parameter because of its links with lichen communities and the differences in snag longevity between managed and natural forests. Although it is currently an unstudied topic, if it is proven that wood-inhabiting fungi associated with fallen kelo trees (Niemelä et al. 2002) require the tree to remain standing for a lengthy period after its death and before its fall, the meaningfulness of time since death would be further reinforced.

High snag longevity is not restricted to Scots pines (*Pinus sylvestris*) but instead appears to be a fairly widespread phenomenon in conifers in the boreal (and, possibly, temperate) zone, although the frequency of snags reaching high longevity varies by tree species. Extended snag longevity has been reported for *Picea abies* (Storaunet 2004), *Thuja plicata* (Daniels et al. 1997), *Larix gmelinii* (Mukhortova et al. 2009), and *Pseudotsuga menziesii* (Everett et al. 1999). In addition, snags of *Larix laricina* have been described as resemblant of kelo trees (Thor et al. 2024). I expect that in all these, lignicolous lichen communities would show similar diversity patterns in relation to time since tree death as on *Pinus sylvestris* snags.

In summary, my thesis supports the view that, on the tree level, epiphyte diversity is at its highest in late succession, i.e., on old trees. In this case, specifically, lignicolous lichen diversity is highest on snags with high values of time since tree death, which is a comparable variable to the age of living trees (**I**). This causes challenges to habitat restoration because the temporal scale at which key structures such as high-longevity snags are restored are very long from a human perspective. Disturbances typically remove high quality substrates by killing old trees (or causing premature snag falls) and may further hinder their formation. Still, the effects of disturbances on epiphyte diversity are complex. Diversity may be upheld in post-disturbance sites by residual structures (**III**). Disturbances also diversify habitats by producing new substrates. Consequently, the stand-level diversity of epiphytic lichens in sites recovering from severe disturbances may be smaller than in late-successional habitats by only a small margin, although community composition is changed substantially (**IV**). The emulation of natural dynamics should be effective in improving the epiphyte diversity of managed forests. The availability of heterogeneous substrates, but particularly old trees (including “old” snags, i.e., high-longevity snags), should be a focus.

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