The response of epiphytic lichens on living and dead *Pinus sylvestris* to prescribed fires of varying severity

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ABSTRACT

Prescribed burning can be used to restore forest ecosystems degraded by anthropogenic pressures. However, some species such as epiphytic lichens may be vulnerable to fire. We studied the effects of fire on epiphytic lichens on living and dead *Pinus sylvestris* (Scots pine) by surveying lichens up to two meters on the trunks 21 years after experimental and replicated prescribed burnings in pine-dominated boreal forests in Finland. We investigated three types of stands that had faced different levels of fire severity: 1) unburned semi-natural mature stands (i.e., control sites), 2) burned semi-natural mature stands, and 3) burned retention groups on clearcut sites. In the semi-natural mature stands, the fires were low-severity surface fires and induced negligible mortality in *P. sylvestris*. In the retention groups, the fires induced high tree mortality and made fresh deadwood the dominant substrate type. Low-severity fires reduced the occurrence of several species, but usually did not eliminate them. High-severity fires eliminated some species, but the abundant deadwood frequently hosted some species that were absent or infrequent on the unburned sites. Thus, the fires had only small effects on total species richness. However, fires substantially changed species composition: they reduced the occurrence of species associated with late-successional habitats, while increasing the occurrence of early-successional species. We also found fires to decrease the occurrence of microlichens and increase that of macrolichens. The magnitude of the compositional changes increased with fire severity. Our findings indicate that the high quantities of fresh deadwood in post-disturbance forests provide habitat only to a limited portion of deadwood-associated lichens. Fire can increase landscape-scale variation in epiphytic lichen communities, but we observed negative effects, which increased with fire severity, on lichen flora of conservation concern. Thus, we recommend prescribed burning to be applied primarily in sites with a history of intensive management. Fire should be avoided in sites with substrates that are fire-sensitive and important to lichen diversity.

1. Introduction

Fire is a key natural disturbance and a major driver of forest dynamics and structure in many forest ecosystems (Fulé et al., 2011; Shorohova et al., 2011). Climate change is currently altering fire regimes worldwide, leading to increased frequency, size and severity of fires. These changes can be devastating to forest ecosystems and carbon storage, and pose a risk to both human and natural wellbeing (Seidl et al., 2014; Abatzoglou and Williams, 2016; Abram et al., 2021). However, while fire activity is expected to increase also in Fennoscandia (Lehtonen et al., 2016), forest fires have been almost non-existent in this region since the late 19th century (Zackrisson, 1977; Niklasson and Granström, 2000). The scarcity of fire is reflected in the current

structure of forests and their future development (Lankia et al., 2012; Aakala, 2018). The scarcity of fire also affects the species assemblages of Fennoscandian boreal forests, since many currently rare species are dependent on or favored by post-fire conditions (Kouki et al., 2001). The reintroduction of fire in the form of prescribed burning can be used as a restoration tool with the aim to expedite the rewilding of previously managed forests, to restore fire-originated structures and dynamics, and to promote species that are favored by fire (Kouki et al., 2001; Kuuluvainen, 2002; Similä and Junninen, 2012; Sandström et al., 2019; Koivula and Vanha-Majamaa, 2020). The concept of prescribed burning entails many approaches and different kinds of goals (Burrows and McCaw, 2013; Ryan et al., 2013; Lindberg et al., 2020), but many aspects of the ecological consequences of these practices remain poorly

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studied. Since restoration via prescribed burning may increase in the coming years due to international agreements on habitat restoration (e. g. European Commission, 2022), and since climate change is increasing fire activity, there is a need for improved understanding on the ecological effects of fires in forests.

In natural forest fire dynamics, fires vary in size and severity, from high-severity stand-replacing fires that kill the majority of trees to low-severity surface fires that usually inflict very low tree mortality (Kuuluvainen, 2002; Lampainen et al., 2004; Perry et al., 2011). Fire dynamics in the boreal forests of Fennoscandia are closely linked with the dominant tree species. In pine-dominated forests, surface fires are more prevalent but stand-replacing fires may occur as well (Wallenius et al., 2004; Kuuluvainen and Aakala, 2011). Surface fires inflict low mortality on mature trunks of the fire-resistant *Pinus sylvestris* (Scots pine), while younger *P. sylvestris* and other tree species are more susceptible (Linder et al., 1998; Kuuluvainen et al., 2002; Kukavskaya et al., 2014). Stand-replacing fires kill nearly all trees and generate large quantities of dead wood (Spies et al., 1988; Junninen et al., 2006), providing habitat for large numbers of wood-inhabiting species such as beetles and fungi (Similä et al., 2002; Junninen et al., 2006).

Epiphytic lichens are a highly diverse group of organisms (Ellis, 2012). The majority of these lichens grow primarily on bark, and many grow facultatively on deadwood. Additionally, about 10 % of epiphytic lichens are obligately associated with deadwood (Spribille et al., 2008). Stand-replacing fires are typically considered highly destructive to epiphytic lichens, resetting the succession of lichen communities and their habitats (Boudreault et al., 2000; Bartels and Chen, 2015; Miller et al., 2022). Surface fires damage lichen communities primarily near tree bases, and the damage increases with fire severity. However, if trees survive, lichen communities are not completely eliminated (Wolseley and Aguirre-Hudson, 1997; Johansson et al., 2006; Hämäläinen et al., 2014; Miller et al., 2018). Lichens depending on tree species with low fire resistance are particularly susceptible to being lost in fires due to the death of host trees (Johansson et al., 2006). Regardless of their destructive effect, severe forest fires also provide substrates by increasing the availability of deadwood and young trees of various tree species, which may be beneficial for lichen diversity (Lõhmus et al., 2018). The effects of fire disturbance on epiphytic lichen communities remain scarcely studied and deficiently understood. In particular, the importance of fire severity has been overlooked. In addition, only scattered attention has been given to the diversity of epiphytic lichens in early-successional deadwood-rich forests.

In this study, we investigated how the species richness and composition of epiphytic lichens on living and dead *Pinus sylvestris* are affected by prescribed fire in boreal pine-dominated forests. Our study includes two types of fires: 1) low-severity surface fires, which were investigated via prescribed burning in semi-natural (or overmature) stands where fire severity was low, and 2) high-severity fires, investigated via prescribed burning in groups of trees retained in clearcut sites, where fire severity was high. In addition, we surveyed unburned semi-natural (or overmature) stands (i.e. control sites). The prescribed burnings had been completed 21 years prior to the lichen surveys. Our study objectives are to 1) examine how fire disturbance affects the species richness and composition of lichen communities, 2) to assess whether these effects differ between fires of low and high severity, and 3) to examine how lichen traits mediate their response to fire disturbance. Our study involves prescribed fires, but we posit that the results may be applied to natural fire dynamics as well. Thus, we aim to provide information on the effects of both prescribed and natural fires on epiphytic lichens. By investigating the effects of stand-replacing fires, we also address the significance of natural young forests as habitats of epiphytic lichens.

2. Methods

2.1. Study area and experimental design

The study was carried out in the municipality of Lieksa in eastern Finland, within and near Patvinsuo national park at around 63.2° N 30.7° E. The study region is at the border of southern and middle boreal vegetation zones, 150–200 m above sea level. The data was collected from 12 study sites, each 3–5 ha in size, which are a part of a large-scale field experiment (https://www.jarikouki.com/fire-experiment). Before experimental treatments, the forests of all the study sites were similar in structure and management history. The stands were sub-xeric and un-even aged, with the dominant trees being approximately 150 years old. *Pinus sylvestris* was the dominant tree species in the overstory. Lower layers were dominated by *Picea abies*. In addition, the stands contained scattered deciduous trees (mainly *Betula* spp.). The mean stock volume in the study sites was 287.9 m³/ha (SD = 71.1), consisting of 72 %, 22 % and 5 % of *Pinus, Picea* and *Betula*, respectively. The study sites had history of selective loggings (Sippola et al., 2001; Uotila et al., 2002), but no loggings had been performed for at least 75 years. Fires have been absent from the region since the late 1800s (Lehtonen and Huttunen, 1997), and time since the previous fire was over 100 years in all study sites.

The experiments of this study included two factors, prescribed burning and harvesting. In the current study, we included the following treatment combinations: 1) unburned and unharvested (i.e. control; three replicates), 2) burned and unharvested (three replicates), and 3) burned and harvested with a retention level of 10 or 50 m³/ha (six replicates, three of each retention level). The retention groups were 200–500 m² in size, consisting of about 15–40 trees. Since the fire had severe effects in the burned and harvested sites (Nirhamo et al., 2023a), they are henceforth referred to as high-severity fire (HSF) sites. The two retention levels were combined for the analyses, since retention level had a minimal effect on the impacts of fire regarding both forest structure and lichen communities. We consider these sites to be representative of the conditions prevailing on sites affected by stand-replacing disturbances. Conversely, in the burned and unharvested sites, fire was significantly less severe, and those sites are henceforth referred to as low-severity fire (LSF) sites. The reduction of humus layer, average scorch height and tree mortality caused by the fires describe the severity of the fires; all of these were higher in the HSF sites than the LSF sites (Table 1a). The experimental treatments were carried out in 2001, i.e. 21 years prior to the surveys of this study.

2.2. Sampling design and tree selection

We surveyed lichens on 420 trees located in 12 sites. Most of the surveyed trees represented the dominant age and size class of the sites, although some smaller trees were also included. We surveyed 10 trees in

Table 1
a) Characterisation of fire severity in LSF and HSF sites based on humus layer reduction, average scorch height and immediate mortality among pine (*Pinus sylvestris*) and spruce (*Picea abies*) caused by the fires. Here, "immediate mortality" refers to mortality within one month of the fires. b) The number of living trees, snags and logs sampled in the unburned, LSF and HSF sites.

	Unburned	LSF	HSF
a) Characterisation of fire severity			
Humus layer reduction	–	8 %	27 %
Average scorch height (m)	–	2.2	4.9
Immediate mortality, pine	–	6.4 %	47.6 %
Immediate mortality, spruce	–	26.8 %	85.3 %
b) Sampled trees			
Living tree	132 (88 %)	134 (89 %)	21 (18 %)
Snag	14 (9 %)	6 (4 %)	23 (19 %)
Log	4 (3 %)	10 (7 %)	76 (63 %)

the sites with a retention level of 10 m³/ha (3 sites), 30 trees in study sites with a retention level of 50 m³/ha (3 sites), and 50 trees in un-harvested sites (6 sites). The goal was to adjust the survey effort in each study site to reflect the density of trees that were present after the treatments of the study sites. With this goal in mind, we also wanted to strike a balance between surveying enough trees in the study sites with the lowest tree density (retention level of 10 m³/ha) and restraining the survey efforts in the sites with the highest tree density (unharvested sites) from being excessive. Thus, the number of trees we surveyed in study sites with different treatments is not directly proportionate to the actual tree densities of the study sites.

All the retention trees in the harvested sites (the trees themselves, not their lichens) were surveyed and mapped in 2021 (Nirhamo et al., 2023a), a year prior to this study. Thus, we had a complete list of all the retention trees in these study sites, including living trees, snags and fallen trees, all species and all sizes. The total number of retention trees on these study sites was 1001. We filtered this list to include only *Pinus sylvestris* trunks with a dbh (diameter at breast height) > 10 cm, resulting in a list of 151 retention trees. From the filtered list, we randomly selected 10 trees in each study site with 10 m³/ha retention and 30 trees in each study site with 50 m³/ha retention. We selected the trees in such a way that the proportions of living trees, snags and logs among the study trees were similar to their proportions at each site. For example, if a site with a retention level of 10 m³/ha contained 50 living trees, 30 snags and 20 logs we would have randomly selected 5 living trees, 3 snags and 2 logs to be study trees.

In the unharvested sites, where the trees had not been previously surveyed, we had to apply a different method for selection of trees. In the burned unharvested sites, the sampling was done within the burned area. In the unburned unharvested sites, we delineated a circle with a radius of 100 m where the central point of the circle was the center of the study site. Within these delineated areas, we randomly assigned co-ordinates for 50 locations. In the field, we walked to these coordinates, and then selected the nearest *Pinus sylvestris* trunk with dbh >10 cm, irrespective of whether it was a living tree, a snag, or a log, to be a study tree. In the case of logs, we measured the distance to the base of the tree. This method allowed us to select living trees, snags and logs propor-tionately to their presence in the study sites, similarly to our procedure in the retention sites.

With this sampling scheme, most sampled trees were living trees in the unburned and LSF sites, and dead trees in the HSF sites (Table 1b). The proportion of living trees was similar in the unburned sites and low-severity fire (LSF) sites, indicating that the fires in the LSF sites induced negligible mortality in *Pinus sylvestris*. In the unburned sites, most dead trees were snags, whereas in the LSF sites, they were primarily logs. Nearly all trees in the high-severity fire (HSF) sites were dead, showing that the fires in those sites induced very high mortality in *P. sylvestris*. The majority of dead trees in HSF sites were logs.

2.3. Lichen surveys and classifications

We recorded presence-absence data of all lichens occurring on the lowest two meters of the trunk of the study trees. On living trees and snags, the limitation to the lowest two meters was for practical reasons, and on logs, the surveyed area was similarly limited to maintain comparability between tree types. On living trees, only lichens on bark were recorded. On dead trees, only lichens on exposed wood were recorded. The purpose of these limitations was to ensure that the sam-ples of living and dead trees represented their characteristic lichen communities. Especially on dead trees, the lichens on bark represent their legacy as living trees and do not reflect their nature as deadwood substrates. When necessary, specimens were collected for later identi-fication with microscopy and chemical spot tests. Lichen nomenclature followed Pykälä et al. (2022).

We categorized lichen species based on their primary substrates and successional stages. For primary substrate, the species were divided into

three categories based on what substrate the species predominantly occur on according to the views of the authors. "Epiphytes" include species that grow primarily on bark, as well as species that occur at a similar frequency on bark and wood. "Lignicolous" species include species that occur exclusively on wood, as well as species with a clear predominance of occurrence on wood, and facultative occurrence on bark. "Terricolous" species include species that grow primarily on the ground, i.e., soil. For successional stages, we split species into three classes: early-successional, late-successional and generalist species. Early-successional species refer to species that occur predominantly on young trees or fresh deadwood, and only rarely on old trees or dead-wood, and vice versa for late-successional species. Generalists refer to species that occur commonly in both early and late stages of succession. To make these classifications, we relied on the information provided by two studies that looked into lichen species composition on living *P. sylvestris* of different ages (Marmor et al., 2011; Bäcklund et al., 2016), as well as a dataset on the succession of lichen communities on standing dead *P. sylvestris* trunks (A. Nirhamo, unpublished data). We did not assign a successional stage to certain species due to lack of data or their context-dependence successional associations. The successional stages of primarily terricolous species were classified based on their occurrence patterns on deadwood and bark. Additionally, we split the observed lichen species to macrolichens (foliose and fruticose growth forms) and microlichens (crustose, leprose and squamulose growth forms).

2.4. Statistical analyses

We performed all statistical analyses in R version 4.2.2 (R Core Team, 2022). Since the number of sampled trees, especially the number of living or dead trees, varied between treatments, we compared the species richness of epiphytic lichens in the unburned, LSF and HSF sites with sample-based rarefaction, where study trees were considered as samples. Rarefaction-extrapolation curves were computed and plotted using the function *iNEXT* in the package *iNEXT* (Hsieh et al., 2016). The rarefaction was based on presence-absence data of species and was done separately for 1) all trees, 2) living trees, and 3) dead trees.

We analyzed the effects of low and high-severity fires to site-scale community composition with non-metric multidimensional scaling (NMDS), using the Bray-Curtis dissimilarity index with the function *metaMDS* in the package *vegan* (Oksanen et al., 2022). Since the data consisted of presence-absence of species on individual trees, the site-scale abundance of a species consisted of the sum of study trees on which its presence was recorded. Species with less than five total oc-currences were excluded from this analysis.

We assessed species-specific responses to fires by analyzing the as-sociations between species and groups of sites, i.e. treatments (De Cáceres and Legendre, 2009). We used the function *multipatt* in the package *indicspecies* (De Cáceres and Legendre, 2009) to calculate the phi coefficient of association (r_Φ) between species and sites, with treatment (unburned, LSF, HSF) as the clustering factor for sites. Since HSF sites were more numerous than other treatments, we used the group-equalized modification of the phi coefficient (Tichý and Chytrý 2006). We considered species that were associated with unburned sites (and, by extension, dissociated with LSF and HSF sites) to be fire-sensitive, and species that were associated with LSF and HSF sites to benefit from low and high-severity fires, respectively. By considering combinations of groups (De Cáceres et al., 2010), we also identified species that benefited from both types of fires (associated with LSF + HSF) and species that were sensitive only to high-severity fires (associ-ated with unburned + LSF) or low-severity fires (associated with un-burned + HSF). We accepted only associations with a high level of statistical significance ($p > 0.01$).

3. Results

We recorded a total of 109 lichen species: 82, 79 and 71 species on

unburned, HSF and LSF sites, respectively (Supplement 1). These included 19 species that are red-listed in Finland (Pykälä et al., 2019); 15, 9 and 7 species on unburned, LSF and HSF sites, respectively. Total species richness was highest in the unburned sites and lowest in the HSF sites, but the differences were small and the confidence intervals (90 %) of the rarefaction curves overlapped. However, the overlap between the confidence intervals of the unburned and the HSF sites was minimal (Fig. 1a). On living trees, species richness was highest on the LSF sites and lowest on the HSF sites (Fig. 1b). On dead trees, species richness was highest on unburned sites and, when differences in sample sizes were taken into account, lowest on the HSF sites (Fig. 1c). Based on the rarefaction curves, species richness on dead trees was clearly restricted in the unburned and the LSF sites by the low number of sampled deadwood. The sample size of deadwood in the unburned and the LSF sites was small due to low deadwood quantity.

The analysis of associations between species and sites identified 21 species as fire-sensitive, with 13 species sensitive to both types of fires and 8 species only to high-severity fires (Table 2). No species were sensitive only to low-severity fires. Furthermore, 30 species were identified to benefit from fires: 11 from both fire severities, 5 from low-severity fires, and 14 from high-severity fires. The fire-sensitive species were mainly late-successional microlichens (e.g. *Chaenotheca ferruginea, Mycoblastus sanguinarius, Xylopsora friesii*). The fire-benefiting species mostly consisted of primarily terricolous macrolichen species as well as early-successional lignicolous microlichen species. In addition, several species were observed on deadwood in the unburned sites, but not on the LSF or HSF sites. However, these species had a low number of total occurrences, and thus they were not recognized by the analysis of associations between species and sites.

Each treatment had a distinct lichen composition (Fig. 2). Overall, fires increased the occurrence of early-successional species, while late-successional species decreased (Fig. 3a, b). Fires also increased the occurrence of macrolichens and reduced the occurrence of microlichens, particularly on living trees (Fig. 3c, d). Fires increased the occurrence of primarily terricolous species on both living and dead trees, whilst the occurrence of epiphytic species on living trees decreased (Fig. 3e, f). Fires also slightly increased the occurrence of lignicolous species on living trees.

4. Discussion

In our study, fires had small effects on lichen species richness on *Pinus sylvestris*, but they caused significant changes in lichen community composition, the magnitude of which increased with fire severity. These changes were characterized by 1) a replacement of late-successional species by early-successional species, 2) a replacement of microlichens by macrolichens, and 3) an increase of primarily terricolous species, which, on living trees, was accompanied by a loss of epiphytic species. Thus, our study showed that the impacts of fire disturbance on epiphytic lichens entail more complexity than merely a destructive effect (see also Lõhmus et al., 2018). Impacts of the fire on epiphytic lichens remained clear 21 years after fires, either via different substrate composition (HSF sites), or scorched bark and changed lichen composition on living trees (LSF sites). Even though high-severity fires generated high quantities of deadwood, lichen diversity on deadwood was at a similar level on the unburned and HSF sites. This indicates that the deadwood on the unburned sites provided habitat of higher quality than the deadwood on the HSF sites. Our results only concern the lowest two meters of the tree trunks. The impacts of fire on lichens may have been different in the upper parts of the trunks which were not reached by the flames, and studying entire trunks could have changed final conclusions substantially.

4.1. Effects of high-severity fires on epiphytic lichens

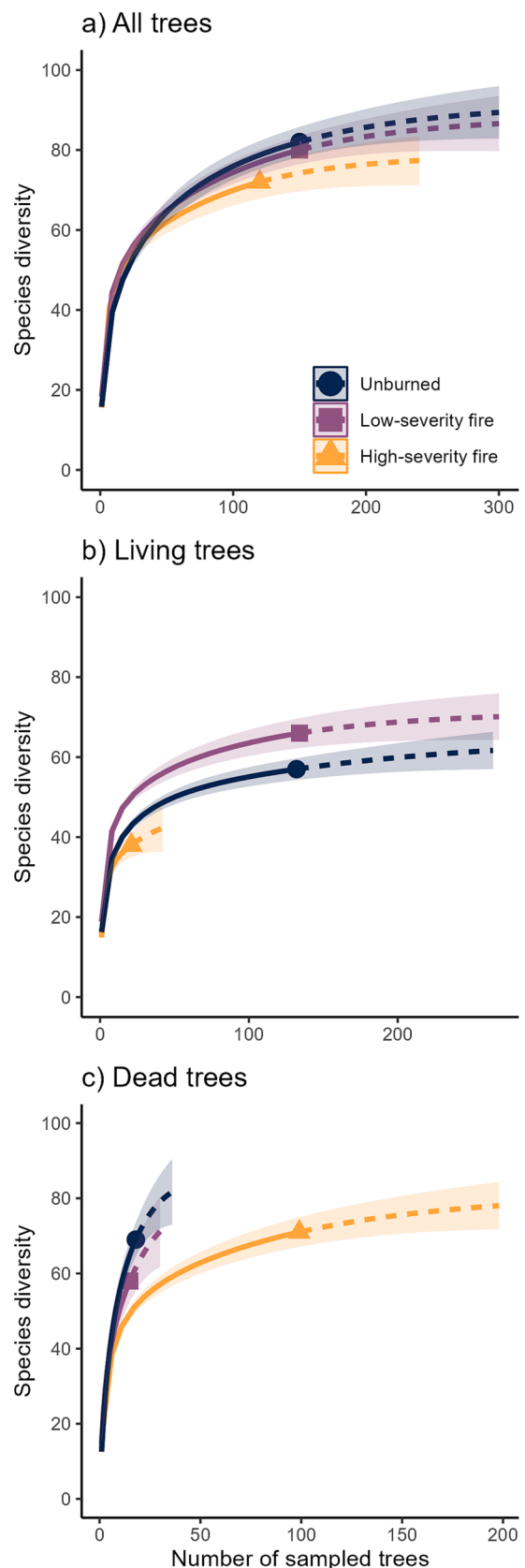The high-severity fires killed almost all trees. Lichen communities on

Fig. 1. Sample-based rarefaction curves (with 90 % CI) showing cumulative numbers of lichen species relative to the number of sampled trees on a) all trees, b) living trees and c) dead trees across the treatment categories. The intact lines refer to interpolated rarefaction, and the dashed lines refer to extrapolated rarefaction.

Table 2

Species with a statistically significant association with a site type or a combination of site types. "IUCN" indicates the IUCN red list status of the species in the Finnish red list (Pykälä et al., 2019). When not specified, species are classified as LC (Least Concern). "rφ" expresses the strength of the association with a range from 0 to 1. Only associations with a high level of statistical significance (p > 0.01) are shown. "Gen" short for "generalist", "Mi" short for "microlichen", "Ma" short for "macrolichen".

Species	IUCN	rφ	Suc. stage	Primary substrate	Growth form
Fire-sensitive species (HSF + LSF)					
Ochrolechia androgyna		0.549	Late	Epiphyte	Mi
Micarea melanea		0.547	Late	Epiphyte	Mi
Chaenotheca ferruginea		0.508	Late	Epiphyte	Mi
Lepraria spp.		0.492	Gen	Epiphyte	Mi
Mycoblastus sanguinarius		0.46	Late	Epiphyte	Mi
Cladonia digitata		0.436	Late	Epiphyte	Ma
Ochrolechia microstictoides		0.416	Late	Epiphyte	Mi
Xylopsora friesii		0.393	Late	Epiphyte	Mi
Violella fucata		0.260	Late	Epiphyte	Mi
Japewia subaurifera	NT	0.256	Late	Epiphyte	Mi
Usnea dasopoga		0.211	Gen	Epiphyte	Ma
Loxospora elatina		0.189	Gen	Epiphyte	Mi
Parmeliopsis hyperopta		0.144	Gen	Epiphyte	Ma
Fire-sensitive species (HSF)					
Lecidea nylanderi		0.597	Gen	Epiphyte	Mi
Hypocenomyce scalaris		0.514	Late	Epiphyte	Mi
Calicium parvum		0.478	Late	Epiphyte	Mi
Hypogymnia physodes		0.406	Gen	Epiphyte	Ma
Bryoria fuscescens		0.345	Gen	Epiphyte	Ma
Lecanora hypoptella		0.336	N/A	Epiphyte	Mi
Platismatia glauca		0.305	Gen	Epiphyte	Ma
Imshaugia aleurites		0.177	Gen	Epiphyte	Ma
Fire-benefiting species (HSF + LSF)					
Cladonia botrytes		0.759	Early	Lignicolous	Ma
Cladonia rangiferina		0.723	Gen	Terricolous	Ma
Vulpicida pinastri		0.652	Gen	Epiphyte	Ma
Cladonia arbuscula		0.573	Gen	Terricolous	Ma
Placynthiella spp.		0.426	Early	Terricolous	Mi
Cladonia gracilis		0.322	Early	Terricolous	Ma
Cladonia cornuta		0.306	Early	Terricolous	Ma
Hypogymnia tubulosa		0.304	Gen	Epiphyte	Ma
Cladonia crispata		0.262	Early	Terricolous	Ma
Tuckermannopsis chlorophylla		0.290	Gen	Epiphyte	Ma
Lecanora symmicta		0.154	Early	Epiphyte	Mi
Fire-benefiting species (LSF)					
Lecidea turgidula		0.298	Early	Epiphyte	Mi
Cladonia deformis		0.256	Gen	Terricolous	Ma
Lecanora cadubriae	VU	0.256	N/A	Epiphyte	Mi
Alectoria sarmentosa	NT	0.243	Late	Epiphyte	Ma
Bryoria fremontii	NT	0.228	Late	Epiphyte	Ma
Fire-benefiting species (HSF)					
Cetraria ericetorum		0.465	Early	Terricolous	Ma
Trapeliopsis granulosa		0.461	Early	Terricolous	Mi
Xylographa parallela		0.447	Early	Lignicolous	Mi
Xylographa vitiligo		0.417	Early	Lignicolous	Mi
Calicium trabinellum		0.416	Early	Lignicolous	Mi
Cetraria sepincola		0.413	Early	Epiphyte	Ma
Calicium glaucellum		0.324	Early	Lignicolous	Mi
Mycocalicium subtile		0.314	Early	Lignicolous	Mi
Xylographa rubescens		0.305	Early	Lignicolous	Mi
Trapeliopsis flexuosa		0.304	N/A	Lignicolous	Mi
Cladonia coniocraea		0.288	Gen	Epiphyte	Ma
Xylographa trunciseda	VU	0.255	Early	Lignicolous	Mi
Lecanora pulicaris		0.231	Early	Epiphyte	Mi
Lecanora circumborealis		0.168	Early	Epiphyte	Mi

Fig. 2. The first two dimensions of the nonmetric multidimensional scaling (NMDS) comparing lichen communities in the 12 study sites by treatment categories. Each symbol represents a study site.

have affected the entire tree. In any case, surviving trees enrich the structure of post-fire stands (Lampainen et al., 2004), consequently leading to more diverse lichen communities (Goward and Arsenault, 2018). Surviving trees may also act as lifeboats, from which lichens may be able to colonize the regenerating trees. In natural high-severity fires, unburned refugial patches are typical (Wallenius et al., 2004), and they probably have an important role in maintaining local epiphyte diversity in fires.

As trees die in high-severity fires, the newly formed deadwood may offer alternative substrates for epiphytes (Löhmus et al., 2018). Still, in our data, total species richness on deadwood was similar in HSF and unburned sites, even though deadwood was much more abundant in the former. We consider this to be because of the higher heterogeneity of deadwood in the unburned sites, most importantly in terms of time since tree death, which is a central factor for lichen communities on deadwood (Santaniello et al., 2017; Saine et al., 2018). In the HSF sites, the deadwood had formed at most 21 years ago, whereas the longevity of snags originating from *Pinus sylvestris* can be over 200 years (Rouvinen et al., 2002a). This range of variability was better represented in the unburned sites. This phenomenon is comparable to a study where relatively fresh high stumps on clearcut sites hosted lower lichen diversity than the more diverse deadwood in mature forests (Hämäläinen et al., 2021). Importantly, the snags on the HSF sites appear to not possess features that enable such high longevity, instead, they have been estimated to remain standing for about 50 years at most (Nirhamo et al., 2023a). As such, the formation of high-longevity standing deadwood from the currently present snags in the HSF sites seems highly unlikely, meaning that these sites would not provide habitat to lichens dependent on high-longevity snags (Santaniello et al., 2017) in the future, either.

4.2. Effects of low-severity fires on epiphytic lichens

The proportion of dead trees was similar in the LSF sites and the unburned sites, indicating that the mortality of *P. sylvestris* caused by the surface fires was negligible. The effect of surface fires was apparent on the surviving trees and persisted 21 years after the fire. In these sites, the fire had scorched only parts of the trunks, and lichen cover had persisted

the surviving trees in the HSF sites were heavily altered by fire, as even though the trees survived, much of the pre-fire lichen communities had been eliminated. In addition to the direct effects of fire, the surviving trees had gone through intense bark peeling, which could have caused further lichen extinctions and hindered recolonization (see Lie et al., 2009). However, we surveyed only the lowest two meters of the trees. Lichens may have survived better in the upper parts of the trunk, which were less affected by the flames, although the possible bark peeling may
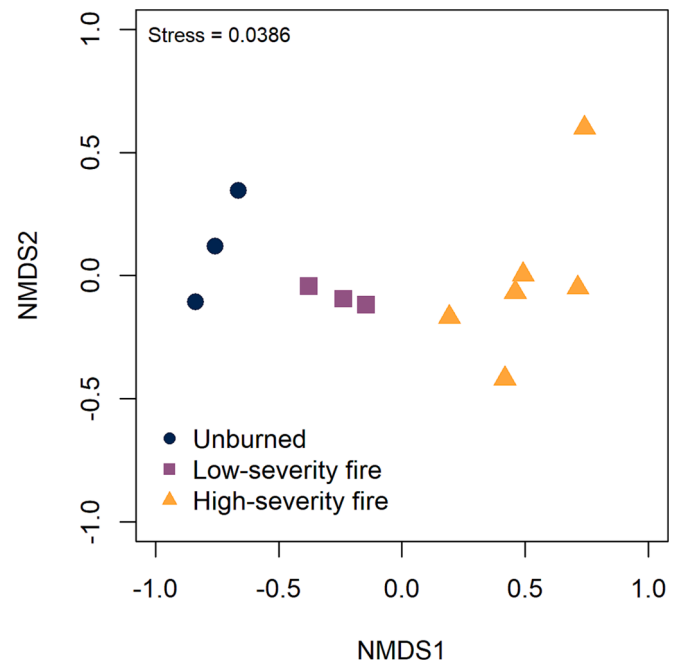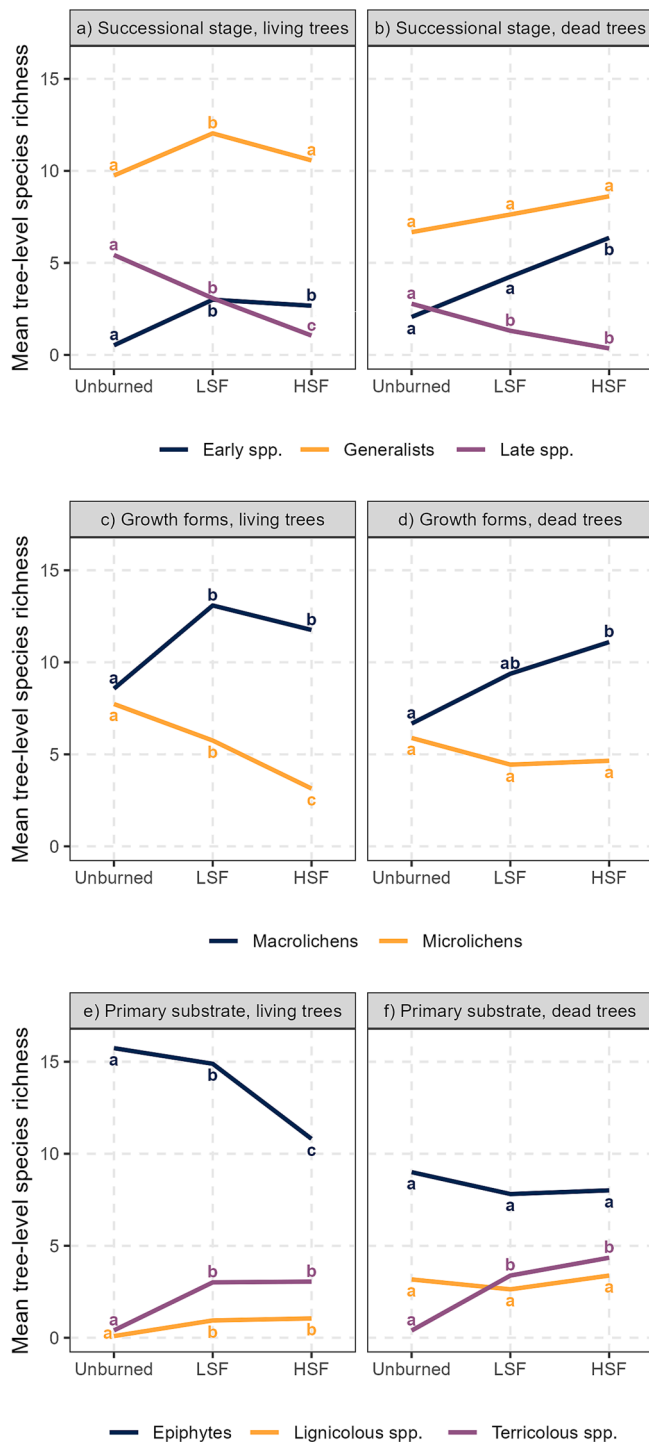
Fig. 3. Mean number of lichen occurrences on living and dead trees by successional stage (a, b), growth form (c, d) and primary substrates (e, f) in unburned sites, low-severity fires and high-severity fires. The letters express the statistical significance of the differences between treatment categories based on Tukey's tests. Statistical significance was less likely to be detected in the occurrence patterns on dead trees due to the small sample size of dead trees in the unburned and LSF sites.

even in some parts of the lowest two meters. Still, some species that were common on the living trees of the unburned sites occurred much more rarely in the LSF sites, even on the non-scorched parts of the trunks. The mechanism causing their disappearance, and apparently preventing or slowing down their recolonization, is not entirely clear, since it seems possible that they could have survived the fire in the non-scorched parts

of the trunks.

Before the fire, the deadwood composition of the LSF sites was presumably similar to that of the unburned sites, including a similar range of variability in time since death. Pre-fire deadwood is, however, vulnerable even to low-severity fires (Horton and Mannan, 1988; Eriksson et al., 2013). The majority of deadwood consisted of snags in the unburned sites and of logs in the LSF sites, suggesting that many of the snags in the LSF sites had fallen as an effect of the fire. If this was the case, it was probably the main reason for the lower lichen richness on deadwood in the LSF sites compared to the unburned sites, since the logs on the LSF sites (i.e. snags that possibly fell as an effect of the fire) hosted rather species-poor lichen communities. Many of these logs were in advanced stages of decay, where epixylic vegetation consists mainly of bryophytes or vascular plants rather than lichens (Söderström, 1988).

4.3. The influence of lichen traits to the response to fire

Our results indicate that species traits are important to understand the responses of epiphytic lichens to fires. As may be expected, fire disturbances caused a shift from late-successional communities to early-successional communities. The former were composed of species that are characteristic to mature and old living trees or high-longevity deadwood, whilst the latter were formed by primarily terricolous species and species found on fresh deadwood. On the HSF sites, this shift was caused by the replacement of late-successional substrates by early-successional substrates, i.e. fresh deadwood consisting mainly of logs. On the LSF sites, the changes in substrate availability were smaller, but the destructive effect of the low-severity fires was specifically directed to late-successional species. The exception to these patterns was found in the occurrence of the pendulous species *Alectoria sarmentosa* and *Bryoria fremontii*, which are usually sensitive to disturbances and associated with late-successional habitats (Esseen et al., 1996). Surprisingly, these species benefited from low-severity fires. The partial opening of the canopy and thus increased light following the mortality of fire-sensitive tree species in the LSF sites may have contributed to their increased occurrence. Positive effects of low-severity fires due to increased light availability would have been plausible even on a wider scale, since epiphytic lichen diversity is generally favored by increased light availability (Ellis, 2012; Marmor et al., 2013; Nirhamo et al., 2023b). However, no clear signs of this were detected.

The fires increased the occurrence of macrolichens and decreased that of microlichens, particularly on living trees. Previous studies have shown similar responses of lichen growth forms to fire (Johansson et al., 2006; Lõhmus et al., 2018). On the other hand, the species benefiting from the abundant deadwood on the HSF sites predominantly were obligately lignicolous species that, like nearly all obligately lignicolous lichens (Spribille et al., 2008), were microlichens. The increase of macrolichens was driven especially by various species of *Cladonia* (see also Lõhmus et al., 2018), many of which were primarily terricolous, which were abundant on the logs in the HSF sites. These species had also colonized the bases (i.e. the most heavily fire-affected parts) of living trees in both types of burned sites. Some studies have shown that microlichens are sensitive to disturbance (Johansson et al., 2006; Lõhmus et al., 2018; Kantelinen et al., 2022), while others have indicated microlichens to follow early-successional strategies (Rogers 1990; Lewis and Ellis, 2010). Thus, the responses of growth forms to disturbance seems to be context-dependent and therefore difficult to predict. However, at least on deadwood, microlichens seem to be the more disturbance-sensitive group (Kantelinen et al., 2022).

4.4. Fire-benefiting and fire-sensitive species

Previous studies have indicated that epiphytic lichens are highly sensitive to fire disturbance (Wolseley and Aguirre-Hudson, 1997; Johansson et al., 2006; Hämäläinen et al., 2014; Miller et al., 2018; Miller et al., 2022), but our analyses revealed a higher number of fire-

benefiting than fire-sensitive species. However, most fire-benefiting species were common generalists or species inhabiting fresh dead-wood. These species were mostly not favored by fire per se, but rather by the abundant formation of deadwood in high-severity fires. In contrast, late-successional species generally were fire-sensitive. Importantly, there are two factors which reduced the number of fire-sensitive species. First, our study exclusively focused on the fire-resistant *Pinus sylvestris*. We excluded fire-sensitive trees (e.g. *Picea abies*) from our study, because examining the effects of fire on lichens on these trees is probably redundant, given the high likelihood of host tree death even in low-severity fires (Linder et al., 1998; Lampainen et al., 2004; Johansson et al., 2006). Thus, including other tree species would undoubtedly have increased the number of fire-sensitive species, and we would have overall observed the fires to have more severe effects on epiphytic lichens.

Second, the unburned sites were not entirely representative of nat-ural pine-dominated forests of the region in terms of deadwood composition. Based on our sample, only about 10 % of the trees in the unburned sites were dead, while in natural pine-dominated forests, coarse woody debris may account for approximately 30 % of total tree volume (Rouvinen et al., 2002b). In particular, large quantities of high-longevity standing deadwood are characteristic for natural pine-domi-nated forests (Linder and Östlund, 1998; Rouvinen et al., 2002a; Kuu-luvainen et al., 2017), but it was scarce in our study sites. We consider the lack of deadwood to be due to management history, specifically selective cuttings performed 100–150 years ago (Sippola et al., 2001; Uotila et al., 2002). We presume that in more natural stands, lichen diversity on deadwood would have been higher, where also the losses in lichen diversity on deadwood caused by both low and high-severity fires would have been more substantial. As such, deadwood-associated spe-cies were heavily underrepresented among fire-sensitive species in our data.

4.5. Implications for management

In natural forest dynamics, early-successional forests sustain high species diversity in various organism groups (Kouki et al., 2001; Swanson et al., 2010; Hilmers et al., 2018). For example, they harbor a higher richness of saproxylic insects and fungi than any other succes-sional stage (Similä et al., 2002; Junninen et al., 2006). However, this is not the case for epiphytic lichens. Much of their diversity is reliant on old living trees or high-longevity deadwood, and the survival of these structures largely determines the impact of fire on epiphytic lichens. As such, fire disturbance can have variable effects on epiphytic lichens contingent upon fire severity. The low amount of deadwood on the unburned sites hosted a similar number of species as the abundant deadwood on the HSF sites, which emphasizes the significance of deadwood quality in addition to deadwood quantity. Other types of disturbances that promote deadwood quantity, such as bark beetle outbreaks (Hlásny et al., 2021), may also be expected to fail in providing habitat to many deadwood-associated lichens due to the lack of high-longevity standing deadwood.

Restorative burning of forests has many ecological benefits (Similä and Junninen, 2012; Burrows and McCaw, 2013; Sandström et al., 2019; Lindberg et al., 2020; Koivula and Vanha-Majamaa, 2020). However, we showed that fire disturbance has harmful impacts, which increase with fire severity, on late-successional lichen communities on living and dead *P. sylvestris* trunks. The intensive and widespread forest management in Fennoscandia has caused significant declines of the habitats and thereby populations of late-successional lichen species (Pykälä et al., 2019; Mönkkönen et al., 2022; Nirhamo et al., 2023b). Therefore, fires, whether natural or prescribed, can be assumed to have considerable negative effects on lichen species of conservation concern. Indeed, we found a higher number of red-listed species on unburned sites than burned sites. This also implies that the amplification of forest distur-bances, including fire, caused by climate change (Lehtonen et al., 2016;

Seidl et al., 2017) poses a significant threat to lichen conservation. Lastly, lichen abundance (i.e. biomass), while not addressed in our study, may be expected to be reduced by fires. This could have harmful effects on the functioning of food webs (Pettersson et al., 1995). Restorative burning is considered a tool mainly to be applied in forests with a history of intensive management, and to be used sparingly and with high caution in more natural forests with high diversity e.g. in the form of high deadwood volume (Similä and Junninen, 2012). Our study supports this notion; prescribed burning should not target sites that contain substrates with special importance to lichen diversity. However, the negative effects of prescribed burning in previously managed and impoverished stands should not be a concern, since the damage caused to epiphytic lichens in such stands is likely to be negligible from a conservation perspective.

CRediT authorship contribution statement

Aleksi Nirhamo: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. **Aino Hämäläinen:** Conceptu-alization, Methodology, Writing – review & editing. **Karoliina Hämäläinen:** Investigation, Writing – review & editing. **Jari Kouki:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121558.

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