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Research article

Effects of boreal ground layer shrubs and bryophytes on the diversity, biomass and composition of lichen communities across contrasting ecosystems

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There has been much recent interest in understanding how abiotic factors such as light, nutrients, and soil moisture affect the composition and biomass of lichen communities. Meanwhile, whether and how ground layer vegetation such as bryophytes and shrubs also influence lichen communities have received much less attention, particularly regarding how these effects vary across environmental gradients. In this study, we used a long-term (19-year) biodiversity manipulation experiment to assess the importance of feather moss and ericaceous dwarf shrub removals on the composition and diversity (assessed via metabarcoding) and biomass (assessed via PLFA markers) of terricolous lichen communities along a 5000-year boreal forest post-fire chronosequence in northern Sweden. Overall, our results showed that shrub removals had a greater impact than moss removals on the biomass and composition of lichen communities. Shrub removals increased lichen alpha-diversity while decreasing lichen beta-diversity. This is mainly because, although the number of lichen species increased in the absence of shrubs, lichen communities were strongly dominated by *Cladonia* spp. However, the effects of shrub removals were context-dependent, with greater effects observed in older ecosystems. Our results highlight that shrubs had a greater impact than moss in shaping terricolous lichen communities in boreal forests, with increasing effects from young ecosystems to older ones. We conclude that the foreseen expansion of vascular plants such as ericaceous shrubs into high latitude regions will probably have negative consequences on lichen cover, but that these effects will be dependent on the environmental context.

Keywords: biodiversity, bryophytes, forest productivity, lichens, metabarcoding, plant functional groups

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Introduction

Lichens are symbiotic associations between fungi (i.e. mycobionts) and green algae and/or cyanobacteria (i.e. photobionts). They provide microhabitats for bacteria, microfauna and mesofauna, and in turn serve as food for both invertebrates and vertebrates such as mites, springtails, slugs and reindeer (Bokhorst et al. 2015, Asplund and Wardle 2017, Roos et al. 2022). Although they are often minor contributors to total biomass in forests, they can still have an important role in driving ecosystem biogeochemistry (Knops et al. 1996, Cornelissen et al. 2007). For instance, some lichens can fix nitrogen (N) from the atmosphere (Belnap 2002), contribute to rock weathering (Adamo and Violante 2000), and enhance soil moisture and nutrient availability (Eldridge et al. 2010, Delgado-Baquerizo et al. 2015). Lichens can also affect plant dispersal and seedling establishment through their beneficial effects on microclimate and soil physicochemical properties, or by acting as a physical barrier to germination (Houle and Filion 2003, Deines et al. 2007, Nystuen et al. 2019). These effects are taxon-specific and depend on local conditions of moisture (Zamfir 2000, Escudero et al. 2007, Nystuen et al. 2019), which suggests that the impact of lichens on plant communities and vice versa in turn depends on environmental context (Favero-Longo and Piervittori 2010).

Changes in environmental conditions such as light exposure, nutrients and soil moisture are central factors that affect the biomass and productivity of lichens (Jonsson et al. 2008, Jonsson Čabrajič et al. 2010, Hämäläinen et al. 2020). For instance, a decrease in light conditions due to canopy closure is detrimental to lichen biomass (Boudreault et al. 2008, 2013), and lichen productivity is often greatest in sunny and open areas (Gustafsson and Eriksson 1995). Although trees are often considered the main driver of shading in forested ecosystems, other plant functional groups in the understory, such as ericaceous dwarf shrubs and mosses, can also significantly influence ground lichen communities. In particular, these plants compete for light and space on the ground surface, which can limit resources available for lichens, potentially influencing lichen cover and productivity (Cornelissen et al. 2001, Wardle et al. 2012, 2020, Fanin et al. 2019). However, the impacts of ericaceous shrubs and mosses on the diversity, composition and biomass of lichens, or how these impacts vary among ecosystems or across environmental gradients, remains largely untested (Pajunen et al. 2011, Chagnon and Boudreau 2019, Chagnon et al. 2021). Furthermore, most previous studies focusing on interactions between lichen and vascular plants, or among different cryptogams, have been conducted on dryland biocrusts, arctic lichen mats and arctic lichen woodlands (Horstkotte and Moen 2019, Pacé et al. 2019, Romero et al. 2020, Sun and Li 2021). As such, the present study, focused on boreal lichen communities, provides valuable new insights into how these interactions play out in different ecosystem states. This is particularly important considering that shrubs are expected to increase in high-latitude ecosystems over the next few decades mainly in response to climate warming (Myers-Smith et al. 2011, Mekonnen et al. 2021). In contrast, moss biomass has shown varying responses to warming, ranging from positive in boreal forests to negative in sub-arctic and alpine ecosystems (Elmendorf et al. 2012, Permin et al. 2022, Økland et al. 2023).

In this study, we explored the impact of experimental ericaceous shrub and moss removals on lichen communities across a long-term (5000-year) boreal forest post-fire chronosequence in northern Sweden. The chronosequence consists of 30 forested islands which vary considerably in time since the most recent fire (Wardle et al. 1997). With increasing time since fire, nutrient limitation on the islands becomes stronger and ecosystem biomass and productivity declines (Wardle et al. 2012). We used a biodiversity manipulation experiment that has been running for 19 years on each of the 30 islands, and includes full factorial removals of ericaceous dwarf shrubs and feather mosses (Wardle and Zackrisson 2005, Gundale et al. 2010, Fanin et al. 2018). We sought to test each of two hypotheses. First, removals of mosses and shrubs both increase lichen diversity and biomass because of reduced competition for space, light and nutrients (H_1). Second, we expected that the effect of moss and shrub removals should be more pronounced on younger islands (i.e. those with a shorter time since fire), as these islands have higher productivity and nutrient availability, making shrubs and mosses more competitive against other vegetation types (H_2) (Wardle et al. 2008, Gundale et al. 2011). As such, this study uses a long-term removal experiment across a strong ecological gradient to advance understanding of how plant functional group impacts on lichen communities may vary across contrasting environmental conditions.

Material and methods

Study site and experimental design

We used a biodiversity manipulation experiment that has been running for 19 years across a chronosequence consisting of 30 forested islands in two adjacent lakes in the boreal zone of northern Sweden, i.e. Lake Hornavan and Lake Uddjaure (65°55′–66°09′N, 17°43′-17°55′E). This lake archipelago serves as an ideal model system for studying the impacts of plant functional group removals, as each island functions as an independent ecosystem, enabling us to investigate ecological processes at meaningful spatial scales. The islands were all formed from glacial till deposited during the retreat of the Fennoscandian ice sheet approximately 9000 years ago. The main abiotic factor that varies across these islands is the frequency of fires that occur as a result of lightning strike; larger islands are struck by lightning more often and have therefore on average burned more recently (Wardle et al. 1997, 2003). Consequently, some larger islands have burned within the last 60 years, while some smaller islands have remained unburned for up to 5000 years (Wardle et al. 2012). As a result, the gradient of island ages represents ‘contrasting environments’, with younger islands being more productive and nutrient-rich compared to older, more nutrient-poor islands. Specifically, previous studies have shown that as time since fire increases, plant biomass and productivity, soil fertility and rates of decomposition and nutrient fluxes decline, while soil organic matter accumulates along this island chronosequence (Wardle et al. 2012, Clemmensen et al. 2013, Fanin et al. 2022, Supporting information). Consistent with previous work in this system (Wardle et al. 2003), we categorized these 30 islands into 10 'large' islands representing early stages of ecosystem development (> 1.0 ha; mean time since fire 585 years), 10 medium islands representing intermediate stages of ecosystem development (0.1–1.0 ha, 2180 years), and 10 small islands representing late stages of ecosystem development (< 0.1 ha, 3250 years) (Kardol et al. 2018, Fanin et al. 2019).

To understand the importance of biodiversity loss on soil communities and their functioning across contrasting ecosystems, we used a removal experiment, as described by Wardle and Zackrisson (2005), Gundale et al. (2010), Fanin et al. (2018) and Fanin et al. (2019). In August 1996, eight plots were established on each of 30 islands (240 plots in total), comprising a full factorial combination of removals of each of the three main plant functional groups present on these islands, i.e. tree root removal (performed by root trenching), ericaceous shrub removal (performed manually), and feather moss removal (performed manually). These plots have been maintained every year since the start of the experiment, with the removals of mosses and shrubs consistently maintained throughout the duration of the study. Specifically, the dominant shrubs were the ericaceous species *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Empetrum hermaphroditum*, while the dominant mosses included the feather mosses *Pleurozium schreberi* and *Hylocomium splendens*. These shrubs often form low-lying, prostrate growth forms, and the mosses develop dense carpets, both of which occupy substantial ground surface area, and compete with lichens for space and light on the forest floor. The three dominant ericaceous shrub species occupy 98% of the total vascular plant biomass species present and the remaining species were removed; mosses other than feather mosses were left in place (Wardle and Zackrisson 2005). As preliminary analyses showed no effect of the tree roots removal treatment on lichen communities, we present the results only for shrub and moss removals in this manuscript.

All plots are 55 × 55 cm, and the removal treatments were applied to the entire surface area. However, only the inner 45 × 45 cm area is used for measurement and sampling. We estimated aboveground dwarf shrub biomass for each species present in each plot by using the point intercept method as described by Wardle et al. (2003) (data presented in Kardol et al. 2018, Wardle et al. 2020). As such, we recorded the total number of times that the vegetation of each species was intercepted by a total of 100 downwardly projected points located throughout the plot. The total number of intercepts for each species was then converted to biomass per unit area through equations previously developed by destructively sampling calibration plots (Wardle et al. 2003). For bryophytes, we used the approach of Lagerström et al. (2007) to determine the biomass of each species (data presented in Fanin et al. 2018), which involved measuring the depth of the live moss layer (i.e. the actively growing, photosynthetic portion) of each species at each of 15 random points throughout the plot, and converting mean depth to biomass using previously established calibration equations.

Soil core sampling was conducted between 3 and 15 August 2015. One sample from the centre of each plot was collected using a stainless-steel cylinder to 10 cm depth for lichen community sequencing, and four additional samples were taken (one at each plot corner) for estimating lichen biomass. Lichens were collected from the entire soil core, which included lichens present on the soil surface, in the aboveground biomass, on twigs and within the moss layer. Mineral soil was excluded when present; this occurred only at the very bottom of some cores on the largest islands that had the shallowest humus layer and accounted for less than 1% of all soil cores. The small rocks and other non-organic debris, though generally minimal, were included in the soil cores during collection but were carefully removed by hand prior to grinding and analysis. All soil samples were frozen (−20°C) for microbial community analyses (i.e. metabarcoding and PLFAs) within a few hours after sampling until further analyses were performed.

Metabarcoding

To assess the lichen community structure of each sample, we utilized metabarcoding with high-throughput sequencing of amplified ITS2 markers, following the method by Ihrmark et al. (2012) and modified by Clemmensen et al. (2016). DNA was extracted from 50 mg of freeze-dried organic matter from the centre core of each plot using the NucleoSpin Soil Kit (Macherey-Nagel, Düren, Germany). Fungal ITS2 fragments were amplified using a combination of gITS7 (Ihrmark et al. 2012) and ITS4 (White et al. 1990) primers, each extended with 8 bp long sample-specific tags. The 30 µl PCR reactions consisted of 0.2 mM dNTPs, 0.75 mM $MgCl_2$, 0.5 µM fITS9 primer, 0.3 µM ITS4 primer and 0.75 U DNA polymerase (DreamTaq Green; Thermo Fisher Scientific). PCR cycling conditions included an initial 95 s at 94°C, followed by 20–35 cycles of 30 s at 94°C, 30 s at 56°C, and 30 s at 72°C, with a final 7 min at 72°C. Template concentrations and PCR cycle numbers were optimized for each sample though preliminary qPCR assays to ensure that amplification occurred in the exponential phase, where it is more quantitatively accurate. Each sample was run in triplicate to minimize stochastic PCR distortion of community composition. Negative controls for DNA extraction and PCR were included to check for contamination and product quality. Amplicons were purified using the Agencourt AMPure kit (Beckman Coulter) and concentrations were measured fluorometrically (Qubit Fluorometer, Invitrogen). Equal amounts of PCR products from each sample were pooled into five composite samples for sequencing. Adaptor ligation and PacBio (PSII) sequencing were carried out by SciLifeLab, Uppsala, Sweden.

Bioinformatics

Fungal sequences were proceeded, and lichen sequences were then identified using the bioinformatics pipeline SCATA (http://scata.mykopat.slu.se/). Sequences with an average quality score below 20 or below 3 at any single position, were discarded. Sequences with missing primer sequences or identification tags, or those with mismatching tags, were also excluded. A total of 520 450 sequences passed this initial quality control step, which represented 33% of the total sequencing output. During the SCATA clustering procedure, sequences were compared for similarity using USEARCH, with a minimum alignment length of 60% of the longest sequence. Pairwise alignments were scored with a mismatch penalty of 1, a gap opening penalty of 0, and a gap extension penalty of 1. Homopolymers were collapsed to 3 base pairs before alignment. Sequences were clustered into operational taxonomic units (OTUs) using single linkage clustering, requiring 98% sequence similarity for OTU inclusion. This threshold is commonly used to assign OTUs at the species level, as it corresponds to the typical intraspecific variation observed in fungal ITS regions. These OTUs were then assigned to functional guilds using comparisons to the UNITE Envir and INSD reference databases via the massBLASTer tool in the UNITE phylogenetic module (https://unite.ut.ee/), and reference sequences downloaded from public databases (Marthinsen et al. 2019). For each sequence, the 10 best-matching references were used for accurate taxonomic assignment. If no reliable taxonomic name was found, manual BLASTn searches were conducted against the INSDC database, using the 500 best-matching sequences. Global singletons were removed. Non-fungal sequences, comprising on average 13.6% of all sequences, were excluded from the analysis. As recommended by Tedersoo et al. (2014), sequences with BLASTn E-values of $< 10^{-50}$ were considered reliable for fungal kingdom assignments, while those $>10^{-20}$ were classified as 'unknown'. Sequences with E-values between 10^{-20} and 10^{-50} were manually verified against the 10 best matches. To account for at least 85% of the fungal sequences in each sample type (95.4% of all reads identified on average), the 514 globally most abundant fungal OTUs, each with at least 50 sequences, were identified. Among them, 14 of these OTUs were assigned to the putative functional guild of lichen. A list of lichens and associated assignments in databases can be found in the Supporting information. On average, lichens were represented by 78 reads per sample, with a range from 0 to 780 reads. The 14 OTUs identified in this study belonged to the class Lecanoromycetes and were spread among three orders: Agyriales, Pertusariales and Lecanorales (Fig. 1). Taxonomic assignments were made based on similarity thresholds of 98.0, 90.0, 85.0, 80.0 and 75.0% for species, genus, family, order and class, respectively. In cases where a high sequence similarity does not allow for a formal taxonomic assignment at a given rank (e.g. species or genus), the taxonomic rank is progressively elevated until a formal assignment can be made. Identification was performed twice independently to ensure objectivity in assigning taxonomic names to each lichen OTU. For the sake of clarity, we will refer to different OTUs

Figure 1. Neighbor-joining tree of representative sequences from obtained clusters and reference sequences belonging to lichens (Lecanoromycetes - Ascomycota) found across all samples. Three orders are present across all samples, each represented by a different color (light blue= Agyriales; yellow = Pertusariales; orange = Lecanorales). All branch nodes with boot-strap values of > 70 are shown with full lines indicating strong support, while those with values < 70 are shown with dashed lines, indicating weaker support. Agyriales and Pertusariales are typically associated with crustose growth forms that adhere tightly to substrate surface, and are often found on rocks, bark or soil.

as ‘lichen taxa’ throughout the manuscript, even though if the identification is made at higher phylum level. Sequence data are archived at the Sequence Read Archive (www.ncbi.nlm.nih.gov/sra) with accession number SRP125544.

Phospholipid fatty acids (PLFAs)

Metabarcoding is a promising strategy as it captures more diversity than traditional lichen inventories (Vondrák et al. 2024). However, this method cannot distinguish between lichen spores, propagules and thalli, thereby highlighting the importance of using complementary methods for assessing quantitative changes in lichen communities (Wright et al. 2019). To address this, we used fungal phospholipid fatty acids (PLFAs; nmol g^{-1}), allowing us to assess an estimation of fungal biomass, and thus obtain a complementary insights with a quantitative approach. In brief, this was done by multiplying the concentration of fungal phospholipid fatty acids (PLFAs; nmol g^{-1}), measured from the four samples collected in each corner of each plot, by the relative abundance of lichen taxa (represented as the percentage of lichen taxa relative to total fungal sequence reads). This quantitative value is used as an indicator of lichen biomass, a metric we refer to as ‘lichen PLFAs’.

The PLFAs were extracted according to Bligh and Dyer (1959) and White et al. (1979) after freeze-drying the sample. The abundance of PLFAs was quantified using a Perkin–Elmer Clarus gas chromatograph equipped with a flame ionization detector, and was converted to nmol PLFA per gram of organic matter using conventional nomenclature. We used the markers 14:0, 15:0, 16:0, 16:1, 17:0, 18:0, 18:1 and 18:2 as indicators for total fungal biomass across various lichen species (Dembitsky et al. 1991, Dembitsky 1992). To confirm the relationship between selected PLFA markers and lichen cover, we collected 30 lichen samples (i.e. 15 samples from open areas and 15 samples from forested shaded areas) across five sites from an independent experimental setup in southwestern France and estimated the lichen cover with the point-intercept method. Because we found significant and positive correlations between ‘lichen PLFAs’ and the percentage cover of lichens estimated directly on the bare ground (Supporting information), we used ‘lichen PLFAs’ for assessing the lichen abundance in response to the removal treatments across our island size gradient. Although this approach is subjected to some uncertainties, notably because these PLFA markers are not specific to lichens and it is impossible to distinguish the contribution of various ascomycete species to fungal biomass (Camenzind et al. 2024), this transformation allows us to convert DNA read abundances into relative quantitative values of different lichen groups (Fanin et al. 2019).

Statistical analyses

To illustrate the distribution of different lichen taxa found across treatments and island size classes, a neighbor-joining tree of representative lichen sequences from obtained clusters belonging to Lecanoromycetes (Ascomycota) was drawn using the ClustalW method in the MEGA-X software. Linear mixed models (LMM) were run to assess the effects of removal treatments, island size class and their interaction on plant and lichen PLFAs, alpha-diversity (measured as the richness of lichen taxa) and the proportions of the different lichen orders (Agyriales, Pertusariales and Lecanorales) using the package ‘nlme’. Island identity was included as a random effect to account for the natural variation among ecosystems. We then applied contrasts and performed post hoc tests (Tukey’s HSD test, $\alpha = 0.05$) to assess significant differences among island size classes or among removal treatments for each of the variable tested using the package ‘multcomp’. For lichen community composition analysis, multivariate analysis of variance was conducted to assess the effect of removal treatments, island size class, and their interaction on the overall structure of lichen communities. We used the package ‘mvabund’, which provides a more robust approach for analyzing multivariate count data using the *manyglm* function, specifying a family of ‘negative binomial’ to account for overdispersion in the count data. p-values were calculated using 999 iterations via PIT-trap resampling (Warton et al. 2012). We then performed non-metric multidimensional scaling (NMDS, 2 dimensions) with the function *metaMDS* in ‘vegan’ using Bray–Curtis dissimilarity matrices on the lichen communities (at the species level) to visualize the effect of shrub and moss removals across island size classes. We used vector fitting based on multiple linear regressions ($n = 999$) using the two NMDS axes as the explanatory variables and the variable of interest (e.g. relative abundance of lichen orders) as the dependent variable. Finally, we calculated lichen beta-diversity using the package ‘vegan’. Beta-diversity, measured as the pairwise difference in overall taxonomic composition between all samples using Bray–Curtis dissimilarity matrices, was analyzed to assess whether and how removal treatments affected the dissimilarity among plots of a given treatment ‘within’ an island size class. Differences in beta-diversity were tested by calculating the centroid for each combination island size × treatment using the function *betadisper*, which is a multivariate analogue of Levene’s test for homogeneity of variances. Subsequently, we used the function *TukeyHSD*, implemented in the package, to assess differences in beta-diversity among treatments. All statistical analyses were done using R ver. 4.0.0 (www.r-project.org).

Results

Lichen biomass estimated using PLFA markers (i.e. ‘lichen PLFAs’) was overall higher for small islands than for large and medium islands ($F_{2,27} = 4.3$, $p = 0.024$) (Table 1, Fig. 2a). Lichen PLFAs was positively affected by shrub removal ($F_{1,194} = 101.2$, $p < 0.001$) and moss removals ($F_{1,194} = 14.1$, $p < 0.001$) (Fig. 2a), which were the treatments that supported the lowest biomass of understory vegetation (Fig. 2b). The effect of shrub removals (but not moss removals) on lichen PLFAs varied among island size classes ($F_{2,194} = 3.5$,

Table 1. Results from full factorial mixed linear models to test for the effects of island size, moss removal, shrub removal, and their interactions on plant and lichen biomass, lichen relative abundance (%OTU representing lichen sequences across all fungal OTUs), lichen diversity and the proportions of lichen orders. Results are presented as F-values and p-values in brackets. F-values represent the statistical results of the models, indicating the strength of the relationship between the factors and the observed variables. Bold values indicate significant effects ($p < 0.05$), and the signs (+) or (–) denote positive or negative effects for the main effects of plant functional group removals, respectively. Lichen orders are represented by their relative abundance (% OTUs) in the lichen community. *Community structure was tested using the package 'mvabund', specifying a distribution family of 'negative binomial' to account for overdispersion in the count data.

Variable	Main effects			Interaction effects			
	Island size (IS)	Moss removal (–M)	Shrub removal (–S)	IS × –M	IS × –S	–M × –S	IS × –M × –S
Main variables							
Shrub + Moss biomass (g m^{-2})	1.9 (0.16)	**222.3 (< 0.0001) (–)**	**249.5 (< 0.0001) (–)**	2.2 (0.11)	1.6 (0.21)	**6.8 (0.01)**	0.9 (0.43)
Lichen PLFAs (nmol g^{-1})	**4.3 (0.024)**	**14.1 (< 0.0001) (+)**	**101.2 (< 0.0001) (+)**	0.9 (0.41)	**3.5 (0.034)**	**11.4 (0.001)**	1.3 (0.29)
Lichen relative abundance (%)	**6.0 (0.007)**	**18.1 (< 0.0001) (+)**	**106.9 (< 0.0001) (+)**	0.5 (0.59)	**4.5 (0.012)**	**14.5 (< 0.0001)**	0.9 (0.40)
Lichen alpha diversity (species richness)	**11.8 (< 0.0001)**	1.1 (0.29)	**132.5 (< 0.0001) (+)**	1.3 (0.28)	**7.8 (0.001)**	0.6 (0.44)	2.3 (0.099)
Lichen community structure*	**126.1 (< 0.001)**	**47.4 (0.012)**	**212.6 (< 0.0.001)**	38.6 (0.22)	**88.2 (0.002)**	25.2 (0.16)	19.9 (0.51)
Lichen orders							
Agyriales (%)	0.7 (0.53)	**4.9 (0.027) (+)**	**38.6 (< 0.0001) (+)**	0.2 (0.84)	0.1 (0.99)	1.6 (0.20)	0.5 (0.61)
Pertusariales (%)	**13.8 (< 0.0001)**	3.8 (0.053)	**106.7 (< 0.0001) (–)**	0.7 (0.50)	**23.0 (< 0.0001)**	0.2 (0.69)	0.3 (0.76)
Lecanorales (%)	**14.3 (< 0.0001)**	0.2 (0.68)	**33.0 (< 0.0001) (+)**	0.5 (0.58)	**21.1 (< 0.0001)**	0.2 (0.65)	0.1 (0.93)

$p = 0.034$) (Table 1), through being more positive on small islands than on large and medium islands (Fig. 2a). There was also an interactive effect of shrub removals and moss removals, with lichen PLFAs being significantly higher when both groups were removed compared to when they were present ($F_{1,194} = 11.4$, $p = 0.010$) (Table 1, Fig. 2). The overall results were very similar when using the relative abundance of lichen taxa, expressed as total OTUs found across all samples (Table 1, Supporting information).

When considering the three different orders of lichens individually, we found that shrub removals reduced the proportions of Pertusariales ($F_{1,194} = 106.7$, $p < 0.001$) while increasing the proportions of Agyriales ($F_{1,194} = 38.6$, $p < 0.001$) and Lecanorales ($F_{1,194} = 33.0$, $p < 0.001$) (Table 1, Fig. 3). The relative abundance of Pertusariales was greatest on small islands, and we found an interactive effect between shrub removals and island size classes on Pertusariales ($F_{2,194} = 23.0$, $p < 0.001$) as removal effects were less consistently positive on large islands (Table 1, Supporting information). Conversely, the relative abundance of Lecanorales was greatest on large islands, and we found an interactive effect between shrub removals and island size classes ($F_{2,194} = 21.1$, $p < 0.001$), with a decrease of Lecanorales in large islands and a relative increase on medium and small islands (Table 1, Supporting information). Finally, our results revealed that moss removals had an overall positive effect on the relative abundance of Agyriales ($F_{1,194} = 21.1$, $p = 0.027$) (Table 1, Supporting information).

Alpha diversity (i.e. species richness) increased from large and medium to small islands ($F_{2,27} = 11.8$, $p < 0.001$) and was promoted by shrub removals ($F_{1,194} = 132.5$, $p < 0.001$) (Table 1, Fig. 4a), with this effect being greater on small islands ($F_{2,194} = 7.8$, $p < 0.001$) (Table 1, Fig. 4a). Beta-diversity was overall lower on large islands than on medium islands with small islands being intermediate ($F_{2,27} = 18.0$, $p < 0.001$), and shrub removals decreased beta-diversity with greater effects on small islands ($F_{2,194} = 32.5$, $p < 0.001$) (Table 1, Fig. 4b). The dissimilarities among lichen communities when shrubs were present were particularly apparent in our NMDS plots (Fig. 5). Further, the structure of lichen communities strongly depended on the presence or the absence of shrubs ($F_{1,229} = 212.6$, $p < 0.001$), and its interaction with island size ($F_{2,226} = 88.2$, $p = 0.002$) (Table 1). As such, we found that Pertusariales were orthogonal to the presence of shrubs, while Agyriales and Lecanorales were inversely associated with shrub presence (Fig. 5). Finally, we did not observe any impact of moss removal ($F_{1,194} = 1.1$, $p > 0.05$), nor any interactive effects between mosses and other factors ($F_{2,194} = 1.3$, $p > 0.05$), on lichen alpha diversity (Table 1). However, we found a significant albeit low effect of moss removal on lichen community composition ($F_{2,194} = 47.4$, $p = 0.012$) (Table 1).

Discussion

Through using a long-term moss and shrub removal experiment set up across a strong environmental gradient, we

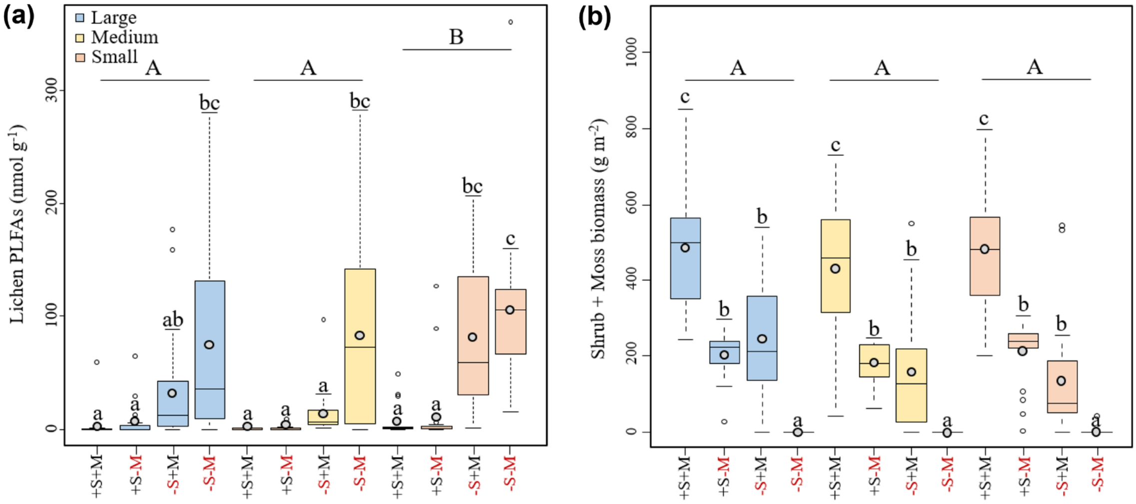

Figure 2. The effects of shrub removals [shrub present (+S) or shrub absent (−S)] and moss removals [moss present (+M) or moss absent (−M)] across contrasting island size classes [Large (red), Medium (blue), and Small (green)] on the biomass of (a) lichens (% OTU corrected by PLFA), or (b) shrubs and mosses (allometric equations). Boxplots represent the central 50% of the data representing lichen or shrub + moss biomass, and the whiskers on the boxplots represent the 95% percentiles. The grey circles within each boxplot represent the mean. Island size classes topped by the same capital letter do not differ, and within island size classes removal treatments topped with the same lower case letter do not differ (Tukey's HSD test, α = 0.05); results of mixed linear model analyses for this data are given in Table 1.

investigated the context-dependency of the effects of plant functional group removal on lichen communities. We found that shrub removals had a higher impact than moss removals on the biomass and composition of lichen communities, with greater effect of removing shrubs in older ecosystems.

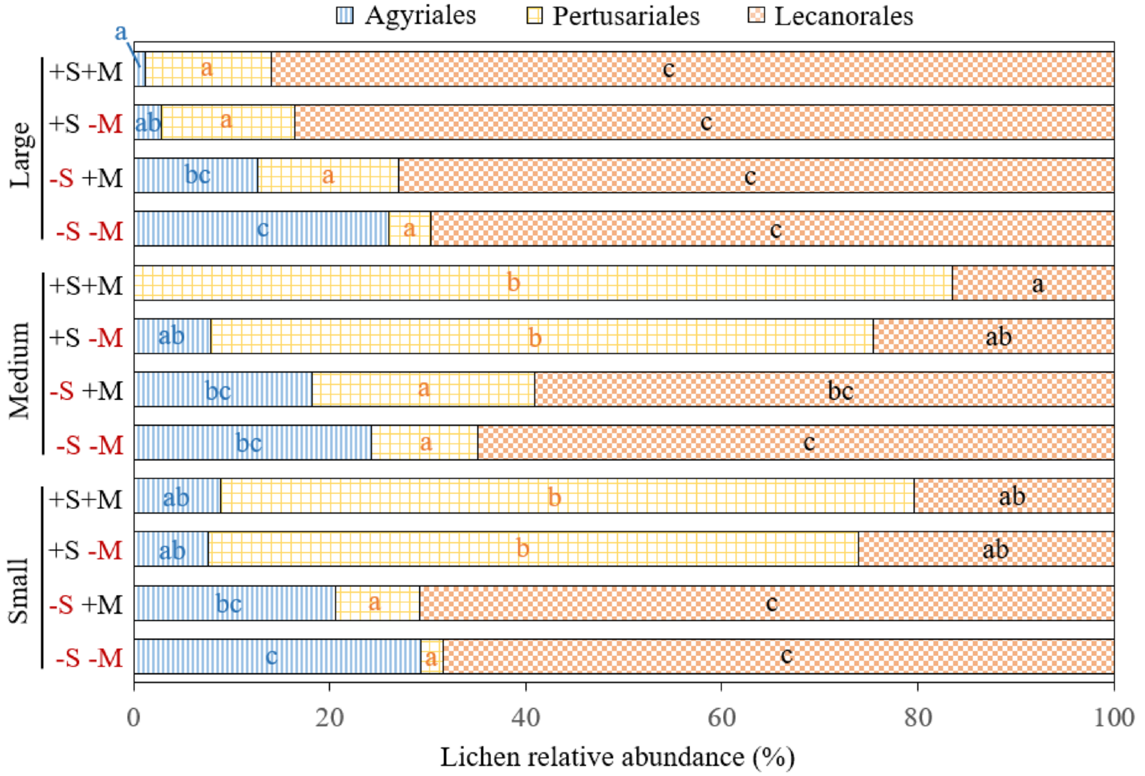

Figure 3. Average relative abundance (% of total OTUs) of each lichen order (Agyriales, Pertusariales and Lecanorales) in the lichen community after shrub removals [shrub present (+S) or shrub absent (−S)] and moss removals [moss present (+M) or moss absent (−M)] across contrasting island size classes. We used Tukey's HSD test to compare the different treatments across island size classes for the orders Agyriales, Pertusariales and Lecanorales. Removal treatments with the same lowercase letter do not differ (Tukey's HSD test, α = 0.05).

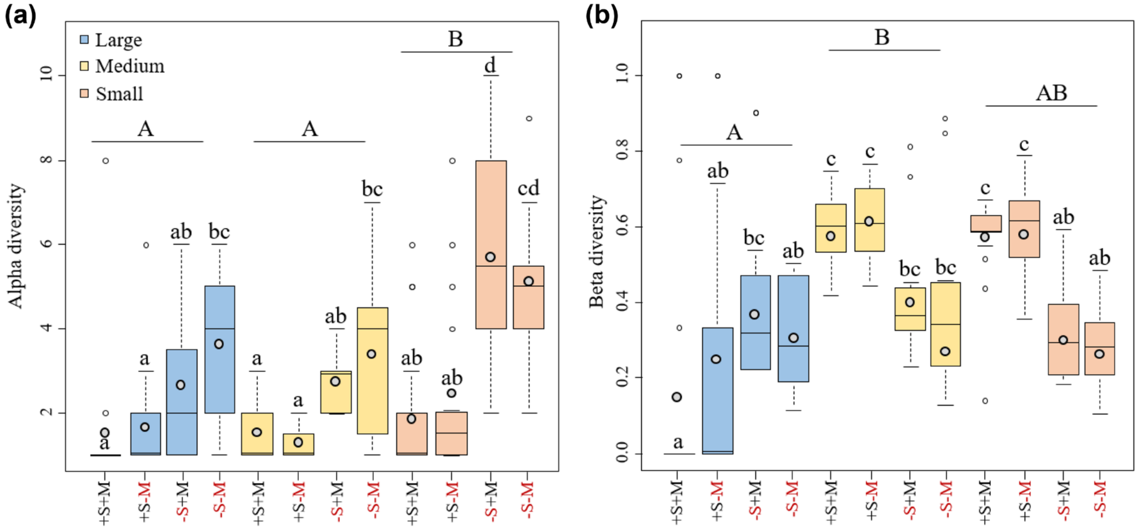

Figure 4. The effects of shrub removals [shrub present (+S) or shrub absent (−S)] and moss removals [moss present (+M) or moss absent (−M)] across contrasting island size classes [Large (red), Medium (blue), and Small (green)] on (a) lichen alpha diversity (species richness), and (b) lichen beta-diversity (dissimilarity among communities). Boxplots represent the central 50% of the data representing beta-diversity (dissimilarity among contrasting lichen communities) and the whiskers on the boxplots represent the 95% percentiles. The grey circles within each boxplot represent the mean. Island size classes topped by the same capital letter do not differ, and within island size classes removal treatments topped with the same lower case letter do not differ (Tukey's HSD test, α = 0.05).

Shrubs and mosses play a negative role on biomass and diversity of lichens

In line with our first hypothesis, we found that removing shrubs and mosses significantly increased lichen biomass, as estimated by PLFAs (Fig. 2). This is most likely because these two plant functional groups compete directly with lichens for space and resources, notably light or because their presence can suppress lichens through litter accumulation, which may limit their establishment and growth (Cornelissen et al. 2001, Elmendorf et al. 2012, Fraser et al. 2014). As such, decreasing the volume and biomass of vascular plants and bryophytes benefited the productivity of lichens, which in turn increased their biomass and allowed them to more completely colonize the soil surface (Fig. 6a). This effect was greater for shrubs than for mosses, which highlights that ericaceous shrubs are more competitive and play a more significant role than mosses in shading lichen communities (Pajunen et al. 2011). Although further research is needed to more accurately identify the precise mechanisms involved, our long-term removal experiment highlights that the understory vegetation, and notably the presence of ericaceous shrubs, strongly influences the biomass and composition of lichen communities in boreal forest ecosystems.

In alignment with our results on lichen PLFAs, we also found that shrub and moss removals significantly increased lichen species richness, probably because these plant functional group removals released more space and a more diverse range of microhabitats, thereby facilitating lichen colonization (Chagnon and Boudreau 2019). This result can be explained in part by the Agyriales genera *Placynthiella* and *Trapeliopsis* often function as pioneer species on bare soil (Kroger and Daniels 1997, Kantvilas and Jarman 2006), whereas *T. granulosa* is known to decline as Ericaceae cover increases (Splawinski et al. 2018). Furthermore, Lecanorales species such as *Cladonia* spp. are known to rapidly increase their abundances in more open micro-habitats after shrub removals (Bloom and Mallik 2004, Boudreault et al. 2013). However, and although removals increased alpha-diversity, we found that both shrub and moss removals significantly decreased beta-diversity. This is likely because the removals led to domination by a few number of lichen species that are well adapted to the new environmental conditions, leading to greater similarity in lichen communities among plots of the same treatment (Jonsson et al. 2016). As such, these lichen species, and notably the 'boreal cup lichen' *Cladonia borealis* (Fig. 6b), which was one of the main lichens present along our boreal island chronosequence, tends to dominate soil surface in open areas created by shrub and moss removals.

The effects of removing shrubs and mosses were greater in older ecosystems

In contrast with our second hypothesis that the effect of plant functional group removals would be higher in younger and more productive ecosystems, we found that shrub removals had a greater effect on lichen biomass later in the chronosequence (i.e. on the small islands), while effects of mosses did not vary across the gradient. This is probably because the amount of light reaching the ground layer vegetation is higher on the small islands due to tree biomass and cover being less than on the more productive large islands (Wardle et al. 2003). This means that the shrubs on the small islands will intercept a larger amount of light and the removal of these shrubs will therefore have a greater impact on light availability for lichen communities. These changes

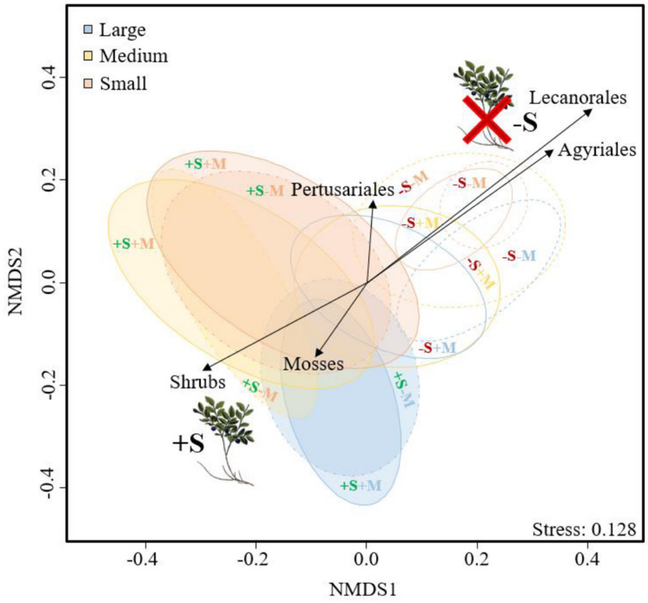

Figure 5. Non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis distances of lichen OTUs, showing the effects of shrub presence (+S; shaded ellipses) versus removal (−S; unshaded ellipses) across contrasting island size classes [Large (red), Medium (blue), and Small (green)]. Vectors represent the goodness-of-fit statistics (r^2) of vegetation parameters fitted to the NMDS.

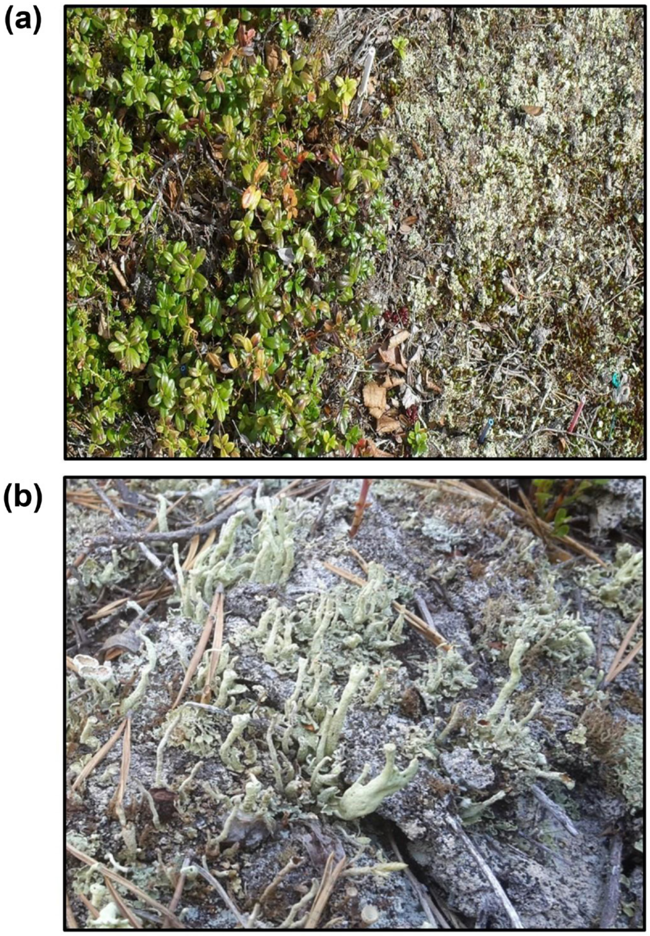

Figure 6. Example of plots showing the colonization of lichens when shrubs and mosses are removed (right) versus present (left) in understorey vegetation layer (a), and colonization of bare soil by crustose and fruticose lichens following removal of shrubs and mosses (b).

in lichen biomass were associated with an increase in lichen alpha diversity, especially on late successional stages. As older forests are more likely to host a greater number of lichen species (Moning and Müller 2009, Boch et al. 2013), this may explain the larger number of lichen species observed after shrub removal on small islands, notably because stands dominated by slow-growing *Picea* are more likely to be older stands compared with those on large and medium islands. However, a larger increase in alpha diversity does not necessarily translate to an increase in beta-diversity, especially since the dominance of a few lichen taxa on small islands may result in strong compositional similarity, despite the increase in local species richness (Fig. 4). This can be due to differences in the ability of some lichen species to recolonize bare soil according to the ecosystem type (Smith 1995). For instance, some lichen species such as *Cladonia* spp. were very responsive to removals mainly in medium and small islands (Supporting information), probably because they are more efficient than other species at recolonizing soils when the habitat is open and luminous (Boudreault et al. 2013). This can also be due to the fact that some lichen species are more sensitive to changes in microclimate and soil moisture, with lichen taxa such as *Cladonia* spp. being more adapted to these altered environmental conditions, and notably to dry conditions (Gheza et al. 2021).

Limitations and perspectives

While this study provides valuable insights into the effects of shrub and moss removal on boreal lichen communities, its results should be interpreted with caution, and generalizing the findings to other ecosystems or environmental contexts warrant careful consideration. First, while the experimental setup allowed us to make inferences about the direct effects of moss and shrub removal on the lichen community, we acknowledge that other indirect effects of environmental factors, such as alteration in local climatic conditions, may also have influenced lichen community responses. These changes are likely to differ between boreal, temperate and arid ecosystems, where variations in moisture, temperature, and light availability can have distinct effects on lichen growth and competition. Second, the metabarcoding approach used to assess lichen communities may include DNA from lichens growing on different substrates, such as rocks and trees, where competition from shrubs and mosses is likely minimal. This can influence the interpretation of the results, especially for taxa like the Pertusariales, which may show weaker responses to removal treatments compared to ground-dwelling lichens such as *Cladonia* and *Placynthiella* species. Finally, although we have used lichen

PLFAs as a complementary method to estimate changes in lichen biomass, PLFAs represent overall fungal biomass and are not specific to lichens, which may affect our ability to directly attribute changes in fungal biomass to lichen-specific responses. Further work, including more precise identification methods, such as the identification of specific lichen biomarkers with HPLC, would help overcome some of these limitations and provide more detailed insights into the response of lichen communities to changes in plant community composition or global change drivers.

Implications for ecosystem functioning

Our study revealed that ericaceous dwarf shrubs are causing a reduction in the biomass and diversity of lichen communities. Because the ongoing climate warming trend is promoting the growth and expansion of these shrubs in high-latitude ecosystems (Mekonnen et al. 2021), the decrease in lichen biomass due to the expansion of shrubs could have significant implications for the carbon balance of these higher latitude ecosystems (Aartsma et al. 2020, 2021). This is notably because if the light-colored lichen covering the Earth's surface were to transition to a darker shrub covering, the surface albedo of the boreal zone would decrease and more solar radiation would be absorbed. This reduction in albedo can result in increased warming, which can in turn further promote shrub growth and create a positive feedback loop that would lead to significant changes in ecosystem carbon exchange (Bernier et al. 2011). Decreases in lichen biomass and diversity through increasing shrub density may also affect rates of overall ecosystem functioning (Asplund and Wardle 2017). For instance, while the seedling establishment of some vascular plants such as *Pinus sylvestris* may be negatively affected by the presence of certain lichen species such as *Cladonia* spp., graminoid or forb species including *Anthoxanthum* and *Bistorta* may not be significantly impacted (Nystuen et al. 2019). This suggests that the influence of lichens on vascular plant establishment can vary depending on the species involved and the ecological conditions present, with a decrease in lichen cover potentially influencing selectively the presence of some vascular species to the detriment of others. Shifts in plant community composition can in turn have repercussions on ecosystem productivity (Fanin et al. 2022), and especially in older ecosystems such as our small islands in which nutrient availability most strongly limits primary productivity (Wardle et al. 2012).

Moreover, as lichens play a particularly vital role in ecosystems with low primary productivity, such as those found in cold or arid environments, a decline in lichen biomass resulting from higher densities of ericaceous shrubs could have cascading effects on higher trophic levels. For example, a decline in lichen biomass can lead to a decline in the populations of specialized herbivores and detritivores that rely on them as food sources, and potentially on their predators. For instance, reindeer directly rely on lichens for their winter diet, which underscores their importance under snow cover in northern ecosystems (Storeheier et al. 2002, Joly et al. 2009). In addition, some lichens form complex structures that provide habitats, shelter and nesting sites for a variety of invertebrates (Bokhorst et al. 2015) and thus can serve as 'foundation species' for multiple taxa in high latitude communities (Roos et al. 2022). As such, it is essential to conserve lichen communities at higher latitudes because they play multiple key roles in the ecosystem, and because of the threat that they face from future shrub expansion due to climate warming (Myers-Smith et al. 2011). In conclusion, our results highlight that the effects of shrub expansion on lichen communities are unlikely to be consistent across ecosystems, and are more likely to impair lichens on unproductive, nutrient limited and later successional ecosystems. Additionally, our findings emphasize the importance of considering the combined effects of multiple factors, notably because the combined effect of moss and shrub removal induced a more pronounced effect on lichen communities than shrub removal alone. Policymakers and conservationists must prioritize measures to enhance the cohabitation of various species and their functioning in the face of climate change, including proactive management of shrub expansion such as soil scarification.

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Author contributions

Nicolas Fanin: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Writing – original draft (lead). **Johan Asplund**: Conceptualization (equal); Investigation (equal); Methodology (equal); Validation (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Michael J. Gundale**: Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Paul Kardol**: Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Marie-Charlotte Nilsson**: Investigation (equal); Methodology (equal); Writing – review and editing (equal). **David A. Wardle**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Validation (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the INRAE Data Repository on data.gouv.fr: https://doi.org/10.57745/L8JRDH (Fanin et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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