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RESEARCH ARTICLE

Response of ground macrolichens to site factors, co-existing plants and forestry in boreal forests

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Abstract

Aim: Ground lichens have declined in boreal and temperate Europe. The potential causes of the decline were explored by analysing the response of lichen cover to forest management, site and stand variables as well as co-existing plants in different boreal vegetation subzones.

Location: Finland.

Methods: Understorey vegetation was surveyed on a systematic network of 1721 sample plots in forests on mineral soil. The response of macrolichen cover to explanatory variables was analysed by generalised linear mixed models (GLMMs).

Results: Ground lichens favoured old *Pinus sylvestris* forests on xeric sites with sufficient light conditions. Intensive forest management regimes, such as regeneration cutting and soil ploughing decreased lichen cover, while lighter scarification methods had less effect on lichens. Lichens benefitted from intermediate cutting on sites with low bryophyte cover. Lichens responded similarly to site and stand variables in all boreal subzones, showing that despite heavy reindeer grazing these response patterns apply also in the northern boreal subzone. Lichens showed both negative (*Vaccinium myrtillus*, *Empetrum nigrum* and *Calluna vulgaris*) and positive (*Vaccinium vitis-idaea*) responses to increasing dwarf shrub cover. Generally, lichens negatively responded to increasing bryophyte cover, indicating either that bryophytes benefit from a decline of lichens or that there is real competition between these groups. The negative relationship between bryophytes and lichens strengthened as the tree canopy becomes denser.

Conclusions: Our study provides new quantitative insights into the effects of forest management and changes in forest structure as underlying factors for lichen decline both inside and outside the reindeer-herding area (i.e., the northern boreal subzone). These factors include increased canopy cover with increased shading as well as disturbance caused by regeneration cutting and soil preparation. The possible effects of the long-term legacy of nitrogen deposition, lack of forest fires and climate change are also discussed.

KEYWORDS
bryophytes, dwarf shrubs, epigeic lichens, forest management, generalised linear mixed models, terricolous lichens, understorey vegetation

1 | INTRODUCTION

Lichen communities growing on the forest floor in boreal forests are most species-rich and abundant at barren oligotrophic sites, but they also grow in smaller amounts on many more common sub-xeric and mesic sites (Oksanen & Ahti, 1982; Ahti & Oksanen, 1990). Besides being important for biodiversity, lichens have a crucial, but often overlooked role in ecosystem processes and food webs (Asplund & Wardle, 2017). A wide range of organisms, from micro-organisms to mammals, depend on lichens (Asplund & Wardle, 2017). Changes occurring in the abundance and distribution of lichens due to increasing human land use and changing climate may therefore have large-scale consequences on the biodiversity and functioning of these ecosystems.

Ground lichens have experienced a major decline in boreal forests during the last 50–100 years (Mäkipää & Heikkinen, 2003; Berg et al., 2008; McMullin et al., 2013; Sandström et al., 2016). A similar trend has also been observed in the temperate forests of Europe (Reinecke et al., 2014; Stefańska-Krzaczek et al., 2018) and alpine and boreal-montane areas in Central Europe (Hauck, 2009). Several factors have been suggested to be behind the decline, ranging from local-level forest management (Johansson, 2008; Kivinen et al., 2010; Nascimbene et al., 2013) to regional level reindeer grazing (Väre et al., 1995; Akujärvi et al., 2014), eutrophication (Reinecke et al., 2014; Stefańska-Krzaczek et al., 2018) and global climate change (Fraser et al., 2014). All these factors, the significance of which depends on the region and the lichen species, indicate direct or indirect impacts of human activities on lichens and lichen-dominated habitats. The consequences of lichen decline are manifold, such as the negative effects on reindeer and caribou populations (Joly et al., 2009) and a decrease of surface albedo due to the gradual darkening of the ground layer due to an increase of shrubs (Cohen et al., 2013; te Beest et al., 2016; Aartsma et al., 2021) or bryophytes (Stoy et al., 2012). Disappearance of light-coloured lichens can cause an increase in soil temperature, which may accelerate the climate change effects in high latitudes (Stoy et al., 2012; Aartsma et al., 2020) and potentially also in sparse forests further south.

Both reindeer grazing and forest management have an impact on the abundance of lichens in northern Fennoscandia (Berg et al., 2008; Kivinen et al., 2010; McMullin et al., 2013; Akujärvi et al., 2014; Korosuo et al., 2014; Sandström et al., 2016). According to Akujärvi et al. (2014), reindeer grazing has a larger impact on lichens than forestry. However, much less is known about the influence of site and stand factors and forest management on the abundance of lichens further south, outside the reindeer-herding area.

In general, nutrients, water and light limit lichen growth and are resources for which lichens compete. Forest management (e.g., cutting and soil preparation) alters the resource conditions of the lichens' growing sites, causes mechanical damage to vegetation and soil, and creates mechanical barriers by leaving logging residues on the ground (Bråkenhielm & Persson, 1980; Roturier & Bergsten, 2006). The recovery of the lichen cover may require decades, although the usage of low-intensity soil preparation methods may somewhat speed up the process (Roturier et al., 2011).

Lichens grow among plant communities of the forest floor, and therefore their occurrence and abundance may also be influenced by competition from faster-growing plants, such as dwarf shrubs and bryophytes growing in the field and ground layer, respectively. The competitive interactions among overstorey and understorey vegetation reflect both the multiple impacts of forest management on plant functional groups and natural successional processes (Bartels & Chen, 2013).

Lichens favour old, sparse forest where light reaches the forest ground layer (Jonsson Čabrajić et al., 2010). Although lichens generally decrease due to forestry, they might benefit from forest cutting in situations where light is a limiting factor (Tonteri et al., 2016). This effect would most likely be greater in southern boreal forests, where tree canopy cover and the competition caused by vascular plants are likely to be higher because of more favourable climate and higher atmospheric nitrogen deposition. Hence it can be expected that the response of lichens to forestry, through its impacts on the forest stand structure and vegetation composition, differs between southern and northern boreal subzones.

In the boreal forests of Finland, the cover of ground macrolichens (mainly reindeer lichens) has decreased since the 1950s (Reinikainen et al., 2000; Mäkipää & Heikkinen, 2003). The decline may, however, have started earlier, since the area of the barren *Cladina* site type forests has decreased in the northern boreal subzone (Lapland) since 1922 (Oksanen & Ahti, 1982; Korhonen et al., 2017). The decline of lichens has continued at least until the early 2000s and it prevails both in northern and southern parts of the country (Tonteri et al., 2016).

The aim of our study was to find potential causes for the lichen decline in Finland by analysing how abundance of ground lichens respond to forest management practices, stand structure influenced by forest management and co-existing plant species. Data collected in a systematic nationwide sampling network was used to construct response models for the total cover of all lichen species and separately for the group of reindeer lichens (*Cladina* spp.) being important winter forage for reindeer in northern Europe.

We tested the following hypotheses:

1. Lichens respond negatively to forest cuttings and soil preparation — the stronger the treatment, the heavier the decline.

2. Forest management effects on lichen cover are similar in the reindeer-herding area and the areas south of it, indicating that long-term heavy grazing has not altered the responses of lichens to stand management and structure.
3. Lichens are negatively associated with co-existing dwarf shrubs and bryophytes.

The results can be applied in developing forest management regimes for maintaining and creating suitable habitats for ground lichens outside and inside the reindeer grazing area in the boreal zone.

2 | MATERIAL AND METHODS

2.1 | Vegetation survey

Understorey vegetation was surveyed in 1985–1986 on a systematic network of 1721 sample plots on mineral soils on productive forest land in Finland (Figure 1). The sample plots are part of a systematic sampling network of 3000 permanent plots established in connection with the 8th Finnish National Forest Inventory (NFI8) (Tonteri et al., 1990; Reinikainen et al., 2000).

Lichen and plant species were identified, and their percentage cover was visually estimated on three to six (usually four) 2-m^2 permanent quadrats within 300-m^2 circular sample plots (Figure 1). In percentage covers between 0 and 1%, cover values at 0.1% intervals were used, and in abundances between 1% and 100%, any cover values at 1% intervals could be used. Crustose lichens were not recorded at all. Species abundances in the quadrats were averaged for each sample plot. Species were classified to groups, and the sum of species percentage cover was calculated for all ground lichens, reindeer lichens, bryophytes and dwarf shrubs. In this study, the genus *Cladonia* was divided into two groups, reindeer lichens (*Cladina*) and cup lichens (*Cladonia*). *Cladina arbuscula*, *C. mitis*, *C. rangiferina* and *C. stellaris* were included in reindeer lichens. The reindeer lichens are called *Cladina* here to make a distinction between them and the cup lichens. They are analysed separately here, because they are important for winter forage of reindeer. The total lichen cover included *Cladina* spp., but also other lichen genera with lower abundances (mean sum 0,5%), such as cup lichens *Cladonia* spp., *Cetraria* spp., *Peltigera* spp., *Nephroma* spp. and *Stereocaulon* spp. Nomenclature follows Suomen lajitietokeskus (2022).

Variables available in the NFI8 data were considered as predictors in modelling (Table 1). The stands were divided into five groups by the categorical variable expressing regeneration (RC) and intermediate cuttings (IC), both 0–5 and 6–10 years since cutting, and using no harvests in the last 10 years (NC) as reference. All cuttings, mainly pre-commercial and commercial thinnings, that took place between RC were classified as IC. A four-level categorical variable was built to describe soil preparation; levels being no treatment, ploughing, ditching and 'other', the last category indicating less intensive methods such as disc trenching, scalping and mounding. In the field, it was possible to record cuttings that occurred 0–10 years before the inventory, but records on soil preparation reached back 25 years.

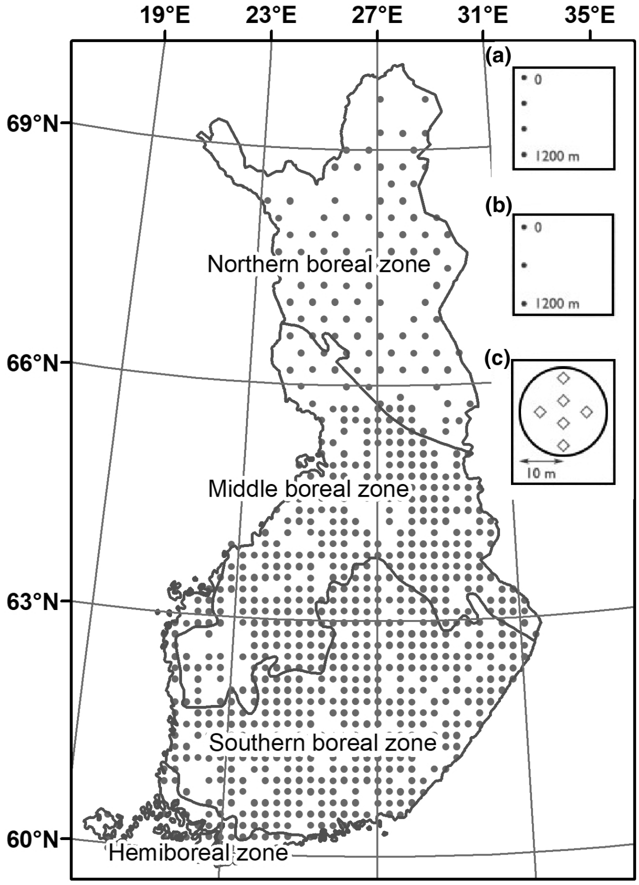


FIGURE 1 Location of subzones of the boreal zone and the sample plots of the vegetation survey ($N = 1721$) used in modelling. Each dot represents a cluster containing one to four sample plots in southern Finland (a) and one to three sample plots in northern Finland (b). Distribution of 2-m^2 vegetation quadrats within each sample plot is shown in diagram (c)

For the boreal subzones (Ahti et al., 1968), the three-level categorical variable zone was formed as follows: HB-SB (hemiboreal and southern boreal subzones merged), MB (middle boreal subzone) and NB (northern boreal subzone).

The forest site type was based on understorey vegetation using a six-point scale where class 1 corresponds to the highest fertility (Cajander, 1949; Hotanen et al., 2008; Pohjanmies et al., 2020). The categorical variable for site type had four levels: 'herb-rich' (Cajander's classes 1 and 2 combined), 'mesic', 'sub-xeric' and 'xeric' (classes 5 and 6 merged) from high to low nutrient and moisture level. Site types also roughly arranged the plots according to the dominant tree species: the herb-rich and mesic sites were mainly Norway spruce (*Picea abies*)-dominated with a variable mixture of Scots pine (*Pinus sylvestris*) and broad-leaved species (mostly *Betula* spp.), while the sub-xeric and xeric sites were mainly *Pinus sylvestris*-dominated and the proportion of other tree species was low. All site types were used in modelling the total cover of all

TABLE 1 The characteristics of variables used in modelling (N = 1721).

Continuous variables	Mean	SD	Median	Min.	Max.
Cover of all lichens, %	3.41	9.22	0.05	0.00	92.75
Cover of *Cladina* spp., %	2.90	8.32	0.00	0.00	72.12
Cover of bryophytes, %	50.58	28.67	52.27	0.00	122.17
Cover of dwarf shrubs, %	25.54	21.24	20.90	0.00	104.17
Cover of herbs, %	7.30	12.90	1.75	0.00	108.80
Cover of graminoids, %	11.03	17.20	2.98	0.00	115.50
Cover of shrubs, %	6.53	9.87	3.50	0.00	109.20
Cover of *Vaccinium myrtillus*, %	10.53	14.08	4.50	0.00	87.50
Cover of *Vaccinium uliginosum*, %	1.52	4.95	0.00	0.00	51.25
Cover of *Vaccinium vitis-idaea*, %	7.34	7.89	4.75	0.00	57.50
Cover of *Calluna vulgaris*, %	2.83	8.12	0.00	0.00	78.75
Cover of *Empetrum nigrum*, %	0.91	3.45	0.00	0.00	42.50
Cover of *Rhododendron tomentosum*, %	0.66	2.73	0.00	0.00	50.00
Altitude, m a.s.l.	132.64	67.75	120	0	410
Temperature sum, d.d.	1098.49	158.13	1120	650	1360
Stand basal area, m^2ha^{-1}	14.43	10.35	14.0	0.0	53.8
Stand age, years	63.35	49.26	55	0	325
Proportion of Scots pine, %	45.59	40.36	39.0	0.0	100.0
Proportion of Norway spruce, %	32.11	35.87	14.9	0.0	100.0
Proportion of deciduous trees, %	17.80	26.27	5.7	0.0	100.0
Canopy cover of trees, %	40.48	25.33	38.0	0.0	147.0
Canopy cover of shrubs, %	6.53	9.87	3.5	0.0	109.0
Categorical variables	Proportion (%) of plots in different categories				
Site type	Herb-rich 18.0%	Mesic 46.5%	Sub-xeric 30.7%	Xeric 4.8%	
Zone	HB-SB 53.8%	MB 30.0%	NB 16.2%		
Cutting	NC 61.4%	RC 0–5 4.4%	RC 6–10 4.7%	IC 0–5 17.6%	IC 6–10 12.0%
Soil treatment	None 85.0%	Ploughing 4.3%	Other 5.4%	Ditching 5.4%	

Note: Abbreviations for the categorical variables zone: HB = hemiboreal, SB = southern boreal, MB = middle boreal and NB = northern boreal subzone, and cutting: NC = no cutting in the last 10 years, RC = regeneration cutting, IC = intermediate cutting, and ranges 0–5 and 6–10 denote years since cutting.

ground lichens. Because the cover of reindeer lichens (*Cladina* spp.) was very low on fertile sites, only their major habitats, i.e., sub-xeric and xeric site types, were included in the modelling data. The data on the total cover of all lichen species consisted of all the sample plots (1721), and the data on the group of reindeer lichens (*Cladina* spp.) consisted of a total of 610 sample plots. The continuous predictors were stand age estimated with an increment core taken from a tree representing the dominant canopy layer of the stand, stand basal area (BA) and the proportions of *Picea abies*, *Pinus sylvestris* and broad-leaved trees of the stand basal area. Stand basal area was estimated using measurements of stem diameter at breast height. The canopy cover of trees higher than 1.5 m and the canopy cover of shrubs (including shrubs >0.5 m in height and trees 0.5–1.5 m) were estimated visually. The canopy covers of trees and shrubs were estimated by species and canopy layers, and thus the total canopy cover can be more than 100% (Table 1). The average effective temperature sum, i.e., the sum of the positive differences between daily mean temperatures and +5°C (d.d.), was calculated for each plot using the method of Ojansuu and Henttonen (1983) to estimate the average of years 1951–1980. The temperature sum of the sample plot was used to describe the south–north variation in growing conditions at the national level.

2.2 | Statistical modelling

Different models were created to explain the variation in the cover of ground lichens, i.e., to test our hypotheses on the response of ground lichens to site factors, co-existing plants (dwarf shrubs and bryophytes) and forestry in boreal forests. Models 1 and 2 were fitted for the total cover of lichens and Model 3 for *Cladina* (reindeer lichens) species only. When analysing the effect of dwarf shrubs, Models 1 and 3 were fitted using both (a) the total cover of all dwarf shrubs and (b) each dwarf shrub species separately one at a time as an explanatory variable. The covariation of bryophytes with lichens was analysed in Model 2. Models 1 and 2 were fitted as separate models, because it appeared that the interpretation of a model including both dwarf shrubs and bryophytes as predictors was not easy. Model 2 with bryophytes was 'simplified' compared to Model 1 since only the strongest effects (cutting, site and zone) were included in Model 2, but not, for example, stand variables. This was done to reduce the overfitting, since lichens and bryophytes occur in the same ground layer and are correlated.

Hypothesis 1 (response to forest management) was tested by fitting the categorical variables for cuttings and soil treatments into Models 1 and 3. Hypothesis 2 (response inside the reindeer-herding area, i.e., the northern subzone) was tested by fitting the interaction terms between zone and cutting, as well as zone and stand structure variables into Models 1 and 3; insignificance of these interactions would support the hypothesis. Hypothesis 3 (response to co-existing plants) was tested by fitting the cover of all or individual dwarf shrub species and its interaction with zone into Models 1 and 3, and correspondingly the cover of bryophytes to Model 2. In addition to variables relevant for hypothesis testing, the most important ecologically relevant and statistically significant ($p < 0.05$) site and stand variables were included in the models. The significance of interaction terms between the main effects were tested to find out if the response of lichens to different variables was dependent on other variables. Non-significant interaction terms were removed from the models.

Generalised linear mixed models with a log link function $\left(\eta_{ij} = \ln\left(\mu_{ij}\right)\right)$ and a quasi-Poisson distribution assumption were used in the modelling of the total cover of lichens (Models 1 and 2) and *Cladina* spp. (Model 3). The highly skewed distribution of lichen cover and the non-integer values in the response variable supported the use of the quasi-Poisson distribution. Clustered observations (sample plots nested within the clusters) were considered by including a cluster-level random effect in the intercept.

Assuming that the response variable (lichen cover) is Y_{ij}, where *i* denotes the observations at the sample plot and *j* those at the cluster level, the mean (*M*) is defined as $M\left(Y_{ij} \mid \eta_{ij}\right) = \mu_{ij}$, where η_{ij} denotes a linear predictor that could be expressed as:

$$\eta_{ij} = \beta_0 + \sum\nolimits_{k_1=1}^{l} \beta_{k_1 i} x_{k_1 i} + \sum\nolimits_{k_2=l+1}^{p} \beta_{k_2 j} x_{k_2 j} + \mu_{0j}, \quad (1)$$

whereβ_0 is the fixed intercept, $\beta_{k_1 i}, \beta_{k_2 j}$ are the coefficients of fixed variables measured at sample plot (*i*) and cluster (*j*) level, $x_{k_1 i}, x_{k_2 j}$ are fixed variables measured at sample plot (*i*) and cluster (*j*) level,μ_{0j} is a random cluster effect (random intercept), k_1, k_2 are the number of fixed variables representing the sample plot and cluster effects, respectively.

The quasi-Poisson distribution denotes that the expected value of the mean may differ from the expected value of variance and will be estimated (overdispersion in our data). As a formula, the variance (V) could be expressed as $V\left(Y_{ij} \mid \eta_{ij}\right) = \phi\mu_{ij}$, where ϕ represents a dispersion parameter. There is no exponential family corresponding to this specification. Rather, the model specifies the conditional mean and variance of Y_{ij} directly (Fox, 2016).

All analyses were performed in the R statistical environment (R Core Team, 2021). The penalised quasi-likelihood (PQL) algorithm was used in the estimation of the model. The function 'glmmPQL' in R package *MASS* (Venables & Ripley, 2002) was used in the modelling. Alternative estimation methods (e.g., Laplace) and other R packages were tried, but they did not converge, or the fit to the data was not better than that achieved using the PQL algorithm. The coefficients for determination (R^2) were computed using the R package *MuMIn* (Barton, 2018). The predictions were computed and plotted using the R package *effects* (Fox, 2003). Additional information on the performance of the models, i.e., the distributions of the observed and predicted lichen covers are presented in Appendix S1.

3 | RESULTS

3.1 | Response of lichens to site factors and forestry

The total cover of all ground lichens responded significantly to categorical variables describing cutting, soil treatment, site type and zone, and continuous variables describing stand age, canopy cover of trees, temperature sum and proportion of *Picea abies* in the total basal area (Table 2). There was a significant interaction between the cover of all dwarf shrubs and zone. In addition, the interaction between zone and site type was significant.

Lichen cover responded to forest management both directly through cuttings and soil treatments and indirectly through the consequent changes in stand structure. In regeneration cut forests, lichen cover was less than half of the cover in uncut forests (Figure 2a). Lichens responded negatively to intensive soil treatments so that on ploughed and ditched sites lichen cover was about a third of that on untreated sites (Figure 2b). On sites with less intensive soil treatment (other), lichens were more abundant than on untreated sites.

Lichen cover responded positively to stand age (Figure 2c), whereas increasing canopy cover of trees (Figure 2d) and proportion of *Picea abies* in the growing stock (Figure 2f) resulted in a negative response. Without any *Picea abies* trees, lichen cover was fourfold cover of a pure *Picea abies* forest.

The cover of all lichens increased with decreasing temperature sum (Figure 2e), indicating the highest cover in the NB subzone (Table 2). On herb-rich, mesic and sub-xeric sites, the fitted cover was scarce (0%–2%). On nutrient-poor xeric sites, the fitted percentage of cover was about 8% in the south and 4% in the north (Figure 2g). On herb-rich and mesic sites, lichen cover was only marginally higher in the northern subzone than in the subzones to the south.

TABLE 2 The generalised linear mixed model for the cover of all lichens using dwarf shrub cover as a predictor (model 1a, $N = 1721$)

Variable	Coefficient	Std.err.	*Df*	*t*/χ2	*p*
Intercept	0.712	1.012	875	0.703	0.481
Cutting (ref. No cutting)			4	91.149	<0.001
- Regeneration cutting in 0–5 years (RC 0–5)	−1.549	0.179	875	−8.636	<0.001
- Regeneration cutting in 6–10 years (RC 6–10)	−0.809	0.211	875	−3.828	<0.001
- Intermediate cutting in 0–5 years (IC 0–5)	−0.044	0.092	875	−0.485	0.628
- Intermediate cutting in 6–10 years (IC 6–10)	−0.010	0.091	875	−0.109	0.913
Zone (ref. HB-SB)			2	17.334	<0.001
- MB	−0.006	1.238	875	−0.005	0.996
- NB	3.170	0.802	820	3.952	<0.001
Site type (ref. Herb-rich)			3	268.308	<0.001
- Mesic	2.317	0.523	875	4.427	<0.001
- Sub-xeric	3.843	0.520	875	7.386	<0.001
- Xeric	5.172	0.531	975	9.741	<0.001
Soil treatment in 25 years (ref. None)			3	71.094	<0.001
- Ploughing	−1.162	0.267	875	−4.351	<0.001
- Other (e.g., disc trenching, scalping)	0.375	0.140	875	2.679	0.008
- Ditching	−1.457	0.226	875	−6.456	<0.001
Stand age (years)	0.002	0.001	875	4.115	<0.001
Proportion of Norway spruce (%)	−0.015	0.002	875	−8.657	<0.001
Temperature sum, d.d.	−0.023	0.007	875	−3.199	0.001
Canopy cover of trees, %	−0.014	0.002	875	−7.949	<0.001
Cover of dwarf shrubs, %	−0.002	0.004	875	−0.577	0.564
Zone * Site type			6	36.579	<0.001
- MB, Mesic	−0.086	1.254	875	−0.069	0.945
- NB, Mesic	−2.426	0.767	875	−3.163	0.002
- MB, Sub-xeric	0.183	1.243	875	0.147	0.883
- NB, Sub-xeric	−2.795	0.762	875	−3.667	<0.001
- MB, Xeric	0.388	1.253	875	0.310	0.757
- NB, Xeric	−3.321	0.779	875	−4.264	<0.001
Zone * Cover of dwarf shrubs, %			2	12.085	<0.001
- MB, Dwarf shrubs	−0.012	0.005	875	−2.675	0.008
- NB, Dwarf shrubs	−0.016	0.005	875	−3.289	0.001
Random effects	Variance	95% cl			
Cluster	1.048	0.875–1.255			

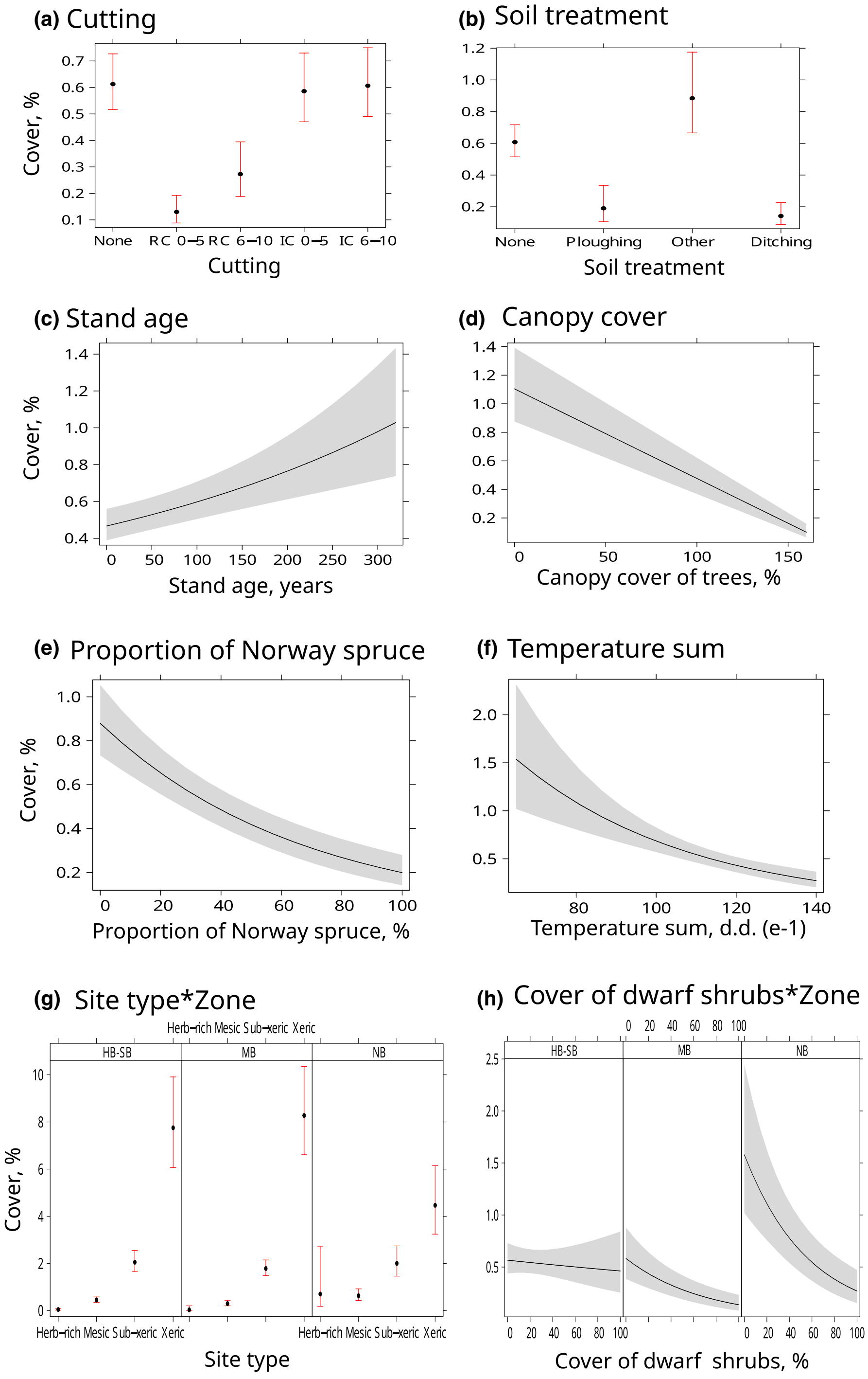
Note: The *t* and χ^2 values are the test values for the parameter estimates and type III Anova (deviance) tests, *df* denotes the degrees of freedom and cl the confidence intervals. R^2 for marginal and conditional model was 56% and 71%, respectively.

3.2 | Response of lichens to dwarf shrubs

Lichen cover showed a negative response to the total cover of dwarf shrubs co-existing in the field layer in the MB and NB subzones (Table 2, Figure 2h). Without any dwarf shrubs, the fitted cover of lichens was about five times higher than that with a dwarf shrub cover of 100%.

The response of lichens to individual dwarf shrub species was species-specific. The higher the cover of deciduous bilberry (*Vaccinium myrtillus)* or evergreen crowberry *(Empetrum nigrum)*, the lower the lichen cover (Table 3, Figure 3a,b). On the other hand, the relationship between evergreen cowberry (*Vaccinium vitis-idaea)* and lichen cover was positive in the NB subzone, but not in the other subzones, which reflects a significant interaction between zone and cowberry (Table 3, Figure 3c). Lichen cover responded negatively to heather (*Calluna vulgaris)* in the middle and northern subzones, whereas in the HB-SB subzones there was a weak positive relationship (Table 3, Figure 3d).

FIGURE 2 Predicted responses and 95% confidence intervals of the cover of all lichens to (a) cutting, (b) soil treatment, (c) stand age, (d) canopy cover of trees, (e) temperature sum, (f) proportion of *Picea abies*, and (g) site type and (h) dwarf shrub cover in southern (HB-SB), middle (MB) and northern (NB) boreal subzones. The predicted effects are based on model 1a (Table 2). Abbreviations: RC, regeneration cutting; IC, intermediate cutting; HB-SB, southern; MB, middle; NB northern boreal subzone



3.3 | Response of lichens to bryophytes

The response of ground lichens to bryophytes co-existing in the same ground layer was studied by including the cover of bryophytes as well as the site type, cutting and zone as the strongest main effects in Model 2. Both zone and cutting interacted significantly with bryophyte cover, but site type did not (Table 4, Figure 4a). Compared to dwarf shrubs, a closer relationship between bryophytes and lichens was found (e.g., higher R^2 values).

Lichen cover responded negatively to bryophytes. This pattern was visible in all cutting treatments and subzones, being strongest in the NB subzone (Table 4, Figure 4b). The smallest negative relationship was found in recently regenerated forests (RC). After intermediate cuttings (IC), lichen cover was relatively high if bryophytes were scarce, but an abundant presence of bryophytes reduced lichen cover (Figure 4c).

3.4 | Response of *Cladina* spp.

The response of reindeer lichens (*Cladina* spp.) to site factors, co-existing plants and forestry was examined by fitting Model 3 for the

TABLE 3 The response of the cover of all lichens to individual dwarf shrub species (model 1b, $N = 1721$)

Variable	Coefficient	Std.err.	*Df*	$t/\chi2$	*p*
Cover of *Empetrum nigrum*, %	−0.034	0.009	877	3.764	<0.001
Cover of *Calluna vulgaris*, %	0.007	0.006	875	1.250	0.212
Zone * Cover of *C. vulgaris*, %			2	6.198	0.045
- MB, *C. vulgaris*	−0.019	0.008	875	−2.380	0.018
- NB, *C. vulgaris*	−0.014	0.008	875	−1.874	0.061
Cover of *Vaccinium myrtillus*, %	−0.017	0.004	877	−4.475	<0.001
Cover of *Vaccinium vitis-idaea*, %	0.014	0.009	875	1.605	0.109
Zone * Cover of *V. vitis-idaea*, %			2	7.535	0.023
- MB, *V. vitis-idaea*	−0.015	0.011	875	−1.333	0.183
- NB, *V. vitis-idaea*	0.013	0.011	875	1.175	0.240

Note: The responses were obtained by replacing the cover of dwarf shrubs in model 1a by the covers of individual dwarf shrub species, one at a time. Other predictors are the same as in model 1a (Table 2). Only the estimates and tests for dwarf shrubs species (*Empetrum nigrum*, *Calluna vulgaris*, *Vaccinium myrtillus* and *V. vitis-idaea*) with significant ($p < 0.05$) responses are presented. The *t* and $\chi2$ values are the test values for the parameter estimates and type III Anova (deviance) tests and *df* denotes the degrees of freedom.

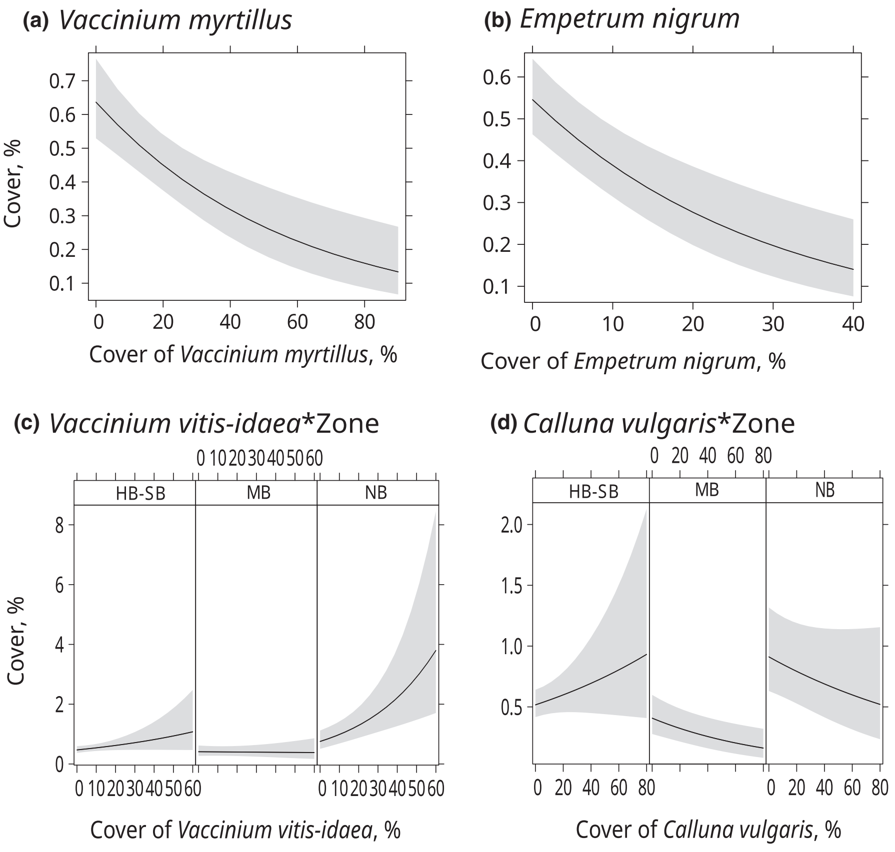


FIGURE 3 Predicted responses and 95% confidence intervals of the cover of all lichens to individual dwarf shrub species: (a) *Vaccinium myrtillus*, (b) *Empetrum nigrum*, (c) *Vaccinium vitis-idaea*, and (d) *Calluna vulgaris* in southern (HB-SB), middle (MB) and northern (NB) boreal subzones. The predicted effects are based on model 1b (Table 3)

cover of *Cladina* spp. on sub-xeric and xeric sites. In modelling, the same predictors were used as in Model 1. The response patterns of *Cladina* spp. to site factors, co-existing plants and forestry were mainly similar to those of all lichens, even though only nutrient-poor sites were included in the model for *Cladina* spp. The results on *Cladina* spp. are presented in Appendix S2.

4 | DISCUSSION AND CONCLUSIONS

Mäkipää and Heikkinen (2003) reported that ground lichens have declined in all kinds of forests throughout Finland during the period from 1951 to 1985, and Tonteri et al. (2016) showed that the declining trend had continued during 1985–2006. Using an extensive

TABLE 4 The generalised linear mixed model for the cover of all lichens using bryophyte cover as a predictor (model 2, $N = 1721$)

Variable	Coefficient	Std.err.	*Df*	*t*/$\chi 2$	*p*
Intercept	−2.676	0.362	884	−7.393	<0.001
Cutting (ref. No cutting)			4	39.425	<0.001
- Regeneration cutting in 0–5 years (RC 0–5)	−1.164	0.263	884	−4.433	<0.001
- Regeneration cutting in 6–10 years (RC 6–10)	−0.636	0.409	884	−1.553	0.121
- Intermediate cutting in 0–5 years (IC 0–5)	0.454	0.179	884	2.534	0.011
- Intermediate cutting in 6–10 years (IC 6–10)	−0.107	0.208	884	−0.514	0.608
Zone (ref. HB-SB)			2	25.041	<0.001
- MB	0.774	0.210	884	3.678	<0.001
- NB	1.068	0.231	820	4.615	<0.001
Site type (ref. Herb-rich)			3	792.644	<0.001
- Mesic	2.307	0.360	884	6.411	<0.001
- Sub-xeric	4.276	0.357	884	11.973	<0.001
- Xeric	5.490	0.362	884	15.163	<0.001
Cover of bryophytes, %	−0.011	0.002	884	−4.267	<0.001
Cutting * Cover of bryophytes, %			4	11.745	0.019
- RC 0–5, Bryophytes	0.001	0.007	884	0.115	0.909
- RC 6–10, Bryophytes	−0.002	0.009	884	−0.186	0.852
- IC 0–5, Bryophytes	−0.011	0.003	884	−3.243	0.001
- IC 6–10, Bryophytes	0.278e-3	3.839e-3	884	0.072	0.942
Zone * Cover of bryophytes, %			2	11.699	0.003
- MB, Bryophytes	−0.010	0.003	884	−3.120	0.002
- NB, Bryophytes	0.472e-3	3.488e-3	884	−0.135	0.892
Random effects	Variance	95% cl			
Cluster	2.373	2.193–2.568			

Note: The *t* and $\chi 2$ values are the test values for the parameter estimates and type III Anova (deviance) tests, *df* denotes the degrees of freedom and cl the confidence intervals. R^2 for marginal and conditional model was 69% and 99%, respectively.

nationwide sampling, we were able to provide new quantitative information on factors influencing lichen cover, especially on those regarding forest management and relationships between lichens and co-existing plants. This information is valuable when evaluating recent lichen decline and predicting potential future changes under increasing human impact and changing climate.

Our study reveals that the abundance of ground lichens is an outcome of intermingled natural and human-influenced factors and interactions among them. The influence of forest management is evident through its disturbance effect but also its effects on forest stand structure that consequently influences the plant succession and competitive interactions among plants.

4.1 | Effects of site factors and stand structure

The negative correlation observed between lichen cover and temperature sum indicates that lichens are more abundant in the more northern locations. Similarly, Akujärvi et al. (2014) found that the lower the temperature sum (i.e., the harsher the climatic conditions), the higher was the lichen biomass in the NB subzone. Also, the cover of lichens increased towards dry and poor site types. In our study, HB-SB and MB subzones showed similar abundance pattern of lichens along the site type gradient, but NB differed from them in terms of lower lichen cover on xeric sites, reflecting the effect of widespread and long-term reindeer grazing in the north (Akujärvi et al., 2014).

Light is a limiting factor for the growth of ground lichens in boreal forests. In our models, lichen cover increased (linearly) with decreasing canopy cover of trees. Most favourable sites were sparse forests with minimal shading of *Picea abies* trees (cf. Petersson et al., 2021). In the earlier study using a part of the present data, the optimal canopy cover for lichens was found to be 25% in mature uncut forests (Tonteri et al., 2016). Other studies have reported optima ranging from canopy cover of 40% (stand basal area of 15 m^2 ha^{-1}, Jonsson Čabrajić, 2009) to 50% (17–19 m^2 ha^{-1}, Matila & Kubin, 1998). The latter studies, however, concentrated on lichen-rich vegetation in *Pinus sylvestris* forests, while we analysed all types of forests on mineral soils, including forests dominated also by *Picea abies* and broad-leaved trees. According to Węgrzyn et al. (Węgrzyn et al., 2020, 2021), lichens thrive better under a canopy of low rather than high *Pinus sylverstris* trees, but

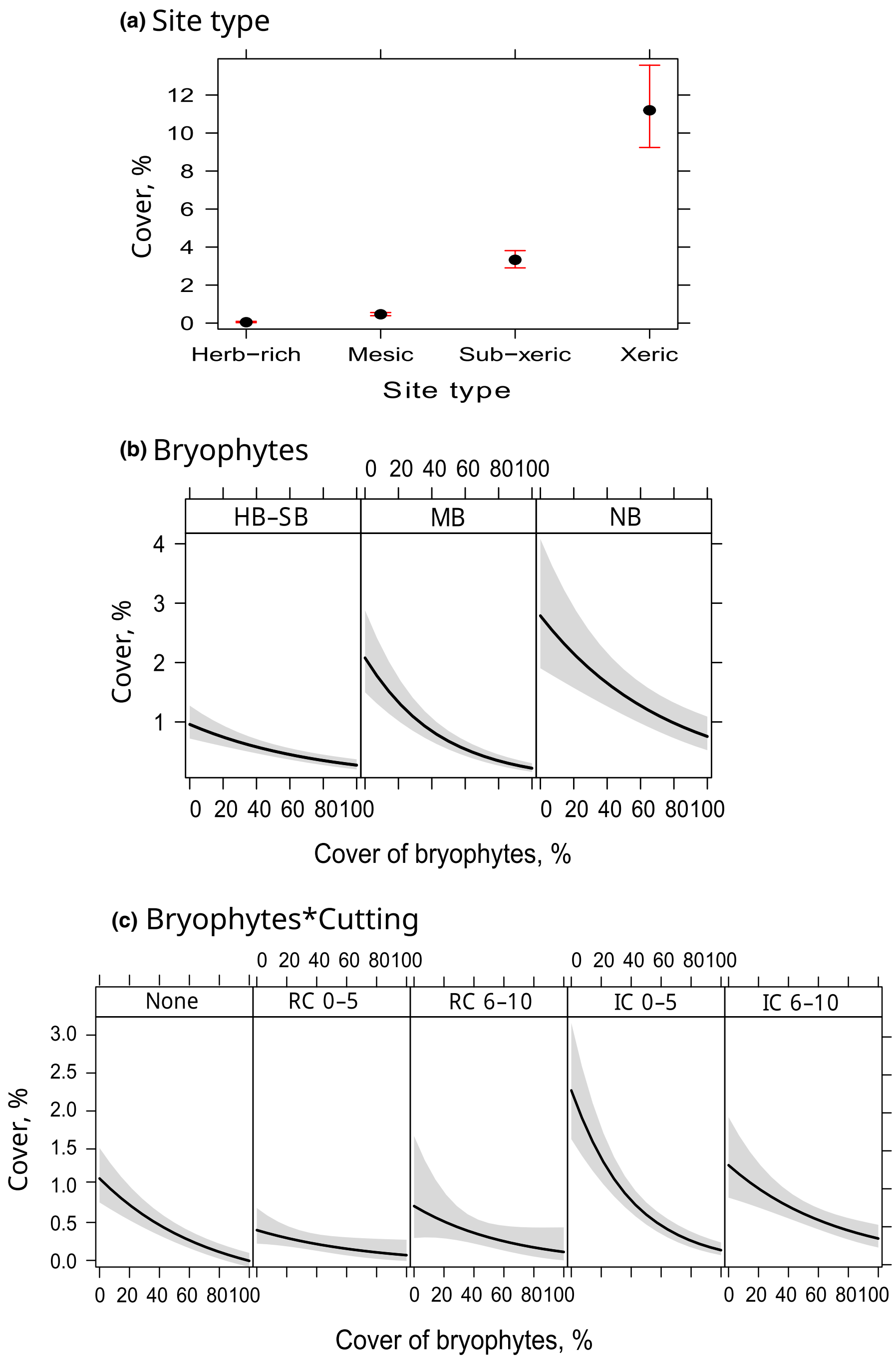


FIGURE 4 Predicted responses and 95% confidence intervals of the cover of all lichens to (a) site type, and (b) bryophyte cover in different subzones of the boreal zone and (c) under different cutting regimes. The predicted effects are based on model 2 (Table 4). Abbreviations: HB-SB, southern; MB, middle; NB northern boreal subzone; RC, regeneration cutting; IC, intermediate cutting

in their case this pattern is possibly connected to variation in site fertility rather than stand structure alone.

Lichens thrive best in old forests (Akujärvi et al., 2014; Kumpula et al., 2014; Sandström et al., 2016), which was confirmed in our study. Old-growth forests may offer optimal light and moisture conditions, but they are also environments where the latest major disturbances have occurred a long time ago. Nevertheless, lichens sometimes are abundant also in early successional stages of boreal forests, especially after RC on mesic, sub-xeric and xeric sites (Tonteri et al., 1990, 2016). This is likely due to the increased availability of light and bare, disturbed soil surface during the short period of the early successional stage, before vascular plants and large bryophytes take over in the secondary succession.

4.2 | Hypothesis 1: Effect of forest management

Regeneration cuttings, mostly clear-cuttings, clearly decreased lichen cover, which supported our first hypothesis. Previous studies have also obtained similar results (Bråkenhielm & Persson, 1980; Helle et al., 1990; Sandström et al., 2016). RC cause a major disturbance to the forest floor through mechanical destruction and with a thick layer of cutting residues. IC, mostly thinnings, cause less disturbance than clear-cuttings, and consequently lichen cover stayed at the same level as in uncut forests or even increased in sites with a low abundance of bryophytes. Moreover, thinning treatment likely makes the growth conditions more favourable for lichens by increasing the amount of light on the forest floor. Kivinen et al. (2010), Boudreault et al. (2013) and Korosuo et al. (2014) even recommended thinning as one of the methods for increasing the abundance of lichens.

Soil preparation methods carried out in connection with RC showed contrasting effects on lichen cover. More intensive methods, that is, ploughing and ditching, caused lichens to decline in our data, thus partly supporting our hypothesis. However, after less intensive treatments, lichen cover was higher than on untreated soil, probably because disc trenching, scalping and mounding create new competition-free microsites for lichens to colonise.

4.3 | Hypothesis 2: Forest management and reindeer grazing

The reindeer-herding area covers almost the entire NB subzone in Finland. Altogether the number of reindeer reaches ca. 200,000 at the end of each year (Anonymous, 2014). Both grazing and trampling have a great impact on lichens in the herding area: in an ungrazed area lichen cover can be fivefold and biomass even 15-fold that in a heavily grazed area (Väre et al., 1995; Akujärvi et al., 2014). In the present study, the lack of ungrazed control plots in the NB subzone limits our ability to show the effect of reindeer grazing on lichen cover in the north. Reindeer move and graze relatively freely in both managed and protected forests in the NB subzone. Therefore, we claim that our finding of 'missing lichen cover' on xeric sites in the north in comparison to that observed on similar sites in the south predominantly results from reindeer grazing (Figure 2g).

Lichens responded similarly to cuttings, soil preparation and stand variables in all boreal subzones representing large biogeographical regions, even though reindeer grazing strongly influences lichen cover in the NB subzone. The result supports our second hypothesis and indicates that long-term heavy grazing has not altered the response patterns of lichens to stand structure and forest management. However, Akujärvi et al. (2014) concluded that the effect of the succession stage and forest management history was slightly stronger on heavily grazed sites than on ungrazed control sites in the NB subzone.

4.4 | Hypothesis 3: Interaction with dwarf shrubs and bryophytes

Dwarf shrubs generally showed a negative impact on lichen cover, which supported our hypothesis. However, the effect depended on the dwarf shrub species and forest site type because different dwarf shrub species dominate on different site types (Cajander, 1949). *Vaccinium myrtillus*, a dominant species on mesic sites, has horizontally positioned branches of shoots (Tolvanen, 1995) and leaves which may overshadow the lichens. In addition, deciduous leaves annually produce a considerable amount of litter on lichens. On sub-xeric and xeric sites, dense clones of *Empetrum nigrum* (Olofsson et al., 2009) and *Calluna vulgaris* (Bråkenhielm & Persson, 1980) leave little space for any other species. *Vaccinium vitis-idaea*, dominating on sub-xeric sites, was the only dwarf shrub having a positive relationship with lichens. Cowberry is evergreen and has straight shoots and a low number of later branches (Tolvanen, 1995). Therefore, compared to *Vaccinium myrtillus*, shading by *Vaccinium vitis-idaea* apparently has less effect on lichens. However, some unknown underlying factors may also explain the positive relationship between lichen and *Vaccinium vitis-idaea*.

Bryophytes and lichens showed a trade-off, which may indicate either that bryophytes benefit from lichen decline (apparent competition), or that a real competition between these two functional groups exists. We found a strong negative relationship between bryophytes and lichens in the NB subzone characterised by reindeer herding. The result may indicate that bryophytes take over the lichen surfaces exposed to reindeer grazing, and thus in such areas an apparent competition is likely to occur (Holt & Bonsall, 2017). However, the negative relationship between bryophytes and lichens was also stronger in the MB 123e in comparison to the HB-SB subzone, both subzones located outside of the reindeer-herding area. The increasing negative correlation towards the north may also be caused by increasing light availability on the forest floor because of decreasing stand density and volume towards the north. Such conditions favour lichens and result in higher variation in their abundance and consequently, in stronger negative correlation between lichen and moss abundance towards the north. Previously, ground lichens and bryophytes have been found to correlate negatively in old boreal forests in Sweden (Dynesius & Zinko, 2006), but in boreal forests of Canada bryophyte cover had no effect on lichen cover (Bartels & Chen, 2013).

In all cutting treatments, the relationship between lichens and bryophytes was negative, indicating (apparent) competition. The negative relationship was stronger in closed stands (no cutting or IC) than in open, recently regenerated stands (RC) (Figure 4c). This is probably because in dense stands humid and dark conditions disfavour lichens, but bryophytes grow vigorously (Bråkenhielm & Persson, 1980; Sulyma & Coxson, 2009; Petersson et al., 2021). In our data, summing the percentages of cover of bryophytes and lichens results in far less than 100% in total immediately after RC, indicating that there is a lot of empty space for both groups to colonise. Despite this, the negative relationship between lichens and bryophytes was observed in RC forests. After IC, lichens benefit from increased light availability especially if bryophyte cover is low, but the positive effect vanishes when the tree canopy later closes.

Although we suggested vascular plants and bryophytes have negative impacts on lichens, the relationship is bidirectional: lichens may have a negative effect on plants (Favero-Longo & Piervittori, 2010), for example through allelopathy (Lawrey, 1984, 1986, 2009), although this has not been found in all studies (Kytöviita & Stark, 2009). Lichens can also prevent or increase seed germination (Sedia & Ehrenfeld, 2003) and affect seedling growth and survival by influencing water and nutrient availability (Riefner Jr. & Bowler, 1995).

4.5 | Many possible reasons for lichen decline

Over the past six decades in Finland, the volume and canopy cover of growing stock have increased, but on the other hand the proportion of regeneration areas and young forests has increased (Korhonen et al., 2017). This means that sparse, light forest stands favourable for lichens have largely been replaced by dense, shaded stands. It is likely that these changes play a major role in the observed decrease of lichens in the HB-SB and MB subzones. In the NB subzone, changes in forest structure most likely have a smaller role.

In addition to forest management and reindeer grazing, previous studies have suggested several other factors to have a negative influence on lichen cover in northern regions. As an effect of climate change, greening of tundra has been observed both in northern Fennoscandia and in North America (Cornelissen et al., 2001; Lang et al., 2012), including the expansion of shrubs and decline of lichens (Fraser et al., 2014; Vuorinen et al., 2017). Villén-Peréz et al. (2020) suggest that global warming may affect the maximum potential abundance of boreal plant species as all functional groups (dwarf shrubs, herbs, grasses, bryophytes and lichens) showed significant responses to temperature, though the direction of effects varied.

The lack of fire's influence in present-day forests may also play a role in observed lichen decline. In the past, fire often swept over xeric forests (Niklasson & Granström, 2000; Wallenius, 2011) maintaining low site fertility favourable for lichens. Moreover, the slash-and-burn agriculture that in Finland lasted until ca. 1900, had a similar influence on slightly more productive soils.

In the HB-SB and MB subzones, anthropogenic nitrogen and sulphur deposition was largest in the 1970s and has decreased since then (Ruoho-Airola et al., 2004). However, their accumulated legacy may still affect forest habitats with negative effects on lichens. Especially the long-term effect of nitrogen deposition may result in eutrophication of forest vegetation and consequently a decrease in lichen cover in southern Finland.

After the collection of our data in 1985–1986, the boreal forests of Finland have faced, for example, climate warming, nitrogen deposition, new forest management practices and intensified reindeer herding. All these changes may have modified the present-day response of ground lichens to the factors analysed in this study. Further, lichens have continued their decline at least until the early 2000s (Tonteri et al., 2016). This study provides new quantitative insights into underlying factors for the lichen decline.

4.6 | What would lichen-friendly forestry look like?

At the stand level, the negative effects of intensive cuttings and soil treatments on ground lichens are clear. However, at the regional level, the simulations of Miina et al. (2020) indicated that the development of the average lichen cover varied only slightly among alternative 30-year regional cutting scenarios with variation in the total harvest removals. They concluded that compared to the overall declining trend observed in lichen cover, the effects of the cutting scenarios were only minor. Our results support these earlier studies: high light availability, low disturbance of the forest ground and maintenance of low site fertility are factors that play a key role in maintaining and creating suitable habitats for ground lichens. Therefore, forest management regimes such as partial cutting (Boudreault et al., 2013), gap felling, selection cuttings and pre-commercial thinning (Korosuo et al., 2014, see also Berg et al., 2008) could be used more commonly than currently to create favourable light and moisture conditions for lichens. Leaving retention trees, prolonging rotation length and maintaining patches of old forest (Kivinen et al., 2010) would also preserve lichen habitats. Further, removal of logging residues, applying lighter soil preparation methods, avoiding extensive fertilisation, and applying prescribed burning on medium fertile sites would maintain and create soil properties suitable for lichens (Kivinen et al., 2010). The effects of forest management and consequent changes in forest structure as underlying factors for lichen decline were similar both inside and outside the reindeer-herding area. Thus, these recommendations on lichen-friendly forestry would also be applicable in the reindeer-herding area.

AUTHOR CONTRIBUTIONS

All authors together formulated the idea of the study. Tiina Tonteri curated the data. Ville Hallikainen and Jari Miina prepared the statistical models. Tiina Tonteri wrote the first draft of the manuscript. All authors commented on the manuscript and contributed to the final version.

DATA AVAILABILITY STATEMENT

The data used in this study are archived in Zenodo. DOI: 10.5281/zenodo.7113609.

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SUPPORTING INFORMATION

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

Appendix S1. Performance of the models.
Appendix S2. Model results for *Cladina* spp.

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