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Original research article

Ground lichen cover and response in relation to forest characteristics in Sweden 1993–2023

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A B S T R A C T

Reindeer husbandry is closely connected to the culture and tradition of the indigenous Sami people, and ground lichens are a key bottleneck resource for winter grazing of the semi-domesticated reindeer. Many factors have been linked to the decrease in ground lichens in the boreal zone. Forestry plays a crucial role in the lichen decline in Swedish forests but is also an important actor with the potential to contribute to a recovery. Forestry is obliged to consider the needs of reindeer husbandry, but important details in the dynamics of how forest measures affect lichen cover are still unknown.

Our analysis of environmental monitoring data shows that ground lichen cover declined by 57 % in the reindeer husbandry area from 1996 to 2015, while there was no declining trend from 2015 to 2021. Comparing lichen cover change for different age classes of forest, we found that lichen cover increase primarily occurred in clear-cut forest and forest aged < 40 years. Our results support previous findings that it is possible to increase lichen cover through adapted forest management. A basal area below 15 m^2ha^{-1} in suitable lichen habitat will increase lichen cover for forest aged 40–80 years. The results of this study can contribute to increasing the knowledge basis for policy decisions, forest management, and local consultations between reindeer herders and forest companies to increase and restore lichen cover.

1. Introduction

Forestry has transformed boreal landscapes and ecosystems over the last century, both worldwide (Noble and Dirzo, 1997; FAO, 2020; Huettmann and Young, 2022) and specifically in Sweden (Lundmark et al., 2013). Significant changes in forest floor vegetation are an effect of a changed forest structure (Kenderes and Standovár, 2003; Hedwall et al., 2013). Ground lichens in the boreal forest of several countries have been declining; this has been shown for the *Cladonia* subgenus *Cladina* in Scandinavia (Nygaard and Ødegaard, 1999; Kumpula et al., 2000; Uotila and Kouki, 2005), Russia (Rees et al., 2003; Uotila and Kouki, 2005), Alaska in the US (Joly et al., 2007; Collins et al., 2011) and Canada (He et al., 2024). In the Swedish reindeer husbandry area (hereafter "reindeer husbandry area"), ground lichen-abundant[1] forests declined by 71 % between 1955 and 2016, from covering 13–3.7 % of the productive forest land (Sandström et al., 2016). This decline affects reindeer husbandry because ground lichens in the boreal forest (mainly *Cladonia* spp. and *Cetraria islandica*) are a bottleneck winter grazing resource for semi-domesticated reindeer (*Rangifer tarandus*, hereafter referred to as

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[1] > 50 % lichen cover of existing bottom layer (SLU, 2018)

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“reindeer”) (Heggberget et al., 2002). Reindeer and reindeer husbandry is closely linked to the Sami indigenous culture and traditions (Lundmark, 2008).

Ground lichens are symbiotic organisms that consist of a fungus together with an algae (Rikkinen, 1995) or a cyanobacteria (Honegger, 2009). Their growth rate is determined by the amount of light they receive while wet, since this is when they are photosynthetically active (Jonsson Čabrajić et al. 2010). Growth rates are negatively correlated with air pollution, acid rain,

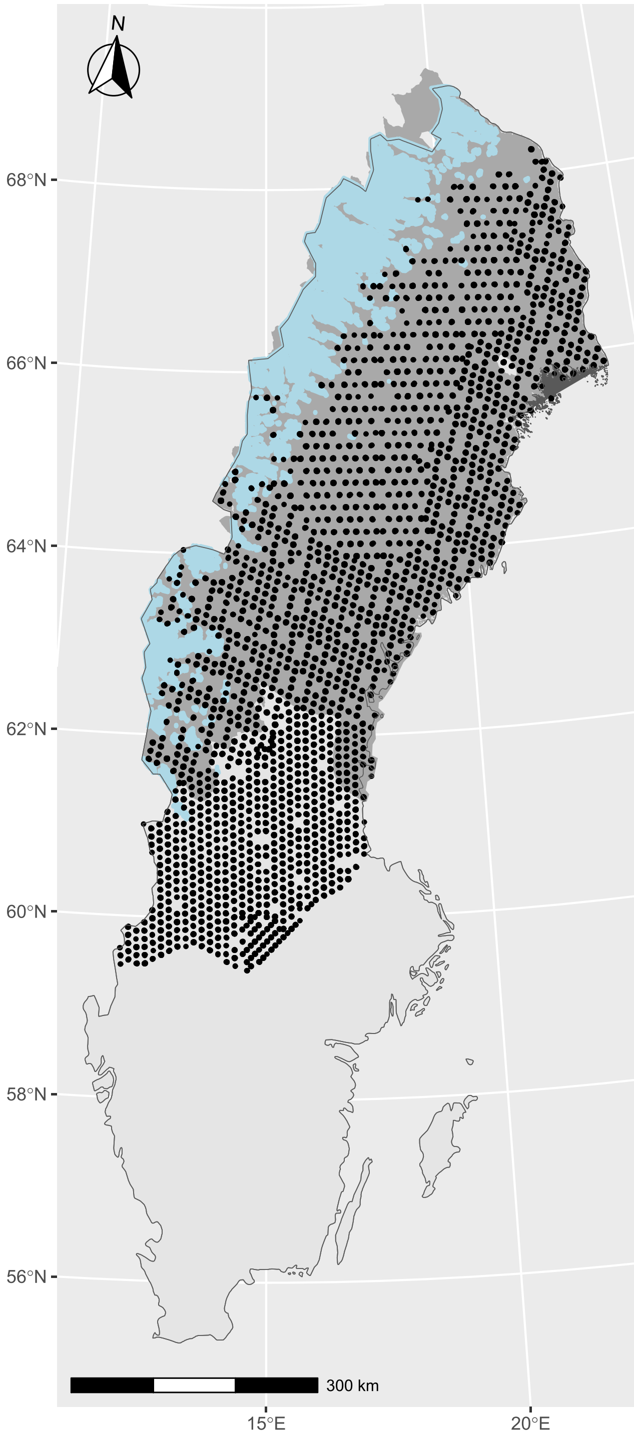

Fig. 1. Map of Sweden. Grey – Reindeer husbandry area (partly overlapping with Norway). Blue – Alpine mountain area. Black points – Sample plots used in this study covering the forested parts of northern Sweden.

accumulation of snow and, for some species, elevation, substrate and temperature (McMullin and Rapai, 2020). Forestry affects ground lichen cover (Berg et al., 2008; Kivinen et al., 2010), and the short-term effects are well known from field and experimental studies (Uboni et al., 2019; Boudreault et al., 2013; Jonsson Čabrajič et al., 2010). Studies on long-term effects are more rare (Horstkotte and Moen, 2019; Mäkipää and Heikkinen, 2003; Tonteri et al., 2016). Forestry affects lichens negatively through e.g. site preparation (Roturier and Bergsten, 2006; Tonteri et al., 2022), fertilisation (Olsson and Kellner, 2006; Strengbom and Nordin, 2008) and planting of *Pinus contorta* (Horstkotte et al., 2023). However, logging can have a positive effect, creating lighter conditions on the forest floor (Boudreault et al., 2013; Coxson and Sharples, 2024; Lafleur et al., 2016). While old growth forests are an important grazing habitat for reindeer, partly due to presence of tree lichen, ground lichen cover has been seen to increase in regenerated (Kivinen et al., 2010) and young (Horstkotte and Moen, 2019) forests. As canopy cover increases, lichens are more likely to be outcompeted by mosses (Kivinen et al., 2010; Tonteri et al., 2022).

Reindeer grazing can be both negative (Akujärvi et al., 2014; Kumpula et al., 2014) and positive (Uboni et al., 2019) for lichen cover. Lichen cover has declined at similar rates both inside and outside the reindeer husbandry area (Sandström et al., 2016), suggesting that factors beyond reindeer grazing – such as site fertility and forest characteristics – play a key role in determining lichen cover. Tonteri et al. (2022) found similar response pattern of lichens to stand variables both within and outside the reindeer husbandry area in Finland, although a negative effect of reindeer grazing on lichen biomass was evident in the northernmost areas. Total reindeer numbers in Sweden have remained relatively stable over time varying around 250 000 in winter stock. For our study period reindeer numbers have varied between 220 000 in 1996 and 260 000 in 2001, and around 230 000 in 2024 (Sametinget, 2025). Minor and temporary increases and decreases of reindeer stock between reindeer herding communities seem not to be coordinated in time.

Important aspects of the relationship between forest management and changes in lichen cover remain poorly understood. Further research is needed to clarify how forestry practices influence ground lichens and to identify effective measures for mitigating lichen decline, thereby supporting the recovery of this vital resource for reindeer husbandry. More knowledge about explanatory factors of lichen habitat and response to forest characteristics will provide an important basis for restoration efforts and the development of reindeer husbandry-adapted forestry in northern Sweden.

Data from the Swedish National Forest Inventory (hereafter "NFI") enable analyses of long-term changes in forest conditions across large spatial scales. Earlier studies on changes in lichen cover in Swedish forests (Horstkotte and Moen, 2019; Uboni et al., 2019; Sandström et al., 2016) were based on general patterns in the changes between different bottom layer cover classes as defined in the NFI (Fridman et al., 2014). Here, the percentage of total lichen cover in relation to mosses in the existing bottom layer is estimated in three classes (lichen-abundant >50 % lichen cover, lichen-moderate 25–50 % and moss dominated <25 %, SLU, 2018). These studies have limitations in detecting lichen cover changes, owing to the used class scale. We instead use continuous values of lichen cover estimates from the revisited sample plots of the NFI, to investigate lichen cover change in relation to forest characteristics. Using continuously measured time series data since 1993, we build models for lichen cover and change with the aim to provide knowledge about explanatory factors for lichen habitat and cover change.

Our research questions are:

1) What is the overall trend in change in lichen cover between 1996 and 2021 within and outside the reindeer husbandry area?

2) How do different forest characteristics explain changes in lichen cover over time between 1993 and 2018?

3) How do different forest characteristics explain lichen cover in the period 1993–1997, and how can this information help us identify areas with potential for restoration?

The reindeer husbandry area does not cover the entire boreal zone, and the forest characteristics and forest management applied within and outside the reindeer husbandry area are similar and therefore suitable for comparing the effects of reindeer grazing on ground lichen. To address the effects of reindeer grazing, we compare lichen cover and height both within and outside the reindeer husbandry area.

This study emphasizes forest characteristics and terminology relevant to Swedish operational forestry, ensuring practical applicability. The selected time periods are determined by the availability of consistent data.

2. Material and method

2.1. Context

The forest industry represents one of Sweden's most important economic sectors, providing significant contributions to employment, exports, and overall value generation (SFIF, 2018). Forestry methods mostly include even-aged, stand-replacement forestry, with profound effects on forests, landscape configuration and conditions (Esseen et al., 1997; Östlund et al., 1997) as well as on reindeer husbandry (Berg et al., 2008; Kivinen et al., 2010, 2012; Sandström, 2015).

Forestry and reindeer husbandry are continual, parallel ongoing land uses on almost all productive forest land in the reindeer husbandry area (Fig. 1). While reindeer husbandry is a small economic sector from a national perspective, it is important for local economic development in many areas in northern Sweden (OECD, 2019). There, reindeer husbandry is a traditional land use form, practised by the indigenous Sami people, and its cultural heritage value may be several times greater than the sector's yearly turnover (Bostedt and Lundgren, 2010). It is a central and highly important part of Sami society, as well as being a carrier of a long cultural tradition and Sami identity (Brännlund, 2015; Sametinget, 2024). Ground lichens are key grazing resources for reindeer (Skuncke, 1969; Danell et al., 1994). Nearly all reindeer in Sweden depend on the availability of these lichen in the boreal forests for four to six months each year. Snow conditions strongly influence ground lichen accessibility, thereby shaping reindeer movements, habitat use, and associated herding practices. The dynamic and intricate interactions among reindeer, lichens, tree cover and snow conditions are fundamental to sustaining the traditional, nature-based grazing practices that underpin Sámi reindeer husbandry (Roturier and Roué, 2009).

Sweden has agreed to promote Sami rights through the Swedish Constitution. Legislation and guidelines stipulate that all owners and stakeholders of the land within the reindeer husbandry area must safeguard and respect the grazing rights as defined in the Swedish Constitution (SFS 1974:152, Chapter 1, §2), the Reindeer Grazing Act (SFS 1971:437) and the Swedish Environmental Code (SFS 1998:808). Sami rights are also promoted through numerous international conventions.[2] The Sami people have the possibility to influence forest management through consultation meetings with large forest owners prior to forest measures (SFS 2010:930). Forest owners are required to consider the needs of reindeer husbandry (SFS 1993:553) but are not required to follow reindeer herders' recommendations.

2.2. Study area

The study area that covers the northern part of Sweden is bounded in the south by *Limes Norrlandicus* (Wastenson et al., 1996) and consists of two parts. The northern part, constituting the sum of all land presently used by the 51 autonomous reindeer herding communities operating in Sweden, is defined by the Sami Parliament as the Swedish Reindeer Husbandry Area (RHA_{in}, Fig. 1, SFS 1971:437; Sametinget, 2024). Forests cover 60 % of the reindeer husbandry area land surface. Of the productive forest land in 2020, 28 % is owned by private corporate companies, 40 % by other private or individual owners, 7 % by other public owners and 25 % by the state or state-owned companies (NFI, 2024).

The southern part of the study area (termed RHA_{out}) is similar to the southern part of RHA_{in} in terms of forest conditions (Appendix, Tables 1 and 2) and forest practice, but with no reindeer grazing occurring. The total size of the study area is 307 136 km^2, with the reindeer husbandry area constituting 226 000 km^2 (55 % of the Swedish land area) and containing 49 % of all productive forest land[3] in Sweden (Sandström et al., 2016). The Scandinavian Mountain Range spans the western section of the study area, crossing east into the boreal forests, interspersed with lakes and mires (Fig. 1). The boreal forests are dominated by Scots pine *(Pinus sylvestris)* and Norway spruce (*Picea abies*), and to a minor proportion birch (*Betula pubescens*) and other broadleaved species.[4] In their natural and primal state the pine forests are fire-prone, but today forest fires has been almost eliminated (Östlund et al., 1997).

2.3. Input data

The NFI's monitoring programme, with its stratified systematic sample plot design, is based on clustered temporary samples since 1953 and permanent revisited plots since 1983, covering all forest land in Sweden.

In the NFI, data on the forest is collected every year at randomly located temporary plots as well as permanent, revisited plots clustered in tracts. It is the permanent plots, established between 1983 and 1987 mainly in order to increase the accuracy of change estimation (Fridman et al., 2014), that constitute the basis for the analysis in this study. Since their establishment they have been revisited at five-year intervals, with some exceptions. NFI's vegetation assessment is done at ten-year intervals on a subsample of the permanent plots (Fridman et al., 2014). This assessment includes a visual estimation of ground cover for species or species groups in both the field layer (vascular plants) and bottom layer (mosses and lichens). Cover is recorded using the following scale: (0, 0.1] m^2, (0.1, 1] m^2 and integer m^2 values up to 100 m^2. Within the bottom layer, *Cladina* spp. (a section within *Cladonia* commonly referred to as reindeer lichens), *Cladonia* spp. (excluding the *Cladina* section) and *Stereocaulun* spp. are registered as separate groups (Walheim et al., 2018). For the present analysis, cover values for *Cladonia* spp., the *Cladina* section, and *Stereocaulon* spp. were aggregated into a single variable termed **"lichen cover."** Other lichen taxa, such as *Cetraria* spp., were therefore not included in this variable. The vegetation assessment also estimates the area of bare soil without vegetation (Skogstaxering, 1993). Vegetation cover at permanent plots is measured based on a circular sample plot with a radius of 5.64 m (100 m^2). Forest variables besides vegetation cover are measured based on a 10 or 20 m-radius plot, with the same centre point (Table 2, Appendix Fig. 1, Holmlund, 2019).

Since 2018, lichen height is registered in the NFI as an area-weighted average height of *Cladina* spp. cover on the 100 m^2 plots (integer number, 0–20 cm, SLU, 2018).

2.4. Data analysis

The data analysis for the four data sets was done in four steps (Table 1). For Steps 1 and 2, the data analyses for RHA_{in} and RHA_{out} were done separately. For Steps 3 and 4, the data for RHA_{in} and RHA_{out} (termed RHA_{all}) was combined to obtain a larger data set and due to the similarities in terms of forest conditions and forest practice between the areas (Appendix, Tables 1 and 2). Details of statistical tests and models are given below separately for each research step.

[2] For instance, the International Covenant on Civil and Political Rights, Article 27; the Council of Europe's Framework Convention for the Protection of National Minorities, Article 5; The United Nations Declaration on the Rights of Indigenous Peoples (UNDRIP).

[3] Productive forest produces more than 1 m^3 timber per ha and year. Unproductive forest land represents 16 % of Sweden's total forest land (Norrbotten 31 %, Västerbotten 20 % and Jämtland 21 % (SCB, 2023)).

[4] Within the reindeer husbandry area, the tree species composition is dominated by Scots pine (48 % of the growing stock), followed by Norway spruce (36 %), birch (*Betula spp.*) (13 %), and other broadleaved species (2 %) (NFI data, year 2020; average for 2018–2022, based on productive forests outside formally set-aside areas).

Table 1
Analyses step, data collection period, study area and number of samples of the datasets in the study.

Analyses step	Data collection period	Study area	Nr. of samples
1. Lichen cover change	1994–2023	RHA_{in} and RHA_{out}	RHA_{in}: 296–656/year RHA_{out}: 153–447/year
2. Lichen height	2018–2023	RHA_{in} and RHA_{out}	RHA_{in}: 1 416 RHA_{out}: 573
3. Lichen cover change and forest characteristics	1993–2023	RHA_{all}	1 008
4. Lichen cover and forest characteristics	1993–1997	RHA_{all}	3 324

For all models developed in this study the open source platform R (R Core Team, 2023) was used, including the libraries mgcv (Wood, 2017) for general additive modelling (GAM) in analyses step 3 and 4, sf (Pebesma Bivand, 2023) and terra (Hijmans, 2025) for spatial operations, and dplyr (Wickham et al., 2023) for handling NFI data base extracted data. For the calculation of the proportion of explained variance for each single variable in relation to the models' total explained variance, the approach described by Eskildsen et al. (2013) was applied. Backward selection (e.g. Hastie and Tibshirani, 2000) was used as the model selection method. Before modelling, we used the VIF (Variance Inflation Factor, e.g. Zuur et al., 2007) to check for collinearity between variables with a threshold of three.

1. Lichen cover change (1996–2021) for RHA_{in} and RHA_{out}
   For the analysis of total change in lichen cover for RHA_{in} and RHA_{out}, we used data from productive forest land in northern Sweden from 1994 to 2023. A ratio estimator was obtained through a Horvits-Thompson estimation (Särndal et al., 2003) between area covered by lichen and the total area for each region and each year. As the design of the NFI covers Sweden after a five-year period, we calculated the mean over each five-year interval and moved this interval. This was done separately within and outside the reindeer husbandry area. To compare the resulting trends, a linear model was applied using year and year*region as predictor variable. If in the model summary year*region is not significant, both trends are similar.
2. Lichen height for RHA_{in} and RHA_{out}
   Lichen height data were only available for the last inventory cycle of the NFI. We compared both cumulative distributions of the collected data using a two-sample Kolmogorov-Smirnov test (Massey, 1951). We also calculate a weighted mean and standard deviations for lichen height inside and outside RHA. The area factor of the sample plot was used as weight for the calculation of standard deviation as well. If the confidence intervals of the means do not overlap (mean ± 1.96*sd) the means are different.
3. Lichen cover change in relation to forest characteristics (1993–2023)

In the change analysis, we include plots with lichen cover > 5 % observed at least once for sample plots inventoried two to four times. To reduce the effect of interobserver variance we ignored changes of less than 5 %. Fig. 2 illustrates the inventories of individual sample plots to clarify the process of data collection. We used data from the individual revisited sample plots to find explanatory factors for change in lichen cover over time.

The data set was divided into four subsets based on forest age classes in order to relate the results to the different phases in rotation forestry practice. Also, some variables are only available for some age categories; for instance, stem number is only available for young forest whereas basal area is not available for very young forest. The data subsets were as follows:

(1) forest with clear-cuts during the study period
(2) young forest aged < 40 years in 2023
(3) mid-aged forest with stand age > 40 years at the start of the study period and < 80 years at the end
(4) mature forest with stand age > 80 years at the start of the study period

To analyse lichen cover change for the period, we used a general additive mixed model (GAMM, Wood, 2017) with plot ID as a random factor and variables listed in Table 1, including year, as explanatory variables. The reason for using GAM was because we did not expect a linear development of lichen over time. As the data consisted of repeated measurements a mixed GAM (GAMM) was applied with sample plot id as a random variable for each data subset.

There were no consistent variables for analysing forest characteristics explaining lichen cover change for clear-cut or young (aged <40 years) forests, due to inventory methodology. Stem number is only measured for trees up to < 7 m in height, while basal area is only measured for trees > 7 m in heigh (Table 1). Therefore, we could not conduct time series analysis on these variables. For all mid-aged and mature forest, we used all available explanatory variables in the data set: mean height, proportion of pine, basal area, stand age and canopy cover.

4. Forest characteristics explaining lichen cover

To identify explanatory variables for lichen cover, we used all plots with lichen cover measure (including zero values) inventoried between 1993 and 1997 ($n = 3\ 324$). This gave a larger sample of plots with lichen cover compared to the end of the study period (2023) because of the lichen cover decline over the period. We built a GAM using the explanatory variables wetness, basal area, proportion of pine, site productivity for pine, mean height, volume and site productivity. The wetness index was derived from a digital elevation model (DEM, Lantmäteriet) using the SAGA package (Brenning et al., 2025) in R, assuming that the DEM had not changed

Table 2
Variables included in the data analysis; radius describes size of inventory plot.

Variable	Definition	Unit	Radius (m)
Basal area	Cross-sectional area of living trees at breast height (for mean height ≥7 m)	m^2ha^{-1}	20
Number of stems	Number (for mean height <7 m)	Number of stems ha^{-1}	20
Stand age	Mean stand age	Years	20
Pine proportion	Proportion of pine	%	20
Mean height	Mean stand height	m	20
Timber volume	Volume of stems including bark	m^3ha^{-1}	10
Site productivity for pine	Maximum mean annual volume increment for pine stands	m^3ha^{-1} and year	10
Reindeer husbandry area	Area where reindeer husbandry is practised 1/0		-
Bottom layer cover	Vegetation cover of mosses and lichens	m^2	5.64
Canopy cover	0–100	%	20
Site index	Site index H100 is a measure of site productivity, indicating the species-specific expected top height of a forest stand at a total age of 100 years, estimated based on site factors (Hägglund and Lundmark 1977).	m (6–50)	10

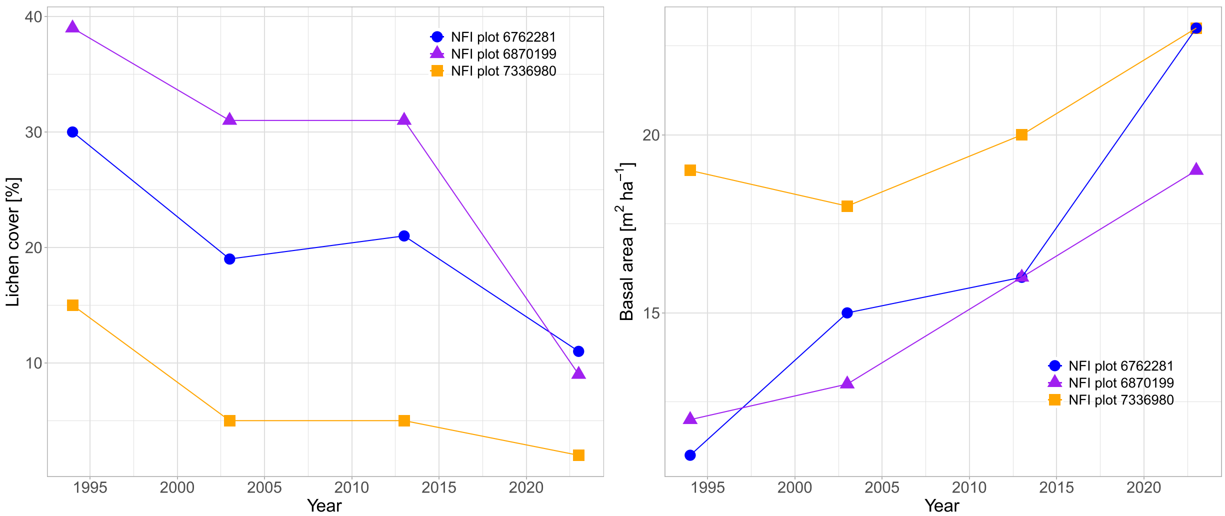

Fig. 2. Development over time of lichen cover (%, left panel) and basal area (m^2ha^{-1}, right panel) for three individual sample plots, revisited three times during the period 1994–2023. Based on Swedish National Forest Inventory data.

over the last 40 years. For modelling, a GAM (Hastie and Tibshirani, 2000; Wood, 2017) was applied using cubic splines and quasi-binomial as family argument (e.g. Schwemmer et al., 2019), dividing lichen cover values by 100. To account for spatial autocorrelation, latitude and longitude were included as an interaction term in the model.

3. Results

3.1. *Lichen cover change (1996–2021) within and outside the reindeer husbandry area*

To assess the total change in lichen cover, we compared temporal trends within and outside the reindeer husbandry area to analyse the effect of reindeer grazing. We found similar declining trends in ground lichen cover in both regions (Fig. 3), indicating that reindeer grazing is not the primary driver of the overall decline. The decrease was continuous until approximately 2015, after which lichen cover appeared to stabilize. Within the reindeer husbandry area, lichen cover declined by 57 % between 1996 and 2015. Over the full study period (1996–2021, based on data from 1994 to 2023), lichen cover for within the reindeer husbandry area decreased by 58 %, from 4.8 % to 2.0 % of the total productive forest land ($n = 296$–656 per year) while for outside it decreased by 40 %, from 4.9 % to 2.9 % ($n = 153$–447 per year). The year-by-region interaction term in the linear model was not statistically significant ($p = 0.10$), suggesting no difference in the overall temporal trends between regions.

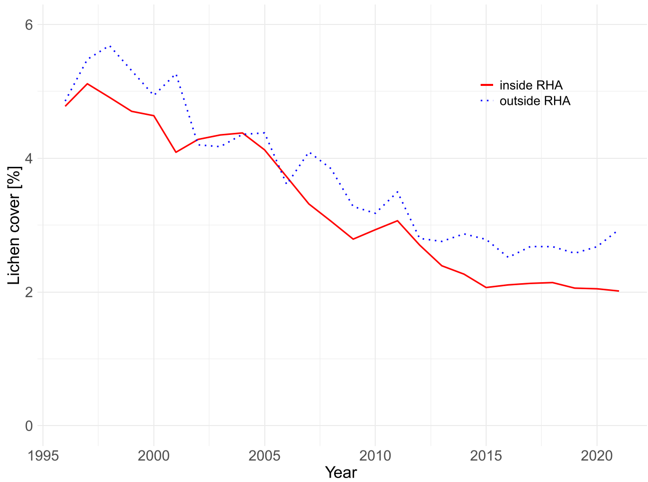

Fig. 3. Change in percentage of lichen cover for the period 1996–2021 within and outside the reindeer husbandry area (RHA) on productive forest land (ratio between lichen cover area and total area, based on five-year moving average 1994–2023). Based on Swedish National Forest Inventory data.

3.2. *Lichen height within and outside the reindeer husbandry area*

We found a significant difference in mean lichen height between areas within and outside the reindeer husbandry area, based on NFI sample plot data from 2018 to 2023 (Fig. 4). The two-sample Kolmogorov-Smirnov test ($D = 0.37294$, $p < 0.01$) indicated a clear difference in the distribution of lichen height between the two regions. Likewise, a test for differences in median height ($W = 291\ 330$, $p < 0.01$) confirmed this result. The weighted mean lichen height was 3.9 cm (± 0.11, $n = 1\ 416$) within the reindeer husbandry area and 7.2 cm (± 0.22, $n = 573$) outside. Although the corresponding 95 % confidence intervals do not overlap, the skewed distribution of height measurements (Fig. 4) warrants cautious interpretation.

3.3. *Lichen cover change in relation to forest characteristics (1993–2023)*

We also analysed changes in lichen cover at individual plot level over time, to compare changes in different age classes. At individual plot level, most plots showed a decline in ground lichen cover in all age classes during the study period (Table 3). Mid-aged and mature forests had the largest proportion of sample plots with a decline in lichen cover, 71 % and 70 % respectively. Sample plots with clear-cuts during the study period had the largest proportion of plots with an increase in lichen cover (41 %).

For clear-cuts, the distribution of sample plots with an increase and a decrease in lichen cover was close to normally distributed around zero, while the distribution of mid-aged forest was most skewed towards negative values (Fig. 5).

Further, we analysed changes in lichen cover in relation to forest characteristics, separated into different age classes. For forest aged 40–80 years ($n = 378$),[5] significant forest characteristics were basal area, stand age and canopy cover (Table 4 and Fig. 6). Basal area above 15 m^2ha^{-1} and stand age over 50 years were negative for lichen cover, while canopy cover between 39 % and 66 % was positive. Basal area was the forest characteristic that best explained change in lichen cover.

For forest aged > 80 years, only two variables of forest characteristics explaining lichen cover change were significant. The significant explanatory variables were year of inventory (F=31.874, $p < 0.001$) and stand age (4.087, 0.05), with increasingly negative effect with age ($n = 613$).

3.4. *Forest characteristics explaining lichen cover*

The explanatory variables for lichen cover at the start of the study period (1993–1997) were different from those explaining the change in lichen cover. The GAM showed that significant variables explaining lichen cover were proportion of pine, site index, wetness and basal area (Table 5 and Fig. 7). A value above the mean lichen cover was found for forest with a high proportion of pine (>48 %), site index H100 pine < 19 and wetness < 10.3. For basal area there was a positive effect below 13 m^2ha^{-1}, between 13 and 30 it was indifferent, and above 30 it was negative. Of the total deviance explained (37.2 %), proportion of pine explains 59.4 %, site index 34.5 %, wetness 4.4 % and basal area 1.8 %. This shows that the site factors, such as wetness and site index – which also largely determine the tree species composition – are more important than more changeable forest characteristics such as basal area.

[5] Number of plots with values for all predictor variables

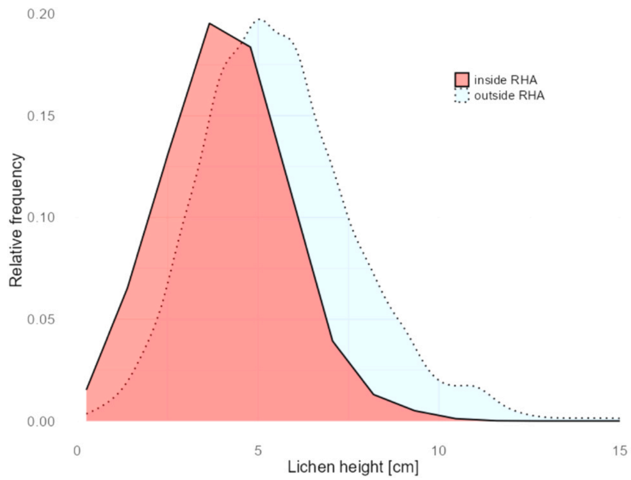

Fig. 4. Lichen height for within and outside the reindeer husbandry area (RHA) measured during the 2018–2023 inventories. Based on Swedish National Forest Inventory data.

Table 3
Total number and proportion (%) of sample plots with lichen cover change distributed on increase, no change (<2 %) and decrease between first and last inventories.

	Clear-cut	Young < 40	Mid-aged 40–80	Mature > 80	Total
Total number of samples	141	199	467	201	1008
With increase (%)	41	29	17	17	23
No change (%)	11	16	12	13	13
With decrease (%)	48	55	71	70	64

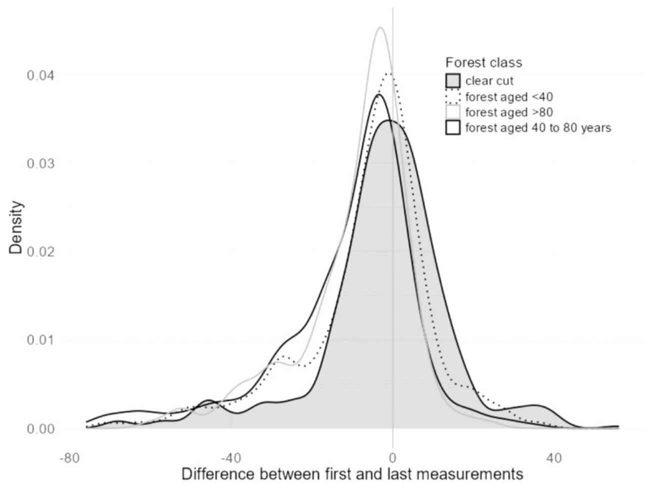

Fig. 5. Change in lichen cover for sample plots, grouped by stand ages. Based on Swedish National Forest Inventory data.

4. Discussion

Our main objective is to find explanatory factors for lichen habitat and lichen cover response. The strength of the study is the large data sets from revisited sample plots over long time series, making it possible to analyse and explain changes in lichen cover for all forests in northern Sweden. Similarly to earlier studies, we found a decline in ground lichen cover. Results showed a decline by almost 60 % in the reindeer husbandry area during the period 1996–2015, where lichen cover change was primarily explained by forest basal area. However, somewhat surprisingly, our results show no declining trend between 2015 and 2021. Another important finding was that sample plots with an increase in lichen cover primarily occurred in forest that was clear-cut during the study period and in forest

Table 4
Summary table of generalized additive mixed model (GAMM) results for significant forest characteristics explaining lichen cover change 1995–2021 for forest aged 40–80 years.

n	Intercept (*t* value; *p* value)	Explanatory variables (*F* value; *p* value)
378	−39.47; < 0.001***	Stand age (3.324;0.0349*) Canopy cover (4.157;0.0139*) Basal area (11.771; <0.001***) Year of inventory (19.735; <0.001***)

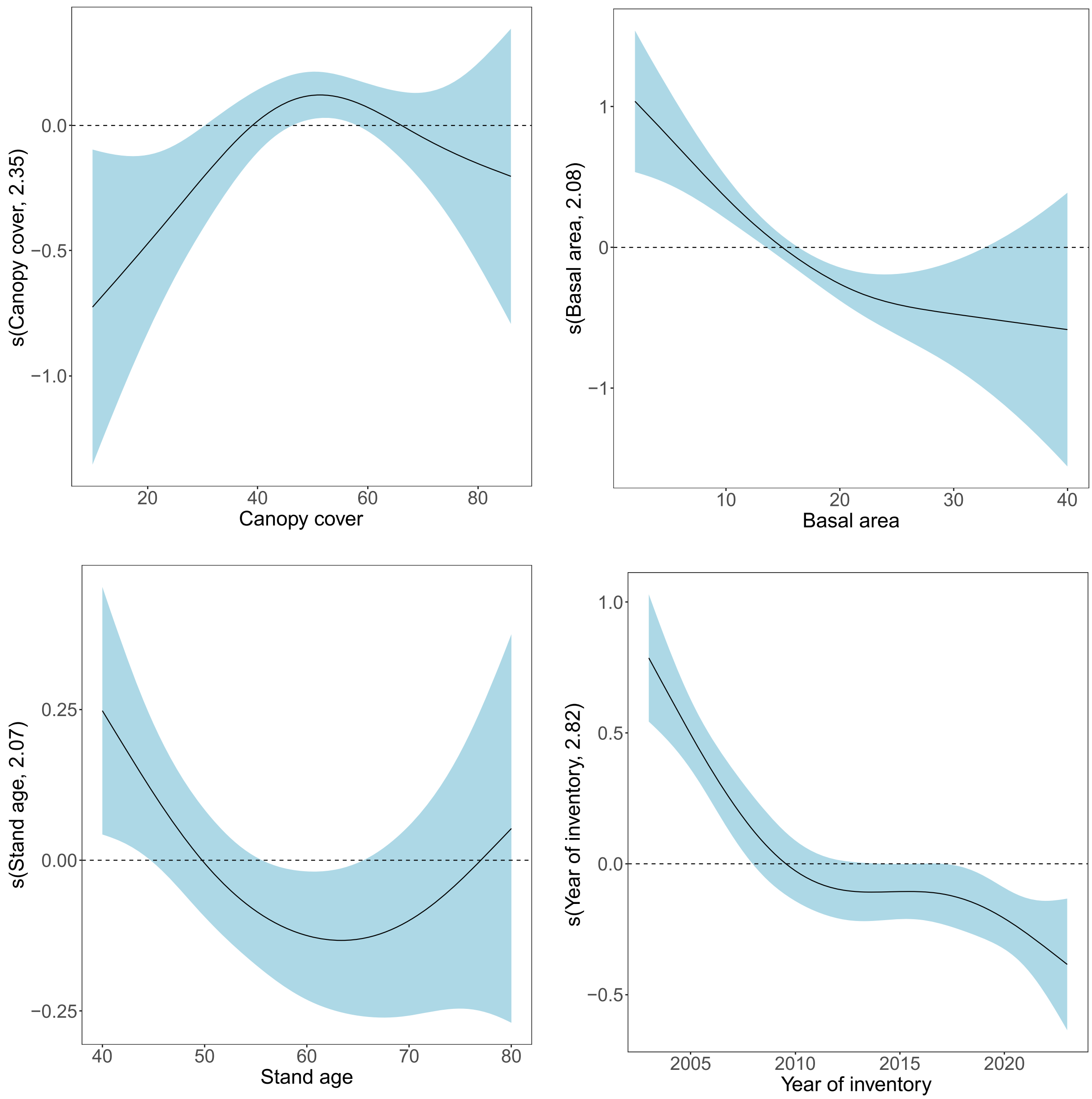

Fig. 6. Change analysis of significant forest characteristics explaining lichen cover change 1995–2021 for forest aged 40–80 years. Negative effect < 0, positive effect > 0.

Table 5
Generalized additive model (GAM) results for the relationship between lichen cover and significant explanatory variables.

n	Intercept (*t* value; *p* value)	Explanatory variables (*F* value; *p* value; expl. dev.)	Explained deviance (%)
3324	−40.87; < 0.001 ***	Wetness (41.005; <0.001***; 4.4 %) Basal area (5.228; <0.001***; 1.8 %) Pine proportion (118.096; <0.001***; 59.4 %) Site index (20.520; <0.001***; 34.5 %)	37.2

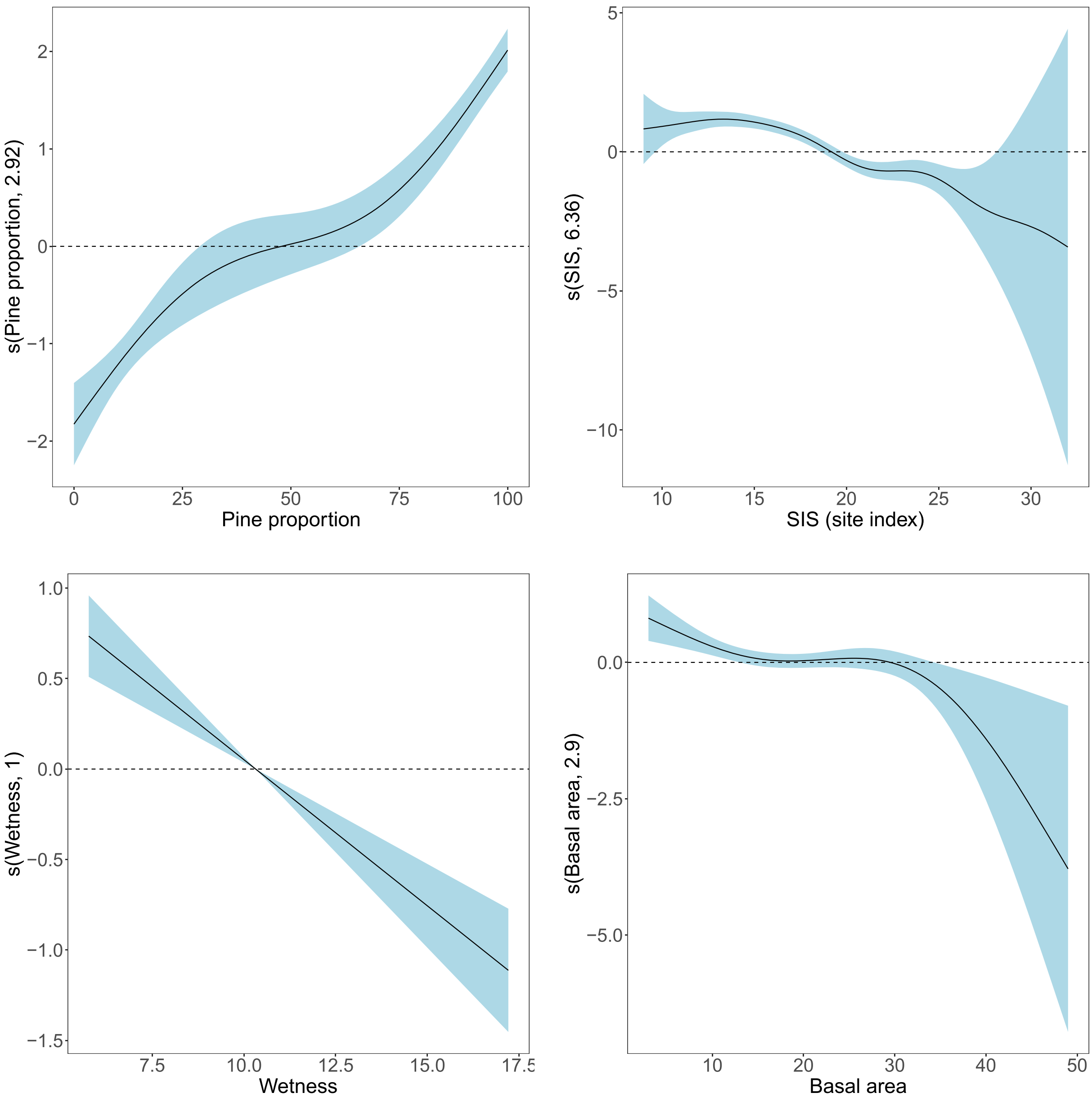

Fig. 7. Forest characteristics significantly explaining lichen cover in the period 1993–1997. Negative effect < 0, positive effect > 0.

aged < 40 years (Table 3). In forest aged 40–80 years, we found a lichen cover increase for basal areas below 15 m^2ha^{-1}.

4.1. Lichen cover change (1996–2021)

Declining ground lichen trends have been shown across the northern hemisphere (McMullin and Rapai, 2020). The decline in Sweden has been described previously (Sandström et al., 2016; Horstkotte and Moen, 2019; Uboni et al., 2019), using different types of data and analysis methods. Sandström et al. (2016) found a decline by 71 % of the lichen-abundant (>50 % lichen cover) forest class area between 1955 and 2016, and Horstkotte and Moen (2019) found a decline by 36 % of the lichen-abundant and lichen-moderate (25–100 % lichen cover) forest classes between 1983 and 2015. Horstkotte and Moen (2019) analysed revisited plots in the NFI and found a decline by 50 % in lichen-abundant forest and by 18 % in lichen-moderate. Sandström et. al (2016) and Uboni et al. (2019) analysed data from the temporary sample plots of the NFI. Here, each sample plot is only visited at one inventory occasion. However, all these three earlier studies were using bottom layer cover class data, where in our study we instead use the continuous values of lichen cover estimates available from the revisited plots. Our approach made it possible to conduct different analyses in comparison to the earlier studies. The bottom layer cover classes used in the other studies are estimations in percentage-classes of lichen or moss dominance, compared to the continuous values of lichen cover in integer square meters in our study. Hence, our data is more precise and for example expresses the decline of lichen cover at plot level ranging from 95 % to 55 %, which would not be detected as a change using the bottom layer-class data.

Uboni et al. (2019) found that lichen cover was positively related to reindeer use of the area; however, other studies from Finland have linked declines in lichen cover to reindeer grazing and trampling (Akujärvi et al., 2014; Kumpula et al., 2014). Our results show a similar declining trend of lichen cover within and outside the reindeer husbandry area (Fig. 3), and our analyses confirms earlier findings that reindeer grazing is not an important factor behind the decline (Sandström et al., 2016). Rather, our results show that changes in forest characteristics occurring both within and outside the reindeer husbandry area are important for lichen cover change (Appendix, Tables 1 and 2). However, our results concern the boreal zone, and e.g. Tonteri et al. (2022) have emphasized that the effect of reindeer is evident in the most northern xeric sites in Finland.

4.2. Lichen height within and outside the reindeer husbandry area

As expected, we found a significant difference in the mean lichen height (2018–2023) inside and outside the reindeer husbandry area, confirming the effect of reindeer grazing. Similarly, Uboni et al. (2019) found that the intensity of reindeer use in an area was negatively and exponentially related to lichen biomass, and negative correlations has been found between reindeer densities and lichen biomass (Kumpula et al., 2014; Cronvall et al., 2025).

As the NFI only provide data for lichen height since 2018, the main part of our analyses address lichen cover. Sustainable reindeer grazing is based on that the consumption of lichen should not exceed the growth as addressed by Cronvall (2025). Here consideration of wastage (Pekkarinen et al., 2017) from trampling and spillage of lichen fragments needs to be included, as well as the effects reindeer grazing could have on spreading i.e. planting lichen. As long-term data on the combination of lichen cover and height become available more specific analyses on the relationship between lichen biomass and forest conditions can be carried out.

4.3. Lichen cover change in relation to forest characteristics (1993–2023)

At individual plot level, a larger number of plots showed a decrease than an increase in lichen cover, for all age classes of forests (Table 2). Interestingly, the proportion of plots with a decrease was lowest for forest with a clear-cut during the study period, with 41 % of the sample plots experiencing an increase in lichen cover and 48 % a decrease (Table 3). Tonteri et al. (2022) found that regeneration cuttings, mostly clear-cuttings, clearly decreased lichen cover for up to ten years after cutting, while our data for lichen change after clear-cutting varies between 10 and 30 years after clear-cut. The number of plots with a lichen cover decline for forest aged < 40 years was moderate (55 %), while the highest number with a decline was found in forest aged 40–80 and > 80 years (71 % and 70 % respectively). This is consistent with earlier studies in which increase in lichen cover has been found for up to 30 years after clear-cutting (Kivinen et al., 2010). Horstkotte and Moen (2019) found that increase in, and persistence of lichen cover occur more often in young forests. During later phases, the canopy closes and lichen are more likely to be outcompeted by mosses (Kivinen et al., 2010; Tonteri et al., 2022).

Forest 'openness' can be described using different variables. In our data, basal area is only measured for forests over a mean height of 7 m. Data analysis was not possible for lichen cover in relation to forest openness for forests with clear-cuts and forest aged < 40 years, due to a lack of enough data on stem number, canopy cover or basal area for these age classes. In addition, the effect of light conditions can be hard to measure for young forests because of the response time in lichen cover change. Our results for the four forest age categories revealed significant relationships between forest characteristics and lichen cover change for forest aged > 80 years and forest aged 40–80 years. From a forest management perspective, the most interesting results are for forest aged 40–80 years, for which a basal area > 15 m^2ha^{-1} was associated with lower lichen cover. As lichens are photosynthesising organisms they are light-dependent; stem basal area has previously been found to be a useful proxy for lichen growth (Jonsson Čabrajič et al. 2010) and thinning has been found to have increased lichen cover (Coxson and Sharples, 2024). However, basal area summarises the area of all stems within one hectare. Hence, a large basal area can mean either a small number of large trees or many small trees in one hectare; these two scenarios can result in very different conditions for the ground vegetation. Low canopy cover (Uboni et al., 2019), low standing volume (Sandström et al., 2016) and low basal area have earlier been found to explain lichen cover (Sandström et al., 2016.;

Uboni et al., 2019; Miina et al., 2020).

4.4. Forest characteristics explaining lichen cover

To gain knowledge, e.g. as a basis for the possible restoration of areas with lost lichen cover, we analysed forest characteristics explaining lichen cover in 1993–1997. This study period contained a much larger data set compared to the latest available NFI data including fewer plots with lichen because of the cover decline. We found that proportion of pine (>48 %), site productivity index H100 pine < 19 and wetness < 10.3 (total deviance explained 37.2 %) were significant forest characteristics explaining lichen cover (Fig. 7). Basal area was also a significant variable but had low explanatory power (1.8 %). As site index is a commonly used variable in practical forest management, it is useful from a lichen restoration perspective. Prevalent lichen cover corresponds to a site index below 19 in the reindeer husbandry area, as reported for 2014–2018 in Eggers et al. (2024), suppl. mat.). The topographic wetness index also showed itself to be a useful indicator explaining lichen cover in combination with other variables. This was not surprising, as ground lichens are not dependent on soil moisture to grow, and dry soils therefore offer them competitive advantages over mosses and vascular plants (Cornelissen et al., 2001, Payette and Delwaide, 2018). The variables stand age, mean height, timber volume and site productivity were not significant in the data analysis.

4.5. Explanations for the general lichen decline

We found basal area, as a proxy for forest density, to be the most important variable affecting lichen cover change. This is similar to earlier findings that forest characteristics affecting light conditions on the ground determine change in lichen cover over time (Miina et al., 2020; Coxson and Sharples, 2024). The overall increase in basal area in Swedish forests, especially in young forests, is likely to explain a large part of the general decline in lichen cover (Fig. 2). Basal area in Sweden increased by an average of 20 % in the last three decades, with the largest increase in northern Sweden (Jonsson et al., 2021). For sample plots in our study area of northern Sweden (RHA_{all}), the basal area for pine forest increased by 19 % between 1995 and 2021, and for pine forest aged < 40 years it increased by 36 % (Appendix, Table 3).

We found that increasing forest age had a negative effect on lichen cover change for forests aged ~50–75 years (Fig. 6) and > 80 years. This is in contrast to Tonteri et al. (2022) who found a positive response of lichen cover for increased stand age for all forest ages. However, Tonteri et al. (2022) used the data from a single inventory (1985–1986) in Finland. This is different from our data, following the lichen cover change over a longer time period for the same sample plots. Finnish pine forests with a high stand age were likely more open and lichen rich at this time, similar to the Swedish situation shown in Sandström et al. (2016), where in the 1950s a high lichen cover was common in the older age classes, but not in the 2010s. As the forests have been regenerated, density has increased with age for mid-aged and mature forests, reflected in a negative effect on lichen cover over time. We found a much lower proportion of plots with an increase in lichen cover for forest aged > 40 years compared to < 40 years (Table 3). The change in forest age distribution between 1995 and 2021 can also partly explain the general decline in lichen cover, as the proportional area of pine forest aged < 40 years in northern Sweden (RHA_{all}) decreased from 47 % to 38 % during that period (Appendix, Fig. 2).

Other factors that we have not been able to address because of lack of sufficient data in the NFI, but can affect lichen cover negatively, are forest management activities such as fertilization (Jacobson et al., 2020; Olsson and Kellner, 2006) and soil scarification (Roturier and Bergsten, 2006; Tonteri et al., 2022), introduction of *Pinus contorta,* natural succession and absence of fire. Furthermore, a warmer climate and increased nitrogen deposition are likely to affect lichen negatively (shown for some lichen taxa, among them *Cladonia arbuscula,* Stevens et al., 2012). *Pinus contorta* has been planted since the 1960s and dominates approximately 520 000 ha, mostly in the northern half of Sweden, circa 4.6 % of the productive forest of that area (Nilsson et al., 2022). The exotic tree species affects lichen negatively compared to Scots pine (Horstkotte et al., 2023). Considering soil scarification, a satisfying forest regeneration can be accomplished by 5–10 % soil disturbance (Söderström et al., 1979; Örlander et al., 1991), however, depending on method up to 75 % soil disturbance occur (Bäcke et al., 1986; Prévost, 1996; Ring and Sikström, 2024). Extensive soil disturbance can explain some of the negative effect on lichen after clear cutting (Table 3). Historically, fire seems to have had positive effects on lichen cover in the long term (Hörnberg et al., 1999, Hörnberg et al., 2018, DeLuca et al., 2013). Natural succession and absence of fire are factors that have probably affected the decline in lichens on a long-term basis. In early succession it is common that the ground is covered by reindeer lichens (Nilsson and Wardle, 2005; Tonteri et al., 2022). The total cover of bottom-layer vegetation declined by 12 % between 1998 and 2019 in Sweden, with the largest decline in the country's northern parts, showing reindeer lichens declined more than mosses. The decline in both bottom-layer and field-layer cover is probably an effect of denser forests, and thereby of light and nutrition competition (Skogsdata, 2024).

4.6. Discussion of the levelling trend in lichen cover change

Our results for 2015–2021 (Fig. 2) show a break in the trend of lichen cover decline. As the break is even more distinguishable outside the reindeer husbandry area, it is not likely that the effect is a result of reindeer husbandry-adapted forestry within the area. A possible reason for the levelling decline is that the forests' densification is also levelling off, which we noted an indication of for basal area, with a yearly increase by 0.7 % in 1995–2021, and by 0.4 % in 2015–2021 for northern Sweden ($RHA_{all,}$ Appendix, Table 3). Following a long period of lichen cover decline it is also possible that equilibrium has been reached, with the areas with increasing lichen cover balancing the decrease in other areas (cf. Table 3).

4.7. Implications of the study

The lichen decline is a severe threat to the survival of Sami reindeer husbandry based on natural grazing grounds, as ground lichen is a bottleneck resource during winter (Heggberget et al., 2002). Forest management has been an important factor in the lichen decline since 1955, but is also the most promising area to adapt in order to contribute to a lichen increase (cf. Eggers et al., 2024). Our results show a potential for adapting forest management in the young forest aged < 40 years, as both increases and decreases in lichen cover are common in this age class. Based on our results, forest management actions to keep basal area < 15 m^2ha^{-1} at site indexes for pine < 19 would be the most important management measure. Pre-commercial thinning to relatively low stem numbers is important both for an economic output (through higher stem diameter) from future thinning as well as to prevent snow and wind damage in the young forest after thinning (Pettersson et al., 2017). Early pre-commercial thinning of smaller trees would also decrease the problem of residues hindering the reindeer from grazing and decreasing the light availability for ground lichens.

In summary, the explanatory variables for lichen cover and lichen cover change open possibilities to find the right sites and methods to apply reindeer husbandry adapted management measures aiming to increase lichen cover. Applying the right measures at the right site can be cost-efficient both from a lichen restoration and a forest management perspective.

Our results indicate that regeneration through clear-cutting generally leads to a lower decline of lichen cover, compared to delaying clear-cuts of mature stands aged > 80 years (48 % compared to 70 % of plots with decreased lichen cover, Table 3). However, it is important to incorporate reindeer adapted forest management throughout the coming forest rotation period to avoid periods of excessively dense forests. Other forest measures such as partial cutting, gap felling, selection cuttings and pre-commercial thinning are alternative forest treatments which would create favorable light conditions for ground lichen cover, but also favour biodiversity in comparison to clear-cutting (Miina et al., 2020; Tonteri et al., 2022). There are also other problems with clear-cuts, e.g. logging residues (Helle et al., 1990) and deeper and harder snow (Kater and Baxter, 2022; Roturier and Roué 2009) which can hinder the reindeers' access to ground lichen. Consequently, clear-cuts may be avoided by reindeer.

4.8. Future studies

The increase in lichen cover was most common in forest that had been clear-cut during the study period: for this age class, there were almost as many sample plots with an increase as with a decrease in lichen cover. Therefore, an important area for future studies is lichen growth response to forest management measures during the clear-cut and regeneration phases. We were not able to address this with our data. Additionally, further research on how the reindeer accessibility to lichen is affected by forestry, and how it can be enhanced, is important. Soil scarification has been shown to have detrimental effects on ground lichens; however, it could also serve a function as a natural disturbance that could favour ground lichen growth. Evaluating the effects of different soil scarification methods in relation to the forest floor vegetation is an important area for future studies. Additionally, the long-term effects of pre-commercial thinning to various stem densities, as well as different treatments of the residues left behind, would be important knowledge for developing reindeer husbandry-adapted forestry. Further studies that take into account the effects of a changing climate and increasing temperature on forests' growth response as well as lichen cover and height are also important.

Furthermore, ecological models linked to forest planning systems to simulate the effects of alternative forest management strategies on reindeer pastures and sustainable reindeer husbandry are needed (e.g. Miina et al., 2020).

4.9. Conclusions

- Ground lichen cover declined by 57 % in the reindeer husbandry area during the period 1993–2015; this supports earlier results based on class-scale lichen cover data.
- Lichen cover generally decreased for all forest ages.
- Adapted forest management offers good possibilities to increase lichen cover:
  - o Basal area below 15 m^2ha^{-1} at lichen habitat will increase lichen cover for forest aged 40–80 years.
  - o Almost half of the clear-cut inventory plots showed an increase in lichen cover; we therefore recommend further studies on how different forest management measures after clear-cut and for young forest can influence lichen cover.
- The results of this study can contribute to increasing the knowledge basis for policy decisions, forest planning and management, and local consultations between reindeer herders and forest companies to increase and restore lichen cover.

CRediT authorship contribution statement

Per Sandström: Writing – review & editing, Funding acquisition, Conceptualization. **Torgny Lind:** Writing – review & editing, Data curation. **Sven Adler:** Writing – review & editing, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Ulrika Roos:** Writing – original draft, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Ulrika Roos reports financial support was provided by Swedish Research Council Formas. Sven Adler has served as reviewer for the journal If there are other authors, they declare that they have no known competing financial interests or personal relationships that

could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03946.

Data Availability

Data will be made available on request.

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