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REPORT

On the decline of ground lichen forests in the Swedish boreal landscape: Implications for reindeer husbandry and sustainable forest management

Per Sandström, Neil Cory, Johan Svensson, Henrik Hedenås, Leif Jougda, Nanna Borchert

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Abstract Lichens are a bottleneck resource for circumpolar populations of reindeer, and as such, for reindeer husbandry as an indigenous Sami land-use tradition in northern Sweden. This study uses ground lichen data and forest information collected within the Swedish National Forest Inventory since 1953, on the scale of northern Sweden. We found a 71 % decline in the area of lichen-abundant forests over the last 60 years. A decline was observed in all regions and age classes and especially coincided with a decrease of >60 year old, open pine forests, which was the primary explanatory factor in our model. The effects of reindeer numbers were inconclusive in explaining the decrease in lichen-abundant forest. The role that forestry has played in causing this decline can be debated, but forestry can have a significant role in reversing the trend and improving ground lichen conditions.

Keywords Large-ungulate grazing · Long-term monitoring · Reindeer lichen · Traditional land-use · Swedish National Forest Inventory

INTRODUCTION

The boreal Fennoscandian landscape contains a variety of forest habitats that all contribute to a rich biodiversity, natural resource, and ecosystem services pool (e.g., Esseen et al. 1997; Gamfeldt et al. 2013; Moen et al. 2014). Forest management and reindeer husbandry represent two extensive land-use systems that utilize the same boreal landscape. For a long time, the forest industry has played an important role in northern Sweden and constitutes an integral part of the national economy (Siiskonen 2013). Modern stand-oriented, even-aged, monoculture forestry has developed in Sweden since the 1950s and has had a profound effect on forest and 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).

The reindeer husbandry system is part of a historical legacy of paramount value that is closely connected to the culture, tradition, local economy, and well-being of the indigenous Sami people (Lundmark 2008). In Sweden, the Reindeer Husbandry Act (1971:437) gives the indigenous Sami people exclusive rights to herd and graze their reindeer (*Rangifer tarandus*) within the reindeer husbandry area, which constitutes the majority of the land within the boreal and alpine biomes in Sweden (see Fig. 1). These grazing rights are acknowledged, independent of land ownership, and other land-uses (Hahn 1990). In fact, reindeer husbandry in Sweden is always carried out in coincidence with other land-uses (Sandström et al. 2003; Sandström 2015). During the 1900s, the reindeer husbandry system has evolved from a more intensive and closely managed system to a more extensive system with larger and more free-ranging herds (Moen and Danell 2003). During this period, also other land-uses changed profoundly, including forest management that has moved from a selective and small scale system to a stand-oriented, intensive system affecting almost all forest lands (Östlund et al. 1997; Lundmark 2008).

The reindeer husbandry system in Sweden is based on the maintenance of grazing and seasonal migration of the reindeer which is similar to the movement patterns of wild and domesticated reindeer in North America and Russia

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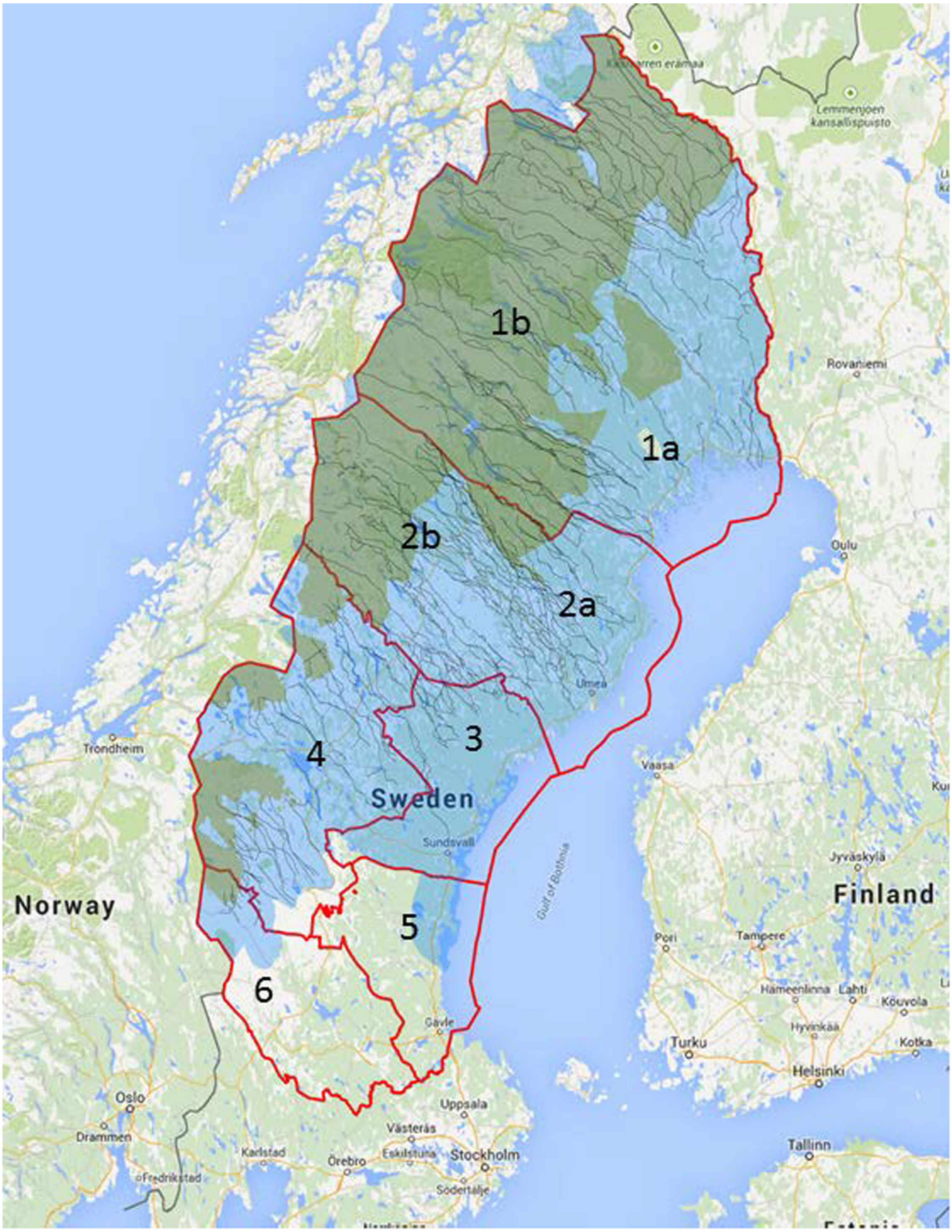


Fig. 1 The Reindeer Husbandry Area (RHA) as defined by the Sami Parliament as an area enclosing all 51 reindeer herding communities (*blue area*). The RHA is further separated into year round areas (*green area*) mostly above the alpine tree line connected with the wintering grazing areas in eastern forests by migration routes (*dark lines*). The county boundaries of Norrbotten (*1a* coastal area and *1b* inland area), Västerbotten (*2a* coastal area and *2b* inland area), Västernorrland (*3*), Jämtland (*4*) Gävleborg (*5*) and Dalarna (*6*) are delineated in *red*

(Vors and Boyce 2009) and in Norway (Panzacchi et al. 2014). The long-range movements of reindeer husbandry in Sweden differ considerably from the situation in Finland where reindeer husbandry is based on a more stationary system (Kumpula et al. 2014). In Sweden, most reindeer migrate from the summer grazing lands in the

Scandinavian mountain range to the winter grazing lands in the interior and coastal boreal forests and back to the mountains again in the spring. For some reindeer herding communities, these yearly migrations can be as long as 700 km. Consequently, a viable and resilient reindeer husbandry system is dependent on boreal landscapes that can provide reindeer movement routes within, as well as between, seasonal grazing lands. In Sweden, such routes usually follow pine-dominated, lichen-rich forests along river beds and ridges (Manker 1953). When continuous grazing lands are maintained intact and connected by migration routes, the seasonal migrations of reindeer represent one of the last remaining, long-range ungulate migrations in the northern hemisphere (Wilcove and Wikelski 2008; Panzacchi et al. 2015), still persisting long after other ungulate populations such as bison (*Bison bison* and *Bison bonasus*) have been eradicated (Vors and Boyce 2009).

A principal component as well as a critical bottleneck in the Swedish reindeer husbandry system is the maintenance of habitats with ground lichens; such as *Cladonia* spp. and epiphytic pendulous lichens such as *Bryoria fuscescens* and *B. fremontii*. Lichens are the pivotal winter grazing resource for reindeer populations in Fennoscandia and Russia (Heggberget et al. 2002; Sandström et al. 2006) as well as for caribou in North America (Bergerud 1972). Lichen has a high carbohydrate concentration and can constitute up to 80 % of the winter diet for reindeer (Heggberget et al. 2002). Hence, knowledge about the status and trends of the lichen resource is a central issue throughout the circumpolar region where wild and semi-domesticated reindeer have been identified as ecological keystone species as well as providing a socioecological cornerstone of circumpolar indigenous cultures (Vors and Boyce 2009).

In Fennoscandia, mat-forming ground lichens are closely associated with sandy or rocky low productive and more open Scots pine (*Pinus sylvestris*) dominated stands (Oksanen and Ahti 1982; Jonsson Cabrajic et al. 2010). In natural ecosystems, pine forests are frequently affected by forest fires that have kept the forests open with a less dense shrub and field layer (Esseen et al. 1997). Natural wildfires are, however, more or less absent as a general disturbance agent in the managed Swedish boreal forest landscape (Esseen et al. 1997). Overall, mat-forming ground lichens constitute an important life form that supports unique biota in the boreal and arctic environments where they occupy the least productive sites but still contribute significantly to biomass production, nutrient and CO_2 cycling as well as to overall biodiversity (Nilsson and Wardle 2005; Falldorf et al. 2014).

So far, no attempt has been made to quantitatively analyze the present status and the long-term trends in forest habitats supporting ground lichen in northern Sweden. The only previous estimates of the status of ground lichen on this broad geographic scale were presented in SOU (2001) and reported by Sandström et al. (2006) as an indicative 50 % decline in lichen cover since the 1950s. Monitoring data from the Swedish National Forest Inventory (NFI; Fridman et al. 2014) provide a unique source for detailed analyses on broad geographic scales.

In this paper, we investigate the following questions for the reindeer husbandry area in Sweden: (1) What are the main landscape characteristics? (2) How has the amount and distribution of ground lichen forest habitats changed in time and space? (3) How does the decline in ground lichen habitat relate to forest conditions, climate, and reindeer population sizes? Further, we discuss the broader implications for land-use and management in a boreal context, in particular with regards to reindeer husbandry and forestry.

MATERIALS AND METHODS

Study area

Our study area consists of the Swedish Reindeer Husbandry Area (RHA), defined by the Sami Parliament of Sweden as the area where the Sami people have the right to carry out reindeer husbandry (Reindeer Husbandry Act 1971; Sametinget 2014). The RHA constitutes the sum of all land presently used by the 51 autonomous reindeer herding communities operating in Sweden (Fig. 1).

Sampling

The Swedish National Forest Inventory (NFI) is a national-scale monitoring program that since 1953 has used a stratified systematic sample based on clustered sample plots and since 1983 also includes permanent, revisited plots (Fridman et al. 2014). The NFI applies a 5-year inventory rotation cycle with a national set of data available for any 5-year moving sample batch. This study is based on estimates of forest floor ground lichen cover where we used three classes of ground layer cover; lichen abundant (>50 % cover of ground lichens), lichen moderate (25–50 % cover of ground lichens), and moss dominant (≤25 % cover of ground lichens). Pine-dominated forest is defined in accordance with the NFI definition as forest where Scots pine comprises at least 65 % of the basal area. In this paper, we apply NFI-data from 1953 up to 2013, thus a time period with marked changes in land-use strategies in the boreal forest landscape.

Two assumptions were made regarding the data. First, the definition of lichen abundant has been slightly re-defined in the NFI protocol. Prior to 1983 lichen abundant was defined as a cover that was "predominantly lichen," but from 1983 lichen abundant is defined as lichen (diffuse) cover >50 % of the ground layer vegetation cover. For the ground layer vegetation data from 1983 to 2013, we found that for 98 % of the sample plots were lichen cover was predominant, the lichen cover exceeded 50 % (Appendix S1). We have therefore assumed that the definition of lichen abundant is consistent throughout the whole study period. Note that the measurement of lichen cover does not take into account grazing pressure and consequently, even intensively grazed lichen areas may be classified as lichen abundant according to the NFI protocol based on the cover of remaining lichens. Second, in 1973 the sample plot size used for vegetation layer definition changed from 6.64 to 10 m radius. We carried out a sensitivity analysis based on data from 2009 to 2013 where we compared the classification of plots classified as lichen abundant based on a 10 m radius plot ($n = 13\,008$) with twin 0.28 m radius plots ($n = 1226$; Appendix S1). The areal estimate of lichen abundant forest was only 2.8 % higher when lichen cover was based on the smaller plot size. This suggests that lichen cover estimates are robust to the effects of plot size change.

Climate and reindeer population data

Within the RHA, annual temperature and annual precipitation for year 1969–2013 were derived from 30 grid squares within the PTHBV data base (Johansson and Chen 2005, and references therein), compiled by the Swedish Meteorological and Hydrological Institute. We thereafter calculated a mean value for these 30 grid squares. A moving 5-year average with the current year plus the four previous years was calculated for the period 1983–2013. Total reindeer population size within the RHA was derived from Official Statistics (1969–1994; Statistics Sweden) and the Sami Parliament of Sweden (1995–2013; www.sametinget.se/statistik_rennaring). We linearly interpolated missing points in the reindeer population data and calculated a lagged moving 5-year average with the current year plus the four previous years was calculated for the period 1983–2013.

Data analysis

We produced maps showing the distribution of ground lichen by interpolating NFI sample plot data. We applied an Inverse Distance Weighted moving window average with a search radius of 25 km, a minimum and maximum number of sample plots set to 1 and 25, respectively, and a distance weighting power of 2 using ArcGIS 10.2. All measurements of standing volume are given in cubic meters (m^3). Standing volume is defined as the trunk volume above a pre-defined tree stump height including the tree top and bark. Productive forest land is defined as land suitable for forest production, i.e., with a forest stock growth of at least 1 m^3 per year. All formally protected forests, as of 2013, have been excluded from productive forest land in our analyses.

We used multi-state models (msm-package, version 1.5; Jackson 2011, 2015) in order to assess the transitions between lichen abundant, lichen moderate and moss dominant sites using the R statistical package (version 3.0.2; Ihaka and Gentleman 1996). We estimated the confidence interval of the transition probabilities using bootstrapping (Jackson 2011). The models were based on permanent plots ($n = 3641$), from 1983 until 2013, that have not been divided into subplots and have been resurveyed at least three times. We also defined a covariate based on tree basal area. Open forest was defined as basal area <15 $m^2\ ha^{-1}$, and dense forest was defined as basal area ≥15 $m^2\ ha^{-1}$ with reference to the study by Jonsson Cabrajic et al. (2010) on growth of ground lichen.

We applied linear models as well as Generalized Additive Models (GAMs; mgcv-package, version 1.8-6; Wood 2006, 2015) using the R statistical package (version 3.0.2; Ihaka and Gentleman 1996) to evaluate whether the change in the areal extent of lichen-abundant pine forest from 1983 until 2013 was related to reindeer population size, annual mean temperature and annual precipitation (moving average based on 5 years) and to the areal extent of the following forest conditions: young (≤60 year old) open pine forest, young dense pine forest, old (>60 year old) open pine forest and old dense pine forest. Open forest was defined as basal area <15 $m^2\ ha^{-1}$, and dense forest as basal area ≥15 $m^2\ ha^{-1}$. Pine forest was defined as >65 % Scots pine based on basal area. We selected the best model by using a best-subset selection procedure. For each possible variable combination, with a maximum of 6 variables, a 10-fold cross validation was provided and the Root Mean Square Error of Prediction (RMSEP; Hastie et al. 2013) and the correlation between predicted and measured value were calculated. The linear model and the GAM with the lowest RMSEP were chosen.

RESULTS

The reindeer husbandry area

Our compilation of data from the Swedish NFI provides the first comprehensive set of accurate summary statistics on the scale of the Swedish RHA (Fig. 1; Table 1a). The total RHA area encompasses 22.6 million ha, representing 55 % of the Swedish land area and about 50 % of all productive forest land in Sweden. The area defined as Plan 78 (SOU 2006) representing an alternative delineation of the RHA

Table 1 Area and proportion of major land cover types (a) and total standing volume of merchantable trees species (b) for the Reindeer Husbandry Area (RHA). Data from the Swedish National Forest Inventory 2009–2013 excluded protected land as of 2013 (SNFI 2014)

	Area land cover type in RHA (1000 ha)	Proportions of land cover types in RHA (%)	Proportions of land cover type in Sweden (%)
(a) Area			
Land areal	22 600	100	55
Productive forest land	11 471	51	50
Mires[a]	3859	17	77
Alpine	5212	23	100
Subalpine forest	956	4	97
Rock surface	352	>1	37
Built-up areas	189	>1	16
Roads and railways	226	>1	45
Agriculture	245	>1	7
Other	89	>1	37
	RHA area of tree species (mill. m^3)	Proportion of standing volume in RHA (%)	Proportion of total standing volume in Sweden (%)
(b) Standing volume			
Total standing volume	1373	100	41
Scots pine	569	41	17
Norway spruce	543	40	16
Broadleaves	233	17	7
Lodgepole pine	28	2	1

[a] Below the sub-montane boundary

covers 21.0 million ha or 47 % of the Swedish land area. All land within the RHA is potentially available for reindeer husbandry, except about 3 % which is made up of urban and developed areas, roads and agricultural lands (Table 1a). Approximately 41 % of Sweden's total standing forest volume is found within the RHA. The state owns 82 % of all land above the sub-montane coniferous forest boundary with the remaining 18 % being privately owned, whereas below this boundary the state owns 26 %, private forest companies 27 % and private household owners 47 %.

Changes in the amount and distribution of lichen-abundant forests

During the 1953–1957 NFI inventory period, 1.4 million ha (13 %) of the productive forest land in the RHA was classified as lichen abundant. This proportion had declined to 0.41 million ha (3.7 %) in the 2009–2013 inventory period (Fig. 2a; Table 2). This constitutes a 71 % decline in the area classified as lichen-abundant forest over the 60-year study period. The amount of lichen-moderate forests constitutes 0.54 million ha and in total, lichen-abundant and lichen-moderate forests cover an area of 0.96 million ha (2009–2013). In comparison, the area of lichen-abundant productive forest land in Sweden outside the RHA, and therefore not subjected to reindeer grazing, declined from 500 000 to 180 000 ha constituting a 64 % decline over the 60-year period.

On a regional scale, the areal decline in forest with classified as lichen-abundant cover differed from north to south within the inland regions with a 78 % decline in inland Norrbotten and an 82 % decline in inland Västerbotten, in comparison with a 55 % decline in Jämtland and Dalarna (all inland). The overall decline for all inland and all coastal areas was 70 and 72 %, respectively, showing a similar, proportionate decreasing trend for the entire RHA (Table 2).

The declining trend for lichen-abundant forests was similar across landowner categories (Fig. 2b). Of the remaining lichen-abundant forests 47 %, equal to 190 000 ha, are located on state-owned land.

Figure 3 shows the 60-year spatiotemporal changes in the proportion of inventory plots classified as lichen-abundant forest for the different inventory periods. The distribution of the highest proportion of lichen-abundant forest land (>20 % of plots classified as lichen-abundant) in the 1953–1957 period was concentrated to large, distinct hotspots in the counties of Jämtland and Dalarna in the south, and in the county of Norrbotten in the north. Some smaller patches occurred in the

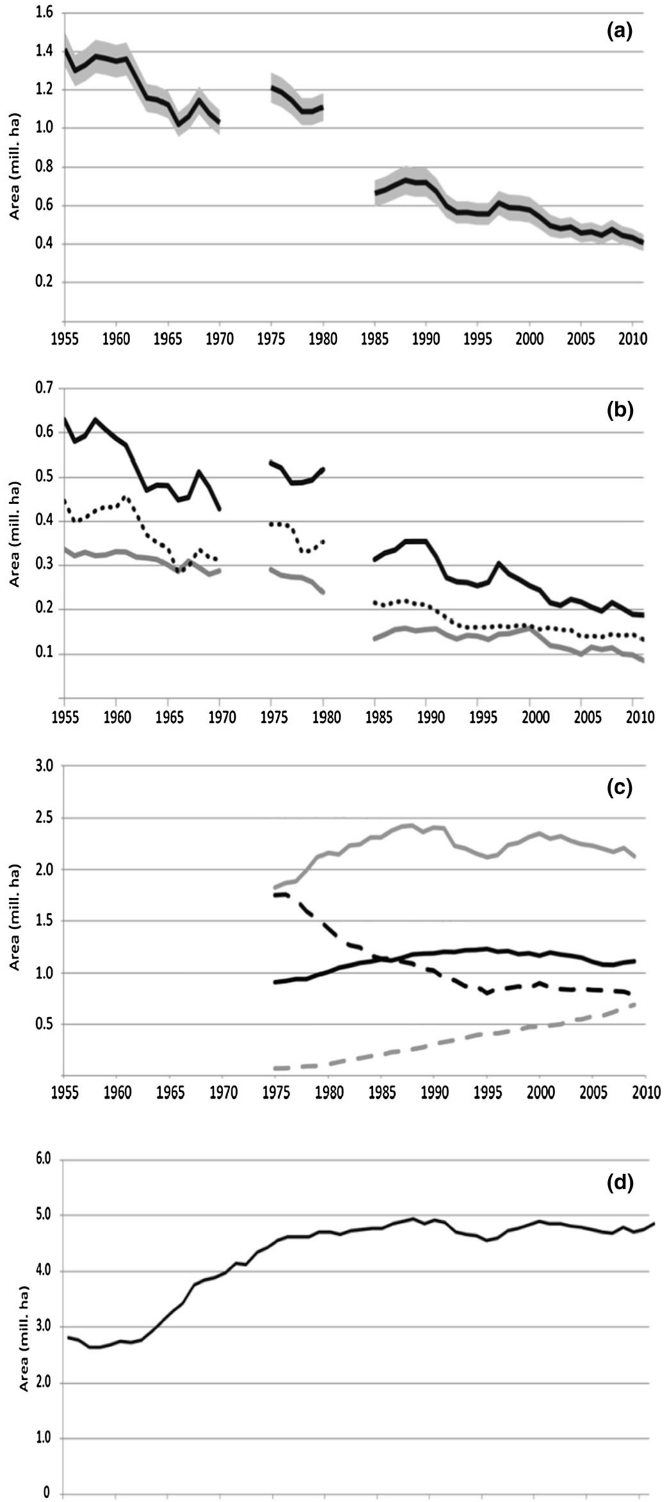


Fig. 2 Area of lichen-abundant productive forest land between 1953 and 2013, for the Reindeer Husbandry Area shown as 5-year mean values for **a** total area with *grey shaded zones* show as standard error and **b** area divided by main land owner categories: state owned land (*solid black line*), private forest companies (*solid grey line*), small private owners and other (*hatched line*). The *curves* are divided by separate periods representing changes in the Swedish National Forest Inventory procedures. **c** Total area of pine forest divided in the following forest types: young ($\leq$60 year old), open (basal area <15 $m^2 ha^{-1}$) pine forest (*grey solid line*); young, dense (basal area $\geq$15 $m^2 ha^{-1}$) pine forest (*grey hatched line*); old (>60 year old), open pine forest (*black hatched line*); old, dense pine forest (*black solid line*). **d** Total area of pine forest defined as $\geq$65 % pine. Data from the Swedish National Forest Inventory for the total area of productive forest land, excluded protected land as of 2013 (SNFI 2014)

Table 2 Area, proportion, and decline of lichen abundant productive forest land in the Reindeer Husbandry Area for the periods 1953–1957 and 2009–2013, for counties divided by inland and coastal areas (Fig. 1). Data from the Swedish National Forest Inventory for the total area of productive forest land, excluded protected land as of 2013. Data shown as a five year average (SNFI 2014)

	Area (1000 ha) and proportion (%) of lichen-abundant forest habitats		Percent area decline in lichen-abundant forest habitats
	1953–1957	2009–2013	
Inland areas	959 (16)	279 (5)	70
Norrbotten	495 (28)	110 (7)	78
Västerbotten	145 (8)	26 (2)	82
Jämtland, Dalarna	318 (12)	142 (6)	55
Coastal areas	454 (10)	127 (3)	72
Norrbotten	220 (13)	57 (3)	74
Västerbotten	123 (10)	42 (3)	66
Västernorrland, Gävleborg	111 (6)	28 (1)	75
All areas	1413 (13)	406 (4)	71

counties of Västerbotten and Västernorrland. The trend during the 1960s and 1970s and onward illustrates a steady decline in lichen-abundant forests. The declining trend became more pronounced from the 1980s and onwards. For northernmost Sweden, only a few patches of the highest proportion class remain. The only large, remaining hotspots of the highest proportion of lichen-abundant forest are now found in the county of Dalarna in the southernmost fringe of the RHA. The 60-year spatiotemporal sequence reveals a turnover in the configuration of lichen-abundant forest on the scale of northern Sweden. Previously, this forest type occurred more or less continuously at proportions of 1–5 % lichen abundance or higher, whereas now levels of 0–1 % dominate with few and fragmented patches at proportions 1–5 % or higher.

Changes in lichen abundance in relation to forest characteristics

Pine-dominated forests have increased from 2.8 million to 4.9 million ha since the 1950s. This increase occurred primarily in the period 1955–1975 and subsequently the areal extent has remained relatively stable (Fig. 2d). Pine-dominated forests presently support 96 % of the lichen-abundant forest and we therefore focused much of our analysis on pine-dominated forests.

During the period 1983–2013, the areal extent of old, open pine forest decreased while young and dense pine forest increased (Fig. 2c). Both the linear model and the GAM used in this study (Table 3) revealed that the decline in the areal extent of lichen-abundant forest coincided with the decline of open pine forest. The best GAM revealed that the strongest explanatory variable for the areal extent of lichen-abundant forest was the area of old open pine forest (68.5 % of the variance explained; positive relationship; Table 3). In addition, precipitation had a significant contribution (17.8 %; negative relationship). The number of reindeer was identified, although not significant, as one of the variables in the best GAM and explained 13.7 % (U-formed relationship) of the variance explained.

Figure 4 shows a matrix of probabilities on how the bottom layer classification has changed or remained the same during 30 years based on revisited NFI field plots. The probabilities of a shift from one bottom layer type to another differed significantly between dense and open forest for all but one change alternative. For example, the probability that a lichen-abundant forest plot remained in the same class after 30 years was 2.8 times higher in an open forest compared to in a dense forest, and the probability that a lichen-abundant forest has changed to a moss-dominated forest was 1.6 times higher in a dense forest compared to in an open forest.

The age structure of the boreal forests of northern Sweden has undergone significant changes during the last 60 years. Within the RHA, the distribution of stand ages in the 1953–1957 periods was dominated by age classes >60 years, while the distribution in 2009–2013 period was dominated by age classes <60 years (Fig. 5). This change in stand age distribution is accompanied by a decline in lichen-abundant forest types in all stand age categories. Our data show that for the NFI-period 2009–2013, the lichen-abundant forest types predominantly occurred in the 3–60 year age classes, with the largest proportion of lichen-abundant plots in the 3–20 class. Furthermore, the clear-cut areas (0–2 year age-class) have a much lower proportion of lichen-abundant plots today compared to the 1953–1957 period (Fig. 5). Apart from clear-cut areas, the highest decline in proportion of lichen-abundant plots was found in stand-age classes over 61 years, and in particular in the classes 61–100 and >160 years, respectively.

Figure 6 describes the relationship between lichen-abundant forests and basal area (Fig. 6a), stand maturity class (Fig. 6b), and standing volume 1953–1957 (Fig. 6c)

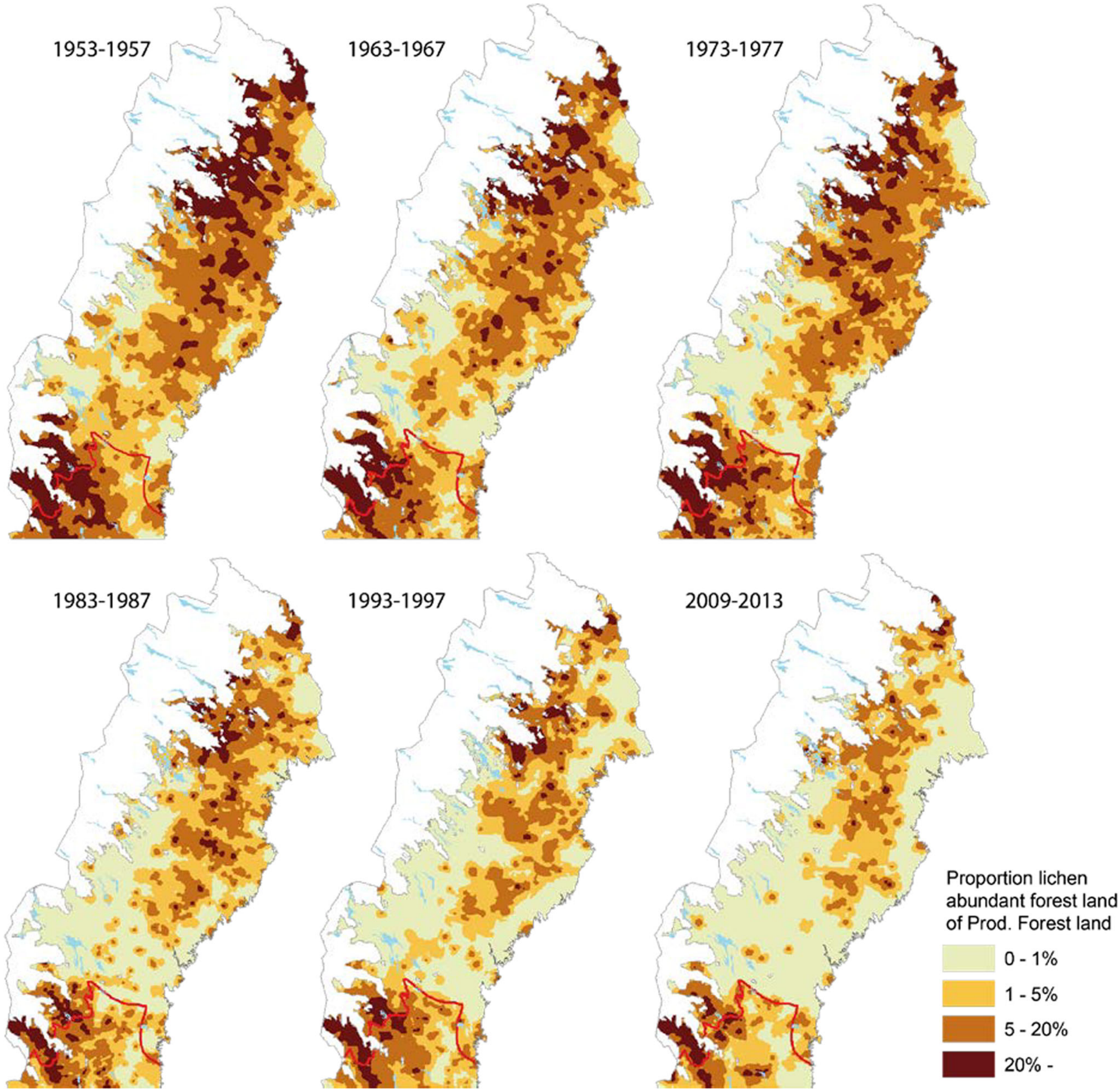


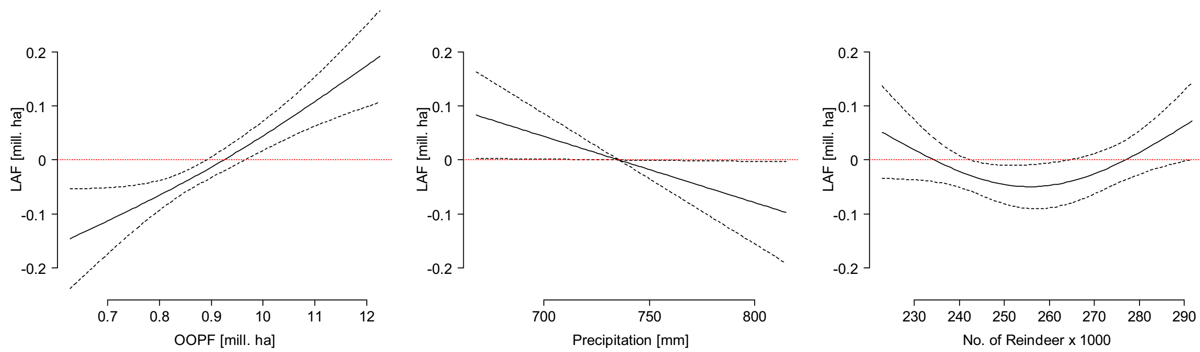
Fig. 3 Distribution of lichen-abundant forest land ($\geq$50 % lichen cover in ground vegetation) within the Reindeer Husbandry Area for a 60-year temporal sequence, expressed as percent of all productive forest land excluding protected forest as of 2013. Interpolation of sample plot data on inventory plots originally classified as lichen abundant from the Swedish National Forest Inventory (SNFI 2014)

compared with 2009–2013 (Fig. 6d). There is obviously a strong covariation between basal area and standing volume, but since detailed basal area figures are not available for the early NFI data, standing volume has also been used. We found an inverse relationship between the occurrence of lichen-abundant plots and basal area, as well as with the standing volume of pine. In other words, there are few lichen-abundant plots in stands with a high pine basal area and volume. Pine stands with volumes >200 m^3 ha^{-1} or basal areas >15 m^2 ha^{-1} appear to represent a threshold value for the decline in lichen abundance. For maturity classes, our data show that more lichen-abundant plots were found in thicket and thinning stage stands compared to recently clear-cut areas, and also compared to old pine forests. When comparing area distributed by standing volume classes for 1953–1957 (Fig. 6c) and 2009–2013 (Fig. 6d), the previously noted increase in area of pine forest (Fig. 2d) is clear. We have moved from a situation

Table 3 The best linear and generalized additive models (GAM) chosen based on cross validations showing the relationship between the area of lichen-abundant forest (LAF) and the variables; young open pine forest (YOPF), old open pine forest (OOPF), mean annual temperature (Temp), precipitation (Prec) and reindeer population size (RD). The figures show the relationship between the selected variables and the area of lichen-abundant forest, in the GAM. Young forest defined as ≤60 year and old as >60 year. Dense forest defined as basal area ≥15 m^2 ha^{-1} and open as basal area <15 m^2 ha^{-1}

Linear model	*N*	Intercept (*t* value; *p* value)	Explanatory variables (*F* value; *p* value)	Adj. R^2(%)	Cor_{cross} (%)	$RMSEP_{cross}$ (ha)	AIC
Best set	31	1.2; 0.232	OOPF (2.2; 0.040), YOPF (2.5; 0.021), Prec (−1.7; 0.094), Temp (−1.5; 0.151)	57.3	69.4	108 742	807.3

GAM-model	*N*	Intercept (*t* value; *p* value)	Explanatory variables (*p* value; *p* value)	Expl. Dev (%)	Cor_{cross} (%)	$RMSEP_{cross}$	AIC
Best set	31	31.4; <0.001	OOPF (16.5; <0.001), Prec (4.3; 0.048), RD (3.3; 0.053)	62.3	68.3	111 588	808.2



Expl. Dev. Explained deviance, *Cor_{cross}* the correlation between predicted and measured value, *RMSEP* Root Mean Square Error of Prediction, *AIC* Akaike information criterion

where a significant proportion of the pine forests were lichen-abundant to a situation where only a small fraction display this forest habitat characteristics.

DISCUSSION

Long-term monitoring in the reindeer husbandry area

The results in this study are based on the first thorough compilation of NFI-data on general land cover types (Table 1), ground lichen status and forest characteristics on a geographical scale as large as the RHA in Sweden. Monitoring data such as the data used in this study allow for analyses of long-term vegetation changes and land-use impact assessments and are invaluable in establishing baselines and trends in landscape and forest changes as essential background for environmental policy development, to define indicators and environmental target precisions and to support adaptive monitoring and management (e.g., Lindenmayer and Likens 2010). Our compilation and analysis can serve as an example of landscape-wide assessments that may be useful in assessment of other land-use systems in the boreal biome.

Decline in ground lichen-abundant forests

There is an evident decline in ground lichen-abundant habitats in the 11.5 million ha boreal forest portion of the Swedish RHA from the 1950s to date. Lichen-abundant habitats have declined from covering 13 % of the productive forest area to 3.7 % constituting a net decline of 71 %. A reduction in ground lichen cover has previously been reported for local studies in Fennoscandia (Berg et al. 2008; Kivinen et al. 2012; Kumpula et al. 2014), but not on the geographical scale or magnitude presented here. Our data show that 0.41 million ha of lichen-abundant forests remain in the RHA. Thus, large areas in northern Sweden have lost lichen-abundant habitat that was previously a part of the natural landscape configuration (Fig. 3).

Our results show that lichen-abundant areas are predominantly found in more open forest stands and that the decline of lichen-abundant habitats coincides with a significant change in forest age distribution, a reduction of old, open pine forests and a significant increase in the

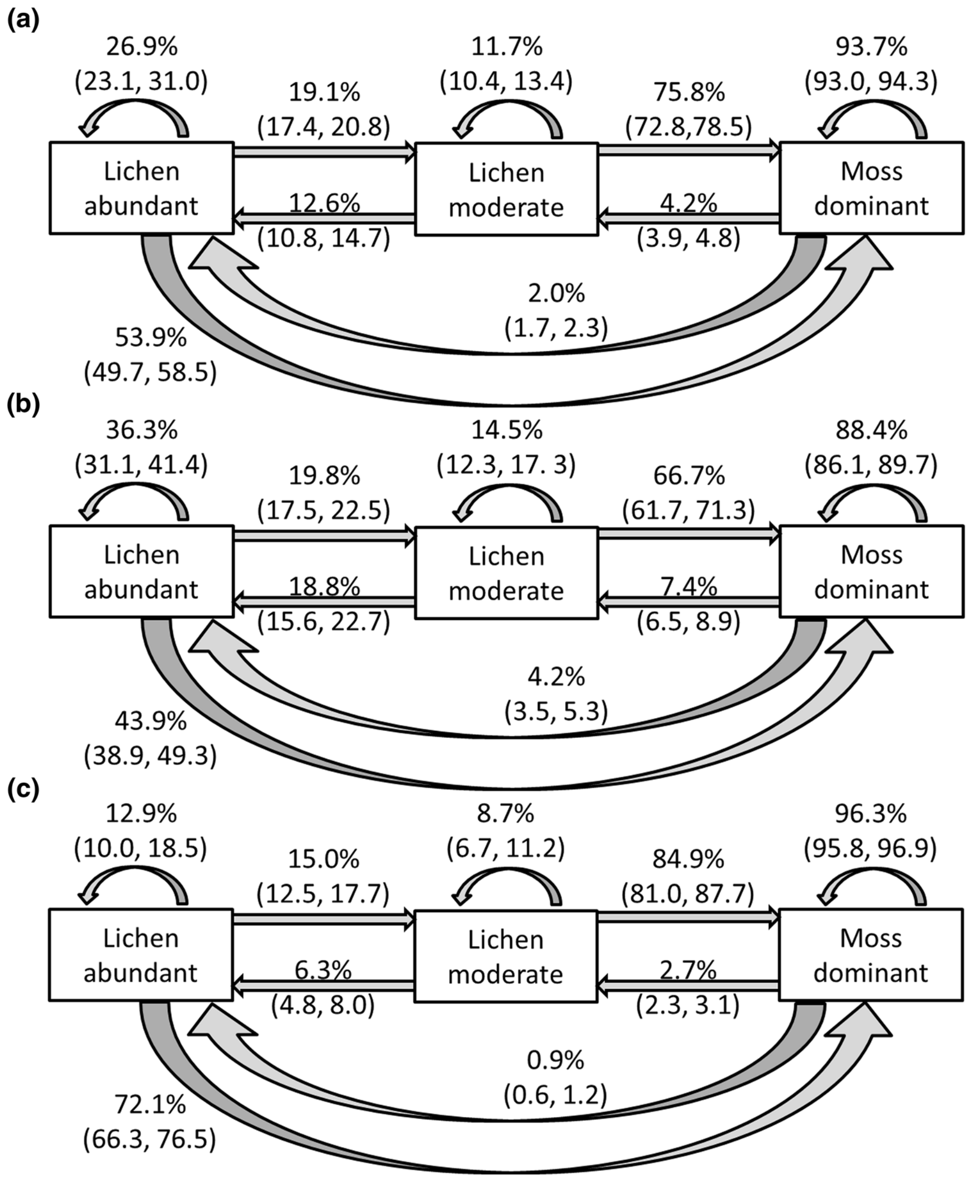


Fig. 4 The probability and confidence interval (in *brackets*) that a sample plot has changed from one forest class to another class after 30 year for **a** all forest plots, **b** plots in open forest (basal area <15 m^2 ha^{-1}) and **c** plots in dense forest (basal area ≥15 m^2 ha^{-1}), respectively. Lichen abundant (>50 % cover of ground lichen), Lichen moderate (25–50 % cover of ground lichens) and moss dominant (≤25 % cover of ground lichens). The probabilities and confidence intervals are the results of a multi-state model

standing volume of pine (Figs. 4, 5, 6). Our analysis of permanent and revisited NFI-plots showed that over a 30-year period, 73 % of the plots classified as lichen abundant had changed into a lower lichen cover class (mainly to moss dominant), and that the probability of change was significantly higher in a dense forest compared to an open forest (Fig. 4). Similarly, 76 % of the plots classified as lichen moderate had changed into a moss-dominant class, and the change was significantly higher in dense forests compared to open forests. Thus, the decline in lichen cover may be explained by younger, denser stands replacing older, open stands which results in insufficient light conditions for the growth of ground lichens (cf. Olsson and Keller 2006; Jonsson Cabrajic et al. 2010). Additionally, previous studies suggest that a higher irradiance decreases the competition effects of bilberry (*Vaccinium myrtillus*; Bråkenhielm and Persson 1980; Kardell 1980; Roturier and Bergsten 2009).

Factors influencing the decline in ground lichen-abundant forests

Previous studies have suggested that grazing by reindeer is a critical factor controlling the lichen resource pool in

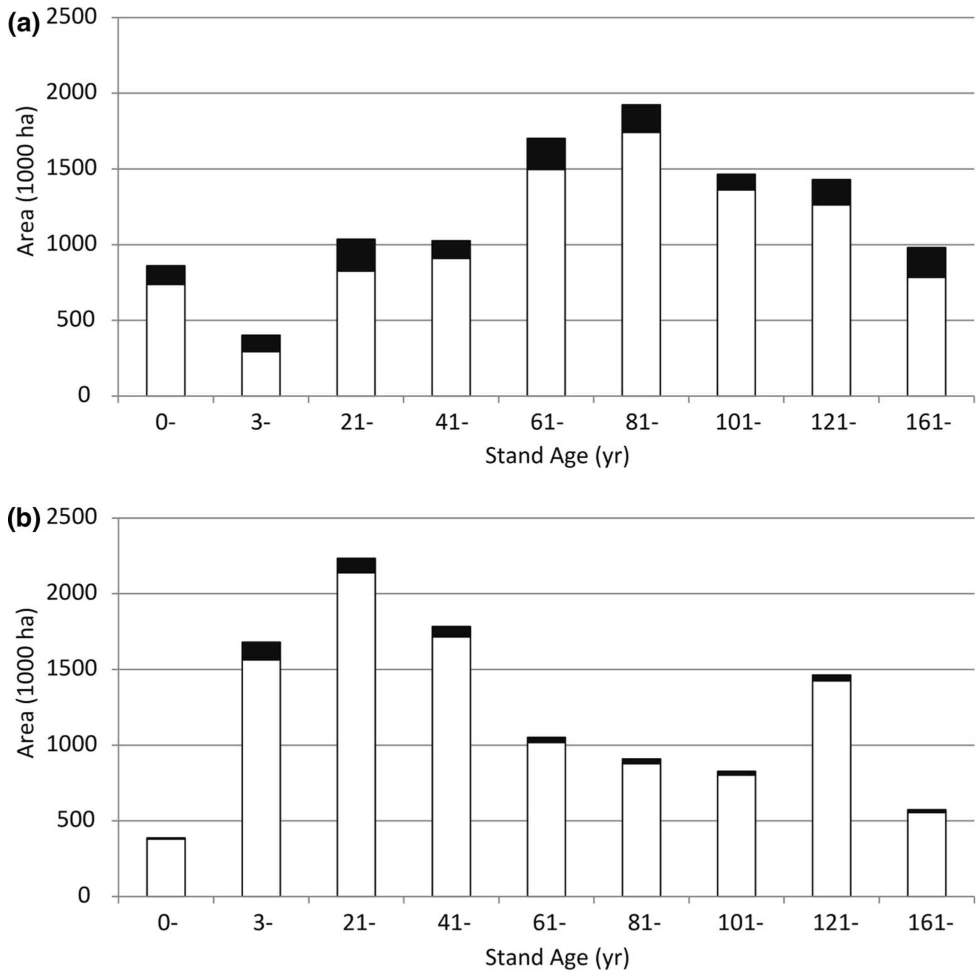


Fig. 5 Proportion of forest land in inventory plots originally classified as lichen abundant (>50 % lichen cover in ground vegetation; *black portion of bars*) on total area forest land (*white portion of bars*) for stand age categories in the periods **a** 1953–1957 and **b** 2009–2013. Data from the Swedish National Forest Inventory for the total area of productive forest land excluded protected land as of 2013 (SNFI 2014)

Finland (Kumpula et al. 2014). We identified reindeer numbers as a contributing variable in the GAM modeling (Table 3). However, the U-shaped relationship with negative effects of both low and high reindeer numbers can be difficult to explain from an ecological perspective. This lack of a clear relationship between reindeer numbers and lichen decline is further supported by our analyses that show a similar decline (64 %) in the area of lichen-abundant forest outside of the Swedish RHA during the same time period. The reindeer husbandry systems differ significantly between Sweden and Finland with the Finnish system relying to a lesser degree on long-range seasonal movements and more on winter time supplemental feeding (Moen and Danell 2003). The reindeer husbandry system in Sweden on the other hand relies to large extent on free-ranging and long-distance migrating herds predominantly feeding on naturally occurring foods. This situation is more similar to that found in North America and Russia (Vors and Boyce 2009) and in Norway (Panzacchi et al. 2014). Additionally, in Sweden most of the reindeer's use of the lichen resource occurs when the ground is snow covered protecting the lichen from being damaged by reindeer trampling. The importance of maintaining a rotational and dynamic grazing system and to avoid the need for supplemental feeding of reindeer can be central in avoiding local overgrazing and decline of the lichen resource.

The observed reduction in amount of ground lichen-abundant forest over the last 60 years coincides with a period of modern forestry policy and practices in the Swedish boreal landscape (Esseen et al. 1997; Östlund et al. 1997). Large-scale logging, intensive reforestation efforts and fire suppression have resulted in a decline in old, open pine-dominated, post-fire successional stands on low productive sites (Esseen et al. 1997) which are important habitats for ground lichens (Oksanen and Ahti 1982). Such stands have instead been replaced by dense, managed forests that favor mosses at

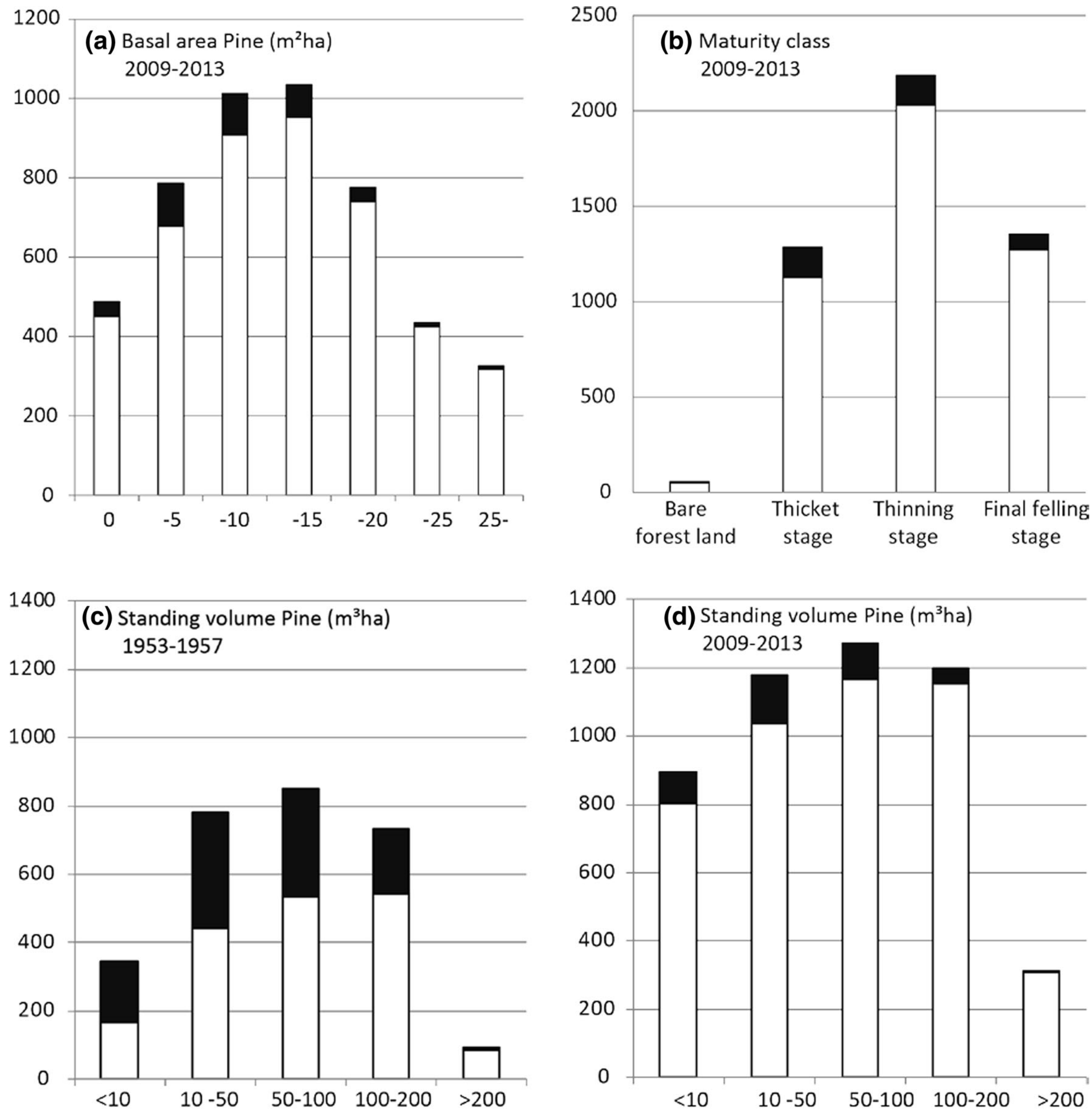


Fig. 6 Proportion lichen-abundant forest (>50 % lichen cover in ground vegetation; *black portion of bars*) of the total area of productive Scots Pine forest in categories of **a** standing volume, **b** basal area and **c** forest stand maturity class. The sample includes inventory plots originally classified as Scots pine dominated (pine proportion >65 % of basal area or number of stems for stands ≥7 or <7 m of height, respectively) and lichen abundant (lichen cover >50 %). Data for the Reindeer Husbandry Area based on 5-year Swedish National Forest Inventory estimates for the period 2009–2013 excluded protected land as of 2013 (SNFI 2014)

the expense of lichens (Kardell and Eriksson 1992; Roturier and Bergsten 2006; Berg et al. 2008), which also is well supported by our findings (Figs. 2c, 5, 6). The loss of these old open pine forests is the most important explanatory variable for the decline in lichen-abundant forests in the RHA (Fig. 4; Table 3). The introduction of lodgepole pine (*Pinus contorta*), on 0.40 million ha of land within the RHA (ref), and fertilization has also been reported to have negative effect on ground lichens (Kardell and Eriksson 1992; Olsson and Keller 2006; Nilsson et al. 2008). Furthermore, damage by soil scarification is found to affect as much as 50 % of the clear-cut surface and therefore substantially decreases both the cover and biomass of ground lichens (Roturier and Bergsten 2006). These previously reported findings correspond well with our results that show an evident decline in the proportion of lichen-abundant forests in clearcuts (Fig. 5). The present low proportion of lichen abundance in clear cuts can be interpreted not only as a response to soil scarification, but also as an effect of a low proportion of mature forests that are lichen abundant (Figs. 5b, 6b).

Both temperature and precipitation have increased over the last decades (Table 3) and may potentially influence the abundance of ground lichens. This study shows that the increase in mean annual precipitation had a small but significant contribution to the decline in lichen-abundant forests (Table 3). However, the relationship between lichen and precipitation is inconclusive. Earlier studies show that vascular plants and mosses replace lichens as the dominant ground cover in moister sites (Esseen et al. 1997); thus, it could be expected that lichens may be outcompeted by vascular plants and mosses with increased precipitation. On the other hand, higher humidity may increase lichen growth in sites with optimal light conditions (Jonsson Cabrajic et al. 2010). In addition, warming experiments have shown that ground lichens may decrease at the expense of other species in the bottom layer with increasing temperature (e.g., Walker et al. 2006). Data for temperature were also incorporated into our analyses but were not found to be a significant explanatory variable.

Implications for reindeer husbandry

The winter-foraging resources are considered the bottleneck for reindeer populations (Heggberget et al. 2002; Sandström et al. 2006) and therefore the decline observed in this study and also in several local studies (e.g., Berg et al. 2008) as well as by active herders (numerous Sami reindeer herder's pers. comm.), are of outmost concern. For the reindeer husbandry system and traditional Sami culture, the overall decline in ground lichen habitats and the associated densification of forest land have both a direct consequence in terms of a lower absolute amount of a critical winter grazing resource, and an indirect but equally important consequence on the spatial availability of the remaining grazing areas. The decline in lichen habitats causes reindeer to use increasingly larger areas for winter grazing; thus subsequently their dependency on connected landscapes raises, which alternatively to natural herd movement which may need to be mitigated by increased use of vehicle transportation. Furthermore, the decline of lichen habitats can contribute to greater need and supplemental feeding of reindeer. It should be noted that epiphytic pendulous lichens (mostly *Bryoria* spp.) are also part of the winter grazing resource for reindeers, but not included in this study due to limited available data. However, other local studies have shown declines in pendulous lichen as a consequence of decreases in the forests with long tree continuity (Esseen et al. 1997; Dettki and Esseen 1998). These findings further underline the importance of the ground lichen resource.

Implications for forest management

The role of forestry practices in relation to the decline of lichen-abundant forest land can be debated. However, the key role that forestry can play to help improve conditions for ground lichens has become clearer. Our results together with other studies (Roturier and Bergsten 2006, 2009) suggest a number of ways in which active forest management can play a central role in reversing the trend of declining ground lichen-abundant forests. First, the fact that Scots pine-dominated forests support 96 % of the remaining lichen-abundant areas can help focus further management of pine. Second, removal of cutting residues can have a positive effect on lichen because of reduced shading and fertilizing effects of the residues (cf. Bråkenhielm and Persson 1980). Third, several studies point at the importance of undertaking careful soil scarification methods on clearcut areas to minimize the impact on the remaining lichens (Roturier and Bergsten 2006; Berg et al. 2008; Kivinen et al. 2010, 2012). Fourth, as an alternative, natural regeneration from seed-trees, continuous cover forestry, or other more careful final harvesting methods could be implemented (Korosuo et al. 2013). Finally, carrying out more pre-commercial and commercial thinnings may improve conditions for the growth of ground lichens (Jonsson Cabrajic et al. 2010; Korosuo et al. 2013). This is especially important as these young forest stands contain the majority of the remaining lichen-abundant forests. Further implementation of the forest management practices discussed above can be mediated by the fact that 47 % of the remaining lichen-abundant areas are on state-owned land. According to SOU (2013), the state is responsible to act as a model landowner and this responsibility can shape national policies.

CONCLUSION

Analysis of 60 years of forest inventory data shows a major decline in the ground lichen resource in Sweden. Such changes can have profound effects on ecosystems and biodiversity in general, and in the case of Sweden, on reindeer husbandry in particular. Adaptive forest policy and practices can provide a key to reversing this trend and restoring the natural landscape configuration.

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AUTHOR BIOGRAPHIES

Per Sandström (✉) has a PhD in Biology. He works at the Department of Forest Resource Management at the Swedish University of Agricultural Sciences. He is a wildlife and landscape ecologist currently working with all reindeer herding communities in Sweden to develop reindeer husbandry and sustainable land-use plans.
Address: Department of Forest Resource Management, Faculty of Forest Sciences, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.
e-mail: per.sandstrom@slu.se

Neil Cory has a PhD in Geochemistry from the Department of Aquatic Sciences and Assessment. He is currently working as an analyst for the Swedish National Forest Inventory at the Department of Forest Resource Management, Swedish University of Agricultural Sciences.
Address: Department of Forest Resource Management, Faculty of Forest Sciences, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.

Johan Svensson has a PhD in Ecology and a background in biodiversity monitoring and landscape sustainability research and currently holds a position as scientific coordinator for the NILS—National Inventory of Landscapes in Sweden—landscape biodiversity program on contract with the Swedish Environmental Protection Agency.
Address: Department of Wildlife, Fish and Environmental Studies, Faculty of Forest Sciences, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.

Henrik Hedenås has a PhD in Ecology from the Department of Ecology and Environmental Science (EMG), Umeå University. He worked as a researcher and a lecturer at EMG, and as a researcher at the Abisko Scientific Research Station. He is currently working as an analyst at the Department of Forest Resource Management, Swedish University of Agricultural Sciences. He is coordinator of the project "Mapping of lichen-rich forests as a tool for landscape planning."
Address: Department of Forest Resource Management, Faculty of Forest Sciences, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.

Leif Jougda works at the Swedish Forest Agency in northern Sweden. He is a senior adviser in land-use and an expert in the field of forest management and reindeer husbandry.
Address: Swedish Forest Agency, Volgsjövägen 27, 912 34 Vilhelmina, Sweden.

Nanna Borchert is an Ecosystem Scientist (MSc University of Bayreyth, Germany), currently working at the Sámi Parliament, leading its Environment Program Eallinbiras.
Address: The Sami Parliament, Box 582, 831 27 Östersund, Sweden.