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Forest Fragmentation and Landscape Transformation in a Reindeer Husbandry Area in Sweden

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Abstract Reindeer husbandry and forestry are two main land users in boreal forests in northern Sweden. Modern forestry has numerous negative effects on the ground-growing and arboreal lichens that are crucial winter resources for reindeer husbandry. Using digitized historical maps, we examined changes in the forest landscape structure during the past 100 years, and estimated corresponding changes in suitability of forest landscape mosaics for the reindeer winter grazing. Cover of old coniferous forests, a key habitat type of reindeer herding system, showed a strong decrease during the study period, whereas clear-cutting and young forests increased rapidly in the latter half of the 20th century. The dominance of young forests and fragmentation of old-growth forests (decreased patch sizes and increased isolation) reflect decreased amount of arboreal lichens as well as a lowered ability of the landscape to sustain long-term persistence of lichens. The results further showed that variation in ground lichen cover among sites was mainly related to soil moisture conditions, recent disturbances, such as soil scarification and prescribed burning, and possibly also to forest history. In general, the results suggest that the composition and configuration of the forest landscape mosaic has become less suitable for sustainable reindeer husbandry.

Keywords Boreal forest · Forestry · Fragmentation · Lichens · *Rangifer tarandus tarandus* · Reindeer husbandry

Introduction

Reindeer husbandry has been practiced by the indigenous Sami people in Swedish boreal forests at least since the 17th century (Lundmark 1982). The current extensive herding system dates back to the early 20th century and is characterized by herds that graze freely over large areas in the western alpine regions in the summer. In Sweden, boreal forests are utilized mainly as winter grazing grounds, although some herding districts use boreal forests also for year-round grazing (for detailed information, see Moen and Danell 2003). During the wintertime, lichens are the principal food source for reindeer (*Rangifer tarandus tarandus* L.). Reindeer winter diet can consist up to 80% of mat-forming terrestrial lichens (mainly *Cladonia* spp.) and arboreal lichens (mainly *Bryoria* spp). Thus, the abundance of lichen-rich pastures in the landscape, and access to them, play an essential role in the reindeer herding system.

Reindeer graze in various habitat types during specific seasons and weather conditions. However, old-growth forests are key pastures as both semi-domesticated reindeer and woodland caribou have been reported to show a high preference for old forests and avoidance of clear-cuts and young stands (Apps and others 2001; Kumpula and others 2007). Biomass of arboreal lichens is strongly related to the stand age, and abundant arboreal lichens are found mainly in old (>100 years) coniferous forests, usually dominated by Norway Spruce (*Picea abies* (L.) Karst.)

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(Esseen and others 1996). Arboreal lichens are a particularly important resource during difficult snow conditions, such as very deep snow or when ice-crust prevents access to ground lichens in late winter. Ground lichens are abundant especially on dry oligotrophic soils in pine (*Pinus sylvestris* L.) heaths. Stand characteristics and related microclimate, such as the availability of light and moisture levels, have a major impact on lichen growth and competitive relationships between ground lichens, bryophytes and vascular plants (Sulyma and Coxson 2001). Open forests with abundant old trees have been found to support higher lichen cover than denser forests (Pharo and Vitt 2000), probably as a result of higher light availability in the more open forests (Jonsson Čabrajič and others 2010).

Forestry is the most important disturbance regime affecting the structure and function of boreal forest ecosystems, and consequently the lichen resources on winter pastures (Sandström and others 2006). The overall structure of Swedish boreal forests was affected mainly by natural disturbances (fires) until selective logging became common in the late 19th century (Östlund and others 1997; Linder and Östlund 1998). Selective logging, targeting the largest trees maintained a forest landscape with a spatially and temporally continuous, multilayered tree cover. Removal of the largest trees opened up the forest structure and potentially improved the growth of ground lichens (Berg and others 2008). Major changes in the forest ecosystems took place after the adoption of modern silvicultural methods, such as clear-cutting, soil scarification, planting and fertilization around the 1950s (Esseen and others 1997; Östlund and others 1997). Clear-cutting disrupts the continuous cover of forests and forms a mosaic forest landscape with sharp edges between single layered forest patches of different ages. In general, forest stands have become younger and denser, and the standing volume has increased during the second part of the 20th century (Berg and others 2008). Modern forest management have had mainly negative impacts on lichens through direct disturbances, such as clear-cutting and site preparation, or unfavourable microclimatic conditions in dense second-growth forests (Morneau and Payette 1989; Eriksson and Raunistola 1990; Roturier and Bergsten 2006; Kivinen and others 2010).

The composition of the forest landscape, i.e. different kinds of habitats and the spatial configuration of habitat patches, can have an impact on both current and future abundances of reindeer winter resources. For example, arboreal lichens disperse locally over relatively short distances and their colonization rates into second-growth forests thus depends on the distribution of old forest patches acting as propagule sources (Dettki and others 2000). The availability of suitable substrate and microclimate further limit the development of arboreal lichens in young stands (Stevenson 1990). The distribution of suitable pastures in the landscape can also affect the utilization of resources (O'Neill and others 1989), as large, closely located patches are probably more easily utilized than small and isolated patches. However, analyses of long-term changes in boreal forest landscape structure are so far relatively few (Axelsson and Östlund 2001; Boucher and others 2009), and none where competing forms of land-use are compared in a historical perspective. Furthermore, landscape structure of boreal forests has been previously studied mainly from a biodiversity perspective relating single species or species richness on the current distribution of habitats (Edenius and Sjöberg 1997; Schmiegelow and others 1997; Fisher and Boutin 2005).

In this paper, we examined forestry-induced long-term changes in the spatial structure of forest landscapes in northern Sweden, and estimated the consequent effects on the general suitability of forest landscapes for reindeer grazing. Landscape structure in two study regions were analyzed in terms of age structure and tree species composition over the past ca. 100 years using digitized historical forest inventory maps. Specifically, our aims were: (1) to study changes in the cover and degree of fragmentation of old-growth forests as an indicator of the general quality of forest landscapes for reindeer husbandry, and (2) to examine the changes in the ability of forest landscapes to sustain the long-term persistence of arboreal lichens. To complement the landscape-level analyses, (3) ground lichen cover was compared between pine-dominated sites with different stand characteristics and forest history.

Materials and Methods

Study Area

The two study regions, Akkajaur-Abraur and Eggelats, are located in the middle-boreal zone in Northern Sweden (18°15′–19°30′E, 65°54′–66°20′N; Fig. 1). They cover together approximately 580 km^2. The landscape is characterized by coniferous forests with Scots pine (*Pinus sylvestris* L.) as a dominant species, and with Norway spruce (*Picea abies* (L.) Karst.) and deciduous trees (mainly *Betula* spp.) occurring to a minor degree.

Eggelats is located within the reindeer herding district of Ståkke, and cover about 6% of the total area of the herding district. Eggelats is mostly used for summer and autumn grazing, but sometimes also all-year-round (Arell 1981). The reindeer number in Ståkke was low from the 1940's to mid-1970's with around 600 reindeer. After two reindeer herders with larger herds moved to the herding district in the mid-1970's, the number of reindeer has fluctuated

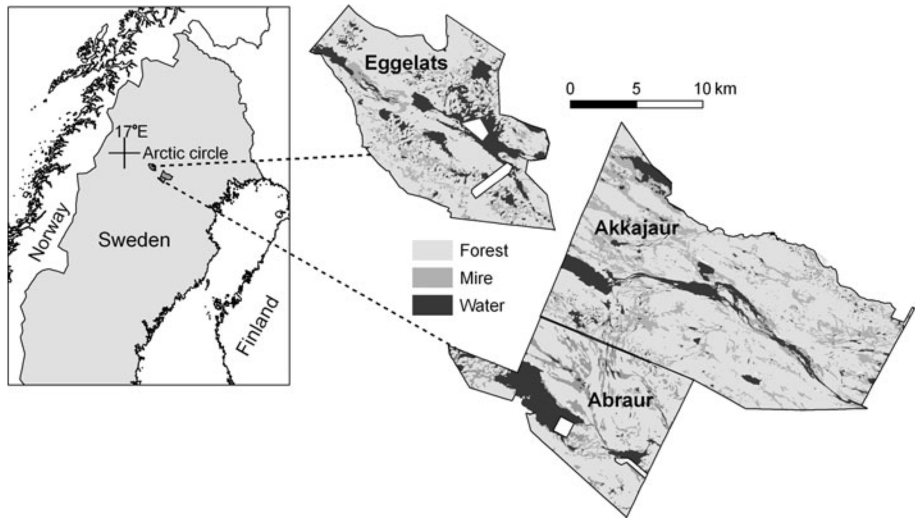

Fig. 1 Locations of the study areas in northern Sweden

between 1,500 and 2,700 animals (data from the Sami Parliament and the Swedish Board of Agriculture).

Akkajaur-Abraur is mostly situated within the herding district of Östra Kikkejaur, although the northernmost part is within both Udtja and Ståkke herding districts. Akkajaur-Abraur constitutes less than 9% of the total area of Östra Kikkejaur, and is used both as summer grazing and as year-round grazing. The number of reindeer has fluctuated between 2,000 and 6,000 animals since the 1940's, more or less in synchrony with the county as a whole (Moen and Danell 2003).

Forest Data

Forest data were derived from forest inventories and management plans consisting of maps and stand descriptions. These records contain information on forest structure, such as tree species composition, tree age, timber volume, etc., for each delimited forest stand. These inventories have been conducted with an interval of approximately twenty years and together covered a period of 111 years, from 1895 to 2006. For the Akkajaur-Abraur area, data were available from 1895 (parts of the area), 1925 (parts of the area), 1936, 1960, and 2006, while for the Eggelats area from 1923, 1936, 1960, 1973, and 2006. The documents from before the 21st century are written documents from the Swedish National Forest Service (Domänverket), obtained from the Provincial Archives in Härnösand, while the 2006 data were obtained from forest stand databases maintained by the present forest owners Sveaskog and Fastighetsverket. For more details on the data, see Berg and others (2008).

The original paper maps were scanned and all subsequent analyses were made with the digital images in ArcGIS 9.2. Each map was geo-referenced using clearly identified structures, such as lakes and streams, and rectified. Each forest stand, together with lakes, mires etc., were digitized on the computer screen, and data from the stand descriptions were added to the maps using unique stand numbers. To facilitate comparisons over time where different age classifications were used, forests were classified into five categories according to their age and species composition: (1) clear-cuts, (2) young pine forests = 1–39 years, (3) middle-aged-pine forests = 40–119 years, (4) old pine forests ≥ 120 years and (5) mixed and spruce forests (for a comparable methodological discussion see Östlund and others 1997 and Axelsson and Östlund 2001).

Spatial Analyses

All spatial analyses were carried out using ArcGIS 9.2 software (Esri Inc.). The digitized forest maps were converted to grids with a 50 m resolution. The class 'continuous old pine forest' was formed in order to analyze the changes in the cover of relatively undisturbed pine forests in both of the study regions between 1895/1923 and 2006. This class consists of old pine forest stands (≥120 years) as well as stands that were temporarily classified as middle-aged pine forests or mixed forests in the early 20th century. These kinds of changes in stand age structure or in species composition result from selective logging that however, does not disrupt the continuity of the forest cover. In the Akkajaur-Abraur region, historical data were partially missing for the southernmost and northernmost parts of the region. Thus, only the central region with a complete coverage of historical data was included in the analyses.

A wide variety of indices has been developed to measure landscape structure and fragmentation. Here, we quantified changes in the forest landscape using the following indices in Fragstats software (McGarigal and Marks 1995). Mean and standard deviation of the patch size and the largest patch index (LPI) were calculated for the cover of continuous old pine forest for each study period. Largest patch index describes the percentage of landscape area occupied by the largest patch of the studied class. Furthermore, the spatial configuration of continuous old pine forest patches was examined using an aggregation index (AI). AI measures the degree of aggregation of the patch type in the landscape. The index is based on the comparison of the number of shared edges with the total possible number of shared edges. AI equals 0 when the patch type is completely disaggregated and 100 with maximal aggregation.

The cover of continuous old coniferous forests was calculated in order to examine changes in the habitat availability for arboreal lichens. The class includes all coniferous forests (pine or spruce-dominated; $\geq$120 years) as well as stands that were temporarily classified as middle-aged pine forests or mixed forests in the early 20th century due to selective loggings. The study of Dettki and others (2000) showed that many arboreal lichen species disperse effectively up to 200 m on a local scale. The ability of the landscape to support the local dispersal of arboreal lichens was studied calculating a 200 m buffer zone around patches of old coniferous forests for the years 1923/1925, 1960 and 2006. The fragmentation of continuous old coniferous forests was analyzed using a mean proximity index (MPI) that distinguishes sparse distributions of small patches from a complex cluster of large patches within a specified search radius. The unitless index value for a focal patch increases as the area of corresponding patch type in the neighborhood increases and is distributed in larger, more contiguous and /or closer patches (McGarigal and Marks 1995). MPI was measured using a 200 m search distance correspondingly with the buffer zone analyses.

Field Work

The aim of the field work was to study the variation in ground lichen cover among sites with different stand characteristics and forest history. Pine-dominated forests in the Akkajaur-Abraur area were divided into a total of eight classes according to moisture, age and forest history. Two soil moisture classes 'xeric' and 'mesic' were derived from Sveaskog's database. Age classes consist of (1) clear-cuts, (2) middle-aged (40–80 years) pine forests and (3) old ($\geq$120 years) pine forests. Old pine forest stands were divided into two groups according to historical maps: (1) old forest from 1895 to 2006 ('OLD1') and (2) succession from a young forest in 1895 to old forest in 2006 ('OLD2'). Similarly, middle-aged pine stands were classified into two categories: (1) old forest before clear-cutting in the mid-20th century ('MIDDLE1') and (2) a history of young forest in 1895/1925 before clear-cutting ('MIDDLE2). The combinations 'xeric OLD2' and 'xeric clear-cuts' are missing from the further analyses, because these forest stands were not common enough to be included in the analyses.

Field work was carried out in the autumn of 2008. A total of 54 forest stands representing the eight forest classes were selected randomly from the maps within a three-km-buffer zone from the existing roads. Each study site consisted of a four orthogonal 25 m transects from a central point (a 50 × 50 m plot) placed randomly within the stand and located with a GPS receiver. Presence or absence of ground lichens (*Cladonia*, *Cetraria*) was measured every 50 cm along the transects and the estimated cover of lichens in the site was calculated dividing the presences with the total number of measurements ($n = 199$). The height of the two highest trees within each plot was measured with a hypsometer and diameter at breast height (1.3 m) was recorded. These trees were cored in order to determine the site age. Basal area was measured using a relascope. The canopy closure, defined as the proportion of sky hemisphere obscured by vegetation when viewed from a single point (Jennings and others 1999), was measured using hemispheric photographs. Five photos—one in a central point and four photos 12.5 m away from the central point along the transects – were taken in each site using a digital camera with a fish-eye lens. The photos were converted to binary images representing the canopy and the sky, and canopy closure was calculated using the Gap Light Analyzer software (version 2.0; Frazer and others 1999). The five photos were pooled for each site.

Statistical Analyses of Ground Lichen Data

Statistical analyses were carried out using a general linear model (GLM) univariate procedure (SPSS Inc, Version 16.0) that provides both regression analysis and analysis of variance. The model was built using all measured study plots excluding clear-cuts ($n = 44$). Following variables were included in the model: moisture (xeric or mesic), age class (old or middle-aged), history ('1' = old forest in 1895/1925 or '2' = young forest in 1895/1925), canopy closure, basal area and site age.

Results

Forest Landscape Structure and Continuous Old Pine Forests

The proportion of the continuous old pine forest of the total land area decreased from 64 to 10% in Akkajaur-Abraur and from 56 to 20% in Eggelats during the past century (1895/1923–2006; Fig. 2). In the beginning of the study period, the landscape in both study regions was mainly dominated by old pine forests (Fig. 3). In the early 20th

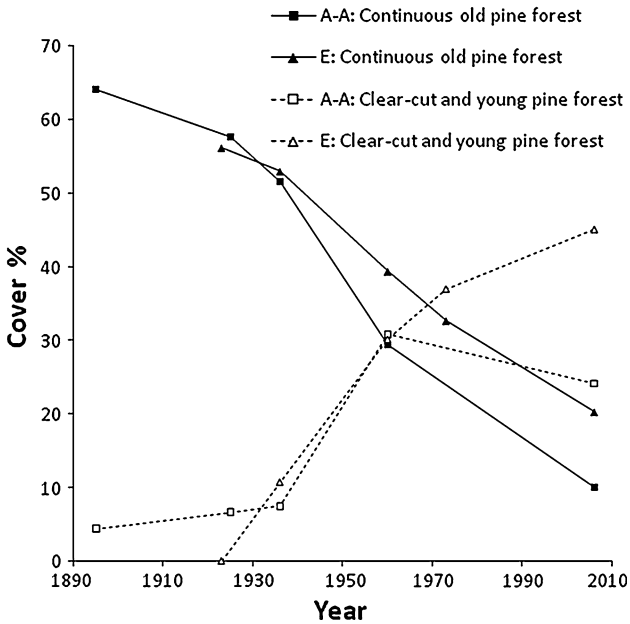

Fig. 2 The proportions of continuous old pine forests and clear-cuts/young pine forests of the total land area in Akkajaur-Abraur (A-A) and Eggelats (*E*)

Table 1 Statistics for the old pine forests

	Patch size (ha)		LPI	AI
	Mean	St dev	%	
Akka-Abr				
1895	321.3	1880.7	48.4	93.7
1923	53.2	572.1	33.4	88.2
1936	34.2	398.1	27.5	87.8
1960	48.1	322.3	13.7	87.5
2006	9.2	23.6	0.7	78.0
Eggelats				
1923	160.2	686.5	22.3	90.9
1936	70.4	551.4	34.1	89.7
1960	51.4	286.6	14.5	88.4
1973	65.2	298.5	13.1	88.1
2006	32.5	111.2	5.6	85.7

LPI Largest patch index, *AI* Aggregation index (see "Materials and Methods" section for more details)

century, part of the old pine forest stands changed into middle-aged or mixed forests as a consequence of selective logging that decreased mean stand age or changed the relative species composition. However, the cover of continuous old pine forest remained high. Selectively logged stands and early clear-cuts were generally located close to the water bodies. The 'clear-cutting wave' proceeded northwards and eastwards in Eggelats during the second part of 20th century, whereas the widest cover of clear-cuts peaked in Akkajaur-Abraur in 1960 (see Östlund 1993). In 2006, young forests and clear-cuts to a lesser extent covered 24 and 45% of the total land area in Akkajaur-Abraur and Eggelats, respectively (Fig. 2).

The mean and standard deviation of the patch size of continuous old pine forest has decreased strongly during the study period (Table 1). The maximum proportion of the total area covered by the largest patch of continuous old pine forest during the study period was 48% in Akkajaur-Abraur (1895) and 34% in Eggelats (1936). Respective

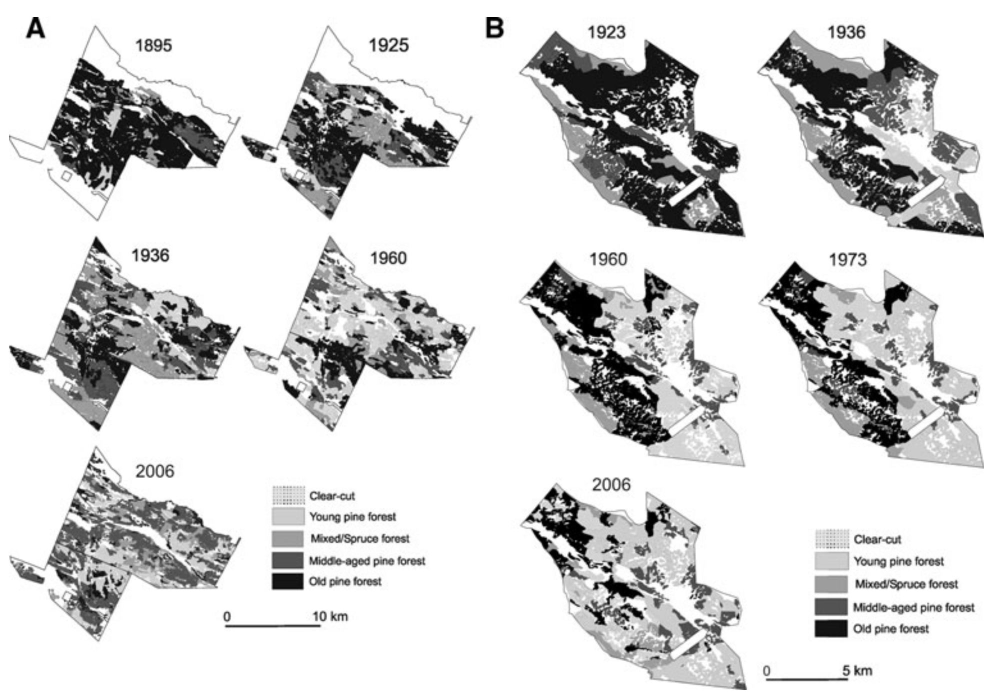

Fig. 3 Changes in the forest landscape in **a** Akkajaur-Abraur in 1895–2006 and in **b** Eggelats in 1923–2006. Other land cover and missing data are marked with *white*

proportions were only 0.7 and 6% in 2006. Aggregation of the continuous old pine forests measured by AI has decreased in both regions, and this development has been more prominent in Akkajaur-Abraur. The maps show that the largest remaining patches of continuous old pine forest are clustered in the north-western part of Eggelats, whereas in Akkajaur-Abraur patches are more scattered in the landscape (Fig. 3).

Habitat Fragmentation of Arboreal Lichens

The proportion of continuous old coniferous forest of the total study area decreased from 56 to 12% in Akkajaur-Abraur, and from 50 to 17% in Eggelats (Fig. 4; Note the different delimitation of the study area and time period compared to the analyses with the continuous old pine forest cover). The joint area of continuous old coniferous forest and the buffer zone of 200 m describing the potential effective dispersal distance of arboreal lichens (Dettki and others 2000) covered a main part of both of the study areas (78–90%) in 1923/1925. The proportion of this area had clearly decreased in 1960, and covered 41 and 40% of Akkajaur-Abraur and Eggelats, respectively, in 2006. Mean proximity index (MPI) decreased notably during the study period in both regions, from 3,721 to 35 in Akkajaur-Abraur and from 2,315 to 112 in Eggelats, indicating decreasing patch sizes and increasing isolation of the patches of continuous old coniferous forests.

Ground Lichen Cover in Relation to Stand Characteristics and Forest History

The highest mean lichen cover was found in xeric MIDDLE2 forests (65%; Fig. 5), and ground lichens were abundant also in other xeric forests. Among mesic forests, OLD2 had notably higher lichen cover compared to OLD1. The lowest mean cover of lichens was found in clear-cuts (24%). The site age determined by the tree-ring analysis varied between 123–521 years for old forests and 36–59 years for middle-aged forests. The mean canopy closure was generally lower in middle-aged forests (xeric = 51%, mesic = 59%) than in old forests (xeric = 62%, mesic = 65%).

No correlation between lichen cover and site age ($r = -0.003$, $P = 0.985$) was found. Instead, lichen cover was significantly negatively correlated with canopy closure and basal area ($r = -0.382$, $P = 0.010$ and $r = -0.306$, $P = 0.043$, respectively). Because of the strong correlation between canopy closure and basal area (0.751, $P < 0.001$), only canopy closure was included in the analyses. Canopy closure was weakly correlated with site age ($r = 0.293$, $P = 0.053$).

The overall GLM ($n = 44$) showed that soil moisture had a significant effect on the lichen cover (Table 2). The main effects of the age class, forest history, canopy closure, and site age were not statistically significant, but there was a significant interaction between age class and forest history (Table 2). In other words, the effect of forest history was not consistent on forests of different age. For old forests, a history of young forest in the early 20th century led to higher lichen cover than a history of old forest (OLD1 = 41.6% and OLD2 = 53.2%). For middle-aged forests, history had no effect on lichen cover (MIDDLE1 = 48.9% and MIDDLE2 = 48.0%). However, the differences in means were not statistically significant (OLD: $F = 1.289$, $P = 0.263$; MIDDLE: $F = 0.010$, $P = 0.922$). Site age was excluded from the final models in order to avoid the redundancy with the age class.

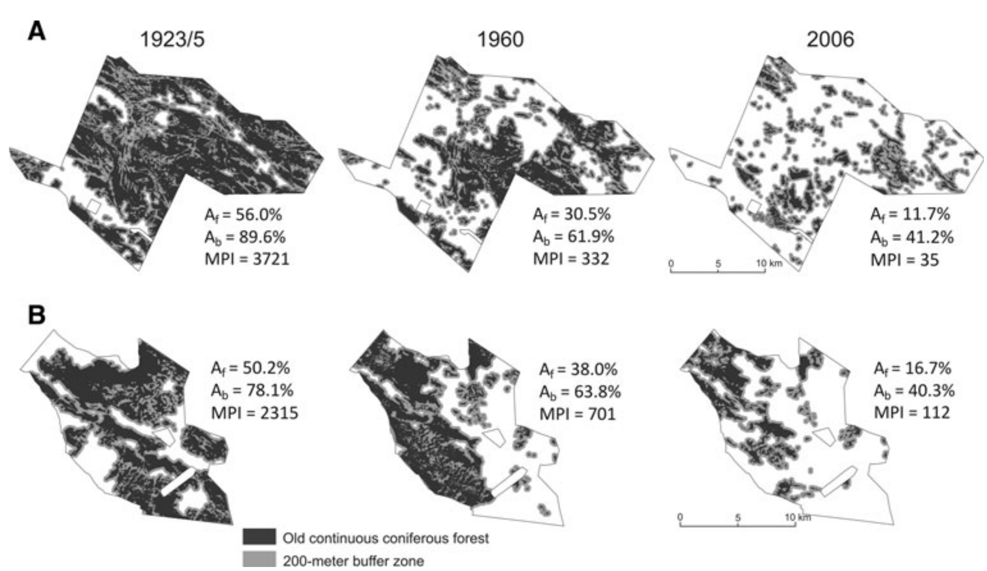

Fig. 4 The proportion of old continuous coniferous forest (A_f) of the total area and the proportion of the joint area covered by the old continuous coniferous forests and 200-meter-buffer zone (A_b) in **a** Akkajaur-Abraur and **b** Eggelats in 1923/1925, 1960, and 2006. Mean proximity index (MPI) is calculated using a 200 m search distance

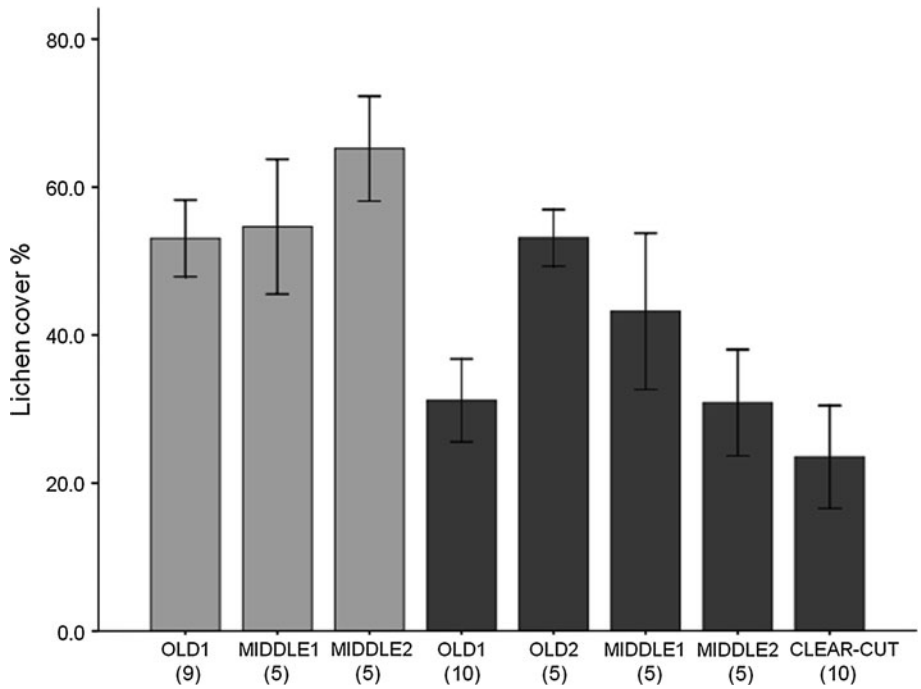

Fig. 5 Mean lichen cover ± S.E. in different forest classes. The number of cases in each class are given in brackets (total $n = 54$). Xeric forests are marked with *light grey bars* and mesic forests with *dark grey bars*

Table 2 An overall GLM for the ground lichen cover constructed using age class (old or middle-aged), moisture (xeric or mesic), history (old forest in 1895/1925, young forest in 1895/1925) and canopy closure (%) as explanatory variables

	SS	*df*	MS	*F*	Sig.
Corrected model	7158.1	7	1022.6	3.62	0.005
Intercept	4266.3	1	4266.3	15.12	0.000
Canopy closure	843.5	1	843.5	2.99	0.092
Moisture	3104.4	1	3104.4	11.00	0.002
Age	686.4	1	686.4	2.43	0.128
History	752.8	1	752.8	2.67	0.111
Moisture*age	232.0	1	232.0	0.82	0.371
Moisture*history	291.1	1	291.1	1.03	0.317
Age*history	1684.9	1	1684.9	5.97	0.020
Error	10157.9	36	282.2		
Total	110521.3	44			
Corrected total	17316.0	43			

$R^2 = 0.413$, Adjusted $R^2 = 0.299$

Discussion

The results showed that the composition and configuration of the forest landscape has changed drastically during the past hundred years. The cover of continuous old forest has decreased particularly rapidly since the mid-20th century. The remaining fragments of the old, relatively undisturbed forests are embedded in a matrix of clear-cuts and second-growth forests. Understanding the complex relationship between the changes of forest landscape structure and reindeer husbandry requires considering a wide range of processes that operate over various spatial and temporal scales.

Forestry is planned and performed on a stand level, but with emergent effects on the landscape levels, and its effects are most obvious for the forest species strongly restricted to certain habitat patches, such as old-growth forests (e.g., Brotons and others 2003). On the contrary, reindeer forage over wide areas during the winter, and reindeer and herders use the landscape in a different spatial scale compared to forestry. There is no single spatial unit in reindeer herding that corresponds to the stand. However, some indications can be found from Ren2000 database (County Administration Boards 2000) that include information on land use of reindeer husbandry. For example, the mean size of the patches where reindeer like to graze over longer periods ('trivselland') is 1,580 ha. In comparison, the average size of the forest stand in Akkajaur-Abraur was approximately 15.2 ha in 2006. The landscape from the reindeer husbandry perspective should be studied as a mosaic consisting of more or less suitable forest patches.

The amount of old forest in the landscape can be considered as one important indicator of the quality of the landscape mosaic. This is supported by a high preference for old woodlands by reindeer and caribou (Apps and others 2001; Kumpula and others 2007). Perhaps the most obvious effect of decreasing cover of old forests on reindeer husbandry is the decreasing abundance of arboreal lichens (Esseen and others 1996). The changes in forest age structure in our study area suggest a significant loss of arboreal lichen resources since the adoption of modern forest management in the mid-20th century. Arboreal lichens disappear immediately after clear-cutting and they have been found to grow more slowly in young dense forests where they generally receive less light than in old forests (Gauslaa and others 2006). The length of the rotation period in Northern Sweden is 120–130 years, but it would normally take longer to reach high biomass of arboreal lichens in a stand (Esseen and others 1996). Furthermore, Dettki and Esseen (1998) found that arboreal lichen abundance can be two times higher in natural landscapes than in managed landscapes. Pasture inventories in Finland have shown that arboreal lichens were lacking in ca. 50% of the forests in the reindeer management area in the beginning of the 21th century (Mattila 2006). In contrast, only a small fraction of forests in national parks in northern Finland has been found to lack arboreal lichens (Jaakkola and others 2006).

The fragmentation of continuous old forests also affects the long-term availability of arboreal lichens. The study of Stevenson (1990) showed that second-growth stands beyond the distance of 400 m from the border of the mature stands with highly abundant arboreal lichens supported almost no arboreal lichens. Our results showed that the area within the estimated effective local dispersal (ca. 200 m; see Dettki and others 2000) has strongly decreased during the past 100 years and today covers less than half of the study areas. This indicates that the sustainable basis for the long-term availability of arboreal lichen resources is declining. In addition to the local dispersal by large fragments or whole thalli, arboreal lichens disperse also by small fragments, soredia, and spores over longer distances, and the significance of regional dispersal may be strongly underestimated (Dettki and others 2000). However, the loss of old forests acting as propagule sources affects negatively also the regional dispersal of arboreal lichens.

The results of the field work showed that, as expected, ground lichen cover was more abundant in xeric forests than in mesic forests. Ground lichens can successfully compete with mosses and vascular plants in light and dry environments (Ahti 1961), and the amount of light reaching the ground is strongly related to lichen growth (Jonsson Čabrajič and others 2010), The amount of light available on the ground layer depends on the canopy closure, and young pine forests are generally denser and more shaded habitats than mature forests (Kuusipalo 1985). In our study, no clear trend between canopy closure and site age was found. However, lichen cover was weakly related to canopy closure.

The results suggest that forest history may have an effect on lichen cover in old mesic forests. Forest fires were the main disturbance agent in the late 19th century in boreal forests. Fire prevents the accumulation of organic matter and consequently the retention of water. This has been reported to benefit lichens that would be otherwise outcompeted by vascular plants and mosses (Zackrisson 1977; Bråkenhielm and Persson 1980; Sulyma and Coxson 2001). Forest history did not have a significant effect on lichen cover in middle-aged forests. The major disturbance in the younger stands has mainly been logging and forest management measures. One explanation for the results could be that different forest practices that have taken place since the mid-20th century may have overridden the possible effects of forest history on the lichen cover (Berg and others 2008).

Our results are in accordance with the study of Helle and others (1990) that found no relationship between ground lichen biomass and stand age and that showed that logging residues in clear-cuts caused a decline in lichen biomass for few years. In our study, lichen cover in clear-cuts was noticeably smaller than in other sites. Clear-cuts formed a rather heterogeneous group of sites where either soil scarification, prescribed burning, or no site preparation at all had taken place. The immediate effects of soil scarification and prescribed burning on the lichen cover are strongly negative (Roturier and Bergsten 2006), and thus, these forestry practices reduce the quality of forest mosaic from a grazing perspective. Our results suggest a strongly reduced availability of ground lichens particularly in 1960's when clear-cutting peaked in the study areas. The long-term effects of clear-cutting and site preparation on the abundance of ground lichens are poorly known (for more discussion, see e.g., Kivinen and others 2010).

In addition to the abundance of lichen resources, the observed changes in the landscape structure can also affect the utilization of remaining resources (O'Neill and others 1989; O'Brien and others 2006). For example, logging residues left on the clear-cuts, tracks and mounds resulting from soil scarification and ditches can hinder reindeer and herders movement in the landscape between suitable pastures (Huusko 2008; Kivinen and others 2010). Besides the availability of resources, reindeer may avoid young dense forests because of poor visibility (Helle 1981). Young dense forests can also hinder practical reindeer herding, such as gathering of herds.

In conclusion, the changes in forest landscape structure suggest that the quality of the winter pastures has decreased substantially during the past hundred years. The landscape mosaics and habitats created by forest fires and selective logging probably provided more abundant winter grazing resources compared to the forest landscape today dominated by clear-cuts and second-growth forests that rarely burn. Unlike conservation of wildlife by protecting habitats and wilderness areas, sustainable reindeer husbandry requires a dynamic approach that integrates land use needs of reindeer husbandry and forestry. The major challenge is to examine the availability of winter resources in a spatial and temporal context. Single changes on forest stand level affect only a small proportion of the landscape mosaic, but the accumulation of negative changes over time inevitably degrades the quality of the landscape for reindeer herding.

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