Consequences of forest landscape changes for the availability of winter pastures to reindeer (*Rangifer tarandus tarandus*) from 1953 to 2003 in Kuusamo, northeast Finland

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Using aerial photographs, we examined the changes in the forest matrix from 1953 to 2003 in the Oulanka National Park and commercial forests in the northern part of the municipality of Kuusamo. The changes concerned the potential winter grazing grounds available to the existing reindeer population. The main changes in the commercial forests took place between 1953 and 1977, during which time the mean forest-patch size shrank by 65%, and the number of patches increased by 78%. From 1953 to 2003, the total area of epiphytic lichens and ground-lichen pastures decreased by 48.6%. The area of ground-lichen pastures decreased by 20%, and the area of common hair grass pastures doubled. The forest matrix transition in the commercial forests changed not only the spatial configuration and areas of different pasture patches, but also the grazing pressure at the remaining pasture sites. In the national park, the changes in grazing pressure were related only to the changes in numbers of reindeer. In general, the conditions of reindeer pastures are a result of interaction between different land-use components.

Introduction

Reindeer husbandry takes place within a large and complex system of pasture environments, in which several factors affect directly or indirectly the state of pastures and the abundance as well as availability of reindeer fodder. Over the past decades, this environment in Finland and Sweden underwent several changes, while the land use intensified and expanded, causing quantity and quality of the most important winter fodder resources to decrease. (Berg *et al.* 2008, Kumpula and Kurkilahti 2010) At the begin-

ning of the 20th century, reindeer in Finland numbered approximately 100 000 (Anon 1934). Due to several factors, the number was doubled by 1984, and in 1992 there were about 265 000 reindeer (data of the Finnish Reindeer Herders' Association). Regardless of the intensification and several changes in the use of pasture environments during the latter part of the 20th century, depletion of lichen ranges (Mattila 1981, 1998, Kumpula *et al.* 1998) was considered to be primarily related to the high numbers of reindeer (Helle and Aspi 1983, Väre *et al.* 1995, Väre *et al.* 1996, Kumpula *et al.* 2000, Moen and Danell

2003). The most important competing form of land use in the reindeer herding area is forest management, as 75%–80% of the reindeer population graze during the winter in the northern boreal forest zone, an important region for commercial forestry since World War II (Helle *et al.* 1990, Kumpula *et al.* 2007, Helle and Jaakkola 2008). Both the intensity of reindeer grazing and forest management correlate with the condition of winter pastures, making it difficult to separate the effects of forestry from those of reindeer husbandry (Kumpula 2001a, Moen and Danell 2003, Kumpula *et al.* 2008).

During winter, the best fodder for reindeer energy expenditure and digestion consists primarily of ground (Cladonia sp. and Cladina sp.) and epiphytic lichens (Alectoria sp. and Bryoria sp.) (Aagnes et al. 1995), though reindeer utilise also dwarf shrubs, sedges, hays and grasses, the most important of which is the common hair grass (Deschampsia flexuosa) (Helle and Tarvainen 1984, Kojola et al. 1991, Kumpula et al. 2007). In the habitat selection studies of the Oraniemi herding district in 2002-2005, Kumpula et al. (2008) found that the most important habitat in late winter is the mesic logging areas, in which plenty of arboreal lichens are available in tree crowns and logging residues. The second important habitat consists of mature and old-growth mesic epiphytic-lichen-rich forests (Kumpula et al. 2008).

Several studies have shown that the effects of forest management on winter pastures for reindeer are for the most part negative (Eriksson and Raunistola 1990, Kumpula 2003, Roturier and Bergsten 2006, Hallikainen et al. 2008, Kivinen et al. 2010, Kumpula and Kurkilahti 2010). It has been observed that clear-cutting as a forest regeneration method reduces the amount and availability of ground lichens at sub-xeric and xeric sites (Helle et al. 1983, Kumpula and Kurkilahti 2010, Kivinen et al. 2010). Clearcutting on mesic and sub-xeric mineral soils frequently gives rise to an abundance of common hair grass, thereby partly compensating for the loss of mature forest due to forestry operations (Colpaert et al. 2003). The highest mean biomasses of common hair grass on mesic sites have been found 5-10 years after clear-cutting (Helle 1975). Unlike ground lichens, epiphytic lichens disappear immediately as a result of clear-cutting (Kivinen et al. 2010). Because forests that are abundant in epiphytic lichens are usually older than forests at the end of the current rotation period, forest management has significantly reduced the availability of epiphytic lichen pastures (Esseen et al. 1996, Jaakkola et al. 2006). In addition to affecting the abundance of lichens, clear-cutting also impacts reindeer access to lichens. Reindeer do not like to graze in clearings or in dense young-growth forests for several reasons: litter and logging residues obstruct digging, snow is likely to be packed harder due to strong wind gusts, and predator visibility in dense young-growth forests is poor (Helle et al. 1990, Kumpula 2001a, Kumpula et al. 2007, 2008). Studies of the interaction between caribou and forestry have shown that caribou may abandon or avoid harvested and partially harvested areas for up to 12 years (Darby and Duquette 1986, Chubbs et al. 1993). Studies of the habitat use of semi-domesticated reindeer in Finland and woodland caribou (Rangifer tarandus caribou) in Canada have shown a strong preference for old-growth forests and an avoidance of clearcuts or young stands (Apps et al. 2001, Kumpula et al. 2007, 2008).

In studying landscape change, five different spatial processes can be distinguished in humanmodified landscapes. These produce more or less isolated patches of habitat and cause habitat loss (Forman 1995). The spatial processes take place simultaneously, and therefore they overlap during the period of land transformation (Forman 1995, Jaeger 2000). The most common ways for land transformation to begin are perforation and dissection, and the process continues through sub-division, shrinkage and attrition (Forman 1995, Fahrig 2003). Classical landscape fragmentation studies concentrate on the different parameters describing habitat areas as well as on the spatial arrangement of the fragments within a landscape. Another approach to studying fragmented landscapes looks at the changes in the conditions in and around the habitat fragments. As the spatial structure of the landscape changes, various factors can act to modify the conditions of landscape elements. These are including both the fragments and the matrix, which are the most extensive and connected

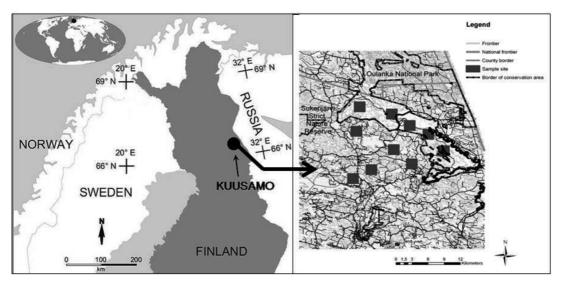


Fig. 1. Location of Kuusamo and the study plots in Oulanka National Park as in the commercial forests (source: National Land Survey of Finland, the Finnish Forest Research Institute, Helsinki; permission number 305/MML/12).

landscape element types (Pickett and Cadenasso 1995, Hobbs 2001). As the degree of modification increases, the land-use intensity in the intact areas increases. Moreover, the remnants of the original vegetation are increasingly influenced by processes originating in modified areas as well as by the original land-use (McIntyre and Hobbs 1999). The decrease in the area of original vegetation may lead to a concentration of moving elements — such as large herbivores in the remaining areas — and changes in temporal and spatial interactions. This is likely to lead to an increase in use of the habitats in the remaining areas (Lovejoy *et al.* 1986).

Our hypothesis suggests that, together with the increase in the reindeer population, the changes in reindeer management methods and the intensification of forest use have resulted in reduced availability of pasture land to reindeer. Simultaneous forest landscape transformation and changes in the numbers of reindeer have together influenced the grazing pressure on the remaining sites of original forest vegetation. In this study, we: (1) defined and quantified the transformation process of the forest landscape in northern part of the municipality of Kuusamo from 1953 to 2003 in the national-park and commercial-forest areas; (2) calculated the mean areas of potential winter grazing grounds for reindeer in the national park and commercial forests during 1953–2003; and (3) related the observed changes in potential winter grazing grounds to the existing numbers of reindeer.

Material and methods

Material used in this study was originally collected for the M.Sc. thesis of the second author (see Heiskanen 2009). For the purpose of this paper, we re-analysed the data to clarify the results, which here are based on the re-classified land-use data. In this study, we used a Mann-Whitney *U*-test, Friedman's test and a Wilcoxon signed-rank test instead of a Kruskall-Wallis one-way analysis of variance, which was applied in Heiskanen (2009). Collection of the original material is briefly described below.

Study area

This study was conducted in the northern part of the municipality of Kuusamo, in northeastern Finland (Fig. 1). The area represents the northern boreal zone within the southern Lapland subzone (Kalela 1961). A part of the study area, the Oulanka National Park, became a protected area in 1956. According to the IUCN classification of nature conservation areas, Oulanka belongs

to Category II. The Oulanka National Park is located 137-395 m a.s.l. Oulanka is dominated by mature forests of Norway spruce (Picea abies) and Scots pine (Pinus sylvetris). The birches present in the area are downy birch (Betula pubescens var pubescens) and silver birch (Betula pendula). The mean snow depth in mid-March (1971-2003) is 0.75-1 m (source http://www. ilmatieteenlaitos.fi/lumitilastot [in Finnish]). The human impact on the primeval forests of northern Fennoscandia had been almost nonexistent until the end of the 19th century (Pohtila 1979). With the exception of few patches of slash-andburn in the coniferous forests, some small-scale selection cutting and felling trees for reindeer, forest use in northern Kuusamo was very limited even at the end of the 19th century; 60.5% of the forests were over 200 years old (Viramo et al. 1980, Ruuttula-Vasari and Juvonen 2006). Until the 1950s, most of the forests in Kuusamo were located beyond what was considered to be the economically profitable limit for industrial forestry (Helle and Jaakkola 2008).

The area under study (1055 km² in total, of which 965 km² are reindeer pastures) belongs to the Alakitka Reindeer Herding Association. The Association maintains 17.6% of the protected area of the Oulanka National Park and the Sukerijärvi Strict Nature Reserve (Nieminen 2008). At the beginning of the 20th century, Alakitka's area was 743 km², and the maximum number of reindeer therein was 900 (Anon 1934). In 1953, the number of reindeer was 1200; in 1977 it was 1500; in 1991 it increased to 2600, and in 2003 it decreased to 1600. The pastures of the Alakitka Reindeer Herding Association are mainly on mesic and sub-xeric upland mineral soils. Alakitka is characterised by a low percentage of xeric pastures that are rich in reindeer lichens as well as a rather high percentage of potential epiphytic lichen pastures. The total area of mires spans 323 km². Percentages of mineral soil sites, potential reindeer lichen pastures, and potential epiphytic lichen pastures were 66.5%, 0.1% and 18.1%, respectively. The pasture area per reindeer (in 2009, the number of reindeer was 1600), area of mire per reindeer, and area of mineral soil pasture per reindeer were 66.0, 20.2 and 40.1 ha, respectively. Presently, some 90%–95% of the Alakitka Reindeer Herding Association's

reindeer are fed in enclosures during winters (November–April) (Nieminen 2008).

Aerial photographs

The landscape change was studied using digital aerial black-and-white photographs obtained from the Topographic Service of the Finnish Defence Forces. The photographs were taken on 11 July 1953, 7 July 1977, and 27 June 2003. Photograph scales were 1:20 000 (1953) and 1:60 000 (1977, 2003). Selection of areas included in the study was based on 90 aerial photographs of northern Kuusamo taken in 1953. In the first phase of sampling, we chose aerial photographs in which the forested areas covered at least $\sim 70\%$ of the picture (estimated visually). We then created two groups of selected photographs based on the primary location (national park vs. commercial forest). There were 5 and 18 independent photographs of the nationalpark area and the commercial forests, respectively, with at least 70% forest cover. From these we randomly chose five non-overlapping photographs (Fig. 1). The photographs were rectified and georeferenced to the Finnish National Grid Coordinate System using ArcGIS 9.3. The aerial photographs from the year 1953 covered an area of 4×4 km. To minimise the distortion of the images close to the edges and the variation of scale-dependent landscape indices, we used the centres of the photographs covering 2 × 2 km. (Löfman and Kouki 2003). The sample squares were manually digitised to the various land-use classes. The visual classification was conducted by delineation and identification of homogenous patches of certain land-use types (Jennings et al. 1999, Paine and Kiser 2003). The digitised classes were mature forest (closed canopy), open forest (canopy cover degree 50%), clear-cut, sapling stand, young forest, seed-tree stand, mire, drained mire, water, roads, open areas (yards), and fields. The original land-use classes were then re-classified into the following new categories: forest (mature forest), open forest (open forest), regeneration area (clear-cut, sapling stands, young forest, seed-tree stand), mire (mire), drained mire (drained mire), water (water), and open area (roads, open areas, fields). To include in the study the edge effect of the impact of landscape transition on epiphytic lichens, 25- and 50-m edges were created within the forest patches. In Swedish studies, the maximum edge effect extended 25–50 m into the Norway spruce forest at moderately exposed sites (Esseen and Renhorn 1998). By subtracting the edge areas from full areas of the patches, we were able to calculate the relative change in the size of the core forest area.

Potential winter grazing grounds

The potential areas of winter pastures were calculated based on the areas of the different classes of digitised patches. The areas of the forest, open forests, and regeneration classes were divided into mesic (57.0%), sub-xeric (41.6%), and xeric (1.4%) sites, based on the results of the 9th National Forest Inventory (Mattila and Mikkola 2009). According to Mattila and Mikkola (2009), xeric and barren forests are primarily groundlichen pastures. However, ground lichens are also found in sub-xeric forests (Kumpula et al. 1999). The mesic sites make the best epiphyticlichen pastures, which are also found at subxeric sites. The mesic and sub-xeric regeneration sites are rich in common hair grass. In addition, the age and structure of the forest affect the abundance of the most important winter fodder resources (Kumpula et al. 1999, Mattila and Mikkola 2008, 2009). However, these factors cannot be estimated reliably from the aerial photographs used in the present study. These calculated areas were then classified into the following types of reindeer pasture: epiphytic lichen (mesic forest areas), epiphytic and ground lichen (sub-xeric forest areas), ground-lichen pastures (sub-xeric forest, xeric forest and xeric open forest areas), and common hair grass (mesic and sub-xeric regeneration areas; Kumpula et al. 1999, Mattila and Mikkola 2009). Other classes were considered as having no winter pasture value.

To show the relative impact of landscape change on the grazing pressure, we divided the calculated areas of potential winter pastures (epiphytic lichen, epiphytic and ground lichen, ground lichen and common hair grass) by the number of reindeer for the years 1953, 1977, and

2003. For 1991, when the number of reindeer was at its highest, the areas of potential pasture types were estimated to be between the values obtained in 1977 and in 2003. First, we calculated the percentages of different pasture types per sample area, and with these percentage figures the areas (km2) of the different pasture types were calculated for the entire herding district. The pasture areas were converted to hectares (ha), and the subsequent value was then divided by the maximum number of reindeer in the herding district in particular years. This calculation was based on the assumption that the pasture-type distribution in the sample squares is similar to that in the entire herding district. Therefore in this study, these results are best applied in comparisons among years and different types of areas.

Statistical analyses

We calculated the landscape spatial pattern statistics using FRAGSTATS (McGarigal et al. 2002). In order to define the landscape structure during different periods, and to estimate the change in the reindeer winter pasture resources, we selected the following six most independent variables for the analysis: number of patches (NP), average patch size, edge density (ED), largest patch index (LPI), Shannon's diversity index (SHDI), and landscape shape index (LSI). The variables are presented as mean values calculated over the sample areas located in the national park and commercial forests. These variables were then grouped into four categories: Patch area, Edge and shape, Diversity, and Configuration (Herold et al. 2002). The first three variables characterise the composition of the landscape and the last one defines the configuration of the landscape. Edge density (ED) describes the length of edge per hectare (m ha-1). Largest patch index (LPI) refers to the percentage of the landscape accounted for by the largest patch and it is a simple measure of dominance. Shannon's diversity index (SHDI) represents the amount of "information" per patch, and it increases as the number of different patch types (i.e., patch richness, PR) increases. Landscape shape index (LSI) measures the perimeter-toarea ratio for the landscape and quantifies the

amount of edge present in a landscape relative to what would be present in a landscape of the same size but with simple geometry. (McGarigal *et al.* 2002).

The data did not meet the assumption of normality, and therefore we applied non-parametric tests to compare results obtained from the national park and commercial forests as well as between among years. A Mann-Whitney U-test was used to determine the statistical significance of the observed differences between the areas (national park vs. commercial forest). To compare the results for different years, Friedman's test was used to determine the statistical significance of the differences. For comparing the areas of pasture types per reindeer between years, the Wilcoxon signed-rank test was used. In the results, the means and standard deviations are presented. The statistical tests were conducted using PASW Statistics ver. 18.0 (SPSS Inc.). Although the Oulanka National Park was established in 1956, this name is used in this study when referring to the data from 1953 for the area covered later by the park.

Results

Landscape changes

The analysis based on the aerial photographs shows that during the period studied, the forest structure changed significantly within the commercial-forest area.

Patch area

In all the studied years, the average areas of the forest patches were significantly larger in the national park as compared with those in the commercial forests (Table 1). The reduction in the mean forest patch size in the commercial forests from 1953 to 2003 was 77%. However, this difference was not statistically significant (Friedman's test: $\chi^2 = 0.667$, p = 0.72). When all the land-use classes were pooled, the mean number of patches increased in both the national park and commercial forests, although the increase was significantly higher in the commercial forests (Fig. 2). In 1953, the average number of patches was slightly higher in the commercial forest than in the national park. In 1977 and 2003, the number of patches in the commercial forest was twice as high as that in the national park. In 1977 and 2003, the difference in the number of patches between the national park and the commercial forests was statistically significant (Mann-Whitney *U*-test: $Z_{both} = -2.6$, $p_{both} =$ 0.008). The changes in the number of patches in the commercial forests were statistically significant among the years ($\chi^2 = 7.6$, p = 0.022).

Edge and shape

There was a statistically significant difference in edge density between the national park and commercial forests in 1977 and 2003 ($Z_{\text{both}} = -2.6$, $p_{\text{both}} = 0.008$). In the commercial forests, the edge

Table 1. The average size (ha) of the forest, open forest, and regeneration area patches within the national park and commercial forests in 1953, 1977 and 2003.

Patch type	Year	Mean area (ha) of patch ± SE (n)		Mann-Whitney <i>U</i> -test
		National Park	Commercial forests	0 1001
Forest	1953	92.5 ± 24.2 (17)	53.8 ± 21.2 (27)	Z = -2.9, p = 0.004
	1977	$85.5 \pm 25.8 (15)$	$17.6 \pm 5.7 (55)$	Z = -3.0, $p = 0.003$
	2003	$89.4 \pm 24.1 (18)$	$12.4 \pm 2.8 (60)$	Z = -4.0, $p < 0.001$
Open forest	1953	$5.0 \pm 1.2 (9)$	4.8 ± 1.3 (6)	Z = 0, p = 1
	1977	$8.1 \pm 4.3 (4)$	4.8 ± 1.2 (32)	Z = 3.0, $p = 0.003$
	2003	2.6 ± 1.4 (6)	$2.5 \pm 0.9 (14)$	Z = 0.8, $p = 0.934$
Regeneration area	1953	13.1 (1)	0.5 (1)	Z = -1.0, $p = 0.317$
	1977	_	$9.8 \pm 2.5 (38)$	_
	2003	0.2 (1)	$9.5 \pm 1.9 (81)$	Z = 1.7, p = 0.087

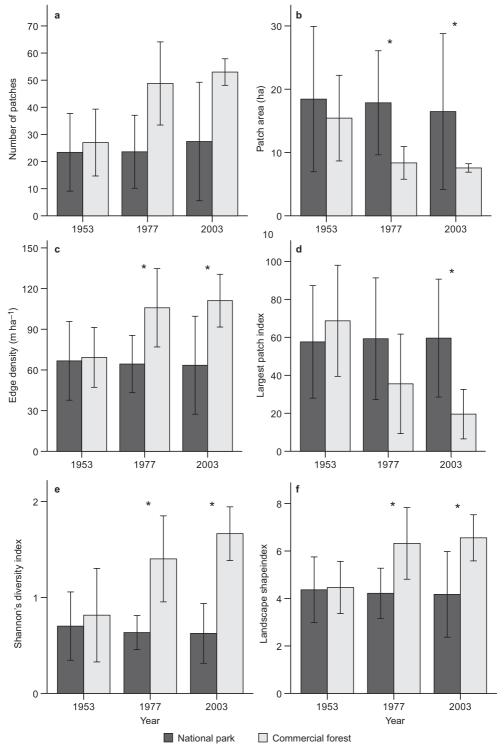


Fig. 2. Comparisons among years (1953, 1977, and 2003) and areas (Oulanka National Park the commercial forest) of (**a**) number of patches, (**b**) area of patches, (**c**) edge density, (**d**) largest patch index, (**e**) Shannon's diversity index, and (**f**) landscape shape index. Vertical lines represent standard deviations. Asterisks indicate significantly different values between Oulanka National Park and commercial forests (Mann-Whitney U-test; p < 0.05).

density increased by 37.6% from 1953 to 2003 ($\chi^2 = 8.4$, p = 0.015) (see Fig. 2).

Diversity

There were no significant differences in the Shannon's diversity index (SHDI) in 1953 between the national park and the commercial forests (Fig. 2). During the periods 1953–1977 and 1977–2003, the SHDI increased within the commercial forests by 42.9% and 17.6%, respectively ($\chi^2 = 8.4$, p = 0.015). The SHDI for the commercial forests was significantly higher than for the national park in 1977 (Z = -2.6, p = 0.008) and in 2003 (Z = -2.6, p = 0.008).

Configuration

In 1953, the largest patch index (LPI) for the national park was 19% lower than that for the commercial forests (Fig. 2). However, in 1977 the LPI was close to being significantly higher for the national park than for the commercial forests (Z = -2.0, p = 0.056). In 2003, the LPI for the national park was significantly higher than that for the commercial forests (Z = -2.6, p = 0.008). The differences among the years were statistically significant for the commercial forests ($\chi^2 = 10.0$, p = 0.007).

The landscape shape index (LSI) for the commercial forests increased by 47% from 1953 to 2003 ($\chi^2 = 8.4$, p = 0.015) (Fig. 2). When compared with the national park figures, LSIs for the commercial forests were significantly higher in 1977 (Z = -2.6, p = 0.008) and 2003 (Z = -2.6, p = 0.008), indicating a more fragmented structure within commercial forests.

Potential winter pastures

In 1953, the areas of epiphytic and ground lichen and ground-lichen pastures were significantly larger in the national park than in commercial forests (Z = -2.6, p = 0.008) (Fig. 3). In 1977 and 2003, the area of epiphytic and ground lichen-pastures was larger in the national park (Z = -2.6, p = 0.008). Interestingly, the area of

epiphytic-lichen pastures was clearly larger in the commercial forests as compared with that in the national park in 1953 and 1977. In 2003, the areas of epiphytic-lichen pastures in the national park and in the commercial forests were the same.

The potential areas of epiphytic-lichen pastures in the commercial forests decreased by 33.0% from 1953 to 1977, and by 23.5% from 1977 to 2003 ($\chi^2 = 8.4$, p = 0.015). The corresponding values for potential epiphytic and ground lichen pastures were 33.1% and 23.2%, respectively ($\chi^2 = 8.4$, p = 0.015). The area of the ground-lichen pastures in the commercial forests was almost three times larger in 1977 than it had been in 1953, and it decreased by 71% during the second period from 1977 to 2003. These differences were statistically significant ($\chi^2 = 68.4$, p = 0.015). As the regeneration areas in mesic and sub-xeric sites are suitable grounds for hair grass, the area of potential hair grass pastures increased by 73% and 109% in 1977 and 2003 respectively. However, the differences were not statistically significant (Fig. 3).

Potential winter pastures per head of reindeer

The available pasture areas per head of reindeer decreased from 1953 to 1977, and further to 1991 (Fig. 4). From 1991 to 2003, the available pasture area per head of reindeer increased in all cases except with regard to the ground-lichen pasture per head of reindeer in the commercial forests. In all the studied years, the areas of epiphytic and ground-lichen pastures per head of reindeer were significantly higher in the national park than in the commercial forests ($Z_{all} = -2.5$, $p_{all} = 0.008$). In 1953, the area of epiphytic-lichen pasture per head of reindeer was significantly higher in the commercial forests than in the national park (Z =-2.6, p=0.008). In 1953 and 2003, the area of ground-lichen pastures per head of reindeer was significantly higher in the national park than in the commercial forests ($Z_{\text{all}} = -2.6$, $p_{\text{all}} = 0.008$).

From 1953 to 2003, the areas of epiphytic and ground-lichen pasture per head of reindeer decreased by 61.5% and 23.4% in the commercial forests and in the national park, respectively.

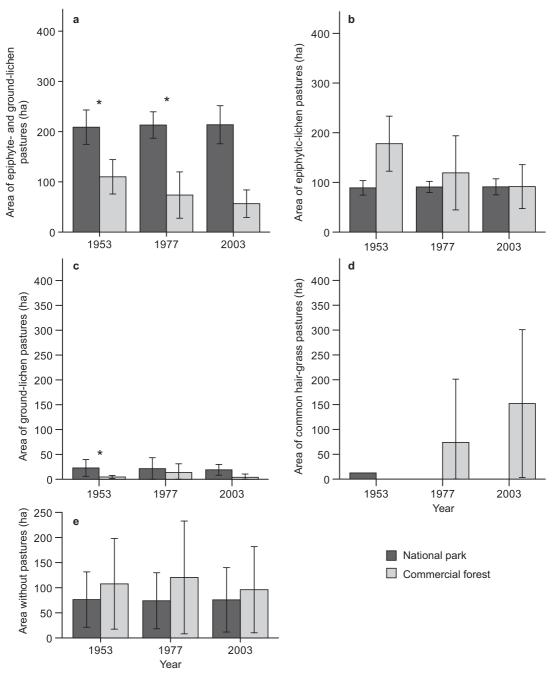


Fig. 3. Total areas of (a) epiphytic- and ground-lichen pastures, (b) epiphytic-lichen pastures, (c) ground-lichen pastures, (d) hair-grass pastures, and (e) without pastures, per sample square in the Oulanka National Park (national park) and commercial forests in 1953, 1977, 1991 and 2003. Vertical lines represent standard deviations. Asterisks indicate significantly different values between Oulanka National Park and the commercial forests (Mann-Whitney U-test; p < 0.05).

The decrease was statistically significant both in the commercial forests ($\chi^2 = 14.0$, p = 0.003) and in the national park ($\chi^2 = 9.6$, p = 0.008). In

the national park, from 1953 to 2003 the area of ground-lichen pasture per head of reindeer decreased by 38% ($\chi^2 = 9.8$, p = 0.02).

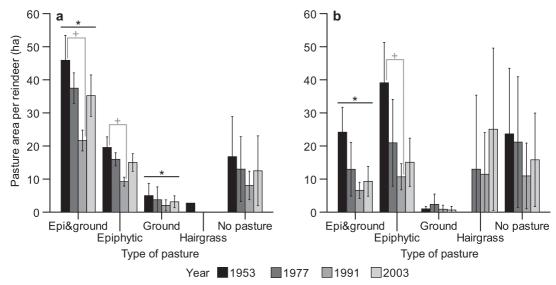


Fig. 4. Areas of different pasture types (epi&ground = epiphytic- and ground-lichen pasture, epiphytic = epiphytic-lichen pasture, ground = ground-lichen pasture, hair grass = hair-grass pasture, and no pasture) per reindeer in 1953, 1977, 1991, and 2003 in (a) Oulanka National Park, and (b) commercial forests. Vertical lines represent standard deviations. Asterisks indicate statistically significant differences between all the years (Friedman test; p < 0.05); plus signs indicate statistically significant differences between the year 1953 and 1991 (Wilcoxon test; p < 0.05).

In order to estimate the impacts of the changing environment and reindeer numbers on pasture availability, we calculated the pasture availability for the year 1991. In the national park, the area of epiphytic- and ground-lichen pasture per head of reindeer in that year was 23% lower as compared with the corresponding value in 1953 (Z = -2.0, p = 0.043). From 1953 to 2003, the area of epiphytic-lichen pasture per head of reindeer in the commercial forests decreased by 61.5% (Z = -2.0, p = 0.043) and in the national park by 23.5% (Z = -2.0, p = 0.043). During the same period, the area of ground-lichen pasture decreased by 60%.

Edge effects

In 1953, the 25-m and 50-m edges reduced the

commercial forest area by an average of 19.9% and 37%, respectively (Table 2). In 2003, the respective values were 35.4% and 57.5%. When comparing the years, between 1953 and 2003 the forest-patch area decreased by an average of 48.5%.

Discussion

After 1950s, even-aged silviculture was an increasingly popular method used for forest regeneration, and this led to an extensive transformation of commercial forest landscape in Fennoscandia in the latter part of the 20th century (Pohtila 1979). In our study area, the middle phase of a typical landscape transition (Forman 1995) was reached during the first 25 years, from 1953 to 1977. A similar pattern, beginning

Table 2. Calculated areas of forest patch, forest core area minus 25-m edge, forest core area minus 50-m edge in 1953 and in 2003 in commercial forests. The areas were calculated from the 400 ha sample plots.

	1953	2003
Forest area (mean ± SE (n), ha)	290.3 ± 20.2 (5)	149.3 ± 16.1 (5)
Forest core area minus 25-m edge (mean \pm SE (n), ha) Forest core area minus 50-m edge (mean \pm SE (n), ha)	$232.4 \pm 20.8 (5)$ $186.0 \pm 21.3 (5)$	96.4 ± 12.2 (5) 63.4 ± 8.4 (5)

already in the 1940s, was detected by Löfman and Kouki (2001) in southern Finland. The forest landscape change in the Kuusamo area started later than in many other parts of northern Finland due to land consolidation, which ended in 1955 (Kortesalmi 1960, Pohtila 1979, Heiskanen 2009). During the period under study, the largest patch index (LPI) decreased in the commercial forests from 70% to 20%, which means that the matrix of homogenous, mature forest is lost for the time it takes a clear-cut forest area to become reforested and matured. Löfman and Kouki (2001) found relatively high LPI values for closed-canopy patches in southern Finland in 1941, 1969 and 1997, indicating that the matrix of closed-canopy was maintained. This result is markedly higher than ours; however, Löfman and Kouki (2001) included the development stages of young, middle-aged, mature and old forests in the closed-canopy classes. According to the current knowledge, landscape indices do not directly indicate suitability of an area for reindeer or caribou. However, it is known that the principal factors affecting the winter habitat selection of the Rangifer species are food biomass and availability, the latter being affected by the characteristics of the snow cover (Pruitt 1979, Helle 1980, Johnson et al. 2002). In addition to high-quality habitat patches, the spatial configuration of habitat in the landscape (i.e. larger clusters of high-quality habitats) is also a strong determinant of the species' winter distribution (O'Brien et al. 2006). According to our results, the patch configurations in the presentday Oulanka National Park and in commercial forests differed from each other even in 1953. Our assumption is that the use of those areas had already been "minimised" from the end of the 19th century, when the idea of establishing the Oulanka National Park was first presented (Komiteanmietintö 1910, 1976).

Due to modern forest practices the multiaged forest matrix has been replaced by a patchwork of forest stands of various ages, most of them being younger than 100 years (Eriksson et al. 2000, Axelsson and Östlund 2001, Berg et al. 2008, Kumpula et al. 2008). The impacts of forest management are only temporary, due to natural and artificial regeneration as well as succession. However, for reasons of eco-

nomical profitability, the applied rotation times are too short to develop forests that are ideal as winter pastures for reindeer (Esseen et al. 1996, Dettki and Esseen 1998). It has also been noted that epiphytic lichens may be strongly affected by the particular environmental conditions of human-induced forest edges (Renhorn et al. 1997, Esseen and Renhorn 1998). During the period under study, the edge-affected area in the commercial forests doubled. This may indicate, together with fragmentation of mature and oldgrowth forest stands, that this development does not support the long-term persistence of epiphytic lichens (Kivinen et al. 2010). Forest management efforts have had mainly negative effects on the abundance of ground lichens through direct disturbances such as clear-cutting, timber transportation and soil scarification; however, availability of ground lichen for reindeer have also been affected by logging residues. Berg et al. (2008) found that during the 20th century in northern Sweden, forestry has caused the area of potentially good ground lichen pastures — i.e. middle-aged and old pine forests — to decrease by about 30%-50%. This is in accordance with our results: the areas of ground- and epiphyticlichen pastures decreased by 20%-50%. In addition to forestry, far-reaching pollutants from different emission sources have affected the amount and growth rate of ground and epiphytic lichens (Kumpula and Kurkilahti 2010).

Forest regeneration increased the area of suitable growth sites for common hair grass. Our results agree with those of Mattila and Mikkola (2009), who found that the biomass of common hair grass increased from the 1970s to the 2000s. In January-March 1974 and 1975, the reindeer of the Alakitka herding district were not feeding in common hair grass pastures, but by the end of the 1970s common hair grass was considered, on average, to be more important than lichens as winter food (Helle and Saastamoinen 1979). This change indicates that the large-scale loggings began in our study area during the late 1960s. The common hair grass biomass in the mesic and sub-xeric sites reaches its peak 5-10 years from logging, and the abundance decreases sharply 35–45 years after clear-cutting (Helle 1975).

While estimating the carrying capacity of winter ranges, an important measure is the avail-

able area of ground-lichen pasture per head of reindeer, although carrying capacity in itself is a theoretical concept that contains a great deal of oversimplification (Kumpula 2001a, Helle et al. 2007). In old estimates, the minimum for moderate-condition lichen pastures was 10-15 ha per head of reindeer (Keisarillisen porolaidunkomissioonin mietintö 1914, Alaruikka 1964). According to Skogland (1986) and Skuncke (1969), with a good pasture rotation system, 7 to 10 ha ground-lichen pastures per animal would satisfy the energy need of reindeer over winter. Compared with these values, our results seem rather high. However, these models can be applied only in conditions, in which alternatives to lichens are not available. Our study area (Alakitka Herding Association), represents a multi-fodder grazing system, in which other pasture types should to be taken into account when calculating carrying capacity (Mattila 1981). According to Mattila and Mikkola (2009), in Alakitka in 2005 the area of epiphytic-lichen pasture per head of reindeer (1600 reindeer in total) was 7.3 ha, and that of ground-lichen pasture 0.1 ha. Respective values in 1995 obtained by Kumpula et al. (1999) were 22.2 and 9.1 ha per head of reindeer (1752 reindeer in total). Mattila and Mikkola (2009) included only xeric sites in ground-lichen class. In contrast to this, Kumpula et al. (1999) included also sub-xeric sites in the ground-lichen pasture class. Our results are closer to the values obtained by Kumpula et al. (1997, 1999), due to similar pasture classification. When comparing the results, it should also be kept in mind that we studied the potential pastures and pasture types per head of reindeer in the national park and commercial forests separately, and the results of Mattila and Mikkola (2009) and Kumpula et al. (1997, 1999) are representative of the entire Alakitka Herding Association, which is one reason why direct comparisons are not possible. According to our study, in 1953 and 1977 the areas of epiphytic-lichen pasture in commercial forests were more important than those in the national park. Currently, the Oulanka National Park is considered to be an important epiphytic lichen pasture (Nieminen 2008).

Our results support the hypothesis that the forest matrix transition changed the spatial configuration of patches, the area of reindeer pastures, and — together with the increase in reindeer numbers — the available pasture area per head of reindeer, which decreased. It is likely that the grazing pressure increased at the unaffected sites, decreasing the biomass of ground lichens. However, supplementary winter feeding that began in the late 1960s as a response to exceptionally difficult weather conditions and inadequacy of epiphytic lichen pastures also had an impact on the condition of the winter pastures (Helle and Saastamoinen 1979, Kumpula et al. 2001, Helle and Jaakkola 2008). According to Helle et al. (1990) and Fischer (2005), the number of winter pellets — an indication of the grazing pressure — at lichen-rich xeric sites in 2004 was only 50% of the value in 1983, and at the same time the mean ground-lichen biomass at xeric sites increased. This is most likely a consequence of the intensive corral feeding (Fischer 2005).

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