
Epiphytic Macrolichens in Managed and Natural Forest Landscapes: A Comparison at Two Spatial Scales
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Epiphytic macrolichens in managed and natural forest landscapes: a comparison at two spatial scales

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To maintain biodiversity in managed forests we must understand how forestry affects various organisms across a wide range of spatial and temporal scales. We compared landscape structure, forest structure, and species richness and abundance of epiphytic macrolichens in three pairs of natural and managed boreal forest landscapes. Study landscapes (2500 ha) were located within and adjacent to three of the largest forest reserves in Sweden (Reivo, Muddus, Jelka). The structural heterogeneity within landscapes was higher in managed forests whereas within-stand structural heterogeneity was higher in natural landscapes. Species richness of macrolichens at the stand level (sample plot) was 23% higher in natural forests but there was no difference at the landscape level. Most (86%) of the common species were more frequent in natural landscapes. Lichen abundance (estimated by lichen litter) was two times higher in natural than in managed landscapes, 5.6 and 2.7 kg ha^{-1} forest (pooled data), respectively. Both species richness and abundance were negatively related to cutting level (number and basal area of cut stumps) and positively related to stand variables (stand age, stem density and basal area). Lichen-rich forest stands were more numerous but covered a smaller area and were more isolated in managed landscapes. This may in turn have important consequences for dispersal of lichen propagules to second-growth forests. In conclusion, the results suggest that effects of forestry on epiphyte diversity and abundance are strongly related to the spatial scale (stand or landscape). To enhance biodiversity in managed forests we must increase structural heterogeneity at the whole range of spatial and temporal scales.

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Recent concern about the loss of biodiversity in managed forests has led to emerging consensus about what kind of knowledge is needed to protect diversity. It is now widely acknowledged that efforts to maintain biodiversity in forests must be based on a thorough understanding on how forestry affects various organisms across a wide range of spatial and temporal scales (Noss 1990, Angelstam 1992, Franklin 1993). Comparative studies of natural and managed forests at different spatial scales may help us to clarify the relative importance of processes that influence diversity and can also provide information on key elements that should be specifically managed for (Roberts and Gilliam 1995). Including the landscape-level in such studies is important for several reasons. First, studies performed over a large geographic area give a more representative picture of the ecological consequences of various forest management methods. Second, comparisons of managed and natural landscapes may provide some insights about the long-term effects of forestry on biodiversity. This is because of the variety of forest management methods, and, hence, great spatial and temporal variability in large areas. Third, many ecological processes operate at a larger, landscape scale rather than at the local, stand scale (Hansson et al. 1995).

Stand-level influences of forestry are best understood (Wigley and Roberts 1997). However, comparisons of animal communities in natural and managed forests

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have recently addressed larger geographic areas such as landscapes and regions (e.g. DeGraaf and Miller 1996, Edenius and Elmberg 1996, Hagan et al. 1996, Mikusiński 1997). In contrast, comparative studies on plant response to forestry have mainly been stand-based. One reason may be that forest plants, being sedentary during their growth phase and mainly long-lived, often show a slower response to large-scale land-transformation processes than mobile animals. Further, studies performed at the landscape level are more difficult as they require more data.

The stand-level focus is, for example, clearly seen in studies addressing forestry effects on epiphytic lichens, which are considered to be particularly sensitive to forestry (Lesica et al. 1991, Tibell 1992, Neitlich 1993, Goward 1994, Rominger et al. 1994, Kuusinen 1995, Esseen et al. 1996). These studies have compared stands with large contrast in forest age or management intensity and have usually found large differences in species composition or abundance between managed and old-growth forests. In contrast, we still have a meagre knowledge about how forestry affects epiphytic lichens at the landscape scale. Some studies suggest that landscape structure may be important to epiphyte communities as it influences dispersal of lichen propagules (Stevenson 1990, Dettki 1998) and microclimatic edge effects (Sillett 1994, Renhorn et al. 1997, Esseen and Renhorn 1998). However, Peck and McCune (1997) found no relationship between current or historic landscape context variables (reflecting propagule availability in older forests) and biomass of epiphytic macrolichens.

We compared three pairs of managed and natural boreal forest landscapes to better understand the effect of forestry on epiphytic macrolichens at two different spatial scales (stand and landscape). The following questions were specifically addressed: 1) what are the major differences in landscape and stand characteristics between intensively managed and unmanaged, natural forest landscapes? and 2) do species richness and abundance of epiphytic macrolichens differ between managed and natural forests at the stand and landscape level?

Methods

Study areas

The study was performed in the interior of the county of Norrbotten (Fig. 1), northernmost Sweden, located in the northern boreal zone. Norrbotten is the most suitable area in Sweden for large-scale comparisons of forestry impact for several reasons. First, it hosts some of the largest forest reserves in north-western Europe surrounded by extensive areas of managed forests. Second, air pollution impact is generally small. Third, there exists a detailed vegetation map over the area. We selected three study areas, each consisting of a forest reserve and surrounding managed forests, based on three of the largest forest reserves in Sweden: Reivo, Muddus National Park and Jelka (Fig. 1). The forest reserves are dominated by old-growth conifer forest but do also contain some younger, post-fire successional stands. Reivo (9600 ha) is one of 20 reference areas in the National Swedish Environmental Monitoring Program (Bernes 1990, Eknert and Bäck 1991). Muddus (57000 ha) is the largest National Park dominated by conifer forest in Sweden. Jelka (16000 ha, including unprotected areas) is known for its large populations of many redlisted plants and fungi, for example, the lichens *Evernia divaricata* and *E. mesomorpha* (Karström 1992). Reivo is located at 65°50′N while both Jelka and Muddus are at 67°N. We arbitrarily defined landscape size as a 5 × 5 km (2500 ha) square. One natural and one managed landscape were selected in each of the three study areas. Natural landscapes were located in accessible parts (close to roads) of the reserves. Managed landscapes were located within a distance of 10–23 km from the reserves (Fig. 1). Managed and natural landscapes were chosen to minimise variation due to landform, altitude and forest-floor vegetation. The forests have relatively open canopies and low to medium productivity. Soils are generally nutrient poor. Fire is the dominant natural disturbance in the region (Engelmark 1987).

Major forestry impact in this region of northern Sweden dates back to late 19th century. The dominant method was selective cutting, mainly focusing on large trees of Scots pine *Pinus sylvestris*. Some stands were repeatedly logged by selecting successively smaller dimensions. Clearcutting was not widely used until the 1940's. Soil scarification by prescribed burning and natural regeneration under seed trees was commonly

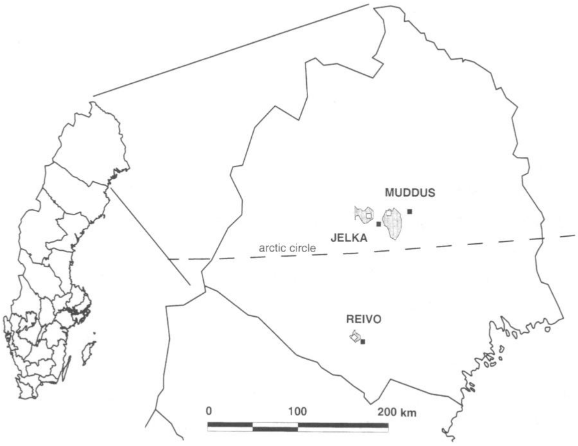

Fig. 1. Map of Norrbotten county, northernmost Sweden, with the three pairs of managed (closed symbols) and natural (open symbols) forest landscapes indicated. Hatched areas denote forest reserves.

used in the 1950's and 1960's. Currently, most clearcuts are mechanically scarified and planted with conifers, particularly *P. sylvestris*, but also *P. contorta*, native to North America, and *Picea abies*. Most stands are thinned at least once during the rotation period. The normal rotation in the region is 120–130 yr. Further details of study areas and forestry in the region are found in Dettki (1993), Hytönen (1995), Esseen et al. (1997) and Engelmark (1998).

Landscape structure

Information on landscape composition was obtained from the vegetation map of Norrbotten which displays the distribution of 40 vegetation types and other landscape elements. It also shows the impact of large-scale forestry (clearcutting) in terms of the distribution of clearcuts, young and mature forest. Stands classified as 'clearcuts' have trees lower than ca 2 m and are regenerated after clearcutting. However, in one of the natural landscapes (Reivo), a stand burnt in 1966 was also included in this category. Young forest are stands with ca 2–10 m high trees and mature forests have trees higher than ca 10 m. We digitised all forest stands (defined by stage of forest development), wetlands (open mires and swamp forests) and water bodies in the six 5 × 5 km landscapes into a geographical information system (GIS, MapInfo) for determination of composition, number and area of major landscape elements. It should be noted, however, that both number of stands and stand area are minimum estimates as forest roads and power line corridors were ignored.

Sample plots

The sampling was undertaken during August–October 1992. Twenty-five circular sample plots (10 m radius, 314 m^2) were allocated to each of the six landscapes by stratified random sampling. Strata represented the three stages of forest development (clearcut, young and mature forest). Number of sample plots per stratum was proportional to stratum area, with a minimum of two plots per stratum, following Krebs (1989). Sample plot locations were determined by random co-ordinates in a 50 × 50 m grid based on the National Grid of Sweden. Because of map scale (1:50000 or 1:100000), plot locations were at least 50 m from stand borders to avoid positional errors. We located the sample plots with a compass and a handheld GPS receiver (Global Positioning System), GARMIN GPS50. To avoid an over-representation of canopy gaps in sample plots, due to our pattern of movement through the forest and the error inherent in absolute GPS positions, we systematically located the centres of sample plots 10 m north of the GPS position.

Stand characteristics

We recorded species, vitality (live/dead), diameter at breast height (1.3 m, DBH) for all stems with DBH ≥ 5 cm in the 150 sample plots. The height of the highest conifer tree (height of dominant trees) was measured with a Suunto hypsometer. Stand age (time since stand-replacing disturbance, i.e. fire or clearcutting) was estimated by coring the two largest conifers at the root collar. The age of the oldest of these trees was used as a minimum estimate of stand age. For clearcuts we obtained information on stand age from the land owners. The extent of previous forestry impact was estimated by counting all cut stumps in each sample plot and by recording stump diameter.

Species richness

We made a thorough reconnaissance of macrolichens (foliose and fruticose species) in the lower canopy in each sample plot. This 'whole plot' method has a high rate of species capture and is suitable for detection of infrequent species. It was found to be the most accurate of three methods at determining species richness by McCune and Lesica (1992). We recorded lichens on trunks (both live and dead) and branches between 0.2 m and 2.0 m above ground. The minimum height of 0.2 m excluded forest floor lichens that had colonised root collars. Branches that stretched inside the plots from trees rooted outside were also included. Representative specimens were collected from each plot and their identity was checked in the laboratory under a dissecting microscope. Standard thallus colour tests and thin layer chromatography (TLC) aided the identifications. The lichen nomenclature follows Santesson (1993).

Abundance

Determining epiphytic lichen biomass by direct sampling in the forest canopy is extremely time consuming and thus usually unrealistic if a large number of stands are to be sampled. As a shortcut we estimated epiphyte abundance by quantifying lichen litter on the forest floor following McCune (1994). He showed that lichen litter was strongly correlated ($r^2 = 0.87$) with in situ epiphyte biomass in conifer forests of different age in Oregon and Washington. However, the method has several potential sources of error, for example, litterfall varies considerably throughout the year (Esseen 1985), and can thus only give rough estimates of lichen abundance. Despite these drawbacks, the litterfall method is sufficiently accurate for large-scale surveys where large differences in epiphyte biomass are expected (McCune 1994). We sampled lichens in late summer-early autumn to avoid the large, unpredictable pulses of litterfall that occur during late autumn and winter (Esseen 1985). We collected all macrolichens (including those on fallen branches and twigs) from one 2×2 m^2 quadrat placed at the centre of each circular sample plot. It was not practical to collect the numerous small lichen fragments, particularly those of filamentous *Bryoria* species, but we estimate that $> 90\%$ of the lichen litter was collected. Litter samples were air-dried to prevent decomposition. All macrolichens were removed from bark, needles, twigs and other non-lichen material and separated into foliose species and two groups of fruticose species (*Alectoria* and *Bryoria*). Lichen samples were then dried for 24 h at 80°C and weighed to the nearest mg. No attempt was made to back-transform the litterfall data to in situ epiphyte standing crop because of lack of information specific to the study area. In Oregon, however, late-summer lichen litter samples had a 1:100 ratio to standing crop (McCune 1994).

Statistical analysis

Mean and standard error for species richness and lichen abundance were estimated by using the formulas for stratified random sampling given by Krebs (1989). We used ANOVA to assess the effect of type of forest landscape (managed/natural) and study area (Reivo, Muddus, Jelka) on species richness and lichen abundance at the stand level. Sample plots were considered as units of replication in this analysis. Both species richness and abundance were rank-transformed prior to such analysis as the raw data did not fulfil the assumptions of parametric analysis (Potvin and Roff 1993, Seaman et al. 1994). The analysis was made with the GLM-procedure (SPSS 1996). Paired t-test was used for comparisons between managed and natural forests at the landscape level. Relationships between lichen and stand variables were analysed with pairwise correlation (Spearman's coefficients, r_s).

Results

Landscape structure

Productive conifer forest constituted between 69% and 84% of total area (2500 ha) in the six landscapes (Table 1). Wetland, dominated by open mires, was the second most important landscape element, constituting between 13% and 30%. Other elements covered relatively small areas, except in the managed landscape in Jelka area, where 7% consisted of conifer forest on rocky ground. The area of water bodies was ten times larger in managed landscapes (4.8%, pooled over study areas) than in natural landscapes (0.5%). This is because access to water for floating of timber was a prerequisite to exploit these forests in the past.

Table 1. Area (in hectares) of major landscape elements in three pairs of managed and natural boreal forest landscapes in northern Sweden. Figures in parentheses are percent of total landscape (2500 ha).

	Reivo	Muddus	Jelka
Managed			
Conifer type	1911 (76.4)	1915 (76.6)	1771 (70.8)
Clearcut	628	849	133
Young	540	333	266
Mature	743	733	1372
Wetland	499 (20.0)	479 (19.2)	388 (15.5)
Water	90 (3.6)	103 (4.1)	167 (6.7)
Other[1]	–	3 (0.1)	175 (7.0)
Natural			
Conifer type	2114 (84.5)	1713 (68.5)	1738 (69.5)
Clearcut	72[2]	–	–
Young	198	–	–
Mature	1843	1713	1738
Wetland	334 (13.4)	740 (29.6)	756 (30.2)
Water	12 (0.5)	22 (0.9)	0 (0.0)
Other[1]	40 (1.6)	25 (1.0)	6 (0.2)

[1] Mainly sub-alpine birch forest and conifer forest on rocky ground; [2] of fire origin.

We found several differences in landscape structure between the two types of landscapes. Mature forest (height > 10 m) dominated in the natural landscapes, constituting 87–100% of the forest, compared to 39–77% in the managed landscapes (Table 1). Clearcuts and young forest comprised 61% and 62% of forest area in the managed landscapes in Reivo and Muddus areas, respectively. However, the impact of large-scale forestry was much smaller in the managed landscape in Jelka area (23% clearcuts and young forest). There was a four-fold difference in mean number of stands per landscape, 42 stands (range 40–43) compared to 11 stands (range 5–18) in managed and natural landscapes, respectively. Mean stand area, in contrast, showed the reversed pattern, being four times higher in natural landscapes (170 ha, range 95–435 ha per landscape) than in managed landscapes (45 ha, range 41–48 ha). The maximum size of individual stands was 1115 ha and 1807 ha, in managed and natural landscapes, respectively.

Stand structure

We found several differences in stand structure between the two types of forest landscapes (Table 2). Mean stand age in natural landscapes (185 yr) was twice that of managed landscapes (92 yr). Old, multi-aged and multi-layered forests dominated in natural landscapes. In contrast, young, even-aged conifer monocultures were most abundant in managed landscapes. Clearcuts had a mean age of 19 yr (range 5–39 yr, n = 19) compared to 50 yr (range 15–145 yr, n = 22) in young forests. Mature stands were 32% older in natural landscapes than in managed areas with overall means of 194 yr (n = 71) and 147 yr (n = 38), respectively. The natural areas differed from the managed landscapes in the following other respects: 41% larger mean height of dominant trees, 21% higher stem density, 17% higher diameter and 74% higher basal area of live trees, two times higher density of large trees (DBH ≥ 20 cm), and 2.8 times higher density, 42% larger diameter and five times higher basal area of dead trees (Table 2). There was also a significant ($p = 0.000$, DF = 140, t-test) difference in within-plot variation in DBH as indicated by the coefficient of variation (CV), with means (± 1 SE) of 0.58 ± 0.02 (n = 74) and 0.46 ± 0.02 (n = 68), in natural and managed landscapes, respectively.

The forests had low tree species diversity: a maximum of four species occurred in a single plot. Number of tree species per sample plot was unaffected by type of landscape, 2.2 ± 0.2 and 2.1 ± 0.1 species ($\bar{X} \pm 1$ SE), in managed and natural landscapes, respectively. However, there was a clear difference in species composition: *Picea abies* dominated in natural landscapes while *Pinus sylvestris* (mainly planted) was most abundant in managed landscapes (Table 2). The amount of deciduous trees (dominated by *Betula pubescens*) showed only minor variation due to type of landscape. However, deciduous trees were considerably more abundant in Muddus (25% of basal area, managed and natural landscapes pooled) and Jelka (30%) than in Reivo (3.5%). Only scattered individuals of other tree species (*Populus tremula*, *Salix caprea* and *Sorbus aucuparia*) occurred.

Density of cut stumps showed a seven-fold difference between managed and natural landscapes, 217 ± 22 stumps ha^{-1} ($\bar{X} \pm 1$ SE, pooled data) and 28 ± 17 stumps ha^{-1}, respectively. Basal area of stumps was four times higher in managed than in natural landscapes with overall means of 3.1 and 0.8 m^2 ha^{-1}, respectively. Thus, the natural landscapes had also been influenced by forestry to some extent (mainly selective cutting of large pines) but the cuttings were generally much older than in managed stands. Signs of previous cutting operations were most frequent in Reivo while there was only minor influence of forestry in the studied parts of Muddus and Jelka.

Composition of the epiphyte community

A total of 35 macrolichens (15 fruticose and 20 foliose) was recorded. The epiphyte community was dominated by green-algal foliose and pendulous, fruticose (alectorioid) species. The most frequent species were *Hypogymnia physodes*, *Vulpicida pinastri*, *Parmeliopsis ambigua*, *P. hyperopta*, *Bryoria fuscescens*, *Parmelia sulcata*, *Bryoria simplicior* and *Cetraria chlorophylla*, in order of decreasing total frequency (Table 3). Interestingly, *Bryoria implexa*, a previously overlooked species (Holien 1989), was found on nearly half of all sample plots. There was only minor differences in overall species composition between the two types of landscapes. Twenty species (57%) were found in all six landscapes and 23 species (66%) were found in both managed and natural landscapes (Table 3). None of the 21 common species (occurring in ≥ 10 sample plots) was exclusively restricted to any of the two landscape types. Further, there was no difference in the number of rare species, both types had eight species. Species frequencies, however, differed considerably due to type of landscape. Eighteen of the 21 common species (86%) were more frequent in natural landscapes. The species most

Table 2. Stand characteristics in managed and natural forest landscapes in northern Sweden. Pooled data from 75 circular sample plots (10-m radius) per type of landscape.

	Managed		Natural	
	$\bar{X} \pm 1$ SE	Maximum	$\bar{X} \pm 1$ SE	Maximum
Stand age (year)	92 ± 9	316	185 ± 9	379
Height of dominant trees (m)	10.7 ± 0.7	22	15.1 ± 0.4	24
Density (stems ha^{-1})				
Live, DBH ≥ 5 cm	712 ± 67	3089	858 ± 47	1943
Live, DBH ≥ 20 cm	70 ± 10	350	135 ± 10	446
Dead, DBH ≥ 5 cm	37 ± 8	318	103 ± 11	446
DBH (cm)				
Live[1]	10.8 ± 0.1	52	12.6 ± 0.1	66
Dead[2]	8.9 ± 0.3	33	12.6 ± 0.2	63
Basal area (m^2 ha^{-1})				
Live	8.7 ± 0.8	27	15.1 ± 0.8	35
Dead	0.4 ± 0.1	5	2.0 ± 0.3	18
Basal area by species (%, live trees)[1]				
Picea abies	36.8		63.0	
Pinus sylvestris	44.7		16.3	
Deciduous trees	18.5		20.7	

[1] total n = 3697; [2] total n = 329.

Table 3. Occurrence (% frequency) of macrolichens in managed and natural forest landscapes. Species are divided into common (found in ≥10 plots) and rare species (in <10 plots) and ordered after increasing ratio of species occurrence between natural and managed landscapes. Pooled data from 75 circular sample plots (10-m radius) per type of landscape.

	Rank position[1]	Managed	Natural	Ratio natural/managed
		$\bar{X} \pm 1$ SE	$\bar{X} \pm 1$ SE	
Common species				
Imshaugia aleurites	20	28 ± 6	20 ± 8	0.71
Bryoria fremontii	17	45 ± 15	33 ± 15	0.74
Melanelia olivacea	10	80 ± 10	80 ± 20	1.00
Bryoria simplicior	7	85 ± 3	92 ± 8	1.08
Cetraria sepincola	9	81 ± 11	88 ± 12	1.08
Vulpicida pinastri	1	91 ± 4	99 ± 1	1.09
Hypogymnia physodes	1	91 ± 4	99 ± 1	1.09
Parmeliopsis hyperopta	4	89 ± 4	97 ± 1	1.09
Parmelia sulcata	5	88 ± 2	96 ± 4	1.09
Parmeliopsis ambigua	3	89 ± 4	99 ± 1	1.10
Bryoria implexa	16	43 ± 16	48 ± 22	1.13
Bryoria fuscescens	5	85 ± 3	99 ± 1	1.16
Cetraria chlorophylla	8	77 ± 3	99 ± 1	1.28
Bryoria capillaris	10	65 ± 6	95 ± 1	1.45
Hypogymnia bitteri	13	56 ± 17	83 ± 9	1.48
Hypogymnia tubulosa	12	63 ± 10	95 ± 3	1.51
Usnea filipendula	19	20 ± 7	31 ± 13	1.53
Platismatia glauca	14	52 ± 6	85 ± 6	1.64
Alectoria sarmentosa	15	39 ± 15	77 ± 11	2.00
Evernia mesomorpha	21	4 ± 4	9 ± 5	2.33
Cladonia spp.	18	13 ± 3	57 ± 7	4.30
Rare species				
Bryoria furcellata	23	4 ± 4	–	–
Bryoria nadvornikiana	28	1 ± 1	–	–
Leptogium saturninum	28	1 ± 1	–	–
Nephroma resupinatum	28	1 ± 1	–	–
Phaeophyscia sp.	28	1 ± 1	–	–
Physcia sp.	28	1 ± 1	–	–
Usnea subfloridana	22	8 ± 7	1 ± 1	0.17
Usnea hirta	25	1 ± 1	1 ± 1	1.00
Collema sp.	28	–	1 ± 1	–
Evernia prunastri	25	–	3 ± 1	–
Hypogymnia austerodes	23	–	4 ± 2	–
Nephroma bellum	25	–	3 ± 1	–
Parmelia saxatilis	28	–	1 ± 1	–
Ramalina dilacerata	28	–	1 ± 1	–

[1] Species are ranked after total frequency.

strongly associated with old forests were *Alectoria sarmentosa*, *Evernia mesomorpha* and tree-base *Cladonia* spp. These species were two to four times more frequent in natural landscapes. In contrast, only two of the common species, *Bryoria fremontii* and *Imshaugia aleurites*, were more frequent in managed landscapes (Table 3).

Species richness

Species richness of macrolichens at the stand (plot) level was higher in natural landscapes in all three study areas (Fig. 2). There was 23% more species per sample plot in natural than in managed landscapes (pooled over the three study areas), with overall means of 16 and 13 species, respectively (Table 4). At the stand level, species richness was affected by both type of landscape ($p = 0.000$) and study area ($p = 0.010$, ANOVA, Table 5). In contrast, at the landscape level, there was no difference in total number of species (29 species in both types) and only a small difference in mean number of species: 23.3 and 24.3 species, in managed and natural landscapes, respectively (Table 4). The null hypothesis could not be rejected at the landscape level ($p = 0.67$, $DF = 2$, paired t-test).

Species richness was strongly influenced by stage of forest development (Table 4). Clearcuts had 60% (pooled data) fewer species and young forests 22% fewer species than mature forests. The change in species richness with stand age was similar in both types of landscapes (Fig. 3). Species richness increased rapidly with stand age in young stands and reached a maximum of ca 16 species/plot around 100 yr. Interestingly, there was a slight decrease in species richness in stands older than ca 200 yr. This is supported by a significant effect of the quadratic term (age^2): a quadratic regression model explained 50% of the variation in species

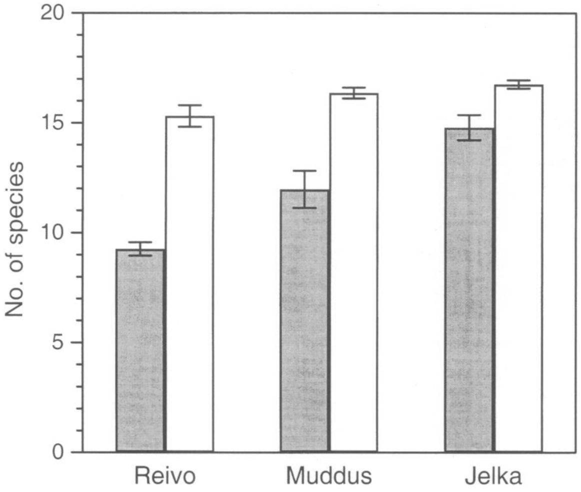

Fig. 2. Number of macrolichen species per sample plot ($\bar{X} \pm 1$ SE) in three pairs of managed (hatched bars) and natural (open bars) forest landscapes.

richness ($p < 0.001$) compared to 27% ($p < 0.001$) for a linear model. Species richness showed a steep increase with basal area at low levels and stabilised at levels exceeding 10 m^2 ha^{-1} (Fig. 3). Species richness was negatively correlated with both density ($r_s = -0.53$, $p < 0.001$) and basal area of cut stumps per hectare ($r_s = -0.41$, $p < 0.001$). In contrast, all five forest stand variables showed significant positive correlations with species richness (Table 6). The highest correlations were found for stem density, basal area and stand age.

Abundance

The abundance of epiphytic macrolichens (indexed by lichen litter) varied from 0 to 23 kg dry mass ha^{-1} in the sample plots. Lichen mass was two times higher in natural landscapes (5.6 ± 0.6 kg ha^{-1} forest, $\bar{X} \pm 1$ SE) than in managed landscapes (2.7 ± 0.6 kg ha^{-1}) pooled over the three study areas. The difference ranged from 1.4 to 2.6 times within each pair of landscapes (Fig. 4). At the stand level, lichen mass per hectare was affected by both type of forest landscape ($p = 0.000$) and study area ($p = 0.000$, ANOVA, Table 5). However, the null hypothesis could not be rejected at the landscape level ($p = 0.18$, $DF = 2$, paired t-test).

Table 4. Species richness of epiphytic macrolichens in relation to stage of forest development and spatial scale (stand and landscape) in managed and natural forests in northern Sweden. Based on data from 150 circular sample plots (10-m radius).

	Managed		Natural	
	$\bar{X} \pm 1$ SE	n	$\bar{X} \pm 1$ SE	n
Stage of forest development				
Clearcut	6.8 ± 1.5	17	5.0 ± 5.0	2
Young forest	12.6 ± 0.7	20	13.5 ± 0.5	2
Mature forest	16.1 ± 0.3	38	16.4 ± 0.2	71
Stand (sample plot) level	13.0 ± 0.6	75	16.0 ± 0.3	75
Landscape level	23.3 ± 1.9	3	24.3 ± 0.3	3

Table 5. Summary of two ANOVA's testing the effect of type of landscape (managed/natural) and study area (Reivo, Muddus, Jelka) on species richness and abundance of epiphytic macrolichens. Analysis on ranked data.

Source	DF	MS	F	p
Species richness				
Type of landscape	1	38720.7	26.23	0.000
Study area	2	7065.8	4.79	0.010
Type × study area	2	4394.5	2.98	0.054
Error	144	1476.0		
Abundance				
Type of landscape	1	49235.0	37.10	0.000
Study area	2	14695.2	11.07	0.000
Type × study area	2	2267.5	1.71	0.185
Error	143	1327.3		

Unfortunately, our litterfall data give biased estimates for the relative contribution of foliose and fruticose lichens to total epiphyte biomass. We have most probably underestimated the abundance of fruticose lichens as alectorioid species decompose considerably faster than foliose lichens (McCune and Daly 1994, Esseen and Renhorn unpubl.). With this precaution in mind, foliose lichens were more abundant than fruticose lichen in managed landscapes while the reverse was found in natural landscapes. Pooled over study areas, there was 1.7 times higher abundance of foliose lichens (2.7 vs 1.6 kg ha^{-1}) and 2.7 times higher abundance of fruticose lichens (2.9 vs 1.1 kg ha^{-1}) in natural landscapes. *Bryoria* spp. were the dominant fruticose lichens (97% of biomass), being nearly 40 times more abundant than *Alectoria sarmentosa* (3%).

Lichen abundance showed larger differences with stage of forest development than species richness. Clearcuts had almost no lichen (0.02 kg ha^{-1}, pooled over the six landscapes). Young stands had 45 times lower abundance than mature stands, 0.13 and 6.0 kg ha^{-1}, respectively. Fruticose lichens had > 100 times higher biomass in mature stands than in young stands, 2.7 and 0.025 kg ha^{-1}, respectively. Foliose lichens, were 27 times more abundant in mature stands than in young stands. Total lichen abundance was strongly related to stand age but there was a large variation among sample plots (Fig. 3). Stands younger than 50–80 yr had very low lichen abundance while maximum lichen mass was reached at an age of ca 150–200 yr. Little or no lichen litter was found in stands with a basal area < 6 m^2 ha^{-1} but it increased rapidly above this value. Lichen abundance was negatively correlated with both density ($r_s = -0.58$, $p < 0.001$) and basal area of cut stumps ($r_s = -0.40$, $p < 0.001$). Abundance

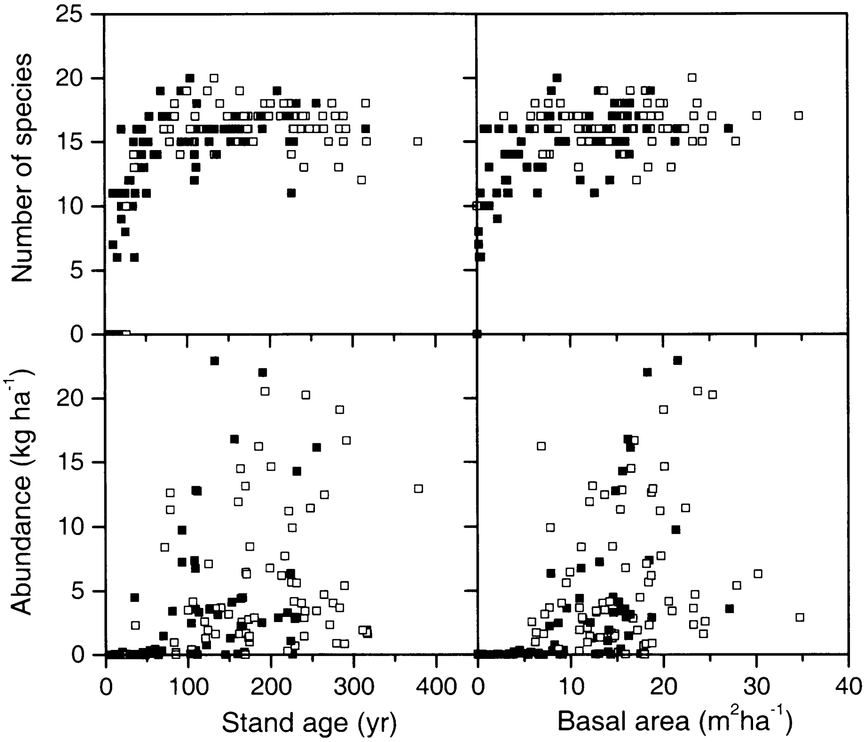

Fig. 3. Relationships between the abundance and species richness of epiphytic macrolichens per sample plot and stand age and basal area. Closed symbols indicate sample plots in managed landscapes (n = 75) and open symbols indicate plots in natural landscapes (n = 75).

showed significant positive correlations with the five forest stand variables but with a slightly different pattern than for species richness (Table 6). The highest correlations were found for basal area, height of dominant trees and stand age.

Both the amount and spatial distribution of lichen-rich forest were strongly affected by the type of landscape (Fig. 5). Mature, lichen-rich forest constituted 29–55% of total landscape in managed landscapes compared to 69–74% in natural landscapes. Lichen-rich patches were more numerous but also smaller and more isolated in managed landscapes due to fragmentation by clearcutting. This was especially the case in the managed landscapes in the Reivo and Muddus areas.

Discussion

Stand and landscape structure

Our analysis shows that the effect of forest management on the structural heterogeneity in forests varies strongly with the spatial scale. At the local level, within-stand structural heterogeneity was greater in natural forest landscapes, paralleling the results of other studies (Kirby et al. 1991, Lesica et al. 1991, Kuuluvainen et al. 1996). This is due to the uneven-aged, multi-layered stands, the high density of large trees and the large amount of coarse woody debris in the natural landscapes. In contrast, at the landscape level, heterogeneity was higher in managed areas in accordance with the findings of Mladenoff et al. (1993).

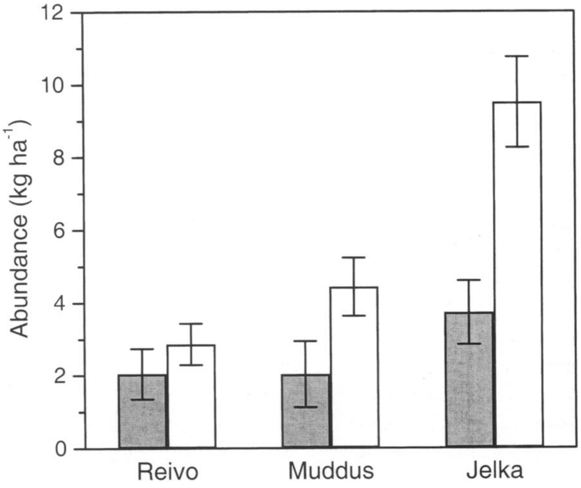

Fig. 4. Abundance ($\bar{X} \pm 1$ SE) of epiphytic macrolichens, expressed as kg (dry weight) lichen litter per hectare forest land, in three pairs of managed (hatched bars) and natural (open bars) forest landscapes.

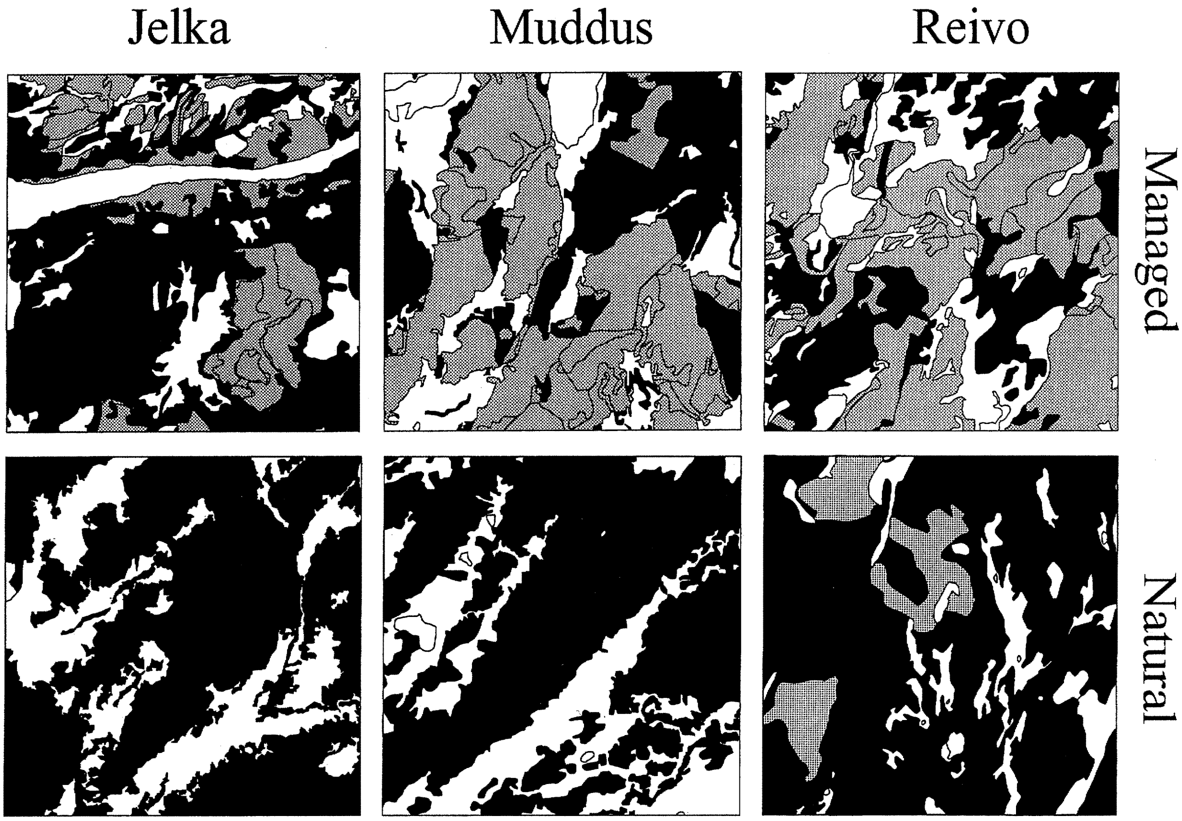

Fig. 5. Simplified spatial distribution of epiphytic lichen abundance in three pairs of managed and natural forest landscapes (each sized 5 × 5 km). Black areas show lichen-rich patches (i.e. mature stands, average lichen litter = 5.7 kg ha^{-1}, data pooled over sample plots, n = 108) while grey areas represent lichen-poor patches (i.e. clearcuts and young stands, average lichen litter = 0.1 kg ha^{-1}, n = 41). White areas indicate other landscape elements (dominated by water and open mires). Lines denote patch borders.

This is exemplified by the higher diversity of succession stages and the higher number of forest patches in the managed landscapes. The natural landscapes were dominated by a few, large patches with complex shape (Fig. 5). As the perception of the landscape differs considerably among species (Angelstam 1992), this suggests that the effects of forestry on biodiversity are strongly related to the spatial scale.

Lichen response at the stand-level

The changes in structural heterogeneity following conversion of diverse old-growth forests to young, conifer monocultures have direct consequences for the composition of the epiphyte communities. It is therefore not surprising that we found large stand-level differences in both species richness and abundance of epiphytic lichens between managed and natural forests in accordance with previous studies (Lesica et al. 1991, McCune 1993, Neitlich 1993, Esseen et al. 1996). In our study, both species richness and abundance were strongly negatively correlated with number and basal area of cut stumps. Forests managed by clearcutting, conifer monocultures and with short rotation are clearly unable to support abundant and diverse epiphyte communities.

Epiphytic lichen communities are controlled by many intercorrelated factors (McCune 1993). The most important local factors are probably substrate availability, substrate quality, stand age and microclimate. In this study, all five stand variables were positively correlated with both species richness and abundance of macrolichens (Table 6, Fig. 3). Unfortunately, since most stand variables change simultaneously it is usually not possible to sort out the effect of individual variables (McCune 1993, Esseen et al. 1996). The interpretation is further complicated by the fact that forest management operations influence many of the variables that regulate epiphyte communities, e.g. microclimate and tree, stand and landscape characteristics. However, our data strongly indicate that basal area (reflecting substrate availability) and stand age (time for lichen colonisation and growth) are two of the most important factors for species richness and abundance of macrolichens. Stand age has previously been shown to be a very critical factor for the development of epiphytic lichen communities (Hyvärinen et al. 1992, McCune 1993, Hilmo 1994, Holien 1996, Esseen et al. 1996). Substrate quality is also an important factor. Several macrolichens and many crustose lichens show a high degree of substrate specificity and are restricted to a single or a small number of tree species. For example, major boreal forest trees have characteristic lichen floras with the most deviating flora on deciduous trees, particularly on *Populus tremula* and *Salix caprea* (Kuusinen 1996). In this study we found a significant correlation between species richness of macrolichens and number of tree species despite the fact that our forests were poor in tree species. Our data indicate that the slight decrease in species richness of macrolichens in the oldest stands (Fig. 3) may have been caused by decreased amount of deciduous trees in late-successional stands.

Lichen response at the landscape level

Both species composition and number of macrolichens were relatively similar to the middle boreal forests in Finland studied by Hyvärinen et al. (1992). Overall species composition was only weakly related to type of forest landscape. However, many species, for example, *Alectoria sarmentosa*, *Evernia mesomorpha*, *Platismatia glauca* and *Usnea filipendula*, were more frequent in natural landscapes (Table 3). In contrast, only two common species, *Bryoria fremontii* and *Imshaugia aleurites*, were more frequent in managed landscapes. This may be explained by the higher basal area of pine in the studied managed forests. Both lichens are most abundant in open pine forests and have low shade tolerance according to Hyvärinen et al. (1992).

There are at least two explanations for the result that species richness of macrolichens at the landscape-level was not related to forest management. First, most of the observed macrolichens were habitat generalists with broad habitat requirements. The observations of rare and mostly specialised species like *Evernia mesomorpha* were too few to significantly influence species richness. Our objective sampling with randomly located sample plots was apparently not effective in locating hotspots of epiphytic lichen diversity. Most redlisted species and high diversity spots are largely confined to specific structural elements (e.g. old trees, deciduous trees) or biotopes (e.g. swamp forests, riparian forests) that occur scattered throughout the landscape mosaic (Berg et al. 1994, Neitlich and McCune 1997, Esseen et al. 1997, Ohlson et al. 1997, Thor 1998). Alternative sampling designs must be used to obtain adequate data for such rare objects. Second, large-scale forestry is rather recent in the region and the managed landscapes therefore had a relatively high proportion (39–77%) of mature forest. The managed landscape near Muddus even included a 100 ha forest reserve. These mature forests were naturally regenerated and sometimes older than the normal rotation in the area (120–130 yr). As a consequence the managed forests still contained some remnant structural elements (old trees, snags) of special importance to cryptogams.

It should be noted, however, that we studied foliose and fruticose lichens. By species numbers, crustose lichens normally dominate the epiphyte flora in boreal forests (Holien 1996, Kuusinen 1996). Further, many specialised crustose lichens, including several redlisted, wood-inhabiting species, are strongly associated with old-growth boreal forests (Tibell 1992). Consequently, forestry has most probably a stronger effect on species richness in crustose lichens than in foliose and fruticose lichens.

Landscape structure may potentially have a strong effect on ecological processes and organisms (Dunning et al. 1992, Forman 1995, Hansson et al. 1995). There are two major aspects of landscape structure: 1) composition, the diversity and amounts of landscape elements, and 2) pattern, the physical distribution of patches in the landscape. Our analysis shows that landscape composition may strongly influence the structure of epiphyte communities. Species richness and lichen abundance at the local (sample plot) level were strongly dependent on stage of forest development. Consequently, the overall epiphyte richness in a managed forest landscape is strongly dependent on the relative contribution of different successional stages. Our study was not specifically designed to test hypotheses relating epiphyte abundance to different aspects of landscape pattern such as patch numbers, size, shape and configuration. Recent works, however, suggest that attributes of the surrounding landscape might have important

Table 6. Correlation matrix (Spearman's coefficients) for combinations of dependent (lichen, 1–2) and independent (stand, 3–7) variables. NS $p > 0.05$, * $p < 0.05$, **$p < 0.01$, ***$p < 0.001$; $n = 150$.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)
(1) Species richness		***	***	***	***	***	***
(2) Abundance	0.54		***	***	***	***	*
(3) Stand age	0.51	0.61		***	***	***	NS
(4) Height of dominant trees	0.47	0.64	0.72		***	***	*
(5) Stem density	0.54	0.50	0.33	0.31		***	***
(6) Basal area	0.53	0.68	0.64	0.76	0.60		**
(7) Number of tree species	0.41	0.20	0.10	0.21	0.42	0.23	

implications for epiphyte communities. For example, species occurrence and composition of epiphytic Caliciales were significantly related to patch area in a large forest-wetland mosaic in northern Sweden (Kruys and Jonsson 1997). Further, changes in microclimate at induced forest edges may influence both growth (Sillett 1994, Renhorn et al. 1997) and abundance (Esseen and Renhorn 1998) of epiphytic lichens.

Limitations of landscape comparisons

Several problems are involved in comparisons of large geographical areas. Specifically, true replication is seldom possible at the landscape level (Hargrove and Pickering 1992). This was partly the case in this study. Despite our intention to minimise variation in other variables than forestry impact it was impossible to avoid some systematic bias at the landscape level. In particular, natural forest landscapes were at somewhat higher elevation (400–610 m) than managed areas (315–560 m). This in turn influenced tree species composition: spruce dominated in natural landscapes while pine was more abundant in managed areas. This is both an effect of the lower natural fire frequency at higher elevations, favouring spruce (Engelmark 1987), and that pine is favoured by forestry. Hence, we cannot exclude that our findings have to some extent been influenced by confounding factors. This implies that one should be cautious to extrapolate our results to other geographical areas. Our findings are probably representative for many areas in the northern boreal zone of Fennoscandia where large-scale forestry is relatively recent and stands of semi-natural character are still locally abundant. However, the results are probably not valid for the middle and southern boreal zones which have a considerably longer history of forest usage. We predict a greater effect of forestry on epiphytic lichen communities in these areas.

Management implications

The results have several implications for the conservation management of biodiversity in forest systems. Our analysis supports the view that efforts to promote diversity in managed forests should focus on increasing the structural heterogeneity at the whole range of spatial and temporal scales (Halpern and Spies 1995). However, it is a particularly complex task to maintain abundant and diverse epiphyte communities in forests managed for commercial purposes due to the ultimate dependence of epiphytes of their hosts. Most importantly, it is crucial to allow old forest to develop because of the slow accumulation of lichen biomass over time. At the stand level, results suggest that stand age and basal area are particularly important for diversity and abundance of macrolichens. Increasing canopy cover over time could be accomplished by prolonged rotations and use of partial cutting rather than clearcutting. To enhance diversity of epiphytic lichens in managed boreal forests we must create mixed stands with a significant proportion of deciduous trees (Kuusinen 1995, Esseen et al. 1997). At the landscape level, we strongly recommend to increase the amount of old (> 150 yr) forest. In addition to providing more habitat for epiphytes, it may also enhance lichen abundance in regenerating stands by increasing the overall supply of lichen propagules. We predict the existence of a lower threshold for the proportion of old, lichen-rich forest in the landscape, below which the long-term persistence of lichens with poor dispersal cannot be sustained. However, more specific guidelines to promote epiphyte diversity and abundance at the landscape level require further investigations on the effect of spatial structure on epiphyte communities.

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