

Epiphytic macrolichens in spruce plantations and native birch forests along a coast-inland gradient in North Norway

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Around 10% of the natural coastal birch forest in North Norway has been converted to spruce plantations. However, little is known about the effects on the affected ecosystems. Our objective was to evaluate differences in macrolichen communities between spruce plantations and native birch-dominated forests. Canonical correspondence ordination shows that birch forests and spruce plantations host distinct macrolichen species compositions. Mean yearly temperature is the most important explanatory environmental variable. Sitka spruce plantations had the lowest recorded species number and diversity, which probably is a result of low-light conditions caused by very long branches. Mixed birch–Norway spruce stands had both highest species number and diversity. Oceanic sites generally have different species composition, and higher species number and bark pH than continental sites. Plantations cause changes in species compositions and partly also declines in species number and diversity, and hence, plantations are far from optimal for conservation of native epiphytic lichen communities.

Introduction

In Norway north of the Arctic Circle, coastal deciduous forests dominated by downy birch (*Betula pubescens*) have been replaced to a large extent by non-native plantations, primarily of Norway spruce (*Picea abies* ssp. *abies*) and Sitka spruce (*P. sitchensis*), and more recently also Lutz spruce (*P. glauca* × *P. sitchensis*) (Hausner 2001, Lid and Lid 2005). Neither of these spruce taxa occurs naturally in the region. At present ca. 10% of the natural birch forest in coastal areas of Norway has been converted, while governmental

initiatives encourage a doubling of the extent of spruce plantation in the region, using subsidies to reach this goal (Hausner 2001, Vennesland *et al.* 2006, Øyen and Nygaard 2007, Norwegian Ministry of Agriculture and Food 2008). Lack of timber and firewood resources over the last 350 years has been the driving force behind the afforestation programme in Norway, which began after the Second World War (Øyen and Nygaard 2007).

Because of the temperature requirements of spruce and the cold climate in North Norway, only some sites are suitable for spruce planting

from a forestry point of view (Stabbetorp and Nygaard 2005, Vennesland *et al.* 2006, Øyen and Nygaard 2007). Thus, in many parts of the region only the climatically and edaphically most favourable sites are selected for spruce planting. Prior to planting, many of these sites probably also host the highest species diversity at local scales.

Research so far indicates that replacement of deciduous forests with conifer plantations leads to increased acidification of the soil and changes in habitat conditions, which can cause a shift in species composition and a reduction in species diversity (Fremstad 1997, Spiecker 2003, Smolander *et al.* 2005). Knowledge on the effects of spruce planting on species diversity in northern Norwegian forests is scanty. The planting is known to negatively affect forest floor vegetation (Sætra 1971), while mature spruce plantations host different species assemblages and less diverse communities of birds, snails and insects, than native birch forests (Hausner *et al.* 2002, Johansson *et al.* 1994, Yoccoz *et al.* 2005, Stabbetorp and Nygaard 2005). Although birch is the dominant tree species in large parts of northern Europe, tall, old-growth low-elevation birch forests, often referred to as “ssp. *pubescens*” in contrast to the short mountain birch referred to as “ssp. *tortuosa*” or “ssp. *czerepanovii*” (Lid and Lid 2005), are becoming less common due to increased land use (Hausner 2001, Stabbetorp and Nygaard 2005, Vennesland *et al.* 2006). Generally, it is this type of birch forest that is replaced by spruce.

Major land use changes in Norway are regulated by law, e.g. by the Planning and Building Act and the Nature Conservation Act. These acts oblige developers to present major land use plans to public authorities for their evaluation and approval. However, conversion of natural forests to spruce plantations is traditionally not considered a major land use change and is therefore not regulated by these acts, but by the Forestry Act, which does not include any such obligations (Hansen 2002). For this reason, land owners are free to plant spruce on their own property, and doing so is even encouraged and subsidized by national authorities. Biodiversity assessments are rarely conducted before planting, and little is therefore known about the origi-

nal vegetation where there currently are mature spruce plantations.

The colonization of epiphytic vegetation, consisting primarily of lichens and bryophytes, in spruce plantations north of the Arctic Circle is poorly studied. There are, however, some indications that plantations provide suitable habitats for some lichen species that are not common in native forests in the same area. For example, the only known localities of the lichen *Pseudevernia furfuracea* in Norway north of the Arctic Circle are in conifer plantations (Bjerke *et al.* 2006a), and some species of *Usnea* tend to be more abundant in spruce plantations than in adjacent native forests (Bjerke *et al.* 2006b). Light and humidity regimes, as well as bark properties, are quite different between spruce plantations and birch forests (Kuusinen 1996). Thus, we hypothesize that the epiphytic vegetation composition differs between plantations and forests. Such differences have been recorded elsewhere where spruce and birch stands occur naturally side by side (e.g. Holien 1997, 1998, Hilmo and Sæstad 2001).

The evaluation of the effect of spruce planting on epiphytic communities would be relevant for conservation purposes. This paper aims at testing the hypothesis that macrolichen species composition and diversity differ between spruce plantations and native birch forests. Considering both the influence of local and large-scale environmental factors this paper further aims at evaluating which factors contribute to explaining the variation in species composition along a coast–inland gradient.

Material and methods

Study area

The study area is situated in the northern part of the Nordland County and the central part of Troms County in North Norway. Along a ca. 220 km long transect from south-west to north-east, 31 sites containing both spruce plantations and native birch forests were selected (Fig. 1). These sites are within the middle boreal (MB) and northern boreal (NB) vegetation zones (Moen 1999, Karlsen *et al.* 2006). ‘Sub-arctic’ is mostly

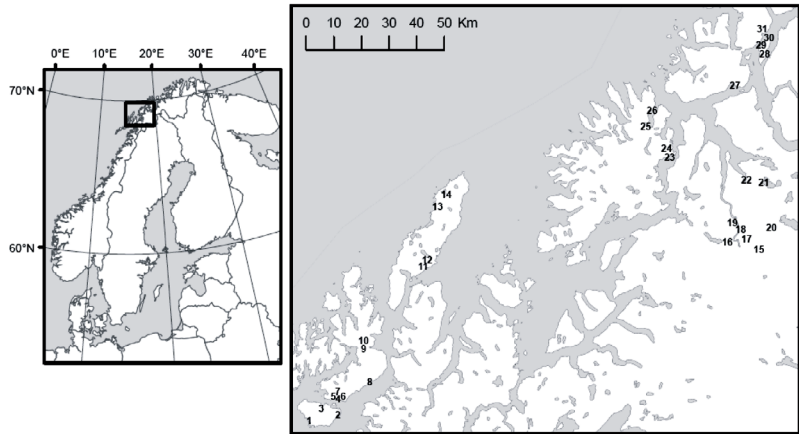


Fig. 1. Map of the study area in North Norway. Field sites are numbered from 1 to 31.

used as an equivalent term to NB, especially by non-Scandinavian researchers, but the definition of sub-arctic is imprecise and highly variable (Hämét-Ahti 1982), and therefore this term is not used here. The division in vegetation zones is based on major shifts in vegetation from south to north as a response to climatic differences, particularly summer temperature (Moen 1999).

Vegetation shifts from coast to inland are divided into vegetation sections. The most important climatic factor for the segregation of vegetation sections is oceanity, which is regulated by air humidity and winter temperature (Moen 1999, Karlsen *et al.* 2006). The study sites are dispersed over three sections; namely the clearly oceanic (O2), the weakly oceanic (O1) and the transition (OC) sections. Vegetation-geographical regions are defined as the combination of vegetation zone and section (Moen 1999), and are here termed by the combination of zonal and sectorial units. Ten sites are situated in MB-O1, eight in MB-O2, four in

NB-O1, four in the transition between MB-O2 and NB-O2, three in MB-OC and two in NB-O2. Typical climatic parameters of these vegetation-geographical regions were discussed by Moen (1999) and are summarized here (Table 1).

Study design

Study sites are clustered within three geographical provinces. These are Vesterålen (sites 1–14 in Fig. 1), central Troms (sites 15–22) and coastal Troms (sites 23–31). These three provinces differ in climatic conditions (both temperature and precipitation rates), which is why they belong to different vegetation-geographical regions. Twenty-five sites were in Norway spruce plantations, and six in Sitka spruce plantations. Within the study area, Sitka spruce plantations are much less common than Norway spruce plantations, and we were therefore not able to increase the number of Sitka spruce sites. However, we con-

Table 1. Typical climatic parameters of the vegetation-geographical regions. Ranges are based on normal values from meteorological stations. Temperature sum is the sum of all monthly averages with values above 5 °C. Frost sum is the sum of all monthly averages with values below 0 °C. Frost sum values are given as approximate averages from at least 10 sites within each region. All data extracted from Moen (1999).

Vegetation-geographical region	July temperature (°C)	Temperature sum (°C)	Frost sum (°C)	Yearly precipitation (mm)
MB-O2	11–13	20–33	10	1000–2500
MB-O1	11–13	20–33	20	800–1500
MB-OC	11–13	20–33	30	700–1200
NB-O2	10–12	12–25	15	1000–2500
NB-O1	10–12	12–25	25	800–1500

sidered six sites as sufficient for undertaking solid statistical calculations. At site 13, the plantation consisted of a mixture of both Norway spruce and Sitka spruce, with Norway spruce as the dominant one. This site is therefore coded as a Norway spruce site. Three quadrates of 10 m × 10 m were established within each site. One quadrate was placed in the central part of the spruce plantation, and at the same altitudinal level as the centre quadrate, a second was placed at the edge of the plantation, thus consisting of half plantation and half native birch-dominated forest. The third quadrate was established at the same altitudinal level as the two other quadrates in native birch forest ca. 100 m from the edge of the plantation, but with certain criteria for being accepted (*see below*). At two of the sites, edge quadrates were not established, primarily because it proved difficult to find a suitable edge area with both birch and spruce trees. Overall, we have five different types of quadrates. They are here abbreviated as follows: BP (birch quadrates), PA (Norway spruce quadrates), PS (Sitka spruce quadrates), EA (edge quadrate with Norway spruce) and ES (edge quadrate with Sitka spruce).

The aim of the study was to evaluate similarities and differences in the structure of epiphytic macrolichen communities in birch forests and spruce plantations. Therefore, forest quadrates were selected such that birch was by far the most dominant tree species, and epiphytic vegetation on other tree species than birch or spruce was not checked. However, all tree species within the quadrates were recorded and counted, and these data were used as environmental variables in the statistical analyses. Abundance of epiphytic lichens was recorded on all birch and spruce trees within the quadrates. At these latitudes, the upper half of the trees generally have rather low species richness and abundance (own observations). Because of this, and the challenges of reaching the upper half of the trees, only the lowermost 4 m were studied in detail (i.e. surveying of all sides of the trunk and every single branch). In addition, binoculars were used to briefly check for dominant epiphytic species higher up in the trees. Our impression is that the upper part of the trees host a minor selection of the species detected in the lower part. Thus,

the lower 4 m of a tree are considered to be an appropriate representation of the entire tree. To avoid the potential influence of ground-dwelling species, the lower 20 cm of the trunks, as well as dead and lying trees, were neglected. Branches that were stretching into the quadrates from trees rooted on the outside were included, but not parts of branches that stretched out of the quadrates.

Species abundance in each quadrate was estimated using a 5-level scale, based on the frequency of each species; 1 = rare (less than five observed thalli); 2 = scattered (6–20 thalli); 3 = frequent (21–80 thalli); 4 = subdominant (81–200 thalli); and 5 = dominant (201 or more thalli). The level selections are based on experiences from previous abundance studies within squares of variable sizes (e.g. Brosø and Elvebakk 2000, Karlsen and Elvebakk 2003). Since many microlichens are difficult to identify in the field, we focused on macrolichens. Nomenclature follows Lid and Lid (2005) for vascular plants and Santesson *et al.* (2004) for lichens, except for *Melanelia s.l.* which follows Blanco *et al.* (2004). Moreover, we did not distinguish between subspecies of *Betula pubescens*, which is in accordance with Jonsell (2000). Some field identifications of macrolichens were controlled in the laboratory, including the use of thin-layer chromatography (Culberson 1972, Orange *et al.* 2001).

Environmental variables

Data on several types of environmental variables were collected (Table 2). Some are site-specific (e.g. remote sensing-derived variables); whereas others are specific to larger areas comprising several sites (e.g. precipitation and temperature values). Most variables were measured at the quadrate level. Tree density includes count data of all individuals taller than 3 m. Mean height and circumference of the two largest trees of birch and spruce in each quadrate (hence in total four trees in the edge quadrates), as evaluated by visual inspection, were measured by means of clinometers and tape measures. Slope angle and aspect of the ground were measured in the quadrates by means of clinometers and compass.

An index of sun light favourability was given as a deviation of aspect, scaled from 0 to 180 degrees. The most favourable aspect in the northern hemisphere is 202.5°, corresponding to SSW, whereas 22.5°, corresponding to NNE, is the most unfavourable (Geiger 1966). Insolation values, which are quite close to the index of favourability, are coded on an ordinal scale ranging from 1 to 16, where SW is 1 and NE is 16. Flat quadrates were given the value 8, which lies between the two extremes.

Monthly values of precipitation (mm) and temperature (°C) (reference period 1961–1990) were provided by the Norwegian Meteorologi-

cal Institute. For each site, data from the nearest meteorological station were used. Data on onset and end of growing season (spring and autumn), as well as the length of the growing season, were extracted from phenological maps, generated in a recent remote sensing study of the phenology of birch in Fennoscandia (Beck *et al.* 2007). These maps have a resolution of 1 km². Thus, the three quadrates at each site were given the same values, as they always were placed in the same kilometre grid square.

Bark pH was determined using the method described in Kermit and Gauslaa (2001). Six-cm-long parts of twigs were cut from random

Table 2. Measured environmental variables.

Environmental variable	Short name used in biplots ¹	Unit	Information on data collection or source
Abiotic variables			
Altitude	Alt	m	ArcGIS
Average annual precipitation		mm	Meteorological data, see text
Average annual temperature	Temperature	°C	Meteorological data, see text
Bark pH	Bark pH	pH	See text
Distance from agricultural area	Agriculture	m	ArcGIS
Distance from large river or lake		m	ArcGIS
Distance from mire		m	ArcGIS
Distance from sea		m	ArcGIS
Distance from settlement		m	ArcGIS
Distance from small stream/brook	Brook	m	ArcGIS
Distance from tree line	Tree line	m	ArcGIS
End of growing season		days	Beck <i>et al.</i> (2007)
Favourability		°	Compass measurements
Insolation		1–16	Ordinal scale; see text
Length of growing season	Season	days	Beck <i>et al.</i> (2007)
Onset of spring		days	Beck <i>et al.</i> (2007)
Slope angle		°	Clinometer measurements
Tree circumference	Circumference	cm	Mean circumference of the two largest trees
Tree height		m	Mean height of the two tallest trees
Biotic variable groups²			
Abundance of tree species		ind.	Abundance of each tree species
Number of epiphytic species and species groups	# Epiphytic species	ind.	See text
Quadrat type	Birch ¹	0/1	Dominant tree species
Shrub density	<i>Sorbus</i> -b ¹	ind. m ⁻²	Shrubs per species (0–3 m)
Total tree density		ind. m ⁻²	Total density of trees
Tree density	<i>Betula</i> -a ¹	ind. m ⁻²	Trees per species taller than 3 m
Tree species	# Tree species	No.	Total number of tree species
Vegetation type	A2 ^{1,3}	0/1	After Fremstad (1997)
Vegetation-geographical region	MB-O2, NB-O2, MB-OC ¹	0/1	After Moen (1999)

¹ Short names only for variables included in the final CCA biplots.

² Each group comprising of one to several variables.

³ Only one vegetation type passed the elimination process. The name of vegetation type A2 is Cowberry-bilberry woodland (*Vaccinium* woodland) (Fremstad 1997).

trees. Twigs with crustose lichens were rejected. The twig cuttings were put in polyethylene bags, and kept cold during transportation. In the laboratory, the vegetation on the twig samples was removed without scratching the cortex. The open twig ends were concealed with wax, such that the resulting pH would reflect the pure bark. The samples were then soaked in a solution of 6 ml 25 mM KCl in a sealed vial for 60 min at 21 °C, and shaken every 10 min. The twigs were removed from the tube, and the pH of the solution was measured. Two samples per quadrat were measured.

Variation in forest floor vegetation was surveyed. This gives an indication of the sites' lushness (fertility level), e.g. with regard to water availability, light and microclimate (Fremstad 1997). Demanding, less common forest floor vegetation types are often accompanied by less common epiphytic communities, and therefore, forest floor vegetation was considered to be of ecological relevance. Dominant species and species composition, as well as photographs from the sites, were used to classify their respective vegetation types according to Fremstad (1997). Plantations were treated as a separate vegetation type by Fremstad (1997), but this type was not used in the current study. Instead, the original vegetation type, regardless of dominant canopy species, was classified according to characteristic forest floor species in the same manner as in birch quadrates. "No vegetation" was used as a separate vegetation type when forest floor was barren.

Data treatment

The 10 m × 10 m quadrates were considered the statistical unit. All statistical analyses were based on the data for epiphytic macrolichen species and environmental parameters. All species data is based on the 5-level abundance scale, and therefore the results depend upon the lowest number of thalli per abundance level recorded (i.e. 1, 6, 21, 81 and 201, see above). The community structure was investigated by means of ordination analyses using Canoco for Windows 4.5 (Microcomputer Power, Ithaca, New York, U.S.A.), according to ter Braak and Šmilauer (2002). Species and continuous environmental

data were log-transformed prior to the analysis, using the formula $\log(1 + x)$. Rare species were downweighted. In order to find the environmental variables that best explain the dispersion of samples and species, a Canonical Correspondence Analysis (CCA) was performed using a Monte Carlo permutation approach. CCA is a direct method of ordination in that it incorporates both the floristic and the environmental dataset within the analysis.

Differences in macrolichen species number, species diversity and sample evenness between the five quadrat types were tested. Species diversity and evenness were calculated using the Shannon diversity index (H') and the equitability index (J) (Magurran 1988). Data sets were checked for homogeneity using Levene's test of equality of error variances and for normality. The H' and J data sets were far from normally distributed, and transformation did not improve normality. All data sets, including the species number data set, were therefore analyzed by the nonparametric Kruskal-Wallis one-way analysis of variance. Pairwise comparisons were undertaken using the Mann-Whitney U -test. A PS quadrat lacking macrolichens (and otherwise only containing minute fragments of a sorediate microlichen) was excluded from the analyses of J , as estimation of J requires two or more species per quadrat. Differences were considered significant at $p < 0.05$. All significance tests were carried out using SPSS 15.0 for Windows (SPSS Inc., Chicago, Illinois, U.S.A.).

Results

At the 31 sites (91 quadrates), there were 770 trunks of Norway spruce, 157 of Sitka spruce and 675 of downy birch. A total of 46 epiphytic macrolichen species were recorded (see Appendix for details). Thirty-nine of these were recorded in BP, 37 in edge quadrates (EA + ES), and 29 in the spruce plantation quadrates (PA + PS). The overall most common species were *Parmelia sulcata* and *Hypogymnia physodes*. In quadrates with birch (BP, EA and ES) *Melanohalea olivacea* was omnipresent, whereas in PA and PS, pendant species of *Bryoria* were most common, although showing some bioclimatic

variation (*see* below). Some primarily terricolous lichens were occasionally recorded as epiphytes (e.g. *Alectoria nigricans*, *Cladonia rangiferina* and *Parmelia omphalodes*). The mean density of trees above 3 m was 1500 individuals per ha in BP, and 2100 per ha in PA and PS.

Species composition

The Monte Carlo permutation test selected 17 environmental variables that are of importance for explaining the variation in species distribution patterns. In this process, several variables were removed due to high inter-correlation, i.e. high inflation rates. The highest variety in species distribution is orientated along the first CCA axis, which has an eigenvalue of 0.146. In total, the first four axes explain 34.9% of the variation in species data (Table 3). The first axis is best correlated with the length of the growing season ($r = 0.679$) and mean annual temperature ($r = 0.649$),

and the second axis is best correlated with the density of birch trees ($r = 0.681$, *see* Table 3).

Two biplots are presented. In the first, species and quadrates are plotted together along the two first axes (Fig. 2). In the second, a polygon has been made for each quadrate category by drawing lines between the outermost dots, representing the outer limit of the quadrates. The polygons are plotted against the vectors of the 17 environmental variables (Fig. 3). Species can be related to environmental variables by comparing Figs. 2 and 3.

The species and quadrates show a wide dispersion along the two first axes (Fig. 2). Hence, there was a considerable variation of macrolichen composition in the study area. BP quadrates and species mostly growing on birch are clustered in the upper half of the biplot. Species associated with birch are, e.g., various species of *Cladonia*, *Nephroma bellum* and *Cetraria sepino-cola*. There is no overlap between BP and PS polygons (Fig. 3), clearly suggesting that mature

Table 3. CCA summary table and CCA correlation matrix of the statistically significant environmental variables. Differences were considered significant at $p < 0.05$. The environmental variables most strongly correlated with axes 1 and 2 are given in boldface.

Axes	1	2	3	4	Total inertia	Sum
Eigenvalues	0.146	0.137	0.069	0.044	1.137	
Species-environment correlations	0.886	0.871	0.834	0.748		
Cumulative percentage variance						
a: of species data	12.9	24.9	31.0	34.9		
b: of species-environment relation	27.3	52.9	65.8	74.1		
Sum of all canonical eigenvalues						0.536
Correlation values of environmental variables						
A2	-0.054	-0.153				
Agriculture	0.260	-0.020				
Alt	0.063	-0.082				
Bark pH	0.235	0.026				
<i>Betula</i> -a	0.132	0.389				
Birch	0.344	0.681				
Brook	0.002	0.034				
Circumference	0.040	-0.232				
# Epiphytic species	0.486	0.014				
MB-O2	0.457	0.209				
MB-OC	-0.434	-0.070				
NB-O2	0.525	-0.151				
Season	0.679	-0.246				
<i>Sorbus</i> -b	0.007	0.067				
Temperature	0.649	-0.204				
Tree line	-0.527	0.022				
# Tree species	-0.089	0.314				

plantations differ considerably from the native forests in which they are planted, both in relation to environmental conditions and species composition. BP is, not surprisingly, correlated with environmental variables related to the number and the size of birch trees. These birch variables are also related to the number of recorded tree species. BP generally had a higher number of tree species, especially of other deciduous trees. On average, each BP quadrat hosted 1.23 trunks taller than 3 m of other deciduous trees [grey alder (*Alnus incana*), willows (*Salix caprea* and *S. myrsinifolia*) and rowan (*Sorbus aucuparia*)]. The values for the other quadrat types are 0.83 (EA), 0.67 (EL), 0.13 (PA) and 0.00 (PL).

PS and PA quadrates, and species more strongly associated with these quadrat types than with BP, are clustered in the lower half of the biplot. This includes species like *Bryoria capillaris*, *B. subcana*, *Hypogymnia tubulosa*, *Platismatia glauca* and *Usnea subfloridana*. The trunk circumference variable is an indicator of tall spruce plantations, as spruce trunks in general had a higher circumference than even the thickest birch trunks. PS quadrates are clustered quite closely together and are surrounded by PA quadrates in the lower right quarter of the biplot. The trunk circumference arrow points towards the PS cluster, which is reasonable, given that PS had higher mean circumference than PA. No species showed any particular affinities to PS.

Species showing continental affinities, e.g. *Bryoria capillaris*, *B. implexa* and *Usnea hirta*, are clustered in the lower left quarter of the biplot, whereas more oceanic species, e.g. *Physcia tenella* var. *tenella*, *Platismatia norvegica* and *Pseudevernia furfuracea*, are clustered in the lower right quarter (Fig. 2). Thus, an oceanicity-continental gradient runs almost parallel to the first axis. This gradient is also correlated with temperature, the length of the growing season and partly also the number of epiphytic species and bark pH (Fig. 3), inferring that oceanic sites generally had higher species number and higher bark pH than the more continental sites.

Close to origo, ubiquitous species such as *Parmelia sulcata*, *Hypogymnia physodes* and *Parmeliopsis ambigua* are clustered. These species did not show any preference for particular environmental conditions within the study area.

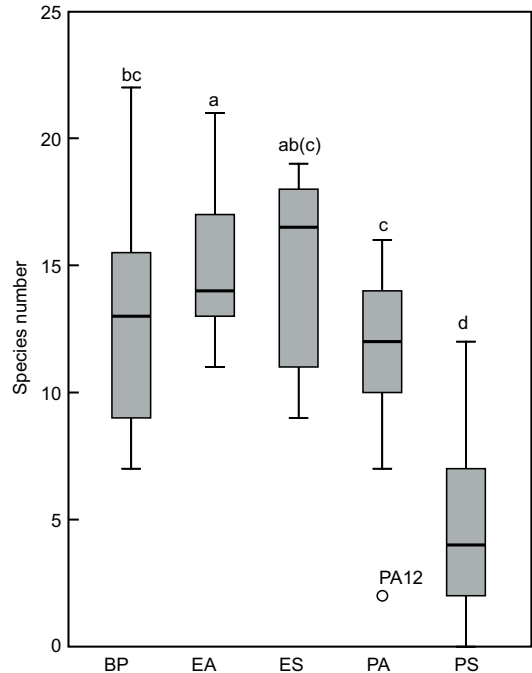


Fig. 4. Number of epiphytic macrolichen species in the five quadrat types. Types as in Fig. 2. The box-plots show the median (horizontal line within box), the inter-quartile range (box), Tukey's hinges (whiskers) and outliers (circles). Quadrat types with different letters are significantly different from each other according to the Mann-Whitney *U*-test. Letter in parentheses denotes a near-significant difference (see text).

EA quadrates are clustered close to origo, but with some outliers in left half of the biplot. The EA polygon coincides noticeably with the PA polygon, but only marginally with the BP polygon, suggesting that the EA quadrates were more strongly influenced by the presence of spruce than by the presence of birch. ES quadrates are slightly different from PS quadrates, as shown by their respective polygons. The species composition in ES was more similar to that of BP and EA than to that of PS.

Species diversity

EA hosted a significantly higher number of species than BP, PA and PS (Fig. 4). Species numbers in ES were very variable and were only significantly different from PS, and near-significantly different from PA ($p = 0.066$). PS had a

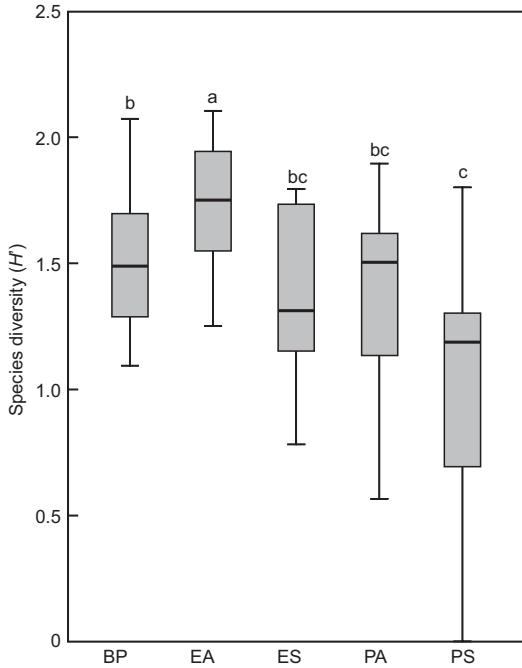


Fig. 5. Species diversity as measured by the Shannon diversity index (H') in the five quadrates types. Types as in Fig. 2. Box-plots as in Fig. 4. Quadrat types with different letters are significantly different from each other according to the Mann-Whitney U -test.

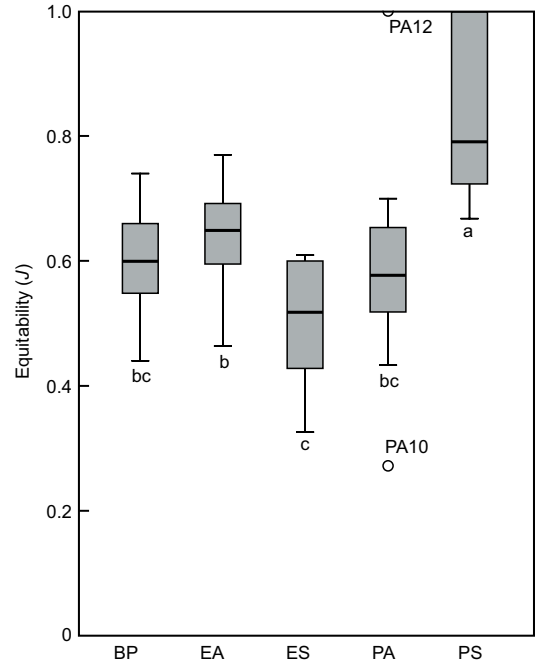


Fig. 6. Evenness as measured by the equitability index (J) in the five quadrates types. Types as in Fig. 2. Box-plots as in Fig. 4. Quadrat types with different letters are significantly different from each other according to the Mann-Whitney U -test.

significantly lower species number than all other categories. Species numbers in BP and PA did not differ from each other.

Species diversity (H') also showed significant differences between some categories (Fig. 5). Diversity in EA was significantly higher than in all other categories, whereas diversity in BP was significantly higher than in PS, but otherwise there were no significant differences.

The equitability index J indicates that evenness was highest in PS (Fig. 6). This was without the quadrates having no recorded species. EA had a significantly even distribution of species than ES, whereas BP, PA and ES did not differ from each other.

Discussion

This study is the first quantitative comparison of the epiphytic macrolichen communities in spruce plantations and natural birch forests in

North Norway. Hence, it is also the first study from this area which shows that species composition differs considerably between birch forests and spruce plantations.

Environmental variation and species composition

The length of the growing season is the variable most strongly correlated with the major variation in the species composition, suggesting that there is a strong climate-induced variation in the epiphytic species composition in these birch forests and spruce plantations. Variables such as the mean annual temperature, NB-O2 and MB-O2, which all are temperature-related, show a similar but slightly weaker correlation.

The changes in species composition are further explained by a selection of local environmental variables. The occurrence and the number of birch trees above 3 m is one of the most

important variables for explaining the variation along the second axis. The variable *Betula*-a indicates that tall, which to a large extent also means old, trees are important for maintaining a high epiphytic diversity in this area. This result is expected considering the results from studies in other areas and forest types (e.g. Esseen *et al.* 1997, Kuusinen and Siitonen 1998, Uliczka and Angelstam 1999, Hilmo *et al.* 2009).

Other deciduous tree species, e.g. rowan, willows and grey alder, recorded in BP generally have a higher bark pH and nutrient level than birch (Werth *et al.* 2005), which facilitates the establishment of more nutrient-demanding species than those that generally occur in pure birch stands (Kuusinen and Siitonen 1998, Werth *et al.* 2005). Thus, occurrences of other tree species within the quadrates may affect the species composition on the birch trees in the quadrates through short-distance dispersal.

Ubiquitous species like *Melanohalea olivacea* and *Hypogymnia physodes* are common both inland and at the coast. Otherwise, species composition within PA, EA and BP differ considerably along the bioclimatic gradient. While oceanic sites host a high proportion of foliose species and shrubby species with band-like lobes (e.g. *Platismatia norvegica*, *P. glauca*, *Melanelixia fuliginosa*, *Evernia prunastri* and *Parmelia omphalodes*), the more continental quadrates are characterized by a higher proportion of pendant species and shrubby species with terete lobes (e.g. *Usnea hirta*, *Bryoria capillaris*, *B. fuscescens*, *B. implexa* and *B. simplicior*). This variation in dominating thallus form is evident in both BP and PA, although with a slightly diverging suite of species. In a gradient study in Scotland, Ellis and Coppins (2006) elucidated that foliose lichens are more abundant at more oceanic sites than at continental sites nearby. This change in growth forms along the bioclimatic gradient might be related to increased drought and frost tolerance (Peterson and McCune 2001, Werth *et al.* 2005). Furthermore, the high abundance of *Bryoria* species in the more continental PA quadrates probably is a result of these lichens' preferences for conifers (Brodo and Hawksworth 1977, Krog *et al.* 1994). Native conifer forests, in this area consisting of Scots pine (*Pinus sylvestris*), are much more common inland, there-

fore facilitating local migration of lichens from pine to inland spruce plantations.

Increased pH at the more oceanic sites might have facilitated, in combination with increased humidity and mean annual temperature, the establishment of the regionally rare species *Evernia prunastri*, *Platismatia norvegica*, *Pseudevernia furfuracea* and *Ramalina farinacea*. Higher bark pH at the oceanic sites is probably due to increased sea salt spray influence.

Species number and diversity

Mixed spruce-birch stands, here represented by the edge quadrates, host epiphytic macrolichens with preferences for both birch and spruce, and this is the likely reason why EA had higher species number and species diversity than pure birch and spruce stands. Planting of spruce in birch forests may therefore lead to an overall increase in the species number and diversity of epiphytic species by introducing a substrate type that does not occur naturally in the area (Humphrey *et al.* 2004). This positive effect of spruce planting on species number is probably often nullified and even inversed when extensive replacements of native forest cause local loss of native forest species.

Tree circumference was inversely related to the number of tree species, which suggests that native trees that were not cut during planting become out-competed by the faster-growing spruce (Framstad and Hofstad 1996, Stabbetorp and Nygaard 2005, Yoccoz *et al.* 2005, Øyen and Nygaard 2007), and that establishment of new native trees within the plantations is a rare or non-existing event. In natural Norway spruce stands, branch length is positively correlated with species number (Holien 1997). However, plantations differ from natural stands by having less space between individual trees and by trees being even-aged (Gauslaa *et al.* 2007, Hilmo *et al.* 2009). Therefore, long branches from one tree reach the branches of adjacent trees, effectively reducing the light penetration and air mass flux through the canopy. This was especially evident in several PS quadrates, as Sitka spruce generally produces much longer branches than Norway spruce (Farjon 1990). The dense, light-

and air-blocking canopy is probably the major reason why PS had a significantly lower species number than the other quadrat types. The PS quadrat that was totally lacking macrolichens was the densest of the studied quadrates. Entering this and similar quadrates was only possible by creeping under the lowermost branches, and photographing inside the plantation was only possible using a flash, even at sunny days around noon. Naturally, the low light levels did not permit any growth of forest floor vegetation.

Concluding remarks

Sitka spruce plantations are identified here as a major threat to lichen species diversity, as the introduced epiphytic substrate is not very suitable for lichens. Norway spruce plantations, however, have a similar number of epiphytic macrolichen species and similar species diversity as adjacent birch forests, and Norway spruce also appears to be a more suitable substrate than birch for some regionally rare, thermophilous species (Holien 1991, Bjerke *et al.* 2006a, 2006b). Therefore, although our results indicate that planting of spruce drastically changes the species composition at the affected sites, the macrolichen species number and diversity are not affected.

We have here compared the macrolichen species composition and diversity in plantations with that of adjacent birch stands. It is known that, in North Norway, single trees or stands of other deciduous trees within the birch forest can host a quite different composition of species than birch (e.g. Gjerde *et al.* 2002, Werth *et al.* 2005, Bjerke *et al.* 2006b). Most of the studied birch forests used in this study are situated close to human settlements and are influenced by a long history of logging and other human activities. None of the sites can be regarded as old-growth forest, although single trees might be quite old. True old-growth birch forests, which are becoming rare in North Norway, probably host a quite higher number of macrolichen species than the thinned birch forests that we have studied. To be able to evaluate in more detail the effects of spruce planting on lichen diversity, plantations should be compared with other native forest trees

and types, and including other groups of species (e.g. epiphytic bryophytes and microlichens).

Indeed, we have shown here that especially one type of plantations, the Sitka spruce, causes declines in species number and diversity. Other studies have shown similar effects of Norway spruce on other organism groups (*see* Introduction). Until more data is available, and given the fact that plantations do have a major impact on the landscape structure (Yoccoz *et al.* 2005), we recommend Norwegian authorities implement field assessment surveys prior to granting of subsidies and planting permissions. When assessments detect native forest patches with high species diversity, especially of red-listed and/or regionally rare species, these should be spared. Moreover, the field assessments may direct the planting activity to areas that from a conservation point of view are less valuable. This recommendation is particularly essential for forest conservation in Norway north of the Arctic Circle where spruce does not occur naturally, except for sporadic stands or individual trees of *Picea abies* ssp. *obovata* in the north-eastern part of the region (Lid and Lid 2005), and where human activity already has caused an extensive reduction of old-growth, deciduous forests (Hausner 2001, Stabbetorp and Nygaard 2005, Vennesland *et al.* 2006).

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Appendix. Recorded epiphytic macrolichen species and their respective number of occurrences in each quadrat type. Types as in Fig. 2.

Scientific name	Short name	BP	EA	ES	PA	PS
<i>Alectoria nigricans</i>	<i>Ale nig</i>	0	0	0	1	0
<i>Bryoria capillaris</i>	<i>Bry cap</i>	0	12	0	12	0
<i>Bryoria fuscescens</i>	<i>Bry fus</i>	19	14	3	7	0
<i>Bryoria implexa</i>	<i>Bry imp</i>	2	17	2	12	0
<i>Bryoria simplicior</i>	<i>Bry sim</i>	13	6	0	7	0
<i>Bryoria subcana</i>	<i>Bry sub</i>	2	6	2	10	1
<i>Cetraria sepincola</i>	<i>Cet sep</i>	8	3	0	2	0
<i>Cladonia bellidiflora</i>	<i>Clu bel</i>	2	0	0	0	0
<i>Cladonia cenotea</i>	<i>Clu cen</i>	1	0	0	0	0
<i>Cladonia chlorophaea</i>	<i>Clu chl</i>	2	1	0	0	0
<i>Cladonia coccifera</i>	<i>Clu coc</i>	2	2	0	0	0
<i>Cladonia coniocraea</i>	<i>Clu con</i>	17	7	3	2	1
<i>Cladonia cornuta</i>	<i>Clu cor</i>	1	1	0	0	0
<i>Cladonia metacorallifera</i>	<i>Clu met</i>	1	0	0	0	0
<i>Cladonia pleurota</i>	<i>Clu ple</i>	1	2	0	0	0
<i>Cladonia pyxidata</i>	<i>Clu pyx</i>	12	5	3	1	0
<i>Cladonia rangiferina</i>	<i>Clu ran</i>	1	1	0	0	0
<i>Cladonia squamosa</i>	<i>Clu squ</i>	1	0	0	0	0
<i>Evernia prunastri</i>	<i>Eve pru</i>	1	2	0	0	0
<i>Hypogymnia physodes</i>	<i>Hyp phy</i>	29	23	6	23	3
<i>Hypogymnia tubulosa</i>	<i>Hyp tub</i>	13	17	6	18	4
<i>Melanelixia fuliginosa</i>	<i>Mel ful</i>	3	4	3	2	0
<i>Melanohalea exasperata</i>	<i>Mel exa</i>	1	1	1	1	1
<i>Melanohalea olivacea</i>	<i>Mel oli</i>	31	23	5	18	3
<i>Nephroma bellum</i>	<i>Nep bel</i>	2	1	0	0	0
<i>Nephroma parile</i>	<i>Nep par</i>	1	1	0	0	0
<i>Parmelia omphalodes</i>	<i>Par omp</i>	5	1	1	0	0
<i>Parmelia saxatilis</i>	<i>Par sax</i>	18	4	3	6	2
<i>Parmelia sulcata</i>	<i>Par sul</i>	31	23	6	22	5
<i>Parmeliopsis ambigua</i>	<i>Par amb</i>	29	23	4	18	0
<i>Parmeliopsis hyperopta</i>	<i>Par hyp</i>	27	16	4	9	1
<i>Physcia tenella</i> var. <i>tenella</i>	<i>Phy ten</i>	0	0	0	1	0
<i>Platismatia glauca</i>	<i>Pla gla</i>	11	16	6	15	1
<i>Platismatia norvegica</i>	<i>Pla nor</i>	1	0	0	1	0
<i>Pseudevernia furfuracea</i>	<i>Pse fur</i>	0	1	0	0	0
<i>Ramalina farinacea</i>	<i>Ram far</i>	2	3	2	3	1
<i>Sphaerophorus globosus</i>	<i>Sph glo</i>	3	0	0	0	0
<i>Tuckermanopsis chlorophylla</i>	<i>Tuc chl</i>	9	21	5	24	3
<i>Usnea filipendula</i>	<i>Usn fil</i>	3	3	1	3	1
<i>Usnea hirta</i>	<i>Usn hir</i>	0	1	0	2	0
<i>Usnea lapponica</i>	<i>Usn lap</i>	1	2	1	1	0
<i>Usnea subfloridana</i>	<i>Usn sub</i>	7	12	4	15	0
<i>Vulpicida pinastri</i>	<i>Vul pin</i>	18	18	5	18	1
<i>Xanthoria candelaria</i>	<i>Xan can</i>	2	3	1	3	0