# Variation in epiphytic vegetation in spruce plantations and adjacent native birch forests in North Norway

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# Master's Thesis in biology (Botanical biodiversity)

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#### **Forord**

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#### **Abstract**

Epiphytic vegetation can contribute to increased knowledge on how planting of spruce in areas where spruce does not occur naturally in the landscape can affect the environment. In the current study, 31 spruce plantations in Troms and Vesterålen in North Norway were investigated, with emphasis on species abundance of macrolichens on tree trunks and branches. The main assumption was that planting of spruce affects the communities of epiphytic vegetation. Sixty-two species/groups of epiphytic vegetation were recorded. Detrended Correspondance Analysis (DCA) and Canonical Correspondence Analysis (CCA) ordination methods displayed prominent differences in species composition between spruce, birch and transition quadrates. Species diversity, species numbers and variance were significantly lower in spruce plantations than in native birch forest. Seventeen major environmental variables were significantly related to the community differences. The variation from coast to inland, differences in temperature and altitude, as well as distance to humid sources is the main regional factors that best explain the variation incommunity structures. In addition, local differences such as various tree characteristics, presence of other tree species, and bark pH also contribute to explaining variation within and between spruce and birch quadrates. As spruce plantations in North Norway mature, these can provide habitats for more rare, shade-tolerant and/ or thermophilous species, as observed in this study. However, plantations do not have a positive effect on the epiphytic biodiversity locally, which in terms may affect other levels of the ecosystem. Investigations on the consequences of spruce planting on the biodiversity in northern birch forests are important to the future planning of new plantations. Habitat-rich areas should not be used for plantations. Moreover, management of plantations, such as selective cutting and thinning, should be attempted in order to enhance species richness and biodiversity within plantations.

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#### Introduction

#### *Spruce plantations and biodiversity*

In North Norway, coastal native birch (*Betula pubescens*) forests have been replaced to a large extent by non-native plantations, primarily of Norway Spruce (*Picea abies*). Spruce planting was initiated in the beginning of the last century, and by today 10 % of the natural birch forest in coastal areas has been converted (Hausner 2001). Knowledge so far indicates that plantations lead to increased acidification of the ground and changes in habitat conditions leading to a shift in species composition and a reduction in biodiversity (Fremstad 1997). The research on the impact of plantations of spruce on the biodiversity in North Norway is scarce. However, an investigation of bird assemblages (Hausner 2001) revealed that mature spruce plantations in North Norway preserve different bird assemblages, as well as a significant lower number of birds, than the surrounding birch forests. An older study from northern Troms County indicates that spruce planting has a severe and destructive effect on the grass and herb vegetation on the forest floor (Sætra 1971).

European forests have been exposed to planting of monocultures of coniferous trees for centuries. This, combined with massive atmospheric deposition of industrial pollutants, has led to serious ecosystem degradation and loss of biodiversity (Emmer et al. 1998). Ewald (2000) claims that the planting of spruce increases the occurrence of coniferous species and acid indicator species on the ground. According to Spiecker (2003), the change in vegetation cover due to spruce planting is accompanied by loss of biodiversity and lower resistance to storm, snow, ice, draught and insect damage.

Forest management has for a long time focused on the production of wood and not taken into consideration the ecological consequences on the forest ecosystems. It has been shown that clear-cutting of forests to give room for plantations has severe outcomes for the epiphytic vegetation related to habitat elimination and edge effects (Kivistö & Kuusinen 2000; Essen & Renhorn 1998; Essen 2006).

#### *Epiphytic lichens and the environment*

Lichens are sensitive to their physical and chemical environment as they are poikilohydric organisms. Wide-ranging macroclimatic factors such as distance from the sea (Werth et al. 2005), altitude (Holien 1997), and mean annual precipitation (Giordani 2006) can have an

impact on where lichens will grow and develop. Also other environmental factors such as light, humidity and temperature determine their distribution (Krog et al. 1994). Characteristic lichen communities develop according to a variety of factors, including local climatic conditions and substrate (Purvis 2000). For example, crustose lichen communities on old European Aspen (Populus tremula) trees die shortly after clear-felling of adjacent forest, which causes detrimental changes in the surrounding climate (Esseen et al. 1997). Bark pH can also be of importance for epiphytic lichen establishment (Kermit & Gauslaa 2001). Birch generally has a higher bark pH than spruce. Therefore, birch trees are normally inhabited by more lichen species than coniferous trees (Moberg & Holmåsen 2000). Knowing that oldgrowth forests provide a more species-rich epiphytic community than younger forests (Detti & Esseen 1998), the level of management is also vital for lichen establishment. An investigation from Central Norway aiming at revealing patterns of species distribution in a native sub-oceanic spruce forest shows that stand age and vegetation type are some of the main causal factors (Holien 1997). The variety of tree species in an area can also be of importance to enhance and maintain the species richness of lichens (Uliczka & Angelstam 1999), which is in contrast to spruce plantations, which are totally dominated by a single tree species.

#### Epiphytic communities in native and planted spruce stands

In Central and south-eastern Norway, where Norway Spruce grows naturally, the knowledge on environmental conditions and epiphytic biodiversity is comprehensive, and thus, can be of value for studies of Norway Spruce plantations beyond its natural distributional limits. In particular, species composition and conservation issues of so-called "old-growth species" have been well documented (e.g. Holien 1997, 1998; Hilmo & Såstad 2001). In relation to forest management issues, the focus on old-growth lichen species as a tool for mimicking and contributing to information on restoring old-growth conditions, has increased (Rolstad et al. 2001). Research on the epiphytic vegetation in deciduous forests in North Norway is limited, with a few exceptions from Troms County (Werth et al. 2005; Bjerke et al. 2006a; Bjerke et al. 2006b). Even less information is publicly available on epiphytic communities in spruce plantations. Werth et al. (2005) elucidated that the main factors determining epiphytic communities in deciduous forests are macroclimatic, particularly the gradient from the coast to the interior. They also revealed that distance from nearby spruce plantations seemed to have an impact on the species distribution in the plots.

Fragmentation and destruction of natural lush, deciduous forests of North Norway may affect the biodiversity of both flora and fauna. The current investigation is a comparative study of epiphytic lichen communities in native birch forests and adjacent spruce plantations. Plantations of various sizes and geographical locations from the outer fjords and islands to inland areas were investigated. The species abundance was recorded at every site. Environmental site information was also collected in terms of direct measurements in field, and gathering of additional data after the field work. Shannon-Wiener diversity index was calculated to detect any possible differences in the species diversity among the different quadrates. Multivariate analyses were performed on the data sets. Detrended correspondence analysis (DCA) was performed on the vegetation data to locate any potential differences in the species preferences, and to assess possible underlying environmental causes for the distribution. Canonical correspondence analysis (CCA) was utilized to look for important environmental variables that might control the species distribution.

#### The primary objectives of this study were:

- To give the first ever assessment of the structure of epiphytic lichen communities in mature spruce plantations versus neighbouring native birch forests in North Norway;
- Determine what main chemical and physical environmental factors that are closely related to the epiphytic species distribution;
- Locate so-called thermophilous or old-growth species that are more common in southerly areas where spruce grows naturally;
- In light of the results, give recommendations for the management of native forest in relation to spruce plantation planning.

#### Materials and methods

#### Study area

The study area is situated in Nordland and Troms County in North Norway (Fig. 1). According to Moen (1998a), these two counties are divided into the vegetation zones; middle boreal (MB), northern boreal (NB) and alpine zones (A). In addition, Nordland has elements of the southern boreal zone (SB) along the coastline in southern parts of the county. The division of the country in vegetation zones is based on changes in vegetation from south to north as a response to climatic differences, particularly summer temperature. In the middle boreal zone, conifer forests dominate in the more continental east, while birch forests are more abundant along the coast (Moen 1998a). Characteristics of middle boreal vegetation are for example the occurrence of well developed forests of Grey Alder (*Alnus incana*) and Bird Cherry (*Prunus padus*) and low herb conifer forests. The northern boreal zone on the other hand, is dominated by Downy Birch (*Betula pubescens*) and other small tree species such as willows (*Salix* spp), European Aspen (*Populus tremula*), and Rowan (*Sorbus aucuparia*). Alpine herbs are also more frequent in the northern boreal zone, and the decrease in thermophilous species is prominent.

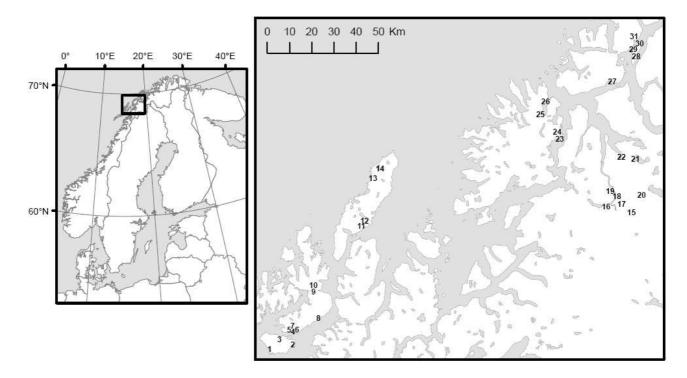


Fig. 1 Map of the study area. The sites are numbered from 1 to 31 according to Table 1, and each site consists primarily of 3 quadrates.

The change in vegetation from coast to inland (west towards east) is divided into sections. The most important climatic factor for the segregation of sections is oceanity; primarily air humidity and winter temperature or frost (Moen 1998a). In the area of investigation is covering three sections; clearly oceanic (02), weakly oceanic (01) and the transition section (OC). Winter temperature, as well as precipitation decreases from 02 to OC. What separates the various sections is the occurrence of certain vegetation types and species that are adapted to these conditions along the oceanity gradient.

By combining the bioclimatic gradients of oceanity (east/west) and summer temperature (south/north) it is possible to deduce bioclimatic regions with characteristic vegetation. These are referred to as vegetation-geographical regions (Moen 1998a), and are areas where both vegetation zones and vegetation sections are combined. In the current study, the vegetation geographical region of each site is taken into consideration in the analysis. At sites where the quadrates are bordering the two bioclimatic regions Nb-02 and Mb-02, these are combined. Table 1 gives an overview of the sites, including Municipality, County and altitudinal range. The quadrates were georeferenced, and transferred into a geographic information system (ArcGIS). The altitude of each quadrate is estimated from the contour lines of the map.

TABLE 1. Overview of the 31 study sites (The vegetation-geographical regions are defined according to Moen (1998b) and Moen at al. (1998)): Mb-01 Middle boreal zone, weakly oceanic section, Mb-02 Middle boreal zone, clearly oceanic section, Nb-02 Northern boreal zone, clearly oceanic section, Nb-01 Northern boreal zone, weakly oceanic section, Mb-OC Middle boreal zone, transition section). \*Two plots only due to lack of time.

	or time.			Vegetation-		
				Altitude geographic N		Number
	Site	Municipality	County	(m a.s.l.)	al region	of plots
1	Melbu	Hadsel	Nordland	Nordland 32-35 Mb-02		3
2	Hadsel Kirke	Hadsel	Nordland	72-79	Mb-02	3
3	Stokmarknes	Hadsel	Nordland	56-62	Nb-02	3
4	Råvoll	Hadsel	Nordland	28-52	Mb-02	3
5	Rå	Hadsel	Nordland	168-170	Nb/Mb-02	3
6	Marka	Hadsel	Nordland	52-74	Mb-02	3
7	Eriklia	Hadsel	Nordland	180-190	Nb-02	3
8	Kleiva	Hadsel	Nordland	64-65	Mb-02	3
9	Vikeidet	Sortland	Nordland	48-52	Mb-02	3
10	Øvre Vikeidet	Sortland	Nordland	148-155	Nb/Mb-02	3
11	Bønna	Andøy	Nordland	66-72	Mb-02	3
12	Lilandskaret	Andøy	Nordland	60-79	Nb/Mb-02	3
13	Stave	Andøy	Nordland	36-38	Mb-02	2*
14	Bleik	Andøy	Nordland	72-88	Nb/Mb-02	3
15	Skoglund	Målselv	Troms	55-80	Mb-OC	3
16	Andselv	Målselv	Troms	106-138	Mb-OC	3
17	Rognmoen	Målselv	Troms	70-77	Mb-OC	3
18	Fredriksberg	Målselv	Troms	20-30	Mb-01	3
19	Fleskmo	Målselv	Troms	36-46	Mb-01	3
20	Litlevoll	Målselv	Troms	168-181	Nb-01	3
21	Vesterli	Balsfjord	Troms	174-178	Nb-01	3
22	Storli	Balsfjord	Troms	74-76	Mb-01	2*
23	Gibostad	Lenvik	Troms	36-82	Mb-01	3
24	Landsøylia	Lenvik	Troms	68-108	Mb-01	3
25	Elverland	Lenvik	Troms	30-60	Nb-01	3
26	Botnhamn	Lenvik	Troms	52-60	Nb-01	3
27	Straumsbukta	Tromsø	Troms	98-123	Mb-01	3
28	Grønnåsen	Tromsø	Troms	120	Mb-01	3
29	Sandnes sør	Tromsø	Troms	26-36	Mb-01	3
30	Sandnes nord	Tromsø	Troms	23-37	Mb-01	3
31	Toften	Tromsø	Troms	57-122	Mb-01	3

#### Study design

#### Sampling of species data

The quadrates of data collection were all associated with spruce plantations of various sizes and ages, whose selection were based on location and access. On each site, three quadrates of  $10 \text{ m} \times 10 \text{ m}$  were established. They were selected by walking a random number of footsteps from the edge of the area of examination (plantation, native forest). One quadrate were placed in the middle of the spruce plantation, another in the transition zone between spruce forest and native vegetation along the edge of the plantation, and finally one quadrate in the natural deciduous, birch-dominated forest at least 100 m from the plantation. The three quadrates from each site are more or less comparable in regard to the surrounding environment, except for the dominant canopy species. At two of the locations (see Table 1), circumstances made it impossible to carry out the data collection in the transition quadrate; hence there are no data from the mixed forest from these sites.

Since the aim of the study is to detect differences in the epiphytic flora between birch and spruce, lichens on other tree species within the plots were neglected. However, all tree species were recorded and counted in each quadrate for use as environmental variables in statistical analyses. Branches of Downy Birch and Norway Spruce, occasionally Sitka spruce (*P. sitchensis*), within each square were first of all investigated for epiphytic vegetation by means of visual inspection. The abundance of epiphytic lichens and bryophytes was recorded on all trees of birch and spruce in the quadrates. Difficult species were collected for later identification in laboratory. 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 inside the plots from trees rooted on the outside were included.

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 studies of lichen abundance, see e.g. Nylund (1997). Since many lichens are difficult to identify in the field, several lichens were pooled in species groups, which may also serve as functional groups. Sorediate crustose lichens (e.g. *Ochrolechia androgyna*, *Japewia subaurifera*, *Biatora vacciniicola*) were joined in one group. Fertile esorediate, lecideoid lichens of the genera *Bacidia*, *Micarea*, *Lecidea* etc. were also joined. Species belonging to

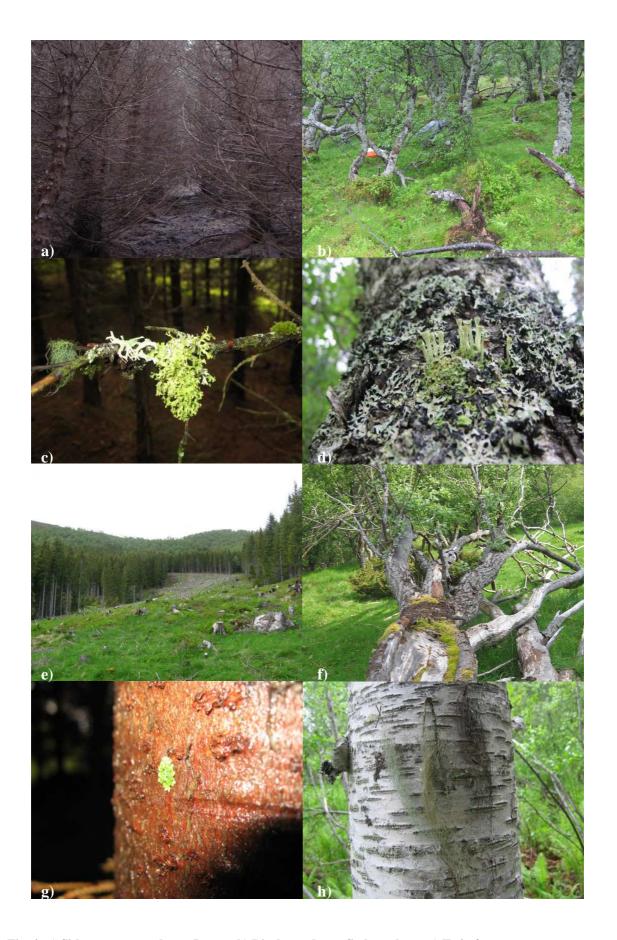


Fig. 2. a) Sitka spruce quadrate, Bønna. b) Birch quadrate, Stokmarknes. c) Twig from a spruce tree at Marka. d) *Cladonia pyxidata* and *Parmelia sulcata* on a birch tree at Fredriksberg. e) Clearcut at Rå. f) Lying willow tree at Bønna. g) A small lichen thallus of *P. sulcata* at Melbu. h) Colour variants of *Bryoria* sp. (from left to right; *B. capillaris*, *B. implexa*, *B. fuscescens*)

the genus *Arthonia* (dot lichens) were joined in the group Arthoniales. Also *Lecanora fuscescens* coll. was considered as one group in the ordination. Another "*Lecanora* cir coll." group was recognized, consisting mainly of *L. circumborealis*, but in several quadrates other *Lecanora* species such as *L. carpinea* and *L. albella* probably made up a considerable part of this group. The bryophytes were divided into the genera *Dicranum* spp., *Orthotrichum* spp. and *Ptilidium* spp. The remaining bryophytes (no liverworts included here) were joined into the group "other mosses". Poorly developed lichen individuals were also identified to genus level only (e.g. *Bryoria* spp., *Caloplaca* spp., and *Cladonia* spp.). Species identifications were mostly done in the field, by means of hand lens and field stereo microscope. The lichen nomenclature in this study follows Santesson et al. (2004). Thin layer chromatographic analyses were carried out using standardized procedures (Culberson 1972, Orange et al. 2001).

#### Potential limitations

To locate all epiphyte species present in an area of  $10 \text{ m} \times 10 \text{ m}$ , every solitary tree had to be investigated. Some species might occasionally have been overlooked, or determined incorrectly. In plantations, the amounts of *Bryoria* species were sometimes large, and might have consisted of several species than those detected. The thallus colour gradient (Fig. 2h) of some *Bryoria* species is very variable, and hard to determine without thin layer chromatography (TLC). In such cases it is not possible to collect all thalli for later analysis, but rather give an estimated abundance to each color variant and later check with identification results in the laboratory. This seemed to work out fine, and the abundance estimates are therefore considered reliable. Concerning the crustose lichens, like *Lecanora*, lecideoids and sorediate lichens, the field identification to species might not have been correct in all situations. This was mostly due to the fact that each plot covered a large area, as well as lack of time or capacity to analyze each crustose thallus.

As for the abundance scaling, the data analyses are based on the lowest number of lichen thalli of each species. This might give a slightly wrong outcome in the diagrams. But this probably affects only the dominant species, which in the analyses are constricted to 201 thalli. The actual number might in many cases have reached far beyond. The other values are reliable since they are less abundant and easier to estimate.

Sampling of environmental data

Several environmental variables were collected for each quadrate (Table 2).

TABLE 2. Division of the environmental variables into abiotic and biotic factors

Environmental variable:	Unit:	Information on data collection:
Liivii Oiliileittai variabie.	Oilit.	information on data confection.
Abiotic factors:		
Average annual precicitation	mm	The Norwegian Meteorological Institute (1961-1990)
Average annual temperature	${\mathfrak C}$	The Norwegian Meteoro logical Institute (1961-1990)
Slope	0	Slope angle of quadrate measured in degree s
Distance from sea	m	Geographical Information System ArcGIS
Distance from small stream	m	Geographical Information System ArcGIS
Distance from large river or lake	m	Geographical Information System ArcGIS
Distance from mire	m	Geographical Information System ArcGIS
Distance from settlement	m	Geographical Information System ArcGIS
Distance from tree limit	m	Geographical Information System ArcGIS
Distance from agriculture area	m	Geographical Information System ArcGIS
Altitude	m	Geographical Information System ArcGIS
Start of spring	days	Beck et al (2006); Beck personal communication)
Start of autumn	days	Beck et al (2006); Beck personal communication)
Season length	days	Beck et al (2006); Beck personal communication)
Unfavorability	1-360°	Compass measurements
Insolation	1-16	Coded on an ordinal scale (Werth et al. 2005)
Tree circumference	cm	Mean circumference of the two largest trees in the quadrate
Tree height	m	Mean height of the two largest trees in the quadrate Measured by the methods described in Kermit and Gauslaa
Bark pH	рН	(2001)
Soil pH	рН	Measured by the methods described in Anonymous (1981)
Biotic factors:		
Abundance of tree species	No	Abundance of each tree species in the quadrates
Tree density-a	No/m <sup>2</sup>	Total density of all tree species above three meters
Tree density-b	No/m <sup>2</sup>	Total density of all tree species below three meters
Total tree density	No/m <sup>2</sup>	Total density of all trees in the quadrate
Tree species	No	Number of all tree species in the quadrate
Vegetation type	-	According to Fremstad (1997)
Vegetation- region	-	According to Moen (1997)
Number of epiphytic species	No	Classified by the 5-level abundance scale

The tree density was determined by counting individuals of all woody species, distinguishing between specimens reaching above or below 3 m. Mean height and circumference of the two largest trees in each quadrate, as evaluated by visual inspection, were measured by means of a clinometer (Suunto PM-5/360 PC) and measuring bands. In the transition quadrates, mean height and circumference was measured on four trees (two largest birch trees and two largest spruce trees). Slope angle and aspect of the ground were measured in the quadrates by means of clinometer and compass, using a 360° scale. An index of unfavourability was given as a

deviation of aspect, scaled from 0 to 180 degrees. The most favourable aspect is 202.5° SSW, while 22.5° NNE is the most unfavourable. The insolation values are coded on an ordinal scale (Werth et al. 2005) ranging from 1 to 16. Plots with no slope were given the value 8, which lies between the two extremes.

In addition to altitude, other distance parameters (see Table 2) were determined by distance measurement operations in the ArcGIS programme. Monthly values of precipitation (mm) and temperature (°C) (reference period 1961-1990) were provided by the Climate Department at the Norwegian Meteorological Institute (DNMI). Data on start and end of growing season (spring and autumn), as well as the length of the season were collected from a recent study of the phenology of birch in Fennoscandia (P. Beck personal communication; Beck et al. 2006). Soil samples were collected in all quadrates, and subsequently used to determine the soil pH. The layer used was mainly the subsoil, due to an irregular and sometimes absent humus layer. The soil was collected using a core sampler, and put in paper bags to dry. The pH of the soil was then determined in the laboratory using standardized methods (Anonymous 1981). One soil sample was collected in each quadrate, except in the transition quadrate where one sample was taken from the spruce section and another from the birch section.

Bark pH was determined using the method described in Kermit and Gauslaa (2001). A 6 cm long part of a twig was cut from a random tree in each quadrate. The twig cuttings were put in polyethylene bags, and kept cold during transportation. In the laboratory, the lichens on the twig samples were removed without scratching the cortex. The open twig ends were concealed with wax, so 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. In the transition plots, the pH values of spruce and birch were combined, giving one value forlater analysis.

Forest floor vegetation was surveyed in the majority of the quadrates (see Appendix B). Dominant species and species composition, as well as photographs from the sites, were used to classify their respective vegetation types according to the treatment of Norwegian vegetation types by Fremstad (1997). The vegetation types of the quadrates within spruce plantations were sparingly developed and strongly modified by the acidic spruce litterfall, and thus hard to identify. Fremstad (1997) treated plantations as a separate vegetation type, but this was not used in the current study. Instead, the original vegetation type, irregardless of dominant canopy species, was classified in the same manner as the other quadrates. In other

cases where the vegetation in the quadrates within the spruce plantations was so scarce that it was impossible to classify, it was given the same type as in the associated quadrate at the edge of the plantation. In other cases where there was no vegetation at all on the forest floor, quadrates were classified as no vegetation (NV).

#### Statistical design and analyses

The  $10 \text{ m} \times 10 \text{ m}$  quadrates were considered as the statistical unit. All statistical analyses were based on the quantitative data for epiphytic vegetation, and the qualitative environmental data. All quantitative species data is based on the 5-level abundance scale, and therefore the results rely upon the lowest number of thalli per abundance level recorded (i.e. 1, 6, 21, 81 and 201 – see chapter 2.2). This is a log-linear scale. The community structure was investigated by means of ordination diagrams made in the software CANOCO 4.5 (ter Braak and Smilauer 2002). Also species diversity, species richness, evenness of samples and variance of samples were calculated to compare properties between the three quadrate categories.

The floristic and the environmental data sets were log-transformed prior to the analysis, using the formula log (1+X). The log-transformation is a procedure for normalizing the variability within the data. Hence, variance is no longer correlated with the mean. Several rare species were only recorded with single thalli in one or a few quadrates. Therefore six species with a total abundance of 1 (1-5 thalli) (*Alectoria nigricans, Cladonia cenotea, Cladonia metacorallifera, Cladonia squamosa, Physcia tenella and Pseudevernia furfuracea*) were made supplementary in the analysis. These species are passive in that they will not influence the axes. They are added in the diagram after the analysis, and can still be judged according to their relation to other species (ter Braak & Smilauer 2002).

Detrended Correspondence Analysis (DCA) was performed on the floristic dataset, examining the similarities and dissimilarities of the vegetation samples. This is an indirect and non-linear method of ordination, and is a useful technique for displaying the internal floristic variation in the dataset, not taking the environmental variables into account (Kent & Coker 1992). In order to find the environmental variables that best explains the floristic variation, a Canonical Correspondence Analysis (CCA) was performed on both data sets. CCA is a direct method of ordination in that it incorporates both the floristic and the environmental dataset within the analysis. The aim of this technique is to reveal the relationships between the species and each of the environmental variables (Kent & Coker 1992). A CCA combined with

Monte Carlo permutation test (with manual selection of variables) was performed on the environmental variables. The Monte Carlo permutation test involves multiple testing of the environmental variables on the set of species data. The number of permutations was set to 499, which is the default value in CANOCO. It is an adequate number to test at the 5 % significance level (ter Brak & Smilauer 2002), and was performed under a full model. The CCA biplots display the environmental variables as vectors, whereas study samples and/or species are plotted as points, indicating the patterns of variation in species composition explained by the environmental variables (ter Braak 1986).

The differences between the forest types concerning species diversity and evenness of samples were investigated using the Shannon-Wiener diversity index (H'), and the values of evenness (J). These calculations are procedures which combine species richness with relative abundance of the species, and is probably the most widely used among plant ecologists (Kent & Coker 1992). The formulas are as follows:

Shannon-Wiener diversity index (H') = 
$$\sum p_i \ln p_i$$
  
Equitability (J) = H'/ln s

, where s= number of species present in the community  $p_i = abundance \ of \ the \ \emph{i}th \ species \ expressed \ as \ a \ proportion \ of \ total \ abundance$ 

The three different quadrate categories investigated in this study are birch forest, transition zone and spruce plantation. The differences in species number, species richness, species diversity and species evenness were investigated by one-way ANOVA (Analysis of Variance), followed by TukeyHSD post hoc test. These analyzes were performed in R (R Development Core Team 2005)

#### **Results**

Epiphytic vegetation on 1602 trees of *Picea abies* (770), *P. sitchensis* (157) and *Betula pubescens* (675) were investigated. A total of 62 species, or groups of species, were recorded. Fifty-five of these were found on birch in the birch quadrates, 54 were found in transition quadrates, while 41 species were found on trees in spruce plantations. Eighteen species were recorded only in the birch quadrates, whereas four species were recorded only in spruce plantations. The overall most common species were *Parmelia sulcata* and *Hypogymnia physodes*. In the birch and transition quadrates *Melanohalea olivacea* and Arthoniales also made up a conspicuous part, while in spruce plantations, *Bryora* species, particularly *B. implexa*, were common. Seventy-two species were recorded in the understorey vegetation, including mosses, ferns, shrubs, herbs and trees, but this list of species is not exhaustive. The DCA and CCA ordination diagrams display clear distinctions between species that prefer birch and spruce, respectively (Figs. 3 and 4). Total inertia as well as the eigenvalues are generally low in both analyses.

#### Community structure

According to the DCA ordination, the spread of species is evident, with a relatively large gradient along the two first axes, indicating that two major environmental gradients are present. Appendix C provides the DCA summary table. Axis one has the highest eigenvalue (0.166), and seems to be the axis that best reveals the distribution in species composition on birch trees vs. spruce trees. 14.3 % of the variance is explained by the first axis. Species placed at the central and lower right of the diagram are species that prefer birch, e.g. several Cladonia species, Sphaerophorus globosus and Nephroma parile. Species at the central and upper left are species that were most abundant on spruce trees. These are, e.g., Bryoria capillaris and Tuckermannopsis chlorophylla. Species located in the upper central and upper right, like Hypogymnia physodes, Parmelia sulacata and Vulpicida pinastri are common species, and likely to be found on both spruce and birch. The gradient length is longest on the second axis, with a value of 2.43, which implies that species on each side of this gradient will rarely occur in the same quadrates. The second axis seems to reveal a gradient in air humidity, most likely from the coast (lower) to inland (upper), with inland species such as Bryoria implexa and Usnea hirta at one side, and Sphaerophorus globosus, demanding high air humidity, at the other. The total variance explained in the dataset is 38.4 %.

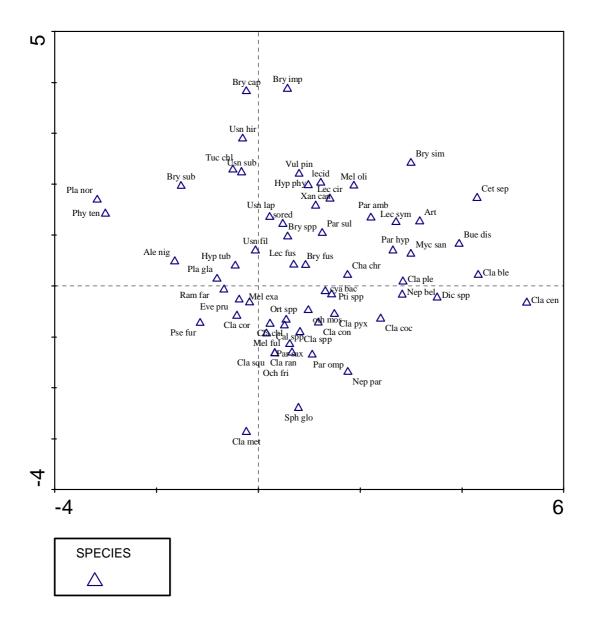


Fig. 3 DCA ordination species plot (n = 62) displaying the species ( $\Delta$ ) optima along the first two axes. For explanation of the abbreviation of species names, see Appendix A. Units along the axis are plot eigenvector.

The CCA, with Monte Carlo permutation test, verifies that the species distribution in this study can be explained by at least 17 environmental variables. The ordination diagram (Fig. 6) displays to some extent the same pattern as in the DCA, with a gradient ranging from birch to spruce (lower to upper parts). The highest variety of species is here placed below the first axis, which has an eigenvalue of 0.131.

Appendix E presents the correlation matrix on the first two axes in the CCA. The most important factor for explaining the vegetation patterns along the first axis is temperature, with

a positive correlation of 0.42. The number of Rowans below 3 m (Sorbus-b) is the second most correlated factor, though; this does not contribute much to the explanation due to the short arrow it is represented by. Other variables that have some explanatory value are the vegetation-geographical region Nb-02 and the number of tree species.

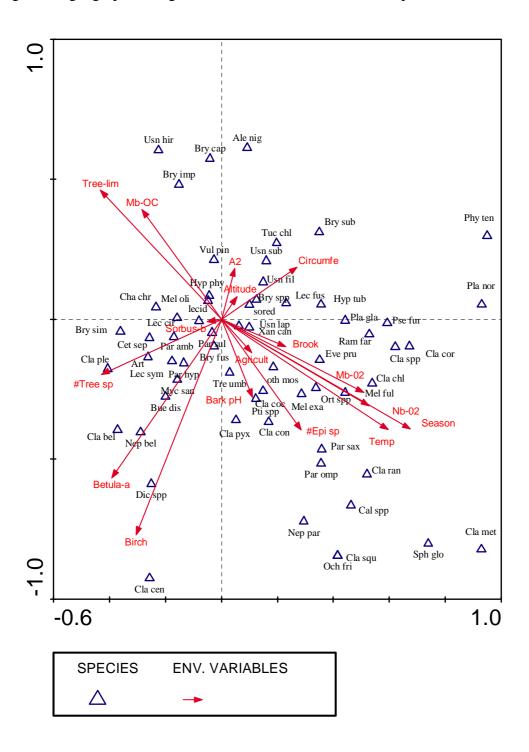


Fig. 4 CCA ordination biplot along the first two axis, displaying species (n = 62) and the statistically significant environmental factors (n = 17). It illustrates how the species  $(\Delta)$  are related to the environmental factors shown as biplot arrows  $(\rightarrow)$ , and which environmental variables that best explain the variation in community structure. For explanation of the abbreviation of species names, see App. A

The second axis has an eigenvalue of 0.121, ca. the same as the first axis. The most important variables along the second axis are the presence of birch trees, with a correslation value of -0.68. This result is not surprising since this is one of the criteria for selecting birch quadrates. Other more relevant factors are the vegetation-geographical region Mb-OC, and the number of birch trees above 3 m. The latter is more or less correlated with the presence of birch trees, and is more informative when evaluating species distribution patterns. According to the ordination, temperature increases in the same direction as the increase in epiphytic species richness, season length in days, and the presence of Mb-02 and Nb-02. These variables are more or less correlated. Appendix D provides the CCA summary table. The total variance of species data explained by the environmental data along all four axes in the CCA is 30.7 %.

#### *The distribution of quadrates*

The DCA ordination on the sample distribution (Fig. 5) reveals a similar pattern as can be traced in the DCA species ordination. This is not surprising as they are both determined by the species distribution. Species found in ca. the same area as the samples, are most abundant there. The ordination gives a clear indication that quadrates inside the spruce plantations have a different species composition than quadrates in the native birch forest. Furthermore, the spruce quadrates seem to have more internal variation, since the diagram area occupied by spruce quadrates is larger than the areas occupied by transition and birch quadrates, respectively (Fig. 5). The largest variation in the data is revealed along the second axis and is between the P. abies quadrates at Lilandskaret (Pa37) and Andselv (Pa66). These two quadrates only have one 'species' (the group of sorediate lichens) in common. The difference can be explained by several environmental factors. In particular, the geographical range is prominent, as Lilandskaret is located on an island (Andøya), whereas Andselv is situated in the more continental parts (Målselv). Also the range in altitude is evident, as Andselv is situated c. twice as high up as Lilandskaret. The reason why these two quadrates lay closer together in the CCA is probably due to the constrictions of the environmental variables on the community data in this sort of analysis. The group of quadrates located in plantations where P. sitchensis dominate, are clustered in the middle. These are quadrates with a relatively low species number and species diversity.

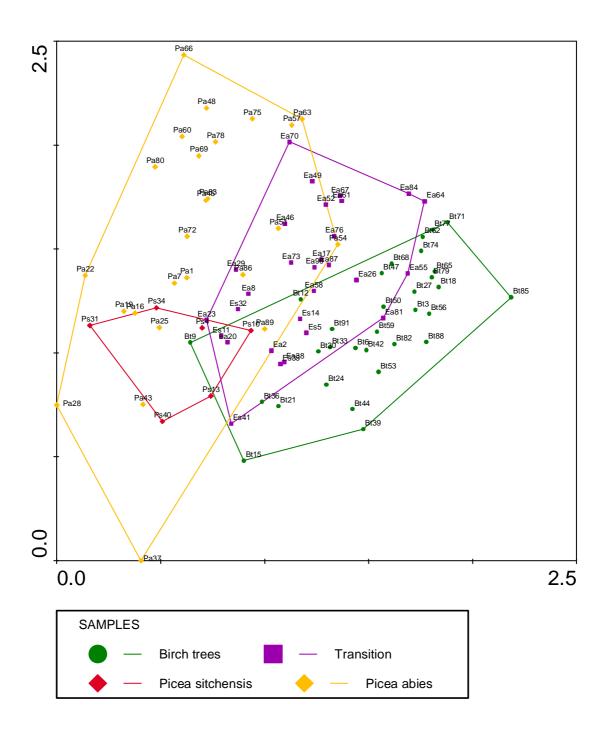


Fig. 5 DCA ordination sample plot classified into birch Bt (n=31), transition Ea/s (n=29), Norway Spruce Pa (n=24) and Sitka Spruce Ps (n=7) plots along the two first axes.

As well as for the spruce quadrates, the variation among the birch quadrates is largest between a coastal (Stokmarknes, Bt15) and an inland (Rognmo, Bt71) quadrate. Stokmarknes, in fact, hosts more than twice as many species as Rognmo. Moreover, the change in species composition is also clear when comparing one of the southernmost birch quadrates (Hadsel, Bt9) with the northernmost one (Toften, Bt85).

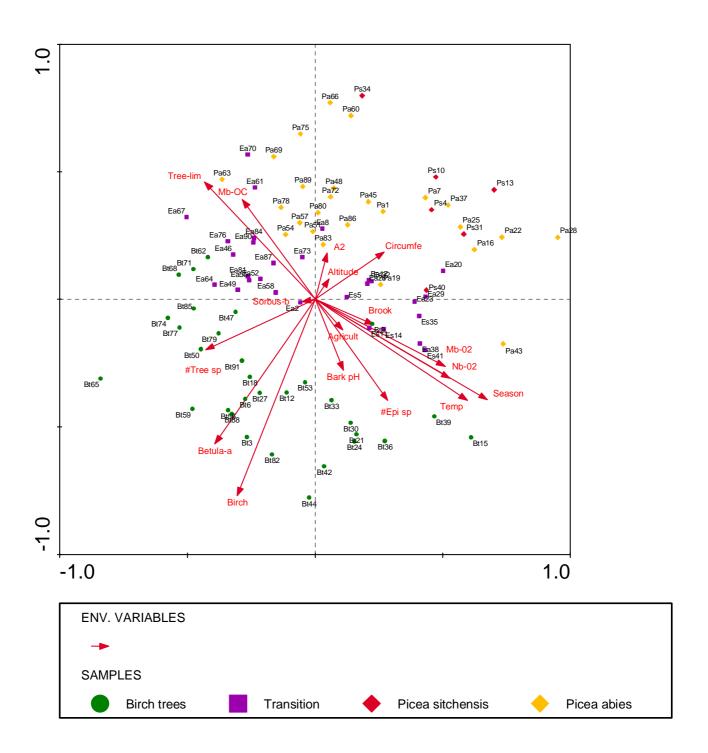


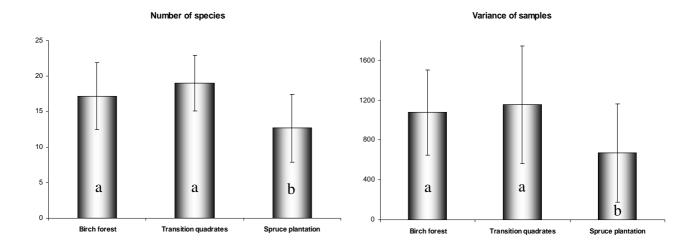
Fig. 6 CCA ordination biplot of samples (n = 62) and the statistically significant environmental variables  $(\rightarrow)$  (n = 17).

The relationship between the quadrates and the environmental variables in the CCA is illustrated in Fig. 6. These environmental variables are the same as those in the CCA species ordination (Fig. 4). The birch quadrates in the lower and slightly left parts of the ordination are explained by the presence of birch trees, the number of tree and epiphytic species in the quadrates, lower bark pH, etc. The quadrates located in the upper area of the biplot are characterized by, e.g., larger circumference, the presence of the vegetation type A2 (berry

heather forest) and fewer tree species in the quadrates. These represent quadrates in spruce plantations. The transition quadrates are for the most part around the centre, as is also displayed in the DCA ordination (Fig. 5).

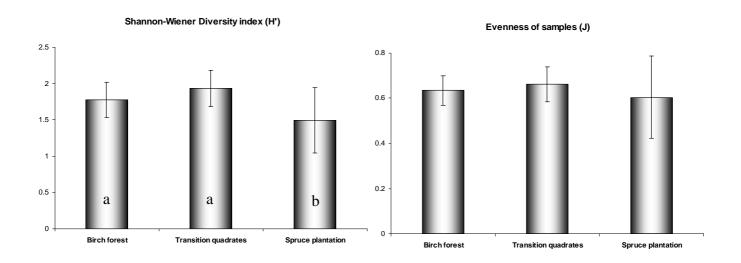
Species number, species variance, species diversity and species evenness

Figure 7 displays the mean species number in the three quadrate categories. The results from the ANOVA indicate that there are significant differences between the means of the forest types (p << 0.05). The Tukey test revealed that there is no statistical difference between the birch forest and the transition quadrates (p = 0.272). Figure 8 displays the mean variance of species among the quadrates between the three quadrate categories. The ANOVA results indicate that there is a significant statistical difference between the category means (p << 0.05). The Tukey revealed that the birch forest and the transition quadrates are statistically identical (p = 0.824).



Figs. 7 and 8. Diagram of the three different classes Birch (n=31), transition (n=29) and Spruce (n=31), plotted against number of species (left) and variance of samples (right). Bars with similar letters are not statistically different from each other. Error bars are  $\pm 1$  standard deviation (SD).

Figure 9 displays the mean values in Shannon-Wiener species diversity. The results from the ANOVA indicate that there are significant differences between the means of the three classes (p << 0.05). However, the Tukey tests revealed that there is no statistical difference between the birch forest and the transition quadrates (p = 0.167). Figure 10 displays the mean values in evenness of species among the quadrates. The ANOVA results indicate that there is no statistically significant difference between the means.



Figs. 9 and 10 Diagram of the three different classes Birch (n = 31), transition (n = 29) and Spruce (n = 31), plotted against the Shannon-Wiener diversity index (left) and evenness of samples (right). Bars with similar letters are not statistically different from each other. Error bars are  $\pm 1$  standard deviation (SD).

#### **Discussion**

This study is the first quantitative comparison of the epiphytic species communities in spruce plantations in contrast to the natural surrounding birch forest in North Norway; hence it is also the first confirmation from this area of major community differences and geographical variation between and within plantations and native forests. The DCA and CCA ordinations show that there is a clear segregation in epiphytic community patterns between forests of Downy Birch and plantations of Norway Spruce and occasionally Sitka Spruce, in terms of species preferences and species richness. This is verified by ANOVA, which reveals that there statistically are more species and higher species diversity in native birch forests than in spruce plantations.

The DCA and CCA both have relatively low percentages, respectively 38.4 and 30.7, in the explanation of the species distribution pattern. The constrained eigenvalue in the CCA is very low (0.520) compared to the unconstrained eigenvalue in the DCA (1.163). The CCA requires a good set of environmental data to match the species data (Kent & Coker 1992). Apparently, the environmental variables selected for this study were not sufficient for explaining the variation in species and samples. Other non-measured variables might contribute more to the explanation. Another detail is the sampling strategy. The areas of sampling were not completely randomly selected, as certain criterions had to be made in terms of access as well as the rejection of epiphytes on other tree species.

#### Local variation

The distributions of the epiphytic species are governed by a substantial set of local environmental variables, as most of them are best explained along the first CCA axis. The occurrence and number of birch trees above 3 meters is one of the most important variables for explaining the community structure. Number of trees is of value for lichen establishment, due to increased patch availability. A high number of birch trees above 3 meters indicate an older forest, which points out that the occurrence of old, deciduous trees may be of importance for the distribution of epiphytic species, as verified by other studies (Uliczka & Angelstam 1999, Essen et al 1997, Aastrup 2007, Kuusinen & Siitonen 1998). The occurrence of other tree species, such as European Aspen, willows, Rowan and Grey Alder, in the quadrates is another important factor for explaining the variance in the data. This is due to

their different bark pH (Werth et al 2005), and consequently facilitating different lichen communities, which again can affect epiphytic diversity on neighboring tree species (Kuusinen & Siitonen 1998, Aastrup 2007). In this study, the birch forest had up to six different tree species in the quadrates, in contrast to the spruce quadrates with three different species at the maximum.

Species associated with spruce plantations are related to increased circumference at breast height, which can be said to characterize mature spruce stands. The tree circumference is one of the most important variables along the first CCA axis. The direction of the variable in the ordination implies that increased circumference contribute to a decline in epiphytic species richness, as few species are closely related to this variable. This can be explained in relation to the variation inside the spruce stands. The trees in the examined plantations vary in age and size. In younger stands, branches were normally needle-rich, whereas in more mature plantations the branches had lost their needles, and dead branches were more common. The occurrence of needles on the branches is important for a successful colonization (Hilmo et al. 2005). The decay of dead, lower branches has also been observed in other studies, where this process has been related to stand age and consequently a more dense canopy cover (Aastrup 2007). Another study revealed that branch length is important for species number in natural spruce stands (Holien 1997). However, plantations differ from natural stands by having less space between individuals. In this study, the mean densities of trees above 3 meters were 0.15 in birch quadrates, and 0.21 in spruce quadrates, revealing a slightly higher density in the plantations. Thus, long branches in plantations may actually reduce species number, as was seen in several Sitka Spruce quadrates. Branches from one tree reached the branches of adjacent trees, effectively reducing the access of light to the lower branches. At a few locations the trees had lost all of the lower branches, or they had been cut off such that sheep could pass through the plantations. In branch-poor Norway Spruce quadrates, the species abundance was reduced as compared to spruce quadrates with more branches and better light conditions.

Moberg & Holmåsen (2000) states that birch trees generally have a higher bark pH than spruce, and therefore are inhabited by more lichen species. This is also verified by the current study. Spruce is characterized by nutrient-poor, acidic bark which causes dominance of acidophilic epiphytic communities (Holien 1997). In this study, the spruce plantations were often dominated by species of *Bryoria*, but some other generalist species like *Hypogymnia physodes* and *Parmelia sulcata* and *Platismatia glauca* (Holien 1997, Krog et al. 1994) also made up a conspicuous part of the lichen biomass. However, according to Kermit & Gauslaa

(2001), bark pH of *P. abies* stands vary vertically. Twigs from lower parts might receive organic acids leached from the canopy above, including its epiphytic species. Lichen-rich branches on the ground were observed in several plantations in the current study. Consequently, the uppermost canopy, being more exposed to rainfall, might have a different bark pH and consequently host a different lichen community than that of the lower branches.

Birch forest quadrates have a more diverse epiphytic flora than the spruce quadrates. Ubiquitous species like *H. physodes, Melanohalea olivacea* and *P. sulcata* generally dominated, but additional species, (e. g. several *Cladonia* species, *Parmelia omphalodes*, *P. saxatilis, Nephroma* spp., *Sphaerophorus globosus* and *Xanthoria candelaria*) occurred above all in birch quadrates. Many of these species are also common on other substrates, such as rocks, soil and decaying wood. According to the CCA these species are related to areas of high species diversity (e. g. Bønna, Stokmarknes and Liland), indicating preferable conditions for the epiphytes there.

#### Regional variation

The quadrates are exposed to a series of varying environmental conditions, stretching from outer islands to more continental areas, and from south to north, covering two vegetation regions and three vegetation sections (Moen 1998a). Temperature is one of the most important and remarkable regional environmental variables in explaining the variance in the data, having a close correlation with the second CCA axis and being represented by a long arrow in the ordination. Other environmental variables such as season length, Nb-02 and Mb-02, are factors positively correlated with temperature in the ordination. These are again associated with a mild climate and increased precipitation. Werth et al (2005) concluded that the most important factors for regulating the macrolichen community composition in North Norway were oceanity, precipitation and local temperature sums. Thus, these two studies both understate, not surprisingly, the regulatory importance of temperature-related factors for lichen distribution. Increased distance to the tree limit and Mb-OC are, not surprisingly, negatively correlated with these factors. It seems to be higher epiphytic species richness at lower areas, which is due to the occurrence of thermophilous species that do not thrive at colder sites near the tree limit. For instance, species of *Usnea*, regarded as thermophilous within the study area, only sporadically occur within the NB vegetation region and close to the tree limit (Bjerke et al. 2006a). Altitude was also pointed out as a significant variable

along the second axis and may play a part in the pattern of species distribution, which is in accordance with other observations (Holien 1997).

Humidity from close-by humid areas, such as brooks, also contribute to the explanation of the species distribution in the current study. Humidity is reckoned as one of the main environmental factors in determining the distribution of lichens (Krog et al. 1994), which this observation understates. A study on old-growth species in a coastal spruce forest in central Norway (Rolstad et al. 2001) acknowledges the presence of branch-rich brook ravines on the occurrence of several of these lichens. The variation in epiphytic lichen distribution and their controlling environmental factors in North Norway can be related to a recent case-study in Liguria, north western Italy (Giordani 2006). Both areas have steep environmental gradients, where average yearly temperatures, rainfall, bark pH and texture are associated with the main axes of variability.

#### *Spruce plantations – A threat to the biodiversity?*

This study has revealed that species richness, species diversity, species number and variance is significantly lowered in spruce plantations contra native birch forest, which proves that potentially important epiphytic species communities may suffer major reductions in areas of substantial spruce planting in North Norway. The forest floor vegetation inside spruce plantations is markedly changed or strongly impoverished (Sætra 1971), indicating a loss of productivity. A reduction in diversity-rich cryptogamic epiphytic communities may affect the diversity of other associated organisms, such as invertebrates (Petterson et al. 1995). Important linkages between the occurrence of lichens and birds have also been discussed (Uliczka & Angelstam 2000, Petterson et al. 1995), comparing managed and natural stands of coniferous forests. These studies understate that the loss of lichen species might influence the occurrence of birds in these forest. Hausner et al. (2001) revealed a loss of bird assemblages in spruce plantations, as well as a reduction of birds in less productive birch habitats, as compared to the lush deciduous birch forest in North Norway.

The transition quadrates, consisting of both spruce and birch trees, reach a peak in species diversity and variance in the samples. This can be explained by the occurrence of both tree species in the quadrates, making it possible for both shade-tolerant species within the plantation, as well as species associated with the richer and sunnier birch stand, to live there. Several studies have dealt with the edge effects on lichen distribution (Esseen & Renhorn 1998, Kivistö & Kuusinen 2000, Hilmo et al. 2005), in terms of changed environmental

properties, for example light intensity (Renhorn et al. 1997) and wind speed (Esseen & Renhorn 1998). The relatively high diversity of epiphytes in the transition quadrates might give a contribution to the argument for mixed forest stands (Emmer et al. 1998, Knoke et al. 2005) in forest management issues.

Spruce plantations might give room for species that are more common in areas where spruce occur naturally in the landscape. The finding of a thallus of *Pseudevernia furfuracea* on *Picea abies* at Rå, is the fifth record of this species from Norway north of 67° northern latitude. The previous four records of this species are also from plantations (Bjerke et al. 2006), indicating that the species is gradually spreading northwards, facilitated by the establishment and maturation of spruce plantations. Another species associated with coastal and/or old-growth habitats is *Platismatia norvegica* (Roland et al. 2001). This species was found at two locations, growing both on spruce and birch. The species most likely has a short generation time and a high reproduction capacity, and is observed to colonize spruce plantations rapidly where the species grows naturally in the surrounding forest (Aastrup 2007).

Forestry means cutting down trees for industrial use. Obviously, this activity eradicates the substrate for epiphytic organisms. Even though lichens disperse into the plantations from the surrounding native forests, some species are not very well adapted to the non-native, shady habitat. This results in a decrease in species richness and diversity. As Rolstad et al. (2001) suggests, moderate selective cuttings may prove positive on the lichen establishment in plantations. This may be an acceptable strategy for the plantations of North Norway, imitating the more open, native birch forests of these areas. Furthermore, results from this study understate the importance of old-growth birch-dominated forests as hosts for rich and diverse epiphytic communities in North Norway. To conserve the remaining patches of such forest, future plans for establishment of spruce plantations should await the results of biodiversity surveys of the potentially affected sites. Thus, the Government, in collaboration with the Directorate for Nature Management, should work towards a plan for introduction of compulsory impact assessment reports prior to establishment of new spruce plantations, in a similar way as impact assessments are required for other major land use plans in Norway. A general recommendation is that future spruce planting should be restricted to areas with low habitat quality, such as semi-natural landscapes, as was also recommended by Humphrey et al. (2004) for plantation establishment in the United Kingdom. Moderate selective cutting and thinning may also sustain and improve potential important epiphytic communities, leading to a healthier environment in these non-native plantations.

#### **Conclusion**

Although spruce plantations may occasionally host some uncommon, shade-tolerant epiphytic species, the communities are generally more species-poor and less diverse than those of the native birch forests. Consequently, the spruce plantations, which can cover very large areas, may have great impact on the native flora and fauna due to the fragmentation of the natural forest and the decline of epiphytic biodiversity. Epiphytic communities are not randomly distributed, but respond to environmental variation at both local and regional scales. The results from this study confirm that:

- The structure of the epiphytic lichen communities in mature spruce plantations
  versus neighboring native birch forests is different in terms of species
  preferences. Species diversity, species richness and variance are reduced in
  spruce plantations as compared to the surrounding native birch forests.
- The epiphytic species distribution is determined by both local and regional
  environmental gradients, where tree characteristics, number of other tree
  species in the area, and pH of bark are the main local variables, while
  temperature and variations along an east-west gradient are the most important
  regional variables.
- Species like the thermophilous *Pseudevernia furfuracea and Alectoria sarmentosa* ssp. *sarmentosa* and species related to old-growth forests, like *Platismatia norvegica*, were recorded. These species might be steadily more common as spruce plantations in North Norway mature.
- Comprehensive research on the impact of spruce plantations on the biodiversity should be central in the planning of new plantations. It is here recommended that future forest management should focus on mixed stands, preferably in areas of low habitat quality such as semi-natural landscapes. Also moderate selective cutting and thinning should be practiced in spruce plantations, to imitate the surrounding, open birch forests.

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# Appendix A – Complete species list

Abbreviation	Latin name	Norwegian name
Ale nig	Alectoria nigricans	jervskjegg
Art	Arthoniales	, , , , ,
	Bryoria capillaris	flekklav gr.
Bry cap		bleikskjegg
Bry fus	Bryoria fuscescens	mørkskjegg
Bry imp	Bryoria implexa	vrangskjegg
Bry sim	Bryoria simplicior	buskskjegg
Bry sub	Bryoria subcana Buellia disciformis	gråskjegg
Bue dis		
Cal sp.	Caloplaca sp.	h. Controller
Cet sep	Cetraria sepincola	bjørkelav
Cha chr	Chaenotheca chrysocephala	gulgrynnål
Cla bel	Cladonia bellidiflora	blomsterlav
Cla chl	Cladonia chlorophaea	pulverbrunbeger
Cla cen	Cladonia cenotea	meltraktlav 
Cla coc	Cladonia coccifera	grynrødbeger
Cla con	Cladonia coniocraea	stubbesyl
Cla cor	Cladonia cornuta	skogsyl
Cla met	Cladonia metacorallifera	skjellrødbeger
Cla ple	Cladonia pleurota	pulverrødbeger
Cla pyx	Cladonia pyxidata	kornbrunbeger
Cla ran	Cladonia rangiferina	grå reinlav
Cla squ	Cladonia squamosa	fnaslav
Eve pru	Evernia prunastri	bleiktjafs
Hyp phy	Hypogymnia physodes	vanlig kvistlav
Hyp tub	Hypogymnia tubulosa	kulekvistlav
Lec cir coll	Lecanora circumborealis	bjørkekantlav
Lec fus coll	Lecanora fuscescens coll.	
Lec sym	Lecanora symmicta	halmkantlav
Mel ful	Melanelixia fuliginosa	stiftbrunlav
Mel exa	Melanohalea exasperata	vortebrunlav
Mel oli	Melanohalea olivacea	snømållav
Myc san	Mycoblastus sanguinarius	bloddråpelav
Nep bel	Nephroma bellum	glattvrenge
Nep par	Nephroma parile	grynvrenge
Och fri	Ochrolechia frigida	fjellkorke
Par omp	Parmelia omphalodes	brun fargelav
Par sax	Parmelia saxatilis	grå fargelav
Par sul	Parmelia sulcata	bristlav
Par amb	Parmeliopsis ambigua	gul stokklav
Par hyp	Parmeliopsis hyperopta	grå stokklav
Phy ten	Physcia tenella var. tenella	frynserosettlav
Pla gla	Platismatia glauca	vanlig papirlav
Pla nor	Platismatia norvegica	skrukkelav
Pse fur	Pseudevernia furfuracea	elghornslav
Ram far	Ramalina farinacea	barkragg
Sph glo	Sphaerophorus globosus	brun korallav
Tuc chl	Tuckermanopsis chlorophylla	kruslav
Usn fil	Usnea filipendula	hengestry
Usn hir	Usnea hirta	glattstry
Usn lap	Usnea lapponica	pulverstry
oon ap	Conod ideponiod	parroidity

Usn sub	Usnea subfloridana	piggstry
Vul pin	Vulpicida pinastri	gullroselav
Xan can	Xanthoria candelaria	grynmessinglav
Lecid	Lecideoid	lecideoide skorpelav
Sored	Sorediate	sorediøse skorpelav
Tre umb	Trentepohlia umbrata	brunflass
Dic sp.	Dicranum sp.	sigdmose sp.
Pti sp.	Ptilidium sp.	frynse sp.
Ort sp.	Orthotrichum sp	bustehette sp.
Oth mos	Other mosses	andre moser

# Appendix B – Vegetation types according to Fremstad (1997).

Type:	Name:	Description:
	Cowberry-bilberry	Few to many trees; birch, pine, spruce. Field layer with dominance of
A2	woodland	heather species. Dense ground layer with mosses.
	Heather- bog bilberry	Few to many trees, birch pine, spruce. Heather species dominates the
A3	woodland	field layer. Often Sphagnum species in the ground layer.
		Few to many trees, birch, pine, spruce, rowan, juniper. Species poor,
		but in some variants affected by culture species. Field layer dominated
A4	Bilberry woodland	by bilberry. Well developed moss ground layer.
		Well developed tree layer; birch, pine, spruce. Same species as A4,
		but small ferns dominate the field layer. In some variants, herbs and
A5	Small fern woodland	grasses enter into. Well developed moss ground layer.
		Open forest; birch, pine, juniper. Low dense field layer of grass species
	Poor, grass dominated	and short-grown, less demanding herbs. Heather species not
A7	woodland	important. Well developed moss ground layer.
		Productive forest; birch, spruce. Grey alder can enter into. Humid
		areas. Rich in large ferns, with dominance of Athyrium filix-femina
		and/or <i>Dryopteris expansa</i> in the field layer. Tall herbs and small weed
C1	Tall fern woodland	can enter into. Heather species not important.
	Tall herb, downy birch	Species rich forest, mostly birch. Tall herbs, large grass species and
00	and Norway spruce	ferns. On higher altitudes smaller herbs and alpine species can enter
C2	woodland	into.
040	Damp, medium nutrient	V B
G12	rich grassland	Very variable. Dense, low field layer. Moist demanding herbs.
NV	No vegetation	Mosses and/or litter

# Appendix C – DCA summary table

Axes	1	2	3	4	Total inertia
Eigenvalues	0.166	0.145	0.075	0.061	1.163
Lengths of gradient	2.186	2.434	1.801	1.498	
Cumulative percentage variance					
of species data	14.3	26.7	33.1	38.4	
Sum of all eigenvalues					1.163

## Appendix D – CCA summary table

Axes	1	2	3	4	Total inertia
Eigenvalues	0.131	0.121	0.061	0.043	1.163
Species-environment correlations	0.900	0.872	0.858	0.748	
Cumulative percentage variance					
of species data	11.3	21.7	26.9	30.7	
of species-environment relation	25.2	48.4	60.2	68.5	
Sum of all eigenvalues					1.163
Sum of all canonical eigenvalues					0.520

 $\label{eq:appendix} \begin{tabular}{ll} Appendix $E-CCA$ correlation matrix of the two first axes and the environmental variables. The environmental variables most correlated with the axes are in bold. \end{tabular}$ 

Env var	Axis 1	Axis 2
Altitude	-0.0903	0.1682
Birch	-0.1822	-0.6786
Brook	0.0340	-0.1278
Tree-lim	-0.0273	0.1777
Agricult	-0.0003	-0.1227
Temp	0.4218	0.1955
Circumfe	0.2753	-0.1660
Bark pH	-0.0096	-0.1412
Mb-02	0.2199	-0.1636
Nb-02	0.3333	-0.2147
Mb-OC	0.3291	0.2982
A2	0.1686	0.0308
# Epi sp	0.0970	-0.1714
# Tree sp	-0.3302	-0.1278
Sorbus-b	0.3531	0.1073
Betula-a	-0.1500	-0.2180
Season	0.2846	0.0603