

**Regional gradients in epiphytic macrolichen communities of northern
Norway**

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Abstract

Question: What is the relative influence of human impact, macroclimate, spatial configuration and environmental differences on species composition of boreal epiphytic macrolichen communities?

Location: Troms county in northern Norway

Methods: DCA revealed the main gradient structure in lists of epiphytic macrolichen species from deciduous forests. By CCA with variance partitioning, the relative amount of variance in macrolichen species composition attributable to human impact, macroclimate, spatial context and environmental differences was quantified.

Results: There was no significant effect of human impact on species composition of epiphytic macrolichens of deciduous forests. Macroclimate was the most important factor determining epiphytic macrolichen communities, which were also strongly influenced by spatial context and ecological difference such as forest stand properties.

Conclusions: Epiphytic macrolichen communities are determined by a macroclimatic gradient from the coastline to the interior of central North Norway. In marked contrast, the species composition of epiphytic macrolichen communities seems to be unaffected by human impact in the study area, where air pollution was marginal.

1 **Keywords**

2 Ordination, variance partitioning, lichens, human impact, spatial variation,
3 macroclimate, environmental variation

4

5 **Nomenclature**

6 Santesson et al. (2004); Lid & Lid (1994)

1 Introduction

2 Understanding patterns in species composition along environmental gradients is of
3 primary interest to community ecology, yet establishing causal relationships between
4 communities and gradients is a difficult task. Various multivariate methods now enable
5 community ecologists to test specific hypotheses on relationships between communities and
6 environmental gradients (Borcard et al. 1992; Økland & Eilertsen 1994). Even though the
7 number of studies testing explicit hypotheses at the community level increased in recent years
8 (Borcard et al. 1992; Méot et al. 1998), little hypothesis testing has been performed on regional,
9 e.g. macroclimatic gradients (but see Graae et al. 2004; Ohmann & Spies 1998; Qian et al. 2003).
10 In particular human impact is a topic of general interest onto which future research activities
11 should be directed (Lubchenco et al. 1991; Meffe & Carroll 1997).

12 Lichens are good model organisms to assess the effects of human impact on ecosystems
13 because of their sensitivity to various types of human impact such as logging (Rose 1992; Wirth
14 1995), land use (Wirth 1999; Wirth et al. 1996) or air pollution (Garty et al. 1993; Hawksworth
15 & Rose 1970; Kricke & Feige 2001; Richardson 1992). The latter has lead to the depauperation
16 of lichen communities over large areas of Europe. However, in other areas such as northern
17 Fennoscandia, the negative effects of air pollution are marginal (van Herk et al. 2003). It has
18 been speculated that land use and logging were of primary importance here.

19 In the present study, partial CCA, which is a powerful tool for testing specific
20 hypotheses about community - environmental relationships (Birks 1993; Borcard et al. 1992;
21 Økland & Eilertsen 1994), was applied to a data set of epiphytic macrolichen communities from
22 coastal boreal deciduous forests of northern Norway. We tested the hypothesis that human impact

is indeed an important factor for epiphytic macrolichen communities when other sources of variance in species composition (e.g. macroclimate, forest stand properties, spatial structure) are accounted for.

Methods

Sampling of epiphytic macrolichen communities

In 1999 and 2000, epiphytic macrolichen communities were sampled along a regional gradient in central and southern parts of Troms county in northern Norway. The gradient represents a transition from an oceanic to a more continental climate (Moen et al. 1999). The spatial extent of the study area was 126 km in the North-South direction and 113 km in the East-West direction. In North Norway, air pollution is relevant in parts of northeastern Finnmark county, but is neglectable in the study area in Troms county (Tømmervik et al. 2003). Only deciduous forests at altitudes below 500 m were included in the analyses. The tree-line in the area is formed by *Betula pubescens* (Bjune et al. 2004) and lies between 150 m on the outermost northwestern islands of Troms and 750 m in the southeastern valleys in the interior of Troms at present, according to topographic maps (Norwegian Mapping Authority). A total of 32 locations situated in the main valleys of central and southern Troms county were sampled (Fig. 1). Since we were interested in a regional gradient in species composition rather than in fine-scale within-site variation, we used large study plots as recommended by Økland (1990), leading to an increased species capture (McCune & Lesica 1992). Per location, one study plot of 400 m² was selected randomly within each of the forest types included in the analyses, which were alder forests (*Alnus incana*), alder-willow swamp forests (*Salix pentandra*, *S. myrsinifolia*), nutrient rich birch forests, nutrient-poor birch forests, dry willow forests in slopes (*S. caprea*) and aspen

forests (*Populus tremula*). This selection represented the most common and characteristic types of deciduous forests in the study area (Fremstad 1997). The forest stands to be sampled were selected subjectively. Within a particular forest stand, a study plot was selected randomly by walking a random number of up to 100 steps from the centre of the stand in a random direction. Aspen and dry willow forests were often too small to follow this randomization procedure and then, the study plot to be analyzed was located in the centre of the respective forest patch. Plots were rejected if closer than two meters to the nearest forest edge, if containing less than three trees above four cm in collar diameter or if more than 30 % of the study plot area was an open water surface. Presence-absence data of epiphytic macrolichen species were recorded on lower stems (≤ 2 m) of deciduous trees in a total of 69 study plots. Macrolichens were defined as the species included by Krog et al. (1994). Due to the great efforts needed to obtain reliable species determinations, the genus *Cladonia* was excluded from the analyses.

Explanatory variables

A total of 68 explanatory variables was used to characterize the plots and they were grouped into four sets of explanatory variables, firstly {C}, a set of 13 macroclimatic, microclimatic and topographic variables, secondly {E}, a set consisting of 33 forest structure and growth substrate related environmental variables – referred to as environmental variables in the following. The third set, {H}, consisted of ten human impact variables, whereas the fourth set, {S}, was composed of twelve spatial variables.

As climatic variables {C}, monthly normal values for precipitation, annual normal precipitation and annual temperature sums as calculated for temperatures above 0°C or 4°C were included. All these data refer to a reference period of 1961 – 1990 (Aune 1993; Førland 1993).

Extrapolated data for the study plots were provided by The Norwegian Meteorological Institute, Klimaavdelingen. Oceanity of climate was determined from maps in Moen et al. (1999). Moisture and light conditions of the plots were estimated with a five-point scale, ranging from dry to wet and from low light to high light situations, respectively. Average plot elevation was obtained from 1:50,000 topographic maps (Norwegian Mapping Authority) to the nearest 10 m. In addition to a heat index (Parker 1988), a 15-point irradiation index with highest values for S and SSW exposure of the study plots was used. Further variables were the average slope angle of the plot, plot aspect, and un-favorability, that is, the deviation of aspect from SSW exposure (Økland 1996). These latter variables characterize the plots' microclimate.

In the set of environmental variables {E}, a rock suitability index, giving a rough indication of the quality of a given study plot's rock habitats for lichen growth was included. This was done since some lichens which are predominantly epiphytic in Central or Southern Europe (Türk & Wunder 1999; Wirth 1995) grow frequently on both rocks and bark substrates in northern Norway (Krog et al. 1994), e.g. *Degelia plumbea*, *Lobaria scrobiculata*, *L. pulmonaria*, and *Pannaria conoplea*. Suitable rock substrates can be important as a refuge of such lichen species in the case of forest disturbance. Based on the number and diameter of tree stems (dbh $\geq$ 5 cm) in a subplot of 100 m², tree density and basal area were calculated. Tree species composition was identified as presence-absence of species. For tree individuals with more than one stem, only the largest stem was measured, but the number of stems was counted, and included as a proportional variable to the total number of trees per plot. Maximum and median tree diameter were also taken into account. Diameter, number, density, position and decay class of dead wood (basal diameter $>$ 10 cm) was recorded in subplots of 100 m². Decay classes follow the classification of Linder et al. (1997). The number and density of all young trees (dbh $<$ 5 cm)

present in subplots of 100 m² was recorded, as well as the type of deciduous forest, coded as binary variables. Distances to the closest river and/or lake were determined from topographic maps, because they were assumed to be indicative of the moisture level of the study plots. Landscape patchiness was defined by means of the sum of the length of boundaries between forest and non-forested mires and lakes, as taken from topographical maps in circular areas of 500 m in radius around the study plots. The resulting index reflected the degree of patchiness of the landscape.

In the set of human impact-related variables {H}, the presence or absence of spruce (*Picea* spp.) or larch (*Larix* spp.) plantations in visibility distance from the study plots was recorded (binary variable). At the 500 m radius area mentioned above, the distance to and length of outlines of structures related to human settlements, e.g. roads (three-point scale from topographic maps), gravel pits or residential areas (closest house) and of clearly human-induced deforestation (e.g. meadows) were estimated from topographic maps. Recently, parameters similar to the latter were used successfully to define an index of human impact by Gombert et al. (2004). The overall human impact of a plot was estimated using criteria suggested by Trass et al. (1999): (1) landscape un-affectedness, (2) tree age, (3) quantity of logs, (4) decay of logs, (5) intensive cutting and (6) other human impact. For our purpose, the 13-point human impact scale of Trass et al. (1999) was reversed, with the starting point of 1 (lowest value of human impact). Note that the three highest human impact categories were missing in our data set.

To enable the detection of complex large-scale spatial patterns (Méot et al. 1998) in the data set, latitude and longitude, and their quadratic and cubic combinations defining a polynomial three-dimensional trend surface were included, as recommended by Borcard et al. (1992). Geographic location of plots was included (binary variable), defined by their affiliation to the

municipalities of Bardu, Tromsø, Storfjord and Målselv. In addition, distances to open sea and closest seashore were included in the set of spatial variables {S}, as taken from topographic maps.

Statistical analysis

We performed DCA ordination (Hill & Gauch 1980) to reveal the main gradient structure of the data set; non-metric multidimensional scaling (Kruskal 1964) gave results comparable to DCA.

All explanatory variables recorded on a continuous measurement scale were transformed to zero skewness, followed by ranging (Graae et al. 2004; Økland et al. 2001). Variables were selected by forward selection followed by Monte Carlo permutation tests, where the overall threshold statistical significance value for inclusion of a variable in a particular set of explanatory variables was Bonferroni-corrected to $\alpha=0.05$. Forward selection procedure was applied separately for each of the four sets of variables. Statistically significant variables were checked for collinearity, and the rejection criterion was a variance inflation factor exceeding nine.

Using partial CCA (ter Braak 1988), we partitioned variance in macrolichen community composition to the four sets of explanatory variables following Økland (2003). For all statistical analyses, the programs CANOCO for Windows 4.0 (ter Braak & Šmilauer 1998) and PC-ORD (McCune & Mefford 1999) were used.

Results

A total of 71 epiphytic macrolichen species was found among the 69 study plots (Tab. 1). Many of these species are common in Norway, such as *Hypogymnia physodes*, *Melanelia olivacea*, *Parmelia sulcata* and *Parmeliopsis ambigua* (Krog et al. 1994). Only one of the species

found is red-listed in Norway and considered as vulnerable, *Lobaria hallii* (DN 1999; Tønsberg et al. 1996). *Collema fasciculare*, *Degelia plumbea*, *Lobaria amplissima*, *L. hallii* and *Pannaria conoplea* are responsibility species of Norway (Tønsberg et al. 1996). *Collema fasciculare* has not been found in Troms county before (Krog et al. 1994; Santesson et al. 2004). Its new northernmost locality in Norway is Tune, Bardu municipality at 68°55' N. Another rare species in North Norway is *Melanelia exasperatula*, which was found at the outermost coastal site investigated. This species is also new to Troms (Krog et al. 1994; Santesson et al. 2004). *Degelia plumbea* and *Pannaria conoplea* are oceanic and normally corticolous species which are rare in northern Norway. The latter species were found exclusively on rock habitats in an inland site at Brennfjellet in the Skibotn valley. *Phaeophyscia nigricans* from the same site is also a rare species, previously only known from three localities in North Norway (Timdal 1987). *Phaeophyscia ciliata*, which was recorded from the same site in the Skibotn valley, is another species which does not seem to have been reported so far North in Fennoscandia before (Santesson et al. 2004).

The DCA ordination axis 1 (Fig. 2) reflected the gradient from coastal to inland sites, with *Xanthoria parietina*, *X. candelaria* and *Physcia tenella* as typical coastal species and *L. amplissima*, *L. pulmonaria*, *L. hallii* and *Collema fasciculare* as characteristic interior species. As opposed to chlorolichens (sensu Lange & Wagenitz 2003), cyanolichens and tripartite lichens containing both cyanobacteria and green algae as photobionts were associated with low values on axis 1. With the exception of *Bryoria capillaris*, all alectorioid and pendulous lichens were associated with high scores on DCA axis 2. Gradient lengths of axis one to three were 2.781, 2.383, and 2.021, respectively, implying that at least two rather short gradients were present in the data. Gradient lengths are short when variation in the species data is low, e.g. if there are

species occurring along the entire gradient. Such widely distributed lichen epiphytes were for example *Hypogymnia physodes*, *Melanelia olivacea*, *Parmelia sulcata*, *Parmeliopsis ambigua* and *Bryoria fuscescens*, species sharing a preference for acidic bark. The species *Phaeophyscia sciastra*, *Physcia caesia*, *P. dubia* and *Xanthoria elegans* at the bottom of the ordination diagram represent a group of species most commonly found on rocks with relatively high nutrient availability (Moberg & Holmåsén 1982). These species were found as rare rich bark epiphytes in interior sites. Another member of this species group, *Phaeophyscia ciliata*, is a typical epiphyte of aspen trees (Krog et al. 1994).

Ten out of 68 explanatory variables were statistically significant, exhibited neglectable collinearity and were therefore included in the partial CCA analyses. Highly significant variables included in {C} were oceanity, precipitation and temperature sum, and in {E} the presence of *Populus tremula* forest and of *Alnus incana*. The selected model explained 26 % of total inertia (3.46 inertia units, IU). All reduced sets of explanatory variables except for the set of human impact variables explained statistically significant amounts of variance, when covariance with the remaining sets of variables had been removed (Tab. 2).

In Fig. 3, variance in epiphytic macrolichen communities accounted for by four sets of explanatory variables {S}, spatial variance, {C}, macroclimate, {H}, human impact and {E}, environmental variance is given and shows that the largest amount of variance was explained by the set of macroclimatic variables (35.0 %), followed by the set of spatial variables (25.5 %) and environmental variables (17.0 %). It is noteworthy that human impact only explained 5.2 % of the variance. All sets of explanatory variables shared variance except for the pair of environmental and human impact variables. Covariance was largest between the sets of macroclimatic and spatial variables.

Discussion

Human impact can not be considered as a key factor structuring epiphytic macrolichen communities in deciduous forests of central Troms county. This result is in good accordance with those of a study of forest vegetation in the northwestern USA investigating higher plant species. Here, clearfellings accounted for only 2 % of the total variation explained (Ohmann & Spies 1998). The effect of logging on the population of a lichen species depends on its population size as well as its habitat preferences. Rare species will face a higher chance of going locally extinct because of logging than common species. Logging will probably only have a long-term negative effect at all in species restricted to certain habitat types. These species are hence often rare and irregularly distributed in a landscape. The ability to disperse to suitable habitat may become a problem if logging is going to reduce not only total amount of available habitat, but also the latter's occurrence in the landscape as it has been hypothesized for deciduous forests of Central Europe (Wirth 1976; Wirth 1999). However, none of the studies proposing lichen species as indicators of human impact on forests (Pfefferkorn & Türk 1996) or ecological continuity of forests (Rose 1976; Rose 1992) used a statistical data analysis. This perpetuates the problem of confounding of habitat qualities with human impacts such as logging regimes. Forests that remained undisturbed for a longer time usually contain many particular habitats suitable for growth of different epiphytic lichens such as large old trees, logs and snags (Jüriado et al. 2003; Peterson & McCune 2001; Uliczka & Angelstam 1999). This is mainly due to a shift in forest structure with ongoing succession, and may thus be independent of logging per se. The results of a study performed in central Norwegian coastal spruce forests in which the covariance between

environmental and human effects was corrected for led to the conclusion that moderate selective logging did not have significant effects on several epiphytic macrolichen species (Rolstad et al. 2001). The latter study included several old growth associated lichens belonging to the Lobarion community, which were classified as indicators of forest continuity (Kuusinen 1996; Rose 1976; Rose 1992) or hemerophoby (Trass et al. 1999).

Logging is likely to lead to an increase of solar radiation on remnant trees to levels destructive for several old forest lichens (Gauslaa & Solhaug 1999; Gauslaa & Solhaug 2000). In valley bottom sites in northern Norway receiving a low amount of solar irradiation due to a low sun angle, this effect is probably not of importance.

Forest thinning did not have the anticipated negative effect on old-growth dependent cyanolichens, but rather led to a slight increase of alectoroid and dry-resistant lichens in a study performed in the northwestern United States (Peterson & McCune 2001). However, the latter form of forest management affected neither the density and nor the frequency of large old trees, which may act as source of lichen propagules, enhancing the colonization of trees remaining after management.

The climate of Troms county can be characterized as oceanic to suboceanic, with the climatically most favorable sites for Lobarion lichens situated in the valley bottoms of the inland. Under a favorable oceanic climate, species belonging to the Lobarion community find optimal climatic conditions, which may lead to a quicker colonization of young stands (Peterson & McCune 2001). Several lichens may thus show a higher resilience to logging than under growth conditions further off their climatic optimum (Anonby 1994). In contrast, for thermophilic lichen species reaching their northern distribution limits in northern Norway, logging and other human

1 impacts were assumed to have strong effects. However, no evidence of this effect was found in
2 the present data set.

3 The CCA results showed a strong response of epiphytic macrolichen communities to
4 macroclimatic factors. The primary importance of macroclimate for lichen communities
5 coincides with the findings of McCune et al. (1997) and Peterson & McCune (2001) from the
6 USA. In a Swedish investigation of epiphyllic algae on spruce needles and epiphytic lichens on
7 trunks of *Pinus sylvestris*, however, macroclimatic variation only accounted for 14.1 % of the
8 total variance in species composition (Liu & Bråkenhielm 1995). In the present study,
9 particularly oceanity and local temperature sums determined macrolichen community
10 composition. There may be several reasons for this finding. First, there is a strong climatic
11 gradient in the study area from oceanic coastal sites with low temperature sums and high annual
12 precipitation to inland sites characterized by a more continental climate with high temperature
13 sums and lower annual precipitation (Aune 1993; Førland 1993). There could well be a trade-off
14 between precipitation and temperature demands of thermophilic lichens in northern Norway –
15 demands for precipitation ask for a coastal distribution, temperature demands for climatically
16 favorable interior sites. Species with an oceanic distribution in Central Europe such as *Collema*
17 *fasciculare*, *C. nigrescens*, *Degelia plumbea*, *Lobaria amplissima*, *L. pulmonaria*, *L.*
18 *scrobiculata*, *Pannaria conoplea* and *Sphaerophorus globosus* (Schauer 1965; Wirth 1995) may
19 be limited by low temperature sums in coastal sites of northern Fennoscandia. In Troms and
20 Finnmark county, these oceanic species are instead restricted to moist habitats at the most
21 continental sites, where both their temperature and humidity demands are met (Elvebakk &
22 Sandvik 1980).

Many lichen species represent good indicators of favorable local climatic conditions in northern Norway (Ingebrigtsen 2000). As many as 26 of the recorded species can be considered thermophilic in northern Fennoscandia, meaning that their distributions are limited by the thermically defined middle boreal zone (Moen et al. 1999). These species are confined to interior sites characterized by high summer temperatures.

An alternative explanation why many epiphytic lichens may only be found in interior sites of northern Norway is limited dispersal capacity. Dispersal limitation has been suggested as a reason why some lichens are locally restricted to old growth forests (Dettki et al. 2000; Sillett et al. 2000). Long distance dispersal events are rare in most organisms (Hanski & Gaggiotti 2004). Some lichen species might just not have been reaching or colonizing the coastal sites so far, but would, in principle, be able to grow under the ecological conditions at the coast. Results from a transplantation experiment of lichen species restricted to interior sites (unpublished data) suggest that ecological conditions of coastal sites may not be limiting survival of species restricted to the interior. At least one year after the establishment of transplants, there was no significant difference in the survival rate of transplants of *Lobaria scrobiculata* and *L. hallii* between coastal and inland sites of Troms county.

Another factor is that forests along the coast have been severely diminished due to agricultural practice for centuries, which is witnessed by the massive invasion of juvenile trees now taking place in Troms, when farms are abandoned and grazing is strongly reduced. However, in the inland, most of the thermophilic lichens recorded in this study have occurrences on rocks. Such occurrences are very rare halfway along the transect, even though suitable rock substrates are present in the whole study area. This increase in habitat specialization towards coastal sites indicates that climatic factors might be decisive, speaking against the preliminary

results of the transplantation experiment. Further studies of the thermophilic saxicolous lichen flora at thermically favorable and unfavorable sites are necessary to solve this question.

The second major gradient in epiphytic macrolichen communities determined in this study, next to climate, was spatial variance, accounting to 25.5 % of total variance explained. This is comparable to what Liu & Bråkenhielm (1995) found in a study of lichen communities on Scots Pine performed in Sweden, where spatial variance accounted for 27.2 % of the total variance. Ohmann & Spies (1998), on the other hand, found a considerably lower amount of spatial variation for forest vegetation in the northwestern USA (15.0 %). In the present study, geographic location is more important for lichen communities than geographic extent of the study area, which is also in accordance with the results of Ohmann & Spies (1998). Organisms are distributed neither regularly nor at random within communities, but they are assembled along gradients, or aggregated in patches (Legendre & Fortin 1989). Many population processes work at small spatial scales (e.g. dispersal, Nathan & Müller-Landau 2000), leading to spatial patterns in species distribution and to spatial autocorrelation.

The last significant gradient detected was variance in substrate conditions, accounting for 17.0 % of the total variance (Fig. 3). Substrate-related variance in epiphyte communities has been emphasized in many local-scale studies (Barkman 1958; Brodo 1973; Burgaz et al. 1994; Oksanen 1988). Variation due to forest stand properties, carrier tree species and bark properties is often considered significant (Bates 1992; Gauslaa 1985; Gustafsson & Eriksson 1995; Hyvärinen et al. 1992). In our study, two of the forest-stand related environmental variables, *Populus* forest and presence of *Alnus incana* were significant. *Populus tremula* has a rich circumneutral bark (Gustafsson & Eriksson 1995) and is inhabited by specialized lichen species (Hedenås & Ericson 2000; Kuusinen 1994; Kuusinen 1996), which accounts for some of the variance found in the

1 epiphytic macrolichen communities. *Alnus incana* is also a rich bark tree species, but has a more
2 acidic bark than *Populus tremula* (unpublished data). Therefore, the variance explained by forest-
3 stand variables was caused by the presence of rich bark tree species.

4 The DCA ordination reflected the main gradient structure detected by CCA, and gave
5 further evidence that the interpretation of the main gradients was reliable.

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Tables

Table 1. Species list. The table includes abbreviations (Abbr.), thermophily (T), growth form (GF), photobiont (PB) and frequencies in coastal (35) and inland (34) study plots. The symbol “+” indicates that a species is thermophilic, i.e. restricted to the middle boreal zone, with the symbol “c” added in cases where only occurrences in corticolous habitats can be considered thermophilic. For functional groups, A = alectorioid, F = folious, P = shrub-formed pendulous and S = shell-formed lichen. For photobionts, C = cyanobiont and G = chlorobiont.

Taxon	Abbr.	T	GF	PB	Frequency	
					Coast	Inland
<i>Bryoria capillaris</i>	Bry cap		A	G	1	0
<i>Bryoria fuscescens</i>	Bry fus		A	G	19	16
<i>Bryoria glabra</i>	Bry gla	+	A	G	2	1
<i>Bryoria implexa</i>	Bry imp		A	G	2	0
<i>Bryoria simplicior</i>	Bry sim		A	G	11	20
<i>Cetraria sepincola</i>	Cet sep		F	G	2	2
<i>Collema fasciculare</i>	Col fas	+	F	C	0	1
<i>Collema furfuraceum</i>	Col fur	+	F	C	0	8
<i>Collema nigrescens</i>	Col nig	+	F	C	1	1
<i>Evernia prunastri</i>	Eve pru	+	P	G	2	1
<i>Hypogymnia austerodes</i>	Hyp aus		F	G	0	4
<i>Hypogymnia bitteri</i>	Hyp bit	+	F	G	0	3
<i>Hypogymnia physodes</i>	Hyp phy		F	G	32	34
<i>Hypogymnia tubulosa</i>	Hyp tub	+	F	G	7	3
<i>Imshaugia aleurites</i>	Ims ale		F	G	1	3
<i>Leptogium saturninum</i>	Lep sat		F	C	9	11
<i>Lobaria amplissima</i>	Lob amp	+	F	CG	0	1
<i>Lobaria hallii</i>	Lob hal	+	F	C	1	5
<i>Lobaria pulmonaria</i>	Lob pul	+	F	CG	1	2
<i>Lobaria scrobiculata</i>	Lob scr	+	F	C	9	20
<i>Melanelia exasperata</i>	Mel eta	+	F	G	8	10
<i>Melanelia exasperatula</i>	Mel ela	+	F	G	1	0
<i>Melanelia fuliginosa</i>	Mel ful	+	F	G	2	0
<i>Melanelia olivacea</i>	Mel oli		F	G	33	34
<i>Melanelia subaurifera</i>	Mel sub	+	F	G	19	26
<i>Nephroma bellum</i>	Nep bel		F	C	21	25
<i>Nephroma expallidum</i>	Nep exp		F	CG	1	1
<i>Nephroma parile</i>	Nep par		F	C	18	21
<i>Nephroma resupinatum</i>	Nep res	+	F	C	7	11

<i>Parmelia omphalodes</i>	Par omp		F	G	2	1
<i>Parmelia saxatilis</i>	Par sax		F	G	15	11
<i>Parmelia sulcata</i>	Par sul		F	G	35	34
<i>Parmeliella triptophylla</i>	Par tri		S	C	4	7
<i>Parmeliopsis ambigua</i>	Par amb		F	G	34	33
<i>Parmeliopsis hyperopta</i>	Par hyp		F	G	27	28
<i>Peltigera aphthosa</i>	Pel aph		F	CG	0	4
<i>Peltigera canina</i>	Pel can		F	C	2	5
<i>Peltigera collina</i>	Pel col	+	F	C	1	5
<i>Peltigera degenii</i>	Pel deg		F	C	1	0
<i>Peltigera didactyla</i>	Pel did		F	C	1	2
<i>Peltigera leucophlebia</i>	Pel leu		F	CG	1	1
<i>Peltigera malacea</i>	Pel mal		F	C	0	2
<i>Peltigera membranacea</i>	Pel mem		F	C	15	8
<i>Peltigera neopolydactyla</i>	Pel neo		F	C	2	6
<i>Peltigera ponojensis</i>	Pel pon		F	C	1	0
<i>Peltigera praetextata</i>	Pel pra		F	C	6	7
<i>Peltigera retifoveata</i>	Pel ret		F	C	0	1
<i>Peltigera rufescens</i>	Pel ruf		F	C	0	1
<i>Phaeophyscia ciliata</i>	Pha cil	+	F	G	2	0
<i>Phaeophyscia nigricans</i>	Pha nig	+	F	G	1	0
<i>Phaeophyscia orbicularis</i>	Pha orb		F	G	1	1
<i>Phaeophyscia sciastra</i>	Pha sci		F	G	1	0
<i>Physcia adscendens</i>	Phy ads	+	F	G	1	0
<i>Physcia aipolia</i>	Phy aip		F	G	14	19
<i>Physcia caesia</i>	Phy cae		F	G	1	0
<i>Physcia dubia</i>	Phy dub		F	G	1	0
<i>Physcia stellaris</i>	Phy ste		F	G	6	10
<i>Physcia tenella</i>	Phy ten	+c	F	G	2	0
<i>Physconia distorta</i>	Pho dis	+	F	G	6	8
<i>Physconia perisidiosa</i>	Pho per	+	F	G	1	0
<i>Platismatia glauca</i>	Pla gla		F	G	3	4
<i>Protopannaria pezizoides</i>	Pro pez		S	C	7	5
<i>Psoroma hypnorum</i>	Pso hyp		S	CG	5	1
<i>Ramalina farinacea</i>	Ram far	+	P	G	2	1
<i>Sphaerophorus globosus</i>	Sph glo		P	G	1	2
<i>Tuckermanopsis chlorophylla</i>	Tuc chl		F	G	13	5
<i>Usnea subfloridana</i>	Usn sub	+	P	G	6	5
<i>Vulpicida pinastri</i>	Vul pin		F	G	23	33
<i>Xanthoria candelaria</i>	Xan can		F	G	2	0
<i>Xanthoria elegans</i>	Xan ele		F	G	0	1
<i>Xanthoria parietina</i>	Xan par	+c	F	G	0	1

Table 2. Partitioning of the variation in epiphytic macrolichen communities on the four sets of explanatory variables: forest and environmental variables {E}, macroclimate, microclimate and topography {C}, human impact {H} and spatial variables {S}. Variation explained (VE) is given in inertia units, IU (total inertia was 3.460 IU) as well as fraction of the total variation explained (FTVE) where the total variation explained was 0.912 IU. The Bonferroni-corrected significance level (p) was 0.0025. The symbols “ $\cup$ ” and “ $\cap$ ” indicate unions and intersections of variable sets, while “ $\neg$ ” stands for the Boolean operator NOT.

Constraining variables	Co-variables	Variation explained				Remarks
		Denotation	VE	FTVE	p	
{C}	none	C	.449	49.2	.0005	Variance explained by macroclimate
{E}	none	E	.223	24.5	.0005	Variance explained by environmental differences
{H}	none	H	.076	8.3	.0030	Variance explained by human impact
{S}	none	S	.348	38.2	.0005	Variance explained by geography
{C}	{E, H, S}	$C (E \cup H \cup S)$	.319	35.0	.0005	Variance explained by {C} not shared with any other variable sets, i.e. purely macroclimatic variance
{E}	{C, H, S}	$E (C \cup H \cup S)$	.155	17.0	.0015	Pure environmental variance; statistically significant
{H}	{C, E, S}	$H (C \cup E \cup S)$	.047	5.2	.3438	Strictly human impact variance; statistically not significant
{S}	{C, E, H}	$S (C \cup E \cup H)$	.233	25.5	.0005	Strictly spatial variance; statistically significant
{E}	{C}	$E C$	.175	19.2	.0020	$E \cap C = E - E C = 0.048$ (5.3 %), i.e. covariance of macroclimatic and environmental variables.
{E}	{H}	$E H$	.224	24.6	.0005	$E \cap H = E - E H = 0.000$ (0.0%)
{E}	{S}	$E S$	.185	20.3	.0005	$E \cap S = E - E S = 0.038$ (4.2 %), i.e. spatially structured environmental variance.
{C}	{H}	$C H$	.434	47.6	.0005	$C \cap H = C - C H = 0.015$ (1.6 %)
{C}	{E}	$C E$	.401	44.0	.0005	$C \cap E = C - C E = 0.048$ (5.3 %)
{C}	{S}	$C S$	.355	38.9	.0005	$C \cap S = 0.094$ (10.3 %), i.e. spatially structured macroclimatic variance.
{S}	{C}	$S C$	.254	27.9	.0005	$S \cap C = 0.094$ (10.3 %)
{S}	{H}	$S H$	.338	37.1	.0005	$S \cap H = 0.010$ (1.1 %)
{S}	{E}	$S E$	.308	33.8	.0005	$S \cap E = 0.040$ (4.4 %)
{H}	{C}	$H C$	.061	6.7	.0880	$H \cap C = 0.015$ (1.6 %)
{H}	{E}	$H E$	.077	8.4	.0040	$H \cap E = 0.000$
{H}	{S}	$H S$	.066	7.2	.0480	$H \cap S = 0.010$ (1.1 %)
{C}	{H, S}	$C (H \cup S)$	.343	37.6	.0005	$C \cap H \cap S = C - C (H \cup S) - C H - C S = 0.003$
{C}	{E, S}	$C (E \cup S)$	.333	36.5	.0005	$C \cap E \cap S = C - C (E \cup S) - C E - C S = 0.026$; $C \cap E \cap S \cap H = 0$ ($H \cap E = 0$); $(S \cap C) (H \cup E) = 0.065$

Figures

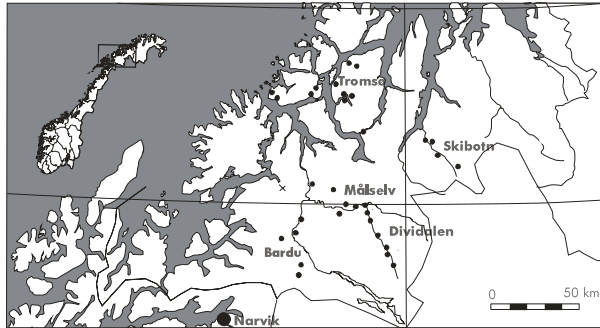


Figure 1. Map of the study area in central and southern Troms county, northern Norway. Small dots indicate sampling locations.

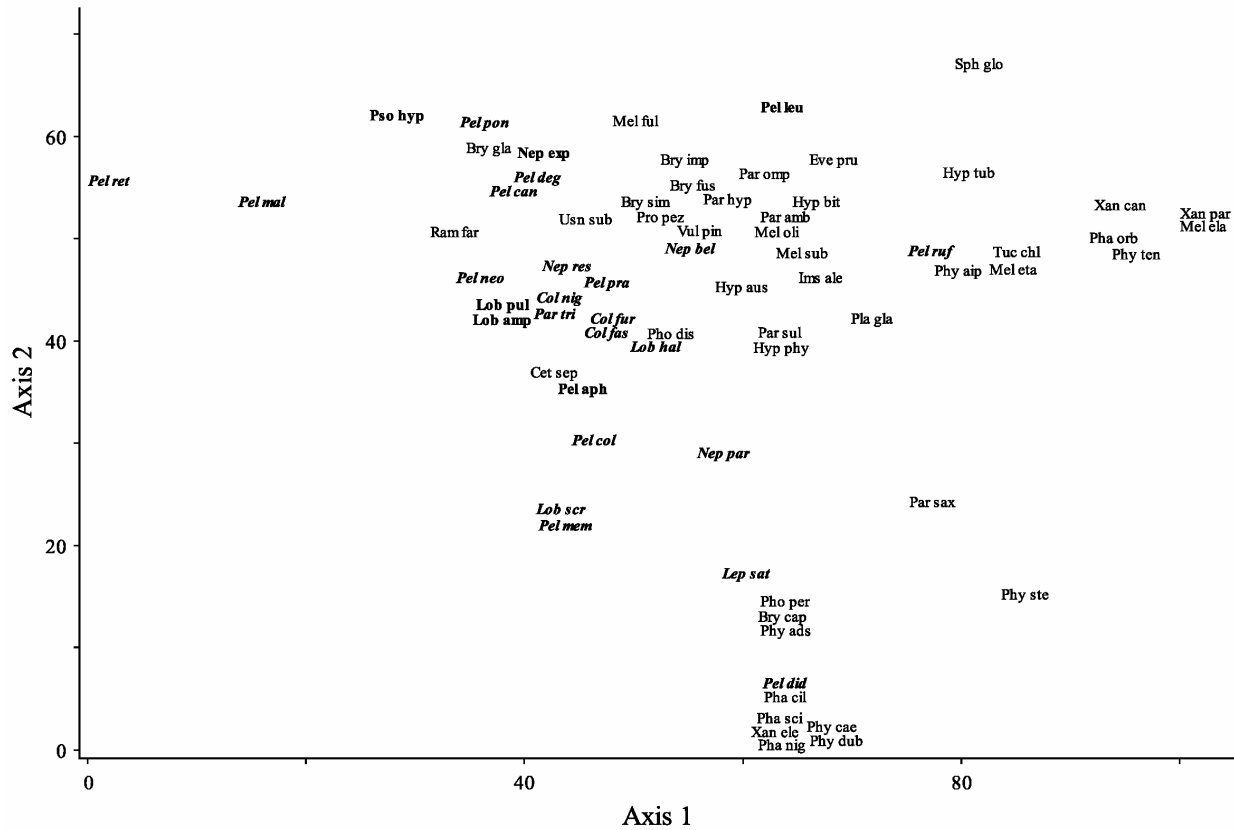


Figure 2. DCA ordination diagram of macrolichens from northern Norway showing the species optima along the first two axes. Cyanolichens are shown with bold italics, tripartite lichens with bold text; the remaining macrolichen species are chlorolichens.

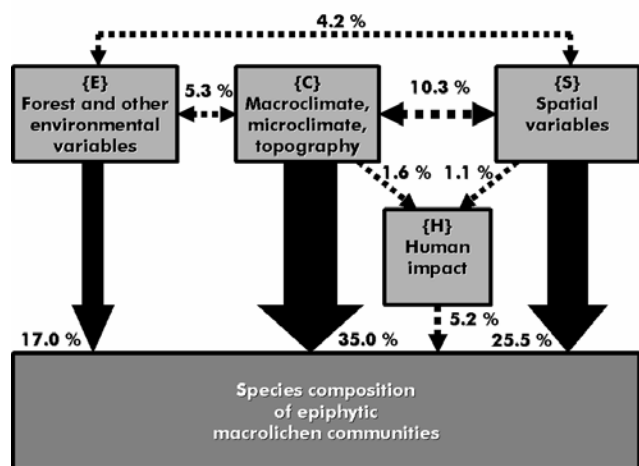


Figure 3. Fraction of total variation explained (FTVE) and shared variance in epiphytic macrolichen communities of northern Norway, partitioned to four sets of explanatory variables: forest and environmental variables {E}, macroclimate, microclimate and topography {C}, human impact {H} and spatial variables {S}. Arrows among variable sets indicate their shared FTVE. Arrows pointing to macrolichen species composition show the fraction of the total variance which was explained by a respective set of explanatory variables, when covariance with all remaining sets had been removed. Dashed lines indicate that a specific FTVE was not statistically significant ($p \geq 0.0025$).