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Epiphytic macrolichen communities along regional gradients in northern Norway

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Abstract

Question: What are the relative influences of human impact, macroclimate, geographic location and habitat related environmental differences on species composition of boreal epiphytic macrolichen communities?

Location: Troms county in northern Norway.

Methods: Detrended Correspondence Analysis revealed the main gradient structure in lists of epiphytic macrolichen species from deciduous forests. By Canonical Correspondence Analysis 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 ecological differences 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.

Keywords: Environmental variation; Human impact; Lichen; Macroclimate; Ordination; Spatial variation; Variance partitioning.

Nomenclature: Santesson et al. (2004); Lid & Lid (1994).

Introduction

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

Lichens are good model organisms to assess the effects of human impact on ecosystems because of their sensitivity to various types of human impact such as logging (Rose 1992; Wirth 1995; Hedenås & Ericson 2003), land use (Wirth 1999) or air pollution (Richardson 1992; Gombert et al. 2004). The latter has caused depauperation of lichen communities over large areas of Europe. However, in other areas, such as northern Fennoscandia, the negative effects of air pollution are marginal (van Herk et al. 2003). It has been speculated that land use and logging are of primary importance here.

In the present study, partial CCA (Canonical Correspondence Analysis), which is a powerful tool for testing specific hypotheses about community - environment relationships (Birks 1993; Økland & Eilertsen 1994), was applied to a data set of epiphytic macrolichen communities from 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 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 negligible in the study area in Troms county (Tømmervik et al. 2003). Only deciduous forests at altitudes below 500 m a.s.l. were included in the analyses. The tree line in the area is formed by *Betula pubescens* and presently lies between 150 m a.s.l. on the outermost northwestern islands of Troms and 750 m a.s.l. in the southeastern valleys in the interior of Troms, 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). We were interested in a regional gradient in species composition rather than in fine-scale within-site variation, so we used large study plots as recommended by Økland (1990), leading to an increased species capture (McCune & Lesica 1992). One study plot of 400 m² was selected randomly within each of the forest types at each location included in the analyses, which were alder forests (*Alnus incana*), alder-willow swamp forests (*Salix pentandra*, *S. myrsinifolia*), nutrient-rich *Betula* forests, nutrient-poor *Betula* forests, dry

willow forests on 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. *P. tremula* and *S. caprea* forests were often too small to follow this randomisation procedure. In these cases the study plot to be analysed was located in the centre of the respective forest patch. Plots were rejected if closer than 2 m to the nearest forest edge, if containing less than three trees > 4 cm in collar diameter or if > 30 % of the study plot area was open water. Presence-absence data of corticolous, epiphytic macrolichen species were recorded on lower stems (< 2 m) of deciduous trees in a total of 69 study plots. The sampling of trunk habitats did not include the lowest parts of the trunks with a terricolous bryophyte cover, often with terricolous/muscicolous lichens such as *Peltigera* spp. and *Cladonia* spp. extending continuously upwards, often to stem heights of 3 cm. Macrolichens were defined as the species treated 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 71 explanatory variables was used to characterise the plots. They were grouped into four sets of explanatory variables: {C}, a set of 15 macroclimatic,

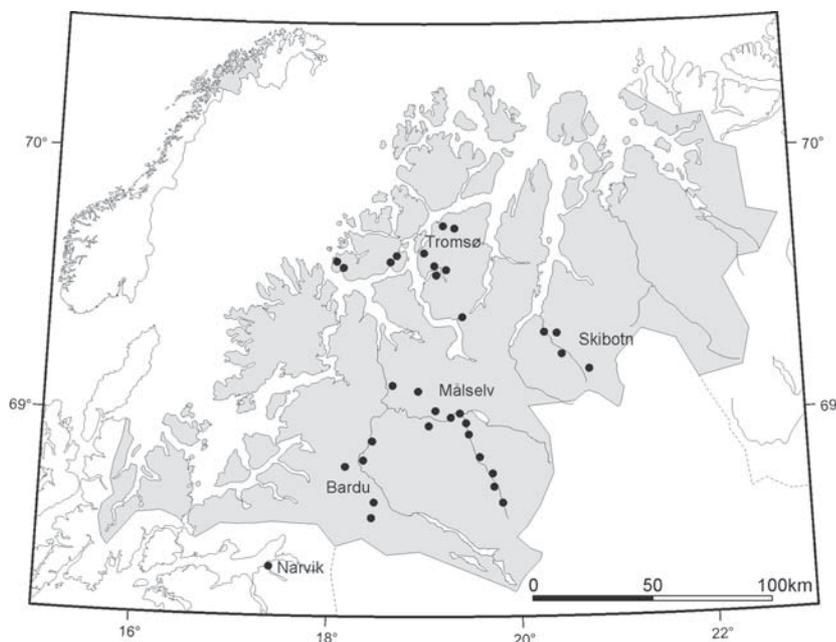


Fig. 1. Map of the study area in central and southern Troms county, northern Norway. Dots indicate sampling locations.

microclimatic and topographic variables; {E}, a set consisting of 34 forest structure and growth substrate related environmental variables – referred to as environmental variables in the following; {H}, consisting of 10 human impact variables and {S}, composed of 12 spatial variables. Details about all explanatory variables are given in App. 1.

Monthly and annual normal values (reference period 1961-1990; Aune 1993; Førlund 1993) for precipitation and annual temperature sums were included in set {C}. Extrapolated data for the study plots were provided by The Norwegian Meteorological Institute, Klimaavdelingen. Climatic oceanicity was determined from a map in Moen (1999), distances to open sea and closest seashore were determined from maps of scale 1:500 000. Moisture and light conditions of the plots were estimated using a five-point scale, ranging from dry to wet and from low light to high light situations, respectively. Further variables were the mean slope angle of the study plot, plot elevation, plot aspect, a plot heat index (Parker 1988), a 15 point irradiation index with highest values for S and SSW exposure and aspect unfavourability, i.e. the deviation of aspect from SSW exposure (T. Økland 1996). Most of these latter variables characterize the microclimate of the plots.

In the set of environmental variables {E}, a rock suitability index, giving an approximate 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 (Wirth 1995) frequently grow 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 > 5 cm) in a 100-m² subplot, tree density and basal area were calculated. Tree species composition was identified as presence-absence of species. The type of deciduous forest was determined and coded as binary variables. Decay class (Linder et al. 1997), diameter, number, density, position and decay class of dead wood (basal diameter > 10 cm) was recorded in 100-m² subplots. The number and density of all young trees (DBH < 5 cm) present in 100-m² subplots was recorded. 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. A landscape patchiness index 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 radius around the study plots.

In the set of human impact related variables {H}, the

presence or absence of *Picea* spp. or *Larix* spp. plantations in visible distance from the study plots was recorded. In the 500-m radius area mentioned above, the distance to and length of outlines of structures related to human settlements and of clearly human induced deforestation 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 on a plot was estimated using criteria suggested by Trass et al. (1999). For our purpose, the 13 point human impact scale of Trass et al. (1999) was reversed, with the starting point of 1. Note that the three highest human impact categories were missing in our data set.

To enable detection of complex, large-scale spatial patterns, 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). In addition, geographic location of plots was included as binary variables, defined by plot affiliations to the municipalities of Tromsø, Storfjord and Målselv.

A bark sample was collected from a specimen of the dominant tree species in each study plot. Bark pH was measured with a pH-meter after soaking bark samples in double distilled water for three hours. The age of the largest deciduous tree in a study plot was determined from a core taken 10 cm above ground level.

Statistical analysis

We performed DCA (Detrended Correspondence Analysis) ordination (Hill & Gauch 1980) to reveal the main gradient structure of the data set. Global non-metric multidimensional scaling (Kruskal 1964) gave results comparable to DCA and thus corroborated DCA results (R. Økland 1996). Kendall's τ correlation coefficients between environmental variables and DCA axes and their significance was calculated (Sokal & Rohlf 1995). Since we were unable to interpret DCA axes three and four in a biologically meaningful way, results are only shown for the first two axes.

All explanatory variables recorded on a continuous measurement scale were transformed to zero skewness, followed by ranging (Økland et al. 2001). As a prelude to variation partitioning, variables were selected separately for each of the four sets by the forward selection procedure in CANOCO, followed by Monte Carlo permutation tests. The threshold statistical significance value for inclusion of a variable in a particular set of explanatory variables was Bonferroni corrected to $\alpha = 0.05$. Statistically significant variables were checked for collinearity, and the rejection criterion was a variance inflation factor >5.

Using partial CCA (ter Braak 1988), we partitioned variance in macrolichen community composition onto 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 R software Version 2.0.0 (Anon. 2004) were used.

Results

A total of 71 epiphytic macrolichen species was found in the 69 study plots (Table 1). Gradient lengths of the first two DCA axes were 1.950 and 1.899, implying that two short gradients were present in the data. The first DCA axis was significantly related to *Betula pubescens* forest, poor in nutrients, and to the study plots' location in Tromsø municipality in the coastal part of the study area (Table 2, Fig. 2). DCA axis two was significantly correlated with latitude, combinations of latitude and longitude, oceanicity and the amount of precipitation (see also App. 2). Most of the variables significantly related to DCA axis two were strongly correlated with each other (Fig. 2). Species optima for lichens associated with green algal photobionts were separated from optima of lichens associated with cyanobacteria along DCA axes 1 and 2 (Fig. 3).

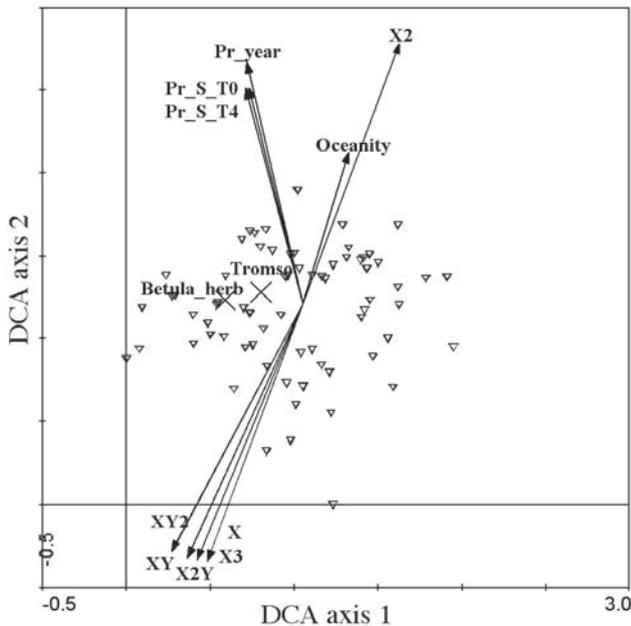


Fig. 2. DCA ordination diagram of macrolichen communities in deciduous forests of northern Norway. The biplot shows study plots (▽) and significantly correlated environmental variables (arrows and X) along the first two axes.

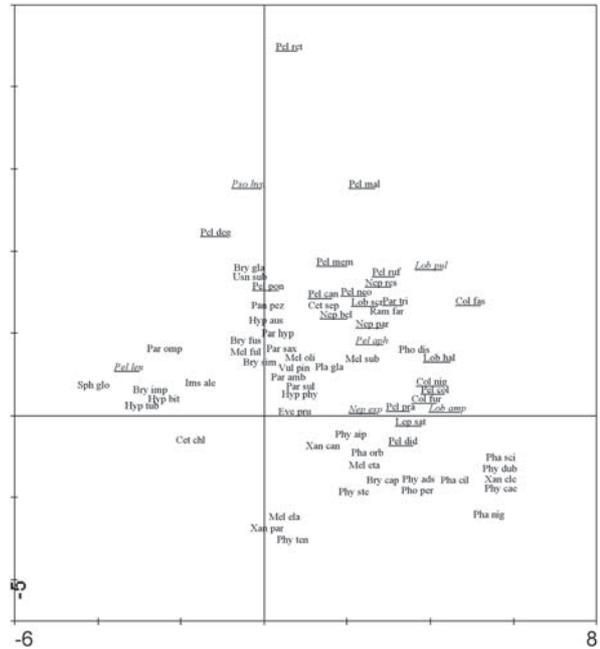


Fig. 3. DCA ordination diagram of macrolichen communities in deciduous forests of northern Norway showing the species optima along the first two axes. Cyanolichens are underlined, tripartite lichens underlined and in italics; the remaining macrolichen species are chlorolichens.

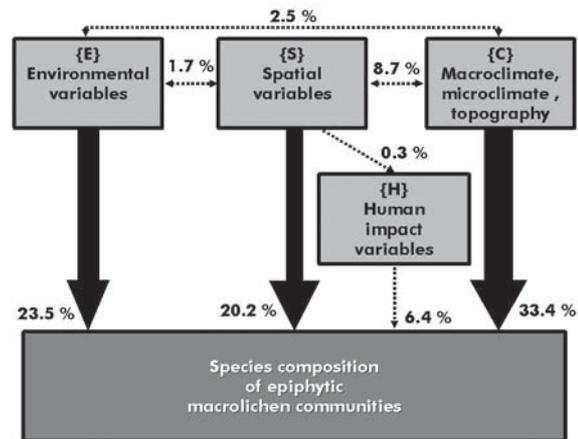


Fig. 4. Fraction of the total variation explained (FTVE) and shared variance in epiphytic macrolichen communities of northern Norway, partitioned to four sets of explanatory variables: forest and environmental variables {E}, macroclimate, microclimate and topography {C}, human impact {H} and spatial 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.

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 = foliose; P = shrub-formed pendulous and S = squamulose lichen. For photobionts, C = cyanobiont and G = chlorobiont.

Taxon	Abbr.	T	GF	PB	Frequency	
					Coast	Inland
<i>Bryoria capillaris</i>	Bry cap		A	G	1.4	0.0
<i>Bryoria fuscescens</i>	Bry fus		A	G	27.5	23.2
<i>Bryoria glabra</i>	Bry gla	+	A	G	2.9	1.4
<i>Bryoria implexa</i>	Bry imp		A	G	2.9	0.0
<i>Bryoria simplicior</i>	Bry sim		A	G	15.9	29.0
<i>Collema furfuraceum</i>	Col fas	+	F	C	0.0	1.4
<i>Collema fasciculare</i>	Col fur	+	F	C	0.0	11.6
<i>Collema nigrescens</i>	Col nig	+	F	C	1.4	1.4
<i>Evernia prunastri</i>	Eve pru	+	P	G	2.9	1.4
<i>Hypogymnia austerodes</i>	Hyp aus		F	G	0.0	5.8
<i>Hypogymnia bitteri</i>	Hyp bit	+	F	G	0.0	4.3
<i>Hypogymnia physodes</i>	Hyp phy		F	G	46.4	49.3
<i>Hypogymnia tubulosa</i>	Hyp tub	+	F	G	10.1	4.3
<i>Imshaugia aleurites</i>	Ims ale		F	G	1.4	4.3
<i>Leptogium saturninum</i>	Lep sat		F	C	13.0	15.9
<i>Lobaria amplissima</i>	Lob amp	+	F	CG	0.0	1.4
<i>Lobaria hallii</i>	Lob hal	+	F	C	1.4	7.2
<i>Lobaria pulmonaria</i>	Lob pul	+	F	CG	1.4	2.9
<i>Lobaria scrobiculata</i>	Lob scr	+	F	C	13.0	29.0
<i>Melanelia exasperata</i>	Mel eta	+	F	G	11.6	14.5
<i>Melanelia exasperatula</i>	Mel ela	+	F	G	1.4	0.0
<i>Melanelia fuliginosa</i>	Mel ful	+	F	G	2.9	0.0
<i>Melanelia olivacea</i>	Mel oli		F	G	47.8	49.3
<i>Melanelia subaurifera</i>	Mel sub	+	F	G	27.5	37.7
<i>Nephroma bellum</i>	Nep bel		F	C	30.4	36.2
<i>Nephroma expallidum</i>	Nep exp		F	CG	1.4	1.4
<i>Nephroma parile</i>	Nep par		F	C	26.1	30.4
<i>Nephroma resupinatum</i>	Nep res	+	F	C	10.1	15.9
<i>Pannaria pezizoides</i>	Par omp		F	G	2.9	1.4
<i>Parmelia omphalodes</i>	Par sax		F	G	21.7	15.9
<i>Parmelia saxatilis</i>	Par sul		F	G	50.7	49.3
<i>Parmelia sulcata</i>	Par tri		S	C	5.8	10.1
<i>Parmeliopsis ambigua</i>	Par amb		F	G	49.3	47.8
<i>Parmeliopsis hyperopta</i>	Par hyp		F	G	39.1	40.6
<i>Peltigera aphthosa</i>	Pel aph		F	CG	0.0	5.8
<i>Peltigera canina</i>	Pel can		F	C	2.9	7.2
<i>Peltigera collina</i>	Pel col	+	F	C	1.4	7.2
<i>Peltigera didactyla</i>	Pel deg		F	C	1.4	0.0
<i>Peltigera degenii</i>	Pel did		F	C	1.4	2.9
<i>Peltigera leucophlebia</i>	Pel leu		F	CG	1.4	1.4
<i>Peltigera malacea</i>	Pel mal		F	C	0.0	2.9
<i>Peltigera membranacea</i>	Pel mem		F	C	21.7	11.6
<i>Peltigera neopolydactyla</i>	Pel neo		F	C	2.9	8.7
<i>Peltigera ponojensis</i>	Pel pon		F	C	1.4	0.0
<i>Peltigera praetextata</i>	Pel pra		F	C	8.7	10.1
<i>Peltigera retifoveata</i>	Pel ret		F	C	0.0	1.4
<i>Peltigera rufescens</i>	Pel ruf		F	C	0.0	1.4
<i>Phaeophyscia ciliata</i>	Pha cil	+	F	G	2.9	0.0
<i>Phaeophyscia nigricans</i>	Pha nig	+	F	G	1.4	0.0
<i>Phaeophyscia orbicularis</i>	Pha orb		F	G	1.4	1.4
<i>Phaeophyscia sciastra</i>	Pha sci		F	G	1.4	0.0
<i>Physcia adscendens</i>	Phy ads	+	F	G	1.4	0.0
<i>Physcia aipolia</i>	Phy aip		F	G	20.3	27.5
<i>Physcia caesia</i>	Phy cae		F	G	1.4	0.0
<i>Physcia dubia</i>	Phy dub		F	G	1.4	0.0
<i>Physcia stellaris</i>	Phy ste		F	G	8.7	14.5
<i>Physcia tenella</i>	Phy ten	+c	F	G	2.9	0.0
<i>Physconia distorta</i>	Pho dis	+	F	G	8.7	11.6
<i>Physconia perisidiosa</i>	Pho per	+	F	G	1.4	0.0
<i>Platismatia glauca</i>	Pla gla		F	G	4.3	5.8
<i>Protopannaria pezizoides</i>	Pro pez		S	C	10.1	7.2
<i>Psoroma hypnorum</i>	Pso hyp		S	CG	7.2	1.4
<i>Ramalina farinacea</i>	Ram far	+	P	G	2.9	1.4
<i>Sphaerophorus globosus</i>	Sph glo		P	G	1.4	2.9
<i>Tuckermanopsis chlorophylla</i>	Cet chl		F	G	18.8	7.2
<i>Tuckermanopsis sepincola</i>	Cet sep		F	G	2.9	2.9
<i>Usnea subfloridana</i>	Usn sub	+	P	G	8.7	7.2
<i>Vulpicida pinastri</i>	Vul pin		F	G	33.3	47.8
<i>Xanthoria candelaria</i>	Xan can		F	G	2.9	0.0
<i>Xanthoria elegans</i>	Xan ele		F	G	0.0	1.4
<i>Xanthoria parietina</i>	Xan par	+c	F	G	0.0	1.4

Table 2. The ten variables most strongly correlated (Kendall's τ) with two DCA axes. Asterisks indicate that a respective correlation is significant at a Bonferroni-corrected overall significance level $\alpha=0.05$.

Variable	Explanation	Kendall's Tau	Axis
Betula_herb	Study plot situated in birch forest poor in nutrients	*-0.39	DCA1
Tromso	Study plot located in Tromsø municipality	*-0.29	DCA1
Aln_inc	Presence of <i>Alnus incana</i>	0.27	DCA1
Dist_town	Distance to closest town	-0.23	DCA1
TM_SUM4	Temperature sum of all months exceeding 4°C mean air temperature	0.23	DCA1
Bet_pub	Presence of <i>Betula pubescens</i>	-0.21	DCA1
Sal_cap	Presence of <i>Salix caprea</i>	0.19	DCA1
Sor_auc	Presence of <i>Sorbus aucuparia</i>	0.19	DCA1
Tree_age	Tree age	-0.18	DCA1
Open_forest	Proportion of open area to forested area	-0.16	DCA1
X	Longitude	*-0.38	DCA2
X2	Longitude ^2	*0.38	DCA2
X3	Longitude ^3	*-0.38	DCA2
X2Y	Longitude ^2*Latitude	*-0.37	DCA2
XY	Longitude *Latitude	*-0.36	DCA2
XY2	Longitude *Latitude^2	*-0.34	DCA2
Pr_year	Annual normal precipitation	*0.34	DCA2
Pr_S_T4	Sum of precipitation in all months exceeding 4 °C in mean air temperature	*0.33	DCA2
Pr_S_T0	Sum of precipitation in all months exceeding 0 °C in mean air temperature	*0.31	DCA2
Oceanicity	Oceanicity of climate	*0.30	DCA2

Of 71 explanatory variables, 11 were statistically significant and were therefore used for variation partitioning. Significant variables included in {C} were oceanicity, distance to open sea, precipitation and temperature sum; in {E} the suitability of rock habitats, the presence of *Alnus incana* and *Betula pubescens* forest with a field layer dominated by herbs; in {H} the overall human impact index only and in {S} longitude and location of study plots in Tromsø and Storfjord municipalities. The full model (with all 11 significant variables) explained 26 % of the total inertia (3.44 inertia units, IU).

The largest amount of variance was explained by the set of macroclimatic variables (48.0%), followed by the set of spatial variables (33.7%) and environmental variables (30.3%). It is noteworthy that human impact only explained 9.1 % of the variance (Table 3). None of the variable sets alone explained statistically significant amounts of variance, when variance due to the remaining sets had been partialled out (Table 3; Fig. 4). The variance attributable to second, third and fourth order partial intersections of variable sets was marginal (< 1.7%).

The bark pH ranges of most deciduous tree species were higher than expected (i.e. ca. 2 pH units; Table 4). There was no significant difference in the bark pH of *Alnus incana* and *Populus tremula* (t -test, $p = 0.061$). The maximum age found for tree cores of *Salix pentandra*, *S. caprea* and *Prunus padus* was ca. 70 years, whereas that of *Betula pubescens* was 180 years.

Table 3. 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}. The denotation of the respective term calculated (Denotation), the sum of all canonical eigenvalues (EV), the fraction of the total variance explained (FTVE), and the p -value of the respective term (p) are shown in the table. Variation explained (EV) is given in inertia units, IU (total inertia was 3.44 IU, total variance explained was 0.909 IU) as well as fraction of the total variation explained (FTVE). The symbols '∪' and '∩' indicate unions and intersections of variable sets, while '!' stands for the Boolean operator NOT; n.p. no test performed. Asterisks indicate that a respective fraction of total explained variance is statistically significant at a Bonferroni-corrected α of 0.05.

Denotation	EV	FTVE	p
E	0.276	*30.3	< 0.001
C	0.436	*48.0	< 0.001
S	0.306	*33.7	< 0.001
H	0.083	9.1	0.011
E (C ∪ H ∪ S)	0.214	23.5	0.005
C (E ∪ H ∪ S)	0.304	33.4	0.005
S (E ∪ H ∪ C)	0.184	20.2	0.015
H (E ∪ S ∪ C)	0.058	6.4	0.302
(E ∩ S) (C ∪ H)	0.015	1.6	n.p.
(E ∩ H) (C ∪ S)	0.000	0.0	n.p.
(E ∩ C) (H ∪ S)	0.023	0.3	n.p.
(S ∩ H) (E ∪ C)	0.002	0.0	n.p.
(S ∩ C) (E ∪ H)	0.080	0.8	n.p.
(H ∩ C) (E ∪ S)	0.000	0.0	n.p.
(C ∩ H ∩ S) E	0.007	0.8	n.p.
(E ∩ H ∩ S) C	0.001	0.1	n.p.
(E ∩ C ∩ H) S	0.007	0.8	n.p.
(E ∩ S ∩ C) H	0.007	0.8	n.p.
E ∩ C ∩ H ∩ S	0.010	1.1	n.p.

Discussion

Our DCA and partial CCA results show that human impact is not a key factor structuring epiphytic macrolichen communities in deciduous forests of central Troms county. This finding is in accordance with that of a study of forest vascular plant vegetation in the northwestern United States in which clearfelling accounted for only 2 % of the total variation explained (Ohmann & Spies 1998). The effect of logging on lichen species depends on population size and habitat preferences. Rare species are at higher risk of becoming locally extinct because of logging than common species. Logging will probably have a long-term negative effect only on species restricted to certain habitat types; species that are rare and irregularly distributed in a landscape. Dispersal ability may become a restricting factor if logging not only reduces the total area of available habitat, but also number of favourable landscape patches as has been hypothesised for deciduous forests of central Europe (Wirth 1999).

Proposals for lichen species that can be used as indicators of human impact on forests (Pfefferkorn & Türk 1996) or ecological continuity of forests (Rose 1992) are rarely built on statistical analysis of empirical data. This perpetuates the problem of confounding habitat qualities with human impacts such as logging regimes. Forests that have remained undisturbed for a longer time usually contain many specific habitats suitable for the growth of different epiphytic lichens, such as large old trees, logs and snags (Peterson & McCune 2001; Jüriado et al. 2003). This is mainly due to a shift in forest structure with time since disturbance, 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 (Rose 1992; Kuusinen 1996) or hemerophoby (Trass et al. 1999). Likewise, forest thinning did not have the anticipated negative effect on old-growth dependent cyanolichens, but rather led to a slight increase of alectoroid and drought-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 nor the frequency of large old trees, which may act as source of lichen propagules for enhanced colonisation of trees remaining after management. In contrast, in a study focusing on branch macrolichen communities,

Table 4. pH value of deciduous tree bark in the study area in Troms county, showing species (Tree species), minimum pH (Min), mean pH (Mean), maximum pH value measured (Max), number of bark samples analysed to determine the latter values (n), maximum age among all tree cores of a species (Maxage) and the number of tree cores taken (Cores).

Tree species	Min	Mean	Max	n	Maxage	Cores
<i>Alnus incana</i>	4.5	5.3	6.7	26	103	17
<i>Betula pubescens</i>	4.1	4.8	6.1	33	180	48
<i>Populus tremula</i>	5.0	5.7	6.9	8	92	7
<i>Prunus padus</i>	5.1	5.5	5.8	3	64	3
<i>Salix caprea</i>	4.8	5.3	6.9	18	76	12
<i>Salix myrsinifolia</i>	4.8	5.9	6.6	25	106	9
<i>Salix pentandra</i>	5.5	5.7	6.1	15	63	3
<i>Sorbus aucuparia</i>	4.6	5.8	6.4	21	114	12

cyanolichens were common in old-growth stands, but virtually absent in secondary, even-aged stands (Radies & Coxson 2004). Logging is likely to lead to an increase of solar radiation on remnant trees to levels destructive for several old forest lichens (Gauslaa & Solhaug 2000). In valley bottom sites in northern Norway that receive a low amount of solar irradiation due to a low sun angle, this effect is probably not of importance; explaining the low importance of human impact found in our study.

The climate of Troms county can be characterised as oceanic to suboceanic, with the climatically most favourable sites for lichens belonging to the *Lobarion-pulmonariae* alliance situated in inland valley bottoms. The habitat of the *Lobarion* is closely related to macroclimate, in particular humidity (Barkman 1958). In a favourable oceanic climate, *Lobarion* species more quickly colonise young stands than in drier climates (Peterson & McCune 2001) and may, therefore, be more resilient to logging than under growth conditions further from their climatic optimum (Anonby 1994). In contrast, for thermophilic lichen species reaching their northern distribution limits in northern Norway, logging and other human impacts were assumed to have strong effects. However, no evidence of such an effect is found in the present data set.

Both the DCA and the CCA results show strong relationships between epiphytic macrolichen species composition and macroclimatic factors. DCA axis two reflected the gradient from moist coastal to drier interior sites. Typical coastal species with low optima along this axis are *Xanthoria parietina*, *X. candelaria* and *Physcia tenella*, while *Lobaria amplissima*, *L. pulmonaria*, *L. hallii* and *Collema fasciculare* are characteristic interior species. Fundamental importance of macroclimate for lichen communities accords with the findings of McCune et al. (1997) and Peterson & McCune (2001) from the USA. In a Swedish investigation of epiphytic algae on spruce needles and epiphytic lichens on trunks of *Pinus*

sylvestris, however, macroclimatic variation only accounted for 14.1 % of the total variation in species composition (Liu & Bråkenhielm 1995). Oceanicity, precipitation and local temperature sums are the main determinants of macrolichen community composition in our study. There may be several reasons for this. First, there is a strong climatic gradient in the study area from oceanic coastal sites with low temperature sums and high annual precipitation to inland sites characterised by a more continental climate with high temperature sums and lower annual precipitation (Aune 1993; Førland 1993). Thermophilic lichens in northern Norway may experience a trade-off between demands for precipitation and temperature – demands for precipitation favour a coastal distribution, temperature requirements are satisfied in climatically favourable interior sites. Species with an oceanic distribution in central Europe such as *Collema fasciculare*, *C. nigrescens*, *Degelia plumbea*, *Lobaria amplissima*, *L. pulmonaria*, *L. scrobiculata*, *Pannaria conoplea* and *Sphaerophorus globosus* (Schauer 1965; Wirth 1995) may be limited by low temperature sums in coastal sites of northern Fennoscandia. In Norway, at latitudes exceeding 68° N these oceanic species are restricted to locally moist habitats at the most continental sites, where demands for temperature and humidity are both met (Elvebakk & Sandvik 1980).

Some lichen species are good indicators of favourable local climatic conditions in northern Norway (Ingebrigtsen unpubl.). As many as 26 of the recorded species can be considered thermophilic in northern Fennoscandia, in the sense that their distributions are limited to the thermally defined middle boreal zone (Moen 1999). These species are confined to interior sites characterised by high summer temperatures. The presence of a thermophilic species group is also reflected in the DCA ordination, in which cyanolichens and tripartite lichens (that contain both cyanobacteria and green algae as photobionts), many of which are considered thermophilic in northern Norway (Ingebrigtsen unpubl.), obtain low optima on DCA axis one. Contrary to the suggestions of Barkman (1958), species typical of the nitrophilous *Xanthorion parietinae* alliance do not seem to be thermally limited in Troms. Many of these species may, however, be favoured by nutrient richness, e.g. brought about by shoreline dust: thus *Xanthoria parietina*, *X. candelaria*, *Physcia tenella* and *Melanelia exasperatula* were only found at coastal sites in Troms, where they occurred sparsely as epiphytes close to rock habitats by the shoreline where the species were abundantly present.

Another major gradient in epiphytic macrolichen communities found in this study by DCA ordination was due to environmental variation, and in CCA, environ-

mental variables accounted for 30.3 % of the total variation explained. Substrate-related variation in epiphyte communities has been emphasized in many local scale studies (Oksanen 1988; Burgaz et al. 1994). Variation due to forest stand properties, carrier tree species and bark properties is often considered significant (Bates 1992; Hyvärinen et al. 1992; Gustafsson & Eriksson 1995). In our study, the presence of *Alnus incana* was significantly influencing epiphytic macrolichen communities. The bark pH conditions of *A. incana* are commonly considered as acidic. However, in calcareous areas or in habitats influenced by dust, tree species normally with acidic bark may have higher pH and epiphyte communities characteristic of rich bark habitats may establish (Du Rietz 1944). This effect was also prevalent in the study area, where the bark pH values of *A. incana* did not differ significantly from those of the rich bark tree species *Populus tremula*. These particular bark conditions, as well as the ability of *A. incana* to live longer than other floodplain tree species (e.g. *Salix pentandra*, *Prunus padus*), may account for its particular importance for epiphytic macrolichen communities. The significance of a rock suitability index in CCA indicates that suitable rock habitats are important for macrolichen communities in the study area, where they might operate as lichen refuges from forest disturbance.

Spatial variation was also proven important by DCA ordination and variation partitioning, accounting for 33.7% of the total variation. This is comparable to the 27.2% of the total variation accounted for by spatial variables in the study of lichen communities on *Pinus sylvestris* in Sweden by Liu & Bråkenhielm (1995). In the present study, geographic location was more important for lichen communities than geographic extent of the study area, which is in accordance with the results of Ohmann & Spies (1998). Organisms are distributed neither regularly nor randomly within communities, but respond to gradients, or aggregate in patches (Legendre & Fortin 1989). Future research should be directed towards the spatial distribution of species and to their dispersal biology, since the latter is crucial for our understanding of immigration and species turnover in communities.

Acknowledgements. We thank the Norwegian Meteorological Institute for providing climate data and Tove Midtun, University of Tromsø, for help with the figures. Furthermore, we thank Rolf Holderegger for his very helpful comments on an earlier draft of the manuscript. Funding for this project was provided by the Norwegian Research Council, the German Academic Exchange Service, the Kometen Fund (University of Tromsø) and the Norwegian Institute of Nature Research. This study was supported by the Swiss National Science Foundation (SNF) under the NCCR Plant Survival.

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Received 23 September 2004;

Accepted 9 February 2005.

Co-ordinating Editor: R.H. Økland.

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www.opuluspress.se

App. 1. Explanation of environmental variables used to characterise the study plots, variable name (Variable), method used to determine variable and explanation of variable (method and explanation), units of measurement (units), explanatory variable set the variable was included into, E= environmental and forest variables, S= Spatial variables, C= Micro- and macroclimatic variables, H= human impact variables (VS), transformation formula (Trans), c value used in transformation (c), minimum value (Min), mean value (Mean), maximum value (Max), n.a. not applicable. Variables marked with (*) were ranged prior to transformation to zero skewness.

Variable	Method and explanation	Units	VS	Trans	c	Min	Mean	Max
Aln_inc	Presence/absence of <i>Alnus incana</i> in study plot.		E	None	n.a.	0.0	0.5	1.0
Aln_Sal_for	Study plot situated in alder-willow forest, composed of <i>Alnus incana</i> , <i>Salix pentandra</i> and/or <i>S. myrsinifolia</i> , (type E3a in Fremstad 1997).		E	None	n.a.	0.0	0.1	1.0
Alnus_for	Study plot situated in <i>Alnus incana</i> forest (type C3 in Fremstad 1997).		E	None	n.a.	0.0	0.3	1.0
Altit	Average plot altitude above sea level, approximated from GPS position and topographical maps.	m	C	$\ln(c+x)$	69.80378	10.0	122.8	440.0
Bas_logs	Basal area of logs, calculated from measurements of log diameters. In tree stumps, the top diameter was measured, and in logs the collar diameter.	m ² /ha	E	$\ln(c+x)$	2.12570	0.0	8.9	38.6
Bas_trees	Basal area of trees, calculated from circumference measurements of deciduous trees in 1.3 m stem height.	m ² /ha	E	$\ln(c+x)$	10.69264	1.9	26.3	71.5
Bet_pub	Presence/absence of <i>Betula pubescens</i> in study plot.		E	None	n.a.	0.0	0.9	1.0
Betula_forb	Study plot situated in nutrient-rich birch forest with a field layer dominated by forbs (type C1 and C2 in Fremstad 1997).		E	None	n.a.	0.0	0.2	1.0
Betula_herb	Study plot situated in nutrient-poor birch forest, dominated by dwarf shrubs (types A3, A4, A5 in Fremstad 1997).		E	None	n.a.	0.0	0.2	1.0
D_Salix_for	Presence/absence of dry <i>Salix caprea</i> forest in study plot.		E	None	n.a.	0.0	0.1	1.0
Dens_young	Density of young trees. The number of young trees (collar diameter lesser than or equal to 5 cm) was counted, and the number of young trees per ha was calculated.	#/ha	E	$\ln(c+x)$	0.00853	0.0	0.3	12.0
Dist_house	The distance to the closest house, determined from topographical maps.	km	H	$\ln(c+x)$	0.10958	0.1	1.4	7.6
Dist_open	The distance to the closest area cleared from forest, determined from topographical maps.	km	H	$\ln(c+x)$	0.01996	0.0	0.7	9.4
Dist_river	The distance to the closest river was measured from topographical maps.	km	E	$\ln(c+x)$	0.00890	0.0	0.2	1.1
Dist_road	The distance to the closest road, determined from topographical maps.	km	H	$\ln(c+x)$	0.03922	0.0	0.4	2.6
Dist_sea	The distance to the closest sea shore, determined from maps of scale 1:500000.	km	C	$\ln(c+x)$	11.15712	0.1	17.6	54.5
Dist_town	The distance to the closest town, determined from topographical maps.	km	H	$\ln(c+x)$	2.84107	0.2	12.3	38.5
Forest_total	The proportion of forest edge length to total length of edge was determined in circular macroplots of radius 500m surrounding the study plots. The length of forest edge and the total edge length were determined from topographical maps.	%	E	e^{cx}	0.00651	16.1	53.6	87.6
Heat_index	Study plot heat index (Parker 1988), calculated as $\tan \alpha_1 * \cos \alpha_2$, where α_1 was plot inclination and α_2 was unfavourability.		C	$\ln(c+x)$	6.73740	-6.1	2.6	185.7
Hum_imp	The overall human impact index was recorded following the classification of Trass et al. (1999). Trass' 13-point human impact scale was reversed, the		H	None	n.a.	1.0	4.6	10.0

	beginning point was set to 1 (lowest value of human impact).							
Human_nat	The proportion of human derived edge length to natural edge length was determined in macroplots (see above) from topographical maps; defined as "human derived" were settlements, gravel pits, paths, powerlines, football pitches and farming area. Defined as "natural edge" were outlines of mire, lakes, rivers, and alike.	%	H	$\ln(c+x)$	0.07630	0.0	0.3	1.3
Human_total	The proportion of human derived edge length to total length of edge. Measured from topographical maps; defined as "human derived" were settlements, gravel pits, and farming area.	%	H	$\ln(c+x)$	22.14012	0.0	21.2	56.0
Insolation	15-point insolation index with highest values in S and SSW. Plots with a slope of 0 were given the value zero.		C	None	n.a.	0.0	5.7	15.0
Landsc	Landscape unaffectedness, following the scale in Trass et al. (1999). 1= strongly affected, 3= unaffected.		H	None	n.a.	1.0	2.1	3.0
Light	Study plot light conditions, 1= shady, 5= sunny.		C	None	n.a.	2.0	3.3	5.0
Log_dec	Log decay, following the classification in Linder et al. (1997). 1= weakly decayed, 3= strongly decayed.		E	None	n.a.	1.0	2.2	3.0
Log_dens	Density of logs, determined by counting all logs exceeding 10 cm collar diameter, and calculating the density per ha.	#/ha	E	$\ln(c+x)$	0.01384	0.0	0.1	0.4
M_Salix_for	Study plot situated in moist <i>Salix</i> forest, i.e. swamp-forests comprising <i>Salix pentandra</i> and/or <i>S. myrsinifolia</i> .		E	None	n.a.	0.0	0.0	1.0
Maalselv	Location of study plot in Målselv municipality, as determined from topographical maps.		S	None	n.a.	0.0	0.3	1.0
Max_log	Maximum log diameter of study plot, determined from measurements of log diameters.	cm	E	$\ln(c+x)$	17.30933	0.0	19.9	51.0
Max_tree	Maximum tree diameter of study plot, calculated by transforming tree circumference values at 1.3 m stem height to diameters, and selecting the maximum tree diameter of each plot	cm	E	$\ln(c+x)$	7.06790	8.2	27.9	64.6
Med_tree	Median tree diameter of study plot, calculated from tree circumference at 1.3 m stem height, transformed to diameter.	cm	E	$\ln(c+\ln(c+x))$	0.39422	6.3	13.5	38.0
Moist	Study plot moisture conditions. 1=Wet to moist. Area either within the floodplains of a river, showing a strong seasonal pattern in moisture, or in a swamp forest, permanently moist with surface water in brooks or small pools, water table at or near the forest ground. Rich in moisture-indicating plants such as <i>Caltha palustris</i> , <i>Climacium dendroides</i> , <i>Potentilla palustris</i> , <i>Sphagnum</i> sp. or <i>Matteuccia struthiopteris</i> . 2=Between moist and mesic. Little permanent water on the ground, indicators of both moist and mesic conditions. 3=Mesic. Little or no permanent water on the ground, and plants such as <i>Vaccinium myrtillus</i> , <i>Gymnocarpium dryopteris</i> , <i>Phegopteris connectilis</i> . 4=Between mesic and dry. No permanent water on the ground, a mixture of species of mesic and dry conditions. 5=Dry. No permanent water on the ground. Often with plant species showing adaptations to dry conditions. Higher plant vegetation with <i>Empetrum nigrum</i> , <i>Vaccinium vitis-idaea</i> , and/or <i>Polystichum lonchitis</i> .		C	None	n.a.	1.0	2.9	5.0

App. 1. Internet supplement to: Werth, S.; Tømmervik, H. & Elvebakk, A. 2005. Epiphytic macrolichen communities along regional gradients in northern Norway. J. Veg. Sci. 16: 199-208.

Nat_nr	Number of naturally derived lines, line segments and patches, as determined for macroplots from topographical maps. Mires, lakes and river segments were taken into consideration.		E	ln(c+x)	1032.955	0.0	0.5	1.0
Nat_total	Proportion of naturally derived edge length to total length of edge. Measured from topographical maps; defined as "natural edge" were outlines of bogs, fens, forest, lakes and rivers.	%	E	ln(c+x)	24.85430	0.0	25.1	71.2
Nr_landsc_elem	Total number of lines, line segments and patches, corresponding to the number of landscape elements in a macroplot. Determined for using topographical maps.		E	ln(c+x)	32890	0.0	0.5	1.0
Oceanity	Oceanity of climate, determined from maps of oceanity of the study area shown in Moen et al. (1999).		C	None	n.a.	1.0	2.3	4.0
Open_forest	Proportion of edge length of non-forested area to edge length of forested area, determined for macroplots using topographical maps.	%	E	ln(c+x)	0.07370	0.0	0.7	4.0
Plantation	Presence of tree plantation (spruce, larch) in visibility of the study plot.		H	None	n.a.	0.0	0.6	1.0
pH-lab	Soil pH value.		E	ln(c+ln (c+x))	2813663.2346	4.1	5.5	7.7
Pop_tre	Presence of <i>Populus tremula</i> in study plot.		E	None	n.a.	0.0	0.1	1.0
Populus_for	Study plot situated in <i>Populus tremula</i> forest.		E	None	n.a.	0.0	0.1	1.0
Pr_S_T0	Sum of monthly precipitation for all months exceeding 0°C in mean air temperature (reference period 1961-1990), interpolated for the locations of the study plots.	mm	C	ln(c+x)	229.56638	208.0	440.6	837.0
Pr_S_T4	Sum of monthly precipitation in all months exceeding 4°C in mean air temperature (reference period 1961-1990), interpolated for the locations of the study plots.	mm	C	ln(c+x)	225.36732	171.0	310.4	477.0
Pr_year	Annual normal precipitation (reference period 1961-1990), interpolated for the locations of the study plots.	mm	C	e^cx	0.00019	319.0	808.4	1275.0
Road_cat	Category of road closest to the study plot, with the categories following the key of topographical maps.		H	None	n.a.	1.0	1.8	3.0
Rock_suit	Suitability of rock substrates, calculated as A+B+C. (A) Bedrock type, (1) gneiss or granite, (2) acidic to neutral schist or arkose, or (5) calcareous schist. (B) Surface conditions, (1) hard, (2) intermediate, or (-1) eroded. (C) Height of exposed rock surface, (1) 0.00 - 0.49m, (2) 0.5 - 0.9 m, (3) > 0.9 m.		E	None	n.a.	1.0	3.3	10.0
Sal_cap	Presence of <i>Salix caprea</i> in study plot.		E	None	n.a.	0.0	0.2	1.0
Sal_myrr	Presence of <i>Salix myrsinifolia</i> in study plot.		E	None	n.a.	0.0	0.3	1.0
Sal_pen	Presence of <i>Salix pentandra</i> in study plot.		E	None	n.a.	0.0	0.1	1.0
Sea_west	Distance to open sea, as determined from maps of scale 1:500000.	km	C	e^cx	11.15712	0.1	17.6	54.5
Sib	Percentage of trees with more than one stem.	%	E	ln(c+x)	0.25687	0.0	0.3	1.0
Slope	Slope angle of study plot, as determined with clinometer.	°azimuth	C	ln(c+x)	6.55405	0.0	11.2	39.0
Sor_auc	Presence of <i>Sorbus aucuparia</i> in study plot.		E	None	n.a.	0.0	0.2	1.0
Storfjord	Study plot located in Storfjord municipality.		S	None	n.a.	0.0	0.1	1.0
TM_SUM0	Temperature sum of all months exceeding 0°C (reference period 1961-1990).	°C	C	e^cx	0.11612	38.4	50.3	54.7
TM_SUM4	Temperature sum of all months exceeding 4°C (reference period 1961-1990).	°C	C	e^cx	0.13445	35.6	48.0	52.4

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Tree_age	Approximate age of tree layer, 1= young forest, 3= old forest.		E	None	n.a.	1.0	2.2	3.0
Tree_dens	Density of trees. The number of trees (collar diameter larger than 5 cm) was counted, and the number of trees per ha was calculated.	#/ha	E	$\ln(c+\ln(c+x))$	0.54047	0.1	0.6	30.0
Tromso	Study plot located in Tromsø municipality, determined from topographical maps.		S	None	n.a.	0.0	0.3	1.0
Unfav	Unfavourability of plot aspect, i.e. the absolute deviation of plot aspect from SSW (202.5°).	°	C	$\ln(c+x)$	1.80244	0.0	45.5	162.5
Water_total	Proportion of water edge length to total length of edge. Determined using topographical maps.	%	E	$\ln(c+x)$	11.03673	0.0	15.5	79.6
X (*)	(*) Longitude		S	$\ln(c+x)$	0.29023	384268.0	422761.6	487446.0
X2 (*)	(*) Longitude ²		S	e^{cx}	-1.80436	1.476 *10 ¹¹	1.793 *10 ¹¹	2.376 *10 ¹¹
X2Y (*)	(*) Longitude ² *Latitude		S	$\ln(c+x)$	0.23539	1.140 *10 ¹⁸	1.377 *10 ¹⁸	1.824 *10 ¹⁸
X3 (*)	(*) Longitude ³		S	$\ln(c+x)$	0.15735	5.674 *10 ¹⁶	7.642 *10 ¹⁶	1.158 *10 ¹⁷
XY (*)	(*) Longitude*Latitude		S	$\ln(c+x)$	0.36348	2.967 *10 ¹²	3.245 *10 ¹²	3.743 *10 ¹²
XY2 (*)	(*) Longitude*Latitude ²		S	$\ln(c+x)$	0.42230	2.267 *10 ¹⁹	2.491 *10 ¹⁹	2.874 *10 ¹⁹
Y (*)	(*) Latitude		S	$\ln(c+x)$	0.89363	7618977.0	7676801.5	7737570.0
Y2 (*)	(*) Latitude ²		S	e^{cx}	-0.77010	5.804 *10 ¹³	5.893 *10 ¹³	5.986* 10 ¹³
Y3 (*)	(*) Latitude ³		S	$\ln(c+x)$	0.84303	4.422 *10 ²⁰	4.524 *10 ²⁰	4.632 *10 ²⁰

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App. 2. Kendall's Tau correlation of the first four DCA axes with environmental variables investigated. Asterisks indicate that the significance of a correlation at a Bonferroni-corrected level of $\alpha = 0.05$.

Variable	DCA1	DCA2	DCA3	DCA4
Aln_inc	-0.05	-0.11	-0.04	0.18
Aln_Sal_for	-0.05	-0.11	-0.04	0.18
Alnus_for	-0.10	0.15	0.19	-0.16
Altit	0.08	-0.27	0.28	-0.15
Bas_logs	-0.09	-0.16	-0.16	0.15
Bas_trees	0.15	-0.14	-0.22	-0.14
Bet_pub	0.12	-0.17	-0.14	0.14
Betula_forb	0.00	*0.10	0.10	-0.14
Betula_herb	*0.02	0.10	0.04	0.14
D_Salix_for	-0.03	-0.18	-0.12	0.13
Dens_young	0.19	0.13	0.08	-0.13
Dist_house	-0.16	0.06	-0.20	0.12
Dist_open	0.23	-0.20	-0.06	0.12
Dist_river	0.06	0.05	0.02	-0.12
Dist_road	0.13	-0.12	-0.20	-0.11
Dist_sea	0.10	-0.06	0.17	-0.11
Dist_town	-0.04	0.05	0.16	-0.11
Forest_total	-0.04	-0.18	-0.12	0.11
Heat_index	0.07	0.02	0.00	0.09
Hum_imp	0.19	0.27	-0.08	0.08
Human_nat	0.07	0.18	-0.02	-0.08
Human_total	0.15	0.28	0.09	0.07
Insolation	0.07	0.11	-0.08	0.07
Landsc	0.11	-0.15	0.22	-0.06
Light	-0.03	0.01	0.08	-0.06
Log_dec	0.04	-0.11	0.04	0.06
Log_dens	0.09	0.07	-0.03	0.06
M_Salix_for	0.01	-0.13	-0.02	0.06
Maalselv	0.05	-0.15	-0.21	-0.05
Max_log	0.07	-0.04	-0.18	-0.05
Max_tree	-0.14	0.07	-0.17	-0.05
Med_tree	0.14	-0.07	0.17	0.05
Moist	-0.14	0.07	-0.17	-0.05
Nat_nr	0.08	-0.09	0.13	-0.05
Nat_total	0.15	-0.18	-0.08	0.05
Nr_landsc_elem	0.06	-0.12	0.08	0.05
Oceanity	-0.13	*-0.38	0.06	-0.05
Open_forest	0.13	0.38	-0.06	0.05
pH_lab	-0.13	-0.38	0.06	-0.05
Plantation	-0.01	-0.11	-0.02	0.05
Pop_tre	-0.29	0.15	-0.24	-0.04
Populus_for	0.09	-0.21	0.19	-0.04
Pr_S_T0	-0.04	*0.20	-0.19	-0.04
Pr_S_T4	0.05	*-0.05	-0.13	-0.04

Pr_year	0.06	*0.12	0.11	-0.04
Road_cat	-0.21	0.04	0.08	0.04
Rock_suit	-0.13	-0.37	0.06	-0.04
Sal_cap	-0.14	-0.36	0.06	-0.04
Sal_my	0.06	0.01	-0.05	-0.04
Sal_pen	-0.16	-0.34	0.04	-0.04
Sea_west	0.09	-0.09	0.02	0.04
Sib	-0.39	0.03	0.26	0.03
Slope	0.04	0.27	0.17	-0.03
Sor_auc	0.12	0.05	-0.17	-0.03
Storfjord	-0.07	0.34	-0.14	-0.03
TM_SUM0	0.15	-0.05	-0.11	0.03
TM_SUM4	-0.04	0.11	0.10	-0.03
Tree_age	0.15	0.00	-0.09	0.03
Tree_dens	0.05	0.04	-0.27	0.02
Tromso	*-0.05	0.33	-0.17	-0.02
Unfav	-0.05	0.31	-0.16	-0.02
Water_total	-0.18	0.11	0.14	0.02
X	-0.04	*0.11	0.10	-0.02
X2	0.09	*0.30	-0.08	0.02
X2Y	0.05	*0.12	0.06	-0.02
X3	0.01	*0.07	-0.04	-0.02
XY	-0.01	*-0.15	-0.03	0.02
XY2	0.15	*0.11	-0.01	-0.01
Y	-0.23	-0.17	0.10	0.00
Y2	0.12	0.24	0.06	0.00
Y3	0.27	-0.15	0.01	0.00