Key factors for epiphytic macrolichen vegetation in deciduous forests of Troms county, northern Norway: human impact, substrate, climate or spatial variation?

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Abstract

Epiphytic macrolichen vegetation was sampled on lower stems ($\leq$ 2 m) of deciduous trees in plots of size 400 m^2 along a regional macroclimatic gradient in Troms county, northern Norway. Canonical Correspondence Analysis (CCA) with variation partitioning revealed the following key factors for macrolichen vegetation:

1. Macroclimate was the primary factor controlling epiphytic macrolichen vegetation, with strictly macroclimatic variation accounting for 35 % of total variation explained (TVE).

2. Two other key factors were spatial variation and tree substrate, amounting to 25.5 % and 17 % of TVE, respectively.

3. Human impact explained little - 5.2 % of TVE, forest fragmentation and natural patchiness none of the variation in species composition.

The largest amount of shared variation was pooled between the sets of spatial and climatic variables, while the set of human impact variables shared no variation with forest and other environmental variables. The reliability of species groupings was confirmed by DCA (Detrended Correspondence Analysis), showing ecologically sound clusters of the species optima. The importance of the different factors is discussed in relation to lichen ecology, physiology and distribution patterns. The response of macrolichens to macroclimate might be mainly attributable to the temperature demands of thermophilous species reaching their northern distribution limits in northern Norway.

Introduction

These days, there are no areas left on our planet that have not experienced changes directly or indirectly connected to human activities (Meffe & Carroll 1997). With the world population growing by about 81 million each year (United Nations 1998), human impact on ecosystems will keep on increasing, and is becoming a topic of primary interest in community ecology. For future conservation purposes, it will become a crucial task to develop methods allowing a straightforward identification of areas altered little by human activities. This can be done by means of indicator species or communities (Werth et al. in prep.).

Lichens are affected by air pollution, e.g. by sulphur dioxide emissions (Richardson 1992; Purvis 2000). Air pollutants may act on small as well as on large spatial scales; often not only in areas adjacent to pollution sources, but also regions far away are affected since air pollutants can be dispersed over large distances. Effects of air pollution on lichen vegetation are documented from many parts of central Europe such as Great Britain (Hawksworth et al. 1973), the Netherlands (van Dobben 1996) and Germany (Wirth 1976; Wirth 1995; Kricke & Feige 2001). Since the 1980's, the deposition of airborne pollutants decreased strongly in some central European areas which were severely polluted in the past, such as the German Ruhr area, and lichens are reinvading (Kricke & Feige 2001). But air pollution is high in Central Europe compared to northern Fennoscandia (see App. 7, Fig. I).

Lichens are also sensitive to disturbance and habitat destruction (Wirth 1976; Gilbert 1977; Pfefferkorn & Türk 1996). Many lichens are confined to ecosystems with low disturbance regimes, such as old-growth forests (Goward 1994). Old-growth dependent lichens have been used as indicators of low disturbance levels ("ecological continuity") in woodlands of Europe (Rose 1976; Rose 1992; Tibell 1992; Kuusinen 1996; Kondratyuk & Coppins 1998) and North America (Goward 1994).

Lichens react to disturbances and habitat alterations for several reasons. Firstly, some lichen species are dependent on favourable microclimatic conditions. Many human activities such as road building (Degelius 1935), drainage of wetlands, and canalisation of river systems (Schöller 1997) lead to a decline of air humidity over large areas, which is harmful to oceanic lichens (Barkman 1958b). Settlement and forest management activities

are often associated with deforestation, which results in a decrease in air humidity (Renhorn et al. 1997), affecting large areas adjacent to the deforested land. At the same time, wind velocities increase when the forest disappears (Renhorn et al. 1997), leading to higher evaporation rates, which affect particularly the hygrophilic oceanic lichen species such as members of the families *Lobariaceae* and *Pannariaceae* (Schöller 1997). Many old-growth dependent lichens are more sensitive to light stress than lichens of young forests (Gauslaa & Solhaug 1996). This is one reason why old-growth lichens disappear from forests after logging events, even if remnant trees are retained.

Another reason why lichens depend on old-growth is that forests which have long remained undisturbed, develop microhabitats differing from those available in young forests (Lesica et al. 1991; Nordén & Appelqvist 2001). This may be a factor leading to the disappearance of certain lichens from forests disturbed by humans, such as some species of Caliciales, which are dependent on particular old-growth microhabitats (Selva 1994) such as snags and tree substrates with coarse, dry and stable bark (Holien 1996).

Rose (1976) suggests that low dispersal ability in certain lichens leads to their dependence on old woodlands. Sillett et al. (2000) recently verified this hypothesis in an experimental study of North-American Douglas-fir forests. In addition, they were able to demonstrate that neither microclimate nor substrate specificity were the factors limiting lichen establishment in forests, provided that sufficient diaspores were available. Also results of an observational study performed in boreal Scot's Pine forests of Northern Europe support the hypothesis that the abundance of old-growth dependent lichens in forests is limited by dispersal (Dettki et al. 2000).

Given their sensitivity to environmental disturbances and habitat alterations, epiphytic lichens may prove to be suitable model organisms functioning as indicators of human impact in forest ecosystems. In particular epiphytic macrolichens have high potential as indicators because they are relatively conspicuous and often fairly easy to identify in the field. Analysing the species composition of epiphytic macrolichen communities may give valuable information about the severity of human impact on particular forest stands.

Human impact on forest ecosystems has a multitude of features – among others pollution, logging, forest fragmentation because of settlement activities and changes in community composition following plantations of non-native tree species.

Since the effects of long-distance air pollution are rather marginal in the study area (see App. 7), the effects of other human impacts are being focused on, such as logging and settlement, leading to forest fragmentation.

Developments in multivariate methods during the last decades have made it possible to test hypotheses on relationships between vegetation and environmental factors (Økland & Eilertsen 1994). Partial constrained ordination is a technique enabling the quantification of variation in vegetational composition explained by specific explanatory variables or sets of explanatory variables (Borcard et al. 1992). Partial Canonical Correspondence Analysis with variation partitioning combined with Monte Carlo permutation tests (Borcard et al. 1992) represents a powerful tool for testing specific null hypotheses about vegetation-environment relationships (Birks 1993; Økland & Eilertsen 1994), which is used in this paper. Relations between the composition of epiphytic lichen vegetation and environmental factors have seldom been tested statistically, and almost no partial constrained ordination with variation partitioning has been used for this purpose (but see Liu & Bråkenhielm 1995).

The central question of this study is whether human impact is a key factor for epiphytic macrolichen communities in boreal deciduous forests, and how important the factors macroclimate, forest- and other environmental variation and spatial variation are for macrolichen communities in Troms county, compared to human impact.

Material and methods

Study area

The study area is situated in central Troms county in northern Norway (Fig. 1), an area dominated by deciduous forests, particularly birch forests (Moen et al. 1998).
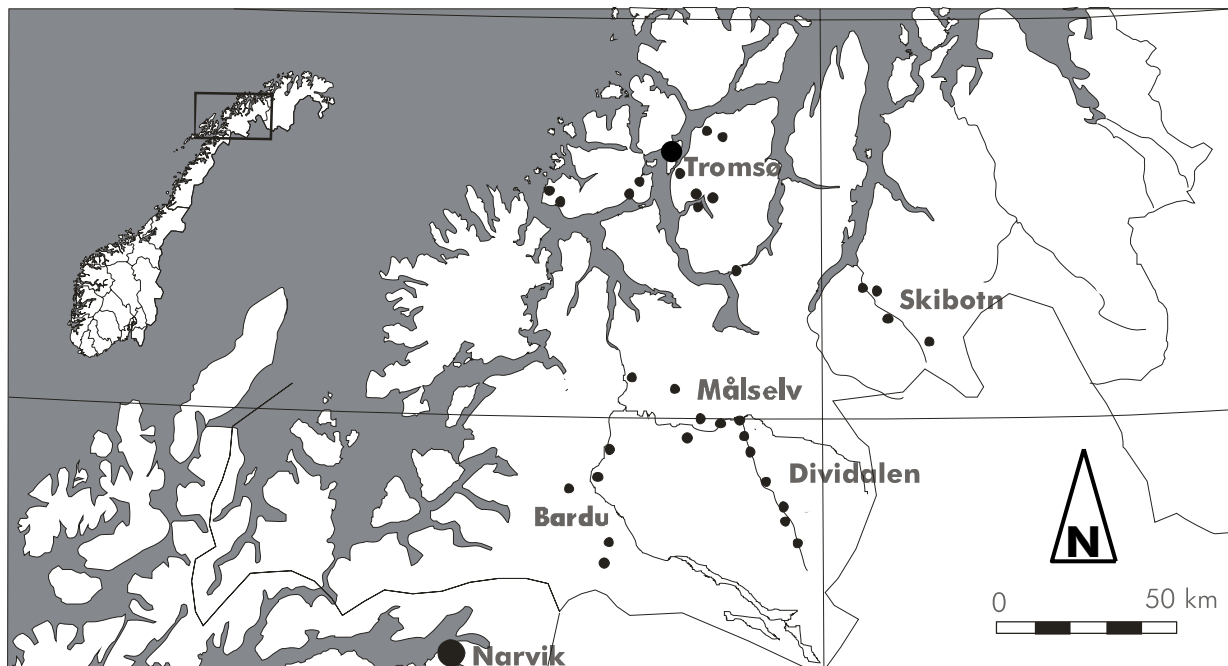
Figure 1. Map of the study area in Troms county, northern Norway. Small points indicate the location of one or several plots.

Selection of epiphytic lichen species

All analyses of macrolichen vegetation were restricted to lichens growing on tree substrates. Lichen species were selected according to the following criteria: (1) The species should be fairly easily visible and (2) relatively easy to be defined in the field. Thus, only macrolichens following the definition of Krog et al. (1994) were selected. An exception were the crustose lichen *Icmadophila ericetorum*. The genus *Cladonia* was excluded from sampling, since it did not meet the second criterion.

Identification of species

Doubtful specimens were collected for identification in the laboratory. In some cases the chemistry of collected specimens was studied by means of chemical spot tests (Walker & James 1980) and/or thin layer chromatography (Culberson & Ammann 1979).

Nomenclature follows Timdal (1998). Species were identified using Krog et al. (1994) and, in some cases, Purvis (1992). In the genus *Peltigera*, the monographs by Vitikainen (1994) and Holtan-Hartwig (1993) were additionally used to ensure the correctness of identifications. Voucher specimens are placed in TROM, the herbarium of Tromsø Museum. Higher plants were determined using Lid et al. (1994).

Figure 2. *Lobaria pulmonaria* (left picture), *L. scrobiculata* (middle) and *L. hallii*, (right) three macrolichens typical of rich, often moist deciduous forest types in the interior of Troms county. *L. hallii* is a red-listed lichen species in Norway (DN 1999).

Abundance scale

All statistical analyses are based on presence/absence data of epiphytic macrolichen species in 69 plots. Species raw data are presented in App. 1; abbreviations of species names are given in App. 2.

Plot size

Square plots of size 400 m^2 were used for the analysis of macrolichen vegetation, while square subplots of 100 m^2 were used for forest stand properties. To study forest fragmentation, circular macroplots of radius 457.2 m, i.e. 500 yd, corresponding to 656,360 m^2 were analysed on M711 topographic maps 1:50,000.

Forest types investigated

The study was restricted to deciduous forests. The following forest types were investigated:

(1) **Alder forests along riversides and on hillsides** (type C3 in Fremstad 1997).
(2) **Alder-willow swamp forests**, composed of *Alnus incana*, *Salix pentandra* and/or *S. myrsinifolia*, (type E3a in Fremstad 1997).
(3) **Moist willow forests**, i.e. swamp-forests comprising *Salix pentandra* and/or *S. myrsinifolia*.
(4) **Birch forests rich in nutrients** with a field layer dominated by forbs (type C1 and C2 in Fremstad 1997).
(5) **Birch forests intermediate in nutrients**, not being either type (4) or (6), showing character species of both nutrient rich and nutrient poor birch forest.
(6) **Birch forests poor in nutrients** dominated by dwarf shrubs (types A3, A4, A5 in Fremstad 1997).
(7) **Dry willow forests in slopes** dominated by *Salix caprea* (type B2c in Fremstad 1997).
(8) **Aspen (*Populus tremula*) forests.**

These eight forest types were substituted by seven binary dummy variables, which were included in the explanatory variable set {E}. When including n categories of a variable such as forest type as binary variables into a data set, the nth category is superfluous because all remaining data points will automatically be in this category. Thus only $n - 1$ binary variables should be included into the data set to avoid redundancy of variables (Kleinbaum et al. 1998).

Stratified random sampling within a vegetation type

Macrolichens were sampled on lower stems of living and dead trees ($\leq$ 2 m height). Also the lower stems of trees lying on the ground were sampled. The forest stands to be sampled were selected subjectively. Within a particular forest stand, a plot was selected randomly by walking a random number of steps from the centre of the forest stand in a random direction. Random numbers between 1 and 100, and 1 and 360 were gained by using a random function in MS Excel; sheets with printed random numbers were used in the field. Patches of aspen and dry willow forests were often too small to follow this randomisation procedure. In these cases, the plots were located in the centre of the respective forest patch.

Criteria for rejection of plots

Plots were rejected if:

1. plots were closer than 2 m to the forest edge;

2. more than 30 % of the area was an open water surface;

3. containing less than three trees above four cm in collar diameter;

4. the forest layer was composed of more than 10 % coniferous trees.

These criteria were used on 400 m² plots as well as on 100 m² subplots.

Macroclimatic, microclimatic and topographic variables

Macroclimatic variables

The following macroclimatic variables were included in the analyses: monthly normal values for precipitation and temperature sums (reference period 1961-1990), calculated for temperatures above 0°C and 4°C, respectively, oceanity of climate (following Moen et al. 1998), and annual normal precipitation. All temperature and precipitation data were supplied by Det Norske Meteorologiske Institutt, Klimaavdelingen.

Raw data of the macroclimatic variables, as well as of all other explanatory variables are given in App. 3, and explanations of variable names in App. 4.

Microclimatic variables

Moisture and light conditions of the plots were estimated on five-point scales, ranging from dry to wet and from low light to high light intensity, respectively. Some plots are permanently flooded, for example plots located in swamp forests. Other plots that lie within the inundation zone of large rivers are temporarily flooded during the snowmelt in spring, and fall dry in summer. All such plots were placed in the category 1, wet to moist.

Five-point scaling of moisture
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 *Caltha palustris*, *Climacium dendroides*, *Potentilla palustris*, or *Matteuccia struthiopteris*.
2=Between moist and mesic. Little permanent water on the ground, indicators of both moist and dry conditions.
3=Mesic. Little or no permanent water on the ground, and plants such as *Vaccinium myrtillus*, *Gymnocarpium dryopteris, Phegopteris connectilis*.
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 *Empetrum nigrum, Vaccinium vitis-idaea,and/or Polystichum lonchitis*

Five-point scaling of light conditions
1=shady
2=shady to diffuse
3=diffuse
4=diffuse to sunny
5=sunny

Topographic variables

Average plot elevation was extrapolated from altitudinal lines in M711 topographic maps 1:50,000 to the nearest 10 m. The slope angle of the plot, α1, was measured using a clinometre (360° scale). Plot aspect was measured by means of a compass, using a 360° scale. Unfavourability, α2, is the deviation of aspect from SSW, 202.5° (Økland 1996). Fig. 3 shows the scaling of unfavourability.

Figure 3.

Scale used for unfavourability. SSW (202.5°) is the most favorable aspect, while NNE (22.5°) is the most unfavourable one.
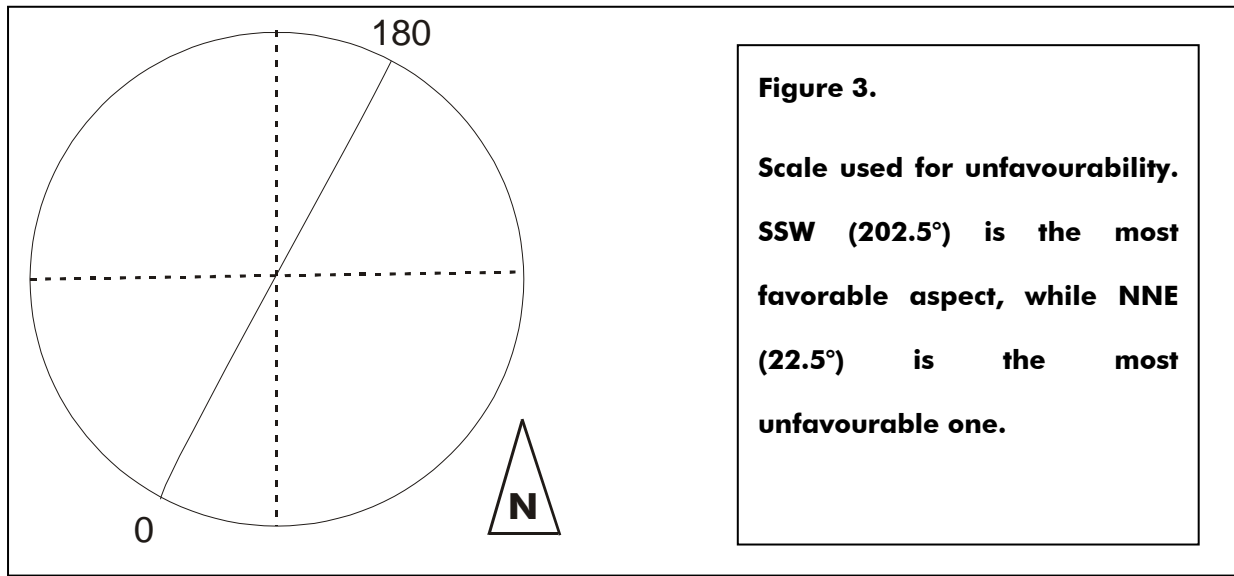
A plot heat index, P, (Parker 1988), was calculated as $P = \tan\alpha1 * \cos\alpha2$, where $\alpha1$ is plot inclination and $\alpha2$ is plot unfavourability. Additionally, a 15-point insolation index with highest value in S and SSW was used, altering Goldsmith's (1973) 10-point scale to a 16-point scale (see Fig. 4). Plots with a slope of 0° were given the value zero.
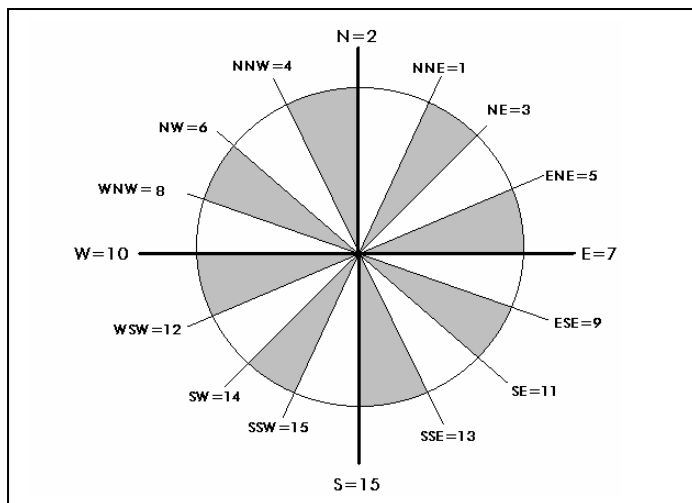
Figure 4. Scaling of the 16-point insolation index, based on Goldsmith (1973).

Forest- and other environmental variables

Rock suitability index

The suitability of rock substrates may be important for epiphytic lichen vegetation since rock habitats may work as a regeneration refuge for lichens able to grow on saxicolous as well as corticolous habitats. When a forest stand is disturbed and epiphytic lichen vegetation is destroyed, lichens may be able to recolonise regrowing trees more rapidly when surviving the disturbance on a rock refugium.

The rock suitability index gives a rough indication of the quality of rock habitats for lichen growth. A particularly high emphasis is put on the growth conditions for Lobarion lichens, which prefer circumneutral schists and silicious rocks in Troms (Elvebakk, personal communication). Since calcareous schists provide by far the best growth conditions for Lobarion lichens, they were given a high emphasis in the scaling (5 points). Both slates and arkoses provide better rock substrates than gneisses or granites, and thus the former were given a slightly higher value than the latter. Not only bedrock type, but also surface conditions are important for lichen growth. Eroded rock surfaces are very unfavourable for lichen growth, and they were therefore given a negative value. Hard surfaces are better than eroded ones, but still not optimal for lichen growth. The optimal surface is intermediate between hard and eroded, and was given the highest possible value for surface. The height of exposed rock surface gives an estimate of the amount of rock surface available for lichen growth. Small rocks do not have a large amount of exposed rock surface, and are often overgrown by vegetation.

Table 1 : Scaling of the rock suitability index

Bedrock type (A)	Surface conditions (B)	Height of exposed rock surface (C)
Gneiss or granite = **1**	Hard = **1**	0-0.49 m = **1**
Slate or arkose = **2**	Intermediate = **2**	0.5 – 0.9 m =**2**
Calcareous schists = **5**	Eroded = **-1**	> 0.9 m = **3**

To obtain the index of rock suitability of a respective plot, the values of (A), (B) and (C) are added (see Tab. 1). Absence of rock habitats were automatically given a rock suitability index of 1.

Forest stand parameters

Based on the number of tree stems in a subplot, tree density was calculated. Tree density is the number of tree stems per area unit. Tree species composition is given in presence/absence of tree species (n − 1 binary variables, see above).

Basal area, BA_{ij}, is gained by adding the stem area in breast height of all tree stems in a plot, and dividing by the plot area. This value was calculated for 100 m² subplots, and transformed to the common units of measurement (m²/ha).

$BA_{ij} = \sum_{i=1}^{l} (r_{ij}^2 \pi)$, where BA_{ij} is the basal area of subplot j, r_{ij} is the diameter of the i-th tree in plot j, $i = 1, \ldots, l$ and $j = 1, \ldots, n$.

BA_{ij} was calculated separately for the tree layer, for coarse woody debris and for tree stumps resulting of logging activities. For the latter two, the diameter recorded was not the diameter in breast height. In tree stumps, the tree diameter at the top of the stump was used, and in logs the collar diameter.

Measurements of tree species composition, tree density and BA_{ij} were done for all trees exceeding four cm in collar diameter. In trees consisting of more than one main stem, the biggest stem alone was measured. The number of such so-called sibling trees was counted, and the proportion of sibling trees to the total number of trees was calculated. Maximum and median tree diameter were included into the set of forest- and other environmental explanatory variables, {E}.

Number, position and decay class of logs were recorded in the subplots of 100 m², in addition to collar diameter of logs. Decay classes follow the classification in Linder et al. (1997). Densities of logs were calculated based on these data, as well as maximum log diameter.

Young trees are defined as trees 5 cm or less in collar diameter. The number of all young trees present in subplots was recorded, and densities were calculated.

pH of tree bark

The bark pH of 8 tree species was determined. For the measurements, the dried samples were cut into pieces of about 1 cm². To every 5 g sample, 25 ml distilled water was added, and the probe was stirred. The bark pH was measured after 2 hours by means of a pH electrode, the error of the pH electrode being 0.05 pH units. The raw data are presented in App. 8.

Forest fragmentation and natural patchiness

Habitat fragmentation is the partition of a previously continuous landscape into small and isolated patches of habitat (Saunders et al. 1991). The term forest fragmentation refers to the same process, the original habitat type being a forest. Landscapes are often naturally heterogeneous, the heterogeneity created through the apportionment by river and lake systems, patches of mires or cliffs. In this study, the term natural patchiness is used for this natural heterogeneity in landscapes. Forest fragmentation and natural patchiness were defined by means of the length of lines or outlines of landscape elements. All measurements were made on the basis of M711 topographic maps with scale 1:50,000. For this purpose, map details around the plot positions were scanned and enlarged. For all plots, fragmentation and patchiness were studied in circular macroplots surrounding the respective plots.

Human impact variables

Presence of plantation

Presence or absence of spruce (*Picea* spp.) or larch (*Larix* spp.) plantation in visibility from the plots' edges was recorded, and included into the human impact variable set as a binary variable.

Length of outlines and lines in macroplots

For two-dimensional landscape elements, a rough estimate of forest fragmentation and natural patchiness was obtained by measuring the length of all outlines of the respective landscape elements with a map distance measurer, and adding them. The map distance measurer used was produced by K&R, Germany. In the case of one-dimensional landscape elements, the length of lines was measured and added for a respective macroplot.

Lengths of the following 12 landscape elements were measured for each macroplot:

Rivers, roads, paths, power lines, lakes, patches of mire, patches of forest, naturally not-forested patches other than mires (i.e. avalanche patches, areas above the tree line, rock faces, cliffs), patches of cultivated land, patches of seashore vegetation, areas covered by sea, as well as patches of "settlement structures" in the broadest sense (i.e. residential

areas, football pitches, gravel pits). Paths and small rivers up to a size of about 10 m were not utilised for defining borders between patches.

The edge length derived from human activity was calculated by adding the length of outlines of cultivated land and other patches cleared from the original forest, of residential areas and football pitches and suchlike, plus the length of paths and powerlines. All other outlines and lengths were used to define natural patchiness.

From the measurements of landscape elements, the following variables were calculated:

i)   **Proportion of human derived edge length to total length of edge**

ii)   **Proportion of human derived edge length to natural edge length**

iii)   **Number of naturally derived lines, line segments and patches**

iv)   **Total number of lines, line segments and patches**

v)   **Proportion of forest edge length to total length of edge**

vi)   **Proportion of naturally derived edge length to total length of edge**

vii)   **Proportion of edge length of non-forested area to edge length of forested area**

viii)   **Proportion of water edge length to total length of edge**

The variables i) and ii) were included in the set of human impact explanatory variables, providing an approximate image of macroplot forest fragmentation. All other variables were included in the set of forest- and other environmental variables, supplying a measure of the natural patchiness of the macroplot (see Tab. 3 and 5).

Overall human impact scale

Overall human impact HI_k of a plot was estimated using the criteria i suggested by Trass et al. (1999): (1) Landscape unaffectedness, (2) tree age, (3) quantity of logs, (4) decay of logs, (5) intensive cutting, (6) other human impact. For more details, see App. 6. Trass' 13-point human impact scale was reversed, the beginning point was set to 1 (lowest value of human impact). The resulting variable is on a 10-point scale since the three highest categories of the new scale were missing in the data set. For counting logs, 10 cm was used as a minimum log diameter.

The criterion landscape unaffectedness was included as a separate variable in the set of human impact explanatory variables. Log decay and tree age were included into the set of environmental variables.

Distance to landscape elements

Landscape elements are hereby defined as objects forming a landscape, e.g. roads, rivers, towns. Based on M711 topographic maps 1: 50,000, the distance from a respective plot to several landscape elements was measured. If distances were below 100 m, they were estimated in the field to the nearest 10 m.

The following distances were measured:

- **Distance to closest farm house, and to boundary of closest city or town**
- **Distance to closest road**
- **Distance to closest area cleared from forest**
- **Distance to nearest river or stream**

Farm houses were defined as in the key of M711 topographic maps 1:50,000. Olsborg, Setermoen and Skjold were regarded as towns, and Tromsø as a city. Of the distances measured, the following were categorised as human impact variables: distance to closest house, town, road and cleared area. Those were included in the human impact explanatory variable set, {H}. All others were included in the set of environmental explanatory variables, {E}.

Road category

The category of the road closest to the plot was determined in a three-point scale, following the key given in M711 topographic maps.

1. **Small road with low traffic, e.g. cart track or private road**
2. **Road with intermediate traffic, e.g. national road, district road or road situated in residential area**
3. **Large road with high traffic, e.g. trunk road or European route.**

Spatial variables

To enable the detection of complex spatial patterns in the data set, latitude and longitude, and their quadratic and cubic combinations defining a 3-dimensional trend surface were included, as recommended by Borcard et al. (1992). This polynomial of the geographic coordinates allows the detection of large-scale spatial patterns in the data (Méot et al. 1998). In addition to geographic extent and its polynomial combinations, geographic location was included in the data set as binary variables, defined by the affiliation of plots

to the municipalities Bardu, Tromsø, Storfjord and Målselv. Only the latter three were included as variables, since the information gained by a fourth variable would have been redundant. Bardu was excluded as a variable, since macrolichen species composition of plots taken in Bardudalen valley was almost similar to that of plots in Målselvdalen valley.

In addition, distance to open sea and to closest seashore were included in the set of spatial variables. Since both variables were measured on a map with scale 1:500,000 if distance to sea was over 500 m, the resulting estimate is rather a rough one. In cases where the distance was below 500 m, it was measured from a topographic M711 map 1:50,000.

The sets of explanatory variables used in all statistical analyses were the following:

{C}, a set consisting of 13 macroclimatic, microclimatic and topographic variables

{E}, a set consisting of 33 forest and other environmental variables

{H}, a set containing 10 human impact variables

{S}, a set of 12 spatial variables

Statistical analysis

Variable transformations

It was attempted to transform all variables to zero skewness (Økland 2001), followed by ranging (Økland 1990). The formulas used for transformation were $\ln(c+x)$, e^{cx} or $\ln[c+\ln(c+x)]$. Since transformation to zero skewness proved impossible for some variables in set {S}, the values were transformed to the smallest possible skewness value which lay below 0.6 for all variables, and ranged afterwards.

Detrended correspondence analysis, DCA

The ordination technique DCA was utilised to display species optima of all epiphytic macrolichen species. Axes were detrended and rescaled[1] by segments. All species were given equal weights.

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[1] The DCA iteration algorithm differs from the CA algorithm in the detrending and rescaling steps.

Significance of variables

The significance of variables to be included in the model was tested by a set of sequential Monte Carlo permutation tests in CCA ("manual forward selection of variables"), separately applied to each explanatory variable set, taking the set of explanatory variables to be tested as constraining variables. The number of permutations used was 2000, and permutations were performed under full model. Selecting variables by a forward selection procedure involves multiple testing. In the case of multiple testing, the significance level has to be lowered to avoid the inclusion of non-significant variables in the model. This was done by a Bonferroni correction: dividing the desired overall significance level (α=0.05) by the number of variables, e.g. 10 in explanatory variable set {H}. The corrected significance level[2] is then 0.05/10 = 0.005. Non-significant variables were excluded from further statistical analyses. Statistical significant variables were checked for collinearity (see App. 5). The Bonferroni-correction, which is rather strict, was used because there were almost as many explanatory variables as plots. In such a case, all explanatory variables provided would be able to explain about 100 % of the variation in species composition, even if there was no relationship between environmental variables and the species at all (Økland 2001). Therefore, only significant explanatory variables have to be included in the model, to make it meet the demand of parsimony (Yoccoz & Ims 2000).

Partial CCA with variation partitioning

Partial Canonical Correspondence Analysis (CCA) with variation partitioning (ter Braak 1988) can be used to estimate the proportions of variation in the macrolichen species data explained by single sets of explanatory variables, after effects of other sets have been removed. In a CCA using the explanatory variable set {H} as constraining variables and no covariables, H is obtained, that is the amount of variation explained by explanatory variable set {H}. To remove the effect of the explanatory set {C} from explanatory variables set {H}, {H} has to be used as constraining variables and {C} as covariables in a partial CCA (ter Braak 1988). The amount of variation obtained by this procedure is termed H|C, that is the amount of variation in {H} not shared by {C}. The amount of variation shared by the explanatory variable sets {H} and {C} can be calculated by

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[2] Note that because of the Bonferroni correction, α differs between explanatory variable sets, but the overall α of each variable set is still 0.05.

subtracting H|C from H. Økland (2001) proposes a procedure to calculate the amount of variation shared by three sets of explanatory variables (see equations 2. and 4. below).

In the following, I suggest the formulae which may be used to calculate shared variation for four sets of explanatory variables:

$$(1.) \; E \cap S \cap C \cap H = E \cap C \cap H - (E \cap C \cap H)|S$$
$$(2.) \; E \cap C \cap H = E + E|(C \cup H) - E|C - E|H$$
$$(3.) \; (E \cap C \cap H)|S = E \cap H - E \cap S \cap H$$
$$(4.) \; E \cap S \cap H = E + E|(S \cup H) - E|S - E|H$$

The symbol "∩" indicates an intersection, and "∪" a union of variable sets, while "|" means "without". Amounts of variation which could be obtained directly from CCA were tested for statistical significance using Monte Carlo permutation tests, using 2000 unrestricted permutations under full model. For shared variation, significance testing is not possible, but these amounts of variation may be compared to similar ones which could be tested directly, and thus it can be evaluated whether or not a certain amount of shared variation may be statistically significant (Økland 2001).

Results

Bark pH

There is considerable variation in tree bark pH (see Fig. 5). The pH value of bark samples from *Populus tremula, Salix myrsinifolia, S. pentandra* and *Sorbus aucuparia* is higher than that of *Alnus incana* and *Salix caprea*. Bark of *Betula pubescens* is more acidic than that of any other tree species, but at the same time the variation of values is high. The three samples taken from *Prunus padus* do not permit a proper evaluation of the bark pH of this species, but it tends to be intermediate, comparable to *Alnus incana* or *Salix caprea*.
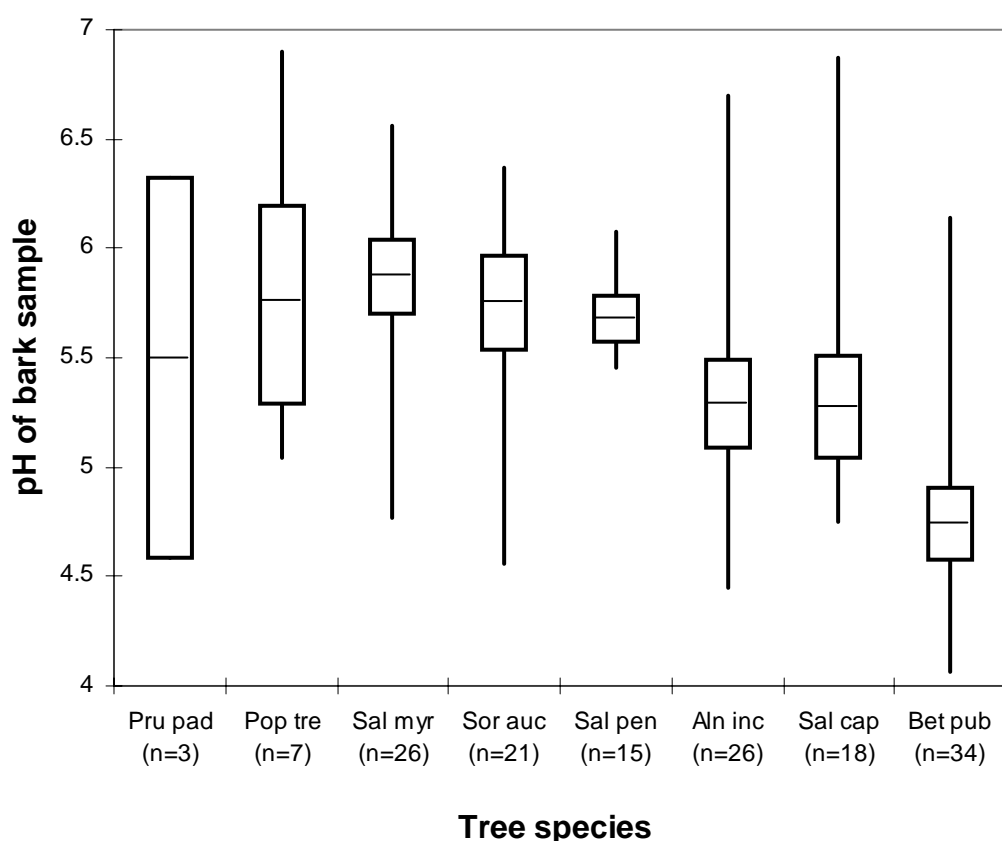
Figure 5. pH value of tree bark samples, showing mean values with 95 % confidence intervals (boxes), maximum and minimum values (whiskers). Abbreviations of tree species: *Prunus padus* Pru pad; *Populus tremula* Pop tre; *Salix myrsinifolia* Sal myr; *Sorbus aucuparia* Sor auc; *Salix pentandra* Sal pen; *Alnus incana* Aln inc; *Salix caprea* Sal cap; *Betula pubescens* Bet pub. The number of samples is indicated for each tree species.

Epiphytic macrolichen vegetation on deciduous trees

A total of 72 macrolichen species were found growing on trees in the plots (App. 1). Many of the species are very common in Norway, such as *Hypogymnia physodes, Melanelia olivacea, Parmelia sulcata* and *Parmeliopsis ambigua* (Timdal 2001).

Collema fasciculare is rare in northern Norway, and has not been found in Troms before (Krog et al. 1994; Timdal 2001). Its new northernmost locality in Norway is now Tune, Bardu municipality at 68°55,565' N. Another rare species for northern Norway is *Melanelia exasperatula*, which was found at the outermost coastal site investigated, close to Brensholmen. This species has also been found only north to Nordland county before (Krog et al. 1994; Timdal 2001). A third rare species for Troms is *Physcia adscendens*, found in Skibotndalen valley. Two other species rare in northern Norway are *Hypogymnia austerodes* and *H. bitteri*, which were found in Dividalen valley, Målselv municipality. Other species which are relatively rare and close to their northern distribution borders in Troms county are *Ramalina farinacea, Usnea subfloridana* and *Evernia prunastri* (Timdal 2001). Only one species which was found is red-listed in Norway, *Lobaria hallii* (DN 1999). A photograph of this species is presented in Fig. 2.

Some primarily terricolous and/or saxicolous species like *Icmadophila ericetorum, Sphaerophorus globosus, Xanthoria elegans* and *Peltigera* spp. were found on the bases of trees covered by bryophytes, or on trunks lying on the ground (Tab. 2).

Table 2. List of species reported as old-growth dependent in Central (Rose 1992) and Northern Europe (Kuusinen 1996) and the US (Goward 1994), found at two sites in Skibotndalen valley.

Species	Brennfjell (plot number A 37)			Kavelnes (plot number A 39)		
	Stone	*Populus*	*Juniperus*	Stone	*Betula*	*Sorbus*
Degelia plumbea	x			x		
Leptogium saturninum		x	x			
Lobaria pulmonaria	x			x		
Lobaria scrobiculata	x	x	x	x	x	x
Nephroma bellum			x			
Nephroma parile			x	x		
Pannaria conoplea	x					
Parmeliella triptophylla	x		x			
Peltigera collina	x		x	x		
Sphaerophorus globosus				x	x	

DCA ordination of epiphytic macroclichens

Fig. 6 presents the species optima in a DCA ordination. Gradient lengths of axis one to three are 2.781, 2.383, and 2.021, respectively. DCA provides a good overview of the main gradient structure of data sets, and was therefore used here to give additional evidence that the interpretation of the main gradients is reliable. Correlations between significant explanatory variables and the first three DCA axes are given in App. 9.

DCA ordination of epiphytic macrolichens
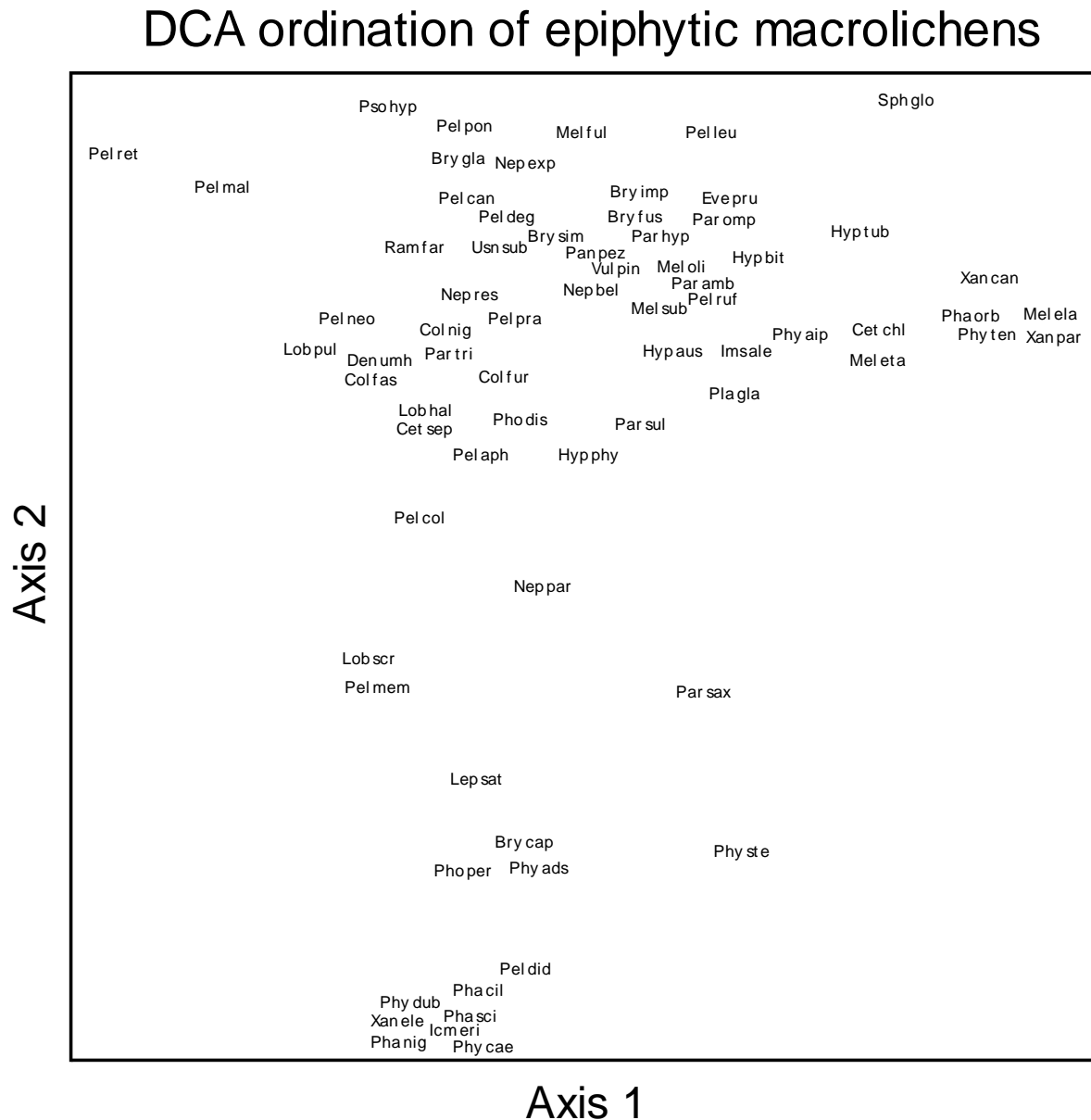
Figure 6. DCA ordination diagram showing species optima along the first two axes in DCA (options used: rescaling of axes, no downweighting of rare species). For abbreviations of species names, see App. 2.

There are three distinct clusters of species. At the bottom of the diagram, there is a cluster of species including several *Phaeophyscia* species, *Physcia dubia*, *Xanthoria elegans* and others. In the corner to the very right side of the diagram, there is a second distinct cluster consisting of *Xanthoria candelaria, X. parietina, Melanelia exasperatula, Phaeophyscia orbicularis* and *Physcia tenella*. Then, there is a third large group of species comprising *Physcia aipolia, Melanelia olivacea, Pannaria pezizoides, Lobaria pulmonaria, Peltigera collina* and many others. Comparable results were obtained when linear non-metric multidimensional scaling was performed instead of DCA.

Significance of variables in CCA

Tab. 3 shows results of a forward selection of variables in the set of human impact explanatory variables, {H}. Only one single variable, presence of plantation of non-native tree species in visibility distance, was significant for lichen species composition at α = 0.005.

Table 3. Human impact variables. Variables were transformed to zero skewness, which was below 10^{-10} after transformation for all variables. Variables significant at α=0.005 were included in further analyses. N. d. = not determinable.

Variable name	Units of measurement	Potential range	Skewness prior to transformation	Transformation formula used	Ran-ging	p	F
Overall human impact		1 – 10	0.512	ln(c+x)	Yes	.0070	1.71
Distance to closest town	km	0 - ∞	0.970	ln(c+x)	Yes	.0145	1.52
Presence of tree plantation (spruce, larch) in visibility		0 – 1	N. d.	None	No	**.0025**	1.50
Category of closest road		1 – 3	0.459	ln(c+x)	Yes	.0360	1.41
Distance to closest farmhouse	km	0 - ∞	2.024	ln(c+x)	Yes	.1154	1.30
Distance to closest area cleared from forest	km	0 - ∞	4.734	ln(c+x)	Yes	.1089	1.29
Proportion of human derived edge length to total length of edge	%	0 - 100	0.703	ln(c+x)	Yes	.1854	1.19
Proportion of human derived edge length to natural edge length	%	0 - ∞	1.692	ln(c+x)	Yes	.2144	1.17
Landscape unaffectedness		1 – 3	-0.145	e^{α}	Yes	.4148	1.03
Distance to closest road	km	0 - ∞	2.314	ln(c+x)	Yes	.6242	.91

From the set of spatial variables, two of three areas, namely the municipalities of Storfjord and Tromsø were significantly related to lichen vegetation, as well as latitude (see Tab. 4). The significance level was α=0.00417.

Table 4. Spatial variables. Variables were transformed to lowest possible skewness, which lay below 0.558 for all variables. Only variables significant at α=0.00417 were included into further analyses. Latitude and longitude refer to the Universal Transverse Mercator (UTM) coordinate system, map datum is WGS 84, grid zone designation 34 W. N. d. not determinable.

Variable name	Units of measure-ment	Potential range	Skewness prior to transfor-mation	Transformation formula used	Skewness after transfor-mation	Ranging of variable	p	F
Storfjord Municipality		0 – 1	N. d.	None	N. d.	No	**.0015**	2.647
Latitude		0 – ∞	.689	ln(c+ln(c+ln(c+x)))	0.556	Yes	**.0005**	2.219
Tromsø Municipality		0 – 1	N. d.	None	N. d.	No	**.0005**	2.252
Distance to open sea	km	0 – ∞	-.308	e^{cx}	$<10^{-8}$	Yes	.0445	1.436
Longitude		0 – ∞	.206	ln(c+ln(c+ln(c+x)))	.202	Yes	.1574	1.246
Latitude*Longitude		0 – ∞	.664	ln(c+x)	.537	Yes	.1694	1.227
Latitude*Longitude^2		0 – ∞	.625	ln(c+x)	.491	Yes	.1754	1.236
Longitude^3		0 – ∞	.215	ln(c+ln(c+ln(c+x)))	.202	Yes	.1504	1.246
Målselv municipality		0 – 1	N. d.	None	N. d.	No	.1709	1.227
Latitude^2*Longitude		0 – ∞	.805	ln(c+x)	.555	Yes	.1884	1.211
Distance to closest seashore	km	0 – ∞	-.308	ln(c+x)	$<10^{-8}$	Yes	.3983	1.005
Latitude^3		0 – ∞	.936	ln(c+ln(c+ln(c+x)))	.557	Yes	1.0000	.004

In the set of forest and other environmental variables, presence of *Populus* forest and of *Alnus incana* trees were significant at α=0.00151 (see Tab. 5). The variation explained by this set of environmental variables is therefore to be interpreted as variation in growth substrate and will be termed "substrate variation" from here on.

Table 5. Forest- and other environmental variables. Skewness after transformation was below 10^{-10}. Only variables significant at α=0.00151 were included in further statistical analyses. N. d. not determinable.

Variable name	Units of measure-ment	Potential range	Skew	Transformation formula used	Ranging	p	F
Presence of moist *Salix* forest		0 – 1	n. d.	None	No	.0315	3.16
Presence of *Populus* forest		0 – 1	n. d.	None	No	**.0015**	2.68
Presence of *Salix pentandra*		0 – 1	n. d.	None	No	.0100	2.32
Proportion of edge length of non-forested area to edge length of forested area	%	0 – ∞	2.910	ln(c+x)	Yes	.0100	1.84
Presence of *Alnus incana*		0 – 1	n. d.	None	No	**.0005**	1.82
Proportion of forest edge length to total length of edge	%	0 – 100	-.295	e^{cx}	Yes	.0100	1.85

Variable name	Units of measurement	Potential range	Skew	Transformation formula used	Ranging	p	F
Tree age		1 – 3	-.350	e^{cx}	Yes	.0040	1.76
Number of naturally derived lines, line segments and patches		0 – ∞	.228	ln(c+x)	Yes	.0085	1.67
Total number of lines, line segments and patches		0 – ∞	1.006	ln(c+x)	Yes	.0085	1.65
Presence of birch forest rich in nutrients		0 – 1	n. d.	None	No	.0245	1.62
Presence of birch forest poor in nutrients		0 – 1	n. d.	None	No	.0110	1.58
Distance to closest river	km	0 – ∞	1.543	ln(c+x)	Yes	.0345	1.50
Presence of *Salix myrsinifolia*		0 – 1	n. d.	None	No	.0265	1.50
Suitability of rock substrates		1 – 10	.877	ln(c+ln(c+x))	Yes	.0365	1.44
Percentage of sibling trees	%	0 – 100	.873	ln(c+x)	Yes	.0590	1.39
Presence of *Salix caprea*		0 – 1	n. d.	None	No	.0740	1.39
Proportion of naturally derived edge length to total length of edge	%	0 – 100	.568	ln(c+x)	Yes	.1114	1.29
Tree density	#/ha	0 – ∞	8.301	ln(c+ln(c+x))	Yes	.1299	1.28
Maximum log diameter	cm	0 – ∞	.730	ln(c+x)	Yes	.1124	1.28
Basal area of logs	m²/ha	0 – ∞	1.143	ln(c+x)	Yes	.1154	1.26
Presence of *Betula pubescens*		0 – 1	n. d.	None	No	.1869	1.23
Maximum tree diameter	cm	0 – ∞	1.037	ln(c+x)	Yes	.1919	1.20
Density of young trees	#/ha	0 – ∞	8.115	ln(c+x)	Yes	.1619	1.21
Basal area of tree layer	m²/ha	0 – ∞	1.143	ln(c+x)	Yes	.2459	1.15
Presence of *Sorbus aucuparia*		0 – 1	n. d.	None	No	.2849	1.10
Log decay		1 – 3	-.435	e^{cx}	Yes	.3123	1.09
Presence of dry *Salix* forest		0 – 1	n. d.	None	No	.3308	1.06
Proportion of water edge length to total length of edge	%	0 – 100	2.157	ln(c+x)	Yes	.4898	.98
Density of logs	#/ha	0 – ∞	3.629	ln(c+x)	Yes	.4973	.96
Presence of alder forest		0 – 1	n. d.	None	No	.6062	.93
Median tree diameter	cm	0 – ∞	1.728	ln(c+ln(c+x))	Yes	.5997	.92
Presence of *Populus tremula*		0 – 1	n. d.	None	No	.4453	.93
Presence of alder-willow forest		0 – 1	n. d.	None	No	.5582	.91

From the set of macroclimatic, microclimatic and topographic variables, the sum of precipitation of all months exceeding 4°C in mean air temperature was significant to epiphytic macrolichen vegetation (Tab. 6). Also the temperature sums exceeding 4°C and 0°C were significant, as well as oceanity. Since only variables connected with macroclimatic parameters were significant, the variation explained by this set will be referred to as macroclimatic variation further on. The significance level used for this set of explanatory variables was α=0.00385.

Table 6. Macroclimatic, microclimatic and topographic variables. Skewness after transformation below 10⁻¹⁰ for all variables. α was 0.00385. N. d. not determinable.

Variable name	Units of measurement	Potential range	Skew-ness	Formula used for transformation	Ranging	p	F
Sum of precipitation in all months exceeding 4°C in mean air temperature	mm	$0 - \infty$	.309	$\ln(c+x)$	Yes	**.0005**	2.500
Oceanity of climate		$1 - 4$	-.409	e^α	Yes	**.0005**	2.740
Annual normal precipitation	mm	$0 - \infty$	-.095	e^α	Yes	.0125	2.573
Temperature sum for all months exceeding 4°C in average air temperature	°C	$0 - \infty$	-1.546	e^α	Yes	**.0025**	1.823
Temperature sum of all months exceeding 0°C in mean air temperature	°C	$0 - \infty$	-1.141	e^α	Yes	**.0005**	2.205
Light conditions		$1 - 5$	.239	$\ln(c+x)$	Yes	.0065	1.804
Slope angle of plot	°azimuth	$0 - 90$	.524	$\ln(c+x)$	Yes	.0195	1.669
Moisture conditions		$1 - 5$	-.104	e^α	Yes	.0345	1.684
Sum of precipitation in all months exceeding 0°C in mean air temperature	mm	$0 - \infty$	.391	$\ln(c+x)$	Yes	.0155	1.683
Unfavourability	°	$0 - 180$	-.518	e^α	Yes	.0195	1.646
Insolation index		$0 - 15$	.413	$\ln(c+x)$	Yes	.0195	1.601
Average plot altitude above sea level	m	$0 - \infty$	1.012	$\ln(c+x)$	Yes	.0865	1.347
Parker's heat index		$-\infty - +\infty$	8.267	$\ln(c+x))$	Yes	.5707	.822

Variation partitioning

Tab. 7 shows the results of variation partitioning in CCA. Pure macroclimatic variation, that is the amount of variation explained by the macroclimatic, microclimatic and topographic explanatory variable set not shared with any other sets is statistically significant (see Tab. 7). Also the amounts of variation explained by this climatic variable set alone plus that shared with other sets of explanatory variables are statistically significant (such as e.g. C|(H∪S) or C|S). Also pure spatial and pure "forest and other environmental" variation are statistically significant. Variation in macrolichen species composition explained by human impact is not statistically significant at $\alpha = 0.0025$.

Table 7. Partitioning of the variation in epiphytic macrolichen vegetation on the four sets of explanatory variables forest and other 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 TI is 3.460 IU) as well as fractions of the total variation explained, FTVE, where the total variation explained, TVE, is 0.912 IU. The Bonferroni-corrected significance level α is 0.0025 (0.05/20). The symbols "∪" and "∩" indicate unions and intersections of variable sets, while "|" stands for "without".

Constraining variables	Covariables	Variation explained					Remarks
		Denotation	VE	FTVE	p	F	
{C}	none	C	.449	49.2	**.0005**	2.383	Variation explained by macroclimate
{E}	none	E	.223	24.5	**.0005**	2.270	Variation explained by substrate
{H}	none	H	.076	8.3	.0030	1.499	Variation explained by human impact
{S}	none	S	.348	38.2	**.0005**	2.420	Variation explained by geography
{C}	{E, H, S}	C|(E∪H∪S)	.319	35.0	**.0005**	1.816	The variation explained by {C} not shared with any other variable sets, i.e. purely macroclimatic variation.
{E}	{C, H, S}	E|(C∪H∪S)	.155	17.0	**.0015**	1.760	Pure substrate variation. Statistically significant.
{H}	{C, E, S}	H|(C∪E∪S)	.047	5.2	.3438	1.070	Strictly human impact variation. N. s.
{S}	{C, E, H}	S|(C∪E∪H)	.233	25.5	**.0005**	1.766	Strictly spatial variation. Significant.
{E}	{C}	E|C	.175	19.2	**.0020**	1.910	E∩C = E − E|C = 0.048 (5.3 %). Variation shared between substrate and macroclimate.
{E}	{H}	E|H	.224	24.6	**.0005**	2.303	E∩H= E − E|H = 0.000
{E}	{S}	E|S	.185	20.3	**.0005**	1.974	E∩S = E − E|S = 0.038 (4.2 %)
{C}	{H}	C|H	.434	47.6	**.0005**	2.316	C∩H = C − C|H = 0.015 (1.6 %)
{C}	{E}	C|E	.401	44.0	**.0005**	2.190	C∩E = C − C|E = 0.048 (5.3 %)
{C}	{S}	C|S	.355	38.9	**.0005**	1.964	C∩S = 0.094 (10.3 %)
{S}	{C}	S|C	.254	27.9	**.0005**	1.875	S ∩C = 0.094 (10.3 %)
{S}	{H}	S|H	.338	37.1	**.0005**	2.365	S∩H = 0.010 (1.1 %)
{S}	{E}	S|E	.308	33.8	**.0005**	2.212	S∩E = 0.040 (4.4 %)
{H}	{C}	H|C	.061	6.7	.0880	1.303	H∩C = 0.015 (1.6 %)
{H}	{E}	H|E	.077	8.4	.0040	1.585	H∩E = 0.000
{H}	{S}	H|S	.066	7.2	.0480	1.385	H∩S = 0.010 (1.1 %)
{C}	{H, S}	C|(H∪S)	.343	37.6	**.0005**	1.906	C∩H∩S = C − C|(H∪S) − C|H − C|S = 0.003
{C}	{E, S}	C|(E∪S)	.333	36.5	**.0005**	1.895	C∩E∩S = C − C|(E∪S) − C|E − C|S = 0.026; C∩E∩S∩H = 0 (H∩E = 0); (S∩C)|(H∪E) = 0.065

The macroclimate explains the largest amount of variation in epiphytic macrolichen species data, followed by geography and substrate (see Fig. 7 and 8). Human impact explains least of the variation in epiphytic macrolichen vegetation. However, all these latter amounts of variation include variation shared with other sets of explanatory variables.

All sets of explanatory variables share variation except for human impact and substrate (see Tab. 7, Fig. 7). The largest amount of shared variation is pooled between geography and macroclimate, amounting to 10.3 % of total variation explained, TVE, followed by variation shared by the set of substrate and macroclimate, 5.3 % of TVE. Human impact shares a small amount of variation with macroclimate, 1.6 % of TVE, as well as with geography, 1.1 % of TVE. The spatially structured component of all environmental variation in the data set, that is $(C \cup E \cup H) \cap S$, may be computed by substracting $S|(C \cup H \cup E)$ from S, and amounts to 12.6 % of TVE.
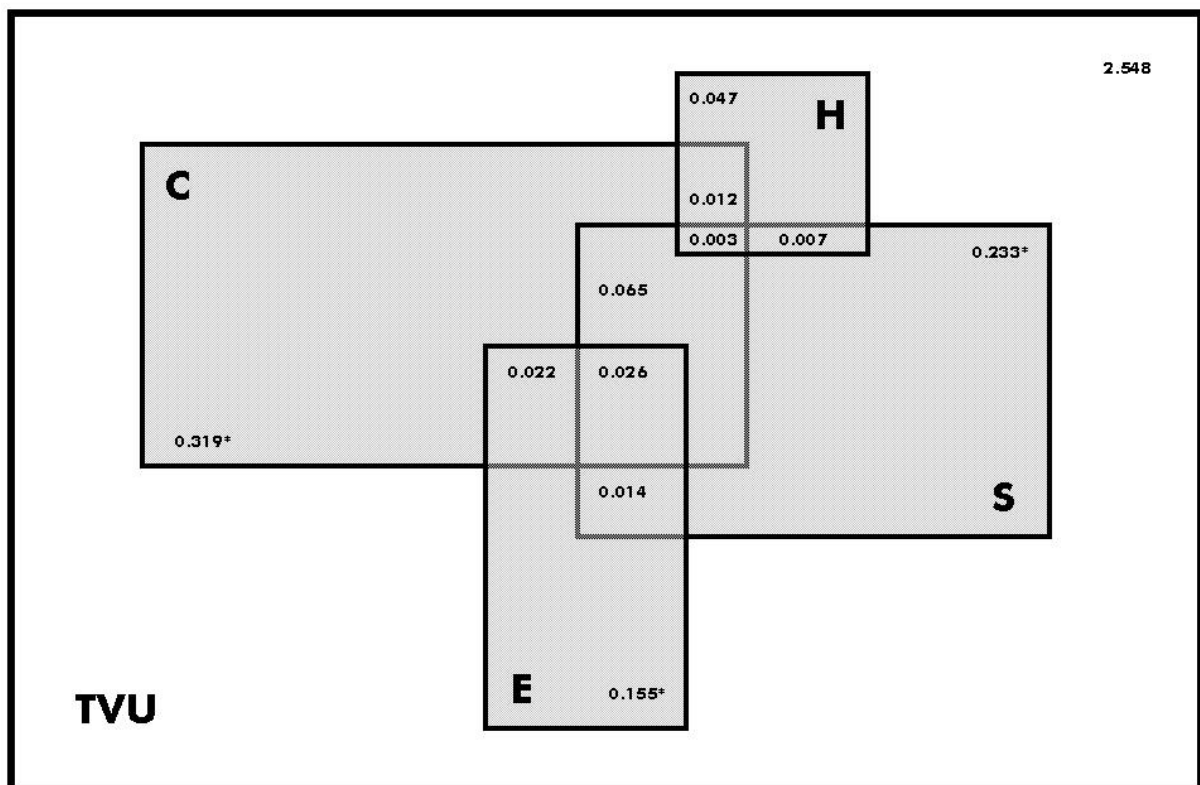
Figure 7. Variation explained by S (spatial variation), C (macroclimate), H (human impact) and E (substrate). Units of measurement are inertia units (IU). Statistically significant amounts of variation are indicated by asterisks. For abbreviations, see Tab. 3 to 6. Total variation explained, TVE is 0.912 IU (area crosshatched grey), and total variation unexplained, TVU, is 2.548 IU. For more details see Tab. 7.

Strictly macroclimatic variation is the largest fraction of total variation explained by a single set of explanatory variables when effects of all other sets of variables had been removed, and amounts to 35 % of TVE. Also strictly spatial variation explains a high proportion of the variation in epiphytic macrolichen vegetation, namely 25.5 % (see Fig. 8), followed by

variation strictly attributable to substrate with 17 % of TVE. Strictly human impact variation is as low as 5.2 % (see Fig. 8).
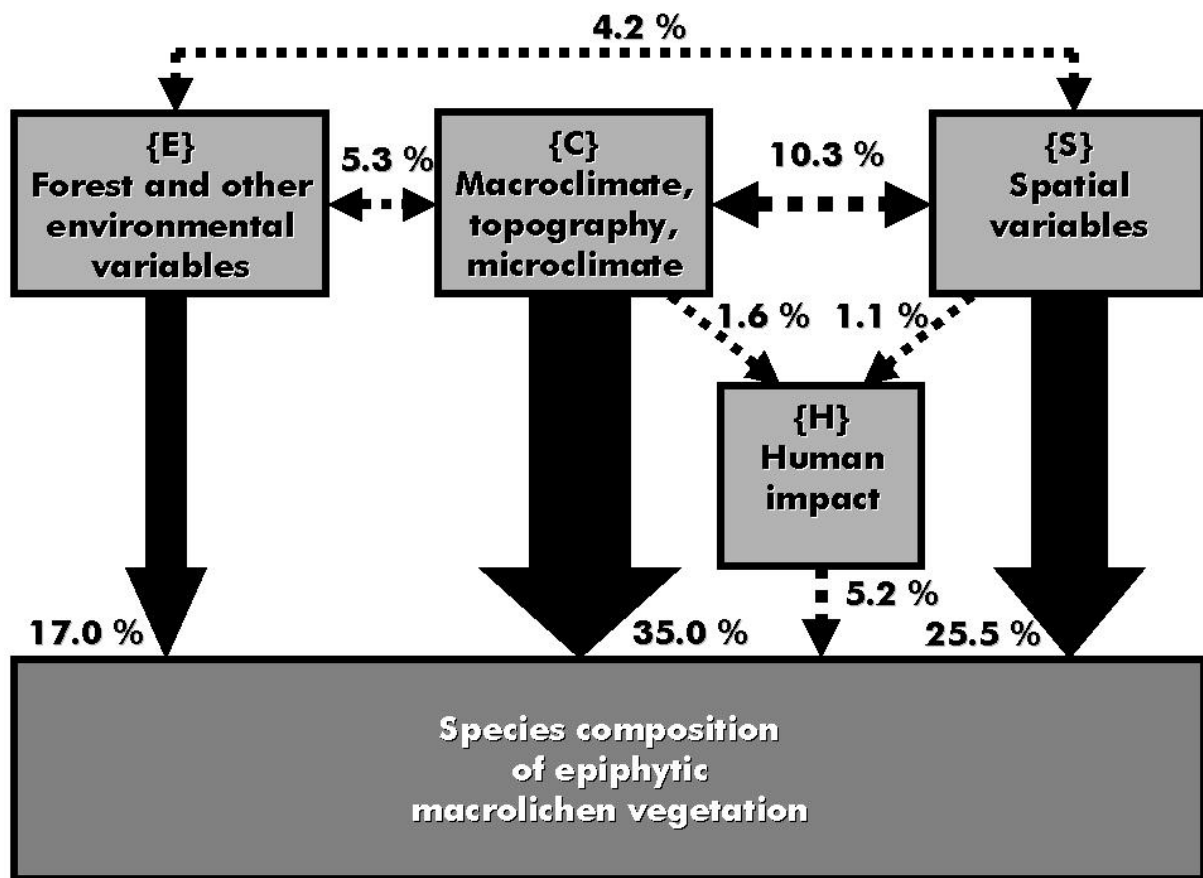
Figure 8. Path diagram showing fractions of total variation explained by four sets of explanatory variables, {C}, {E}, {H}, and {S}, and shared variation between variable sets. Fractions of total variation explained, FTVE, are indicated by arrows. An arrow pointing to another variable set indicates the FTVE shared by the variable sets. An arrow directly pointing from a given variable set to species composition shows the FTVE attributable to this set of variables, when the effects of all other sets of explanatory variables had been removed. Dotted lines indicate that a specific FTVE is not statistically significant at $\alpha = 0.0025$.

Discussion

Synopsis

Macroclimate, substrate and spatial variation explain most of the variation in epiphytic macrolichen composition. Even though human impact – or the lack of it – is often assumed to be a major factor structuring lichen vegetation (Rose 1992; Tibell 1992; Pfefferkorn & Türk 1996; Kuusinen 1996; Trass et al. 1999), in the present study the effects of human impact on macrolichen community composition are not statistically significant. Species commonly regarded as faithful indicators of continuity of the tree canopy in Central Europe such as *Degelia plumbea, Pannaria conoplea*, *Parmeliella triptophylla* and others occur either on rocks in the study area – such as the former two, or on diverse substrates – such as the latter one, but were rarely or never found in typical old-growth habitats.

Are the selected methods adequate for the present purpose?

Abundance estimate used

Presence/absence of species is the roughest possible species abundance estimate, but has the advantage of being straightforward. In comparison to other abundance estimates such as frequency in subplots or cover, sampling of presence/absence of species in plots is far less time-consuming when used in field vegetation surveys, and provides a more observer-independent, reliable estimate than cover estimates.

Scale of study

The scale is the spatial context a study is operating in. The purpose of this very study leads to the selection of a large spatial scale, a regional rather than local scale - in this investigation, the distance between the westernmost and easternmost plot is 113 km, and that between the northernmost and southernmost plot is 126 km. The determination of factors important for macrolichen vegetation, valid for the entire region of central and southern Troms county would be impossible on a local scale. The region is richly structured by mountain chains, which gives rise to strong differences in environmental

conditions between localities. Under such topographic conditions, it is treacherous to interpolate from a small investigation area to a whole region. An investigation on a local scale would not recover important gradients in species composition operating on a large spatial scale.

It was aimed at including as many localities in central and southern Troms county as possible in order to optimise the representativity of the sample, reflecting typical climatic and topographical conditions of the region.

Plot size

The choice of plot size is a critical point in vegetation ecological studies. Large plot sizes imply filtering out all information on scales finer than the plot size, and low noise in the data set obtained (Bellehumeur et al. 1997). Small plot sizes do recover fine-scale gradients (Økland 2001), but those are not always of interest.

The plot size should reflect the scale on which the variation of interest occurs. As it is being focused on a broad, regional scale, the plot size has to be large for adequately representing this scale. A second point to be focused on is that the larger the plots are, the more time it takes to analyse them, and thus fewer plots will be obtained in a given time (Økland 2001). In addition, the larger the plot, the more difficult it becomes to record all elements of the plot, which implies that the data may become less faithful.

Økland (1990) recommends to use the smallest plot size which adequately represents the spatial scale of interest, which may be between $25 - 100$ m^2 when studying the tree layer in forest vegetation. This latter recommendation refers to vegetation comprised of higher plants, and may not be useful at all when applied to epiphytic lichen vegetation. Here, specific considerations have to be taken into account. Many macrolichen species show a high degree of habitat specialism (Barkman 1958a). In situations where the tree species preferred is not dominating the tree layer, the spatial distribution of habitat specialised lichens will be either clumped or scattered, following the distribution of the preferred tree species. When small plot sizes are used under such conditions, the danger of overestimating species abundance is high if a plot by chance includes a preferred phorophyte tree. Otherwise, species abundance is underestimated if a plot fails to include appropriate phorophyte trees. Under such circumstances, the most precise abundance of such species will be obtained by using large plot sizes.

Square plots of size 400 m^2 were used for the analysis of macrolichen vegetation in this study, while square subplots of 100 m^2 were used for forest stand properties. This solution seems to be adequate for recovering clumped species distributions, and to avoid too much time-consumption for analysing forest stand parameters.

Number of plots

Several considerations have to be taken into account when determining plot number: the expected variation in ecological conditions in the study area, the method used for selecting plots, the plot size, the necessary representation of each combination of complex gradients or vegetation types, and time available for field work (Økland 1990).

When assuming the variation in ecological conditions to be high, plot numbers should be maximised. When making use of random or systematic sampling, plot numbers have to be higher than when employing stratified random or subjective sampling, since the former two sampling methods tend to fail representing rare vegetation types which can be specifically sampled in the latter sampling strategies. The larger the plot size, the fewer plots are needed (Økland 1990).

Here, it was focused on getting the highest possible total number of plots by analysing as many as possible localities. The plot number was 69. According to Økland (2001), for the detection of two gradients in species composition by the ordination technique DCA, at least 50 plots have to be supplied.

It was aimed at analysing one plot per selected deciduous forest type present at a given locality. This constraint had to be violated when the number of deciduous forest types in a given locality was low, and then several plots of the same forest type were analysed instead.

Stratified random sampling within a vegetation type

To be able to detect possible macroclimatic differences in epiphytic macrolichen vegetation, it was attempted to place plots with a regular spacing along the coastline-interior gradient. Some middle-gradient areas were slightly undersampled, as for example the Balsfjord area.

To obtain optimal results in gradient analysis, the whole gradient along which the species occur should be sampled, at best with regularly placed plots (Økland 2001). Otherwise,

one might face a risk of obtaining a data set with a disjunction in floristic dissimilarity. None of the gradient analysis techniques are able to cope with disjunctive data sets, since species optima may not be adequately calculated. The gradient lengths of such data sets become very large, i.e. exceeding 4 S.D. units, if two ends of the sampled gradient are floristically completely dissimilar, lacking shared species (Jongman et al. 1987).

In the present study, however, the gradient length of the macrolichen data set is rather low, i.e. below 2.8 S.D. units on the first two axes in DCA. A large amount of species is found almost anywhere along the gradient, such as *Hypogymnia physodes, Melanelia olivacea, Parmelia sulcata, Parmeliopsis ambigua* and the like. Under such conditions, it is rather unimportant that the middle part of the coastline-interior gradient was undersampled to some extent. Increasing the number of middle-gradient plots would probably not add any significant changes to the results obtained.

Criteria for rejection of plots

In vegetation ecological studies, it is of primary importance to define criteria for rejection of plots prior to sampling. Rejecting plots of certain properties implies a filtering of the data obtained (Økland 2001), and may lead to biased data. When objective criteria are given to reject certain types of plots, however, this filtering of data may be desired.

The criteria used lead to the avoidance of plots which can not be considered representative samples. The first criterion of excluding plots closer than 2 m to the forest edge leads to the exclusion of plots comprising the most severe parts of forest edges. Lichens are influenced by edge effects (Esseen & Renhorn 1998). Excluding the most severe part of the forest edge means a reduction of noise in the data set obtained, which is rather advantageous since the statistical method employed, CCA, is sensitive to noisy data. However, it might also prevent a detection of the most severe effects of forest fragmentation. By the second and third criterion, plots consisting of either a large water surface or a small number of trees are rejected – plots which can hardly be defined as forest. The fourth criterion seeks to avoid including forest types comprised of more than 10 % coniferous trees. The lichen flora of coniferous trees such as Scots pine, for instance, is very different from that of deciduous trees (Kuusinen 1994b). Since it is attempted to study macrolichen vegetation of deciduous forests, the lichen flora of coniferous trees is not of interest to this study, and would only be an additional source of noise in the data.

Ordination versus constrained ordination

The concept of constrained ordination is fundamentally different from that of ordination (Økland 1996; Økland 1999). Ordination is designed to reveal coenoclines, i.e. gradual changes in species composition (Jongman et al. 1987). Plots and species are grouped by using the species data alone (Palmer 1993). This variation in species composition can be related to a set of explanatory variables a posteriori, allowing the generation of hypotheses about important underlying complex gradients[1] (Økland 1996).

Constrained ordination aims at detecting patterns of variation in species composition that can be explained by the observed environmental variables (Jongman et al. 1987). Plots and species are grouped along axes of variation in species composition, optimizing the fit to a set of explanatory variables (Økland 2001). With regard to the iteration algorithm, a constrained ordination solution can be obtained by adding a multiple regression step into any of the ordination algorithms after the calibration step (ter Braak & Prentice 1988; Palmer 1993; Økland 2001). This multiple regression step provides plot scores which are linear combinations of the trial plot scores and the explanatory variables supplied, the "maximally constrained plot scores" (Økland 2001), "LC site scores" (Palmer 1993), or "LC scores" (McCune 1997). By adding a multiple regression step into a given ordination algorithm, a constrained parallel to any of the ordination methods in the Correspondence Analysis - family can be provided (ter Braak & Prentice 1988). The most commonly used constrained techniques are Redundancy Analysis (RDA) which is a constrained parallel of Principal Component Analysis (PCA) and Canonical Correspondence Analysis (CCA), which is a constrained parallel of Correspondence Analysis (CA) (Jongman et al. 1987).

The fundamental difference between ordination and constrained ordination is, that in constrained ordination all variation in vegetation not related to the explanatory variables provided is discarded (Økland 1996), whereas ordination reveals all variation in species composition, regardless of environmental variables. This implies that in constrained ordination, only variation in vegetation which was assumed to be important a priori may be discovered, as defined by the choice of explanatory variables. In other words, the results of a constrained ordination are dependent on which explanatory variables were considered important prior to sampling. As a consequence, the possibility of generating

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[1] A complex gradient is a set of ecological factors, which are varying more or less parallel.

new hypotheses about vegetation-environment relationships is lost in constrained ordination (Økland 1996).

The constrained ordination technique CCA is sensitive to noise in environmental data and provides strongly distorted gradients in such cases (McCune 1997). This is another argument for not using CCA in studies where the purpose is detecting gradients in species composition. It remains questionable whether other constrained ordination techniques show the same weakness when supplied with noisy data; no tests have so far been performed on e.g. RDA.

General-purpose vegetation ecological studies attempt to recover the most important gradients in species composition. Ordination axes reflect gradients in species composition optimally. Hence, ordination is the adequate method for this kind of ecological studies.

However, if the purpose of a study is testing hypotheses about vegetation-environment relationships, then constrained ordination may be the method of choice (Økland 1996; Økland 2001). The reason for this is, that constrained ordination associated with Monte Carlo tests allows statistical significance testing of the relationships between species and environmental variables (ter Braak & Smilauer 1998).

CCA versus RDA

CCA and RDA are different with respect to the species response model. In RDA, a linear relationship between explanatory variables and species abundances is assumed, while the assumption of CCA is an unimodal relationship. CCA is recommended when the longest gradient is exceeding 2 S.D. units, while RDA is more appropriate when the longest gradient falls below 2 S.D. units (Jongman et al. 1987).

The concept of variation in CCA

Two types of axes may be gained in CCA: constrained axes with a high correlation to environmental variables, and unconstrained distortion axes. The latter give a measure of residual variation remaining in the data when the variation associated with the constraining variables has been extracted. In CCA, the total variation in the data, total inertia, TI, is calculated by adding the eigenvalues[2] of all CCA axes, while total variation

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[2] Eigenvalues give a measure of the dispersion of scores along an axis, which shows how well the plots can be separated by their species composition.

explained, TVE, is the sum of eigenvalues of all constrained axes (Økland 2001). Variation remaining after the extraction of constrained axes may be due to lack of fit of the data to the model, resulting in polynomial distortion axes. The "variation explained" by those distortion axes is not actually of interest for the interpretation of the data, since it merely shows that the data do not fit perfectly to the model (Økland 2001). Also a deficiency in the sampling of environmental data results in residual variation by the exclusion of important variables or by using wrong scales of measurement. Unfortunately, the sources of residual variation can not be separated, which means that the interpretation of residual or "unexplained" variation is hardly possible (Økland 2001).

Possible pitfalls in CCA

Any method based on regression – such as CCA – will be affected by collinearity of variables. Collinear variables are those correlated strongly with each other ($r^2 \geq 0.9$; variation inflation factor >10) (Kleinbaum et al. 1998). Collinear variables were therefore excluded from analyses in this study, and the variation inflation factor was smaller than or equal to 8 for all variables used for calculations of fractions of total variation explained.

CCA is susceptible to noise in the data as well as to the inclusion of superfluous environmental data into the model (McCune 1997). This problem will remain whenever we sample environmental data – no data set is free of noise.

Monte Carlo permutation tests

The Monte Carlo permutation test is a randomisation test. Randomisation tests are non-parametric tests which can be used in cases where the demands for statistical independence of observations are not met with, or when it can not be guaranteed that they are met with (Manly 1997). The null hypothesis to be tested is that the relationship between the response variable and the other variables is not stronger than expected by chance (Økland 2001). Using Monte Carlo permutation tests, it is possible to test the significance of variation in vegetation explained by a constrained ordination axis, an explanatory variable or a set of explanatory variables (Økland 1996).

Detrended Correspondence Analysis, DCA

According to Økland (personal communication), it is preferable in vegetation ecology to employ several different methods of gradient analysis in parallel. Is the same general conclusion obtained independently by different methods, it may be assumed to be reliable. For this reason, the ordination technique DCA was used in parallel to the constrained ordination technique CCA. Correlations between plot scores in DCA and significant variables of CCA (App. 9) reveal a pattern very similar to that of the CCA, with two macroclimatic, one spatial and one substrate variable significantly correlated to the first axis in DCA (correlation coefficient used: Kendall's τ), three macroclimatic and two spatial variables and the human impact variable significantly correlated to the second axis in DCA.

The gradient lengths of the first three DCA-axes exceed 2.0 - implying that at least two rather short gradients are present in the species 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 epiphytes are for example the foliose *lichens Hypogymnia physodes, Melanelia olivacea, Parmelia sulcata, Parmeliopsis ambigua* and the fruticose lichen *Bryoria fuscescens*, species sharing a preference for strongly acidic bark. Among the species with a more limited distribution are *Hypogymnia bitteri, H. austerodes, Physcia caesia* and *Physconia perisidiosa*. The latter two are mostly found as epilithic individuals.

Two ecologically distinct species groups are found within the large central cluster of species optima in the ordination diagram (Fig. 6). There is a gradual shift from habitat-specialised species with a low distribution range to the left to less specialised species on the right side of the ordination diagram, common and widely distributed in the study area. The former are *Peltigera collina, Collema nigrescens*, *Lobaria pulmonaria,* and adjacent species, growing predominantly on circumneutral to weekly acidic bark in the interior of Troms county, many of which belong to the Lobarion community (Barkman 1958a). *Cetraria sepincola* is an exception in this pattern, a species rarely found in the plots due to its habitat preference for small branches. The placement of this species within the group of habitat-specialised interior species is probably incorrect due to the low number of plots where the species was present. Many of the species around *Xanthoria parietina* in the upper right corner of the ordination diagram are species occurring predominantly in coastal sites in Troms, all of them preferring habitats with high nutrient availability such as

cliffs manured by birds, cliffs within reach to the sea spray zone, and rich bark tree species (Moberg 1982; Timdal 2001). The species *Phaeophyscia sciastra, Physcia caesia, Physcia dubia* and *Xanthoria elegans* at the bottom of the ordination diagram represent a group of species mostly found on stone with differing nutrient availability (Moberg 1982). These species were mostly found in interior sites. *Phaeophyscia ciliata,* however, is a typical epiphyte of aspen trees (Moberg 1982).

The DCA ordination reveals a pattern in species optima of epiphytic macrolichens which may be directly related to substrate conditions and spatial variation, and possibly indirectly to macroclimate, but the single factors can hardly be separated.

To conclude, apart from the scale used to estimate forest fragmentation, which was presumably slightly too large to enable the detection a response of macrolichens on forest fragmentation, in my opinion the methods employed in this study can be regarded as adequate.

Human impact

In boreal deciduous of Troms county, human impact can not be considered as a key factor structuring epiphytic macrolichen vegetation in deciduous forests of central Troms county. These results are in accordance with those of a study of forest vegetation in the Northwest US comprised of higher plant species, where clearfellings accounted to only 2 % of total variation explained (Ohmann et al. 1998). When effects of covariation have been corrected for, variation due to human impact – that is, the presence of tree plantations close to the plots – explains a statistically non-significant amount of 5.2 % of total variation explained. Box 1 summarises possible physiological mechanisms underlying the sensitivity of lichens to human impact, Box 2 presents the results of a case study at Brennfjellet (Tab. 2), and Box 3 gives an outline of forest management history in Troms county.

From the set of human impact explanatory variables, the variable indicating the presence of a plantation in visibility is significant for epiphytic macrolichen vegetation. It is not a very reliable variable because plantations are difficult to see if the planted trees are still small. Additionally, visibility is presumably dissimilar in different forest types, and is lower in dense forests. The interpretation of the variation accounted for by this variable has to be subject to reservations. In Troms county, areas to be planted are cleared from the original tree

layer to a varying extent by logging either before alien trees are planted, or some years later (Tømmervik, personal communication). Since lichens were not recorded on spruce trees, it is evident to interpret the variation explained by plantation as a generally high level of human impact in the plot's surroundings.

Box 1. Possible underlying physiological mechanisms causing the sensitivity of lichens to human impact.

High light stress may cause chlorophyll degradation in lichens, particularly in species confined to old forests; this is one reason why lichens are harmed by logging (Gauslaa & Solhaug 1996). Low tolerance to heat stress may be another factor, as shown for the old forest lichen *Lobaria pulmonaria,* and the two factors might work together (Gauslaa & Solhaug 1999). Sufficiently high thallus water content is a crucial factor for photosynthesis in lichens; if the thallus does not contain enough water, respiration may exceed photosynthesis (Purvis 2000). Low air humidity may cause a decrease in time available for photosynthesis, leading to reduced lichen growth (Sillett 1994). In forests of Switzerland, thalli of the old forest lichen *Lobaria pulmonaria* were photosynthetically active over periods of on average one hour per day (Scheidegger unpublished data). It is evident that a further reduction of the short time available for photosynthesis might be fatal. Periods of low air humidity reduce the competitive ability of oceanic lichen species (Schauer 1965). For these reasons, lichens react to habitat changes involving deforestation, such as logging and forest fragmentation.
Also pollution can be regarded as a human impact (Liu & Bråkenhielm 1995; Pfefferkorn & Türk 1996). Lichen algae were shown to be directly harmed by sulphur dioxide and ozone fumigation (Le Blanc & Rao 1973; Holopainen 1983; Holopainen & Kärenlampi 1984; Garty et al. 1993; Scheidegger & Schröter 1995). According to McCune et al. (1997), epiphytic lichens are sensitive to air pollution mainly because of their reliance on atmospheric nutrition sources and their lack of a cuticle .

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 events than common species. Is all available habitat suitable to and colonised by a lichen species in a forest landscape, logging will probably have no long-term effects at all. Is the species restricted to certain habitat types, and are those rare, irregularly distributed throughout the landscape, and interesting for logging activities, then the species may face a particularly high risk of local extinction owing to logging. The accessibility of suitable habitat may then become a problem for the species since the total amount of available habitat declines, leading to a decrease in the probability of a lichen diaspore to be dispersed to suitable habitat. These circumstances have been hypothesised for deciduous forests situated in Central Europe (Wirth 1976; Wirth 1999).

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; Kondratyuk & Coppins 1998; Kuusinen 1996), except for the latter, involve a statistical analysis of the data - the findings are therefore restricted to reservations. Confounding of habitat qualities and logging regimes, for instance, is a problem which can not be coped with in such studies. As opposed to younger forests, forests that remained undisturbed for a longer time contain more particular habitats suitable for growth of epiphytic lichens such as large trees, logs and snags. This difference is mainly due to a shift in forest structure with ongoing succession, and may be completely independent of logging. Studies in which the effects of covariation created by habitat properties is not corrected for, are unable to evaluate the importance of logging, or other human impacts faithfully.

Box 2. Case study of "old-growth dependent" macrolichens at two sites in Skibotndalen valley, focussing on habitat preferences.

Macrolichen species which are old-growth dependent in Central Europe such as *Degelia plumbea* or *Pannaria conoplea* do not prefer exactly the same habitat types in Troms county – instead they show a tendency of growing on rock habitats . This may be due to an increased availability of suitable rock habitats compared to areas in Central Europe, as well as to the lack of sufficiently old trees at Brennfjell and suitable tree species at Kavelnes. The forest stand at Brennfjell is a young aspen forest located on a south-exposed hillside, growing on top of a boulder field, with the largest aspen tree about 54 years old. At this site, yet another curiosity is visible: instead of growing on aspen, the dominant tree species, a large number of "old-growth" macrolichens grow on tiny juniper shrubs (see Tab. 2). Of the old-growth species listed in Tab. 2, only *Leptogium saturninum* and *Lobaria scrobiculata* actually grow on trees in plot A37 at Brennfjell. As for *Lobaria scrobiculata*, only a single individual grows on an aspen tree, probably recruited from the large saxicolous population growing right beside.
A similar habitat pattern is found in Kavelnes, with *Degelia plumbea*, *Lobaria pulmonaria* and *Peltigera collina* exclusively growing on rocks. *Lobaria scrobiculata* and *Sphaerophorus globosus* are the only species from the list presented in Tab. 2 which grow both as saxicolous and as corticolous.

The results of a study performed in central Norwegian coastal spruce forests in which the effects of covariation were corrected for, led to the conclusion that historical selective logging did not have significant effects on selected epiphytic macrolichen species (Rolstad et al. 2001). Several of the species investigated were species belonging to the Lobarion community, considered as indicators of ecological continuity of woodlands in Great Britain (Rose 1976; Rose 1992) and Finland (Kuusinen 1996), and as hemerophobic species in Estonia (Trass et al. 1999). Four species are reckoned as old-growth dependent or

preferring in Northern America (Lesica et al. 1991; Goward 1994). Rolstad et al. (2001) did not detect negative long-term effects of selected logging on these species.

For the entire set of macrolichen species, no effects of human impact were detected in the present study. In areas characterised by an highly oceanic climate, such as coastal central Norway (Ahti et al. 1968), species belonging to the Lobarion community have almost optimal climatic conditions (Gauslaa, personal communication). Under such conditions they may show a higher tolerance to logging than under growth conditions further off the climatic optimum (Gauslaa, personal communication). The climate of Troms county can be characterised as oceanic to suboceanic (Ahti et al. 1968). It is possible that at least some lichen species may respond comparatively little to logging because of climatic conditions favourable to them. On the other hand, regarding thermophilous lichen species reaching their northern distribution limits in northern Norway such as *Hypogymnia tubulosa* and *Ramalina farinacea* (Timdal 2001), logging or other human impacts were assumed to have stronger effects because they are already climatically limited. This hypothesis will be tested in Werth et al. (in prep.).

Forest fragmentation and natural patchiness

In fragmented landscapes, communities are influenced by edge effects (Noss & Csuti 1997). Forest fragmentation leads to a change in forest microclimate: areas characterised by sunny, dry forest edge microclimate with relatively high wind speeds increase (Renhorn et al. 1997). In a study of Norway spruce forests in northern Sweden, epiphytic lichens were affected by edge effects, but significant edge effects were not found further away than 50 m from the forest edge (Esseen & Renhorn 1998).

None of the variables indicating forest fragmentation or natural patchiness were statistically significant in the present study. On the spatial scale studied, no effects of forest fragmentation or natural patchiness on epiphytic macrolichen vegetation were detected.

Measurements on the basis of topographical maps give certainly the roughest possible estimate of forest fragmentation, and it is doubtful whether the most recent changes in the landscape are mapped. But at least the information provided by topographical maps gives a general image of forest fragmentation. To estimate the degree of forest fragmentation, circular macroplots of radius 457 m were employed, corresponding to 656,360 m^2. This seems to be about the finest spatial scale where the resolution of the topographical maps

1:50,000 is high enough to give appropriate estimates of forest fragmentation, and yet this scale was probably too large to enable the detection of a response in macrolichen vegetation.

Box 3. A brief outline of forest management history in Troms county.

It is very likely that Sami people were already living as nomads in Troms county for centuries when the first settlers of Norwegian origin arrived (Eggen 1959; Sveli 1987), and were making use of the forest resources in the areas they were living in. Sami housing grounds are reported from places in the interior of Troms county such as in Målselv municipality at the lake Takvatnet (Ruden 1911), as well as from places closer to the coastline such as the Malangen area (Hauglid 1981). Sami resting-places are known from the floodplains of the river Barduelva in Bardu municipality, for instance (Eggen 1950). Ruden (1911) is of the opinion that Sami people destroyed large forest areas in Troms county. Contrary to Ruden (1911), Sveli (1987) stresses the fact that Sami people did not affect forests to a significant degree, since they were never long enough at one place to make ample use of the forest resources. Barth (1858) confirms this view for forests in Finnmark county.

Non-nomadic settlers had a by far more severe effect on forests in northern Norway. Already in the age of the Viking explorations, the forest resources were used intensively at the outer coastline and the fjord areas of Troms county, where most of the population was living at that time (Sveli 1987). In the 7th century, Hillesøy got established as a trading place, and thereafter the adjacent area was settled thinly, followed by a period of more intensive settlement in the 8th century (Bertheussen, 1988). In the outermost area of the fjord Malangen, first settlements began in the 12th century, but an intensive period of settlement did not start before the 14th century (Ytreberg 1943). By the 20th century, almost no forest was left along the coastline of Troms county partly because of intensive cattle, sheep and reindeer grazing and partly because of logging for firewood and other purposes (Sveli 1987). The inland areas were settled much later than the coastline of Troms, mostly in the 18th and 19th century; in Bardujord in Bardu municipality, for example, the first farms were established in 1791 (Eggen 1950), and in Alapmoen, inner Målselvdalen valley, in 1829 (Kiil 1981). Logging of coniferous trees, however, is reported from Målselv already in the 17th century (Ytreberg 1943).

Substrate variation

The third major gradient in species composition is variation in substrate conditions, accounting for 17 % of total variation explained (see Tab. 6). It is interesting that in this investigation performed on a comparatively broad spatial scale along a regional climatic gradient, substrate conditions are determined as one of the key factors for epiphytic macrolichen vegetation. Tab. 2 gives a list of the growth substrates at the sites Brennfjell and Kavelnes in Storfjord municipality, found for lichens which are reported as old-growth dependent in Central Europe. This case study is discussed further in Box 2.

Substrate-related variation in epiphyte communities has been emphasised in many local-scale studies (Barkman 1958a; Brodo 1973; Seaward 1982; Oksanen 1988; Bates 1992; Hyvärinen et al. 1992; Burgaz et al. 1994). Variation due to forest stand properties (Oksanen 1988; Hyvärinen et al. 1992; Gustafsson & Eriksson 1995), phorophyte species (Oksanen 1988; Bates 1992; Hyvärinen et al. 1992; Burgaz et al. 1994), and bark properties (Gauslaa 1985; Bates 1992; Hyvärinen et al. 1992; Gustafsson & Eriksson 1995) is often considered significant. Another important gradient in lichen species composition operating on an even finer spatial scale is the vertical zonation of lichen communities on tree boles (McCarthy 1980).

In the set of forest- and other environmental variables, two variables defining the forest type, *Populus* forest and indicating the presence of *Alnus incana* trees in the plots, are significant for epiphytic macrolichen vegetation. *Populus tremula* represents a rich bark tree species, with circumneutral to slightly acidic bark pH in the study area (see Fig. 5). *Populus* trees are inhabited by many specialised lichen species (Kuusinen 1994a). *Populus* forest plots form a group with a specific lichen flora, which contributes to the explanation of some of the variation in epiphytic macrolichen vegetation. Obviously, there is a pattern in epiphytic macrolichen vegetation which can be explained by the presence of *Alnus incana* trees. *Alnus incana* is a rich bark tree species, but more acidic than *Populus tremula* (see Fig. 5). Both significant variables in the set of forest- and other environmental explanatory variables are connected with the presence of rich bark trees. Interpreting the set of environmental explanatory variables as variation in the species data created by substrate features, more specifically by substrate alkalinity, therefore seems to be reasonable.

Macroclimate

Macroclimate is the most important factor controlling the regional gradient in macrolichen species composition, amounting to 35 % of total variation explained. The primary importance of macroclimate for lichen vegetation coincides with the findings of McCune et al. (1997), who performed a regional-scale study of lichen vegetation in the Southeast US. However, no information about the amount of variation explained by macroclimate is supplied, since the statistical method employed, non-metric multidimensional scaling, does not enable to provide such. Also in a regional study of forest vegetation in the Northwest

US using partial and stepwise CCA, macroclimate was found to be the most important factor for species composition, contributing to 49 % of total variation explained, and 46 % to 60 % for the subregions investigated (Ohmann & Spies 1998). In an investigation of epiphyllic algae on spruce needles and epiphytic lichens on Scots pine trunks employing partial Redundancy Analysis, RDA, performed in Sweden, strictly macroclimatic variation in lichen species composition was as low as 14.1 % of total variation explained, TVE. The joint effects of macroclimatic and spatial variation accounted to 13.3 % of TVE (Liu & Bråkenhielm 1995).

Among the significant variables from the set of macroclimatic, microclimatic and topographical explanatory variables were the temperature sum of all month exceeding 4°C and that of all months exceeding 0°C. For higher plants, temperature sums are often defined as the sum of mean air temperatures of all months exceeding 4°C or 5°C (Tuhkanen 1984). Since many lichens are physiologically active at very low temperatures (Kappen 1988), 0°C may be regarded as an equally appropriate limit for defining temperature sums for lichen vegetation as 4°C, as far as boreal and arctic environments are concerned.

Also the oceanity of the climate as well as the amount of precipitation in all months exceeding an average monthly air temperature of 4°C were statistically significant. In the species *Lobaria amplissima,* only the cyanomorph was found in the present study. *Lobaria amplissima* is reckoned an oceanic lichen species in Fennoscandia (Degelius 1935) and Central Europe (Schauer 1965). The ecological demands of photomorphs can differ greatly, however. In the species *Sticta felix* found in New Zealand, for instance, the chloromorph grows under dry high-light conditions, while the cyanomorph grows under low-light conditions and constantly high humidity (James & Henssen 1976). Lichens such as *Collema fasciculare, C. nigrescens, L. amplissima*, *L. pulmonaria, L. scrobiculata* and *Sphaerophorus globosus* are reckoned oceanic lichens in Central Europe (Schauer 1965). Of those, only *Collema fasciculare* and *L. amplissima* have a strictly oceanic distribution in Norway. *Lobaria scrobiculata* and *L. pulmonaria* (see Fig. 2) show a slightly oceanic tendency in their distribution pattern in Norway (Timdal 2001). It is interesting that these species were only found in the interior of Troms county. The following species which were found in the plots are regarded as thermophilic in northern Norway: *Collema furfuraceum, C. nigrescens, Hypogymnia tubulosa, Lobaria pulmonaria, L. scrobiculata, L. amplissima,*

Melanelia exasperata, Nephroma resupinatum, Peltigera collina, Physconia distorta, Usnea subfloridana, and as an epiphyte *Xanthoria parietina* (Ingebrigtsen 2000). *Lobaria hallii* is predominantly distributed in interior sites in northern Norway (Timdal 2001), which might indicate that it could be a thermophilic species as well. Given that elevations are comparable, temperature sums are higher and precipitation values lower in inland than in coastal sites. There seems to be a trade-off between precipitation and temperature demands in thermophilic lichens – demands to precipitation asking for a coastal distribution, and temperature demands for the interior. In Troms county, temperature demands seem to prevail. Evaporation is temperature dependent – the higher the temperature, the more water is evaporated. Compared to areas in central Europe, where the time available for photosynthesis may be as low as one hour per day because of insufficient thallus water contents (Scheidegger, unpublished data), lichens tolerating the comparably lower temperatures may have brilliant conditions for photosynthesis in boreal areas (Scheidegger, personal communication). This is mainly due to longer times with sufficiently high thallus water contents because of reduced evaporation rates.

The temperature regime seems to be the limiting factor for growth of oceanic lichens in Troms county. They may have sufficient time available for photosynthesis even when living in interior areas with low annual precipitation, since evaporation is reduced because of comparatively low air temperatures. Additionally, the oceanic lichens listed above and *L. hallii* tend to prefer moist forest types in interior sites of Troms county, and those might provide relatively high air humidity.

Box 4. Possible underlying mechanisms causing the response of lichens to macroclimatic gradients.

Since lichens gain most of their nutrients from atmospheric sources and lack mechanisms regulating the uptake and loss of water, they are able to respond to changes in climate (Esseen & Renhorn 1998). The net rate of photosynthesis is dependent on the temperature regime, and on the thallus water content of lichens. Is thallus water below a certain limit, photosynthesis stagnates. Lichens of arctic tundra ecosystems were shown to gain carbon at temperatures as low as –10°C, while temperature optima of lichen net photosynthesis were ranging from 11 to 22°C (Lange et al. 1996). Dispersal of lichen soredia is strongly dependent on macroclimatic conditions (Armstrong 1991). This could be another factor leading to a response of lichens to macroclimatic conditions.

Spatial variation

None of the variables defining a three-dimensional trend surface is significant, except for latitude. Obviously, there is no complex large-scale spatial structure in the data, but a simple east-west gradient.

Geographic location, that is the area the plots are situated in, is more important than geographic extent, namely the east-west gradient. Interpreting the significance of variables indicating the presence of a plot in a certain area proves to be quite intricate. There might be a systematic difference between areas because of forest management history, as outlined in Box 3. A precise reconstruction of forest management history on plot basis appears to be problematical, since spatially explicit and high-resolution historical forest data are lacking, and no continuous series of aerial images are available for all plots for the time of interest. An indirect picture of the importance of forest history for epiphytic macrolichen vegetation may be obtained by considering the area where the plots are situated in, since plots situated in the same area are likely to have a similar management history. The significance of the two area-related variables may indicate that forest history could have at least some significance for macrolichen vegetation, even though on the basis of the present data set, effects of forest history can not be separated from other effects such as spatial autocorrelation or unmeasured environmental variables.

In communities, organisms are distributed neither regularly nor at random, but they are assembled along gradients, or aggregated in patches (Legendre & Fortin 1989). Many population processes work on fine spatial scales, leading to spatial patterns in species distribution, and to spatial autocorrelation (Økland 2001). Dispersal is not a random process, for instance, but spatially explicit (Nathan & Muller-Landau 2000). Yet another possible explanation for the importance of the areas Skibotn and Tromsø to lichen vegetation is the existence of one or several underlying environmental factors which were not measured, leading to a systematic difference between the areas. To summarise, the significance of two variables indicating which area the plots are situated in might have three different explanations: systematic differences in forest history between the areas, spatial autocorrelation, or variation created by one or several unmeasured environmental factors. It can hardly be evaluated which explanation is the most plausible.

The second major gradient in epiphytic macrolichen communities is spatial variation, strictly geographic variation accounting to 25.5 % of total variation explained, TVE. This

amount is comparable to that found by Liu & Bråkenhielm (1995) in a study of lichen vegetation on Scots pine performed in Sweden, where strictly spatial variation accounted to 27.2 % of TVE. Ohmann & Spies (1998), on the other hand, found a considerably lower amount of strictly spatial variation for forest vegetation in the Northwest US, explaining 15 % of TVE. McCune et al. (1997) determined pollution as the second gradient of importance for lichen species composition in the Southeast US, and they did not consider spatial variation to be of any significance. In the present study, geographic location is more important for lichen vegetation than geographic extent, which is in accordance with the results of Ohmann & Spies (1998). A relatively high amount of environmental variation is spatially structured. This study is one of the examples where spatial structure was found to be a key factor for living organisms – in this case, macrolichens – and where spatially structured components of ecological variation were high.

Conclusions & future research needs

72 species of epiphytic macrolichens were found in 69 plots examined in central and southern Troms county, northern Norway. Gradient analysis revealed three major gradients in macrolichen species composition. The most important gradient corresponds to a macroclimatic gradient from the coastline to the interior of Troms county. The second and third major gradients in species composition are due to spatial and substrate variation. In deciduous forests of Troms county, human impact explained little of the variation in species composition, when the covariation with other factors had been removed. The results of this study may be assumed to be valid within boreal deciduous forests of Norway.

Forest fragmentation and its effects on lichen species offer interesting possibilities for future research in Troms, and also the effects of plantations of non-native tree species on lichen populations or communities require more detailed investigations. Little is known about habitat preferences of lichens, and even less about dispersal of lichens in general. Modern molecular techniques offering species-specific markers give the opportunity of studying the flux of lichen diaspores and its apportionment on dispersal vectors.

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References

Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968) Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* **5**: 169-211.

Armstrong, R. A. (1991) The influence of climate on the dispersal of lichen soralia. *Environmental and Experimental Botany* **31**(2): 239-245.

Barkman, J. J. (1958a) *Phytosociology and ecology of cryptogamic epiphytes*. Assen: Van Gorcum.

Barkman, J. J. (1958b) *On the ecology of cryptogamic epiphytes with special reference to the Netherlands*. Leiden: Van Gorcum.

Barth, J. B. (1858) *Om skovforholdene i Finmarken : indberetning til Departementet for det Indre*.

Bates, J. W. (1992) Influence of chemical and physical factors on *Quercus* and *Fraxinus* epiphytes at Loch Sunart, western Scotland: a multivariate analysis. *Journal of Ecology* **80**: 163-179.

Bellehumeur, C., Legendre, P. & Marcotte, D. (1997) Variance and spatial scales in a tropical rain forest: Changing the size of sampling units. *Plant Ecology* **130**(1): 89-98.

Bertheussen, C. (1988) *Kulturbilder fra gamle Hillesøy*. Tromsø: Lenvik og Tromsø kommuner.

Birks, H. J. B. (1993) Is the hypothesis of survival on glacial nunataks necessary to explain the present-day distributions of Norwegian mountain plants? *Phytocoenologia* **23**: 399-426.

Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology* **73**(3): 1045-1055.

Brodo, I. M. (1973) Substrate ecology. In *The Lichens.* (V. Ahmadjian & M. E. Hale eds.): 401-441. New York: Academic Press.

Burgaz, A. R., Fuertes, E. & Escudero, A. (1994) Ecology of cryptogamic epiphytes and their communities in deciduous forests in mediterranean Spain. *Vegetatio* **112**: 73-86.

Culberson, C. F. & Ammann, K. (1979) Standardmethode zur Dünnschichtchromato-graphie von Flechtensubstanzen. *Herzogia* **5**: 1-24.

Degelius, G. (1935) Das Ozeanische Element der Strauch- und Laubflechtenflora von Skandinavien. Dissertation. *Acta Phytogeographica Suecica* **7**: 1-411.

Dettki, H., Klintberg, P. & Esseen, P. A. (2000) Are epiphytic lichens in young forests limited by local dispersal? *Ecoscience* **7**(3): 317-325.

DN (1999) *Nasjonal rødliste for truete arter i Norge 1998. Norwegian Red List 1998.* Trondheim: Direktoratet for Naturforvaltining.

DNMI (2001) Oslo: Det Norske Meteorologiske Institutt, Klimaavdelingen.

Eggen, E. B. (1950) *Bardu bygdebok*. Bardu: Bygdeboknemnda.

Esseen, P. A. & Renhorn, K. E. (1998) Edge effects on an epiphytic lichen in fragmented forests. *Conservation Biology* **12**(6): 1307-1317.

Fremstad, E. (1997) *Vegetasjonstyper i Norge.* Trondheim: Norsk Institutt for Naturforskning.

Garty, J., Karary, Y. & Harel, H. (1993) The impact of air-pollution on the integrity of cell-membranes and chlorophyll in the lichen *Ramalina duriaei* (Denot) Bagl transplanted to industrial sites in Israel. *Archives of Environmental Contamination and Toxicology* **24**(4): 455-460.

Gauslaa, Y. (1985) The ecology of Lobarion pulmonariae and Parmelion caperatae in *Quercus* dominated forests in south-west Norway. *Lichenologist* **17**(2): 117-140.

Gauslaa, Y. & Solhaug, K. A. (1996) Differences in the susceptibility to light stress between epiphytic lichens of ancient and young boreal forest stands. *Functional Ecology* **10**: 344-354.

Gauslaa, Y. & Solhaug, K. A. (1999) High-light damage in air-dry thalli of the old forest lichen *Lobaria pulmonaria* - interactions of irradiance, exposure duration and high temperature. *Journal of Experimental Botany* **50**(334): 697-705.

Gilbert, O. L. (1977) Lichen conservation in Britain. In *Lichen ecology* (M. R. D. Seaward, ed.): 415-436. London: Academic Press.

Goldsmith, F. B. (1973) The vegetation of exposed sea cliffs at South Stak, Anglesey. I. The multivariate approach. *Journal of Ecology* **61**(3): 787-818.

Goward, T. (1994) Notes on oldgrowth-dependent epiphytic macrolichens in inland British Columbia, Canada. *Acta Botanica Fennica* **150**: 31-38.

Gustafsson, L. & Eriksson, I. (1995) Factors of importance for the epiphytic vegetation of aspen *Populus tremula* with special emphasis on bark chemistry and soil chemistry. *Journal of Applied Ecology* **32**: 412-424.

Hauglid, A. O. (1981) *Balsfjorden og Malangens historie*. Storsteinnes: Balsfjord kommune.

Hawksworth, D. L., Rose, F. & Coppins, B. J. (1973) Changes in the lichen flora of England and Wales attributable to pollution of the air by sulphur dioxide. In *Air pollution and lichens* (B. W. Ferry, M. S. Badderley & D. L. Hawskworth, eds.): 330-367. London: Athlone Press.

Holien, H. (1996) *Studies of lichens in spruce forest of central Norway. Diversity, old growth species and the relationship to site and stand parameters.* Department of Botany, Faculty of Chemistry and Biology. Trondheim: Norwegian University of Science and Technology.

Holopainen, T. (1983) Ultrastructural changes in epiphytic lichens, *Bryoria capillaris* and *Hypogymnia physodes*, growing near a fertilizer plant and a pulp mill in central Finland. *Annales Botanici Fennici* **20**: 169-185.

Holopainen, T. & Kärenlampi, L. (1984) Injuries to lichen ultrastructure caused by sulphur dioide fumigations. *New Phytologist* **98**: 285-294.

Holtan-Hartwig, J. (1993) The lichen genus *Peltigera*, exclusive of the *P. canina* group, in Norway. *Sommerfeltia* **15**: 1-77.

Hyvärinen, M., Halonen, P. & Kauppi, M. (1992) Influence of stand age and structure on the epiphytic lichen vegetation in the middle-boreal forests of Finland. *Lichenologist* **24**(2): 165-180.

Ingebrigtsen, K. (2000) *Bioklimatologisk kartlegging av et topografisk variert granittområde i ytre Efjorden, Ballangen, Nordland.* Department of Biology, Faculty of Sciences. Tromsø: University of Tromsø.

James, P. W. & Henssen, A. (1976) The morphological and taxonomic significance of cephalodia. In *Lichenology: Progress and Problems* (D. H. Brown, D. L. Hawsworth and R. H. Bailey, eds.): 27-77. London: Academic Press.

Jongman, R. H. G., ter Braak, C. J. F. & van Tongeren, O. F. R (1987) *Data analysis in community and landscape ecology*. Wageningen: Pudoc.

Kappen, L. (1988) Ecophysiological relationships in different climatic regions. In *CRC handbook of lichenology, Volume 2* (M. Galun, ed.): 37-100. Boca Raton, Florida: CRC Press.

Kiil, A. & Eilertsen, T. F. (1981) *Målselv bygdebok*. Moen: Målselv kommune.

Kleinbaum, D. G., Kupper, L. & Muller, K. E. (1998) *Applied regression analysis and other multivariable methods*. Boston: PWS-KENT Publishing Company.

Kondratyuk, S. Y. & Coppins, B. J. (1998) *Lobarion lichens as indicators of the primeval forests of the Eastern Carpathians*. Kiev: Phytosociocentre.

Kricke, R. & Feige, G. B. (2001) Biomonitoring with lichens in the Ruhr area for air quality assessment - 1966 to 2000. *Gefahrstoffe - Reinhaltung der Luft* **61**(4): 163-166.

Krog, H., Østhagen, H. & Tønsberg, T. (1994) *Lavflora : norske busk- og bladlav*. Oslo: Universitetetsforlag.

Kuusinen, M. (1994a) Epiphytic lichen flora and diversity on *Populus tremula* in old-growth and managed forests of southern and middle boreal Finland. *Annales Botanici Fennici* **31**: 245-260.

Kuusinen, M. (1994b) Epiphytic lichen diversity on *Salix caprea* in old-growth southern and middle boreal forests of Finland. *Annales Botanici Fennici* **31**: 77-92.

Kuusinen, M. (1996) Cyanobacterial macrolichens on *Populus tremula* as indicators of forest continuity in Finland. *Biological Conservation* **75**: 43-49.

Lange, O. L., Hahn, S. C., Muller, G., Meyer, A. & Tenhunen, J. D. (1996) Upland tundra in the foothills of the Brooks Range, Alaska: Influence of light, water content and temperature on CO_2 exchange of characteristic lichen species. *Flora* **191**(1): 67-83.

Le Blanc, F. & Rao, D. N. (1973) Effects of sulphur dioxide on lichen and moss transplants. *Ecology* **54**: 612-617.

Legendre, P. & Fortin, M. J. (1989) Spatial pattern and ecological analysis. *Vegetatio* **80**(2): 107-138.

Lesica, P., McCune, B., Cooper, S. V. & Hong, W. S. (1991) Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. *Canadian Journal of Botany* **69**: 1745-1755.

Lid, J., Lid, D. & Elven, R. (1994) *Norsk flora*. Oslo: Samlaget.

Linder, P., Elfving, B. & Zackrisson, O. (1997) Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management* **98**: 17-33.

Liu, Q. H. & Bråkenhielm S. (1995) A statistical approach to decompose ecological variation. *Water Air and Soil Pollution* **85**(3): 1587-1592.

Manly, B. F. J. (1997) *Randomization, bootstrap and Monte Carlo methods in biology*. London: Chapman & Hall.

McCarthy, P. M. (1980) Vertical zonation of lichens on alder (*Alnus glutinosa* (L.) Gaertn.) near Cork, Ireland. *The scientific Proceedings of the Royal Dublin Society*. *Series A* **6**(14): 397-405.

McCune, B. (1997) Influence of noisy environmental data on Canonical Correspondence Analysis. *Ecology* **78**(8): 2617-2623.

McCune, B., Dey, J., Peck, J., Heiman, K. & Willwolf, S. (1997) Regional gradients in lichen communities of the Southeast United States. *Bryologist* **100**(2): 145-158.

Meffe, G. K. & Carroll, C. R. (1997) What is conservation biology? In *Principles of conservation biology* (G. Meffe, K. & C. R. Carroll, eds.): 3-27. Sunderland: Sinauer.

Méot, A., Legendre, P. & Borcard, D. (1998) Partialling out the spatial component of ecological variation: questions and propositions in the linear modelling framework. *Environmental and Ecological Statistics* **5**: 1-27.

Moberg, R. & Holmåsen, I. (1982) *Lavar : en fälthandbok*. Stockholm: Interpublishing.

Moen, A., Odland, A. & Lillethun, A. (1998) *Nasjonalatlas for Norge: Vegetasjon*. Hønefoss: Norwegian Mapping Authority.

Nathan, R. & Muller-Landau, H. C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* **15**(7): 278-285.

Nordén, B. & Appelqvist T. (2001) Conceptual problems of ecological continuity and its bioindicators. *Biodiversity and Conservation* **10**: 779-791.

Noss, R. F. & Csuti, B. (1997) Habitat fragmentation. In *Principles of conservation biology* (G. K. Meffe & C. R. Carroll, eds.): 269-304. Sunderland: Sinauer.

Ohmann, J. L. & Spies, T. A. (1998) Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecological Monographs* **68**(2): 151-182.

Oksanen, J. (1988) Impact of habitat, substrate and microsite classes on the epiphyte vegetation: interpretation using exploratory and canonical correspondence analysis. *Annales Botanici Fennici* **25**: 59-71.

Økland, R. H. (1990) Vegetation ecology: theory, methods and applications with reference to Fennoscandia. *Sommerfeltia supplement* **1**: 1-233.

Økland, R. H. (1996) Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? *Journal of Vegetation Science* **7**: 289-292.

Økland, R. H. (1999) On the variation explained by ordination and constrained ordination axes. *Journal of Vegetation Science* **10**: 131-136.

Økland, R. H. (2001). Gradient analysis. Lecture notes 2001 update. Oslo: University of Oslo.

Økland, R. H. & O. Eilertsen (1994) Canonical Correspondence Analysis with variation partitioning: some comments and an application. *Journal of Vegetation Science* **5**: 117-126.

Økland, T. (1996) Vegetation-environment relationships of boreal spruce forests in ten monitoring reference areas in Norway. *Sommerfeltia* **22**: 1-349.Palmer, M. J. (1993) Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* **74**(8): 2215-2230.

Parker, K. C. (1988) Environmental relationships and vegetation associates of columnar cacti in the northern Sonoran Desert. *Vegetatio* **78**: 125-140.

Pfefferkorn, V. & Türk, R. (1996) Flechten als Zeiger des Hemerobiegrades in terrestrischen Biotopen. *Sauteria* **8**: 181-192.

Purvis, O. W. (1992) *The lichen flora of Great Britain and Ireland.* London: Natural History Museum Publications in association with The British Lichen Society.

Purvis, W. (2000) *Lichens*. London: The Natural History Museum.

Renhorn, K. E., Esseen, P. A., Palmqvist, K. & Sundberg, B. (1997) Growth and vitality of epiphytic lichens. I. Responses to microclimate along a forest edge-interior gradient. *Oecologia* **109**: 1-9.

Richardson, D. H. S. (1992) *Pollution monitoring with lichens.* Slough: Richmond Publishing.

Rolstad, J., Gjerde, I., Storaunet, K.O. & Rolstad, E. (2001) Epiphytic lichens in Norwegian coastal spruce forest: historic logging and present forest structure. *Ecological Applications* **11**(2): 421-436.

Rose, F. (1976) Lichenological indicators of age and environmental continuity in woodlands. In *Lichenology: progress and problems* (D. H. Brown, D. L. Hawksworth & R. H. Bailey, eds.): 279-307. London: Academic Press.

Rose, F. (1992) Temperate forest management: its effects on bryophyte and lichen floras and habitats. In *Bryophytes and lichens in a changing environment* (J. W. Bates & A. M. Farmer, eds.): 211-233. Oxford: Oxford Scientific Publications, Clarendon Press.

Ruden, I. (1911) Fremstilling av en del av den skade som de svenske flytlapper og ren har voldt paa skogen i Tromsø amt: avfattet paa grundlag av undersøkelser og befaringer foretat i henhold til skogdirektørens skrivelse av 11te mai 1909. Kristiania: Grøndahl & Søns bogtrykkeri.

Saunders, D. A., Hobbs, R. J. & Margules, C. R. (1991) Biological consequences of ecosystem fragmentation - a review. *Conservation Biology* **5**(1): 18-32.

Schauer, T. (1965) Ozeanische Flechten im Nordalpenraum. *Portugaliae Acta Biologiae. (B)* **8**: 17-229.

Scheidegger, C. & Schroeter, B. (1995) Effects of ozone fumigation on epiphytic macrolichens - ultrastructure, CO_2 gas-exchange and chlorophyll fluorescence. *Environmental Pollution* **88**(3): 345-354.

Schöller, H. (1997) *Flechten: Geschichte, Biologie, Systematik, Ökologie, Naturschutz und kulturelle Bedeutung; Begleitheft zur Ausstellung "Flechten - Kunstwerke der Natur"*. Frankfurt am Main: Kramer.

Seaward, M. R. D. (1982) *Lichen ecology*. London: Academic Press.

Selva, S. B. (1994) Lichen diversity and stand continuity in the northern hardwoods and spruce-fir forests of northern New England and western New Brunswick. *Bryologist* **97**(4): 424-429.

Sillett, S. C. (1994) Growth-rates of 2 epiphytic cyanolichen species at the edge and in the interior of a 700-year-old douglas-fir forest in the Western Cascades of Oregon. *Bryologist* **97**(3): 321-324.

Sillett, S. C., McCune, B., Peck, J. E., Rambo, T. R. & Ruchty, A. (2000) Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecological Applications* **10**(3): 789 - 799.

Sveli, A. (1987) *Skogbruk i Nord-Norge : streiftog gjennom historien*. Mosjøen: Nord-Norges skogsmannsforbund.

ter Braak, C. J. F. (1988) Partial canonical correspondence analysis. In *Classification and related methods of data analysis : proceedings of the First Conference of the International Federation of Classification Societies (IFCS), Technical University of Aachen, F.R.G., 29 June-1 July, 1987* (H. H. Bock, ed.): 551-558. Amsterdam: Elsevier Science Publishers.

ter Braak, C. J. F. & Prentice, I. C. (1988) A theory of gradient analysis. *Advances in Ecological Research* **18**: 272-317.

ter Braak, C. J. F. & Smilauer, P. (1998) *CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4)*. Ithaca, NY, USA: Microcomputer Power.

Tibell, L. (1992) Crustose lichens as indicators of forest continuity in boreal coniferous forests. *Nordic Journal of Botany* **12**: 427-450.

Timdal, E. (1998) *Checklist of Norwegian lichens*. (Latest update 03.12.1998). http://www.toyen.uio.no/botanisk/bot-mus/lav/bmlnosj.htm

Timdal, E. (2001) *Search the Norwegian Lichen Database*. (First posted 16.04.1997, latest update 06.11.2001). http://www.toyen.uio.no/botanisk/bot-mus/lav/soklavherb.htm

Trass, H., Vellak, K. & Ingerpuu, N. (1999) Floristical and ecological properties for identifying of primeval forests in Estonia. *Annales Botanici Fennici* **36**: 67-80.

Tuhkanen, S. (1984) A circumboreal system of climatic-phytogeographical regions. *Acta Botanica Fennica* **127**: 1-50.

United Nations (1998) *World population prospects. The 1996 revision*. New York: Department of Economic and Social Affairs, Population Division.

van Dobben, H. F. (1996) Decline and recovery of epiphytic lichens in an agricultural area in The Netherlands (1900-1988). *Nova Hedwigia* **62**: 477-485.

Vitikainen, O. (1994) Taxonomic revision of *Peltigera* (lichenized Ascomycotina) in Europe. *Acta botanica Fennica* **152**: 96.

Walker, F. J. & James, P. W. (1980) A revised guide to microchemical techniques for the identification of lichen products. *Bulletins of the British Lichen Society* **46** (Supplement): 13-29.

Werth, S., Elvebakk, A., & Tømmervik, H. (in prep.) What epiphytic macrolichens do indicate in the absence of air pollution - a case study from northern Norway. *Ecological Indicators.*

Wirth, V. (1976) Veränderungen der Flechtenflora und Flechtenvegetation in der Bundesrepublik Deutschland. *Schriftenreihe für Vegetationskunde* **10**: 177-203.

Wirth, V. (1995) *Die Flechten Baden-Württembergs.* Stuttgart: Eugen Ulmer.

Wirth, V. (1999). Gefährdete Flechtenbiotope in Mitteleuropa. *Natur und Museum* **129**(1): 12-21.

Yoccoz, N. G. & Ims, R. A. (2000) *Ecological methodology: study design and statistical analysis. Compendium in Bio-310A.* Oslo: University of Oslo.

Ytreberg, N. A. (1943) *Malangen bygdebok.* Trondheim: Malangen bygdebok-komite.

Plot number	Bry cap	Bry fus	Bry gla	Bry imp	Bry sim	Cet chl	Cet sep	Col fur	Col fas	Col nig	Den umh	Eve pru	Hyp aus	Hyp bit	Hyp phy	Hyp tub	Icm eri	Ims ale	Lep sat	Lob hal	Lob pul	Lob scr	Mel eta	Mel ela	Mel ful
A42	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
A43	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0
A44	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
A45	0	1	0	0	1	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0
A46	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
A47	0	1	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	0	0
A48	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1	0	0	0
A49	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
A50	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0
A51	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
A52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0
A53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
A54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
A55	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0
A56	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0
A57	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0
A58	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0
A59	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
A60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
A61	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
A62	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0
A63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0
A64	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
A65	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
A66	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
A67	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
A68	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
A69	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0

Plot number	Mel oli	Mel sub	Nep bel	Nep exp	Nep par	Nep res	Pan pez	Par omp	Par sax	Par sul	Par tri	Par amb	Par hyp	Pel aph	Pel can	Pel col	Pel did	Pel deg	Pel leu	Pel mal	Pel mem	Pel neo	Pel pon	Pel pra	Pel ret
A1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
A2	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A3	1	0	0	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
A4	1	1	1	0	1	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0
A5	1	1	1	0	1	1	1	0	1	1	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0
A6	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0
A7	1	1	1	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0
A8	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A9	1	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
A10	1	1	1	0	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	1	0
A11	1	1	1	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	1	1	0	0	1
A12	1	0	1	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0	0	0	1	0	0	0	0
A13	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A14	1	1	1	0	1	1	0	0	1	1	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0
A15	1	1	1	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
A16	1	0	1	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0
A17	1	0	1	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
A18	1	0	1	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0
A19	1	1	1	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A20	1	1	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A21	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
A22	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A23	1	1	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0
A24	1	1	1	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A25	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
A26	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1
A27	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A28	1	1	1	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	1	0	1	1	0
A29	1	1	1	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
A30	1	1	1	1	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A31	1	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A32	1	1	1	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
A33	1	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
A34	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A35	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
A36	1	0	1	0	1	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A37	1	1	1	0	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0
A38	1	1	1	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A39	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A40	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Plot number	Mel oli	Mel sub	Nep bel	Nep exp	Nep par	Nep res	Pan pez	Par omp	Par sax	Par sul	Par tri	Par amb	Par hyp	Pel aph	Pel can	Pel col	Pel did	Pel deg	Pel leu	Pel mal	Pel mem	Pel neo	Pel pon	Pel pra	Pel ret
A41	1	0	1	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0
A42	1	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A43	1	1	1	0	1	1	1	0	0	1	0	1	0	1	0	1	1	0	0	0	0	1	0	0	0
A44	1	1	1	0	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
A45	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A46	1	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A47	1	1	1	0	1	0	1	0	1	1	0	1	1	1	0	0	1	0	0	0	1	0	0	0	0
A48	1	1	0	0	1	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A49	1	1	1	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A50	1	1	1	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0
A51	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
A52	1	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
A53	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A54	1	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0
A55	1	1	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
A56	1	1	1	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0
A57	1	1	1	0	1	1	0	0	1	1	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0
A58	1	1	1	0	1	1	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
A59	1	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
A60	1	1	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
A61	1	1	1	0	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0
A62	1	1	1	0	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
A63	1	1	1	0	1	1	0	0	0	1	0	1	1	0	0	1	0	0	0	1	0	0	0	1	0
A64	1	1	1	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A65	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0
A66	1	1	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A67	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A68	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
A69	1	0	1	0	1	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0

Plot number	Pel ruf	Pha cil	Pha nig	Pha orb	Pha sci	Pho per	Phy ads	Phy aip	Phy cae	Phy dub	Phy ste	Phy ten	Pho dis	Pla gla	Pso hyp	Ram far	Sph glo	Usn sub	Vul pin	Xan can	Xan ele	Xan par
A1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
A2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A4	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0
A5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
A6	0	1	1	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0
A7	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
A8	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A9	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0
A10	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0
A12	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0
A13	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0
A14	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	1	0	0	0
A15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
A16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
A18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A19	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	1
A20	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0
A21	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
A22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A23	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
A24	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
A25	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
A26	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
A27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A28	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0
A29	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0
A30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
A31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
A32	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
A34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
A37	0	1	0	0	0	1	1	1	0	0	1	0	1	1	0	0	0	0	0	1	0	0
A38	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
A39	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0
A40	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0

Plot number	Pel ruf	Pha cil	Pha nig	Pha orb	Pha sci	Pho per	Phy ads	Phy aip	Phy cae	Phy dub	Phy ste	Phy ten	Pho dis	Pla gla	Pso hyp	Ram far	Sph glo	Usn sub	Vul pin	Xan can	Xan ele	Xan par
A41	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A43	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0
A44	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A45	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0
A46	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
A47	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0
A48	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A50	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A51	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A52	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
A53	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0
A54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A55	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0
A56	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
A57	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
A58	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
A59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A61	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A62	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
A63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A64	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0
A65	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A66	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A69	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0

Par hyp	*Parmeliopsis hyperopta* (Ach.) Arnold
Pel aph	*Peltigera aphthosa* (L.) Willd.
Pel can	*Peltigera canina* (L.) Willd.
Pel col	*Peltigera collina* (Ach.) Schrader
Pel did	*Peltigera didactyla* (With.) J.R. Laundon
Pel deg	*Peltigera degenii* Gyelnik
Pel leu	*Peltigera leucophlebia* (Nyl.) Gyelnik
Pel mal	*Peltigera malacea* (Ach.) Funck
Pel mem	*Peltigera membranacea* (Ach.) Nyl.
Pel neo	*Peltigera neopolydactyla* (Gyelnik) Gyelnik
Pel pon	*Peltigera ponojensis* Gyelnik
Pel pra	*Peltigera praetextata* (Sommerf.) Zopf
Pel ret	*Peltigera retifoveata* Vitik.
Pel ruf	*Peltigera rufescens* (Weis) Humb.
Pha cil	*Phaeophyscia ciliata* (Hoffm.) Moberg
Pha nig	*Phaeophyscia nigricans* (Flörke) Moberg
Pha orb	*Phaeophyscia orbicularis* (Necker) Moberg
Pha sci	*Phaeophyscia sciastra* (Ach.) Moberg
Phy ads	*Physcia adscendens* (Fr.) H. Olivier
Phy aip	*Physcia aipolia* (Ehrh.) Fürnr.
Phy cae	*Physcia caesia* (Hoffm.) Fürnr.
Phy dub	*Physcia dubia* (Hoffm.) Lettau
Phy ste	*Physcia stellaris* (L.) Nyl.
Phy ten	*Physcia tenella* (Scop.) DC.
Pho dis	*Physconia distorta* (With.) J.R. Laundon
Pho per	*Physconia perisidiosa* (Erichsen) Moberg
Pla gla	*Platismatia glauca* (L.) W. Culb. & C. Culb.
Pso hyp	*Psoroma hypnorum* (Vahl) S.F. Gray
Ram far	*Ramalina farinacea* (L.) Ach.
Sph glo	*Sphaerophorus globosus* (Hudson) Vainio
Usn sub	*Usnea subfloridana* Stirton
Vul pin	*Vulpicida pinastri* (Scop.) J.-E. Mattsson & M. J. Lai
Xan can	*Xanthoria candelaria* (L.) Th. Fr.
Xan ele	*Xanthoria elegans* (Link) Th. Fr.
Xan par	*Xanthoria parietina* (L.) Th. Fr.

Plot number	Altitude	Heat index	Insolation	Light	Moisture	Oceanity	Pr_S_T>0	Pr_S_T>4	Pr_year	Slope	TM_SUM>0	TM_SUM>4	Unfavorability
A40	30	0.000	0	3	1	1	238	171	413	0	54.3	51.2	0.0
A41	210	0.180	15	3	3	1	250	203	486	15	46.4	45.8	-4.5
A42	440	2.391	12	4	3	1	208	184	497	14	38.4	35.6	51.5
A43	90	0.000	0	3	1	2	374	279	759	0	51.9	50.3	0.0
A44	100	0.000	2	3	3	2	361	275	736	22	51.3	49.8	155.5
A45	240	0.000	0	4	3	1	221	196	345	0	48.8	47.5	0.0
A46	230	0.000	0	2	2	1	221	195	343	0	49.2	47.9	0.0
A47	300	0.147	12	3	3	1	217	186	319	19	46.7	45.7	50.5
A48	360	0.124	12	4	4	1	217	186	319	25	44.7	43.9	47.5
A49	10	0.000	0	4	1	3	437	293	790	0	54.7	51.5	0.0
A50	10	0.000	0	3	2	3	437	293	790	0	54.6	51.4	0.0
A51	10	0.000	0	3	3	3	436	292	789	0	54.6	51.4	0.0
A52	80	0.142	14	2	3	3	431	286	786	10	51.9	49.4	17.5
A53	180	-0.009	13	2	3	2	364	267	775	22	48.2	47	-34.5
A54	150	0.130	15	2	3	2	367	268	779	25	49.3	47.9	-28.5
A55	70	0.544	7	3	3	2	360	272	690	12	52.7	50.9	-110.5
A56	90	-0.479	6	2	3	3	431	286	787	10	51.5	49.1	115.5
A57	160	0.005	6	4	3	3	438	311	855	22	49.2	48.3	101.5
A58	170	0.056	10	4	4	3	438	311	856	23	48.9	48	89.5
A59	60	0.000	0	2	3	3	436	310	850	0	52.8	51.4	0.0
A60	50	0.000	0	3	2	3	425	317	810	0	53.2	51.7	0.0
A61	110	-0.009	15	3	4	3	431	320	820	22	51.2	50	-9.5
A62	160	0.194	6	3	3	3	404	303	783	12	49.4	48.4	117.5
A63	160	1.372	6	5	4	3	404	303	783	21	49.4	48.4	109.5
A64	180	-0.867	3	2	3	2	372	297	783	18	48.8	48	-151.5
A65	280	0.467	12	3	4	1	303	238	518	10	46.7	45.6	49.5
A66	50	0.282	15	3	2	3	535	350	982	35	51.9	48.2	-13.5
A67	70	0.000	0	3	3	3	573	388	1057	0	51	47.5	0.0
A68	50	-1.177	4	3	3	3	480	325	900	24	51.9	48.3	145.5
A69	260	-0.623	3	3	3	2	373	297	784	10	46.1	45.6	-160.5

Plot number	Presence of Alnus	Alnus-Salix forest	Alnus forest	Basal area trees	Basal area logs	Presence of Betula	Betula herb forest	Betula forb forest	Forest/Total	Log decay	Log density	Maximum tree diameter	Nat/Total	Nat_nr	Open/forest	Presence of Populus	Populus forest
A1	1	0	1	1.9	4.5	1	0	0	43.7	2	0.00	8.25	48.9	0.758	1.000	0	0
A2	1	0	0	10.8	0.4	1	1	0	44.3	1	0.01	25.25	55.7	0.681	0.950	0	0
A3	1	0	1	24.4	8.3	1	0	0	43.6	1	0.03	40.86	11.9	0.515	1.021	0	0
A4	1	1	0	29.1	20.2	1	0	0	33.3	1	0.08	33.47	11.0	0.600	1.671	0	0
A5	1	1	0	28.2	21.2	1	0	0	36.0	2	0.07	27.93	8.0	0.425	1.557	0	0
A6	0	0	0	37.6	0.6	1	0	0	53.1	2	0.03	24.84	14.0	0.720	0.619	1	1
A7	1	0	1	23.4	7.1	0	0	0	35.7	2	0.07	33.44	51.8	0.471	0.604	0	0
A8	0	0	0	19.0	0.9	1	0	1	56.9	1	0.02	27.77	21.2	0.118	0.487	0	0
A9	1	0	1	21.0	25.6	0	0	0	47.6	3	0.16	37.32	39.9	0.378	0.694	0	0
A10	0	0	0	4.8	3.4	0	0	0	50.6	2	0.07	10.99	42.7	0.558	0.593	0	0
A11	0	0	0	11.1	1.8	1	0	1	53.0	2	0.03	21.02	22.7	0.425	0.656	0	0
A12	0	0	0	12.8	13.9	1	0	1	47.7	2	0.06	23.76	43.8	0.720	0.742	0	0
A13	0	0	0	16.3		1	1	0	36.4	2	0.03	23.50	9.8	1.000	1.506	0	0
A14	1	0	0	29.5	4.1	1	0	1	34.5	2	0.02	25.19	9.7	0.600	1.667	0	0
A15	0	0	0	27.2	10.0	1	0	0	41.3	3	0.13	30.61	55.1	0.329	1.087	0	0
A16	0	0	0	16.6	2.5	1	0	0	25.7	1	0.05	24.87	45.7	0.329	2.179	1	1
A17	0	0	0	5.4	1.0	1	1	0	49.8	2	0.02	9.94	48.3	0.935	0.614	0	0
A18	0	0	0	25.1	6.8	1	0	0	52.8	3	0.13	36.18	47.2	0.425	0.657	0	0
A19	0	0	0	36.7	10.0	1	0	0	16.1	3	0.08	24.70	71.2	0.681	3.967	0	0
A20	1	0	1	26.7	38.6	1	0	0	62.8	2.5	0.14	34.08	26.0	0.681	0.179	0	0
A21	1	0	1	19.5	20.5	1	0	0	57.6	2	0.13	27.42	14.2	0.515	0.736	0	0
A22	0	0	0	25.8	0.0	1	0	0	49.8	1	0.00	26.08	19.4	0.720	0.671	0	0
A23	1	1	0	34.6	25.6	1	0	0	61.6	3	0.08	22.26	24.3	0.831	0.315	0	0
A24	1	1	0	15.6	20.8	1	0	0	54.6	3	0.08	17.52	18.4	0.795	0.496	0	0
A25	1	0	1	53.9	7.3	0	0	0	67.7	2.5	0.08	27.52	18.8	0.600	0.199	0	0
A26	1	0	1	24.3	10.1	1	0	0	63.7	2	0.09	19.81	28.5	0.720	0.122	0	0
A27	1	0	0	30.9	3.3	1	1	0	60.8	2.5	0.04	26.11	20.8	0.425	0.360	0	0
A28	0	0	0	29.0	3.2	1	0	0	68.6	3	0.10	40.19	10.3	0.173	0.354	0	0
A29	1	0	1	65.1	31.2	1	0	0	51.7	3	0.07	38.54	42.8	0.720	0.589	0	0
A30	1	0	0	28.8	5.5	1	0	1	55.4	3	0.04	19.59	36.4	0.681	0.510	0	0
A31	0	0	0	38.1	11.3	1	1	0	59.1	2	0.13	30.67	33.6	0.378	0.556	0	0
A32	1	0	1	38.8	7.0	0	0	0	46.4	3	0.06	22.61	34.4	0.831	0.814	0	0
A33	0	0	0	16.1	13.8	1	1	0	41.3	3	0.03	22.96	48.7	0.795	1.236	0	0
A34	1	0	1	24.1	4.0	1	0	0	38.0	2.5	0.06	31.59	50.1	0.866	1.403	0	0
A35	0	0	0	14.6	6.2	1	1	0	48.6	1	0.14	17.99	51.4	0.279	1.058	0	0
A36	1	0	1	59.7	6.9	1	0	0	44.6	3	0.05	51.59	40.6	0.758	0.953	0	0
A37	0	0	0	23.4	0.5	1	0	0	61.5	1	0.02	22.52	12.0	0.758	0.430	1	1
A38	0	0	0	5.5	1.9	1	1	0	63.9	2	0.03	20.00	15.6	0.558	0.372	0	0
A39	0	0	0	8.4	4.1	1	1	0	51.0	2	0.05	18.22	17.0	0.720	0.626	0	0

Plot number	Presence of Alnus	Alnus-Salix forest	Alnus forest	Basal area trees	Basal area logs	Presence of Betula	Betula herb forest	Betula forb forest	Forest/Total	Log decay	Log density	Maximum tree diameter	Nat/Total	Nat_nr	Open/forest	Presence of Populus	Populus forest
A40	1	1	0	26.6	24.8	1	0	0	52.0	1	0.39	21.91	17.4	0.831	0.588	0	0
A41	0	0	0	19.3	10.5	1	0	1	87.6	3	0.04	22.64	2.5	0.378	0.112	0	0
A42	0	0	0	10.7	3.0	1	1	0	56.1	2	0.03	23.25	43.9	0.329	0.299	0	0
A43	1	1	0	41.9	7.0	1	0	0	44.5	3	0.10	30.16	42.7	0.378	0.806	0	0
A44	0	0	0	27.2	0.9	1	1	0	71.1	2	0.03	51.59	9.3	0.425	0.323	0	0
A45	0	0	0	7.6	20.1	1	1	0	59.7	3	0.05	19.04	14.7	0.227	0.429	0	0
A46	1	0	1	27.8	5.3	0	0	0	66.5	3	0.04	20.76	11.2	0.173	0.336	0	0
A47	0	0	0	64.5	4.7	1	0	0	69.2	3	0.04	64.59	0.0	0.060	0.444	0	0
A48	0	0	0	22.0	19.5	1	0	0	73.7	3	0.03	27.45	0.0	0.000	0.358	1	1
A49	1	0	1	17.0	8.7	1	0	0	66.9	3	0.08	18.47	7.3	0.329	0.386	0	0
A50	1	1	0	27.9	9.4	1	0	0	52.1	3	0.03	23.66	34.0	0.600	0.578	0	0
A51	0	0	0	20.0	9.6	1	0	1	54.3	3	0.06	43.82	30.7	0.515	0.571	1	0
A52	1	0	0	20.5	8.6	1	0	1	58.9	2.5	0.04	25.41	24.8	0.173	0.276	0	0
A53	0	0	0	27.1	0.6	1	0	0	46.1	1	0.03	12.74	14.8	0.681	0.955	1	0
A54	1	0	0	17.1	1.0	1	0	0	42.3	1	0.05	12.52	13.9	0.795	1.124	1	1
A55	1	0	0	60.0	7.7	1	0	0	69.7	3	0.05	35.16	17.3	0.279	0.240	1	1
A56	1	0	0	39.8	10.2	1	0	1	65.0	2	0.05	48.06	35.0	0.227	0.039	0	0
A57	1	0	0	34.2	26.8	1	0	1	62.0	3	0.06	34.43	26.6	0.279	0.184	0	0
A58	1	0	1	21.3	9.4	0	0	0	69.5	2	0.05	26.91	21.9	0.173	0.124	0	0
A59	0	0	0	13.4	3.8	1	1	0	56.7	1	0.03	22.45	16.4	0.681	0.498	0	0
A60	1	0	1	15.6	3.6	0	0	0	50.5	2	0.06	23.22	19.9	0.378	0.634	0	0
A61	0	0	0	22.4	0.2	1	0	0	51.9	1	0.01	25.22	10.0	0.173	0.780	0	0
A62	0	0	0	46.7	11.1	1	0	1	62.9	3	0.06	39.52	0.0	0.227	0.590	0	0
A63	1	0	1	22.0	5.6	0	0	0	60.8	3	0.05	25.80	0.0	0.227	0.646	0	0
A64	1	0	1	22.8	2.9	1	0	0	64.4	1	0.07	55.00	11.2	0.329	0.379	0	0
A65	0	0	0	71.5	12.4	1	0	0	74.6	3	0.02	55.00	7.8	0.227	0.314	1	1
A66	1	0	1	57.3	7.3	0	0	0	48.1	2	0.07	30.13	28.2	0.681	0.613	0	0
A67	0	0	0	19.4	2.3	1	1	0	58.6	2	0.03	16.11	10.9	0.227	0.690	0	0
A68	0	0	0	9.8	0.3	1	1	0	30.0	2	0.01	10.45	20.1	0.378	1.858	0	0
A69	0	0	0	20.4	6.1	1	0	1	62.4	2	0.04	30.48	20.4	0.471	0.276	0	0

Plot number	Distance to river	Presence of dry Salix forest	Presence of moist Salix forest	Presence of Salix caprea	Percentage of sibiling trees	Presence of Salix myrsinifolia	Presence of Sorbus aucuparia	Presence of Salix pentandra	Rock suitability	Total number of landscape elements	Median tree diameter	Tree age	Tree density	Water / total	Density of young trees
A1	0.007	0	0	0	0.04	0	1	0	1	0.6283	6.37	1	0.06	0.000	0.68
A2	0.010	0	0	0	0.00	0	0	0	1	0.4969	12.42	2	0.07	15.094	0.05
A3	0.015	0	0	0		1	0	0	1	0.8010	14.39	2	0.10	9.663	0.04
A4	0.005	0	0	0	0.29	0	0	1	1	0.8623	12.93	2	0.14	11.398	0.08
A5	0.010	0	0	0	0.23	1	0	0	1	0.8010	15.96	2	0.13	11.617	0.00
A6	0.030	0	0	0	0.06	0	0	0	10	0.6283	10.56	1	0.34	11.986	0.11
A7	0.200	0	0	0	0.60	0	1	0	7	0.4138	28.03	2	0.05	16.078	0.17
A8	0.200	0	0	0	0.14	0	1	0	1	0.1291	18.09	2.5	0.07	79.562	0.29
A9	0.010	0	0	1	0.69	0	0	0	3	0.3124	6.56	2	0.13	9.013	0.56
A10	0.020	0	1	0	1.00	1	0	1	1	0.4432	9.39	1	0.07	16.854	0.40
A11	0.250	0	0	1	0.22	0	0	0	1	0.4969	11.56	2	0.09	21.053	0.30
A12	0.000	0	0	0	0.50	1	1	0	1	0.5885	11.86	2	0.08	9.441	0.24
A13	0.200	0	0	0	0.73	0	0	0	6	1.0000	12.20	2	0.11	12.069	0.11
A14	0.050	0	0	0	0.41	1	1	0	10	0.7454	14.01	2.5	0.17	11.681	0.01
A15	0.150	1	0	1	0.11	0	0	0	6	0.2730	11.37	2	0.19	16.168	0.00
A16	0.400	0	0	0	0.27	0	0	0	6	0.4432	7.61	2	0.15	7.566	0.50
A17	0.200	0	0	0	0.46	0	0	0	6	0.6470	6.59	2	0.13	21.132	0.16
A18	0.300	0	0	0	0.13	0	1	0	5	0.3124	8.03	3	0.15	26.943	0.02
A19	0.150	0	1	0	0.36	1	0	1	1	0.5673	14.25	2	0.22	6.332	0.01
A20	0.015	0	0	0	0.83	0	0	0	1	0.5673	19.78	2.5	0.07	44.925	0.00
A21	0.500	0	0	0	0.37	0	0	0	1	0.5450	7.93	2	0.19	14.239	0.33
A22	0.020	0	0	0	0.31	0	1	0	1	0.7600	12.68	3	0.13	0.000	0.34
A23	0.005	0	0	0	0.13	1	0	1	1	0.6822	10.97	2	0.24	20.520	0.33
A24	0.100	0	0	0	0.54	1	0	0	1	0.7304	12.00	2	0.13	18.093	0.19
A25	0.003	0	0	0	0.43	0	0	0	1	0.4969	15.35	3	0.21	23.759	0.08
A26	0.000	0	0	0	0.37	1	0	0	1	0.5673	9.01	2	0.30	17.966	0.15
A27	0.005	0	0	0	0.50	0	0	0	1	0.4432	10.02	2.5	0.22	29.167	0.00
A28	0.300	1	0	1	0.18	0	0	0	1	0.2298	11.43	2.5	0.17	27.027	0.02
A29	0.005	0	0	0	0.20	0	0	0	1	0.5673	17.79	2.5	0.20	4.000	0.02
A30	0.025	0	0	0	0.22	0	1	0	1	0.5216	12.61	2.5	0.18	21.561	0.33
A31	0.050	0	0	0	0.00	0	0	0	1	0.3488	18.15	3	0.13	16.058	0.04
A32	0.020	0	0	0	0.19	0	0	0	1	0.7149	16.27	2	0.16	4.641	0.03
A33	0.007	0	0	0	0.14	0	0	0	1	0.6283	16.40	3	0.07	17.401	0.46
A34	0.001	0	0	0	0.13	0	0	0	1	0.6988	9.68	2	0.16	7.127	0.13
A35	0.650	0	0	0	0.00	1	0	0	6	0.1822	7.77	1	0.19	16.064	0.22
A36	0.002	0	0	0	0.29	1	0	0	1	0.6988	11.75	2.5	0.17	0.000	0.12
A37	0.150	0	0	1	0.06	0	0	0	10	0.6988	11.62	2	0.17	13.480	0.25
A38	0.250	0	0	1	1.00	0	0	0	1	0.5885	6.27	1	0.07	20.082	0.23
A39	0.150	0	0	0	0.63	0	0	0	7	0.6649	10.27	2	0.08	8.798	0.00

Plot number	Distance to river	Presence of dry *Salix* forest	Presence of moist *Salix* forest	Presence of *Salix caprea*	Percentage of sibiling trees	Presence of *Salix myrsinifolia*	Presence of *Sorbus aucuparia*	Presence of *Salix pentandra*	Rock suitability	Total number of landscape elements	Median tree diameter	Tree age	Tree density	Water / total	Density of young trees
A40	0.000	0	0	0	0.52	1	0	1	1	0.7741	8.28	2	0.29	13.647	0.20
A41	0.100	0	0	0	0.33	1	0	0	6	0.3488	13.42	3	0.12	36.422	0.09
A42	0.650	0	0	0	1.00	0	1	0	7	0.2298	15.25	2	0.05	3.337	0.09
A43	0.004	0	0	0	0.58	1	0	0	1	0.3124	21.16	2	0.12	19.091	0.03
A44	0.250	0	0	1	0.23	1	1	0	5	0.4432	9.90	1	0.31	15.926	0.43
A45	0.100	0	0	0	0.40	0	0	0	7	0.2730	9.78	3	0.05	7.583	0.00
A46	0.000	0	0	0	0.36	1	0	0	3	0.2298	8.61	2	0.28	15.736	0.22
A47	0.500	1	0	1	0.50	0	0	0	5	0.2298	14.63	3	0.08	16.923	0.18
A48	0.700	0	0	0	0.50	0	0	0	5	0.0000	17.71	3	0.08	0.000	0.28
A49	0.000	0	0	0	0.33	0	0	0	1	0.4432	13.31	2	0.12	0.000	0.00
A50	0.000	0	0	0	0.00	0	0	1	1	0.5216	17.82	2.5	0.12	7.120	0.20
A51	0.005	0	0	0	0.17	0	0	0	1	0.4708	11.78	3	0.05	18.333	0.31
A52	0.150	0	0	0	0.10	0	1	0	5	0.1822	16.13	3	0.10	34.109	0.37
A53	0.150	0	0	0	0.12	0	0	0	1	0.8010	8.95	2	0.41	6.386	0.33
A54	0.070	0	0	0	0.36	1	0	0	7	0.8954	9.20	2	0.25	8.508	0.10
A55	0.250	0	0	0	0.12	0	1	0	7	0.2730	22.93	2	0.17	31.712	0.08
A56	0.000	0	0	1	0.29	0	1	0	1	0.1291	17.87	3	0.07	21.368	0.02
A57	0.650	0	0	1	0.45	0	1	0	6	0.3124	11.56	3	0.11	24.051	0.06
A58	0.700	0	0	0	0.71	0	0	0	1	0.1291	20.16	2	0.07	32.813	12.00
A59	0.200	0	0	0	0.11	0	0	0	1	0.6470	13.98	3	0.09	7.671	0.59
A60	0.050	0	0	0	0.75	0	0	0	1	0.5216	17.10	2	0.08	19.164	0.16
A61	0.450	1	0	1	0.31	0	1	0	6	0.3824	10.81	2	0.16	17.301	0.11
A62	1.000	0	0	0	0.23	1	0	0	10	0.3824	20.92	3	0.13	11.828	0.01
A63	1.050	0	0	0	0.63	0	1	0	7	0.3824	19.25	2	0.08	0.000	0.00
A64	0.150	0	0	1	0.20	0	0	0	10	0.3824	9.09	1	30.00	0.000	0.03
A65	0.750	0	0	0	0.50	0	0	0	1	0.2298	38.01	3	0.06	13.659	0.76
A66	0.070	0	0	0	0.26	1	0	0	4	0.7304	14.24	2.5	0.27	1.301	0.10
A67	0.500	0	0	0	0.29	0	0	0	1	0.4138	10.16	2	0.21	31.270	0.11
A68	0.600	0	0	0	0.15	0	0	0	6	0.5885	7.87	2	0.20	0.567	0.09
A69	0.250	0	0	1	0.00	0	0	0	1	0.4432	19.75	3	0.06	17.921	0.01

Plot number	Distance to town	Cultivated / natural	Distance to closest farmhouse	Human impact	Human / Total	Landscape	Distance to closest area cleared from forest	Plantation	Road category	Distance to closest road
A1	7.65	0.080	0.85	8.0	7.407	2.0	0.100	1	1	0.250
A2	7.45	0.000	1.15	7.0	0.000	2.0	0.350	1	1	0.600
A3	0.20	0.802	0.20	7.0	44.494	1.0	0.015	0	2	0.250
A4	0.15	1.257	0.15	9.0	55.699	1.0	0.050	0	2	0.150
A5	0.15	1.275	0.15	5.0	56.036	1.0	0.070	0	2	0.150
A6	5.10	0.490	2.10	8.0	32.877	2.0	0.150	0	3	0.250
A7	20.00	0.143	0.65	5.0	12.549	2.0	0.100	0	2	0.550
A8	11.00	0.280	1.20	6.5	21.898	3.0	0.350	1	2	1.200
A9	11.00	0.142	1.05	5.0	12.446	2.0	0.350	1	2	1.150
A10	4.20	0.072	0.75	6.0	6.742	2.0	0.700	1	3	1.150
A11	3.90	0.321	0.40	5.0	24.291	2.0	0.350	1	3	0.750
A12	4.00	0.092	0.70	5.0	8.462	2.0	0.600	1	3	2.200
A13	23.50	1.167	0.25	6.0	53.860	2.0	0.150	0	1	0.150
A14	17.00	1.260	0.25	4.5	55.752	2.0	0.100	1	2	0.550
A15	30.00	0.037	0.75	4.0	3.593	2.0	0.500	1	2	0.750
A16	30.00	0.401	0.35	6.0	28.618	2.0	0.300	0	2	0.250
A17	29.50	0.019	1.30	4.0	1.887	3.0	1.300	1	2	1.500
A18	29.50	0.000	2.50	1.0	0.000	3.0	2.400	1	2	2.550
A19	35.00	0.145	0.07	5.0	12.665	1.0	0.010	0	1	0.070
A20	6.00	0.126	0.55	3.0	11.211	3.0	0.550	1	2	0.650
A21	7.50	0.392	0.20	6.0	28.155	2.0	0.100	1	2	0.010
A22	0.60	0.445	0.35	8.0	30.806	2.0	0.100	1	2	0.250
A23	1.30	0.165	0.35	3.5	14.162	2.5	0.350	0	1	0.050
A24	11.50	0.371	0.65	3.0	27.078	2.0	0.200	1	2	0.015
A25	31.00	0.156	2.50	2.5	13.475	2.0	0.070	0	2	0.200
A26	33.00	0.085	1.15	4.5	7.797	3.0	0.350	0	2	0.300
A27	38.50	0.226	7.55	3.0	18.403	3.0	2.600	0	1	0.100
A28	6.15	0.267	2.75	3.5	21.081	3.0	0.050	1	1	0.150
A29	6.95	0.059	1.70	3.5	5.538	2.0	0.350	0	1	0.300
A30	4.60	0.089	3.30	2.5	8.178	3.0	2.550	1	1	1.650
A31	5.75	0.079	2.45	2.0	7.299	3.0	1.150	1	1	0.350
A32	6.25	0.238	0.50	3.0	19.198	2.0	0.300	1	1	0.040
A33	8.25	0.111	1.65	3.0	9.977	3.0	1.550	0	1	0.500
A34	8.00	0.135	1.35	4.0	11.879	2.0	1.150	0	1	0.250
A35	11.00	0.000	3.60	5.5	0.000	3.0	3.100	0	1	1.500
A36	7.50	0.174	0.45	4.0	14.789	2.0	0.300	1	1	0.150
A37	5.40	0.360	4.35	9.0	26.471	2.0	0.100	1	3	0.150
A38	6.75	0.258	5.60	6.0	20.492	2.0	0.850	0	3	0.150

Plot number	Distance to town	Cultivated / natural	Distance to closest farmhouse	Human impact	Hum an / Total	Landscape	Distance to closest area cleared from forest	Plantation	Roadc ategory	Distance to closest road
A39	5.80	0.470	4.75	5.0	31.965	2.0	0.350	0	1	0.002
A40	6.25	0.441	5.25	6.0	30.588	2.0	0.300	0	3	0.200
A41	16.50	0.109	3.35	3.0	9.844	2.0	9.400	0	3	0.150
A42	22.00	0.000	4.50	4.0	0.000	3.0	4.400	0	3	0.600
A43	5.50	0.146	1.07	3.0	12.727	2.0	0.300	0	1	0.550
A44	9.50	0.244	0.70	7.0	19.630	2.0	0.650	0	2	0.020
A45	34.50	0.344	1.75	2.0	25.592	2.0	1.250	1	2	0.120
A46	33.00	0.288	1.60	3.0	22.335	2.0	1.000	0	2	0.030
A47	32.50	0.444	0.50	1.5	30.769	2.5	0.250	1	1	0.300
A48	32.00	0.358	0.75	1.0	26.347	3.0	0.400	1	1	0.500
A49	1.00	0.348	0.80	5.0	25.828	1.0	0.650	0	1	0.070
A50	1.25	0.162	0.85	2.5	13.916	2.0	0.750	0	1	0.200
A51	1.20	0.176	0.87	1.5	15.000	2.5	0.770	0	1	0.250
A52	1.75	0.194	0.65	2.0	16.279	3.0	0.450	0	1	0.650
A53	11.35	0.643	0.25	9.0	39.146	2.0	0.150	1	3	0.300
A54	11.35	0.779	0.10	10.0	43.803	1.0	0.100	1	3	0.100
A55	0.90	0.149	0.65	4.0	12.973	2.0	0.550	1	1	0.200
A56	2.50	0.000	0.95	2.0	0.000	3.0	0.950	1	1	0.600
A57	8.00	0.129	1.60	3.0	11.392	2.0	0.650	1	2	0.400
A58	8.00	0.094	1.55	3.0	8.594	3.0	0.700	1	2	0.450
A59	8.00	0.367	1.20	8.0	26.849	1.0	0.005	1	2	0.010
A60	1.10	0.421	0.25	4.0	29.617	2.0	0.200	1	3	0.200
A61	1.75	0.615	0.50	6.0	38.062	2.0	0.150	1	1	0.150
A62	1.65	0.590	1.05	2.0	37.097	2.0	0.200	1	1	0.400
A63	1.65	0.646	0.95	2.5	39.247	2.5	0.200	1	1	0.400
A64	18.50	0.323	1.00	6.0	24.400	2.0	0.400	1	1	0.010
A65	33.00	0.213	1.00	2.0	17.561	2.0	0.900	0	1	0.030
A66	9.80	0.310	0.10	5.5	23.646	1.0	0.150	1	3	0.010
A67	12.50	0.438	0.70	5.0	30.455	2.0	0.050	0	2	0.650
A68	12.00	0.994	0.10	6.0	49.858	2.0	0.020	0	2	0.007
A69	18.00	0.208	1.45	4.5	17.204	2.0	0.800	1	1	0.030

Plot number	Seadis	SeaWest	Latitude	Latitude^2 * Longitude	Latitude^3	Latitude . Longitude	Latitude . Longitude^2	Longitude	Longitude^3
A1	1.0	29	411200	1.30627E+18	6.95279E+16	3.17673E+12	2.45418E+19	7725500	4.61084E+20
A2	1.0	29	411200	1.30622E+18	6.95279E+16	3.1766E+12	2.45399E+19	7725200	4.6103E+20
A3	2.3	37	423166	1.3837E+18	7.57761E+16	3.26988E+12	2.5267E+19	7727191	4.61387E+20
A4	0.7	37	422853	1.38171E+18	7.56081E+16	3.26759E+12	2.52503E+19	7727487	4.6144E+20
A5	1.0	37	422966	1.38242E+18	7.56687E+16	3.2684E+12	2.5256E+19	7727337	4.61413E+20
A6	7.3	135	474198	1.72943E+18	1.0663E+17	3.64707E+12	2.80498E+19	7691033	4.5494E+20
A7	2.6	99	437429	1.47311E+18	8.36995E+16	3.36764E+12	2.59266E+19	7698721	4.56306E+20
A8	28.0	161	421973	1.36292E+18	7.5137E+16	3.22987E+12	2.47221E+19	7654216	4.48438E+20
A9	28.0	161	422084	1.36363E+18	7.51963E+16	3.2307E+12	2.47282E+19	7654154	4.48427E+20
A10	15.5	151	388593	1.1535E+18	5.86793E+16	2.96839E+12	2.2675E+19	7638813	4.45736E+20
A11	15.5	151	388668	1.15395E+18	5.87133E+16	2.969E+12	2.26799E+19	7638900	4.45751E+20
A12	15.5	151	388567	1.15334E+18	5.86675E+16	2.96818E+12	2.26733E+19	7638784	4.45731E+20
A13	32.5	168	400877	1.22439E+18	6.44219E+16	3.05427E+12	2.32704E+19	7618977	4.42273E+20
A14	31.0	168	401275	1.22807E+18	6.4614E+16	3.06042E+12	2.33411E+19	7626752	4.43628E+20
A15	0.8	35	390504	1.17658E+18	5.95493E+16	3.01298E+12	2.3247E+19	7715625	4.59318E+20
A16	0.3	35	390436	1.1761E+18	5.95182E+16	3.01227E+12	2.32402E+19	7715153	4.59234E+20
A17	1.5	35	391099	1.18026E+18	5.98219E+16	3.01781E+12	2.32861E+19	7716221	4.59424E+20
A18	2.6	35	391025	1.18003E+18	5.97879E+16	3.01778E+12	2.32901E+19	7717626	4.59675E+20
A19	0.1	21	384268	1.14039E+18	5.67417E+16	2.96769E+12	2.29194E+19	7722975	4.60632E+20
A20	23.0	175	438063	1.46921E+18	8.40639E+16	3.35387E+12	2.56777E+19	7656132	4.48775E+20
A21	25.5	178	437319	1.46385E+18	8.36363E+16	3.34733E+12	2.56212E+19	7654217	4.48438E+20
A22	24.5	170	431000	1.42241E+18	8.0063E+16	3.30025E+12	2.52707E+19	7657200	4.48962E+20
A23	24.0	170	432543	1.43254E+18	8.0926E+16	3.3119E+12	2.53586E+19	7656810	4.48894E+20
A24	30.0	185	439857	1.47972E+18	8.5101E+16	3.36408E+12	2.57289E+19	7648130	4.47369E+20
A25	48.5	212	446280	1.5201E+18	8.88837E+16	3.40616E+12	2.5997E+19	7632347	4.44605E+20
A26	50.0	212	447381	1.52693E+18	8.95432E+16	3.41303E+12	2.60378E+19	7628919	4.44006E+20
A27	54.5	212	449405	1.53978E+18	9.0764E+16	3.42627E+12	2.61219E+19	7624010	4.4315E+20
A28	3.1	38	430873	1.43609E+18	7.99922E+16	3.33299E+12	2.57821E+19	7735424	4.62863E+20
A29	1.9	38	430800	1.43594E+18	7.99516E+16	3.33319E+12	2.57895E+19	7737200	4.63182E+20
A30	3.6	38	429700	1.42811E+18	7.93407E+16	3.32351E+12	2.57057E+19	7734500	4.62697E+20
A31	3.0	38	430064	1.43063E+18	7.95425E+16	3.32654E+12	2.57308E+19	7734995	4.62786E+20
A32	0.8	38	429508	1.4274E+18	7.92344E+16	3.32335E+12	2.57146E+19	7737570	4.63248E+20
A33	1.75	29	410527	1.30192E+18	6.91871E+16	3.17134E+12	2.44987E+19	7725034	4.61E+20
A34	1.4	29	410700	1.30306E+18	6.92746E+16	3.17278E+12	2.45107E+19	7725300	4.61048E+20
A35	3.9	26	408269	1.28746E+18	6.80517E+16	3.15346E+12	2.43573E+19	7723979	4.60811E+20
A36	0.5	29	411472	1.30809E+18	6.9666E+16	3.17905E+12	2.45615E+19	7726042	4.61181E+20
A37	7.0	135	474312	1.73026E+18	1.06707E+17	3.64793E+12	2.80562E+19	7690987	4.54932E+20
A38	8.3	135	475331	1.73749E+18	1.07396E+17	3.65534E+12	2.81098E+19	7690084	4.54772E+20
A39	7.3	135	474565	1.73198E+18	1.06878E+17	3.64961E+12	2.8067E+19	7690427	4.54832E+20

Plot number	Seadis	SeaWest	Latitude	Latitude^2 · Longitude	Latitude^3	Latitude · Longitude	Latitude · Longitude^2	Longitude	Longitude^3
A40	7.8	135	474931	1.73458E+18	1.07125E+17	3.65228E+12	2.80864E+19	7690118	4.54778E+20
A41	18.0	185	483166	1.79369E+18	1.12795E+17	3.71237E+12	2.85238E+19	7683434	4.53593E+20
A42	23.5	190	487446	1.82468E+18	1.15819E+17	3.74334E+12	2.8747E+19	7679503	4.52897E+20
A43	28.5	161	422507	1.36639E+18	7.54226E+16	3.234E+12	2.4754E+19	7654308	4.48454E+20
A44	26.0	161	422519	1.36674E+18	7.54291E+16	3.23474E+12	2.47646E+19	7655840	4.48723E+20
A45	52.0	212	448311	1.53317E+18	9.01028E+16	3.41988E+12	2.60881E+19	7628373	4.43911E+20
A46	50.0	212	448168	1.53225E+18	9.00166E+16	3.41892E+12	2.60818E+19	7628662	4.43961E+20
A47	49.0	212	448148	1.53258E+18	9.00045E+16	3.41981E+12	2.60966E+19	7630990	4.44368E+20
A48	48.5	212	448165	1.53272E+18	9.00148E+16	3.41999E+12	2.60983E+19	7631098	4.44387E+20
A49	16.8	115	404252	1.25411E+18	6.60627E+16	3.1023E+12	2.38076E+19	7674183	4.51956E+20
A50	16.8	115	404628	1.2565E+18	6.62472E+16	3.10531E+12	2.38316E+19	7674480	4.52009E+20
A51	16.8	115	404632	1.25651E+18	6.62492E+16	3.10532E+12	2.38315E+19	7674426	4.51999E+20
A52	18.0	115	406046	1.2653E+18	6.69462E+16	3.11614E+12	2.39144E+19	7674363	4.51988E+20
A53	17.5	135	415700	1.32515E+18	7.18357E+16	3.18775E+12	2.4445E+19	7668400	4.50935E+20
A54	17.5	135	415414	1.32336E+18	7.16875E+16	3.18565E+12	2.44295E+19	7668617	4.50974E+20
A55	24.0	170	430500	1.41911E+18	7.97847E+16	3.29642E+12	2.52414E+19	7657200	4.48962E+20
A56	18.0	112	406020	1.26518E+18	6.69333E+16	3.11604E+12	2.39144E+19	7674606	4.52031E+20
A57	25.0	143	399219	1.21894E+18	6.36259E+16	3.0533E+12	2.33522E+19	7648183	4.47378E+20
A58	25.0	143	399258	1.19916E+18	6.36445E+16	3.05357E+12	2.3354E+19	7648109	4.47365E+20
A59	25.0	143	398941	1.21727E+18	6.3493E+16	3.05126E+12	2.33372E+19	7648396	4.47416E+20
A60	20.5	141	393293	1.18234E+18	6.08343E+16	3.00627E+12	2.29794E+19	7643838	4.46616E+20
A61	20.0	142	393296	1.18245E+18	6.08357E+16	3.00652E+12	2.29831E+19	7644412	4.46717E+20
A62	20.0	143	395404	1.19495E+18	6.18192E+16	3.02209E+12	2.3098E+19	7643046	4.46477E+20
A63	21.5	143	395388	1.19484E+18	6.18117E+16	3.02195E+12	2.30968E+19	7643000	4.46469E+20
A64	30.5	168	399900	1.21918E+18	6.3952E+16	3.04872E+12	2.32425E+19	7623700	4.43096E+20
A65	39.5	196	442800	1.49793E+18	8.68206E+16	3.38286E+12	2.5844E+19	7639700	4.45891E+20
A66	0.3	69	424900	1.39337E+18	7.67115E+16	3.27929E+12	2.53089E+19	7717800	4.59706E+20
A67	1.3	68	430200	1.4287E+18	7.9618E+16	3.32101E+12	2.56372E+19	7719700	4.60046E+20
A68	0.2	72	427600	1.41099E+18	7.81831E+16	3.29979E+12	2.54645E+19	7717000	4.59563E+20
A69	29.5	168	399446	1.21644E+18	6.37344E+16	3.04532E+12	2.3217E+19	7623849	4.43122E+20

Plot number	Tromsø kommune	Storfjord kkommune	Målselv kommune	Locality
A1	1	0	0	Håkøybotn Sørelva
A2	1	0	0	Håkøybotn Sørelva
A3	1	0	0	Tromsdalen
A4	1	0	0	Tromsdalen
A5	1	0	0	Tromsdalen
A6	0	1	0	Skibotn, Brennfjell
A7	1	0	0	N of Laksvatnet
A8	0	0	1	Tverrelvflata
A9	0	0	1	Tverrelvflata
A10	0	0	0	Moan
A11	0	0	0	Moan
A12	0	0	0	Moan
A13	0	0	0	Sørdalen, Solheim
A14	0	0	0	Sørdalen, Lundeng
A15	1	0	0	Greipstad
A16	1	0	0	Greipstad, Falkberget
A17	1	0	0	Greipstad, behind Vardhaugen
A18	1	0	0	Greipstad, Sløykdalshøgda
A19	1	0	0	Brensholmen
A20	0	0	1	Holt
A21	0	0	1	Dividalen, Åsen
A22	0	0	1	Skjold
A23	0	0	1	Skjold
A24	0	0	1	Dividalen, Øvre Steinvoll
A25	0	0	1	Dividalen, near the pine plantation at Frihetsli
A26	0	0	1	Dividalen, Frihetsli, where Skaktarelva meets Divielva
A27	0	0	1	Dividalen, end of the road
A28	1	0	0	Tønsvik
A29	1	0	0	Tønsvik, Høgmelelva
A30	1	0	0	Tønsvik, southern bank of Tønsvikselva
A31	1	0	0	Tønsvik, southern bank of Tønsvikelva
A32	1	0	0	Tønsvik, northern bank of Tønsvikelva
A33	1	0	0	Håkøybotn Finnvikelva
A34	1	0	0	Håkøybotn Finnvikelva
A35	1	0	0	Straumsbukta
A36	1	0	0	Håkøybotn
A37	0	1	0	Skibotn, Brennfjell
A38	0	1	0	Skibotn, Bærfjell
A39	0	1	0	Kavelnes
A40	0	1	0	Campingsite behind Brennfjell Camping

Plot number	Tromsø kommune	Storfjord kkommune	Målselv kommune	Locality
A41	0	1	0	Rovvejokkafossen
A42	0	1	0	Lávvajohka, Helligskogen
A43	0	0	1	Tverrelvflata
A44	0	0	1	Alapmoen
A45	0	0	1	Skakterdalen
A46	0	0	1	Skakterdalen
A47	0	0	1	Frihetsli
A48	0	0	1	Frihetsli
A49	0	0	1	Olsborg, Brorstadbekken
A50	0	0	1	Olsborg, Brorstadbekken
A51	0	0	1	Olsborg, Brorstadbekken
A52	0	0	1	Sollia, on a hillside
A53	0	0	1	Bjørkli near Takvatnet
A54	0	0	1	Bjørklia, Takvatnet
A55	0	0	1	Eggum, near Øverbygd
A56	0	0	1	Sollia
A57	0	0	0	Tune, Sæterbekken
A58	0	0	0	Tune
A59	0	0	0	Tune
A60	0	0	0	Høgtverrelva
A61	0	0	0	Svartbergan
A62	0	0	0	Holtet
A63	0	0	0	Holtet
A64	0	0	0	Melhusdalen
A65	0	0	0	Devddesjávri
A66	1	0	0	Kalvebakken
A67	1	0	0	Ramfjordmoen
A68	1	0	0	Hans-Larsa-neset
A69	0	0	0	Sørdalen, Melhusdalen

Presence of moist *Salix* forest	Presence of moist Salix forest
Presence of *Salix caprea*	Presence of Salix caprea trees in plot
Percentage of sibiling trees	Percentage of sibling trees in plot
Presence of *Salix myrsinifolia*	Presence of Salix myrsinifolia trees in plot
Presence of *Sorbus aucuparia*	Presence of Sorbus aucuparia trees in plot
Presence of *Salix pentandra*	Presence of Salix pentandra trees in plot
Rock suitability	Suitability of rock habitats for lichens
Total number of landscape elements	Total number of lines, line segments and patches
Median tree diameter	Median tree diameter of trees in plot
Tree age	Tree age
Tree density	Density of trees in plot
Water / total	Proportion of water edge length to total length of edge
Density of young trees	Density of young trees in plot
Distance to town	Distance to closest city (Tromsø) or town (Olsborg, Setermoen, Skjold)
Cultivated / natural	Proportion of human derived edge length to natural edge length
Distance to closest farmhouse	Distance from plot to closest farmhouse
Human impact	Overall human impact scale of plot
Hum an / Total	Proportion of human derived edge length to total length of edge
Landscape	Landscape unaffectedness
Distance to closest area cleared from forest	Distance to closest area cleared from forest by humans
Plantation	Presence of plantation of *Picea* spp. or *Larix* spp. in visibility distance
Road category	Category of closest road
Distance to closest road	Distance from plot to closest road
Seadis	Distance to closest seashore
SeaWest	Distance to open sea
Latitude	Latitude. Map projection used is Universal Transverse Mercator, UTM, datum WGS 84.
Latitude^2 x Longitude	Latitude^2 x Longitude
Latitude^3	Latitude^3
Latitude x Longitude	Latitude x Longitude
Latitude x Longitude ^{2}	Latitude $_*$ Longitude ^{2}
Longitude	Longitude. Map projection used is Universal Transverse Mercator, UTM, datum WGS 84.
Longitude^3	Longitude^3
Locality	Locality where a respective plot is situated in.

Appendix 5: Correlations between variables used in CCA

Pearsons product-moment correlation (R^2)

	Latitude	TROMSØ	STORFJORD	PR_S_T>4	OCEANITY	TM_SUM>0	TM_SUM>4	PLANTATION	ALN_B	POPULUS
Latitude	**1.00**	-0.20	0.69	-0.59	-0.63	-0.06	-0.09	-0.33	0.00	0.21
TROMSØ	-0.20	**1.00**	-0.24	0.77	0.57	0.06	-0.34	-0.10	0.02	-0.14
STORFJORD	0.69	-0.24	**1.00**	-0.55	-0.36	0.03	0.00	-0.28	-0.24	0.21
PR_ST_4	-0.59	0.77	-0.55	**1.00**	0.74	0.11	-0.14	0.13	0.12	-0.29
OCEANITY	-0.63	0.57	-0.36	0.74	**1.00**	0.31	0.11	0.08	0.03	-0.16
TM_SUM>0	-0.06	0.06	0.03	0.11	0.31	**1.00**	0.88	-0.23	0.34	-0.04
TM_S_4	-0.09	-0.34	0.00	-0.14	0.11	0.88	**1.00**	-0.11	0.28	-0.03
PLANTATION	-0.33	-0.10	-0.28	0.13	0.08	-0.23	-0.11	**1.00**	-0.02	0.01
ALN_B	0.00	0.02	-0.24	0.12	0.03	0.34	0.28	-0.02	**1.00**	-0.15
POPULUS	0.21	-0.14	0.21	-0.29	-0.16	-0.04	-0.03	0.01	-0.15	**1.00**

Tolerance (1-R^2)

	Latitude	TROMSØ	STORFJORD	PR_S_T>4	OCEANITY	TM_SUM>0	TM_SUM>4	PLANTATION	ALN_B	POPULUS
Latitude	**0.00**	1.20	0.31	1.59	1.63	1.06	1.09	1.33	1.00	0.79
TROMSØ	1.20	**0.00**	1.24	0.23	0.43	0.94	1.34	1.10	0.98	1.14
STORFJORD	0.31	1.24	**0.00**	1.55	1.36	0.97	1.00	1.28	1.24	0.79
PR_ST_4	1.59	0.23	1.55	**0.00**	0.26	0.89	1.14	0.87	0.88	1.29
OCEANITY	1.63	0.43	1.36	0.26	**0.00**	0.69	0.89	0.92	0.97	1.16
TM_SUM>0	1.06	0.94	0.97	0.89	0.69	**0.00**	0.12	1.23	0.66	1.04
TM_S_4	1.09	1.34	1.00	1.14	0.89	0.12	**0.00**	1.11	0.72	1.03
PLANTATION	1.33	1.10	1.28	0.87	0.92	1.23	1.11	**0.00**	1.02	0.99
ALN_B	1.00	0.98	1.24	0.88	0.97	0.66	0.72	1.02	**0.00**	1.15
POPULUS	0.79	1.14	0.79	1.29	1.16	1.04	1.03	0.99	1.15	**0.00**

Variance Inflation Factor (VIF) = 1/Tolerance

	Latitude	TROMSØ	STORFJORD	PR_S_T>4	OCEANITY	TM_SUM>0	TM_SUM>4	PLANTATION	ALN_B	POPULUS
Latitude		1	3	1	1	1	1	1	1	1
TROMSØ	1		1	4	2	1	1	1	1	1
STORFJORD	3	1		1	1	1	1	1	1	1
PR_ST_4	1	4	1		4	1	1	1	1	1
OCEANITY	1	2	1	4		1	1	1	1	1
TM_SUM>0	1	1	1	1	1		8	1	2	1
TM_S_4	1	1	1	1	1	8		1	1	1
PLANTATION	1	1	1	1	1	1	1		1	1
ALN_B	1	1	1	1	1	2	1	1		1
POPULUS	1	1	1	1	1	1	1	1	1	

Appendix 6: Classification of human impact HI_k following Trass et al. (1999). Bold values are used in the calculations of HI_k.

Changes made: points III and IV – log diameter > 10 cm instead of > 20 cm. The original 13-point scale was reversed (low values – low human impact; high values – high human impact). Since three categories of highest human impact were missing in the data, the scale is a 10-point scale.

Formula used for calculations:

$HI_k = 1 + \left(\sum_{i=1}^{6} X_{ik} \right)$, where HI_k is human impact in plot k, $k=1,…,69$, and X_{ik} is the value of the variable i used for defining human impact in the k-th plot; $i=1,…,6$.

| i		
1 (landscape unaffectedness):	**2** =	The forest forms an islet in a landscape that has been strongly altered by human activity
	1 =	The surrounding landscape has been altered by intermediate human activity.
	0 =	The forest is surrounded by a natural landscape little disturbed by human activity, the width of the surrounding zone must be at least 0.5 km.
2 (tree age)	**2** =	Young forest (max. 40 years).
	1 =	Middle-aged forest (40-80 years), main tree species more or less of similar age.
	0 =	Old forest with forest gaps, main tree species belonging to at least three age classes, the age of the oldest class being more than 80 years.
3 (logs, windfall, d>10 cm)	**2** =	Absent or cleared away.
	1 =	Few (on average 2-5 per 400 m2).
	0 =	Many (6 or more per 400 m2).
4 (decay of logs, d>10cm)	**2** =	The majority of the logs are quite fresh, bryophyte coverage is absent or low (small, young patches).
	1 =	At least half of the logs are moderately decayed, bryophyte coverage on them up to 50%.
	0 =	At least one third of the logs are strongly decayed, bryophyte coverage on them 50-100%.
5 (latest intensive cutting)	**2** =	Less than 10 years ago.
	1 =	10-40 years ago.
	0 =	More than 40 years ago or never cut.
6 (other human impact)	**2** =	Clearly visible (intensive cutting, trampling that has strongly damaged the ground layer, heavy vehicle tracks, fresh ditches etc.)
	1 =	Intermediate (moderate cutting, tracks or trampling, old ditches etc.).
	0 =	No clearly visible damage, may belong the limitation zone or reservate of a nature reserve.

Appendix 7: Environmental data on air pollution
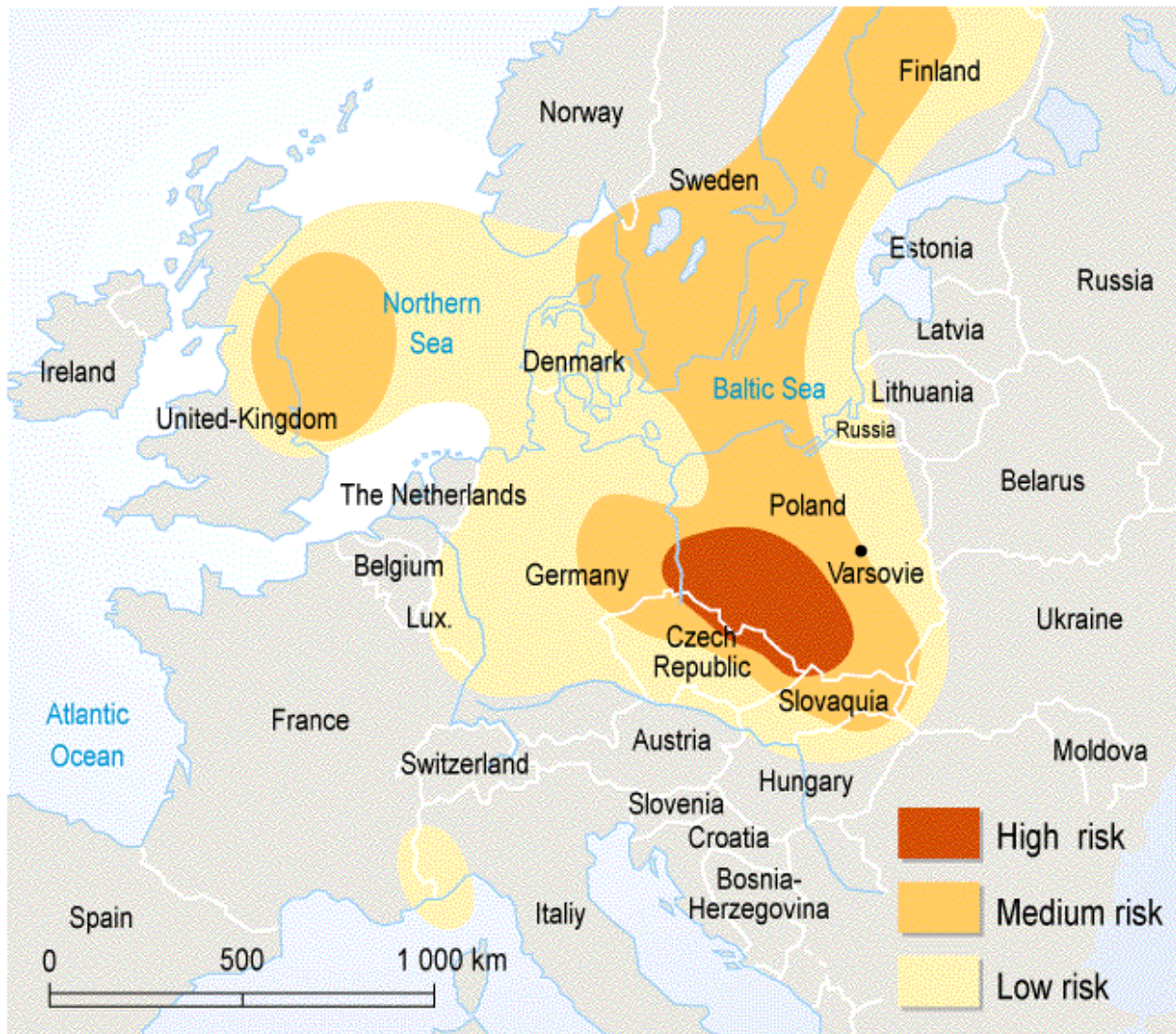
Figure I: Map on risk of acid rain in central Europe; source: Ed. Hatier, Paris, 1993, in UNEP GRID-Arendal (http://www.grida.no)
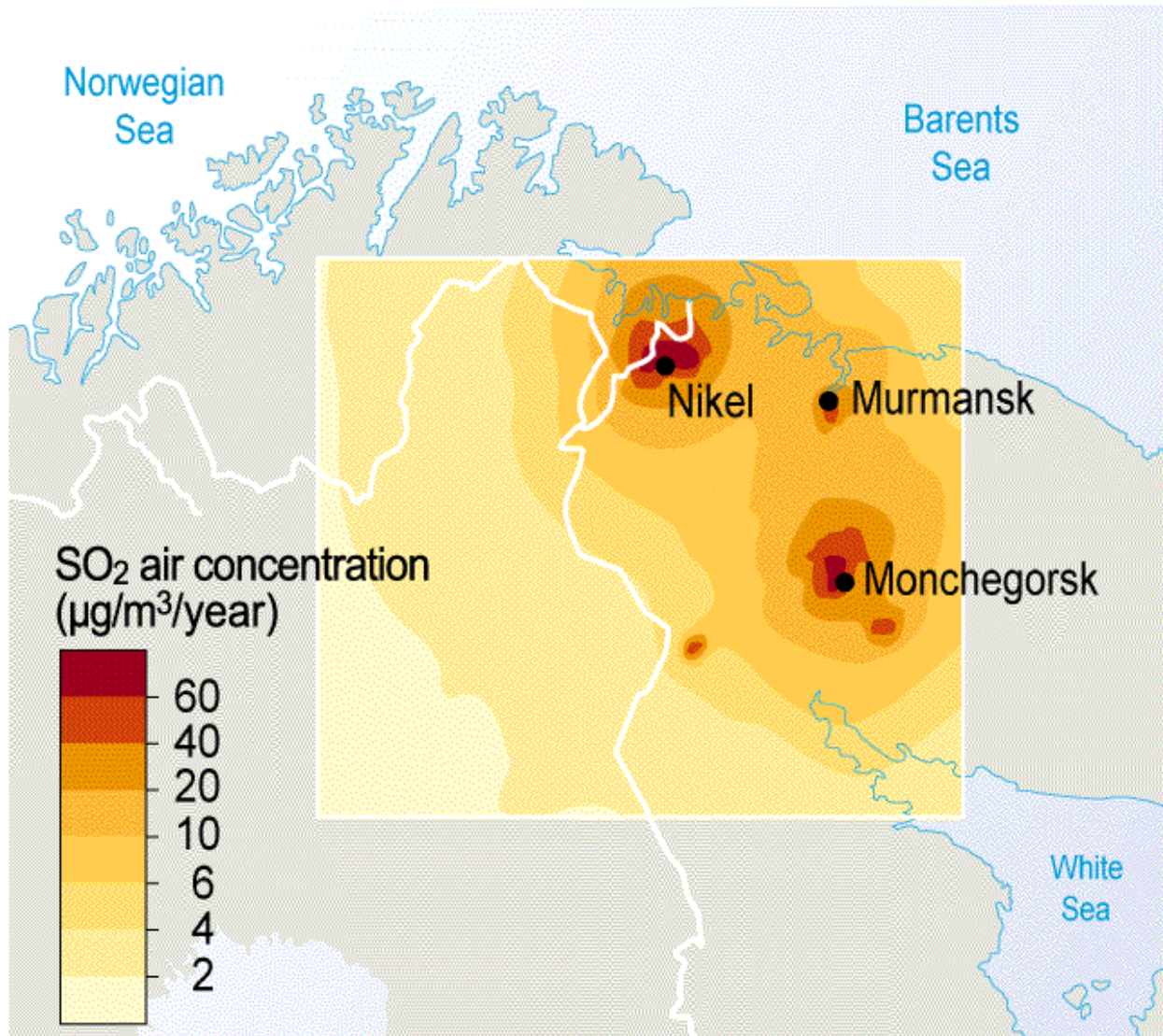
Figure II: SO2 air concentration in the Barent area, source: Norut, Bellona, SoEAR 1996, The Nordic Arctic Environment 1997, Le Monde Diplomatique 1996, AMAP 1997 in UNEP GRID-Arendal (http://www.grida.no)
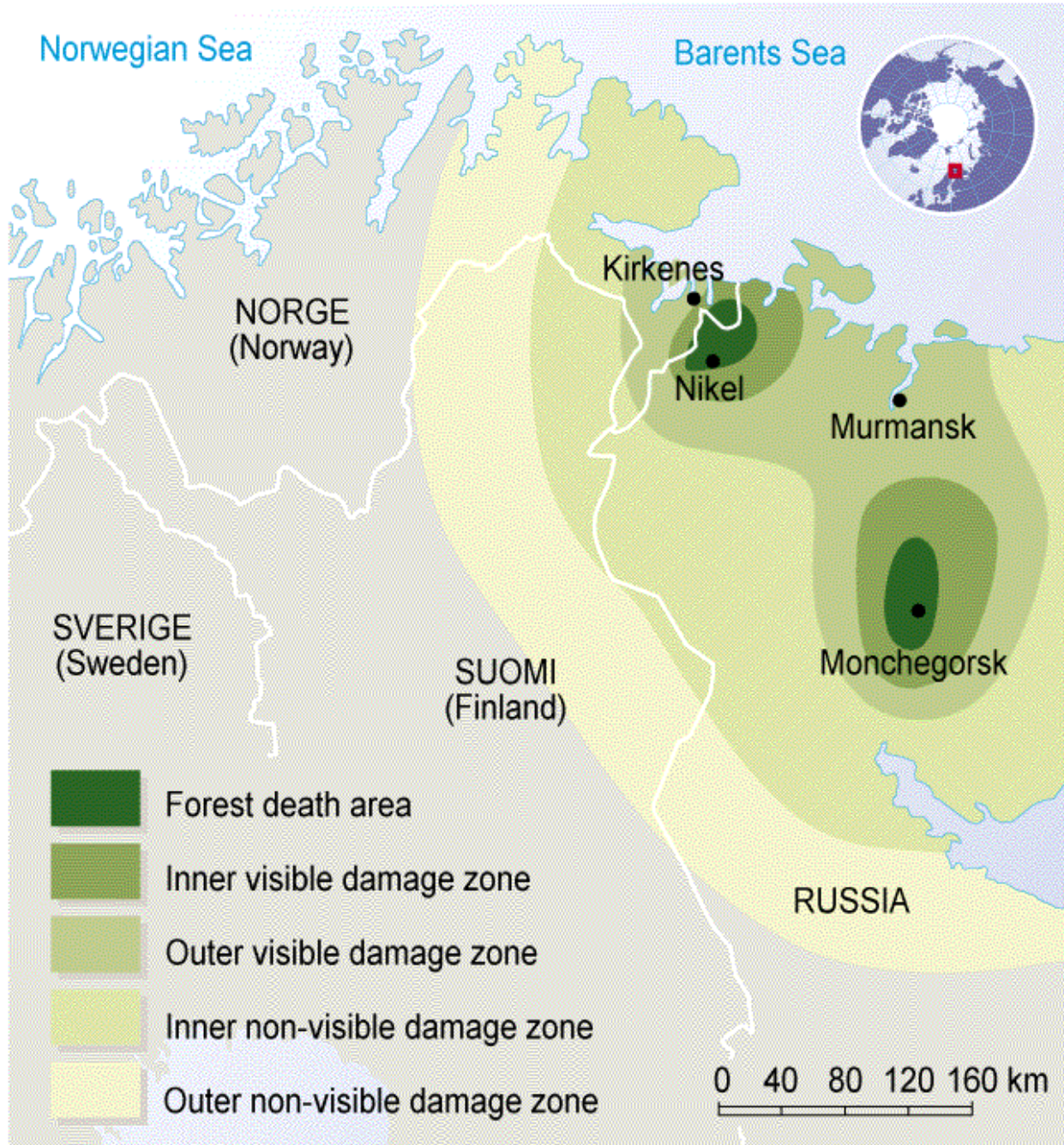
Figure III: Forest damage in the Barents area; sources: Norut, Bellona, SoEAR 1996, The Nordic Arctic Environment 1997, Le Monde Diplomatique 1996, AMAP 1997 in UNEP GRID-Arendal (http://www.grida.no)

Appendix 8: pH value of bark samples

Alnus incana	Betula pubescens	Populus tremula	Prunus padus	Salix caprea	Salix myrsinifoli	Salix pentandra	Sorbus aucuparia
4.45	4.06	5.04	5.77	6.87	6.37	5.67	5.98
4.47	4.16	5.66	5.51	5.64	6.13	5.75	5.37
4.64	4.16	5.71	5.08	4.99	6.07	5.48	5.41
4.69	4.18	5.49		5.08	5.60	5.47	5.52
4.90	4.20	6.03		5.04	5.84	5.52	5.31
5.00	4.43	6.90		4.99	5.65	5.72	5.97
5.00	4.43	5.61		5.36	5.32	5.54	4.56
5.14	4.45	5.49		5.16	5.79	5.98	6.36
5.14	4.48			4.75	5.79	5.45	5.86
5.15	4.49			5.24	5.79	5.90	6.18
5.16	4.49			4.97	6.20	5.76	6.22
5.17	4.58			4.83	6.14	5.75	5.71
5.19	4.58			5.47	6.40	6.08	6.03
5.19	4.62			5.19	6.56	5.63	4.82
5.29	4.64			5.27	6.35	5.47	6.37
5.31	4.65			5.12	6.15		6.05
5.42	4.66			5.58	5.25		5.66
5.44	4.67			5.42	5.51		5.62
5.49	4.68				6.00		6.12
5.58	4.72				6.08		5.68
5.67	4.75				6.29		5.98
5.69	4.76				5.98		5.08
5.77	5.00				5.55		
5.88	5.08				5.75		
6.03	5.13				4.77		
6.70	5.19				5.29		
	5.22						
	5.25						
	5.30						
	5.37						
	5.75						
	6.14						
	4.08						
	4.84						

Appendix 9: Kendall's τ correlation for the first three axes of CCA and DCA and the significant environmental variables.

Økland (2001) recommends the non-parametric Kendall's τ correlation coefficient to check correlations between environmental variables and (constrained) ordination axes, since this correlation coefficient performs best with similar plot variable values for many plots. The absolute values of Kendall's τ are always smaller than those of Pearson's r.

Correlations of CCA axes

Correlated axis/variable	Kendall's τ	p-level
CCA_1 & LATITUDE	-0.1514	0.06590
CCA_1 & TROMSØ	**0.2285**	**0.00549**
CCA_1 & STORFJORD	**-0.3825**	**0.00000**
CCA_1 & PR_SUM_T>4	**0.2786**	**0.00071**
CCA_1 & OCEANITY	-0.0829	0.31348
CCA_1 & TM_SUM_T>0	**-0.2901**	**0.00042**
CCA_1 & TM_SUM_T>4	**-0.3028**	**0.00023**
CCA_1 & PLANTATION	0.1516	0.06548
CCA_1 & ALNUS TREES	0.0527	0.52219
CCA_1 & POPULUS FOREST	**-0.3964**	**0.00000**
CCA_2 & LATITUDE	**0.3910**	**0.00000**
CCA_2 & TROMSØ	**0.2310**	**0.00499**
CCA_2 & STORFJORD	**0.2260**	**0.00604**
CCA_2 & PR_SUM_T>4	-0.1237	0.13284
CCA_2 & OCEANITY	**-0.2499**	**0.00239**
CCA_2 & TM_SUM_T>0	-0.1354	0.09991
CCA_2 & TM_SUM_T>4	**-0.2770**	**0.00076**
CCA_2 & PLANTATION	-0.1408	0.08719
CCA_2 & ALNUS TREES	**-0.4142**	**0.00000**
CCA_2 & POPULUS FOREST	0.0456	0.57962
CCA_3 & LATITUDE	-0.1292	0.11648
CCA_3 & TROMSØ	**0.5776**	**0.00000**
CCA_3 & STORFJORD	0.0535	0.51551
CCA_3 & PR_SUM_T>4	**0.3728**	**0.00001**
CCA_3 & OCEANITY	**0.3651**	**0.00001**
CCA_3 & TM_SUM_T>0	**0.1904**	**0.02068**
CCA_3 & TM_SUM_T>4	0.0185	0.82245
CCA_3 & PLANTATION	**-0.3020**	**0.00024**
CCA_3 & ALNUS TREES	**-0.1831**	**0.02606**
CCA_3 & POPULUS FOREST	**-0.2022**	**0.01402**

Correlated axis/variable	Kendall's τ	p-level
DCA_1 & LATITUDE	-0.1357	0.0991
DCA_1 & TROMSØ	**-0.2142**	**0.0093**
DCA_1 & STORFJORD	0.0318	0.6988
DCA_1 & PR_SUM_T>4	-0.0851	0.3011
DCA_1 & OCEANITY	0.0950	0.2485
DCA_1 & TM_SUM_T>0	**0.1843**	**0.0251**
DCA_1 & TM_SUM_T>4	**0.2588**	**0.0017**
DCA_1 & PLANTATION	0.0997	0.2258
DCA_1 & ALNUS TREES	**0.2308**	**0.0050**
DCA_1 & POPULUS FOREST	0.1413	0.0859
DCA_2 & LATITUDE	**0.3163**	**0.0001**
DCA_2 & TROMSØ	0.0816	0.3217
DCA_2 & STORFJORD	**0.1651**	**0.0448**
DCA_2 & PR_SUM_T>4	**-0.1723**	**0.0363**
DCA_2 & OCEANITY	**-0.1915**	**0.0200**
DCA_2 & TM_SUM_T>0	**0.1653**	**0.0446**
DCA_2 & TM_SUM_T>4	0.1022	0.2144
DCA_2 & PLANTATION	**-0.2566**	**0.0018**
DCA_2 & ALNUS TREES	0.0613	0.4565
DCA_2 & POPULUS FOREST	0.0129	0.8751
DCA_3 & LATITUDE	-0.0420	0.6099
DCA_3 & TROMSØ	0.1595	0.0527
DCA_3 & STORFJORD	-0.0777	0.3452
DCA_3 & PR_SUM_T>4	0.1101	0.1809
DCA_3 & OCEANITY	0.1179	0.1521
DCA_3 & TM_SUM_T>0	-0.0605	0.4624
DCA_3 & TM_SUM_T>4	-0.0850	0.3015
DCA_3 & PLANTATION	0.0024	0.9766
DCA_3 & ALNUS TREES	0.0042	0.9592
DCA_3 & POPULUS FOREST	-0.1036	0.2082