

Bryophyte and lichen diversity under simulated environmental change compared with observed variation in unmanipulated alpine tundra

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Abstract. Effects of simulated environmental change on bryophyte and lichen species richness and diversity in alpine tundra were investigated in a 5-year experiment at Latnjajaure, northern Sweden. The experiment had a factorial design including fertilisation and temperature enhancement in one meadow and one heath plant community. Responses in species richness, biodiversity, and species composition of bryophytes and lichens to experimental treatments were compared to the observed variation in six naturally occurring plant communities. The combination of fertilisation and enhanced temperature resulted in a species impoverishment, for bryophytes in the bryophyte-dominated community, and for lichens in the lichen-dominated communities, but the species composition stayed within the observed natural variation. During the course of the study, no species new to the investigated mid-alpine landscape were recorded, but that scenario is realistic within a decade when comparing with the processes seen in vascular plants.

Introduction

Global change, as understood today, is composed of three major, interactive components, i.e. climate change, land use change, and environmental pollution, their relative importance varying across the biomes of the Earth. Climate change in terms of global warming is anticipated to be most pronounced at high latitudes (Mitchell et al. 1990; Maxwell 1992). The impact can already be visualised in the decrease of annual snow cover extent in the Northern hemisphere (EEA 2004), decrease of arctic sea ice (Johannessen et al. 2002), and decrease of glaciers (Dyurgerov 2003; EEA 2004). Expected environmental changes include increases in air surface temperatures, which have already been observed in the Alaskan Arctic and Europe (Overpeck et al. 1997; Keyser et al. 2000; Serreze et al. 2000; EEA 2004), and increases in nutrient availability (Nadelhoffer et al. 1991, 1992; Bonan and Van Cleve 1992; Jonasson et al. 1993), leading to profound effects on community composition and ecosystem

functioning (Van Wijk et al. 2003). The impact of global change on plants is expected to be particularly pronounced in arctic and alpine regions as the plants here are limited by the low temperatures and nutrient availability.

Ecosystems at high latitudes exhibit a large proportion of bryophytes and lichens that are highly significant in terms of species richness (Longton 1982; Matveyeva and Chernov 2000), biomass (Longton 1984; Nash 1996; Lange et al. 1998), and nutrient cycling (Crittenden 1983; Longton 1984; Nash 1996; Kielland 1997; Longton 1997). The relative abundance of bryophytes and lichens increases with increasing latitude, an indirect effect of the more rapid decline in vascular plant species richness (Vitt and Pakarinen 1977; Wielgolaski et al. 1981). Bryophytes and lichens at these high latitudes make important contributions to the species diversity on a global scale (Longton 1997; Matveyeva and Chernov 2000). Given the high abundance, and the occasionally high dominance of bryophytes and lichens in these areas, they are important components of the ecosystem functioning (Cornelissen et al. 2001). Consequently, it is important to gain knowledge on their responses to global change.

Global change poses a potential threat to biodiversity, and may cause irreversible effects (Kappelle et al. 1999); the temperature change may affect biodiversity of the biota in arctic and alpine areas (Chapin and Körner 1995). To date, most studies on the effects of simulated global change have been focused on biomass or cover of vascular plants (e.g. Arft et al. 1999; Van Wijk et al. 2003), whereas biodiversity and species richness have received less attention. Lack of studies on the effect of global change on species diversity is one of the areas identified by EEA (2004), however, even fewer studies have been focused on the bryophyte and lichen diversity (cf. Molau and Alatalo 1998). The few studies that exist on how bryophyte and lichen species richness or diversity is affected by fertiliser and temperature enhancement show diverse results, from no changes to decreases in bryophytes, and from decreases to increases in lichens (Jonasson 1992; Molau and Alatalo 1998; Press et al. 1998). Thus, so far, a clear response pattern to the effects of global change on the richness and diversity of bryophytes and lichens is lacking.

It has been argued that a problem of the existing *in situ* experiments is that they only include one or a few plant community types, making it difficult to distinguish between ecosystem and/or site specific responses (see Van Wijk et al. 2003). Plant communities with different initial species compositions may show contrasting responses to *in situ* experiments (Molau and Alatalo 1998). If findings from the experiments could be compared with e.g. natural gradients, patterns of environmental variation, or different temporal or spatial scales, the results from the experimental manipulations would have stronger validity (Van Wijk et al. 2003). Similarly, a comparison between the change in diversity and species richness within *in situ* experiments and the naturally occurring variation in a number of contrasting local plant communities, could show if the responses of the *in situ* experiments fall within a natural range of variation. If so, this indicates the future direction for bryophyte and lichen plant community

change, and, if not, the effect on bryophytes and lichens is perhaps more negative than expected.

The aim of this study was to investigate: (1) if species richness and diversity of bryophytes and lichens are negatively affected by *in situ* experiments of simulated environmental change; and (2) if the magnitudes of responses in species richness, diversity, and species composition in these *in situ* experiments fall within the range of the observed variation in natural plant communities.

We conducted a 5-year factorial experiment of fertilisation and temperature enhancement in two subarctic-alpine tundra plant communities, and compared the magnitude of responses with the variation observed in six natural local plant community types. We have previously reported on the biodiversity of whole plant communities (Molau and Alatalo 1998) and bryophyte growth and cover (Jägerbrand et al. 2003) after three seasons of simulated environmental change at the same site.

Materials and methods

Site description

The study was conducted at the Latnjajaure Field Station (LFS; 68°21'N, 18°29'E, 1000 m a.s.l.) in northern Swedish Lapland. The Latnjajaure area is phytogeographically regarded as subarctic-alpine tundra, but has a typically arctic climate with a mean annual temperature between -1.5 to -2.9 °C, and a total annual precipitation between 605 and 990 mm (Table 1). The valley is covered by snow about 8 months of the year. The bedrock in Latnjajaure belongs to the upper Caledonian nappe (called Kōli nappe) composed of mica-garnet schists and with inclusions of marble on the west facing slopes. Intrusions of acidic granites can be found in the northern part of Latnjavagge ('vagge or 'vaggi is Sami for valley). The lower part of Latnjavagge's floor is

Table 1. Climate data from the years 1993–2002 for the Latnjajaure valley.

Year	Mean annual temperature (°C)	Total precipitation (mm)	Mean summer temperature (°C, June–August)	Total summer precipitation (mm, June–August)
1993	-2.7	990	5.5	187
1994	-2.4	680	6.0	126
1995	-2.9	808	5.2	268
1996	-2.2	605	6.8	201
1997	-2.0	742	8.0	99
1998	-2.7	813	6.6	219
1999	-1.9	829	6.0	254
2000	-1.5	857	6.1	219
2001	-2.3	826	7.1	285
2002	-1.8	855	7.3	158

dominated by the Lake Latnjajaure and a series of moraine ridges, 10–20 m high with material of granitic origin. The crests are snow-free during most of the winter and many boulders are windpolished on the north-facing sides. Solifluction and gelifluction are present on the gentle slopes and are expressed as slowly moving lobes and sheets. Sorted polygons are frequent on the valley floor, even though they today may be regarded as inactive, sub-fossil remainings, as there is no indication of permafrost in the valley floor any longer (Beylich et al. 2004).

Abbreviations of plant communities and experimental plots are presented in Table 2. The OTC (Open-Top Chamber, see Marion et al. 1997) experiment was set up in two plant communities ca. 500 m apart: (1) a dry heath plant community on an acidic moraine ridge (H; dry heath, described below) with sparse vegetation, and (2) a meadow on a calcareous terrace (M; mesic meadow, described below) with a continuous vegetation cover.

The dry heath (HD) is of the *Loiseleuria procumbens*-*Arctostaphylos alpinus*-*Empetrum hermaphroditum*-type (Nordic Council of Ministers 1995), and occurs on windblown, dry, acidic moraines, mostly glacial end moraines of alloctonous origin. Usually there are some active frost processes, expressed as small mudboils or solifluction lobes, although most of the ground is stable. The vegetation is more or less snow-free throughout the winter or with an early snowmelt at the beginning of June. The vascular plant species richness is low with a discontinuous vascular plant canopy dominated by *Betula nana*, *Empetrum hermaphroditum*, *Vaccinium vitis-idaea*, *Salix herbacea*, *Diapensia lapponica* and *Carex bigelowii*. The bottom layer is species rich with, e.g.

Table 2. Abbreviation list for plant community types of the experimental treatments and natural community types at Latnjajaure.

Abbreviation	Plant community type	Number of plots
<i>Natural vegetation plots</i>		
HD	Dry heath	16
HP	Patterned heath	16
HSS	Heath snowbed	12
MM	Mesic meadow	12
MV	Moist meadow	10
MRF	Medium rich fen	10
<i>Experimental plots</i>		
H	All heath plots of 1995	20
HC	Heath control plots (1999)	8
HF	Heath fertilised plots (1999)	4
HT	Heath temperature plots (1999)	4
HTF	Heath temperature and fertilised plots (1999)	4
M	All meadow plots of 1995	20
MC	Meadow control plots (1999)	8
MF	Meadow fertilised plots (1999)	4
MT	Meadow temperature plots (1999)	4
MTF	Meadow temperature and fertilised plots (1999)	4

Kiaeria starkei, *Dicranum fuscescens*, *Dicranum groenlandicum*, *Polytrichum juniperinum*, and *P. piliferum*. Some dominant lichens are *Sphaerophorus globosus*, *Ochrolechia frigida*, and *Cladonia spp.*

The patterned heath (HP) vegetation type develops on the ground with active frost processes forming sorted polygons, and the vegetation consists of a small-scale mosaic of dry to wet heath vegetation. All components of the mosaic can be found within 1–5 m². The vegetation is poor on the polygon summits, resembling that of the dry heath vegetation (see above) and wetter in the depressions between the polygons. Plant communities formed under the influence of underlying permafrost, such as the patterned heath, are not present in the regional classification system in use (i.e. Nordic Council of Ministers 1995).

Heath snowbed (HSS) is of the *Cassiope hypnoides*-*Salix herbacea*-type (Nordic Council of Ministers 1995), and is common on unstable acidic soils. In drier areas, the vascular plant canopy is discontinuous and characterised by a few species, e.g. *Salix herbacea*, *Gnaphalium supinum*, *Carex lachenalii*, *Ranunculus glacialis*, and *Cassiope hypnoides*. The bryophyte cover is extensive and contains dominant species from the family Dicranaceae. In moister areas with a continuous water supply, grasses can be found, e.g. *Phippsia algida* and *Deschampsia alpina*, as well as bryophytes such as *Polytrichastrum sexangulare*, and *Warnstorfia sarmentosa*. Lichens are generally less frequent.

Mesic meadow (MM) of the *Cassiope tetragona*-type (Nordic Council of Ministers 1995) develops on calcareous ground with little sign of frost processes, despite good snow protection in winter, snowmelt comes relatively early. The community is dominated by the evergreen dwarf shrub *Cassiope tetragona*, but there are also substantial amounts of *Rhododendron lapponicum*, *Dryas octopetala*, and *Saxifraga oppositifolia*. Herbs are well represented with species such as *Tofieldia pusilla*, *Potentilla crantzii*, *Bartsia alpina*, *Bistorta vivipara*, *Campanula uniflora*, *Thalictrum alpinum* and *Astragalus alpinus*. Sedges are mainly represented by *Carex* species. In the bottom layer the bryophytes prevail, e.g. *Aulacomnium turgidum*, *Cyrtomnium hymenophyllum*, *Ditrichum flexicaule*, *Hylocomium splendens*, *Polytrichastrum alpinum*, *Polytrichum strictum*, *Ptilidium ciliare*, *Rhytidium rugosum*, *Tomentypnum nitens*, and *Tritomaria quinque-dentata*. Lichens are mainly represented by *Cetraria spp.* and *Peltigera spp.*

The moist meadow (MV) is of the *Potentilla crantzii*-*Bistorta vivipara*-type (Nordic Council of Ministers 1995), a low herb plant community that develops in areas with calcareous ground, good snow protection and an early snowmelt. Herbs are frequent, but there are also some *Salix* species, and sedges are common, e.g. *Carex vaginata*, *C. fuliginosa*, *C. atrata*, as well as the grass *Poa arctica*. The bryophyte flora recalls that of the mesic meadow (see above) but with a lower cover, while lichens are less frequent.

Medium rich fen (MRF) of the *Salix herbacea*-*Paludella squarrosa*-type (Nordic Council of Ministers 1995) is an important component in nutrient rich moist – wet sites of the valley. The canopy is dominated by graminoids, mainly the sedges *Carex lachenalii*, *C. bigelowii*, and *C. parallela*. In wetter parts

Eriophorum angustifolium, *E. scheuchzeri*, *Juncus biglumis*, *Carex fuliginosa*, *Carex lachenalii*, *Carex capillaris* and *Poa arctica* are the most frequent species. The bottom layer has an almost complete cover dominated by bryophytes, e.g. *Scorpidium revolvens*, *Bryum pseudotriquetrum*, *Rhizomnium pseudopunctatum*, *Polytrichastrum alpinum*, *Paludella squarrosa*, and *Sphagnum* spp. Lichens are less frequent.

Experimental treatments

The experiment was set up to cover one heath (H) and one meadow (M) plant community type. For each plant community, 20 plots (1 × 1 m) with homogeneous vegetation cover were chosen in 1995, and randomly assigned to treatments in a factorial design. There were 8 control plots and 4 plots for each of the following three treatments: fertilisation, temperature, and fertilisation and temperature combined. The temperature was enhanced by using open-top chambers of ITEX design, which increase the temperature on average by 1.5–3 °C compared to control plots (Marion et al. 1997; Molau 2001). Fertiliser addition consisted of 5 g N (as NH_4NO_3) and 5 g P (as P_2O_5) per m^2 , dissolved in 10 l of meltwater. In 1995, the fertiliser treatment was implemented directly after the initial vegetation mapping, and in subsequent years a few days after snowmelt. The experiment followed the BACI design (Before/After Control/Impact; see Bernstein and Zalinski 1983; Stewart-Oaten et al. 1986; Underwood 1991, 1992). Vegetation mapping was undertaken in July 1995, and again in July 1999. Species composition was analysed by the point-frame method (described in Walker 1996; Molau and Alatalo 1998) by measuring relative abundances of bryophytes and lichens. In order to receive the same sample plot size as the measurements of the natural plant communities, only the central 0.25 m^2 of the plots were used in the analyses.

Measurements of natural plant communities

In 1998, a staked grid with a 50 × 50 m mesh size and encompassing 118 grid points (in total 0.5 km^2) was set up. The vegetation at each grid point was investigated within 10 × 10 m for dominant vascular plant species and bryophytes, and the plant communities were classified according to the Scandinavian classification system (Nordic Council of Ministers 1995). As a basis of this study, we selected the six most dominant plant communities encountered within the grid (see Molau et al. 2003). In the summer of 2002, a detailed recording of species composition was performed by point-framing one 0.25 m^2 plot at each grid point falling within the chosen plant communities. As these six plant communities have somewhat different abundances, the number of plots sampled varied between 10 and 16 per community (see Table 2). Nomenclature follows Nilsson (1991) for vascular plants, Söderström and

Hedenäs (1998) for bryophytes, and Moberg and Holmåsén (2000) for lichens. For a complete species list of all bryophytes and lichens, see Appendix A.

Abiotic data and soil measurements

Snow depth was measured from the last week of May until the date of final snow melt 1999–2002 at all grid points by using an avalanche sond. Soil moisture was measured at each point using a Theta-Probe (Delta-T Devices, Cambridge, UK) during the whole snow free period in 1999–2002 with an interval of 10 days between each measurement. The values that were used in the statistical analyses were calculated as a mean of the whole snow-free period.

The soil sampling took place in the above mentioned permanent grid in 1999. Two samples ($n = 2$) within 2 m from each grid point corresponding to the plant community of interest were collected with a soil sample cylinder (\varnothing 70 mm). After removing the litter, the soil surface layer (0–5 cm) was strained through a 2 mm mesh sieve. All sieved samples were air-dried at 20 °C before all analyses were started. The soil organic matter (SOM) was determined from ignited dried (105 °C) soil samples in a muffle furnace at 550 °C for 24 h.

Two subsamples of 5.0 g each from each sample were extracted in 50 ml 1 M KCl and 50 ml 1 M NH_4Ac (adjusted to pH 7.0), respectively, in 250-ml plastic bottles by shaking for 30 min. The solutions were then filtered and collected in 100-ml brown glass bottles. About 20 ml was taken out from the KCl solution to a 250-ml E-flask and a couple of drops of phenolphthalein were added. The sample was titrated with 0.05 M NaOH to colour alteration and the consumed amount NaOH was used to calculate the exchangeable acidity. One drop 0.05 M HCl was added to make sure that the sample was not overtitrated and the sample became colorless. Then 5 ml 4% NaF was added and if the sample contained Al^{3+} the sample again became colored by the formation of OH^- . The coloured sample was then titrated with 0.05 M HCl to colour alteration and the consumed amount HCl was used to calculate the extractable Al^{3+} (Balsberg 1975). Both titrations were made with Metrohm 665 Dosimat. In the remaining part of the KCl solution, pH was measured with Jenco microcomputer pH meter model 6209. 0.2 ml of the NH_4Ac solution was diluted with 5.0 ml 1% LaCl_3 /0.1% CsCl solution in a 30-ml plastic beaker. The sample was then analysed for extractable Ca^{2+} , Mg^{2+} and K^+ on a Perkin-Elmer model 380 AAS. Samples from the rich areas had to be diluted further with 5–40 ml 1% LaCl_3 /0.1% CsCl solution (Balsberg 1975).

Data analyses

Patterns of diversity were investigated by calculating species richness (species number per unit area), Simpson's diversity index D (Simpson 1949), Brillouin diversity index HB (Brillouin 1962), and the Brillouin based evenness measure EB

(Zar 1996). Both Simpson's and Brillouin's diversity indexes were included as Simpson's diversity index is reliable even when a small sample size is available (Mouillot and Leprêtre 1999), whereas the Brillouin's diversity index is appropriate when samples are obtained nonrandomly from a population (Zar 1996). The Brillouin based evenness measure was included as a measurement of the homogeneity or relative diversity of the species (Pielou 1966). Prior to analyses of species richness and diversity, data were transformed to meet normality assumptions by achieving homogeneity of variances by log transformation and adding a constant (for further details, see Økland et al. 2003).

A correlation analysis and Z-test was used to analyse if species richness and the diversity indexes were interrelated (Zar 1996). As all of the indexes were significantly correlated, some of the indexes were excluded from some of the figures and tables (they are presented in Appendix B). Richness and diversity changes in experimental treatments were analysed as relative changes between years (1995–1999). Differences (in richness and diversity) among treatments, and between experimentally treated and natural plant communities were analysed by ANOVA, and if significant, followed by Tukey-Kramer *post hoc* tests, which can be used for unequal sample sizes. However, in one case (richness of lichens in the heath) this test did not reveal any differences, and we therefore excluded every other value from control plots, receiving equal sample sizes, and then used Fisher's *post hoc* test. Finally, PCA (principal component analysis) was used to analyse trends in the species composition of experimental and natural plant communities. In the PCA, species with less than five counts were excluded as they would have little impact. Log-transformation was used to reduce the impact of very dominant species. The PCA was conducted on correlations and the species was centered and standardised. To make graphical presentations possible, the PCA was performed on mean values (see Table 2). For ANOVA, *post hoc* tests, and correlation analysis, Statview[®] 5.0.1 was used, and for PCA CANOCO 4.5 (ter Braak and Šmilauer 2002). Sample sizes are shown in Table 2.

Results

The plant communities were found to have different relative abundance of bryophytes and lichens (Figure 1). For the bryophytes in the meadow, the ANOVA showed that the species richness ($F_{3,16} = 4.4$, $p = 0.019$), and the Simpson's diversity index D ($F_{3,16} = 5.92$, $p = 0.007$) were significantly different between experimental treatments. *Post hoc* tests showed that the species richness and diversity were significantly lower in the combined fertilised and temperature enhanced treatment compared with the fertiliser treatment in the meadow (Figure 2 a, b). There were no significant treatment effects found for the bryophytes in the heath (species richness, $F_{3,16} = 2.37$, $p = 0.109$; D, $F_{3,16} = 0.17$, $p = 0.914$). For lichens in the heath, the ANOVA showed significant differences between the treatments in the species richness ($F_{3,16} = 3.69$, $p = 0.034$), and the *post hoc* test showed that richness was lower

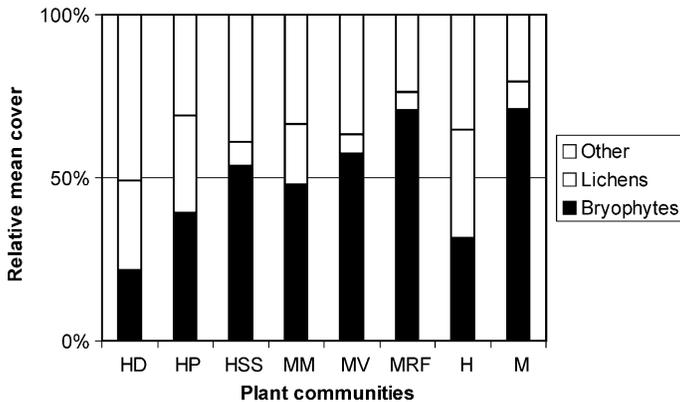


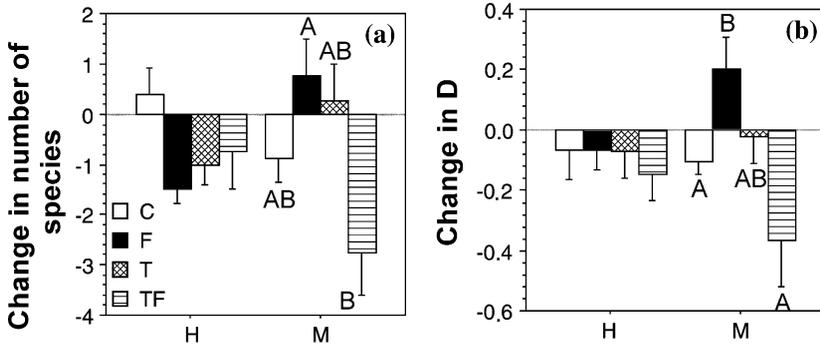
Figure 1. Mean relative cover of bryophytes, lichens and others in the natural plant communities at Latnjajaure. For abbreviations see Table 2. $n = 16$ (HD, HP), 12 (HSS, MM), 10 (MV, MRF), and 20 (H, M).

in the fertiliser and the combined fertiliser and temperature treatments compared to the increase in temperature enhancement plots (Figure 2c). No other significant treatment effect was found by the ANOVA for lichens (in the heath, D, $F_{3,16} = 2.28$, $p = 0.119$, and in the meadow, species richness $F_{3,16} = 0.69$, $p = 0.569$; D, $F_{3,16} = 0.03$, $p = 0.994$; Figure 2d).

There were significant differences in experimental treatments and natural plant communities, for bryophytes in the species richness (ANOVA, $F_{15,140} = 5.46$, $p < 0.0001$), and D ($F_{15,140} = 3.53$, $p < 0.0001$), and for lichens in the species richness ($F_{15,140} = 11.57$, $p < 0.0001$), and D ($F_{15,140} = 8.59$, $p < 0.0001$). For richness and D in bryophytes, MTF was significantly different from all other plots except HD (Figure 3 a, b, and Table 3). For lichens, HT and HC were significantly different in species richness and D from HSS, MV and MRF, but not from HD and HP (Figure 3 c, d, and Table 3).

PCA axes 1 and 2 for the species composition of bryophytes has the eigenvalues 0.285 and 0.196, respectively, and explains 48.1% of the variation. In PCA 1, all natural plant communities except HD were situated in the right part of the diagram, whereas the experimental treatments and controls were in the left part (Figure 4a). For PCA 2, all meadow plots (both experimental and natural) were situated in the upper part of the diagram, whereas all heath plots were in the lower part (Figure 4a). This pattern seems to correspond to the natural plant communities differences in soil characteristics (Table 4). The heath plant communities (HD, HP, HSS) generally have lower pH and base saturation than the meadow plant communities (MM, MV, MRF). Further, the heath also had lower levels of extractable calcium and magnesium, but higher acidity and extractable aluminium levels (Table 4). One exception was the meadow plots of the combined treatment of increased nutrients and temperature, situated closer to the heath part of the diagram, which probably reflect the loss of diversity of bryophytes in the combined treatment.

Bryophytes



Lichens

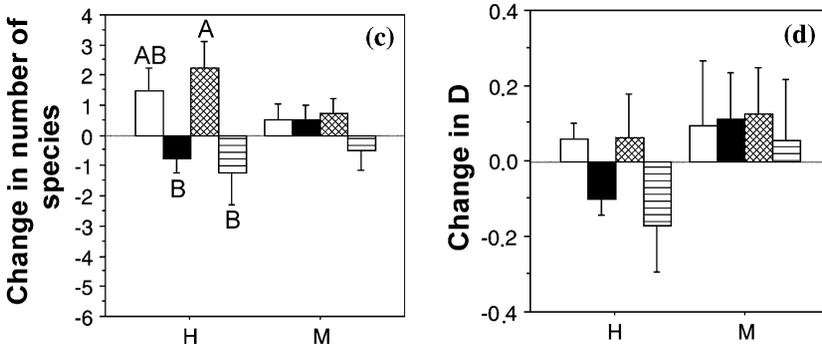


Figure 2. Change in species richness and Simpson's diversity index (D) of bryophytes and lichens in the experiments simulating environmental change at Latnjajaure. Relative changes between 1995–1999 are shown. Different letters on bar charts indicate significant differences between the treatments at $p < 0.05$, analysed by *post hoc* tests. Treatments: C = control plots, F = fertilised, T = temperature, TF = temperature and fertiliser. H = heath, M = meadow. $n = 8$ (controls) and 4.

For the species composition of the lichens, the eigenvalues of the first two PCA axes are 0.323 and 0.200, respectively, and are explaining 52.3% of the variance. In PCA 1 for lichens the heath plots were situated in the right part of the diagram (except HSS, HTF), whereas meadow plots were situated in the left part, irrespective of natural or experimental origin (Figure 4b), and does not seem to follow any of the measured soil characteristics (Table 4).

Discussion

Responses to simulated environmental change

The combination of fertilisation and temperature enhancement caused a decline in bryophyte richness and diversity in the meadow. No significant changes

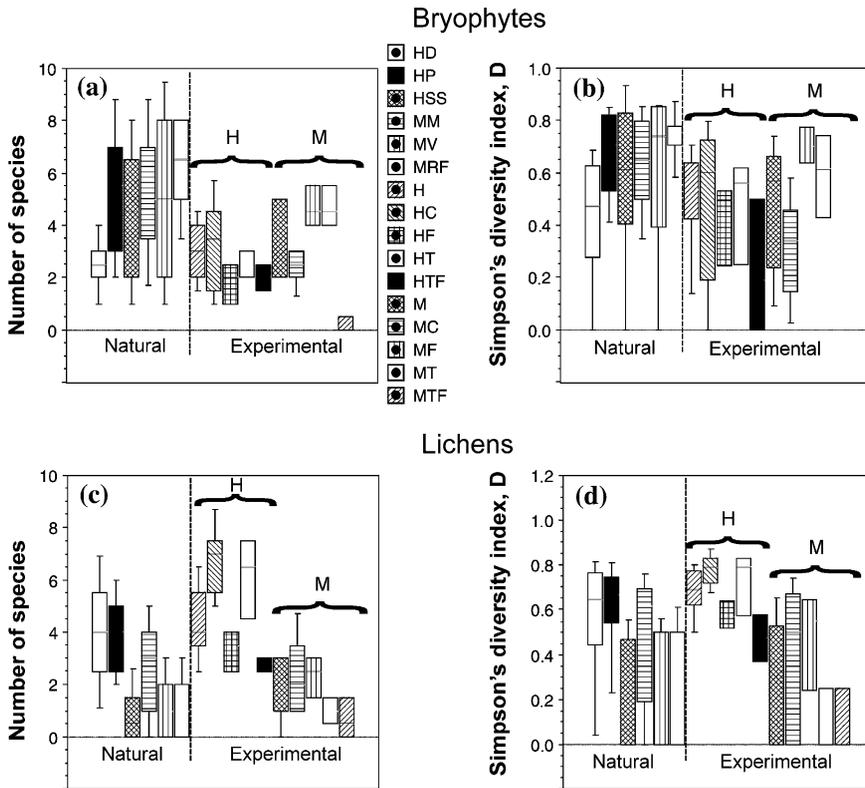


Figure 3. Box plots of natural plant communities 'Natural', and the experiments simulating environmental change 'Experimental' at Latnjajaure. (a) Number of bryophyte species. (b) Simpson's diversity index (D) for bryophytes. (c) Number of lichen species. (d) Simpson's diversity index (D) for lichens. H = Heath, M = meadow. Box plot shows the 10th to the 90th percentile of the data. For abbreviations and sample size see Table 2. Significant differences are shown in Table 5.

were found in the heath community, but there was a clearly negative trend in species richness in all treatments. Lichen richness declined in the combined treatment of fertilisation and temperature enhancement in the heath, compared with the increase in control and temperature enhancement plots. Previous results at the same site by Molau and Alatalo (1998), showed that after three seasons, bryophyte richness did not change with any treatments, whereas lichen richness showed a significant increase in the combined treatment of added fertiliser and temperature enhancement, compared with a decrease in control plots. Studies on vascular plants (Chapin et al. 1995; Graglia et al. 2001) have shown that the responses of species richness to simulated global change may shift over time. Our results on bryophyte and lichen richness support these findings. Depending on the cryptogam-vascular plant dominance relationships, one might therefore expect that total species richness of tundra plant communities may change at different time-scales.

Table 3. Significant differences in number of species (N*) and Simpson's diversity index (D) between non-manipulated (natural) plant communities and the environment change experimental treatments for bryophytes and lichens at Latnjajaure.

	HD		HP		HSS		MM		MV		MRF	
	N	D	N	D	N	D	N	D	N	D	N	D
<i>Bryophytes</i>												
HD												
HP												
HSS												
MM												
MV												
MRF	S											
H												S
HC												
HF												S
HT												
HTF												S
M												
MC												S
MF												S
MT												
MTF			S	S	S	S	S	S	S	S	S	S
<i>Lichens</i>												
HD												
HP												
HSS	S	S	S	S								
MM												
MV	S	S	S	S								
MRF	S	S	S	S								
H						S			S	S	S	S
HC					S	S	S		S	S	S	S
HF												
HT					S	S			S	S	S	S
HTF												
M	S	S	S	S								
MC												
MF												
MT	S		S									
MTF	S		S									

Analysed by ANOVA and Tukey-Kramer *post hoc* test. S = Significance level $p < 0.05$. For abbreviations and sample size see Table 2.

The fact that the previously reported results on species richness change in bryophytes and lichens from experimental *in situ* studies simulating global change are drawn from different time scales (e.g. three seasons; Molau and Alatalo 1998; and five seasons; Press et al. 1998) and experimental designs, limits the possibility to make comparisons. However, it can be noted that the change in bryophyte species richness and/or diversity is most often zero to negative in fertilisation experiments, at least when a few years have passed since

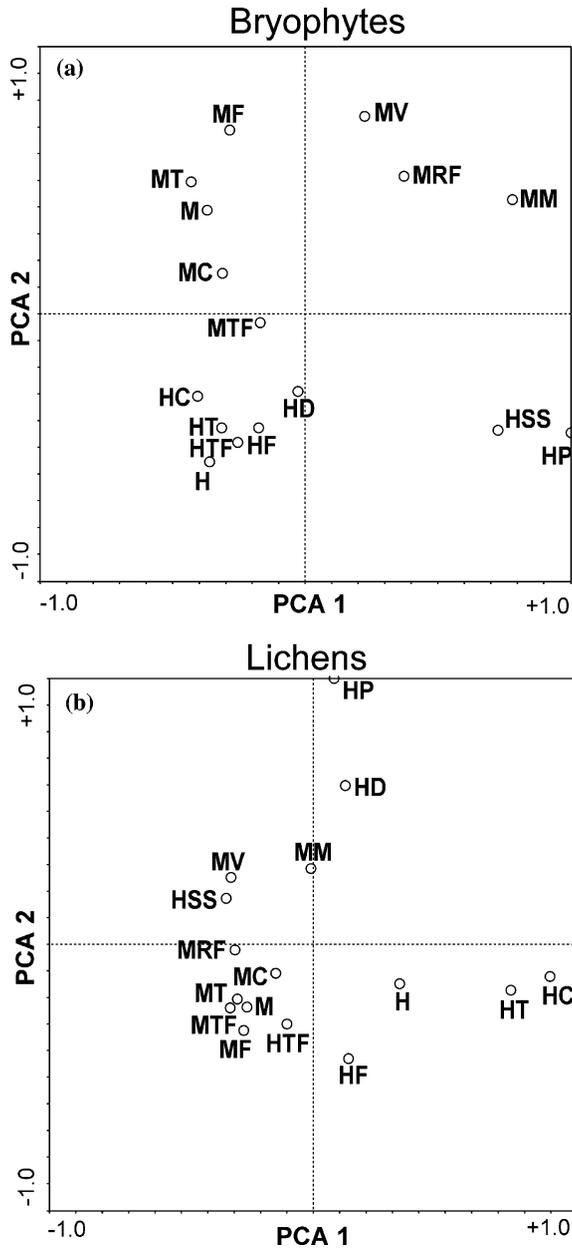


Figure 4. Principal component analysis of the species composition from plots in the experiments simulating environmental change and the (non-manipulated) natural vegetation at Latnjajaure. (a) Bryophytes. Eigenvalues for PCA 1: 0.285, and for PCA 2: 0.196. (b) Lichens. Eigenvalues for PCA 1: 0.323, and for PCA 2: 0.200. For abbreviations see Table 2. $n = 16$ (mean values for the species composition of the plots were used).

Table 4. Abiotic data and soil variables in the permanent grid at Latnjajaure, northern Sweden.

Plant community type	pH	Extr. acidity (μ mol _l /g)	Extr. aluminum (kg/ha)	Extr. calcium (kg/ha)	Extr. magnesium (kg/ha)	Extr. potassium (kg/ha)	Base saturation (%)	Soil organic matter (%)	Soil moisture (%)	Snow depth (cm)	Final snow melt (day number)
HD (dry heath)											
Mean \pm SE	3.9 \pm 0.2	24.9 \pm 11.3	56.3 \pm 23.3	61.1 \pm 102.1	12.9 \pm 10.8	4.2 \pm 1.8	29.0 \pm 23.2	13.2 \pm 10.8	23.8 \pm 8.1	24 \pm 43	152.9 \pm 12.6
HP (patterned heath)											
Mean \pm SE	4.0 \pm 0.2	16.4 \pm 7.5	54.5 \pm 17.7	26.6 \pm 22.8	7.1 \pm 5.0	3.5 \pm 4.4	22.9 \pm 16.3	6.3 \pm 3.9	32.5 \pm 9.3	70 \pm 50	165.4 \pm 11.5
HSS (heath snowbed)											
Mean \pm SE	4.0 \pm 0.2	19.9 \pm 10.0	42.7 \pm 21.0	79.9 \pm 122.5	12.0 \pm 9.6	4.7 \pm 3.0	38.1 \pm 26.1	13.3 \pm 9.6	38.2 \pm 14.6	148 \pm 67	181.7 \pm 15.3
MM (mesic meadow)											
Mean \pm SE	4.5 \pm 0.6	9.2 \pm 10.3	18.1 \pm 21.3	407.2 \pm 357.7	36.0 \pm 21.6	2.2 \pm 1.1	77.4 \pm 26.5	19.6 \pm 13.4	40.3 \pm 10.9	59 \pm 60	160.7 \pm 11.2
MV (moist meadow)											
Mean \pm SE	4.7 \pm 0.5	5.4 \pm 6.2	11.0 \pm 16.0	334.4 \pm 201.8	27.4 \pm 15.0	2.2 \pm 1.2	85.6 \pm 24.5	30.4 \pm 20.0	44.2 \pm 10.2	73 \pm 55	158.3 \pm 10.9
MRF (medium rich fen)											
Mean \pm SE	4.4 \pm 0.3	8.7 \pm 8.0	16.1 \pm 18.3	253.8 \pm 269.9	19.2 \pm 16.6	2.1 \pm 1.8	78.0 \pm 26.0	31.5 \pm 18.9	56.3 \pm 6.4	48 \pm 50	164.0 \pm 12.6

Extractable acidity, aluminum, calcium, magnesium, and potassium as well as pH, base saturation, and soil organic matter were measured in 1999. Soil moisture measured as growing season mean 1999–2002. Snow depth measured during the last week of May 1999–2002 and Julian date of final snowmelt were measure 1999–2002.

the onset of the experiment (Jonasson 1992; Molau and Alatalo 1998; Press et al. 1998). Similarly, Jonasson (1992) and Press et al. (1998) reported a negative impact from added nutrients on lichen species richness (but see Molau and Alatalo 1998). Non-vascular plants may be vulnerable to the direct addition of nutrients on the photosynthetic tissues, but responses are probably too slow to be significant (Van Wijk et al. 2003).

In a fertilisation experiment in the Front Range of Colorado, Seastedt and Vaccaro (2001) hypothesised that the decrease in species richness of vascular plants could be related to increased acidity. This increased acidity, according to Seastedt and Vaccaro (2001), could have been caused by enhanced nitrification due to increased biotic activity. However, our data on bryophyte species composition (Figure 4a), do not support that conclusion, as the fertilised and the combined treatment of added nutrients and increased temperature show contrasting results. Furthermore, it is not likely that increased N addition (5 g N m^{-2}) will have such an impact on the microbial activity that it could change the acidity and thereby be able to alter species richness and diversity.

The reported decrease in bryophytes and lichens is probably rather an indirect effect of the dramatic increase of vascular plant cover/biomass in the fertiliser and combined fertiliser and temperature treatments as shown in other studies (e.g. Molau and Alatalo 1998; Press et al. 1998; Cornelissen et al. 2001; Graglia et al. 2001; Van Wijk et al. 2003; Jägerbrand 2005). The increase in vascular plant abundance is thought to increase competition and shading which may have negative effects on bryophytes and lichens (e.g. Molau and Alatalo 1998; Graglia et al. 2001). The increase of litterfall due to increased vascular plant cover/biomass also causes a long-term decline in mosses and lichens (Chapin et al. 1995).

In our study, the increase in lichen richness in the heath control and temperature enhancement plots indicates a positive response to the increase in temperature and precipitation during this time period. The years 1991–2000 were warm and wet; it was in fact the warmest decade since the 1930s in Sweden (Klingbjer and Moberg 2003; Raisanen and Alexandersson 2003). As lichens are poikilohydric plants, their photosynthesis and growth may increase with water availability (Nash 1996). They may also respond positively to a temperature increase as was shown for example in Alaskan tundra (Lange et al. 1996). It is therefore possible that poikilohydric plants may show a positive response when precipitation (i.e., water availability) and temperature are enhanced, as long as they are not outcompeted by vascular plants (see Sandvik and Heegaard 2003). However, these plants are probably not representative of the typical high altitudinal or high latitudinal bryophytes and lichens, as these may have their growth optima at lower temperatures (cf. Kallio and Heinonen 1973).

Comparisons between experimentally treated communities and natural communities

Natural heath and meadow communities differed largely in species structure, particularly in bryophyte composition. This separation is a reflection of the

abiotic conditions in their distribution. The distribution of meadow communities at the landscape level in the Latnjajaure catchment follows the same pattern, as the meadows have high pH and base saturation (Molau et al. 2003), quite in congruence with our study. R.G. Björk (personal communication) have also shown increased net mineralisation rates with increasing pH, where meadow communities also have higher amounts of inorganic nitrogen concentrations as well as higher net mineralisation rates than the heath communities at Latnjajaure. Although, species richness and diversity generally did not seem to differ between heaths and meadows, the abiotic variables are providing basic conditions for species to flourish in a particular site that is reflected in the species structure.

The observed variation in bryophyte species richness and diversity in natural communities, and the response in experimentally treated communities, showed that the combined treatment of added nutrients and increased temperature had a strong negative effect in the meadow. The species composition patterns revealed largest differences between the natural plant communities and all the experimental plots. This indicates that the underlying natural species distribution patterns among the treatment plots and natural communities differed. The reason might be that the natural communities were sampled in a random manner over a larger area than that of the experimental plots, incorporating a larger underlying habitat heterogeneity.

For lichens, the decline in species richness to the combined treatment of fertilisation and temperature enhancement was found to be within the limits of the variation found in the natural communities, also supported by the results from the species composition analysis. In fact, many of the natural plant communities had very low lichen richness and diversity. In general, it is likely that in this study the response time for bryophytes and lichens are rather short in terms of arrival and establishment of new species to fundamentally change the plant community composition. Results from the landscape-level studies in the Latnjajaure valley reveal a rather slow immigration of vascular plant species from the lower alpine and subalpine zones: despite a significant warming trend only five species have been recorded as new since 1990 (U. Molau, personal communication).

To conclude, even though the manipulation (the combined treatment of added nutrients and temperature) had a negative effect on the richness and diversity of bryophytes in one plant community, the species structure stayed within the naturally occurring variation. More importantly, the combination of added nutrients and enhanced temperature resulted in a species impoverishment, for bryophytes in the bryophyte-dominated community, and for lichens in the lichen-dominated communities.

Future projections

Although our results from the experiments on bryophyte and lichen diversity did show significant changes in the simulation of Global Change, our results

may not directly be interpreted as a projection of climate change-induced vegetational alteration in a long-term scenario. Plant community responses to Global Change are complex and the outcome depends on many factors such as natural underlying climatic conditions, initial species composition and their responsiveness (Jónsdóttir et al. 2005). Still, small scaled experiments are necessary tools as their results indicate the possible future climate-changed induced vegetational changes.

In mountain regions of Europe, higher temperatures and longer growing seasons have made it possible for new species to migrate upwards and now compete with the endemic mountain species (Grabherr et al. 1994; Gottfried et al. 1999), resulting in devastating effects on the endemic flora (i.e. 'biodiversity disasters', Grabherr et al. 1995). Ongoing warming in the Alps has enabled spruce and pine species to increase in the sub-alpine region (Pauli et al. 2001) and sub-alpine shrubs to establish themselves on summits (Theurillat and Guisan 2001). In Sweden, the warming in the 20th century has caused the treeline advance, so that trees and shrub species have migrated upwards 120–375 m in elevation and are now colonizing moderate snow-bed communities (Kullman 2001, 2002). The anticipated and observed altitudinal/northward movement of vegetation zones will cause the current ecosystems to change, and if movements of vegetation zones will coincide with warming and increased nutrient availability for plants (see e.g. Jonasson et al. 2000), and increased cover of vascular plants (i.e. 'filling effects', Grabherr et al. 1995), contemporary areas of typical high altitude alpine ecosystems with large fractions of bryophytes and lichens will certainly be invaded, accompanied by a dramatic decrease in species richness of their original bryophyte and lichen flora. Today's bryophyte and lichen flora consists mainly of very long-lived slow-growing species, adapted to the extreme conditions of their habitats, and it therefore seems unlikely that these may respond in similar manner and move northwards. Even if they could, the areas available for new establishment are very limited as the effects of Global Change are currently affecting the temperatures (e.g. Overpeck et al. 1997; Serreze et al. 2000), vegetation (Chapin et al. 1995; Sturm et al. 2001), as well as the plant growth in the Arctic (Myneni et al. 1997). Hence, it is possible that the cryptogamic flora of current times will be replaced by more southern or low altitude species (boreal or thermophilic), leading indirectly to a global diversity impoverishment. It will be difficult to protect threatened species for two reasons. Firstly, it would hardly be logistically possible to conserve individual species as cold region bryophytes and lichens are hard to keep in *ex situ* cultivation. Secondly, prospects of *in situ* conservation are poor, as the entire tundra is synchronously affected by the strongest impact of climate change on the planet (ACIA 2004). Consequently, international discussions are urgently needed in order to implement the best conservation practice possible at this stage.

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Appendix

Appendix A. Species list of all bryophytes and lichens encountered in the plots at Latnjajaure, northern Sweden.

Bryophytes		Lichens
<i>Anastrophyllum minutum</i>	<i>Lophozia sudetica</i>	<i>Alectoria nigricans</i>
<i>Andreaea obovata</i>	<i>Lophozia ventricosa</i>	<i>Alectoria ochroleuca</i>
<i>Anthelia juratzkana</i>	<i>Marchantia alpestris</i>	<i>Cetraria cucullata</i>
<i>Aulacomnium palustre</i>	<i>Meesia uliginosa</i>	<i>Cetraria delisei</i>
<i>Aulacomnium turgidum</i>	<i>Nardia geoscyphus</i>	<i>Cetraria nivalis</i>
<i>Barbilophozia binsteadii</i>	<i>Oncophorus wahlenbergii</i>	<i>Cladina arbuscula</i>
<i>Barbilophozia floerkei</i>	<i>Paludella squarrosa</i>	<i>Cladina rangifera</i>
<i>Barbilophozia kunzeana</i>	<i>Philonotis fontana</i>	<i>Cladonia ecmocyna</i>
<i>Barbilophozia lycopodioides</i>	<i>Plagiochila porelloides</i>	<i>Cladonia furcata</i>
<i>Barbilophozia</i> sp.	<i>Plagiothecium curvifolium</i>	<i>Cladonia gracilis</i>
<i>Blepharostoma trichophyllum</i>	<i>Pleurocladula albescens</i>	<i>Cladonia macrophylla</i>
<i>Brachythecium glaciale</i>	<i>Pleurozium schreberi</i>	<i>Cladonia macrophyllodes</i>
<i>Bryum pseudotriquetrum</i>	<i>Pogonatum</i> sp.	<i>Cladonia pyxidata</i>
<i>Bryum</i> sp.	<i>Pogonatum urnigerum</i>	<i>Cladonia squamosa</i>
<i>Campyllum stellatum</i>	<i>Pholia cruda</i>	<i>Cladonia</i> sp.
<i>Cephalozia ambigua</i>	<i>Pohlia</i> sp.	<i>Cladonia uncialis</i>
<i>Cephalozia bicuspidata</i>	<i>Pohlia wahlenbergii</i>	<i>Coelocaulon aculeatum</i>
<i>Cephalozia</i> sp.	<i>Polytrichastrum alpinum</i>	<i>Coelocaulon muricatum</i>
<i>Cephaloziella</i> sp.	<i>Polytrichastrum sexangulare</i>	<i>Gyalecta foveolaris</i>
<i>Conostomum tetragonum</i>	<i>Polytrichum hyperboreum</i>	<i>Nephroma articum</i>
<i>Cyrtomnium hymenophylloides</i>	<i>Polytrichum piliferum</i>	<i>Ochrolechia frigida</i>
<i>Cyrtomnium hymenophyllum</i>	<i>Polytrichum juniperinum</i>	<i>Parmelia glabratula</i>
<i>Dicranella</i> sp.	<i>Polytrichum strictum</i>	<i>Peltigera aphthosa</i>
<i>Dicranoweisia crispula</i>	<i>Preissia quadrata</i>	<i>Peltigera scabrosa</i>
<i>Dicranum brevifolium</i>	<i>Pseudobryum cinclidioides</i>	<i>Solorina crocea</i>
<i>Dicranum elongatum</i>	<i>Ptilidium ciliare</i>	<i>Sphaerophorus globosus</i>
<i>Dicranum fuscescens</i>	<i>Racomitrium fasciculare</i>	<i>Stereocaulon alpinum</i>
<i>Dicranum groenlandicum</i>	<i>Racomitrium lanuginosum</i>	<i>Thamnomlia vermicularis</i>
<i>Dicranum laevidens</i>	<i>Rhizomnium pseudopunctatum</i>	<i>Umbilicaria nylanderiana</i>
<i>Dicranum scoparium</i>	<i>Rhytidium rugosum</i>	<i>Umbilicaria proboscidea</i>
<i>Dicranum</i> sp.	<i>Sanionia uncinata</i>	
<i>Diplophyllum taxifolium</i>	<i>Scapania</i> sp.	

Appendix A. (Continued)

Bryophytes		Lichens	
<i>Ditrichum flexicaule</i>	<i>Scorpidium revolvens</i>		
<i>Gymnomitrium corallioides</i>	<i>Sphagnum balticum</i>		
<i>Gymnomitrium concinatum</i>	<i>Sphagnum capillifolium</i>		
<i>Gymnomitrium</i> sp.	<i>Sphagnum fimbriatum</i>		
<i>Hylocomium splendens</i>	<i>Sphagnum</i> sp.		
<i>Hylocomiastrum pyrenacium</i>	<i>Sphagnum warnstorffii</i>		
<i>Jungermannia exsertifolia</i>	<i>Straminergon stramineum</i>		
<i>Jungermannia</i> sp.	<i>Tetralophozia setiformis</i>		
<i>Kiaeria falcata</i>	<i>Tamentypnum nitens</i>		
<i>Kiaeria starkei</i>	<i>Tortella tortuosa</i>		
<i>Leiocolea heterocolpos</i>	<i>Tritomaria polita</i>		
<i>Lescuraea incurvata</i>	<i>Tritomaria quinquedentata</i>		
<i>Lophozia grandiretis</i>	<i>Warnstorffia sarmentosa</i>		
<i>Lophozia</i> sp.			

Appendix B. Mean values \pm 1 S.E. of Simpson's diversity index = D, Brillouin's diversity index = HB, and Brillouin's evenness index = EB of bryophytes and lichens in all plant communities at Latnjajaure, northern Sweden. For abbreviations see Table 2. n = number of plots.

	n	Bryophytes						Lichens					
		D	± 1 S.E.	HB	± 1 S.E.	EB	± 1 S.E.	D	± 1 S.E.	HB	± 1 S.E.	EB	± 1 S.E.
HD	16	0.43	0.07	0.21	0.04	0.64	0.09	0.57	0.07	0.32	0.04	0.71	0.08
HP	16	0.65	0.06	0.41	0.05	0.69	0.06	0.60	0.06	0.34	0.04	0.75	0.06
HSS	12	0.57	0.09	0.37	0.07	0.66	0.09	0.18	0.08	0.06	0.04	0.24	0.12
MM	12	0.62	0.07	0.41	0.06	0.72	0.08	0.47	0.09	0.24	0.05	0.61	0.11
MRF	10	0.74	0.03	0.51	0.04	0.77	0.03	0.17	0.09	0.07	0.04	0.29	0.15
MV	10	0.57	0.11	0.40	0.09	0.64	0.11	0.16	0.08	0.07	0.04	0.28	0.14
H	20	0.49	0.05	0.26	0.03	0.67	0.06	0.68	0.02	0.38	0.03	0.82	0.02
HC	8	0.48	0.11	0.27	0.07	0.59	0.13	0.78	0.03	0.54	0.02	0.82	0.03
HF	4	0.39	0.13	0.16	0.06	0.64	0.22	0.58	0.05	0.30	0.05	0.71	0.07
HT	4	0.43	0.15	0.23	0.08	0.61	0.20	0.70	0.11	0.48	0.10	0.76	0.07
HTF	4	0.25	0.15	0.11	0.07	0.40	0.23	0.48	0.08	0.23	0.03	0.75	0.09
M	20	0.46	0.06	0.30	0.04	0.60	0.06	0.20	0.15	0.08	0.03	0.29	0.09
MC	8	0.31	0.07	0.18	0.04	0.51	0.10	0.39	0.12	0.18	0.06	0.57	0.17
MF	4	0.71	0.04	0.42	0.03	0.81	0.05	0.44	0.12	0.18	0.06	0.65	0.22
MT	4	0.59	0.11	0.39	0.07	0.69	0.14	0.13	0.06	0.04	0.04	0.25	0.25
MTF	4	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.13	0.04	0.04	0.25	0.25

References

ACIA 2004. Impacts of a Warming Arctic: Arctic Climate Impact Assessment. Cambridge University Press. See also <http://www.acia.uaf.edu>.

- Arft A.M., Walker M.D., Gurevitch J., Alatalo J.M., Bret-Harte M.S., Dale M.R.T., Diemer M.C., Gugerli F., Henry G.H.R., Jones M.H., Hollister R.D., Jónsdóttir I.S., Laine K., Lévesque E., Marion G.M., Molau U., Mølgaard P., Nordenhäll U., Raszhivin V., Robinson C.H., Starr G., Stenström A., Stenström M., Totland Ø., Turner P.L., Walker L.J., Webber P.J., Welker J.M. and Wookey P.A. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecol. Monogr.* 64: 491–511.
- Balsberg A.-M. 1975. Handledning i kemiska metoder vid växtekologiska arbeten. Meddelanden från Avdelningen för Ekologisk Botanik Årg. 3, Nr 2. Lunds Universitet, Lund. (In Swedish).
- Bernstein B.B. and Zalinski J. 1983. An optimum sampling design and power tests for environmental biologists. *J. Environ. Manage.* 16: 35–43.
- Beylich A.A., Kolstrup K., Thyrsted T., Linde N., Pedersen L.B. and Dysenius L. 2004. Chemical denudation in arctic-alpine Latnjavagge in relation to regolith as assessed by radio magnetotelluric-geophysical profiles. *Geomorphology* 57: 303–319.
- Bonan G.B. and Van Cleve K. 1992. Soil-temperature, nitrogen mineralisation, and carbon source sink relationships in boreal forests. *Can. J. For. Res.* 22: 629–639.
- Brillouin L. 1962. *Science and Information Theory*. Academic Press, New York, pp. 351
- Chapin F.S. III and Körner C. 1995. Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Springer-Verlag, Berlin.
- Chapin F.S. III, Shaver G.R., Giblin A.E., Nadelhoffer K.J. and Laundre J.A. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76: 694–711.
- Cornelissen J.H.C., Callaghan T.V., Alatalo J.M., Michelsen A., Graglia E., Hartley A.E., Hik D.S., Hobbie S.E., Press M.C., Robinson C.H., Henry G.H.R., Shaver G.R., Phoenix G.K., Gwynn-Jones D., Jonasson S., Chapin F.S. III, Molau U., Neill C., Lee J.A., Melillo J.M., Sveinbjörnsson B. and Aerts R. 2001. Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *J. Ecol.* 89: 984–994.
- Crittenden P.D. 1983. The role of lichens in the nitrogen economy of subarctic woodlands: nitrogen loss from the nitrogen-fixing lichen *Stereocaulon paschale* during rainfall. In: Lee J.A., McNeill S. and Rorison I.H. (eds), *Nitrogen as an Ecological Factor*. Oxford, Blackwell, pp. 43–68.
- Dyrugerov M. 2003. Mountain and subpolar glaciers show an increase in sensitivity to climate warming and intensification of the water cycle. *J. Hydrol.* 282: 164–176.
- EEA 2004. *Impacts of Europe's changing climate, an indicator-based assessment*. European Environmental Agency EEA Report 2, Luxembourg: Office for Official Publications of the European Communities, Copenhagen.
- Gottfried M., Pauli H., Reiter K. and Grabherr G. 1999. A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. *Divers. Distrib.* 5: 241–251.
- Grabherr G., Gottfried M. and Pauli H. 1994. Climate effects on mountain plants. *Nature* 369: 448.
- Grabherr G., Gottfried M., Gruber A. and Pauli H. 1995. Patterns and current changes in alpine plant diversity. In: Chapin F.S. III and Körner C. (eds), *Arctic and Alpine Biodiversity: Patterns, Causes, and Ecosystem Consequences*. Springer-Verlag, Berlin, pp. 167–181.
- Graglia E., Jonasson S., Michelsen A., Schmidt I.K., Havström M. and Gustavsson L. 2001. Effects of environmental perturbations on abundance of subarctic plants after three, seven and ten years of treatments. *Ecography* 24: 5–12.
- Johannessen O.M., Bengtsson L.B., Miles M.W., Kuzmina S.I., Semenov V.A., Alekseev G.V., Nagurnyi A.P., Zakharov V.F., Bobylev L.P., Pettersson L.H., Hasselmann K. and Cattle H.P. 2002. Arctic climate change: observed and modelled temperature and sea-ice variability. *Tellus* 56A: 328–341.
- Jonasson S. 1992. Growth responses to fertilisation and species removal in tundra related to community structure and clonality. *Oikos* 63: 420–429.
- Jonasson S., Havström M., Jensen M. and Callaghan T.V. 1993. *In situ* mineralization of nitrogen and phosphorus of Arctic soils after perturbations simulating climate change. *Oecologia* 95: 179–186.

- Jonasson S., Callaghan T.V., Shaver G.R. and Nielsen L.A. 2000. Arctic terrestrial ecosystems and ecosystem function. In: Nuttall M. and Callaghan T.V. (eds), *The Arctic: Environment, People, Policy*. Harwood Academic Publishers, Reading, pp. 275–313.
- Jónsdóttir I.S., Magnússon B., Gudmundsson J., Elmarsdóttir Á. and Hjartarson H. 2005. Variable sensitivity of plant communities in Iceland to experimental warming. *Global Change Biol.* 11: 553–563.
- Jägerbrand A.K., Molau U. and Alatalo J.M. 2003. Responses of bryophytes to simulated environmental change at Latnjajaure, northern Sweden. *J. Bryol.* 25: 163–168.
- Jägerbrand A.K. 2005. Subarctic bryophyte ecology: phenotypic variation and responses to simulated environmental change. Ph.D. Thesis, Göteborg University, Sweden.
- Kallio P. and Heinonen S. 1973. Ecology of *Rhacomitrium lanuginosum* (Hedw.) Brid. *Rep. Kevo Subarctic Res. Stat.* 10: 43–54.
- Kappelle M., van Vuuren M.M.I. and Baas P. 1999. Effects of climate change on biodiversity: a review and identification of key research issues. *Biodivers. Conserv.* 8: 1383–1397.
- Keyser A.R., Kimball J.S., Nemani R.R. and Running S.W. 2000. Simulating the effects of climate change on the carbon balance of North American high-latitude forests. *Global Change Biol.* 6(suppl 1): 185–195.
- Kielland K. 1997. Role of free amino acids in the nitrogen economy of arctic cryptogams. *Écoscience* 4: 75–79.
- Klingbjer P. and Moberg A. 2003. A composite monthly temperature record from Tornedalen in northern Sweden, 1808–2002. *Int. J. Climatol.* 23: 1465–1494.
- Kullman L. 2001. 20th century climate warming and tree-limit rise in the Southern Scandes of Sweden. *Ambio* 30: 72–80.
- Kullman L. 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J. Ecol.* 90: 68–77.
- Lange O.L., Hahn S.C., Mueller G., Meyer A. and Tenhunen J.D. 1996. Upland tundra in the foothills of the Brooks Range, Alaska: influence of light, water content and temperature on CO₂ exchange of characteristic lichen species. *Flora* 191: 67–83.
- Lange O.L., Hahn S.C., Meyer A. and Tenhunen J.D. 1998. Upland tundra in the foothills of the Brooks range, Alaska, U.S.A. lichen long-term photosynthetic CO₂ uptake and net carbon gain. *Arctic Alpine Res.* 30: 252–261.
- Longton R.E. 1982. Bryophyte vegetation in polar regions. In: Smith A.J.E. (ed.), *Bryophyte Ecology*. Chapman and Hall, London, pp. 123–165.
- Longton R.E. 1984. The role of bryophytes in terrestrial ecosystems. *J. Hattori Bot. Lab.* 55: 147–163.
- Longton R.E. 1997. The role of bryophytes and lichens in polar ecosystems. In: Woodin S.J. and Marquiss M. (eds), *Ecology of Arctic Environments*. Oxford, Blackwell Science, pp. 69–96.
- Matveyeva N. and Chernov Y. 2000. Biodiversity of terrestrial ecosystems. In: Nuttall M. and Callaghan T.V. (eds), *The Arctic: Environment, People, Policy*. Harwood Academic Publishers, Reading, pp. 233–273.
- Maxwell B. 1992. Arctic climate: potential for change under global warming. In: Chapin F.S.III, Jefferies R.L., Reynolds J.F., Shaver G.R. and Svoboda J. (eds), *Arctic Ecosystems in a Changing Climate. An Ecophysiological Perspective*. Academic Press, San Diego, pp. 11–34.
- Marion G.M., Henry G.H.R., Freckman D.W., Johnstone J., Jones G., Jones M.H., Lévesque E., Molau U., Mølgaard P., Parsons A.N., Svoboda J. and Virginia R.A. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biol.* 3(suppl 1): 20–32.
- Mitchell J.F.B., Manabe S., Meleshko V. and Tokioka T. 1990. Equilibrium climatic change and its implications for the future. In: Houghton J.T., Jenkins G.J. and Ephraim J.J. (eds), *Climatic Change. The IPCC scientific assessment*. Cambridge University Press, Cambridge, pp. 131–172.
- Moberg R. and Holmåsén I. 2000. *Lavar: En fälthandbok*. Interpublishing, Stockholm. (In Swedish).
- Molau U. 2001. Tundra plant responses to experimental and natural temperature changes. *Mem. Natl Inst. Polar Res. Spec. Issue* 54: 445–466.

- Molau U. and Alatalo J.M. 1998. Responses of subarctic-alpine plant communities to simulated environmental change: biodiversity of bryophytes, lichens, and vascular plants. *Ambio* 27: 322–329.
- Molau U., Kling J., Lindblad K., Björk R., Dänhardt J. and Ließ A. 2003. A GIS assessment of alpine biodiversity at a range of scales. In: Nagy L., Grabherr G., Körner C. and Thompson D.B.A. (eds), *Alpine Biodiversity in Europe*. Ecological Studies 167, Springer-Verlag, Berlin, pp. 221–229.
- Moullot D. and Leprêtre A. 1999. A comparison of species diversity estimators. *Res. Popul. Ecol.* 41: 203–215.
- Myneni R.B., Keeling C.D., Tucker C.J., Asrar G. and Nemani R.R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386: 698–702.
- Nadelhoffer K.J., Giblin A.E., Shaver G.R. and Laundre J.A. 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. *Ecology* 72: 242–253.
- Nadelhoffer K.J., Giblin A.E., Shaver G.R. and Linkins A.E. 1992. Microbial processes and plant nutrient availability in arctic soils. In: Chapin F.S. III, Jeffries R.L., Reynolds J.F., Shaver G.R. and Svoboda J. (eds), *Arctic Ecosystems in a Changing Climate*. Academic Press, San Diego, pp. 281–300.
- Nash T.H. III 1996. *Lichen Biology*. Cambridge University Press, Cambridge.
- Nilsson Ö. 1991. *Nordisk fjällflora*. Bonniers fakta bokförlag, Stockholm. (In Swedish).
- Nordic Council of Ministers 1995. *Vegetation types of the Nordic Countries*. TemaNord 1998: 510.
- Overpeck J., Hughen K. and Hardy D. 1997. Arctic environmental changes of the last four centuries. *Science* 278: 1251–1256.
- Økland R.H., Rydgren K. and Økland T. 2003. Plant species composition of boreal spruce swamp forests: closed doors and windows of opportunity. *Ecology* 84: 1909–1919.
- Pauli H., Gottfried M. and Grabherr G. 2001. High summits of the Alps in a changing climate. The oldest observation series on a high mountain plant diversity in Europe. In: Walther G.-R., Burga C.A. and Edwards P.J. (eds), *Fingerprints of Climate Change-adapted Behaviour and Shifting Species Ranges*. Kluwer Academic Publishers, New York, pp. 139–149.
- Pielou E.C. 1966. The measurement of diversity in different types of biological collections. *J. Theoret. Biol.* 13: 131–144.
- Press M.C., Potter J.A., Burke M.J.W., Callaghan T.V. and Lee J.A. 1998. Responses of a subarctic dwarf shrub heath community to simulated environmental change. *J. Ecol.* 86: 315–327.
- Raisanen J. and Alexandersson H. 2003. A probabilistic view on recent and near future climate change in Sweden. *Tellus Ser. A: Dyn. Meteorol. Oceanogr.* 55: 113–125.
- Sandvik S.M. and Heegaard E. 2003. Effects of simulated environmental changes on growth and growth form in a late snowbed population of *Pohlia wahlenbergii* (Web. et Mohr.) Andr. *Arctic Antarctic Alpine Res.* 35: 341–348.
- Seastedt T.R. and Vaccaro L. 2001. Plant species richness, productivity, and nitrogen and phosphorus limitations across a snowpack gradient in alpine tundra, Colorado, U.S.A. *Arctic, Antarctic Alpine Res.* 33: 100–106.
- Serreze M.C., Walsh J.E., Chapin F.S. III, Osterkamp T., Dyrgerov M., Romanovsky V., Oechel W.C., Morison J., Zhang T. and Barry G. 2000. Observational evidence of recent change in the northern high-latitude environment. *Clim. Change* 46: 159–207.
- Simpson E.H. 1949. Measurement of diversity. *Nature* 163: 688.
- Stewart-Oaten A., Murdoch W.W. and Parker K.R. 1986. Environmental impact assessment: “pseudoreplication” in time? *Ecology* 67: 929–940.
- Sturm M., Racine C. and Tape K. 2001. Increasing shrub abundance in the Arctic. *Nature* 411: 546–547.
- Söderström L. and Hedenäs L. 1998. Checklista över Sveriges mossor- 1998. *Myrinia* 8: 58–90.
- Ter Braak C.J.F. and Šmilauer P. 2002. *CANOCO Reference Manual and Canodraw for Windows User’s Guide: Software for Canonical Community Ordination (Version 4.5)*. Microcomputer Power, Ithaca, NY.

- Theurillat J.P. and Guisan A. 2001. Potential impact of climate change on vegetation of European Alps: A review. *Clim. Change* 50: 77–109.
- Underwood A.J. 1991. Beyond BACI: experimental designs for detecting human environmental impacts on temporal variations in natural populations. *Austral. J. Mar. Freshwater Res.* 42: 569–587.
- Underwood A.J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. *J. Exp. Mar. Biol. Ecol.* 161: 145–178.
- Van Wijk M.T., Clemmensen K.E., Shaver G.R., Williams M., Callaghan T.V., Chapin F.S. III, Cornelissen J.H.C., Gough L., Hobbie S.E., Jonasson S., Lee J.A., Michelsen A., Press M.C., Richardson S.J. and Rueth H. 2003. Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biol.* 10: 105–123.
- Vitt D.H. and Pakarinen P. 1977. The bryophyte vegetation production and organic components of Truelove Lowland. In: Bliss L.C. (ed.), *Truelove Lowland, Canada: A high arctic ecosystem*. University of Alberta Press, Edmonton, pp. 225–244.
- Walker M. 1996. Community baseline measurements for ITEX studies. In: ITEX manual Ed.2. Molau U. and Mølgaard P. (eds), *International Tundra Experiment*. Danish Polar Centre, Copenhagen, pp. 39–41.
- Wielgolaski F.E., Bliss L.C., Svoboda J. and Doyle G. 1981. Primary production of tundra. In: Bliss L.C., Heal O.W. and Moore J.J. (eds), *Tundra Ecosystems: A Comparative Analysis*. Cambridge university press, Cambridge, pp. 187–226.
- Zar J.H. 1996. *Biostatistical Analysis*. Prentice-Hall, Upper Saddle River, NJ, USA.