

1 Seven years of experimental warming and nutrient addition causes decline of bryophytes and  
2 lichens in alpine meadow and heath communities

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15

16 **Abstract**

17 Global change is predicted to have large and rapid impact on polar and alpine regions.  
18 Bryophytes and lichens increase their importance in terms of biomass, carbon/nutrient  
19 cycling, cover and ecosystem functioning at higher latitudes/altitudes. Here we report from a  
20 seven year factorial experiment with nutrient addition and warming on the abundance of  
21 bryophytes and lichens in an alpine meadow and heath community. Treatments had  
22 significant negative effect on relative change of total abundance bryophytes and lichens, the  
23 largest decline to the nutrient addition and the combined nutrient addition and warming  
24 treatments, bryophytes decreasing most in the meadow, lichens most in the heath. Nutrient  
25 addition, and the combined nutrient addition and warming brought rapid decrease in both  
26 bryophytes and lichens, while warming had a delayed negative impact. Of sixteen species that  
27 were included the statistical analyses, we found significant negative effects on seven species.  
28 We show that impact of simulated global change on bryophytes and lichens differ in in time  
29 and magnitude among treatments and plant communities. Our results underscore the  
30 importance of longer-term studies to improve the quality of climate change models, as short-  
31 term studies are poor predictors of longer-term responses of bryophytes and lichens, similar to  
32 what have been shown for vascular plants. Species-specific responses may differ in time, and  
33 this will likely cause changes in the dominance structures of bryophytes and lichens over  
34 time.

35

## 36 **Introduction**

37 Global change is affecting large areas of the globe through increased climate variability as  
38 well as increased nutrient deposits. Both factors are mainly driven by deposits and emissions  
39 from anthropogenic activities (Grandy *et al.* 2008; IPCC 2013; Clark *et al.* 2013). For  
40 example, in China that has among the richest biodiversity in the world (Zhang *et al.* 2014),  
41 climate change have been predicted to have great impact on wide variety of ecosystems in  
42 priority areas of biodiversity conservation (Wu *et al.* 2014), and extinction risk of protected  
43 plants is predicted to increase (Zhang *et al.* 2014). Climate change is also thought to have the  
44 potential to rapidly affect polar and alpine regions. As the same regions are often nutrient  
45 limited (Chapin *et al.* 1995; Mack *et al.* 2004), a combination of climate change and  
46 increasing nutrient levels can be expected to have large impact on their ecosystems. The  
47 number of studies on climate change has increased substantially and the pace seem to be  
48 increasing (Andrew *et al.* 2013; Shen & Ma 2014). Some of the changes that have been  
49 detected in a number of ecosystems around the world have been attributed to global change,  
50 either as response to nutrient deposition or existing climate warming trend. The changes  
51 include changes in species richness, composition of plant communities, poleward or upward  
52 movement of species (Post *et al.* 2009; Maskell *et al.* 2010; Callaghan *et al.* 2011; Stöckli *et*  
53 *al.* 2011; Pauli *et al.* 2012; Clark *et al.* 2013). However, the causes behind shifts in species  
54 distributions can be difficult to pinpoint as a study on northward movement of vascular plants  
55 in Great Britain using data from 1978 to 2011 found (Groom 2013). The results indicated that  
56 the significant northward movement of plants was likely not due to climate warming, instead  
57 the reason was likely due to other changes resulting from anthropogenic activities (Groom  
58 2013). Global change can also have contrasting effects on species richness depending on the  
59 nutrient status of the ecosystem (Chalcraft *et al.* 2008), and it is likely that the combination of  
60 increased nutrient levels and warming can have interactive effects in cold and nutrient limited

61 ecosystems in polar and high alpine regions (Chapin *et al.* 1995; Mack *et al.* 2004). A  
62 worrying example of how increased nutrient level can potentially impact climate change  
63 comes from an experiment with 20 years of nutrient addition in Alaskan tundra where they  
64 showed that increased nutrient availability caused a net ecosystem loss of carbon which could  
65 lead to a positive feed back to climate warming (Mack *et al.* 2004). Other studies have  
66 reported contrasting short and medium term responses, revealing non-linear responses to  
67 treatments over time, indicating that longer-term responses may be difficult to predict  
68 (Alatalo & Little 2014; Alatalo *et al.* 2014b).

69           Bryophytes and lichens tend to make up larger part of the cover and biomass on  
70 higher altitudes and latitudes as the environment becomes harsher, this is partly an effect of  
71 that the vascular plants become smaller in stature (Longton 1984; Jägerbrand *et al.* 2006). At  
72 the same time their relative importance in the high altitude/latitude ecosystems increases due  
73 to their influence on factors such as recruitment of vascular plants (Soudzilovskaia *et al.*  
74 2011), permafrost stability (Harden *et al.* 2006; Romanovsky *et al.* 2010; Turetsky *et al.*  
75 2012), water, carbon and nitrogen cycling (Turetsky 2003; Turetsky *et al.* 2012). Many of the  
76 bryophyte and lichen species found in polar regions exhibits wide distributions, some being  
77 circumpolar, making them important parts of ecosystem functioning even on global scale.  
78 Recent research also show that migratory birds can transfer bryophyte diaspores bilpolarly,  
79 supporting bryophyte long range dispersal (Lewis *et al.* 2014). Bryophytes and lichens also  
80 fill important roles in biological soil crusts in deserts world wide (Zhang 2005; Li *et al.* 2013).  
81 Yet the number of experimental global change studies on bryophytes and lichens is small  
82 compared to the number of studies on vascular plants in these severe environments, at least  
83 when it comes to having a resolution at the species level, or community responses that include  
84 bryophyte and lichen diversity (Potter *et al.* 1995; Alatalo 1998; Molau & Alatalo 1998;  
85 Jägerbrand, Molau & Alatalo 2003; Jägerbrand *et al.* 2006, 2009; Klanderud 2008; Lang *et al.*

86 2009, 2012; Bjerke *et al.* 2011; Olsen & Klanderud 2014; Alatalo, Jägerbrand & Molau  
87 2014a). In most cases when bryophytes are included in experimental global change studies,  
88 they are grouped as “mosses” or “lichens” (Graglia *et al.* 2001; Hill & Henry 2011). This is  
89 likely due to that ecologist commonly have problems to identify bryophytes and lichens to  
90 species level (Turetsky *et al.* 2012). It is unsatisfactory that modeling studies on the impact of  
91 climate change often seem to lack data on bryophytes and lichens as their predictions will be  
92 of less value for high altitude, polar and desert regions due to their increasing importance in  
93 severe environments.

94 Here we report on the impact of a seven-year factorial study with experimental  
95 nutrient addition and warming on total community and individual species abundances of  
96 dominant bryophytes and lichens in two contrasting alpine plant communities in subarctic  
97 Sweden.

## 99 **Material and Methods**

### 100 *Study area*

101 Fieldwork took place at the Latnjajaure Field Station (LFS) in northern Sweden, at 1000 m  
102 elevation in the valley of Latnjavagge (68°21'N, 18°29'E). Continuous climate data were  
103 provided from the early spring of 1992 onwards. Climate is classified as sub-arctic (Polunin  
104 1951) with snow cover for most of the year, cool summers, and relatively mild, snow-rich  
105 winters. Mean annual temperatures ranged from  $-2.0$  to  $-2.7^{\circ}\text{C}$  between 1993 and 1999, with  
106 winter minima of  $-27.3$  to  $-21.7^{\circ}\text{C}$ . Mean annual precipitation during this time period was  
107 808 mm, with individual years ranging from a low 605 mm in 1996 up to 990 mm in 1993.  
108 The warmest temperatures come in July, which had mean temperatures ranging from  $+5.4^{\circ}\text{C}$   
109 in 1992 to  $+9.9^{\circ}\text{C}$  in 1997. Physical conditions in the valley vary from dry to wet and poor

110 and acidic to base-rich, with a variety of plant communities to match (Molau & Alatalo 1998;  
111 Lindblad, Nyberg & Molau 2006; Alatalo *et al.* 2014b).

112

### 113 *Experimental design*

114 In July 1995, 20 plots (1 x 1 m) with homogenous vegetation cover were chosen in both the  
115 meadow and heath plant communities and randomly assigned to treatments in a factorial  
116 design. There were 8 control (CTR) plots and 4 plots for each of the experimental treatments  
117 in each plant community: warming (T for temperature enhancement), nutrient addition (N)  
118 and combined warming and nutrient addition (TN). Warming was induced by Open Top  
119 Chambers (OTCs) that increase temperature by 1.5 to 3°C compared to control plots with  
120 ambient temperature (Marion *et al.* 1997; Molau & Alatalo 1998). Nutrient addition consisted  
121 of 5 g of nitrogen (as NH<sub>4</sub>NO<sub>3</sub>) and 5 g of phosphorus (P<sub>2</sub>O<sub>5</sub>) per m<sup>2</sup>, dissolved in 10 L of  
122 meltwater. In 1995 all plots were analyzed with a point-frame method (Walker 1996) to  
123 determine the species occurrences under natural conditions before implementing the  
124 experimental treatments. The OTCs were then left on plots with warming treatments year-  
125 around, and nutrient addition was applied directly after the initial vegetation analyses in 1995  
126 and a few days after snow melt in the subsequent years (1996-2001). The nutrient treatments  
127 were then terminated after 2001.

128

### 129 *Measurements*

130 The majority of bryophytes and lichens in the plots were identified to the species level (with  
131 help from experienced bryophyte taxonomist Sven Franzén), and cover of each species was  
132 assessed using a 1 x 1 m frame with 100 grid points (Walker 1996) in the middle of the 1995,  
133 1999, and 2001 growing seasons. To ensure accuracy and reproducibility, the same grid frame  
134 was used for each measurement, and fixed points at the corner of each plot allowed the frame

135 to be placed in the same position within the plot at each different measuring point. This  
136 method has been shown to be accurate in detecting changes in tundra vegetation (May &  
137 Hollister 2012).

138

### 139 *Data analysis*

140 From the point-frame data, we summed the number of touches to pins within each plot to  
141 produce plot-level abundance measures for each species. This was then used to calculate  
142 relative changes in abundances. We included only the most dominant species in the analyses,  
143 i.e. excluding those with less than 100 hits from the point framing (Table 1). For responses in  
144 relative changes of total abundances of the most dominant bryophytes and lichens, GLM  
145 (general linear model) was used to analyze significant responses of sites and treatments (both  
146 as fixed factors) and their interactions. Species abundance was highly skewed and therefore  
147 did not meet assumptions of normality, so instead of GLM we used nonparametric tests.  
148 Kruskal-Wallis Test was used for analyzing the effect of all treatments as group on relative  
149 changes of species specific abundances. When significant, Mann-Whitney U Test was used to  
150 analyze the effect between treatments. All analyses were executed in SPSS version 19 (IBM).

151

## 152 **Results**

### 153 **Impact on total abundance of the most dominant bryophytes and lichens**

154 Total abundances of the most dominant bryophytes declined among years in response to the  
155 treatments, with the largest decline found to the nutrient addition and the combined nutrient  
156 addition and warming treatments (Figure 1, Tables 2, 3). The decline in bryophytes was  
157 significantly larger in the rich meadow than in the poor heath community (Figure 1, Tables 2,  
158 3). The treatments had somewhat different responses over time, nutrient addition and the  
159 combined nutrient addition and warming causing a rapid decrease that then did not fall much

160 further between 1999 and 2001. In contrast warming had larger negative impact in the  
161 meadow (but not in the heath) between 1999 and 2001, exhibiting a more delayed response  
162 pattern compared to the nutrient addition (Figure 1). Bryophytes in control plots tended to  
163 increase in both communities, with the increase extending though the whole period (Figure 1).

164 Total abundance of the most dominant lichens declined among years in response  
165 to all treatments in the poor heath, the nutrient addition and combined nutrient addition and  
166 warming having the largest negative impact (Figure 1, Tables 2, 3). This negative impact of  
167 nutrient addition and the combined nutrient addition and warming extended throughout the  
168 whole period. In the heath, treatments had no significant effect in the later period (1999 –  
169 2001), when lichens decreased significantly in all treatments at the heath compared to the  
170 meadow community (Figure 1, Tables 2, 3). The decline of lichens was significantly larger in  
171 the poor heath compared to the rich meadow in both periods; 1995-2001 and 1999-2001  
172 (Figure 1, Tables 2, 3).

#### 174 **Species specific responses of bryophytes and lichens**

175 Out of sixteen most dominant species that had more 100 hits from the point framing and thus  
176 included the statistical analyses, we found significant negative effects of treatments on seven  
177 species; *Aulacomnium turgidum* (Wahlenb.) Schwägr. (acrocarpous bryophyte), *Cetrariella*  
178 *delisei* (Bory ex Schaer.) Kärnfelt & A. Thell (lichen), *Gymnomitrium sp.* (liverwort), *Kiaeria*  
179 *starkei* (F. Weber & D. Mohr) I. Hagen (acrocarpous bryophyte), *Stereocaulon alpinum*  
180 Laurer (lichen), *Hylocomium splendens* (Hedw.) Schimp. (pleurocarpous bryophyte),  
181 *Cladonia arbuscula* (Wallr.) Flot. (lichen). All significant treatment responses were negative  
182 when found, regardless if in the rich meadow or the poor heath community, with nutrient  
183 addition and the combined nutrient addition and warming having the largest negative effect  
184 on relative change of abundance among years (Figures 2, 3, Table 4). In control plots, most



185 species tended to slightly increase in relative abundance between both 1995-2001 and 1999-  
186 2001.

187

## 188 **Discussion**

189 Previous studies have shown highly heterogenic response patterns for experimental nutrient  
190 addition and warming. For example, a long-term study in Alaska and subarctic Sweden,  
191 combined nutrient and warming was shown to have significant negative effect on lichens and  
192 bryophytes, in the same study nutrient addition alone caused significant decrease in lichens  
193 biomass but had no significant effect on bryophytes, while warming caused no significant  
194 responses (Van Wijk *et al.* 2003). Experimental nutrient addition has been shown to have  
195 positive effect on bryophytes (Jonasson 1992; Robinson *et al.* 1998), and lichens in open high  
196 arctic and alpine vegetation (Jonasson 1992), decrease of both bryophyte and lichens to nine  
197 years if nutrient addition in a subarctic birch forest (Richardson *et al.* 2002). Likewise,  
198 warming has been shown to cause arbitrary impact on bryophytes and lichens, with no  
199 responses of bryophytes (Chapin *et al.* 1995; Van Wijk *et al.* 2003; Lang *et al.* 2009;  
200 Jägerbrand *et al.* 2009; Alatalo *et al.* 2014a), negative effect on bryophytes (Press *et al.* 1998;  
201 Lang *et al.* 2012; Sistla *et al.* 2013), no effect on lichens (Jägerbrand *et al.* 2009; Alatalo *et al.*  
202 2014a), negative effect on lichens (Press *et al.* 1998; Lang *et al.* 2012; Sistla *et al.* 2013), and  
203 positive effect on lichens (Chapin *et al.* 1995; Alatalo 1998; Biasi *et al.* 2008; Jägerbrand *et*  
204 *al.* 2009). The contrasting response patterns have been hypothesized to be caused by  
205 competitive interactions between cryptogams and vascular plants, and also to be attributed to  
206 how well the cryptogams are adapted to light competition (Alatalo 1998). Bryophyte species  
207 have been shown to have different responses to shading effects (Jägerbrand & During 2005).  
208 In sites with existing dense canopies the bottom layer cryptogam communities are thought to  
209 be dominated by shade-tolerant species while cryptogams in more open canopies are thought

210 to be dominated by shade-intolerant species, an increase in canopy closure due to warming  
211 and/or increased nutrient levels is hypothesized to affect the shade-intolerant species most  
212 (Alatalo 1998). Therefore, cryptogams in sites with more developed vascular plant canopies  
213 are expected to be more resistant to global change with increased temperature and nutrient  
214 levels. Experimental support for the hypothesis has been found in a cross continental study on  
215 macro-lichens that included more southern parts of arctic where the vegetation canopy was  
216 more dense compared to vegetation with more open canopy in high arctic or arctic alpine sites  
217 (Cornelissen *et al.* 2001), and in a study in alpine subarctic Sweden on the effect of  
218 neighboring vascular plants on bryophytes in contrasting plant communities (Jägerbrand *et al.*  
219 2012). However, our results from the present study show that after seven years both the  
220 nutrient and warming treatments had significant negative effect in both the rich meadow and  
221 the poor heath community, thus not supporting the hypothesis. Bryophytes decreased the most  
222 in the meadow and the lichens decreased most in the heath, which is in accordance with  
223 previous findings (Jägerbrand *et al.* 2006). Nutrient addition and the combined nutrient  
224 addition and warming caused a more rapid response compared to the more delayed response  
225 of warming *per se*. Thus, it might be that long term warming will cause other shifts in the  
226 environment such as an increased accumulated thickness of litter that may have a more  
227 detrimental effect than live canopy. An increased production of litter could lead to that  
228 cryptogams get “covered” while live canopy cover will still leave “space” for the cryptogams.  
229 This could potentially be an artifact of using OTCs that may hinder litter to disperse outside  
230 the OTCs. Optimally, new experiments would include litter removal as one of the factors  
231 together with warming and nutrient addition in factorial set up. That long-term warming can  
232 cause drastic shifts in cryptogam communities is evident after two decades of experimental  
233 warming in Alaska which caused lichens to decrease by 99% and bryophytes by 63% (Sistla  
234 *et al.* 2013). However, the time needed for the negative effects to be expressed may differ

235 among species and plant communities, as is shown in our study. After seven years of warming  
236 seven out of sixteen species included in the statistical analyses in our study were negatively  
237 affected. When we compare this to a previous study in the same sites on the impact of five  
238 years of warming, there were no significant effects from warming on bryophyte and lichens at  
239 the community level, in fact only one lichen species *Cetraria nivalis*, displayed a significant  
240 negative response to warming in the heath (Jägerbrand *et al.* 2009). These results point out the  
241 importance of longer-term studies to improve the quality of climate change models. Our  
242 results indicate that short-term studies are poor predictors of longer-term responses of  
243 bryophytes and lichens, similar as have been shown for vascular plants (Alatalo & Little  
244 2014; Alatalo *et al.* 2014b). The results also show that species specific responses may differ  
245 in time, and that this will likely cause changes in the dominance structures of bryophytes and  
246 lichens over time. The potential role of litter for cryptogam development also need to be  
247 studied in controlled experiments to determine if canopy development or litter accumulation  
248 are the main driving forces behind the decrease of cryptogams found in longer-term global  
249 change experiments.

250

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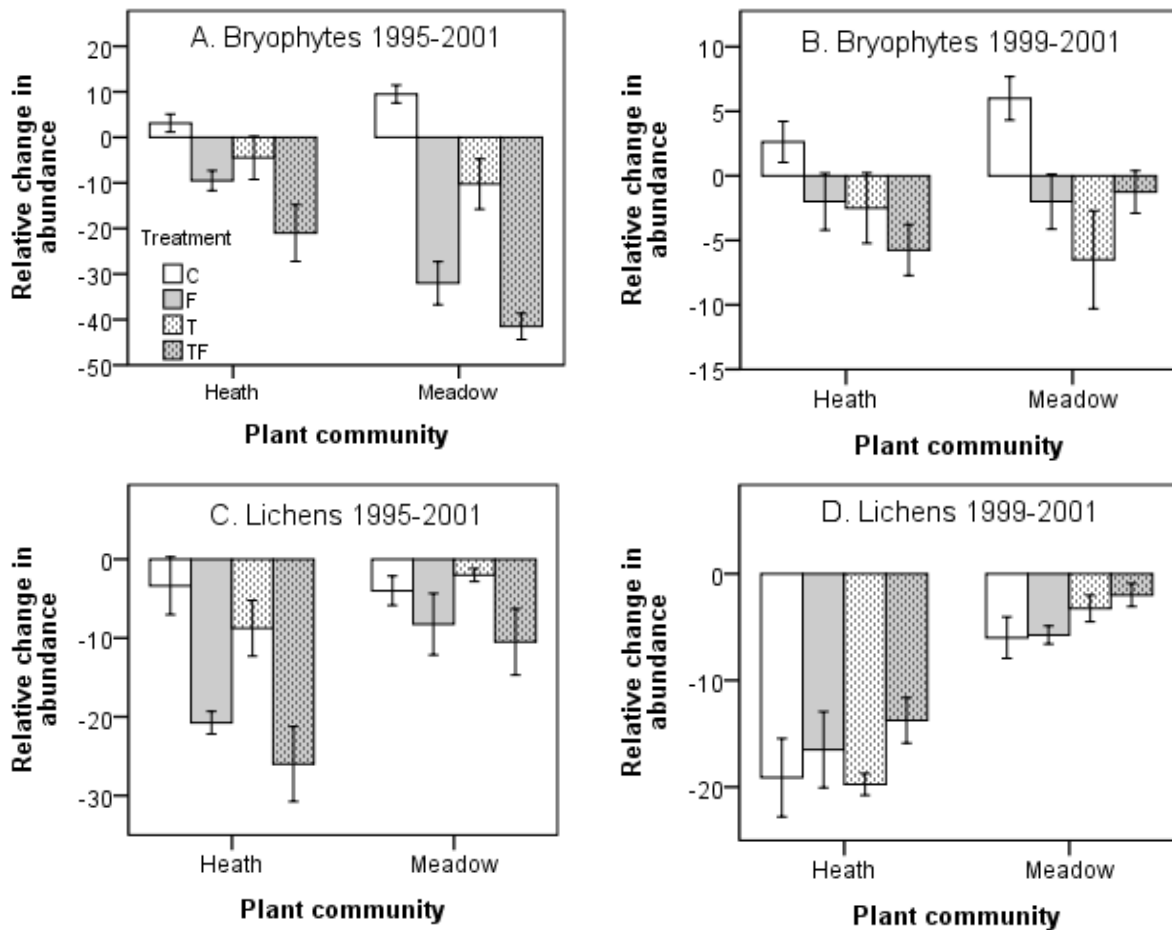


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436 **Figure 1.** Relative changes in total abundances (mean  $\pm$  1 SE) of bryophytes and lichens to  
 437 experimental manipulations in a poor heath and rich meadow, at Latnjajaure, subarctic  
 438 Sweden. A) Change in relative total abundance of bryophytes between 1995-2001, B) change  
 439 in relative total abundance of bryophytes between 1999-2001, C) change in relative total  
 440 abundance of lichens between 1995-2001, D) change in relative total abundance of lichens  
 441 between 1999-2001. Treatments: C = control, T = temperature treatment, F = fertilizer  
 442 treatment, TF = temperature and fertilizer treatments. N = 4 for T, F and TF, N = 8 for C.  
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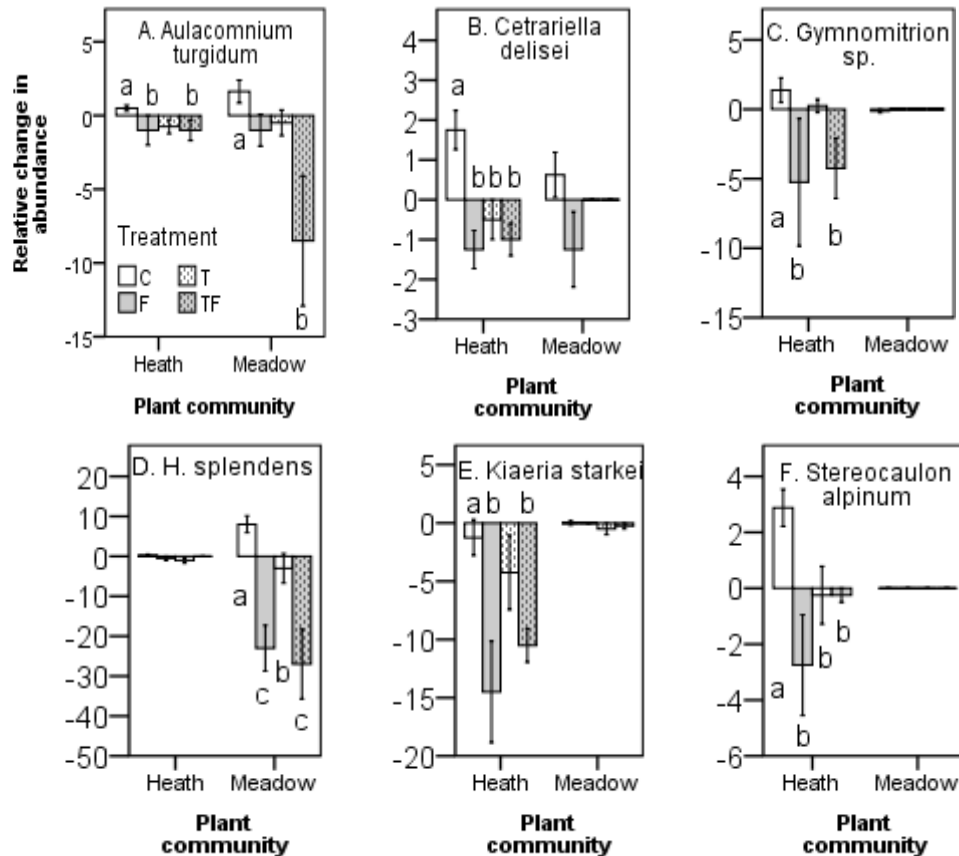


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446 Figure 2. Relative changes in species specific abundances (mean  $\pm$  1 SE) for bryophytes and  
 447 lichens between 1995-2001 to experimental manipulations in a poor heath and rich meadow,  
 448 at Latnjajaure, subarctic Sweden. Treatments: C=control, T=temperature treatment,  
 449 F=fertilizer treatment, TF = temperature and fertilizer treatments. Different letters indicate  
 450 significant differences analyzed by Mann-Whitney U-test. N = 4 for T, F and TF, N = 8 for C.  
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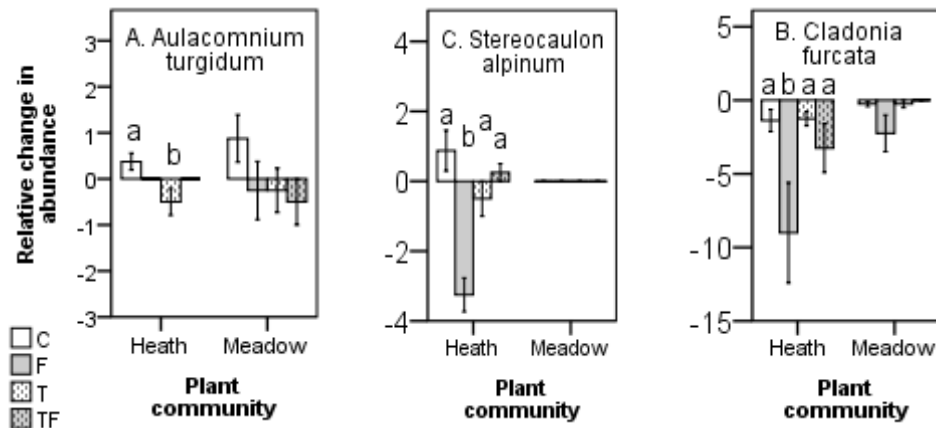
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456 Figure 3. Relative changes in species specific abundances (mean  $\pm$  1 SE) for bryophytes and  
 457 lichens between 1999-2001 to experimental manipulations in a poor heath and rich meadow,  
 458 at Latnjajaure, subarctic Sweden. Treatments: C = control, T = temperature treatment, F =  
 459 fertilizer treatment, TF = temperature and fertilizer treatments. Different letters indicate  
 460 significant differences analyzed by Mann-Whitney U-test. N = 4 for T, F and TF, N = 8 for C.

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465 **Table 1.** The most dominant species of bryophytes and lichens at two the different plant  
 466 communities (heath and meadow) at Latnjajaure, Northern Sweden.

Species	Group
<i>Aulacomnium turgidum</i> (Wahlenb.) Schwägr.	Bryophyte
<i>Cetrariella delisei</i> (Bory ex Schaer.) Kärnfelt & A. Thell	Lichen
<i>Cladonia arbuscula</i> (Wallr.) Flot.	Lichen
<i>Cladonia furcata</i> (Huds.) Schrad.	Lichen
<i>Cladonia uncialis</i> (L.) F. H. Wigg.	Lichen
<i>Dicranum groenlandicum</i> Brid.	Bryophyte
<i>Flavocetraria cucullata</i> (Bellardi) Kärnefelt & A. Thell	Lichen
<i>Flavocetraria nivalis</i> (L.) Kärnefelt & A. Thell	Lichen
<i>Gymnomitrium</i> sp.	Bryophyte
<i>Hylocomium splendens</i> (Hedw.) Schimp.	Bryophyte
<i>Kiaeria starkei</i> (F. Weber & D. Mohr) I. Hagen	Bryophyte
<i>Ochrolechia frigida</i> (Sw.) Lynge	Lichen
<i>Polytrichum juniperinum</i> Hedw.	Bryophyte
<i>Ptilidium ciliare</i> (L.) Hampe	Bryophyte
<i>Sphaerophorus globosus</i> (Huds.) Vain.	Lichen
<i>Stereocaulon alpinum</i> Laurer	Lichen

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469 **Table 2.** Test of model effects of the generalized linear model (GLM) on responses in relative  
 470 abundance of bryophytes and lichens between 1995 - 2001, and between 1999 - 2001, to  
 471 experimental manipulations at two different plant communities at Latnjajaure, Northern  
 472 Sweden. Only the most dominant species were included, see Table 1.

Source	Wald chi- squa re	df	P
<b>Bryophytes 1995-2001</b>			
Intercept	131.7	1	<0.0001
Plant community	21	1	<0.0001
Treatments	181	3	<0.0001
Plant community *	32	3	<0.0001
Treatments			
<b>Bryophytes 1999-2001</b>			
Intercept	3.9	1	0.048
Plant community	0.5	1	0.5
Treatments	31.1	3	<0.0001
Plant community *	5.2	3	0.16
Treatments			
<b>Lichens 1995-2001</b>			
Intercept	88.9	1	<0.0001
Plant community	14.8	1	<0.0001
Treatments	33	3	<0.0001
Plant community *	9.7	3	0.02
Treatments			
<b>Lichens 1999-2001</b>			
Intercept	138.4	1	<0.0001
Plant community	50.7	1	<0.0001
Treatments	3.9	3	0.28
Plant community *	1.2	3	0.75
Treatments			

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**Table 3.** Results of generalized linear model (GLM) explaining the responses in relative abundance of bryophytes and lichens between 1995 - 2001, and between 1999 - 2001, to experimental manipulations at two different plant communities at Latnjajaure, Northern Sweden. Only significant variables are shown. Coefficient (B), SE = standard error and P, significance levels.

Variable	Coefficient	SE	P
<b>Bryophytes 1995-2001</b>			
Intercept	-41.5	3.5	<0.0001
Heath	20.5	4.9	<0.0001
Control	51.0	4.3	<0.0001
Temperature	31.3	4.9	<0.0001
Heath * Control	-26.9	6.1	<0.0001
Heath * Temperature	-14.8	7.0	0.035
<b>Bryophytes 1999-2001</b>			
Control	7.3	2.7	0.006
Heath * Temperature	8.5	4.3	0.05
<b>Lichens 1995-2001</b>			
Intercept	-10.5	3.4	0.002
Heath	-15.5	4.7	0.001
Heath * Control	16.1	5.8	0.005
<b>Lichens 1999-2001</b>			
Heath	-11.8	3.9	0.003

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**Table 4.** Mann-Whitney U-tests for species specific abundances of bryophytes and lichens between treatments, among years in the heath and meadow communities. Significance values ( $P < 0.05$ ) in bold. C = Control plots; T = warming (OTC); TF = combined warming and nutrient addition. Species: At = *Aulacomnium turgidum* (Wahlenb.) Schwägr. (acrocarpous bryophyte), Cetd = *Cetrariella delisei* (Bory ex Schaer.) Kärnfelt & A. Thell (lichen), Gym = *Gymnomitrium sp.* (liverwort), Kias = *Kiaeria starkei* (F. Weber & D. Mohr) I. Hagen (acrocarpous bryophyte), Stea = *Stereocaulon alpinum* Laurer (lichen), HS = *Hylocomium splendens* (Hedw.) Schimp. (pleurocarpous bryophyte), Cl dof = *Cladonia arbuscula* (Wallr.) Flot. (lichen). Species abbreviations with a number 2 attached (example At2) means that the Mann-Whitney U-test were performed for differences between 1999 and 2001, species abbreviations without a number means that the Mann-Whitney U-test was performed on difference between 1995-2001

HEATH		At	Cetd	Gym	Kias	Stea	At2	Stea2
C	T	<b>0,048</b>	<b>0,011</b>	0,48	0,49	<b>0,03</b>	<b>0,035</b>	0,158
C	F	0,11	<b>0,007</b>	<b>0,029</b>	<b>0,033</b>	<b>0,006</b>	0,18	<b>0,008</b>
C	TF	<b>0,048</b>	<b>0,007</b>	<b>0,024</b>	<b>0,008</b>	<b>0,006</b>	0,176	0,257
T	F	0,74	0,27	0,1	<b>0,083</b>	0,24	0,127	<b>0,017</b>
T	TF	0,88	0,35	<b>0,076</b>	0,19	0,74	0,127	0,169
F	TF	0,74	0,65	0,88	0,25	0,12	1	<b>0,017</b>
MEADOW		At	HS	Cl dof2				
C	T	0,172	<b>0,013</b>	1				
C	F	<b>0,093</b>	<b>0,006</b>	<b>0,014</b>				
C	TF	<b>0,005</b>	<b>0,006</b>	0,29				
T	F	0,66	<b>0,043</b>	<b>0,04</b>				
T	TF	<b>0,08</b>	<b>0,043</b>	0,32				
F	TF	0,14	0,56	<b>0,011</b>				