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2

3   Title: Changes in plant composition and diversity in an Alpine heath and meadow after 18 years of

4   experimental warming

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27

28   **Abstract**

29   **Background and aim** Global warming is expected to have large impacts on high alpine and Arctic

30   ecosystems in future. Here we report the effects of 18 years of experimental warming on two

31   contrasting high alpine plant communities in subarctic Sweden.

32   **Methods** Using open-top chambers (OTCs), we analysed the effects of long-term passive experimental

33   warming on two high alpine plant communities, a species- and nutrient-poor heath and a more nutrient-

34   and species-rich mesic meadow. We determined the impact on species composition, species diversity (at

35   the level of rare, frequent and dominant species in each community), and phylogenetic and functional

36   diversity.

37   **Key results** Long-term warming drove differentiation in the species composition in both heath and

38   meadow vegetation, with the warmed plots having distinctly different species composition in 2013

39   compared with 1995. In addition, variability in species composition increased in the meadow, while it

40   decreased in the heath. The long-term warming had a significant negative effect on the three orders of

41   phylogenetic Hill diversity in the meadow. There was a similar tendency in the heath, but only the

42   phylogenetic diversity of dominant species was significantly affected. Long-term warming caused a

43   reduction in graminoids in the heath, while deciduous shrubs increased. In the meadow, cushion-

44   forming plants showed an increase in abundance from 2001 to 2013 in the warmed plots.

45   **Conclusions** Responses in species and phylogenetic diversity to experimental warming varied over both

46   time (medium vs long-term responses) and space (i.e. between the two neighbouring plant communities

47   heath and meadow). The meadow community was more negatively affected in terms of species and

48   phylogenetic diversity than the heath community. A potential driver for the changes in the meadow may

49   be decreased soil moisture caused by the long-term warming.

50

53

1. Introduction

54

55   Environmental changes are likely to cause large vegetation shifts in many polar and alpine regions

56   (Rowland et al. 2016). Global warming may pose a serious threat to isolated endemic alpine species

57   when neither upward nor poleward distribution shift is possible (Kidane et al. 2019). In addition, global

58   warming may seriously shrink suitable habitats (Ferrarini et al. 2019) and cause local extinction of

59   species at the extreme of their distribution range (Hampe and Petit 2005; Ferrarini et al. 2016). Global

60   warming has already been shown to cause range shifts (Kullman 2002; Chen et al. 2011) and

61   composition shifts (Evangelista et al. 2016; Koltz et al. 2018). A widespread trend at many alpine and

62   Arctic sites is an increase in shrubs (Jägerbrand et al. 2009; Myers-Smith et al. 2011; Maliniemi et al.

63   2018; Vowles and Björk 2019). However, many plant species in polar and alpine regions are long-lived

64   (Morris and Doak 1998; Ferrarini et al. 2019). Thus, even when conditions at a site become unfavourable

65   due to environmental change, plant species can be expected to persist for more years than animals and

66   short-lived species, as the plants are confined to the site and cannot migrate once established. In

67   addition, longer-lived plant species have been suggested to be less vulnerable to increased climate

68   variability than short-lived species (Morris et al. 2008). However, there have been very few experimental

69   studies applying increased variability/different warming scenarios, while those conducted to date are

70   short-term (Jonasson et al. 1999; Marchand et al. 2006; Alatalo et al. 2016).

71   Solar radiation and temperature have been shown to be dominant factors controlling net

72   primary production in alpine meadows and grasslands on the Tibetan plateau (Wang et al. 2018; Zheng

73   et al. 2020), while summer precipitation is an important driver for species richness (Li et al. 2020).

74   Extreme warming events that are accompanied by drought have been shown to have more severe

75   effects on plant communities than warming without accompanying drought (Bragazza 2008; De Boeck et

76   al. 2016). From the growing number of experimental global change experiments performed, we have

77 learned that short-, medium- and longer-term responses may differ (Hollister et al. 2005; Alatalo and

78 Little 2014; Alatalo et al. 2015b; Kremers et al. 2015; Baruah et al. 2018; Walker et al. 2020)

79   In addition, different types of environmental disturbance may have different effects on plant

80 communities and invasive species (Erfanian et al. 2019b). Strong evidence of the importance of both

81 duration of experimental manipulations and number of disturbances is provided by a global study that

82 included data from more than 100 experiments. The study showed that the greater the number of

83 experimental perturbations and the longer the experiment, the less resistant plant communities were to

84 the experimental treatments (Komatsu et al. 2019). Plant communities were in general resistant to

85 experiments that ran for less than 10 years, while experiments lasting more than 10 years showed larger

86 changes. In addition, plant communities that were exposed to three or more experimental treatments

87 showed larger changes in the plant community than plant communities that experienced fewer

88 environmental manipulations (Komatsu et al. 2019). Thus, short-term responses may be poor predictors

89 of potential long-term changes. It is therefore important to try to ensure that global change experiments

90 are maintained and re-sampled over longer periods than normally covered by external funding for

91 research projects.

92   Climate change experiments have been conducted at Latnjajaure field station in northern

93 Sweden since 1993. An increasing number of studies at the field station are now covering potential

94 impacts of climate change on different organism groups and ecosystem properties. In an experiment

95 established at the station 1995 on a nutrient- and species-poor heath and a more species- and nutrient-

96 rich mesic meadow, we have previously reported short and medium-term responses and the impact of

97 long-term warming on lichens (Alatalo et al. 2017a), bryophytes (Alatalo et al. 2019) and soil fauna

98 (Alatalo et al. 2015a, 2017b).

99   In this paper, we test the effect of 18 years of experimental warming on the vascular plant

100 communities. Specifically, we focus on the impact on species composition, species diversity (at the level

101   of rare, frequent and dominant species of each community), and the phylogenetic and functional

102   diversity of vascular plants. We hypothesise that the effect of experimental warming will be larger at the

103   end of the experiment compared to the early years of the experiment (Komatsu et al. 2019), and that

104   the effect of experimental warming will be larger on the meadow community compared to the heath

105   community, as the meadow community has higher nutrient content in the soil and larger species pool.

106

107   **2. Materials and Methods**

108   **2.1 Study area**

109   The study was conducted at Latnjajaure field station, which is located in the Latnjavagge valley (68°21´N,

110   18°29´E; 1000 m a.s.l.) in northern Sweden. The climate at the site is classified as subarctic (Polunin

111   1951), with snow cover for most of the year, cool summers and relatively mild, snow-rich winters. The

112   growing season starts in late May and ends in early September (Molau et al. 2005). Climate data were

113   collected throughout the year at the weather station at Latnjajaure field station, with hourly means,

114   maxima and minima recorded. Mean annual air temperature in the study period (1993-2013) ranged

115   from -0.76 to -2.92°C (Alatalo et al. 2017a). Mean monthly temperature was highest in July, ranging

116   from 5.9°C in 1995 to 13.1°C in 2013 (Alatalo et al. 2017a). Mean annual precipitation during the period

117   was 846 mm, but in individual years it ranged from a low of 607 mm (1996) to a high of 1091 mm (2003)

118   (Alatalo et al. 2017a). Detailed monthly mean, max and min temperature data and precipitation data are

119   supplied in electronic supplementary materials (Alatalo et al. 2017a). Physical conditions in the soils in

120   the valley vary from dry to wet and poor and from acidic to base-rich, with an associated variation in

121   plant communities (Lindblad et al. 2006; Björk et al. 2007; Alatalo et al. 2017b).

122   The mesic meadow community has a more developed vegetation cover (67% canopy cover)

123   (Alatalo et al. 2017a), dominated by *Carex vaginata*, *Carex bigelowii*, *Festuca ovina*, *Salix reticulata*, *Salix*

124   *polaris*, *Cassiope tetragona*, *Bistorta vivipar*a and *Thalictrum alpinum* (Molau and Alatalo 1998; Alatalo

125   et al. 2014). The more sparsely vegetated poor heath community (54% canopy cover) (Alatalo et al.

126   2017a) is dominated by *Betula nana*, *Salix herbacea* and *Calamagrostis lapponica* (Molau and Alatalo

127   1998; Alatalo et al. 2015c).

128

129   **2.2 Experimental design and measurements**

130   In July 1995, twelve 1 m x 1 m plots with homogeneous vegetation cover were marked out in an alpine

131   mesic meadow plant community and in a heath plant community and randomly assigned to treatments

132   (control and experimental warming) in a factorial design. At the start of the experiment, there were

133   eight control plots and four plots with experimental warming (total 12) in each plant community.

134   However, as we could not identify all initial control plots in 2013, we only made measurements in four

135   control and four experimental warming plots in each community in that year. Experimental warming is

136   applied at the site using open-top chambers (OTCs) left on plots with warming treatment all year

137   around. In the initial years, the temperature in the control and OTC plots was monitored with Delta[TM]

138   and Tinytag[TM] loggers (Molau and Alatalo 1998). As found in other studies (Marion et al. 1997; Molau

139   and Alatalo 1998; Hollister and Webber 2000), the OTCs increased the air temperature by 1.5-3°C

140   compared with control plots with ambient temperature. OTCs have also been shown to decrease canopy

141   moisture (Hollister and Webber 2000), causing earlier snow melt and prolonging the growing season

142   (Molau and Alatalo 1998; Hollister and Webber 2000).

143   Abundance of all species was assessed using a 1 m × 1 m frame with 100 grid points (Walker

144   1996) in the middle of the growing season in 1995, 1999, 2001, and 2013. Due to their hexagonal shape,

145   the OTCs reduced the number of points per plot to 77-87 and thus warmed plots had fewer pin-point

146   intercepts than control plots. To compensate for this, we analysed the relative changes from 1995 (see

147   data analyses below). Fixed points at the corner of each plot allowed the grid frame to be placed in the

148 same position on the plot on each measuring occasion. This method has been shown to be accurate in

149 detecting changes in tundra vegetation (May and Hollister 2012).

150

151 **2.3 Data analysis**

152 **2.3.1 Community composition**

153 The effect of the warming treatment over time on species composition in both heath and meadow plant

154 communities was evaluated using principal response curves (PRC) (van den Brink et al. 2009). Also,

155 Monte Carlo permutation tests were performed to evaluate the statistical significances of the

156 differences between each treatment and control. The PRC and permutations were performed by using

157 the vegan package (Oksanen et al. 2017)

158   We also evaluated changes in species composition within the samples from each year (i.e.

159 within-site beta diversity), to test whether small-scale (i.e. plot) conditions lead to different responses in

160 the patches of each community in the area. Hellinger distance (i.e. Euclidean distance of the Hellinger-

161 transformed data) was used as a measure of within-site beta diversity. This dissimilarity index was

162 calculated using the *vegdist* function in the vegan package. For each year, mean and 95% confidence

163 intervals (CIs) of these indices were calculated. The CIs were estimated using a one-mean t-procedure

164 (Zar 2010). All of the calculated indices were relativised using within-site beta diversity in 1995 as the

165 base value. R version 3.5.3 was used for the analyses (R Core Team 2019).

166 **2.3.2 Species diversity**

167 Hill species diversity indices were calculated to compare changes in the species diversity of the heath

168 and meadow communities between the sampling years. These indices are considered as the standard

169 framework for calculating and comparing species diversity (Erfanian et al. 2019b). We considered the

170 species richness (q=0 in the Hill species diversity formula), the exponential of the Shannon diversity

171 (q=1) and the reciprocal of the Simpson index (q=2). These indices evaluate the species diversity of a

172   community at the level of rare, frequent and dominant species (Chao et al. 2014b, a; Erfanian et al.

173   2019a). The sampling in the present study was conducted during several years. Unequal sampling effort

174   between sampling years, which greatly affects biodiversity estimates, is a typical limitation of this type

175   of studies (Kent 2012). To eliminate the effects of this limitation on our inferences, we used a coverage-

176   based rarefaction/extrapolation method where the species diversities in the different years were

177   calculated at the same coverage (i.e. sampling effort) level (Chao and Jost 2012; Chao et al. 2014b). The

178   95% confidence intervals (CIs) for the estimated diversities were calculated, using a bootstrapping

179   approach. These analyses were performed in the iNEXT package, using the *estimateD* function (Hsieh et

180   al. 2016). All of the calculated indices were relativised using the species diversity in 1995 as the base

181   value.

182

183   **2.3.3 Phylogenetic diversity**

184   The phylogenetic diversity of the communities was used since it reflects the evolutionary history of the

185   assemblages and is related to their conservation value (Faith and Baker 2006; Faith 2016). The

186   phylogenetic tree of the vascular plants collected from plots was estimated using the V.PhyloMaker

187   package (Jin and Qian 2019). Hill diversity indices of phylogenetic diversity at the level of rare (q=0),

188   frequent (q=1) and dominant (q=2) species were considered. The coverage-based

189   rarefaction/extrapolation method was employed to calculate these indices at the same coverage level.

190   The iNEXT-PD package was used for the calculations (Chao et al. 2010; Hsieh et al. 2016). The results

191   obtained were relativised using the phylogenetic diversity in 1995 as the base value.

192

193   **2.3.4 Functional diversity**

194   Changes in five functional groups of vascular plants (cushion-forming plants, deciduous shrubs,

195   evergreen shrubs, forbs and grasses) were evaluated. The ranges of these functional types in each

196   sampling year in control and temperature plots were drawn. The Hellinger distance was calculated

197   separately for each functional group, to assess the species turnover within groups. Using 1995 as the

198   base year, the relative change in species composition was calculated for 1999, 2001 and 2013.

199

200   **3 Results**

201   **3.1 Species composition**

202   The PRC analysis results showed that there was a significant difference (p-value = 0.039, F-value =7.166)

203   between control and warming plots of the heath community as long as their species compositions is

204   considered. Also, the PRC analysis result showed that 16 % of variance was attributed to the warming

205   treatment and that 15.35 % of the variances is explained by first axis. For the meadow vegetation, the

206   PRC analysis could not detect a significant difference (p-value = 0.659, F-value = 1.814) between species

207   composition of control and warming plots. About 9% percent of variance was explained by the PRC

208   analysis and 7.56 % of this variance contributed to the first axis. The PRC results are presented in Figure

209   1. Only species with relative frequency sum above 1 is shown. For meadow vegetation, *Carex vaginata*

210   showed the greatest abundance increase and *Cassiope tetragona* experienced the most decrease in the

211   abundance. In the heath vegetation, *Betula nana* showed an increased abundance and *Empetrum*

212   *hermaphroditum* had the greatest abundance loss.

213   Long-term warming led to a decreased beta diversity in the species composition of patches in

214   the heath plots (Figure 2a), but increased variability in the species composition of patches in the

215   meadow plots (Figure 2b). Control plots showed a similar trend, but at a lower magnitude. However, by

216   2013, the beta diversity of control and warmed plots was similar.

217   **3.2 Species diversity**

218   For meadow vegetation, except for the year 1999, there were significant differences between control

219   and warmed plots in all three orders of Hill species diversity (i.e. q = 0, 1 and 2). Warmed plots generally

220   showed lower species diversity than control plots. Comparing diversity among the years, in control plots,

221   2013 showed a significantly higher species diversity than that of the year 2001; 2001 have a significantly

222   lower diversity than that of the 1999. Comparing 1999 and 1995, except for the exponential of the

223   Shannon diversity (i.e., q=1), there was a significant difference between 1995 and 1999. The species

224   richness (q=0) of 1999 was lower than that of the 1995, contrary, 1999 showed a higher species diversity

225   at q=2 than that of the 1995. Comparing diversity of warming plots among the years, except for the q=2,

226   no significant difference was observed between 2013 and 2001. However, 2001 showed a significantly

227   lower species diversity than that of the 1999. Also, except for the q=2, no significant difference were

228   observed between 1995 and 1999. Moreover, among the years, a decreasing trend from 1995 to 2001

229   and an increasing trend from 2001 to 2013 could be detected (Figure 3).

230   For heath vegetation, except for q=2 in 2001, there were no significant differences in species

231   diversity (i.e. species richness (q=0), the exponential of Shannon diversity (q=1) and the reciprocal of the

232   Simpson index (q=2)) between warming and control plots (Figure 3). Comparing species diversity among

233   the years, in control plots, species richness (q=0) and the exponential of the Shannon diversity (q=1) of

234   2013 was significantly lower than that of the 2001. No significant differences were observed among the

235   2001 and 1999. However, species richness (q=0) and the exponential of the Shannon diversity (q=1) of

236   1999 was significantly higher than that of the 1995. For warming plots, only at the level of q=2 a

237   significant decrease was observed from 1995 to 1999.

238   **3.3 Phylogenetic diversity**

239   The results of phylogenetic diversity (hereafter PD) estimation comparing control and warming plots in

240   the meadow showed that there was significant difference between these two treatments in the 2001

241   (Figure 4). In the 1999 PD at the level of q=1 and 2 significantly differed between two treatments. In the

242   2013, only PD at the level of q=1 showed significant difference between control and warming plots.

243   Among the years, in the control plots, PD in 1999 and 2001 was significantly lower than that of the 1995

244   at the level of q=0. At the levels of q=1 and 2, PD of the control plots in 1999 was significantly higher

245   than those of 1995. No significant differences were revealed comparing the PD of 2013 to the other

246   years. For the warming plots, comparing among the years, 2013 showed a higher PD than that of 2001

247   and a lower PD than that of the 1995. The PD of 2001 were significantly lower than that of the 1999.

248   In the heath vegetation, at the level of q=2 warming plots showed a significantly lower PD than

249   those of the control plots. This was also observed in the 2013 at the level of q=1. No significant

250   difference was detected between control and warming plots at the level of q=0 PD. Comparing the

251   years, in the control plots, PD at the level of q=1 and q=2 was significantly lower than that of the 1995.

252   The same differences were also observed for the warming plots at the three levels of PD.

253   **3.4 Functional diversity**

254   Our results revealed that, in heath vegetation, graminoids decreased in the warmed plots, while

255   deciduous shrubs increased. For the meadow vegetation, cushion-forming plants and forbs showed an

256   increase in the warmed plots in 2013 (Figure 5).

257   Changes in the species composition of each functional group, measured using the Hellinger

258   dissimilarity measure, are presented in Table 1. Cushion-forming plants, deciduous shrubs and

259   evergreen shrubs showed low species turnover in both warmed and control plots. However, forbs and

260   graminoids showed moderate species turnover from 1995 to 2013 in both warmed and control plots.

261

262   **Discussion**

263   Long-term warming (18 years) drove differentiation in the species composition of the heath vegetation

264   over time, with the warmed plots ending up with distinctly different species composition in 2013

265   compared with 1995. Also, warming causes a shrub (i.e., *Betula nana*) increases in heath and graminoids

266   (e.g. *Carex vaginata* and *Festuca ovina*) increased in meadow communities. However, a previous study

267   at the same site found that seven years of experimental warming caused sedges to decline in the

268   meadow (Alatalo et al. 2014). Thus, the short-term and longer-term responses differed. As

269   hypothesised, and similar to previous studies that found that effects from experiments are increased by

270   with time (Komatsu et al. 2019), the majority of changes occurred in the later part of the 18-year study

271   period. Many previous studies have reported increased occurrence of shrubs in alpine and arctic tundra

272   ecosystems, and have attributed this to ongoing climate change (Jägerbrand et al. 2009; Maliniemi et al.,

273   2018; Myers-Smith et al., 2011; Myers-Smith and Hik, 2018; Vowles and Björk, 2019). Our results show

274   that the responses can vary considerably even on local scale, as deciduous shrubs increased markedly in

275   the heath plots, but not in the nearby meadow plots studied at the site. Deciduous shrubs showed

276   similar positive effect from experimental warming in the initial five year response at our site (Jägerbrand

277   et al. 2009), and in Alaskan Tundra (Chapin III and Shaver 1985, 1996). Also, the variability in species

278   composition within the meadow community could be related to the increase in abundance of cushion

279   plants that can modify microclimatic condition at the plot-scale (Cavieres et al. 2007). In addition, our

280   results contradict findings in a long-term monitoring study in High Arctic Canada experiencing natural

281   warming that evergreen shrubs, but not deciduous shrubs, increased over a period of 27 years (Hudson

282   and Henry 2009).

283   Changes in species composition have also been reported for grasslands in Tibet (Liu et al. 2018),

284   Oklahoma (Shi et al. 2018) and the Pyrenees (Boutin et al. 2017), for snowbed and nival vegetation in

285   the European Alps (Matteodo et al. 2016; Lamprecht et al. 2018) and for tussock tundra in Alaska

286   (Leffler et al. 2016).

287   Variability in the species composition of plots increased in the meadow vegetation, while it

288   decreased in the heath vegetation. This finding suggests that patches in the meadow vegetation

289   responded to climate changes in different ways. Patches of heath vegetation showed a poor adaptive

290   response, and we observed compositionally homogenised communities. This is a negative change, as

291   homogenised communities can potentially be more vulnerable to future disturbances. Considering the

292   differing responses of heath and meadow communities, we conclude that the heath vegetation was

293   more susceptible to climate change impacts. A previous study in the Swiss Alps revisiting 63 sites

294   experiencing natural warming over time found that arrival of new species resulted in homogenization of

295   the plant communities (Matteodo et al. 2016). However, the stability of species composition varied

296   between plant communities, with snowbed communities being more vulnerable than grassland

297   communities (Matteodo et al. 2016).

298   A monitoring study over 40 years in alpine Colorado found that species richness declined in all

299   three plant communities studied (dry meadow, moist meadow and shrub tundra), with the largest

300   decline in the shrub community (Scharnagl et al. 2019). Similarly, the two plant communities at our

301   study site in northern Sweden responded with contrasting patterns at different levels of species

302   diversity (rare, frequent and dominant species) to the ambient temperature and experimental warming

303   treatments over time. Experimental warming caused an initial negative responses in within site diversity

304   in the heath (Alatalo et al. 2015c) which remained negative in the long term (this study). Also, dominant

305   species of the heath vegetation were more susceptible to shrubification. The meadow community

306   showed an initial rapid negative response (until 2001), after which it started to recover, but it had not

307   returned to its initial status after 18 years of warming. In terms of phylogenetic diversity, the long-term

308   warming caused a significant negative effect on the three orders of phylogenetic Hill diversity in the

309   meadow. While there was a similar tendency in the heath, only phylogenetic diversity of dominant

310   species was significantly affected. The observed reduction in phylogenetic diversity of both communities

311   can be considered an indication of loss of rare and phylogenetically diverse species, as the final

312   colonising species have lower phylogenetic diversity because they come from related taxa. Notably,

313   forbs and graminoids showed a larger turn-over in species composition during 18-year experiment in

314   meadow, while shrubs showed a much lower turn-over in the heath. However, this difference in species

315   turn-over could potentially be explained by differences in their longevity. With forbs and graminoids

316   including more short-lived species compared to shrub species.

317   In a previous study at our site, seven years of warming caused a significant decline in total

318   species richness (Alatalo et al. 2014). These results confirm findings in other studies that mesic meadow

319   communities tend to be more vulnerable than drier sites in terms of species loss (Elmendorf et al. 2012).

320   At our study site, long-term warming has caused a decrease in soil moisture in the meadow community,

321   but not in the heath community (Alatalo et al. 2017b). This could potentially help to explain the

322   differences in responses between these plant communities. Decreased soil moisture due to

323   experimental warming has been reported to be accompanied by an decrease in sedges and an increase

324   in grasses and forbs in a meadow community in Tibet following short-term experimental warming (Peng

325   et al. 2017). However, in our meadow site we found a more complex response pattern over time,

326   initially sedges decreased (Alatalo et al. 2014), while they increased over long-term (this study). This

327   later increase in sedges was mainly driven by *Carex vaginata,* while the initial shorter term responses

328   were dominated by changes in abundance of *Carex bigelowii* (Jägerbrand et al. 2009). Thus, negative

329   effects on species and phylogenetic diversity may be driven by an indirect effect of decreased moisture

330   levels due to warming, not by the warming itself. In addition, both the responses, and major drivers

331   (species), may also change over time.

332   Cushion-forming plants are important in alpine areas due to their function as facilitator species

333   (Cavieres et al. 2014; Anthelme et al. 2014). The shorter-term results (1995-2001) from our experiment

334   showed that the dominant cushion-forming plant at the site, *Silene acaulis*, was highly plastic in its

335   phenotypic responses in terms of growth-related plant traits to nutrient addition and combined nutrient

336   addition and warming, while warming alone had no effect on growth and abundance (Alatalo and Little

337   2014). In the present longer-term study, the PCR showed that *S. acaulis* only decreased slightly in

338   response to 18 years of warming, thus, the studied population is likely resistant to warming that is not

15

339   accompanied by an increase of nutrients. The dominant cushion plant in the meadow *Silene acaulis* has

340   a taproot, thus as the soil became drier in the warmed plots (Alatalo et al. 2017b), having taproot could

341   have become an advantage compared to more shallow-rooted species over the longer term. However, a

342   previous study has shown that *S. acaulis* populations across the species distribution range may respond

343   in different ways, with southern populations of *S. acaulis* having higher growth rates than northern

344   populations in North America, but lower survival and recruitment (Doak and Morris 2010). That study

345   also found that the warmest years had a negative effect on survival and fruit production, but that

346   moderately warmer years had a positive effect (Doak and Morris 2010). In contrast, a recent study

347   showed that northern populations of *S. acaulis* may decline while more southern populations may

348   remain stable (Peterson et al. 2018). This highlights the difficulty in predicting plant species responses to

349   climate change, as both life history plasticity and local adaptation will affect species responses to

350   warming (Peterson et al. 2018).

351

352   **Conclusions**

353   This study found that responses in plant species composition and phylogenetic diversity to experimental

354   warming varied both in time (medium vs long-term) and space (neighbouring heath and meadow

355   communities). The heath community was more negatively affected in terms of species composition and

356   patch-scale responses than the meadow community. However, the meadow community showed a larger

357   decrease in species and in phylogenetic diversity than the heath community. Long-term warming caused

358   differentiation in species composition in both communities, with shrubification and decreases in

359   graminoids being observed in the heath community and increases in cushion-forming plants in the

360   meadow community. A potential driver for the changes in the meadow community may be decreased

361   soil moisture caused by the long-term warming (18 years).

362

370

371   **Authors' contributions**

372   JMA and UM designed the experiment, JMA, AJ and UM carried out fieldwork. JMA, MBE and SC carried

373   out data analyses, MBE prepared the figures and tables. JMA and MBE drafted the manuscript. All

374   authors read, commented on and approved the final manuscript.

375

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Figure 1. Principal response curve showing the effect of warming treatment over time on vascular plant species in heath and meadow vegetation at Latnjajaure, northern Sweden.
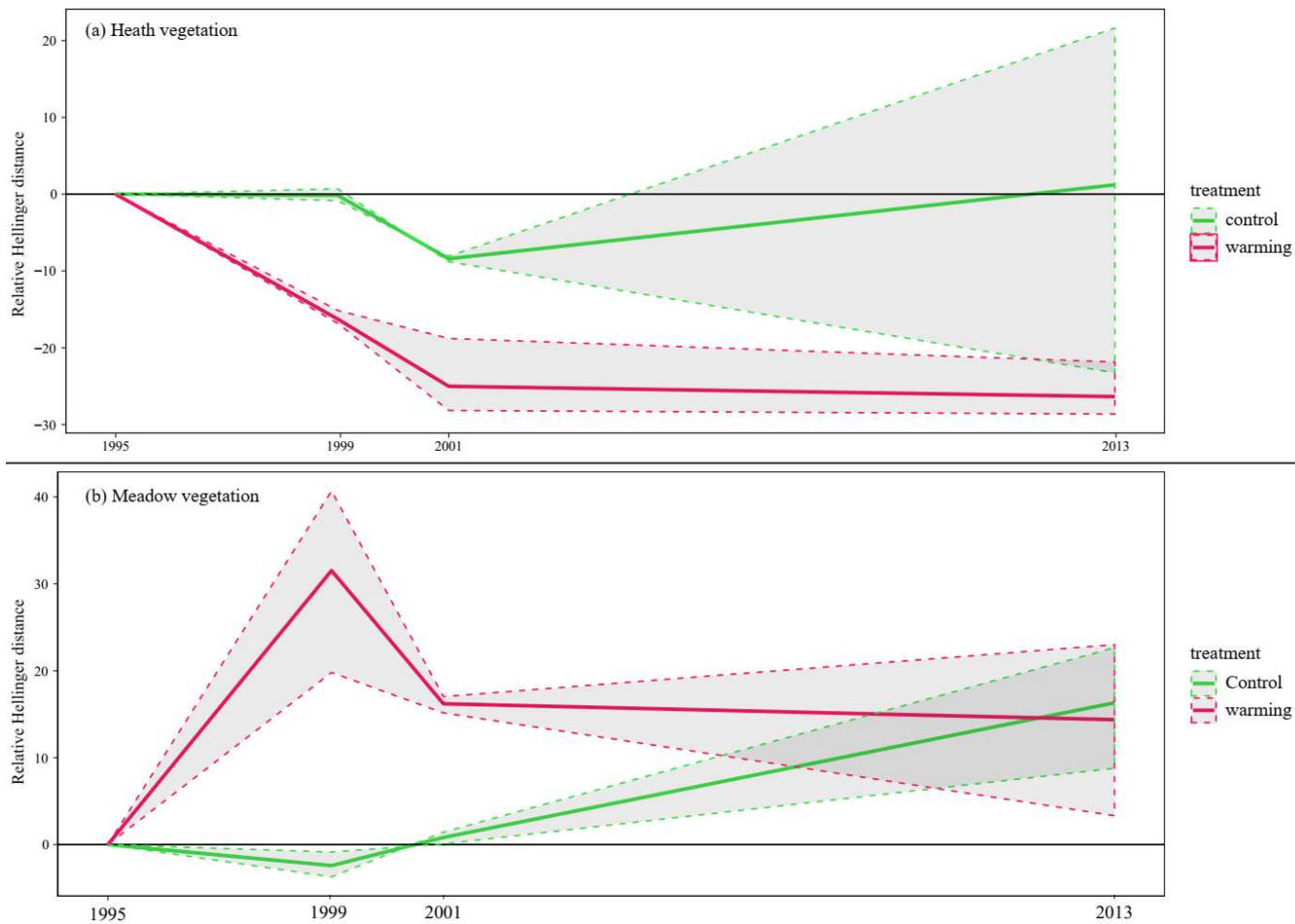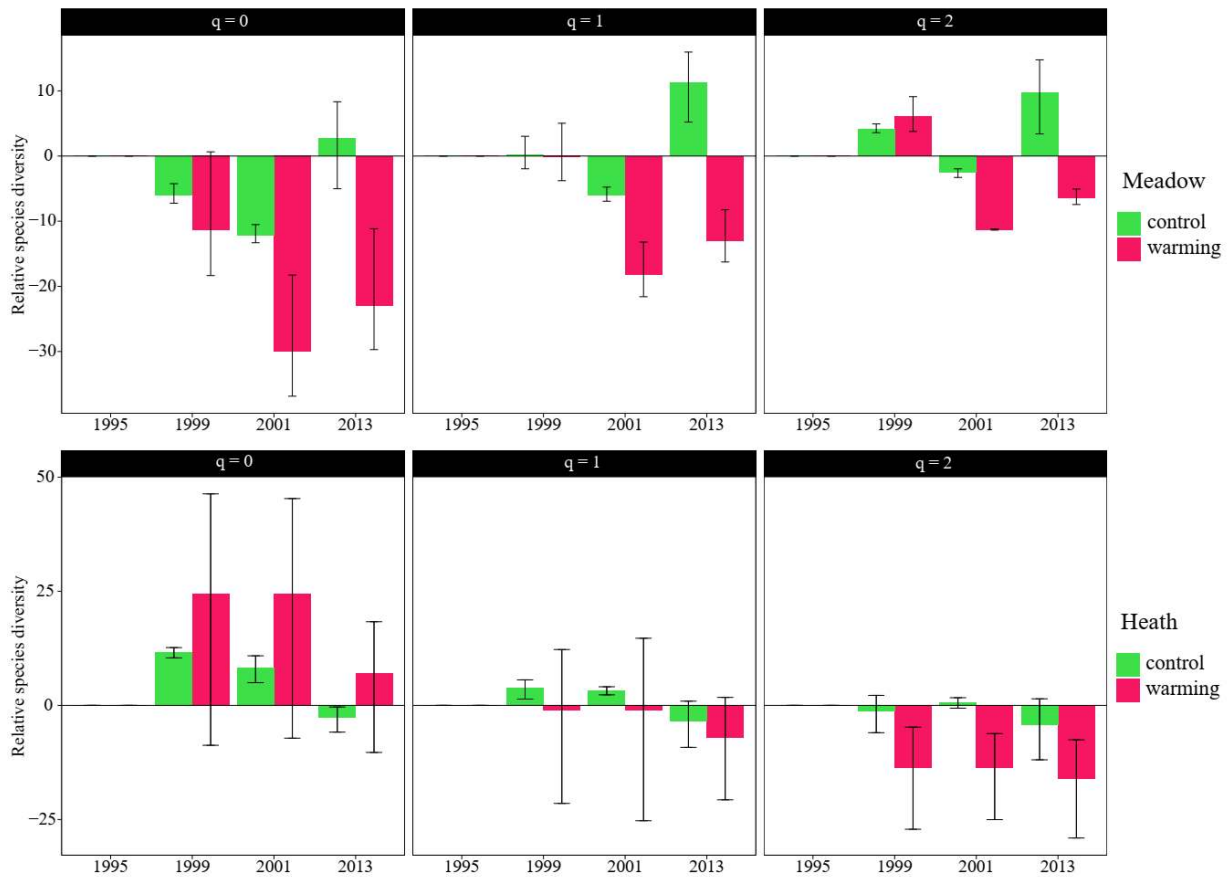
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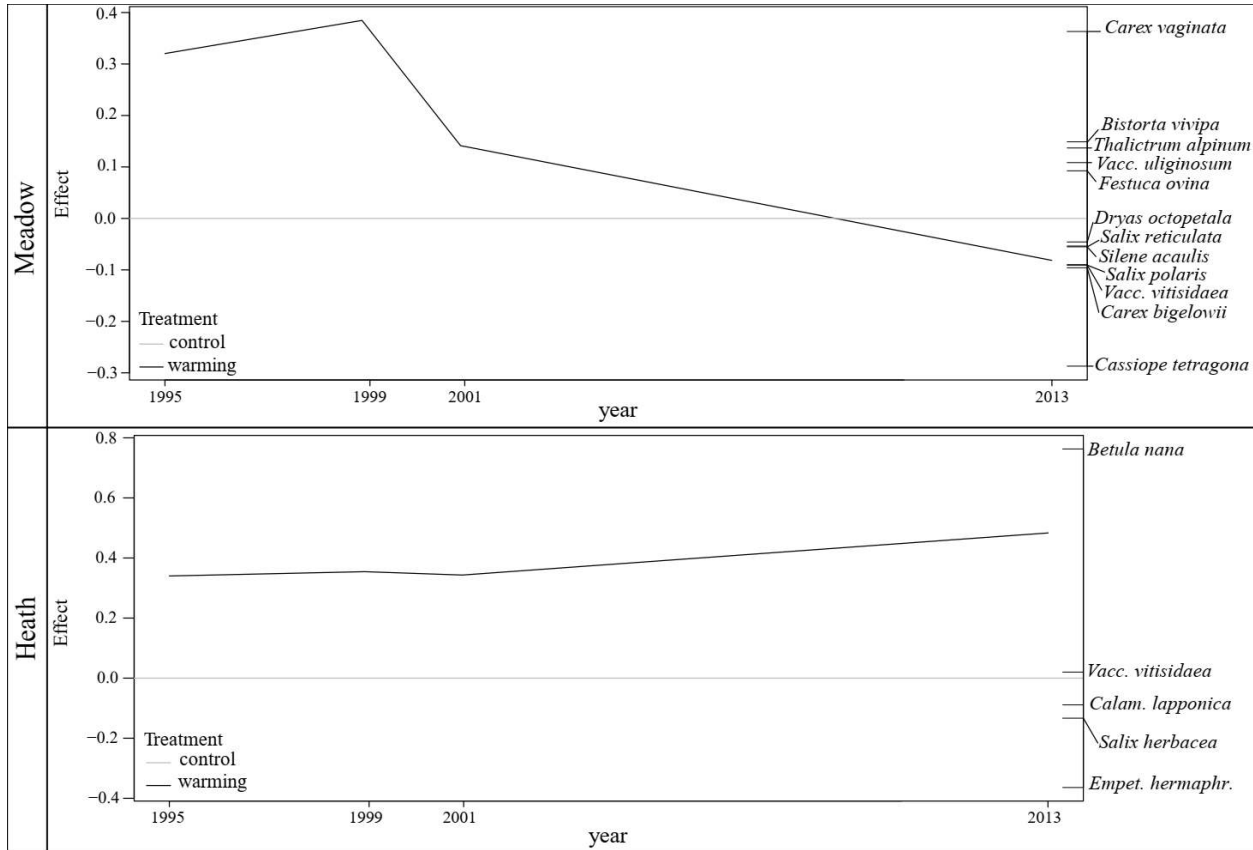
586

587

588   Figure 2. Relative changes in within-site beta diversity in response to long-term warming (1995-2013) in

589   an alpine heath community and a meadow community at Latnjajaure, subarctic Sweden. Values

590   represent mean and 95% confidence intervals.

591

592

593   Figure 3. Changes in species diversity in response to long-term warming (1995-2013) in an alpine heath

594   community and a meadow community at Latnjajaure, subarctic Sweden. Species diversity at the level of

595   rare, frequent and dominant species in the community, indicated by q = 0 (species richness, in the Hill

596   species diversity formula), q =1 (exponential of Shannon diversity, effective number of species) and q = 2

597   (reciprocal of Simpson index), respectively.

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603   Figure 4. Changes in phylogenetic diversity (Hill diversity indices at the level of rare (q=0), frequent

604   (q=1), and dominant (q=2) species) in response to long-term warming (1995-2013) in an alpine heath

605   community and a meadow community at Latnjajaure, subarctic Sweden. Values represent mean and

606   95% confidence intervals.

607

608

609   Figure 5. Dominance structure (% of total cover) of different plant functional groups, by treatment

610   (warming, control) and year (1995, 1999, 2001, 2013), in a long-term warming experiment in an alpine

611   heath community and a meadow community at Latnjajaure, subarctic Sweden.
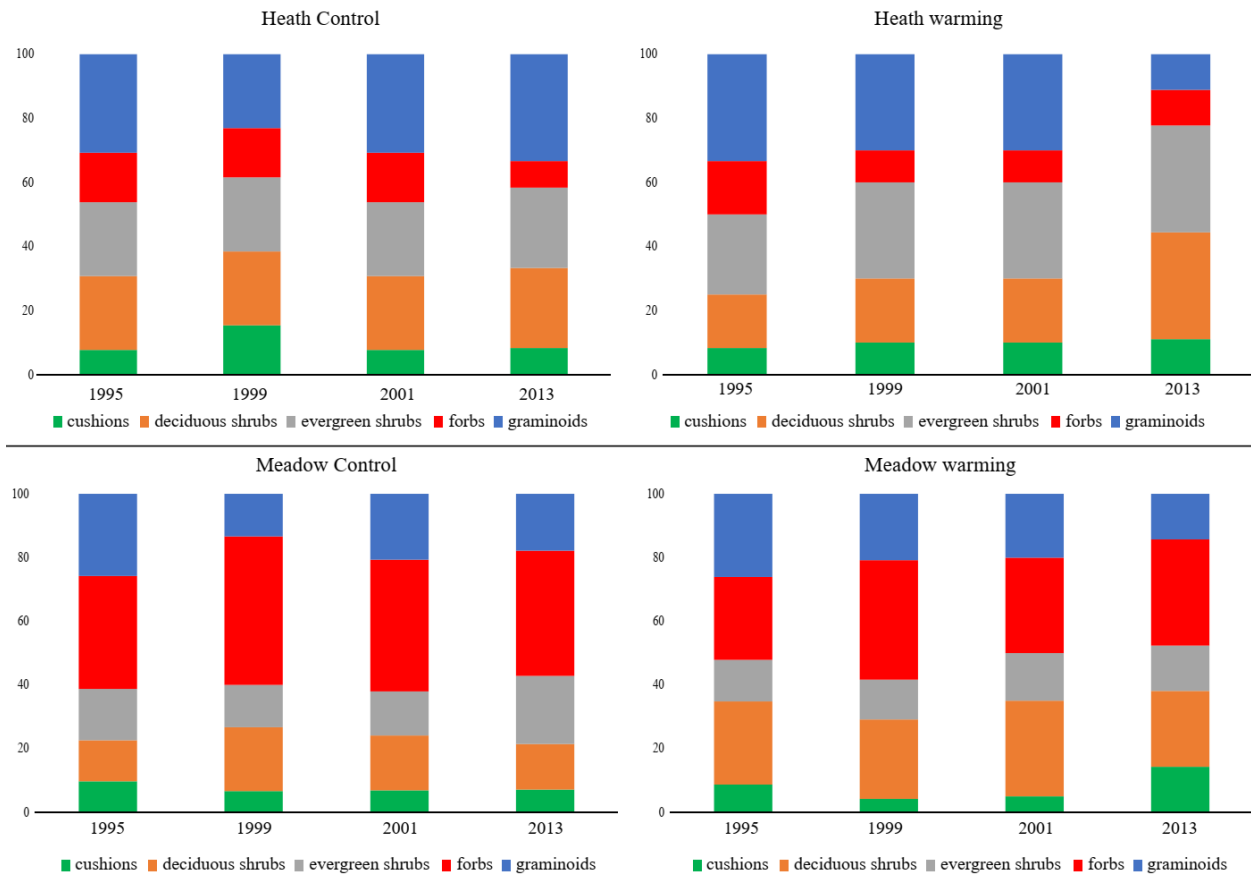
612

613

614   Table 1. Changes in species composition (measured as Hellinger dissimilarity) of different plant

615   functional groups in response to long-term warming (1995-2013) in an alpine heath community and a

616   meadow community at Latnjajaure, subarctic Sweden. Cushions = cushion-forming plants, D. =

617   deciduous shrubs, E. = evergreen shrubs

Heath		Functional gp.	Year	Meadow	
Warming	Control			Control	Warming
0.00	0.27	Cushions	1999	0.09	0.12
0.00	0.00	Cushions	2001	0.10	0.12
0.00	0.00	Cushions	2013	0.08	0.10
0.08	0.03	D. shrubs	1999	0.10	0.24
0.09	0.03	D. shrubs	2001	0.11	0.24
0.15	0.17	D. shrubs	2013	0.19	0.30
0.04	0.09	E. shrubs	1999	0.03	0.05
0.38	0.04	E. shrubs	2001	0.08	0.02
0.08	0.06	E. shrubs	2013	0.12	0.09
1.00	0.47	Forbs	1999	0.03	0.38
0.52	0.38	Forbs	2001	0.08	0.22
0.52	1.00	Forbs	2013	0.12	0.45
0.15	0.14	Graminoids	1999	0.20	0.19
0.18	0.07	Graminoids	2001	0.24	0.20
0.35	0.15	Graminoids	2013	0.25	0.23

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