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

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Abstract

Background and aim Global warming is expected to have large impacts on high alpine and Arctic ecosystems in future. Here we report the effects of 18 years of experimental warming on two contrasting high alpine plant communities in subarctic Sweden.

Methods Using open-top chambers (OTCs), we analysed the effects of long-term passive experimental warming on two high alpine plant communities, a species- and nutrient-poor heath and a more nutrient- and species-rich mesic meadow. We determined the impact on species composition, species diversity (at the level of rare, frequent and dominant species in each community), and phylogenetic and functional diversity.

Key results Long-term warming drove differentiation in the species composition in both heath and meadow vegetation, with the warmed plots having distinctly different species composition in 2013 compared with 1995. In addition, variability in species composition increased in the meadow, while it decreased in the heath. The long-term warming had a significant negative effect on the three orders of phylogenetic Hill diversity in the meadow. There was a similar tendency in the heath, but only the phylogenetic diversity of dominant species was significantly affected. Long-term warming caused a reduction in graminoids in the heath, while deciduous shrubs increased. In the meadow, cushion-forming plants showed an increase in abundance from 2001 to 2013 in the warmed plots.

Conclusions Responses in species and phylogenetic diversity to experimental warming varied over both time (medium vs long-term responses) and space (i.e. between the two neighbouring plant communities heath and meadow). The meadow community was more negatively affected in terms of species and phylogenetic diversity than the heath community. A potential driver for the changes in the meadow may be decreased soil moisture caused by the long-term warming.

Keywords: Arctic; climate change; effective number of species; functional diversity; global warming; long-term warming; phylogenetic diversity; species, diversity; species richness; tundra

1. Introduction

Environmental changes are likely to cause large vegetation shifts in many polar and alpine regions (Rowland et al. 2016). Global warming may pose a serious threat to isolated endemic alpine species when neither upward nor poleward distribution shift is possible (Kidane et al. 2019). In addition, global warming may seriously shrink suitable habitats (Ferrarini et al. 2019) and cause local extinction of species at the extreme of their distribution range (Hampe and Petit 2005; Ferrarini et al. 2016). Global warming has already been shown to cause range shifts (Kullman 2002; Chen et al. 2011) and composition shifts (Evangelista et al. 2016; Koltz et al. 2018). A widespread trend at many alpine and Arctic sites is an increase in shrubs (Jägerbrand et al. 2009; Myers-Smith et al. 2011; Maliniemi et al. 2018; Vowles and Björk 2019). However, many plant species in polar and alpine regions are long-lived (Morris and Doak 1998; Ferrarini et al. 2019). Thus, even when conditions at a site become unfavourable due to environmental change, plant species can be expected to persist for more years than animals and short-lived species, as the plants are confined to the site and cannot migrate once established. In addition, longer-lived plant species have been suggested to be less vulnerable to increased climate variability than short-lived species (Morris et al. 2008). However, there have been very few experimental studies applying increased variability/different warming scenarios, while those conducted to date are short-term (Jonasson et al. 1999; Marchand et al. 2006; Alatalo et al. 2016).

Solar radiation and temperature have been shown to be dominant factors controlling net primary production in alpine meadows and grasslands on the Tibetan plateau (Wang et al. 2018; Zheng et al. 2020), while summer precipitation is an important driver for species richness (Li et al. 2020). Extreme warming events that are accompanied by drought have been shown to have more severe effects on plant communities than warming without accompanying drought (Bragazza 2008; De Boeck et al. 2016). From the growing number of experimental global change experiments performed, we have learned that short-, medium- and longer-term responses may differ (Hollister et al. 2005; Alatalo and Little 2014; Alatalo et al. 2015b; Kremers et al. 2015; Baruah et al. 2018; Walker et al. 2020)

In addition, different types of environmental disturbance may have different effects on plant communities and invasive species (Erfanian et al. 2019b). Strong evidence of the importance of both duration of experimental manipulations and number of disturbances is provided by a global study that included data from more than 100 experiments. The study showed that the greater the number of experimental perturbations and the longer the experiment, the less resistant plant communities were to the experimental treatments (Komatsu et al. 2019). Plant communities were in general resistant to experiments that ran for less than 10 years, while experiments lasting more than 10 years showed larger changes. In addition, plant communities that were exposed to three or more experimental treatments showed larger changes in the plant community than plant communities that experienced fewer environmental manipulations (Komatsu et al. 2019). Thus, short-term responses may be poor predictors of potential long-term changes. It is therefore important to try to ensure that global change experiments are maintained and re-sampled over longer periods than normally covered by external funding for research projects.

Climate change experiments have been conducted at Latnjajaure field station in northern Sweden since 1993. An increasing number of studies at the field station are now covering potential impacts of climate change on different organism groups and ecosystem properties. In an experiment established at the station 1995 on a nutrient- and species-poor heath and a more species- and nutrient-rich mesic meadow, we have previously reported short and medium-term responses and the impact of long-term warming on lichens (Alatalo et al. 2017a), bryophytes (Alatalo et al. 2019) and soil fauna (Alatalo et al. 2015a, 2017b).

In this paper, we test the effect of 18 years of experimental warming on the vascular plant communities. Specifically, we focus on the impact on species composition, species diversity (at the level of rare, frequent and dominant species of each community), and the phylogenetic and functional diversity of vascular plants. We hypothesise that the effect of experimental warming will be larger at the end of the experiment compared to the early years of the experiment (Komatsu et al. 2019), and that the effect of experimental warming will be larger on the meadow community compared to the heath community, as the meadow community has higher nutrient content in the soil and larger species pool.

2. Materials and Methods

2.1 Study area

The study was conducted at Latnjajaure field station, which is located in the Latnjavagge valley (68°21´N, 18°29´E; 1000 m a.s.l.) in northern Sweden. The climate at the site is classified as subarctic (Polunin 1951), with snow cover for most of the year, cool summers and relatively mild, snow-rich winters. The growing season starts in late May and ends in early September (Molau et al. 2005). Climate data were collected throughout the year at the weather station at Latnjajaure field station, with hourly means, maxima and minima recorded. Mean annual air temperature in the study period (1993-2013) ranged from -0.76 to -2.92°C (Alatalo et al. 2017a). Mean monthly temperature was highest in July, ranging from 5.9°C in 1995 to 13.1°C in 2013 (Alatalo et al. 2017a). Mean annual precipitation during the period was 846 mm, but in individual years it ranged from a low of 607 mm (1996) to a high of 1091 mm (2003) (Alatalo et al. 2017a). Detailed monthly mean, max and min temperature data and precipitation data are supplied in electronic supplementary materials (Alatalo et al. 2017a). Physical conditions in the soils in the valley vary from dry to wet and poor and from acidic to base-rich, with an associated variation in plant communities (Lindblad et al. 2006; Björk et al. 2007; Alatalo et al. 2017b).

The mesic meadow community has a more developed vegetation cover (67% canopy cover) (Alatalo et al. 2017a), dominated by *Carex vaginata*, *Carex bigelowii*, *Festuca ovina*, *Salix reticulata*, *Salix polaris*, *Cassiope tetragona*, *Bistorta vivipar*a and *Thalictrum alpinum* (Molau and Alatalo 1998; Alatalo et al. 2014). The more sparsely vegetated poor heath community (54% canopy cover) (Alatalo et al. 2017a) is dominated by *Betula nana*, *Salix herbacea* and *Calamagrostis lapponica* (Molau and Alatalo 1998; Alatalo et al. 2015c).

2.2 Experimental design and measurements

In July 1995, twelve 1 m x 1 m plots with homogeneous vegetation cover were marked out in an alpine mesic meadow plant community and in a heath plant community and randomly assigned to treatments (control and experimental warming) in a factorial design. At the start of the experiment, there were eight control plots and four plots with experimental warming (total 12) in each plant community. However, as we could not identify all initial control plots in 2013, we only made measurements in four control and four experimental warming plots in each community in that year. Experimental warming is applied at the site using open-top chambers (OTCs) left on plots with warming treatment all year around. In the initial years, the temperature in the control and OTC plots was monitored with Delta^{TM} and Tinytag^{TM} loggers (Molau and Alatalo 1998). As found in other studies (Marion et al. 1997; Molau and Alatalo 1998; Hollister and Webber 2000), the OTCs increased the air temperature by 1.5-3°C compared with control plots with ambient temperature. OTCs have also been shown to decrease canopy moisture (Hollister and Webber 2000), causing earlier snow melt and prolonging the growing season (Molau and Alatalo 1998; Hollister and Webber 2000).

Abundance of all species was assessed using a 1 m × 1 m frame with 100 grid points (Walker 1996) in the middle of the growing season in 1995, 1999, 2001, and 2013. Due to their hexagonal shape, the OTCs reduced the number of points per plot to 77-87 and thus warmed plots had fewer pin-point intercepts than control plots. To compensate for this, we analysed the relative changes from 1995 (see data analyses below). Fixed points at the corner of each plot allowed the grid frame to be placed in the same position on the plot on each measuring occasion. This method has been shown to be accurate in detecting changes in tundra vegetation (May and Hollister 2012).

2.3 Data analysis

2.3.1 Community composition

The effect of the warming treatment over time on species composition in both heath and meadow plant communities was evaluated using principal response curves (PRC) (van den Brink et al. 2009). Also, Monte Carlo permutation tests were performed to evaluate the statistical significances of the differences between each treatment and control. The PRC and permutations were performed by using the vegan package (Oksanen et al. 2017)

We also evaluated changes in species composition within the samples from each year (i.e. within-site beta diversity), to test whether small-scale (i.e. plot) conditions lead to different responses in the patches of each community in the area. Hellinger distance (i.e. Euclidean distance of the Hellinger-transformed data) was used as a measure of within-site beta diversity. This dissimilarity index was calculated using the *vegdist* function in the vegan package. For each year, mean and 95% confidence intervals (CIs) of these indices were calculated. The CIs were estimated using a one-mean t-procedure (Zar 2010). All of the calculated indices were relativised using within-site beta diversity in 1995 as the base value. R version 3.5.3 was used for the analyses (R Core Team 2019).

2.3.2 Species diversity

Hill species diversity indices were calculated to compare changes in the species diversity of the heath and meadow communities between the sampling years. These indices are considered as the standard framework for calculating and comparing species diversity (Erfanian et al. 2019b). We considered the species richness ($q=0$ in the Hill species diversity formula), the exponential of the Shannon diversity ($q=1$) and the reciprocal of the Simpson index ($q=2$). These indices evaluate the species diversity of a community at the level of rare, frequent and dominant species (Chao et al. 2014b, a; Erfanian et al. 2019a). The sampling in the present study was conducted during several years. Unequal sampling effort between sampling years, which greatly affects biodiversity estimates, is a typical limitation of this type of studies (Kent 2012). To eliminate the effects of this limitation on our inferences, we used a coverage-based rarefaction/extrapolation method where the species diversities in the different years were calculated at the same coverage (i.e. sampling effort) level (Chao and Jost 2012; Chao et al. 2014b). The 95% confidence intervals (CIs) for the estimated diversities were calculated, using a bootstrapping approach. These analyses were performed in the iNEXT package, using the *estimateD* function (Hsieh et al. 2016). All of the calculated indices were relativised using the species diversity in 1995 as the base value.

2.3.3 Phylogenetic diversity

The phylogenetic diversity of the communities was used since it reflects the evolutionary history of the assemblages and is related to their conservation value (Faith and Baker 2006; Faith 2016). The phylogenetic tree of the vascular plants collected from plots was estimated using the V.PhyloMaker package (Jin and Qian 2019). Hill diversity indices of phylogenetic diversity at the level of rare (q=0), frequent (q=1) and dominant (q=2) species were considered. The coverage-based rarefaction/extrapolation method was employed to calculate these indices at the same coverage level. The iNEXT-PD package was used for the calculations (Chao et al. 2010; Hsieh et al. 2016). The results obtained were relativised using the phylogenetic diversity in 1995 as the base value.

2.3.4 Functional diversity

Changes in five functional groups of vascular plants (cushion-forming plants, deciduous shrubs, evergreen shrubs, forbs and grasses) were evaluated. The ranges of these functional types in each sampling year in control and temperature plots were drawn. The Hellinger distance was calculated separately for each functional group, to assess the species turnover within groups. Using 1995 as the base year, the relative change in species composition was calculated for 1999, 2001 and 2013.

3 Results

3.1 Species composition

The PRC analysis results showed that there was a significant difference (p-value = 0.039, F-value =7.166) between control and warming plots of the heath community as long as their species compositions is considered. Also, the PRC analysis result showed that 16 % of variance was attributed to the warming treatment and that 15.35 % of the variances is explained by first axis. For the meadow vegetation, the PRC analysis could not detect a significant difference (p-value = 0.659, F-value = 1.814) between species composition of control and warming plots. About 9% percent of variance was explained by the PRC analysis and 7.56 % of this variance contributed to the first axis. The PRC results are presented in Figure 1. Only species with relative frequency sum above 1 is shown. For meadow vegetation, *Carex vaginata* showed the greatest abundance increase and *Cassiope tetragona* experienced the most decrease in the abundance. In the heath vegetation, *Betula nana* showed an increased abundance and *Empetrum hermaphroditum* had the greatest abundance loss.

Long-term warming led to a decreased beta diversity in the species composition of patches in the heath plots (Figure 2a), but increased variability in the species composition of patches in the meadow plots (Figure 2b). Control plots showed a similar trend, but at a lower magnitude. However, by 2013, the beta diversity of control and warmed plots was similar.

3.2 Species diversity

For meadow vegetation, except for the year 1999, there were significant differences between control and warmed plots in all three orders of Hill species diversity (i.e. q = 0, 1 and 2). Warmed plots generally showed lower species diversity than control plots. Comparing diversity among the years, in control plots, 2013 showed a significantly higher species diversity than that of the year 2001; 2001 have a significantly lower diversity than that of the 1999. Comparing 1999 and 1995, except for the exponential of the Shannon diversity (i.e., q=1), there was a significant difference between 1995 and 1999. The species richness (q=0) of 1999 was lower than that of the 1995, contrary, 1999 showed a higher species diversity at q=2 than that of the 1995. Comparing diversity of warming plots among the years, except for the q=2, no significant difference was observed between 2013 and 2001. However, 2001 showed a significantly lower species diversity than that of the 1999. Also, except for the q=2, no significant difference were observed between 1995 and 1999. Moreover, among the years, a decreasing trend from 1995 to 2001 and an increasing trend from 2001 to 2013 could be detected (Figure 3).

For heath vegetation, except for q=2 in 2001, there were no significant differences in species diversity (i.e. species richness (q=0), the exponential of Shannon diversity (q=1) and the reciprocal of the Simpson index (q=2)) between warming and control plots (Figure 3). Comparing species diversity among the years, in control plots, species richness (q=0) and the exponential of the Shannon diversity (q=1) of 2013 was significantly lower than that of the 2001. No significant differences were observed among the 2001 and 1999. However, species richness (q=0) and the exponential of the Shannon diversity (q=1) of 1999 was significantly higher than that of the 1995. For warming plots, only at the level of q=2 a significant decrease was observed from 1995 to 1999.

3.3 Phylogenetic diversity

The results of phylogenetic diversity (hereafter PD) estimation comparing control and warming plots in the meadow showed that there was significant difference between these two treatments in the 2001 (Figure 4). In the 1999 PD at the level of q=1 and 2 significantly differed between two treatments. In the 2013, only PD at the level of q=1 showed significant difference between control and warming plots. Among the years, in the control plots, PD in 1999 and 2001 was significantly lower than that of the 1995 at the level of q=0. At the levels of q=1 and 2, PD of the control plots in 1999 was significantly higher than those of 1995. No significant differences were revealed comparing the PD of 2013 to the other years. For the warming plots, comparing among the years, 2013 showed a higher PD than that of 2001 and a lower PD than that of the 1995. The PD of 2001 were significantly lower than that of the 1999.

In the heath vegetation, at the level of q=2 warming plots showed a significantly lower PD than those of the control plots. This was also observed in the 2013 at the level of q=1. No significant difference was detected between control and warming plots at the level of q=0 PD. Comparing the years, in the control plots, PD at the level of q=1 and q=2 was significantly lower than that of the 1995. The same differences were also observed for the warming plots at the three levels of PD.

3.4 Functional diversity

Our results revealed that, in heath vegetation, graminoids decreased in the warmed plots, while deciduous shrubs increased. For the meadow vegetation, cushion-forming plants and forbs showed an increase in the warmed plots in 2013 (Figure 5).

Changes in the species composition of each functional group, measured using the Hellinger dissimilarity measure, are presented in Table 1. Cushion-forming plants, deciduous shrubs and evergreen shrubs showed low species turnover in both warmed and control plots. However, forbs and graminoids showed moderate species turnover from 1995 to 2013 in both warmed and control plots.

Discussion

Long-term warming (18 years) drove differentiation in the species composition of the heath vegetation over time, with the warmed plots ending up with distinctly different species composition in 2013 compared with 1995. Also, warming causes a shrub (i.e., *Betula nana*) increases in heath and graminoids (e.g. *Carex vaginata* and *Festuca ovina*) increased in meadow communities. However, a previous study at the same site found that seven years of experimental warming caused sedges to decline in the meadow (Alatalo et al. 2014). Thus, the short-term and longer-term responses differed. As hypothesised, and similar to previous studies that found that effects from experiments are increased by with time (Komatsu et al. 2019), the majority of changes occurred in the later part of the 18-year study period. Many previous studies have reported increased occurrence of shrubs in alpine and arctic tundra ecosystems, and have attributed this to ongoing climate change (Jägerbrand et al. 2009; Maliniemi et al., 2018; Myers-Smith et al., 2011; Myers-Smith and Hik, 2018; Vowles and Björk, 2019). Our results show that the responses can vary considerably even on local scale, as deciduous shrubs increased markedly in the heath plots, but not in the nearby meadow plots studied at the site. Deciduous shrubs showed similar positive effect from experimental warming in the initial five year response at our site (Jägerbrand et al. 2009), and in Alaskan Tundra (Chapin III and Shaver 1985, 1996). Also, the variability in species composition within the meadow community could be related to the increase in abundance of cushion plants that can modify microclimatic condition at the plot-scale (Cavieres et al. 2007). In addition, our results contradict findings in a long-term monitoring study in High Arctic Canada experiencing natural warming that evergreen shrubs, but not deciduous shrubs, increased over a period of 27 years (Hudson and Henry 2009).

Changes in species composition have also been reported for grasslands in Tibet (Liu et al. 2018), Oklahoma (Shi et al. 2018) and the Pyrenees (Boutin et al. 2017), for snowbed and nival vegetation in the European Alps (Matteodo et al. 2016; Lamprecht et al. 2018) and for tussock tundra in Alaska (Leffler et al. 2016).

Variability in the species composition of plots increased in the meadow vegetation, while it decreased in the heath vegetation. This finding suggests that patches in the meadow vegetation responded to climate changes in different ways. Patches of heath vegetation showed a poor adaptive response, and we observed compositionally homogenised communities. This is a negative change, as homogenised communities can potentially be more vulnerable to future disturbances. Considering the differing responses of heath and meadow communities, we conclude that the heath vegetation was more susceptible to climate change impacts. A previous study in the Swiss Alps revisiting 63 sites experiencing natural warming over time found that arrival of new species resulted in homogenization of the plant communities (Matteodo et al. 2016). However, the stability of species composition varied between plant communities, with snowbed communities being more vulnerable than grassland communities (Matteodo et al. 2016).

A monitoring study over 40 years in alpine Colorado found that species richness declined in all three plant communities studied (dry meadow, moist meadow and shrub tundra), with the largest decline in the shrub community (Scharnagl et al. 2019). Similarly, the two plant communities at our study site in northern Sweden responded with contrasting patterns at different levels of species diversity (rare, frequent and dominant species) to the ambient temperature and experimental warming treatments over time. Experimental warming caused an initial negative responses in within site diversity in the heath (Alatalo et al. 2015c) which remained negative in the long term (this study). Also, dominant species of the heath vegetation were more susceptible to shrubification. The meadow community showed an initial rapid negative response (until 2001), after which it started to recover, but it had not returned to its initial status after 18 years of warming. In terms of phylogenetic diversity, the long-term warming caused a significant negative effect on the three orders of phylogenetic Hill diversity in the meadow. While there was a similar tendency in the heath, only phylogenetic diversity of dominant species was significantly affected. The observed reduction in phylogenetic diversity of both communities can be considered an indication of loss of rare and phylogenetically diverse species, as the final colonising species have lower phylogenetic diversity because they come from related taxa. Notably, forbs and graminoids showed a larger turn-over in species composition during 18-year experiment in meadow, while shrubs showed a much lower turn-over in the heath. However, this difference in species turn-over could potentially be explained by differences in their longevity. With forbs and graminoids including more short-lived species compared to shrub species.

In a previous study at our site, seven years of warming caused a significant decline in total species richness (Alatalo et al. 2014). These results confirm findings in other studies that mesic meadow communities tend to be more vulnerable than drier sites in terms of species loss (Elmendorf et al. 2012). At our study site, long-term warming has caused a decrease in soil moisture in the meadow community, but not in the heath community (Alatalo et al. 2017b). This could potentially help to explain the differences in responses between these plant communities. Decreased soil moisture due to experimental warming has been reported to be accompanied by an decrease in sedges and an increase in grasses and forbs in a meadow community in Tibet following short-term experimental warming (Peng et al. 2017). However, in our meadow site we found a more complex response pattern over time, initially sedges decreased (Alatalo et al. 2014), while they increased over long-term (this study). This later increase in sedges was mainly driven by *Carex vaginata,* while the initial shorter term responses were dominated by changes in abundance of *Carex bigelowii* (Jägerbrand et al. 2009). Thus, negative effects on species and phylogenetic diversity may be driven by an indirect effect of decreased moisture levels due to warming, not by the warming itself. In addition, both the responses, and major drivers (species), may also change over time.

Cushion-forming plants are important in alpine areas due to their function as facilitator species (Cavieres et al. 2014; Anthelme et al. 2014). The shorter-term results (1995-2001) from our experiment showed that the dominant cushion-forming plant at the site, *Silene acaulis*, was highly plastic in its phenotypic responses in terms of growth-related plant traits to nutrient addition and combined nutrient addition and warming, while warming alone had no effect on growth and abundance (Alatalo and Little 2014). In the present longer-term study, the PCR showed that *S. acaulis* only decreased slightly in response to 18 years of warming, thus, the studied population is likely resistant to warming that is not accompanied by an increase of nutrients. The dominant cushion plant in the meadow *Silene acaulis* has a taproot, thus as the soil became drier in the warmed plots (Alatalo et al. 2017b), having taproot could have become an advantage compared to more shallow-rooted species over the longer term. However, a previous study has shown that *S. acaulis* populations across the species distribution range may respond in different ways, with southern populations of *S. acaulis* having higher growth rates than northern populations in North America, but lower survival and recruitment (Doak and Morris 2010). That study also found that the warmest years had a negative effect on survival and fruit production, but that moderately warmer years had a positive effect (Doak and Morris 2010). In contrast, a recent study showed that northern populations of *S. acaulis* may decline while more southern populations may remain stable (Peterson et al. 2018). This highlights the difficulty in predicting plant species responses to climate change, as both life history plasticity and local adaptation will affect species responses to warming (Peterson et al. 2018).

Conclusions

This study found that responses in plant species composition and phylogenetic diversity to experimental warming varied both in time (medium vs long-term) and space (neighbouring heath and meadow communities). The heath community was more negatively affected in terms of species composition and patch-scale responses than the meadow community. However, the meadow community showed a larger decrease in species and in phylogenetic diversity than the heath community. Long-term warming caused differentiation in species composition in both communities, with shrubification and decreases in graminoids being observed in the heath community and increases in cushion-forming plants in the meadow community. A potential driver for the changes in the meadow community may be decreased soil moisture caused by the long-term warming (18 years).

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Authors' contributions

JMA and UM designed the experiment, JMA, AJ and UM carried out fieldwork. JMA, MBE and SC carried out data analyses, MBE prepared the figures and tables. JMA and MBE drafted the manuscript. All authors read, commented on and approved the final manuscript.

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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.

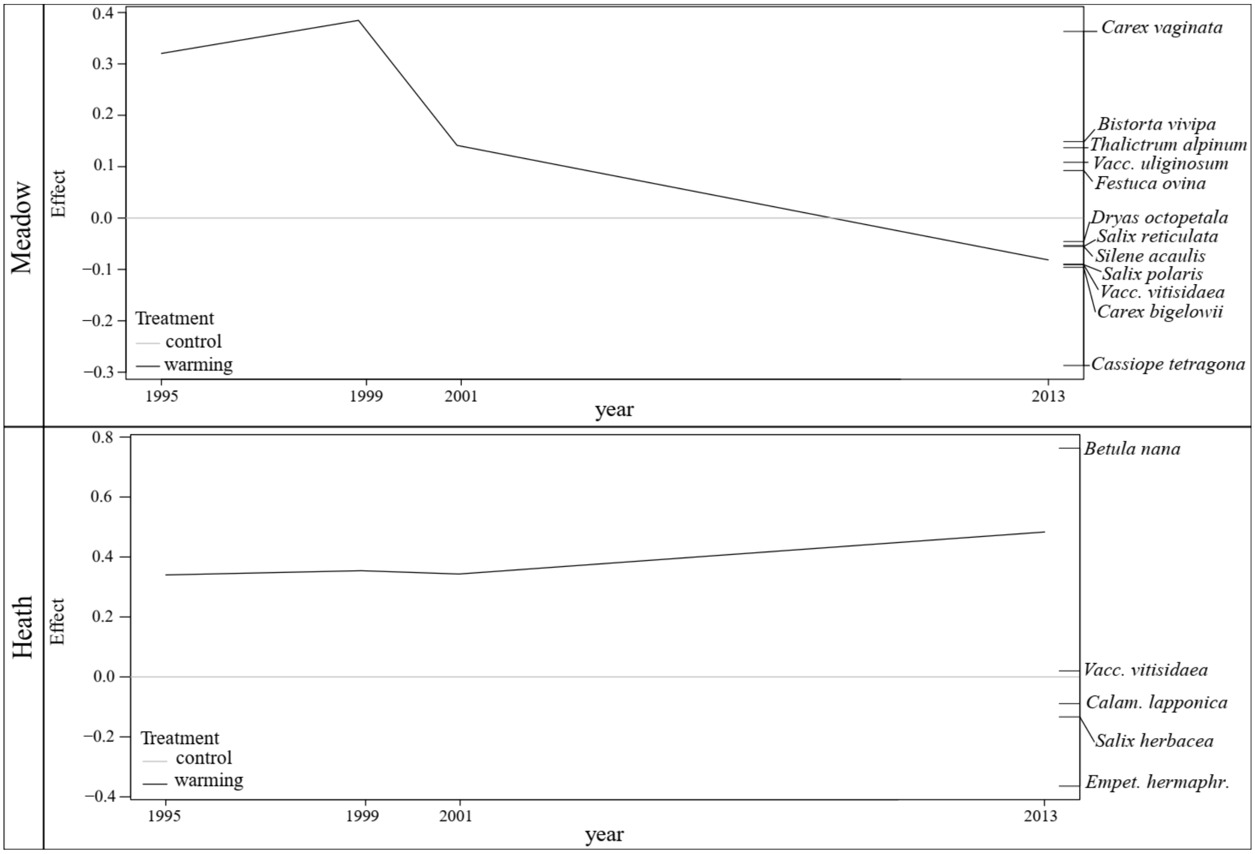

Figure 2. Relative changes in within-site beta diversity in response to long-term warming (1995-2013) in an alpine heath community and a meadow community at Latnjajaure, subarctic Sweden. Values represent mean and 95% confidence intervals.

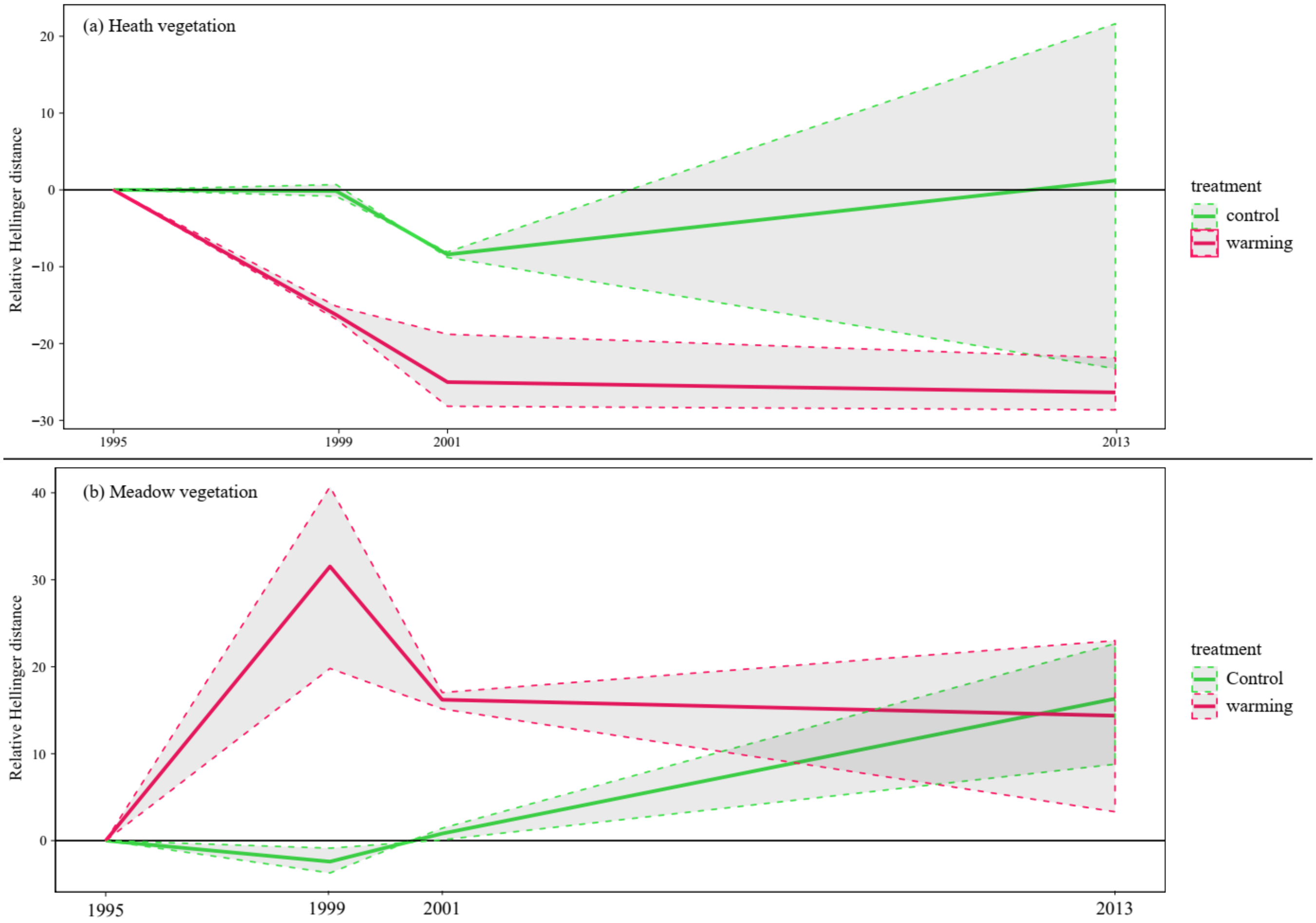

Figure 3. Changes in species diversity in response to long-term warming (1995-2013) in an alpine heath community and a meadow community at Latnjajaure, subarctic Sweden. Species diversity at the level of rare, frequent and dominant species in the community, indicated by q = 0 (species richness, in the Hill species diversity formula), q =1 (exponential of Shannon diversity, effective number of species) and q = 2 (reciprocal of Simpson index), respectively.

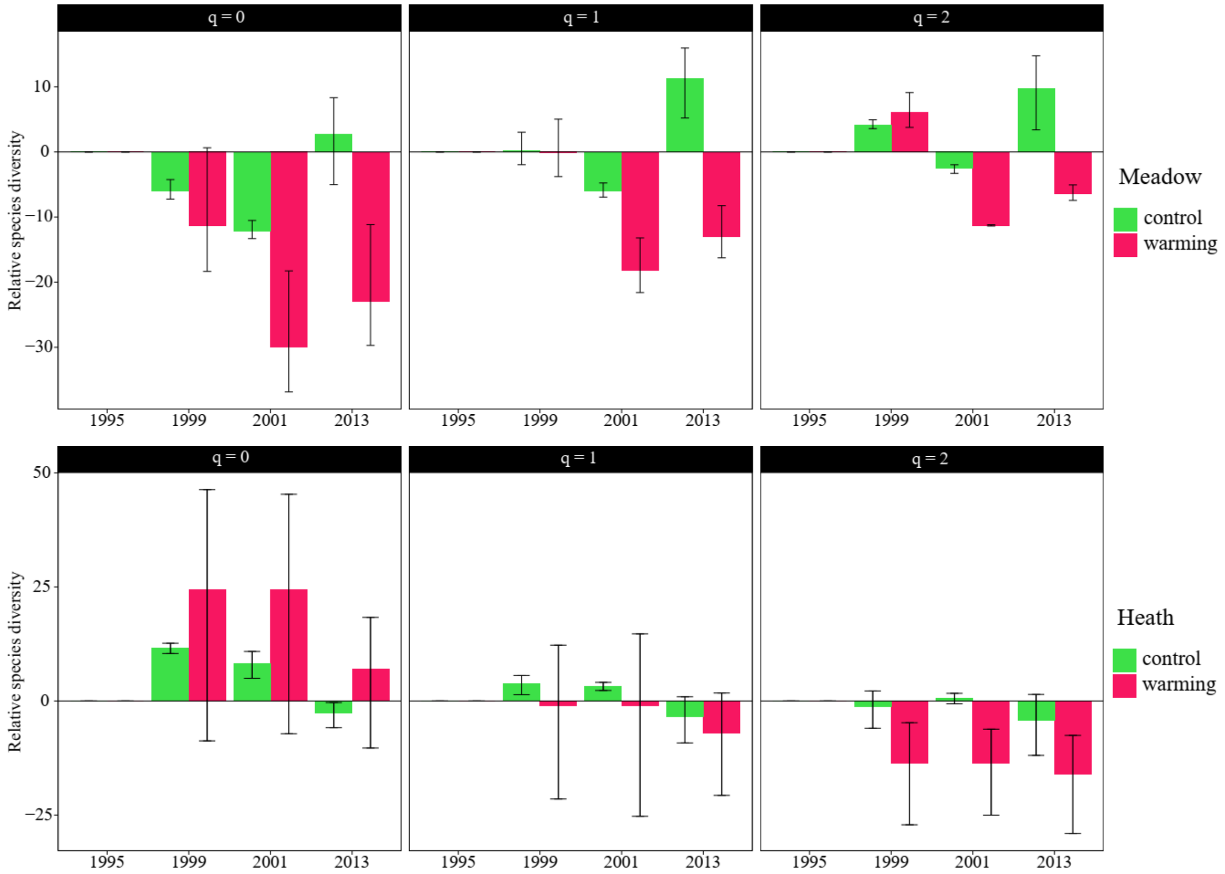

Figure 4. Changes in phylogenetic diversity (Hill diversity indices at the level of rare (q=0), frequent (q=1), and dominant (q=2) species) in response to long-term warming (1995-2013) in an alpine heath community and a meadow community at Latnjajaure, subarctic Sweden. Values represent mean and 95% confidence intervals.

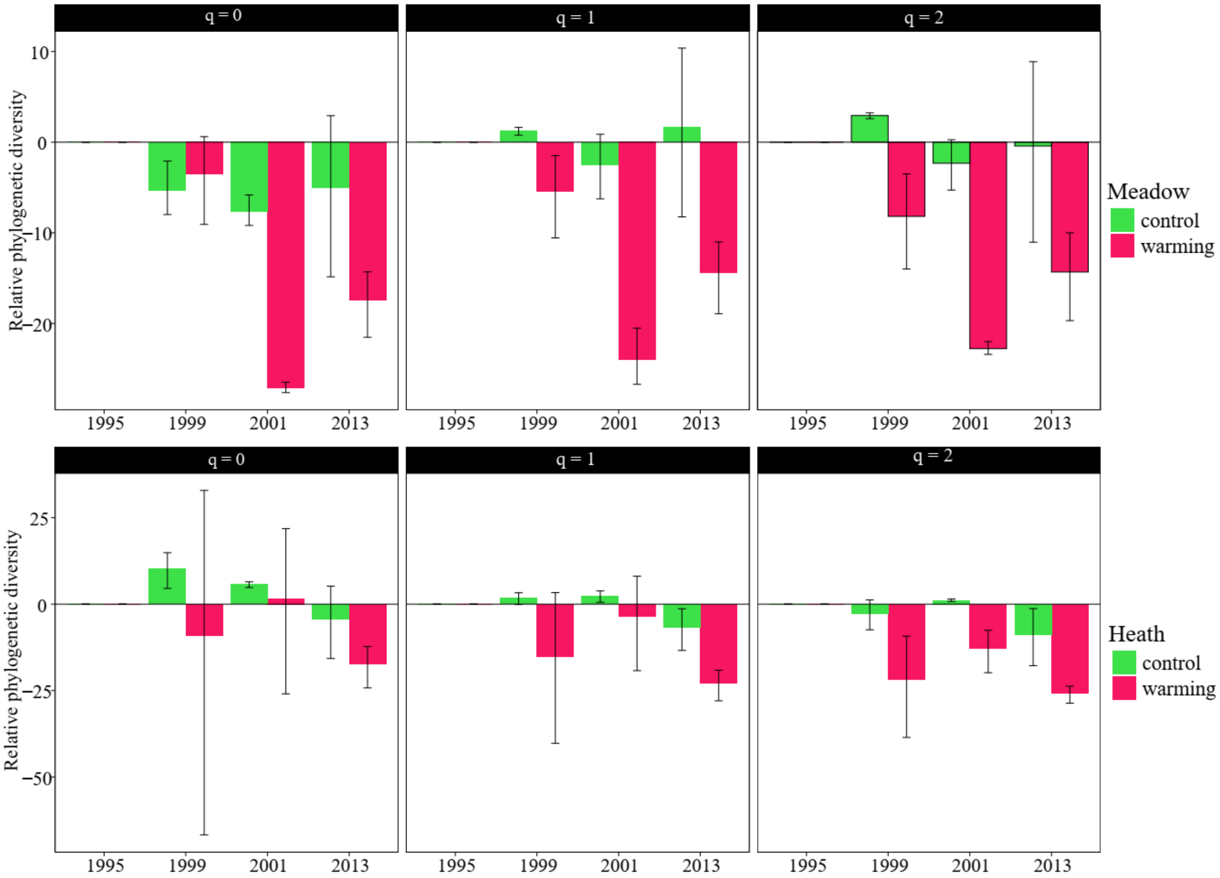

Figure 5. Dominance structure (% of total cover) of different plant functional groups, by treatment (warming, control) and year (1995, 1999, 2001, 2013), in a long-term warming experiment in an alpine heath community and a meadow community at Latnjajaure, subarctic Sweden.

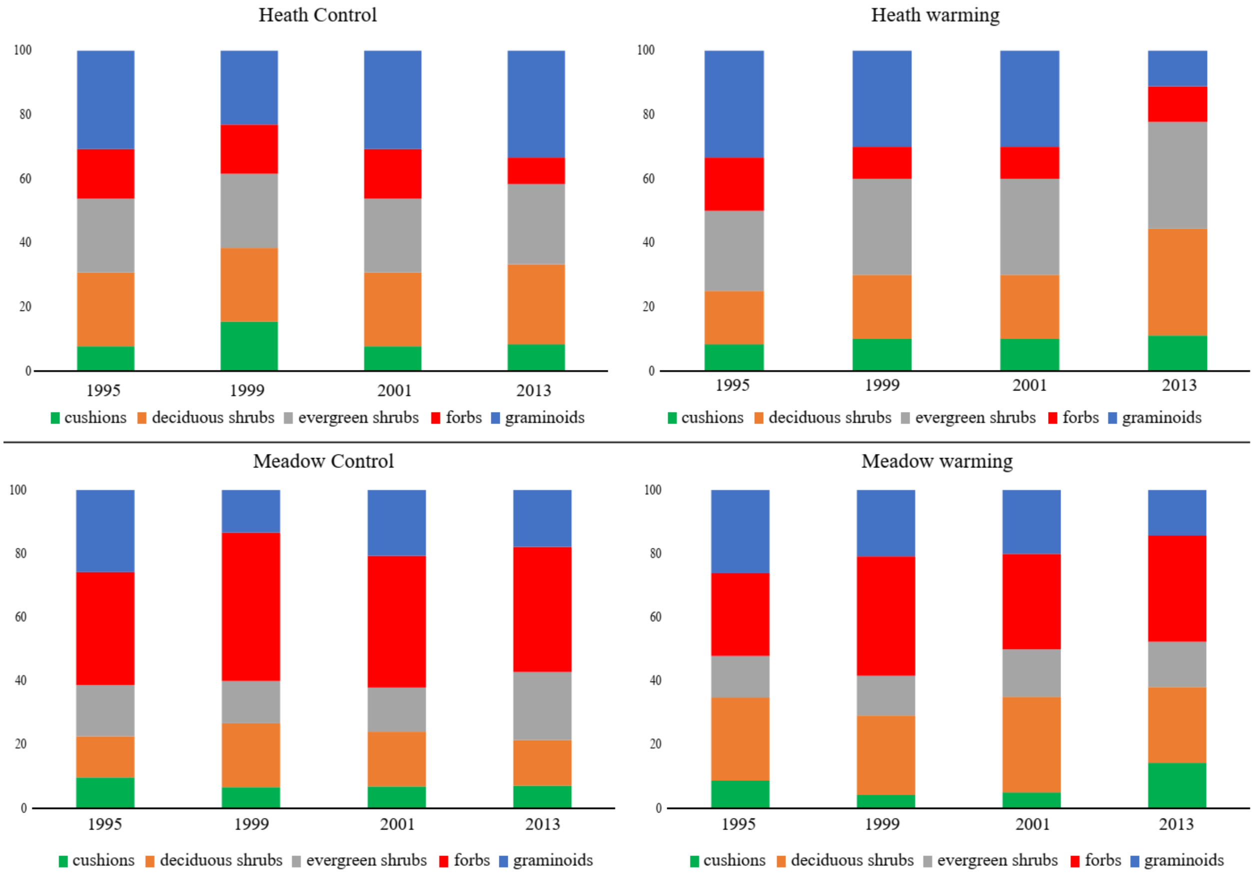

Table 1. Changes in species composition (measured as Hellinger dissimilarity) of different plant functional groups in response to long-term warming (1995-2013) in an alpine heath community and a meadow community at Latnjajaure, subarctic Sweden. Cushions = cushion-forming plants, D. = deciduous shrubs, 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