



# Changes in plant composition and diversity in an alpine heath and meadow after 18 years of experimental warming

Juha M. Alatalo<sup>1</sup> · Mohammad Bagher Erfanian<sup>2</sup> · Ulf Molau<sup>3</sup> · Shengbin Chen<sup>4</sup> · Yang Bai<sup>5</sup> · Annika K. Jägerbrand<sup>6</sup>

Received: 7 February 2021 / Accepted: 28 September 2021 / Published online: 9 October 2021  
© Swiss Botanical Society 2021

## Abstract

Global warming is expected to have large impacts on high alpine and Arctic ecosystems in the future. Here we report effects of 18 years of experimental warming on two contrasting high alpine plant communities in subarctic Sweden. Using open-top chambers, we analysed effects of long-term passive experimental warming on a heath and a meadow. We determined the impact on species composition, species diversity (at the level of rare, common and dominant species), and phylogenetic and functional diversity. Long-term warming drove differentiation in species composition in both communities; warmed plots, but not control plots, had distinctly different species composition in 2013 compared with 1995. Beta diversity increased in the meadow, while it decreased in the heath. Long-term warming had significant negative effects on the three orders of phylogenetic Hill diversity in the meadow. There was a similar tendency in the heath, but only phylogenetic diversity of dominant species was significantly affected. Long-term warming caused reductions in forbs in the heath, while evergreen shrubs increased. In the meadow, deciduous and evergreen shrubs showed increased abundance from 2001 to 2013 in warmed plots. Responses in species and phylogenetic diversity to experimental warming varied over both time (medium (7 years) vs long-term (18 years)) and space (between two neighbouring plant communities). 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 long-term warming.

**Keywords** Arctic · Climate change · Species diversity · Species richness · Tundra

## 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 shifts are possible (Kidane et al. 2019). In addition, global warming may seriously shrink suitable habitats (Ferrarini et al. 2019a) and cause local extinction of species at the extreme of their distribution range (Ferrarini et al. 2016; Hampe and Petit 2005). Global warming has already been shown to cause range shifts (Chen et al. 2011; Kullman 2002; Steinbauer et al. 2019) and composition shifts (Evangelista et al. 2016; Koltz et al. 2018; Liberati et al. 2019; Rosbakh et al. 2014). A widespread trend at many alpine and Arctic sites is an increase in shrubs (Jägerbrand et al. 2009; Maliniemi et al. 2018; Myers-Smith et al. 2011; Vowles and Björk 2019). Other plant groups (forbs and graminoids) have more inconsistent responses (Elmendorf et al. 2012; Vowles

✉ Juha M. Alatalo  
jalatalo@qu.edu.qa

<sup>1</sup> Environmental Science Center, Qatar University, PO Box 2713, Doha, Qatar

<sup>2</sup> Quantitative Plant Ecology and Biodiversity Research Lab, Department of Biology, Faculty of Science, Ferdowsi University of Mashhad, Mashhad, Iran

<sup>3</sup> Department of Biological and Environmental Sciences, University of Gothenburg, PO Box 461, 405 30 Gothenburg, Sweden

<sup>4</sup> College of Ecology and Environment, Chengdu University of Technology, Chengdu 610041, China

<sup>5</sup> Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Mengla 666303, Yunnan, China

<sup>6</sup> Department of Environmental and Biosciences, School of Business, Innovation and Sustainability, Halmstad University, P.O. Box 823, 301 18 Halmstad, Sweden

et al. 2017). However, a meta-analysis of 61 warming experiments in tundra vegetation found that graminoids tended to increase at colder sites, while showing neutral or negative responses at warmer sites (Elmendorf et al. 2012). Cushion plants, such as the widespread *Silene acaulis*, are predicted to be vulnerable to climate change in alpine areas (Doak and Morris 2010; Ferrarini et al. 2019a, b). However, many plant species in polar and alpine regions are long-lived (Ferrarini et al. 2019a; Morris and Doak 1998). Thus, even when conditions at a site become unfavourable due to environmental change, long-lived 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, we are not aware of any long-term (> 10 years) experimental studies that have tried to mimic the predicted increase of interannual variability of climatic factors, or different types of warming scenarios (ex. different levels of warming, increased warming with years, or occasional heat waves). Those conducted to date are short term. One previous study has applied a high level of warming, simulating a heat wave for 2 weeks in Greenland (Marchand et al. 2006), one study has applied low level, high level and increasing warming for 4 years in sub-arctic alpine Sweden (Alatalo et al. 2016), and one study has applied low and high levels of warming for 5 years in sub-arctic alpine Sweden (Jonasson et al. 1999).

Solar radiation and temperature have been shown to be dominant factors controlling net primary production in alpine meadows and grasslands in Tibet (Wang et al. 2018; Zheng et al. 2020) and Scotland (Gimona et al. 2006), while summer precipitation is an important driver for species richness in Tibet (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 learnt that short- (1–3 years), medium- (4–7 years) and longer term (> 10 years) responses may differ (Alatalo et al. 2015b; Alatalo and Little 2014; Baruah et al. 2018; Hollister et al. 2005; Kremers et al. 2015; Walker et al. 2020).

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 in 1995, on a nutrient- and species-poor heath and a more species- and nutrient-rich mesic meadow, we have previously reported on short- and medium-term responses and the impact of long-term warming on lichens (Alatalo et al. 2017a), bryophytes (Alatalo

et al. 2020), soil fauna (Alatalo et al. 2015a, 2017b), and plant traits (Baruah et al. 2017).

In the present study, we examined the effect of 18 years of experimental warming on vascular plant communities. Specifically, we determined the impact on species composition, species diversity (at the level of rare, common and dominant species of each community), and phylogenetic and functional diversity of vascular plants. We hypothesised that (1) the effect of experimental warming is greater over time compared with in the early years of the experiment (Komatsu et al. 2019). Specifically, we hypothesised that long-term warming would have (2) a negative impact on species richness and diversity in the meadow, with well-developed vegetation cover, due to increased competition between species following lower environmental stress (as temperature increases), and (3) a positive impact on species richness and diversity in the heath, with its less developed vegetation cover allowing species to colonise new space.

## Materials and methods

### 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 around 8 months of the year (usually from October to May), 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 (Alatalo et al. 2017a) are supplied in electronic supplementary materials to this paper. Physical conditions in the soils in the valley vary from dry, acidic and nutrient-poor to wet, base-rich and more nutrient-rich, with an associated variation in plant communities (Alatalo et al. 2017b; Björk et al. 2007; Lindblad et al. 2006; Sarneel et al. 2020).

The mesic meadow community has a vegetation averaging 67% canopy cover (Alatalo et al. 2017a), dominated by *Carex vaginata*, *Carex bigelowii*, *Festuca ovina*, *Salix reticulata*, *Salix polaris*, *Cassiope tetragona*, *Bistorta vivipara* and

*Thalictrum alpinum* (Alatalo et al. 2014; Molau and Alatalo 1998). The more sparsely vegetated poor heath community (average 54% canopy cover) (Alatalo et al. 2017a) is dominated by *Betula nana*, *Salix herbacea* and *Calamagrostis lapponica* (Alatalo et al. 2015c; Molau and Alatalo 1998). The mesic meadow has thicker soil cover and higher soil nutrient and moisture content than the heath (for details, see Alatalo et al. (2017b)).

## Experimental design and measurements

In July 1995, twelve 1 m × 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 2013. The experimental site was dismantled in 2016 (2013 being the last year of plant measurements). For 1995–2001, we used data from eight control plots. 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™ and Tinytag™ loggers (Molau and Alatalo 1998). As found in other studies (Hollister and Webber 2000; Marion et al. 1997; Molau and Alatalo 1998), the OTCs increased the air temperature by 1.5–3 °C compared with control plots with ambient temperature (Molau and Alatalo 1998). OTCs have also been shown to decrease canopy moisture (Hollister and Webber 2000), causing earlier snow melt and prolonging the growing season (Hollister and Webber 2000; Molau and Alatalo 1998).

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 as suggested by Kent et al. (2011). 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).

## Data analysis

### Community composition

The effect of the warming treatment over time on species composition in both plant communities was evaluated using principal response curves (PRC), which show the community-level treatment effects over time compared with the control and enable species-level changes to be interpreted (Van den Brink and Braak 1999). Monte Carlo permutation tests were performed to evaluate the statistical significance of differences between each treatment and the control. The PRC and permutation tests were performed using the vegan package (Oksanen et al. 2017).

We also evaluated temporal variation in species composition within each plant community in each year (i.e., within-site beta diversity), to test whether small-scale (i.e., plot) conditions can lead to different responses in the plant communities 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) 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).

### 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 the standard tool for calculating and comparing species diversity (Erfanian et al. 2019a). We considered species richness ( $q=0$  in the Hill species diversity formula), the exponential of Shannon diversity ( $q=1$ ) and the reciprocal of the Simpson index ( $q=2$ ), which reveal the diversity of rare, common and dominant species, respectively (Chao et al. 2014a, b; Erfanian et al. 2019b). 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 study (Kent 2011). 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 et al. 2014b; Chao and Jost 2012). The 95% 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. Positive and negative values of relativised diversity indicate higher or lower diversity, respectively, compared with the 1995 baseline.

### 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 2016; Faith and Baker 2006). 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 ( $q=0$ ), common ( $q=1$ ) 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.

### Functional diversity

Changes in the dominance structure of five functional groups of vascular plants (cushion-forming plants, deciduous shrubs, evergreen shrubs, forbs and grasses) were evaluated. Cushion plants included *Diapensia lapponica*, *Harrimanella hypnoides*, *Saxifraga oppositifolia* and *Silene acaulis*. All these species can form more or less dense cushions depending on the physical conditions at the growing site. For example, the growth form of *S. acaulis* can change substantially

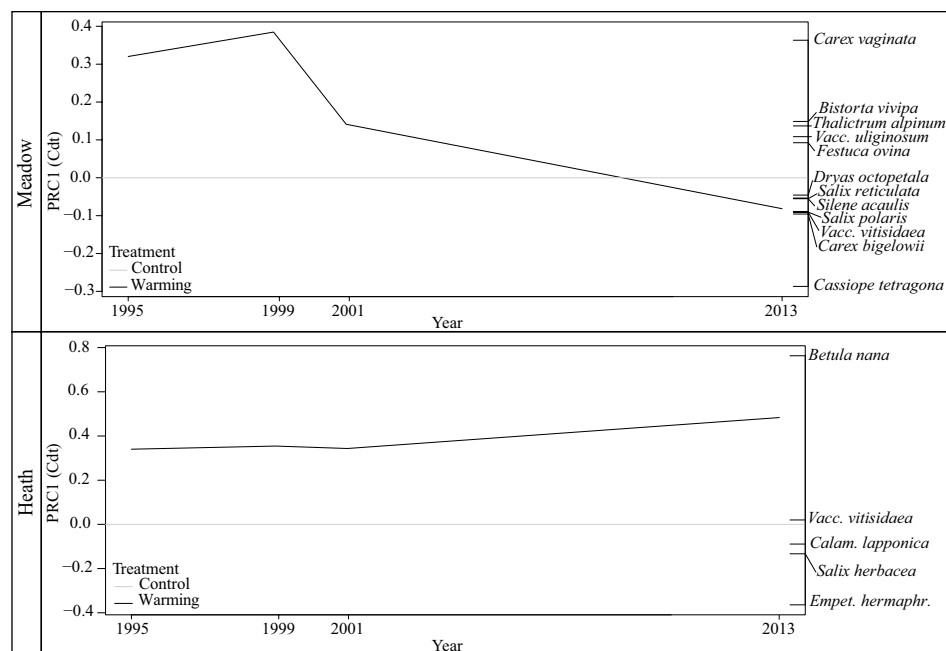
along an elevation gradient (Bonanomi et al. 2015). Due to low numbers of observations in some groups, we could not statistically compare these results. Boxplots were drawn to visualise relative changes in functional group abundance between control and warming plots. For relativisation, abundance data for control and warming plots were subtracted from the median of the abundance of control plots in 1995. The resulting value was divided by the median abundance in control plots in 1995. This result was multiplied by 100, to show the percentage change in functional group abundance during the 18 years of the experiment. Thus, negative values in boxplots indicate decreased abundance, while positive values show increased abundance of functional types compared with the median of the control community. For visualisation, the percentage values were log-transformed. The Hellinger distance was calculated separately for each functional group, to assess the species turnover within groups.

## Results

### Species composition

The PRC analysis results revealed a significant difference ( $p$  value = 0.039,  $F$  value = 7.166) between control and warming plots of the heath community in terms of species composition. The PRC analysis explained 16% of the variance, and 15.35% of this variance contributed to the first axis (Fig. 1). For the meadow vegetation, the PRC analysis did not detect a significant difference ( $p$  value = 0.659,  $F$  value = 1.814) between species composition of control and warming plots. About 9% of variance was explained by the PRC analysis

**Fig. 1** Principal response curve (PRC) showing the effect of warming treatment over time on vascular plant species in heath and meadow vegetation at Latnjajaure, northern Sweden. Only species with relative frequency sum > 1 are shown



and 7.56% of this explained variance contributed to the first axis. Only species with relative frequency sum above 1 are shown in Fig. 1. In meadow vegetation, *Carex vaginata* showed the greatest average abundance increase and *Cassiope tetragona* showed the greatest average abundance decrease (Fig. 1). In heath vegetation, *Betula nana* showed the greatest increase in average abundance and *Empetrum hermaphroditum* showed the greatest decrease (Fig. 1).

Long-term warming led to a significant decrease in beta diversity in the heath plots over time (Fig. 2), but to increased beta diversity in the meadow plots (Fig. 2). From 2001 to 2013, the beta diversity in warming plots stabilised for both vegetation types. In 2013, for both vegetation types, there was no significant difference between beta diversity of control and warming plots. In the heath, the difference between control and warming plots was significant from 1999 until 2001, while in 2013 the confidence intervals overlapped slightly. In the meadow, the difference between control and warming plots was significant in 1999 and 2001. In meadow control plots, beta diversity started to increase from 2001.

## Species diversity

For meadow vegetation, except in the year 1999, warming had a significant negative effect on all three orders of Hill species diversity (i.e.,  $q=0$ , 1 and 2) compared with the control (Fig. 3).

For heath vegetation, except for dominant species in 2001, there were no significant differences in species diversity (i.e., species richness ( $q=0$ , including rare species), the

exponential of Shannon diversity ( $q=1$ , or common species) and the reciprocal of the Simpson index ( $q=2$ , or dominant species)) between warming and control plots (Fig. 3).

## Phylogenetic diversity

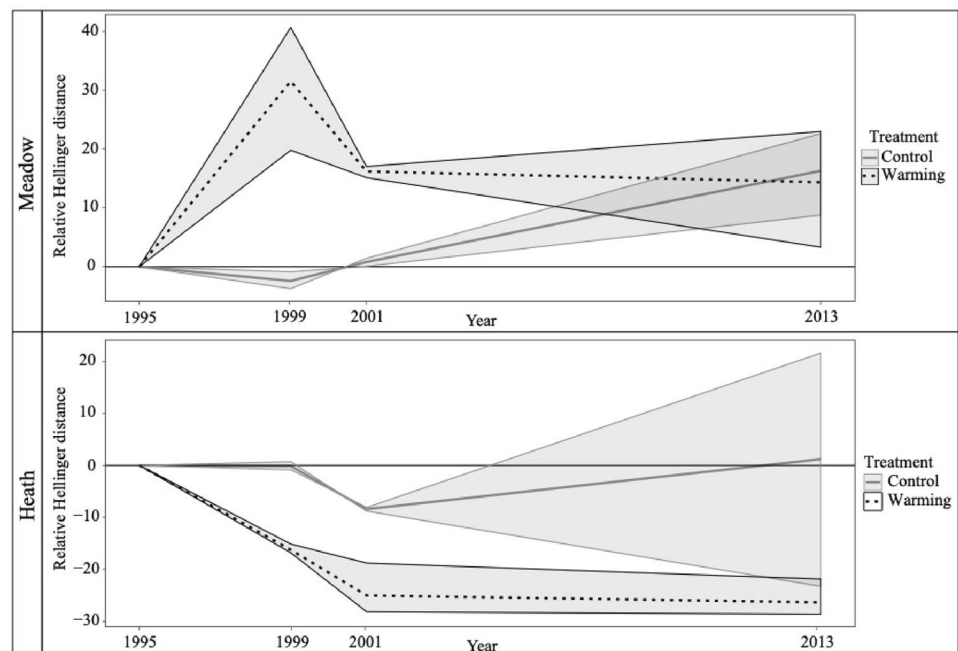
Comparison of phylogenetic diversity (hereafter PD) estimates for control and warming plots in the meadow showed that there was a significant difference between these two treatments in the 2001 inventory (Fig. 4). In 1999, PD at the level of  $q=1$  (common species) and 2 (dominant species) differed significantly between the control and warming treatment. In 2013, only PD at the level of  $q=1$  (common species) showed a significant difference between control and warming plots. In all the above cases, warming had a negative effect.

In the heath vegetation, at the level of  $q=2$  warming plots showed significantly lower PD than control plots (Fig. 4). This was also observed in 2013 at the level of  $q=1$ . No significant difference was detected between control and warming plots at the PD level of  $q=0$ .

## Functional diversity

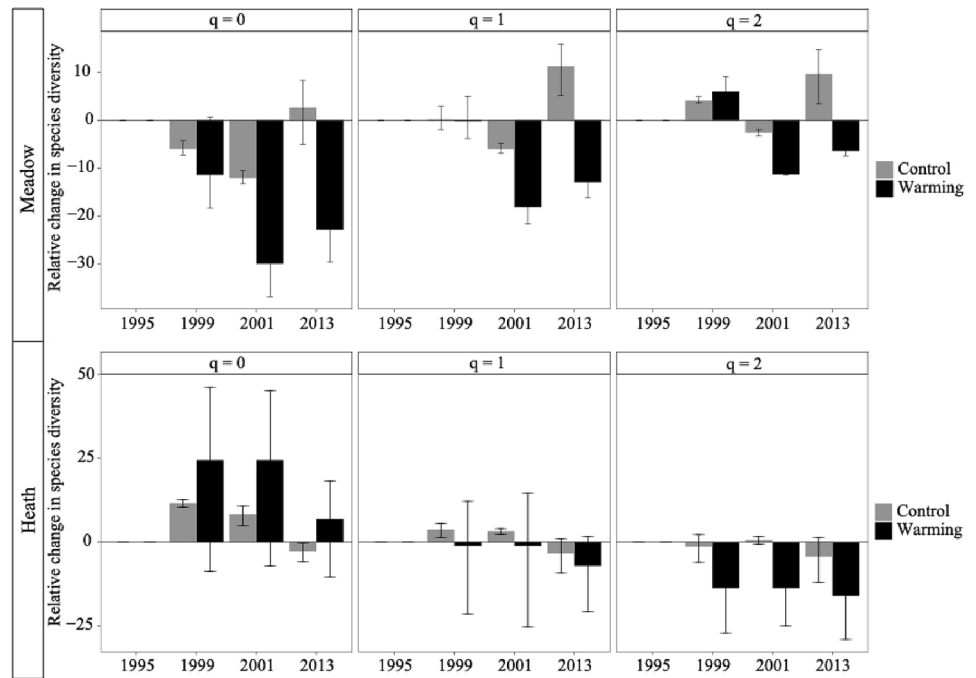
In meadow warming plots, abundance of cushion plants remained unaffected over time, but abundance of deciduous shrubs increased (Fig. 5). Control plots of both vegetation types also showed increased abundance of deciduous shrubs from 1995 until 2001. However, by 2013, the abundance of deciduous shrubs had decreased in the control plots in both communities (Fig. 5). In the meadow,

**Fig. 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. 1995 data used as baseline

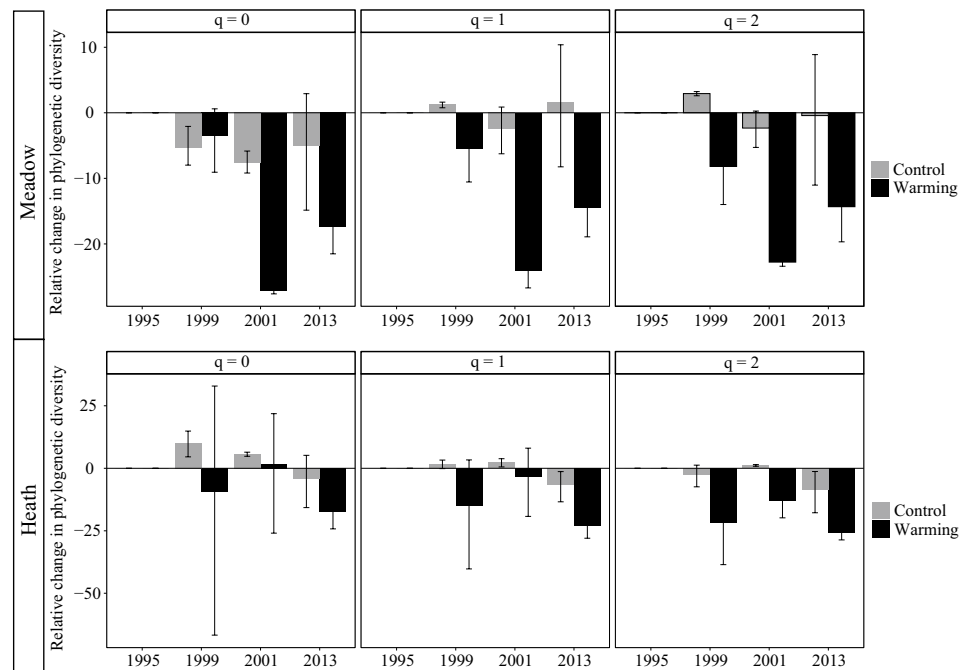




**Fig. 3** Changes in species diversity in response to long-term warming (1995–2013) in an alpine heath community and a meadow community at Latnjajaure, subarctic Sweden. Species diversity is shown at the level of rare, common and dominant species in the community, indicated by  $q=0$  (species richness),  $q=1$  (exponential of Shannon diversity) and  $q=2$  (reciprocal of Simpson index), respectively. 1995 data used as baseline



**Fig. 4** Changes in phylogenetic diversity (Hill diversity indices at the level of rare ( $q=0$ ), common ( $q=1$ ), 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. 1995 data used as baseline

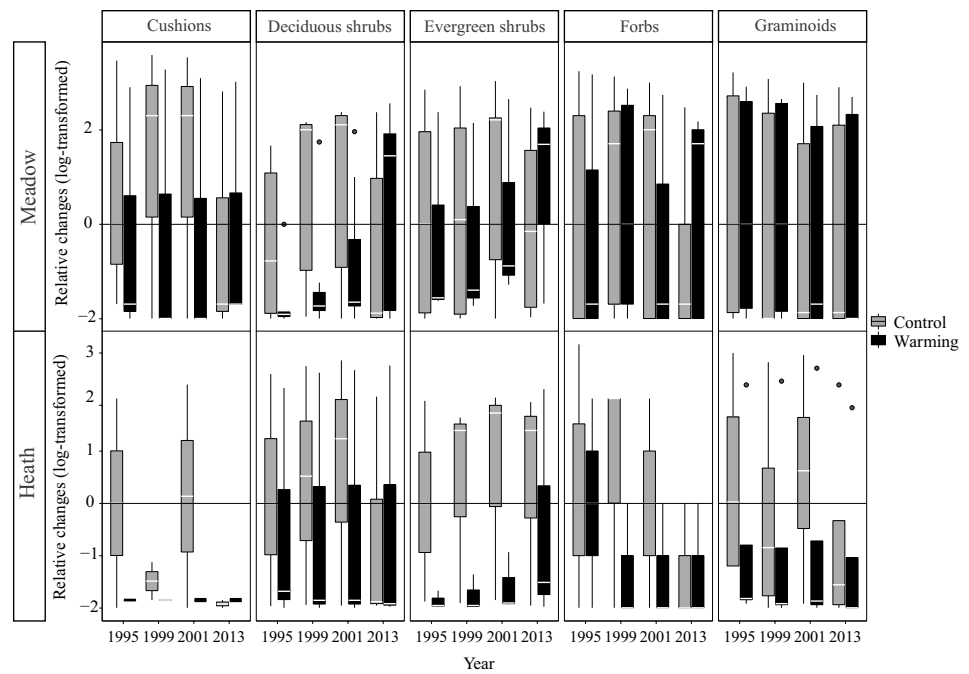


evergreen shrub abundance remained similar over time in control plots, but increased in warming plots. In the heath, abundance of evergreen shrubs increased over time in both warming and control plots (Fig. 5). Forb abundance remained unchanged in the warming plots in the meadow, while it decreased over time in the warming plots in the heath (Fig. 5). Graminoid abundance remained stable over time in both control and warming plots in the meadow,

and in warming plots in the heath. However, graminoid abundance decreased in the control plots in 2013 (Fig. 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

**Fig. 5** Boxplots showing relative changes in abundance of cushion plants, deciduous shrubs, evergreen shrubs, forbs and graminoids over time in control (green) and warmed (red) plots in meadow (top panel) and heath (bottom panel) vegetation at Latnjajaure, northern 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

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

Cushions = cushion-forming plants, D. = deciduous shrubs, E. = evergreen shrubs

low species turnover in both warmed and control plots. In contrast, forbs and graminoids showed moderate species

turnover from 1995 to 2013 in both warmed and control plots.

### Discussion

This study examined the impact of long-term experimental warming on species composition and species, phylogenetic and functional diversity. Our hypothesis (1) was partially supported, since the effect of experimental warming was greater from year seven of the experiment in the meadow, but not in the heath. Moreover, in the meadow, the 7-year responses were more pronounced than the responses in year 18. Our hypothesis (2) was fully supported, as long-term warming had a negative impact on species richness and diversity in the meadow. However, long-term warming had no positive effect on species richness and diversity in the heath, contradicting our hypothesis (3).

Ambient temperature at the experimental site showed an increase of around 2 °C during the study period (Alatalo et al. 2017a). Thus, plants growing in control plots also experienced warmer conditions and plants in the warmed plots were exposed to a greater temperature increase than initially intended (~2 °C experimental warming plus ~2 °C ambient warming). Long-term warming (18 years) drove differentiation in species composition of the heath vegetation over time, with the warmed plots ending up with distinctly different species composition in 2013 compared with 1995. In the meadow, warming caused deciduous and evergreen shrubs to increase in abundance, while graminoids as a group remained stable. However, warming caused some

graminoid species (e.g. *Carex vaginata* and *Festuca ovina*) to increase in abundance in the meadow. A previous study at the same site found that 7 years of experimental warming caused sedges to decline in the meadow (Alatalo et al. 2014). Thus, the short-term and longer term responses differed. Previous studies have found that the effects of experimental treatments increase with time (larger effects after 10 years) (Komatsu et al. 2019). Similarly, we found that the majority of changes occurred from year 7 in our 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 warming increased deciduous shrubs markedly in the meadow plots, but not in the nearby heath plots studied at the site, while evergreen shrubs increased in both communities. Deciduous shrubs showed a similar positive effect of experimental warming in the initial 5-year response at our site (Jägerbrand et al. 2009), and in Alaskan Tundra (Chapin III and Shaver 1985, 1996). In addition, a long-term monitoring study in High Arctic Canada experiencing natural warming found 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 (Lamprecht et al. 2018; Matteodo et al. 2016) 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 the meadow vegetation responded to climate changes in different ways. 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 concluded 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 homogenisation 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).

While not applying experimental warming, 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). The

two plant communities at our study site in northern Sweden responded with contrasting patterns at different levels of species diversity (rare, common and dominant species) to the ambient temperature and experimental warming treatments over time. Experimental warming caused an initial negative response in within-site diversity in the heath (Alatalo et al. 2015c), which remained negative in the long term (this study). While the heath experienced a decrease in dominant species ( $q=2$ ) evergreen shrubs increased in abundance. In alpine Colorado, increases in shrub abundance and plant litter under ambient climate conditions was accompanied by a decrease in forbs, graminoids and non-vascular plants (Scharnagl et al. 2019). The meadow community at our study site 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 had 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 in meadow showed larger turnover in species composition during the 18-year experiment, while shrubs showed much lower turnover in the heath. However, these differences in species turnover could potentially be explained by differences in their longevity, with forbs and graminoids including more short-lived species than shrubs.

In a previous study at our site, it was shown that 7 years of warming caused a significant decline in total species richness (Alatalo et al. 2014). These results support indications in other studies that mesic meadow communities tend to be more vulnerable than drier sites in terms of species loss (Elmendorf et al. 2012). However, several studies have shown that plants in tundra and alpine ecosystems are often nutrient-limited (Eskelinen et al. 2017; Haag 1974; Soudzilovskaia et al. 2005). As nitrogen mineralisation has been shown to increase due to increased microbial activity in response to warming, plants on thicker, more nutrient-rich soils that are normally limited by temperature/short growing season can be expected to respond more positively to warming/extended growing season than plants growing in thinner soils with nutrient-poor conditions (Rustad et al. 2001). However, microbial responses to warming in alpine areas also depend on precipitation levels (Hu et al. 2020). In our long-term experiment, long-term warming 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 a 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), with meadows becoming more similar to heaths in alpine Sweden (Scharn et al. 2021). However, at our meadow site we found a more complex response pattern over time, as sedges decreased initially (Alatalo et al. 2014), but increased over the longer 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 indirectly by decreased moisture levels due to warming, not by the warming itself (Scharn et al. 2021). In addition, both the responses and major drivers (species) may change over time.

Cushion-forming plants are important in alpine areas due to their function as facilitator species (Anthelme et al. 2014; Cavieres 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 PRC showed that *S. acaulis* only decreased slightly in response to 18 years of warming, so the studied population is likely resistant to warming that is not accompanied by an increase in nutrients. The dominant cushion plant in the meadow, *S. acaulis*, has a taproot. As the soil became drier in the warmed plots (Alatalo et al. 2017b), having a taproot could have provided an advantage over more shallow-rooted species in 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 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).

In addition, different types of environmental disturbance, such as grazing and land degradation status (depending on the status of human land use intensity) (Erfanian et al. 2019a), experimental warming, nutrient addition and changes in light regime (Jonasson et al.

1999), may have different effects on plant communities. 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 (Komatsu et al. 2019). 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 community composition 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. Unfortunately, our experimental site was dismantled in 2016.

## 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 community-level 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 the two communities, with shrubification in both communities and decreases in forbs in the heath community. A potential driver for the changes in the meadow community may be decreased soil moisture caused by the long-term warming.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00035-021-00272-9>.

**Acknowledgements** The authors thank the staff of Abisko Scientific Research Station for their help and hospitality, and Matthias Molau for assistance in the field. We thank two anonymous reviewers for their constructive criticism that improved the manuscript.

**Author 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, and JMA and MBE drafted the manuscript. All authors read, commented on and approved the final manuscript.

**Funding** This study was supported by Carl Tryggers stiftelse för vetenskaplig forskning and Qatar Petroleum to JMA.

**Data availability statement** Data used for analyses are included in the electronic supplementary materials.

## Declarations

**Conflict of interests** None to declare.

## References

- Alatalo JM, Little CJ (2014) Simulated global change: contrasting short and medium term growth and reproductive responses of a common alpine/Arctic cushion plant to experimental warming and nutrient enhancement. *Springerplus* 3:157. <https://doi.org/10.1186/2193-1801-3-157>
- Alatalo JM, Little CJ, Jägerbrand AK, Molau U (2014) Dominance hierarchies, diversity and species richness of vascular plants in an alpine meadow: contrasting short and medium term responses to simulated global change. *PeerJ* 2:e406. <https://doi.org/10.7717/peerj.406>
- Alatalo JM, Jägerbrand AK, Čuchta P (2015a) Collembola at three alpine subarctic sites resistant to twenty years of experimental warming. *Sci Rep* 5:18161. <https://doi.org/10.1038/srep18161>
- Alatalo JM, Jägerbrand AK, Molau U (2015b) Testing reliability of short-term responses to predict longer-term responses of bryophytes and lichens to environmental change. *Ecol Ind* 58:77–85. <https://doi.org/10.1016/j.ecolind.2015.05.050>
- Alatalo JM, Little CJ, Jägerbrand AK, Molau U (2015c) Vascular plant abundance and diversity in an alpine heath under observed and simulated global change. *Sci Rep* 5:10197. <https://doi.org/10.1038/srep10197>
- Alatalo JM, Jägerbrand AK, Molau U (2016) Impacts of different climate change regimes and extreme climatic events on an alpine meadow community. *Sci Rep* 6:21720. <https://doi.org/10.1038/srep21720>
- Alatalo JM, Jägerbrand AK, Chen S, Molau U (2017a) Responses of lichen communities to 18 years of natural and experimental warming. *Ann Bot* 120:159–170
- Alatalo JM, Jägerbrand AK, Juhanson J, Michelsen A, Euptáčík P (2017b) Impacts of twenty years of experimental warming on soil carbon, nitrogen, moisture and soil mites across alpine/subarctic tundra communities. *Sci Rep* 7:44489. <https://doi.org/10.1038/srep44489>
- Alatalo JM, Jägerbrand AK, Bagher Erfanian M, Chen S, Sun S-Q, Molau U (2020) Bryophyte cover and richness decline after 18 years of experimental warming in Alpine Sweden. *AoB PLANTS* plaa061. <https://doi.org/10.1093/aobpla/plaa061>
- Anthelme F, Cavieres LA, Dangles O (2014) Facilitation among plants in alpine environments in the face of climate change. *Front Plant Sci*. <https://doi.org/10.3389/fpls.2014.00387>
- Baruah G, Molau U, Bai Y, Alatalo JM (2017) Community and species-specific responses of plant traits to 23 years of experimental warming across subarctic tundra plant communities. *Sci Rep* 7:2571. <https://doi.org/10.1038/s41598-017-02595-2>
- Baruah G, Molau U, Jägerbrand AK, Alatalo JM (2018) Impacts of seven years of experimental warming and nutrient addition on neighbourhood species interactions and community structure in two contrasting alpine plant communities. *Ecol Complex* 33:31–40
- Björk RG, Klemedtsson L, Molau U, Harndorf J, Ödman A, Giesler R (2007) Linkages between N turnover and plant community structure in a tundra landscape. *Plant Soil* 294:247–261. <https://doi.org/10.1007/s11104-007-9250-4>
- Bonanomi G, Stinca A, Chirico GB, Ciaschetti G, Saracino A, Incerti G (2015) Cushion plant morphology controls biogenic capability and facilitation effects of *Silene acaulis* along an elevation gradient. *Funct Ecol* N/a-N/a. <https://doi.org/10.1111/1365-2435.12596>
- Boutin M, Corcket E, Alard D, Villar L, Jiménez J-J, Blaix C, Lemaire C, Corriol G, Lamaze T, Pornon A (2017) Nitrogen deposition and climate change have increased vascular plant species richness and altered the composition of grazed subalpine grasslands. *J Ecol* 105:1199–1209. <https://doi.org/10.1111/1365-2745.12743>
- Bragazza L (2008) A climatic threshold triggers the die-off of peat mosses during an extreme heat wave. *Glob Change Biol* 14:2688–2695. <https://doi.org/10.1111/j.1365-2486.2008.01699.x>
- Cavieres LA, Brooker RW, Butterfield BJ, Cook BJ, Kikvidze Z, Lortie CJ, Michalet R, Pugnaire FI, Schöb C, Xiao S, Anthelme F, Björk RG, Dickinson KJM, Cranston BH, Gavilán R, Gutiérrez-Girón A, Kanka R, Maalouf J-P, Mark AF, Noroozi J, Parajuli R, Phoenix GK, Reid AM, Ridenour WM, Rixen C, Wipf S, Zhao L, Escudero A, Zaitchik BF, Lingua E, Aschehoug ET, Callaway RM (2014) Facilitative plant interactions and climate simultaneously drive alpine plant diversity. *Ecol Lett* 17:193–202. <https://doi.org/10.1111/ele.12217>
- Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93:2533–2547. <https://doi.org/10.1890/11-1952.1>
- Chao A, Chiu C-H, Jost L (2010) Phylogenetic diversity measures based on Hill numbers. *Philosoph Transact Royal Soc b Biol Sci* 365:3599–3609. <https://doi.org/10.1098/rstb.2010.0272>
- Chao A, Chiu C-H, Jost L (2014a) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through hill numbers. *Annu Rev Ecol Syst* 45:297–324. <https://doi.org/10.1146/annurev-ecolsys-120213-091540>
- Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014b) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol Monogr* 84:45–67. <https://doi.org/10.1890/13-0133.1>
- Chapin FS III, Shaver GR (1985) Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* 66:564–576
- Chapin FS III, Shaver GR (1996) Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology* 77:822–840
- Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026. <https://doi.org/10.1126/science.1206432>
- De Boeck HJ, Bassin S, Verlinden M, Zeiter M, Hiltbrunner E (2016) Simulated heat waves affected alpine grassland only in combination with drought. *New Phytol* 209:531–541. <https://doi.org/10.1111/nph.13601>
- Doak DF, Morris WF (2010) Demographic compensation and tipping points in climate-induced range shifts. *Nature* 467:959–962. <https://doi.org/10.1038/nature09439>
- Elmendorf S, Henry G, Hollister R, Alatalo J, Björk R, Björkman A, Callaghan T, Collier L, Cooper EJ, Cornelissen J, Day T, Fosaa A, Gould W, Grétarsdóttir J, Harte J, Hermanutz L, Hik D, Hofgaard A, Jarrad F, Jónsdóttir I, Keuper F, Klanderud K, Klein JA, Koh S, Kudo G, Lang SI, Loewen V, May JL, Mercado J, Michelsen A, Molau U, Myers-Smith IH, Oberbauer SF, Pieper S, Post E, Rixen C, Robinson CH, Schmidt NM, Shaver GR, Stenström A, Tolvanen A, Totland O, Troxler T, Wahren C-H, Webber PJ, Welker JM, Wookey P (2012) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space

- and time. *Ecol Lett* 15:164–175. <https://doi.org/10.1111/j.1461-0248.2011.01716.x>
- Erfanian MB, Ejtehadi H, Vaezi J, Moazzeni H (2019a) Plant community responses to multiple disturbances in an arid region of northeast Iran. *Land Degrad Dev* 30:1554–1563. <https://doi.org/10.1002/ldr.3341>
- Erfanian MB, Ejtehadi H, Vaezi J, Moazzeni H, Memariani F, Firouz-Jahantigh M (2019b) Plant community responses to environmentally friendly piste management in northeast Iran. *Ecol Evol* 9:8193–8200. <https://doi.org/10.1002/ece3.5388>
- Eskelinen A, Kaarlejärvi E, Olofsson J (2017) Herbivory and nutrient limitation protect warming tundra from lowland species' invasion and diversity loss. *Glob Change Biol* 23:245–255. <https://doi.org/10.1111/gcb.13397>
- Evangelista A, Frate L, Carranza ML, Attorre F, Pelino G, Stanisci A (2016) Changes in composition, ecology and structure of high-mountain vegetation: a re-visitation study over 42 years. *AoB PLANTS*. <https://doi.org/10.1093/aobpla/plw004>
- Faith DP, Baker AM (2006) Phylogenetic diversity (pd) and biodiversity conservation: some bioinformatics challenges. *Evol Bioinforma* 2:121–128. <https://doi.org/10.1177/117693430600200007>
- Faith DP (2016) The PD phylogenetic diversity framework: linking evolutionary history to feature diversity for biodiversity conservation. In: Pellens R, Grandcolas P (Eds) *Biodiversity conservation and phylogenetic systematics topics in biodiversity and conservation* Springer, Cham. [https://doi.org/10.1007/978-3-319-22461-9\\_3](https://doi.org/10.1007/978-3-319-22461-9_3)
- Ferrarini A, Selvaggi A, Abeli T, Alatalo JM, Orsenigo S, Gentili R, Rossi G (2016) Planning for assisted colonization of plants in a warming world. *Sci Rep* 6:28542. <https://doi.org/10.1038/srep28542>
- Ferrarini A, Alsafran MH, Dai J, Alatalo JM (2019a) Improving niche projections of plant species under climate change: *Silene acaulis* on the British Isles as a case study. *Clim Dyn* 52:1413–1423. <https://doi.org/10.1007/s00382-018-4200-9>
- Ferrarini A, Dai J, Bai Y, Alatalo JM (2019b) Redefining the climate niche of plant species: A novel approach for realistic predictions of species distribution under climate change. *Sci Total Environ* 671:1086–1093
- Gimona A, Birnie RV, Sibbald AR (2006) Scaling up of a mechanistic dynamic model in a GIS environment to model temperate grassland production at the regional scale. *Grass Forage Sci* 61:315–331. <https://doi.org/10.1111/j.1365-2494.2006.00539.x>
- Haag RW (1974) Nutrient limitations to plant production in two tundra communities. *Can J Bot* 52:103–116
- Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecol Lett* 8:461–467. <https://doi.org/10.1111/j.1461-0248.2005.00739.x>
- Hollister RD, Webber PJ (2000) Biotic validation of small open-top chambers in a tundra ecosystem. *Glob Change Biol* 6:835–842. <https://doi.org/10.1046/j.1365-2486.2000.00363.x>
- Hollister RD, Webber PJ, Tweedie CE (2005) The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. *Glob Change Biol* 11:525–536. <https://doi.org/10.1111/j.1365-2486.2005.00926.x>
- Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol Evol* 7:1451–1456. <https://doi.org/10.1111/2041-210X.12613>
- Hu Y, Wang S, Niu B, Chen Q, Wang J, Zhao J, Luo T, Zhang G (2020) Effect of increasing precipitation and warming on microbial community in Tibetan alpine steppe. *Environ Res* 189:109917. <https://doi.org/10.1016/j.envres.2020.109917>
- Hudson JMG, Henry GHR (2009) Increased plant biomass in a High Arctic heath community from 1981 to 2008. *Ecology* 90:2657–2663. <https://doi.org/10.1890/09-0102.1>
- Jägerbrand AK, Alatalo JM, Chrimes D, Molau U (2009) Plant community responses to 5 years of simulated climate change in meadow and heath ecosystems at a subarctic-alpine site. *Oecologia* 161:601–610. <https://doi.org/10.1007/s00442-009-1392-z>
- Jin Y, Qian H (2019) VPhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography*. <https://doi.org/10.1111/ecog.04434>
- Jonasson S, Michelsen A, Schmidt I, Nielsen E (1999) Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic. *Ecology* 80:1828–1843
- Kent M (2011) *Vegetation description and data analysis: a practical approach*. John Wiley & Sons
- Kidane YO, Steinbauer MJ, Beierkuhnlein C (2019) Dead end for endemic plant species? A biodiversity hotspot under pressure. *Global Ecol Conserv* 19:e00670. <https://doi.org/10.1016/j.gecco.2019.e00670>
- Koltz AM, Schmidt NM, Høye TT (2018) Differential arthropod responses to warming are altering the structure of Arctic communities. *Royal Soc Open Sci* 5:171503. <https://doi.org/10.1098/rsos.171503>
- Komatsu KJ, Avolio ML, Lemoine NP, Isbell F, Grman E, Houseman GR, Koerner SE, Johnson DS, Wilcox KR, Alatalo JM, Anderson JP, Aerts R, Baer SG, Baldwin AH, Bates J, Beierkuhnlein C, Belote RT, Blair J, Bloor JMG, Bohlen PJ, Bork EW, Boughton EH, Bowman WD, Britton AJ, Cahill JF, Chaneton E, Chiariello NR, Cheng J, Collins SL, Cornelissen JHC, Du G, Eskelinen A, Firm J, Foster B, Gough L, Gross K, Hallett LM, Han X, Harmens H, Hovenden MJ, Jägerbrand A, Jentsch A, Kern C, Klanderud K, Knapp AK, Kreyling J, Li W, Luo Y, McCulley RL, McLaren JR, Megonigal JP, Morgan JW, Onipchenko V, Pennings SC, Prev y JS, Price JN, Reich PB, Robinson CH, Russell FL, Sala OE, Seabloom EW, Smith MD, Soudzilovskaia NA, Souza L, Suding K, Suttle KB, Svejcar T, Tilman D, Tognetti P, Turkington R, White S, Xu Z, Yahdjian L, Yu Q, Zhang P, Zhang Y (2019) Global change effects on plant communities are magnified by time and the number of global change factors imposed. *Proc Natl Acad Sci* 116:201819027. <https://doi.org/10.1073/pnas.1819027116>
- Kremers KS, Hollister RD, Oberbauer SF (2015) Diminished response of arctic plants to warming over time. *PLoS ONE* 10:e0116586. <https://doi.org/10.1371/journal.pone.0116586>
- Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J Ecol* 90:68–77. <https://doi.org/10.1046/j.0022-0477.2001.00630.x>
- Lamprecht A, Semenchuk PR, Steinbauer K, Winkler M, Pauli H (2018) Climate change leads to accelerated transformation of high-elevation vegetation in the central Alps. *New Phytol* 220:447–459. <https://doi.org/10.1111/nph.15290>
- Leffler AJ, Klein ES, Oberbauer SF, Welker JM (2016) Coupled long-term summer warming and deeper snow alters species composition and stimulates gross primary productivity in tussock tundra. *Oecologia* 181:287–297. <https://doi.org/10.1007/s00442-015-3543-8>
- Li M, Zhang X, Niu B, He Y, Wang X, Wu J (2020) Changes in plant species richness distribution in Tibetan alpine grasslands under different precipitation scenarios. *Global Ecol Conserv* 21:e00848. <https://doi.org/10.1016/j.gecco.2019.e00848>
- Liberati L, Messerli S, Matteodo M, Vittoz P (2019) Contrasting impacts of climate change on the vegetation of windy ridges and snowbeds in the Swiss Alps. *Alp Bot* 129:95–105. <https://doi.org/10.1007/s00035-019-00223-5>
- Lindblad KEM, Nyberg R, Molau U (2006) Generalization of heterogeneous alpine vegetation in air photo-based image classification, Latnjajaure catchment, northern Sweden. *Pirineos* 161:74–79. <https://doi.org/10.3989/pirineos.2006.v161.1>
- Liu H, Mi Z, Lin L, Wang Y, Zhang Z, Zhang F, Wang H, Liu L, Zhu B, Cao G, Zhao X, Sanders NJ, Classen AT, Reich PB, He J-S



- (2018) Shifting plant species composition in response to climate change stabilizes grassland primary production. *Proc Natl Acad Sci* 115:4051–4056. <https://doi.org/10.1073/pnas.1700299114>
- Maliniemi T, Kapfer J, Saccone P, Skog A, Virtanen R (2018) Long-term vegetation changes of treeless heath communities in northern Fennoscandia: Links to climate change trends and reindeer grazing. *J Veg Sci* 29:469–479. <https://doi.org/10.1111/jvs.12630>
- Marchand FL, Verlinden M, Kockelbergh F, Graae BJ, Beyens L, Nijs I (2006) Disentangling effects of an experimentally imposed extreme temperature event and naturally associated desiccation on Arctic tundra. *Funct Ecol* 20:917–928. <https://doi.org/10.1111/j.1365-2435.2006.01203.x>
- Marion G, Henry GHR, Freckrnan DW, Johnstone I, Jones G, Jones MH, Levesque E, Molau U, Molgaard P, Parsons AN, Svoboda J, Virginia RA (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. *Glob Change Biol* 3:20–32. <https://doi.org/10.1111/j.1365-2486.1997.gcb136.x>
- Matteodo M, Ammann K, Verrecchia EP, Vittoz P (2016) Snowbeds are more affected than other subalpine–alpine plant communities by climate change in the Swiss Alps. *Ecol Evol* 6:6969–6982. <https://doi.org/10.1002/ece3.2354>
- May JL, Hollister RD (2012) Validation of a simplified point frame method to detect change in tundra vegetation. *Polar Biol* 35:1815–1823. <https://doi.org/10.1007/s00300-012-1224-1>
- Molau U, Alatalo JM (1998) Responses of subarctic-alpine plant communities to simulated environmental change: biodiversity of bryophytes, lichens, and vascular plants. *Ambio* 27:322–329
- Molau U, Nordenhäll U, Eriksen B (2005) Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland. *Am J Bot* 92:422–431. <https://doi.org/10.3732/ajb.92.3.422>
- Morris WF, Doak DF (1998) Life history of the long-lived gynodioecious cushion plant *Silene acaulis* (Caryophyllaceae), inferred from size-based population projection matrices. *Am J Bot* 85:784–793. <https://doi.org/10.2307/2446413>
- Morris W, Pfister C, Tuljapurkar S, Haridas CV, Boggs CL, Boyce MS, Bruna E, Church D, Coulson T, Doak D, Forsyth S, Gaillard J, Horwitz C, Kalisz S, Kendall B, Knight T, Lee C, Menges ES (2008) Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* 89:19–25. <https://doi.org/10.1890/07-0774.1>
- Myers-Smith IH, Hik DS (2018) Climate warming as a driver of tundra shrubline advance. *J Ecol* 106:547–560. <https://doi.org/10.1111/1365-2745.12817>
- Myers-Smith IH, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klaassen U, Lévesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Collier LS, Weijers S, Rozema J, Rayback SA, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen C, Ménard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker J, Grogan P, Epstein HE, Hik DS (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ Res Lett* 6:045509. <https://doi.org/10.1088/1748-9326/6/4/045509>
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2017) *Vegan*. *Community Ecol Package* 1:1–295
- Peng F, Xue X, Xu M, You Q, Jian G, Ma S (2017) Warming-induced shift towards forbs and grasses and its relation to the carbon sequestration in an alpine meadow. *Environ Res Lett* 12:044010. <https://doi.org/10.1088/1748-9326/aa6508>
- Peterson ML, Doak DF, Morris WF (2018) Both life-history plasticity and local adaptation will shape range-wide responses to climate warming in the tundra plant *Silene acaulis*. *Glob Change Biol* 24:1614–1625. <https://doi.org/10.1111/gcb.13990>
- Polunin N (1951) The real arctic: suggestions for its delimitation, subdivision, and characterization. *J Ecol* 39:308–315
- R Core Team (2019) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna
- Rosbakh S, Bernhardt-Römermann M, Poschod P (2014) Elevation matters: contrasting effects of climate change on the vegetation development at different elevations in the Bavarian Alps. *Alp Bot* 124:143–154
- Rowland EL, Fresco N, Reid D, Cooke HA (2016) Examining climate-biome (“cliome”) shifts for Yukon and its protected areas. *Global Ecol Conserv* 8:1–17. <https://doi.org/10.1016/j.gecco.2016.07.006>
- Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC, Gurevitch J, GCTE-NEWS (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126:543–562
- Sarneel JM, Sundqvist MK, Molau U, Björkman MP, Alatalo JM (2020) Decomposition rate and stabilization across six tundra vegetation types exposed to >20 years of warming. *Sci Total Environ* 724:138304. <https://doi.org/10.1016/j.scitotenv.2020.138304>
- Scharn R, Little CJ, Bacon CD, Alatalo JM, Antonelli A, Björkman MP, Molau U, Nilsson RH, Björk RG (2021) Decreased soil moisture due to warming drives phylogenetic diversity and community transitions in the tundra. *Environ Res Lett*. <https://doi.org/10.1088/1748-9326/abfe8a>
- Scharnagl K, Johnson D, Ebert-May D (2019) Shrub expansion and alpine plant community change: 40-year record from Niwot Ridge, Colorado. *Plant Ecol Divers* 12:407–416. <https://doi.org/10.1080/17550874.2019.1641757>
- Shi Z, Lin Y, Wilcox KR, Souza L, Jiang L, Jiang J, Jung CG, Xu X, Yuan M, Guo X, Wu L, Zhou J, Luo Y (2018) Successional change in species composition alters climate sensitivity of grassland productivity. *Glob Change Biol* 24:4993–5003. <https://doi.org/10.1111/gcb.14333>
- Soudzilovskaia NA, Onipchenko VG, Cornelissen JHC, Aerts R (2005) Biomass production, N:P ratio and nutrient limitation in a Caucasian alpine tundra plant community. *J Veget Sci* 16:399–406. <https://doi.org/10.1111/j.1654-1103.2005.tb02379.x>
- Steinbauer K, Lamprecht A, Semenchuk P, Winkler M, Pauli H (2019) Dieback and expansions: species-specific responses during 20 years of amplified warming in the high Alps. *Alp Bot*. <https://doi.org/10.1007/s00035-019-00230-6>
- Van den Brink PJ, Braak CJT (1999) Principal response curves: Analysis of time-dependent multivariate responses of biological community to stress. *Environ Toxicol Chem Int J* 18:138–148
- Vowles T, Björk RG (2019) Implications of evergreen shrub expansion in the Arctic. *J Ecol* 107:650–655. <https://doi.org/10.1111/1365-2745.13081>
- Vowles T, Gunnarsson B, Molau U, Hickler T, Klemetsson L, Björk RG (2017) Expansion of deciduous tall shrubs but not evergreen dwarf shrubs inhibited by reindeer in Scandes mountain range. *J Ecol* 105:1547–1561
- Walker TW, Janssens IA, Weedon JT, Sigurdsson BD, Richter A, Peñuelas J, Leblans NIW, Bahn M, Bartrons M, Jonge CD, Fuchslueger L, Gargallo-Garriga A, Gunnarsdóttir GE, Marañón-Jiménez S, Oddsdóttir ES, Ostonen I, Poellau C, Prommer J, Radujković D, Sardans J, Sigurdsson P, Soong JL, Vicca S, Wallyander H, Ilieva-Makulec K, Verbruggen E (2020) A systemic overreaction to years versus decades of warming in a subarctic grassland ecosystem. *Nature Ecol Evol* 4:101–108. <https://doi.org/10.1038/s41559-019-1055-3>
- Walker MD (1996) Community baseline measurements for ITEX studies. In: Molau U, Mielgaard P (Eds) *ITEX Manual* (2nd ed.). Danish Polar Centre: Copenhagen, Denmark, 39–41
- Wang L, Yu H, Zhang Q, Xu Y, Tao Z, Alatalo J, Dai J (2018) Responses of aboveground biomass of alpine grasslands to climate

- changes on the Qinghai-Tibet Plateau. *J Geog Sci* 28:1953–1964. <https://doi.org/10.1007/s11442-019-1573-y>
- Zar JH (2010) *Biostatistical Analysis*. Prentice Hall, New Jersey
- Zheng Z, Zhu W, Zhang Y (2020) Seasonally and spatially varied controls of climatic factors on net primary productivity in alpine grasslands on the Tibetan Plateau. *Global Ecol Conserv* 21:e00814. <https://doi.org/10.1016/j.gecco.2019.e00814>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.