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Bryophyte cover and richness decline after 18 years of experimental warming in Alpine Sweden

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Abstract

Background and Aims: Climate change is expected to affect alpine and Arctic tundra communities. Most previous studies have examined vascular plants, but this study examined potential impacts of long-term warming on bryophyte communities.

Methods: Experimental warming with open-top chambers (OTCs) was applied for 18 years to a mesic meadow and a dry heath alpine plant community. Species abundance was measured in 1995, 1999, 2001 and 2013.

Key results: Species composition changed significantly from the original communities in the heath, but remained similar in the mesic meadow. Experimental warming increased beta diversity in the heath community. Bryophyte cover and richness both declined with long-term warming, while diversity showed no significant responses. Over the 18-year period, bryophyte cover decreased from 43% to 11% in heath and from 68% to 35% in meadow (75% and 48% decline, respectively, in original cover), while richness declined by 39% and 26%, respectively. There was a strong negative relationship between deciduous shrub cover and bryophyte cover, but not bryophyte richness, in both plant communities.

Conclusions: This study showed that bryophyte species do not all respond similarly to climate change. Total bryophyte cover declined in both dry heath and mesic meadow communities under long-term warming (by 1.5-3°C), driven by general declines in many species. Bryophytes in the heath community were more affected by long-term warming than those in the meadow community. Species loss was slower than the general decline in bryophyte abundance, as diversity remained similar in both communities. Increased litter fall with increasing deciduous shrub cover led to a steep decline in bryophyte cover and a smaller decrease in bryophyte richness.

Keywords: Climate change; global warming; mosses; plant-climate interactions; plant-plant interactions; species richness

1 Introduction

Ecosystems and ecosystem services world-wide are being affected by climate change, which is likely to continue in future (Shen and Ma 2014; Wu et al. 2014; Zhang et al. 2014; Hao et al. 2017). Arctic and alpine ecosystems are likely to experience a faster rate of warming than the global average (Chapin et al. 1995; Mack et al. 2004; IPCC 2013). Climate change is therefore likely to cause shifts in the range and relative abundance of Arctic/alpine organisms. Bryophytes in particular are predicted to be vulnerable to climate change, as many have low-temperature optima for photosynthesis and a narrow range of suitable temperatures for net photosynthetic gain (He et al. 2016). A long-term study on the relative abundance of bryophytes based on biological collections in Switzerland found that 16 species declined, four showed an increase and seven remained stable (Hofmann et al. 2007).

Bryophytes in Arctic and alpine regions are important in terms of biodiversity (Matveyeva and Chernov 2000; Bahuguna et al. 2016; Mateo et al. 2016), cover and biomass (Longton 1984; Cornelissen et al. 2007). For example, bryophyte cover has been found to increase along an altitudinal transect from 2000-4200 m above sea level (a.s.l.) in Gongga Mountains, China (Sun et al. 2013). In addition, bryophytes can host nitrogen-fixing bacteria and increase nitrogen inputs in ecosystems (During and Van Tooren 1990; Turetsky 2003), as well as acting as a food source for both invertebrates and vertebrates (Herbert and Prins 1982; Crafford and Chown 1991; Hodkinson et al. 1994; Smith et al. 2001; Imada and Kato 2016). Despite this, vascular plants have been the focus of most climate change studies to date (Arft et al. 1999; Walker et al. 2006; Elmendorf et al. 2012a, b; Dumais et al. 2014; Alatalo et al. 2014b; Wheeler et al. 2016; Zhang et al. 2016). Moreover, many studies on bryophytes provide no information about species-level responses, while only a few have collected species-level data to study the impact on species or bryophyte diversity and richness (Molau and Alatalo 1998; Jägerbrand et al. 2003; Wahren et al. 2005; Klanderud and Totland 2008; Klanderud 2008; Lang et al. 2012; Alatalo et al. 2014a, 2015a; Sun et al. 2017). Most previous studies have shown that bryophyte biomass and/or cover is sensitive to long-term warming (8-20 years) at alpine and Arctic sites (Chapin et al. 1995; Wahren et al. 2005; Elmendorf et al. 2012a; Lang et al. 2012; Sistla et al. 2013), but an increase in bryophyte cover has also been reported (Hudson and Henry 2010). Shorter-term studies (2-7 years) report contrasting results more frequently (Press et al. 1998; Jägerbrand et al. 2003; Bates et al. 2005; Klanderud 2008; Lang et al. 2009; Alatalo et al. 2014a; Koncz et al. 2018). Furthermore, the response of bryophytes to climate warming may be context-specific, depending on potential competition from vascular plants (Molau and Alatalo 1998; Jägerbrand et al. 2012) and the origin of the sampled population (Jägerbrand et al. 2014). Recent studies have reported increasing shrubification of alpine and Arctic tundra ecosystems, a process that is predicted to increase in future due to climate change (Myers-Smith et al. 2011; Maliniemi et al. 2018; Myers-Smith and Hik 2018; Vowles and Björk 2019). It is likely that shrubification will affect bryophyte communities, although previous studies have found inconsistent relationships between bryophytes and vascular plant abundance (Lang et al. 2012).

In the present study, bryophyte communities were examined following 18 years of experimental warming in two contrasting alpine sub-Arctic plant communities (mesic meadow and dry heath) in northern Sweden. The hypotheses tested were that: 1) Bryophyte community composition is altered by long-term warming; 2) bryophyte cover, richness and diversity are decreased by long-term warming; 3) bryophyte cover and richness are negatively related to deciduous shrub cover and litter cover; and 4) the negative impacts of warming are greater for mesic meadow, with its more developed vascular plant community, than for poor heath, with its sparser vascular plant community.

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 sub-Arctic (Polunin 1951), with snow cover for 7-8 months 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). 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). Climate data were collected throughout the year at the weather station at Latnjajaure field station, with hourly means, maxima and minima recorded (Molau and Alatalo 1998). Physical conditions in the valley soils vary from dry to wet, and from acidic to base-rich, with an associated variation in plant communities (Molau and Alatalo 1998; Lindblad et al. 2006; Björk et al. 2007; Alatalo et al. 2014b, 2017b). The mesic meadow community has a more developed vegetation cover (67% canopy cover) (Alatalo et al. 2017a), dominated by *Carex vaginata*, *C. bigelowii*, *Festuca ovina*, *Salix reticulata*, *S. polaris*, *Cassiope tetragona*, *Bistorta vivipara* and *Thalictrum alpinum* (Molau and Alatalo 1998; Alatalo et al. 2014b). 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. 2015b).

2.2 Experimental design and measurements

In July 1995, 12 plots (1 m × 1 m) with homogeneous vegetation cover were marked out in the alpine mesic meadow and the heath plant communities and randomly assigned to treatments (control, experimental warming) in a factorial design. At the start of the experiment, there were eight control plots and four plots with experimental warming in each plant community (total 12 in each plant community). However, all initial control plots could not be identified in 2013, so measurements were only made in four control and four experimental warming plots in each community in that year. Experimental warming was applied using hexagonal open-top chambers (OTCs), which were left in place on plots with warming treatment all year around. In the initial years (1995-1998), the temperature in the control and OTC plots was monitored with DeltaTM and TinytagTM loggers (Molau and Alatalo 1998). As found in other studies (Marion et al. 1997; Molau and Alatalo 1998; Hollister and Webber 2000), OTCs increased the air temperature by 1.5-3°C compared with control plots with ambient temperature. It has also been shown that OTCs decrease canopy moisture (Hollister and Webber 2000), causing earlier snowmelt and prolonging the growing season (Molau and Alatalo 1998; Hollister and Webber 2000).

The species present in the plots (see Table S1) were identified in the field or with the help of experienced bryophyte taxonomist Sven Franzén. Nomenclature for bryophyte species was retrieved from the literature (Hallingbäck and Holmåsen 1985; efloras.org 2015). Coverage of each 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 (five years of warming treatment), 2001 (seven years of treatment) and 2013 (18 years of treatment). 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, relative changes between years/treatments were determined in the statistical analyses. To ensure accuracy and reproducibility, the same grid frame was used for each measurement, and fixed points at the corner of each plot allowed the frame to be replaced in the same positions within 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 Statistical analyses

2.3.1 Species composition

The effect of the warming treatment over time on species composition in the heath and meadow vegetation types was evaluated using principal response curves (PRC) (van den Brink et al. 2009). Because of unbalanced data for each year, we opted not to conduct a formal permutation test and instead used analysis of similarity (ANOSIM) with 999-time permutations to test whether the species composition in control and warming plots differed significantly in 1995 and 2013. We also tested the difference between 1995 and 2013 control and warming plots using ANOSIM. The *anosim* function in the vegan software package was used for this analysis (Oksanen et al. 2017).

To test whether climate change affected beta diversity within treatment in each year (i.e. variation in the species composition of the plots in each treatment), a separate Hellinger distance matrix was created for control and warming plots in each year, using the vegan package (Oksanen et al. 2017; Oksanen 2018). We used the Hellinger distance approach because it is not affected by double zeros (Erfanian et al. 2019). Average dissimilarity for each distance matrix was then calculated, and one-mean confidence intervals for each calculated average were determined using a t-procedure (Zar 2010). The results were relativised using beta diversity in 1995 as a base and reported as percentage change in dissimilarity. Finally, graphs showing changes in beta diversity for the heath and meadow vegetation types were created using the ggplot2 package (Wickham 2009).

2.3.2 Species diversity and bryophyte cover

Bryophyte cover, species richness and diversity community parameters were calculated for comparison of the bryophyte assemblages. From the point-frame data, the number of hits was summed up at pins within each plot to produce plot-level abundance measures for each species. These values were used to calculate total bryophyte cover, richness (species number per unit area) and diversity as Simpson's diversity index D (Simpson 1949). The calculated values were then transformed to relative change (ratio) for the whole period of the study (1995-2013), with 1995 data for each plot taken as the starting value. Relative change was used as the response variable because the number of hits per plot differed between treatments and because plots differed in their starting values of cover, richness and species composition. Thus, we opted to analyse relative changes between 1995 and 2013 instead of the actual number of hits per species per plot. Simpson's diversity index was chosen since it is reliable even when the sample size is small (Mouillot and Lepretre 1999). In addition, it considers the diversity at the level of dominant species (Chao et al., 2017). The species richness metric considers the diversity of species without giving weight to the species (i.e. without considering their abundances), but Simpson's diversity index (hereafter called 'diversity') gives higher weight to dominant species and rare species do not change its value. Data on bryophyte cover, species richness, diversity and species abundance were checked for normality assumptions using the Shapiro-Wilk test, and for homogeneity of variance using the Bartlett test. The Shapiro-Wilk test revealed that species abundance, cover, richness and diversity data were highly skewed, and therefore did not meet the assumption of normality. Therefore the Mann-Whitney U test, a robust non-parametric test, was used to examine the effect of the experimental warming treatment on the relative change between 1995-2013 in bryophyte species abundance, cover, richness and diversity for the heath and meadow ecosystems. These tests were conducted using R software (R Core Team 2019).

2.3.3 Relationships between bryophyte richness and cover, deciduous shrub cover and litter cover

Due to the small number of samples, we opted not to use any inferential statistical method and instead used graphical comparison of the relationships between bryophyte richness and cover, deciduous shrub cover and litter cover. Boxplots were used to demonstrate changes in bryophyte cover, bryophyte richness, litter cover and deciduous shrub cover over time. The boxplots were drawn in R (R Core Team 2019).

3. Results

3.1 Species composition

The principal response curve (PRC) for the heath, with 1995 used as reference, showed that community changes were abrupt after 2001 (Fig. 1). *Ptilidium ciliare* showed a strong increase in presence in plots over time, whereas *Kiaeria starkei* and *Gymnomitrion concinnatum* presence in plots was greatly reduced (Fig. 1). Analysis of similarities indicated that in the heath community, species composition had changed significantly in both the control and warmed plots after 18 years of warming (Table 1).

The PRC for the meadow, with 1995 used as reference, indicated that the species composition of the warming and control plots became similar over time (Fig. 2). Analysis of similarity tests on the species composition of meadow bryophytes, comparing the control and warming plots in 1995 vs. 2013, and comparing 2013 vs. 1995, showed that species composition did not differ between treatments, either at the start of the experiment or after 18 years of warming. *Sphagnum capillifolium* and *Ptilidium ciliare* showed the greatest increase in presence, and *Hylocomium splendens* and *Polytrichum alpinum* the greatest decrease in presence, in the meadow community over time (Fig. 2). However, analysis of the relative changes in total abundance (not species presence/absence) showed that *Ptilidium ciliare* declined significantly in abundance (P=0.021) after 18 years of experimental warming in the meadow, but not in the heath (Table 1). While no other species showed any significant changes in abundance in response to experimental warming over 18 years, there was a trend for a decrease in abundance of *Aulacomnium turgidum*, *Dicranum groenlandicum*, and *Hylocomium splendens* in the meadow, and *Polytrichum juniperinum*, *Gymnomitrion concinnatum*, and *Kiaeria starkei* in the heath.

For the heath vegetation type, long-term warming led to increased beta diversity (Fig. 3). Control plots also initially showed increased beta diversity, which seemed to stabilise later. For the meadow vegetation type, in 2001 both control and warming plots showed significant differences from their 1995 condition, but by 2013 both warming and control plots had reached a stabilised state (Fig. 3).

3.2 Bryophyte cover, species diversity and richness

Bryophyte cover declined significantly in the both heath (P=0.029) and meadow (P=0.020) after 18 years of experimental warming (Fig. 4, Fig. S1). In 1995, bryophyte cover was on average 43% and 68% in the heath and meadow, respectively, while after 18 years of experimental warming it was 11% and 35%, respectively (Fig. 4, Fig. S1). This represented a decline in bryophyte cover relative to the original cover in the long-term warming plots of 75% in the heath and 48% in the meadow. In the control treatments, bryophyte cover showed smaller and inconsistent changes, decreasing from 27% to 21% in the heath and increasing from 69% to 80% in the meadow during the 18-year period (Fig. 4, Fig. S1).

Bryophyte richness declined significantly in response to experimental warming in the heath (P=0.018), while it did not change significantly in the meadow (Fig. 4). In 1995, richness was 6.1 and 7.1 (species per OTC plot) in the heath and meadow, respectively. After 18 years of experimental warming, richness was 3.75 and 5.25 in the heath and meadow, respectively (Fig. 4). This represented a decline in richness of 39% in the heath and 26% in the meadow. After 18 years in the control treatment, richness was 7.3 and 6.25 in the heath and meadow, respectively (Fig. 4).

Bryophyte diversity did not show any significant response to experimental warming over 18 years in either the heath or meadow ecosystems (Fig. 4). However, there was a non-significant decline trend in diversity in the heath (P=0.083).

3.3 Relationships between bryophyte richness and cover, deciduous shrub cover and litter cover

Changes in bryophytes species richness and cover relative to canopy cover of deciduous shrubs and litter cover are shown in Figs. 5 and 6. For the heath vegetation (Fig. 5), in the control plots litter cover was greatly reduced over time and deciduous shrub cover showed a slight decrease. However, both litter cover and deciduous shrub cover increased in the warmed plots. In these plots, the increase in litter cover was related to the increase in canopy cover of deciduous shrubs.

For the meadow vegetation, in the control plots litter cover remained relatively similar through the study period, but deciduous shrub cover increased over time (Fig. 6). In the warmed plots of the meadow vegetation type, litter cover and deciduous shrub cover both increased over time (Fig. 6).

4. Discussion

4.1 Changes in species composition in bryophyte communities under long-term warming

Principal response curve analysis showed that bryophyte species did not all respond to the experimental warming provided by OTCs in the same manner. This is in line with previous findings of both contractions and expansions in bryophyte species in Europe (Bergamini et al. 2009; Désamoré et al. 2012; Hodd et al. 2014). For example, a study on bryophytes using 10,521 specimens from biological collections in Switzerland found that 16 species had declined since 1850-1939, while four had increased. Bryophyte species can be expected to differ in their responses to warming, as they differ in their temperature optima, desiccation tolerance and shading tolerance (Furness and Grime 1982; Humbert et al. 2007; He et al. 2016). In the present study, we found that species composition (based on presence/absence data relative to 1995) of bryophytes in the meadow vegetation became more similar over time in the warming and control plots. In contrast, there were significant differences in species composition in the heath vegetation between control and warming plots. Thus, the hypothesis that bryophytes in mesic meadow are more vulnerable was not supported by the data. Instead, the results suggested that bryophytes in alpine heath vegetation are more susceptible to warming than those in meadow vegetation, supporting the suggestion that bryophyte communities may be less resistant in drier environments than in wetter habitats (Turetsky et al. 2012). Depending on the variable considered (presence/absence or abundance), some species showed contrasting response patterns. For example *Ptilidium ciliare* increased in presence in warmed plots (as indicated by the PRC analysis), while at the same time its abundance decreased significantly due to the warming treatment. Thus, while *P. ciliare* was present in more plots, the total abundance of the species decreased in response to warming.

A study on alpine bryophyte communities in Northern Italy showed that species track specific climate conditions along elevation gradients, leading to the prediction that climate change will increase species turnover of bryophyte communities rather than leading to species loss (Nascimbene and Spitale 2017). In contrast, a study in the Canadian Rocky mountains found that bryophytes had a wide tolerance to temperature and elevation-related factors, thus having broader habitats and lower beta diversity along elevation gradients (Lee and La Roi 1979). While the present study did not include elevation gradients, the results showed that response patterns of beta diversity differed between sites, with the meadow community being more resistant to warming than the heath, and that plot-scale (i.e. small-scale) features are likely to have an important role in determining the resulting communities. In addition, the medium-term (1995-2001) and long-term (2001-2013) responses showed contrasting patterns. The latter underscores the importance of maintaining long-term monitoring and experimental studies to better understand community dynamics. Similarly, other studies have found that it is difficult to predict longer term responses from the initial responses in experimental warming treatments (Hollister et al. 2005).

4.2 Impacts of climate change on bryophyte cover, species richness and diversity

As hypothesised, bryophyte cover and richness both declined under long-term experimental warming. Similar negative responses have been reported in previous experimental studies (Elmendorf et al. 2012a; Lang et al. 2012; Sistla et al. 2013). In a study on Alaskan tundra, 20 years of experimental warming decreased bryophyte cover by 63% (Sistla et al. 2013). In shorter-term studies in Sweden and Tibet, bryophytes only started to decrease at the end of the experiments (Alatalo et al. 2015a; Sun et al. 2017), suggesting that changes in bryophyte communities may take time. However, bryophyte responses to long-term warming are not always negative (Van Wijk et al. 2003; Hudson and Henry 2010; Bokhorst et al. 2016). For example, 15 years of experimental warming resulted in an increase in bryophyte cover in High Arctic Canada (Hudson and Henry 2010). In the present study, bryophyte cover declined in experimentally warmed plots in both the meadow and heath community, but it tended to increase in the control plots in the meadow community, but not in the heath. This may be because Latnjajaure experienced natural warming of roughly 2 °C in the period 1993-2013, which may have caused a greater increase in vascular plant canopy in the heath community than in the meadow community (Alatalo et al. 2017a). Bryophytes are generally highly dependent on external water (He et al. 2016) and variations in annual rainfall could therefore potentially affect their photosynthesis and growth. Annual precipitation varied substantially between years in the study period, with 2012 and 2013 not having the highest or lowest annual precipitation (Alatalo et al. 2017a). Thus, it is unlikely that precipitation was the cause of changes in bryophyte cover. In a previous large-scale study involving 61 experimental sites, polar and alpine bryophytes were found to be more negatively affected by experimental warming at wetter sites than at drier sites (Elmendorf et al. 2012a). While that study did not include data on the effect of warming on soil moisture, the findings indicated that bryophytes inhabiting sites with higher soil moisture could be more vulnerable to warming-related decreases in soil moisture. In the present experiment, long-warming in the meadow (but not in the heath) had a negative effect on soil moisture compared with the control plots (Alatalo et al. 2017b). This could partly explain the decreases in bryophyte cover and richness, as the responses to water stress can vary among bryophyte species (Davey 1997; Turetsky 2003). In addition, OTCs could potentially have hindered colonisation by bryophytes from outside the warmed plots. However, as the warming chambers have an open top, they are not likely to prevent colonisation by spores from outside. A previous study in High Arctic Canada found that seed production in a wind-pollinated willow was not reduced by OTCs and that insect visitation was also unaffected (Robinson and Henry 2018). Thus, it is unlikely that the OTCs used in our study had a negative effect on wind-dispersed spores.

4.3 Impact of shrubification on bryophyte cover, species richness and diversity

Previous studies have reported an increase in deciduous shrub cover in alpine and Arctic tundra (Myers-Smith et al. 2011; Vowles et al. 2017; Maliniemi et al. 2018), so in the present study we examined the correlation between this group of vascular plants and bryophytes. The reported increase in deciduous shrubs is in line with previous predictions that increased temperature and nutrient mineralisation will increase the productivity of vascular plants, which could have a negative effect on bryophytes (Molau and Alatalo 1998; Van der Wal et al. 2005). Our hypothesis of a negative correlation between deciduous shrub cover and bryophyte cover and richness was partly supported by the data. However, due to the low number of samples, we opted to not perform statistical inference on the results.

We also examined the relationships between litter cover, bryophyte cover and richness, and deciduous shrub cover. The results indicated a positive correlation between litter increase and shrubification in the warmed plots in both heath and meadow vegetation and a strong negative correlation between bryophyte cover and litter/deciduous shrub cover. A similar, but weaker, relationship was observed between bryophytes richness and litter/deciduous shrub cover. This difference in strength of relationship may be because bryophyte species loss takes longer to occur than a decrease in bryophyte cover. However, the differences in litter cover between control and warmed plots may be an artefact caused by the constant presence of OTCs preventing litter from being blown away by the wind, and thus artificially increasing the litter cover. Previous studies have shown that both bryophytes and lichens are negatively correlated with vascular plant canopy (Löbel et al. 2006; Pajunen et al. 2011; Jägerbrand et al. 2012; Alatalo et al. 2017a). Therefore, the widespread shrubification reported in alpine and Arctic tundra (Myers-Smith et al. 2011; Maliniemi et al. 2018; Myers-Smith and Hik 2018) could potentially have large impacts on cryptogam communities. In addition, long-term experimental warming has been found to cause a drastic increase in cover of *Betula nana* (dwarf birch), a common circumpolar deciduous shrub also found at our site in Sweden. For example, experimental warming increased *B. nana* cover by 94% in Alaska (Sistla et al. 2013), while this species increased in cover and grew higher and with larger leaves under experimental warming in Sweden (Jägerbrand et al. 2009; Baruah et al. 2017). However, this is not always the case (Løkken et al. 2019) and the responses may differ between deciduous and evergreen shrubs, and between sites (Walker et al. 2006; Elmendorf et al. 2012a, b; Vowles et al. 2017; Maliniemi et al.

2018). For example, a study using data from Latnjajaure, Sweden, and Toolik Lake, Alaska, found no negative relationship between bryophytes and abundance of vascular plants (Lang et al. 2012). As shrubification of alpine and Arctic tundra is expected to increase due to climate change, the effect of shrub encroachment on bryophytes needs to be monitored more closely in areas experiencing shrubification.

5. Conclusions

Climate change is increasing at a more rapid rate than previously predicted, with widespread impacts on Arctic/alpine regions. This study showed that the important but relatively understudied Arctic/alpine bryophytes are likely to be adversely affected in the longer term. The species composition of heath vegetation appeared to be more susceptible to experimental warming than that of meadow vegetation. Bryophyte cover and richness both declined over 18 years of experimental warming and the rate of decline increased over time. However, bryophyte diversity did not show any significant responses to warming. The decline in total bryophyte cover in both heath and meadow communities was driven by a general decline in multiple species. Many of the most common species did not show any detectable changes, but the cumulative change was significant. There were indications that species loss was slower than the general decline in bryophyte abundance. Bryophytes in the meadow community were expected to be more susceptible to warming, but the results showed that bryophyte communities in the drier heath habitat were more susceptible. Over the 18-year study period, there was a strong negative relationship between deciduous shrub/litter cover and bryophyte cover, and a weaker negative relationship between deciduous shrub/litter cover and bryophyte richness, probably due to a more delayed decline in species richness than in abundance in response to long-term warming. There was a positive correlation between litter cover and shrubification in warmed plots in both heath and meadow vegetation. Thus widespread shrubification across the Arctic is likely to have a negative impact on the important bryophyte group, reducing their richness and cover.

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Authors' contributions

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

Additional Information

Supplementary information accompanies this paper electronically.

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Data availability

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

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Figure captions

Fig. 1. Principal response curve showing the effect of warming treatment over time on presence of bryophyte species in heath vegetation at Latnjajaure, northern Sweden. CTR = control plots, T = warmed plots (open-top chambers).

Fig. 2. Principal response curve showing the effect of warming treatment over time on presence of bryophyte species in meadow vegetation at Latnjajaure, northern Sweden. CTR = control plots, T = warmed plots (open-top chambers).

Fig. 3. Effect of warming treatment over time on beta-diversity in heath and meadow vegetation at Latnjajaure, northern Sweden. Control = ambient plots, temperature = warmed plots.

Fig. 4. Relative changes after 18 years (1995-2013) in (A) bryophyte cover, (B) bryophyte richness and (C) bryophyte diversity in heath and meadow vegetation at Latnjajaure, northern Sweden. CTR = control, T = warming treatment. Boxplots show minimum, first quartile, median, third quartile and maximum values. * = significant difference ($P<0.05$).

Fig. 5. Boxplots showing changes in bryophyte cover, bryophyte richness, litter cover and deciduous shrub cover over time in control (green) and warmed (red) plots in heath vegetation at Latnjajaure, northern Sweden.

Fig. 6. Boxplots showing changes in bryophyte cover, bryophyte richness, litter cover and deciduous shrub cover over time in control (green) and warmed (red) plots in meadow vegetation at Latnjajaure, northern Sweden.

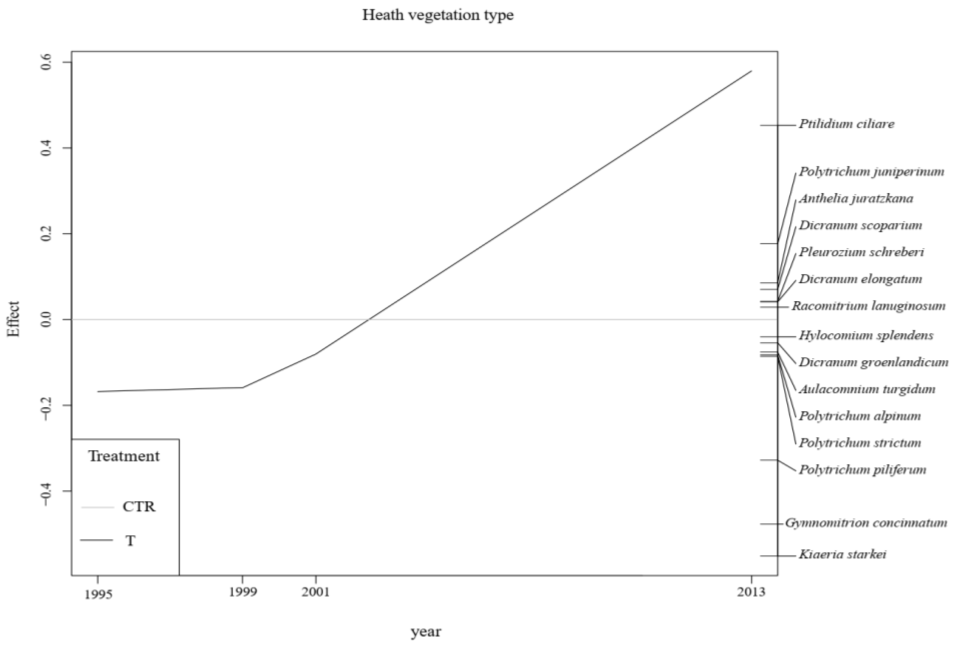
Heath vegetation type
Effect
0.6
0.4
0.2
0.0
−0.2
−0.4
year
1995
1999
2001
2013
Treatment
CTR
T
Ptilidium ciliare
Polytrichum juniperinum
Anthelia juratzkana
Dicranum scoparium
Pleurozium schreberi
Dicranum elongatum
Racomitrium lanuginosum
Hylocomium splendens
Dicranum groenlandicum
Aulacomnium turgidum
Polytrichum alpinum
Polytrichum strictum
Polytrichum piliferum
Gymnomitrion concinnatum
Kiaeria starkei

Fig. 1

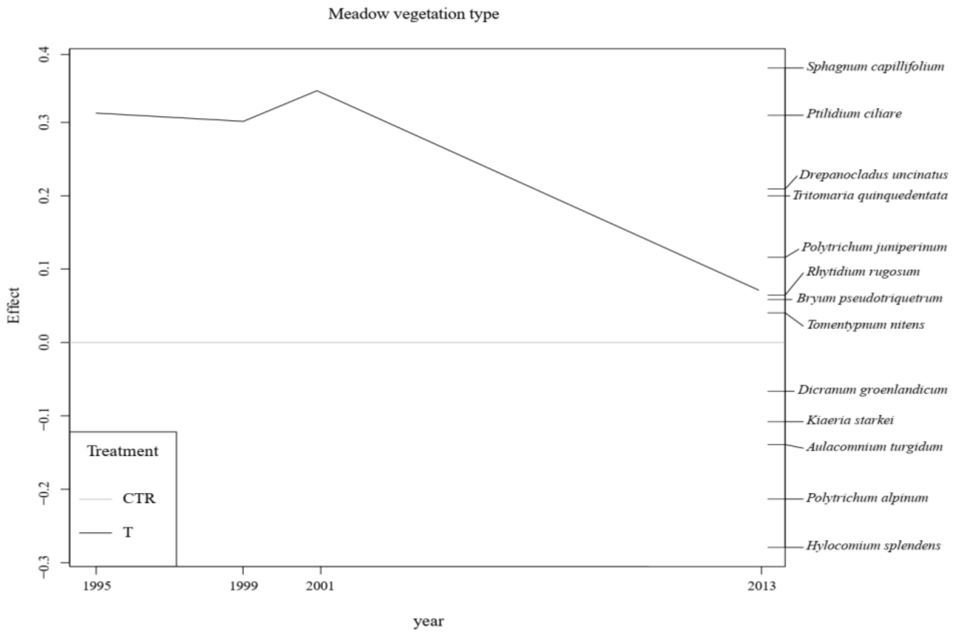
Meadow vegetation type
Effect
0.4
0.3
0.2
0.1
0.0
−0.1
−0.2
−0.3
year
1995
1999
2001
2013
Treatment
CTR
T
Sphagnum capillifolium
Ptilidium ciliare
Drepanocladus uncinatus
Tritomaria quinquedentata
Polytrichum juniperinum
Rhytidium rugosum
Bryum pseudotriquetrum
Tomentypnum nitens
Dicranum groenlandicum
Kiaeria starkei
Aulacomnium turgidum
Polytrichum alpinum
Hylocomium splendens

Fig. 2

Relative dissimilarity
40
20
0
1995
1999
2001
2013
Heath
control
temperature
Relative dissimilarity
20
0
−20
−40
1995
1999
2001
2013
Meadow
control
temperature

Fig. 3

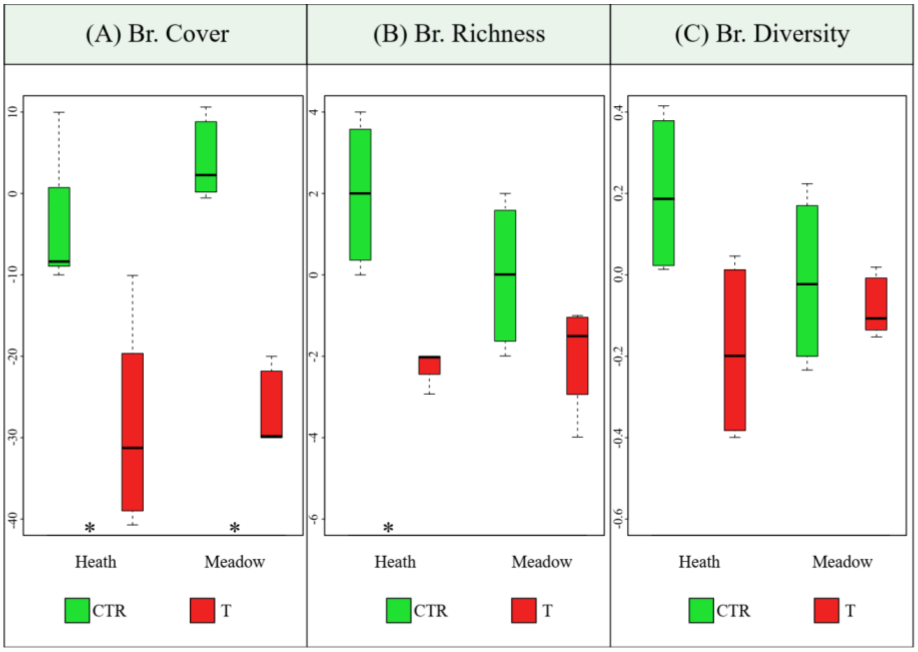
(A) Br. Cover
(B) Br. Richness
(C) Br. Diversity
10
0
-10
-20
-30
-40
4
2
0
-2
-4
-6
0.4
0.2
0.0
-0.2
-0.4
-0.6
*
*
*
Heath
Meadow
Heath
Meadow
Heath
Meadow
🟩 CTR
🟥 T
🟩 CTR
🟥 T
🟩 CTR
🟥 T

Fig. 4

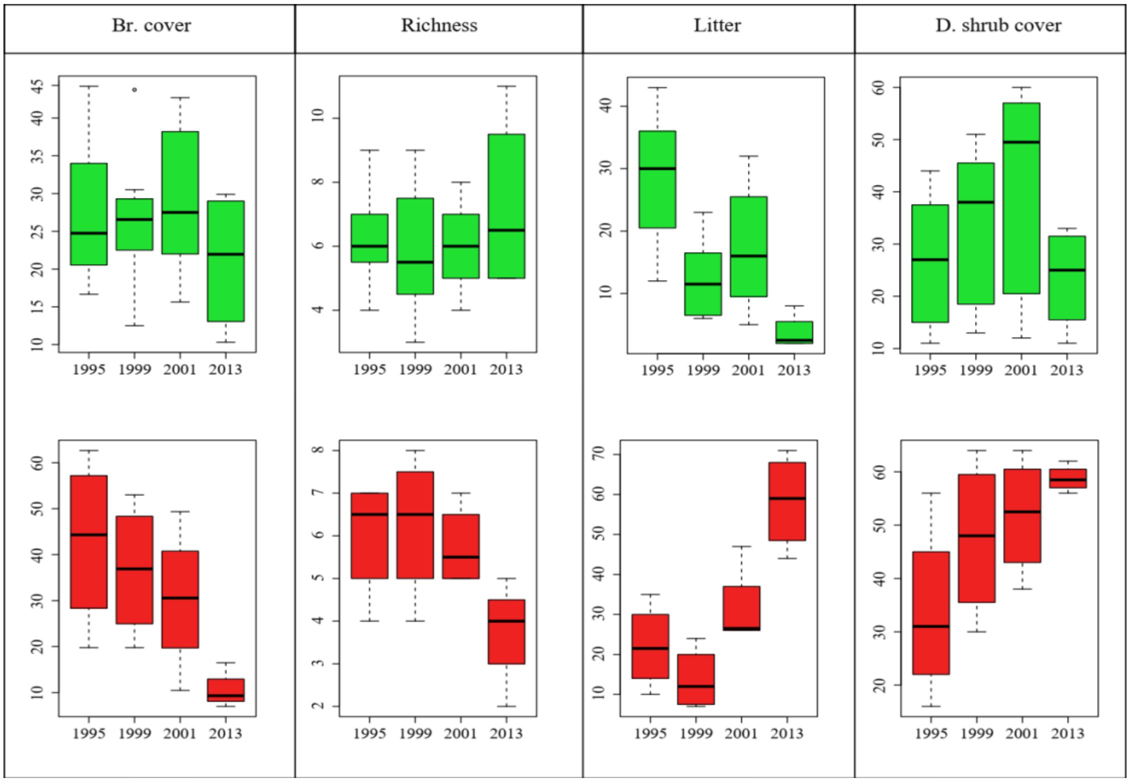
Br. cover
Richness
Litter
D. shrub cover
10 15 20 25 30 35 40 45
4 6 8 10
10 20 30 40
10 20 30 40 50 60
10 20 30 40 50 60
2 3 4 5 6 7 8
10 20 30 40 50 60 70
20 30 40 50 60
1995 1999 2001 2013

Fig. 5

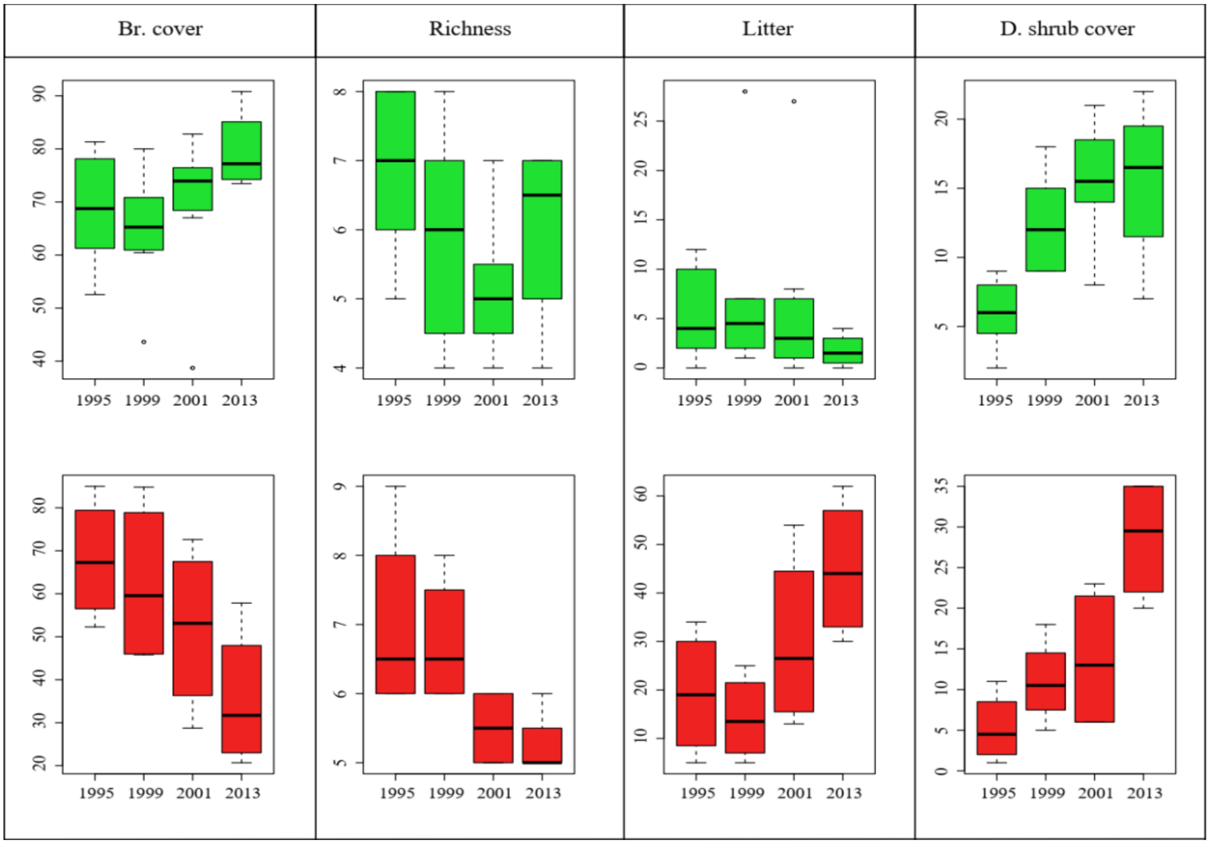

Fig. 6

Table 1. Analysis of similarity results comparing differences in bryophyte species composition in control (CTR) vs. warming (Temp) plots in meadow and heath vegetation at Latnjajaure, northern Sweden, in 1995 and 2013, and 1995 vs. 2013

Vegetation type	Year	Treatment	p-value	R
Meadow	1995	CTR vs Temp	0.084	0.2353
Meadow	2013	CTR vs Temp	0.386	0.02083
Meadow	1995 VS 2013	CTR	0.521	-0.0294
Meadow	1995 VS 2013	Temp	0.796	-0.156
Heath	1995	CTR vs. Temp	0.371	0.0275
Heath	2013	CTR vs. Temp	0.093	0.2812
Heath	1995 VS 2013	CTR	**0.002**	0.6783
Heath	1995 VS 2013	Temp	**0.029**	0.7344