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

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Summary

1. Bryophytes in the Arctic and Alpine regions are important in terms of biodiversity, cover and biomass. However, climate change and widespread shrubification of alpine and arctic tundra is predicted to increase in the future, with potentially large impacts on bryophyte communities.
2. We studies the impact of 18 years of experimental warming with open top chambers (OTCs) on bryophyte cover, richness and diversity in an alpine mesic meadow and a heath plant community in Northern Sweden. In addition we investigated the relationship between deciduous shrubs and bryophytes.
3. Cover and richness of bryophytes both declined due to long-term warming, while diversity did not show any significant responses. After 18 years, bryophyte cover had decreased by 71% and 26 in the heath and meadow, while richness declined by 39% and 26%, respectively.
4. *Synthesis*. Decline in total bryophyte cover in both communities in response to long-term warming was driven by a general decline in many species, with only two individual species showing significant declines. Although most of the species included in the individual analyses did not show any detectable changes, the cumulative change in all species was significant. In addition, species loss was slower than the general decline in bryophyte abundance. As hypothesized, we found significant negative relationship between deciduous shrub cover and bryophyte cover, but not bryophyte richness, in both plant communities. This is likely due to a more delayed decline in species richness compared to abundance, similar to what was observed in response to long-term warming.

Keywords: Arctic, climate change, global warming, mosses, plant-climate interactions, plant-plant interactions, species richness, tundra.

Introduction

Ecosystems and ecosystem services across the globe are likely to be impacted by climate change (Hao et al., 2017; Shen & Ma, 2014; Wu et al., 2014; Yinbo Zhang, Wang, Zhang, & Ma, 2014). In particular, arctic and alpine ecosystems are likely to experience a faster rate of climate change than the global average (Chapin, Shaver, Giblin, Nadelhoffer, & Laundre, 1995; IPCC, 2013; Mack, Schuur, Bret-Harte, Shaver, & Chapin, 2004). Climate change is therefore likely to cause species shifts. Some evidence of this has already been reported (Bergamini, Ungricht, & Hofmann, 2009; Callaghan et al., 2013; Capers & Stone, 2011; Erschbamer, Unterluggauer, Winkler, & Mallaun, 2011; Grytnes et al., 2014). For example, rapid latitudinal and elevation range shift has been observed in a study on more than 1000 species (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011), while a re-survey in Svalbard 85 years after the first survey showed that 11 species had increased and 11 species had decreased over the period (Kapfer & Grytnes, 2017).

Bryophytes are specifically predicted to be vulnerable to climate change, as many have low temperature optima for photosynthesis and a narrow range of temperatures for net photosynthetic gain (He, He, & Hyvönen, 2016). A long-term study 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). However, range shifts can also be due to other human activities such as agriculture, forestry and grazing that alter the environment (Groom, 2013). Moreover, extinction risks may increase worldwide, as habitats can disappear due to climate change (Colwell, Brehm, Cardelús, Gilman, & Longino, 2008; Dirnböck, Essl, & Rabitsch, 2011; Engler et al., 2011; Ferrarini, Alsafran, Dai, & Alatalo, 2019; Ferrarini, Dai, Bai, & Alatalo, 2019; Raxworthy et al., 2008).

Bryophytes in arctic and alpine regions are important in terms of biodiversity (Bahuguna, Gairola, Uniyal, & Bhatt, 2016; Mateo et al., 2016; Matveyeva & Chernov, 2000), cover and biomass (Cornelissen, Lang, Soudzilovskaia, & During, 2007; Longton, 1984). Bryophyte cover has been found to increase along an altitudinal transect from 2000-4200 m above sea level (m a.s.l.) in Gongga Mountains, China (Sun et al., 2013). In addition, bryophytes can host N_2-fixing bacteria and increase N inputs in ecosystems (During & Van Tooren, 1990), as well as act as a food source for both invertebrates and vertebrates (Crafford & Chown, 1991; Herbert & Prins, 1982; Hodkinson et al., 1994; Imada & Kato, 2016; Smith, Young, & Marquiss, 2001). Despite this, vascular plants have been the focus of most climate change studies to date (Alatalo, Little, Jägerbrand, & Molau, 2014; Arft et al., 1999; Dumais, Ropars, Denis, Dufour-Tremblay, & Boudreau, 2014; Wheeler et al., 2016; Yangjian Zhang, Wang, & others, 2016). Many studies on bryophytes lack information about species-level responses and only a few gather species-level data to study the impact on species or on bryophyte diversity and richness (Alatalo, Jägerbrand, & Molau, 2014, 2015; Jägerbrand, Molau, & Alatalo, 2003; Kar Klanderud & Totland, 2008; Kari Klanderud, 2008; Lang et al., 2012; Molau & Alatalo, 1998; Sun et al., 2017; Wahren, Walker, & Bret-Harte, 2005). 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; Elmendorf et al., 2012; Lang et al., 2012; Sistla et al., 2013; Wahren et al., 2005), while shorter-term studies (2-7 years) report contrasting results (Alatalo, Jägerbrand, et al., 2014; Bates, Thompson, & Grime, 2005; Jägerbrand et al., 2003; Kari Klanderud, 2008; Koncz, Hermanutz, Marino, Wheeler, & Cranston, 2018; Lang et al., 2009; Press, Potter, Burke, Callaghan, & Lee, 1998). Furthermore, the response of bryophytes to climate warming may be context-dependent, depending on potential competition with vascular plants (Jägerbrand, Kudo, Alatalo, & Molau, 2012; Molau & Alatalo, 1998) and the origin of the sampled population (Jägerbrand, Alatalo, & Kudo, 2014). Recent studies have reported an increasing shrubification of alpine and arctic tundra ecosystems and this process is predicted to increase in future due to climate change (Maliniemi, Kapfer, Saccone, Skog, & Virtanen, 2018; Myers-Smith et al., 2011; Myers-Smith & Hik, 2018; Vowles & Björk, 2019). It is likely that shrubification may affect bryophyte communities. However, previous studies how found mixed relationships of bryophytes with vascular plant abundance (Lang et al., 2012). Thus, a second aim of this study was to determine the potential impact of deciduous shrub cover on bryophytes.

We examined bryophyte communities following 18 years of experimental warming in two contrasting alpine subarctic plant communities, mesic meadow and dry heath, in Sweden. We hypothesized that 1)) bryophyte cover and richness are negatively related with the cover of deciduous shrubs; 2) bryophyte cover, richness and diversity are negatively affected (decreased) by long-term warming, and 3) 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.

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 most of the year, cool summers and relatively mild, snow-rich winters. The growing season starts in late May and ends in early September (Molau, Nordenhäll, & Eriksen, 2005). Mean annual air temperature in the study period (1993-2013) ranged from -0.76 to -2.92°C (Alatalo, Jägerbrand, Chen, & Molau, 2017). Mean monthly temperature was highest in July, ranging from 5.9°C in 1995 to 13.1°C in 2013 (Alatalo, Jägerbrand, Chen, et al., 2017). 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, Jägerbrand, Chen, et al., 2017). Climate data were collected throughout the year at the weather station at Latnjajaure field station, with hourly means, maxima and minima recorded. Physical conditions in the soils in the valley vary from dry to wet and poor and from acidic to base-rich, with an associated variation in plant communities (Alatalo, Jägerbrand, Juhanson, Michelsen, & Ľuptáčik, 2017; Alatalo, Little, et al., 2014; Björk et al., 2007; Lindblad, Nyberg, & Molau, 2006; Molau & Alatalo, 1998). The mesic meadow community has a more developed vegetation cover (67% canopy cover) (Alatalo, Jägerbrand, Chen, et al., 2017), dominated by *Carex vaginata*, *C. bigelowii*, *Festuca ovina*, *Salix reticulata*, *S. polaris*, *Cassiope tetragona*, *Bistorta vivipar*a and *Thalictrum alpinum* (Alatalo, Little, et al., 2014; Molau & Alatalo, 1998). The more sparsely vegetated poor heath community (54% canopy cover) (Alatalo, Jägerbrand, Chen, et al., 2017) is dominated by *Betula nana*, *S. herbacea* and *Calamagrostis lapponica* (Alatalo, Little, Jägerbrand, & Molau, 2015; Molau & Alatalo, 1998).

Experimental design and measurements

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

Species in the plots were identified in the field or with the help of experienced bryophyte taxonomist Sven Franzén. Nomenclature for bryophyte species was retrieved from the literature (efloras.org, 2015; Hallingbäck & Holmåsen, 1985). 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 treatments). 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 between years/treatments 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 & Hollister, 2012).

Statistical analyses

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 species hits, total bryophyte cover, richness (species number per unit area), Simpson's diversity index D (hereafter called ‘diversity’) (Simpson, 1949) and the relative changes (ratio) for the whole period of the study (1995-2013), with 1995 data being the starting value. The use of relative change as response variable was due the fact that the number of hits per plot differed between treatments, and that 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 actual numbers. The cover, species richness and diversity community parameters were calculated for comparison of the bryophyte assemblages. Simpson’s diversity index was chosen since it is reliable even when sample size is small (Mouillot & Lepretre, 1999). In addition, nine species with more than a total of 25 hits during all four years of inventory (i.e. 1995, 1999, 2001 and 2013) were chosen in order to analyse relative changes for individual species between 1995 and 2013 (Table 1). For community changes (richness and diversity) all species occurrences were included in the analyses (Table 1).

Data on cover, species richness, diversity and individual species occurrence were checked for normality assumptions by the Shapiro-Wilk test and for homogeneity of variance by 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. We therefore used the Mann-Whitney U test, a robust non-parametric test, to examine the effect of the experimental warming treatments on relative changes between 1995-2013 in species abundances, litter, cover, richness and diversity for the heath and meadow ecosystems. We used two-tailed Spearman correlation to test the relationship between bryophytes (total cover and total richness) and deciduous shrub cover.

R version 3.4.4. (R Core Team, 2019) was used for analyses of results from the Shapiro-Wilks, Bartlett and Mann-Whitney U tests . Spearman correlations were performed in IBM© SPSS© Statistics Version 25.

Results

Bryophyte cover (-0.554) (P=0.01), but not bryophyte richness (-0.085) (P=0.432), was shown to be negatively correlated with cover of deciduous shrubs (Figure 1).

Bryophyte cover declined significantly in both heath (P=0.029; Z=-2.18) and meadow (P=0.020; Z=-2.32) after 18 years of experimental warming (Figure 2A, 2B, Figure 3A). In 1995, bryophyte cover was 31% and 59% in the heath and meadow, respectively, while after 18 years of temperature treatment it was 9% and 30%, in the heath and meadow, respectively (Figure 2A, 2B). Bryophyte cover decreased by 71% in the heath and by 50% in the meadow. In the control treatments, bryophyte cover had smaller changes, decreasing from 27% to 21 % in the heath, and increasing from 69% to 80% in the meadow during the same period (Figure 2A, 2B).

Richness declined in response to experimental warming in the heath (P=0.018; Z=-2.37), while it was not significantly different in the meadow (Figure 2C, 2D, Figure 3B) after 18 years of warming. In 1995, richness was 6.1 and 7.1 (species per 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 (Figure 2C, 2D). This represented a decline in richness of 39% in the heath and 26% in the meadow. In the control treatment, richness was 7.3 and 6.25 after 18 years in the heath and meadow, respectively (Figure 2C, 2D).

Diversity did not show any significant responses to experimental warming over 18 years in either the heath or the meadow ecosystem (Figure 2E, 2F, Figure 3C). However, there was a trend of decline in diversity in the heath (P=0.083; Z=-1.73).

Anthelia juratzkana declined significantly in abundance (P=0.038; Z=-2.07) after 18 years of experimental warming in the heath, but not in the meadow (Figure 4A, Figure S1). *Ptilidium ciliare* declined significantly in abundance (P=0.021; Z=-2.31) after 18 years of experimental warming in the meadow, but not in the heath (Figure 4H, Figure S1). No other species showed any significant changes in response to experimental warming after 18 years (Figure 4). In the experimental warming plots, there was a trend for a decrease in *A. juratzkana* in the meadow (Figure 4A, Figure 5B), *Dicranum groenlandicum* in the meadow (Figure 4B, Figure S1), *Polytrichum juniperinum* in the heath (Figure 4G, Figure S1), *Gymnomitrion concinnatum* in the heath (Figure 4C, Figure 6A), *Hylocomium splendens* in the meadow (Figure 4D, Figure S2) and *Kiaeria starkei* in the heath (Figure 4E, Figure S2).

The abundance of litter increased significantly after 18 years of experimental warming in both the heath (P=0.021; Z=-2.31) and meadow (P=0.021; Z=-2.31) (Figure 4J, Figure S3).

Discussion

As hypothesised, both cover and richness of bryophytes declined under long-term experimental warming. After 18 years, the bryophyte cover had decreased by 71% in the heath and by 50% in the meadow. Similar negative responses have been reported in previous studies (Elmendorf et al., 2012; 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, Jägerbrand, et al., 2015; Sun et al., 2017), suggesting that changes in bryophyte communities may take time. However, bryophyte responses to long-term warming are not always negative (Bokhorst, Convey, Huiskes, & Aerts, 2016; Van Wijk et al., 2003).

In the present study, the decline in total bryophyte cover in both the heath and meadow was driven by a general decline in multiple species, with only two individual species showing a significant decline: *Anthelia juratzkana* in heath and *Ptilidium ciliare* in meadow. Thus, while most of the individual species that were analysed did not show any detectable changes, the cumulative changes became significant. In addition, the responses differed among plant communities. Importantly, the decline in bryophyte cover and richness increased with time in the experimental warming plots. Unfortunately the long-term experiment was terminated in 2017, and it is therefore not possible to study whether further warming will cause the bryophyte cover and richness to decrease further. While bryophyte cover declined in the experimentally warmed plots in both the meadow and heath community, it tended to increase in the control plots in the meadow community, but not in the heath. This may be due to the fact that 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, Jägerbrand, Chen, et al., 2017). Bryophytes are generally highly dependent on external water (He et al., 2016) and variation in annual rainfall could therefore potentially affect their photosynthesis and growth. However, the annual precipitation varied substantially among years with 2012 or 2013 having neither the highest nor the lowest annual precipitation (Alatalo, Jägerbrand, Chen, et al., 2017). Thus, it is unlikely that the precipitation was the cause of changes in bryophyte cover. The OTCs could potentially have hindered the colonization of bryophytes from outside the warmed plots. However, as the OTCs are open in the top, they are open for colonization by spores from outside.

Previous studies have shown that both bryophytes and lichens are negatively correlated with vascular plant canopy (Alatalo, Jägerbrand, Chen, et al., 2017; Jägerbrand et al., 2012; Löbel, Dengler, & Hobohm, 2006). Therefore, the widespread shrubification reported in alpine and arctic tundra (Maliniemi et al., 2018; Myers-Smith et al., 2011; Myers-Smith & 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*, which is a common circumpolar deciduous shrub also found at our site in Sweden. For example, in Alaska *B. nana* cover increased by 94% (Sistla et al., 2013), while they both increased in cover and grew higher and with larger leaves in Sweden (Baruah, Molau, Bai, & Alatalo, 2017; Jägerbrand, Alatalo, Chrimes, & Molau, 2009). However, this is not always the case (Løkken, Hofgaard, Dalen, & Hytteborn, 2019) and the responses may differ between deciduous and evergreen shrubs, and between sites (Maliniemi et al., 2018; Vowles et al., 2017). As a growing number of studies report an increase in deciduous shrubs in alpine and arctic tundra, we examined the correlation between this group of vascular plants and bryophytes. Our hypothesis of a negative correlation between deciduous cover and bryophyte cover and richness was partly supported. A previous study in northwest Fennoscandia and northwest Russia found a negative correlation between bryophytes (both cover and richness) and deciduous shrub cover (Pajunen, Oksanen, & Virtanen, 2011). We found a significant negative relationship between deciduous shrub cover and bryophyte cover, but not between deciduous shrub cover and bryophyte richness. This may be due to the fact that species loss may take longer to occur compared to decrease in cover. In contrast, a study with 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 need to be followed more closely in areas experiencing shrubification.

Conclusions

Climate change is increasing at a more rapid rate than previously thought with widespread impacts on Arctic/Alpine regions. Here we show that the important but relatively understudied bryophytes are likely to become adversely affected longer term. Both cover and richness have declined after 18 years of experimental warming and the rate of decline increased over time. However, diversity did not show any significant responses to the warming treatment. The decline in total bryophyte cover in both heath and meadow was driven by a general decline in multiple species. Many of the most common species included in the individual analyses did not show any detectable changes, but the cumulative change was significant. The results also indicate that species loss was slower than the general decline in bryophyte abundance. In addition, the widespread shurbification reported across the Arctic is likely to have a negative impact on bryophytes. We found a significant negative relationship between deciduous shrub cover and bryophyte cover, but not between deciduous shrub cover and bryophyte richness, likely due to a more delayed decline in species richness compared to abundance, similar to what was observed in response to long-term warming.

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Authors' contributions

JMA and UM designed the experiment, AKJ, JMA and UM carried out the fieldwork. JMA, AKJ and SC carried out the data analyses, AKJ and JMA made 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.

Competing financial interests: The authors declare no competing financial interests.

Data availability

Data used for analyses is included in the electronic supplementary materials

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Figures

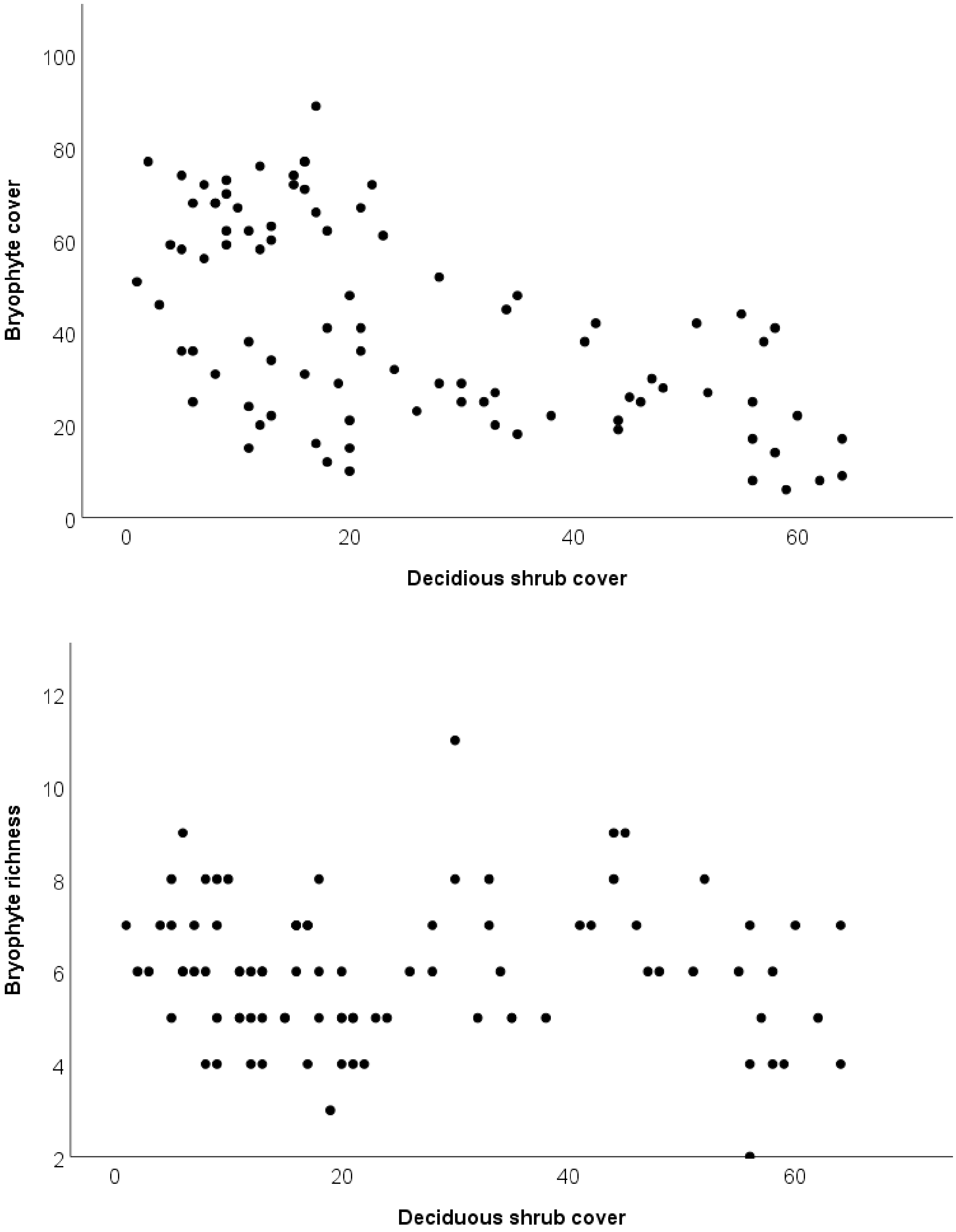

Figure 1. Relationship between (upper diagram) bryophyte cover and deciduous shrub cover and (lower diagram) bryophyte richness and deciduous shrub cover, at Latnjajaure, sub-arctic Sweden. Number of plots: *n* = 88.

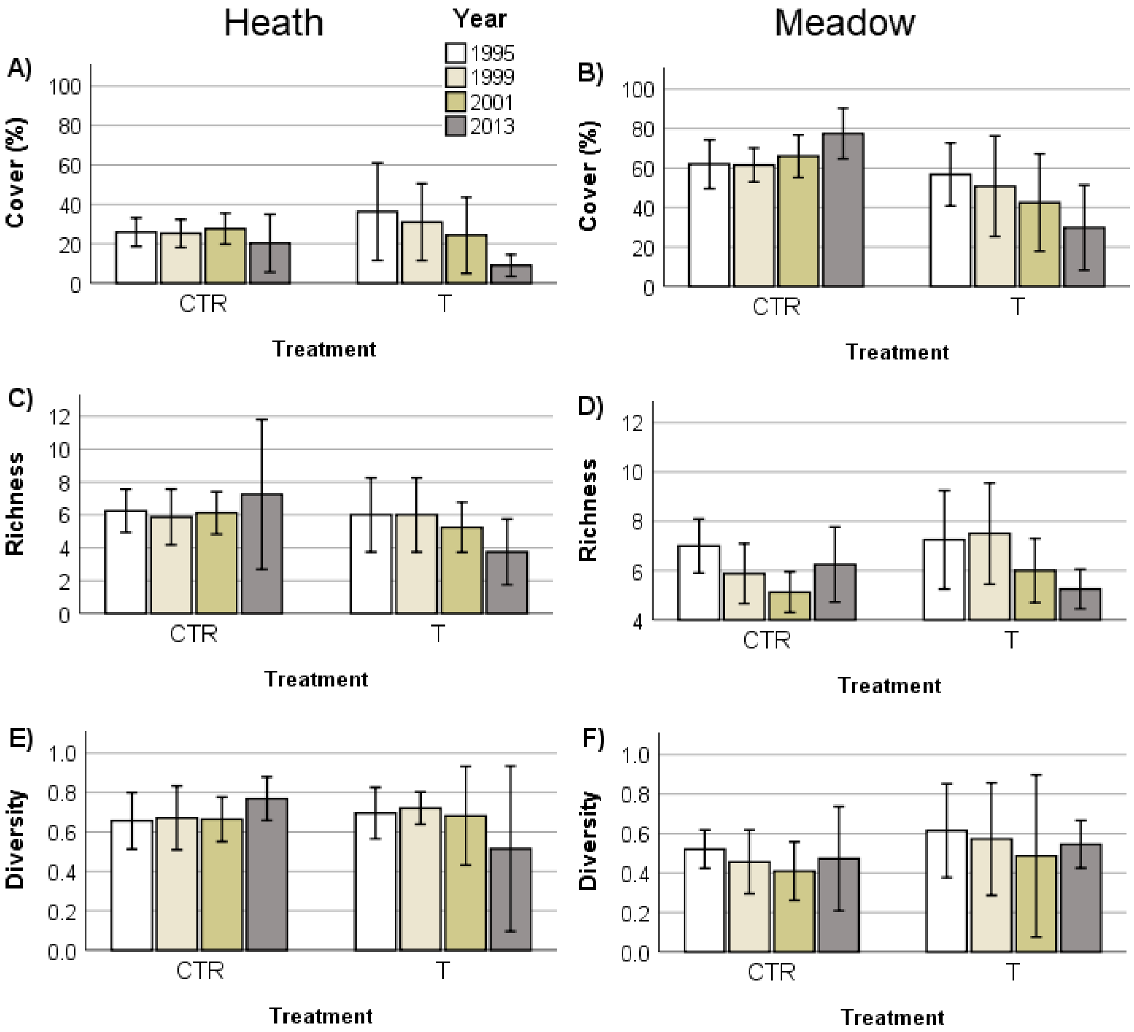

Figure 2. Changes over 18 years in the cover, richness and diversity of bryophytes in the heath and meadow ecosystems. Absolute values (per plot) for the years 1995, 1999, 2001 and 2013. CTR=control treatment, T=experimental warming treatment. Mean value ± 95% C.I. *Note*: Absolute values are shown to make it easier to visualize while relative changes were used for statistical analyses.

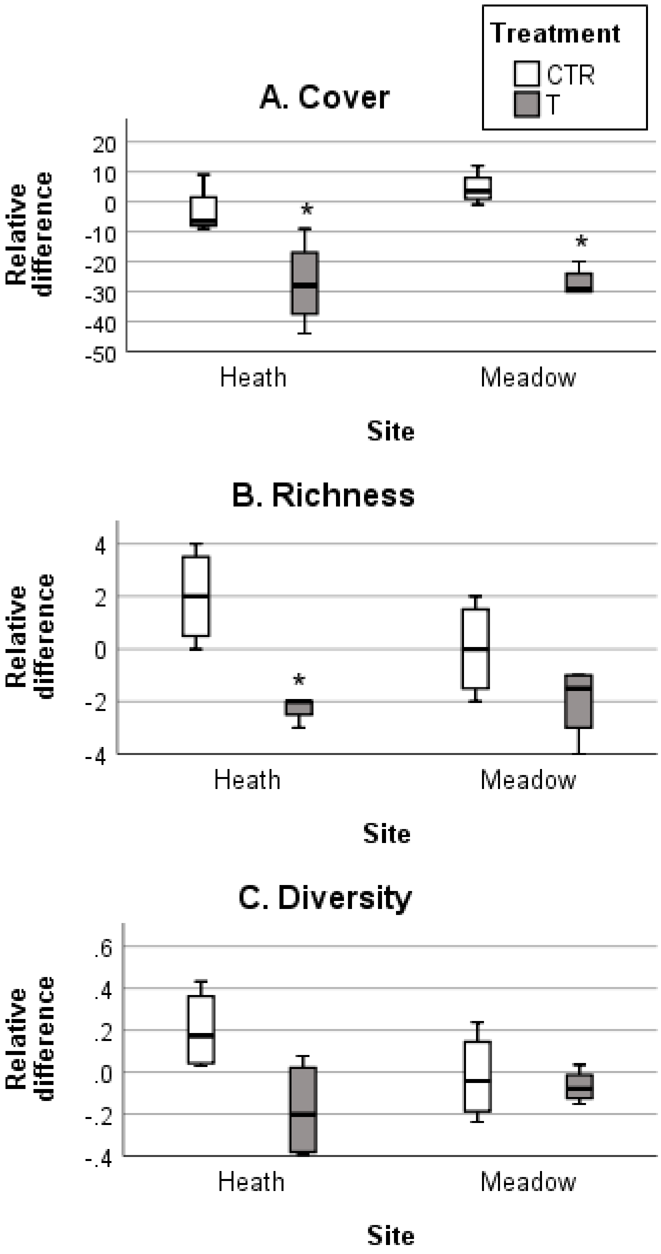

Figure 3. Relative changes after 18 years (1995-2013) in (A) bryophyte cover, (B) bryophyte richness and (C) bryophyte diversity. CTR=control treatment, T= experimental warming treatment. The boxplots show minimum, first quartile, median, third quartile and maximum values. n=4. P<0.05*.

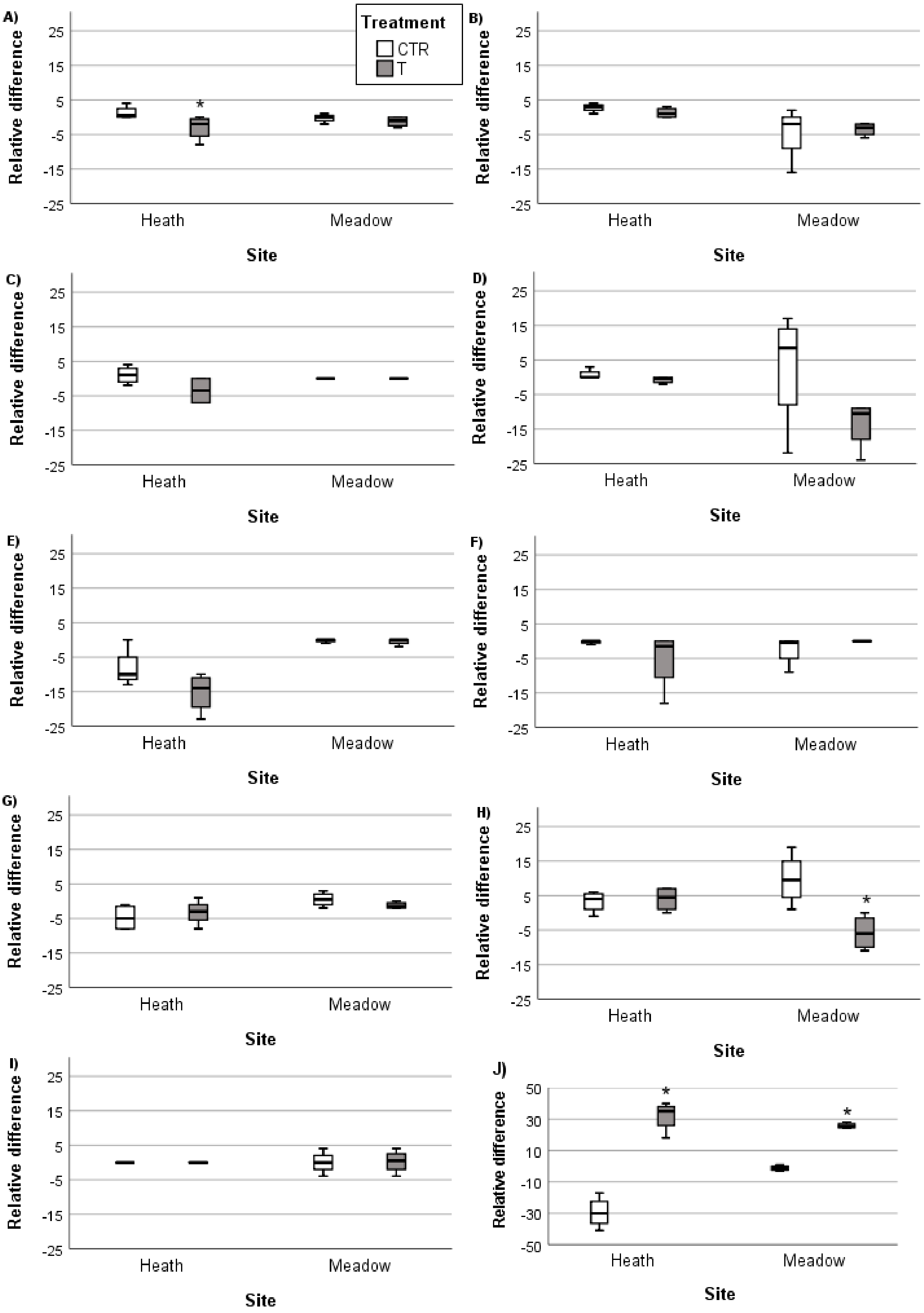

Figure 4. Relative changes in abundance after 18 years (1995-2013) in: A) *Anthelia juratzkana*, B) *Dicranum groenlandicum*, C) *Gymnomitrion concinnatum*, D) *Hylocomium splendens*, E) *Kiaeria starkei*, F) *Polytrichastrum alpinum*, G) *Polytrichum juniperinum*, H) *Ptilidium ciliare*, I) *Rhytidium rugosum* and J) litter. CTR=control treatment, T=experimental warming treatment.

The boxplots show minimum, first quartile, median, third quartile and maximum values. n=4. $P<0.05$ *.

Table 1. Species (31) included in the community analysis (cover, richness and diversity) and their abbreviations, and the nine species that were analysed for individual species level changes in the experimental warming treatment.

Species	Abbreviation	Species analysis
Anthelia juratzkana	Ajur	x
Barbilophozia kunzeana	Barbk	
Barbilophozia lycopodioides	Barblyc	
Bryum pseudotriquetrum	Brps	
Climacium dendroides	Cliden	
Dicranum brevifolium	Dicrb	
Dicranum elongatum	Dicre	
Dicranum fuscescens	Dicrf	
Dicranum groenlandicum	Dicrg	x
Dicranum scoparium	Dicrs	
Gymnomitrion concinnatum	Gym	x
Gymnocolea inflata	Gyminf	
Hylocomium splendens	Hs	x
Kiaeria starkei	Kias	x
Leiocolea heterocolpos	Lchc	
Lophozia grandiretis	Lophg	
Marsupella brevissima	Marbr	
Pleurocladula albescens	Plea	
Pohlia nutans	Ponu	
Pohlia nutans subsp. schimperi	Pohsch	
Polytrichastrum alpinum	Polya	x
Polytrichum juniperinum	Polyj	x
Polytrichum piliferum	Polyp	

Polytrichastrum sexangulare	Polysex	
Ptilidium ciliare	Ptc	x
Racomitrium lanuginosum	Rla	
Rhytidium rugosum	Rr	x
Sphagnum capillifolium	Sphc	
Sphagnum warnstorfii	Sphw	
Tritomaria quinquedentata	Trit	