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Responses of lichen communities to 18 years of natural and experimental warming

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- **Background and Aims** Climate change is expected to have major impacts on high alpine and arctic ecosystems in the future, but empirical data on the impact of long-term warming on lichen diversity and richness are sparse. This study report the effects of 18 years of ambient and experimental warming on lichens and vascular plant cover in two alpine plant communities, a dry heath with sparse canopy cover (54 %) and a mesic meadow with a more developed (67 %) canopy cover, in sub-arctic Sweden.
- **Methods** The effects of long-term passive experimental warming using open top chambers (OTCs) on lichens and total vascular plant cover, and the impact of plant cover on lichen community parameters, were analysed.
- **Key Results** Between 1993 and 2013, mean annual temperature increased about 2 °C. Both site and experimental warming had a significant effect on cover, species richness, effective number of species evenness of lichens, and total plant canopy cover. Lichen cover increased in the heath under ambient conditions, and remained more stable under experimental warming. The negative effect on species richness and effective number of species was driven by a decrease in lichens under experimental warming in the meadow. Lichen cover, species richness, effective number of species evenness were negatively correlated with plant canopy cover. There was a significant negative impact on one species and a non-significant tendency of lower abundance of the most common species in response to experimental warming.
- **Conclusions** The results from the long-term warming study imply that arctic and high alpine lichen communities are likely to be negatively affected by climate change and an increase in plant canopy cover. Both biotic and abiotic factors are thus important for future impacts of climate change on lichens.

Key words: Arctic, climate change, effective number of species, global warming, plant–climate interactions, species richness, tundra.

INTRODUCTION

Climate change is predicted to have a large impact on a wide range of ecosystems and ecosystem services (Shen and Ma, 2014; Wu *et al*., 2014; Zhang *et al*., 2014; Hao *et al*., 2017). Polar and high-elevation alpine ecosystems are likely to experience rapid climate change (Chapin *et al*., 1995; Mack *et al*., 2004; Stocker *et al*., 2013). Changes in species composition in alpine and arctic plant communities have already been recorded (Capers and Stone, 2011; Erschbamer *et al*., 2011; Callaghan *et al*., 2013), and a meta-analysis incorporating 1367 species responses provided evidence of a rapid latitudinal and elevational range shift in species across a large geographical range (Chen *et al*., 2011). However, it is not always possible to identify the cause of range shifts, and they may sometimes be due to other changes brought about by human activities (Groom, 2013). The loss of habitat due to climate change is predicted to increase the extinction risks on mountain ranges worldwide (Colwell *et al*., 2008; Raxworthy *et al*., 2008; Dirnböck *et al*., 2011; Engler *et al*., 2011). However, as glaciers retreat, this may uncover new habitats to be colonized, e.g. a number of studies have shown that lichen diversity and abundance is correlated with increasing time since glacier retreat (Bilovitz *et al*., 2014*a*, *b*, 2015*a*). However, the ice-free glacial tills exposed sometimes require several hundred years to reach the climax stage of alpine grassland (Raffl and Erschbamer, 2004). In polar regions and high alpine areas, lichens tend to be more important in terms of cover and biomass for N_2 fixation and as a food source for herbivores as vascular plants become smaller (Longton, 1984; Heggberget *et al*., 2002; Wirtz *et al*., 2003; Nash, 2008; Rees *et al*., 2008; Rai *et al*., 2014). Thus, lichens are a very important part of high-altitude/latitude ecosystems but, despite this, the majority of climate change studies to date focus on vascular plants (Alatalo and Totland, 1997; Arft *et al*., 1999; Dumais *et al*., 2014; Wheeler *et al*., 2016; Zhang and Wang, 2016). Long-term studies have shown that vascular plants have increased in abundance in response to warming (Sturm *et al*., 2001; Myers-Smith *et al*., 2011; Hobbie *et al*., 2017). Most studies on lichens lack information about species-level responses, and only a few incorporate species-level data to study the impact on different species or on lichen diversity and richness (Molau and Alatalo, 1998; Klanderud and Totland, 2005;

Lang *et al*., 2012; Alatalo *et al*., 2014*a*, 2015*a*). However, studies on lichens are currently being initiated worldwide to study potential impacts of climate change and other anthropogenic disturbances on lichen communities (Maphangwa *et al*., 2012; Rai *et al*., 2012*a*, *b*; Darnajoux *et al*., 2015; Shukla *et al*., 2015; Upreti *et al*., 2015; Piercey-Normore *et al*., 2016). Existing long-term studies (9–20 years) show that lichen biomass and/or cover is sensitive to long-term warming at alpine and arctic sites (Chapin *et al*., 1995; Van Wijk *et al*., 2003; Elmendorf *et al*., 2012; Lang *et al*., 2012; Sistla *et al*., 2013), while shorter term studies (2–7 years) report contrasting results (Press *et al*., 1998; Klanderud and Totland, 2005; Biasi *et al*., 2008; Alatalo *et al*., 2014*a*, 2015*a*). Lichen diversity has also been shown to decrease due to warming in arctic Alaska (16 years of warming) and sub-arctic Sweden (9 years of warming) (Lang *et al*., 2012). Furthermore, the response may be context dependent, depending on potential competition with vascular plants (Alatalo, 1998; Cornelissen *et al*., 2001). Modelling studies on the potential impact of climate change on lichens suggest that many lichen species are potentially threatened (Allen and Lendemer, 2016; Nascimbene *et al*., 2016; Rubio-Salcedo *et al*., 2017).

Here we examined lichen communities following 18 years of experimental warming in two contrasting alpine sub-arctic plant communities (mesic meadow and dry, poor heath) in Sweden. The hypotheses tested were that (1) lichen cover and diversity are negatively affected (decreasing) by long-term warming; (2) the negative impacts of warming are greater for a meadow community with a more developed vascular plant community (67 % canopy cover) than a poor heath with a less developed vascular plant community (54 % canopy cover); and (3) more species are lost than gained owing to long-term warming.

MATERIALS AND METHODS

Study area

Fieldwork took place at Latnjajaure field station, which is located in the Latnjavagge valley (68°21′N, 18°29′E; 1000 m above sea level) in northern Sweden. Climate parameters were measured daily from early spring 1992 onwards (by data loggers that collect hourly data on temperature, and by a manned climate station during summers). The climate at the site is classified as sub-arctic (Polunin, 1951), with snow cover for most of the year, cool summers and relatively mild, snow-rich winters. The growing season starts in late May and ends in early September (Molau *et al*., 2005). Mean annual air temperature ranged from -0·76 to -2·92 °C between 1993 and 2013 (Fig. 1; Supplementary Data Fig. S1). The mean temperature was highest in July, with mean temperature ranging from 5·9 °C in 1995 to 13·1 °C in 2013 (Fig. S1). Mean annual precipitation during that period was 846 mm, but in individual years it ranged from a low of 607 mm (1996) to a high of 1091 mm (2003) (Fig. S1). Climate data are collected throughout the year at the weather station at Latnjajaure field station, with hourly means, maxima and minima. Physical conditions in the soils in the valley vary from dry to wet and poor and 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*., 2014*b*). The mesic meadow community is dominated by *Carex vaginata*, *C. bigelowii*, *Festuca ovina*, *Salix reticulata*, *S. polaris*, *Cassiope tetragona*, *Polygonum viviparum* and *Thalictrum alpinum* (Molau and Alatalo, 1998; Alatalo *et al*., 2014*b*). The more sparsely vegetated poor heath community is dominated by *Betula nana*, *S. herbacea* and *Calamagrostis lapponica* (Molau and Alatalo, 1998; Alatalo *et al*., 2015*b*).

Experimental design and measurements

In July 1995, 1 × 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 warming) in a factorial design. At the start of the experiment there were eight control (CTR) plots and four plots with warming in each plant community (a total of 12 in each plant community). However, as we could not identify all initial control plots in 2013, in that year we only made measurements in four control and four warming plots in each community. Warming was applied by open top chambers (OTCs), and we monitored the temperature in control and plots with OTCs in the initial years with Delta^{TM} and Tinytag^{TM} loggers (Molau and Alatalo, 1998). As found in other studies (Marion *et al*., 1997; Molau and Alatalo, 1998; Hollister and Webber, 2000), OTCs increased the air temperature by 1·5–3 °C compared with control plots with ambient temperature. OTCs have also been shown to decrease canopy moisture (Hollister and Webber, 2000), causing earlier snow melt and prolonging the growing season (Molau and Alatalo, 1998; Hollister and Webber, 2000). The OTCs were then left on plots with warming treatment all year around. The majority of lichens in the plots were identified to species level. When necessary, we collected a specimen of the same species outside the experimental plots to be determined in the laboratory. In the case of *Cladonia*, when we were not able to determine the specimen to species level, we labelled it *Cladonia* spp. Coverage of each species was assessed by point-intercept using a 1 ×1 m frame with 100 grid points (Walker, 1996) in the peak of the 1995, 1999, 2001 and 2013 growing seasons. 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.

Statistical analyses

The following community parameters were calculated for comparison of the lichen assemblages: cover, species richness, Shannon's evenness and effective number of species (expH = exponential of Shannon entropy), which is the number of equally abundant species needed for the average proportional abundance of the species to equal that observed in the data set (where all species may not be equally abundant) (Jost, 2006). For vascular plants, we calculated total canopy cover. All data were checked for normality assumptions and homogeneity of variance by the Kolmogorov–Smirnov test and Levene's test of equality of error variances, respectively. We then applied a univariate analysis of variance (ANOVA) with treatment (control or warming) and vegetation type (meadow or heath) as fixed factors, and the ratio of the value in 2013 to the value in 1995 (relative change of the community parameters mentioned above) on each plot as the response variable. The use of the

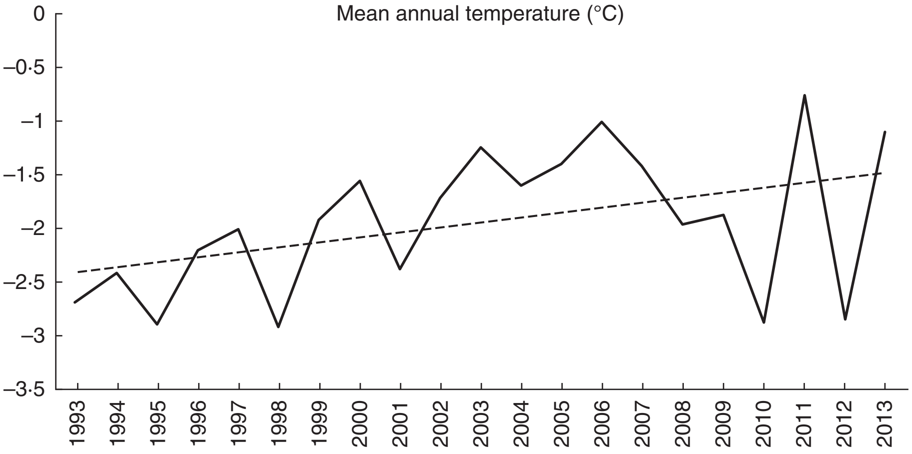

FIG. 1. Mean annual temperature (°C), 1993–2013, at Latnjajaure, Northern Sweden. Solid line, mean annual temperature; dotted line, trend line.

ratio as the response variable was due to 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 ANOVA included the initial value in 1995 of each variable as covariate, which may potentially have affected the response variable. To check for the effect of time on cover, species richness, effective number of species and Shannon's evenness, we applied a repeated measurement ANOVA on relative changes between 1995 and 1999, 1995 and 2001, and 1995 and 2013. As the species-level data did not meet the assumption of normal distribution after transformation, we used the conservative non-parametric Mann–Whitney U-test to analyse the effect of treatment on the relative change between 1995 and 2013 of the most common species. Only species with >100 pin-point intercept hits in total from the years 1995, 1999, 2001 and 2013 were included (Alatalo *et al*., 2015*a*). Two-tailed Pearson correlation was used to analyse correlations between lichen community parameters (total lichen cover, species richness, Shannon's evenness and effective number of species) and vascular plant canopy cover. All analyses were performed in IBM© SPSS© Statistics Version 23.0.0.2.

RESULTS

Initial lichen cover in the heath and meadow control plots was 35·75 % (s.d. ±5·44) and 11·75 % (±5·56), respectively. There was a significant effect of time on lichen total cover ($P < 0{\cdot}001$), species richness ($P = 0{\cdot}009$) and effective number of species ($P = 0{\cdot}004$), but not on Shannon's evenness ($P = 0{\cdot}3160$). Cover of lichens increased by 87 % over the 18 year study period in the heath control plots. Over the same period, lichen cover in control plots in the meadow increased by 21 %. Eighteen years of experimental warming and site both had significant effects on cover, species richness, effective number of species and evenness of lichens (Fig. 2; Table 1). Lichen cover decreased significantly in response to the long-term warming in both heath and meadow communities ($P < 0{\cdot}001$); there was an 8 % decline in lichen cover in the heath and a 31 % decline in the meadow compared with the starting year. A total of 22 lichen species were recorded in the study plots during the course of the study, with 19 in 1995 and 16 in 2013 (three new species recorded and six species lost in 2013) (Table 2). Lichen richness and, effective number of species, and evenness declined significantly ($P < 0{\cdot}001$, $P < 0{\cdot}014$, $P < 0{\cdot}035$, respectively) in response to long-term warming, an effect mainly driven by a decline in the meadow, while species richness and effective number of species both remained more stable in the heath community (Fig. 2). Total lichen cover (-0·542, $P < 0{\cdot}001$), species richness (-0·370, $P < 0{\cdot}001$), effective number of species (-0·350, $P = 0{\cdot}001$), but not Shannon's evenness (0·070, P = 0·545), were negatively correlated with vascular plant canopy cover (Fig. 3). Eighteen years of experimental warming and site both had significant effects on plant canopy cover (Table 3); warming having a positive impact on plant cover, with the largest increase found in the heath (Fig. 4).

Of the eight most common lichen species, there was a significant negative effect of long-term warming on cover of one species, *Flavocetraria cucullata* ($P = 0{\cdot}029$), in the heath, but not in the meadow ($P = 1$). For the other seven species, *Cetrariella delisei* ($P = 0{\cdot}114$, $P = 1$), *Flavocetraria nivalis* ($P = 0{\cdot}114$, $P = 0{\cdot}686$), *Cladina arbuscula* ($P = 0{\cdot}343$, $P = 0{\cdot}486$), *Cladonia unicalis* ($P = 0{\cdot}114$, $P = 0{\cdot}114$), *Ochrolechia frigida* ($P = 1$, $P = 1$), *Sphaerophorus globosus* ($P = 0{\cdot}20$, $P = 0{\cdot}114$) and *Stereocaulon alpinum* ($P = 0{\cdot}114$, $P = 1$), there were no significant effects on cover in either the heath or the meadow (Fig. 5).

DISCUSSION

The results from this long-term experiment confirm predictions that lichens may be less vulnerable in plant communities with less developed plant cover than in communities with more developed plant cover (Alatalo, 1998; Cornelissen *et al*., 2001). As hypothesized, lichens were more vulnerable in the meadow with its more developed plant canopy cover. We found that all lichen community parameters (total lichen cover, species richness, effective number of species and Shannon's evenness) were negatively correlated with plant canopy cover. Similar to

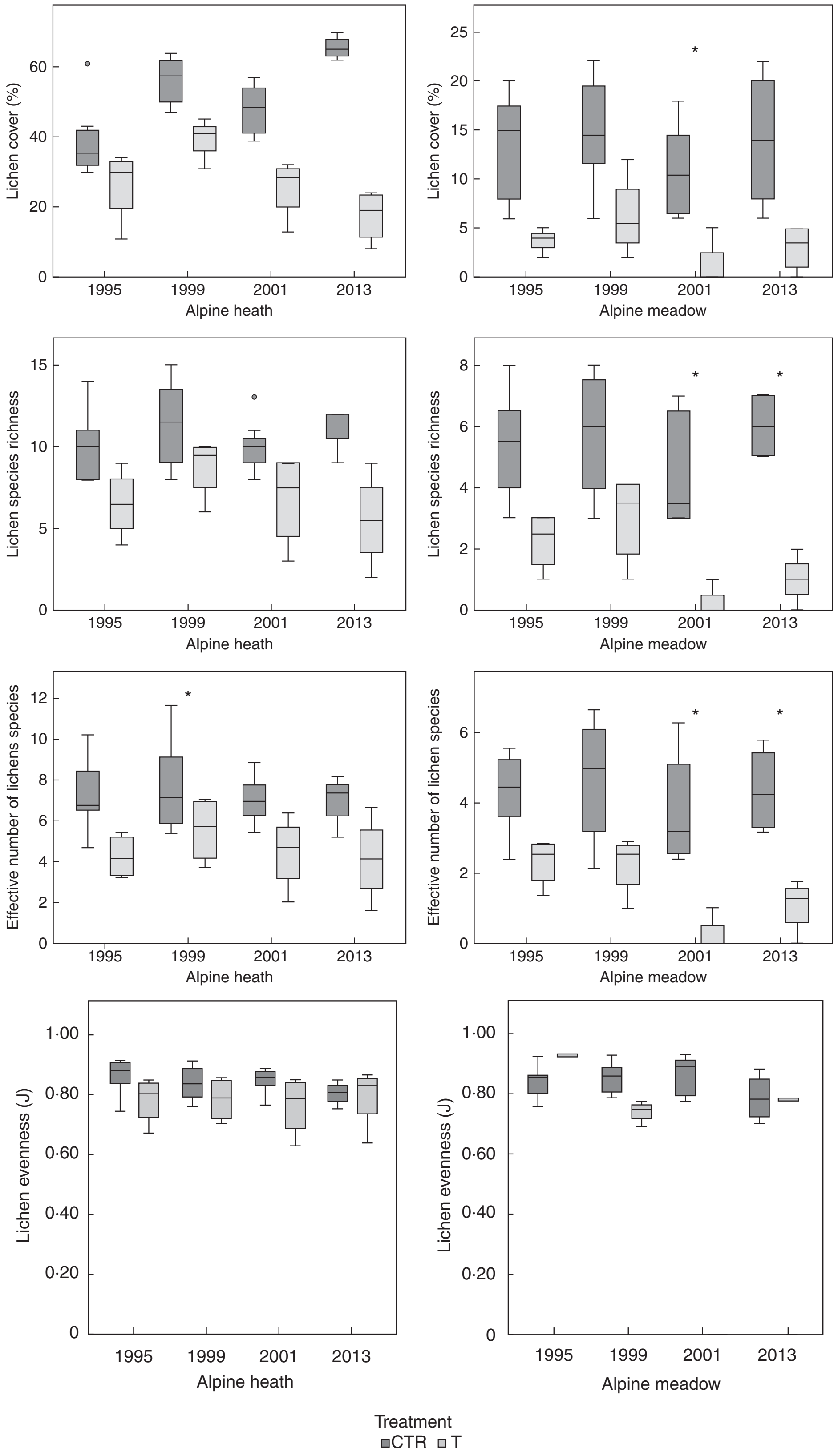

FIG. 2. Boxplots of changes in lichens during an 18 year period (1995–2013) of experimental warming in an alpine heath and an alpine meadow community at Latnjajaure, sub-arctic Sweden. Total cover of lichens (percentage), species richness of lichens, effective number of lichen species (exponential of Shannon's entropy) and Shannon evenness. Boxplots show the 10th–90th percentile of the data. Treatments: CTR, control; T, temperature warming. Number of plots: $n = 4$ for CTR and T at each site. Asterisks (*) indicate significant differences in relative changes between treatments.

TABLE 1. *Result of univariate ANOVAs testing the effects of treatment (18 years of experimental warming) and site (alpine meadow and alpine heath) on relative change in: cover, species richness, effective number of species and evenness for lichens*

Source	Type III sum of squares	*d.f.*	Mean square	*F*	*P*-value
Relative change in cover					
Initial cover	1·900	1	1·900	9·815	0·010
Treatment	4·050	1	4·050	20·926	<0·001
Site	2·652	1	2·652	13·703	0·003
Treatment × Site	0·269	1	0·269	1·388	0·264
Total	29·178	16			
$R^2 = 0{\cdot}704$ (Adjusted $R^2 = 0{\cdot}596$)					
Relative change in species richness					
Initial richness	0·885	1	0·885	8·919	0·012
Treatment	2·142	1	2·142	21·580	<0·001
Site	1·088	1	1·088	10·963	0·007
Treatment × Site	0·259	1	0·259	2·613	0·134
Total	17·714	16			
$R^2 = 0{\cdot}716$ (Adjusted $R^2 = 0{\cdot}613$)					
Relative change in effective number of species					
Initial effective no. sp.	0·839	1	0·839	5·737	0·036
Treatment	1·256	1	1·256	8·594	0·014
Site	1·196	1	1·196	8·180	0·016
Treatment × Site	0·206	1	0·206	1·411	0·260
Total	17·035	16			
$R^2 = 0{\cdot}579$ (Adjusted $R^2 = 0{\cdot}425$)					
Relative change in evenness					
Initial evenness	0·004	1	0·004	0·060	0·811
Treatment	0·397	1	0·397	5·750	0·035
Site	0·677	1	0·6777	9·807	0·010
Treatment × Site	0·660	1	0·660	9·566	0·010
Total	12·352	16			
$R^2 = 0{\cdot}700$ (Adjusted $R^2 = 0{\cdot}591$)					

D.f., degrees of freedom; F, F-statistics; *P*-value, significance level.

TABLE 2. *List of lichens recorded in the heath (H) and meadow (M) alpine vegetation communities at Latnjajaure, sub-arctic Sweden*

Lichen species	1995	1999	2001	2013
Alectoria nigricans	H	H	H	Not recorded
Alectoria ochroleuca	H	H	H	H
Cetrariella delisei	H, M	H, M	H, M	H, M
Cladina arbuscula	H, M	H, M	H, M	H, M
Cladina rangiferina	H	Not recorded	Not recorded	Not recorded
Cladonia spp.	H, M	H, M	H, M	H
Cladonia furcata	H	H, M	H	Not recorded
Cladonia gracilis	Not recorded	H	H	H, M
Cladonia pyxidata	Not recorded	Not recorded	Not recorded	H
Cladonia uncialis	H, M	H, M	H, M	H, M
Cornicularia divergens	H	H	H	Not recorded
Flavocetraria cucullata	H, M	H, M	H, M	H, M
Flavocetraria nivalis	H, M	H, M	H, M	H, M
Nephroma arctica	H, M	H, M	H, M	H
Ochrolechia frigida	H, M	H, M	M	Not recorded
Peltigera aphthosa	H, M	H, M	H, M	H, M
Peltigera scabrosa	H	H	H	H, M
Pertusaria dactylina	Not recorded	Not recorded	Not recorded	H
Solorina crocea	H	H	H	Not recorded
Sphaerophorus globosus	H, M	H, M	H, M	H, M
Stereocaulon alpinum	H	H	H	H
Thamnolia vermicularis	H, M	H, M	H, M	H, M

Species in bold are the eight most common lichen species found.

other studies (Sturm *et al.*, 2001; Myers-Smith *et al.*, 2011; Harte *et al.*, 2015; Hobbie *et al.*, 2017), we found that long-term warming caused a significant increase in total plant canopy cover, with canopy expanding most in the heath. As both lichens (this study) and bryophytes (Jägerbrand *et al.*, 2012) have been shown to be negatively correlated with vascular plant canopy, a future increase in vascular plant canopy is therefore likely to have a detrimental effect on these groups. The differences in canopy cover of vascular plant communities may thus help to explain the significant site effect on all response variables. The negative impact on diversity is in line with previous long-term studies in Alaska showing a decrease in lichen diversity under 16 years of warming (Lang *et al.*, 2012). This highlights the importance of long-term studies, as shorter term studies have tended to find contrasting effects on lichens (Klanderud and Totland, 2005; Alatalo *et al.*, 2014*a*), while longer term studies have typically found negative effects (Chapin *et al.*, 1995; Van Wijk *et al.*, 2003; Elmendorf *et al.*, 2012; Lang *et al.*, 2012; Sistla *et al.*, 2013).

The responses to long-term warming differed between the two plant communities studied, with the meadow experiencing a larger decline in lichen cover relative to the initial year of the study than the heath community (Fig. 2). A similar pattern was found for richness and effective number of species, which declined in the meadow but not in the heath. This shows that both abiotic and biotic interactions may play important roles in lichen responses and reveals the necessity of including different

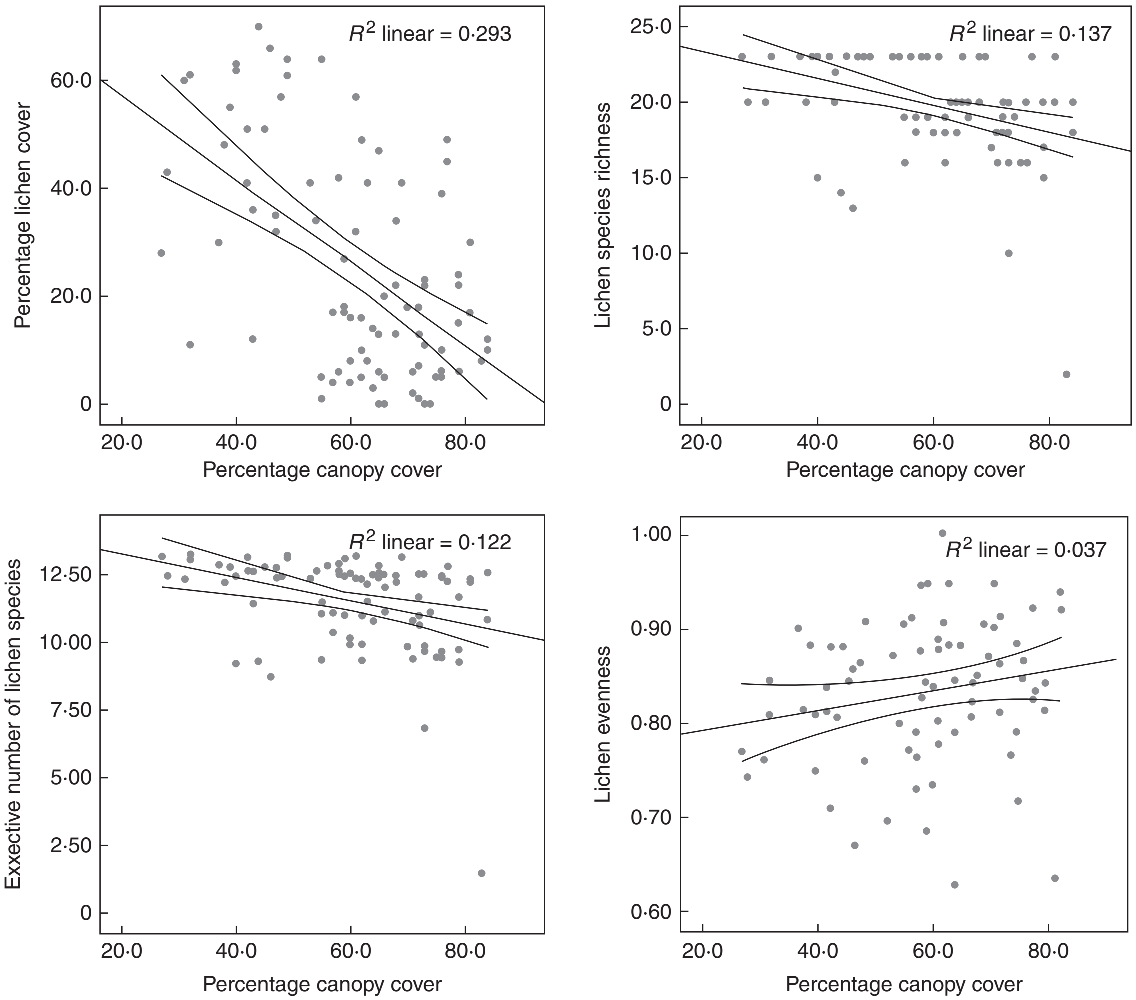

FIG. 3. Relationship between lichens and vascular plant canopy cover at Latnjajaure, sub-arctic Sweden: total cover of lichens, species richness of lichens, effective number of lichen species (exponential of Shannon's entropy) and Shannon evenness. Number of plots: $n = 88$.

TABLE 3. *Result of univariate ANOVAs testing the effects of treatment (18 years of experimental warming) and site (alpine meadow and alpine heath) on relative change in vascular plant canopy cover*

Source	Type III sum of squares	d.f.	Mean square	F	P-value
Relative change in cover					
Initial cover	2·247	1	2·247	54·156	<0·001
Treatment	0·698	1	0·698	16·831	0·002
Site	0·194	1	0·194	4·664	0·054
Treatment × Site	0·456	1	1·018	24·542	<0·001
Total	36·623	16			
$R^2 = 0{\cdot}906$ (adjusted $R^2 = 0{\cdot}872$)					

plant communities in experimental studies. In our study, of the eight most common species, we only found a significant negative impact on one species, *F. cucullata*, in the heath, but not in the meadow. However, while there were no significant effects on the other species, there was a general tendency for lower abundance of the most common species in the plots experiencing long-term warming. Thus, it is likely that the increase in evenness observed in our long-term study may have been caused by an overall decline in dominant lichen species over the study period.

The long-term data from our control plots also indicate that bare ground in high alpine areas that has been ice free for a long period (since the retreat of glaciers) can continue to be colonized by lichens, similarly to the plant progression that occurs when glaciers retreat (Raffl and Erschbamer, 2004; Bilovitz *et al.*, 2015*a*, 2015*b*).

In fact, Latnjajaure experienced a natural increase in mean annual temperature of about 2 °C between 1995 and 2013. Thus, the lichens in control plots were also exposed to natural climate warming, which may have contributed to the positive effect on lichen cover seen in control plots. It is likely that the main driver for the significant difference between treatments was the increase in lichen cover in the control plots, not the decrease in lichen cover in long-term warming plots. Thus, while the lichens within the warming plots declined less over the study period in the heath compared with the meadow community, the difference compared with the control plots was larger in the heath than in the meadow community. Another potential

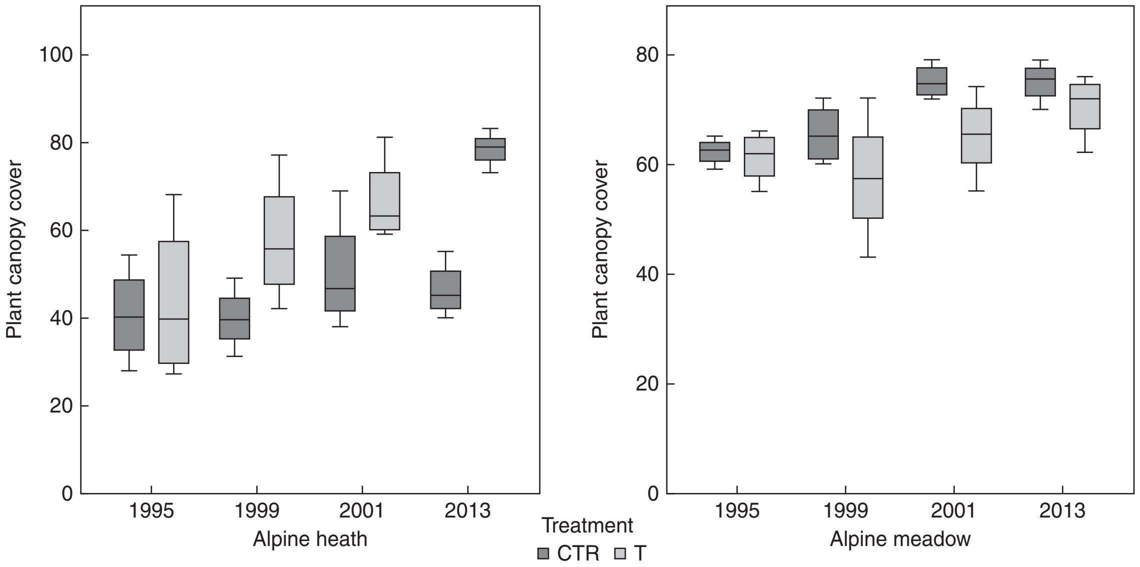

Fig. 4. Boxplots of changes in vascular plant canopy cover during an 18 year period (1995–2013) of experimental warming in an alpine heath and an alpine meadow community at Latnjajaure, sub-arctic Sweden. Boxplots show the 10th–90th percentile of the data. Treatments: CTR, control; T, temperature warming. Number of plots: $n = 4$ for CTR and T at each site.

explanation for the large difference in increase in cover may be differences in initial levels of bare ground and vascular plant cover between the plant communities, with the meadow having less bare ground and a more developed initial plant cover (Molau and Alatalo, 1998). Thus, the heath both offered more bare ground to be colonized by lichens and experienced less competition from vascular plants. The fact that lichen cover, species richness, and effective number of species were all negatively correlated to plant canopy cover indicates that lichens were most probaby outcompeted, or overgrown, by vascular plants.

It should be noted that a constant level of warming is not the most realistic scenario for future climate change, which will most probably increase both the variability and magnitude of climate events (Stocker *et al*., 2013). For example, increased precipitation during winter could potentially increase snow accumulation, and this in turn may reduce survival and growth of dominant arctic–alpine lichens (Bidussi *et al*., 2016). However, if an increase in precipitation during winter is accompanied by an earlier onset of spring due to warmer climate, this may be counterbalanced. While we did not measure precipitation or snow accumulation in our study, the experimental long-term warming caused a loss of soil carbon, nitrogen, C/N ratio and soil moisture in the mineral soil layer of the meadow (Alatalo *et al*., 2017). However, the warming did not have any effect on the soil parameters in the thin organic soil layers in the meadow or heath (Alatalo *et al*., 2017). As lichens do not have a well-developed root system, drying of deeper soil layers is therefore unlikely to have had a direct effect on lichens. However, OTCs have been shown to decrease moisture in the canopy layer (Hollister and Webber, 2000), which may potentially have had a negative effect on lichens that depend on moisture levels for their photosynthesis and growth. There are very few experimental studies that examine different warming scenarios across years (Jonasson *et al*., 1999; Alatalo *et al*., 2014*a*, 2016), and none is long term. The one existing short-term study (3 years) applying different climate change scenarios to lichens in an alpine meadow found the lichens to be highly resistant to a constant level of warming, a stepwise increase in warming and a single season of high-level pulse warming (Alatalo *et al*., 2014*a*). However, as the short-term and longer term responses of lichens have been shown to differ (Alatalo *et al*., 2015*a*), there is a need to initiate long-term experiments that incorporate different warming and precipitation scenarios.

Overall, 18 years of experimental warming brought a significant decline in lichen cover, species richness and, effective number of species, and evenness. The results showed that lichen responses are most probably dependent on both biotic and abiotic interactions and that responses differ among communities. Specifically, lichens increased more under ambient conditions in heath with a less developed plant community and decreased more under experimental warming in meadow with a more developed plant community. Species richness and effective number of species remained stable in the heath, but decreased under experimental warming in the meadow. Lichen cover, species richness, effective number of species and evenness were all negatively correlated with plant canopy cover.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of Figure S1: mean, minimum and maximum monthly temperatures (°C), and monthly precipitation (mm) January 1993–December 2013, at Latnjajaure, Northern Sweden.

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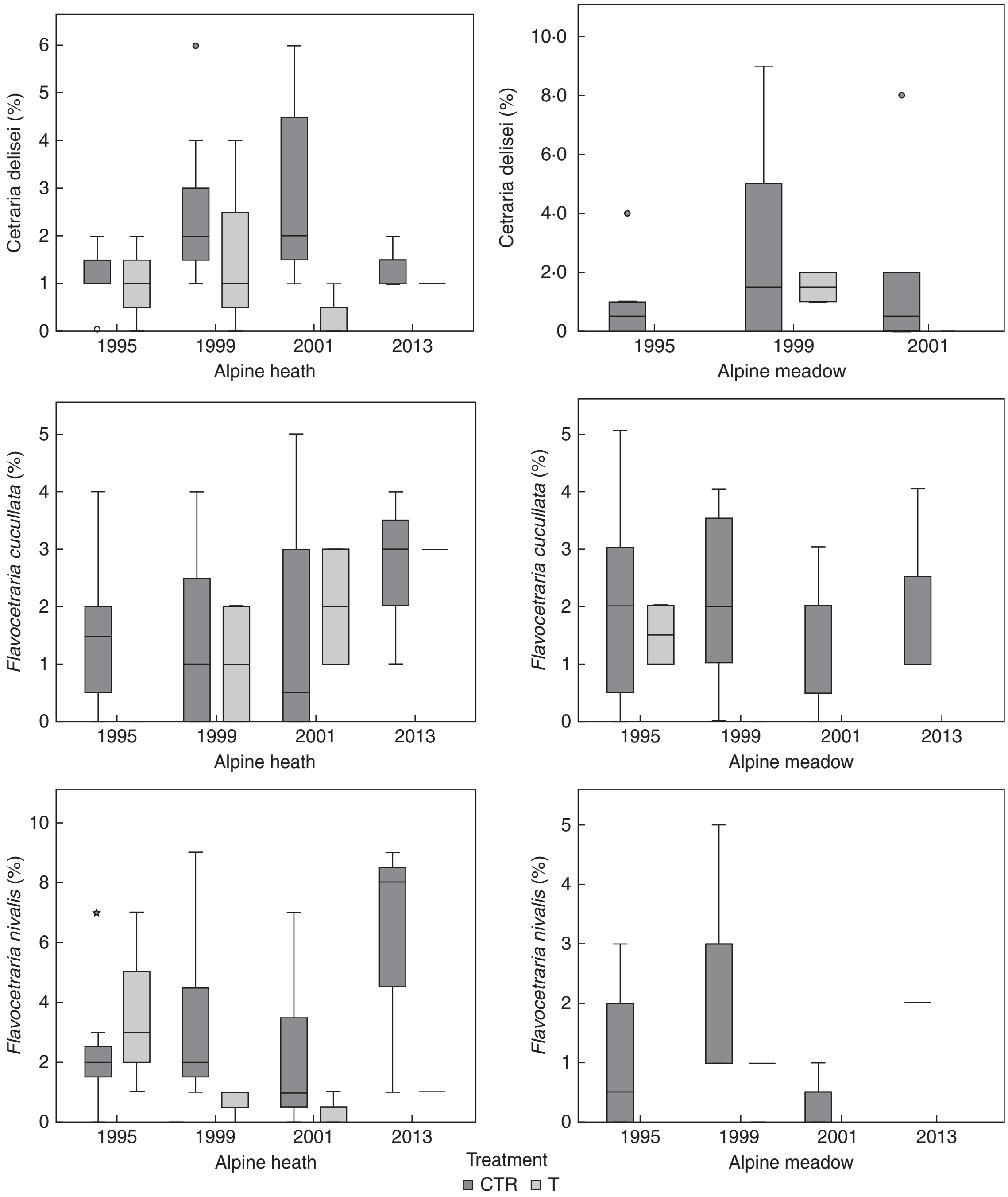

FIG. 5. Boxplots of species-specific responses of lichen cover (percentage) during an 18 year period (1995–2013) of experimental warming in a poor alpine heath and a rich alpine meadow community at Latnjajaure, sub-arctic Sweden. Boxplots show the 10th–90th percentile of the data. Treatments: CTR, control, T, temperature warming. Number of plots: $n = 4$ for CTR and T at each site.

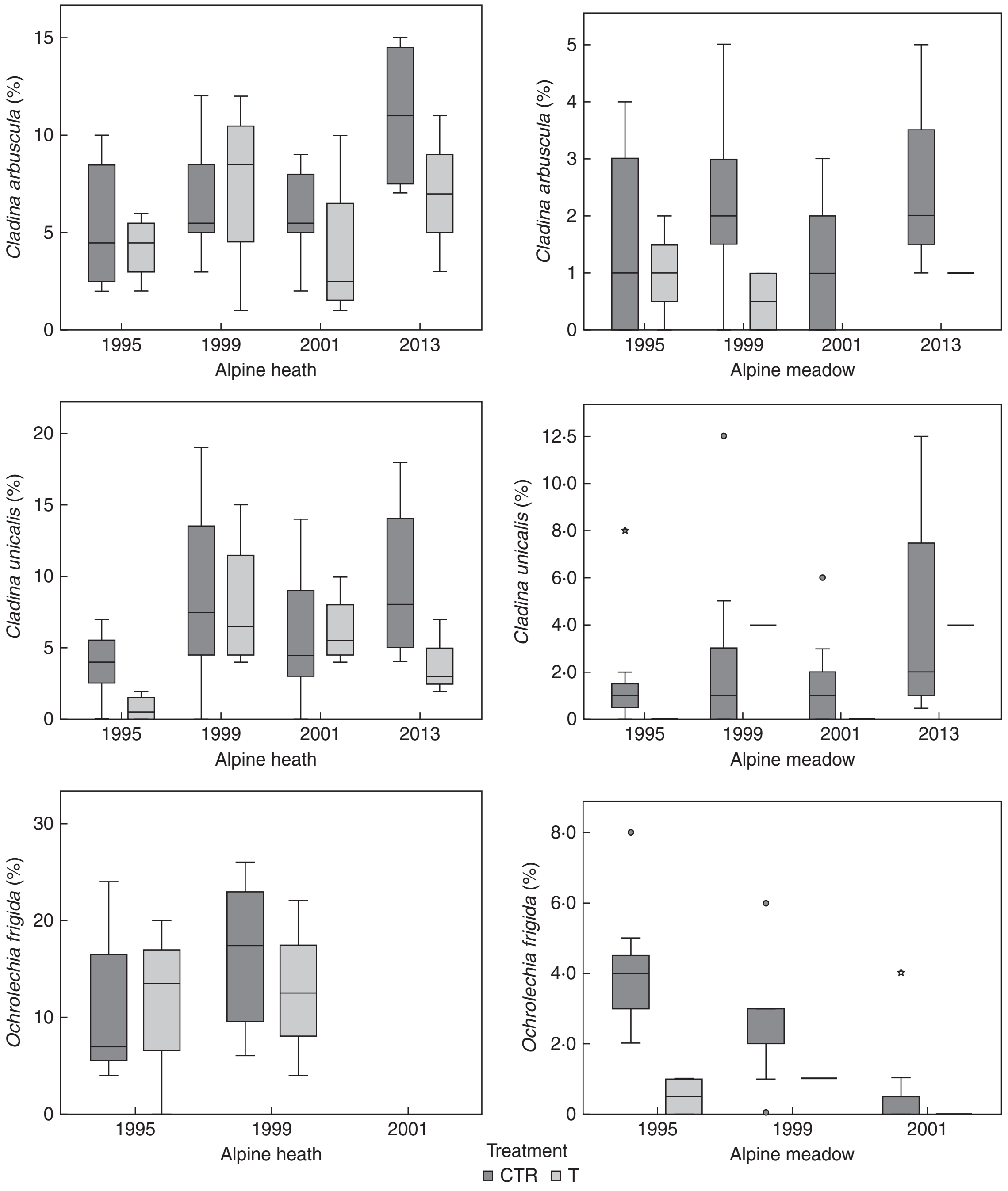

FIG. 5. Continued

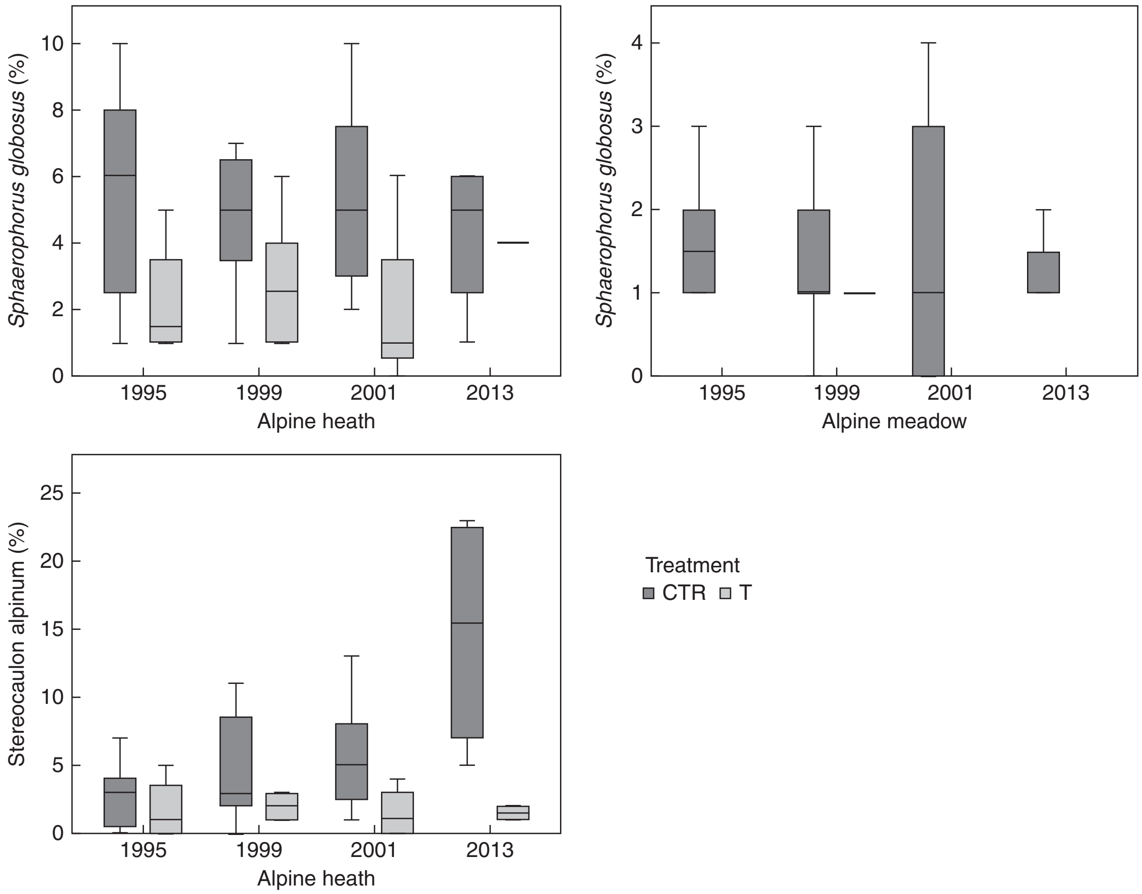

Fig. 5. Continued

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AUTHOR CONTRIBUTIONS

J.M.A and U.M. designed the experiment, J.M.A. and U.M. carried out fieldwork. J.M.A., A.K.J. and S.C. carried out data analyses, J.M.A. and A.K.J. made the figures, and J.M.A. made the tables. J.M.A. drafted the manuscript. All authors read, commented on and approved the final manuscript. The authors declare no competing financial interests.

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