Seven years of experimental warming and nutrient addition causes decline of bryophytes and lichens in alpine meadow and heath communities

Authors: Juha M. Alatalo[a]*, Annika K. Jägerbrand[b] and Ulf Molau[c]

[a] Department of Ecology and Genetics, Uppsala University, Campus Gotland, SE-621 67 Visby, Sweden; [b] VTI, Swedish National Road and Transport Research Institute, Box 55685, 102 15 Stockholm, Sweden; [c] Department of Biological and Environmental Sciences, University of Gothenburg, PO Box 461, SE-405 30 Gothenburg, Sweden.

*Corresponding author: E-mail: juha.alatalo@ebc.uu.se

Keywords: Arctic, climate change, cryptogams, dominant species, environmental change, global change, meadow, heath, mosses, polar region, tundra

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.672v1 | CC-BY 4.0 Open Access | rec: 6 Dec 2014, publ: 6 Dec 2014

Abstract

Global change is predicted to have large and rapid impact on polar and alpine regions. Bryophytes and lichens increase their importance in terms of biomass, carbon/nutrient cycling, cover and ecosystem functioning at higher latitudes/altitudes. Here we report from a seven year factorial experiment with nutrient addition and warming on the abundance of bryophytes and lichens in an alpine meadow and heath community. Treatments had significant negative effect on relative change of total abundance bryophytes and lichens, the largest decline to the nutrient addition and the combined nutrient addition and warming treatments, bryophytes decreasing most in the meadow, lichens most in the heath. Nutrient addition, and the combined nutrient addition and warming brought rapid decrease in both bryophytes and lichens, while warming had a delayed negative impact. Of sixteen species that were included the statistical analyses, we found significant negative effects on seven species. We show that impact of simulated global change on bryophytes and lichens differ in in time and magnitude among treatments and plant communities. Our results point out the importance of longer-term studies to improve the quality of climate change models, as short-term studies are poor predictors of longer-term responses of bryophytes and lichens, similar to what have been shown for vascular plants. Species-specific responses may differ in time, and this will likely cause changes in the dominance structures of bryophytes and lichens over time.

Introduction

Global change is affecting large areas of the globe both increased climate variability and increased nutrient deposits. Both factors are mainly driven by deposits and emissions from anthropogenic activities (Grandy *et al.* 2008; IPCC 2013; Clark *et al.* 2013). For example, in China that has among the richest biodiversity in the world (Zhang *et al.* 2014), climate change have been predicted to have great impact on wide variety of ecosystems in priority areas of biodiversity conservation (Wu *et al.* 2014), and extinction risk of protected plants is predicted to increase (Zhang *et al.* 2014). Climate change is also thought to have the potential to rapidly affect polar and alpine regions. As the same regions are often nutrient limited (Chapin *et al.* 1995; Mack *et al.* 2004), a combination of climate change and increasing nutrient levels can be expected to have large impact on their ecosystems. The number of studies on climate change has increased substantially and the pace seem to be increasing (Andrew *et al.* 2013; Shen & Ma 2014). Some of the changes that have been detected in a number of ecosystems around the world have been attributed to global change, either as response to nutrient deposition or existing climate warming trend. The changes include changes in species richness, community composition of plant communities, poleward or upward movement of species (Post *et al.* 2009; Maskell *et al.* 2010; Callaghan *et al.* 2011; Stöckli *et al.* 2011; Pauli *et al.* 2012; Clark *et al.* 2013). However, the causes behind shifts in species distributions can be difficult to pinpoint as a study on northward movement of vascular plants in Great Britain using data from 1978 to 2011 found (Groom 2013). The results indicated that the significant northward movement of plants was likely not due to climate warming, instead the reason was likely due to other changes resulting from anthropogenic activities (Groom 2013). Global change can also have contrasting effects on species richness depending on the nutrient status of the ecosystem (Chalcraft *et al.* 2008), and it is likely that the combination of increased nutrient levels and warming can have interactive effects in cold and nutrient limited ecosystems in polar and high alpine regions (Chapin *et al.* 1995; Mack *et al.* 2004). A worrying example of how increased nutrient level can potentially impact climate change comes from an experiment with 20 years of nutrient addition in Alaskan tundra where they showed that increased nutrient availability caused a net ecosystem loss of carbon which could lead to a positive feed back to climate warming (Mack *et al.* 2004). Other studies have reported contrasting short and medium term responses, revealing non-linear responses to treatments over time, indicating that longer-term responses may be difficult to predict (Alatalo & Little 2014; Alatalo *et al.* 2014b).

Bryophytes and lichens tend to make up larger part of the cover and biomass on higher altitudes and latitudes as the environment becomes harsher, this is partly an effect of that the vascular plants become smaller in stature (Longton 1984; Jägerbrand *et al.* 2006). At the same time their relative importance in the high altitude/latitude ecosystems increases due to their influence on factors such as recruitment of vascular plants (Soudzilovskaia *et al.* 2011), permafrost stability (Harden *et al.* 2006; Romanovsky *et al.* 2010; Turetsky *et al.* 2012), water, carbon and nitrogen cycling (Turetsky 2003; Turetsky *et al.* 2012). Many of the bryophyte and lichen species found in polar regions exhibits wide distributions, some being circumpolar, making them important parts of ecosystem functioning even on global scale. Recent research also show that migratory birds can transfer bryophyte diaspores bilpolary, supporting bryophyte long range dispersal (Lewis *et al.* 2014). Bryophytes and lichens also fill important roles in biological soil crusts in deserts world wide (Zhang 2005; Li *et al.* 2013). Yet the number of experimental global change studies on bryophytes and lichens are small compared by the number of studies on vascular plants in these severe environments, at least when it comes to having a resolution on species level, or community responses that include bryophyte and lichen diversity (Potter *et al.* 1995; Alatalo 1998; Molau & Alatalo 1998; Jägerbrand, Molau & Alatalo 2003; Jägerbrand *et al.* 2006, 2009; Klanderud 2008; Lang *et al.*

2009, 2012; Bjerke *et al.* 2011; Olsen & Klanderud 2014; Alatalo, Jägerbrand & Molau 2014a). In most cases when bryophytes are included in experimental global change studies, they are grouped as "mosses" or "lichens" (Graglia *et al.* 2001; Hill & Henry 2011). This is likely due to that ecologist commonly have problems to identify bryophytes and lichens to species level (Turetsky *et al.* 2012). It is also worrying that modelling studies on the impact of climate change often seem to lack data on bryophytes and lichens as their predictions will be of less value for high altitude, polar and desert regions due to their increasing importance in severe environments.

Here we report on the impact of a seven year factorial study with experimental nutrient addition and warming on total community and individual species abundances of dominant bryophytes and lichens in two contrasting alpine plant communities in subarctic Sweden.

Material and Methods

Study area

Fieldwork took place at the Latnjajaure Field Station (LFS) in northern Sweden, at 1000 m elevation in the valley of Latnjavagge (68°21´N, 18°29´E). Continuous climate data were provided from the early spring of 1992 onwards. Climate is classified as sub-arctic (Polunin 1951) with snow cover for most of the year, cool summers, and relatively mild, snow-rich winters. Mean annual temperatures ranged from –2.0 to –2.7°C between 1993 and 1999, with winter minima of –27.3 to –21.7°C. Mean annual precipitation during this time period was 808 mm, with individual years ranging from a low 605 mm in 1996 up to 990 mm in 1993. The warmest temperatures come in July, which had mean temperatures ranging from + 5.4°C in 1992 to +9.9°C in 1997. Physical conditions in the valley vary from dry to wet and poor and acidic to base-rich, with a variety of plant communities to match (Molau & Alatalo 1998; Alatalo *et al.* 2014b).

Experimental design

In July 1995, 20 plots (1 x 1 m) with homogenous vegetation cover were chosen in both the meadow and heath plant communities and randomly assigned to treatments in a factorial design. There were 8 control (CTR) plots and 4 plots for each of the experimental treatments in each plant community: warming (T for temperature enhancement), nutrient addition (N) and combined warming and nutrient addition (TN). Warming was induced by Open Top Chambers (OTCs) that increase temperature by 1.5 to 3°C compared to control plots with ambient temperature (Marion *et al.* 1997; Molau & Alatalo 1998). Nutrient addition consisted of 5 g of nitrogen (as NH_4NO_3) and 5 g of phosphorus (P_2O_5) per m^2, dissolved in 10 L of meltwater. In 1995 all plots were analyzed with a point–frame method (Walker 1996) to determine the species occurrences under natural conditions before implementing the experimental treatments. The OTCs were then left on plots with warming treatments year-around, and nutrient addition was applied directly after the initial vegetation analyses in 1995 and a few days after snow melt in the subsequent years (1996-2001). The nutrient treatments were then terminated after 2001.

Measurements

The majority of bryophytes and lichens in the plots were identified to species level (with help from experienced bryophyte taxonomist Sven Franzen), and cover of each species was assessed using a 1 x 1 m frame with 100 grid points (Walker 1996) in the middle of the 1995, 1999, and 2001 growing seasons. 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 placed in the same position within the plot at each different measuring point. This method has been shown to be accurate in detecting changes in tundra vegetation (May & Hollister 2012).

Data analysis

From the point-frame data, we summed the number of touches to pins within each plot to produce plot-level abundance measures for each species. This was then used to calculate relative changes in abundances. We included only the most dominant species in the analyses, i.e. excluding those with less than 100 hits from the point framing (Table 1). For responses in relative changes of total abundances of the most dominant bryophytes and lichens, GLM (general linear model) was used to analyse significant responses of sites and treatments (both as fixed factors) and their interactions. Species abundance was highly skewed and therefore did not meet assumptions of normality, so instead of GLM we used nonparametric tests. Kruskal-Wallis Test was used for analyzing the effect of all treatments as group on relative changes of species specific abundances. When significant, Mann-Whitney U Test was used to analyze the effect between treatments. All analyses were executed in SPSS version 19 (IBM).

Results

Impact on total abundance of the most dominant bryophytes and lichens

Total abundances of the most dominant bryophytes declined among years in response to the treatments, with the largest decline found to the nutrient addition and the combined nutrient addition and warming treatments (Figure 1, Tables 2, 3). The decline in bryophytes was significantly larger in the rich meadow than in the poor heath community (Figure 1, Tables 2, 3). The treatments had somewhat different responses over time, nutrient addition and the combined nutrient addition and warming causing a rapid decrease that then did not worsen much further between 1999 and 2001. In contrast warming had larger negative impact in the meadow (but not in the heath) between 1999 and 2001, exhibiting a more delayed response pattern compared to the nutrient addition (Figure 1). Bryophytes in control plots tended to increase in both communities, with the increase extending though the whole period (Figure 1).

Total abundance of the most dominant lichens declined among years in response to all treatments in the poor heath, the nutrient addition and combined nutrient addition and warming having the largest negative impact (Figure 1, Tables 2, 3). This negative impact of nutrient addition and the combined nutrient addition and warming extended throughout the whole period. In the heath, treatments had no significant effect in the later period (1999 – 2001), when lichens decreased significantly in all treatments at the heath compared to the meadow community (Figure 1, Tables 2, 3). The decline of lichens was significantly larger in the poor heath compared to the rich meadow in both periods; 1995-2001 and 1999-2001 (Figure 1, Tables 2, 3).

Species specific responses of bryophytes and lichens

Out of sixteen most dominant species that had more 100 hits from the point framing and thus included the statistical analyses, we found significant negative effects of treatments on seven species; *Aulacomnium turgidum* (Wahlenb.) Schwägr. (acrocarpous bryophyte), *Cetrariella delisei* (Bory ex Schaer.) Kärnfelt & A. Thell (lichen), *Gymnomitrion sp*. (liverwort), *Kiaeria starkei* (F. Weber & D. Mohr) I. Hagen (acrocarpous bryophyte), *Stereocaulon alpinum* Laurer (lichen), *Hylocomium splendens* (Hedw.) Schimp. (pleurocarpous bryophyte), *Cladonia arbuscula* (Wallr.) Flot. (lichen). All significant treatment responses were negative when found, regardless if in the rich meadow or the poor heath community. With nutrient addition and the combined nutrient addition and warming having the largest negative effect on relative change of abundance among years (Figures 2, 3, Table 4). In control plots, most species tended to slightly increase in relative abundance between both 1995-2001 and 1999-2001.

Discussion

Previous studies have shown highly heterogenic response patterns for experimental nutrient addition and warming. For example, in a long-term study in Alaska and subarctic Sweden, combined nutrient and warming was shown to have significant negative effect on lichens and bryophytes, in the same study nutrient addition alone caused significant decrease in lichens biomass but had no significant effect on bryophytes, while warming caused no significant responses (Van Wijk et al. 2003). Experimental nutrient addition has been shown to have positive effect on bryophytes (Jonasson 1992; Robinson *et al.* 1998), and lichens in open high artic and alpine vegetation (Jonasson 1992), decrease of both bryophyte and lichens to nine years if nutrient addition in a subarctic birch forest (Richardson *et al.* 2002). Likewise, warming has been shown to cause arbitrary impact on bryophytes and lichens, with no responses of bryophytes (Chapin *et al.* 1995; Van Wijk *et al.* 2003; Lang *et al.* 2009; Jägerbrand *et al.* 2009; Alatalo *et al.* 2014a), negative effect on bryophytes (Press *et al.* 1998; Lang *et al.* 2012; Sistla *et al.* 2013), no effect on lichens (Jägerbrand et al. 2009; Alatalo et al. 2014a), negative effect on lichens (Press *et al.* 1998; Lang *et al.* 2012; Sistla *et al.* 2013), and positive effect on lichens (Chapin *et al.* 1995; Alatalo 1998; Biasi *et al.* 2008; Jägerbrand *et al.* 2009). The contrasting response patterns have been hypothesised to be caused by competitive interactions between cryptogams and vascular plants, and also to be attributed to how well the cryptogams are adapted to light competition (Alatalo 1998). Bryophyte species have been shown to have different responses to shading effects (Jägerbrand & During 2005). In sites with existing dense canopies the bottom layer cryptogam communities are thought to be dominated by shade-tolerant species while cryptogams in more open canopies are thought to be dominated by shade-intolerant species, an increase in canopy closure due to warming and/or increased nutrient levels is hypothesised to affect the shade-intolerant species most (Alatalo 1998). Therefore, cryptogams in sites with more developed vascular plant canopies are expected to be more resistant to global change with increased temperature and nutrient levels. Experimental support for the hypothesis has been found in a cross continental study on macro-lichens that included more southern parts of arctic where the vegetation canopy was more dense compared to vegetation with more open canopy in high arctic or arctic alpine sites (Cornelissen *et al.* 2001), and in a study in alpine subarctic Sweden on the effect of neighbouring vascular plants on bryophytes in contrasting plant communities (Jägerbrand *et al.* 2012). However, our results from the present study show that after seven years both the nutrient and warming treatments had significant negative effect in both the rich meadow and the poor heath community, thus not supporting the hypothesis. Bryophytes decreased the most in the meadow and the lichens decreased most in the heath, which is in accordance with previous findings (Jägerbrand *et al.* 2006). Nutrient addition and the combined nutrient addition and warming caused a more rapid response compared to the more delayed response of warming *per se*. Thus, it might be that long term warming will cause other shifts in the environment such as an increased accumulated thickness of litter that may have a more detrimental effect than live canopy. An increased production of litter could lead to that cryptogams get “covered” while live canopy cover will still leave “space” for the cryptogams. This could potentially be an artefact of using OTCs that may hinder litter to disperse outside the OTCs. Optimally, new experiments would include litter removal as one of the factors together with warming and nutrient addition in factorial set up. That long-term warming can cause drastic shifts in cryptogam communities is evident after two decades of experimental warming in Alaska which caused lichens to decrease by 99% and bryophytes by 63% (Sistla *et al.* 2013). However, the time needed for the negative effects to be expressed may differ among species and plant communities, as is shown in our study. After seven years of warming seven out of sixteen species included in the statistical analyses in our study was negatively affected. When we compare this to a previous study in the same sites on the impact of five years of warming, there were no significant effects from warming on bryophyte and lichens on community level, in fact only one species *Cetraria nivalis,* displayed a significant negative response to warming in the heath (Jägerbrand *et al.* 2009). These results point out the importance of longer-term studies to improve the quality of climate change models. Our results indicate that short-term studies are poor predictors of longer-term responses of bryophytes and lichens, similar as have been shown for vascular plants (Alatalo & Little 2014; Alatalo *et al.* 2014b). The results also show that species specific responses may differ in time, and that this will likely cause changes in the dominance structures of bryophytes and lichens over time. The potential role of litter for cryptogam development also need to be studied in controlled experiments to determine if canopy development or litter accumulation are the main driving forces behind the decrease of cryptogams found in longer-term global change experiments.

References

Alatalo, J. (1998) *Climate Change: Impacts on Structure and Biodiversity of Subarctic Plant Communities*. Göteborg University, Sweden.

Alatalo, J.M., Jägerbrand, A.K. & Molau, U. (2014a) Climate change and climatic events: community-, functional- and species-level responses of bryophytes and lichens to constant, stepwise, and pulse experimental warming in an alpine tundra. *Alpine Botany*, **124**, 81–91.

Alatalo, J.M. & Little, C.J. (2014) Simulated global change: contrasting short and medium term growth and reproductive responses of a common alpine/Arctic cushion plant to experimental warming and nutrient enhancement. *SpringerPlus*, **3**, 157.

Alatalo, J.M., Little, C.J., Jägerbrand, A.K. & Molau, U. (2014b) Dominance hierarchies, diversity and species richness of vascular plants in an alpine meadow: contrasting short and medium term responses to simulated global change. *PeerJ*, **2**, e406.

Andrew, N.R., Hill, S.J., Binns, M., Bahar, M.H., Ridley, E.V., Jung, M.-P., Fyfe, C., Yates, M. & Khusro, M. (2013) Assessing insect responses to climate change: What are we testing for? Where should we be heading? *PeerJ*, **1**, e11.

Biasi, C., Meyer, H., Rusalimova, O., Hämmerle, R., Kaiser, C., Baranyi, C., Daims, H., Lashchinsky, N., Barsukov, P. & Richter, A. (2008) Initial effects of experimental warming on carbon exchange rates, plant growth and microbial dynamics of a lichen-rich dwarf shrub tundra in Siberia. *Plant and Soil*, **307**, 191–205.

Bjerke, J., Bokhorst, S., Zielke, M., Callaghan, T., Bowles, F. & Phoenix, G. (2011) Contrasting sensitivity to extreme winter warming events of dominant sub-Arctic heathland bryophyte and lichen species. *Journal of Ecology*, **99**, 1481–1488.

Callaghan, T.V., Tweedie, C.E., Åkerman, J., Andrews, C., Bergstedt, J., Butler, M.G., Christensen, T.R., Cooley, D., Dahlberg, U., Danby, R.K., Daniëls, F.J.A., Molenaar, J.G. de, Dick, J., Mortensen, C.E., Ebert-May, D., Emanuelsson, U., Eriksson, H., Hedenås, H., Henry, G.H.R., Hik, D.S., Hobbie, J.E., Jantze, E.J., Jaspers, C., Johansson, C., Johansson, M., Johnson, D.R., Johnstone, J.F., Jonasson, C., Kennedy, C., Kenney, A.J., Keuper, F., Koh, S., Krebs, C.J., Lantuit, H., Lara, M.J., Lin, D., Lougheed, V.L., Madsen, J., Matveyeva, N., McEwen, D.C., Myers-Smith, I.H., Narozhniy, Y.K., Olsson, H., Pohjola, V.A., Price, L.W., Rigét, F., Rundqvist, S., Sandström, A., Tamstorf, M., Bogaert, R.V., Villarreal, S., Webber, P.J. & Zemtsov, V.A. (2011) Multi-Decadal Changes in Tundra Environments and Ecosystems: Synthesis of the International Polar Year-Back to the Future Project (IPY-BTF). *AMBIO*, **40**, 705–716.

Chalcraft, D.R., Cox, S.B., Clark, C., Cleland, E.E., Suding, K.N., Weiher, E. & Pennington, D. (2008) Scale-dependent responses of plant biodiversity to nitrogen enrichment. *Ecology*, **89**, 2165–2171.

Chapin, F.I., Shaver, G., Giblin, A., Nadelhoffer, K. & Laundre, J. (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694–711.

Clark, C.M., Morefield, P.E., Gilliam, F.S. & Pardo, L.H. (2013) Estimated losses of plant biodiversity in the United States from historical N deposition (1985–2010). *Ecology*, **94**, 1441–1448.

Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M., Michelsen, A., Graglia, E., Hartley, A.E., Hik, D.S., Hobbie, S.E., Press, M.C., Robinson, C.H., Henry, G.H.R., Shaver, G.R., Phoenix, G.K., Gwynn Jones, D., Jonasson, S., Chapin, F.S., Molau, U., Neill, C., Lee, J.A., Melillo, J.M., Sveinbjornsson, B. & Aerts, R. (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, **89**, 984–994.

Graglia, E., Jonasson, S., Michelsen, A., Schmidt, I.K., Havström, M. & Gustavsson, L. (2001) Effects of environmental perturbations on abundance of subarctic plants after three, seven and ten years of treatments. *Ecography*, **24**, 5–12.

Grandy, A.S., Sinsabaugh, R.L., Neff, J.C., Stursova, M. & Zak, D.R. (2008) Nitrogen deposition effects on soil organic matter chemistry are linked to variation in enzymes, ecosystems and size fractions. *Biogeochemistry*, **91**, 37–49.

Groom, Q.J. (2013) Some poleward movement of British native vascular plants is occurring, but the fingerprint of climate change is not evident. *PeerJ*, **1**, e77.

Harden, J., Manies, K., Turetsky, M. & Neff, J. (2006) Effects of wildfire and permafrost on soil organic matter and soil climate in interior Alaska. *Global Change Biology*, **12**, 2391–2403.

Hill, G.B. & Henry, G.H.R. (2011) Responses of High Arctic wet sedge tundra to climate warming since 1980. *Global Change Biology*, **17**, 276–287.

IPCC. (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.

Jägerbrand, A.K., Alatalo, J.M., Chrimes, D. & Molau, U. (2009) Plant community responses to 5 years of simulated climate change in meadow and heath ecosystems at a subarctic-alpine site. *Oecologia*, **161**, 601–610.

Jägerbrand, A.K. & During, H.J. (2005) Effects of Simulated Shade on Growth, Number of

Branches and Biomass in Hylocomium splendens and Racomitrium lanuginosum. *Lindbergia*, **30**, 117–124.

Jägerbrand, A.K., Kudo, G., Alatalo, J.M. & Molau, U. (2012) Effects of neighboring vascular plants on the abundance of bryophytes in different vegetation types. *Polar Science*, **6**, 200–208.

Jägerbrand, A.K., Lindblad, K.E.M., Björk, R.G., Alatalo, J.M. & Molau, U. (2006) Bryophyte and Lichen Diversity Under Simulated Environmental Change Compared with Observed Variation in Unmanipulated Alpine Tundra. *Biodiversity and Conservation*, **15**, 4453–4475.

Jägerbrand, A.K., Molau, U. & Alatalo, J.M. (2003) Responses of bryophytes to simulated environmental change at Latnjajaure, northern Sweden. *Journal of Bryology*, **25**, 163–168.

Jonasson, S. (1992) Plant Responses to Fertilization and Species Removal in Tundra Related to Community Structure and Clonality. *Oikos*, **63**, 420.

Klanderud, K. (2008) Species-specific responses of an alpine plant community under simulated environmental change. *Journal of Vegetation Science*, **19**, 363–372.

Lang, S.I., Cornelissen, J.H.C., Hölzer, A., ter Braak, C.J.F., Ahrens, M., Callaghan, T.V. & Aerts, R. (2009) Determinants of cryptogam composition and diversity in Sphagnum - dominated peatlands: the importance of temporal, spatial and functional scales. *Journal of Ecology*, **97**, 299–310.

Lang, S.I., Cornelissen, J.H.C., Shaver, G.R., Ahrens, M., Callaghan, T.V., Molau, U., Ter Braak, C.J.F., Hölzer, A. & Aerts, R. (2012) Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. *Global Change Biology*, **18**, 1096–1107.

Lewis, L.R., Behling, E., Gousse, H., Qian, E., Elphick, C.S., Lamarre, J.-F., Bêty, J., Liebezeit, J., Rozzi, R. & Goffinet, B. (2014) First evidence of bryophyte diaspores in the plumage of transequatorial migrant birds. *PeerJ*, **2**, e424.

Li, X., Zhang, Z., Huang, L. & Wang, X. (2013) Review of the ecohydrological processes and feedback mechanisms controlling sand-binding vegetation systems in sandy desert regions of China. *Chinese Science Bulletin*, **58**, 1483–1496.

Longton, R. (1984) The role of bryophytes in terrestrial ecosystems. *J Hattori Bot Lab*, **55**, 147–163.

Mack, M.C., Schuur, E.A.G., Bret-Harte, M.S., Shaver, G.R. & Chapin, F.S. (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature*, **431**, 440–443.

Marion, G., Henry, G.H.R., Freckrnan, D.W., Johnstone, I., Jones, G., Jones, M.H., Levesque, E., Molau, U., Molgaard, P., Parsons, A.N., Svoboda, J. & Virgina, R.A. (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, **3**, 20–32.

Maskell, L.C., Smart, S.M., Bullock, J.M., Thompson, K. & Stevens, C.J. (2010) Nitrogen deposition causes widespread loss of species richness in British habitats. *Global Change Biology*, **16**, 671–679.

May, J.L. & Hollister, R.D. (2012) Validation of a simplified point frame method to detect change in tundra vegetation. *Polar Biology*, **35**, 1815–1823.

Molau, U. & Alatalo, J.M. (1998) Responses of Subarctic-Alpine Plant Communities to Simulated Environmental Change: Biodiversity of Bryophytes, Lichens, and Vascular Plants. *Ambio*, **27**, 322–329.

Olsen, S.L. & Klanderud, K. (2014) Exclusion of herbivores slows down recovery after experimental warming and nutrient addition in an alpine plant community. *Journal of Ecology*.

Pauli, H., Gottfried, Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J.L.B., Coldea, G., Dick, J., Erschbamer, B., Calzado, R.F., Ghosn, D., Holten, J.I., Kanka, R., Kazakis, G., Kollár, J., Larsson, P., Moiseev, P., Moiseev, D., Molau, U., Mesa, J.M., Nagy, L., Pelino, G., Puşcaş, M., Rossi, G., Stanisci, A., Syverhuset, A.O., Theurillat, J.-P., Tomaselli, M., Unterluggauer, P., Villar, L., Vittoz, P. & Grabherr, G. (2012) Recent Plant Diversity Changes on Europe’s Mountain Summits. *Science*, **336**, 353–355.

Polunin, N. (1951) The real arctic: suggestions for its delimitation, subdivision, and characterization. *Journal of Ecology*, **39**, 308–315.

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., Wal, R. van der, Welker, J., Wookey, P.A., Schmidt, N.M. & Aastrup, P. (2009) Ecological Dynamics Across the Arctic Associated with Recent Climate Change. *Science*, **325**, 1355–1358.

Potter, J., Press, M., Callaghan, T. & Lee, J. (1995) Growth responses of Polytrichum commune and Hylocomium splendens to simulated environmental change in the sub-arctic. *New Phytologist*, **131**, 533–541.

Press, M., Potter, J., Burke, M., Callaghan, T. & Lee, J. (1998) Responses of a subarctic dwarf shrub heath community to simulated environmental change. *Journal of Ecology*, **86**, 315–327.

Richardson, S.J., Press, M.C., Parsons, A.N. & Hartley, S.E. (2002) How do nutrients and warming impact on plant communities and their insect herbivores? A 9-year study from a sub-Arctic heath. *Journal of Ecology*, **90**, 544–556.

Robinson, C., Wookey, P., Lee, J., Callaghan, T.V. & Press, M. (1998) Plant community responses to simulated environmental change at a high arctic polar semi-desert. *Ecology*, **79**, 856–866.

Romanovsky, V., Drozdov, D., Oberman, N., Malkova, G., Kholodov, A., Marchenko, S., Moskalenko, N., Sergeev, D., Ukraintseva, N., Abramov, A., Gilichinsky, D. & Vasiliev, A. (2010) Thermal state of permafrost in Russia. *Permafrost and Periglacial Processes*, **21**, 136–155.

Shen, Z. & Ma, K. (2014) Effects of climate change on biodiversity. *Chinese Science Bulletin*, **59**, 4637–4638.

Sistla, S.A., Moore, J.C., Simpson, R.T., Gough, L., Shaver, G.R. & Schimel, J.P. (2013) Long-term warming restructures Arctic tundra without changing net soil carbon storage. *Nature*, **497**, 615–618.

Soudzilovskaia, N., Graae, B., Douma, J., Grau, O., Milbau, A., Shevtsova, A., Wolters, L. & Cornelissen, J. (2011) How do bryophytes govern generative recruitment of vascular plants? *New Phytologist*, **190**, 1019–1031.

Stöckli, V., Wipf, S., Nilsson, C. & Rixen, C. (2011) Using historical plant surveys to track biodiversity on mountain summits. *Plant Ecology & Diversity*, **4**, 415–425.

Turetsky, M. (2003) The role of bryophytes in carbon and nitrogen cycling. *The Bryologist*, **106**, 395–409.

Turetsky, M.R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A.D. & Tuittila, E.-S. (2012) The resilience and functional role of moss in boreal and arctic ecosystems. *The New phytologist*, **196**, 49–67.

Walker, M.D. (1996) Community baseline measurements for ITEX studies. *ITEX Manual (2nd ed.)* (eds U. Molau & P. Miolgaard), pp. 39–41. Danish Polar Centre, Copenhagen, Denmark.

Van Wijk, M.T., Clemmensen, K.E., Shaver, G.R., Williams, M., Callaghan, T.V., Chapin, F.S.I., Cornelissen, J.H.C., Gough, L., Hobbie, S.E., Jonasson, S., Lee, J.A., Michelsen, A., Press, M.C., Richardson, S.J. & Rueth, H. (2003) Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology*, **10**, 105–123.

Wu, X., Lin, X., Zhang, Y., Gao, J., Guo, L. & Li, J. (2014) Impacts of climate change on ecosystem in Priority Areas of Biodiversity Conservation in China. *Chinese Science Bulletin*, **59**, 4668–4680.

Zhang, Y. (2005) The microstructure and formation of biological soil crusts in their early developmental stage. *Chinese Science Bulletin*, **50**, 117–121.

Zhang, Y., Wang, Y., Zhang, M. & Ma, K. (2014) Climate change threats to protected plants of China: an evaluation based on species distribution modeling. *Chinese Science Bulletin*, **59**, 4652–4659.

Figure 1. Relative changes in total abundances (mean ± 1 SE) of bryophytes and lichens to experimental manipulations in a poor heath and rich meadow, at Latnjajaure, subarctic Sweden. A) Change in relative total abundance of bryophytes between 1995-2001, B) change in relative total abundance of bryophytes between 1999-2001, C) change in relative total abundance of lichens between 1995-2001, D) change in relative total abundance of lichens between 1999-2001. Treatments: C=control, T=temperature treatment, F=fertilizer treatment, TF= temperature and fertilizer treatments. N = 4 for T, F and TF, N = 8 for C.

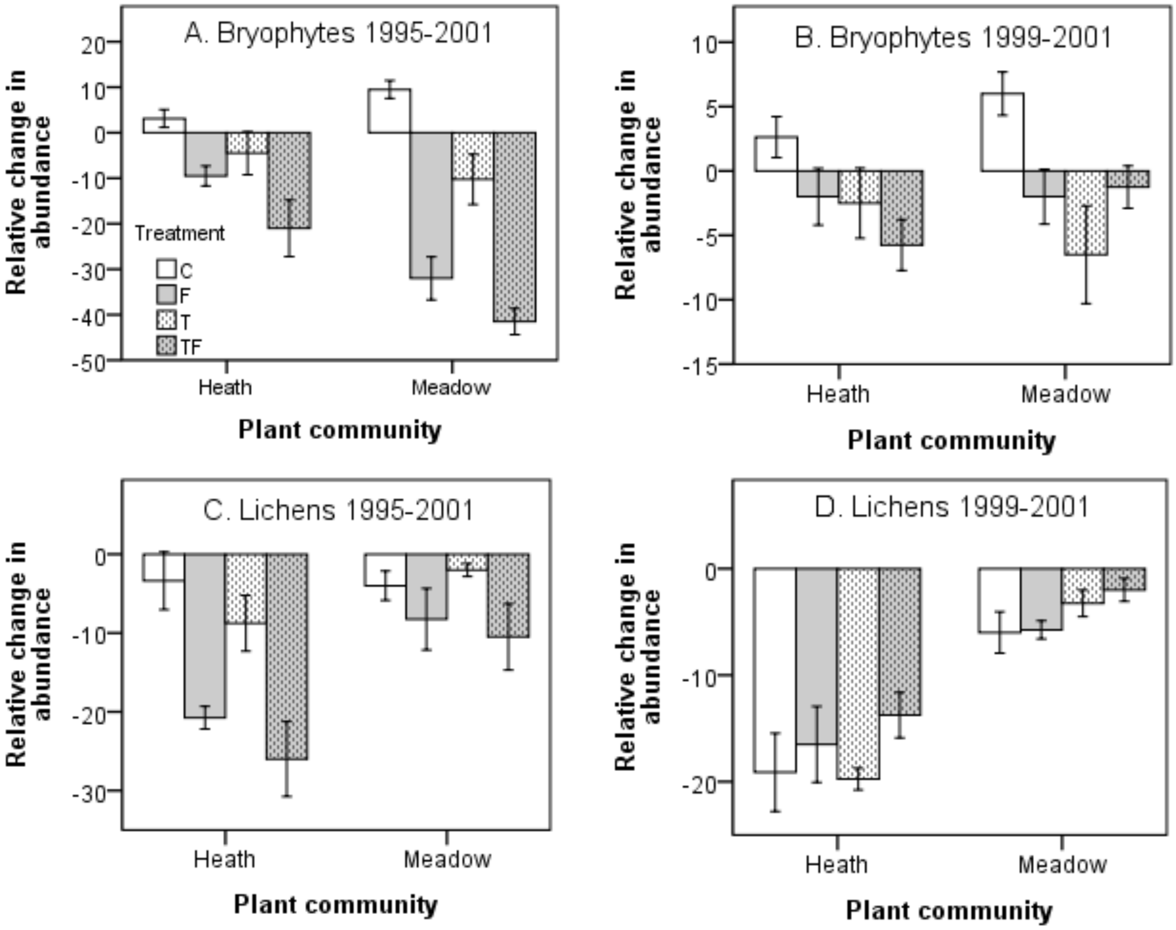

Figure 2. Relative changes in species specific abundances (mean ± 1 SE) for bryophytes and lichens between 1995-2001 to experimental manipulations in a poor heath and rich meadow, at Latnjajaure, subarctic Sweden. Treatments: C=control, T=temperature treatment, F=fertilizer treatment, TF= temperature and fertilizer treatments. Different letters indicate significant differences analysed by Mann-Whitney U-test. N = 4 for T, F and TF, N = 8 for C.

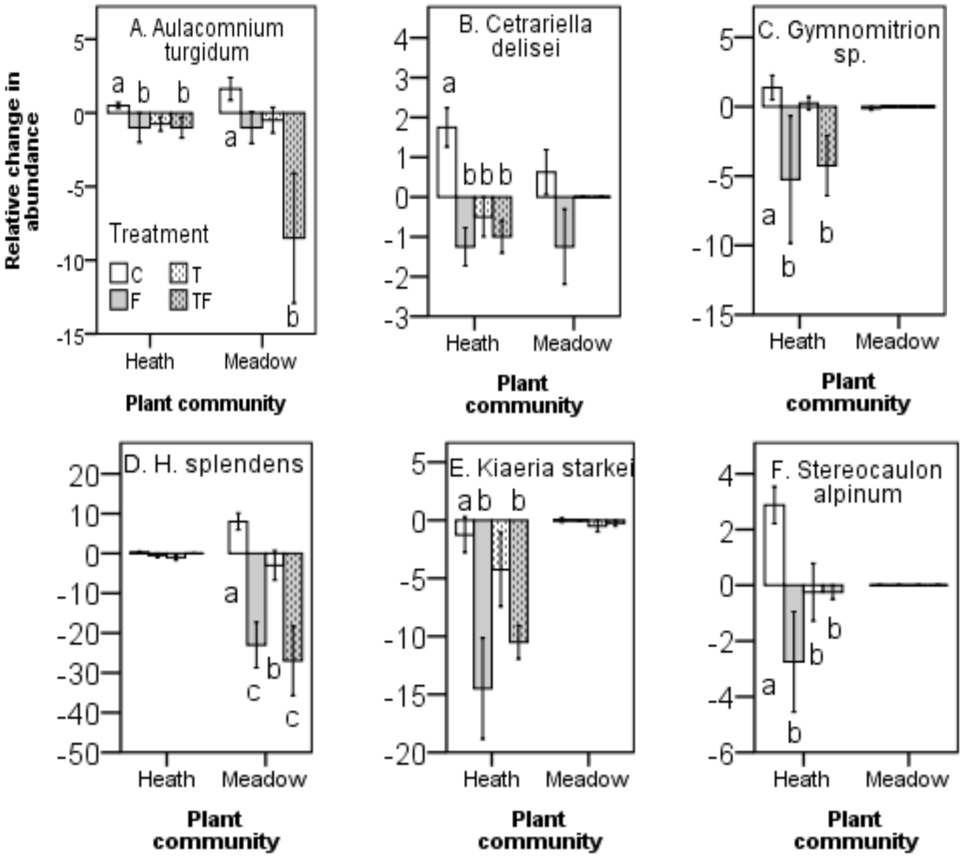

Figure 3. Relative changes in species specific abundances (mean ± 1 SE) for bryophytes and lichens between 1999-2001 to experimental manipulations in a poor heath and rich meadow, at Latnjajaure, subarctic Sweden. Treatments: C=control, T=temperature treatment, F=fertilizer treatment, TF= temperature and fertilizer treatments. Different letters indicate significant differences analysed by Mann-Whitney U-test. N = 4 for T, F and TF, N = 8 for C.

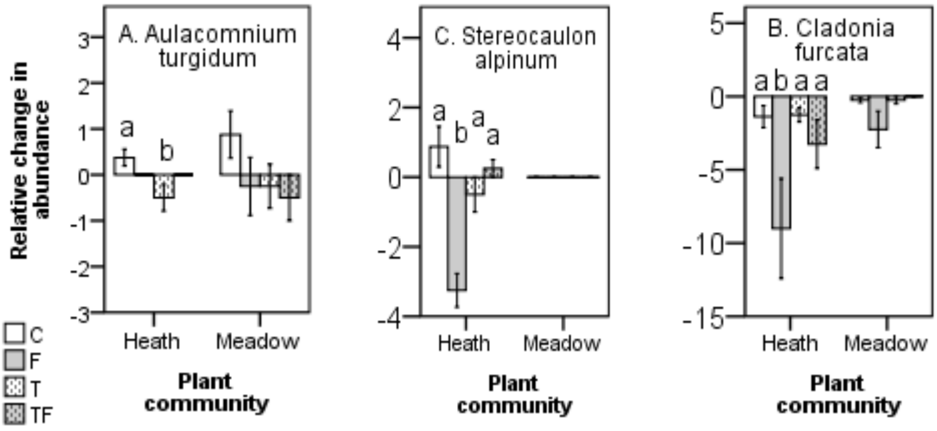

Table 1. The most dominant species of bryophytes and lichens at two the different plant communities (heath and meadow) at Latnjajaure, Northern Sweden.

Species	**Group**
Aulacomnium turgidum (Wahlenb.) Schwägr.	Bryophyte
Cetrariella delisei (Bory ex Schaer.) Kärnfelt & A. Thell	Lichen
Cladonia arbuscula (Wallr.) Flot.	Lichen
Cladonia furcata (Huds.) Schrad.	Lichen
Cladonia uncialis (L.) F. H. Wigg.	Lichen
Dicranum groenlandicum Brid.	Bryophyte
Flavocetraria cucullata (Bellardi) Kärnefelt & A. Thell	Lichen
Flavocetraria nivalis (L.) Kärnefelt & A. Thell	Lichen
Gymnomitrion sp.	Bryophyte
Hylocomium splendens (Hedw.) Schimp.	Bryophyte
Kiaeria starkei (F. Weber & D. Mohr) I. Hagen	Bryophyte
Ochrolechia frigida (Sw.) Lynge	Lichen
Polytrichum juniperinum Hedw.	Bryophyte
Ptilidium ciliare (L.) Hampe	Bryophyte
Sphaerophorus globosus (Huds.) Vain.	Lichen
Stereocaulon alpinum Laurer	Lichen

Table 2. Test of model effects of the generalized linear model (GLM) on responses in relative abundance of bryophytes and lichens between 1995 - 2001, and between 1999 - 2001, to experimental manipulations at two different plant communities at Latnjajaure, Northern Sweden. Only the most dominant species were included, see Table 1.

Source	Wald chi-square	df	P
Bryophytes 1995-2001			
Intercept	131.7	1	<0.0001
Plant community	21	1	<0.0001
Treatments	181	3	<0.0001
Plant community * Treatments	32	3	<0.0001
Bryophytes 1999-2001			
Intercept	3.9	1	0.048
Plant community	0.5	1	0.5
Treatments	31.1	3	<0.0001
Plant community * Treatments	5.2	3	0.16
Lichens 1995-2001			
Intercept	88.9	1	<0.0001
Plant community	14.8	1	<0.0001
Treatments	33	3	<0.0001
Plant community * Treatments	9.7	3	0.02
Lichens 1999-2001			
Intercept	138.4	1	<0.0001
Plant community	50.7	1	<0.0001
Treatments	3.9	3	0.28
Plant community * Treatments	1.2	3	0.75

Table 3. Results of generalized linear model (GLM) explaining the responses in relative abundance of bryophytes and lichens between 1995 - 2001, and between 1999 - 2001, to experimental manipulations at two different plant communities at Latnjajaure, Northern Sweden. Only significant variables are shown. Coefficient (B), SE=standard error and P, significance levels.

Variable	Coefficient	SE	P
Bryophytes 1995-2001			
Intercept	-41.5	3.5	<0.0001
Heath	20.5	4.9	<0.0001
Control	51.0	4.3	<0.0001
Temperature	31.3	4.9	<0.0001
Heath * Control	-26.9	6.1	<0.0001
Heath * Temperature	-14.8	7.0	0.035
Bryophytes 1999-2001			
Control	7.3	2.7	0.006
Heath * Temperature	8.5	4.3	0.05
Lichens 1995-2001			
Intercept	-10.5	3.4	0.002
Heath	-15.5	4.7	0.001
Heath * Control	16.1	5.8	0.005
Lichens 1999-2001			
Heath	-11.8	3.9	0.003

Table 4. Mann-Whitney U-tests for species specific abundances of bryophytes and lichens between treatments, among years in the heath and meadow communities. Significance values ($P < 0.05$) in bold. C = Control plots; T = warming (OTC); TF = combined warming and nutrient addition. Species: At = *Aulacomnium turgidum* (Wahlenb.) Schwägr. (acrocarpous bryophyte), Cetd = *Cetrariella delisei* (Bory ex Schaer.) Kärnfelt & A. Thell (lichen), Gym = *Gymnomitrion sp*. (liverwort), Kias = *Kiaeria starkei* (F. Weber & D. Mohr) I. Hagen (acrocarpous bryophyte), Stea = *Stereocaulon alpinum* Laurer (lichen), HS = *Hylocomium splendens* (Hedw.) Schimp. (pleurocarpous bryophyte), Cldof = *Cladonia arbuscula* (Wallr.) Flot. (lichen). Species abbreviations with a number 2 attached (example At2) means that the Mann-Whitney U-test were performed for differences between 1999 and 2001, species abbreviations without a number means that the Mann-Whitney U-test was performed on difference between 1995-2001

HEATH		At	Cetd	Gym	Kias	Stea	At2	Stea2
C	T	**0,048**	**0,011**	0,48	0,49	**0,03**	**0,035**	0,158
C	F	0,11	**0,007**	**0,029**	**0,033**	**0,006**	0,18	**0,008**
C	TF	**0,048**	**0,007**	**0,024**	**0,008**	**0,006**	0,176	0,257
T	F	0,74	0,27	0,1	**0,083**	0,24	0,127	**0,017**
T	TF	0,88	0,35	**0,076**	0,19	0,74	0,127	0,169
F	TF	0,74	0,65	0,88	0,25	0,12	1	**0,017**

MEADOW		At	Hs	Cldof2
C	T	0,172	**0,013**	1
C	F	**0,093**	**0,006**	**0,014**
C	TF	**0,005**	**0,006**	0,29
T	F	0,66	**0,043**	**0,04**
T	TF	**0,08**	**0,043**	0,32
F	TF	0,14	0,56	**0,011**