Testing reliability of short-term responses to predict longer-term responses of bryophytes and lichens to environmental change

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ABSTRACT

Environmental changes are predicted to have severe and rapid impacts on polar and alpine regions. At high latitudes/altitudes, cryptogams such as bryophytes and lichens are of great importance in terms of biomass, carbon/nutrient cycling, cover and ecosystem functioning. This seven-year factorial experiment examined the effects of fertilizing and experimental warming on bryophyte and lichen abundance in an alpine meadow and a heath community in subarctic Sweden. The aim was to determine whether short-term responses (five years) are good predictors of longer-term responses (seven years). Fertilizing and warming had significant negative effects on total and relative abundance of bryophytes and lichens, with the largest and most rapid decline caused by fertilizing and combined fertilizing and warming. Bryophytes decreased most in the alpine meadow community, which was bryophyte-dominated, and lichens decreased most in the heath community, which was lichen-dominated. This was surprising, as the most diverse group in each community was expected to be most resistant to perturbation. Warming alone had a delayed negative impact. Of the 16 species included in statistical analyses, seven were significantly negatively affected. Overall, the impacts of simulated warming on bryophytes and lichens as a whole and on individual species differed in time and magnitude between treatments and plant communities (meadow and heath). This will likely cause changes in the dominance structures over time. These results underscore the importance of longer-term studies to improve the quality of data used in climate change models, as models based on short-term data are poor predictors of long-term responses of bryophytes and lichens.

1. Introduction

Increased climate variability and increased nutrient deposition are affecting large areas of the world. Both factors are mainly driven by emissions and deposits resulting from human activities (Clark et al., 2013; Grandy et al., 2008; IPCC, 2013). For example, in China, which has some of the richest biodiversity in the world (Zhang et al., 2014), climate change is predicted to have great impacts on a wide variety of ecosystems in priority areas of biodiversity conservation (Wu et al., 2014). Consequently, the extinction risk to protected plants is predicted to increase (Zhang et al., 2014). Climate change is also believed to have the potential to rapidly affect polar and alpine regions. As these 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 greatly affect their ecosystems. There is a growing number of studies on climate change (Andrew et al., 2013; Shen and Ma, 2014). Some of the changes detected in a number of ecosystems around the world have been attributed to ecosystem response to nutrient deposition or current climate warming. These changes affect species richness, the composition of plant communities and species location, with poleward or northerly movement of species (Callaghan et al., 2011; Clark et al., 2013; Maskell et al., 2010; Pauli et al., 2012; Post et al., 2009; Stöckli et al., 2011). However, the causes behind shifts in species distribution can be difficult to pinpoint, as shown in a study on northward movement of vascular plants in Great Britain using data for the period of 1978–2011 (Groom, 2013). That study concluded that the significant northward movement of plants was most likely not due to climate warming, but to other changes resulting from anthropogenic activities (Groom, 2013). Fertilizing and warming can also have contrasting effects on species richness depending on the

nutrient status of the ecosystem (Chalcraft et al., 2008). It is likely that a combination of increased nutrient levels and climate warming can have interactive effects in the cold, nutrient-limited ecosystems prevailing in polar and high alpine regions (Chapin et al., 1995; Mack et al., 2004). A worrying example of how increased nutrient level can potentially interact with climate change was provided by a study on 20 years of fertilizing in the Alaskan tundra (Mack et al., 2004). It showed that increased nutrient availability caused net ecosystem loss of carbon, which could lead to positive feedback on climate warming. Other studies have reported contrasting short- and medium-term responses, resulting in non-linear reactions to treatments over time, indicating that longer-term impact may be difficult to predict (Alatalo et al., 2014b; Alatalo and Little, 2014).

Bryophytes and lichens (cryptogams) tend to make up much of the ground cover and biomass at higher altitudes and latitudes as the environment becomes harsher. This is partly an effect of the vascular plant community becoming smaller in stature (Jägerbrand et al., 2006; Longton, 1984). At the same time, their relative importance in 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) and water, carbon and nitrogen cycling (Turetsky, 2003; Turetsky et al., 2012). Bryophytes and lichens also play an important role in biological soil crusts in deserts worldwide (Li et al., 2013; Zhang, 2005). Despite this, the number of experimental environmental change studies on bryophytes and lichens is small. While numerous studies have investigated vascular plants in these severe environments, there are few that have resolution at species level or community responses that include bryophyte and lichen diversity (Bjerke et al., 2011; Klanderud, 2008; Lang et al., 2012; Olsen and Klanderud, 2014; Potter et al., 1995). Bryophytes and lichens are frequently used as ecological indicator species (Cristofolini et al., 2014; Mölder et al., 2015), but in experimental environmental change studies bryophytes and lichens are not usually identified at species level (Graglia et al., 2001; Hill and Henry, 2011). This is probably because ecologists commonly have problems identifying bryophytes and lichens to species level (Brunialti et al., 2012; Turetsky et al., 2012). It is unsatisfactory that modelling studies on the impact of climate change often lack data on bryophytes and lichens, as the resulting simulations will be of lower value for high altitude, polar and desert regions due to the major importance of bryophytes and lichens in such severe environments.

In a previous 5 year study on the responses to five years of fertilizing and experimental warming we found contrasting responses of bryophytes and lichens that varied with plant community and treatments (Jägerbrand et al., 2009). Here, we wanted to test if these initial short-term (5 years) responses of bryophytes to fertilizing and experimental warming are good predictors for longer-term responses (7 years). This as studies on vascular plants have shown contrasting short- and medium-term responses (Alatalo et al., 2014b; Alatalo and Little, 2014). We carried out a seven-year factorial study to examine the effects of fertilizing and experimental warming on total community and individual species abundance of dominant bryophytes and lichens in two contrasting alpine plant communities in subarctic Sweden, an alpine meadow and a heath. The results were then compared to the initial responses of a previous 5 year study (Jägerbrand et al., 2009). Specifically, we hypothesized that similar to vascular plants (a) initial short-term responses of bryophytes and lichens reported in a previous study would be poor predictors for longer-term responses, and (b) that bryophytes and lichens in the rich meadow community would be more resistant to perturbations than bryophytes in the poor heath.

2. Material and methods

2.1. Study area

Fieldwork took place at the 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 continuously from early spring 1992 onwards. 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. Mean annual air temperature ranged from −2.0 to −2.7 °C between 1993 and 1999, with a winter minimum of −27.3 to −21.7 °C. Mean annual precipitation during that period was 808 mm, but in individual years it ranged from a low of 605 mm (1996), to a high of 990 mm (1993). The temperature was highest in July, with mean temperature ranging from 5.4 °C in 1992 to 9.9 °C in 1997. Physical conditions of the soils in the valley vary from dry to wet and poor and acidic to base-rich, with an associated variation in plant communities (Alatalo et al., 2014b; Lindblad et al., 2006; Molau and Alatalo, 1998).

2.2. Experimental design

In July 1995, 20 plots (1 m × 1 m) with homogeneous vegetation cover were marked out in an alpine meadow plant community and 20 in a heath plant community and randomly assigned to treatments in a factorial design. There were eight control (CTR) plots and four plots for each of the following experimental treatments in each plant community: warming (or temperature enhancement, T), fertilizing (F) and combined warming and fertilizing (TF). Warming was induced by Open Top Chambers (OTCs), which increase the temperature by 1.5–3 °C compared with control plots with ambient temperature (Marion et al., 1997; Molau and Alatalo, 1998). Fertilizing consisted of supplying each plot with 5 g nitrogen (as NH_4NO_3) and 5 g phosphorus (P_2O_5) per m^2, dissolved in 10 L meltwater from snow adjacent to the experimental plots. In 1995, all plots were analyzed with a point-frame method (Walker, 1996) to determine species occurrence under natural conditions before the experimental treatments were established. The OTCs were then left on plots with a treatment involving warming (T, TF) all year around. Fertilizing was performed directly after the initial vegetation analyses in 1995 and a few days after snow melt in the six subsequent years (1996–2001). The fertilizing treatments were then terminated.

2.3. Measurements

The majority of bryophytes and lichens in the plots were identified to species level (with the help of experienced bryophyte taxonomist Sven Franzén), and functional group (acrocarpous bryophytes, pleurocarpous bryophytes, liverworts, lichens). Coverage of each species was assessed using a 1 m × 1 m frame with 100 grid points (Walker, 1996) in the middle of the 1995, 1999 (after five years of treatments) and 2001 (after seven years of treatments) 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 replaced in the same positions within the plot on each measuring occasion. This method has been shown to be accurate in detecting changes in tundra vegetation (May and Hollister, 2012). The habitat preference for the bryophyte and lichen species was retrieved from literature (efloras.org, 2015; Hallingbäck and Holmåsen, 1985; Moberg and Holmåsen, 1990).

2.4. Data analysis

From the point-frame data, the number of hits was summed up at pins within each plot to produce plot-level abundance measures