



Original Research Article

Impacts of seven years of experimental warming and nutrient addition on neighbourhood species interactions and community structure in two contrasting alpine plant communities



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ABSTRACT

Global change is predicted to have major impacts on alpine and arctic ecosystems. Plant fitness and growth will be determined by how plants interact with each other at smaller scales. Local-scale neighbourhood interactions may be altered by environmental perturbations, which could fundamentally affect community structure. This study examined the effects of seven years of experimental warming and nutrient addition on overall changes in the community structure and patterns of interspecific interaction between neighbouring plant species in two contrasting alpine plant communities, mesic meadow and poor heath, in subarctic Sweden. We used a network approach to quantify the dissimilarity of plant interaction networks and the average number of interspecific neighbourhood interactions over time in response to different environmental perturbations. The results revealed that combined warming and nutrient addition had significant negative effects on how dissimilar plant interaction networks were over time compared with the control. Moreover, plant–plant neighbourhood interaction networks were more dissimilar over time in nutrient-poor heath than in nutrient-rich mesic meadow. In addition, nutrient addition alone and combined nutrient addition and warming significantly affected neighbourhood species interactions in both plant communities. Surprisingly, changes in interspecific neighbourhood interactions over time in both communities were very similar, suggesting that the nutrient-poor heath is as robust to experimental environmental perturbation as the mesic meadow. Comparisons of changes in neighbouring species interactions with changes in evenness and richness at the same scale, in order to determine whether diversity drove such changes in local-scale interaction patterns, provided moderate evidence that diversity was behind the changes in local-scale interspecific neighbourhood interactions. This implied that species might interact at smaller scales than those at which community measures were made. Overall, these results demonstrated that global change involving increased nutrient deposition and warming is likely to affect species interactions and alter community structure in plant communities, whether rich or poor in nutrients and species.

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1. Introduction

Global change is predicted to significantly affect plant community structure, mediated through plant traits, their interactions and growth (Baruah et al., 2017; Niu and Wan 2008). A better understanding is needed of how interactions among plants can shift due to global change. Plant interactions

shape large-scale evolutionary processes, which are important in maintaining species diversity (Isbell et al., 2011). The local-scale processes and biotic interactions among plants are very complex and changes are therefore difficult to predict (Ricklefs, 2004), but such interactions are key to regional diversity (Tilman et al., 1997; Allesina and Levine 2011). It is thus very important to study changes in these local-scale interactions, which can consist of positive and negative interactions and complex combinations of both (Callaway, 1995). For example, global changes or even local changes can cause demographic change due to increased negative

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plant interactions and changes in litter accumulation (Olsen and Klanderud, 2014).

Plant–plant interactions are an important component in understanding the response of plant communities to predicted global change, which will affect plant communities either directly or indirectly (Adler et al., 2012; Brooker 2006; Gilman et al., 2010; Lortie et al., 2004). Plant–plant interactions play an important role in regulating plant community structure. Many studies have demonstrated the importance of network analysis in understanding community dynamics (Albert and Barabási, 2002), in particular in response to environmental change (Tylianakis et al., 2008; Bascompte and Jordano 2013). Due to the nested structure of plant networks, plant–plant interactions can be facilitative and thereby prevent extinction (Verdú and Valiente-Banuet, 2008).

It is unclear, however, to what extent community responses are sensitive to variations in local-scale neighbourhood interactions. It has been demonstrated that species competition increases as the number of neighbour species increases and that the degree of competition can vary depending on the type of communities present (Wiegand et al., 2007). Thus the importance of neighbourhood interactions cannot be ignored in light of climate change. Although measurements of diversity using indices such as evenness can roughly sum up the community structure and link it to the productivity of the community, such measures may miss interactions at smaller, local scales (McKenna and Yurkonis, 2016). Changing neighbourhood species interactions could substantially affect community productivity and plant diversity–productivity relationships if the scale of interactions between plant species in a community is localised within a few metres (Lamošová et al., 2010; Zhang et al., 2014). Such local-scale interactions in a particular habitat could be identified with the help of neighbourhood interaction analyses. Moreover, in a habitat it might be possible for evenness to remain the same over the years, but neighbourhood associations between species in that habitat can potentially decrease. This might occur for example, in a hypothetical case where there are different plant species in a small habitat, but not all are neighbours to all others. This is possible when there are non-random aggregations of a particular species and its con-specifics, such that all plant species are far apart and hence there are no direct neighbours (at a scale of 0.1 m). Such non-random aggregations of conspecifics might allow weaker competitors to persist through delayed competitive exclusion (Stoll and Prati, 2001). The resulting communities would presumably be more diverse, yet less productive, than non-aggregated communities (McKenna and Yurkonis, 2016). Diverse communities are generally more productive and stable, with a linear relationship between plant productivity and diversity (Mulder et al., 2004). However, recent studies suggest that the diversity–productivity relationship may be affected if neighbour species compete at a very small spatial scale (Zhang et al., 2014). The spatial pattern of plants in a particular habitat can have a significant effect on the outcome of competition and, consequently, alter the biodiversity yield (Lamošová et al., 2010). Hence the importance of such local-scale neighbourhood species associations should not be ignored.

Many experiments and studies have been conducted on the potential effects of global warming on biodiversity in arctic and alpine environments (Alatalo 1998; Alatalo et al., 2014b, 2015; Elmendorf et al., 2012; Jägerbrand et al., 2009). The network approach of calculating interactions in a plant community can reveal changes in the overall community structure and would also allow the robustness of plant communities to environmental change to be analysed (Proulx et al., 2005). Robustness can be measured by perturbing the current network structure, for example by removing focal species in the network or by changing the environment of the plant communities by increasing/decreasing stress levels over time. Whether a plant community

is robust to changes in the environment would be manifested in the number of plant–plant interactions in the plant community.

In this study, a factorial experimental design was used, with warming and nutrient addition as treatments, to study and compare changes in neighbourhood species interactions over time in two contrasting alpine tundra plant communities: a species-rich meadow and a species-poor heath. Specifically, with the experimental set-up, we tested the following five hypotheses: 1) The overall topological structure of networks differs over time in response to warming and nutrient addition and such changes in topological structure vary between the two contrasting plant communities. 2) Interspecific neighbourhood interactions change significantly in mesic meadow and poor heath communities due to warming and nutrient addition; 3) Changes in interspecific neighbourhood interactions at a scale of 0.1 m differ between nutrient-limited poor heath and mesic meadow; 4) Changes in neighbourhood interactions are independent of changes in diversity; 5) Interspecific interactions among dominant species respond to changes in the experimental environmental change in both mesic meadow and poor heath communities.

2. Methods

2.1. Study area

Fieldwork took place at Latnjajure field station, which is located in the Latnjavagge valley (68°21'N, 18°29'E; 1000 m above sea level) in northern Sweden. A total of 40 plots (1 m × 1 m) with homogeneous vegetation cover were chosen in July 1995 at sites representing contrasting resource availability: 20 plots for a mesic meadow community with higher nutrient availability and 20 plots for a poor heath with lower nutrient availability. We have previously reported on the vascular plant abundance and diversity in these communities (Alatalo et al., 2014a, 2015). Treatments were randomly assigned in a factorial design experiment to eight control (CTR) plots and four plots for each of three experimental treatments: warming (T), nutrient addition (N) and combined warming and nutrient addition (TN). Warming was induced by open top chambers (OTCs), which increased the air temperature by 1.5–3.0 °C during the snow-free summer period. Nutrients were added in similar amounts as used in previous studies in Alaskan Tundra (Chapin et al., 1995) and consisted of application (per m²) of 5 g nitrogen (as NH₄NO₃) and 5 g phosphorus (P₂O₅) dissolved in 10 L snowmelt water. As part of a BACI (Before-After-Control-Impact) approach (Underwood, 1996), in 1995 all plots were analysed with a point frame method (described below) to determine species occurrence under natural conditions, prior to application of experimental treatments. The OTCs were then left on plots with warming treatments year-round, while the nutrient solution was applied directly after the initial vegetation analyses in 1995 and a few days after snowmelt in subsequent years (1996–2001). The nutrient treatments were terminated after the 2001 season.

2.2. Measurements

All vascular plants in the plots were identified to species level and cover of each species was assessed, using a 1 m × 1 m frame with 100 grid points, in the middle of the 1995, 1999 and 2001 growing seasons (Walker, 1996). 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 on each measuring occasion, allowing us to ‘hit’ (measure) the same points in the grid in each plot in different years. Only the first hit of each species was recorded. This method has been shown to be accurate in detecting

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