

# Community and species-specific responses to simulated global change in two subarctic-alpine plant communities

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**Abstract.** Long-term observational studies have detected greening and shrub encroachment in the subarctic attributed to current climate change, while global change simulations have showed that community composition and productivity may shift drastically in arctic, subarctic, and alpine tundra plant communities in the future. However, responses to global change can be highly species- and context-dependent. We examined community-level and species-specific responses to a six-year factorial temperature and nutrient (nitrogen and phosphorus) amendment experiment in two alpine plant communities in northern Sweden: a species-poor dwarf shrub heath, and a more species-rich meadow. We hypothesized that abundance responses to global change would be variable within commonly defined vascular plant functional groups (e.g., forbs, evergreen shrubs, deciduous shrubs) and that new species would appear in experimental plots over time due to the ameliorated growing conditions. We found that within most functional groups, species were highly individualistic with respect to the global change simulation, particularly within the forbs, whereas within the shrubs, responses were neutral to negative and widely variable in magnitude. In the heath community the response of the graminoid functional group was driven almost entirely by the grass *Calamagrostis lapponica*, which increased in abundance by an order of magnitude in the combined temperature and nutrient treatment. Furthermore, community context was important for species' responses to the simulations. Abundance of the pan-arctic species *Carex bigelowii* and *Vaccinium vitis idaea* responded primarily to the temperature treatment in the meadow community whereas the nutrient treatment had stronger effects in the heath community. Over six growing seasons, more new species appeared in the experimental plots than in control plots in the meadow community, whereas in the heath community only one new species appeared. Our results from two closely situated but different plant communities show that functional groups do not predict individual species responses to simulated global change, and that these responses depend to a large extent on pre-existing physical conditions as well as biotic interactions such as competition and facilitation. It may be difficult to apply general trends of global change responses to specific local communities.

**Key words:** *Calamagrostis lapponica*; *Carex bigelowii*; global change; heath; Latnjajaure, Sweden; meadow; nutrient addition; plant community composition; subalpine tundra; *Vaccinium vitis idaea*; warming.

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## INTRODUCTION

Global change is already affecting high-latitude and high-altitude ecosystems, however responses in the Arctic and subarctic have been highly heterogeneous because of the complexity and diversity of natural systems (IPCC 2014). For vascular plant communities, extensive effects of global change, including changes in temperature, nutrients, CO<sub>2</sub>, and the frequency of storms and fires, have already been observed at the community (Hudson and Henry 2009, Wilson and Nilsson 2009, Hill and Henry 2011, Callaghan et al. 2013), functional group (Molau 2010, Myers-Smith et al. 2011), and species levels (Chapin et al. 1995). Models have suggested that there will be widespread redistribution of plant functional groups in the Arctic, with woody shrubs increasing by as much as 50% (Pearson et al. 2013), and experimental studies have found strong responses in tundra communities at the global scale (Walker et al. 2006, Elmendorf et al. 2012). The rapid expansion or loss of one or several dominant species could have major effects on ecosystem functioning (Smith and Knapp 2003). Changes in plant abundance and diversity also have important effects across trophic levels, including on insect and mammalian herbivores through changes in forage availability and quality (Post et al. 2009).

Measuring and predicting these changes in vascular plant communities are challenging. Many studies focus only on one study site, and generalizing results across the tundra biome may not be appropriate. Meta-analyses of warming experiments have addressed this, combining results of multiple studies to report trends in phenology, vascular plant cover, and community diversity, as well as drawing conclusions about vascular plant functional groups in a global change context (Arft et al. 1999, Walker et al. 2006). The functional group theory states that vascular plants will show consistent responses to global change within their functional group (Chapin et al. 1996), a concept particularly useful to compare between or generalize across many unique ecosystems with varying community composition. In subalpine and tundra ecosystems plant functional groups have been mainly defined as growth forms, for instance deciduous and evergreen shrubs, forbs, or graminoids (e.g.,

Chapin et al. 1996). Besides tracking changes in abundance in response to global change, these functional groups have been used to assess its effects on aspects of ecosystem functioning and interactions across trophic levels (e.g., Haugwitz and Michelsen 2010, Yano et al. 2013). However, there is considerable debate about the utility of functional groups, how many groups should be used, and how they should be defined (Lavorel et al. 1997, Jeltsch et al. 2008, Woodward and Cramer 2009). For example, arguments have been made for using trait-based categorization of species, independent of growth form, including such traits as size, dispersal ability, resource requirements, or fecundity (Soudzilovskaia and Onipchenko 2005, Suding et al. 2008). Additionally, the specificity of local ecosystems may also limit the utility of the functional group theory, as local biotic and physical conditions may contribute to determining responses to global change (Elmendorf et al. 2012).

Several studies have taken a more detailed approach, assessing responses by multiple highly abundant species within a given community (e.g., Klanderud 2008, Wipf 2010, Wang et al. 2012). This has allowed a more nuanced understanding of interactions within the ecosystem. Species within a functional group can have different timeframes for responding to manipulations, and some responded more strongly to changes in temperature while others responded more to changes in nutrient availability or grazing. For example, in an alpine heath in Norway, different species of *Carex* sedge showed varying responses to global change simulations by increasing or decreasing in abundance (Klanderud 2008). Abundance changes of dominant species or dominance shifts as a result of global change simulations may be particularly important in competitive interactions (Niu and Wan 2008).

Furthermore, novel species have been colonizing alpine ecosystems as the temperature has warmed over the last several decades (Klanderud and Birks 2003, Stöckli et al. 2012, Callaghan et al. 2013). Many endemic alpine plants are poor competitors, and thus may be outcompeted by new colonists that are better adapted to warmer, more productive environments (Billings and Mooney 1968). In some cases, novel species may have substantial enough impacts to affect

ecosystem functioning, for instance changing the microbial community in the soil and thus soil respiration and enzymatic activity (Kourtev et al. 2002). Occasionally novel species in alpine systems can become invasive (Pauchard et al. 2009), completely changing the previously established dominance hierarchies. This is not only relevant in terms of shifting functional group dominance, but because competition between species within the same functional group can also be crucial for structuring alpine plant communities (Theodose and Bowman 1997a).

Thus in this complex system, it is important to understand whether using broad functional group categorizations is useful in predicting community responses to global change. To further explore species-specific responses to global change and appearance of novel species in harsh subalpine environments, we assessed species-level responses over six years of factorial temperature and nutrient manipulations in two neighboring communities in northern Sweden. Rarely have global change simulations in the arctic or alpine zones included multiple community types (see Theodose and Bowman 1997b, Hollister et al. 2005, but few in Europe). We hypothesized the following.

- (1) Species-specific responses to the experimental manipulations vary within functional groups, based in part on plant functional traits within these groups. For instance, while shrub encroachment is common in the Arctic and subarctic, one might expect taller shrubs to respond more positively to ameliorating conditions while prostrate dwarf shrubs might be limited by increased competition for light and thus negatively affected. Thus, we hypothesize that using a more taxonomic approach, looking at the species or genus level, may be more accurate than using a functional group approach to predict climate change responses;
- (2) Furthermore, community context is important to the response of individual species to simulated and real global change. Using two species common in both of two different communities with differing abiotic and biotic characteristics, we hypothesize that changes in cover will result not

only from focal species' release from limitation by key abiotic factors, but also due to other species that may respond in ways which alter competitive interactions; and

- (3) Experimental perturbations would cause new species to appear in the warmed and fertilized plots. While abundant species were primarily addressed in the previous two hypotheses, rare and novel species are also important to community functioning. We hypothesize that species that had previously been excluded from these communities due to the harsh abiotic conditions (low nutrient, low temperature) would be able to establish and become competitive, potentially at the expense of already-present species that are adapted to low-nutrient or cold conditions but which may be poor competitors when conditions change.

## METHODS

### *Study sites and experimental design*

Fieldwork was conducted at Latnjajajure Field Station at 1000 m elevation in the Latnjavagge valley in northern Sweden (68°21' N, 18°29' E). There are a wide range of vegetation communities distributed in patches on the slopes surrounding the lake as terrain varies from rocky to smooth and soil substrate from acidic to more base-rich, including tussock tundra, wet streambeds, meadow, and heath communities. This supports populations of reindeer, lemmings, and birds as well as insect herbivores. The valley is geographically representative of a subarctic-alpine climate, but climate data collected continuously from the early spring of 1992 onwards show temperature and precipitation more representative of the Low Arctic. Snow cover persists for most of the year, with cool summers and relatively mild, snow-rich winters. Mean annual temperatures ranged from  $-1.5$  to  $-2.9^{\circ}\text{C}$  between 1995 and 2001, with winter minima of  $-21.7$  to  $-28.8^{\circ}\text{C}$ . Annual precipitation during this time period was consistently between 800 and 860 mm, with the exception of a particularly dry season in 1996 with only 605 mm. The warmest temperatures come in July, with maxima between  $18.3^{\circ}$  and  $20.5^{\circ}\text{C}$ . This field experi-

ment comprised two contrasting plant communities: a richer meadow community on calcareous bedrock, and a much more species-poor heath community on a glacial moraine (Jägerbrand et al. 2009).

Within each community (meadow and heath), 20 plots (1 × 1 m) with homogenous vegetation cover were selected in a systematic fashion in July 1995. In the heath community, plots were chosen based on the presence of the dominant species *Betula nana* and in the meadow community based on the dominant species *Cassiope tetragona*. Before implementing the treatments in 1995, all plots were analyzed with a point-frame method (described below) to determine the species occurrences under natural conditions. After this initial relevé, plots were randomly assigned to treatments in a factorial design. In each plant community, there were 8 control (CTR) plots and 4 plots for each of the experimental treatments: warming (T for temperature enhancement), nutrient addition (N) and combined warming and nutrient addition (TN). For the N and TN treatments, 5 g of nitrogen (as  $\text{NH}_4\text{NO}_3$ ) and 5 g of phosphorus ( $\text{P}_2\text{O}_5$ ) per  $\text{m}^2$  were dissolved in 10 L of meltwater and added to the plots a few days after snowmelt in each of the subsequent years (1996–2001). For the T and TN treatments, Open Top Chambers (OTCs) induced a temperature increase of 0.7–2.6°C compared to the ambient temperature in the control plots (Molau and Alatalo 1998), and OTCs were left on the plots year-round.

Vascular plant cover in each plot was assessed using a 1 × 1 m frame with 100 grid points spaced 10 cm apart (Walker 1996) in the peak of the 1995, 1999, and 2001 growing seasons. The canopy layer was measured by identifying the species of the tallest plant to hit each of 100 pins within the frame (Jägerbrand et al. 2009). Species were categorized into the following plant functional groups: cushion plants, deciduous shrubs, evergreen shrubs, forbs, grasses, and a group denoted “sedges” which included both rushes and sedges. The number of hits by each species, hereafter referred to as “cover,” was used as an estimate of species abundance. 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 each year. This

allowed us to tabulate species gained and lost from the plots from one year to another.

### Statistical analyses

All statistics and graphing were done in R version 3.1.0 (R Core Team 2013). Changes in the species composition of plots from 1995 to 2001 were examined using detrended correspondence analysis (DCA) using the package ‘vegan’ version 2.0-10 (Oksanen et al. 2012). The meadow and heath communities were examined separately because of their widely different composition (47 species in the meadow vs. 16 in the heath; Appendix: Table A1) and since short-term responses in abundance and diversity have been shown to differ substantially in the two communities at Latnjajaure (Molau and Alatalo 1998, Jägerbrand et al. 2009). Species cover matrices of 60 × 47 for the meadow community and 60 × 16 for the heath community were assessed using DCA and the standard settings. As in a similar study in Alaska which downweighted rare species, there were few differences in the configuration of plots in the DCA space compared to when using untransformed data (Wahren et al. 2005), so we did not weight species based on abundance. DCA axes were of short to intermediate lengths (between 1.5 and 4 SD). To assess the effects of treatment, year, and their interaction on community composition, we used a constrained gradient technique and examined the outcomes from both canonical correspondence analysis (CCA) and redundancy analysis (RDA; Oksanen et al. 2012). RDA provided a better fit for the data with higher eigenvalues and a larger percent of the variation explained on the first two axes. The significance of the constraints of treatment by year were tested using up to 1,000 Monte Carlo permutations.

To further address the fidelity of global change responses within vascular plant functional groups, we examined the effects of experimental treatments on 12 of the most dominant species from 1995 to 2001. Focal species were selected for analysis if they were present in at least 15 of the 20 plots in a community type, with the exception of the *Salix* species complex (including *S. herbacea*, *S. lanata*, *S. polaris*, and *S. reticulata*), which should be explored separately in relation to one another. In the heath community, *B. nana* and *Calamagrostis lapponica* were chosen. In the



meadow community, *Carex vaginata*, *Cassiope tetragona*, *Dryas octopetala*, *Equisetum scirpoides*, *Festuca ovina*, *Polygonum viviparum*, *Thalictrum alpinum*, and *Vaccinium uliginosum* were included. Several of the focal species chosen for the heath and meadow sites were also present in the other community, but in only <15 plots. *Carex bigelowii*, and *Vaccinium vitis-idaea* were sufficiently abundant to be analyzed in both communities. We built generalized linear models with nutrient manipulation and temperature manipulation as fixed factors and year as a random factor using the lme4 package (Bates et al. 2012). For each response variable, normality and homogeneity of variance were assessed using standard diagnostic procedures. We modeled each species' cover as a binomial function of total vascular plant cover in the plot, as OTC plots were somewhat smaller than control plots and could not fit all 100 points of the point-frame. The models were fit using restricted maximum likelihood (REML) and BOBYQA optimization (Powell 2009). Backward model selection from a full factorial model to, if necessary, a random-effects model, was performed using second-order AIC (Akaike's information criterion) scores or AIC<sub>c</sub> (Mazerolle 2013), which slightly modify the AIC to account for small sample size and prevent overfitting of the model. For model validation, we examined residuals, q-q plots, and marginal  $r^2$  using the 'MuMIn' package (Barton 2013). Where the interaction of the fixed factors was significant, multiple comparisons of treatment types were performed as part of the selected generalized linear model using the 'multcomp' package (Hothorn et al. 2008).

## RESULTS

### *Species-specific responses in the meadow community*

The first two axes of the constrained RDA explained 97% of the variation in the meadow community (Appendix: Table A2) and permutation tests showed that the constraints of treatment by year were significant ( $F_{7,52} = 4.415$ ,  $P = 0.005$ ). Plots were mixed with few discernible patterns in 1995 (Appendix: Fig. 1A), with displacement over time shown in Fig. 1B and C with the N and TN plots showing the most extreme displacement in the DCA space. The

direction of movement was driven by diverse species, and species within defined functional groups did not group together in the RDA space (Fig. 1D). For instance, the three species with the strongest effects on directional movement were *E. hermaphroditum* and *C. tetragona*, both evergreen shrubs but with loadings in the opposite direction from one another on both axes, and the grass *Festuca vivipara*.

For individual species analyzed in the meadow community, one or both of the components of the global change simulation was included in the mixed-effects species cover model with the best fit (Table 1). In the meadow community, the forbs *E. scirpoides* (Fig. 2A), *T. alpinum* (Fig. 2B), and *P. viviparum* (Fig. 2C) showed trends of declining cover over time in both control plots and experimental treatments. For all three species, the most significant cover differences were between CTR and N treatments, and sometimes between the CTR and TN treatments (linear comparisons for these and all other species are summarized in Table 2). For *T. alpinum* and *P. viviparum*, but not for *E. scirpoides*, cover increased in at least one experimental treatment before finally declining.

The dominant graminoid species increased in response to experimental treatments. The sedge *C. vaginata* had significantly higher cover in all of the experimental treatments than in the control plots (Fig. 2D). The grass *F. ovina* showed the strongest response to experimental treatments, showing no effect of temperature on its own but a strong effect of nutrient addition (Fig. 2E). While *C. vaginata* cover declined after initial strong response to nutrient addition, *F. ovina* cover maintained and even intensified its gains from 1999 to 2001.

Shrub species showed few consistent patterns with respect to the global change simulations and tended to differ primarily due to preexisting differences in cover before the treatments were implemented. *C. tetragona* and *D. octopetala* showed significant differences between almost every pair of treatment types (Fig. 2F and G). *V. uliginosum* cover did not differ between CTR plots and any experimental treatment plots, however cover was significantly different between N plots and T and TN plots (Fig. 2H).

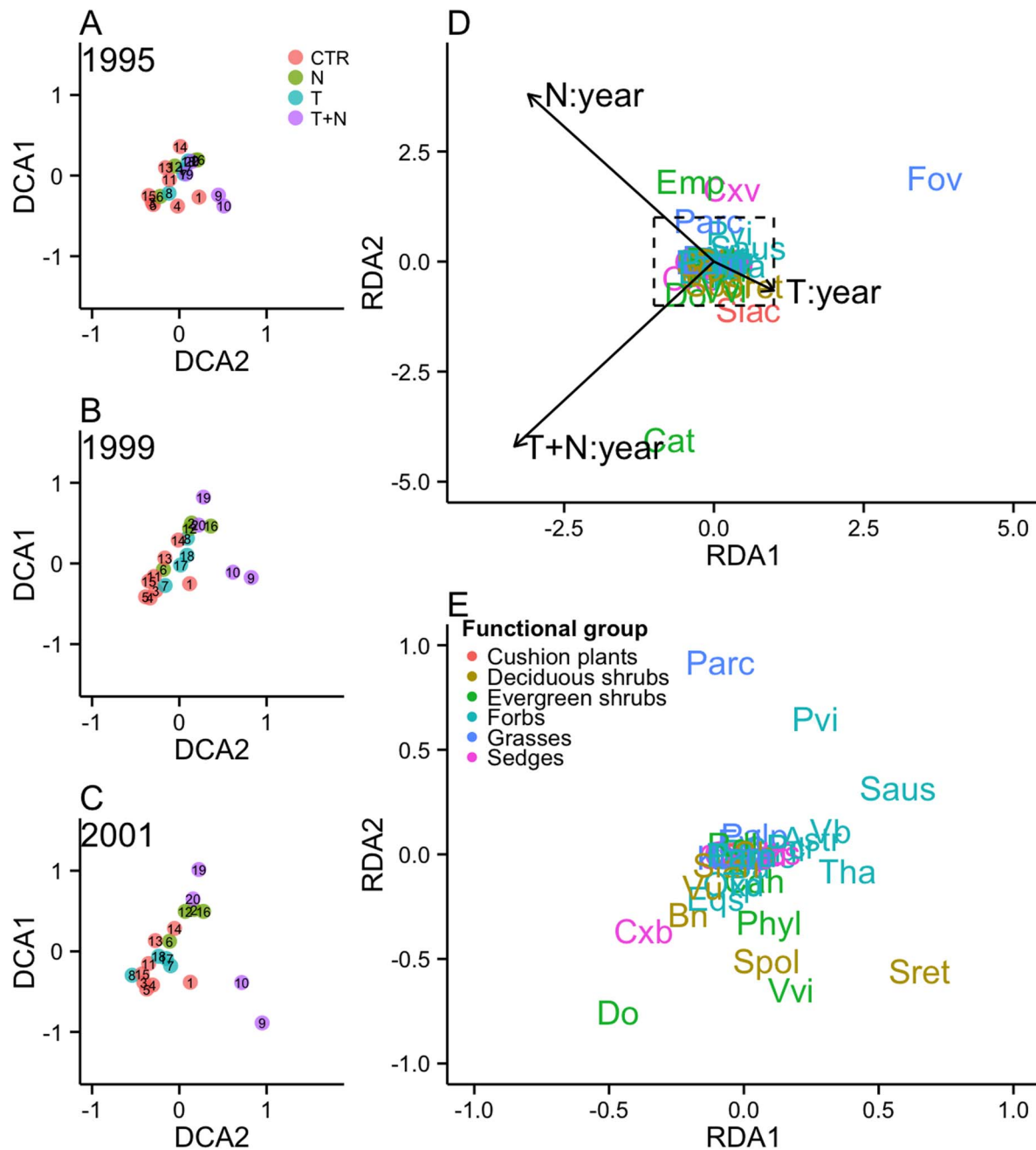


Fig. 1. Change in species composition in plots in the meadow community plots (numbered within each color-coded point) according to detrended correspondence analysis from pre-treatment conditions in 1995 (A) and after the global change simulation had been applied through 1999 (B) and 2001 (C). The axes are the same for all three panels. Redundancy analysis showed differing shifts through time according to treatment, with some species (abbreviated as described in Appendix: Table A1) more associated with a specific treatment type (D); closely clustered species, outlined in the dashed line, are shown in more detail in panel (E).

Table 1. AIC<sub>c</sub> scores for different generalized mixed-effects models for each of the vascular plant species examined using univariate analyses, with an indication of which community type the cover measurements were collected (for *C. bigelowii* and *V. vitis idaea*, models were fit for both community types). The “best” model is indicated by bolding of its AIC<sub>c</sub> score; its effects are described using marginal *R*<sup>2</sup>, the proportion of variance explained by the fixed factors alone.

Species	Location	Factorial†	Additive‡	Nutrient§	Temperature¶	Random#	Marginal <i>R</i> <sup>2</sup> of best model
<i>Betula nana</i>	heath	<b>821.45</b>	825.60				0.13
<i>Calamagrostis lapponica</i>	heath	597.81	597.12	<b>594.82</b>	1214.20	1224.76	0.23
<i>Carex bigelowii</i>	heath	240.39	<b>238.24</b>	249.32	296.80		0.20
	meadow	<b>371.82</b>	376.20				0.02
<i>Carex vaginata</i>	meadow	<b>387.73</b>	407.29				0.16
<i>Cassiope tetragona</i>	meadow	<b>811.50</b>	818.57				0.18
<i>Dryas octopetala</i>	meadow	<b>265.45</b>	282.14				0.34
<i>Equisetum scirpoides</i>	meadow	<b>143.02</b>	143.45				0.94
<i>Festuca ovina</i>	meadow	<b>576.83</b>	591.29				0.13
<i>Polygonum viviparum</i>	meadow	<b>331.06</b>	332.67				0.03
<i>Thalictrum alpinum</i>	meadow	<b>326.27</b>	343.35				0.04
<i>Vaccinium uliginosum</i>	meadow	351.80	<b>349.82</b>	360.06	352.40		0.02
<i>Vaccinium vitis idaea</i>	heath	262.97	261.98	<b>259.80</b>	323.71	323.86	0.18
	meadow	284.76	<b>282.41</b>	286.55	285.08		0.02

Notes: As backward model selection was used, blank cells indicate that a more complex model was already selected and thus there was no need to calculate AIC<sub>c</sub> scores for the model in question. For example, if the additive model had a lower AIC<sub>c</sub> score than the factorial model, then neither the nutrient nor temperature only models were fit. The fixed and random effects of each model are footnoted as below.

† Factorial: nutrient × temperature + random(year).

‡ Additive: nutrient + temperature + random(year).

§ Nutrient: nutrient + random(year).

¶ Temperature: temperature + random(year).

# Random: random(year).

### Species-specific responses in the heath community

The first two RDA axes explained a smaller proportion of variation in the heath community (87%; Appendix: Table A2), but again the constraints of treatment showed a significant association with plot position in the multivariate space ( $F_{7,52} = 11.070$ ,  $P = 0.005$ ). Over the course of the experiment the N and TN plots were displaced towards the negative side of the first axis, characterized by the grass *Calamagrostis lapponica* and the sedge *Carex bigelowii*, while the CTR and T plots were on the positive side characterized by *E. hermaphroditum* (Fig. 3A, B, and C). The constrained RDA shows that interactions with year pulled the N and T manipulations in opposite directions, with the T treatment trending towards the previously dominant deciduous shrub *Betula nana*, while the TN was characterized by an increase in *C. lapponica* (Fig. 3D).

As was the case for the meadow community, individual species covers were best predicted by one or both aspects of the global change simulation (Table 1). For the dominant graminoid *C. lapponica* the N treatment had a very significant

positive effect on cover, increasing it by a factor of four or more (Fig. 4A), with effects increasing over time. The dominant shrub, deciduous *B. nana*, responded differently to each treatment type: but there was a trend of decreasing *B. nana* cover in the N and TN treatments but *B. nana* showed a slight recovery by the end of the 2001 growing season (Fig. 4B). Nevertheless, by 2001, tall, upright species such as *C. lapponica* and *C. bigelowii* had taken over the N and TN plots in the heath community, and *B. nana* was no longer the dominant species (Fig. 5C).

### Responses by species present in both communities

For the sedge *C. bigelowii*, cover in the meadow decreased in all plots and in the T and TN plots in particular (Fig. 5A). In the heath, *C. bigelowii* started at a low cover and greatly increased in the N and TN plots over four years, before declining somewhat by the sixth year (Fig. 5B).

Cover of the evergreen shrub *V. vitis-idaea* differed only between the T treatments and the unwarmed CTR and N treatments in the meadow (Fig. 5C). In the heath, nutrient perturbation immediately decreased the cover of *V. vitis-idaea*

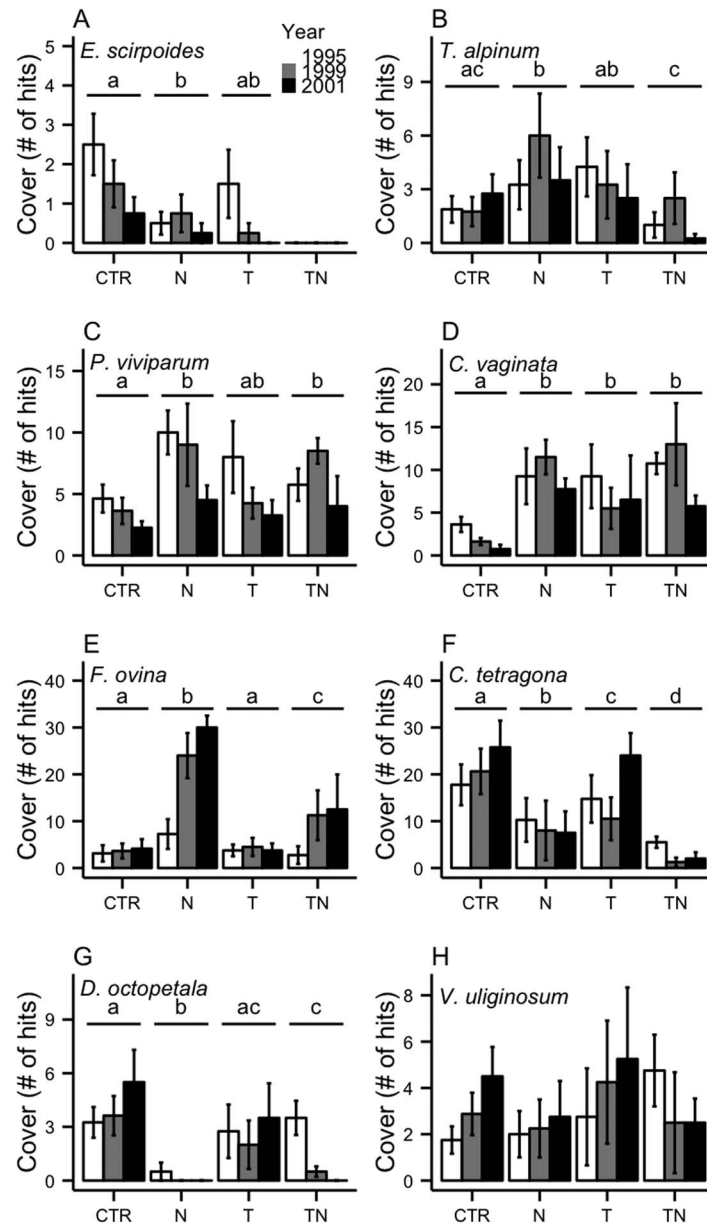


Fig. 2. Cover in the meadow community, measured by point-frame analyses with a maximum of 100 points, for three common forbs (*Equisetum scirpoides*, *Thalictrum alpinum*, and *Polygonum viviparum*, A C), two common graminoids (*Carex vaginata* and *Festuca ovina*, D E), two evergreen shrubs (*Cassiope tetragona* and *Dryas octopetala*, F G) and one deciduous shrub (*Vaccinium uliginosum*, H). Cover as measured in three different years from 1995 to 2001, and represented by treatment (CTR = control, N = nutrient addition, T = temperature enhancement, TN = nutrient plus temperature enhancement). Error bars represent standard error of the mean. Bars not sharing a common letter indicate significant differences between treatments, as measured across the whole timespan of the experiment (linear comparisons,  $p < 0.05$ ).



Table 2. Linear comparisons between treatment types for species where an additive or factorial model was the best explanation for species cover. For treatment types, CTR designates control plots, N designates fertilization plots, T designates warmed plots, and TN designates combined warming and fertilization plots. Thus, CTR-N represents the comparison between control and fertilized plots. Comparisons were made across the entire length of the experiment (1995–2001), not for years separately. Significant differences within the comparisons ( $p < 0.05$ ) are highlighted in bold.

Species	Location	CTR N	CTR T	CTR TN	N T	N TN	T TN
<i>Betula nana</i>	heath	<0.001	<0.001	<0.001	<0.001	0.003	<0.001
<i>Carex bigelowii</i>	heath	<0.001	0.29	0.01	<0.001	0.01	0.003
	meadow	0.001	0.11	0.23	0.68	0.44	0.99
<i>Carex vaginata</i>	meadow	<0.001	<0.001	<0.001	0.99	0.02	0.06
<i>Cassiope tetragona</i>	meadow	<0.001	0.36	<0.001	<0.001	<0.001	<0.001
<i>Dryas octopetala</i>	meadow	<0.001	0.52	<0.001	<0.001	0.006	0.06
<i>Equisetum scirpoides</i>	meadow	0.006	0.09	0.99	0.79	0.99	0.99
<i>Festuca ovina</i>	meadow	<0.001	0.41	<0.001	<0.001	<0.001	<0.001
<i>Polygonum viviparum</i>	meadow	<0.001	0.007	<0.001	0.93	0.96	0.75
<i>Thalictrum alpinum</i>	meadow	0.03	0.02	0.54	0.99	0.008	0.005
<i>Vaccinium uliginosum</i>	meadow	0.20	0.06	0.69	<0.001	0.04	0.69

to almost zero in N and TN (Fig. 5D), a decline from which it could not recover.

#### Gain and loss of species in experimental plots

In the meadow, three shrub species and two cushion plants were lost completely in the point-frame analysis from at least one of the experimental treatment types (Table 3A). In most cases, these species were either never present in the control plots or were initially present and then also lost in control plots. An exception is the evergreen shrub *Phyllodoce caerulea* which was maintained in control plots from 1995–2001, representing a divergence in the experimental plots. In addition, two forbs, three grasses, one sedge, and two rushes were gained in at least one experimental treatment type. In five cases, these species were either never present in the control plots, or had been present and then disappeared from the point-frame analysis over the course of the study. In the other three cases, the species had originally been present in the control plots but not in experimental plots, and were still maintained in the control plots by the end of the study.

In the heath, an evergreen shrub, a forb, a grass, and two rush species were lost from the point-frame analysis of the experimental plots but either never counted or counted and maintained at their original level in the control plots (Table 3B). In addition, the forb *P. viviparum* was lost in the experimental plots, but gained over the course of the study in the control plots.

## DISCUSSION

#### Lack of functional group fidelity in responses to perturbations

The most abundant species in both communities showed varying and sometimes no responses to the global change simulations. Furthermore, as hypothesized, responses within functional groups were not consistent. This can be primarily illustrated through three broad groups: the forbs, the shrubs, and the graminoids.

**Forbs.**—In the forb functional group, species' responses between treatments were not consistent in their direction or magnitude. The two most common species in the meadow, *E. scirpoides* and *P. viviparum*, showed trends of declining cover in not only the manipulated plots but also the control plots, while the third-most common species *T. alpinum* had higher cover in N and T treatments but showed no difference between the CTR and TN treatment.

**Shrubs.**—Within the shrub functional group, we found a trend of decreasing cover when nutrients were added in almost every species and across both the heath and meadow sites. However, the magnitude of this response varied greatly between species. Research in a high arctic semi-desert also showed that *D. octopetala* can greatly increase its biomass through clonal growth when nutrient supply improves (Wookey et al. 1995), but we did not find an increase in *D. octopetala* cover in our T or TN plots, nor to our knowledge have global change simulations been

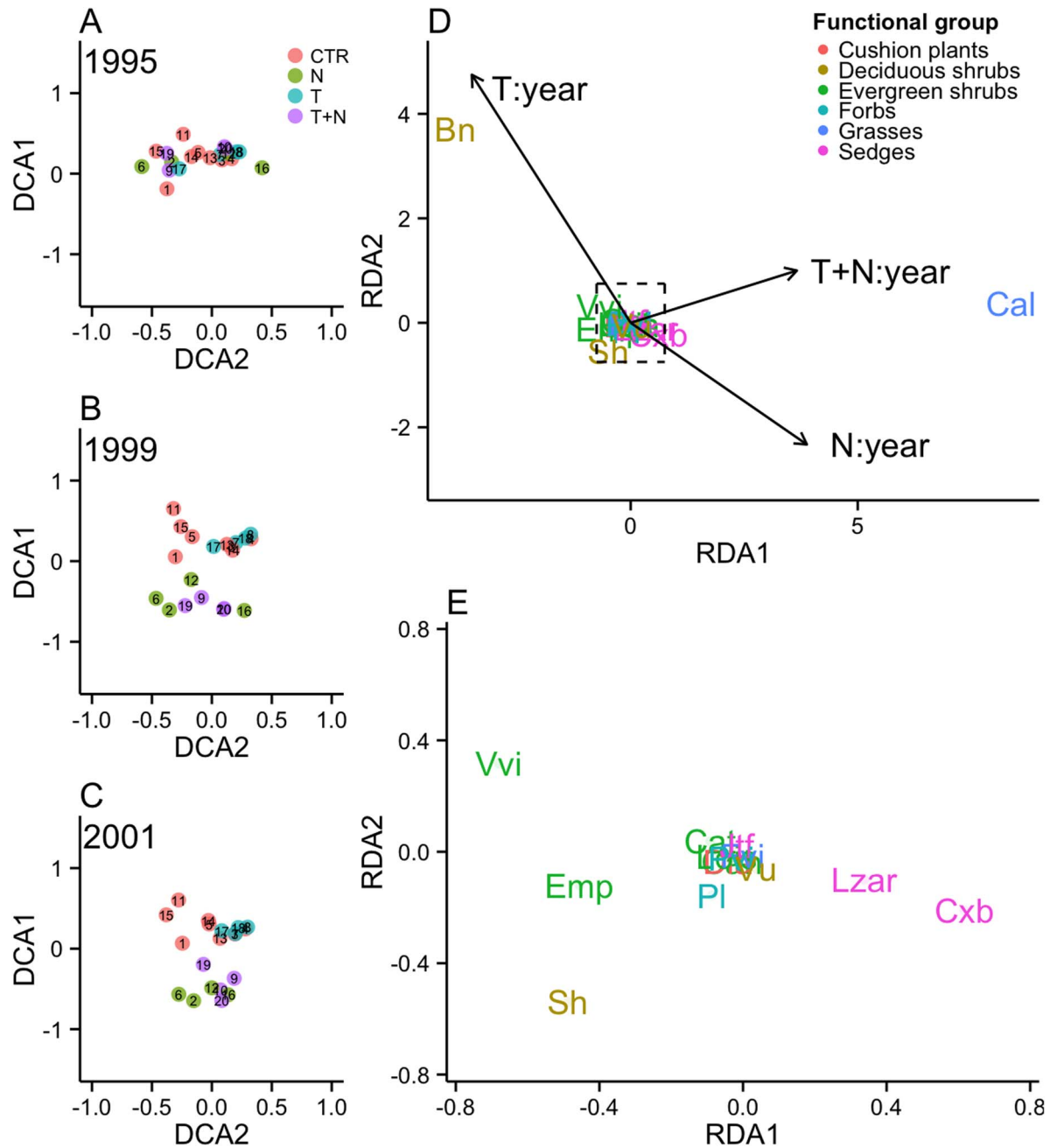


Fig. 3. Change in species composition in plots (numbered within each color-coded point) in the heath community according to detrended correspondence analysis from pre-treatment conditions in 1995 (A) and after the global change simulation had been applied through 1999 (B) and 2001 (C). The axes are the same for all three panels. Redundancy analysis showed differing shifts through time according to treatment, with some species (abbreviated as described in Appendix: Table A1) more associated with a specific treatment type (D); closely clustered species, outlined in the dashed line, are shown in more detail in panel (E).

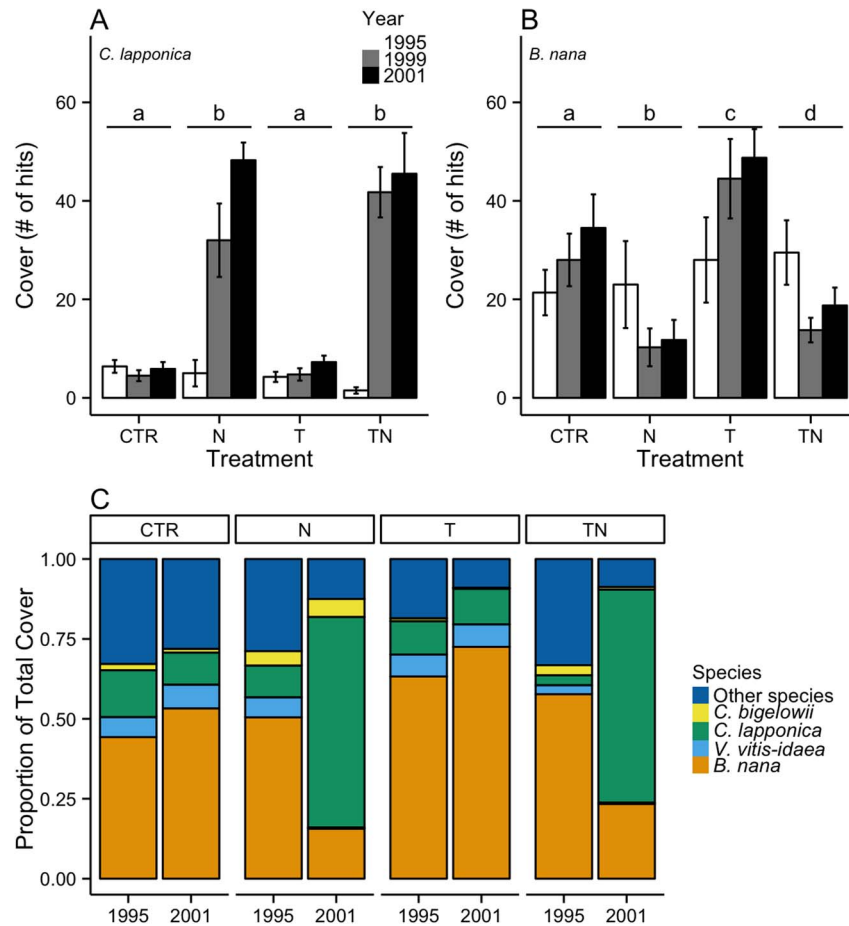


Fig. 4. Cover in the heath community, measured by point-frame analyses with a maximum of 100 points, for a dominant sedge (*Carex bigelowii*; A) and a dominant deciduous shrub (*Betula nana*; B). Cover as measured in three different years from 1995 to 2001, and represented by treatment (CTR = control, N = nutrient addition, T = temperature enhancement, TN = nutrient plus temperature enhancement). Error bars represent standard error of the mean. Bars not sharing a common letter indicate significant differences between treatments, as measured across the whole timespan of the experiment (linear comparisons,  $p < 0.05$ ). Experimental treatments also caused shifts in dominance from 1995 to 2001 (C).

shown to change *C. tetragona* or *V. uliginosum* abundance at the community level in comparable meadow systems. Several studies have found responses by these species in heath systems, while a comparative study of *C. tetragona* has shown widely differing responses among different types of ecosystems (Havström et al. 1993). Thus our results, combined with a previous study at a nearby site where *C. tetragona* was shown to be fairly unresponsive to warming treatments and also a poor competitor under warmer conditions (Molau 1997), indicate that individual shrub species may not contribute to

this trend of shrub expansion dependent on prior community composition and the availability, or lack thereof, of commonly limiting abiotic factors. Furthermore, *C. tetragona*, *D. octopetala*, and *V. uliginosum* have all been shown to be poor germinators from the high Arctic seed bank (Cooper et al. 2004), and in southern Sweden, there is also evidence that *V. uliginosum* relies on recruitment “windows of opportunity,” i.e., dispersal to open patches of a specific substrate (Eriksson and Froberg 1996). Thus, low recruitment levels may be one factor limiting these shrubs’ competitive ability compared to other

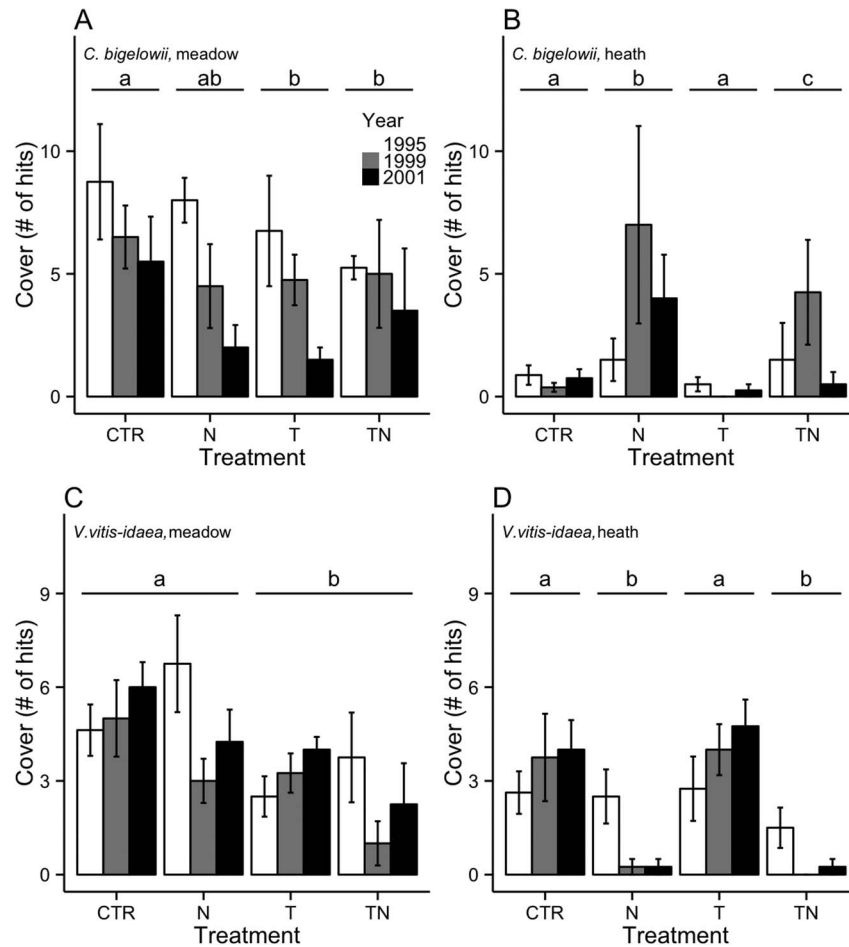


Fig. 5. Cover, measured by point-frame analyses, for four common heath species from 1995 to 2001. Treatment abbreviations, bar colors, and indicators of significance as in Fig. 2.

species when the environment becomes warmer and more fertile.

**Graminoids.**—Grass-dominated tundra has also contributed to the greening trend in the subarctic (McManus et al. 2012). In research regarding functional group responses to global change, grasses, sedges, and rushes have been treated in various ways, from as one combined “graminoid” group (Wang et al. 2012), to grasses separately from sedges and rushes (Chapin et al. 1996, Dormann and Woodin 2002), and finally to each group being considered separately (Elmendorf et al. 2012). We found strong positive responses to N treatment by several grasses; *F. ovina* in the meadow and *C. lapponica* in the heath ended up as the most dominant species in the N plots in their respective communities. However,

deeming this as a family- or functional group-response may be misleading as in each case the strong response was due primarily to a single species. We furthermore found examples of divergent responses even within narrowly defined functional groups. Within the sedges, both *C. vaginata* and *C. bigelowii* decreased in response to perturbations in the meadow community, while *C. bigelowii* initially increased, but then dramatically decreased in cover under nutrient amendment in the meadow. As has been documented previously, sedges and grasses differ significantly in their responses to fertilization in alpine and subalpine systems (Soudzilovskaia and Onipchenko 2005, Onipchenko et al. 2012, Alatalo et al. 2014). Our results add credence to the idea of separating the various subgroups of



Table 3. Cover change by species that were present in experimental plots in the meadow community (A) and heath community (B) either only before the treatments were applied (i.e., they were lost after treatments began) or only after the treatments were applied (i.e., they were gained after treatments began), along with their behavior in the control plots (i.e., lost, gained, never present, or “maintained” as present throughout the experiment).

Species	Functional group	Change in treatments	Behavior in controls
A) Meadow			
<i>Diapensia lapponica</i>	cushion plant	lost	lost
<i>Saxifraga oppositifolia</i>	cushion plant	lost	never counted
<i>Salix herbacea</i>	deciduous shrub	lost	never counted
<i>Phyllocladus caerulea</i>	evergreen shrub	lost	maintained
<i>Rhododendron lapponicum</i>	evergreen shrub	lost	never counted
<i>Oxyria diyna</i>	forb	gained	maintained
<i>Parnassia palustris</i>	forb	gained	never counted
<i>Festuca vivipara</i>	grass	gained	never counted
<i>Poa alpina</i>	grass	gained	lost
<i>Poa arctica</i>	grass	gained	never counted
<i>Carex norvegica</i>	sedge	gained	never counted
<i>Juncus trifidus</i>	rush	gained	maintained
<i>Luzula multiflora</i>	rush	lost	never counted
<i>Luzula spicata</i>	rush	gained	maintained
B) Heath			
<i>Cassiope tetragona</i>	evergreen shrub	lost	maintained
<i>Pedicularis lapponica</i>	forb	lost	maintained
<i>Polygonum viviparum</i>	forb	lost	gained
<i>Festuca vivipara</i>	grass	lost	never counted
<i>Juncus trifidus</i>	rush	gained in +N, lost in +TN	maintained
<i>Luzula arcuata</i>	rush	lost	never counted

graminoids instead of grouping them together at the functional group level, but even this may be insufficient to predict individual species responses.

Our results draw further into question the assumption that global change will create predictable responses from a given functional group (Dormann and Woodin 2002, Dorrepaal 2007, Onipchenko et al. 2012). A meta-analysis of 61 manipulative warming experiments suggested that regional heterogeneity in functional group responses was likely due to environmental conditions such as soil moisture, nutrient availability, and ambient temperature and the community composition prior to experimental implementation (Elmendorf et al. 2012). Furthermore, attributing dominance shifts to functional groups rather than species may prevent investigation of important effects of a dominant species on competition or ecosystem functioning. *C. lapponica*, which came to dominate the fertilized heath plots, has a well-documented, strong response to nutrient amendment which results in, for example, increased cover (Graglia et al. 2001), increased flowering (Lee et al. 1995), or overall increased productivity (Lee et al. 1995,

Press et al. 1998). Such a strong response will likely affect the microenvironment not only for other functional groups, for instance short-stature dwarf shrubs which may begin to lose competition for light and other resources, but also for other members of the same functional group. No investigation of competitive effects of *C. lapponica* for available soil resources has been performed to date, but this could be an important question given that it could become a dominant species in heath ecosystems in the future. Furthermore, the dominance of *C. lapponica* in the heath and *F. vivipara* in the meadow eroded diversity and evenness (unpublished data). Impact on diversity may persist for years even after perturbations themselves are reversed (Isbell et al. 2013). Lower biodiversity also has costs in terms of ecosystem functioning and services (Balvanera et al. 2006). Consequently, if functional group responses are a first measure of the effect of global change simulations, they should be used as a tool to identify and then examine the responses of key species, especially when such species are crucial in shaping the community character as perturbations continue.

### *Lack of within-species fidelity in responses to perturbations*

We also found that two common species present in both the heath and the meadow behaved differently with respect to the global change simulation in the heath compared to the meadow community. The sedge *C. bigelowii* and the evergreen shrub *V. vitis-idaea* showed opposite responses to simulations depending on the habitat type, with each responding to the temperature manipulation in the meadow community but to the nutrient manipulation in the heath community. While this is in some ways surprising, previous work has shown that a species may respond differently to global change depending on community productivity or climate history (for example, Pakeman 2004, Penning et al. 2005, Friedrichs et al. 2009). Meta-analyses of tundra experiments have found heterogeneity of vegetation responses to global change, and suggested that soil nutrient pools, herbivory pressure, winter climate, and species composition may lead to differing effects on species and communities (Elmendorf et al. 2012).

The difference in responses of *C. bigelowii* and *V. vitis-idaea* in the meadow compared to the heath may be because the heath is a more nutrient-limited ecosystem, and thus the addition of extra nitrogen and phosphorus may offer a more substantial release from environmental pressure. In a previous study of these sites, it was found that the meadow had about twice the total nitrogen load of the heath, which also had more acidic soil, lower soil moisture, and a comparatively shallower organic horizon (Björk et al. 2007). This pattern has also been found in other tundra gradients, for example in Japan where the grass *Deschampsia caespitosa* showed different abundance responses to manipulative warming from fjellfield to snowbed communities (Kudo et al. 2010). The heath community also had a much greater proportion of bare ground at the beginning of the experiment, which has likely allowed the proliferation of *C. lapponica* and *C. bigelowii* under the nutrient amendments. This may have directly contributed to the strong decline of *V. vitis-idaea* in the heath N plots, whereas in the meadow the lack of such a dramatic dominance shift probably resulted in *V. vitis-idaea* maintaining its proportional cover even when the ecosystem became more fertile.

These results highlight the highly context-dependent nature of responses to global change, even within a single species.

### *More novel species in the meadow than the heath community*

We hypothesized that new species (i.e., those which had not previously been detected by point-framing in the specific community) would begin to appear in the treatment plots due to amelioration of temperature and nutrient limitations. Previous work in the Latnjajaure area has shown that there is substantial seed rain, with propagules sometimes dispersing hundreds of meters in elevation higher than the upper limit of their extant distribution (Molau and Larsson 2000). Thus it is not necessarily dispersal which is limiting current species distribution, but likely also physical and biotic conditions.

We found this to be true in the meadow community, where new species appeared in plots where climate and nutrients were manipulated and the environment became less harsh. New species were found only rarely in control plots, in contrast to longer-term repeated sampling efforts in the same region, which found high species turnover attributed to currently observed climate change (Callaghan et al. 2013). Instead, it appears that the qualitative difference in abiotic conditions between control and experimental plots in the meadow allows novel species to establish in the treatment plots. An amelioration of growing conditions may in fact allow species that require warmer temperatures or higher, more consistent nutrient supply rates to colonize and flourish, invading at the expense of native or endemic species. Notably, however, evenness did not significantly decline in the meadow treatment plots (Alatalo et al. 2014), showing that at least in this mid-term timeframe, the appearance of novel species does not necessarily increase competition to a level detrimental to the established vegetation community.

However, not all experimental studies have found that new species can colonize as conditions change. A major challenge in ecology is that establishment success of new species can be unpredictable and community-context dependent (Gray et al. 2015). Indeed, while we found successful establishment of new species in the meadow community, in the different context of

the heath community we did not detect substantial species turnover and in fact found that existing species were lost from treatment plots, rather than new species being gained. This may be due to the heath's lower nutrient availability prior to experimental implementation. This is contrary to previous findings from northern Fennoscandia, where more species-rich communities lost richness with observed climate change, but comparatively species-poor communities gained new species (Virtanen et al. 2010). However, other harsh and species-poor high-latitude and high-altitude tundra communities have been shown to lose species in response to global change (Klein et al. 2004) or to have reduced richness of initially rare species (Chapin et al. 1995). In some cases, this reduction in species richness was hypothesized to be due to increasing vegetative productivity and competition. In the heath, the lack of new species appearing in treatment plots may be due to the rapid and extreme proliferation of *C. lapponica*, which likely limited the space available for new species to colonize. Thus the ability of new species to colonize warming or increasingly nutrient-rich communities is likely to be context-dependent based on other environmental factors, availability of space, and the community's starting composition.

## CONCLUSIONS

Over six years of global change simulations, we found species- and site-specific responses to warming and nutrient enrichment in northern Sweden. As hypothesized, for each ecosystem individually, species within a functional group did not necessarily respond in the same way. While responses to simulated global change were consistently negative within the shrub functional groups, the magnitude of these responses varied considerably. Discrepancies within functional groups were particularly noticeable for the forbs, but we also found evidence that previously identified graminoid responses may in fact be due to increases only of grass cover, or perhaps even of a single grass species. Thus, analysis at the broad functional group level may mask important information about the changing character of vegetation communities. Furthermore, we found strong evidence that species respond

differently to global change depending on the biotic and abiotic starting conditions of their community. This was demonstrated both using individual species (*C. bigelowii* and *V. vitis-idaea*), which responded to different aspects of the global change simulation in the heath compared to the meadow community, and by the fact that many more novel species began to appear in experimental treatment plots in the meadow than in the heath community. Our results support previous work which has suggested that functional groups are not particularly useful in predicting changes in ecosystem functioning due to climate change (Dorrepaal 2007, Bret-Harte et al. 2008). Thus, we urge caution when applying predictions of climate change effects based on meta-analyses and/or models because such results may be inadequate for predicting specific responses at local sites.

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## SUPPLEMENTAL MATERIAL

### ECOLOGICAL ARCHIVES

The Appendix is available online: <http://dx.doi.org/10.1890/ES14-00427.1.sm>