

UC Riverside

UC Riverside Previously Published Works

Title

Indirect effects of global change accumulate to alter plant diversity but not ecosystem function in alpine tundra

Permalink

<https://escholarship.org/uc/item/1hq2r0bw>

Journal

Journal of Ecology, 103(2)

ISSN

0022-0477

Authors

Farrer, Emily C
Ashton, Isabel W
Spasojevic, Marko J
[et al.](#)

Publication Date

2015-03-01

DOI

10.1111/1365-2745.12363

Peer reviewed

Indirect effects of global change accumulate to alter plant diversity but not ecosystem function in alpine tundra

Emily C. Farrer^{1*}, Isabel W. Ashton², Marko J. Spasojevic³, Shiyang Fu¹,
David J. X. Gonzalez¹ and Katharine N. Suding¹

¹Department of Environmental Science, Policy & Management, University of California, 137 Mulford Hall #3114, Berkeley, CA 94720-3114, USA; ²Rocky Mountain National Park, National Park Service, Estes Park, CO 80517, USA; and ³Department of Biology, Campus Box 1137, Washington University in St. Louis, St. Louis, MO 63130, USA

Summary

1. Environmental change can affect species directly by altering their physical environment and indirectly by altering the abundance of interacting species. A key challenge at the interface of community ecology and conservation biology is to predict how direct and indirect effects combine to influence response in a changing environment. In particular, little is known about how direct and indirect effects on biodiversity develop over time or their potential to influence ecosystem function.

2. We studied how nitrogen (N), winter precipitation (snow) and warming influenced diversity and ecosystem function over 6 years in alpine tundra. We used path analyses to partition direct effects of environmental manipulations from indirect effects due to changes in the abundance of two dominant plants. We hypothesize that (i) indirect effects will develop more slowly but will become stronger than direct effects over time and (ii) after 6 years, indirect effects will more strongly influence diversity while direct effects will influence ecosystem function.

3. Indirect effects of N on diversity were consistently stronger than direct effects and actually developed quickly, prior to direct effects. Direct effects of snow on diversity were detected in year 2 but then subsequently were reversed, while indirect effects were detected in year 4 and grew stronger over time. Overall in year 6, indirect effects were much stronger than direct effects on diversity.

4. Direct effects predominated for three of four ecosystem functions we measured (productivity, N mineralization, winter N availability). The only indirect effects we found were that N and snow indirectly affected microbial biomass N by influencing *Geum* abundance. Across all four ecosystem measures, indirect effects were infrequent and weaker than direct effects.

5. *Synthesis.* Increasing indirect effects on diversity over time indicate that short-term experiments or monitoring of natural systems may underestimate the full magnitude of global change effects on plant communities. Moreover, explicitly accounting for changes in dominant plant abundance may be necessary for forecasting plant community response to environmental change. Conversely, weak indirect effects for ecosystem processes suggest that predicting ecosystem function without knowledge of plant responses to global change may be possible.

Key-words: climate change, ecosystem function, nitrogen fertilization, Niwot Ridge, path analysis, plant–climate interactions, precipitation, snow, temperature, time-lags

Introduction

Environmental change can both directly affect a species by altering the physical environment and indirectly affect a species by altering the abundance of coexisting species and thus their interaction network (Tylianakis *et al.* 2008; Walther 2010). Recent work demonstrates that indirect effects can be

as or more important than direct effects in influencing a species response to a changing environment (Davis *et al.* 1998; Suttle, Thomsen & Power 2007; Tylianakis *et al.* 2008; Adler, Leiker & Levine 2009; Gilman *et al.* 2010). However, it remains unclear how to incorporate indirect effects into predictions of ecological response to global environmental change. Specifically, little is known about how the relative strengths of direct and indirect effects develop over time or the potential for indirect effects to influence ecosystem

*Correspondence author. E-mail: ecfarrer@berkeley.edu

function. Understanding which components of systems are most influenced by indirect effects and how these processes may change over time has the potential to illuminate when modelling complexity is necessary in forecasting biodiversity and ecosystem response to future environmental change.

Several frameworks describing ecological responses to environmental change emphasize a temporal hierarchy of response (Shaver *et al.* 2000; Smith, Knapp & Collins 2009), where individual-level physiological responses occur first, followed by reordering of species abundances in the community as some species are favoured by the changing conditions at the expense of others. It is this second stage of species reordering where environmental change can influence the abundance of competitors and the strength of per-capita competitive effects (Klanderud 2005; Adler, Leiker & Levine 2009; Kardol *et al.* 2010a; Adler, Dalglish & Ellner 2012; Farrer *et al.* 2014a; but see Levine *et al.*, 2010). Thus, indirect effects through altered interactions may take longer to manifest compared with direct physiological effects (Suttle, Thomsen & Power 2007). As the dominant species often control the majority of resources and most strongly affect species interactions (Keddy 2001; Smith, Knapp & Collins 2009), changes in abundance of dominant species may be where indirect effects on diversity predominate (Kardol *et al.* 2010a).

Species reordering, by shifting the distribution of species functional traits within a community, can also affect ecosystem processes (Shaver *et al.* 2001; Antoninka *et al.* 2009). As the traits of dominant species often contribute more to ecosystem processes (Grime 1998; Shaver *et al.* 2000; Hooper *et al.* 2005), changes in abundance of dominant species may be where indirect effects on ecosystem function predominate and the magnitude of these effects should depend on similarities in functional traits among the species (Kardol *et al.* 2010b). Indirect effects on ecosystem function may take longer to manifest than indirect effects on diversity due to time-lags inherent in many pathways by which species traits influence function (e.g. litter deposition and decomposition) (Chapin *et al.* 1995).

Here, we test the relative importance of direct and indirect effects of environmental change on diversity and ecosystem function in alpine tundra. We experimentally manipulated three environmental drivers (alone and in combination) expected to increase by the end of the century: N deposition, winter precipitation and summer temperatures (Dentener *et al.* 2006; IPCC 2007; Galloway *et al.* 2008). We hypothesize that (i) indirect effects through changes in abundance of the dominant species will develop more slowly but will become stronger than direct effects over the 6-year duration of the experiment and (ii) after 6 years, indirect effects will have a stronger effect on diversity compared with measures of ecosystem function.

Materials and methods

STUDY SITE AND GLOBAL CHANGE EXPERIMENT

This experiment was conducted in moist meadow alpine tundra on Niwot Ridge (40°03' N, 105°35' W) in the Front Range of the Rocky Mountains, Colorado, USA. Climate conditions at the field site

(summer temperatures, N deposition, summer and winter precipitation) over the length of the experiment are shown in Fig. S1 in Supporting Information. Moist meadow is common on leeward slopes receiving moderate to heavy snowcover (Frank & Isard, 1986). It is co-dominated by *Deschampsia cespitosa* (a perennial bunchgrass, Poaceae) and *Geum rossii* (a perennial forb, Rosaceae), which together make up over 60% cover. Hereafter, we refer to these dominant species as *Deschampsia* and *Geum*, respectively.

In 2006, we established a factorial manipulative experiment of winter precipitation (snowpack), nitrogen and temperature. The experiment used a split-plot design in which the whole-plot factor was precipitation and N addition and warming were randomized within precipitation treatment. The experiment consisted of three blocks of sixteen 1 m² plots (48 total plots, six replicates for each treatment combination). Precipitation was manipulated using snow fences running the length of the centre of each block so that the windward eight plots received ambient snow and the leeward eight plots received additional snowpack. This design allowed each N and warming treatment combination to be replicated twice within each split-plot. Snow fences elevated snow depth in treatment plots by an average of 40 cm throughout the winter (2.2× control plots) and treatment plots experienced 6–8 weeks more snow cover. Nitrogen was added as osmocote slow release fertilizer (urea 40-0-0 N-P-K), initially at a rate of 28 g N m⁻² year⁻¹ and reduced to 10 g N m⁻² year⁻¹ in 2011; due to incomplete release of the fertilizer pellets and high surface water flow at the beginning of the growing season, we estimate that the actual N made available in each plot was 14 and 5 g N m⁻² year⁻¹, respectively (Bowman *et al.* 1993; Suding *et al.* 2008). Ambient N deposition in the tundra was approximately 5 kg N ha⁻¹ year⁻¹ (0.5 g N m⁻² year⁻¹) over this time period (Fig. S1b). Growing season temperature (June through August) was increased using open-topped chambers which increased air temperature by 1 °C.

PLANT COMMUNITY AND ECOSYSTEM MEASUREMENTS

Species composition was measured in each of the 48 plots in 2006–12 using the point-intercept method, yielding a per cent cover for each species within each plot. Presence was assessed at 100 evenly spaced points per plot; species that were present in the plot but not hit were recorded as 0.5 (indicating < 1% cover). We used the Shannon Index as a measure of species diversity, incorporating both richness and evenness in one metric, $H = -\sum(p_i \ln p_i)$, where p_i is the relative abundance of species i . The 2006 data were taken prior to the initiation of the manipulative treatments. Because plots varied considerably in their initial species composition and diversity, 2007–12 data are presented as a change (Δ) from 2006 values.

In 2012, we measured four ecosystem processes in order to capture global change effects on processes important to system carbon and nutrient cycling: net primary productivity, microbial biomass N, winter N availability and N mineralization. Indirect effects through changes in dominant plant species have the potential to impact some of these ecosystem processes. While *Deschampsia* and *Geum* do not differ in biomass production (Steltzer & Bowman 1998; Suding *et al.* 2008), they differ substantially in litter quality which affects microbial biomass N (Bowman *et al.* 2004; Suding *et al.* 2008), N mineralization (Steltzer & Bowman 1998; Suding *et al.* 2008) and winter litter N immobilization (Steltzer & Bowman 2005).

We quantified net primary productivity by clipping above-ground live biomass to ground level in one 20 × 20 cm area within each plot at peak biomass, drying at 60 °C, and weighing.

We measured microbial biomass in late June of 2012 in each plot, from soil cores (3.4 cm diameter) sampled to a depth of 10 cm. Soil cores were brought back to the laboratory on ice, sieved (2 mm), and gravimetric soil moisture was measured (by drying at 105 °C). Chloroform-labile N and C was determined using the chloroform fumigation extraction technique (Robertson *et al.* 1999). Briefly, a 10 g subsample of the soil was extracted immediately, and another subsample was fumigated with chloroform to kill microbes and then extracted with 0.5 mol L⁻¹ K₂SO₄. Total dissolved nitrogen (TDN, by persulfate digestion) was measured on a chemiluminescence gas analyzer (TOC-V CSN; Shimadzu Corp, Kyoto, Japan) and microbial biomass N was calculated as the difference between fumigated and unfumigated samples. To correct for extraction efficiency, microbial biomass N was divided by 0.54 (Brookes *et al.* 1985).

Net N mineralization was measured using a portion of the soil core from microbial biomass. In the field, the soil core was split in half and one part was put inside a gas-permeable bag and was returned to the hole for *in situ* N mineralization measurements (Eno 1960). After 28 days, the incubated soils were retrieved, sieved and extracted with 0.5 mol L⁻¹ K₂SO₄. Initial and incubated samples were analysed for nitrate and ammonium as above. N mineralization was calculated as the increase in NH₄⁺ and NO₃⁻ over the 28-day incubation period.

Nitrogen availability was measured using ion exchange resins [Rexyn I-300 (H-OH); Fisher Scientific, Pittsburgh, PA, USA]. We placed two ion exchange resin tubes (2.54 cm diameter × 2 cm height wrapped in nylon mesh) at a depth of 10 cm in each plot. Winter N availability (mid-August to mid-June) was measured over the 2011–12 winter. Resins were extracted with 2 mol L⁻¹ KCl and analysed for nitrate (QuikChem 8000 continuous-flow autoanalyzer; Lachat Instruments, Milwaukee, WI, USA) and ammonium (Synergy 2 Multidetector Microplate Reader; BioTek Instruments, Inc., Winooski, VT, USA) in the Kiowa Environmental Chemistry Laboratory (Boulder, CO, USA). Summer N availability (mid-June to mid-August) was also measured in 2012; it confirmed our N addition treatment and was so tightly correlated with the N addition treatment that it was dropped from further analyses.

STATISTICAL ANALYSIS

We assessed net effects of environmental change treatments on dominant species cover and diversity using repeated-measures linear mixed models in R (R Core Team 2013) package NLME (Pinheiro *et al.* 2013). We included pre-treatment cover as a covariate in the models. We modelled nitrogen, snow and temperature and all two-way treatment interactions as fixed effects. We also tested for changes in treatment effects over time by modelling year (as a factor) and all two-way and three-way interactions between year and treatments. Repeated measurements were modelled by including plot (within snow and block) as a random effect with compound symmetry error structure. Net effects of treatments on ecosystem properties (productivity, winter resin N, N mineralization and microbial biomass N) were analysed as above but without year effects or a random plot effect, as they were only measured in 2012.

The direct and indirect effects of the three environmental manipulations on diversity were assessed using separate path analyses on each year of data. Prior to path analyses, all variables were examined for distributional properties and the linearity of relationships. We then constructed an initial model which included the direct effects of treatments (N, snow, temperature, N × snow, N × temperature and snow × temperature) on the cover of the two dominant plant species (*Deschampsia* and *Geum*) and diversity, the direct effects of the

dominant plants on diversity and the covariance between *Deschampsia* and *Geum* (Fig. S2). Treatments were modelled as binary (0 for control, 1 for treatments); interactive effects were modelled as additional binary variables representing the product of the two treatments (0 for control and single treatments, 1 for two treatments). In this analysis, dominant plant cover and diversity were corrected for pre-treatment starting conditions (measured as a Δ from 2006). All variables were standardized so that effects could be directly compared. For each year, we fit the model using maximum likelihood in the LAVAAN package (Rosseel 2012) in R. We removed variables to find the model with the lowest AIC (Spasojevic *et al.* 2014) to balance model fit and parsimony (Grace & Pugeseck 1997) and assessed final model fit with the χ^2 statistic and the root mean square error of approximation (RMSEA). Chi-squared values associated with a *P*-value > 0.05 (suggesting that observed and expected covariance matrices are not different) and a RMSEA < 0.05 indicate a good model fit (Kline 2010). Z-statistics were used to determine the significance of each pathway. Indirect effects were deemed significant when the two individual pathways making up the indirect effect were significant by the Z-test.

We then compared the magnitude of direct vs. indirect effects of N, snow, and temperature on diversity. Direct effects are quantified by their standardized regression coefficient (standardized coefficients are used so that all variables are weighted equally regardless of measurement units) (McCune & Grace 2002; Grace 2006); indirect effects are calculated by multiplying standardized regression coefficients along pathways through the dominant plant species and summing (McCune & Grace 2002; Grace 2006). Covariances were not used in calculating magnitude of direct or indirect effects. In order to check that backwards selection (i.e. exclusion of non-significant terms) did not affect calculations of direct and indirect effects over time, we ran models in all years including all explanatory variables and confirmed that it did not qualitatively influence results.

Results were similar using the Shannon diversity index or evenness as the metric of species diversity, with the exception that there were no direct effects on N on evenness (for evenness results, see Figs S2–S4).

We tested the strength of direct and indirect effects on ecosystem function (productivity, microbial biomass, winter N availability, N mineralization) using path analysis in the final year of the experiment (2012). We built an initial model that included direct single factor and two-way interactive effects of treatments on dominant plants and ecosystem properties. We also included effects of *Deschampsia* and *Geum* on ecosystem properties and covariance between *Deschampsia* and *Geum* (Fig. S2). Summer soil moisture was used as a covariate for all variables except winter N availability. Other aspects of model design and fit were performed as above.

Results

NET EFFECTS OF ENVIRONMENTAL CHANGE ON DIVERSITY OVER TIME

Diversity declined in the N and snow addition treatments, and effects grew stronger over time (Fig. 1a, Table 1, for repeated-measure ANOVA results, see Table S1). The warming treatment had little effect on diversity; however, the path analyses indicated that in year 2 temperature combined with N had a negative effect (N × temperature interaction) and in the final year of the experiment temperature alone had a slight positive effect on diversity (Table 1, Fig. 2).

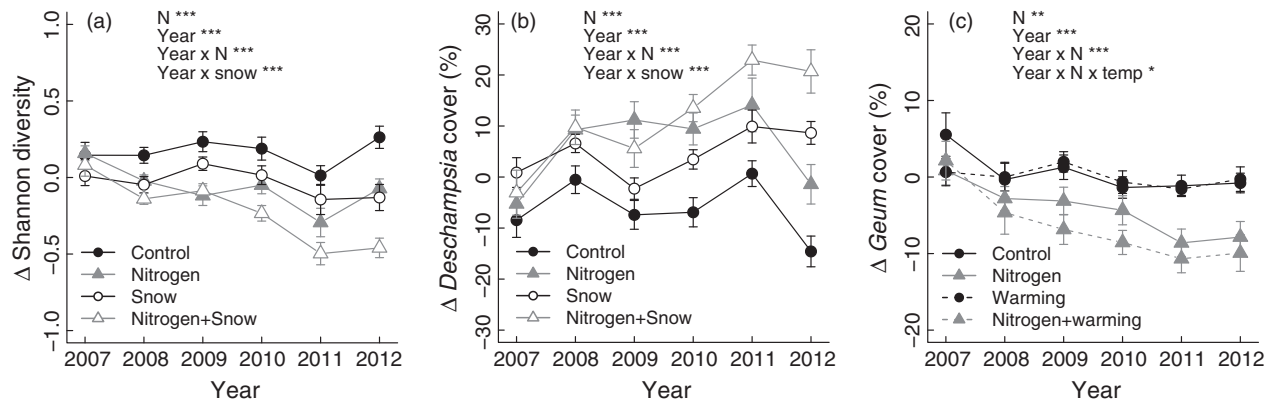


Fig. 1. The effects of environmental change drivers on diversity (a), *Deschampsia* (b) and *Geum* (c) over time. Data are corrected for pre-treatment conditions (Δ diversity and cover from 2006). Only treatments significant in a repeated-measures ANOVA are shown, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (see Table S1), and values are averaged over other treatments for clarity (mean \pm SE).

Table 1. Standardized direct, indirect and net effects of three environmental change drivers (N, snow, temperature) on diversity over time. Only significant ($P < 0.05$) effects are shown

Environmental change	Type of effect	2007	2008	2009	2010	2011	2012
Nitrogen	Direct			-0.22		-0.24	-0.18
	Indirect		-0.26	-0.24	-0.46	-0.37	-0.30
	Net	0.00	-0.26	-0.46	-0.46	-0.61	-0.48
Snow	Direct		-0.28	-0.12			
	Indirect				-0.22	-0.21	-0.40
	Net	0.00	-0.28	-0.12	-0.22	-0.21	-0.40
Temperature	Direct						
	Indirect						0.24
	Net	0.00	0.00	0.00	0.00	0.00	0.24
N \times temperature	Direct		-0.24				
	Indirect						
	Net	0.00	-0.24	0.00	0.00	0.00	0.00

Nitrogen addition strongly affected the abundance of the two dominant plant species, increasing *Deschampsia* cover and decreasing *Geum* cover (Figs 1b,c and 2, for repeated-measures ANOVA results, see Table S1). Snow addition also increased *Deschampsia* cover especially in the last 3 years of the experiment (Figs 1b and 2). The snow treatment and the combined N plus temperature treatment reduced *Geum* cover, although the magnitudes of these effects were more variable across years (Figs 1c and 2). The effect of environmental change treatments on the dominant species generally increased in strength over time (Fig. 2). *Deschampsia* and *Geum* also exhibited significant negative covariance in all years (Fig. 2).

DIRECT AND INDIRECT EFFECTS ON DIVERSITY OVER TIME

We identified both direct and indirect effects of nitrogen, snow, and less so, temperature, on diversity (Figs 2 and 3, Table 1). In the year following the initiation of treatment (2007), no treatment effects on diversity, either direct or indirect, were evident (Fig. 2a). Nitrogen directly reduced species diversity starting in year 3, and this diversity reduction

persisted in years 5 and 6 (Figs 2 and 3a). Snow directly reduced diversity starting in year 2, but unlike the direct effect of N, diversity recovered from the direct effect after year 3 (i.e. plots that had lost species in year 2 regained them again in year 3), so that direct effects did not play a role in long-term response to snow (Figs 2 and 3b). No direct effect of temperature alone was detected, only an N \times temperature interaction in year 2 (Fig. 2b, Table 1).

Indirect effects, through changed abundances of *Deschampsia* and *Geum*, were detected for all three environmental change treatments and displayed different patterns of development over time (Fig. 3). Nitrogen indirectly reduced diversity by increasing the abundance of *Deschampsia* starting in year 2, and the indirect effects increased slightly in magnitude over time (Figs 2 and 3a). Nitrogen also indirectly increased diversity through decreasing the abundance of *Geum* in year 3, though this effect was small (Fig. 2c). Snow indirectly reduced diversity via increased *Deschampsia* abundance starting in year 4 and effects increased over time (Figs 2 and 3b). The only evidence of an indirect effect of warming on diversity was in the last year of the experiment, where warming reduced the abundance of *Deschampsia* (Figs 2 and 3c). After 6 years, for all environmental change treatments (N, snow,

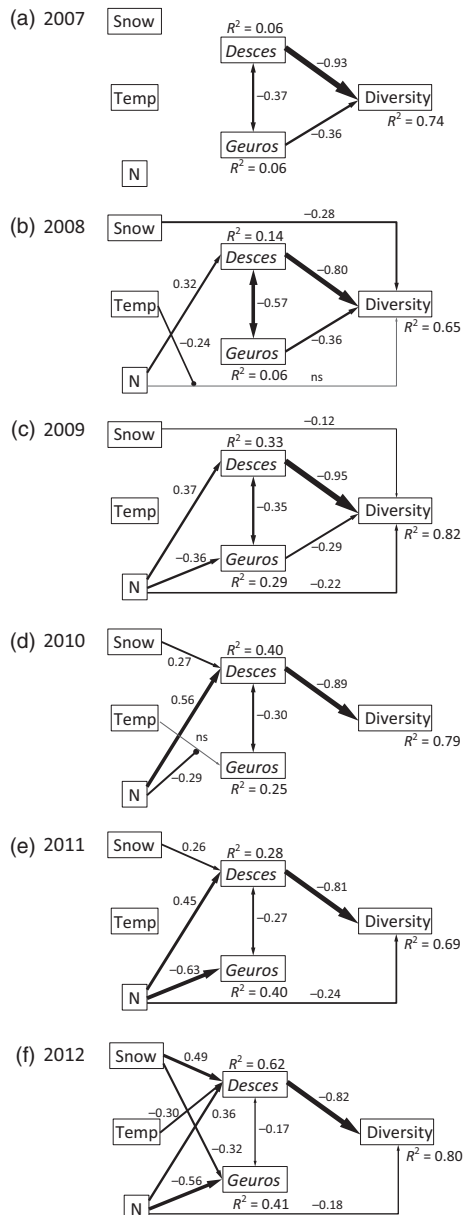


Fig. 2. Path analyses showing significant ($P < 0.05$) causal relationships among environmental drivers, abundance of dominant plant species and diversity from 2007 to 2012 (a–f). The width of the arrow corresponds to the strength of the correlation; an arrow pointing to another arrow indicates an interactive effect. *Desces* = *Deschampsia cespitosa*, *Geuros* = *Geum rossii*. Models had a good overall fit in every year ($\chi^2 > 0.5$, $P > 0.53$, root mean square error of approximation < 0.001 in each year). When interactive effects are significant but main effect is not, the main effect is labelled 'ns'.

temperature), indirect effects were stronger than direct effects on diversity (Fig. 3, Table 1).

DIRECT AND INDIRECT EFFECTS ON ECOSYSTEM FUNCTION

Direct effects of environmental manipulations on ecosystem function predominated 6 years after the initiation of the experiment (Fig. 4, for ANOVA results, see Table S1). Productivity

was positively affected by snow but only in the absence of warming (snow \times temperature effect, Figs 4 and 5a). Snow addition decreased winter N availability, especially in the N addition treatment (N \times snow effect, Figs 4 and 5b). N addition increased net N mineralization (Figs 4 and 5c) and decreased microbial biomass N (Figs 4 and 5d). Only one of the four ecosystem function variables we measured, microbial biomass N, was affected by changes in abundance of the dominant plant species: snow and N indirectly decreased microbial biomass N via negative effects on *Geum* cover (Fig. 4), and the magnitude of these effects was small (Table 2). While experimental treatments affected *Deschampsia* abundance, these effects did not translate to indirect effects on ecosystem function. Overall, indirect effects on ecosystem function were much weaker than indirect effects on diversity (Tables 1 and 2).

Discussion

Understanding how indirect effects develop over time and which components of ecological systems are most influenced by indirect effects is essential for assessing the impact of global change on systems and forecasting future change. Theoretical expectations of the temporal progression of effect of environmental change on systems, from initial physiological change to subsequent species reordering (Shaver *et al.* 2000; Smith, Knapp & Collins 2009), suggest the development of indirect effects may lag behind direct effects. Consistent with theory, we found that direct effects of snow on diversity occurred initially but then were reversed, while indirect effects developed more slowly and accumulated over time. Conversely, indirect effects of N on diversity were detected earlier than direct effects; both increased and then stabilized over time with indirect effects consistently stronger than direct effects. The indirect effects of species reordering, however, did not extend to the ecosystem level: after 6 years, direct effects were much stronger than indirect effects on measures of ecosystem function.

NET EFFECTS OF ENVIRONMENTAL CHANGE TREATMENTS

In high-elevation mountain ecosystems, plant species are thought to be strongly limited by environmental factors (Harsch *et al.* 2009; Engler *et al.* 2011; Carlson *et al.* 2013). For instance, wind redistributes snow along topographic gradients, slope and aspect affect temperature and radiation, and both temperature and snowpack influence the timing of snowmelt. This strong control may cause these systems to be particularly responsive to environmental change. For example, within the alpine tundra zone, the timing of snowpack controls the growing season length, a fundamental control on plant species composition (Kikvidze *et al.* 2005; Scherrer & Körner 2011; Spasojevic *et al.* 2013). Increased atmospheric deposition of N may also relax N limitation on plant growth (Bowman *et al.* 1993, 2006). We manipulated three key environmental controls that are predicted to change in our study system:

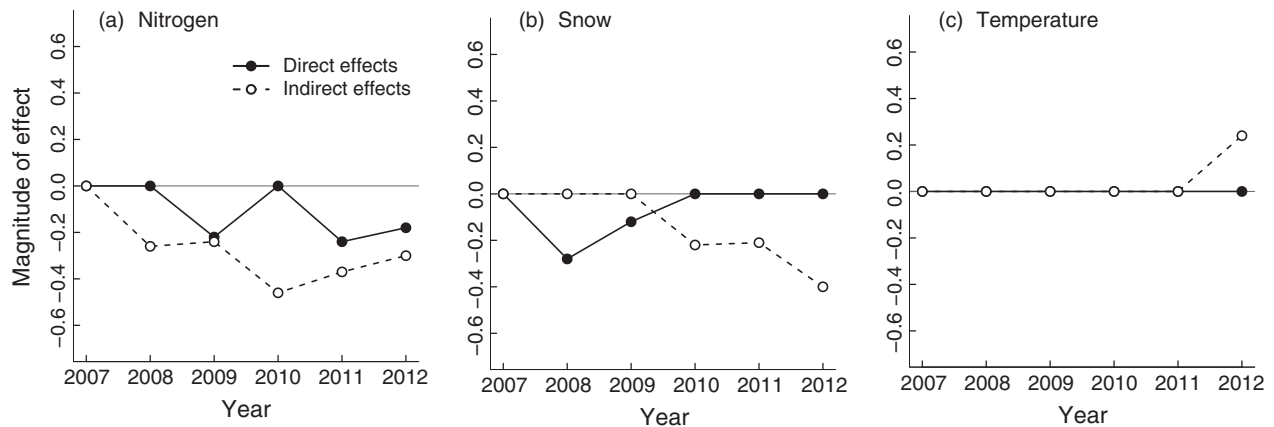


Fig. 3. Magnitude of direct and indirect effects of nitrogen (a), snow (b) and temperature (c) on diversity over time. Indirect effects occur through changes in the dominant plant species. Path diagrams for each year are shown in Fig. 2. Direct effects are the standardized regression coefficients; indirect effects are calculated by multiplying standardized regression coefficients along pathways through the dominant plant species and summing.

Table 2. Standardized direct and indirect effects of three environmental change drivers (N, snow, temperature) on ecosystem properties in 2012. Only significant ($P < 0.05$) effects are shown

Ecosystem property	Environmental change	Direct effect	Indirect effect
Productivity	Snow	0.45	
	Snow \times temperature	-0.56	
Microbial biomass	N	-0.46	-0.13
	N \times temperature		0.09
	Snow		-0.12
Winter N availability	N	0.85	
	N \times snow	-0.52	
N mineralization	N	0.44	

snowpack, nitrogen and temperature. Although we manipulated these factors alone and in combination, interactive effects were surprisingly infrequent (also see Farrer *et al.* 2014a).

Snow addition

Snowpack and snow duration exert strong controls on where species can persist in alpine tundra landscapes (Litaor, Williams & Seastedt 2008). Increased snow can benefit fast-growing species that thrive under high moisture conditions, such as one dominant species in our system, *Deschampsia*, as well as protect plants from spring frost events. However, increased snow generally has been shown to decrease diversity, as we found here, due to the loss of species that cannot tolerate a shortened growing season (Seastedt & Vaccaro 2001; Wahren, Walker & Bret-Harte 2005; Wipf & Rixen 2010). For example, carbon limitation from a shorter growing season due to increased snowpack can cause species decline (Bell & Bliss 1979). The reduction in growing season length caused by increased snowpack is also generally found to decrease productivity (Wipf & Rixen 2010); however, in this study, production was only decreased when increased snow

was combined with warming (particularly in 2012, the warmest of the experimental years). In the absence of warming, increased snow increased biomass production, likely due to reduced water limitation.

Elevated snowpack can also have profound impacts on winter nutrient dynamics, which contribute disproportionately to annual nutrient cycling in tundra systems (Brooks, Williams & Schmidt 1995). Typically, increased snowpack leads to high rates of N mineralization in the winter due to insulation by the snow, followed by high rates of immobilization at snowmelt (Schimel, Bilbrough & Welker 2004). Because the duration of our winter resin N measurements included both winter insulation and snowmelt periods, the negative effect of increased snow on winter N availability, particularly with N addition, indicate that high rates of immobilization in plots with elevated snow more than compensates for any excess N mineralization that occurred in those plots through the winter. This immobilization likely leads to reduced N availability to plants during snowmelt, which could be one factor related to the negative effect of increased snow on diversity. It also suggests that future increases in precipitation will help to reduce export of inorganic N to surface waters (Brooks, Williams & Schmidt 1998).

Warming

Increased minimum temperatures (McGuire *et al.* 2012) have been causing an earlier spring melt and a longer, drier growing season at our study site (Cain 2010) and in many tundra areas world-wide. While temperature is generally perceived as a major abiotic control in alpine tundra (Callaghan *et al.* 2011; Gottfried *et al.* 2011), our warming treatment using passive ITEX chambers created a small increase (1 °C) in ambient summer temperature and did not cause consistent biotic responses. While 1–3 °C warming has been shown to reduce diversity in experiments across the tundra biome (Walker *et al.* 2006; Elmendorf *et al.* 2012), as well as alter ecosystem processes, particularly productivity and soil N

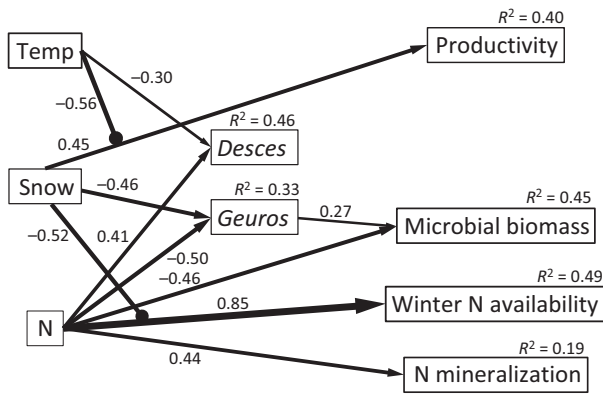


Fig. 4. Path diagram comparing direct and indirect effects of global change on ecosystem function in 2012. Only significant ($P < 0.05$) paths are shown. The width of the arrow corresponds to the strength of the correlation; an arrow pointing to another arrow indicates an interactive effect. *Desces* = *Deschampsia cespitosa*, *Geuros* = *Geum rossii*. The model had a good overall fit ($\chi^2_{35} = 22.85$, $P = 0.943$, root mean square error of approximation < 0.001). Interactive effects on the dominant species are not shown for simplicity (snow \times temperature for *Deschampsia* and N \times temperature for *Geum*). The effect of the covariate soil moisture on *Geum* ($r = -0.32$, $P = 0.01$) and microbial biomass N ($r = 0.55$, $P < 0.001$) is not shown for simplicity.

change (Farrer *et al.* 2014a), and possibly ecosystem change, at Niwot Ridge in the long term.

Nitrogen addition

Although the alpine tundra is in general a low-nutrient system, nutrient availability varies within the alpine tundra zone, increasing along a snowpack gradient from dry to moist to wet meadow communities (Bowman *et al.* 1993; Fisk, Schmidt & Seastedt 1998). Current atmospheric N deposition rates (near 6 kg N ha⁻¹ year, Williams & Tonnessen 2000) have been increasing significantly over the last several decades (Williams & Tonnessen 2000; Mladenov *et al.* 2012). These rates are in the range of the critical loads measured for changing individual species abundance (4 kg N ha⁻¹ year) and for overall community change (10 kg N ha⁻¹ year) (Bowman *et al.* 2006), as well as our N fertilization treatment.

Diversity decline with N fertilization, as we found in this study, is a classic response in many ecosystems (Stevens *et al.* 2004; Clark *et al.* 2007) including moist and wet meadow alpine tundra (Theodose & Bowman 1997; Suding *et al.* 2008). Response to N differed between the two dominant plant species, with N increasing abundance of *Deschampsia* and decreasing abundance of *Geum*. These responses were expected based on several previous studies (Suding *et al.* 2004, 2008; Farrer *et al.* 2013) and were likely due to differences in N uptake and growth rate characteristics of the two species (Theodose *et al.* 1996; Miller & Bowman 2003).

dynamics (Rustad *et al.* 2001), effects have been inconsistent and largely constrained to specific functional groups (shrubs, lichens) not abundant at our study site. Predicted temperature change over the next century is much greater (4 °C), and simulations suggest that temperature will drive tundra community

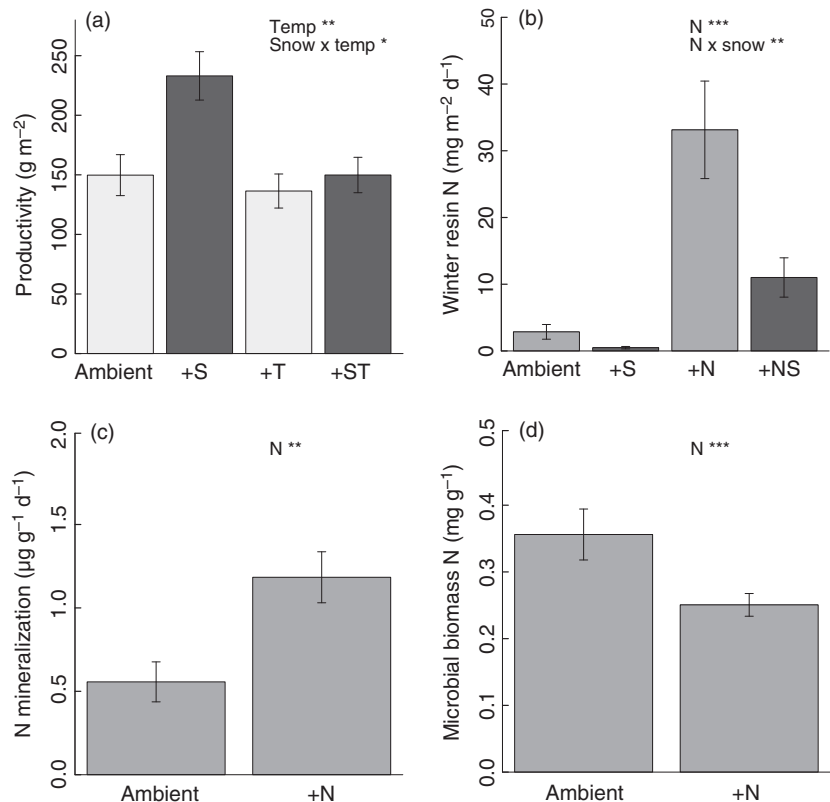


Fig. 5. Effects of environmental change drivers on ecosystem function in 2012, productivity (a), winter resin N (b), N mineralization (c) and microbial biomass N (d). Only treatments significant in an ANOVA are shown, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (see Table S1), and values are averaged over other treatments for clarity (mean \pm SE). +S = snow addition, +T = increased temperature, +N = nitrogen addition.

We found N fertilization increased summer net N mineralization, a response that is common across systems and is likely the result of increased plant litter N content (McNulty & Aber 1993; Fisk & Schmidt 1996; Matson, Lohse & Hall 2002). Concurrent with an increase in N mineralization, microbial biomass decreased with N addition. Together this suggests carbon limitation in soil microbes in N addition plots, which is expected because N deposition can reduce plant allocation below-ground, reduce ligninase activity and react chemically with soil compounds to produce recalcitrant products (Treseder 2008). While lower microbial biomass can result in lower soil CO₂ emissions (Treseder 2008), this will likely not appreciably offset the strong effects of warming on the tundra as a carbon source (Natali *et al.* 2011; Belshe, Schuur & Bolker 2013).

INDIRECT EFFECTS ON DIVERSITY AND ECOSYSTEM FUNCTION

We extended the frameworks of environmental change that emphasize a temporal hierarchy of response (Shaver *et al.* 2000; Smith, Knapp & Collins 2009) to predictions about how indirect effects may propagate through a system. We hypothesized that direct effects of environmental change, involving individual-level physiological responses, should occur first and then level off in magnitude following a period of species loss or adaptation. We found that direct effects of nitrogen and snow develop within 2–3 years and then level off or reverse, indicating that declines in species unable to tolerate the changed environmental conditions occur fairly quickly.

Based on the environmental change frameworks, we also hypothesized that indirect effects should develop more slowly, as they will depend on reordering of species abundances in the community as some species are favoured by the changing conditions at the expense of others and competitive interactions play out. As hypothesized, indirect effects of snow on diversity manifested more slowly than direct effects but became stronger over time (Fig. 3b). However, indirect effects of N on diversity developed rapidly, within 2 years, prior to direct effects; they increased and then appeared to stabilize over the 6-year experiment at a level higher than direct effects. Indirect effects were largely mediated by one of the dominant plants, *Deschampsia*, a fast-growing, competitive species that increased dramatically in abundance with N and snow. Increased competition from fast-growing, opportunistic dominants may be a general case where indirect effects are strong (Adler & Hille Ris Lambers 2008; Kardol *et al.* 2010a; Farrer *et al.* 2014a). Interestingly, in the case of *Deschampsia*, indirect effects were driven by population growth of the species rather than change in per-capita effects (path coefficients linking *Deschampsia* to diversity remained constant over time).

In contrast to diversity, dominant plant species mediated few effects on ecosystem function. While *Deschampsia* and *Geum* have similar biomass production (Steltzer & Bowman 1998; Suding *et al.* 2008) and so may not mediate large

changes in production, they have been shown to have species-specific effects on other ecosystem functions that could cause indirect effects. For instance, *Deschampsia* and *Geum* are known to differentially affect microbial biomass (Bowman *et al.* 2004; Suding *et al.* 2008), N mineralization (Steltzer & Bowman 1998; Suding *et al.* 2008), and litter N immobilization over the winter (Steltzer & Bowman 2005) through differences in litter quality. Consistent with *Geum*'s effect on microbial biomass N, snow and N treatments indirectly decreased microbial biomass N via negative effects on *Geum* cover. Even though we did not find strong indirect effects on ecosystem function through dominant plants, other intermediaries might be important. For example, it is possible that if we included soil microbial community structure in our analysis, we may have detected indirect effects on soil processes via microbial communities (Antoninka *et al.* 2009). It also may be that we need to follow the experimental treatment responses longer than 6 years to identify indirect effects on ecosystem function. Time-lags inherent in many pathways by which species traits influence function (e.g. litter deposition and decomposition) (Chapin *et al.* 1995) may require a decade or more.

Implications

The strong indirect effects of global change on plant diversity found here and in many other studies across systems (Klanderud 2005; Adler & Hille Ris Lambers 2008; Antoninka *et al.* 2009; Kardol *et al.* 2010a; Adler, Dalgleish & Ellner 2012) imply that multispecies approaches must be taken when forecasting plant community response to global change. For example, because we found that competition from *Deschampsia* drives declines in diversity with global change, diversity declines might not be predicted for sites where *Deschampsia* is not abundant. Moreover, the development of increasing indirect effects on diversity over time suggests that short-term experiments or monitoring of natural systems undergoing environmental change may underestimate the full magnitude of global change effects on plant communities. Conversely, the weak indirect effects on ecosystem processes suggest that predicting ecosystem function without knowledge of plant responses to global change may be possible. Overall, understanding which components of systems are most influenced by indirect effects and how they play out over time will help us identify when modeling complexity is necessary in forecasting ecosystem response to future environmental change.

Acknowledgements

We thank Krista Beckley, Kurt Chowanski, Adam Formica, Eva Franzova, Yvette Gault, Liana Nichols, Julia Reich, Charlotte Riggs, Keishla Rodriguez, Trang Pham, Jane Smith, Warren Sconiers, Robert Weller and Lucas Zukiewicz for their assistance in the field. We also thank Christine Seibold and Holly Hughes at the Iowa laboratory for running nutrient analyses. Three anonymous referees gave thoughtful comments on earlier drafts of this manuscript. Funding was provided by the National Science Foundation (DEB-0919569 and Niwot Ridge LTER, DEB-0423662 and DEB-1027341) and the Andrew W. Mellon Foundation.

Data accessibility

Data are available from the Dryad Digital Repository (Farrer *et al.* 2014b) and can be accessed on the Niwot Ridge LTER website: <http://niwot.colorado.edu/index.php>.

References

- Adler, P.B., Dalglish, H.J. & Ellner, S.P. (2012) Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? *Journal of Ecology*, **100**, 478–487.
- Adler, P.B. & Hille Ris Lambers, J. (2008) The influence of climate and species composition on the population dynamics of ten prairie forbs. *Ecology*, **89**, 3049–3060.
- Adler, P.B., Leiker, J. & Levine, J.M. (2009) Direct and indirect effects of climate change on a prairie plant community. *PLoS ONE*, **4**, e6887.
- Antoninka, A., Wolf, J.E., Bowker, M., Classen, A.T. & Johnson, N.C. (2009) Linking above- and belowground responses to global change at community and ecosystem scales. *Global Change Biology*, **15**, 914–929.
- Bell, K.L. & Bliss, L.C. (1979) Autecology of *Kobresia bellardii*: why winter snow accumulation limits local distribution. *Ecological Monographs*, **49**, 377–402.
- Belshe, E.F., Schuur, E.A.G. & Bolker, B.M. (2013) Tundra ecosystems observed to be CO₂ sources due to differential amplification of the carbon cycle. *Ecology Letters*, **16**, 1307–1315.
- Bowman, W.D., Theodose, T.A., Schardt, J.C. & Conant, R.T. (1993) Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology*, **74**, 2085–2097.
- Bowman, W.D., Steltzer, H., Rosenstiel, T.N., Cleveland, C.C. & Meier, C.L. (2004) Litter effects of two co-occurring alpine species on plant growth, microbial activity and immobilization of nitrogen. *Oikos*, **104**, 336–344.
- Bowman, W.D., Gartner, J.R., Holland, K. & Wiedermann, M. (2006) Nitrogen critical loads for alpine vegetation and terrestrial ecosystem response: are we there yet? *Ecological Applications*, **16**, 1183–1193.
- Brookes, P.C., Landman, A., Pruden, G. & Jenkinson, D.S. (1985) Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biology & Biochemistry*, **17**, 837–842.
- Brooks, P.D., Williams, M.W. & Schmidt, S.K. (1995) Snowpack controls on soil nitrogen dynamics in the Colorado alpine. *Biogeochemistry of Seasonally Snow-Covered Catchments (Proceedings of a Boulder Symposium, July 1995)*, IAHS Publ. no. **228**, 283–292.
- Brooks, P., Williams, M. & Schmidt, S. (1998) Inorganic nitrogen and microbial biomass dynamics before and during spring snowmelt. *Biogeochemistry*, **43**, 1–15.
- Cain, N. (2010) Recent hydrologic change in a Colorado alpine basin: an indicator of permafrost thaw? *Annals of Glaciology*, **51**, 130–134.
- Callaghan, T.V., Tweedie, C.E., Akerman, J., Andrews, C., Bergstedt, J., Butler, M.G. *et al.* (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.
- Carlson, B., Randin, C., Boulangeat, I., Lavergne, S., Thuiller, W. & Choler, P. (2013) Working toward integrated models of alpine plant distribution. *Alpine Botany*, **123**, 41–53.
- Chapin, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694–711.
- Clark, C.M., Cleland, E.E., Collins, S.L., Fargione, J.E., Gough, L., Gross, K.L., Pennings, S.C., Suding, K.N. & Grace, J.B. (2007) Environmental and plant community determinants of species loss following nitrogen enrichment. *Ecology Letters*, **10**, 596–607.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.
- Dentener, F., Drevet, J., Lamarque, J.F., Bey, I., Eickhout, B., Fiore, A.M. *et al.* (2006) Nitrogen and sulfur deposition on regional and global scales: a multimodel evaluation. *Global Biogeochemical Cycles*, **20**, Gb4003.
- Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Björkman, A.D., Callaghan, T.V. *et al.* (2012) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters*, **15**, 164–175.
- Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araújo, M.B. *et al.* (2011) 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, **17**, 2330–2341.
- Eno, C.F. (1960) Nitrate production in the field by incubating the soil in polyethylene bags. *Soil Science Society of America Journal*, **24**, 277–279.
- Farrer, E.C., Herman, D.J., Franzova, E., Pham, T. & Suding, K.N. (2013) Nitrogen deposition, plant carbon allocation, and soil microbes: changing interactions due to enrichment. *American Journal of Botany*, **100**, 1458–1470.
- Farrer, E.C., Ashton, I.W., Knape, J. & Suding, K.N. (2014a) Separating direct and indirect effects of global change: a population dynamic modeling approach using readily available field data. *Global Change Biology*, **20**, 1238–1250.
- Farrer, E.C., Ashton, I.W., Spasojevic, M.J., Fu, S., Gonzalez, D.J.X. & Suding, K.N. (2014b) Data from: indirect effects of global change accumulate to alter plant diversity but not ecosystem function in alpine tundra. *Dryad Digital Repository*, doi: 10.5061/dryad.kk61p.
- Fisk, M.C. & Schmidt, S.K. (1996) Microbial responses to nitrogen additions in alpine tundra soil. *Soil Biology & Biochemistry*, **28**, 751–755.
- Fisk, M.C., Schmidt, S.K. & Seastedt, T.R. (1998) Topographic patterns of above- and belowground production and nitrogen cycling in Alpine tundra. *Ecology*, **79**, 2253–2266.
- Frank, T.D. & Isard, S.A. (1986) Alpine vegetation classification using high-resolution aerial imagery and topoclimatic index values. *Photogrammetric Engineering and Remote Sensing*, **52**, 381–388.
- Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z.C., Freney, J.R., Martinelli, L.A., Seitzinger, S.P. & Sutton, M.A. (2008) Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science*, **320**, 889–892.
- Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010) A framework for community interactions under climate change. *Trends in Ecology & Evolution*, **25**, 325–331.
- Gottfried, M., Hantel, M., Maurer, C., Toechterle, R., Pauli, H. & Grabherr, G. (2011) Coincidence of the alpine–nival ecotone with the summer snowline. *Environmental Research Letters*, **6**, 014013.
- Grace, J.B. (2006) *Structural Equation Modeling and Natural Systems*. Cambridge University Press, Cambridge, UK.
- Grace, J.B. & Pugsek, B.H. (1997) A structural equation model of plant species richness and its application to a coastal wetland. *The American Naturalist*, **149**, 436–460.
- Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.
- Harsch, M.A., Hulme, P.E., McGlone, M.S. & Duncan, R.P. (2009) Are tree-lines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, **12**, 1040–1049.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- IPCC (2007) Climate change 2007: synthesis report. *Contribution of Working Groups I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Core Writing Team, R.K. Pachauri & A. Reisinger), pp. 104. IPCC, Geneva, Switzerland.
- Kardol, P., Company, C.E., Souza, L., Norby, R.J., Weltzin, J.F. & Classen, A.T. (2010a) Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. *Global Change Biology*, **16**, 2676–2687.
- Kardol, P., Cregger, M.A., Company, C.E. & Classen, A.T. (2010b) Soil ecosystem functioning under climate change: plant species and community effects. *Ecology*, **91**, 767–781.
- Keddy, P.A. (2001) *Competition*. Kluwer Academic Publishers, Dordrecht.
- Kikvidze, Z., Pugnaire, F.I., Brooker, R.W., Choler, P., Lortie, C.J., Michalet, R. & Callaway, R.M. (2005) Linking patterns and processes in alpine plant communities: a global study. *Ecology*, **86**, 1395–1400.
- Klanderud, K. (2005) Climate change effects on species interactions in an alpine plant community. *Journal of Ecology*, **93**, 127–137.
- Kline, R.B. (2010) *Principles and Practice of Structural Equation Modeling*. Guilford Press, New York, NY.
- Levine, J.M., McEachern, A.K. & Cowan, C. (2010) Do competitors modulate rare plant response to precipitation change? *Ecology*, **91**, 130–140.
- Litaor, M.I., Williams, M. & Seastedt, T.R. (2008) Topographic controls on snow distribution, soil moisture, and species diversity of herbaceous alpine vegetation, Niwot Ridge, Colorado. *Journal of Geophysical Research: Biogeosciences*, **113**, G02008.

- Matson, P., Lohse, K.A. & Hall, S.J. (2002) The globalization of nitrogen deposition: consequences for terrestrial ecosystems. *Ambio*, **31**, 113–119.
- McCune, B. & Grace, J.B. (2002) *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, OR.
- McGuire, C.R., Nufio, C.S.R., Bowers, M.D. & Guralnick, R.P. (2012) Elevation-dependent temperature trends in the rocky mountain front range: changes over a 56- and 20-year record. *PLoS ONE*, **7**, e44370.
- McNulty, S.G. & Aber, J.D. (1993) Effects of chronic nitrogen additions on nitrogen cycling in a high-elevation spruce-fir stand. *Canadian Journal of Forest Research*, **23**, 1252–1263.
- Miller, A. & Bowman, W. (2003) Alpine plants show species-level differences in the uptake of organic and inorganic nitrogen. *Plant and Soil*, **250**, 283–292.
- Mladenov, N., Williams, M.W., Schmidt, S.K. & Cawley, K. (2012) Atmospheric deposition as a source of carbon and nutrients to an alpine catchment of the Colorado Rocky mountains. *Biogeosciences*, **9**, 3337–3355.
- Natali, S.M., Schuur, E.A.G., Trucco, C., Hicks Pries, C.E., Crummer, K.G. & Baron Lopez, A.F. (2011) Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra. *Global Change Biology*, **17**, 1394–1407.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2013) *nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-109* available at <http://CRAN.R-project.org/package=nlme>.
- R Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Robertson, G.P., Coleman, D.C., Bledsoe, C.S. & Sollins, P. (1999) *Standard Soil Methods for Long-Term Ecological Research*. Oxford University Press, New York, NY, USA.
- Rossee, Y. (2012) lavaan: an R package for structural equation modeling. *Journal of Statistical Software*, **48**, 1–36.
- Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J., Gurevitch, J. & Gcte, N. (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543–562.
- Scherrer, D. & Körner, C. (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, **38**, 406–416.
- Schimel, J.P., Bilbrough, C. & Welker, J.A. (2004) Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology & Biochemistry*, **36**, 217–227.
- Seastedt, T.R. & Vaccaro, L. (2001) Plant species richness, productivity, and nitrogen and phosphorus limitations across a snowpack gradient in alpine tundra, Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research*, **33**, 100–106.
- Shaver, G.R., Canadell, J., Chapin, F.S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L. & Rustad, L. (2000) Global warming and terrestrial ecosystems: a conceptual framework for analysis. *BioScience*, **50**, 871–882.
- Shaver, G.R., Bret-Harte, S.M., Jones, M.H., Johnstone, J., Gough, L., Laundre, J. & Chapin, F.S. (2001) Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology*, **82**, 3163–3181.
- Smith, M.D., Knapp, A.K. & Collins, S.L. (2009) A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, **90**, 3279–3289.
- Spasojevic, M.J., Bowman, W.D., Humphries, H.C., Seastedt, T.R. & Suding, K.N. (2013) Changes in alpine vegetation over 21 years: are patterns across a heterogeneous landscape consistent with predictions? *Ecosphere*, **4**, art117.
- Spasojevic, M.J., Grace, J.B., Harrison, S. & Damschen, E.I. (2014) Functional diversity supports the physiological tolerance hypothesis for plant species richness along climatic gradients. *Journal of Ecology*, **102**, 447–455.
- Steltzer, H. & Bowman, W.D. (1998) Differential influence of plant species on soil nitrogen transformations within moist meadow Alpine tundra. *Ecosystems*, **1**, 464–474.
- Steltzer, H. & Bowman, W. (2005) Litter N retention over winter for a low and a high phenolic species in the alpine tundra. *Plant and Soil*, **275**, 361–370.
- Stevens, C.J., Dise, N.B., Mountford, J.O. & Gowing, D.J. (2004) Impact of nitrogen deposition on the species richness of grasslands. *Science*, **303**, 1876–1879.
- Suding, K.N., Larson, J.R., Thorsos, E., Steltzer, H. & Bowman, W.D. (2004) Species effects on resource supply rates: do they influence competitive interactions? *Plant Ecology*, **175**, 47–58.
- Suding, K.N., Ashton, I.W., Bechtold, H., Bowman, W.D., Mobley, M.L. & Winkelman, R. (2008) Plant and microbe contribution to community resilience in a directionally changing environment. *Ecological Monographs*, **78**, 313–329.
- Suttle, K.B., Thomsen, M.A. & Power, M.E. (2007) Species interactions reverse grassland responses to changing climate. *Science*, **315**, 640–642.
- Theodose, T.A. & Bowman, W.D. (1997) Nutrient availability, plant abundance, and species diversity in two alpine tundra communities. *Ecology*, **78**, 1861–1872.
- Theodose, T.A., Jaeger, C.H., Bowman, W.D. & Schardt, J.C. (1996) Uptake and allocation of 15N in alpine plants: implications for the importance of competitive ability in predicting community structure in a stressful environment. *Oikos*, **75**, 59–66.
- Treseder, K.K. (2008) Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies. *Ecology Letters*, **11**, 1111–1120.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.
- Wahren, C.H.A., Walker, M.D. & Bret-Harte, M.S. (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, **11**, 537–552.
- Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M. et al. (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 1342–1346.
- Walther, G.-R. (2010) Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 2019–2024.
- Williams, M.W. & Tonnessen, K.A. (2000) Critical loads for inorganic nitrogen deposition in the Colorado Front Range, USA. *Ecological Applications*, **10**, 1648–1665.
- Wipf, S. & Rixen, C. (2010) A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Research*, **29**, 95–109.

Received 13 June 2014; accepted 15 December 2014

Handling Editor: Sandra Lavorel

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. ANOVA results showing the effect of global change treatments on ecosystem and plant community properties.

Figure S1. Mean summer temperatures, N deposition, summer precipitation and winter precipitation at Niwot Ridge over the length of the experiment.

Figure S2. Initial form of the path analysis models.

Figure S3. Treatment effects on evenness.

Figure S4. Path diagram of environment, dominant species, and evenness over time.

Figure S5. Magnitude of direct and indirect effects of environmental change on evenness over time.