Ecol Res (2016) 31: 935–945
DOI 10.1007/s11284-016-1403-6

ORIGINAL ARTICLE

**Arshad Ali · Ulf Molau · Yang Bai ·
Annika K. Jägerbrand · Juha M. Alatalo**

Diversity-productivity dependent resistance of an alpine plant community to different climate change scenarios

Received: 15 July 2016 / Accepted: 29 September 2016 / Published online: 6 October 2016

Abstract Here we report from a experiment imposing different warming scenarios [control with ambient temperature, constant level of moderate warming for 3 years, stepwise increase in warming for 3 years, and one season of high level warming (pulse) simulating an extreme summer event] on an alpine ecosystem to study the impact on species diversity–biomass relationship, and community resistance in terms of biomass production. Multiple linear mixed models indicate that experimental years had stronger influence on biomass than warming scenarios and species diversity. Species diversity and biomass had almost humpback relationships under different warming scenarios over different experimental years. There was generally a negative diversity–biomass relationship, implying that a positive diversity–biomass relationship was not the case. The application of different warming scenarios did not change this tendency. The change in community resistance to all warming scenarios was generally negatively correlated with increasing species diversity, the strength of the correlation varying both between treatments and between years within treatments. The strong effect of experimental years was consistent with the notion that niche complementarity effects increase over time, and hence, higher biomass productivity over experimental years. The strongest negative relationship was found in the first year of the pulse treatment, indicating that the community had weak resistance to an extreme event of one season of abnormally warm climate. Biomass production started recovering during the two subsequent years. Contrasting biomass-related resistance emerged in the different treatments, indicating that micro sites within the same plant community may differ in their resistance to different warming scenarios.

Keywords Biomass · Climate variability · Community resistance · Extreme climatic events · Species diversity

Introduction

The increasing loss of global biodiversity has highlighted the question of the functional importance of diversity in ecosystems (Loreau 2000). Another long-term consideration is the extent to which the relationship between diversity and productivity can stabilise ecosystems in the face of climate change (Loreau 1998, 2000; Hooper et al. 2005). The resistance of a plant community to perturbation is a vital factor for determination of ecosystem stability and productivity (Pimm 1984; Pfisterer and Schmid 2002). Productivity, measured as biomass, has been recognised as one of the basic ecosystem processes (Huston 1997; Wilsey and Potvin 2000) and is an important variable in response to perturbation. Experimental warming can be expected to increase biomass production in Arctic and Alpine Tundra (Arft et al. 1999: Jonasson et al. 1999), but there are also contrasting results (Press et al. 1998; Carlyle et al. 2013).

A. Ali
School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China

A. Ali
Forest Ecosystem Research and Observation Station in Putuo Island, Zhoushan 316100 Zhejiang, China

A. Ali
Tiantong National Forest Ecosystem Observation and Research Station, Ningbo 315114 Zhejiang, China

U. Molau
Department of Biological and Environmental Sciences, University of Gothenburg, PO Box 461, 405 30 Gothenburg, Sweden

Y. Bai
Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla 666303 Yunnan, China

A. K. Jägerbrand
VTI, Swedish National Road and Transport Research Institute, Box 55685, 102 15 Stockholm, Sweden

J. M. Alatalo (✉)
Department of Biological and Environmental Sciences, College of Arts and Sciences, Qatar University, P.O. Box 2713, Doha, Qatar
E-mail: jalatalo@qu.edu.qa

However, the relationship between diversity and biomass can vary between regions, as revealed in a study across 295 grasslands in Germany (Klaus et al. 2013).

In alpine plant communities, changes in environmental conditions may cause large variations in productivity and subsequent species interactions and community stability (Klanderud and Totland 2008; Alatalo et al. 2014b). For example, timing of snowmelt influences the spatial distribution of species richness and abundance (Domènech et al. 2014). These alpine and tundra ecosystems are highly variable in productivity, and primary production can range between 10 g m^{-2} per year in polar deserts to 1000 g m^{-2} per year in willow shrublands (Virtanen et al. 2013). A recent study involving systematic sampling of 27 sites across the Eurasian tundra biome tested two main theories on the relationship between diversity and productivity, namely the productivity-species pool hypothesis, which predicts a positive productivity-species richness relationship, and the productivity-interaction hypothesis, which predicts a humpbacked productivity-species richness relationship. That study found general support for the latter (Virtanen et al. 2013). A similar humpbacked relationship between diversity and biomass was found in a study using data from south-eastern Alps (Austria, Italy and Slovenia) (Poldini et al. 2011). There is also some experimental support for diversity peaking in mid-productive alpine tundra systems (Alatalo et al. 2014b). In general, after the humpbacked relationship, a positive productivity–diversity relationship seems to be the next most common pattern (Mittelbach et al. 2001).

Climate change is generally assumed to be one of the most important factors driving changes in biodiversity. Climate change is predicted to impact on a number of ecosystems, increasing the risk of extinction of many rare and protected plants (Wu et al. 2014; Zhang et al. 2014). The importance of climate variability is especially true in ecosystems with low temperatures, such as polar and high alpine areas. These are thought to be especially vulnerable to climate change as they are predicted to experience a very rapid and relatively large increase in temperature (IPCC 2014). This will most likely cause species losses in the near future or cause shifts in dominance structures (Sun et al. 2011; Kravtsova and Loshkareva 2013; Zhao et al. 2013). Furthermore, studies have shown that climate change can also alter species interactions within a plant community (Bret-Harte et al. 2004; Klanderud and Totland 2005), and that the responses can be non-linear over time (Alatalo and Little 2014; Alatalo et al. 2015).

The majority of experimental studies to date have applied open-top chambers (OTCs) which give a constant level of warming. This is not the most realistic simulation, as climate change is thought to increase climate variability, giving more frequent and extreme climate events (IPCC 2007). At present there are very few experimental studies that have applied different warming scenarios in alpine and tundra ecosystems (Jonasson et al. 1999; Marchand et al. 2005, 2006a; b; Alatalo et al. 2014a, 2016). None of these has examined the impact of different climate change scenarios on the relationship between species diversity and productivity (biomass), or the role of the diversity–productivity relationship for community resistance. A number of experimental studies on grasslands have found that resistance to drought perturbations is related to species richness (Mulder et al. 2001; Pfisterer and Schmid 2002). However, this is not always the case, e.g. an experimental study on grassland examining the role of species diversity for biomass production and drought resistance found no support for the diversity resistance hypothesis or any correlation between species diversity and biomass production (Wang et al. 2007). Instead, it found that experimental plots with lower biomass were more resistant to drought than plots with higher biomass (Wang et al. 2007). Consequently, we hypothesize that resistance of plant communities in terms of species diversity—biomass relationship performs better or similar under warming scenarios than natural environment in an alpine ecosystem.

In the present study, we aimed to distinguish between the impacts of different climate change scenarios on the relationship between species diversity and productivity (biomass) and their role for plant community resistance. We have previously reported the impact of climate change on community structure, functional groups and species-specific responses of bryophytes and lichens (Alatalo et al. 2014a). Specific objectives in the present study were to determine: (1) the relationship between species diversity and productivity, measured as aboveground biomass, and the response to different warming scenarios; (2) whether community resistance of biomass production to warming depends on species diversity and/or productivity.

Methods

Study area and vegetation

This study was conducted at the Latnjajaure Field Station (LFS) in the Latnjavagge valley in northern Sweden (68°21′N, 18°29′E, elevation of 1000 m asl.). The experiment was conducted in a rich meadow alpine community (Alatalo et al. 2014a) around 300-m southeast of the LFS, on a gentle northwest-facing slope with an abundant groundwater supply. The vegetation in the valley comprises a wide range of communities, and the environment varies from dry to wet and from acidic to base-rich.

The valley is covered with snow for most of the year and the climate is characterised by cool summers and relatively mild, snow-rich winters. The site is classified as subarctic, with mean annual temperature of −2.0 to −2.7 °C (data for 1993–1999) and an annual minimum of −27.3 to −21.7 °C. July is the warmest month, with mean temperature ranging from +5.2 °C (1995) to +8.0 °C (1997). Mean annual precipitation ranges from

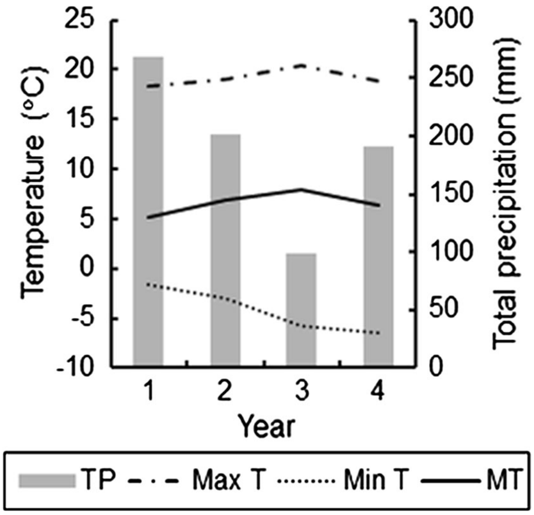

Fig. 1 Climate data for the Latnjajaure Field Station during summer (1 June–31 August) in the period 1995–1998. *TP* total precipitation, *Max T* maximum temperature, *Min T* minimum temperature, *MT* mean temperature

a low of 605 mm (1996) to a high of 990 mm (1993), with the mean for the period 1990–1999 being 808 mm. For summer climate data for the period 1995–1998, see Fig. 1.

Experimental design

In July 1995, four blocks, each with four 1 m × 1 m plots, were marked out and numbered. All blocks and plots were as similar as possible with respect to the floristic composition and edaphic conditions. At the end of the 1995 season, the subsequent treatments were distributed within the blocks using a simple lottery. Within each of the four blocks, four different kinds of warming: (1) control, (2) standard OTC warming, (3) press warming (annual stepwise increase of warming) and (4) pulse warming (a initial single summer of high level of warming), were implemented starting in June 1996 (Alatalo et al. 2014a). The OTC experiments were configured according to hexagonal polycarbonate chambers with a base diameter of 1 m (Marion et al. 1997), which were fixed to the ground from early June 1996 to late August 1998. In the press warming manipulation, an OTC was installed in the plot on 10 cm-high pylons throughout the 1996 season; this OTC was affixed to the ground during the 1997 season and a polyethylene lid was used throughout the 1998 season, thus increasing the experimental warming each year. In the pulse treatment, a closed-top chamber (CTC; a standard OTC with a polyethylene lid as in the press warming case) was installed in the plot during the 1996 season only and was removed in late August of the same year (Alatalo et al. 2014a).

The different treatments resulted in different warming levels. The temperature increase using the standard OTC remained at an average of 1.87 ± 0.25 °C (mean ± SE, $n = 7$ runs) above the ambient surface temperature in the adjacent control plots (Alatalo et al. 2014a). At the same time, the ventilated OTCs in the first treatment year in the stepwise warming treatment caused a more moderate increase of 1.00 ± 0.42 °C ($n = 2$), whereas the CTC treatment in the stepwise warming (year 3) and pulse treatments caused a greater increase of 3.54 ± 0.24 °C ($n = 3$). Thus, the treatments generated three different warming scenarios for comparison (Alatalo et al. 2014a). The different experimental warming treatments can also be illustrated as three temperature units of ~1 °C each, where the OTCs (2 units) and press warming (1, 2 and 3 units for the different years) had an equal cumulative sum (total of six units) after 3 years of treatment. However, the single-year pulse treatment (3 units) only had three units above the control for the same period (Alatalo et al. 2014a).

The experiment was designed using the BACI (before-after-control-impact) approach, and all plots were mapped in the first year (1995) prior to any manipulation (Underwood 1994). The experiment was ended after the final data collection period in August 1998.

Measurements of vegetation structure

All 16 plots were mapped in early August of each year (1995–1998) in the same sequence, such that each individual plot was mapped on roughly the same date every year. For mapping, a 1 m × 1 m grid frame was used. At each of the 100 grid points, the specific identity of the top-most canopy (if present) and bottom-most layer species (if present) were noted, together with the height (1 cm accuracy) from the ground to the point of interception (canopy species only). In the square 1 m × 1 m control plots, there were always 100 sampling points for the canopy and 96 points for the bottom layer, where four points were sacrificed for orientation screws with 5 mm head diameter, which enabled accurate re-installation of the grid frame each year. This method has been shown to be accurate in detecting changes in tundra vegetation (May and Hollister 2012). Due to their hexagonal shape, the OTCs reduced the number of points per plot to 87–94. Solifluction at the study site was very low and totalled less than 1 cm in horizontal distance over the 4 years of the study.

Variables used in analyses

The aboveground biomass of the various functional groups of vascular plants (Table 1) was estimated using the life form-specific allometric equations developed for the site (Table 2, Karlsson 1998; Molau 2010). The total aboveground biomass of a plot was estimated through summation of biomass of all life forms present in the plot.

Table 1 Mean estimated aboveground biomass (g m^{-2}) of different functional plant groups in different years and treatments

Functional groups	1995				1996				1997				1998			
	Ctrl	OTC	Press	Pulse	Ctrl	OTC	Press	Pulse	Ctrl	OTC	Press	Pulse	Ctrl	OTC	Press	Pulse
Acrocarp	93	97	83	83	88	90	78	96	71	84	68	91	82	99	67	113
Cushion	13	3	7	11	16	3	6	15	21	7	8	18	22	8	8	14
Deciduous	17	14	20	24	19	18	25	38	26	24	33	46	29	26	42	34
Evergreen	72	41	81	45	89	62	102	84	110	99	139	95	137	119	202	107
Graminoids	30	32	27	32	23	31	23	37	19	26	20	27	21	35	40	19
Herbs	4	3	2	6	3	4	3	10	6	7	4	10	8	8	12	16
Lichens	13	11	19	9	13	14	19	12	13	12	17	9	11	8	15	8
Pleurocarp	58	77	44	71	65	80	55	75	71	82	50	89	69	75	45	72
Sphagnum	70	44	95	26	71	49	99	28	81	50	106	30	87	58	127	37

Acrocarp mosses, vascular cushion plants, deciduous dwarf shrubs, evergreen dwarf shrubs, gaminoids, herbs, lichens, pleurocarp mosses, *Sphagnum* spp

Ctrl control, *OTC* open-top chamber

Table 2 Regression data used to calculate aboveground biomass based on percentage of cover (bottom layer) and volume (canopy layer). Modified from Karlsson (1998) and Molau (2010)

Functional groups	R^2	Equation for regression
Graminoids	0.80	$B = 0.393 \times V$
Herbs	0.35	$B = 0.204 \times V$
Evergreen shrubs	0.86	$B = 1.370 \times V$
Deciduous shrubs	0.53	$B = 1.007 \times V$
Cushion plants	0.82	$B = 2.992 \times C$
Lichens	0.41	$B = 0.785 \times C$
Acrocarp mosses	0.44	$B = 2.973 \times C$
Pleurocarp mosses and liverworths	0.61	$B = 2.787 \times C$
Sphagnum spp.	0.89	$B = 4.252 \times C$

Dry biomass in g m^{-2} (B), cover (C), above ground volume in cm^3 (V)

The Shannon–Wiener biodiversity index was used to quantify species diversity, because it reflects both species evenness and richness (Magurran 2013). Based on relative species abundance, species diversity (H) was calculated for each plot as:

$$H = -\sum_{i=1}^{s} p_i \times \ln p_i \tag{1}$$

where p_i is the relative abundance of the ith species and s is the number of plant species in a plot. The analysis on the Shannon–Wiener index was performed using the "*vegan*" in R 3.2.2 (Oksanen et al. 2013; R Core Team 2015).

As the control plots and treatment plots differed in size (warming treatments decreasing the number of hits), resistance to warming was measured as the ratio of aboveground biomass production between different years (1996, 1997 and 1998) of experimental warming (OTC, press and pulse) and the initial year without warming treatment (Eq. 2).

$$R = ln\left(\frac{B_{warming-year}}{B_{warming-1995}}\right) \tag{2}$$

where warming is control, OTC, press or pulse warming treatment, while year is 1996, 1997 or 1998. The proportional resistance to different warming scenarios was examined as the relationship between community biomass in initial year without warming and biomass in different treatment years. A slope < 1 of the log–log relationship was taken to indicate that resistance to warming is negatively biomass-dependent and a slope > 1 indicated a positive relationship.

Statistical analyses

For statistical analysis, the following steps were conducted. First, we conducted bivariate relationships between observed species diversity and biomass under different warming scenarios over different experimental years, using regression analysis. Specifically, we fit each pair of variables using simple linear regression and multiple linear regressions by adding quadratic and cubic polynomial terms to test for bivariate relationships of species diversity and biomass, by using pooled data from warming scenarios and/or experimental years. Our analyses indicated that multiple linear regressions by adding quadratic and cubic polynomial terms was the best in describing bivariate relationships based on the Akaike information criterion (AIC).

Second, to evaluate how biomass is determined by species diversity, experimental years and warming scenarios, we performed multiple linear mixed models incorporating fixed and random factors (Eq. 3).

$$Y = \mathrm{poly}(X, 3) + \varepsilon \tag{3}$$

where, Y is natural-logarithm transformed biomass (*ln*AGB), poly (X, 3) is the polynomial (linear, quadratic, and cubic terms) of natural-logarithm transformed species diversity (*ln*H), and ε is the random factor(s) i.e. experimental treatments and/or experimental years (grouping variables).

Specifically, we tested the following three multiple linear mixed models, by incorporating polynomial terms (linear, quadratic and cubic) to account for nonlinear effects of species diversity on biomass.

$$ln\text{AGB} \sim (\text{poly}(ln\text{H}, 3)) + (1 + \text{Treatments}|\text{Years}) \quad \text{model (1)}$$
$$ln\text{AGB} \sim (\text{poly}(ln\text{H}, 3)) + \text{Years} + (1|\text{Treatments}) \quad \text{model (2)}$$
$$ln\text{AGB} \sim (\text{poly}(ln\text{H}, 3)) + \text{Treatments} + (1|\text{Years}) \quad \text{model (3)}$$

We calculated the conditional (c) and marginal (m) R^2 for the each multiple linear mixed model following (Nakagawa and Schielzeth 2013). Conditional R^2 (R^2_c) indicates the variance explained by both fixed and random factors, whereas marginal R^2 (R^2_m)indicates the variance explained by fixed factors only. When R^2_m value is close to R^2_c, then most of the variation explained in the biomass is caused by the predictors (fixed factors), rather than by random effect. Linear mixed models were conducted using the "*lme4*" and "*MuMIn*" packages (Bates et al. 2015; Barton 2016) in R 3.2.2 (R Core Team 2015).

Third, we examined the relationship between species diversity (in reference plots) and warming resistance (calculated by Eq. 2) with multiple linear regressions by adding quadratic and cubic polynomial terms, using pooled data from experimental years. In addition, we have also conducted simple linear regression relationship between species diversity (in reference plots) and biomass ratio (calculated by Eq. 2) under each experimental warming scenarios for each experimental year. Species diversity in reference plots refers to the species diversity in the initial year (i.e. 1995) under same warming scenario.

Fourth, we examined the power–law relationship between biomass production under the warming scenario ($\text{B}_{\text{warming}}$) and the biomass production in reference plot ($\text{B}_{\text{reference}}$) with Eq. (4) (Harms et al. 2000). $\text{B}_{\text{reference}}$ is the biomass production in the initial year (i.e. 1995) of the subplot under the same warming scenario.

$$\text{B}_{\text{warming}} = a\text{B}^{b}_{\text{reference}} \tag{4}$$

where a is a constant.

The $\text{B}_{\text{warming}}$–$\text{B}_{\text{reference}}$ relationship was conducted using simple linear regressions of natural-logarithm transformed biomass values. A value of fitted constant b less than 1 was taken to indicate that warming resistance is inversely related to biomass production. Because of the small sampling size ($n = 4$' in case of third and fourth steps of the analyses), correlation coefficients in range 0.00–0.10 were generally considered neutral, 0.11–0.40 weak, 0.41–0.70 moderate and > 0.71 strong. The direction of correlations is highlighted with a negative or positive sign. Although most of the relationships or effects in our study were not significant while the coefficients were high (probably resulted due to small sampling size), the general trends were clear to draw the conclusions.

Prior to the all statistical analyses, Shapiro–Wilk goodness-of-fit test was used to assess the normality for all variables. All numerical variables including biomass and species diversity were natural-logarithm transformed and standardized in order to meet the assumptions of normality and linearity, and to allow comparisons among multiple predictors and models (Zuur et al. 2009). The dataset used in the analyses is provided in Appendix S1.

Results

Relationships between biomass and species diversity under different warming scenarios over different experimental years

When species diversity was considered as a fixed factor, and warming treatments and experimental years as random factors in the linear mixed model (model 1, Table 3), the result indicate that biomass was significantly negatively related to the quadratic term of species diversity ($\beta = -0.24$, $P = 0.013$), but not to the linear

Table 3 Linear mixed models for the relationships between Shannon's species diversity and aboveground biomass under different warming scenarios over different experimental years

Predictors	β	t	P	R^2_m	R^2_c
Model 1 (treatments and years are random factors, while *ln*(H) is a fixed factor					
ln(H1)	−0.15	−1.74	0.087	0.09	0.57
ln(H2)	−0.24	−2.57	**0.013**		
ln(H3)	0.11	1.26	0.214		
Model 2 (treatments is a random factor, while *ln*(H) and years are fixed factors					
ln(H1)	−0.15	−2.01	**0.048**	0.55	0.67
ln(H2)	−0.21	−2.63	**0.011**		
ln(H3)	0.04	0.52	0.605		
Years	0.72	9.52	**< 0.001**		
Model 3 (years is a random factor, while *ln*(H) and treatments are fixed factors					
ln(H1)	−0.15	−1.78	0.080	0.07	0.53
ln(H2)	−0.19	−2.03	**0.046**		
ln(H3)	0.11	1.26	0.211		
Treatments	−0.04	−0.02	0.632		

Standardized regression coefficient (β), t test, P value, conditional (c) and marginal (m) R^2 (R^2_c = both fixed and random effects, and R^2_m = fixed effects only) are given. $P < 0.05$ is shown in bold

H1, H2 and H3 represent the polynomial terms for Shannon's species diversity (H); *ln* = natural-logarithm

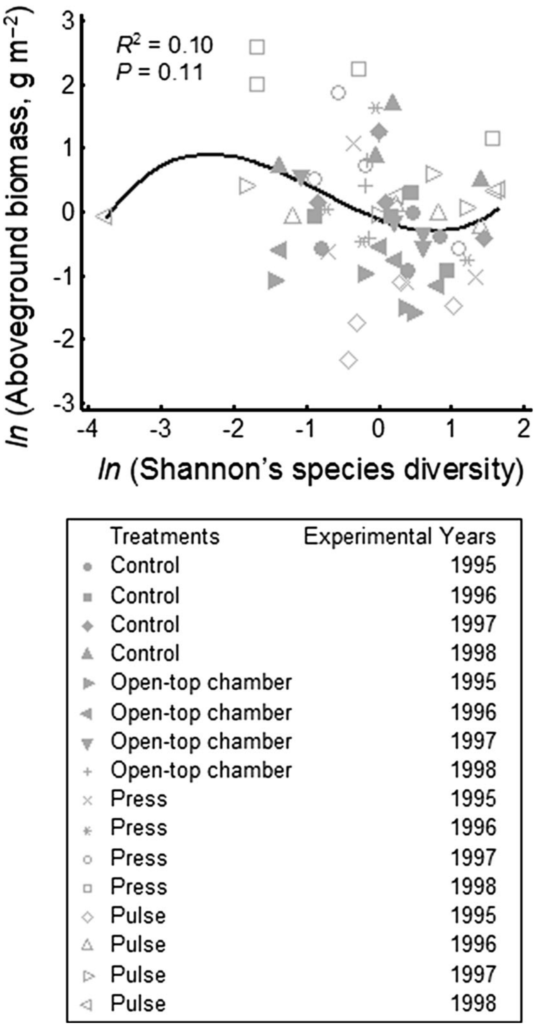

Fig. 2 Relationship between aboveground biomass and Shannon's species diversity. Data from warming scenarios over different experimental years were pooled for, $n = 64$. *Different symbols* represent different warming scenarios, and different colours (*light grey* to *dark grey*) represent different experimental years (1995–1998). Key legend is provided at the end of the graph. The *curve* represents cubic polynomial function ($Y = aX^3 + bX^2 + cX + d$). Both X and Y variables are natural-logarithm (*ln*) transformed

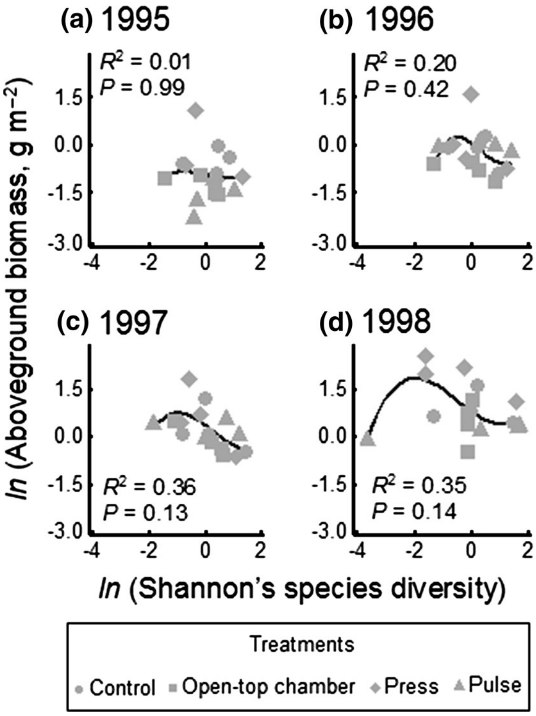

Fig. 3 Relationships between aboveground biomass and Shannon's species diversity over different experimental years, 1995–1998. Experimental years are shown in the *top panel* of the graph. Data from warming scenarios were pooled for each experimental year, $n = 16$. *Different symbols* represent different warming scenarios (key legend is provided at the end of the graph). The *curve* represents cubic polynomial function ($Y = aX^3 + bX^2 + cX + d$). Both X and Y variables are natural-logarithm (*ln*) transformed

term ($\beta = -0.15$, $P = 0.087$), or to the cubic term of species diversity ($\beta = 0.11$, $P = 0.214$). However, species diversity did contributes weakly to biomass ($R^2_m = 0.09$), whereas random factors such as experimental years and warming treatments did contribute strongly ($R^2_c = 0.57$, thus their $R^2_m = 0.48$). We also found that species diversity and biomass had almost humpback relationship, when pooled data from warming treatments and experimental years (Fig. 2).

When species diversity and experimental years were considered as fixed factors, and warming treatments as a random factor (model 2, Table 3), the result indicated that biomass was significantly positively related to experimental years ($\beta = 0.72$, $P < 0.001$), the quadratic ($\beta = -0.21$, $P = 0.011$) and linear ($\beta = -0.15$, $P = 0.048$) terms of species diversity, but not to the cubic term of species diversity ($\beta = 0.04$, $P = 0.60$). Fixed factors such as species diversity and experimental years did contribute strongly to biomass ($R^2_m = 0.55$), whereas random factor such as warming treatments did contribute weakly ($R^2_c = 0.67$, thus its $R^2_{\mathrm{m}} = 0.12$). This result indicate that experimental years had stronger influence on biomass than warming treatments and species diversity. We also found that species diversity and biomass had almost humpback relationships over different experimental years, when pooled data from warming treatments (Fig. 3).

By considering species diversity and warming treatments as fixed factors, and experimental years as a random factor in the linear mixed model (model 3, Table 3), the result showed that biomass was significantly negatively related to the quadratic term of species diversity ($\beta = -0.19$, $P = 0.046$), but not to the linear term ($\beta = -0.15$, $P = 0.080$), cubic term of species diversity ($\beta = 0.11$, $P = 0.21$), or warming treatments ($\beta = -0.04$, $P = 0.63$). However, fixed factors such as species diversity and warming treatments did contribute weakly to biomass ($R^2_m = 0.07$), whereas random factor such as experimental years did contributes strongly ($R^2_c = 0.53$, thus its $R^2_m = 0.46$). This result again indicate that experimental years had stronger influence

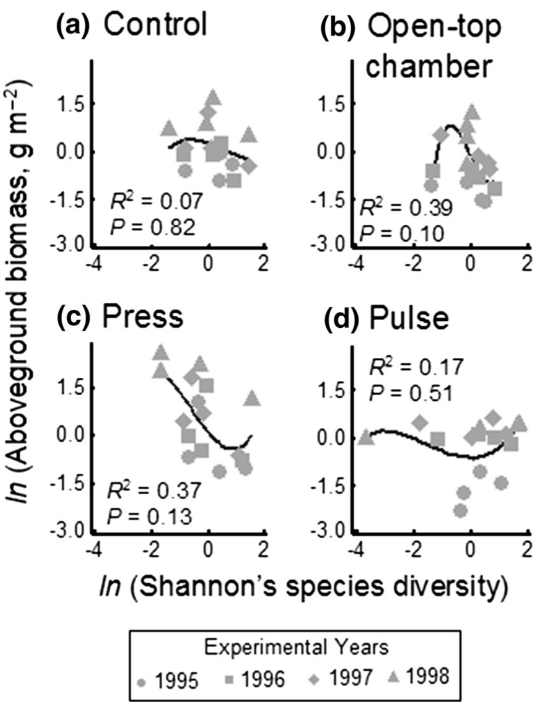

Fig. 4 Relationships between aboveground biomass and Shannon's species diversity under different experimental warming scenarios. Experimental warming scenarios are shown in the *top panel* of the graph. Data from experimental years were pooled for each experimental warming scenario, $n = 16$. *Different symbols* represent different experimental years (key legend is provided at the end of the graph). The *curve* represents cubic polynomial function ($Y = aX^3 + bX^2 + cX + d$). Both X and Y variables are natural-logarithm (*ln*) transformed

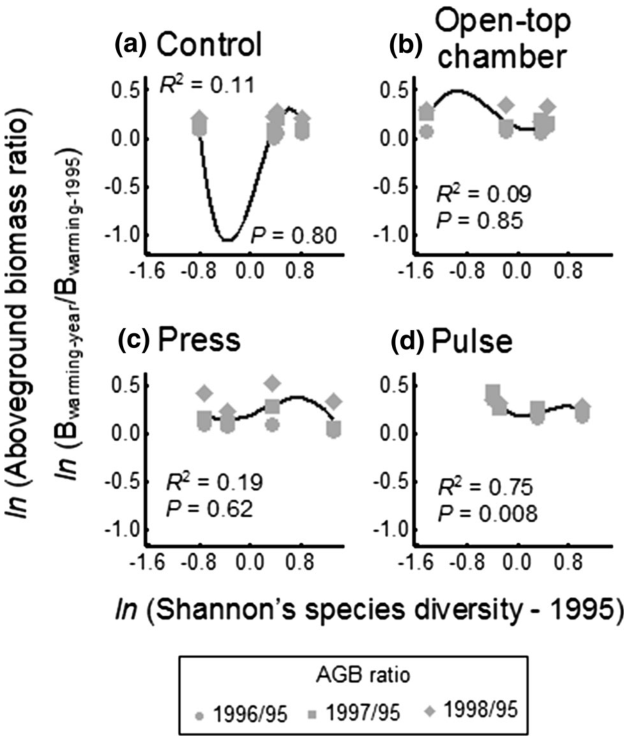

Fig. 5 Relationships between community proportional resistance of biomass production and Shannon's species diversity (initial year) to different experimental warming scenarios. Data from experimental years were pooled for each experimental warming scenario, $n = 12$. *Different symbols* represent aboveground biomass ratio over different experimental years (key legend is provided at the end of the graph). The *curve* represents cubic polynomial function ($Y = aX^3 + bX^2 + cX + d$). Both X and Y variables are natural-logarithm (*ln*) transformed

on biomass than warming treatments and species diversity. We also found that species diversity and biomass had almost humpback relationships under different warming treatments particularly under OTC treatment, when pooling data from experimental years (Fig. 4).

Diversity-dependent resistance to warming scenarios over different experimental years

Plant community resistance to natural climate variability (control) in terms of biomass production [$ln(B_{\text{control-year}}/B_{\text{control-1995}})$] showed V-shaped trend with species diversity under control environment of the initial year ($lnH_{\text{control-1995}}$), when biomass ratio data was pooled across experimental years (Fig. 5a). More specifically, we found that biomass ratio at each experimental year, i.e. $ln(B_{\text{control-1996}}/B_{\text{control-1995}})$, $ln(B_{\text{control-1997}}/B_{\text{control-1995}})$ and $ln(B_{\text{control-1998}}/B_{\text{control-1995}})$, varied from moderately negative ($r = -0.58$) to neutral ($r = -0.04$), to weakly positive ($r = 0.24$) with species diversity of the reference year ($lnH_{\text{warming-1995}}$) (Table 4).

In contrast, we found almost humpback relationship between biomass production [$ln(B_{\text{warming-year}}/B_{\text{warming-1995}})$] and species diversity of the initial year ($lnH_{\text{warming-1995}}$) under each of OTC (Fig. 5b) and press treatments (Fig. 5c). There were no clear patterns in the resistance of biomass production correlated with the species diversity in OTC of the initial year without experimental warming, against the constant level of warming applied by OTC from 1995 to 1996, 1995 to 1997, and 1995 to 1998. The diversity–resistance relationship varied from weakly positive in 1996 ($r = 0.25$) to strongly negative in 1997 ($r = -0.73$) and weakly negative in 1998 ($r = -0.28$; Table 4). The responses in diversity–resistance relationship of biomass production in the press warming treatment compared with the species diversity for the initial year without experimental warming, i.e. $lnH_{\text{press-1995}}$, increased with the level of warming applied. As the experimental warming increased between 1996 and 1998, the diversity–resistance relationship changed from strongly negative in 1996 ($r = -0.80$) to moderately negative in 1997 ($r = -0.30$) to neutral in 1998 ($r = 0.10$; Table 4).

In contrast, we found almost U-shaped or unimodal pattern between biomass production [$ln(B_{\text{pulse-year}}/B_{\text{control-1995}})$] and species diversity of the initial year ($lnH_{\text{pulse-1995}}$) under pulse treatment (Fig. 5d).The resistance of biomass production in the pulse warming treatment (with one season of pulse warming applied in 1996), compared with the species diversity of the initial year without

Table 4 Shannon's species diversity and biomass-dependent resistance of plant community to different warming scenarios over different experimental years ($n = 4$)

(a) Diversity-dependent resistance	*r*	(b) Biomass-dependent resistance	*r*
$\mathit{ln}(B_{\text{Ctrl-1996}}/B_{\text{Ctrl-1995}}) = 0.05 - 0.03\ \mathit{ln}(H_{\text{Ctrl-1995}})$	−0.58	$\mathit{ln}(B_{\text{Ctrl-1996}}) = -1.52 + 1.27\ \mathit{ln}(B_{\text{Ctrl-1995}})$	0.94
$\mathit{ln}(B_{\text{Ctrl-1997}}/B_{\text{Ctrl-1995}}) = 0.12 - 0.003\ \mathit{ln}(H_{\text{Ctrl-1995}})$	−0.04	$\mathit{ln}(B_{\text{Ctrl-1997}}) = -4.41 + 1.77\ \mathit{ln}(B_{\text{Ctrl-1995}})$	**0.96**
$\mathit{ln}(B_{\text{Ctrl-1998}}/B_{\text{Ctrl-1995}}) = 0.23 + 0.01\ \mathit{ln}(H_{\text{Ctrl-1995}})$	0.24	$\mathit{ln}(B_{\text{Ctrl-1998}}) = -1.46 + 1.29\ \mathit{ln}(B_{\text{Ctrl-1995}})$	0.94
$\mathit{ln}(B_{\text{OTC-1996}}/B_{\text{OTC-1995}}) = 0.08 + 0.01\ \mathit{ln}(H_{\text{OTC-1995}})$	0.25	$\mathit{ln}(B_{\text{OTC-1996}}) = 1.86 + 0.69\ \mathit{ln}(B_{\text{OTC-1995}})$	0.74
$\mathit{ln}(B_{\text{OTC-1997}}/B_{\text{OTC-1995}}) = 0.18 - 0.05\ \mathit{ln}(H_{\text{OTC-1995}})$	−0.73	$\mathit{ln}(B_{\text{OTC-1997}}) = -0.37 + 1.10\ \mathit{ln}(B_{\text{OTC-1995}})$	0.70
$\mathit{ln}(B_{\text{OTC-1998}}/B_{\text{OTC-1995}}) = 0.28 - 0.03\ \mathit{ln}(B_{\text{OTC-1995}})$	−0.28	$\mathit{ln}(B_{\text{OTC-1998}}) = -4.24 + 1.78\ \mathit{ln}(B_{\text{OTC-1995}})$	0.79
$\mathit{ln}(B_{\text{press-1996}}/B_{\text{press-1995}}) = 0.09 - 0.03\ \mathit{ln}(H_{\text{press-1995}})$	−0.80	$\mathit{ln}(B_{\text{press-1996}}) = -0.05 + 1.02\ \mathit{ln}(B_{\text{press-1995}})$	**0.99**
$\mathit{ln}(B_{\text{press-1997}}/B_{\text{press-1995}}) = 0.17 - 0.03\ \mathit{ln}(H_{\text{press-1995}})$	−0.30	$\mathit{ln}(B_{\text{press-1997}}) = 1.26 + 0.82\ \mathit{ln}(B_{\text{press-1995}})$	0.83
$\mathit{ln}(B_{\text{press-1998}}/B_{\text{press-1995}}) = 0.39 + 0.01\ \mathit{ln}(H_{\text{press-1995}})$	0.10	$\mathit{ln}(B_{\text{press-1998}}) = 3.99 + 0.39\ \mathit{ln}(B_{\text{press-1995}})$	0.66
$\mathit{ln}(B_{\text{pulse-1996}}/B_{\text{pulse-1995}}) = 0.27 - 0.11\ \mathit{ln}(H_{\text{pulse-1995}})$	−0.82	$\mathit{ln}(B_{\text{pulse-1996}}) = 6.12 - 0.03\ \mathit{ln}(B_{\text{pulse-1995}})$	−0.09
$\mathit{ln}(B_{\text{pulse-1997}}/B_{\text{pulse-1995}}) = 0.33 - 0.09\ \mathit{ln}(H_{\text{pulse-1995}})$	−0.67	$\mathit{ln}(B_{\text{pulse-1997}}) = 5.52 + 0.09\ \mathit{ln}(B_{\text{pulse-1995}})$	0.15
$\mathit{ln}(B_{\text{pulse-1998}}/B_{\text{pulse-1995}}) = 0.31 - 0.05\ \mathit{ln}(H_{\text{pulse-1995}})$	−0.54	$\mathit{ln}(B_{\text{pulse-1998}}) = 4.37 + 0.29\ \mathit{ln}(B_{\text{pulse-1995}})$	0.75

(a) Relationship between community proportional resistance of biomass production and species diversity to warming over experimental years, 1995–1998. (b) Proportional resistance to different warming scenarios, as relationship between community biomass (in initial year without warming) and biomass (in different treatment years). The slope of the log–log relationships was < 1, indicating that resistance to warming is negatively biomass-dependent

ln natural-logarithm, *B* aboveground biomass, *H* Shannon's species diversity, *r* Pearson's correlation coefficient, *Ctrl* control, *OTC* open-top chamber

experimental warming, i.e. $\mathit{ln}H_{\text{pulse-1995}}$, varied from strongly negative in 1996 ($r = -0.82$) to moderately negative in 1997 ($r = -0.67$) to moderately negative in 1998 ($r = -0.54$; Table 4). Thus, the largest impact occurred during the year of the pulse treatment, the impact becoming less pronounced in the two following years after the one summer season of high-level warming.

Biomass-dependent resistance and plant community performance to warming scenarios over different experimental years

We found contrasting patterns between treatments and years. In control plots experiencing natural climate variability, where the relationship for biomass changed between years, the slopes of log–log relationships was >1 in all 3 years (1996–1998), with strong positive Pearson correlation values (ranging from $r = 0.94$ to $r = 0.96$; Table 4).

For the OTC treatment, the slope of log–log relationships in plots experiencing a constant level of experimental warming changed from a negative relationship in 1996 (0.69, the first year with warming applied) to a positive relationship in 1997 (1.10) and 1998 (1.78), with strong positive Pearson correlations (ranging from $r = 0.70$ to $r = 0.79$; Table 4). For the press warming treatment, the slope of log–log relationships in plots changed from a positive relationship in 1996 (1.02, the year with the lowest level of experimental warming applied) to a negative relationship with increasing level of warming (0.82 in 1997 and 0.39 in 1998, with the highest level of warming applied). The corresponding positive Pearson correlation decreased in strength from 0.99 in 1996 to 0.66 in 1998 (Table 4). For the pulse treatment, which imposed a single season of high-level warming in 1996, we found that the slope of log–log relationships was negative in all 3 years, –0.03 in 1996 (the year with pulse warming applied), 0.09 in 1997 and 0.29 in 1998 (with no warming applied). The corresponding Pearson correlation coefficient increased from neutral in 1996 and 1997 ($r = -0.09$ and $r = 0.15$) to a strong positive relationship in 1998 ($r = 0.75$, Table 4).

Discussion

To our knowledge, this is the first experimental study to apply different warming scenarios in an alpine ecosystem to study the impact on the relationship between species diversity and biomass production, and community resistance in terms of biomass production.

While the small sample size did not allow for more detailed study on the effect of diversity on biomass production, the slopes obtained were in general negative. This implies that a positive diversity–biomass relationship was not present. Thus, the results are in line with previous findings on the relationship between diversity and plant biomass production indicating humpbacked relationships in alpine and Arctic areas (Poldini et al. 2011; Virtanen et al. 2013; Alatalo et al. 2014b). The application of different experimental warming scenarios did not change this tendency. Furthermore, the relationships between species diversity and biomass in the initial year (1995) in different warming scenarios were slightly humpbacked. Even when high species diversity is not critical for maintaining ecosystem processes under constant or benign environmental scenarios, it might nevertheless be important for maintaining them under changing scenarios. The insurance hypothesis (Yachi and Loreau 1999) and related hypotheses (Tilman 1996) propose that species diversity provides an "insurance" or a buffer, against environmental changes, because different species respond differently to these changes, leading to more predictable ecosystem properties or functions. In this hypothesis, species that are functionally redundant for biomass at a given time are no longer redundant through time (Loreau 2000). Therefore, the negative relationship between species diversity and biomass in this study, might also be attributed to species redundancy, producing negative interspecific interactions through competition (Walker 1992).

In this study, we found that experimental years compared to species diversity and warming scenarios had strong positive effect on biomass productivity. Generally, it is plausible that biomass productivity is mainly driven by the initial biomass of vegetation. It is suggesting that vegetation quantity (initial biomass) is more important than vegetation quality (e.g., species diversity) because most plants initially present survive during the census, and the more biomass they initially have, the faster they can grow over time (Lohbeck et al. 2015). Therefore, our findings were consistent with the notion that niche complementarity effects increase (linear or non-linear) over time (e.g., experimental years in our study) via species and/or structural diversity of the vegetation (Zhang and Chen 2015; Ali et al. 2016), and hence, higher biomass productivity over experimental years in the alpine plant communities.

While there are no comparable data, previous studies on diversity-dependent drought resistance (Tilman 1996; Huston 1997; Mulder et al. 2001; Pfisterer and Schmid 2002; Wang et al. 2007) have observed that the effect of species diversity on community resistance to drought scenarios can vary. Consistent with the pattern reported for species diversity of herbaceous plants along a gradient of resource supply (Grime 1973), we found almost humpbacked relationship for community resistance in terms of species diversity and biomass production to OTC and press warming over experimental years (Fig. 5). Specifically, we found that change in community resistance of biomass production to all warming scenarios was generally negatively correlated with increasing species diversity, the strength of the correlation varying both between treatments and between years within treatments (Table 4). The strongest negative relationship was found in the first year of the pulse treatment and it decreased in the subsequent 2 years after the treatment, indicating that the community had weak resistance to the treatment simulating the extreme event of one season of abnormally warm climate. However, the biomass production was able to start recovering during the two subsequent years as the negative relationship decreased. In contrast, the stepwise press warming treatment, which applied an increasing level of warming between years, gave a strong negative relationship in the first year of warming (with the lowest level of warming), and a neutral relationship in the last year that experienced a similar level of warming as in the first year of the pulse treatment. Thus this treatment showed the opposite trend to warming compared with the experimental plots receiving the pulse treatment. This indicates that a gradual increase in warming may not be detrimental and that plant communities may be able to adapt to a gradual increase in warming between years. More gradual warming may not be as harmful as an extreme event with an abrupt increase in warming. Furthermore, small-scale heterogeneity in alpine landscapes may offer short-distance migration to refugia for plant species (Opedal et al. 2014). Meanwhile, in the experimental plots experiencing the intermediate level of constant warming (OTCs), the relationship changed from weakly positive to moderately negative.

A previous study on resistance to drought in grasslands found that resistance was higher in communities with lower biomass production than in communities with higher biomass production (Wang et al. 2007). In contrast, we found differing biomass-related resistance in the different treatments, indicating that plant communities may vary in their resistance to different warming scenarios. However, warming and drought can be expected to differ in impact on plant biomass production. While the impact of drought is generally negative, the impact of warming may differ between climate regions. For example, in cold areas such as alpine and polar areas, plants may be temperature limited for growth and thus warming can be expected to have a more positive impact than in regions with warmer climate conditions. Furthermore, different warming scenarios may have different impacts on plant biomass production. Short-term warming with OTCs that apply moderate warming has previously been shown to have only a small impact on biomass production (Press et al. 1998), while a higher level of warming has been shown to have a positive effect on biomass (Jonasson et al. 1999). While not measuring biomass, experiments in Greenland simulating heat waves also found contrasting effects on plant cover (which is positively correlated with biomass in the Arctic), ranging from positive to neutral and negative (Marchand et al. 2005, 2006a; b).

Conclusions

The change in community resistance of biomass production to all warming scenarios in this study was generally negatively correlated with increasing species diversity, the strength of the correlation varying both between treatments and between years within treatments. The strongest negative relationship was found in the first year of the pulse treatment and decreased in the subsequent 2 years after treatment. This indicates that the community had weak resistance to an extreme event of one season of abnormally warm climate. The strong effect of experimental years was consistent with the notion that niche complementarity effects increase (linear or non-linear) over time, and hence, higher biomass productivity over experimental years in the alpine plant communities. However, biomass production was able to start recovering during the two subsequent years as the negative relationship decreased. Furthermore, contrasting biomass-related resistance emerged in the different treatments, indicating that microsites within the same plant community may differ in their resistance to different warming scenarios.

Acknowledgments We thank the staff of Abisko Scientific Research Station for help and hospitality and Vivian Aldén, Björn Aldén and Olga Khitun for assistance in the field. This study was supported by an NFR Grant (B-AA/BU 08424) to Professor Ulf Molau. Constructive comments from two anonymous reviewers helped to substantially improve an earlier version of this manuscript.

References

Alatalo JM, Jägerbrand AK, Molau U (2015) Testing reliability of short-term responses to predict longer-term responses of bryophytes and lichens to environmental change. Ecol Indic 58:77–85. doi:10.1016/j.ecolind.2015.05.050

Alatalo JM, Jägerbrand AK, Molau U (2014a) Climate change and climatic events: community-, functional- and species-level responses of bryophytes and lichens to constant, stepwise, and pulse experimental warming in an alpine tundra. Alp Bot 124:81–91. doi:10.1007/s00035-014-0133-z

Alatalo JM, Jägerbrand AK, Molau U (2016) Impacts of different climate change regimes and extreme climatic events on an alpine meadow community. Sci Rep 6:21720. doi:10.1038/srep21720

Alatalo JM, Little CJ (2014) Simulated global change: contrasting short and medium term growth and reproductive responses of a common alpine/Arctic cushion plant to experimental warming and nutrient enhancement. SpringerPlus 3:157. doi:10.1186/2193-1801-3-157

Alatalo JM, Little CJ, Jägerbrand AK, Molau U (2014b) Dominance hierarchies, diversity and species richness of vascular plants in an alpine meadow: contrasting short and medium term responses to simulated global change. PeerJ 2:e406. doi:10.7717/peerj.406

Ali A, Yan E-R, Chen HY et al (2016) Stand structural diversity rather than species diversity enhances aboveground carbon storage in secondary subtropical forests in Eastern China. Biogeosciences 13:4627–4635

Arft AM, Walker MDM, Gurevitch J et al (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. Ecol Monogr 69:491–511

Barton K (2016) MuMIn: Multi-Model Inference. R package version 1.15.6, pp. Model selection and model averaging based on information criteria (AICc and alike)

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. doi:10.18637/jss.v067.i01

Bret-Harte MS, García EA, Sacré VM et al (2004) Plant and soil responses to neighbour removal and fertilization in Alaskan tussock tundra. J Ecol 92:635–647

Carlyle CN, Fraser LH, Turkington R (2013) Response of grassland biomass production to simulated climate change and clipping along an elevation gradient. Oecologia. doi:10.1007/s00442-013-2833-2

Domènech M, Komac B, Peñuelas J, Conesa JA (2014) Site-specific factors influence the richness and phenology of snowbed plants in the Pyrenees. Plant Biosyst Int J Deal Asp Plant Biol:1–9

Grime JP (1973) Competitive exclusion in herbaceous vegetation. Nat UK 242:344–347

Harms KE, Wright SJ, Calderón O et al (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404:493–495

Hooper DU, Chapin FS, Ewel JJ et al (2005) Effect of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35. doi:10.1890/04-0922

Huston MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110:449–460

IPCC (2014) Climate change 2014: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fifth Assessment Report of the IPCC. Cambridge University Press, Cambridge

IPCC (2007) Climate change 2007: impacts, adaptation and vulnerability: Working Group II Contribution to the Fourth Assessment Report of the IPCC Intergovernmental Panel on Climate Change. Cambridge

Jonasson S, Michelsen A, Schmidt I, Nielsen E (1999) Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic. Ecology 80:1828–1843

Karlsson U (1998) Evaluation of pointframe cover assessment for estimating biomass in alpine tundra. B.Sc. Thesis, University of Gothenburg

Klanderud K, Totland Ø (2008) Diversity-stability relationships of an alpine plant community under simulated environmental change. Arct Antarct Alp Res 40:679–684. doi:10.1657/1523-0430(07-075)

Klanderud K, Totland Ø (2005) Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. Ecology 86:2047–2054

Klaus VH, Hölzel N, Boch S et al (2013) Direct and indirect associations between plant species richness and productivity in grasslands: regional differences preclude simple generalization of productivity-biodiversity relationships. Preslia 85:97–112

Kravtsova VI, Loshkareva AR (2013) Dynamics of vegetation in the tundra-taiga ecotone on the Kola Peninsula depending on climate fluctuations. Russ J Ecol 44:303–311. doi:10.1134/S1067413613040085

Lohbeck M, Poorter L, Martínez-Ramos M, Bongers F (2015) Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. Ecology 96:1242–1252

Loreau M (2000) Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91:3–17

Loreau M (1998) Biodiversity and ecosystem functioning: a mechanistic model. Proc Natl Acad Sci 95:5632–5636

Magurran AE (2013) Measuring biological diversity. Wiley, Oxford

Marchand FL, Kockelbergh F, Van de Vijver B et al (2006a) Are heat and cold resistance of arctic species affected by successive extreme temperature events? New Phytol 170:291–300

Marchand FL, Mertens S, Kockelbergh F et al (2005) Performance of High Arctic tundra plants improved during but deteriorated after exposure to a simulated extreme temperature event. Glob Change Biol 11:2078–2089

Marchand FL, Verlinden M, Kockelbergh F et al (2006b) Disentangling effects of an experimentally imposed extreme temperature event and naturally associated desiccation on Arctic tundra. Funct Ecol 20:917–928. doi:10.1111/j.1365-2435.2006.01203.x

Marion G, Henry GHR, Freckrnan DW et al (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. Glob Change Biol 3:20–32

May JL, Hollister RD (2012) Validation of a simplified point frame method to detect change in tundra vegetation. Polar Biol 35:1815–1823. doi:10.1007/s00300-012-1224-1

Mittelbach GG, Steiner CF, Scheiner SM et al (2001) What is the observed relationship between species richness and productivity? Ecology 82:2381–2396

Molau U (2010) Long-term impacts of observed and induced climate change on tussock tundra near its southern limit in northern Sweden. Plant Ecol Divers 3:29–34. doi:10.1080/17550874.2010.487548

Mulder CPH, Uliassi DD, Doak DF (2001) Physical stress and diversity-productivity relationships: the role of positive interactions. Proc Natl Acad Sci 98:6704–6708

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142

Oksanen J, Guillaume Blanchet, F Kindt R, Legendre P et al (2013) Community Ecology Package, Package "vegan."

Opedal ØH, Armbruster WS, Graae BJ (2014) Linking small-scale topography with microclimate, plant species diversity and intra-specific trait variation in an alpine landscape. Plant Ecol Divers:1–11

Pfisterer AB, Schmid B (2002) Diversity-dependent production can decrease the stability of ecosystem functioning. Nature 416:84–86

Pimm SL (1984) The complexity and stability of ecosystems. Nature 307:321–326

Poldini L, Sburlino G, Buffa G, Vidali M (2011) Correlations among biodiversity, biomass and other plant community parameters using the phytosociological approach: a case study from the south-eastern Alps. Plant Biosyst Int J Deal Asp Plant Biol 145:131–140. doi:10.1080/11263504.2010.547673

Press M, Potter J, Burke M et al (1998) Responses of a subarctic dwarf shrub heath community to simulated environmental change. J Ecol 86:315–327. doi:10.1046/j.1365-2745.1998.00261.x

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Sun J, Li XZ, Wang XW et al (2011) Latitudinal pattern in species diversity and its response to global warming in permafrost wetlands in the Great Hing'an Mountains, China. Russ J Ecol 42:123–132. doi:10.1134/S1067413611020111

Tilman D (1996) Biodiversity: population versus ecosystem stability. Ecology 77:350–363

Underwood A (1994) On beyond BACI: sampling designs that might reliably detect environmental disturbances. Ecol Appl 4:3–15

Virtanen R, Grytnes J-A, Lenoir J et al (2013) Productivity–diversity patterns in arctic tundra vegetation. Ecography 36:331–341. doi:10.1111/j.1600-0587.2012.07903.x

Walker BH (1992) Biodiversity and ecological redundancy. Conserv Biol 6:18–23

Wang Y, Yu S, Wang J (2007) Biomass-dependent susceptibility to drought in experimental grassland communities. Ecol Lett 10:401–410

Wilsey BJ, Potvin C (2000) Biodiversity and ecosystem functioning: importance of species evenness in an old field. Ecology 81:887–892

Wu X, Lin X, Zhang Y et al (2014) Impacts of climate change on ecosystem in priority areas of biodiversity conservation in China. Chin Sci Bull 59:4668–4680. doi:10.1007/s11434-014-0612-z

Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc Natl Acad Sci 96:1463–1468

Zhang Y, Chen HY (2015) Individual size inequality links forest diversity and above-ground biomass. J Ecol 103:1245–1252

Zhang Y, Wang Y, Zhang M, Ma K (2014) Climate change threats to protected plants of China: an evaluation based on species distribution modeling. Chin Sci Bull 59:4652–4659. doi:10.1007/s11434-014-0642-6

Zhao J, Liu W, Ye R et al (2013) Responses of reproduction and important value of dominant plant species in different plant functional type in Kobresia meadow to temperature increase. Russ J Ecol 44:484–491. doi:10.1134/S1067413613060131

Zuur AF, Ieno EN, Walker N et al (2009) Mixed effects models and extensions in ecology with R. Springer, New York