Oecologia (2020) 193:689–699
https://doi.org/10.1007/s00442-020-04713-w

COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Beyond resource limitation: an expanded test of the niche dimension hypothesis for multiple types of niche axes

Xuebin Yan[1] · **Jeffrey Diez**[2] · **Kailing Huang**[1] · **Shaopeng Li**[3,4] · **Xi Luo**[1] · **Xinyu Xu**[1] · **Fanglong Su**[1] · **Lin Jiang**[5] · **Hui Guo**[1] · **Shuijin Hu**[1,6]

Received: 12 March 2020 / Accepted: 14 July 2020 / Published online: 17 July 2020

Abstract

The niche dimension hypothesis predicts that more species can coexist given a greater number of niche axes along which they partition the environment. Although this hypothesis has been broadly supported by nutrient enrichment experiments, its applicability to other ecological factors, such as natural enemies and abiotic stresses, has not been vigorously tested. Here, we examined the generality of the niche dimension hypothesis by experimentally manipulating both resource and non-resource niche dimensions—nitrogen limitation, pathogens and low-temperature stress—in a Tibetan alpine meadow. We found that decreases in niche dimensions led to a significant reduction in species richness, consistent with results from nutrient addition studies. However, different niche variables uniquely affected the plant communities. While nitrogen had largest effects on both community biomass and species richness, pathogens and low-temperature stress, in combination with nitrogen, had synergistic effects on them. Our results provide direct evidence demonstrating that both resource and non-resource niche dimensions can influence species coexistence. These findings suggest that other non-resource factors need to be taken into consideration to better predict the community assembly and control over biodiversity, particularly under the future multifaceted global change scenarios.

Keywords Niche dimensionality · Species diversity · Biomass · Tibetan plateau · Alpine meadow

Introduction

Elucidating the mechanisms of biodiversity maintenance is one of primary objectives of ecology (Chesson 2000). Understanding how species stably coexist has become even more critical as anthropogenic environmental change has led to rapid losses of biodiversity and associated disruption of ecosystem functions and services (Tilman et al. 2014; Newbold et al. 2016; Turnbull et al. 2016). One of the most common theoretical explanations for species coexistence is the niche dimension hypothesis, which posits that greater dimensionality of niches, often defined by the number of limiting factors, allows more species to coexist (Hutchinson 1957). Conversely, this theory predicts that decreases in the number of limiting niche dimensions would reduce species diversity (Kneitel and Chase 2004; Harpole et al. 2017).

Numerous nutrient addition experiments with plants have provided empirical support for the niche dimension hypothesis in the past two decades (Harpole and Tilman 2007; Silvertown et al. 2009; Ren et al. 2010; Harpole and Suding 2011; Harpole et al. 2016). The primary productivity

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Communicated by Kendi Davies.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00442-020-04713-w) contains supplementary material, which is available to authorized users.

✉ Hui Guo
hui.guo@njau.edu.cn

[1] College of Resources and Environmental Sciences, Nanjing Agricultural University, Nanjing 210095, Jiangsu, China

[2] Department of Botany and Plant Sciences, University of California, Riverside, CA 92521, USA

[3] Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China

[4] Institute of Eco-Chongming (IEC), Shanghai 200062, China

[5] School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA 30332, USA

[6] Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695, USA

of many terrestrial ecosystems is commonly co-limited by multiple nutrients (Fay et al. 2015). Addition of these limited nutrients can, thus, reduce the dimensionality of niches by alleviating resource limitation or decreasing the heterogeneity of these nutrients, ultimately leading to decreased number of coexisting species (Harpole et al. 2016). Alleviation of limiting resources may also increase aboveground biomass of plants and cause a shift from nutrient competition belowground to light competition aboveground (Harpole and Tilman 2007; Ren et al. 2010; Harpole and Suding 2011; Harpole et al. 2016). This shift in the identity of limiting factors is thought to be an indirect pathway reducing niche dimensionality, thereby leading to species exclusion (DeMalach et al. 2017; Harpole et al. 2017).

Niche dimensionality can be defined according to different types of factors. Chase and Leibold (2003) emphasized that niche should include a species' requirement for and impacts on a factor, where requirements refer to the conditions allowing a species to maintain positive population growth and impacts refer to the effect that species has on the factor. The niche concept can also be extended to two or more dimensions to show how factors interact to determine the two components of the niche of an organism (Chase and Leibold 2003). To potentially coexist locally, species must differentiate in their requirements and impacts, which have often been addressed as trade-offs (Chase and Leibold 2003; Harpole et al. 2016). Specifically, trade-offs may occur when a trait of an organism that confers advantage for one function but simultaneously confers a disadvantage for another function (Chase and Leibold 2003).

Besides nutrients, other factors, such as natural enemies and environmental stresses, could also drive trade-offs among plant species and potentially influence species coexistence. For instance, a competition-defense trade-off, where better competitors for resources are more vulnerable to natural enemies than those with weaker competitive ability, is considered as an important contributor to diversity maintenance in plant communities (Borer et al. 2007; Elser et al. 2007; Viola et al. 2010). Pathogens and herbivores have been found to promote species diversity in plant communities by enhancing negative frequency-dependent interactions, in effect penalizing species as they become more abundant (Viola et al. 2010; Bagchi et al. 2014; Bever et al. 2015). Similarly, a trade-off between resource competition and stress tolerance may also be necessary for species coexistence (Bestelmeyer 2000; Kneitel and Chase 2004). In most ecosystems, when stress is relieved, such as through warming of alpine and tundra ecosystems, plant species diversity often declines (Klein et al. 2004; Elmendorf et al. 2012).

Therefore, trade-offs in species' abilities to compete for multiple resources, defend against natural enemies and tolerate environmental stresses may all contribute to species coexistence (Viola et al. 2010; Robinson et al. 2012; Eskelinen et al. 2017). Amelioration of these factors is, thus, predicted to reduce the niche dimensionality of the community, decrease their role in mediating species coexistence, and lead to species losses.

Here, we describe the first experimental test, to our knowledge, of the niche dimension hypothesis that explicitly focused on different types of limiting factors. We conducted a 2-year field experiment in an alpine meadow on the Tibetan plateau by alleviating nitrogen limitation, low-temperature stress, and pathogen pressure. We first identified that these manipulated factors were limiting by measuring plant biomass responses. Then, we tested whether the number of limiting factors (i.e., niche axes) was associated with the alteration in species richness. In addition, we also explored the specific effects of each limiting factors on species richness. Further, we used structural equation models (SEMs) to examine the relative strength of direct and indirect effects of these niche axes on species diversity. Our overall hypothesis was that both resource and non-resource limiting factors can affect species diversity. Two specific hypotheses guided our research. First, decreases in the number of limiting factors would reduce species richness. Second, each limiting factor would have a unique effect on species diversity. Specifically, nitrogen addition would decrease species richness due to light limitation caused by increased biomass, and warming would have a similar effect through directly relieving temperature stress and indirectly enhancing soil nutrient availability. In contrast, fungicide application would have the largest effect on species evenness through reducing pathogen pressure on dominant species.

Materials and methods

The study site

Our study site is located in the eastern Tibetan plateau, in Maqu county, Gansu Province, China (33° 67′ N, 101° 87′ E, 3500 m a.s.l.). This site has a mean annual temperature of 1.2 °C, ranging from − 10 °C in January to 11.7 °C in July, and a mean annual precipitation of 620 mm, with most of the rain falling during the summer growing season (ranges from the end of May to early September). The vegetation is an alpine meadow community dominated by perennial herbs, including *Kobresia graminifolia* (Cyperaceae), *Elymus nutans* (Poaceae), *Thermopsis lanceolata* (Leguminosae), *Anemone rivularis* (Ranunculaceae) and *Anemone obtusiloba* (Ranunculaceae).

Experimental design

The field experiment was established in May 2016 in an alpine meadow on a south-facing slope, which had been previously fenced to exclude large herbivores (e.g. yaks, sheep and horses). We applied factorial treatments of fertilizer nitrogen (N), fungicide (F) and warming (W), including the untreated control for each factor leading to a total of eight treatment combinations. Plots of all eight treatment combinations (1.5 m × 1.5 m each) were randomly arranged in five replicate blocks, with all plots separated by 0.5 m buffer zones. For the nitrogen addition treatment, chemical nitrogen (urea) was added annually at a rate of 12 g N m^{-2} $year^{-1}$ in the early growing season (early June). This amount is very high compared to the natural nitrogen deposition but represents a reasonable level after considering nitrogen fertilizers used to raise forage productivity or restore the degraded grasslands (Harris 2010, Liu et al. 2016). For the fungicide addition treatment, a foliar fungicide-Amistar (Syngenta Crop Protection Inc., NC, USA; suspension concentrate; active ingredient: azoxystrobin) was sprayed weekly on the plant leaves throughout the whole growing season. This fungicide provides a broad-spectrum control of many fungal-borne diseases, including leaf spots, smut, blights, brown spots, and powdery mildew, which affect plant growth at our study site (Liu et al. 2016). For the warming treatment, hexagonal open top chambers (OTCs) with a maximum basal diameter of 150 cm were used. The OTC is a commonly used and well-documented method for assessing warming impacts on ecosystems, especially in arctic and alpine ecosystems (Marion et al. 1997; Kaarlejärvi et al. 2017; Hopping et al. 2018). This passive warming method is the favored option in the Tibetan plateau because of the limitation of electricity and the high wind velocity (Hopping et al. 2018). In our study, the OTCs were remained on the plots year-round and they increased the air temperature by 1.47 °C on average during the growing season.

Plant community responses

To estimate the responses of plant diversity and community composition, we randomly sampled one 0.5 m × 0.5 m quadrat in each plot and recorded the abundance of each species at peak primary productivity (in the middle of August) in 2016 and 2017. Species richness (S) was measured as the total number of plant species observed in each plot, and species evenness was calculated with the equation $H/\ln(S)$, where H is Shannon's diversity. We quantified beta diversity among plots under the same treatment using the Bray–Curtis dissimilarity metric (Anderson et al. 2006). We estimated aboveground biomass in each year by clipping green (live) fractions of plants rooted within the quadrats in each plot at the ground level, oven-drying at 65 °C for 48 h and weighing. Plant species were classified into four functional groups for assessing how life histories affect responses experimental treatments: grasses, sedges, legumes and forbs. We measured photosynthetically active radiation (PAR) above the plant canopy and at ground surface in each plot (using AccuPAR LP-80 Ceptometer, Decagon Devices, WA, USA) in August 2017, and calculated light penetration as the proportion of transmitted light through the canopy to the ground surface.

Soil analyses and quantification of arbuscular mycorrhizal fungi (AMF) colonization of plant roots

While relieving limitations of nitrogen, pathogens and temperature, our manipulations might simultaneously exert negative effects on plants, such as decreased soil pH induced by nitrogen addition, suppression of mycorrhizae by fungicide and thermal or water stress caused by warming (Mitchell 2003; Klein et al. 2004; Chen et al. 2013). Therefore, we determined soil pH, AMF colonization and the ratio of soil microbial biomass carbon and nitrogen to detect these possible negative effects. In late August 2017, soil cores (2.5 cm dia., 20 cm depth) were collected from three random locations in each plot and combined for one composite soil sample. The fresh soils were sieved through 2 mm mesh to remove rocks, visible roots and debris, and separated into two halves in laboratory. All the root samples were collected and carefully washed for determination of AMF colonization (see more details below). One half of each soil sample was maintained fresh at 4 °C to determine soil moisture, soil pH, soil ammonium and nitrate, and soil microbial biomass carbon and nitrogen; the remaining half was air-dried to determine soil-available phosphorus. Soil microbial biomass carbon was estimated by the fumigation–extraction method (Vance et al. 1987) and microbial biomass nitrogen was determined following alkaline digestion (Cabrera and Beare 1993). A random subset of plant roots was sampled to determine the AMF colonization. Mycorrhizal colonization of roots was microscopically determined after the roots were stained with Trypan Blue and were scored using gridline intersection (McGonigle et al. 1990).

Data analyses

To examine whether treatment factors (nitrogen, warming and fungicide) were limiting or co-limiting in this system, we calculated increased amount of biomass (IAB): $\mathrm{IAB} = \mathrm{Biomass}_{\mathrm{Treatment}} - \mathrm{Biomass}_{\mathrm{control}}$ for each treatment. Multi-factor treatments are considered synergistic when they have IAB values that are greater than the sum of the individual treatments, additive when they are equivalent, and sub-additive when they are less than the sum of individual factors (Harpole et al. 2011; Fay et al. 2015).

To test the niche dimension hypothesis, we categorized experimental treatments by the number of factors applied to a plot. Specifically, 0 = control, 1 = nitrogen addition (N), fungicide addition (F) or warming treatment (W), 2 = any combination of two of the three treatments, and 3 = the combination of nitrogen addition, fungicide addition and warming. We fit two sets of linear mixed-effects models (LMMs) to assess how different community properties (species richness, evenness, beta diversity, aboveground total biomass, and biomass of four plant functional groups) responded to: (i) the number of manipulated factors (0–3), and (ii) specific treatments. Models were fit using the 'lme4' package (Bates et al. 2017) for linear mixed-effects models in R (R Core Team 2017). Each model included 'block' as the random effect, and statistical significance of treatments relative to the control was determined using the Satterthwaite's degrees of freedom method in the 'lmerTest' package (Kuznetsova et al. 2017). Pairwise contrasts between treatments were estimated using Tukey multiple comparisons via the glht function in the 'multcomp' package (Hothorn et al. 2008).

To tease apart direct and indirect effects of the number of manipulated factors or specific treatment factors on species loss, we formulated two full piecewise structural equation models (SEMs) in which soil resources, biomass and light penetration were included as intermediate variables between the number of manipulated factors (or specific treatment factors) and species richness (Electronic Supplementary Material Fig. S1). Individual models comprising each SEM were linear mixed-effects models in which block was treated as a random effect. We also calculated the Spearman rank–order correlation between variables in the piecewise SEMs (Electronic Supplementary Material Fig. S2) and estimated variance inflation (VIF). This demonstrated that multi-collinearity did not affect parameter estimates ($VIF < 3$). Then, we sequentially eliminated non-significant pathways in the full piecewise SEMs until attaining the final models according to Akaike information criterion (AIC). Overall, fits of the piecewise SEMs were evaluated using Fisher's C statistic and AIC in the 'piecewiseSEM' package (Lefcheck 2016). The 'soil resources' factor in piecewise SEMs was characterized by the first principal component of soil moisture, available phosphorus, soil ammonium and nitrate (Electronic Supplementary Material Fig S3).

Results

Resource and non-resource limiting factors

Increased amount of biomass (IAB) of single-factor and multiple-factor treatments showed that these factors were likely to be limiting or co-limiting in our study alpine meadow (Table 1). Specifically, combinations of two or three factors (i.e. F + N, F + W, N + W and F + N + W) had synergistic effects on community biomass compared with the sum of the individual treatments in 2016. In contrast, only treatment F + W showed a synergistic effect in 2017, while F + N, N + W and F + N + W treatments had sub-additive effects relative to the sum of their individual effects. When the data of both years were combined, F + W and F + N + W treatments had synergistic effects on biomass relative to the sum of the individual treatments, whereas F + N and N + W treatment had sub-additive effects on biomass relative to summed F and N treatments (Table 1).

No potential negative effects of three treatment factors on plant growth were found in our experiment. Specifically, nitrogen addition did not cause a decrease in soil pH (Fig. 1a). Fungicide did not significantly affect AMF colonization of plant roots and the ratio of soil microbial biomass carbon and nitrogen (Fig. 1b, c).

Numbers and identities of limiting factors

The experimental treatments of nitrogen addition, fungicide application, and warming had significant effects on community diversity and composition. Both species richness and beta diversity were negatively associated with the number of manipulated niche factors (Fig. 2a, e). However, species evenness was not significantly related to the number of factors manipulated (Fig. 2c).

Nitrogen, fungicide and warming exhibited differential effects on the community-level properties examined. Species richness was significantly lower under the combination of all treatment factors (F + N + W) than the F + W treatment

Table 1 Increased amount of biomass showing co-limitation in two years (2016 and 2017) in the field experiment

Year	F	N	W	F + N		F + W		N + W		F + N + W	
	IAB	IAB	IAB	IAB	Type	IAB	Type	IAB	Type	IAB	Type
2016	6.2196	19.8871	− 13.4717	32.1490	Synergistic	1.0811	Synergistic	17.7201	Synergistic	48.8690	Synergistic
2017	− 1.3190	67.7665	− 1.2558	55.5083	Sub-additive	16.7602	Synergistic	53.7886	Sub-additive	53.4377	Sub-additive
All	2.4503	43.8268	− 7.3638	43.8287	Sub-additive	8.9207	Synergistic	35.7543	Sub-additive	51.1533	Synergistic

We calculated increased amount of biomass (IAB): $IAB = Biomass_{Treatment} - Biomass_{control}$ for each treatment. Multi-factor treatments are considered synergistic when they have IAB values that are greater than the sum of the individual treatments, additive when they are equivalent, and sub-additive when they are less than the sum of individual factors. F, N and W represent fungicide addition, nitrogen addition and warming, respectively. IAB represents increased amount of aboveground biomass

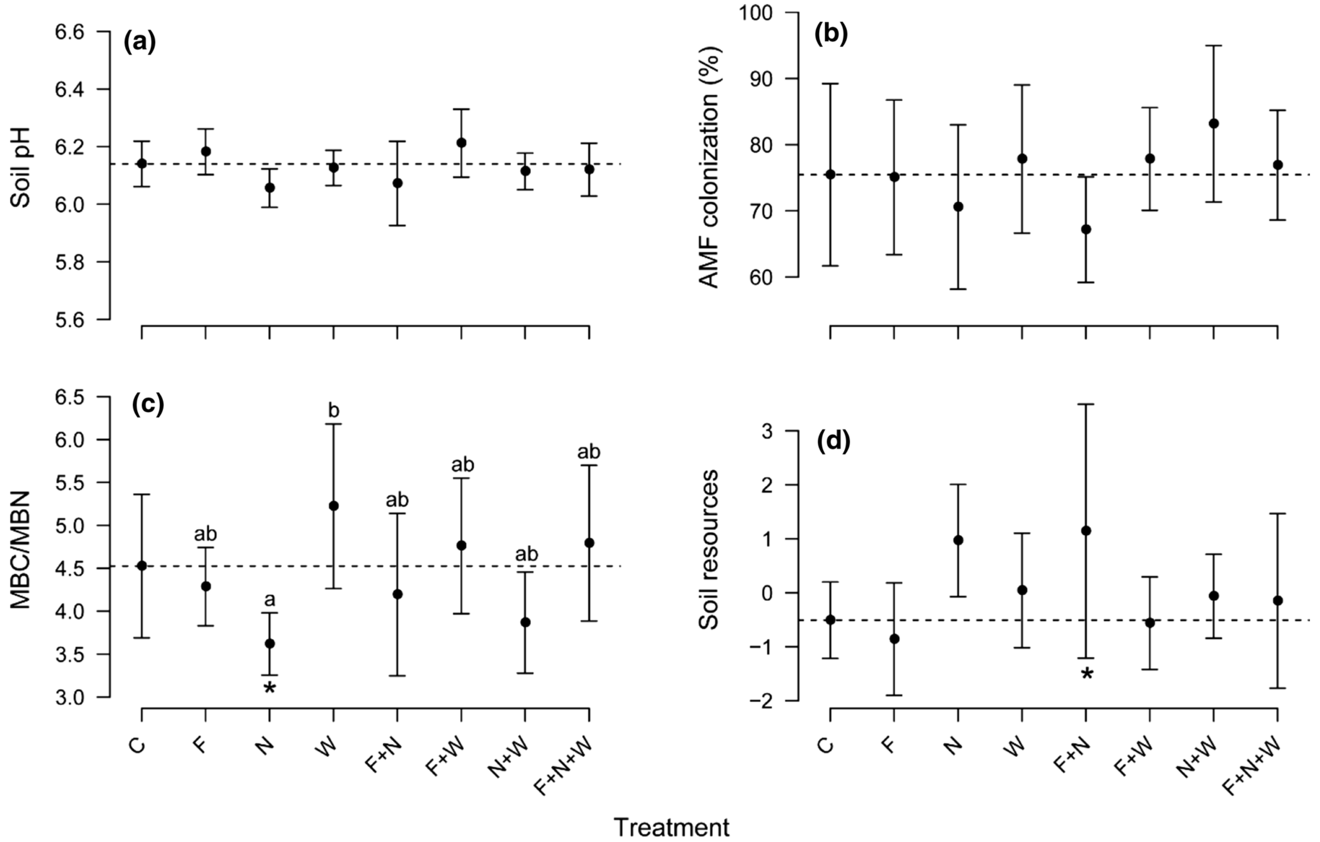

Fig. 1 Responses of **a** soil pH, **b** AMF colonization of plant roots, **c** ratio of microbial biomass carbon and nitrogen (MBC/MBN), and **d** soil resources (the first principal component of soil moisture, available phosphorus, soil ammonium and nitrate) under different experimental treatments: F, N and W represent fungicide addition, nitrogen addition and warming, respectively. Data are mean ± 1 standard deviation. Within each graph, values that do not share a letter are significantly different from each other ($P < 0.05$). Asterisks indicate that values of the treatments are significantly different from the control through testing by the linear mixed-effects model ($P < 0.05$). Horizontal dashed lines mark the mean value in the control plots

(Fig. 2b). The F + N + W treatment also decreased species evenness relative to the control (Fig. 2d). Also, treatments of N, F + N, F + W, N + W, and F + N + W induced significant decline in beta diversity relative to the control (Fig. 2f). In addition, all of interactive treatments containing warming (F + W, N + W, F + N + W) led to lower beta diversity than warming alone (Fig. 2e). These interactive effects indicated that warming effects on species homogenization may depend on nitrogen and pathogens in the environment.

Direct and indirect effects

The piecewise SEM showed that reduced niche dimensionality (increased number of manipulated factors) significantly contributed to increased aboveground biomass, which lead to a significant decrease in light penetration through the canopy (Fig. 3a). However, reduced light penetration was not significantly related to species richness. The number of manipulated factors negatively affected species richness (Fig. 3a). However, the piecewise SEM including specific treatment factors instead of numbers of manipulated factors showed that only nitrogen had a direct significant effect on species richness (Fig. 3b). Also, nitrogen addition significantly increased soil resources and aboveground biomass and, reduced light penetration, but it did not significantly influence species richness through these indirect pathways (Fig. 3b).

Discussion

Numerous experimental manipulations of resources have provided strong empirical support for the niche dimension hypothesis (Harpole and Tilman 2007; Ren et al. 2010; Harpole and Suding 2011; Harpole et al. 2017). Results from our study extend that body of work to show that relaxing niche constraints of both resources and non-resource factors can affect species richness (Fig. 2a). However, the effect of each niche variable was not equal, raising interesting questions about the relative importance of different types of niche axes

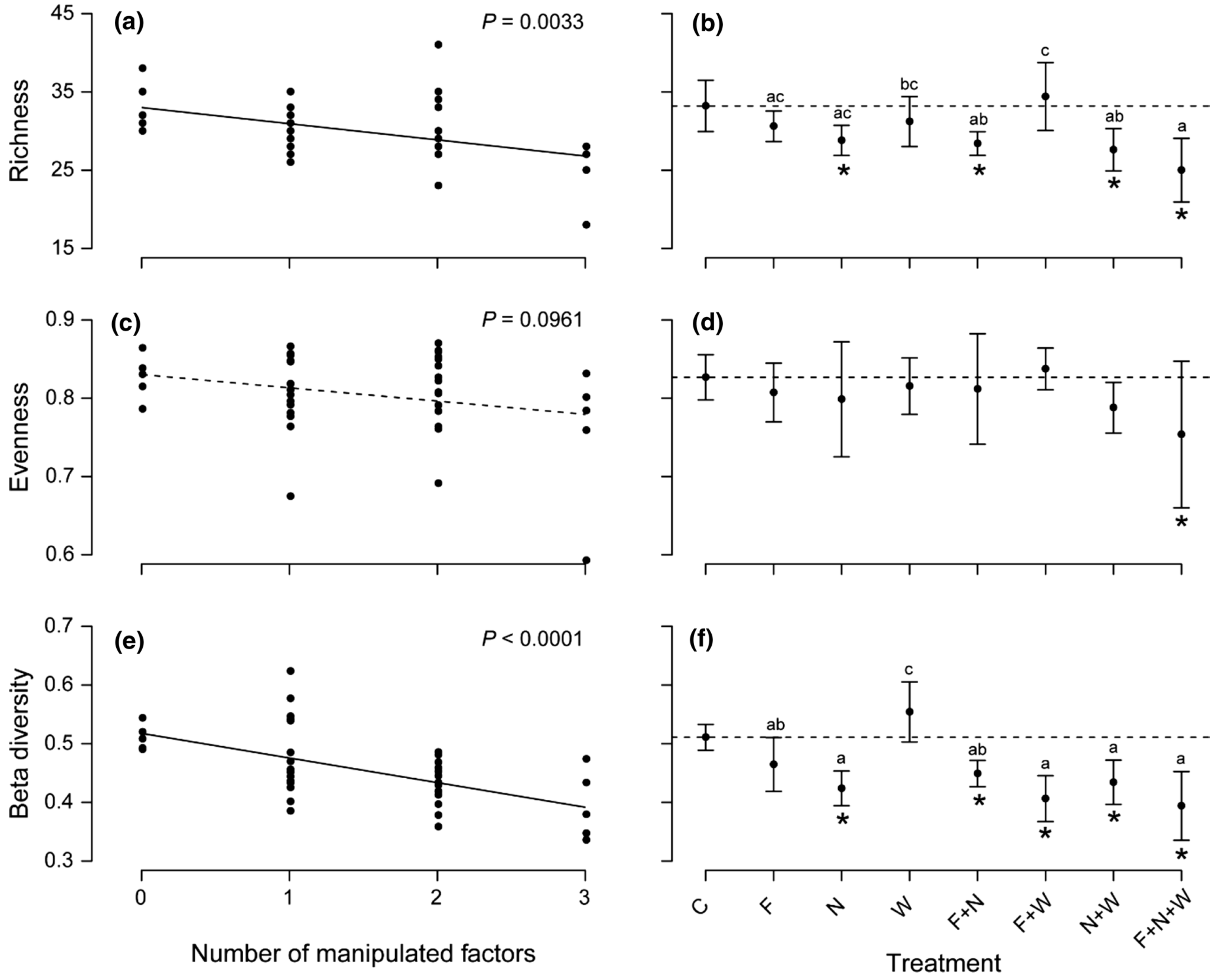

Fig. 2 Responses of **a**, **b** species richness, **c**, **d** evenness, **e**, **f** beta diversity to the number of manipulated factors and each treatment (F, N and W represent fungicide addition, nitrogen addition and warming, respectively). In panel **a**, **c** and **e**, black lines are regression lines estimated by linear mixed-effects models and only significant relationships ($P < 0.05$) are shown. In panel **b**, **d** and **f**, data are mean ± 1 standard deviation. Within each graph, values that do not share a letter are significantly different from each other ($P < 0.05$). Asterisks indicate that values of the treatments are significantly different from the control through testing by the linear mixed-effects model ($P < 0.05$). Horizonal dashed lines mark the mean value in the control plots. Data are shown here for 2017 alone, but 2016 data are included in Supplementary Electronic Supplementary Material Figure S5

for regulating species diversity. Also, the piecewise SEM results (Fig. 3) suggest that the decrease in species richness may be primarily driven by the direct effects of reduced niche dimensions rather than their indirect effects.

Resource and non-resource limiting factors

One critical step in testing niche-related hypotheses is to ensure that the factor manipulated is indeed a limiting factor to plants (Chase and Leibold 2003). First, a limiting factor should directly and/or indirectly limit the productivity of plants (Harpole et al. 2011; Fay et al. 2015). Our IAB analysis showed that the three manipulated factors (nitrogen, pathogen and temperature) co-limited plant biomass (Table 1). Second, a treatment of ameliorating a limiting factor should not generate indirect effects that may create new limitations on plants (Harpole and Suding 2011). However, nitrogen addition may induce soil acidification (Chen et al. 2013), warming may lead to water or thermal stress on plants and soil microbes, and fungicide applications may have non-target effect by suppressing saprophytic fungi (Hu et al. 1995) and/or arbuscular mycorrhizal fungi (Wilson et al. 2009). We found no significant nitrogen-induced decrease in soil pH (Fig. 1a), no warming-induced thermal or water stress to plants and microbes (Electronic Supplementary Material Fig. S4), and no fungicide suppression on

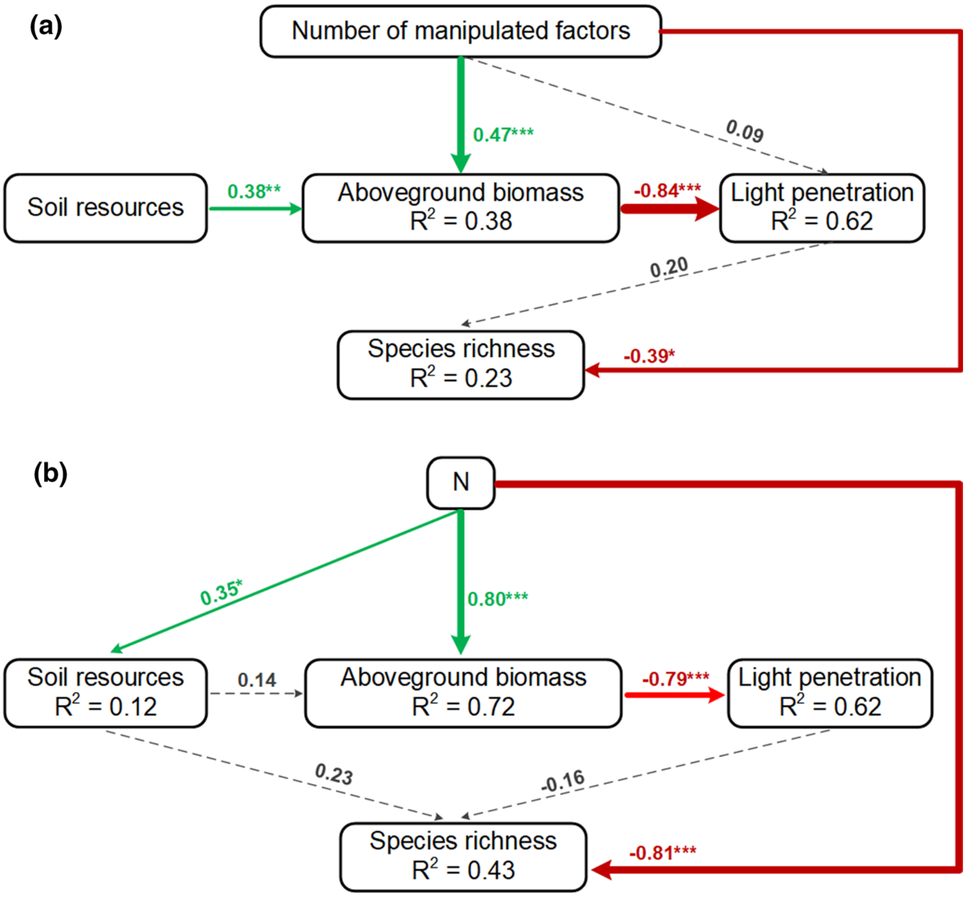

Fig. 3 **a** The final (reduced) piecewise structural equation models (SEMs) relating the number of manipulated factors or **b** specific treatment factors and species richness. Green and red arrows represent significant positive and negative pathways, respectively, and grey dashed arrows indicate non-significant pathways. Arrow width is proportional to the strength of the relationship. Numbers indicate the standard path coefficients and asterisks indicate statistical significance ($*P<0.05$, $**P<0.01$, $***P<0.001$). The R^2 is the marginal R^2, which indicates the variance explained by fixed effects in the mixed model. The 'Soil resources' is the first principal component of soil moisture, available phosphorus, soil ammonium and nitrate. In panel **b**, the 'N' represents nitrogen addition. The final (reduced) models adequately fitted the data: **a** Fisher $C=6.34$, $df=6$, $P=0.39$; Akaike information criteria (AIC) = 36.33; **b** Fisher $C=5.37$, $df=6$, $P=0.50$; AIC = 43.37

soil microbes and AMF (Fig. 1b, c). Together, these results indicate that the factors manipulated in our study, i.e., low available nitrogen, fungal pathogens, low temperature, represent important niche axes in the alpine meadow, and that alleviation of these can reduce the niche dimensionality of the system and causes species loss.

Numbers and identities of limiting factors

In this study, we found that species richness declined and biomass increased with increasing numbers of manipulated niche variables, consistent with previous studies of nutrient enrichment alone (Harpole and Suding 2011; Harpole et al. 2017). The increase in biomass appeared to be mainly attributed to the increase in biomass of sedges and grasses (Electronic Supplementary Material Fig. S6a, b). A portion of this increase in biomass may result from changes in allocation, as growth-defense trade-offs may result in increased allocation to growth when the multiple limitations of nitrogen, pathogens and low temperature were relieved (Lind et al. 2013). In addition, the significant reduction in beta diversity with increasing number of manipulated factors (Fig. 2e) suggests that reduced niche dimensionality not only caused great loss of species, but also induced homogenization of community composition (Anderson et al. 2006).

The effects of specific treatments showed that not all factors had equivalent effects. Nitrogen addition had consistently positive effects on community biomass (Electronic Supplementary Material Fig. S4b, d), indicating a significant nitrogen limitation in this alpine meadow ecosystem. There was also a significant negative effect of nitrogen addition on species richness. Several previous studies have shown that compared to phosphorous, potassium and water, nitrogen had greater impacts on plant species richness and community productivity in the alpine meadow (Ren et al. 2010; Fay et al. 2015). In addition to species richness and plant biomass, nitrogen can also affect some important ecosystem progress in the alpine grasslands, such as ecosystem carbon uptake and release (Song et al. 2017; Ma et al. 2018). Our results also showed that nitrogen had the largest effect on both plant biomass and species richness. These findings suggest that the alpine meadow is a nitrogen-limiting system and nitrogen did play an important role in this ecosystem.

Although the effects of fungicide and warming treatments were not as strong as nitrogen addition, they also had synergistic effects on the community in combination with nitrogen. When fungicide was applied along with warming, the marginal increase in biomass suggests that the release from pathogens' negative effects on plants may be enhanced under warmer temperatures (Electronic Supplementary Material Fig. S4b). Although fungicide addition alone did not significantly affect species richness and species evenness, it altered beta diversity marginally alone and more significantly in synergy with the warming treatment (Fig. 2f). This suggests that pathogens may have asymmetric effects on species depending on their relative abundance (Mordecai 2011), thereby playing an important role in maintaining beta diversity.

In addition to nutrients and pathogens, low temperature is another critical ecological factor limiting plant growth and reproductive output and success in cold alpine regions (Klein et al. 2004). In this study, the lack of effects of experimental warming alone on community biomass or richness was surprising for an alpine community. It appears more likely that temperature acts as a synergistic variable, amplifying the effects of other niche factors. For instance, F + W had marginally more biomass than F, suggesting a possible release from fungal pathogens under warmer conditions (Electronic Supplementary Material Fig. S4b).

Together, these results showed that reduced niche dimensions led to an increase in community biomass but a decrease in species richness. Moreover, different niche variables uniquely affected the plant communities. Nitrogen had largest effects on both community biomass and species richness. Pathogens affected species composition rather than species richness. Low-temperature stress acted as a synergistic variable, amplifying the effects of other niche factors. As suggested by previous tests on the niche dimension hypothesis, in addition to the direct reduction in the number of limiting resources, both changes in the balance or decreases in heterogeneity of these limiting resources could also reduce the niche dimension and, therefore, affect species richness (Harpole and Tilman 2007; Harpole et al. 2017). Therefore, these limiting factors may not affect the niche dimension separately. Instead, they act synergistically to determine the niche dimension and species coexistence. For example, the effect of pathogens removal on species richness may depend on temperature or soil nitrogen condition. Together, these results suggest that we not only need to focus on specific roles of each limiting factor, but also need to consider the role of their interactive effects.

Direct and indirect effects

Results from our study also showed that the negative effects of the relaxation of limiting factors on diversity were primarily driven by their direct effects. The piecewise SEMs confirmed that increased biomass led to a reduction in light penetration through the canopy (Fig. 3), which is expected to increase light competition for these meadow species. Competition for light is an important mechanism exerting negative effects on species richness (Hautier et al. 2009). However, there was no direct linkage between light penetration and species richness in both piecewise SEMs. We have considered three mechanisms that may potentially underlie this phenomenon. First, environmental conditions could alter the importance of light levels in controlling plant richness (Dickson and Foster 2011). For example, higher light levels were generally associated with decreased plant richness in drought years but increased plant richness in wet years (Dickson and Foster 2011). Therefore, variations in these environmental conditions (e.g. soil temperature and moisture, air temperature and humidity) may accentuate light effects on species richness. Second, the light levels in our study were not directly manipulated but resulted from changes in plant biomass. The magnitude of change in light penetration might be not sufficient to induce a significant decline in species richness. Third, the light intensity in the Tibetan alpine meadow is much higher than many other areas, so that some decreases due to plant biomass may not lead to any significant effect on plants. Although there was no relationship between light and species richness, biomass was negatively related to species richness in a bivariate model (Electronic Supplementary Material Fig. S7). These results suggest that light competition may not always be the primary mechanism by which increasing biomass decreases species diversity even though it is important in many plant communities. For example, increased biomass can attract herbivores and increase the risks of rare species loss through herbivory (Post and Pedersen 2008). Although not studied here, herbivores can also impact plant diversity through alternation in trait-dependent species losses and gains (Borer et al. 2007; Kaarlejärvi et al. 2017). These potential limiting factors can interact with nutrient, temperature and pathogen and cause species loss in complex ways. To reveal the potential mechanisms of species loss caused by these limiting factors, additional experiments manipulating multiple types of factors at once will be helpful.

The effects of increased light asymmetry caused by increased biomass may often mask the direct contributions of reduced niche dimensionality to diversity loss. Recent debate has highlighted the potentially complex, combined importance of niche dimensionality, productivity and light competition in driving diversity loss under resources addition (DeMalach and Kadmon 2017; Harpole et al. 2017). Our piecewise SEMs highlight that the decrease in species richness was primarily driven by the direct effects of relieved multiple limitations rather than indirect effects of increasing light competition.

Conclusion, caveats, and future directions

Overall, this study suggests that expanding the niche dimension hypothesis to include other non-resource factors may lead to interesting insights into the mechanisms of community regulation. Nonetheless, significant questions remain about the mechanisms by which each limiting factor contributes to species loss and how they act synergistically. For example, nitrogen addition, having the largest effect in our study, was expected to reduce species richness by causing asymmetric light competition, but this indirect effect was not significant in the piecewise SEMs (Fig. 3b). Treatments including nitrogen addition did have significant direct negative effects on species richness, however, suggesting that alternative mechanisms exist. These alternatives could include nitrogen effects on microbial communities or belowground competition (Farrer and Suding 2016; Hautier et al. 2009). Trade-offs among species for multiple limiting factors to species coexistence are also likely to be trait-dependent (Kraft et al. 2015), suggesting a need to quantify physiological, morphological and stoichiometric traits that mediate species coexistence under multiple limiting factors in natural communities.

A final uncertainty remaining after this study is the temporal dynamics of communities following changes in multiple niche axes. Our experimental duration is only two years and the observed changes may be conservative estimates of the long-term effects on communities. It is plausible that the effects of alleviation of both resource and non-resource factors would sustain over time. Several nutrient addition experiments have shown that the effect of nutrient enrichment accumulated over time (Harpole et al. 2016; Yang et al. 2011). A synthesis of experimental warming studies also indicated that the warming effect on plant diversity amplified over time (Elmendorf et al. 2012). In an N-enriched environment, plant pathogens may become more important in maintaining plant biodiversity as they may prevent the dominance of a few species (Mitchell et al. 2003; Bever et al. 2015). A latest synthesis of over 100 studies showed that more numbers of global change factors imposed had greater effects on plant community and these effects are often magnified over time (Komatsu et al. 2019). In addition, sustained alleviation of these resource and non-resource limiting factors may benefit establishment of invasive plants, further affecting species diversity and composition of local community (Eskelinen et al. 2017). Together, these results highlight the importance of long-term studies of multiple limiting factor effects on species diversity and community composition.

In summary, relaxing the limitation by multiple types of ecological factors in this experiment led to a decline in species richness directly, supporting the niche dimension hypothesis. Hutchinson (1959) in fact anticipated this finding near the end of his famous "*Homage to Santa Rosalia*," reflecting that other types of factors, besides just food or nutrition, may serve as critical niche axes along which species partition the environment:

> "We may, therefore, conclude that the reason why there are so many species of animals is at least partly because a complex trophic organization of a community is more stable than a simple one, but that limits are set by the tendency of food chains to shorten or become blurred, by unfavorable physical factors, by space, by the fineness of possible subdivision of niches, and by those characters of the environmental mosaic which permit a greater diversity of small than of large allied species."

Thus, a more complete exploration of different types of niche axes may lead to a richer 'niche dimensions' hypothesis. The effects of different variables will not likely always be equal, and they may only act in synergy with other niche axes, so exploring this space will be challenging but hopefully useful for better understanding community assembly mechanisms in global change scenarios.

Acknowledgements We thank Juanjuan Zhang, Fuwei Wang, Yangguang Ji, Yi Yang, Fei Yang, and Ying Wang for help in experimental maintenance and sampling in field, and Xiaoqing Shao, Huixin Zhang, Zirong Ren and Jiatong Wang for help in lab analyses. We also thank Dr. Zhengwei Ren for helpful suggestions. We are grateful to the Research Station of Alpine Meadow and Wetland Ecosystem Tibetan Plateau of Lanzhou University for providing support in the field. This study was supported by National Natural Science Foundation of China (31971435) and National Key Research and Development Program of China (2017YFC0503902).

Author contribution statement H.G., S.H. and X.Y. designed the research. X.Y., K.H., X.L., X.X. and F.S. conducted the field experiment. X.Y. performed the lab analyses. X.Y., H.G. and J.D. analyzed the data. X.Y. and H.G. wrote the first draft of the manuscript. J.D., L.J., S.L. and S.H. contributed substantially to revisions.

Data accessibility statement We confirm that if our manuscript is accepted, the data supporting the results will be archived in an appropriate public repository.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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