Short-term responses of an alpine meadow community to removal of a dominant species along a fertilization gradient

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Abstract

Aims

The relationship between biodiversity and ecosystem functioning has intrigued ecologists for several decades, but the effect of loss of a dominant species on community structure and functioning along a nutrient gradient remains poorly understood. The aim of this paper was to test the effect of a dominant species on community structure and function by conducting a species removal experiment along a fertilization gradient.

Methods

We removed the population of a dominant species (*Elymus nutans*) in a long-term fertilization field in an alpine meadow on the Tibetan Plateau, China. Univariate general linear models were used to evaluate the effects of fertilization and removal on above-ground vegetation characteristics, including photosynthetically active radiation in the understory, species richness, Shannon–Weiner diversity index, Simpson's dominance index, above-ground biomass (including different functional groups) and seedling richness and density.

Important Findings

Results revealed that after two plant growing seasons, there was no significant effect of the removal of a dominant species on species richness and diversity of the remaining vegetation, but the biomass of forbs and seedling recruitment were significantly increased indicative of the potential for long-term effects. Moreover, removal had a large effect at high fertilization levels, but little effect when fertilization levels were low. Our studies indicated that community response to loss of a dominant species was mainly dependent on resource availability and the remaining functional group identities. We also found seedling recruitment was usually more sensitive to the influence of competition of dominant species than the established vegetation in the short term.

Keywords: alpine meadow, competition, dominant species, fertilization, removal, Tibetan Plateau

Received: 28 May 2014, Revised: 28 October 2014, Accepted: 22 November 2014

INTRODUCTION

Fertilization can cause species diversity loss and a shift in species dominance and composition, and these changes further affect productivity, litter decomposition and seedling recruitment (Chapin *et al.* 1998; Dickson *et al.* 2014; Gross *et al.* 2005).

The magnitudes of the responses of species diversity and community productivity to fertilization appear to mainly depend on traits of dominant species, which is an important driver factor, both in the short term by affecting seedling recruitment and in the long term, by driving soil processes that regulate nutrient supply for other species (Clark *et al.* 2007).

Over the past several decades, ecologists have focused on studies of 'biodiversity–ecosystem functioning', i.e. the relationship between species diversity and composition in an ecosystem and the functioning of this ecosystem (Balvanera *et al.* 2006; Duffy 2009). Data predict that losses in species diversity will have a negative effect on ecosystem functioning, including productivity and soil nutrient cycling (Balvanera *et al.* 2006; McLaren and Turkington 2010). Early experiments about biodiversity–ecosystem functioning often showed that effects of the identity of species or functional groups in a community may have as much of an impact as the number of species. The 'mass ratio hypothesis' proposed by Grime (1998) predicts that the influence of a species or functional group on ecosystem functioning or stability is proportional to their input to primary production. According to this hypothesis, the functioning of ecosystems is determined to a large extent by the traits of the dominant species. Experimental tests also have supported this hypothesis (Laughlin 2011). In contrast, other studies have shown that functional diversity (the extent of trait differences between species in a given community) is also important in driving ecosystem functioning (Flynn *et al.* 2011; Mason *et al.* 2013). Recently, removal experiments have been promoted for biodiversity–ecosystem functioning studies in natural communities (McLaren and Turkington 2010).

Removal experiments have long been used to examine the interactions among species or functional groups in a community (Aksenova *et al.* 1998; McLaren and Turkington 2010). More recently, experiments removing a species from a community have been used to examine the effects of local non-random species loss on both community functioning and the remaining plant community properties (Longo *et al.* 2013; McLaren and Turkington 2010). Removal experiments can demonstrate competitive interactions among species if removals cause increases in diversity or biomass of the remaining community (Aksenova *et al.* 1998), facilitation interactions if the remaining community decreases in diversity or biomass (Shevtsova *et al.* 1997) and neutral interactions if there is no response (Bret-Harte *et al.* 2004).

Much of classical ecology theory relies on the assumption that competition is a major biotic factor determining the structure of plant communities (Hutchinson 1959; MacArthur 1970; MacArthur and Levins 1967). For example, light competition hypotheses propose that as productivity increases, availability of light in the understory is reduced, leading to the mortality or competitive exclusion of shorter species (Hautier *et al.* 2009; Newman 1973). Conversely, Grime's theories (1977) predict that competition can be unimportant in structuring plant communities of low productivity. Correspondingly, Grime's hypothesis predicts that facilitation, rather than competition, will become more important as environments become more stressful (Mitchell *et al.* 2009).

The types of interactions that occur among species or functional groups, or the effects of removal, may be dependent on the environmental context or limiting resource. For example, the competitive ability of a species can change along resource gradients, and the ability of species to colonize after removals is likely to depend on environmental conditions (McLaren and Turkington 2011; Tilman 1984). Therefore, we chose to test the interaction of resource availability (fertilization) with a dominant species removal.

Dominant species may be the best competitors by rapidly drawing down resources (Li *et al.* 2011a) or by surviving resource suppression (Goldberg and Landa 1991). Alternatively, these dominant species may use positive soil feedbacks (Bever 2003) or colonize open space quickly (Wildová *et al.* 2012). In recent years, however, the frequency with which competition occurs between dominant species and other species in nature and the importance of dominant competition in structuring communities has been the subject of debate (Freckleton *et al.* 2009; Rees 2013). Several studies in grassland ecosystems demonstrate that reduction in the abundance of the dominant grasses may result in competitive release of subordinate grass and forbs species (Silletti *et al.* 2004). An inverse relationship between grass dominance and diversity also has been documented in many restored grasslands (Baer *et al.* 2004). In contrast, many studies have shown that increased dominance of particularly stable grass species can increase community temporal stability (Yang *et al.* 2011). The relative importance of potential limiting resources (e.g. light, soil nutrients) is likely to vary in grasslands. For example, fertilization may result in higher nutrient availability, whereas seedling recruitment and plant establishment may be affected by lower light availability at the soil surface (Foster and Gross 1998; Hautier *et al.* 2009).

Experiments demonstrating the dramatic effects of the removal of a dominant competitor on community structure have been conducted in different systems (Busch *et al.* 2005; Kunte 2008). More recently, removal experiments in natural communities have been promoted for biodiversity–ecosystem functioning studies (Longo *et al.* 2013; McLaren and Turkington 2011). The role of a particular species in an intact community can be determined by observing how a community functions with a full complement of species compared with a community with that species removed. Most experimental studies of competition in natural plant communities have examined the effects of competition on the growth of plants of a single species, or estimated the competitive effects of community components. It has often been observed that experimental enhancement of soil fertility in plant communities can lead to an increase in productivity, a dramatic reduction in species diversity, but an increase in the dominance of a few species (Yang *et al.* 2011). Such changes in community composition have commonly been attributed to the exclusion of other species by competitively superior dominants where soil nutrients are high and rapid growth is possible. In addition, perturbations (e.g. grazing, mowing or target species removal) can decrease vegetative biomass and height, but facilitate seedling recruitment by creating available microsites and decreasing competition (Gallego *et al.* 2004) with tall plants.

The purpose of this experiment was to examine the effect of a dominant species on community structure (species richness, Shannon–Weiner diversity index, Simpson's dominance index) and function (above-ground biomass) along a gradient of fertility by simultaneously manipulating soil resources and the presence of the dominant species in an alpine meadow on the Tibetan Plateau, China. Ecosystem capacity to respond to a perturbation such as fertilization may therefore depend on the characteristics of the species that becomes dominant (Yang *et al.* 2011). We tested the hypotheses that (i) removing the dominant species can increase light availability in the understory, leading to competitive release of other subordinate species, (ii) removal of dominant species can affect species richness and diversity, and the community biomass can be compensated by the remaining functional groups, (iii) the effect of dominant species removal varies with level of soil fertility, such that removal of dominant species at higher soil fertility levels has a greater effect on community response compared with the removal at lower soil fertility levels and (iv) dominant species removal has a significant effect on seedling recruitment or community recovery after perturbation.

MATERIALS AND METHODS

Study site description

The experiment was conducted at the research station of alpine meadow and wetland ecosystems of Lanzhou University (N33°58′, E101°53′) on the eastern Tibetan plateau, 3500 m a.s.l., Gansu, China, The average yearly temperature is 1.2°C, ranging from −10°C in January to 11.7°C in July, with ~270 frost days. Average annual precipitation over the last 35 years is 620 mm (most in summer). The annual cloud-free solar radiation is ~2580 h (Li *et al.* 2011a). The sub-alpine meadow soil has relatively low P availability (<2 mg available P kg⁻¹ dry soil). The vegetation, typical of Tibetan alpine meadows, is dominated by clonal *Kobresia* spp., *Elymus nutans, Festuca ovina, Poa poophagorum, Agrostis* spp., *Saussurea* spp. and *Anemone rivularis* (Li *et al.* 2011a). The experimental site has been overgrazed in the past, but has been fenced and only grazed in winter and early spring (October to April in the following year) since 2000.

Experimental design

The long-term fertilization experiment was established on a flat field (slope is <1°) in this experimental site in March 2000. Sixteen 6×10-m² plots composed of four fertilization levels with four replicates were distributed in four columns and four rows with a randomized block design. Each plot was separated from the others by a 1-m buffer strip. The fertilization treatment was generated with different amounts of $(NH_4)_2\ HPO_4$ fertilizer applied annually since 2000 at the beginning of the growing season (usually in the middle of May). Fertilizer applications of 0, 30, 60 and 120 g m⁻² year⁻¹ are hereafter referred to as F0, F30, F60 and F120, which corresponds to 0, 6.3, 12.6 and 25.2 g N m⁻² year⁻¹ and 0, 7.0, 14.0 and 28.0 g

P m⁻² year⁻¹, respectively. The fertilizer was applied in May each year during a rain event (Li *et al.* 2011a). The original goal of this experiment was to test the relationship between productivity and diversity and other ecological questions (e.g. Luo *et al.* 2006; Niu *et al.* 2008; Yang *et al.* 2011).

We carried out a removal experiment (beginning on 17 May 2009) in this long-term fertilization field to test the important impacts of a dominant species on community function and structure. Four 0.5×0.5 m² permanent quadrats were established in each plot. The quadrat location was randomly selected with the constraint that it was at least 0.5 m from the margin to avoid edge effects. Half of the quadrats were randomly assigned for removal treatments. All tillers and root crowns of the dominant species, *E. nutans*, were removed by clipping at the soil surface, with all other vegetation left undisturbed. After establishment of the removal treatments in 2009, some below-ground stems remained and regrowth occurred. Treatments were maintained by removing the regrowth of target species in summer.

Vegetation monitoring

Community measurements were conducted from 2 to 4 September 2011. We estimated the cover of each species and recorded the number of seedlings in each quadrat before being clipped and brought to the lab. For clonal species, an individual plant was defined as a group of tillers connected by a crown (Luo *et al.* 2006). Seedlings were counted as separate individuals. The cover of each species in each plot was estimated as a percentage using a canopy interception technique based on cardboard cut-outs of various shapes and sizes as visual guides. Summed cover of all species frequently exceeded 100%. For above-ground biomass, we distinguished between sedges, grasses, legumes and other forbs. All samples were dried at 80°C for 48 h and weighed to the nearest 0.01 g.

In each plot, we measured light with a Decagon Sunfleck ceptometer (Decagon, Pullman, Washington, DC) at the time of vegetation monitoring on 1 September 2011. Light readings were taken on a cloudless day (11:00–13:00 h). Photosynthetically active radiation (PAR) was recorded at 10 cm above the soil surface (under the plants) and at the top of the canopy. The ratio between these two measurements was taken as a proxy for PAR reaching the understory.

Data analysis

From the vegetation harvest data, we calculated the above-ground biomass (including different functional groups), and two indices were selected to estimate diversity according to Pielou (1969). The first index is plant species richness, represented by the number of species recorded in each quadrat. The second, the Shannon–Weiner diversity index is $H' = -\sum_{i=1}^{S} P_i \log_2 P_i$, where P_i is the relative abundance of species i (P_i = cover of each a species in a quadrat/total cover of all species in a quadrat) and S is the species richness. In addition, we calculated the community Simpson's dominance index,

which is the sum of the species' squared relative abundances (Simpson 1949).

The effects of the long-term fertilization on the soil characteristics and the cover and height of *E. nutans* were tested by one-way analysis of variance before conducting a species removal experiment.

All analyses included block, fertilizer treatment and removal treatment as categorical factors, and the interaction of fertilization × removal was also tested. Univariate general linear models were used to estimate the effects of fertilization and removal on above-ground vegetation characteristics, including PAR in the understory, above-ground biomass (including different functional groups), species richness, Shannon–Weiner diversity index, Simpson's dominance index and seedling number and richness. *Post hoc* comparisons for different treatments were made using Tukey's Honest Significant Difference. Natural logarithmic transformations were used when data did not meet statistical assumptions (normality of residuals, homogeneity of variance and data linearity). F statistics were considered significant at α = 0.05. All statistical analyses were performed using the software program SPSS, version13.0 (SPSS Inc., Chicago, IL).

RESULTS

Changes of soil properties and *E. nutans* after long-term fertilization treatment

Ten years of fertilization significantly increased the soil available N concentration and available P concentration (Table 1). Fertilization treatment did not change the organic C content ($F_{3, 7} = 0.398$, $P = 0.808$) and soil pH ($F_{3, 7} = 2.497$, $P = 0.077$). The vegetation composition shifted from dominance initially by sedges and forbs, to being dominated by a single grass, *E. nutans*, which became increasingly dominant ($F_{3, 7} = 1193.68$, $P < 0.001$) and taller ($F_{3, 7} = 27.26$, $P < 0.001$) with fertilization (Table 1).

Effects of fertilization and removal on above-ground vegetation characteristics

Fertilization significantly decreased the PAR in the understory (~10 cm near the soil surface, Table 2; Fig. 1), but removal

significantly increased the PAR in the understory (Table 2; Fig. 1), especially for higher fertilization levels (Fig. 1).

Fertilization significantly decreased species richness (Table 2; Fig. 2A) and diversity (Table 2; Fig. 2B), but significantly increased community dominance (Table 2; Fig. 2C). Increased dominance was mainly driven by the response of the dominant species (*E. nutans*) in our results (Table 1). On the contrary, removal treatment did not change species richness (Table 2; Fig. 2A) and diversity (Table 2; Fig. 2B) of the remaining community, but significantly decreased community dominance (Table 2; Fig. 2C), which was associated with the removal of the dominant species (*E. nutans*), and the exclusion of strong light limitation (Fig. 1). Fertilization by removal interaction had no effects on species richness (Table 2), but had significant effects on Shannon–Weiner diversity index (Table 2) and dominance (Table 2). Block and the interaction of fertilization × removal effects were unimportant in this experiment. We therefore mainly focused on nutrient and removal effects on vegetation and diversity.

As expected, fertilization significantly increased above-ground biomass (Table 2; Fig. 3A), including grass biomass (Table 2; Fig. 3B), sedge biomass (Table 2; Fig. 3C), forb biomass (Table 2; Fig. 3D) and legume biomass (Table 2; Fig. 3E). Removal significantly decreased the above-ground biomass (Table 2; Fig. 3A), including grass biomass (Table 2; Fig. 3B). Removal had no effects on sedge biomass (Table 2; Fig. 3C) and legume biomass (Table 2; Fig. 3E), but significantly increased forb biomass (Table 2; Fig. 3E); moreover, removal had a large effect on forb biomass at higher fertilization levels, but little effect when fertilization levels were lower (Fig. 3E).

Fertilization significantly decreased the density (Table 2; Fig. 4A) and richness of seedlings (Table 2; Fig. 4B), but removal significantly increased the density (Table 2; Fig. 4A) and richness of seedlings (Table 2; Fig. 4B), and the seedlings had greater recruitment at higher fertilization levels than at low fertilization levels (Fig. 4).

DISCUSSION

Vegetation in most ecosystems has been altered by plant invasion and species loss from disturbances. It has become crucial,

Table 1: changes for soil properties and *E. nutans* after long-term fertilization treatment

		F0	F30	F60	F120
Soil properties	Soil organic C (%)	1.7 (0.06)	1.6 (0.07)	1.6 (0.08)	1.7 (0.05)
	Soil available N (mg kg^{-1})	17.3 (1.15)c	20.3 (1.32)bc	34.6 (2.34)b	48.9 (3.51)a
	Soil available P (mg kg^{-1})	2.6 (0.64)d	39.9 (2.31)c	82.4 (3.27)b	176.5 (4.11)a
	pH	7.1 (0.12)	6.8 (0.09)	6.7 (0.14)	6.3 (0.21)
E. nutans	Relative cover (%)	6.3 (1.6)d	20.1 (2.1)c	82.6 (5.1)b	99.8 (9.6)a
	Height (cm)	48.9 (3.3)c	69.2 (3.6)b	88.4 (3.1)a	99.3 (4.9)a

Values in the table are means with standard error in parentheses (*n* = 8). F0, F30, F60, F90 and F120 represent $(NH_4)_2HPO_4$ fertilizer applications of 0, 30, 60 and 120 g m^{-2} year^{-1}. Significant differences across treatments within each variable were determined using Tukey's Honest Significant Difference test (*P* < 0.05) after one-way analysis of variance and are indicated by dissimilar letters.

Table 2: GLM of effects of treatments on above-ground vegetation characteristics

Variable	Source	Mean square	*df*	*F*	*P*
Richness	Block	23.355	3	2.836	0.053
	Fertilization	16 688.444	3	202.231	**<0.001**
	Removal	1.000	1	0.124	0.734
	Fertilization × removal	6.293	3	0.764	0.524
Diversity index	Block	0.071	3	0.324	0.808
	Fertilization	32.075	3	145.981	**<0.001**
	Removal	0.148	1	0.675	0.417
	Fertilization × removal	1.022	3	4.051	**0.008**
Dominance index	Block	13.548	3	3.975	0.062
	Fertilization	0.552	3	67.002	**<0.001**
	Removal	2.397	1	290.975	**<0.001**
	Fertilization × removal	0.551	3	66.943	**<0.001**
Above-ground biomass	Block	442.131	3	4.224	0.053
	Fertilization	5446.323	3	15.956	**<0.001**
	Removal	72 671.556	1	212.845	**<0.001**
	Fertilization × removal	17 557.794	3	51.427	**<0.001**
Grasses biomass	Block	382.736	3	5.838	0.059
	Fertilization	18 586.457	3	76.644	**<0.001**
	Removal	143 363.322	1	591.152	**<0.001**
	Fertilization × removal	22 031.309	3	90.843	**<0.001**
Sedges biomass	Block	143.416	3	4.235	0.065
	Fertilization	2217.953	3	65.521	**<0.001**
	Removal	0.191	1	0.015	0.943
	Fertilization × removal	11.095	3	0.337	0.815
Legumes biomass	Block	11.555	3	1.08	0.372
	Fertilization	109.31	3	10.18	**<0.001**
	Removal	0.862	1	0.08	0.781
	Fertilization × removal	0.471	3	0.04	0.852
Forbs biomass	Block	98.714	3	2.23	0.092
	Fertilization	2121.346	3	24.09	**<0.001**
	Removal	11 287.756	1	11 287.65	**<0.001**
	Fertilization × removal	405.038	3	405.03	**0.001**
Seedlings density	Block	109.125	3	1.119	0.356
	Fertilization	3975.424	3	40.769	**<0.001**
	Removal	2575.563	1	26.416	**<0.001**
	Fertilization × removal	716.063	3	7.344	**0.001**
Seedlings richness	Block	4.432	3	1.854	0.157
	Fertilization	132.724	3	55.519	**<0.001**
	Removal	87.891	1	36.365	**<0.001**
	Fertilization × removal	9.057	3	3.789	**0.020**
PAR	Block	617.75	3	1.24	0.698
	Fertilization	339.633	3	15.137	**<0.001**
	Removal	13 838.000	1	616.753	**<0.001**
	Fertilization × removal	4053.533	3	14.48	0.0621

Factors include fertilization and removal on species richness, Shannon–Wiener diversity index, above-ground biomass, grasses biomass, sedges biomass, legumes biomass, forbs biomass, seedlings density, seedlings richness and PAR. The interactions of block with fertilization or removal are not shown in this table. Significant effects (*P* < 0.05) are in bold.

therefore, to understand how species that are added to or lost from plant communities affect ecosystem functions like productivity. Our study was the first to examine the influence of a dominant species on community structure and function in an alpine meadow in Tibetan Plateau, China. Our results revealed that after two plant growing seasons, there was no
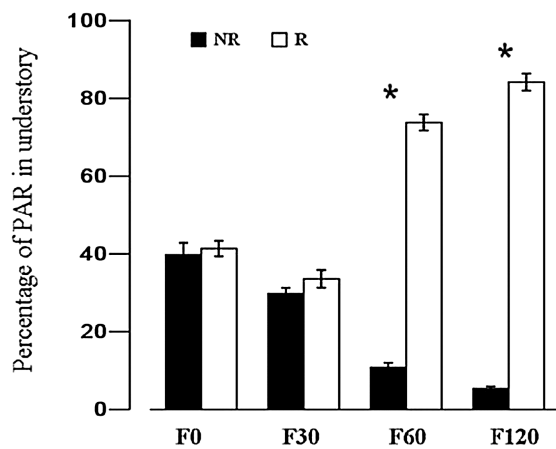
Figure 1: effects of fertilization and removal on PAR in the understory (~10 cm near the soil surface). F0, F30, F60, F90 and F120 represent $(NH_4)_2HPO_4$ fertilizer applications of 0, 30, 60 and 120 g m^{-2} $year^{-1}$. Asterisks (*) indicate a significant difference ($P < 0.05$) between NR and R treatment in each fertilization level. Abbreviations: NR = no removal, R = removal.

significant effect of the dominant species removal on species richness and diversity, whereas forb biomass and seedling recruitment were significantly increased.

Grime (1998) proposed the 'mass ratio' hypothesis, which states that ecosystem functioning and processes are largely controlled by the dominant species. After fertilization of grasslands, grasses commonly become dominant, resulting in overall low species richness and diversity (Li *et al.* 2011a; Silvertown *et al.* 2006; Yang *et al.* 2011). Manipulating factors that decrease grass dominance may provide competitive release for other species (Hartnett *et al.* 1996). Tilman (1988) proposed that light levels at the soil surface can be of critical importance in determining the outcome of competition. In our study, removing the dominant grass, *E. nutans*, led to increased PAR in the understory and forb biomass, but effects on species diversity were limited. The data support the hypothesis that competition with the dominant species, *E. nutans*, limits other species or functional groups in this community. These results were consistent with other short-term studies, which indicate that dominant species removals often impose little effect on community diversity (Belsky 1992; Spackova *et al.* 1998). In contrast, other studies showed that species diversity increased with dominant species removal (Wardle *et al.* 1999). Smith and Knapp (2003) removed dominant grass species over two growing seasons and documented a decrease in aboveground biomass and grass cover with no significant effect on forbs species, resulting from the apparent lack of competitive release from stressful environment conditions (e.g. decreased light) modulated by the dominant species. We interpret that the lack of competition release in our study may result from (i) the area of the quadrat (0.5×0.5 m^2) that we used in this experiment may be smaller compared to the large untreated area and (ii) the short-term nature of the experiment and the fact that species interactions may become more important over a longer time period.
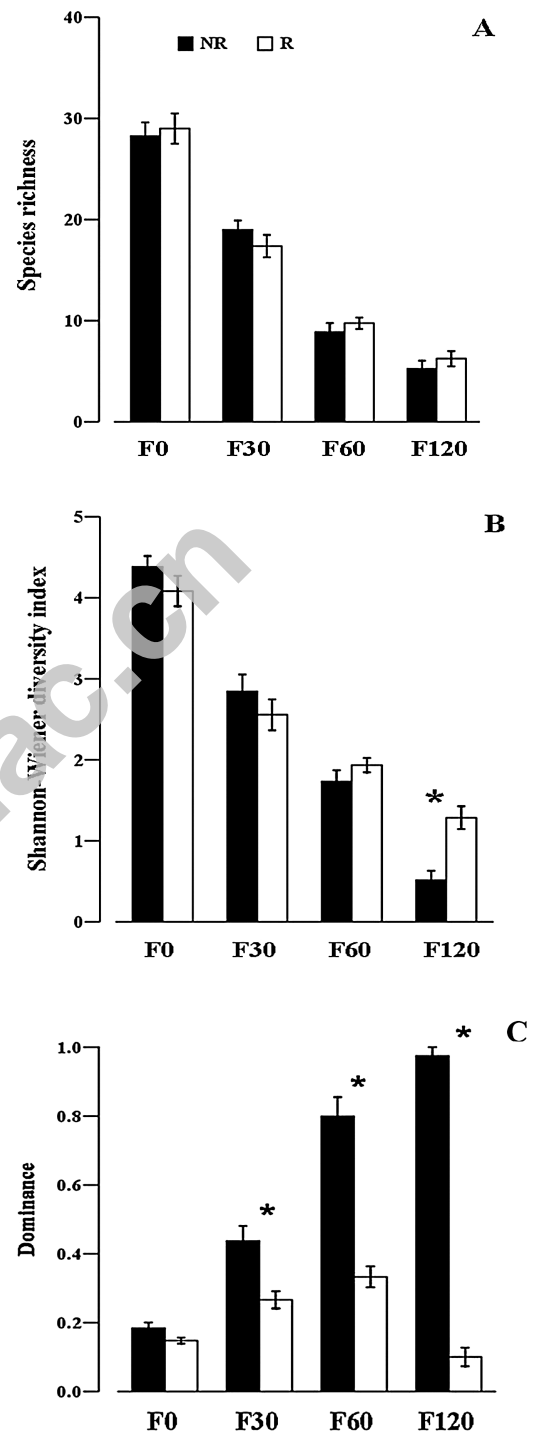

Figure 2: effects of fertilization and removal on species richness (**A**), Shannon–Wiener diversity index (**B**) and dominance (**C**). F0, F30, F60, F90 and F120 represent $(NH_4)_2HPO_4$ fertilizer applications of 0, 30, 60 and 120 g m^{-2} $year^{-1}$. Asterisks (*) indicate a significant difference ($P < 0.05$) between NR and R treatment in each fertilization level. Abbreviations: NR = no removal, R = removal.

By removing an independent dominant species, we can remove the competitive effects from that species (as well as other influences on community properties). No response or
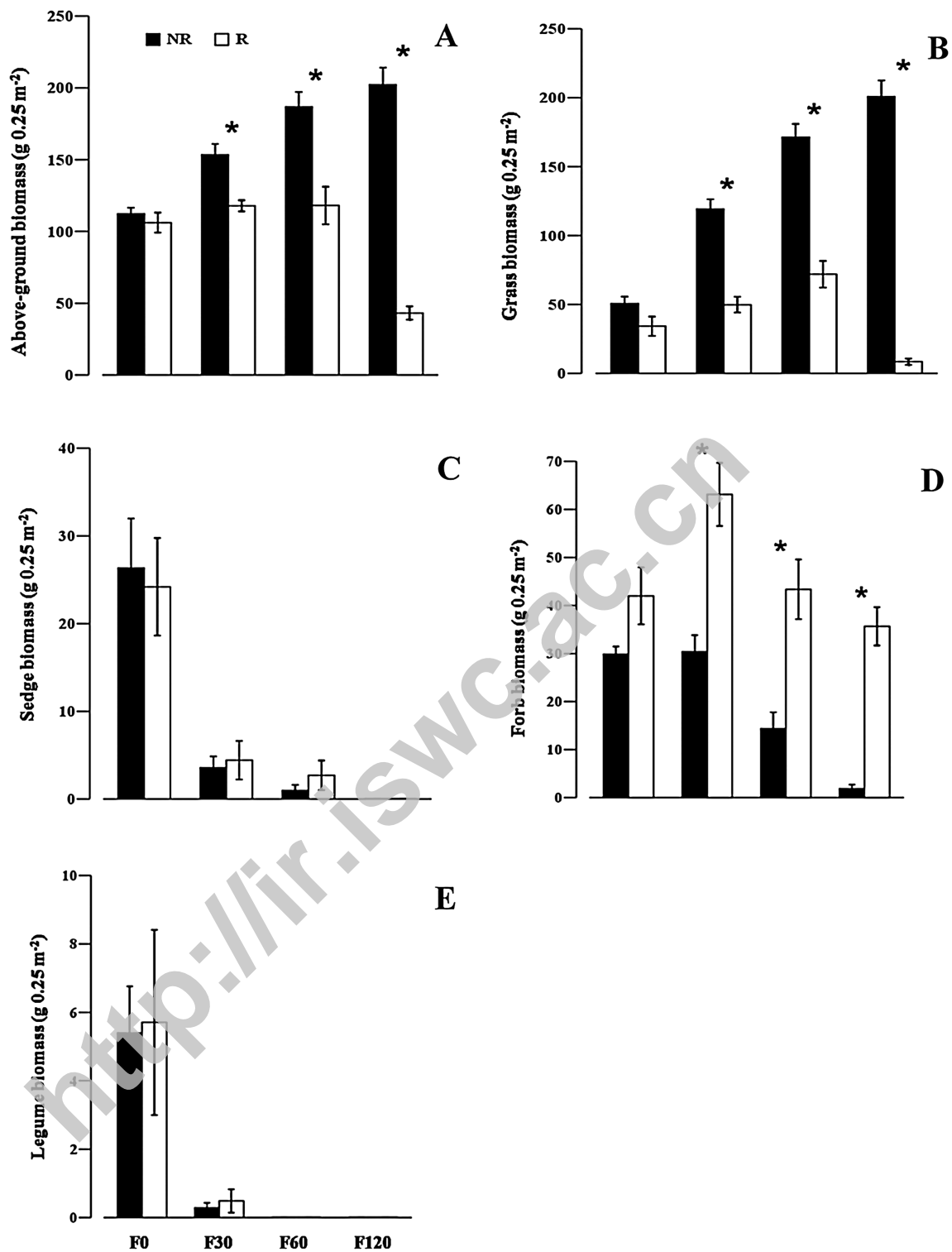
Figure 3: effects of fertilization and removal on above-ground biomass (**A**), grasses biomass (**B**), sedge biomass (**C**), forb biomass (**D**) and legume biomass (**E**). F0, F30, F60, F90 and F120 represent $(NH_4)_2HPO_4$ fertilizer applications of 0, 30, 60 and 120 g m^{-2} year^{-1}. Asterisks (*) indicate a significant difference ($P < 0.05$) between NR and R treatment in each fertilization level. Abbreviations: NR = no removal, R = removal.

delayed response of the remaining functional groups or species to removals may indicate a lack of strong competitive effects of the removed species, supporting predictions that ecosystems may be limited more by harsh environmental conditions than

competitive interactions (Mitchell *et al.* 2009).The degree of bio-mass compensation was affected not only by the identity of the removed species but also by the identity of remaining functional groups. In this community, forbs species comprise the bulk of
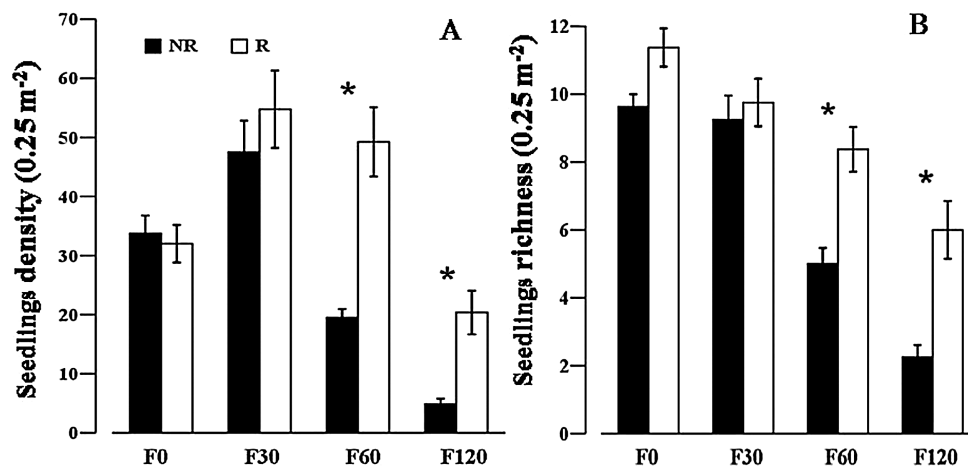
Figure 4: effects of fertilization and removal on seedlings density (**A**) and seedlings richness (**B**). F0, F30, F60, F90 and F120 represent $(NH_4)_2HPO_4$ fertilizer applications of 0, 30, 60 and 120 g m^{-2} year^{-1}. Asterisks (*) indicate a significant difference ($P < 0.05$) between NR and R treatment in each fertilization level. Abbreviations: NR = no removal, R = removal.

species diversity, as in most herbaceous communities (Grime 1998), and removing dominant species may provide competitive release (increased light penetration) for the subordinate species and an opportunity for forbs to increase in biomass. Neither remaining grasses nor sedges and legumes showed any change when a dominant species was removed, suggesting a lack of strong competition. In other words, community response may be functional group-specific. The lack of response or slow response to removal may also have been due to the high elevation (or low temperature) of this experiment. Other studies have shown that the lack of response of the remaining community is likely not due to variation in the effects of removals on soil properties over time (McLaren and Turkington 2010). In addition, much of the biomass in this community is below ground, and root recovery patterns may not parallel the above-ground patterns. Below-ground biomass measurements are destructive for soils, however, and thus were not examined in this study.

Nutrient enrichment can remove the limiting factor and thus allow the species to take best advantage of the resource (Dickson et al. 2014; Li et al. 2011a). Moreover, the suppression of other species by the dominant is strongest at high soil fertility (Grime 2001). Our results support the hypothesis that competition from the dominant species is more important in structuring the community when nutrients are higher than when nutrients are more limited (Grime 2001). The forb biomass was greater at high resource levels than at low (control) resource levels in the removal treatment. It may be that such effects are difficult to detect on less fertile soils, or that species are unable to develop such strong competitive dominance over other species in less fertile environments. From the perspective of diversity-stability relationships, the remaining functional groups (forbs) can maximize community biomass and stability to offset the negative effects of species loss, especially at higher resource levels. In addition, the dominance of *E. nutans* was not obvious at low (control) resource levels in this alpine meadow, in which the vegetation composition was dominated initially by sedges (*Kobresia* spp.).

Seedling regeneration has been shown to be an important factor affecting community composition in a number of studies ranging from experimental to theoretical (Grubb 1977). Plant colonization and species diversity maintenance are often limited by successful seedling recruitment under different habitats in grasslands communities (Li et al. 2011b; Zobel et al. 2000). Due to the almost complete exclusion of light below the canopy at higher resource levels in the no-removal plots, it is very difficult for seedlings of most species (particularly short or rosette-forming species) to establish, grow and persist (Hautier et al. 2009; Lamb et al. 2009). In this study, decreased coverage after dominant species removal led to more sunlight reaching the understory, and therefore significantly increased the seedling richness and density. We also found that the seedlings have more recruitment chance at higher resource levels than at low resource levels, consistent with other studies (Foster and Gross 1998; Hautier et al. 2009). However, some other studies find that the effect is weak or inconsistent (Dickson and Foster 2011; Suding and Goldberg 1999). Moreover, light limitation may affect seedlings more than adult plants because seedlings are smaller than adult plants and fall victim to the unidirectional supply of light and asymmetric light competition. We conclude that shading (canopy shade) is undoubtedly an important factor that influences seedling recruitment in this alpine meadow community.

Our results demonstrated that the responses of established plants and seedlings to removal treatments are very different. The lack of response in the established vegetation is probably due to their response time being longer than that of the seedlings. In any case, the results clearly show that competition by the dominant species is an important factor influencing community structure and seedling recruitment. Together, these results also suggest that management practices that increase canopy openness and light availability (e.g. mowing or target species removal) can increase forb biomass and

species recruitment in this alpine meadow community. It is our intention to continue to maintain these treatments and follow the community dynamics in the future.

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