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Functional group dominance and not productivity drives species richness

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Background: There is a lack of consensus about the productivity–richness relationship, with several recent studies suggesting that it is not productivity but other factors that are the important drivers that determine species richness.
Aims: Here, we examine the relationship between productivity, functional group dominance and plant species richness at the plot scale in Tibetan Plateau meadows. These alpine meadows are ideal to examine the species productivity-richness relationship because they have a very high species richness, a large gradient in productivity, and can be dominated by either graminoids (grasses and sedges) or forbs.
Methods: We measured plant species richness and above-ground biomass along a natural gradient of functional group abundance in 44 plots distributed across five natural, winter-grazed but otherwise undisturbed sites in the eastern part of the Qing-Hai Tibetan Plateau, in Gansu province, China in 2008.
Results: Graminoid abundance (i.e. graminoid biomass as percent of the total above-ground biomass) explained 39% of plot differences in species richness while neither productivity nor the biomass of the three most abundant plant species, either individually or combined, were a significant predictor of species richness.
Conclusions: Our results show that within these alpine meadows, a shift from graminoid to forb dominance, rather than the individual dominant species or productivity itself, is strongly correlated with species richness. Thus, differences in functional group abundance can be a strong driver of observed plant species richness patterns.

Keywords: dominance–richness; functional groups; productivity–richness relationship; species richness; species diversity; graminoid abundance; graminoid dominance; Tibetan Plateau

Introduction

The productivity–richness relationship has been an important research topic, however patterns and their underlying mechanisms remain controversial (Gross and Cardinale 2007; Adler et al. 2011; Cusens et al. 2012; Fraser et al. 2015). The classic study by Al-Mufti et al. (1977) found a hump-shaped relationship between plant standing biomass and species richness. However, in subsequent studies almost any possible patterns have been found (Mittelbach et al. 2001; Adler et al. 2011; Cusens et al. 2012). Overall, there is no consensus and some studies have argued that there is no universal productivity–richness relationship along natural gradients (Grace et al. 2007; Gross and Cardinale 2007), and that productivity is a poor predictor of plant species richness (Adler et al. 2011). However, others have argued that studies at many sites cover too small part of a range of productivity or standing plant biomass to detect a reliable pattern (Fridley et al. 2012) and that combining different vegetation types to have a larger productivity gradient can be problematic especially if the scale or size of plants differs (Chase and Knight 2013; Fraser et al. 2015). However, natural gradients in plant species richness have not only been hypothesised to be driven by (a) productivity (Al-Mufti et al. 1977), but also by other factors such as (b) differences in dominant species (Misra and Misra 1981), (c) differences in functional groups (Rusch and Oesterheld 1997; Gilbert et al. 2009; Miles and Knops 2009a; Dickson and Gross 2013) and (d) abiotic factors including temperature, water, nutrients, light availability, environmental heterogeneity and disturbance (Pausas and Austin 2001; Borer et al. 2014).

Studies that have experimentally increased productivity by nutrient addition almost universally have found a decrease in species richness (Clark and Tilman 2008; Ren et al. 2010). However, these nutrient additions also lead to changes in dominant species or functional group (Tilman 1987; Dickson and Gross 2013), suggesting that changes in species or functional group abundance drive declines in richness due to fertilization (Dickson and Gross 2013). Experiments have shown that dominant species or functional groups can be related to the occurrence of other species in a community (Miles and Knops 2009a) and influence the establishment of new species (Gilbert et al. 2009; Miles and Knops 2009b), also suggesting that

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dominant species or functional groups may be of key importance in determining the overall community dynamics, including community richness and productivity (Grime 1998; Gilbert et al. 2009; Dickson and Gross 2013). Thus, because experimentally induced increases in productivity also change species and functional group abundances, experimental studies can only provide limited insights into how species richness depends on productivity.

Experimental studies have changed the question from how productivity influences species richness to how species richness influences productivity. These studies have shown that plant richness can be an important factor related to higher productivity (Tilman et al. 1996, 2001). However, dominant species (Whittaker 1965; Grime 1998; Vile et al. 2006; Emery and Gross 2007) and functional group compositions (Reich et al. 2004; Wang et al. 2004; Li et al. 2010) also strongly influence productivity. Observational (Grime 1998; Wilsey 2010) and experimental studies (Tilman et al. 1996; Reich et al. 2004) have shown that dominants (Whittaker 1965; Grime 1998; Vile et al. 2006) and functional group differences (Reich et al. 2004; Wang et al. 2004; Li et al. 2010) can be a key driver of species richness and productivity. In addition, experiments manipulating plant species richness have involved either synthetically assembled communities (Tilman et al. 1997; Reich et al. 2004) or species deletions (Symstad and Tilman 2001; Díaz et al. 2003), and both types of artificial communities are less diverse, smaller in size, shorter in duration and much simpler in ecological structure relative to natural communities (Hooper et al. 2005; Cardinale et al. 2007). Synthetically assembled communities are also strongly different from assemblages in natural ecosystems (Guo et al. 2006), and synthetic communities can be unstable with different rates of invasions depending on the community species and functional group composition (Knops et al. 1999; Fridley et al. 2012). Thus, experimental species richness manipulations can only provide limited insights into mechanisms that drive natural gradients in productivity and species richness.

It is clear from these observational and experimental studies that there exists a tangled web between productivity, species richness, dominant species and functional groups. Therefore, to be able to examine the relationship between productivity and species richness, it is required to examine how species richness depends on functional group dominance or functional group composition (Grace et al. 2014). However, the range of functional group composition is often limited along natural gradients, especially for productivity gradients, and graminoids almost always contribute the majority of the productivity within grasslands (Whittaker 1965; Smith and Knapp 2003). Alpine meadows on the Tibetan Plateau provide an ideal system to examine how species richness is influenced by functional group dominance, productivity and plant richness, because these meadows have a large gradient in functional group dominance, a large gradient in productivity and very high species richness. Above-ground productivity varies

from 70 to 560 g/m^2. Abundance (i.e. biomass as percent of total above-ground biomass) varies from 4% to 94% for graminoids (grasses plus sedges), from 3% to 85% for forbs (Wang et al. 2004; Li et al. 2009), and from 1% to 15% for legumes. Approximately, 1900 species occur in the eastern Tibetan Plateau (Qi et al. 2014) and species richness can be as high as 50 species per m^2 (Li et al. 2009). Within these alpine Tibetan meadows, we tested the hypotheses that plant species richness was inversely driven by productivity, supported by an inverse correlation between richness and productivity. The alternative hypothesis was that species richness was not correlated with productivity, and therefore dominant species abundance differences and/or functional group differences drove patterns in species richness.

Materials and methods

Study sites

We measured plant species richness and above-ground biomass in 44 plots distributed across five natural, winter grazed, i.e. grazing between November and May, but otherwise undisturbed sites in the eastern part of the Qing-Hai Tibetan Plateau, in Gansu province, China in 2008 (Table 1). Tibetan herders typically manage the lower elevation meadows as only winter grazing because these are accessible year round, whereas the higher elevations and steeper slopes are only accessible during the summer, hence these meadows are used for summer grazing. In this region, vegetation is mainly grazed by domestic livestock, with stocking density of 0.18–0.25 yaks ha^{-1}, 3.7–4.0 sheep ha^{-1} and much lower density of horses and cattle (Long et al. 2008; Cao et al. 2011; Yang et al. 2012). Domestic livestock grazing has been common in Tibetan meadows for at least 8000 years (Miehe et al. 2014). Native grazers, such as Tibetan antelope (*Pantholops hodgsonii*), Tibetan gazelle (*Procapara picticaudata*), goitered gazelle (*Gazella subgutturosa*), white-lipped deer (*Przewalskium albirostris*) and Tibetan argali (*Ovis ammon hodgsoni*) have low population sizes and are not common in our research area (Mallon and Jiang 2009). Zokors (*Myospalax baileyi*), pikas (*Ochotona curzoniae*), marmots (*Marmota himalayana*) and other small mammals are common and can occur at high densities (Smith and Foggin 1999). Hezuo station (HZS), Behind Hezuo station (BHZ) and Xishanpo (XSP) are located within a 3 km^2 area in Hezuo County. Oula (OL) and Machang (MC) are located 200 km further south, lying within a 4 km^2 area within Maqu County. All study areas are mature meadows with winter grazing by livestock (e.g yak and Tibetan sheep). All grazing occurs between late fall and early spring and no domestic livestock grazing occurs during the remainder of each year. Soil organic matter ranges from 22 to 49 g kg^{-1} at 0–10 cm depth among the five sites in 2008. Soil total N at 0–10 cm depth varies from 2.9 to 4.5 g kg^{-1} among the five sites in 2008. This region is located at an elevation of 2900–3900 m, and

Table 1. Study site characteristics. All sites are located within the Eastern Qinhai-Tibetan Plateau of China.

Study sites	Hezuo station (HZS)	Behind Hezuo station (BHS)	Xishanpo (XSP)	Oula (OL)	Machang (MC)
Geographical position	34°57'N, 102°52'E	34°57'N, 102°52'E	34°58'N, 102°53'E	34°12'N, 101°30'E	33°44'N, 102°06'E
Elevation (m)	2963	2975	3000	3480	3497
Mean annual temperature (°C)	2.9	2.9	2.9	2.1	2.1
Mean annual Precipitation (mm)	552	552	552	502	502
Plots	12	8	10	10	4
Above-ground biomass (m²)	168~560	71~255	86~147	103~277	236~289
Species richness (0.25 m²)	12~24	22~35	14~38	24~31	21~28
Grass abundance (%)	47~94	4~61	12~42	32~63	49~72
Dominant species	*Elymus nutans, Roegneria stricta, Kobresia* sp.	*Kobresia humilis, Polygonum viviparum, Potentilla fragarioides.*	*Kobresia humilis, Elymus nutans*	*Kobresia capillifolia, Elymus nutans, Potentilla fragarioides*	*Kobresia capillifolia, K. humilis, Anemone rivularis*

the climate is cold humid-alpine with mean annual rainfall of 450–780 mm, with 85% of the precipitation during the growing season from June through September. Mean annual temperature is 1.2°C, ranging from −10°C in January to 11.7°C in July, and there are on average 2580 h of sunshine and 270 frost days per year. The timberline in the study region is ca. 2500–4000 m (Li 1993; Zhao et al. 2014). The regional species pool is ca. 12,000 species of 1500 genera (Wu 2008), of which more than 3000 are exclusively alpine (Li et al. 2014) and 1355 angiosperm species are found on the eastern Tibetan Plateau (Qi et al. 2014).The vegetation at our sites was dominated by species, such as *Elymus nutans, Kobresia humilis, Polygonum viviparum, Roegneria nutans, Roegneria stricta, Potentilla fragarioides, Anemone rivularis, Kobresia capillifolia, Poa poophagorum* (Table 1 and Supplemental data).

Field sampling

The minimum sampling area in the alpine meadow plant community has been reported to be ca. 0.2 m^2 (Du et al. 2003), and 50 cm × 50 cm plot size (0.25 m^2) is commonly used in Tibetan alpine meadow studies (Yang et al. 2012; Liu et al. 2014). Within each site, 50 cm × 50 cm sampling plots were randomly arranged and sampled in August 2008, during the peak of the growing season, and every species in each plot was counted. A total of 44 plots were sampled in the five sites (Hezuo, 12 replicate; Behind Hezuo, 8; Xishanpo, 10; Oula, 10; and Machang, 4). We cut all above-ground biomass at soil level, sorted it by species and recorded the weight of each plant species after drying to constant weight for 48 hours at 80 °C. Species richness is the total number of species present within each plot. Graminoid abundance is expressed as graminoid proportion of the total productivity (peak standing above-ground biomass) of each plot (Misra and Misra 1981). Sedge species are strong competitors within Tibetan meadows, especially in the *Kobresia* genus because of their ability to withstand intense grazing and ability to spread horizontally and fill in bare soil (Miehe et al. 2008). We included both grasses and sedges in a graminoid category, as is often done in grassland studies (Tilman 1987).

Data analyses

The two most common functional groups in the Tibetan Plateau herbaceous meadows are graminoids and forbs; legumes are rare, with only five species present in the five sites. The range of legume biomass per plot is 1–13% of total plant biomass, and the average percent biomass per plot is less than 5%. Here, we present the relationships between graminoid abundance, productivity (using the peak above-ground biomass as a proxy for productivity as is commonly done for grasslands [Tilman et al. 1996; Grace et al. 2007; Adler et al. 2011]) and species richness.

In order to directly compare the most likely factor for each hypothesis and to avoid potentially confounding issues from highly correlated factors, we examined single fixed-factor models for graminoid abundance vs. graminoid biomass vs. forb biomass, and the biomass of each of the three most dominant species individually vs. combined. These models were compared via AIC using the R package bbmle. Based on these single fixed-factor models, we selected factors for functional group abundance, species abundance, and productivity for inclusion as fixed effects in mixed model analysis. This avoids extreme issues of collinearity. Sites (N = 5) was included as a random factor so as to account for possible non-independence of plots sampled at the same site. The mixed model analysis was conducted in R using lmer in package lme4. The statistical significance of fixed effects was calculated as likelihood ratio tests conducted in R with Anova from the package car, using type "II" (Fox 2008). The marginal R^2_{GLMM}, a metric which describes the fraction of variation explained by the fixed effects in a mixed effects model (Nakagawa and Schielzeth 2013), was used to quantify the explanatory power of factors.

Results

Species richness ranged from 12 to 38 species per 0.25 m^2 among all plots (Table 1). Graminoid abundance varied from 4% to 94% (Figure 1) and productivity from 70 to 560 g m^{-2} among all plots (Table 1). For the sites, the mean vascular plant species richness varied from 18.3 to 29.6 per 0.25 m^2 plot and the mean productivity varied from 112 to 376 g m^{-2} (dry mass) (Table 1).

We only present graminoid abundance here; however, note that graminoid abundance is inversely correlated with forb abundance; therefore, a decreasing graminoid abundance can also be interpreted as an increasing forb abundance (Supplemental data). We used graminoid abundance (i.e. the percent graminoid biomass of the total plant biomass) instead of graminoid biomass because percent biomass is a biological meaningful metric of relative abundance (Misra and Misra 1981). Furthermore, graminoid abundance has a lower correlation with the remaining factors, decreasing the possibility of collinearity issues in multiple linear regression (Table 2), and based on a ΔAIC model comparison, graminoid abundance is a better fit than graminoid biomass and forb biomass in explaining species richness (Table 3) (Burnham and Anderson 2002). The three dominant species combined also were a better fit than each dominant species individually based on the ΔAIC, hence we included the combined biomass of the three dominant species.

Using a linear mixed effects model (Table 4), we found that only graminoid abundance was a significant explanatory factor of total species richness, whereas productivity and the three dominant species biomass together were non-significant. Inclusion of the three dominant species individually (instead of the combined biomass) produced a qualitatively similar result – significant graminoid
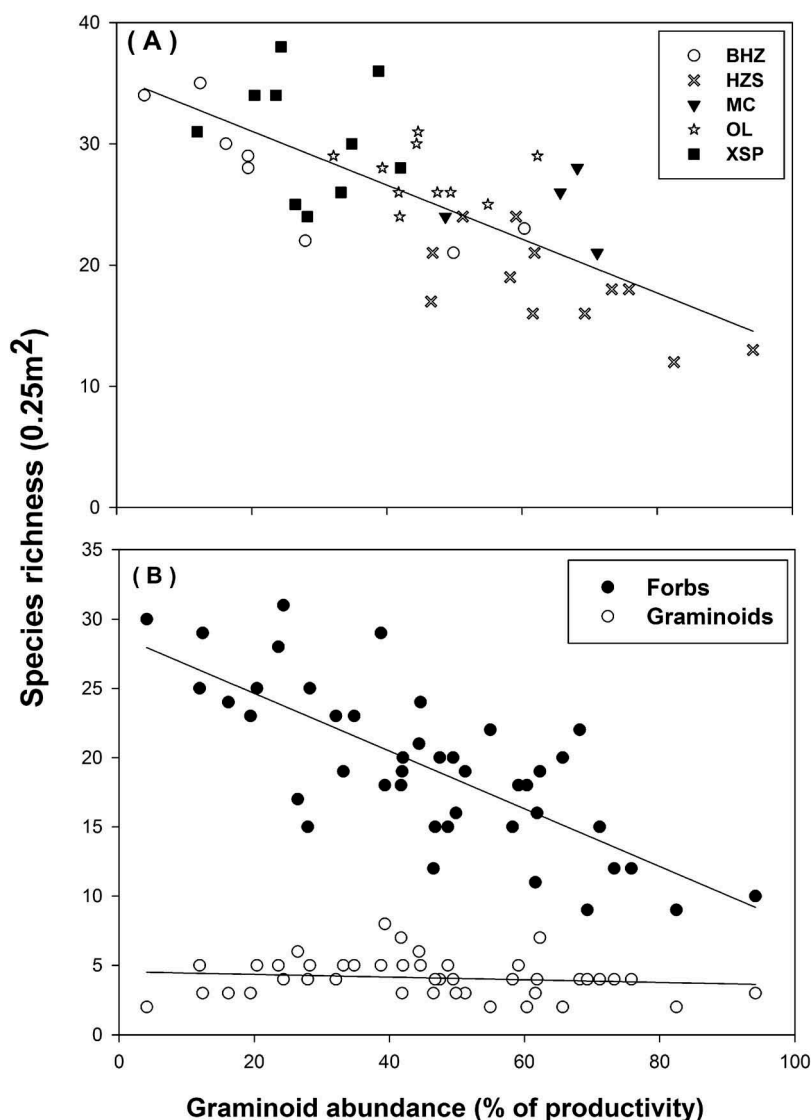
Figure 1. The relationships between (A) total species richness (the number of species per 0.25 m^2), (B) forb, graminoid richness and graminoid abundance (% of total productivity). $N = 44$, different symbols in (A) denote five different sites (Table 1), which was included as a random effect in a linear mixed model (Table 4), $R^2_{GLMM} = 0.390$. Graminoid richness does not change with graminoid abundance ($\chi^2 = 0.609$, df = 1, $P = 0.435$), forb richness decreases with increasing graminoid abundance ($\chi^2 = 32.479$, df = 1, $P < 0.0001$).

Table 2. Correlations among graminoid abundance, graminoid biomass, productivity, the three most abundant species *Elymus nutans, Kobriesia humilus, Polygonum viviparum*, and the three most abundant species biomass combined.

	Graminoid abundance	Graminoid biomass	Forb biomass	Productivity	*Elymus nutans*	*Kobresia humilis*	*Polygonum viviparum*
Graminoid biomass	0.817						
Forb biomass	−0.039	0.356					
Productivity	0.637	0.939	0.639				
Elymus nutans	0.419	0.609	0.079	0.512			
Kobresia humilis	0.235	0.083	−0.065	0.035	−0.134		
Polygonum viviparum	−0.083	−0.049	0.281	0.050	0.002	−0.183	
Three dominant species	0.486	0.611	0.102	0.516	0.908	0.253	0.111

abundance and all other factors were non-significant (data not shown). Also, forb biomass when included in the linear mixed model was not significant ($P > 0.9$) and did

not change the fact that only graminoid abundance was a significant predictor of species richness. Complications from potential collinearity between graminoid abundance

Table 3. Comparison of mixed models explaining species richness, each with the single factor listed as a fixed effect and site included as a random effect. Comparisons are among correlated factors within each area of hypothesis: functional group abundance and species abundance. Models are sorted in order of decreasingly good fit with graminoid abundance being the best model as compared to graminoid and forb biomass; the biomass of the three most dominant species combined being the best model compared to each single species.

Factor	AIC	ΔAIC	N
Graminoid abundance	244.5	0	4
Graminoid biomass	257.8	13.3	4
Forb biomass	258.9	14.3	4
Three dominant species	262.7	0	4
Elymus nutans	262.8	0.2	4
Kobresia humilis	262.9	0.3	4
Polygonum viviparum	264.6	2.0	4

Table 4. Species richness differences as explained by factors and sites in a linear mixed effects model. All factors are fixed effects with the exception of sites ($N = 5$), which is a random effect.

Factor	χ^2	df	*P*-value
Graminoid abundance	23.554	1	**<0.0001**
Productivity	0.110	1	0.740
Three dominant species	0.248	1	0.619

and productivity (Table 2) were not an issue because graminoid abundance was found to be the only significant factor in the linear mixed model (Table 4). In fact, even with productivity included as the sole fixed effect, productivity remained not significant ($\chi^2 = 2.15$, df = 1, $P = 0.643$) because the relationship between productivity and species richness is driven by among site differences, with no additional relationship within sites (Supplemental data). In contrast, the relationship between species richness and graminoid abundance is consistent among sites and within sites (Figure 1) providing more statistical power given our sampling design, and suggesting that this locally driven mechanism is important across a broad scope of inference.

When fitted with restricted maximum likelihood, we found a variance of 9.01 due to sites with a remaining residual variance of 10.98. The full model, which included graminoid abundance explained 39% of the variation in species richness as described by the marginal R^2_{GLMM}. In contrast, a model that excluded graminoid abundance while retaining productivity and the combined biomass of the three dominant species had a marginal R^2_{GLMM} of 2.0%. The large drop in variation explained by the removal of graminoid abundance underscores the important explanatory power of graminoid abundance as compared to other measures of individual species dominance or productivity.

Sampling effect among species has been discussed as a mechanism to explain community-level responses in grasslands (Wardle 1999; Hector et al. 2002). Specifically, in this study, one could hypothesise that, along the graminoid abundance gradient, forb richness decreased while graminoid richness increased, in which case the net reduction in total species richness could be the result of shifting from a species-rich pool of forbs to a species-poor pool of graminoids. However, the evidence is that graminoid species richness remains the same across the graminoid abundance gradient while forb diversity consistently declines (Figure 1B). This result is consistent with Figure 1A, and precludes the simple mechanism that the community is shifting from one species pool to another.

Discussion

We found that within Tibetan alpine meadows, graminoid abundance explained 39% of plot differences in species richness, while productivity and the dominant species were not significant predictors. Graminoid abundance was also strongly correlated with above-ground productivity.

Note that multiple sites were used to expand our scope of inference so as to identify a broad pattern operating across grasslands, but we have inadequate site replication to address diversity differences among sites. Plots are the experimental unit and site is included as a random effect to account for possible non-independence of multiple plots within a site (Šímová et al. 2013).

Our above-ground biomass varied from 70 to 560 g m^{-2}. Other grasslands can have much higher standing biomass, and the relationship between plant diversity in relation to standing plant biomass or productivity may differ at higher productivity (Fraser et al. 2015). However, such theoretical patterns are not important for Tibetan meadows because these meadows do not reach such high levels of productivity, because of the short growing season and other limitations of the alpine environment.

Wang et al. (2004) examined the correlations between plant functional group richness and composition and community productivity in four different Tibetan alpine plant communities and also found that species richness was significantly higher in plant communities with lower graminoid abundance. These results combined suggest that differences in functional group abundance may be an important driver of both species richness and productivity in Tibetan meadows, and that productivity may be only an indirect correlation and not a causal factor driving the relationship between productivity and species richness. Correlation studies have shown that plant species richness decreases with increasing productivity (De Lafontaine and Houle 2007); however as our study shows, such correlation studies may be confounded by differences in functional group abundance (Grime 1998; Wang et al. 2004). While our data are also correlational, the large gradient in functional group abundance, in combination with a productivity gradient, provides a unique viewpoint on the natural dynamics of grasslands.

Experimental studies that manipulated functional group abundance have shown that functional group richness and/or composition can significantly influence productivity (Tilman et al. 1997). Reich et al. (2004) manipulated both species richness and functional group richness to examine their independent effects and indicated that species richness and functional group richness independently influenced biomass accumulation. Jiang et al. (2007) examined the effects of three components of plant diversity (plant species richness, plant functional group richness and plant functional trait richness) on community productivity in artificial plant communities and found that functional group richness and functional trait richness had more important effects on productivity and resource use efficiency than plant species richness. Note, these experimental studies used synthetic communities with manipulated functional group abundance, and thereby also species richness; thus they could not directly examine the impact of functional group abundance differences on species richness. However, one can indirectly examine if functional group differences influence species richness, by examining plant invasions into synthetic communities with different functional group composition. One such study by Symstad (2000) found that removing C_4 grasses significantly increased plant invasions as compared to other functional groups removal. Similarly, a recent removal experiment also reported that removal of the dominant native graminoids significantly increased exotic forb biomass and overall community dynamics (Longo et al. 2013). These experimental results and our observational results are consistent with the notion that graminoid dominance drives higher productivity and graminoid absence drives higher species richness.

Dominance per se does not lead to increased productivity because we found that increased forb dominance was related to decreased biomass. Not all plant canopies are the same and have the same pattern of light interception; graminoids generally have long angled leaves, whereas forbs often have a central stem with leaves horizontally attached to the stem (Craine et al. 2001). The different leaf angles of different functional groups cause a different light interception profile in the plant canopy (Monsi and Saeki 2005), and graminoids have, for a similar leaf area index, lower light interception than others plant types (Monsi and Saeki 2005). Such differences in light extinction between plant canopies can have a strong effect on plant richness (Hautier et al. 2009). Experimental manipulations of light environments in relation to functional group differences, such as the approach that Hautier et al. (2009) used are needed to examine this. Several other grassland studies also have found that graminoid dominance was negatively correlated with plant diversity, and a common mechanism identified has been increased light competition with graminoid dominance. Within Dutch chalk grasslands, increased atmospheric nitrogen (N) deposition leads to increased productivity and dominance by a grass species which in turn leads to lower plant diversity (Bobbink and Willems 1987). The abandonment of haying in Romanian grasslands decreases plant diversity linked with either an increase in grass or forb dominance depending on the species pool (Csergő et al. 2013), again, likely because of increased light competition. However, the identity of the grass species also can matter and different grasses can influence plant diversity in different ways. For instance, in North American grasslands, the dominant C_4 grasses differ in their ability to grow tall and capture light and thereby differ in their impact on plant diversity (Wilsey 2010). Removal of such dominant grass species can lead to decreased light competition and increased plant diversity (McCain et al. 2010). However, in addition to light interception, there are also several other factors that differ between forbs and graminoids, such as the greater competitive ability of graminoids, faster growth, and rapid increase in plant height resulting in high light capture, higher N use efficiency (Peppler-Lisbach and Petersen 2001), and rapidly colonising bare space by spreading horizontally through clonal rhizome growth (Wilsey 2010). Any of these or other factors, may cause the negative correlation between graminoids abundance and species richness.

In North American grasslands, graminoids typically comprise less than 20% of total plant species richness (Sims and Risser 2000), and therefore forbs account for most of species richness. In our five sites, a total of 112 species were present, consisting of six graminoids, five legumes and 101 forbs; thus, graminoids only account for 5% of species richness while forbs account for 92% of total species richness. In other Tibetan alpine sites, Wang et al. (2004) found that forbs also accounted for more than 50% of total species richness. Pokorny et al. (2004) quantified species and functional group richness in an alpine grassland plant community in south-western Montana and found that forbs accounted for 83% of total species richness. These studies suggest that within alpine meadows, forbs contribute much more to higher plant species richness than graminoids.

We estimated productivity based on peak standing above-ground plant biomass in late summer, as many other studies have done (Tilman et al. 2001; Reich et al. 2004; Adler et al. 2011). Grazing may be a potential confounding factor because grazers can have a preference and choose sites that differ in graminoid abundance. This can create patterns of different biomass removal and thereby may influence species richness (Olff and Ritchie 1998). Grazing of the dominant graminoids can also lead to increased richness by decreasing competition for limiting resources (Bakker and Olff 2003), especially light (Collins et al. 1998). However, selective grazing is not likely to influence our results, because within our sites all domestic livestock grazing occurs between late fall and early spring, i.e. winter grazing and typically, grazing in Tibetan grasslands is very uniform (Zhang Weiguo, personal observation). Thus, winter grazing in Tibetan meadows removes all standing dead plant litter over the winter and is essentially the same as a late summer or fall mowing regime as commonly is used in grasslands (Fraser et al. 2015). In the same region of the

Tibetan Plateau, experimentally removing winter grazing with fencing significantly increased plant cover and standing biomass of graminoids and reduced overall plant species density and richness (Wu et al. 2009). Thus, winter grazing which removes dead above-ground biomass likely increased the spring light regime and may benefit many short statured species, which are predominantly forbs. Thus, there is evidence that winter grazing negatively impacts graminoids in Tibetan meadows. However, this does not change our conclusion, because if grazing lowered our estimate of graminoid dominance, we underestimated the positive relationship between graminoid dominance and productivity and negative relationship with species richness.

Rusch and Oesterheld (1997) also found that grazing increased plant diversity within Argentinian pampa grasslands, because of an increase in exotic forbs whereas native species richness did not change. Grazing within these grasslands occurred year round, caused large decreases in both plant standing biomass and productivity during the growing season and a shift in productivity from the summer warm season to the spring cool season. Thus, similar to our study, increased light levels with grazing may facilitate higher plant diversity, but our study differs because at our sites growing season is much shorter, i.e less than 4 months and we do not see a seasonal transition between different plant species, and no exotic species are present. Thus, grazing influence on plant diversity may commonly be through decreased light competition, but how functional groups respond to grazing can differ markedly depending on the climate and growing season length.

In addition to winter livestock grazing, herbivory by zokors, pikas, marmots and small mammals can be important (Zhang and Liu 2003; Wang et al. 2008). Zokors forage below ground and cause high soil disturbance and preferentially impact clonal species with rhizomes and the burrowing activities of zokors favour an increase in species richness in Tibetan alpine meadows (Liu et al. 2012). Pikas and marmots forage above ground, but also can cause significant soil disturbance and can significantly impact plant species composition (Smith and Foggin 1999). However, we do not have data to evaluate the impact of these below- and above-ground herbivores.

Conclusions

Taken together, it is clear that in Tibetan alpine meadows, a shift from graminoid to forb dominance is strongly positively correlated with plant richness, but the exact mechanism – and how important above- and belowground grazing is in controlling this pattern – is less clear. It is clear that productivity and dominant species are less important than changes in relative abundance of functional groups as a driver of species richness.

Disclosure statement

No potential conflict of interest was reported by the authors.

Supplemental data

Supplemental data for this article can be accessed here.

Notes on contributors

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