

Grazing increases functional richness but not functional divergence in Tibetan alpine meadow plant communities

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Abstract Plant community diversity and ecosystem function are conditioned by competition among co-occurring species for multiple resources. Previous studies suggest that removal of standing biomass by grazing decreases competition for light, but coincident grazing effects on competition for soil nutrients remain largely unknown in Tibetan rangelands where grazing tends to deplete soil phosphorus availability. We measured five functional traits indicative of plant productivity and stoichiometry leaf carbon concentration (LCC), leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC), specific leaf area (SLA), leaf dry matter content (LDMC) for component species of plant communities in grazed and ungrazed plots in five Tibetan alpine meadows. We examined the diversity of traits singly Rao index of functional diversity (FD_{rao}) and in aggregate functional richness (FRic), functional divergence (FD_{div}), and functional evenness (FE_{ve}) in response to grazing. We tested whether foliar trait diversity increases with nutrient competition but decreases with light competition when competitive exclusion is reduced by grazing. The FD_{rao} of LPC significantly increased under grazing, but FD_{rao} for LCC, LNC and SLA tended to decrease. The FD_{rao} of LDMC increased at the drier site but decreased at the wettest site. There was a strong negative association between increase in FD_{rao} of LPC and decrease in soil nutrients, especially soil phosphorus availability. The

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FRic for all five traits together increased with species diversity following grazing, but neither FDiv nor FEve differed significantly between grazed and ungrazed plots at most sites. Grazing in Tibetan alpine meadows tends to increase competition for soil phosphorus while decreasing competition for light, resulting in an increase in the functional richness in grazed plant communities without any significant changes in the overall functional diversity of foliar traits. Our study highlights the potential importance of grazing mediated competition for multiple resources in alpine meadow ecosystems.

Keywords Community assembly · Competition · Foliar traits · Functional diversity · Grassland · Leaf economic spectrum

Introduction

The Tibetan plateau has been grazed by both domesticated and wild mammalian herbivores for at least 8000 years (Miehe et al. 2009). Despite longstanding modern recognition of its importance as a grazing highland (Kingdon-Ward 1947), there has been surprisingly little study of the effects of grazing on community assembly in Tibetan rangeland. Theoretically, after filtering by local abiotic environmental factors, species coexistence and community diversity in grazed and ungrazed rangeland should primarily be determined by the balance between competitive exclusion and stabilizing niche differences (Chesson 2000; Hille Ris Lambers et al. 2012). Community diversity generally increases with niche differentiation but decreases with competitive exclusion (Götzenberger et al. 2012; Cardinale 2013). Previous studies support the idea that grazing should promote community diversity by removing standing biomass, hence decreasing competition for light among neighbouring plants (Belsky 1992; Wilsey and Polley 2003; Borer et al. 2014). Conversely the influence of grazing on community diversity attributable to competition for soil nutrients and water is less well known (Bagchi and Ritchie 2010; Pakeman 2011). Competition for soil nutrients may be especially important in Tibetan rangeland where grazing depletes soil phosphorus availability (Yang et al. 2014; Niu et al. 2015), which could increase plant competition and influence both community assembly and ecosystem function.

The nature and consequences of grazing on community assembly can be evaluated by observing shifts in the functional diversity (FD) of traits involved in competition among co-existing plant species for multiple resources (Ricotta and Moretti 2011; Hille Ris Lambers et al. 2012; Spasojevic and Suding 2012; Karadimou et al. 2014). For example, when competitive exclusion was prevented, an increase in the FD of foliar nutrients led to increasing competition that induced niche differentiation among species in response to soil nutrient limitation (Güsewell et al. 2005; Mason et al. 2012; Niu et al. 2015). Similarly, an increase in the FD of specific leaf area (SLA) is associated with an increase in niche differentiation in response to competition for limited light and soil nutrients (Kraft et al. 2008; Dwyer et al. 2014), and an increase in the FD of leaf dry matter content (LDMC) is associated with water and soil nutrient limitations (Hodgson et al. 2011; Bernard-Verdier et al. 2012).

Such responses in the FD of single traits, however, can be constrained by close functional linkages to any number of other traits determining performance at the whole plant level (Marks and Lechowicz 2006a; Reich 2014). Trade-offs in the responses within a suite of traits can create multiple possibilities for combinations of traits that yield approximately

equal performance at the whole plant level and hence a low overall value for change in FD in response to environmental factors (Marks and Lechowicz 2006b; Shipley et al. 2006). To estimate the balance among multiple factors affecting community assembly following grazing, one therefore should consider the FD of traits both singly and in aggregate (Flynn et al. 2009; Pakeman 2011; Mason et al. 2013; Karadimou et al. 2014).

In this paper we assess the functional basis for changes in the diversity of Tibetan alpine meadow communities under grazing by analyzing changes in five traits in the leaf economics spectrum (LES) that interact to determine foliar function (Wright et al. 2004; Shipley et al. 2006). Based on previous work and with regard to the responses of single traits, we expected that:

- (i) removal of biomass would reduce competition for light in grazed communities, leading to a decrease in the FD of foliar carbon content (Niu et al. 2009, 2010; Borer et al. 2014);
- (ii) grazing would decrease competitive exclusion attributable to acquisition of scarce soil nutrients, hence increasing FD in foliar nutrient concentration leaf nitrogen concentration (LNC), and leaf phosphorus concentration (LPC) in these nutrient limited alpine meadows (Yang et al. 2014; Niu et al. 2015);
- (iii) the effect of grazing on the FD of SLA and LDMC will depend on the balance between decreasing light competition and increasing competition for soil nutrients and water (Bagchi and Ritchie 2010).

This anticipated contrast in structural stability (SLA and LDMC) versus stoichiometric lability (LCC, LNC and LPC) under grazing together with the potential for trade-offs among these five foliar traits raises the possibility of grazing responses in three different components of FD—functional richness, functional divergence and functional evenness (Villéger et al. 2008; Mouchet et al. 2010). In this regard, we hypothesized that:

- (i) the increased species richness of alpine meadow communities that occurs when grazing reduces competitive conclusion (Niu et al. 2012) should also enhance functional richness in the suite of LES traits;
- (ii) the countervailing effects of decreased light competition and increased competition for nutrients and water under grazing should leave both functional divergence and functional evenness in the suite of LES traits unchanged because of coordinated trade-offs among the traits (Marks and Lechowicz 2006a; Reich 2014).

In summary, in this paper we investigate the possibility that grazing in Tibetan alpine meadows tends to increase competition for soil phosphorus while decreasing competition for light, resulting in an increase in the functional richness in grazed plant communities without any significant changes in the overall functional diversity of foliar traits.

Materials and methods

Study sites

We conducted a grazing exclusion experiment at five alpine meadows distributed from the eastern to northwestern parts of the Tibetan Plateau: HY site in Hongyuan County of Sichuan province (cf. Zhao et al. 2013), AZ sites (cf. Zhang et al. 2014) and WLK in Maqu County of Gansu province (cf. Niu et al. 2009; Yang et al. 2012), QH site in Mengyuan

County of Qinghai province (cf. Wang et al. 2012) and NQ site in Nagu Prefecture of the Tibet Autonomous Region (cf. Xiong et al. 2014), China (Supplemental Fig. 1).

Overall, on a gradient from eastern (AZ, WLK and HY) to northern (QH) and western (NQ) sites, productivity, the diversity of plant species, soil depth and fertility decrease in conjunction with mean annual temperature and precipitation (Supplemental Table 1; Yan et al. 2013). The mean maximum and minimum monthly temperatures in July and January are about 10 °C and −15 °C, respectively. Precipitation ranges from 690 mm in the east to 400 mm in the west, occurring mainly in the short growing season from early June to late August. All sites are located on relatively level terrain with an annual duration of cloud-free solar radiation greater than 2500 h.

Grazed meadows at all sites are dominated by *Kobresia* species such as *K. setschwanaensis*, *K. capillifolia*, *K. pygmaea* and *K. humilis*, but after exclusion of grazers, grasses such as *Elymus nutans*, *Roegneria nutans*, *Poa pratensis*, *Agrostis hugoniana* become abundant. Total vegetation cover in midsummer exceeds 80 %; vegetation height in grazed meadows ranges from 30 to 50 cm in eastern and 10–20 cm in the northern and western sites (Supplemental Table 1).

Experimental design

At each site we built exclosures (1–13 ha) within a larger area (20–60 ha) of alpine meadow. The exclosures were designed to stop grazing by both wild and domestic mammals. The exclosure at the WLK site was established in 1999, and those at the other four sites in 2005–2006; hence at the time of the study the plant community within the exclosure had been protected from grazing for either 11 (WLK) or 3–5 years (Supplemental Table 1). Grazing was allowed within the exclosures during the non-productive winter months for AZ, WLK and NQ, but excluded throughout the year for YH and QH. Outside of the exclosure, vegetation was moderately grazed by yaks and sheep during all months except for 40–60 days between June and mid-August when the animals were moved to high-altitude pasture (Niu et al. 2010, 2012).

In June 2009–2010, at each site eight 5 × 8 m plots were randomly established within the exclosures and another eight outside the exclosures. The ungrazed plots within the exclosures were separated by 2–8 m, while grazed plots outside the exclosures were separated by 2–20 m. Because the fence used for the grazing exclosures might affect plant growth as well as the activities of small animals, we located our ungrazed plots well away from the exclosures. This resulted in 300–500 m distances between grazed and ungrazed plots, but given the low levels of β diversity and the high levels of soil homogeneity in these meadows on fairly level terrain this should not disrupt comparisons between grazed and ungrazed plots. Each replicate plot was divided into two parts: a 5 × 5 m subplot for measurement of plant traits and a 5 × 3 m subplot for community monitoring, biomass harvest and soil sampling.

Trait measurements

In July 2009 and 2010, we randomly sampled mature leaves from 7 to 10 individuals at fruiting time for all but a few very infrequent species at each site in grazed and ungrazed plots. We first measured specific leaf area (SLA, mm² mg⁻¹) and leaf dry matter content (LDMC, mg g⁻¹) on these individual leaves. To satisfy analytic requirements, we then pooled and ground the sample of 7–10 leaves for each species in grazed and ungrazed plots, and analyzed three subsamples of the pooled and ground tissue for leaf carbon

concentration (LCC, mg g^{-1}), leaf nitrogen concentration (LNC, mg g^{-1}) and leaf phosphorus concentration (LPC, mg g^{-1}). The sampled species (142 species in total, 20–45 species at a site) accounted for 90–98 % of the aboveground biomass and 95–99 % of vegetation cover in the plant community. All measurements of leaf traits followed standardized methods (Cornelissen et al. 2003; He et al. 2008, 2010).

Community and soil measurements

From mid-August to early September in 2009 and 2010, we harvested plants in a 0.5×0.5 m quadrat within each of the 5×3 m subplots at each site. Plants were harvested by species, oven-dried and the biomass of each species determined. After aboveground biomass was harvested in each quadrat, we collected and pooled three soil samples from the 0 to 15 cm soil layer, which were air-dried and sieved (2-mm mesh) for further analyses. Soil total carbon and nitrogen concentrations (mg g^{-1}) were measured using an elemental analyzer, and soil organic carbon concentrations (mg g^{-1}) using the Walkley–Black method (Nelson and Sommers 1982). Soil available phosphorus concentrations for plants (Olsen-P) (mg kg^{-1}) were determined by the molybdate colorimetric test after perchloric acid digestion (Sommers and Nelson 1972).

Data analysis

Diversity indices

For each species in grazed and ungrazed plots in each site, we calculated the means of SLA and LDMC as well as LCC, LNC and LPC. In each quadrat, we calculated the relative abundance of each species as the ratio of aboveground biomass of a given species to the total community aboveground biomass. To measure species diversity in each quadrat, we calculated species richness, Shannon entropy of true species diversity, and the Simpson index of species evenness based on species number and relative abundance (Jost 2006) using the ‘vegetarian’ package (Charney and Record 2009) in R (R Core Team 2014).

To measure single-trait functional diversity (FD) in each quadrat, we calculated Rao’s index of quadratic entropy for each of the five leaf traits (FDrao) using the ‘FD’ package in R (Laliberté and Shipley 2010). The FDrao index is widely used to assess the functional diversity of single traits (Leps et al. 2006; Ricotta and Moretti 2011) and is strongly correlated with other indices of single-trait FD, but less impacted by variation in species richness (Mouchet et al. 2010; De Bello et al. 2011). To assess the functional diversity for the suite of foliar traits in each quadrat, we used three independent components of multi-trait FD—functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve) (Villéger et al. 2008; Mouchet et al. 2010). These indices were calculated based on the species abundance in each quadrat and the ‘Gower’ distance matrices of the five traits in grazed and ungrazed plots using the ‘FD’ package (Laliberté and Shipley 2010) in R.

Grazing effect on diversity indices

To examine the effect of grazing on species diversity on the five traits alone or taken together over our five study sites, we used a linear-mixed model with residual maximum likelihood (REML): $\text{response} \sim \text{Site/Grazing}$, $\text{random} = \sim \text{I|plot}$. Here, the diversity indices were included as response variables along with ‘Grazing’ as nested fixed factors

within each site; individual quadrats were taken as a random factor to account for any spatial autocorrelation. Where necessary, data were log-transformed to meet assumptions of normality and homogeneity of variance. The *lme4* package in R was used to perform the mixed models (Bates et al. 2011). We used generalized canonical discriminant analyses (gCCA) with a nested linear model (grazing nested in site effect) to examine and visualize linkages among the FD of individual traits and soil nutrient availability in grazed and ungrazed plots across the five study sites. The gCCA was performed using the *candisc* package (Friendly and Fox 2013).

Results

Effect of grazing on the functional diversity of traits considered singly

The FD_{rao} for LCC, LNC and SLA tended to decrease at three or four sites, respectively, but the FD_{rao} of LPC significantly increased in grazed plots relative to ungrazed plots at all five sites (Table 1; Fig. 1). The FD_{rao} of LDMC significantly increased in grazed plots at the QH site but decreased at the wetter AZ site (Table 1; Fig. 1). The grazing induced increase in the FD_{rao} of LPC is coupled with decreasing soil organic carbon and soil nutrients (Fig. 1).

Effect of grazing on community functional diversity for the suite of foliar traits

In terms of the suite of foliar traits taken as an integrated whole, functional richness increased with species richness and species diversity in grazed plots relative to ungrazed plots at most sites (Table 1; Fig. 2). Functional divergence did not significantly change in grazed plots relative to ungrazed plots except at the AZ site (Table 1; Fig. 2). Functional evenness did not significantly change due to grazing although species evenness increased in grazed plots at the WLK and QH sites and decreased at the NQ site (Table 1; Fig. 2). Individual density significantly increased in grazed plots relative to ungrazed plots at the HY and WLK sites and standing biomass significantly decreased following grazing at all sites (Table 1). Grazing induced increase in species diversity coupled with increases in functional richness, significantly discriminating grazed plots from ungrazed plots at all five sites (Fig. 2).

Discussion

Moderate grazing often is expected to promote plant community diversity by reducing the opportunity for competitive exclusion of subdominant species (Milchunas et al. 1988; Olf and Ritchie 1998). Many field investigations and experiments support this expectation, typically attributing the response to the reduction in light competition among neighbouring plants as grazing removes standing biomass (Gibson 2009; Borer et al. 2014). We also have found that reduction in light competition is a key mechanism for maintaining various aspects of community diversity under prevailing grazing regimes in Tibetan rangeland (Niu et al. 2012; Yang et al. 2012). For example, in this study, the functional diversity (FD) of both plant mature height (not shown) and LCC decreased with decreasing standing

Table 1 Results of nested linear-mixed modelling for effect of grazing (nested in sites) on functional diversity (FDrao) of traits singly, multi-trait functional diversity for the suite of foliar traits and species diversity

	AIC/BIC	Strength and direction of the grazing effect				
		AZ site	HY site	WLK site	QH site	NQ site
<i>Functional diversity (FDrao) of traits singly</i>						
Leaf carbon concentration (LCC)	-174/-149	-0.05 ± 0.02	-0.08 ± 0.02*	-0.14 ± 0.02*	0.02 ± 0.02	-0.09 ± 0.02
Leaf nitrogen concentration (LNC)	-172/-147	-0.01 ± 0.02	-0.03 ± 0.02	-0.09 ± 0.02*	-0.05 ± 0.02	-0.09 ± 0.02*
Leaf phosphorus concentration (LPC)	-198/-173	0.11 ± 0.02*	0.06 ± 0.02*	0.14 ± 0.02*	0.08 ± 0.02*	0.08 ± 0.02*
Specific leaf area (SLA)	-199/-174	-0.06 ± 0.02	0.01 ± 0.02	-0.03 ± 0.01	-0.07 ± 0.02*	-0.01 ± 0.02
Leaf dry matter content (LDMC)	-193/-168	-0.13 ± 0.02*	0.04 ± 0.02	-0.00 ± 0.02	0.05 ± 0.02	-0.04 ± 0.02
<i>Functional diversity for the suite of foliar traits</i>						
Functional richness (FRic)	465/490	8.2 ± 4.40	12.09 ± 4.36*	-4.9 ± 4.4	9.81 ± 4.4	1.78 ± 4.35
Functional divergence (FDiv)	-146/-121	0.06 ± 0.03	0.003 ± 0.03	-0.04 ± 0.02	-0.02 ± 0.03	0.01 ± 0.03
Functional evenness (FEIV)	-55.6/-30.5	0.001 ± 0.06	0.002 ± 0.06	-0.01 ± 0.06	0.09 ± 0.06	0.1 ± 0.06
<i>Species diversity</i>						
Species richness	351/376	1.6 ± 1.7	11.1 ± 1.7*	1.9 ± 1.8	3.6 ± 1.7	-3.9 ± 1.7
Shannon species diversity	16.7/41.8	-0.08 ± 0.1	0.43 ± 0.1*	0.37 ± 0.1*	0.41 ± 0.1*	-0.27 ± 0.1
Simpson species evenness	-147/-122	-0.05 ± 0.03	0.02 ± 0.03	0.11 ± 0.03*	0.06 ± 0.03	-0.7 ± 0.03
Individual density	734/762	41.8 ± 40.8	184.7 ± 40.4	195.8 ± 40.8	-0.12 ± 40.8	-134.8 ± 40.4*
Standing biomass	524/549	-45.6 ± 7.2*	-34.0 ± 7.1*	-51.9 ± 7.2*	-34.2 ± 7.2*	-13.2 ± 7.2

Value = slope value + standard error with bold entries indicating $p < 0.05$, * indicating $p < 0.01$. Positive and negative values indicate increased and decreased diversity indices, respectively, in grazed plots relative to ungrazed plots. The tabulated values indicate the strength of the grazing effect gauged by the slope of the relationship AIC Akaike information criterion, BIC the Schwarz's Bayesian Information Criteria. Degrees of Freedom = 60

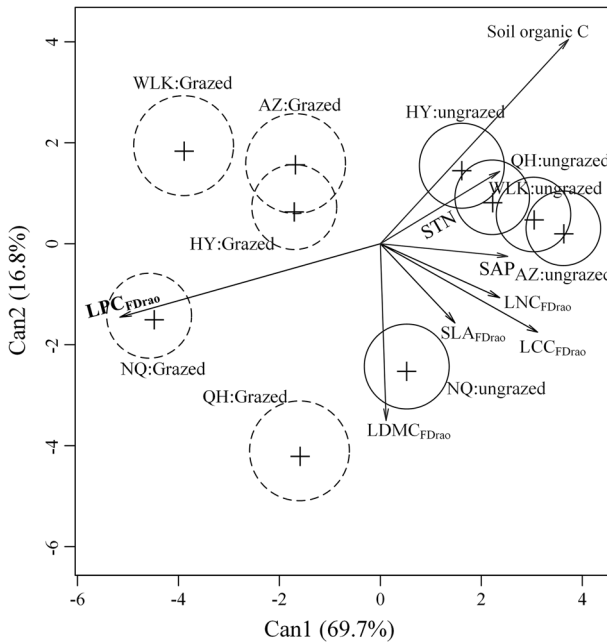


Fig. 1 Generalized canonical discriminant analysis showing links among functional diversity (FDrao) of individual leaf traits and soil nutrient availability in a multivariate linear model (i.e. grazing effect nested in sites effect). The lines at each site bound the 95 % confidence interval around the site-treatment mean. Both grazing and sites effects are significant at $P < 0.01$ test by a Wilks' lambda test. *LCC* leaf carbon concentration, *LNC* leaf nitrogen concentration, *LPC* leaf phosphorous concentration, *SLA* specific leaf area, *LDMC* leaf dry matter content, *STN* soil total nitrogen, *SAP* soil available phosphorous

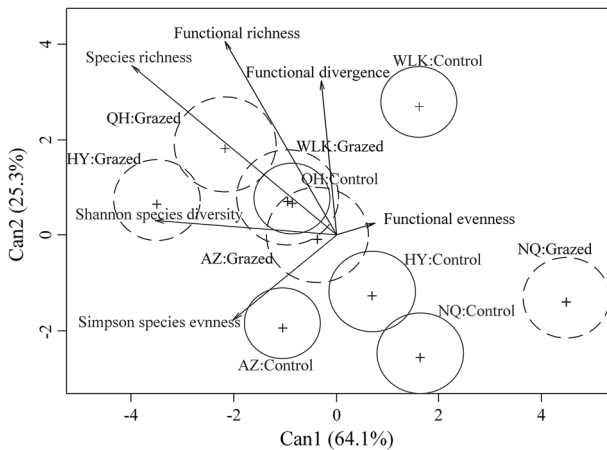


Fig. 2 Generalized canonical discriminant analysis showing the influence of species and functional diversity in the suite of foliar traits on the relationships within and among the grazed and ungrazed communities at each of the five study sites. The broken lines at each site bound the 95 % confidence interval around the site-treatment mean. Both grazing and sites effect are significant at $P < 0.01$ by Wilks' lambda test

biomass following grazing (Fig. 1; Table 1). In addition, however, we also found evidence suggesting that grazing influences plant community diversity through changes in competition for available soil resources, especially soil phosphorus.

Firstly, we found an increase in the FD of LPC under grazing, which indicates an increase in niche differentiation among co-occurring species in their acquisition and use of soil phosphorus (Fig. 1; Table 1) when competitive exclusion is prevented by grazing (Niu et al. 2015). Since the community weighted mean value of LPC also increases (Niu et al. in review) and soil phosphorus availability decreases under grazing, we infer that the intensity of competition for soil available phosphorus is greater in grazed compared to ungrazed Tibetan alpine meadows. This is consistent with the greater density of the rapidly growing and re-growing plants in grazed communities, which increases demand for this limiting nutrient. Both reduced nutrient cycling at low temperature (Chapin III et al. 1978) and the loss of phosphorus in animal products exported outside the region limit availability of soil phosphorus in Tibetan rangeland, further accentuating functional diversification under grazing. In contrast, both nitrogen deposition and return of excreta by grazing animals reduces the likelihood of comparable nitrogen limitation in Tibetan rangeland. Competition for soil nitrogen did not necessarily increase due to grazing, and we found that the FD of LNC even tended to decrease (Fig. 1; Table 1) under grazing although the community weighted mean for LNC did increase. Secondly, because the FD of SLA primarily reflects the joint effect of plant competition for both light and soil resources (Dwyer et al. 2014; Long et al. 2014), the decrease in the FD of SLA suggests that competition for light decreased while competition for soil phosphorus increased under grazing. Similarly, the increase in the FD of LDMC at the relatively dry QH site and its decrease at the wet AZ site is consistent with the expectation that FD in LDMC will primarily be associated with competition for both water and soil resources (Hodgson et al. 2011; Bernard-Verdier et al. 2012). This result supports the idea that the responses of plant communities to grazing in dry Himalayan rangeland may depend on water availability as well as soil fertility (Bagchi and Ritchie 2010).

The forgoing observations on the response of single aboveground traits to grazing bear on questions of limiting resources but are insufficient in assessing the potential effects of grazing for responses at the community and ecosystem level such as productivity or nutrient cycling. For example, while the net productivity of the community arises in abundance weighted contributions of individual species, the performance of individual species depends on differences in their values for traits in the leaf economic spectrum and other suites of functional traits (Reich 2014) that affect performance at the whole plant level. Various combinations of values within a suite of functional traits can yield essentially similar overall foliar function (Marks and Lechowicz 2006a; Shipley et al. 2006). Increases in the FD of a single trait such as LPC can be coupled to decreases in the FD of LNC, SLA and LDMC (Fig. 2; Table 1). As a result, we observed that functional divergence and evenness changed little in response to grazing even though both species diversity and evenness tends to increase under grazing (Fig. 2; Table 1). These results are consistent with many recent observations that the response of functional diversity to environmental change is only loosely related to species diversity (Niu et al. 2014; Šímová et al. 2014) and highlights the potential complexity of community and species responses to grazing (Karadimou et al. 2014). We note that an investigation of FD in belowground traits could usefully extend the insights gained from the foregoing responses to grazing in aboveground traits.

These responses to grazing of aboveground traits taken both singly and in aggregate nonetheless provide insights relevant to biodiversity conservation and ecosystem

functioning. For instance, increases in both the community weighted mean value of LPC (Niu et al. in review) and the FD of LPC suggests that the limitation of soil available phosphorus will be accelerated as plants respond to grazing in rangelands on the Tibetan Plateau, which in turn will increasingly favour the success of smaller over larger mammals (Wise and Abrahamson 2005, 2007). Scarcity in soil available phosphorus will not only limit community productivity but heighten the effects of competitive exclusion that accelerate loss of subdominant plant species in the community (Niu et al. 2012). Decreasing productivity will further accelerate degradation and desertification of the rangeland through top-down and bottom-up processes, resulting in loss of plant species and decline in animal biodiversity and ultimately further depressing productivity. Sustainable rangeland management may be achievable through interventions such as phosphate fertilization, but only with a better understanding of the trait-based influence on the assembly and functioning of the rangeland plant communities.

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