

Grazing-induced shifts in community functional composition and soil nutrient availability in Tibetan alpine meadows

Kechang Niu^{1,2,3*}, Jin-Sheng He² and Martin J. Lechowicz³

¹Department of Biology, Nanjing University, Nanjing 210023, China; ²Department of Ecology, Peking University, Beijing 100871, China; and ³Department of Biology, McGill University, Montréal, QC H3A 1B1, Canada

Summary

1. The functional structure of plant communities can be altered by grazing through two main mechanisms: species turnover (i.e. changes in species occurrence and relative abundance) and intraspecific trait variability (ITV), which is driven by phenotypic responses of individual plants and shifts in the relative abundance of genotypic variants within species. Studies of grassland ecosystem function under grazing often focus on community changes induced by species turnover, which ignores the effects of ITV on biomass productivity, soil carbon or nutrient availability. By quantifying the relative contribution of both effects on shifts in community-wide traits, we highlight the role of ITV in community functional response to grazing and its implications for ecosystem function in Tibetan alpine meadows.

2. We measured three chemical traits (LC: leaf carbon, LN: leaf nitrogen and LP: leaf phosphorus concentrations) and two morphological traits (SLA: specific leaf area, LDMC: leaf dry matter content) that are critical components of plant production and forage quality in grazed and ungrazed plots. Using variance decomposition of community-weighted means (CWM) for these foliar traits, we distinguished the relative importance of ITV vs. change in species occurrence and abundance in response to grazing and the associated changes in soil carbon and nutrient availability.

3. The CWM for foliar nutrients and SLA_{CWM} increased in response to grazing together with decreases in soil carbon and nutrient stores, especially LP_{CWM} enrichment and loss of available soil P. The LP_{CWM} was strongly negatively correlated with $LDMC_{CWM}$, which was significantly higher in ungrazed plots. These community-wide trait responses to grazing were generally best captured by ITV and not changes in species occurrence and abundance, although ITV was consistently correlated with species turnover for all traits.

4. *Synthesis and applications.* In response to continuous grazing, plants in Tibetan alpine meadows increase specific leaf area and foliar nutrients but tend to have lower leaf dry matter content, a response consistent with faster growth and regrowth under grazing. This intraspecific trait variability response drives a shift in community function from conservative, slow-growing resource use in ungrazed meadows to exploitative resource use under grazing. This community-wide functional response enhances forage quality, in turn favouring the secondary productivity of small herbivorous mammal communities, but also contributes to accelerated depletion of soil available phosphorus. We discuss the implications of these results for biodiversity conservation, ecosystem function and rangeland sustainability in the Qinghai–Tibetan Plateau, especially with regard to managing grazing rotation to strike a balance between favouring secondary productivity of domesticated stock vs. small herbivorous mammals.

Key-words: community structure, functional traits, grazing rotation, leaf economics spectrum, plant–herbivore interactions, rangeland sustainability, soil fertility, species turnover

*Correspondence author. E-mail: kechangniu@nju.edu.cn

Introduction

Nomadic pastoralists have been active in the Qinghai–Tibetan Plateau for millennia, gradually expanding grasslands through use of fire and by grazing domesticated yaks, sheep, goats and horses on rangelands also used by wild mammalian herbivores (Miehe *et al.* 2009). In recent decades, this nomadic, free-range grazing regime (*sensu* Briske *et al.* 2011) has increasingly shifted toward intensive, market-oriented grazing. There is evidence that both socio-political and environmental changes in the last century have contributed to degradation of these alpine rangelands. Increasing demand from markets outside the region led to increased grazing pressure, nomadism became restricted, grazing increasingly became concentrated around settlements, the abundance of small mammalian grazers such as the plateau pika increased, and climate change adversely affected ecosystem function (Miehe *et al.* 2009; Harris 2010; Cao *et al.* 2013). There is, however, little or no definitive evidence for widespread degradation driven predominantly by any one of these possible causes (Harris 2010). The alpine plant communities are responding to many interacting factors, varying in influence from place to place. This situation provides an opportunity to investigate how functional responses to grazing at the plant community level can inform management strategies for rangeland sustainability.

A promising way to understand the consequences of grazing for management of rangeland sustainability is to focus on how changes in trait composition at the plant community level affect ecosystem function and services (Lavorel & Garnier 2002; Diaz *et al.* 2007a; Suding *et al.* 2008; Mouillot *et al.* 2013). In this regard, the community-weighted mean (CWM: the abundance-weighted mean of a trait for species comprising a community) is well-established as a meaningful measure of a trait functional composition at the community level (Grime 1998; Garnier *et al.* 2004; Diaz *et al.* 2007a; Lavorel & Grigulis 2012; Laughlin 2014). Changes in CWM, however, can result from shifts not only in species composition (i.e. change in species occurrence and relative abundance) but also in intraspecific trait variability (ITV: Albert *et al.* 2010; Messier, McGill & Lechowicz 2010; Lepš *et al.* 2011) associated with plastic environmental responses in individual plants and shifts in the relative abundance of genotypic variants within species (Diaz *et al.* 2007b; Albert *et al.* 2010). Previous studies of grazing effects have focused on the importance of species turnover in changing community structure and ecosystem function (Grime 2001; Diaz *et al.* 2004; Hooper *et al.* 2005). Only recently have the possible effects of ITV been considered, mostly from the point of view of community assembly (Post *et al.* 2008; Jung *et al.* 2010; Bolnick *et al.* 2011; Siefert *et al.* 2015). The influence of ITV on shifts in ecosystem function following disturbance remains largely

unstudied, especially in the case of biomass production and soil fertility (Mason *et al.* 2011; Mouillot *et al.* 2013).

Species-specific changes in traits due to both phenotypic responses of individual plants and genotypic differentiation following grazing have been well documented (reviewed in Diaz *et al.* 2007b; Gibson 2009; Mason *et al.* 2011). For example, under continuous grazing, grassland plants often decrease individual size (Diaz *et al.* 2007b) and biomass allocation to vegetative growth (Niu *et al.* 2009), but enrich foliar nutrient concentrations (Bai *et al.* 2012) due to regrowth and shifts in nutrient allocation. These patterns of ITV between grazed and ungrazed communities may be more important than species turnover in organizing community structure following grazing (Post *et al.* 2008; Mouillot *et al.* 2013). This is especially true in grasslands dominated by perennial species where grazing can have relatively little effect on species occurrence and/or relative abundance in the short term (Adler *et al.* 2004; de Bello, Lepš & Sebastia 2005; Cingolani, Posse & Collantes 2005; Niu *et al.* 2010; Volf *et al.* 2016). To better understand the importance of ITV on the functioning of rangeland ecosystems, it is necessary to distinguish the relative contributions of ITV and species turnover to the community functional response to grazing (Lepš *et al.* 2011; Pérez-Ramos *et al.* 2012). Hence, in this paper we examine the linkage between community functional structure and soil nutrient availability in response to grazing, and assess the relative importance of ITV in shifting community functional structure following grazing in the alpine meadows of the Qinghai–Tibetan Plateau.

We focus in particular on five well-studied functional traits in the leaf economics spectrum (LES: Wright *et al.* 2004; Shipley *et al.* 2006) that are directly relevant to forage quality: three foliar chemical traits (LC: leaf carbon, LN: leaf nitrogen, LP: leaf phosphorus concentrations) and two foliar morphological traits (SLA: specific leaf area, LDMC: leaf dry matter content) that can be important indicators of both species performance and community functional response to grazing (Lavorel & Garnier 2002; Diaz *et al.* 2007a; Garnier *et al.* 2007; Suding *et al.* 2008). There is a tight trade-offs among these LES traits in response to environmental regimes at both the species level (Shipley *et al.* 2006; Reich 2014) and the community level (Pérez-Ramos *et al.* 2012; Prieto *et al.* 2015) with consequences for the delivery of multiple ecosystem services (Lavorel & Grigulis 2012). For instance, in response to continuous removal of above-ground biomass by grazing, the relative abundance of fast (re)-growing species and individuals (e.g. with high SLA and leaf nutrient but low LDMC) increases within the plant community (Diaz *et al.* 2007b; Niu *et al.* 2010; Mouillot *et al.* 2013), which on the one hand can improve forage quality and digestibility to the benefit of secondary production (Zhang *et al.* 2014) but on the other hand depletes soil nutrient availability to the detriment of sustainability (Mason

et al. 2011). By delving into community-level changes in these foliar traits under grazing, we seek to strengthen our understanding of how and why grazing alters ecosystem function on the Qinghai–Tibetan Plateau.

We use an enclosure experiment in five alpine meadows widely distributed on the Qinghai–Tibetan Plateau to assess: (i) whether grazing induces a community-wide shift in these foliar traits; (ii) the degree to which any shifts involve ITV vs. change in species occurrence and relative abundance; and (iii) whether shifts in these community-wide traits under grazing are associated with changes in soil nutrient availability. We consider these results in relation to factors affecting rangeland sustainability in the Qinghai–Tibetan Plateau and propose a management framework that conserves intraspecific trait variability to help ensure resilience of the rangeland under rotational grazing across sites that vary in environmental conditions.

Materials and methods

STUDY SITES

We compared the functional structure of plant communities in grazed and ungrazed (enclosure) plots at five alpine meadow sites separated by 150 to 1850 km and distributed from the eastern to north-western parts of the Qinghai–Tibetan Plateau (Table 1, Fig. S1, Supporting information). We chose these widely distributed sites not only to account for the impact of variation in the local species pool on the structure of ecological communities (Lessard *et al.* 2012) but also to detect dependence of trait-based community functional response to grazing on possible regional differences in environment and grazing history (de Bello, Lepš & Sebastia 2005; Carmona *et al.* 2012; Eldridge *et al.* 2016). Mean annual temperature and precipitation as well as productivity, biodiversity, soil depth and nutrient availability generally decrease from eastern sites (AZ, WLK and HY) to northern (QH) and western (NQ) sites. Total vegetation cover in midsummer exceeds 80% at all sites. Vegetation height in grazed meadows ranges from 10 to 20 cm in the northern and western sites to 30–50 cm in eastern sites. Grazing has increased substantially at all sites in the last three decades, primarily by domesticated yaks and also sheep at drier sites such as WLK, QH and NQ. Small mammals such as the plateau pika are a significant component of the wild

grazer community that compete with larger domesticated stock (Harris 2010; Wilson & Smith 2015).

EXPERIMENTAL DESIGN

We studied alpine meadows on level terrain, establishing enclosures to prevent grazing during the peak growing season for either 11 (WLK) or 3–5 years (Table 1). The enclosures excluded both large and small vertebrate grazers. Grazing was allowed within the enclosures during the non-productive winter months for AZ, WLK and NQ, but excluded throughout the year for YH and NQ. Outside of the enclosure, vegetation was moderately grazed during all months except for 40–60 days between June and mid-August when yaks and sheep were moved to high-altitude pastures.

In June 2009, eight ungrazed plots separated by 2–8 m were randomly set out within the previously established enclosures and eight grazed plots separated by 2–20 m were randomly placed between 300 and 500 metres outside the enclosure at each site. Each 5 × 8 m plot was subdivided into a 25-m² subplot for measurement of plant traits and a 15-m² subplot for biomass harvest and soil sampling in a 0.25-m² quadrat (Fig. S1, Supporting information). The pairwise separation between quadrats at a site ranged from 10 to 510 m (median = 180 m). The species–area curve at our sites saturates (37–42 species) in the range of only 0.15–0.22 m², and levels of both β diversity and soil heterogeneity generally are low in a locality (Niu *et al.* 2009, 2010, 2012; Yang *et al.* 2012). Given the spatial configuration of our sampling design, this should lead to low spatial autocorrelation effects in our analyses of community composition. Nonetheless, to be conservative in our analyses, we explicitly took account of possible spatial autocorrelation effects in the linear mixed model used to analyse our data (Schank & Koehnle 2009).

TRAIT MEASUREMENTS

We measured three foliar chemical traits [LC: leaf carbon (mg g⁻¹), LN: leaf nitrogen (mg g⁻¹), LP: leaf phosphorus concentrations (mg g⁻¹)] and two foliar morphological traits [SLA: specific leaf area (mm² mg⁻¹), LDMC: leaf dry matter content (mg g⁻¹)] on all but a few infrequent species in the grazed as well as in ungrazed 25-m² subplots at each site. The sampled species (142 in total and 20–45 species in each site) accounted for 90–98% of the above-ground biomass and 95–99% of vegetation cover. In July 2009 and 2010, we sampled leaves from 5 to 20 random individuals to measure foliar traits for each species in

Table 1. Characterization of the five sites used in this study

	AZ	HY	WLK	QH	NQ
Location: Latitude	33°39'N	32°53'N	34°00'N	37°37'N	31°25'N
Longitude	101°52'E	102°36'E	102°00'E	101°12'E	92°00'E
Altitude (m)	3508	3484	3485	3178	4486
Mean annual temperature (°C)	1.2	1.4	1.2	-1.7	-2.1
Mean annual precipitation (mm)	620	690	620	560	406
Vegetation type	Wet meadow	Meadow	Meadow	Meadow	Dry meadow
Grazing allowed in enclosures	Winter	No	Winter	No	Winter
Ungrazed years in enclosures	3	4	11	5	3
Standing biomass in enclosures (g in 0.25 m ²)	130	100	130	120	22
Species richness in enclosures (n in 0.25 m ²)	22	21	28	29	14

grazed and ungrazed plots at each site. For each species in grazed and ungrazed plots at each site, we measured SLA and LDMC on 10 leaves from different individuals, and measured foliar carbon and nutrient concentrations on three samples pooled from the residual leaves to attain sufficient material for analysis. All measurements of leaf traits followed standardized methods (Cornelissen *et al.* 2003; He *et al.* 2006, 2008). This sampling design respects the requirements for the sum of squares decomposition method used to assess the relative importance of intraspecific variability and change in species occurrence and abundance in variation of community traits (Lepš *et al.* 2011; de la Riva *et al.* 2016).

COMMUNITY AND SOIL MEASUREMENTS

From mid-August to early September 2009, we harvested above-ground green parts (stems and leaves) in the 0.25-m² quadrat within each of the 15-m² subplots at all the sites except HY, which was harvested in 2010. We sorted the harvest from each 0.25-m² quadrat by species and oven-dried and weighed the sorted material. We also collected and pooled three soil samples from the 0- to 15-cm soil layer in the 15-m² subplot that were homogenized, air-dried and sieved (2-mm mesh) for soil analyses. Soil total C and N concentrations (mg g⁻¹) were determined by elemental analysis (He *et al.* 2006), soil organic carbon concentrations (mg g⁻¹) by the Walkley–Black method (Nelson & Sommers 1982) and soil available P concentrations (Olsen-P; mg kg⁻¹) by a molybdate colorimetric test after perchloric acid digestion (Sommers & Nelson 1972).

DATA ANALYSIS

We calculated the means of SLA and LDMC (10 replicates) as well as LC, LN and LP (three replicates) for each species in grazed and ungrazed plots in each site. We calculated the relative abundance of each species in each quadrat as a ratio of above-ground biomass of a given species to the community above-ground biomass in each quadrat. The community-weighted means (CWM) of the foliar traits were calculated for each quadrat as

$$\text{CWM} = \sum_{i=1}^n p_i \text{trait}_i$$

where p_i is the relative abundance of species i , and trait_i is the mean trait value of species i in grazed or ungrazed plots in each site.

Grazing effect on community-wide traits and soil nutrients

We used a linear mixed model with residual maximum likelihood (REML) to assess the effect of sites and grazing on variation in the CWM of traits and soil nutrients. The model had the following design: fixed = response – Site/Grazing, random = –1|plot. ‘Grazing’ was nested in the ‘site’ effect, and individual plots were taken as a random factor to account for any spatial autocorrelation. This nested model reflects our focus on assessing the grazing effect on community structure while taking account of any species pool and site effects. Where necessary, data were log-transformed to meet assumptions of normality and homogeneity of variance. For the mixed models, we used *lme* functions in the *lme4* package in R (Bates, Maechler &

Bolker 2011). To visualize the overall relationships among the CWM of leaf traits and soil nutrients in grazed and ungrazed plots, we used generalized canonical discriminant and correlation analyses (gCCA) with a nested linear model (grazing nested in site effect). The gCCA was done in the *candisc* package (Friendly & Fox 2013).

Intraspecific variability vs. change in species occurrence and abundance

To distinguish the relative contribution of ITV vs. change in species occurrence and abundance on changes in the CWM for each foliar trait, we used a sum of squares decomposition following de la Riva *et al.* (2016) adapted from Lepš *et al.* (2011); see also Asplund & Wardle (2014) and Jung *et al.* (2014). Assuming no ITV, we first calculated CWM_{fixed} in each grazed plot from species abundance in the grazed plot, but using the trait values measured in ungrazed plots at each site. This treats the difference between observed CWM (i.e. CWM_{specific}) and CWM_{fixed} in the grazed plots as an estimator of pure effects of intraspecific trait change in response to grazing as though there was no ITV in ungrazed plots. Then, for each ungrazed and grazed plot, we recalculated ^{p/a}CWM_{fixed} by the species presence/absence data and traits in ungrazed plots. Thus, variation in ^{p/a}CWM_{fixed} is solely affected by species occurrence, while difference between CWM_{fixed} and ^{p/a}CWM_{fixed} indicates effects of species abundance change on variation in CWM.

We then used a nested ANOVA (grazing nested in site) to decompose the total sum of squares (SS) into CWM variance components attributable to the site effect, grazing effect and plot effect, and finally quantified the relative contribution of ITV and change in species occurrence and abundance and their covariance for each component effect (Lepš *et al.* 2011; Asplund & Wardle 2014; Jung *et al.* 2014; de la Riva *et al.* 2016). Note that in this approach, the covariation is partitioned into two different components (de la Riva *et al.* 2016): the covariation between ITV and species turnover (Cov I = SS of CWM_{specific}–SS of CWM_{fixed}–SS of ITV) and covariation between species occurrence and abundance [Cov II = SS of CWM_{fixed}–SS of ^{p/a}CWM_{fixed}–SS of abundance effect (CWM_{fixed}–^{p/a}CWM_{fixed})]. All these analyses were performed in R 3.1.0 (R Foundation for Statistical Computing, Vienna, Austria).

Results

LINKING COMMUNITY-WIDE TRAITS TO SOIL NUTRIENT AVAILABILITY IN RESPONSE TO GRAZING

In response to grazing, LC_{CWM}, LN_{CWM}, LP_{CWM} and SLA_{CWM} significantly increased and LDMC_{CWM} decreased with decreased soil carbon and nutrient availability in most sites (Table 2, Fig. 1 and detailed in Table S1, Supporting information). Irrespective of grazing effect, soil nutrient and organic carbon decreased but LDMC_{CWM} increased from the AZ to NQ site (Fig. 1, Table 2).

A strong inverse relationship between the LP_{CWM} and the LDMC_{CWM} separated the grazed vs. ungrazed plots on the first axis of the gCCA, which accounts for 60% of the variance (Fig. 1, $P < 0.001$). The increase in CWM

Table 2. Results of nested linear-mixed model for effect of grazing (nested in sites) on standing biomass, community-weighted mean (CWM) of leaf traits and soil nutrients

	AIC/BIC	Strength and direction of the grazing effect (relative to grazed plots)				Strength and direction of the site effect (relative to AZ)				
		AZ site	HY site	WLK site	QH site	NQ site	HY site	WLK site	QH site	NQ site
Vegetation										
Standing biomass	524/549	-45.6 ± 7.2*	-34.0 ± 7.1*	-51.9 ± 7.2*	-34.2 ± 7.2*	-13.2 ± 7.2	-27.9 ± 6.9*	3.18 ± 6.90	-9.28 ± 6.67	-106 ± 6.9*
CWM of mature height	348/373	-11.12 ± 1.66*	-12.4 ± 1.64*	-13.12 ± 1.65*	-9 ± 1.65	-3.37 ± 1.65	0.24 ± 1.58	-0.01 ± 1.53	-13.35 ± 1.54*	-32.78 ± 1.59*
Community-wide traits										
Leaf carbon _{CWM}	89/114	0.11 ± 0.19	-0.46 ± 0.18	1.29 ± 0.19*	-0.57 ± 0.19*	0.39 ± 0.19	0.68 ± 0.18*	-0.37 ± 0.17	1.03 ± 0.17*	0.41 ± 0.18*
Leaf nitrogen _{CWM}	-54/-29	0.14 ± 0.05	0.18 ± 0.06	0.16 ± 0.06	0.12 ± 0.06	-0.29 ± 0.06	-0.08 ± 0.0	-0.1 ± 0.06	0.02 ± 0.05	0.25 ± 0.06*
Leaf phosphorus _{CWM}	-439/-414	0.02 ± 0.0*	0.01 ± 0.0*	0.02 ± 0.0*	-0.01 ± 0.0	0.01 ± 0.0	-0.01 ± 0.0*	0.01 ± 0.0	0.01 ± 0.0	-0.01 ± 0.0
Specific leaf area _{CWM}	516/541	53.56 ± 6.72*	43.85 ± 6.65*	7.45 ± 6.72	7.13 ± 6.72	15.28 ± 6.64	-24.09 ± 6.44*	5.25 ± 6.22	17.78 ± 6.22*	-21.37 ± 6.43*
Leaf dry matter content _{CWM}	-173/-148	-0.09 ± 0.02*	-0.18 ± 0.02*	-0.10 ± 0.02*	-0.01 ± 0.02	-0.14 ± 0.02	-0.01 ± 0.02	-0.04 ± 0.02	0.01 ± 0.02	0.05 ± 0.02
Soil carbon and nutrients										
Soil organic carbon	46/72	-0.66 ± 0.13*	-0.45 ± 0.13*	-0.31 ± 0.13	-1.33 ± 0.13*	-0.38 ± 0.13*	-0.50 ± 0.13*	-0.46 ± 0.13*	-0.63 ± 0.13*	-0.76 ± 0.13*
Soil total N	-97/-72	-0.16 ± 0.04*	-0.03 ± 0.04	-0.05 ± 0.04	-0.11 ± 0.04	-0.56 ± 0.04	-0.88 ± 0.04*	-0.90 ± 0.04*	-0.70 ± 0.04*	-0.98 ± 0.04*
Soil available P	-76/-51	-0.01 ± 0.05	-0.03 ± 0.05	-0.18 ± 0.05*	0.008 ± 0.05	-0.18 ± 0.05	0.06 ± 0.04	-0.11 ± 0.05	-0.01 ± 0.05	-0.03 ± 0.05

The tabulated values indicate the strength of the grazing (and site) effect gauged by the slope of the relationship (slope value + std). Bold entries indicate $P < 0.05$ and, $*P < 0.01$. Positive and negative values indicate increased vs. decreased variables in grazed plots relative to ungrazed plots (each site relative to AZ site), respectively. d.f. = 60. AIC, Akaike information criterion, BIC, Schwarz's Bayesian information criteria.

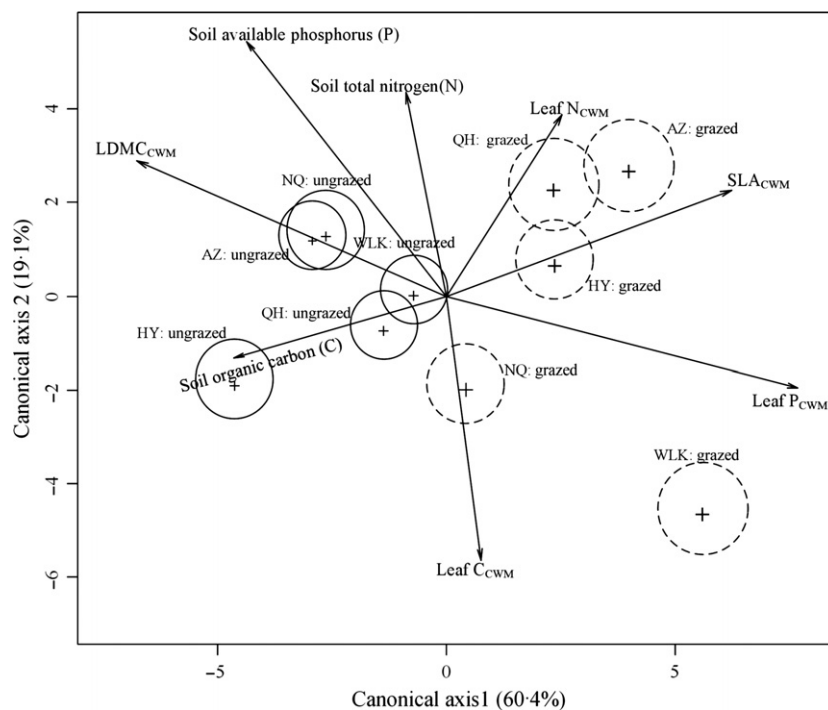


Fig. 1. Generalized canonical discriminant analysis for links among community weighted mean (CWM) values for leaf traits and soil nutrients in a multivariate linear model (i.e. grazing effect nested in sites effect). Both grazing and site effects are significant (Wilks' lambda, $P < 0.01$). The 95% confidence interval is shown around each treatment mean. The vectors map the contributions of leaf traits and soil nutrients to discriminating among responses to grazing across sites; the longer the vector the more its influence acts in the direction shown. SLA, specific leaf area; LDMC, leaf dry matter content.

values for leaf nutrients and for SLA_{CWM} significantly correlated with a decrease in soil nutrients following grazing, especially for enrichment of LP_{CWM} and loss of soil available P (Fig. 1, $P < 0.001$).

INTRASPECIFIC VARIABILITY VS. CHANGE IN SPECIES OCCURRENCE AND ABUNDANCE

Overall, changes in CWM values among sites mostly results from change in species occurrence and abundance, but intraspecific trait variability drives grazing effects on total variation in all leaf traits (Fig. 2). The contributions of ITV to the site effect and the grazing effect on total variation in CWM are significant for all leaf traits (Fig. 2, $P < 0.001$, detailed in Table S2, Supporting information). The contributions of species occurrence and abundance change to site effect are significant for all traits, but the contribution to grazing effect only for some traits (Fig. 2, detailed in Table S2, Supporting information).

Although species turnover is more important than ITV in determining variation in CWM across sites, the large negative covariance results in the site effect being weaker than the grazing effect for total variation in CWM values for all leaf traits except for LP_{CWM} (Fig. 2). In contrast, large ITV coupled with small negative covariance results in the grazing effect dominating the total variation in CWM for all leaf traits (accounting for 30–74% of the variation, Fig. 2, detailed in Table S2, Supporting information).

Discussion

Individual plant species have evolved foliar traits along the leaf economic spectrum (LES) that mediate inherent

trade-offs between growth and competitive abilities (Shipley *et al.* 2006; Donovan *et al.* 2011), which in turn are conditional on resource availability and the risk of herbivory (Wise & Abrahamson 2005, 2007). For example, since mammalian tissues are more N-rich than plant tissues, mammalian foraging and digestive strategies often cue on the N concentration of plant tissues and as a result photosynthetic gains from investment in higher foliar N may well be offset by a greater risk of herbivory. Grazing in turn can adversely impact soil carbon and mineral nutrient stocks via mass effects arising in these functional trait trade-offs at the plant community level (Lavorel & Grigulis 2012). These sorts of three-way interactions among plants, herbivores and soil resources condition the primary and secondary productivity of grasslands (Frank, Kuns & Guido 2002) as well as the availability of carbon, nitrogen and phosphorus in grassland soils (Bai *et al.* 2012; Schipanski & Bennett 2012; McSherry & Ritchie 2013; Xiong *et al.* 2014). Hence, at any point in time in a grassland ecosystem, the community-weighted mean LES values should provide a gauge of the balance struck in the interactions among the plant community, the resources available to the plants and the herbivore community.

Under resource limitation, slow-growing plant species with a conservative strategy of resource use have long-lived leaves with high LDMC and low foliar nutrients in contrast to fast-growing species with an exploitative strategy of resource use that have short-lived leaves with low LDMC and high foliar nutrients (Shipley *et al.* 2006; Reich 2014). Ungrazed or lightly grazed rangeland dominated by species with longer-lived leaves, hence generally should have lower community-weighted mean values for

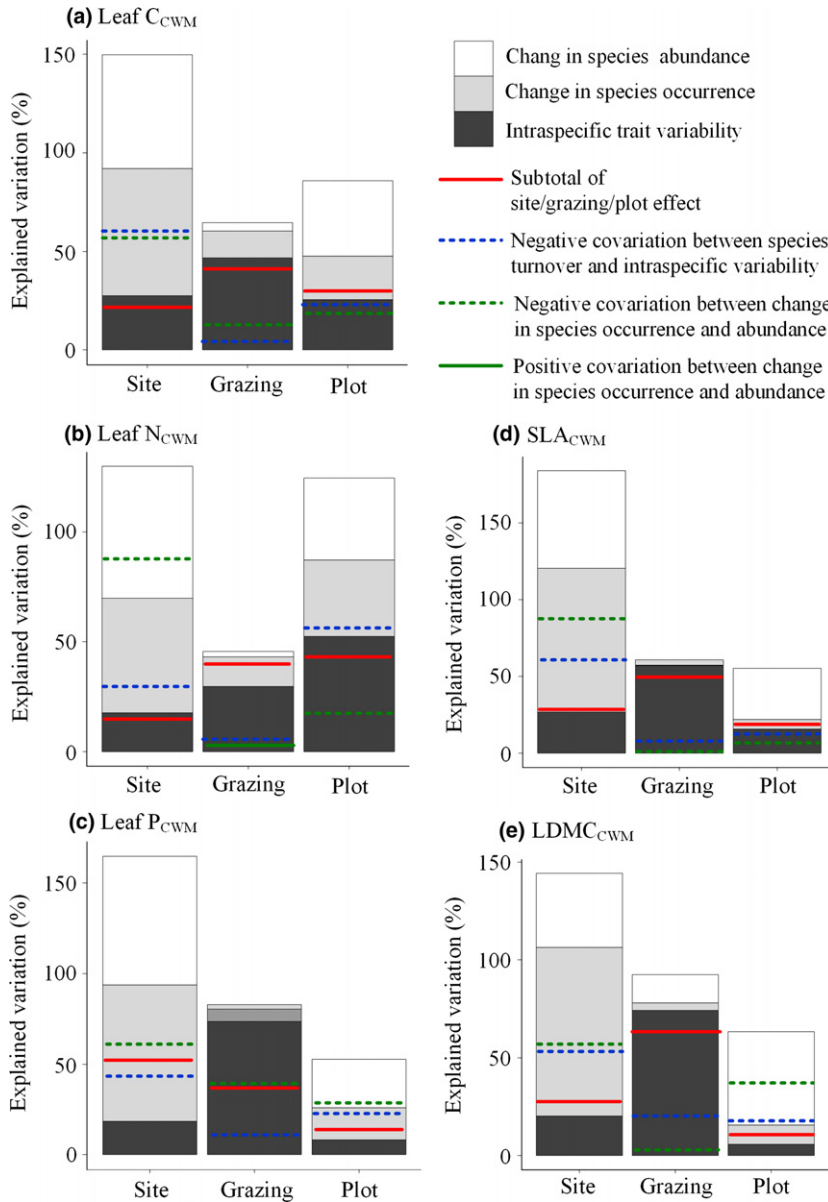


Fig. 2. Disentangling the relative importance of intraspecific trait variability vs. changes in species occurrence and abundance in determining site, grazing and plot effects on variation in community weighted traits (CWM) of leaf chemical traits (a–c) and morphological traits (d and e). All the site and grazing effects as well as the contributions of intraspecific trait variability are significant at $P < 0.01$ (detailed in the Table S2, Supporting information). SLA: Specific leaf area, LDMC: Leaf dry matter content

%N and higher LDMC (Pérez-Ramos *et al.* 2012), characteristics favouring larger herbivores such as sheep and yaks with foregut fermentation that requires and can more efficiently process large quantities of lower-quality forage (Müller *et al.* 2013). Conversely, rangeland dominated by plant species with shorter-lived leaves should have higher community-weighted mean values for %N and lower LDMC – characteristics favouring smaller herbivores such as pikas, marmots and hares with hindgut fermentation that depend more on lower quantities of higher-quality forage (Müller *et al.* 2013). The shifts observed in community-wide LES traits in response to removal of grazing pressure at our Tibetan alpine sites suggest that these three-way interactions involving grazers, plants and soil resources have reduced availability of soil phosphorus and shifted the alpine meadow communities to an exploitive resource use strategy that favours

small, hindgut fermenters such as pikas to the detriment of large, foregut fermenters such as yaks and sheep.

These three-way interactions among grazers, plants and soil resources are influenced by species turnover across our alpine meadow sites, but are consistently dominated by the effects of intraspecific trait variability in response to grazing at each site. While there are significant differences in the values of the community-wide LES traits both within and among plots at each site, the impact of grazing clearly supersedes both local and regional variation among plots (Figs 1 and 2). Compared with grazed plots, ungrazed plots have notably higher soil carbon and available phosphorus, higher community-wide mean levels of LDMC and lower levels of foliar P and N; these differences increase the longer a site has been protected from grazing (Table 1, Fig. 1). Variation in community-wide mean values for LES traits across sites and among plots

within a site is largely due to change in species occurrence and abundance, while the effects of grazing on community-wide mean values for LES traits are always due more to intraspecific trait variation (Fig. 2). Conversely, variation in the community-wide mean for foliar N is due partly to change in species occurrence, which is consistent with the effects of herbivores selectively feeding on plants with higher foliar N (Müller *et al.* 2013).

While many studies have recognized the role of change in occurrence and/or abundance in affecting changes in the functional structure of communities at sites separated spatially along resource gradients (McIntyre 2008; Albert *et al.* 2010; Messier, McGill & Lechowicz 2010; Lepš *et al.* 2011; Kichenin *et al.* 2013), the consistent changes attributable to intraspecific responses to grazing that we found have only recently been considered (Volf *et al.* 2016). This importance of intraspecific trait variability (ITV) in the functional response of the plant community to grazing is consistent with the expectation that high ITV can confer greater resistance to disturbance at the community level (Mouillot *et al.* 2013; Jung *et al.* 2014). Conversely, a functional response driven by species turnover suggests community function will more likely be disrupted by disturbance (Albert *et al.* 2011; Bolnick *et al.* 2011; Violle *et al.* 2012). Grazing shifted community functional structure in our Tibetan alpine meadows more through variation among individual plants within species than through change in occurrence and/or abundance. Hence, community diversity did not significantly change following grazing (Niu *et al.* 2015a), which favours short-term stability in the rangeland ecosystem (Volf *et al.* 2016).

The community-wide LES response to grazing appears to arise not only in this scale-dependent inversion of LES relationships, but also on fixed individual LES traits. While the increase in CWM values for foliar nutrient and SLA following grazing resulted from large ITV, there is a small negative covariance with species turnover (Fig. 2). This indicates that for dominant species, grazing selects for faster-growing individuals with high foliar nutrient content and SLA, but infrequent conservative species with low foliar nutrient content and SLA have an advantage under grazing (Lepš *et al.* 2011; Volf *et al.* 2016). Consistently, the decrease in LDMC_{CWM} following grazing involves a larger negative covariance between ITV and species turnover, which indicates species with low LDMC dominated in grazed plots, while most species tend to increase in LDMC in response to grazing (Fig. 2e). These negative covariance relationships between ITV and species turnover arise mostly in the contrasting effects of grazing on dominant species vs. infrequent species, for example faster-growing species dominate in grazed plots but infrequent, conservative species can take advantage of grazing-induced release from competition. These covariance effects can also be influenced by various intrinsic constraints: (i) interspecific differences in the evolutionary trade-offs among LES traits in their responses to

environmental factors (Shipley *et al.* 2006; Niu *et al.* 2015b); (ii) interspecific competition organized mainly for light in ungrazed communities vs. soil nutrients in grazed communities (Niu *et al.* 2015a); and (iii) selection pressures for plastic responses in leaf foliar nutrient and SLA that maximize short-term resource acquisition vs. LDMC that maximize long-term competitive ability (Ryser & Eek 2000; Niu *et al.* 2015a). The small negative covariation between effect of species occurrence and abundance change for most traits further supports the balance between maximizing short- vs. long-term fitness (Ryser & Eek 2000), but the positive covariation for LN_{CWM} reflects the strong influence of herbivores selectively feeding on plants with higher foliar N (Müller *et al.* 2013).

Although a shift in community functional composition following grazing was consistently induced by ITV over our five sites, the larger species turnover and negative covariation in site effect suggest that among-sites differences may also be important. For instance, the ITV-induced increase in LP_{CWM} following grazing was significant in meadows at favourable sites such as AZ, HY and WLK, but not at the QH and NQ sites where environmental conditions are relatively harsh (Table 2). Similarly, the decline in soil available P due to grazing was significant at the long-grazed WLK site (relative to ungrazed plots) and at the dry site NQ, but not at the other sites. This sort of site dependence in our results is consistent with many previous studies that report differences in grazing effects attributable to differences in climatological conditions, grazing history and management (Diaz *et al.* 2007b; Carmona *et al.* 2015; Eldridge *et al.* 2016). Finally, we note one other possibility: the large effect of species abundance change within plots indicates a high dissimilarity in trait composition among community replicates. This suggests that we may have underestimated ITV within communities due to (i) taking trait measurements at the treatment rather than plot level and (ii) sampling relatively few community replicates at a small spatial scale. Future studies exploring community responses to grazing should further consider this range of possible effects.

These results have important management implications because grazing shifts alpine meadow communities in the Qinghai–Tibetan Plateau from a resource conservative strategy to a resource exploitative strategy, which favours smaller mammalian herbivores. High levels of herbivory by small mammals combined with intensive stocking of domesticated yaks and sheep for shipment to market in turn have driven down the availability of soil phosphorus (Hong, Wang & Wu 2014; Yang *et al.* 2014) and depleted the soil carbon stock (Xiong *et al.* 2014). Similar decreases in soil carbon, nitrogen and phosphorus due to grazing have been reported world-wide (Schipanski & Bennett 2012; McSherry & Ritchie 2013), and especially in Chinese grasslands (Bai *et al.* 2012; Xiong *et al.* 2014). These decreases are often attributed simply to persistent removal of above-ground biomass (Bai *et al.* 2012; McSherry & Ritchie 2013) or sometimes to more subtle

grazing-induced species turnover that alters community productivity (McIntyre 2008; Pérez-Ramos *et al.* 2012). Here, we show that grazing-induced intraspecific variability can also contribute to changes in community function that amplify the effects of above-ground biomass removal and lead to depletion of soil carbon and available phosphorus. Phosphorus limitation in particular appears to account for the stoichiometric imbalance in soil nutrients (Yang *et al.* 2014) and losses of productivity in the Tibetan (Xiong *et al.* 2014) and Inner Mongolian grasslands (Bai *et al.* 2012) in recent decades. Since the recent work by Siefert & Ritchie (2016) suggests that ITV can drive an effective short-term response to grassland fertilization, phosphate fertilization may prove useful as part of a management strategy to balance the three-way interaction among plants, herbivores and soil resources to sustain plant productivity in these alpine rangeland ecosystems over the long term.

More immediately, however, our results suggest the need to reduce grazing intensity by domesticated stock so that the rangeland is not altered to the advantage of smaller wild herbivores. There is clear evidence that pika numbers are high on badly degraded rangeland (Zhao *et al.* 2013), but current rodent control measures aimed at improving degraded range (Wilson & Smith 2015) do not solve the root cause of degradation in the first place, namely domestic grazer overstocking. There is equally clear evidence that plateau pikas can coexist sustainably with domesticated stock under moderate levels of grazing intensity (Zhao *et al.* 2013), which makes ecological sense in terms of the contrasting foraging strategies associated with differences in mammalian body size (Müller *et al.* 2013). Plateau pika selectively forage on forbs rather than graminoids (Jiang & Xia 1985; Wang *et al.* 1992), leaving graminoids available to the larger-bodied domestic stock that are well adapted to digesting their more fibrous tissues. In principle, ongoing dynamic shifts in the phenotypic traits and genotypic variants within rangeland plant species (i.e. ITV) subject to moderate grazing can ensure rangeland stability and resistance to disturbance (Mouillot *et al.* 2013; Volf *et al.* 2016). With proper stocking levels and good timing of rotational grazing in the Qinghai–Tibetan Plateau, the intrinsic resilience in the alpine meadow community due to ITV can temper the degradation of the range associated with species turnover that is observed under steady, intense grazing pressure (Díaz *et al.* 2004; McIntyre 2008; Pérez-Ramos *et al.* 2012).

Acknowledgements

We thank Professor Shucun Sun, Philippe Choler, Marc Cadotte, Lara Souza and two anonymous referees for valuable discussion and constructive comments on earlier versions of this manuscript. We are especially grateful to Zhenong Jin and Lin Ma from Peking University and Professor Guozhen Du and Dr. Xianhui Zhou from the Research Station of Alpine Meadow and Wetland Ecosystems at Lanzhou University, China, for providing invaluable field and laboratory assistance. The study was supported by the National Science Foundation of China (grant no

31370008) and National Basic Research Program of China (no. 2013CB956304).

Data accessibility

Plant species abundance and trait data are available from Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.r5m20> (Niu, He & Lechowicz 2016).

Conflict of interest

The authors declare no conflict of interest.

References

- Adler, P.B., Milchunas, D.G., Lauenroth, W.K., Sala, O.E. & Burke, I.C. (2004) Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology*, **41**, 653–663.
- Albert, C.H., Thuiller, W., Yoccoz, N.G., Soudant, A., Boucher, F., Saccone, P. *et al.* (2010) Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology*, **98**, 604–613.
- Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G. & Violle, C. (2011) When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics*, **13**, 217–225.
- Asplund, J. & Wardle, D.A. (2014) Within-species variability is the main driver of community-level responses of traits of epiphytes across a long-term chronosequence. *Functional Ecology*, **28**, 1513–1522.
- Bai, Y.F., Wu, J.G., Clark, C.M., Pan, Q.M., Zhang, L.X., Chen, S.P. *et al.* (2012) Grazing alters ecosystem functioning and C: N: P stoichiometry of grasslands along a regional precipitation gradient. *Journal of Applied Ecology*, **49**, 1204–1215.
- Bates, D., Maechler, M. & Bolker, B. (2011). lme4: linear mixed-effects models using Eigen and Eigen. R package version 0.999375-38.
- de Bello, F., Lepš, J.A.N. & Sebastia, M.-T. (2005) Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *Journal of Applied Ecology*, **42**, 824–833.
- Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M. *et al.* (2011) Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, **26**, 183–192.
- Briske, D., Sayre, N.F., Huntsinger, L., Fernandez-Gimenez, M., Budd, B. & Derner, J. (2011) Origin, persistence, and resolution of the rotational grazing debate: integrating human dimensions into rangeland research. *Rangeland Ecology & Management*, **64**, 325–334.
- Cao, J., Yeh, E.T., Holden, N.M., Yang, Y. & Du, G. (2013) The effects of enclosures and land-use contracts on rangeland degradation on the Qinghai-Tibetan plateau. *Journal of Arid Environments*, **97**, 3–8.
- Carmona, C.P., Azcárate, F.M., Bello, F., Ollero, H.S., Lepš, J. & Peco, B. (2012) Taxonomical and functional diversity turnover in Mediterranean grasslands: interactions between grazing, habitat type and rainfall. *Journal of Applied Ecology*, **49**, 1084–1093.
- Carmona, C.P., Mason, N.W., Azcárate, F.M. & Peco, B. (2015) Inter-annual fluctuations in rainfall shift the functional structure of Mediterranean grasslands across gradients of productivity and disturbance. *Journal of Vegetation Science*, **26**, 538–551.
- Cingolani, A.M., Posse, G. & Collantes, M.B. (2005) Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. *Journal of Applied Ecology*, **42**, 50–59.
- Cornelissen, J.H.C., Lavoural, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E. *et al.* (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.
- Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K. & Robson, M. (2007a) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 20684–20689.
- Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Milchunas, D., Casanoves, F. *et al.* (2007b) Plant trait responses to grazing – a global synthesis. *Global Change Biology*, **13**, 313–341.
- Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A. *et al.* (2004) The plant traits that drive ecosystem: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.

- Donovan, L.A., Maherali, H., Caruso, C.M., Huber, H. & de Kroon, H. (2011) The evolution of the worldwide leaf economics spectrum. *Trends in Ecology & Evolution*, **26**, 88–95.
- Eldridge, D.J., Poore, A.G., Ruiz-Colmenero, M., Letnic, M. & Soliveres, S. (2016) Ecosystem structure, function and composition in rangelands are negatively affected by livestock grazing. *Ecological Applications*, **26**, 1273–1283.
- Frank, D.A., Kuns, M.M. & Guido, D.R. (2002) Consumer control of grassland plant production. *Ecology*, **83**, 602–606.
- Friendly, M. & Fox, J. (2013). Visualizing Generalized Canonical Discriminant and Canonical Correlation Analysis. R Package “candisc”, version: 0.6-5.
- Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M. *et al.* (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J. *et al.* (2007) Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, **99**, 967–985.
- Gibson, D.J. (2009) *Grasses and Grassland Ecology*. Oxford University Press Inc., New York, NY.
- Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.
- Grime, J.P. (2001) *Plant Strategies, Vegetation Processes and Ecosystem Properties*. John Wiley Sons, Chichester.
- Harris, R.B. (2010) Rangeland degradation on the Qinghai-Tibetan plateau: a review of the evidence of its magnitude and causes. *Journal of Arid Environments*, **74**, 1–12.
- He, J.-S., Fang, J., Wang, Z., Guo, D., Flynn, D.F. & Geng, Z. (2006) Stoichiometry and large-scale patterns of leaf carbon and nitrogen in the grassland biomes of China. *Oecologia*, **149**, 115–122.
- He, J.-S., Wang, L., Flynn, D.F., Wang, X., Ma, W. & Fang, J. (2008) Leaf nitrogen: phosphorus stoichiometry across Chinese grassland biomes. *Oecologia*, **155**, 301–310.
- Hong, J., Wang, X. & Wu, J. (2014) Stoichiometry of root and leaf nitrogen and phosphorus in a dry alpine steppe on the Northern Tibetan Plateau. *PLoS ONE*, **9**, e109052.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. *et al.* (2005) Effect of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- Jiang, Z. & Xia, W. (1985) Utilization of the food resources by plateau pika. *Acta Theriologica Sinica*, **5**, 251–262.
- Jung, V., Violle, C., Mondy, C., Hoffmann, L. & Muller, S. (2010) Intraspecific variability and trait-based community assembly. *Journal of Ecology*, **98**, 1134–1140.
- Jung, V., Albert, C.H., Violle, C., Kunstler, G., Loucougaray, G. & Spiegelberger, T. (2014) Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. *Journal of Ecology*, **102**, 45–53.
- Kichenin, E., Wardle, D.A., Peltzer, D.A., Morse, C.W. & Freschet, G.T. (2013) Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology*, **27**, 1254–1261.
- Laughlin, D.C. (2014) Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*, **17**, 771–784.
- Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.
- Lavorel, S. & Grigulis, K. (2012) How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology*, **100**, 128–140.
- Lepš, J., De Bello, F., Šmilauer, P. & Doležal, J. (2011) Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography*, **34**, 856–863.
- Lessard, J.-P., Belmaker, J., Myers, J.A., Chase, J.M. & Rahbek, C. (2012) Inferring local ecological processes amid species pool influences. *Trends in Ecology & Evolution*, **27**, 600–607.
- Mason, N.W.H., de Bello, F., Doležal, J. & Lepš, J. (2011) Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *Journal of Ecology*, **99**, 788–796.
- McIntyre, S. (2008) The role of plant leaf attributes in linking land use to ecosystem function in temperate grassy vegetation. *Agriculture Ecosystems & Environment*, **128**, 251–258.
- McSherry, M.E. & Ritchie, M.E. (2013) Effects of grazing on grassland soil carbon: a global review. *Global Change Biology*, **19**, 1347–1357.
- Messier, J., McGill, B.J. & Lechowicz, M.J. (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, **13**, 838–848.
- Miehe, G., Miehe, S., Kaiser, K., Reudenbach, C., Behrendes, L. & Schlütz, F. (2009) How old is pastoralism in Tibet? An ecological approach to the making of a Tibetan landscape. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **276**, 130–147.
- Moullot, D., Graham, N.A., Vileger, S., Mason, N.W. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, **28**, 167–177.
- Müller, D.W., Codron, D., Meloro, C., Munn, A., Schwarm, A., Hummel, J. *et al.* (2013) Assessing the Jarman-Bell principle: scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, **164**, 129–140.
- Nelson, D.W. & Sommers, L.E. (1982) Total carbon, organic carbon, and organic matter. *Methods of Soil Analysis* (eds A. Page, R. Miller & D. Keeney), pp. 539–579. American Society of Agronomy, Madison, WI.
- Niu, K.C., He, J.-S. & Lechowicz, M.J. (2016) Data from: grazing-induced shifts in community functional composition and soil nutrient availability in Tibetan alpine meadows. *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.r5m20>.
- Niu, K.C., Choler, P., Zhao, B.B. & Du, G.Z. (2009) The allometry of reproductive biomass in response to land use in Tibetan alpine grasslands. *Functional Ecology*, **23**, 274–283.
- Niu, K.C., Zhang, S.T., Zhao, B.B. & Du, G.Z. (2010) Linking grazing response of species abundance to functional traits in the Tibetan alpine meadow. *Plant and Soil*, **330**, 215–223.
- Niu, K.C., Schmid, B., Choler, P. & Du, G.Z. (2012) Relationship between reproductive allocation and relative abundance among 32 species of a Tibetan alpine meadow: effects of fertilization and grazing. *PLoS ONE*, **7**, e35448.
- Niu, K.C., He, J.-S., Zhang, S.T. & Lechowicz, M.J. (2015a) Grazing increases functional richness but not functional divergence in Tibetan alpine meadow plant communities. *Biodiversity and Conservation*, doi: 10.1007/s10531-015-0960-2.
- Niu, K.C., Messier, J., He, J.-S. & Lechowicz, M.J. (2015b) The effects of grazing on trait diversity and niche differentiation in Tibetan alpine meadows. *Ecosphere*, **6**, Art150.
- Pérez-Ramos, I.M., Roumet, C., Cruz, P., Blanchard, A., Autran, P. & Garnier, E. (2012) Evidence for a ‘plant community economics spectrum’ driven by nutrient and water limitations in a Mediterranean rangeland of southern France. *Journal of Ecology*, **100**, 1315–1327.
- Post, D.M., Palkovacs, E.P., Schielke, E.G. & Dodson, S.I. (2008) Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology*, **89**, 2019–2032.
- Prieto, I., Roumet, C., Cardinael, R., Dupraz, C., Jourdan, C., Kim, J.H. *et al.* (2015) Root functional parameters along a land-use gradient: evidence of a community-level economics spectrum. *Journal of Ecology*, **103**, 361–373.
- Reich, P.B. (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology*, **102**, 275–301.
- de la Riva, E.G., Pérez-Ramos, I.M., Tosto, A., Navarro-Fernández, C.M., Olmo, M., Marañón, T. & Villar, R. (2016) Disentangling the relative importance of species occurrence, abundance and intraspecific variability in community assembly: a trait-based approach at the whole-plant level in Mediterranean forests. *Oikos*, **125**, 354–363.
- Ryser, P. & Eek, L. (2000) Consequences of phenotypic plasticity vs. interspecific differences in leaf and root traits for acquisition of aboveground and belowground resources. *American Journal of Botany*, **87**, 402–411.
- Schank, J.C. & Koehnle, T.J. (2009) Pseudoreplication is a pseudoproblem. *Journal of Comparative Psychology*, **123**, 421.
- Schipanski, M.E. & Bennett, E.M. (2012) The influence of agricultural trade and livestock production on the global phosphorus cycle. *Ecosystems*, **15**, 256–268.
- Shipley, B., Lechowicz, M.J., Wright, I. & Reich, P.B. (2006) Fundamental trade-offs generating the worldwide leaf economics spectrum. *Ecology*, **87**, 535–541.
- Siefert, A. & Ritchie, M.E. (2016) Intraspecific trait variation drives functional responses of old-field plant communities to nutrient enrichment. *Oecologia*, **181**, 245–255.

- Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A. *et al.* (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, **18**, 1406–1419.
- Sommers, L. & Nelson, D. (1972) Determination of total phosphorus in soils: a rapid perchloric acid digestion procedure. *Soil Science Society of America Journal*, **36**, 902–904.
- Suding, K.N., Lavorel, S., Chapin, F.S. III, Cornelissen, J.H., Diaz, S., Garnier, E. *et al.* (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, **14**, 1125–1140.
- Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C. *et al.* (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, **27**, 244–252.
- Wolf, M., Redmond, C., Albert, Á.J., Le Bagousse-Pinguet, Y., Biella, P., Götzenberger, L. *et al.* (2016) Effects of long- and short-term management on the functional structure of meadows through species turnover and intraspecific trait variability. *Oecologia*, **180**, 941–950.
- Wang, X., Liu, J., Liu, W. & Ji, L. (1992) Studies on the nutritional ecology of herbivorous small mammals: patterns of food selection and food quality for plateau pikas, *Ochotona curzoniae*. *Acta Theriologica Sinica*, **12**, 183–192.
- Wilson, M.C. & Smith, A.T. (2015) The pika and the watershed: the impact of small mammal poisoning on the ecohydrology of the Qinghai-Tibetan plateau. *Ambio*, **44**, 16–22.
- Wise, M.J. & Abrahamson, W.G. (2005) Beyond the compensatory continuum: environmental resource levels and plant tolerance of herbivory. *Oikos*, **109**, 417–428.
- Wise, M.J. & Abrahamson, W.G. (2007) Effects of resource availability on tolerance of herbivory: a review and assessment of three opposing models. *The American Naturalist*, **169**, 443–454.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.
- Xiong, D.P., Shi, P.L., Sun, Y.L., Wu, J.S. & Zhang, X.Z. (2014) Effects of grazing exclusion on plant productivity and soil carbon, nitrogen storage in alpine meadows in northern Tibet, China. *Chinese Geographical Science*, **24**, 488–498.
- Yang, Z., Powell, J.R., Zhang, C. & Du, G. (2012) The effect of environmental and phylogenetic drivers on community assembly in an alpine meadow community. *Ecology*, **93**, 2321–2328.
- Yang, Y.H., Fang, J.Y., Ji, C.J., Datta, A., Li, P., Ma, W.H. *et al.* (2014) Stoichiometric shifts in surface soils over broad geographical scales: evidence from China's grasslands. *Global Ecology and Biogeography*, **23**, 947–955.
- Zhang, T., Wang, Y., Yao, F.-J., Shi, Y.-T., Cui, G.-W. & Hu, G.-F. (2014) Effect of grazing intensity on ecological stoichiometry of *Deyeuxia angustifolia* meadow. *Acta Prataculturae Sinica*, **23**, 20–28.
- Zhao, G., Li, G., Ma, W., Zhao, D. & Li, X. (2013) Impacts of *Ochotona pallasii* disturbance on alpine grassland community characteristics. *Chinese Journal of Applied Ecology*, **24**, 2122–2128.

Received 15 February 2016; accepted 23 June 2016

Handling Editor: Lara Souza

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. The locations of the five study sites.

Table S1. Summary community weighted mean of leaf traits and soil nutrients in grazed and ungrazed plots at five meadows in the Qinghai-Tibetan Plateau.

Table S2. Disentangling the relative importance of changes in species occurrence and abundance vs. intraspecific variability in determining site, grazing and plot effects on variation in community weighted traits.