The effects of grazing on foliar trait diversity and niche differentiation in Tibetan alpine meadows

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Abstract. Niche differentiation arising in functional trait diversity is expected to increase the potential for species coexistence, but empirical evidence for these relationships is sparse. We test whether grazing increases the functional diversity of leaf traits and niche differentiation in phosphorus limited Tibetan alpine meadows. We measured five traits in the leaf economic spectrum (LES; LC, leaf carbon concentration; LN, leaf nitrogen concentration; LP, leaf phosphorus concentration; SLA, specific leaf area; and LDMC, leaf dry matter content) for all species occurring in grazed and ungrazed plots at each of five sites. By comparing indicators of the fundamental and realized niches of co-occurring plants in both grazed and ungrazed plots, we quantified a grazing-mediated competitive effect on trait divergence and convergence. This trait response reflects the relative importance of niche differentiation and competitive exclusion in response to grazing. We found that while grazing induced LP divergence, both LC and LN tended to converge under grazing. Grazing had no effect on either SLA or LDMC diversity. When all five traits are considered together as a functionally integrated suite (LES hypervolume), there is no evidence for either divergence or convergence in response to grazing. Although grazing promotes functionally relevant diversity in LP that enables niche differentiation in competition for scarce soil available P, these results suggest that coordinated shifts in other LES traits sustain effective overall foliar function despite shifts in LP.

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INTRODUCTION

The mechanisms affecting species coexistence and community assembly necessarily involve a balance between trait convergence and divergence among coexisting species. On one hand, the principle of limiting similarity predicts divergence for some traits in coexisting species to reduce interspecific competition (Grime 2006, Kraft and Ackerly 2010, Godoy et al. 2014). On the other hand, abiotic environmental filters determining entry into the community may enforce a degree of trait convergence among coexisting species (Cornwell et al. 2006; Kraft et al., *in press*). Biotic filtering can also cause convergence in traits through competitive interactions that confer dominance to a few species in a community (Mayfield and Levine 2010, Hille

Ris Lambers et al. 2012, Godoy et al. 2014). Ultimately, after removing the effect of abiotic environmental filtering on trait convergence in local communities, species coexistence and community biodiversity should be determined by the balance between two antagonistic forces associated with competition-mediated biotic effects: niche differentiation and competitive exclusion that induce trait divergence and convergence, respectively (Grime 2006, Cornwell and Ackerly 2009). Empirical evidence for niche differentiation promoting species coexistence and community diversity, however, is sparse (Siepielski and McPeek 2010, Thompson et al. 2010, Freschet et al. 2011). This paucity of empirical support can be attributed either to potential trait divergence being offset by counterbalancing abiotic or biotic effects that are simultaneously causing convergence (Swenson and Enquist 2009, Götzenberger et al. 2012) or to methodological constraints in separating the effects of abiotic and biotic process on trait convergence and divergence (Mayfield and Levine 2010, de Bello et al. 2012; Kraft et al., *in press*). In this paper, we report the results of an exclosure experiment in Tibetan alpine meadows that was designed specifically to isolate the biotic effects on trait divergence and convergence in grazed versus ungrazed plant communities.

The Tibetan alpine meadows we studied (Niu et al. 2010) provide a good system in which to isolate biotic filtering effects that could lead to niche differentiation and competitive exclusion in grazed versus ungrazed plots. First, the meadow communities have both high species diversity (e.g., 20–50 species in a 0.25-m^2 quadrat) and high ramet density (e.g., 300–500 individuals in a 0.25-m^2 quadrat), which suggests strong biotic filtering effects should occur (cf. Bagousse-Pinguet et al. 2014). Second, the relatively low dissimilarity of species composition among samples of the meadow community at each study site (modes of Bray-Curtis dissimilarity values from 0.23 to 0.44) suggests relatively weak abiotic filtering within each site (Mayfield and Levine 2010, Götzenberger et al. 2012; Kraft et al., *in press*), which should make it easier to isolate biotic filtering effects. Finally, soil phosphorus availability is a strong limiting factor in these alpine meadows (Yang et al. 2014; Niu et al., *unpublished manuscript*), which suggests that competition for soil phosphorus should promote

biotic filtering effects involving functional diversity in leaf traits (Lambers et al. 2010, Venterink 2011) when competitive exclusion is reduced by grazing. Hence, we hypothesize that increased competition for soil nutrients, especially soil phosphorus, in grazed plots will have led to increased niche differentiation and promoted a greater diversity of leaf traits in communities where competitive exclusion is reduced by grazing.

To test this hypothesis we use a functional species pool framework (de Bello et al. 2012) to distinguish contrasting competitive effects on trait divergence and convergence. The value of this analytic approach depends critically on certain aspects of our experimental design. First, we define the species pool subject to biotic assembly mechanisms at a very fine scale—the community of species co-occurring in a 0.25-m^2 quadrat, which ipso facto have passed the same abiotic filters (Götzenberger et al. 2012). Second, we use mean pairwise distance calculated for a set of covariate foliar traits as a measure of shifts in functional diversity in grazed versus ungrazed plots. Third, we use standardized effect size (SES) to remove the influence of sample size on mean pairwise distance (Mason et al. 2013) and adjust the abundance-weighted mean pairwise distance for differences in species diversity (de Bello et al., *unpublished manuscript*). Finally, we compare the abundance-weighted functional diversity measures to those based on presence–absence to evaluate the degree of niche differentiation in grazed versus ungrazed plots. When abundance-weighted functional diversity in the community exceeds that in the species pool one can infer that niche differentiation promotes higher trait diversity in a more functionally diverse community. Conversely, when there is strong competitive exclusion the abundance-weighted functional diversity in the community will be less than that in the functional species pool (Appendix: Fig. A1; de Bello et al. 2012). In communities without either significant trait divergence or convergence, niche differentiation and competitive exclusion can be inferred to be of similar strength. This combination of experimental design and analytic approach provides a strong test of our hypothesis that competition for soil nutrients, especially soil phosphorus, will lead to increased niche differentiation and

greater functional diversity of leaf traits in communities when competitive exclusion is reduced by grazing in Tibetan alpine meadows.

An additional concern, however, is that it may be difficult to distinguish neutral pattern from niche processes based on the examination of only single traits in isolation (Purves and Pacala 2005). Differences in the functional diversity of traits need not all reflect responses to the same abiotic and biotic factors affecting community assembly (Götzenberger et al. 2012, Hille Ris Lambers et al. 2012, Spasojevic and Suding 2012). For example, variation in the functional diversity of SLA may reflect niche differentiation among species in competition for soil nutrients and water in general while species differences in LDMC are a consistent response to low soil fertility (Hodgson et al. 2011). Similarly, differences in foliar nutrient concentrations may arise in species-specific differences in capture of particular soil nutrients (Mason et al. 2012).

The responses of any particular trait in turn are constrained by its functional linkages with other traits, each potentially responding somewhat differently to abiotic and biotic factors. There is clearly a degree of functional coordination among diverse traits and trade-offs among traits can yield more or less equal performance (Marks and Lechowicz 2006a, Reich 2014), so any mapping of a single trait on a single environmental factor is unlikely to represent the functional basis of community assembly. A community can show a quasi-neutral pattern of species abundance in fact based on a complex underlying niche process involving multiple interacting traits (Purves and Pacala 2005). Consideration of the patterns of divergence and convergence in a suite of functionally linked traits (a trait hypervolume) can help better understand the processes involved in community assembly. Hence, in this paper we also consider whether community biodiversity is promoted through simple or more complex niche differentiation in foliar function by examining the responses of five traits in the leaf economic spectrum (LES; Reich 2014) singly as well as in aggregate.

Methods

Study sites

We compared the functional trait diversity of plant communities in grazed and ungrazed plots at five alpine meadows located from the eastern (WLK, Niu et al. 2009; HY, Zhao et al. 2013; AZ, Zhang et al. 2014) to northern (QH, Wang et al. 2012) and western (NQ, Xiong et al. 2014) parts of the Tibetan Plateau (Appendix: Fig. A2). To account for the impact of variation in the local species pool on the structure of ecological communities, which is critically important for a strong test of local effects on community structure (Lessard et al. 2012), the sites are separated by 150–1850 km. Mean annual temperature and precipitation as well as productivity, biodiversity, soil depth, and nutrient availability decrease significantly both from east to west and from south to north (Appendix: Table A1). Total vegetation cover in midsummer exceeds 80% at all sites. Vegetation height and individual density in 0.25-m^2 plots in ungrazed meadows ranges from 10 to 20 cm and 500 individuals in the northern and western sites to 30–50 cm and 300 individuals in eastern sites. Outside exclosures, the meadows are primarily grazed by domesticated yaks and at drier sites such as WLK, QH, and NQ also by sheep. In our exclosures, the meadows are either wholly ungrazed or only lightly grazed during winter.

Experimental design

At each site, we studied alpine meadows on level terrain by establishing large fenced exclosures preventing grazing during the peak growing season for either 11 (WLK) or 3–5 years (Appendix: Table A1). Both large and small vertebrate grazers were allowed within the exclosures during the non-growing season (winter months) for AZ, WLK, and NQ, but excluded throughout the year for HY and QH. Outside of the exclosure, 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-elevation pastures.

At each site in June 2009, we randomly set up eight 5 × 8 m ungrazed plots separated by 10–200 m within the exclosure, as well as eight 5 × 8 m grazed plots outside the exclosure separated by 10–510 m and 300–1000 m from the ungrazed

plots inside the exclosure (Appendix: Fig. A2). Each replicate plot was divided into two parts: a 5 × 5 m subplot for measurement of plant traits and a 5 × 3 m subplot, in which a 0.5 × 0.5 m (0.25-m^2) quadrat was set out for community monitoring, biomass harvest, and soil sampling (Appendix: Fig. A2). Our 0.25-m^2 quadrats provide independent replicates for assessing variation in community composition at each site because (1) the species-area curve saturates between 0.15 and 0.22 m^2 in these alpine meadows and (2) the 10–510 m pairwise separation between quadrats (median = 180 m) ensured negligible spatial autocorrelation effects.

Trait measurements

Using standard protocols for functional traits, we measured five LES traits in July 2009 and 2010 on a total of 32,852 plants: SLA (mm^2 × mg), LDMC (mg × g), LC (mg × g), LN (mg × g), and LP (mg × g). Details for the trait measurements are provided in He et al. (2006, 2008). For each species at each site, we measured SLA and LDMC using samples collected near our 0.25-m^2 quadrats in each plot. In the case of foliar LN, LP, and LC, the biomass of the less abundant species at the plot level was insufficient for analysis so we pooled leaf material by species and treatment (grazed vs. ungrazed plots) at each site. The sampled species accounted for 90–98% and 95–99% of the aboveground biomass and vegetation cover in these alpine meadows, respectively. Taking trait measurements on plants growing in close proximity to the 0.25-m^2 quadrats used to sample grazed and ungrazed community composition at each site allowed us to examine trait responses among co-occurring species subject to closely similar abiotic environments.

Community and soil measurements

From mid-August to early September 2009, we harvested standing aboveground biomass (stems and leaves) of plants sorted by species in the 0.25-m^2 quadrats within each of the 5 × 3 m subplots at all the sites except HY, which was harvested in 2010. We determined the standing oven-dry biomass of each species and calculated the relative abundance of each species as a fraction of the total oven-dry biomass in each ¼ m^2 quadrat. We also collected and pooled three soil

samples from the 0–15 cm soil layer near each quadrat. The soil samples were homogenized, air-dried, and sieved (2-mm mesh) for measurement of soil total C and N concentrations (mg × g) by elemental analysis (He et al. 2006), soil organic carbon concentrations (mg × g) by the Walkley–Black method (Nelson and Sommers 1982), and soil available P concentrations (Olsen-P; mg × kg) by a molybdate colorimetric test after perchloric acid digestion (Sommers and Nelson 1972).

Data analysis

Measuring and quantifying the functional diversity in foliar traits.—We calculated the means of SLA and LDMC (7–10 replicates) as well as LC, LN, and LP (three replicates) for each species in grazed and ungrazed plots. We calculated functional diversity using a mean pairwise distance (MPD) approach (Pavoine and Bonsall 2011, de Bello et al. 2012) referenced against a null model to calculate standardized effect size (SES) of functional diversity (MPD$_{SES}$; Mason et al. 2013). The calculation of MPD is mathematically similar to other indices of functional diversity that calculate the mean trait dissimilarity among all possible pairs of species comprising each community (i.e., our 0.25-m^2 quadrats). Since MPD is independent of species number (Table 1; Pavoine and Bonsall 2011), we calculated a standardized effect size to remove any effect of sample size (and therefore abundance). These MPD$_{SES}$ values for each of the five foliar traits as well as for the LES hypervolume based on the combination of all five traits were calculated in R using the picante package. The calculation is based on the species abundance data using a weighted Gower distance matrix of the trait data compared against a null distribution of trait values. The null distribution of trait values was generated using 9,999 randomizations of the species names in the trait distance matrices

$$\text{MPD}_{SES} = \frac{\text{MPD}_{comm} - \text{mean}(\text{MPD}_{rand})}{\text{sd}(\text{MPD}_{rand})} \quad (1)$$

where MPD$_{comm}$ is the observed community MPD and MPD$_{rand}$ is the null expectation.

A positive MPD$_{SES}$ indicates community trait diversity is larger than that expected in a random community of equal species richness, and a negative MPD$_{SES}$ value indicates less trait diver-

Table 1. Results of nested linear-mixed modelling for effect of grazing (nested in sites) on observed functional diversity ($^{abund}MPD_{SES}$) of leaf traits. The tabulated values indicate the strength of the grazing effect gauged by the slope of the relationship. Positive and negative values indicate increased and decreased traits in grazed plots relative to ungrazed plots.

$^{abund}MPD_{SES}$	AIC/BIC	Intercept	Strength and direction of the grazing effect				
			AZ	HY	WLK	QH	NQ
Leaf C	172.46/197.59	−0.91 ± 0.21*	0.02 ± 0.38	−1.63 ± 0.37*	−3.02 ± 0.38*	0.49 ± 0.38	−0.91 ± 0.38
Leaf N	174.58/199	−1.00 ± 0.25*	0.32 ± 0.39	−0.65 ± 0.39	−2.76 ± 0.39*	−1.32 ± 0.39*	−1.80 ± 0.39*
Leaf P	152.96/178.09	−1.30 ± 0.21*	2.39 ± 0.33*	1.32 ± 0.33*	2.16 ± 0.33*	0.54 ± 032	1.16 ± 0.32*
SLA	165.95/191.08	−0.10 ± 0.23	−0.12 ± 0.36	0.13 ± 0.36	−1.26 ± 0.36*	−1.42 ± 0.36*	0.93 ± 0.36
LDMC	172.30/197.43	1.76 ± 0.25*	−1.91 ± 0.38*	0.26 ± 0.37	−0.74 ± 0.38	1.81 ± 0.38*	0.23 ± 0.37
All leaf traits	169.98/195.11	−0.48 ± 0.125	0.10 ± 0.37	−0.05 ± 0.37	−2.02 ± 0.37*	−0.07 ± 0.38	−0.25 ± 0.37

Notes: Value = slope value + SE with boldface entries indicating p < 0.05 and an asterisk indicating p < 0.01; df = 60. Abbreviations are: AIC, Akaike information criterion; BIC, the Schwarz's Bayesian information criteria.

sity than expected. For each community (i.e., each 0.25-m^2 quadrat), we calculated both a presence-absence based estimate of trait diversity in the species pool ($^{P/a}MPD_{SES}$) and a measure of trait diversity weighted by relative abundance in the community ($^{abund}MPD_{SES}$). The values of $^{abund}MPD$ were normalized against Simpson species diversity (de Bello et al., *unpublished manuscript*). We then compared the ratio of $^{abund}MPD_{SES}$ and $^{P/a}MPD_{SES}$ to identify trait divergence and convergence in each community.

Assessing trait divergence and trait convergence.— To distinguish the relative importance of niche differentiation and competitive exclusion in controlling trait divergence and convergence, we followed the functional species pool framework proposed by de Bello et al. (2012) with some modification allowing for our specific sampling and experimental designs. We used $^{abund}MPD_{SES}$ and $^{P/a}MPD_{SES}$ of traits as indicators of the realized and fundamental niche, respectively. The trait diversity in a sampled community can be interpreted as indicative of niche differences among co-occurring species after abiotic filtering (Violle and Jiang 2009, Spasojevic and Suding 2012) and $^{P/a}MPD$ as a measure of trait diversity in the species pool available for community assembly (de Bello et al. 2012). Hence when $^{abund}MPD_{SES}$ is plotted against $^{P/a}MPD_{SES}$, a community located above the 1:1 line indicates competition-induced trait divergence has occurred, and a community below the 1:1 line indicates trait convergence (de Bello et al. 2012).

Working in this conceptual framework, we used standardized major axis regressions (War-

ton et al. 2006, Niu et al. 2009) to quantify the relationship between $^{abund}MPD_{SES}$ and $^{P/a}MPD_{SES}$ for each trait and for the combination of all traits in grazed and ungrazed plots at each site and across all five sites. We compared the regression to the 1:1 line expected when trait divergence and convergence are of similar strengths (de Bello et al. 2012). We also tested the difference in elevations and slope of regressions between grazed plots and ungrazed plots in each sites and across five sites. All regressions and tests of the shifts in elevation and slope were conducted using the smatr package (Warton et al. 2014).

Response of functional diversity to grazing.—To examine the effect of grazing on community functional diversity ($^{abund}MPD_{SES}$) of the individual traits over five sites, we used a linear-mixed model with residual maximum likelihood (REML): fixed = response ~ site/grazing, random = ~1|plot. Here, grazing was included as a nested fixed factor, and individual plots taken as a random factor to account for the (unlikely) possibility of spatial autocorrelation. Where necessary, data were log-transformed to meet assumptions of normality and homogeneity of variance. This mixed model was tested using the lme functions of the lme4 package (Bates et al. 2011). Last, we used generalized canonical discriminant analyses (gCCA) with a nested linear model (grazing nested in site effect) to visualize the relationships among the $^{abund}MPD_{SES}$ values for leaf traits in relation to soil nutrients in grazed and ungrazed plots across the five sites. The gCCA was performed using the candisc package (Friendly and Fox
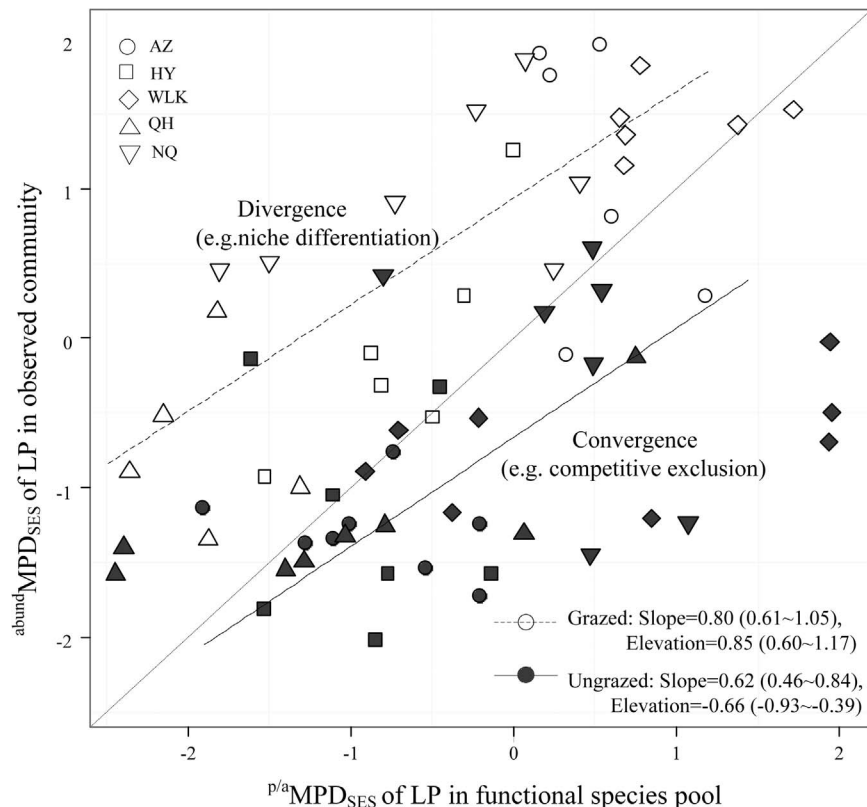
Fig. 1. The functional diversity (MPD_{SES}) of leaf P in observed communities ($^{abund}MPD_{SES}$, calculated based on species relative abundance) is compared with that in a functional species pool, based on species presence and absence ($^{p/a}MPD_{SES}$) for both grazed and ungrazed communities across five sites. A point located above the 1:1 line indicates trait divergence induced by niche differentiation and a point below the 1:1 line indicates trait convergence caused by competitive exclusion. The $^{abund}MPD_{SES}$-$^{p/a}MPD_{SES}$ relationship was quantified using standardized major axis regression and the mean and 95% confidence interval of slope and elevation used to test differences in the $^{abund}MPD_{SES}$-$^{p/a}MPD_{SES}$ regression between grazed and ungrazed communities, as well as deviation from the 1:1 line.

2013). All statistical analyses and figures were performed in R 3.1.0 (R Development Core Team 2007).

RESULTS

Trait divergence versus trait convergence

In terms of LP, grazed communities shift toward trait divergence (i.e., fall above the 1:1 line in Fig. 1) irrespective of site, and most ungrazed communities tend to trait convergence (i.e., fall below the 1:1 line). This shift of grazed communities toward trait divergence is associated with increasing elevation of the $^{abund}MPD_{SES}$-$^{p/a}MPD_{SES}$ regression without change in slope (Fig. 1). The slopes of the

$^{abund}MPD_{SES}$-$^{p/a}MPD_{SES}$ regression both in grazed and ungrazed plots are below 1, which indicates that the importance of competitive exclusion increases as trait diversity increases (Fig. 1). There is no significant interaction between grazing and site effects on shifts in the balance of trait divergence and convergence.

In terms of LC (Fig. 2A) and LN (Fig. 2B), grazed communities tend toward convergence with elevation of the $^{abund}MPD_{SES}$-$^{p/a}MPD_{SES}$ regression less than zero. In contrast, most ungrazed communities tend toward divergence with the elevation of the $^{abund}MPD_{SES}$-$^{p/a}MPD_{SES}$ regression tend to be greater than zero (Fig. 2A, B). For both LC and LN, grazed communities
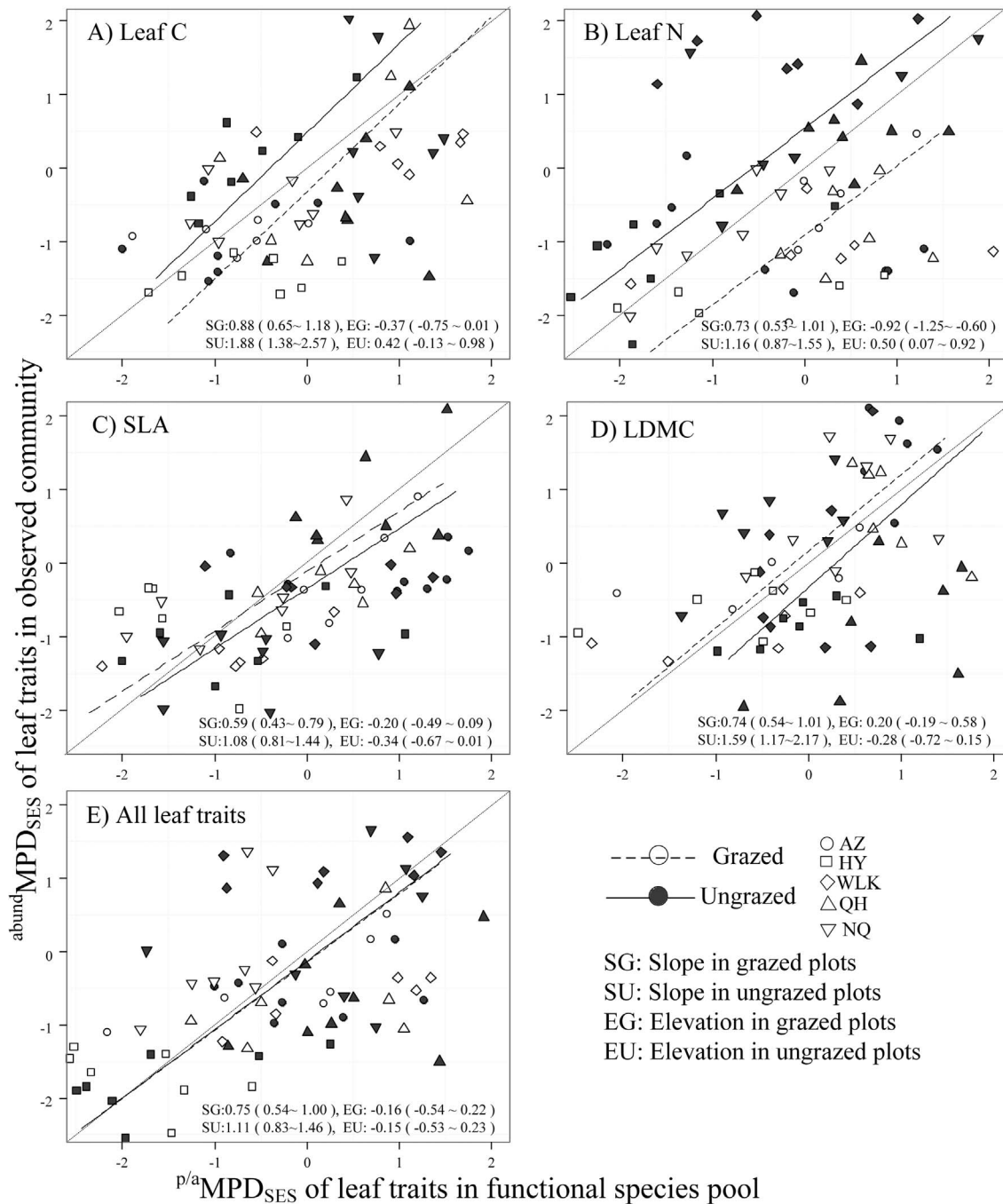
Fig. 2. The functional diversity (MPD_{SES}) for leaf traits in observed communities based on species relative abundance ($^{abund}MPD_{SES}$) compared with that in functional species pool based on species presence and absence ($^{p/a}MPD_{SES}$) for both grazed and ungrazed communities across five sites. A point located above the 1:1 line indicates trait divergence induced by niche differentiation and a point below the 1:1 line indicates trait convergence caused by competitive exclusion. The $^{abund}MPD_{SES}$-$^{p/a}MPD_{SES}$ relationship was quantified using standardized major axis regression and the mean and 95% confidence interval of slope and elevation used to test differences in the $^{abund}MPD_{SES}$-$^{p/a}MPD_{SES}$ regression between grazed and ungrazed communities as well as deviation from the 1:1 line.
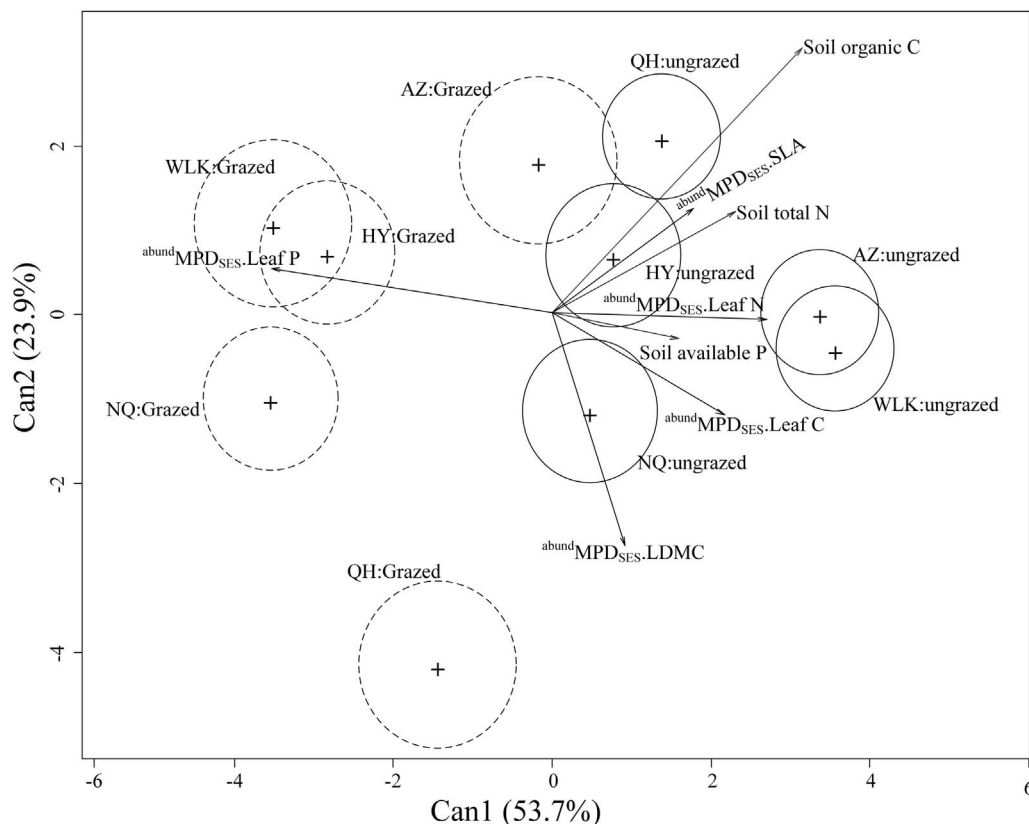
Fig. 3. Generalized canonical discriminant analysis showing the influence of functional diversity of leaf traits in the observed communities (^{abund}MPD$_{SES}$) and soil nutrients on relationships among the grazed and ungrazed communities at each of the five study sites. The continuous and broken circles bound the 95% confidence interval around the site-treatment mean in ungrazed and grazed communities, respectively.

tend to exhibit lower ^{abund}MPD$_{SES}$-$^{P/a}$MPD$_{SES}$ regression slopes. This pattern is opposite from the response of LP to grazing (Fig. 1).

In terms of SLA (Fig. 2C), LMDC (Fig. 2D), and the LES hypervolume (Fig. 2E), the slopes of the ^{abund}MPD$_{SES}$-$^{P/a}$MPD$_{SES}$ regression slightly increased in grazed communities relative to ungrazed, but not the elevations. Grazed communities did not significantly differ from ungrazed communities in convergence versus divergence of these traits (Fig. 2C–E).

Response in the functional diversity of leaf traits under grazing

In term of the functional diversity for individual leaf traits, the ^{abund}MPD$_{SES}$ of LP significantly increased in grazed communities at four of five sites (Table 1). The ^{abund}MPD$_{SES}$ of LC and LN also significantly decreased in grazed communi-

ties at two and three sites, respectively (Table 1). The ^{abund}MPD$_{SES}$ of SLA significantly decreased in grazed communities at the WLK and QH sites but increased at NQ, while MPD$_{SES}$ of LDMC increased in QH but decreased at AZ (Table 1). The ^{abund}MPD$_{SES}$ for all traits combined did not differ significantly between grazed and ungrazed communities at four of our five sites (Table 1). Note that for the longest established experimental site (WLK, 11 years), grazing induced an increase in diversity of LP and decrease in diversity of LC, LN, SLA, and LDMC.

Overall, the first axis of the generalized canonical discriminant analysis shows that the increase in ^{abund}MPD$_{SES}$ of LP is coupled with decreases in soil organic carbon and soil nutrients (Fig. 3). At most sites, the ^{abund}MPD$_{SES}$ values for LC, LN, and SLA all tend to decrease in response to grazing (Table 1, Fig. 3). Site also

significantly impacted the $^{abund}MPD_{SES}$ of leaf traits, but accounted for less variation than the grazing effect, e.g., $^{abund}MPD_{SES}$ of LDMC tends to decrease from AZ and WLK to HY, NQ, and QH (Fig. 3).

DISCUSSION

Niche differentiation is widely assumed to be a fundamental factor promoting greater community diversity, yet field studies have often failed to find strong evidence for the prevalence of niche differentiation effects in community assembly. A related expectation is that niche differentiation can be overwhelmed or neutralized by strong abiotic and biotic filtering effects (Purves and Pacala 2005, Swenson and Enquist 2009, Mayfield and Levine 2010, Götzenberger et al. 2012). Theoretically, once species pass abiotic filters that mediate colonization in a locality, community assembly is then dominated by biotic effects on coexistence. When niche differentiation is greater than competitive exclusion, species can form a stable community with both high trait divergence and high biodiversity. In contrast, when the effects of competitive exclusion are greater than those of niche differentiation, competitively inferior species will be lost from the community and the remaining species will share traits associated with good competitive ability (Grime 2006, Hille Ris Lambers et al. 2012). In this study, by removing the abiotic effect on trait convergence, we found that divergence in leaf P occurred under grazing and was associated with both increased leaf P diversity and species diversity. These results support the idea that niche differentiation drives high community trait diversity when competitive exclusion is prevented but there are further biological details that merit discussion.

It is important to recognize that intensive grazing during recent decades (Miehe et al. 2009) has shifted the plant community in these Tibetan alpine meadows to exploitive resource use and accelerated depletion of soil available P. Competition for soil available P, rather than light or nitrogen, now most limits plants growth and regrowth in grazed plots (Yang et al. 2014). The divergence of leaf P among species in grazed communities generally is driven by niche differentiation due to competition for this limiting

resource, but the dynamics are complicated. The slope below one in the $^{abund}MPD_{SES}$-$^{p/a}MPD_{SES}$ regression across sites (Fig. 1) indicates a larger increase in competitive exclusion relative to niche differentiation with increases in functional diversity. This may be caused by larger niche overlap at species-rich sites with less stressful environments (e.g., WLK and HY in our study; Bagousse-Pinguet et al. 2014) or with facilitation promoting niche differentiation among co-occurring species in stressful environments (Valiente-Banuet and Verdú 2013) with low functional diversity (e.g., NQ and QH in our study).

This complication aside, increasing competition for soil available P generally promotes greater trait diversity because several factors weaken the influence of competitive exclusion. First, unlike size-asymmetric light competition, a larger plant does not have a particularly great advantage over a smaller plant for uptake of soil available P (Rajaniemi 2003, Lambers et al. 2010). Second, in response to grazing, plants tends to increase leaf nutrient content for fast growth and regrowth (Niu et al., *unpublished manuscript*), which often accelerates growth rates at the expense of competitive ability (Vrede et al. 2004, Lambers et al. 2010). This is especially true for tall dominant species, which tend to be more heavily grazed (Niu et al. 2010). Third, the response in foliar nutrients under grazing arises primarily in plastic intraspecific variability (Niu et al., *unpublished manuscript*), which allows a greater trait diversity through favorable pairings of neighboring plants. Finally, the presence of grazers creates local disturbance that favors coexistence of conservative species with high competitive ability and exploitative species with better colonization ability in grazed meadows (Niu et al. 2012).

Although leaf C and leaf N increased with increase of leaf P in response to grazing for both dominant and rare species (Klein et al. 2007, Mi et al. 2015; Niu et al., *unpublished manuscript*), increases in leaf C and N in dominant species are small compared to the increases in rare species, which results in convergence of leaf C and N among occurring species (Figs. 2A, B and 3). It is also possible that taller dominant plants invest less structural C and N due to weakened light competition in grazed plots. In contrast, in grazed plots plants need more P to meet the

demands of faster regrowth as well as seed production (Niu et al. 2009, Lambers et al. 2010), especially for rare species with higher growth rates and reproductive allocation (Niu et al. 2012). In short, these results suggest that plastic intraspecific variation in response to grazing plays a central role in driving functional diversity and organizing community assembly (Niu et al., *unpublished manuscript*). These interactions among plastic responses, competition and community assembly under grazing merit further study.

Finally, we draw attention to the risk of gauging the role of functional diversity in community assembly using single traits, which is commonly done but can be misleading. For example, changes in the functional diversity of easily measured traits such as SLA and LDMC are often used to distinguish biotic and abiotic processes in trait-based community assembly. This makes some sense in that variation in SLA and LDMC within and among species reflects difference in capture of light, soil nutrient, and water resources (Reich 2014), but SLA and LDMC are only part of a functionally linked suite of foliar traits that includes LP, LN, A_{max}, and R_{dark} (Shipley et al. 2006, Reich 2014). Any single trait in this leaf economic spectrum responds to multiple environmental factors in ways constrained by functional linkages to other foliar and non-foliar traits reflecting a variety of plant functions at the whole plant level (Marks and Lechowicz 2006*b*, Reich 2014). This creates multiple possibilities for combinations of traits that yield approximately equal performance at the whole plant level (Marks and Lechowicz 2006*a*). Although the LES is strong across broad scales, it is typically much weaker on small gradients and within communities (e.g., Funk and Cornwell 2013), so that along the main LES trade-off axes, traits retain a significant ability to vary independently of each other, i.e., show scatter perpendicular to an LES trade-off axis. Here, we found that although diversity in leaf phosphorus concentration increased with grazing, diversity in the LES hypervolume did not. This result can be accounted for if traits in the leaf economic spectrum that interact to determine foliar function differ in their responses to resource availabilities, hence increasing the number of viable alternative combinations of trait

values in a given environmental regime. For example, in grazed plots, increase in competition for soil available P can counterbalance decreases in light competition such that there is little change in overall trait convergence and divergence following grazing (cf. Figs. 2C–E and 3). These results support the idea that the integrated effects of functionally linked traits may lead to low overall functional diversity due to approximately equal fitness among species in a locality (Marks and Lechowicz 2006*a*) and that communities can arise with an apparently neutral pattern based on an underlying, complex trait-based niche process (Purves and Pacala 2005).

Acknowledgments

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Characteristics of the five Tibetan alpine meadows in this study.

| Characteristic	AZ	HY	WK	QH	NQ
Latitude, longitude	33°39′ N, 101°52′ E	32°53′ N, 102°36′ E	34°00′ N, 102°00′ E	37°37′ N, 101°12′ E	31°25′ N, 92°00′ E
Elevation (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 exclosures	winter	no	winter	no	winter
Ungrazed years in exclosures	3	4	11	5	3
Average standing biomass in exclosures (g/0.25 m^2)	130	100	130	120	22
Average species richness in exclosures (no./0.25 m^2)	22	21	28	29	14
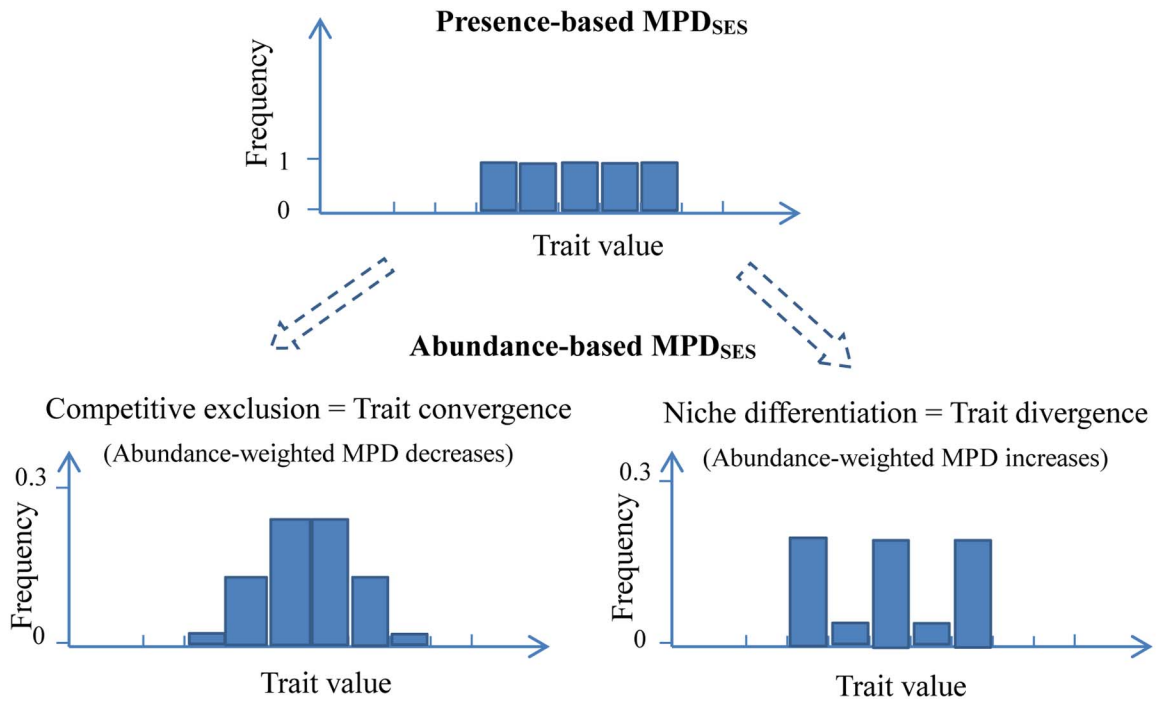
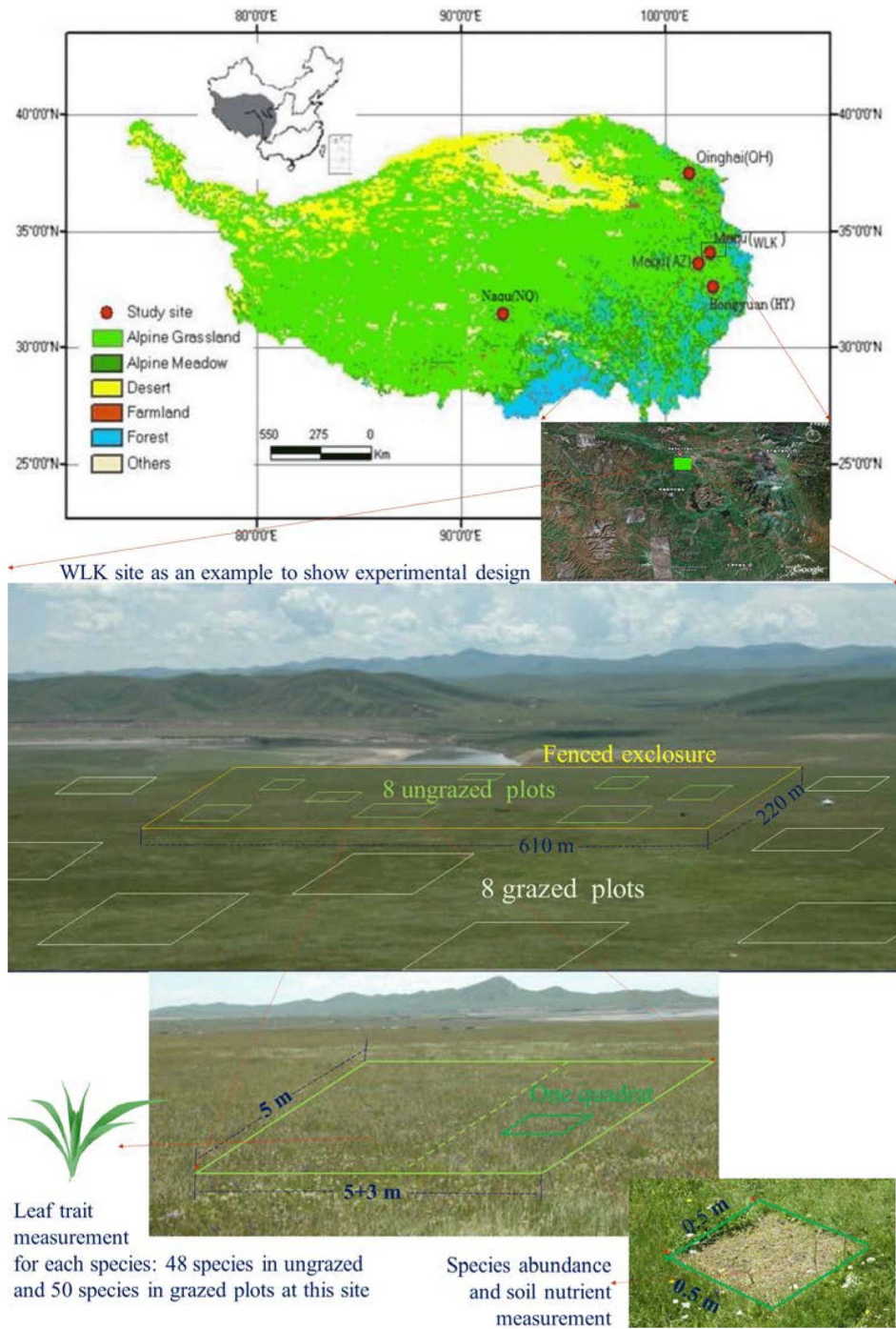Fig. A1. Conceptual illustration of divergent and convergent patterns in a trait.

Fig. A2. Location of the five study sites; site WLK used to illustrate the sampling design.