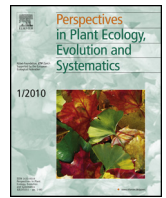


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## Foliar phosphorus content predicts species relative abundance in P-limited Tibetan alpine meadows



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### ABSTRACT

Traits that favor rapid plant growth are expected to have an important influence on species relative abundance (SRA) in semi-natural grasslands where competitive exclusion is reduced by grazing. However, which traits are more strongly associated with variation in SRA remains largely unknown, especially in P-limited but species-rich grasslands. We assessed the relative importance of traits predicting SRA in P-limited Tibetan alpine meadows subject to long term grazing. We assessed abundance in terms of both aboveground biomass and ramet numbers in relation to seven traits (specific leaf area, LDMC: leaf dry matter content, leaf carbon concentration, leaf nitrogen concentration, LPC: leaf phosphorus concentration, mature height, and seed size) for all component species in grazed and ungrazed plots in each of three contrasting sites on the Tibetan Plateau. We used CATS regression (*i.e.* regression for Community Assembly through Trait Selection) to quantify the relative importance of different traits in predicting SRA, and tested dependence of trait importance values on both environmental context and alternative measures of abundance. Species were primarily differentiated along a trade-off axis involving traits promoting nutrient acquisition for fast growth vs resource conservation and competitive ability. A higher LPC consistently was the most important trait predicting species abundance in grazed plots, while species with low LPC but higher LDMC held an advantage in ungrazed plots. This suggests that in competition-released communities, species with a high ability to uptake soil available P tend to become abundant, while in competition-dominated communities, species using fixed P efficiently do better. The relative importance of traits in ungrazed plots did not change across sites, but in grazed plots species that have traits associated with nutrient conservation were favored in colder and drier conditions. The results highlight the importance of traits affecting acquisition of soil available P in these Tibetan alpine meadow communities. Species tradeoffs in nutrient acquisition *versus* conservation are a primary determinant of SRA, but the relative importance of traits depended on both environmental context and whether SRA was estimated as above-ground biomass or as number of ramets.

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### 1. Introduction

Plant community ecologists have a reasonably comprehensive and well-established conceptual framework in which to address the mechanistic basis for the assembly of plant communities (Weiher et al., 2011; Kraft et al., 2015a). The idea of limiting similarity that traces back to Darwin combines well with a multivariate view of the niche (Hutchinson, 1957) to allow evaluation of the likelihood that species similarity limits co-occurrence (Holt, 2009;

Leimar et al., 2013). That likelihood, which lies at the heart of the concept of species coexistence (Kraft et al., 2015b), is considered to be affected by traits that are essential if a species is to successfully establish in given environmental regime. Contemporary theory to explain the coexistence of species focuses on the influence of stabilizing niche differences and relative fitness differences (Chesson, 2000; Hille Ris Lambers et al., 2012) that can be tied to variation in functional traits (Kraft et al., 2015b). In turn, the origin of interspecific trait variation lies in adaptive evolution, raising the question of the degree to which phylogenetic relatedness constrains the likelihood that two species occur together (Cadotte et al., 2013; Godoy et al., 2014). While this conceptual framework governing coexistence and community assembly can help us make *post hoc* sense of a great deal of the voluminous observational records for plant distri-

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bution and abundance, two seemingly intractable problems make it difficult to operationalize current theory in a way that yields robust predictions of community assembly and species relative abundance (SRA) in a particular environmental context (Lawton, 1999; Cadotte et al., 2015).

The difficulties arise in uncertainties at the interface between the processes of environmental filtering and dispersal. Dispersal, the necessary prerequisite to establishment in a community, is an intrinsically stochastic, distance-weighted process characterized by probability distributions in which slight variations in infrequent events weigh heavily in determining successful outcomes (Clobert et al., 2012). Since the shape of these dispersal functions varies among species, the probability distribution for arrival of propagules at a site is a complex function of the geospatial distribution of species populations around the site (Ricklefs, 2015). By comparison environmental filtering can be fairly straightforward at spatial scales from biomes to habitat, but at the scale of a local community, where interactions among neighboring plants are in play, stochasticity driven by fine-scale spatiotemporal heterogeneity predominates (Morin and Lechowicz, 2008; Kraft et al., 2015a). Hence it is difficult to discern what trait or combination of traits determines the success or failure of a propagule in the face of both biotic and abiotic environmental factors in a locality, a challenge made all the more difficult by interactions between the trait dependencies and the spatiotemporal heterogeneity. Given the compounded uncertainty that a propagule will both disperse to a site and have the requisite traits to successfully establish, one might well despair of there ever being a predictive theory for community assembly (Lawton, 1999).

In this paper we explore the utility of an approach called “community assembly through trait selection” (CATS: Shipley, 2010; Shipley et al., 2012), which aims to identify traits that best predict species relative abundance. The CATS approach has proven effective in identifying traits that affect changes in community structure in an experimental study of rangeland management strategies on a decadal time scale in New Zealand (Laliberte et al., 2012). The experiment reported in Laliberte et al. (2012) involved sowing 25 grass and legume species into a degraded tussock grassland, which was then broken into experimental plots subjected to treatments involving various combinations of grazing and, for the first 19 years, annual fertilization with sulphur-superphosphate. A CATS regression of species relative abundance (*i.e.*% cover) on 12 functional traits in this experimental system showed that after 27 years species with traits promoting rapid growth were favored in high fertility treatments, and those with traits promoting plant nutrient conservation were favored under nutrient limiting treatments (Laliberte et al., 2012). Considering the dynamic interplay between competition for light *versus* soil resources under grazing that is typical in grasslands (Suding et al., 2005; Hautier et al., 2009; Borer et al., 2014; Niu et al., 2015a), these outcomes after 27 years will have arisen in a potentially complex series of changes over time that may have favored different traits during successional change in each treatment regime. In the present study, to extend this promising line of inquiry, we evaluate the utility of the CATS approach with an emphasis on identifying traits affecting short-term changes in species relative abundance under release from grazing.

To do so, we conducted a short-term (*i.e.* 3–5 years) grazing exclusion experiment in three contrasting Tibetan alpine meadows (Niu et al., 2015a) that have been subjected to grazing by wild and domesticated animals for millennia (Miehe et al., 2009). Previous studies show that plant competition for limited soil available P controls plant diversity (Hong et al., 2014; Yang et al., 2014; Niu et al., 2015a) and niche differentiation among co-occurring species in these Tibetan meadows (Niu et al., 2015b). Using trait values determined at both grazed and ungrazed plots to better allow for the effects of trait plasticity (Albert et al., 2011; Violle et al., 2012)

in response to grazing, we considered seven functional traits (SLA: specific leaf area, LDMC: leaf dry matter content, LCC: leaf carbon concentration, LNC: leaf nitrogen concentration, LPC: leaf phosphorus concentration, mHeight: mature height, and seed size) that might influence species relative abundance in these alpine meadows. To better differentiate the effects of the establishment and growth of individual plants *versus* the effects of vegetative spread of individuals, we assessed species relative abundance on the basis of both harvested above-ground biomass and number of ramets. To further strengthen our ability to detect the influence of traits that affect species relative abundance we used a recently developed CATS regression model (Warton et al., 2015), which generalized the CATS approach by relaxing the constraints to facilitate analyses over multiple sites along environmental gradients. In summary, we assessed the influence of traits on species relative abundance in grazed as well as ungrazed plots in each of three contrasting Tibetan alpine meadows using a generalized CATS approach.

In grazing exclusion plots where competition for limited nutrients drives community assembly, succession and fitness difference drive SRA, and lack of competition promotes species abundance (Hille Ris Lambers et al., 2012; Niu et al., 2015a), we expected species with higher leaf dry matter content (Wright et al., 2004; Laughlin 2014) and lower foliar phosphorus (Hidaka and Kitayama, 2013; Maire et al., 2015) should be favored. In grazed plots where competition is reduced by removal of aboveground biomass (Tilman, 1988; Collins and Glenn, 1990; Gibson, 2009), niche differences drive SRA, and fast (re)growth underpins species abundance (Hille Ris Lambers et al., 2012; Niu et al., 2015b), we expected species with high foliar nutrient content and high specific leaf area (Rivas-Ubach et al., 2012; Hidaka and Kitayama, 2013; Maire et al., 2015) would be favored. Because species that spread by rhizomes or stolons can quickly command open space under grazing, we also anticipated that SRA would be better related to traits if measured in terms of aboveground biomass in ungrazed plots and in terms of ramet numbers in grazed plots. Finally, we anticipated that the relative importance of traits in determining species fitness and SRA would depend on environmental context (Shipley et al., 2016), hence varying across our three study sites. To test all these expectations we combined generalized CATS regression (Warton et al., 2015) with an automated model selection procedure (Calcagno and de Mazancourt, 2010) to quantify the relative importance of different traits in predicting SRA cross the environmental regimes represented by our three study sites.

## 2. Material and methods

### 2.1. Study sites

We carried out this field experiment in alpine meadows distributed from east to north on the Tibetan Plateau: HY site in Hongyuan County of Sichuan province (see. Zhao et al., 2013), AZ sites (see. Zhang et al., 2014) and QH site in Mengyuan County of Qinghai province (see. Wang et al., 2012), China. The sites ranged in elevation from 3178 m at the QH site (37°37'N, 101°12'E) to 3484 m at the HY site (32°53'N, 102°36'E) and 3508 m at the AZ site (33°39'N, 101°52'E). Climate in all three sites is cold, continental and characterized by a short and cool spring, summer and autumn and a long winter. The soils have a high organic content and low available N and P (*cf.* Niu et al., 2015a). The three sites fall along gradients of moisture, temperature and productivity: AZ is a wet alpine meadow with relatively high daytime temperatures and growing season precipitation, deep soil, and high productivity; HY is a typical alpine meadow with intermediate productivity and QH is a dry, cold alpine meadow with a short growing season, shallow soil and low productivity (see. Niu et al., 2015a).

There is a long history of grazing by both wild and domesticated species in the Tibetan plateau, but grazing by domesticated yaks and Tibetan sheep has increased markedly at all sites in the last three decades (Miehe et al., 2009). Grazed meadows are dominated by *Carex rigescens* at the AZ site, by *Kobresia capillifolia* at the HY site and by *Stipa aliena* at the QH site; subdominants, which also vary from site to site, include sedges such as *C. atrofusca*, grasses such as *Elymus nutans* and *Deschampsia cespitosa*, and forbs such as *Potentilla anserina*, *P. saundersiana* and *Gueldenstaedtia diversifolia*. Nitrogen-fixing legumes are only a minor component of these alpine meadows. Complete species abundance and trait data for both grazed and ungrazed meadows at the three study sites are in the supplemental material. Total vegetation cover in midsummer exceeds 80%; vegetation height in ungrazed meadows is 70–100 cm at the AZ site, 50–80 cm at the HY site and 40–60 at the QH site (see Niu et al., 2015b).

## 2.2. Experimental design

In a 20–30 ha area of reasonably uniform alpine meadow at each site, we built exclosures (1–5 ha) in 2005–2006 that were designed to exclude grazing by both small and large mammals. At the time of this study the alpine meadow within the exclosure had been protected from grazing for 3–5 years. Grazing was excluded throughout the year at HY and QH but occasionally allowed within the exclosures during the non-productive winter months at AZ. Outside of the exclosure, the meadows were moderately grazed by yaks and sheep during all months except for 40–60 days between June and mid-August when herds were moved to high-elevation pasture (Niu et al., 2010, 2012).

In June 2009–2010, at each site eight 5 × 8 m plots were randomly established within the exclosures and another eight in the meadow surrounding the exclosures. The grazed plots outside the exclosures were separated by 5–15 m, while ungrazed plots within the exclosures were separated by 2–5 m. This should ensure that spatial autocorrelation effects (e.g. any issue of pseudo-replication) among the sampled communities (0.25 m<sup>2</sup>) will be negligible considering the low  $\beta$  diversity and the fact that the species-area curve in these meadows saturates at 0.15–0.22 m<sup>2</sup> (Niu et al., 2009, 2010, 2015b). There were 300–400 m between grazed and ungrazed plots. Each replicate plot was divided into two parts: a 5 × 5 m subplot for measurement of plant traits and a 5 × 3 m subplot for community monitoring, counting of individual ramets, biomass harvest and soil sampling.

## 2.3. Trait and abundance measurements

In July 2009 and 2010, we randomly sampled a mature leaf from 7 to 10 individuals at fruiting time for all but a few very infrequent species in the 5 × 5 m subplots in grazed and ungrazed plots at each site. We measured specific leaf area (SLA, mm<sup>2</sup> mg<sup>-1</sup>), leaf dry matter content (LDMC, mg g<sup>-1</sup>), leaf carbon concentration (LCC, mg g<sup>-1</sup>), leaf nitrogen concentration (LNC, mg g<sup>-1</sup>), and leaf phosphorus concentration (LPC, mg g<sup>-1</sup>) using these leaves and measured mature height (mHeight, cm) and seed size (mg) on the same individuals (Niu et al., 2015a). The sampled species accounted for 90–98% of the aboveground biomass and 95–99% of vegetation cover in the meadow community. All measurements of functional traits followed standardized methods (He et al., 2010; Pérez-Harguindeguy et al., 2013).

From mid-August to early September 2009 and 2010, we harvested plants in the 0.5 × 0.5 m quadrat within each of the grazed and ungrazed 5 × 3 m subplots at each site. Individual ramets were counted and harvested by species, and the oven-dried biomass of each species determined (Niu et al., 2010). These data were used

to calculate species relative abundance (SRA) as described subsequently.

## 2.4. Data analysis

### 2.4.1. SRA and functional traits

In each 0.5 × 0.5 m<sup>2</sup> quadrat in grazed and ungrazed plots, we calculated the relative abundance of each species as the percentage of 1) the total aboveground biomass and 2) the ramet numbers represented by each species in the quadrat. This provides eight replicate estimates for two complementary measures of SRA in grazed and ungrazed plots in the meadow community at each site (Niu et al., 2010). We calculated the means of SLA, LDMC and mHeight (7–10 replicates) as well as LCC, LNC, LPC and seed size (3 replicates) for each species in grazed and ungrazed plots in each of three sites.

We used principal component analysis (PCA) to visualize the interrelationships among the seven plant functional traits for the component species in grazed and ungrazed plots at the three sites. The angles between trait vectors in the PCA biplot (using type-II scaling) reflect correlations among traits, with a small angle indicating a high correlation. Statistical significance of the correlations among traits was tested by Pearson correlation and differences between treatments (grazed vs. ungrazed nested in sites) were tested by ANOVA. These analyses as well as those described subsequently were conducted in the R environment.

### 2.4.2. CATS regression

Since there is no theory to suggest *a priori* a particular model predicting SRA from functional traits under alternative grazing regimes, we used CATS regression to explore a number of alternative models for predicting SRA as a function of our species-specific data on foliar traits, plant stature and seed size for grazed plots and ungrazed plots separately. These CATS analyses use the mean of the eight quadrats in each site-treatment combination. As is the case for  $\lambda$ -values in the CATS model (Shipley, 2010),  $\beta$ -values in CATS regression can be directly compared to estimate the relative importance of different traits in determining SRA (Warton et al., 2015). A positive  $\beta$ -value for a given trait indicates that when other traits are held constant, species with greater values for this trait are relatively more abundant in the local community than could be expected by chance, while negative  $\beta$ -values indicate the opposite. A  $\beta$ -value of zero suggests that a trait does not influence SRA (Shipley, 2010; Warton et al., 2015).

In a first round of analyses, we regressed all seven traits on SRA estimated either as aboveground biomass or ramet numbers to estimate relative importance of each trait in predicting SRA over our three sites (Warton et al., 2015). We fitted this model using Poisson regression for both biomass and ramet estimates of SRA; we also tried a negative binomial regression for SRA based on ramet counts because count data are often over-dispersed compared to the Poisson distribution (O'Hara and Kotze, 2010). Since we did not know SRA for the regional species pool, we used a uniform prior in the CATS regression; this may influence the accuracy of estimates for trait importance in determining SRA but will not significantly impact comparison of the relative importance of different traits (Shipley, 2010). We evaluated the significance of model and regression coefficients ( $\beta$ ) in the CATS regression using a Wald-test in resampling-based inference (n = 999; Warton et al., 2015). The interaction between site and trait variables was tested by an ANOVA on the matrix of bootstrap values (n = 999) in the CATS regression (Warton et al., 2015).

We then explored the statistical structure of the relationships among the seven traits using the 'glmulti' package (Calcagno and de Mazancourt, 2010) to identify a minimal combination of the traits that could provide robust predictions of SRA. Although the seven



traits we studied are well established components of plant function (Wright et al., 2004; Díaz et al., 2016), their relative importance in affecting SRA will depend on both environmental context and life history variation in the species that comprise the local community (Laughlin and Messier, 2015; Shipley et al., 2016). Since there will be some degree of functional coordination and hence statistical collinearity among the traits (Wright et al., 2004; Díaz et al., 2016) the best model for predicting SRA may not be immediately apparent (Shipley, 2010; Laliberte et al., 2012). Hence we considered generalized linear model (GLM) regressions using both Poisson and negative binomial approaches to predict SRA, and decided among the many alternative models based on comparison of the Akaike Information Criteria (AIC); the model with the minimum AIC was selected. Using trait(s) in the best GLM model, we re-analysed the trait-SRA relation with the multi-site analysis of CATS regression mentioned above, and re-estimated  $\beta$ -values as well as tested the significance of the model and  $\beta$ -values.

Finally, since there were few significant interactions between sites and trait variables in the multi-site analysis, we performed single-site analyses using CATS regression to quantify  $\beta$ -values for each of seven traits at each of the three study sites using both Poisson and negative binomial regression. We report the results from Poisson regression and present the results from negative binomial regression in Supplemental Materials Fig. S1; the  $\beta$ -values were consistent in both cases, although significance levels differed slightly due to inevitable variation inherent in the pit.trap resampling for the Wald-test.

### 3. Results

#### 3.1. Relationship among traits

Not surprisingly, plant height declined significantly following grazing and also was lower at the cold, dry QH site ( $P < 0.05$ , Fig. 1), but due to the large variance component associated with species ( $P > 0.05$ , Fig. 1) neither the grazing nor site factors significantly influenced any other traits or the main axis of the PCA. Although trait correlations often are weak among species in local communities, there are significant negative relationships between traits associated with nutrient conservation and traits involved in nutrient acquisition. For example, LDMC is negatively correlated with SLA ( $r = 0.41$ ,  $P < 0.05$ , Fig. 1) and with LPC ( $r = 0.25$ ,  $P < 0.05$ , Fig. 1), a contrast that organizes the first axis of the PCA, which accounts for 23.1% of the variance in these data (Fig. 1). Similarly, the second axis of the PCA, accounting for 19.3% of the variance, is organized by the negative correlation ( $r = 0.16$ ,  $P < 0.05$ ) between seed size and LNC (Fig. 1). It is noteworthy that the positive correlation between SLA and LPC ( $r = 0.24$ ,  $P < 0.05$ , Fig. 1) is stronger than that of SLA and LNC ( $r = 0.13$ ,  $P < 0.05$ ). Seed size is positively correlated with mature height ( $r = 0.25$ ,  $P < 0.05$ , Fig. 1).

#### 3.2. Relative importance of traits in grazed plots

Although the prediction of SRA from traits in grazed plots is relatively weak (pseudo  $R^2$  ranges from 0.32 to 0.57), in all models a higher LPC is the trait most strongly associated with species abundance (Fig. 2a,b and Table 1). Indeed, in comparisons among alternative models, the two best models used only LPC or LPC and mature height to predict SRA (Table 1). Species with low SLA and larger seed size also tended to be more abundant in grazed plots, more significantly when SRA was measured as aboveground biomass (Table 1, Fig. 2a).

In all the variants of multi-site CATS regression for grazed plots, no models found a significant site effect. There were some significant interactions between site and traits (Table S1), suggesting that

the relative importance of traits can change from site to site (Fig. 2). Overall, however, the relative importance of traits in grazed plots differs only slightly across sites (Table S1). Species with low SLA and larger seed tend to abundant at the QH site relative to the wetter AZ site (Fig. 2a,b and Table S1). When SRA is measured as ramet numbers, more abundant species not only have a higher LPC but also are higher in LDMC at the harsh QH site relative to the AZ and HY sites (Fig. 2b and Table S1).

#### 3.3. Relative importance of traits in ungrazed plots

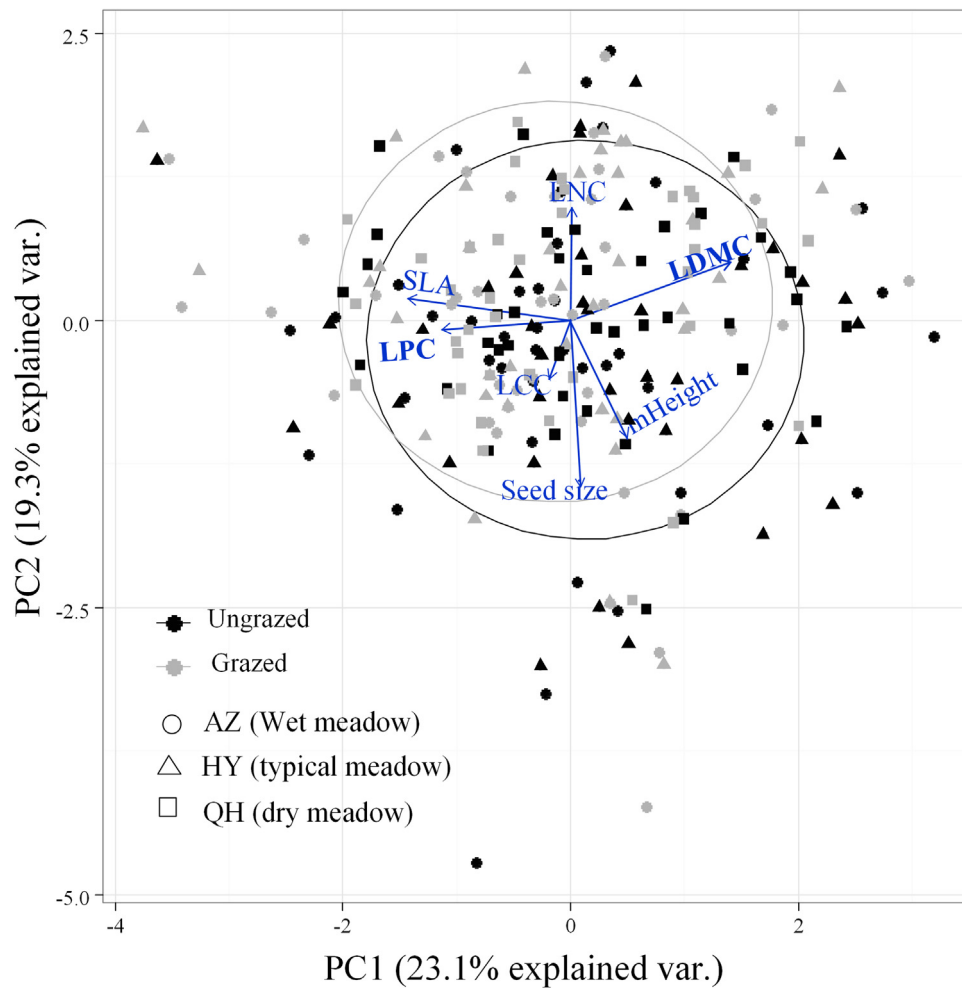
Although the prediction of SRA from traits is also relatively weak (pseudo  $R^2 = 0.35$ – $0.52$ ) in ungrazed plots, alternative models in the CATS regressions show a consistent pattern of relative importance for the different traits (Table 1 and Fig. 2c,d). In contrast to grazed plots, SRA in ungrazed plots is positively associated with LDMC but negatively correlated with leaf nutrients, most notably LPC (Table 1 and Fig. 2c,d). These patterns hold whether the CATS regression is based on all seven traits or any subset of traits selected in comparisons among alternative models (Table 1). Neither regression approach (Poisson or negative binomial) nor alternative measures of SRA (aboveground biomass vs. ramet numbers) significantly changed the relative values of regression coefficients (Table 1 and Fig. 2c,d). Low LPC and high LDMC, respectively, were the first and second most important traits associated with species abundance in ungrazed plots; when abundance was measured with biomass, low SLA also was significantly, but more weakly, associated with species abundance (Table 1 and Fig. 2c,d). There was no significant trait  $\times$  site interaction (Table S1), indicating no significant change in the relative importance of traits in ungrazed plots among sites (Fig. 2), but larger SLA and seed size tended to be more important for species abundance at the HY site (Table S1, Fig. 2c,d).

### 4. Discussion

#### 4.1. Foliar phosphorus content indicates species position along a gradient from exploitive nutrient-acquisition to nutrient-use efficiency in Tibetan alpine meadows

Studies at broad spatial scales suggest there is a tradeoff between nutrient acquisition vs. conservation that is reflected in foliar traits (Wright et al., 2004; He et al., 2009; Reich, 2014). Some species have foliar characteristics associated with high rates of resource uptake (e.g. larger SLA and leaf nutrient concentrations) in contrast to traits involved in nutrient-use efficiency (e.g. larger LDMC and long lifespan). Specifically, in light or nitrogen limited ecosystems, higher SLA and LNC, which are associated with higher uptake of the limiting resource and greater growth rate, are strongly negatively correlated with LDMC at the species level (Wright et al., 2004; Raouda et al., 2005; Ordoñez et al., 2009; Hodgson et al., 2011; Dwyer et al., 2014). Similarly, in a P limited ecosystem, LPC should increase with ability to acquire soil available P (Ordoñez et al., 2009; Maire et al., 2015) and should also be strongly negatively correlated with LDMC at the species level (Rivas-Ubach et al., 2012; Hidaka and Kitayama, 2013).

Studies reporting a negative LPC-LDMC relationship among species, however, are surprisingly few. Our results show that LPC, rather than either LNC or SLA, is negatively correlated with LDMC at the species level in Tibetan alpine meadow communities (Fig. 1), and that the correlation becomes stronger when we focus on common species or community level patterns ( $R^2 = 0.46$ – $0.68$ ). Domínguez et al. (2012) reported similar results at the community level in Mediterranean woodlands. These results and the fact that root phosphorus content is strongly correlated to LPC (Geng et al., 2014) suggest that LPC indicates species position along a gradient



**Fig. 1.** Principal component analysis correlation biplot showing the relationships among seven traits for all component species in grazed and ungrazed communities at all three sites. LCC: leaf carbon concentration, LNC: leaf nitrogen concentration, LPC: leaf phosphorus concentration, SLA: specific leaf area, LDMC: leaf dry matter content, mHeight: mature height. Apart from a decline in mHeight with grazing and from AZ to QH, there are no significant changes in traits among sites or between grazed vs. ungrazed plots in a site.

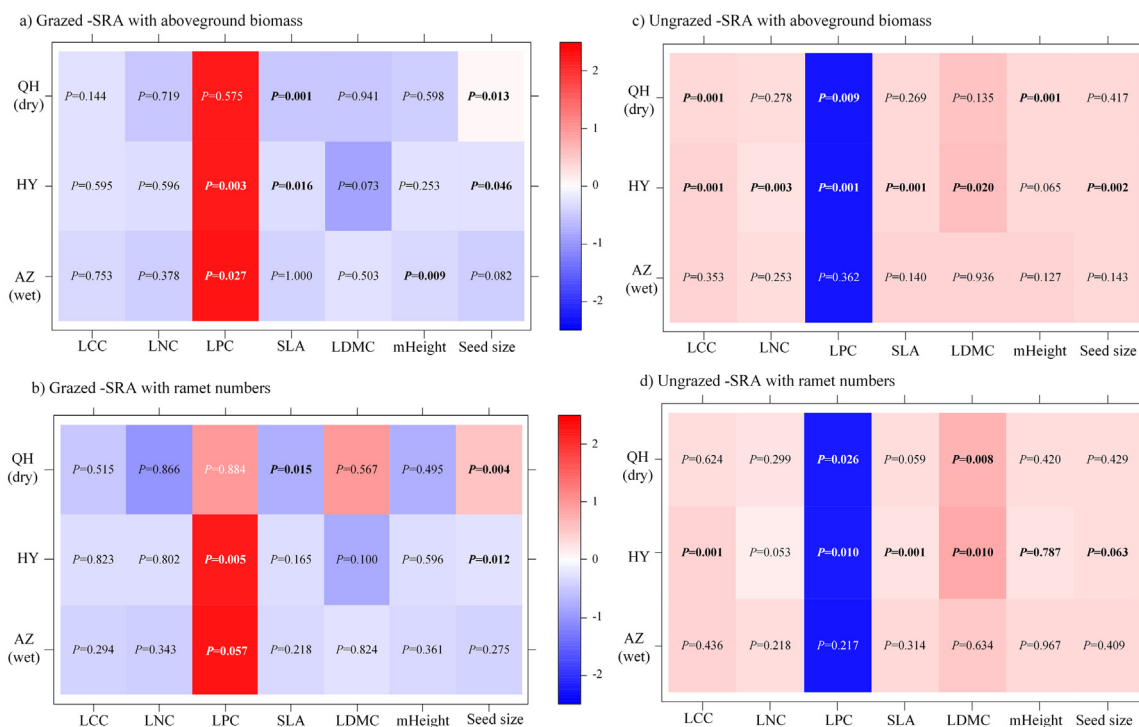
trading off nutrient-acquisition against nutrient-use efficiency in these P-limited alpine meadows. Species with fast (re)growth and weak competitive ability have high LPC but lower LDMC compared to slower-growing species with efficient use and conservation of fixed P and strong competitive ability.

#### 4.2. Foliar phosphorus content is associated with greater species relative abundance

Overall, our results show that in P-limited Tibetan alpine meadows abundant species are those with greater ability to uptake soil available P and/or to efficiently use fixed P. In the grazed community, we assumed that uptake of soil P is the most important factor determining plant growth and species abundance when size-dependent competition for soil nutrients and light are reduced by removal of aboveground biomass (Borer et al., 2014; Niu et al., 2015a). In grazed communities higher LPC indicates that acquiring limited soil P for fast (re)growth is the most important trait associated with greater species abundance (Table 1 and Fig. 2a,b). Interestingly, we found that LPC, LDMC and seed size also are important for predicting SRA (Fig. 2d) at the dry and cold site QH. This indicates that not only nutrient acquisition but also the ability to conserve and efficiently use fixed P can become important in harsh environments. In contrast, our result shows that higher LDMC (and LCC) but lower LPC are the most important traits affect-

ing species abundance in ungrazed communities (Fig. 2c,d). This supports our previous assumption that traits promote competition for limited soil available P as well as conservation and that efficient use of fixed P is more important in a competition dominated community when grazing is excluded. Although neither height, LCC, LNC or SLA were important influences on species abundance under grazing, there is evidence that these traits involved with competition for light and soil N do influence species abundance in ungrazed alpine meadows (Hille Ris Lambers et al., 2012; Niu et al., 2015b).

To summarize, these results suggest that traits promoting resource acquisition for fast (re)growth are critical for affecting high species abundance in disturbed communities, while traits associated with nutrient conservation are more important in a competition dominated community. This result supports ideas that SRA in a local community is organized by interspecific variation along a gradient in nutrient conservation versus acquisition (Tilman, 1988; Grime, 2001). Additionally, the importance of seed size, LDMC and height at our dry and cold study site suggests that species with these traits hold an advantage in seed dispersal and seedling establishment in this relatively harsh alpine environment. This supports the prediction that plant regeneration and recruitment by asexual reproduction will predominate in favorable environments but reproduction by seed in more stressful environments (Bazzaz, 1996). In this regard, by considering ramet numbers as a measure of SRA we were able to better discern the contribution of traits to



**Fig. 2.** Results from CATS regressions at single sites using a Poisson distribution to show the relative importance of individual traits in predicting species relative abundance (SRA) in grazed (a–b) and ungrazed plots (c–d) in term of both biomass (a, c) and ramet numbers (b, d) at each of the three study sites. Color indicates positive (red) and negative (blue) trait association with SRA; the magnitude of values indicates the relative importance of traits in predicting SRA. *P*-values indicate the significance of regression coefficients used to gauge the relative importance of traits as determined by a Wald-test using 999 resampling iterations in the CATS regression. LCC: leaf carbon concentration, LNC: leaf nitrogen concentration, LPC: leaf phosphorous concentration, SLA: specific leaf area, LDMC: leaf dry matter content, mHeight: mature height. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**  
The relative importance of traits in predicting species relative abundance (SRA) in grazed and ungrazed plots estimated in a multi-site CATS regression using both Poisson and negative binomial (NegBin) approaches. The SRA was estimated either in terms of both ramet numbers and aboveground biomass. Regression coefficients (proportional to relative importance) for different traits are estimated either from CATS regression with all seven traits or with fewer traits selected in alternative models assessed using the Akaike information criterion (AIC). The tabulated values are the regression coefficients of individual traits in predicting SRA. The magnitude of the regression coefficient indicates the relative importance of traits in predicting SRA and the sign positive or negative association with SRA. The significance of models and regression coefficients was assessed using a Wald-test based on 999 iterations in pit.trap resampling with bold entries indicating  $P < 0.10$ , \*indicating  $P < 0.05$ . LCC: leaf carbon concentration, LNC: leaf nitrogen concentration, LPC: leaf phosphorous concentration, SLA: specific leaf area, LDMC: leaf dry matter content, mHeight: mature height. Note that we tabulate the trait  $\times$  site interactions in Table S1, as few are significant.

	Grazed plots				Ungrazed plots			
	Ramets		Biomass		Ramets		Biomass	
	Poisson	NegBin	Poisson	NegBin	Poisson	NegBin	Poisson	NegBin
Abundance regressed on all key traits								
AIC	603.171	509.457	617.456	477.215	555.275	477.690	476.558	409.071
Significance ( <i>P</i> )	<b>0.024*</b>	0.433	<b>0.001*</b>	<b>0.063</b>	<b>0.001**</b>	<b>0.014*</b>	<b>0.001**</b>	0.164
Trait effect								
LCC	-0.196	-0.196	0.067	0.065	0.179	<b>0.317</b>	0.247	0.323
LNC	-0.380	-0.128	-0.424	-0.144	-0.598	<b>-0.785*</b>	-0.572	-0.726
LPC	8.986	8.834	<b>22.089*</b>	11.909	<b>-24.902</b>	<b>-30.93*</b>	-17.305	-21.538
SLA	0.002	0.003	0.001	-0.002	-0.005	<b>-0.006</b>	<b>-0.009</b>	<b>-0.011</b>
LDMC	0.298	0.017	1.124	-0.573	1.044	1.926	0.229	0.240
mHeight	0.019	0.020	<b>0.068**</b>	<b>0.073</b>	0.002	-0.008	<b>0.028*</b>	0.029
Seed size	-0.245	-0.092	<b>-0.417</b>	-0.24	-0.183	0.011	<b>-0.330*</b>	-0.087
Abundance regressed on traits selected from model comparison								
Selected trait(s) in best model	LPC		LPC + mHeight		LCC + LNC + LPC + LDMC		LCC + LPC + SLA + LDMC + Seed size	
AIC	664.176	500.068	736.34	472.959	573.834	470.455	533.495	421.892
Significance ( <i>P</i> )	0.254	0.36	<b>0.001**</b>	<b>0.014</b>	<b>0.001**</b>	<b>0.001**</b>	<b>0.001**</b>	<b>0.011*</b>
Trait effect								
LCC					0.195	<b>0.334</b>	0.254	0.333
LNC					<b>-0.729*</b>	<b>-0.874</b>		
LPC	11.71	13.474	<b>24.785*</b>	15.800	<b>-24.546</b>	<b>-33.651</b>	-7.495	-12.231
SLA							<b>-0.014*</b>	<b>-0.016*</b>
LDMC					<b>2.516**</b>	<b>3.062</b>	0.520	0.268
mHeight			<b>0.0659*</b>	<b>0.071</b>				
Seed size							-0.217	0.049

variation in SRA under grazing. Species relative abundance is usually assessed in terms of biomass, but the relative importance of traits depends not only on environmental context but also on the measure of abundance, especially in grazed communities (Fig. 2a,b and Table S1). Site by trait interactions are more significant when abundance is measured by ramet numbers, which especially for graminoids provides a measure better allied with the potential for regrowth in response to grazing (Niu et al., 2009).

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2016.08.002>.

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