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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 though 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).

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