Intraspecific variation in traits reduces ability of trait-based models to predict community structure

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Abstract

Questions: Is it possible to predict the composition of local plant assemblages? Trait-based approaches have offered some promise, especially in cases where deterministic processes such as environmental filtering and niche differentiation shape communities. In this study, we asked how much intraspecific variation contributes to trait distributions within and among plant communities, and whether trait distributions resulting from environmental filtering and niche differentiation can predict accurately the relative species abundances of montane plant species in local communities.

Location: West Elk Mountains, Colorado, USA.

Methods: We collected functional trait, species composition and environmental data from 14 sites along a broad climate gradient in Colorado, USA, ranging in elevation from 2480 to 3560 m. We partitioned the variation within and among sites into intraspecific and interspecific components, and compared the results to values from a recent global meta-analysis, which examined intraspecific trait variability patterns. We also used these data to parameterize statistical models that have been shown to reproduce patterns associated with the processes of environmental filtering and niche differentiation. We fit two models to the data, one assuming that niche differentiation is invariant among sites, and another assuming that niche differentiation varies among sites.

Results: We found that the trait-based models were worse at predicting species relative abundances in local communities than a null model assuming equal abundances of all species. One plausible explanation for the poor performance of the models is that intraspecific variation in functional traits, which in our system was higher than the global averages documented in the meta-analysis, swamped the effects of interspecific variation in functional traits along the climatic gradient. In particular, almost all variation in root traits was within rather than among species, even among sites.

Conclusion: Our results suggest that a greater focus be placed on measuring intraspecific trait variability and determining its consequences for community assembly and ecosystem properties.

Introduction

Community ecologists seek to describe the ways in which environmental conditions and interactions among organisms influence patterns in the distribution and abundance of species across space and time. Ignoring for now the sometimes heated debate over whether stochastic or deterministic processes shape communities, ample evidence shows that easily measured organismal traits often correlate with environmental tolerances and can determine the outcomes of biological interactions (Grime 1979; Lavorel & Garnier 2002; Lavorel 2013; Díaz et al. 2016). This key insight has led to a massive research effort aimed at linking functional traits of species to ecosystem function and community assembly, especially in plant communities (McGill et al. 2006; Levine 2016). Here, functional traits are defined as any property of an organism that is correlated either with its niche or its fitness. The functional trait approach might offer a way to deal with a bugbear of community ecologists: results of community ecology studies

are often difficult to interpret or generalize. This is because community assembly processes often depend heavily on the specific local composition of the species pool and on small-scale environmental variation; hardly any two communities are the same (Lawton 1999; Ricklefs 2008). By measuring functional traits instead of focusing on species identity, ecologists can make quantitative comparisons among species assemblages (McGill et al. 2006; Webb et al. 2010). Furthermore, functional traits are not only correlated with climate but also with emergent ecosystem-level properties such as carbon turnover (De Deyn et al. 2008; Reichstein et al. 2014). The ultimate goal of functional trait ecology, which has been described as the holy grail of the field (Lavorel & Garnier 2002; Funk et al. 2016), should be to predict variation and change in community composition and ecosystem function from functional traits.

Despite its promise, the functional trait approach has borne the brunt of several critical reviews (Violle et al. 2007; Laughlin & Messier 2015). In particular, the correlational nature of many trait studies is problematic because the correlations between environment and traits are often examined in isolation. This ignores processes such as filtering, selection and plasticity that might have generated the observed trait and species distributions. Moreover, in many trait-based ecological studies, functional traits have often been used as proxies for species, but they should instead be thought of as ways to represent processes occurring at the organism level. Traits are poor proxies for species identity for three reasons: the multidimensional nature of traits (Albert et al. 2010), the strong relationship between traits and environmental conditions (Laughlin & Messier 2015), and high levels of intraspecific variability even in similar environments. Ecological outcomes such as herbivore damage can be predicted only when accounting for complex interactions of traits along multidimensional axes (Loranger et al. 2013). In addition, individual responses to environmental gradients are necessary to explain species distributions and diversity patterns, as has been shown for forest trees (Clark et al. 2011) – when examining the relationship between traits and fitness, we must account for the trait–environment interaction (McGill et al. 2006; Shipley et al. 2016).

Perhaps the worst omission in many previous studies has been documenting or including intraspecific variation in traits and acknowledging that intraspecific variation might influence community assembly (Crutsinger et al. 2008). For example, earlier trait-based assembly models such as MaxEnt (Shipley et al. 2006, 2011) are based solely on species means. Other studies have examined how variation in traits within a particular dominant (Crutsinger et al. 2009) or foundation (Whitham et al. 2006) species might influence assembly of associated communities. However, few studies have considered how intraspecific variation in key functional traits among all species might influence community assembly, especially along climatic gradients.

In this study, we suggest new approaches to move the field of functional trait ecology forward in two key ways. First, we explicitly incorporate intraspecific variation into our statistical models, building on previous work (Laughlin & Laughlin 2013; D'Amen et al. 2017; Laughlin et al. 2015). Second, we quantify how much the variation in trait values within and among species contributes to observed species abundance distributions within local communities. To do this, we fit a predictive statistical model that incorporates both filtering (i.e. relative fitness differences) and niche differentiation processes (HilleRisLambers et al. 2012) and includes variation in these processes along environmental gradients (Read et al. 2014). Both relative fitness differences and stabilizing niche differences contribute to the realized abundance distribution at a given site. Our approach uses functional traits to tackle the most important problem in ecology: describing the linkages between environment and species and predicting future change in those linkages. In this study, we established plots at 14 observational sites along a transect where we collected data on relative species abundance and functional traits of the most abundant species. We used these data to ask a series of related questions:

- How much does intraspecific variation contribute to trait distributions observed within and among plant communities? How does intraspecific variation in this system compare to levels observed globally? How does this differ above-ground and below-ground, and what does this mean for the processes that drive community assembly?
- How do environmental filtering and niche differentiation interact to structure plant communities across a landscape, and can we use the trait distributions resulting from these processes to predict relative species abundances given climate?

Methods

Site description

The study region is in the West Elk range of the southern Rocky Mountains in Colorado, USA, near the Rocky Mountain Biological Laboratory. Elevations of the study sites range from 2480 to 3560 m a.s.l. Mean annual temperatures, derived from the Worldclim data set (Hijmans et al. 2005) range from -1.8 to 2.7 °C, and mean annual precipitation from 355 to 679 mm·yr^{-1}. The long-term temperature averages derived from the Worldclim data are closely correlated with temperature data we collected at

the sites in 2015 (R^2 = 0.67); these temperatures likely represent the long-term climatic filters that have acted on these (mostly) perennial species, rather than just a one-off measure of local temperature. The study sites are located on an elevational gradient along which temperature decreases and precipitation increases with increasing elevation (Appendix S1). In addition, soils at higher elevations have increased available P and decreased available N (J. Lynn, unpublished data). We selected 14 open meadow sites without tree cover. At each of the study sites, we established a permanently marked 10 m × 10 m plot.

Data collection

Plant community

In the summer of 2015, we measured the relative abundance of plant species at each site. We placed a 0.25-m^2 quadrat at ten random locations in the 10 m × 10 m plot, and visually estimated the above-ground cover of all vascular plant species within each quadrat, identifying them to species. Species with <10% relative cover were estimated to the nearest 1%, while species with >10% were estimated to the nearest 5%. At each plot, we surveyed relative abundance during both the early season and peak season. We used the relative cover of the plant species to determine which plant species to collect for plant traits, as well as to validate model predictions of relative species abundances.

Plant traits

In 2014 and 2015, we collected leaves and roots from at least five individuals of at least five of the most abundant species at each site within the marked plot. Two sites were sampled more intensively (10–20 individuals of 5–15 species) as part of a related study. For most sites, we have plant trait information for the species that make up at least 80% of the above-ground plant cover within the sites. We followed standardized trait measurement protocols (Pérez-Harguindeguy et al. 2013) to measure plant height, leaf mass:area ratio, leaf dry matter content, leaf N:P ratio and SRL. In total, we measured traits on 891 individuals of 52 species across the 14 sites. We measured the full suite of traits on 421 of those individuals, which we used for model fitting. We measured plant height of all individuals from the base to the tip of the topmost leaf blade, measuring perpendicular to the ground rather than along the stem.

We collected at least three mature and fully expanded leaves from each individual that we sampled for leaf traits. We transported the leaves on moist paper towels and scanned them on an Epson flatbed scanner. We weighed the scanned leaf material, dried it for 48 h at 60 °C, and then weighed it again. We pooled the dried leaf material with additional leaves that were collected for chemical analysis.

We collected two to four 2.5-cm diameter, 15-cm long soil cores from directly below the base of each plant that we sampled for root traits, following protocols from other published studies (e.g. Tjoelker et al. 2005; Orwin et al. 2010; Kraft et al. 2015). We extracted as much fine root material as possible from the soil cores, washing the soil over a 2-mm sieve if necessary. We scanned ten to 20 intact pieces of fine root from each individual on an Epson flatbed scanner after floating the root pieces in a transparent tray of water. We dried the root material for 48 h at 60 °C and weighed it.

To measure N and P content by mass (total Kjeldahl N and P) of the dried tissue samples (both leaf and root), we first ground the tissue samples with a mortar and pestle. We weighed 75 mg, or as much as was available, of the ground sample and folded it into a piece of adhesive-free cigarette paper. We digested the sample for 5 h at 350 °C in 5 ml H_2SO_4 in a Kjeldatherm digestion block (Gerhardt, Königswinter, DE). After the digests cooled, we added 45 ml deionized water to each sample. We used a SmartChem 200 discrete analyser (Unity Scientific, Brookfield, CT, US) to measure total Kjeldahl N and P, expressed as mg·g^{-1} tissue.

We measured the area of the scanned leaf images, and the total length of the scanned root images, with ImageJ software (v 1.45s; Schneider et al. 2012), using the IJRhizo macro (Pierret et al. 2013) to automatically trace all the roots in each image. We calculated leaf mass:area ratio (LMA; g·m^{-2}) for each individual plant by summing the mass and area of each individual and dividing the dry mass by the scanned area. Leaf dry matter content (LDMC; g·g^{-1}) was calculated as the dry leaf mass divided by the leaf mass before drying. We calculated specific root length (SRL; m·g^{-1}) for each individual plant by dividing the total root length by the dry root mass.

Partitioning of intraspecific variability

All analyses were conducted in R (v 3.2.3; R Foundation for Statistical Computing, Vienna, AT), with packages listed where appropriate. To determine the contribution of intraspecific trait variation to total trait variation both within our study communities and among communities, we used previously published variance partitioning equations (de Bello et al. 2011; Siefert et al. 2015). For each trait at each site, we calculated within-community intraspecific trait variability (wITV), the relative contribution of intraspecific trait variability to total within-site trait variability. Also, for each trait across all sites, we calculated among-community intraspecific trait variability (aITV), the log ratio of variance due to intraspecific trait variability

to variance due to species turnover across sites. We report wITV as a proportion between 0 and 1, where higher values indicate larger contribution of intraspecific variability to the total, and we report aITV as the natural logarithm of a ratio, where a positive number indicates that intraspecific variability is relatively more important than species turnover across sites. We used ANOVA to compare wITV values among traits and sites, and we also compared the wITV and aITV values to the global means reported by Siefert et al. (2015). Unfortunately, no mean variability values for root traits were reported in the meta-analysis.

Predictions of species abundances

We used a model that mathematically represents assembly of local communities from a regional species pool through the selective processes of environmental filtering and niche differentiation. The model is modified from the Traitspace model (Laughlin et al. 2012). The model predicts species abundances at locations with differing environmental conditions, using species traits to connect species identities with environmental conditions. The Traitspace model captures two key processes that contribute to patterns of species abundance among local communities. First, in order for a species from the regional species pool to be able to establish at a particular site, it must possess traits that enable it to tolerate the environmental conditions at that site. Species with traits conferring higher fitness given a particular set of environmental conditions should have higher abundance. Second, in addition to these relative fitness differences, niche differentiation among species resulting from interactions among individuals is an additional filter that determines the species composition and abundance distribution at a given site. Biotic processes might contribute to increased trait dispersion both within and among species.

We fit Traitspace models with two types of priors: uninformative priors and priors that used each species' global range size as *a prior* estimate of its local abundance. Across both types of prior, we fit models with two structures of trait variance: one in which trait variance, and thus the strength of disruptive selection within species, was assumed constant across sites, and one in which it was assumed to vary across sites. We expected that the model allowing trait variance to differ among sites would lead to

improved predictions of species abundance, because the niche breadths of species tend to decrease with increasing elevation (Stevens 1992). We fit these four variants of the Traitspace model to all 31 possible subsets of the five plant traits we measured, for a total of 124 model fits (Table 1 summarizes the different models that were fit). For each of these model fits, we output predictions of relative species abundances at each of the study sites and compared them to the observed abundances.

We followed a multi-step process to fit the Traitspace model to the data; see Appendix S2 for a full description of this process. First, we fit trait-by-environment regressions using trait and environmental data from each of the 14 observational sites. For each trait, we combined all the individual measurements, without information on species, and fit a weighted multiple quadratic regression model with environmental variables as predictors. Next, we calculated the trait distribution, parameterized as a multivariate normal distribution, for each species across all sites where it occurred. Next, we sampled from the trait distribution at each site, independent of species, with the appropriate variance structure for each Traitspace model fit. Next, we used the sampled trait data and the previously fit trait distributions for each species to calculate the likelihood, or the probability, of each species being present given each trait sample. In a subset of the models, we used a flat discrete prior, and in another subset of the models, we scaled the prior for each species by the global range size of that species, estimated from publicly available global occurrence data (see Appendix S3 for how these range sizes were estimated). Finally, we integrated out the traits using Monte Carlo integration to get the posterior predictions of relative species abundances.

We fit the models using all possible subsets of these five traits: plant height, leaf mass:area ratio (LMA; the ratio of dry mass to scanned leaf area), SRL (ratio of root length to dry root mass), leaf dry matter content (LDMC; the ratio of dry leaf mass to wet leaf mass) and leaf tissue N:P ratio. We assessed model predictive accuracy using root mean squared error (RMSE). We compared the accuracy of model predictions with all the possible subsets of traits, with and without variation in niche differentiation processes across the landscape, and with and without the incorporation of prior information on species range sizes (Table 1). In addition, we compared all these model

Table 1. Summary of factors that varied across model fits.

Factor	Levels Used in Different Model Fits	
Prior Information	Uninformative prior	Prior for each species proportional to its global range size
Trait Variance	Variance of each trait assumed constant across sites	Variance of each trait assumed to vary across site
Traits Used	All 31 possible subsets of the following traits: LMA, SRL, height, LDMC, leaf N:P ratio	

predictions to a null model for which all 46 species in the data set were assumed to have equal relative abundances at each site. R files containing functions (Appendix S4) and scripts (Appendix S5) to reproduce our analyses are included as a supplement.

Results

Local plant communities

The plant communities at the 14 sites varied in total richness along the elevational gradient. The lowest richness was 13 species at the lowest elevation site (2480 m; median 5.0 species·quadrat^{-1}), and peak richness was 34 species at 2806 m a.s.l. (median 10.5 species·quadrat^{-1}), including species for which we did not measure functional traits. Median site-level richness across elevations was 24.5 species, and median quadrat-level richness was 10.75 species per quadrat. The ten most common species across all sites and their elevational ranges are given in Table 2. Both leaf and root traits, including LMA SRL and LDMC, tended to vary independently of one another both among species within a site and among sites (Fig. 1a). However, variation in plant height was somewhat more constrained (Fig. 1b). In general, species co-occurring at a site tended to overlap in trait space, especially in LMA and SRL.

Partitioning of intraspecific variability

Within sites, intraspecific trait variation (wITV) varied widely but unpredictably for above-ground traits, with proportions of within-species variation in individual traits at individual sites ranging from under 0.2 to over 0.95 (Fig. 2). The magnitude of intraspecific variation across sites was unrelated to any climatic variable. Variation in SRL within sites was uniformly dominated by within-species variation, with proportions ranging from 0.67 to 0.97 (Fig. 3). Among sites, SRL, leaf N:P ratio and LDMC had positive aITV values, indicating the variation in functional

Table 2. The ten most common species in the study plots and their elevational ranges.

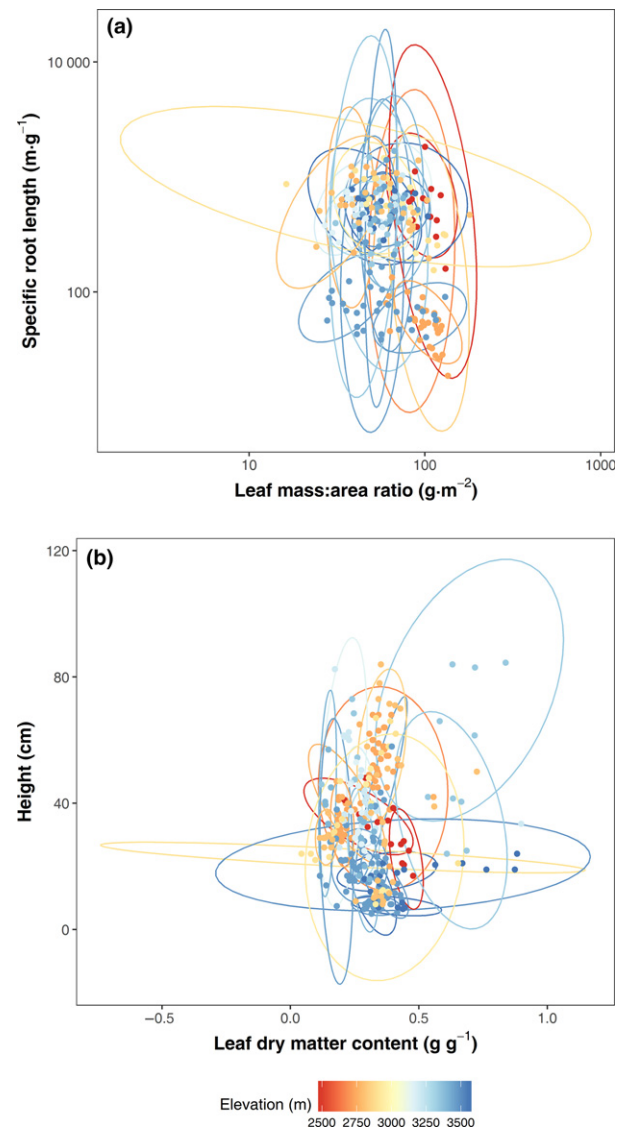| Species	Elevational Range (m a.s.l.)	
	Minimum	Maximum
Poa pratensis	2769	3200
Festuca thurberi	2740	2943
Bromopsis inermis	2740	3392
Helianthella quinquenervis	2769	3392
Erigeron speciosus	2740	3392
Potentilla gracilis	2740	3460
Lathyrus leucanthus	2740	3335
Artemisia tridentata	2480	2806
Thalictrum fendleri	2806	3392
Ligusticum porteri	2769	3460

Fig. 1. Individual measurements of LMA and SRL (**a**) and LDMC and height (**b**). In each panel, measurements are coloured by site elevation above sea level. For each species, an ellipse is drawn around the central 95% mass of the multivariate normal distribution of the two traits. Ellipses are coloured by the mean elevation of each species. [Colour figure can be viewed at wileyonlinelibrary.com]

traits within species among sites was greater than the variation caused by turnover of species among sites. In contrast, LMA, root N:P ratio and plant height had negative aITV values (Fig. 2), indicating that species turnover among sites made up the majority of variation in LMA and plant height among sites, with intraspecific variation making up a smaller proportion.

We also compared the observed wITV and aITV to values recorded in a recent global meta-analysis and found that the values for intraspecific trait variability in our study were generally higher than the global means in the
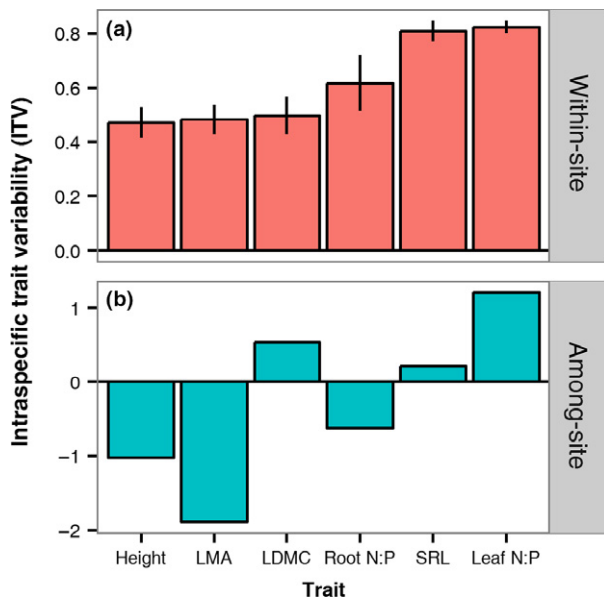
Fig. 2. Bar plots of intraspecific trait variability. (**a**) Bar plot of the proportion of intraspecific variability (wITV) at each site for each of the six traits; error bars represent SEM. A value of 0 would indicate no intraspecific variability. (**b**) For each trait, the log ratio of variation among sites due to intraspecific variability to variation among sites due to species turnover (aITV). A positive number means that intraspecific variability contributes more than species turnover, and 0 would mean the effects are of the same magnitude. [Colour figure can be viewed at wileyonlinelibrary.com]

meta-analysis (Siefert et al. 2015). The global mean wITV values for LMA, plant height and LDMC were all approximately 0.3 (0.29, 0.30, and 0.29 respectively), albeit with high variability among studies. In contrast, the mean wITV values we observed were >0.4 for all traits, indicating that the role of within-site intraspecific variability of each trait was higher than the global mean in our study region. The three mean aITV values were all negative in the global meta-analysis and ranged between −0.3 and −0.9 (−0.86, −0.33 and −0.65, respectively), although none significantly differed from zero. In our study, the aITV values for LMA and plant height were more negative than the global mean, but the aITV value for LDMC was positive. These results indicate that within sites in our system, species vary more in their LMA and height than the global average, and that among sites differences in LDMC are driven by individual-level variation to a greater degree than is typical globally.

Trait-by-environment regressions

Overall, we found that the predictive power of trait–environmental relationships was relatively weak (Fig. 3; model fit statistics in Appendix S6; note R^2 values). Across all sites, plant height had a unimodal relationship with both

summer precipitation and summer temperature, while leaf mass:area ratio was highest at sites with high temperature and low precipitation (low elevation). LDMC was lowest at sites with intermediate temperature and precipitation (mid-elevation), and leaf N:P ratio had a moderate peak at intermediate sites. As SRL varied so widely within sites, there were no significant across-site relationships with climatic variables.

Predictions of species abundances

The performance of all models, whether incorporating variation in functional diversity among sites or not, whether incorporating information about global range sizes, and regardless of which traits were included, was remarkably poor (Fig. 4). Model performance was not affected by the assumption of variable trait variances across sites or by the incorporation of prior information (Fig. 4). In fact, essentially all models performed worse at predicting relative species abundances than a null model assuming equal species abundances across all sites: the RMSE of the null model was 0.054, and the lowest RMSE across all 124 model fits was also 0.054. The poor performance of the 124 variants of the trait-based model indicates that relative abundance distributions of species in the study region are not driven by the relationship between environment and species traits, at least for the traits and environmental conditions that we considered (Appendix S7).

In general, the models under-predicted the abundance of most of the common species and predicted that some species that were present but rare would have a relative abundance approaching zero. In addition, the predictions of species abundance distributions were much more even than those we observed: median Simpson's evenness across sites was 0.15, but across all model runs median evenness across sites was 0.49 (between 0.33 and 0.87 in 95% of runs). Across all sites, the models tended to under-predict the abundances of exotic species, including *Bromopsis inermis* and *Taraxacum officinale*. The models over-predicted the abundances of some species that were locally common at one or two sites, but not found elsewhere, including *Poa* spp., *Symphoricarpos rotundifolius*, *Geum rossii* and *Chrysothamnus viscidiflorus*. Within sites where they were present, the local abundance of grass species, including *Poa* and *Festuca* spp., tended to be underestimated.

Discussion

Trait-based ecology has made great progress in accounting for patterns in nature, despite largely failing to account for the obvious fact that traits vary among individuals within species, and that this variation matters for how species interact with their environment and with each other.
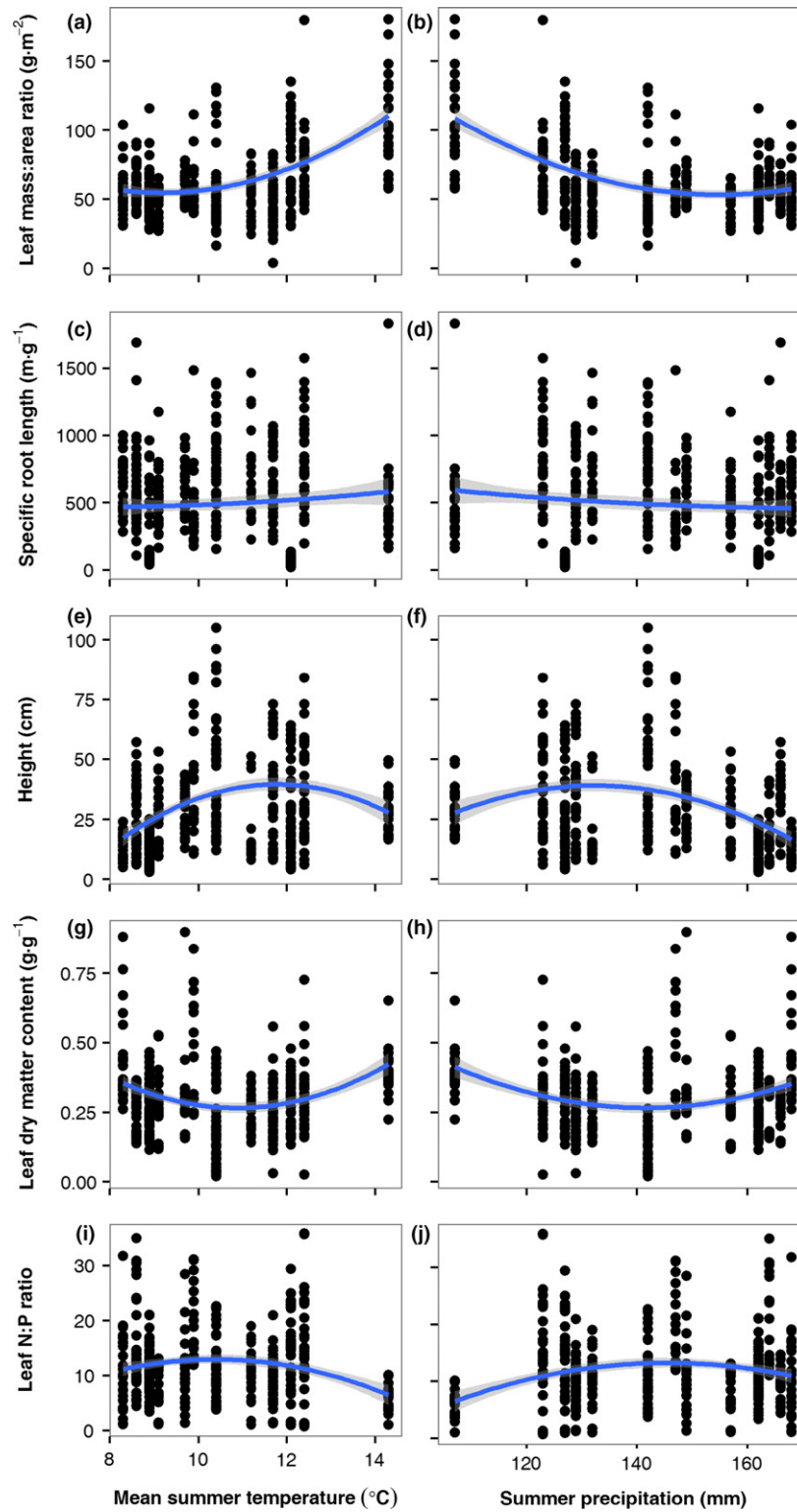
Fig. 3. Trait-by-environment scatterplots showing, from top to bottom, leaf mass:area ratio, SRL, plant height, LDMC and leaf N:P ratio plotted against mean summer temperature (left panels; **a**, **c**, **e**, **g** and **i**) and total summer precipitation (right panels; **b**, **d**, **f**, **h** and **j**). Each point represents a trait value for an individual plant at a particular site, ignoring species identity. Quadratic abundance-weighted regression fits are plotted, along with a band representing the SE of the fits. [Colour figure can be viewed at wileyonlinelibrary.com]
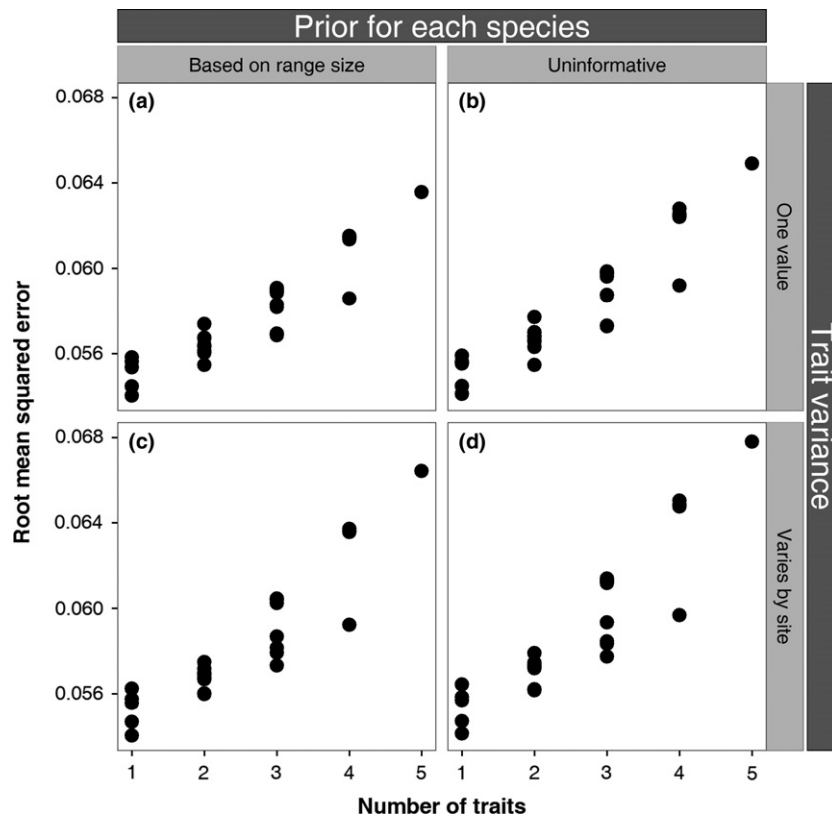
Fig. 4. Root mean squared errors (RMSE) of all model fits. Within each panel, RMSE is plotted against the number of traits used to fit the model. The top two panels (**a** and **b**) show RMSE of models with a single trait variance value used across sites, and the bottom two panels (**c** and **d**) show RMSE of models in which trait variance was allowed to vary across sites. The left two panels (a and c) show RMSE of models with uninformative priors, and the right two panels (**b** and **d**) show RMSE of models with informative priors based on species global range sizes.

Here, we sought to link trait variation both among and within species to the assembly of montane plant communities. Our results suggest that different plant traits are involved with different assembly processes occurring simultaneously. For instance, high ITV below-ground may suggest that processes such as soil resource partitioning are the dominant driver of variation in root traits, whereas leaf traits were less variable within species at each site and may be influenced more by environmental filtering. The predictive model showed that the functional traits we measured do not explain the distributions of species across sites (Appendix S7). In addition, incorporating functional diversity to account for niche spread did not improve predictive accuracy at all (Fig. 4). Overall, the poor performance of traits in predicting species relative abundances indicates that more than just trait-based filtering from the regional species pool determines which species establish at a site and how abundant they become. Observed species distributions were much less even than modelled distributions, indicating that the model does not adequately account for species dominance patterns that arise during local community assembly. The high level of intraspecific trait

variability in our study system is a plausible explanation for the lack of predictive power of our models. In addition, a variety of other processes may be more important than trait-based filtering. Among these processes may be historical and biogeographic effects, effects of spatial scale, soil resource heterogeneity or the fact that these functional traits may not capture the processes leading to community assembly patterns in the study region.

Intraspecific variability

It is notable that the intraspecific variation in root traits within sites was greater than the intraspecific variation in either leaf traits or plant height. This may indicate that there is higher competition among individuals, regardless of species, below-ground that is driving niche differentiation (Westoby & Wright 2006), or large differences in soil resource availability (Hutchings et al. 2003). Further, the high variability in root traits may mean that root traits are not very useful for predicting species abundances at a given site, because most of the variation is within species. It is also possible that root traits vary at different spatial scales

and in response to different environmental drivers, neither of which are well captured by this study. Individual plants exhibit morphological plasticity in roots in response to environmental change, presumably to achieve optimal resource co-limitation (Hutchings et al. 2003; Freschet et al. 2015). Adjustments in SRL and root biomass allocation may explain most of the community-level variation in root morphology that we recorded.

In comparison to the values from the global meta-analysis of Siefert et al. (2015), the wITV values from the study region were higher, while the aITV values for LMA and height were comparable. This shows that LDMC and SRL are explained more by individual variability than by species turnover across sites, but LMA and height are explained more by species turnover. Taken together, these results may indicate that LMA, root N:P ratio and plant height determine which species from the regional species pool pass through environmental filters and become established at each site, but that SRL may be involved with interactions among conspecific individuals that tend to increase the niche breadth of a species. The correlation of LMA and height with species turnover across sites appears to suggest that those traits would be the most useful for predicting species presence across the study sites. However, LMA and height are not useful for predicting relative abundance due to high intraspecific variability within sites, which helps explain the poor model performance we observed.

Our results lend support to the calls for an increased appreciation of individual trait variability in ecology (Bolnick et al. 2011; Violle et al. 2012; Rosindell et al. 2015). They suggest that intraspecific variation is a crucial driver of global change response, in agreement with previous work (Siefert et al. 2014; Moran et al. 2016). The high intraspecific trait variability in our study system would suggest that multiple species at a given site could be functionally equivalent (Hubbell 2005). The high degree of overlap in trait values among species made it difficult to predict which species should achieve the highest abundance at a given site from their traits alone. Our models failed to predict species dominance patterns: predicted distributions of species abundance were relatively even, but in reality one or a few species dominated at each site. We discuss potential reasons for this mismatch below.

Mismatch in temporal and spatial scales

One potential reason that our models failed to predict species relative abundance in local communities is that differences in the relative abundances of species among sites separated by hundreds of meters of elevation may be controlled by historical and biogeographic factors rather than deterministic ecological processes. These contingent historical events have interfered with the deterministic outcomes of filtering and niche differentiation. There may be dispersal barriers that prevent plants with appropriate traits from reaching optimal sites (Clark et al. 2002), perhaps due to topographic barriers in the mountainous study region (Engler et al. 2009). In addition, species relative abundance may shift from year to year due to temporal stochasticity (Alonso et al. 2006). Another potential explanation for the mismatch between traits and environment is that we measured species composition at a single time point and attempted to correlate it with static measures of climate (mean annual temperature and precipitation). However, plant species relative abundance may respond more sensitively to climatic fluctuations at a rapid time scale (Fukami & Nakajima 2011), leading to year-by-year turnover in dominant species identity (Allan et al. 2011). Furthermore, coarse-scale measurements of climatic factors may not adequately account for heterogeneity in microclimate and soil characteristics, either of which may act as a strong determinant of relative abundance at the plot scale (Levin 1992). Such small-scale variation in climate and soil properties may be an important cause of the intraspecific variation we recorded.

Mismatch between traits and community assembly processes

The trait-based models may have performed poorly because we failed to measure the plant traits or environmental factors that ultimately drive community assembly, assuming that community assembly is not entirely stochastic (Wills et al. 1997). Interestingly, our models tended to predict relative abundance distributions that were much more even than those we observed, and to predict the presence of many species that did not occur at particular study sites (Appendix S7). The under-prediction of the abundance of common species may indicate that the models do not capture processes that generate uneven abundance distributions. Furthermore, the assumption that probability of presence at a site corresponds to relative abundance within a community, common to Traitspace and other trait-based community models (e.g. Maxent; Shipley et al. 2006), often leads to under-prediction of common species. In addition, empirical studies have often failed to detect significant functional differences among dominant and minor species (Walker et al. 1999), indicating that neutral processes may be more important for generating relative abundance distributions (Hubbell 2005).

Another potential explanation for the low predictive power of the models is that the trait–environment relationship was relatively weak (Appendix S6; note R^2 values), at least for the traits we selected. Given the relatively high overlap of co-occurring species in trait space, the signature

of filtering may not be detectable; this effect may have been exacerbated through high levels of intraspecific variation within sites. In addition, the predictive power of models including more traits was lower, possibly because fewer individuals per species had measurements for all of the traits. Using fewer individuals reduced the information used to generate the multivariate density estimations, which may have led to worse model performance. Finally, our approach did not directly model competitive interactions among species. Although we indirectly accounted for the effect of limiting similarity (Abrams 1983) on community assembly by modelling trait variance, our model would not have detected a strong trait-based competitive hierarchy (HilleRisLambers et al. 2012). Future trait-based models of environmental filtering should explicitly include both types of interactions to capture more of the community assembly process.

Conclusion

In order for trait-based ecology to fulfill its early promises (McGill et al. 2006), traits must be used to predict, rather than solely describe patterns in an *ad hoc* manner (Laughlin et al. 2012; Violle et al. 2014). However, because trait distributions reflect the outcome of selective processes acting at the level of the individual organism, they may not be good predictors of species abundances within communities, especially when trait plasticity or variation is high (Messier et al. 2010; Siefert et al. 2015). We recommend that future model development focus on accounting for individual variation and plasticity and their consequences for community assembly. In addition, we suggest that researchers measure root traits that capture trade-offs in resource acquisition below-ground, because what plants do below-ground can obviously influence interactions, and ultimately their relative abundance, above-ground.

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Supporting Information

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

Appendix S1. Maps showing temperature and precipitation variability in the study region.
Appendix S2. Expanded description of Traitspace model fitting.
Appendix S3. Method of estimation of global range sizes.
Appendix S4. R functions used in data analysis.
Appendix S5. R scripts to recreate data analysis.
Appendix S6. Model fit statistics for trait-by-environment regressions.
Appendix S7. Predicted versus observed relative abundance for one model fit.