Competitive hierarchy or niche packing? An examination of the effects of competition on community functional trait distributions

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Abstract

Competitive dynamics play an important role in community assembly but are often difficult to study in natural systems due to their complexity. Here, I examine the effects of competition on community functional trait distributions. Many studies of competition have found competitive hierarchies, where dominant species with optimal traits for their environment competitively exclude less well-adapted species. I recast this model to provide predictions for the relationship between functional trait values and dominance. I analyzed these distributions of four functional traits in meadow communities along an elevation gradient and at multiple spatial scales to examine the relative role of these two processes. Height displayed generally hierarchical dynamics across variation in elevation and spatial scale, while other traits showed more mixed results. These results indicate that competition may be acting differently on different traits and resources within plant communities on many scales.

Introduction

Competition has long been thought of as a driving factor in ecology and community assembly. The role of competition traces back to Darwin (1859) who proposed that closely related species will compete more strongly than distantly related species. This has led to the 'niche packing theory,' which predicts functional and phylogenetic overdispersion in communities. While there have been many studies claiming support of Darwin's hypothesis (e.g. Cavender-Bares et al. 2004, Elton 1946) there have been several other studies that have found evidence of phylogenetic clustering or a lack of overdispersion (e.g. Cahill et al. 2008). From findings of clustering, a second hypothesis has been developed that makes predictions opposite those of the niche packing theory. This 'competitive hierarchy theory' predicts that the species with the best-suited traits for a given environment will ultimately be dominant. Over time, species with poorly suited traits would be competitively excluded, leading to functional and phylogenetic clustering around the dominant species. These hypotheses have traditionally been tested through species-level measures, such as phylogenetic modelling and species richness. However, these approaches assume that the traits acted upon by natural selection are phylogenetically conserved, which is not necessarily true for every trait (Webb et al. 2002).

Here, I recast these two contrasting hypotheses of competitive dynamics to predict functional trait distributions within plant communities. Functional traits are plant attributes such as leaf size and thickness, plant height, seed mass and tissue density that are markers for different life-history strategies and competitive abilities. Measuring functional traits within communities allows generalization of effects across different ecosystems and modeling of plant differences in a more direct manner than phylogenetic analysis (Grime 2006, McGill et al. 2006, Westoby 1998). Leaf traits such as specific leaf area (SLA) and leaf dry matter content (LDMC) are particularly important as measures of relative plant investment in structural support and photosynthetic output. Together with other leaf traits, these are known as the leaf economics spectrum (Wright et al. 2004). Measuring these traits allows description of where a plant falls along a distribution from long-lived, slow-growing plants (or plant parts) to short-lived, fast-growing plants (or plant parts), an important axis of variation for competition.

Effect of competition on functional trait distributions

The competitive hierarchy hypothesis predicts a narrow distribution of traits within a community. Successful species will have trait values clustered around those of the dominant species, while rare species may have different trait values. While older studies have attributed

convergence in functional traits within systems to environmental filtering (Weiher and Keddy 1995), competitive effects could also result in a much smaller range of traits present in a system and mechanistically explain contractions in the realized niches of species that appear well-adapted for a given environment. If this hypothesis best explains how competition proceeds, traits should converge within each community around those of the dominant species.

The niche packing hypothesis, on the other hand, predicts that competition will lead to a wide distribution of functional traits within communities (e.g. Silvertown et al. 1999). If this hypothesis is correct, there should be relatively little overlap between species' functional trait values and no relationship between abundance and functional trait values. This hypothesis argues that traits within a community will be more widely dispersed than predicted by chance because species will separate into distinct niches to avoid competition, while species that are too similar to each other will be competitively excluded. If this hypothesis best explains competition, traits within each community should diverge into separate niches.

Abiotic factors such as moisture availability generally determine the range of traits that can occur in a given environment, but the balance of trait-convergent and trait-divergent outcomes of competition creates the distribution of functional traits within communities by narrowing fundamental niches. This balance can change depending on several sampling and environmental factors. For instance, when environmental variation within a community is high or difference in competitive ability is low, competition may be reduced, promoting coexistence (Fig. 2, Mayfield and Levine 2010, see also Chesson 2000, de Bello et al. 2013). Spatial scale can also be important, with hierarchical factors dominating at small spatial scales where interaction between individuals is most relevant while niche packing tends to dominate at larger scales where environmental variability becomes relevant (de Bello et al. 2013, Silvertown et al. 2006). To integrate the influences of these effects, I will measure functional trait variation in forbs over several spatial scales along an elevation gradient.

In this study, I tested the competitive hierarchy theory's ability to predict the distribution of functional traits within plant communities. I then determined whether patterns of hierarchical dynamics were related to (1) differences over three spatial scales (plot level, 0.25 m^2; site level, ~ 25 m^2; landscape level, 14.3 km with 800 m elevation gain), (2) differences between functional traits (height, wet to dry ratio, SLA and LDMC) and (3) differences among sites across an elevation gradient.

Methods

Research system

Here, I examined competition through functional trait distributions in five sites along an elevation gradient in the Elk Mountain range of Colorado near Gothic, CO (Figure 1). These sites ranged from 2697 to 3463 m above sea level, and had primarily forb communities with some shrubs and grasses. At each site, I found communities of 16-20 species, with a total of 76 species across the landscape. Lower elevation sites had longer growing seasons, higher average temperatures and lower annual precipitation. However, soil moisture was generally highest during the growing season at the mid to high elevation sites. Snowmelt also occurred earlier at lower elevation sites, potentially increasing water stress.

Field methods

Between July 2 and August 7 2014 I harvested biomass and measured traits at each of the five different study sites (Figure 1). I established five plots at each site to measure plant

abundances and functional traits. Each plot was 0.25 m^2 (0.5 x 0.5 m), and plots were placed haphazardly throughout each site (roughly 25 m^2) in areas with relatively high diversity of forbs. Within each plot, I identified all species of forbs (excluding grasses and shrubs for experimental feasibility and consistency in trait measurements) and measured the height of five (or all, if fewer than five) individuals of each species. Species that could not be identified were assigned a morphospecies name to differentiate from other species and identified later in the lab. I then harvested all above-ground biomass by species and stored in a cooler until processing (no more than 6 hours). All plants were gathered near the peak season biomass for each site, with higher elevation sites analyzed later in the season than lower elevation sites.

Lab methods

Within samples from each plot, I determined the wet weight of each species, then collected five mature leaves per species to measure leaf traits. For each of these leaves, I measured leaf area, wet weight and dry weight to calculate SLA and LDMC (Cornelissen et al. 2003). In addition, I determined the dry weight of the total biomass to calculated wet to dry ratio. Dry weight for both leaves and full biomass was determined after a minimum of 72 hours (or longer, in cases of large plants) in a drying oven at 65° C. Leaf area was calculated by scanning each leaf individually using a scanner and then analyzing the images with ImageJ. SLA was calculated at the ratio of leaf area to dry leaf mass. LDMC was calculated as the ratio of leaf wet mass to leaf dry mass. Dry to wet ratio was calculated as the ratio of whole plant wet mass to whole plant dry mass, including the masses of leaves removed for leaf trait analysis.

Analysis

For each plot (n=25) and site (n=5) as well as for the dataset as a whole (landscape scale), I determined the dominant species (using wet biomass). I then determined mean functional trait values (height, dry:wet mass ratio, SLA and LDMC) for these dominant species and calculated the deviation of functional trait values of all other species from the dominants. Where grasses were dominant, I compared each species to the second most dominant species (dominant forb). I repeated this analysis on each spatial scale using dominant species and functional trait values for each plot and site.

I then ran linear regressions on each resulting dataset to determine the relationship between biomass and deviation in functional trait values from the mean. Biomass was log transformed to improve normality. For these models, I excluded the dominant species to avoid skewing the data (since the dominant species will always have a deviation of zero). All analyses were conducted in R (R Core Team 2014).

Results

Plot-level analysis

Evidence for competitive hierarchies was strongest in tests using height. The deviation in height from the dominant species was significantly correlated ($p<0.05$) with species biomass (log transformed) for nine out of 25 plots, and this correlation was marginally significant ($0.05 < p < 0.10$) in an additional five plots. Evidence in other traits was less strong; however, total mass dry to wet ratio was significantly correlated with biomass (log transformed) for six plots and marginally correlated in an additional two plots. SLA was correlated with biomass (log transformed) in one case and marginally correlated in one other, while LDMC was significantly related in two cases and marginally related in an additional three cases (Table 1).

Site-level analysis

Height was marginally correlated with log transformed biomass at two sites and significantly correlated at two others. Dry to wet biomass ratio was significantly correlated with log transformed biomass at one site and marginally correlated at two others. SLA and LDMC were not correlated with log transformed biomass at any sites (Table 2).

Landscape analysis

On the landscape scale, height and dry to wet ratio were significantly correlated with log transformed biomass. LDMC was marginally significantly correlated (Table 2).

Discussion

Evidence for competitive hierarchical dynamics was most clear based on variation in plant height across all spatial scales (Figure 2). This is in line with results of other studies and theoretical models, which predict that height variation should display highly hierarchical dynamics (e.g. Mayfield and Levine 2010). Evidence for competitive hierarchies were weaker in whole plant dry to wet ratios and nearly absent for leaf traits. These traits are less obviously hierarchical, since they are not direct markers for plant competition as height is through shading. However, as measures of the leaf economic spectrum and plant allocation of resources to growth or structure, they can describe plant strategies for competition on a more integrated scale. Further work on these data using multivariate modeling may produce a better picture of how plant competition plays out across a number of resources. More robust modeling would also allow testing of the niche packing theory more directly by determining whether species differ in predictable patterns within a multivariate trait space.

Effects of elevation and abiotic harshness

While evidence for elevational differences in competition was not clear, there was some indication that higher elevation sites had more hierarchical dynamics, although this was not the case at the highest elevation site (Figure 3). While there are many possible explanations for this pattern (including random chance), several interesting possibilities emerge. First, higher elevation sites could have decreased total trait space (due to harsh conditions or short growing season), leading to more hierarchical competition. For example, the total range of heights was larger for the mid-high elevation sites than for the lower elevation sites. At the lowest elevation site, the range of heights was only 30.5 cm, while at the second highest (and most hierarchical) the range was 109.5 cm. However, for many traits the highest elevation site had the lowest total trait space, but it still did not display hierarchical dynamics.

Second, more intense competition could occur in the middle to higher elevation sites due to greater total biomass (Figure 4). Increased biomass could increase the magnitude of competition as plants are growing more close together. Therefore, some of the results that I describe here could be an effect of increased importance of competition at mid-elevation sites rather than a change in competitive dynamics. Other studies have predicted that competition will be more intense and more hierarchical when there is larger variation in competitive ability (Mayfield and Levine 2010). All of these mechanistic explanations also describe the lack of hierarchical dynamics at the highest elevation site, which had low total biomass, more harsh (dry) abiotic conditions and a low range of heights. In addition, the dominant species at the highest elevation site was very short, while at other sites the dominant tended to be tall.

Based on data from summer 2013 on this elevation gradient, soil moisture (gravimetric %) generally increases across the gradient in a similar pattern to observed evidence for competitive hierarchies (Figure 5). Actual values for soil moisture may differ this year, but the general pattern of changes should be similar. This pattern does not fit exactly with the patterns that I found, but soil moisture may still be a driving factor in competitive dynamics, particularly as abiotic harshness increases with decreasing moisture. Measured soil moisture was high at the Cinnamon site, but for this study I used plots that were slightly higher up and on a rockier soil type which likely had much lower moisture.

The effects of abiotic harshness and other factors related with elevation could be teased apart with additional replication of this study along other gradients in different biomes, particularly if precipitation and temperature were linked in different ways (for example, along a gradient where precipitation decreases with elevation, or along a latitudinal gradient with changes in growing season length accompanied by a range of environmental conditions). The results at the highest elevation site provide some insight into the factors that could lead to competitive hierarchies but without additional data strong conclusions cannot be drawn.

Implications for competitive dynamics theories

While more complex modeling is necessary, these preliminary results suggest that competition may act in fundamentally different ways on different traits or axes of competition. That is, rather than competition acting either through niche differentiation or through hierarchies, community assembly may occur through a mix of these two kinds of dynamics, even on the level of individual plants or species. Some traits, such as height, lend themselves to more hierarchical dynamics, while other traits, such as SLA, are markers of different strategies that plants may use to avoid competition. Work on a wider variety of traits, as well as modeling of multivariate trait space may help to determine which trait distributions are best explained by different theories.

If true, the simultaneous action of different models for competition has several important implications for community structure. Communities primarily limited by different resources may have different competitive dynamics. Where light or other resources are limiting, hierarchies may develop. On the other hand, when plant communities are limited by abiotic harshness or other factors that affect all individuals equally, niche differentiation may be more important. For example, Fynn *et al.* (2005) found that the difference in competitive ability between short and tall species was more pronounced when soil fertility was high and not limiting. However, defining harshness in the systems that I examined is more difficult; higher elevation sites tend to be colder and have shorter growing seasons, but lower elevation sites tend to be moisture-limited due to low precipitation. A previous study along this same elevation gradient found predictable changes in intraspecific trait values with elevation, which could provide further evidence for the existence of optimal trait assemblages at different sites (Sides et al. 2014). Individual species may respond to changes along the elevation gradient differently, shaping the role of competitive forces and community structure through both interspecific and intraspecific variation.

Spatial scale

I did not find any clear difference in competitive dynamics when analyzing results at different spatial scales (Figure 6). This is in contrast to previous studies including de Bello (2013) which found that hierarchical dynamics prevailed only at small spatial scales. de Bello posited that this was due to lack of environmental variability on small scales preventing niche differentiation. The results of the current study are not in agreement with this model since

environmental conditions varied greatly across the elevation gradient and some evidence of competitive hierarchies was seen at all sites. This is true even with high species turnover between sites, which could lead to highly differentiated communities. These communities may be differentiated on variables such as leaf characteristics, but even on a landscape-wide scale, variation in height seems to exhibit hierarchical dynamics. However, previous studies that have found differences in competitive dynamics over different spatial scales have used smaller spatial scales than I used here. For example, while my smallest spatial scale was 0.25 m^2, de Bello (2013) used areas that were just 0.01 m^2. Here, I was unable to test dynamics on such very small spatial scales.

Future work

Here, I have used single-trait modeling to test the value of the competitive hierarchy theory for predicting trait distributions in communities. However, these data could also be combined in a multivariate trait space to examine changes within the overall plant type across the elevation gradient and with dominance. In addition, testing of intraspecific variation within these data could allow comparison between the competitive hierarchy theory and the niche packing theory. Since niche differentiation could be based on a number of traits (for example, species could overlap in their range of heights but have different shade-tolerance levels), it is difficult to analyze the role of this process when looking at single traits. Combining traits into a multivariate analysis could show either separation of species, indicating differentiation, or large niche overlap, indicating that this process is unimportant.

These different mechanisms of competition could co-occur in different traits, spatial scales or sites. Improving this data analysis would allow determination of whether the predictions of niche packing play out with patterns similar to or different from those of competitive hierarchies. If there is evidence for both at the same sites, this could indicate that the total magnitude of competition is higher in some areas. However, there may be more evidence for niche packing in areas without evidence for hierarchies, indicating that one process predominates in each community.

Conclusions

While trends in the predictive power of the competitive hierarchy theory were not clear across different analyses, there was strong evidence that hierarchical dynamics shaped community functional trait distributions in some tests. This was particularly strong in height and in the middle sites along the elevation gradient. These data provide interesting insight into a new framework for studying competition in plant communities. Further analysis and testing using multivariate statistics could yield additional results and test the balance between competitive hierarchy and niche packing within these communities.

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Tables

Table 1. Relationships between dominance (log biomass) and functional traits on smallest spatial scale. Sites are ordered by elevation; all results are based on linear regressions. Significant ($p < 0.05$) results are in bold, marginal ($0.05 < p < 0.10$) results are also listed.

Plot	Dominant sp	# species[1]	Height[2]	Dry:wet[2]	SLA[2]	LDMC[2]
CBT1	Chrysanthemum	8	0.0767, 0.4316	**0.0315, 0.5651**	--	**0.0464, 0.5107**
CBT2	Taraxacum	8	--	**0.0129, 0.6707**	**0.0269, 0.5858**	--
CBT3	Geum	4	**0.0015, 0.9970**	--	--	--
CBT4	Chrysanthemum	9	**0.0202, 0.5611**	--	**0.0108, 0.6291**	--
CBT5	Erigeron	3	--	--	--	0.0973, 0.9768 [3]
Road1	Erigeron	5	--	--	--	--
Road2	Potentilla	6	0.0650, 0.6145	--	--	--
Road3	Valeriana	4	--	--	--	--
Road4	Valeriana	4	--	**<0.0001, 0.9999**	--	--
Road5	Valeriana	4	--	--	--	--
Pf1	Veratrum	7	0.0828, 0.4835	--	--	--
Pf2	Veratrum	6	--	**0.0189, 0.7841**	--	0.0693, 0.6030
Pf3	Veratrum	6	**0.0320, 0.7227**	0.0765, 0.5849	--	--
Pf4	Veratrum	5	**0.0088, 0.9258**	--	--	--
Pf5	Veratrum	4	--	--	--	--
PBM1	Veratrum	9	**0.0266, 0.5278**	0.0845, 0.3656	--	--
PBM2	Veratrum	6	**0.0006, 0.9615**	--	--	--
PBM3	Chamerion	7	**0.0165, 0.7153**	**0.0386, 0.6082**	--	0.0996, 0.4489
PBM4	Veratrum	7	0.0744, 0.5029	**0.0492, 0.5929** [3]	--	0.0611, 0.5368
PBM5	Veratrum	8	**0.0002, 0.9193**	--	--	--

Cin1	Arctostaphylos	8	--	--	--	--
Cin2	Arctostaphylos	6	**0.0351, 0.7105**[3]	--	--	--
Cin3	Arctostaphylos	7	--	--	--	--
Cin4	Arctostaphylos	3	--	--	--	--
Cin5	Arctostaphylos	7	0.0643, 0.5282	--	--	--

1: Number of species in regression; excludes the dominant and species for which functional traits were not measured (eg *Equisetum*, grasses, and rare species with no healthy mature leaves)
2: results of linear regression: blank if p>0.10, otherwise p, r^2
3: slope is positive (negative in all other listed cases)

Table 2. Relationships between dominance (log biomass) and functional traits on site and landscape spatial scales. Sites are ordered by elevation; all results are based on linear regressions.

Site	Dominant sp	# species[1]	Height[2]	Dry:wet[2]	SLA[2]	LDMC[2]
CBT	Chrysanthemum [3]	15	--	0.0510, 0.2622	--	--
Road	Valeriana	12	**0.0235, 0.4163**	--	--	--
Pfeiler	Veratrum	15	0.0701, 0.2305	0.0649, 0.2383	--	--
PBM	Veratrum	15	**0.0017, 0.5451**	**0.0493, 0.2656**	--	--
Cin	Arctostaphylos	14	0.0607, 0.2632[4]	--	--	--
All	Veratrum	57	**<0.0001, 0.3682**	**0.0004, 0.1884**	--	0.0656, 0.0603

1: Number of species in regression; excludes the dominant and species for which functional traits were not measured (eg *Equisetum*, grasses, and rare species with no healthy mature leaves)
2: results of linear regression: blank if p>0.10, otherwise p, r^2
3: Grasses were dominant overall, daisy was 2nd most dominant
4: slope is positive (negative in all other listed cases)

Figures

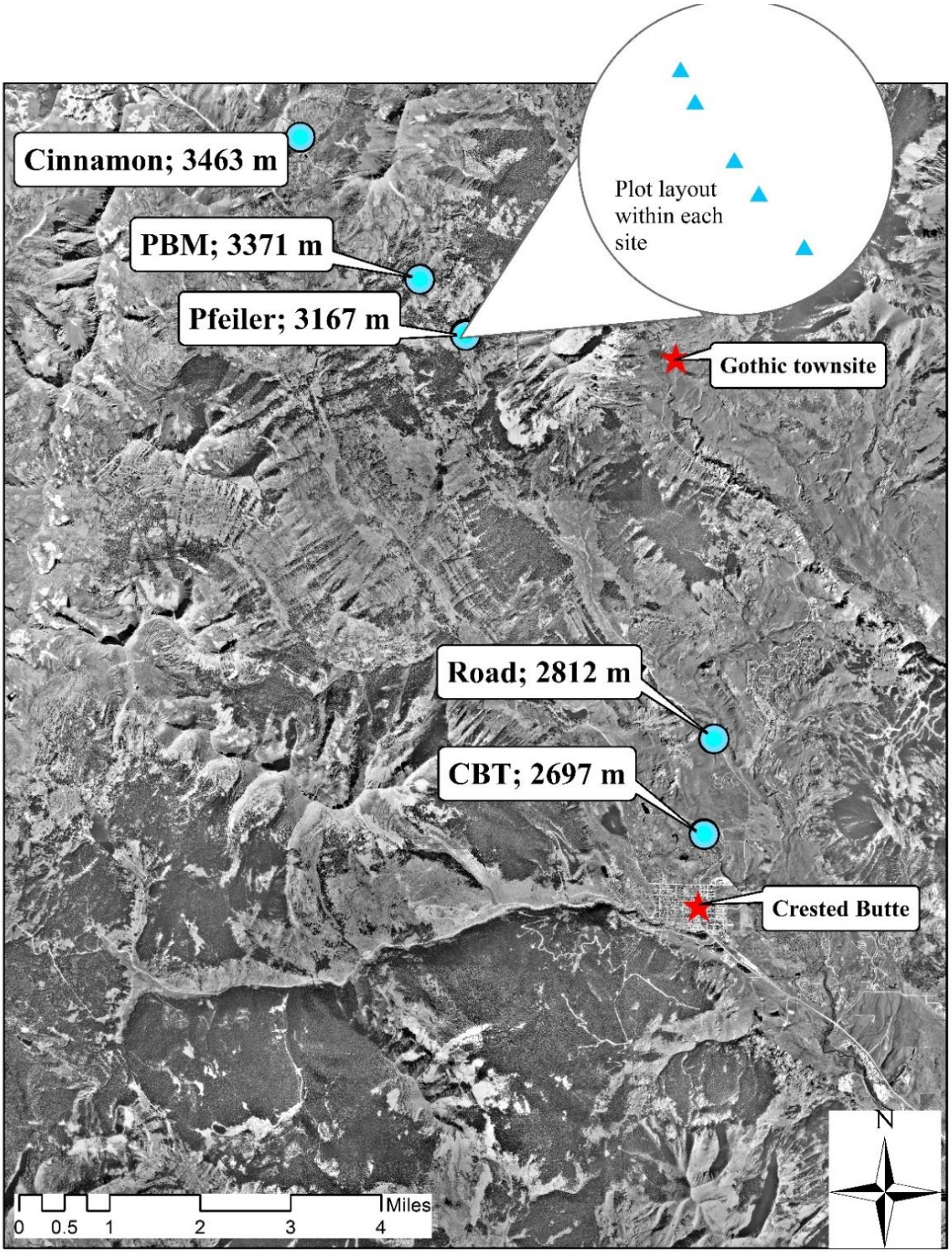

Figure 1. Map of research sites. Inset shows representative layout of plots within a research site.

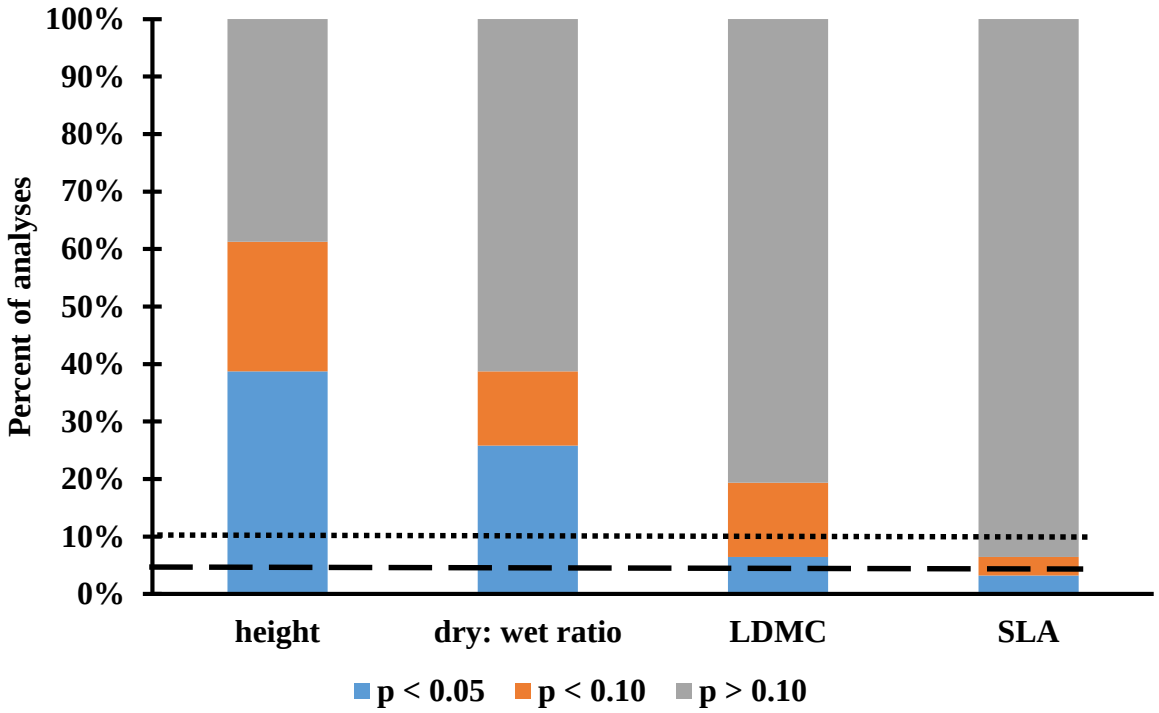

Figure 2. Differences in relationship with dominance for different functional traits. Dashed line represents expected number of significant analyses at $p < 0.05$; dotted line represents expected number at $p < 0.10$.

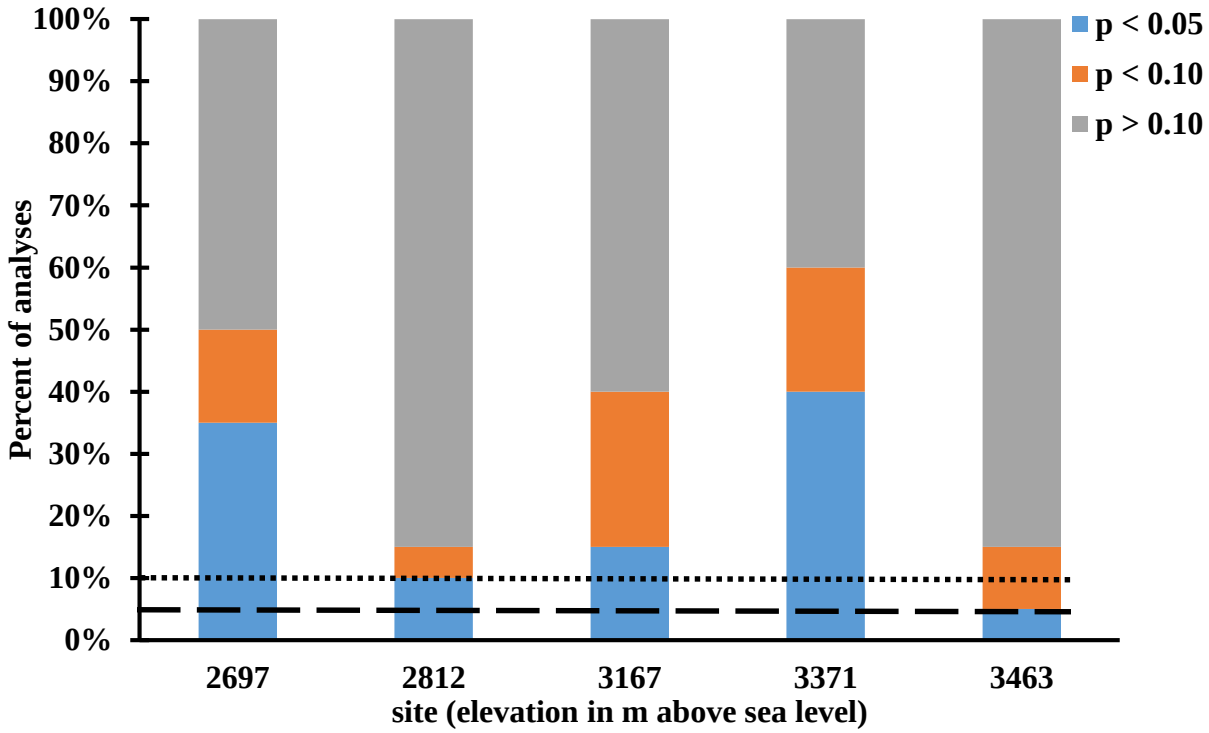

Figure 3. Differences in relationship between functional traits and biomass across sites of different elevations. Soil moisture and total biomass were highest in the sites at 3167 and 3371 m

above sea level. Dashed line represents expected number of significant analyses at $p < 0.05$; dotted line represents expected number at $p < 0.10$.

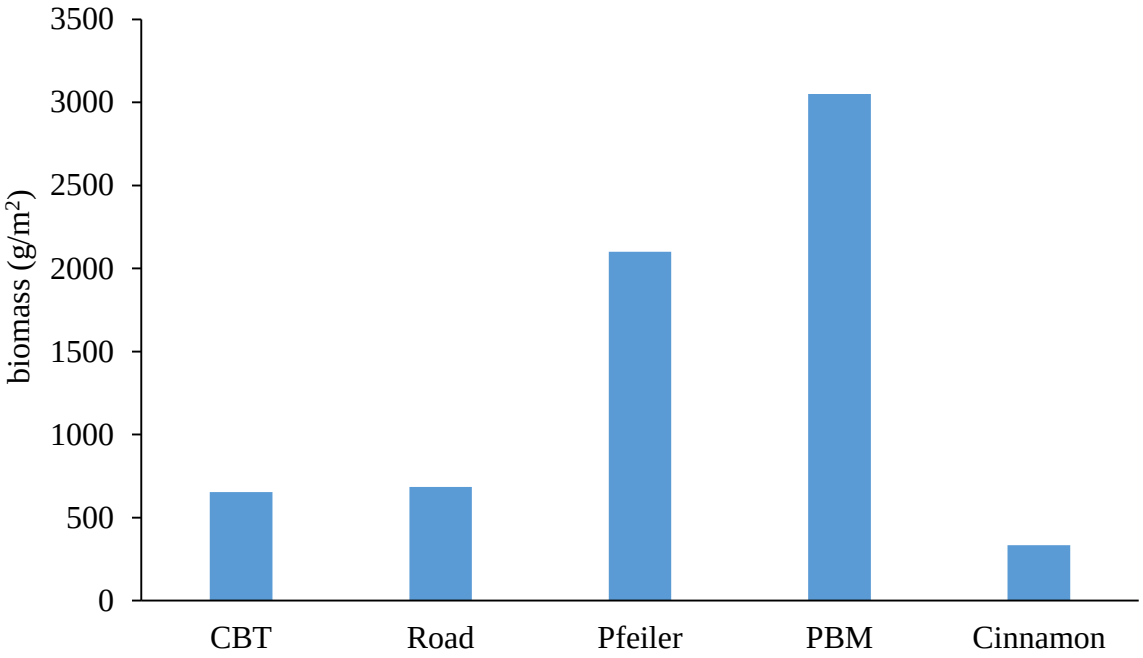

Figure 4. Total aboveground wet biomass at each site (arranged by elevation from left to right)

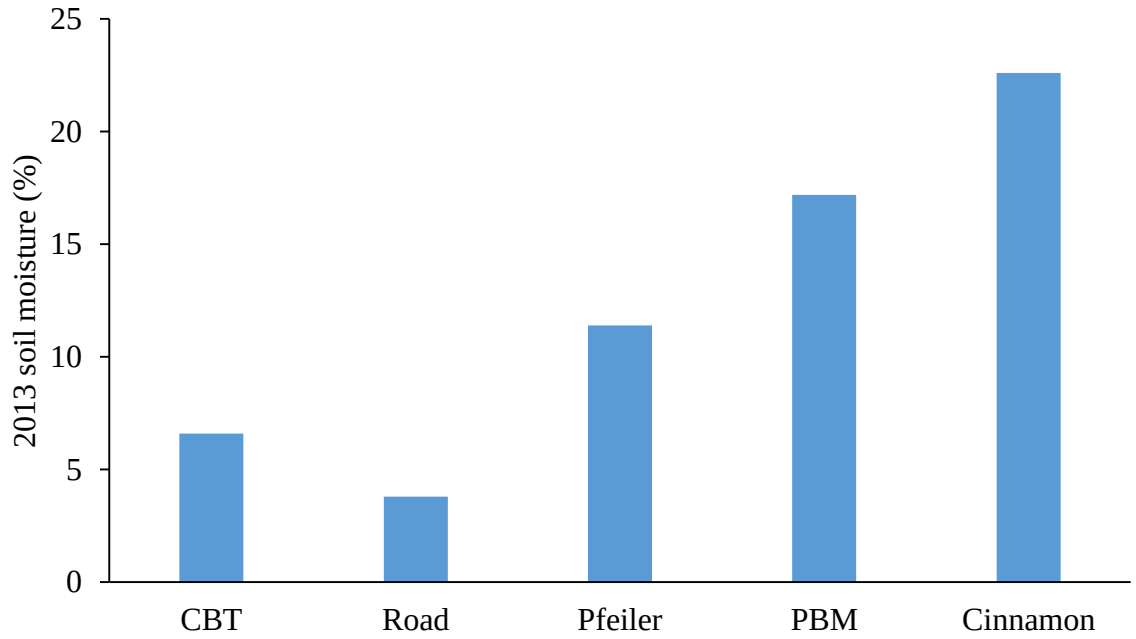

Figure 5. Gravimetric soil moisture from 2013 measurements. Soil moisture was measured in same general area as plots used in this study, but differed slightly. This was particularly true at Cinnamon, where sites used for this project were higher up on a rocky outcrop and likely had much lower soil moisture.

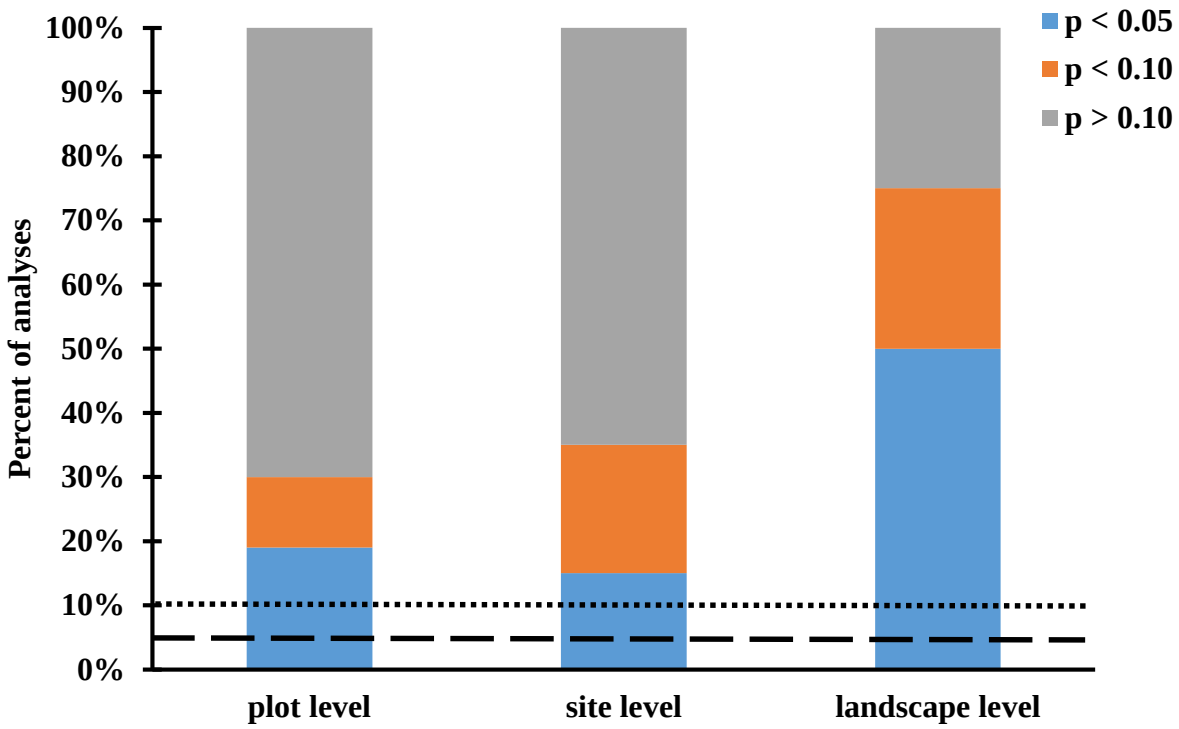

Figure 6. Differences in relationship between functional traits and biomass across different spatial scales. Note that plot level n = 100, site level n = 20 and landscape level n = 4. Dashed line represents expected number of significant analyses at $p < 0.05$; dotted line represents expected number at $p < 0.10$.

Literature Cited

Cahill, J. F., S. W. Kembel, E. G. Lamb, and P. A. Keddy. 2008. Does phylogenetic relatedness influence the strength of competition among vascular plants? Perspectives in Plant Ecology, Evolution and Systematics 10:41-50.

Cavender-Bares, J., D. Ackerly, D. Baum, and F. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. The American Naturalist 163:823-843.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343-366.

Cornelissen, J., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. Gurvich, P. Reich, H. Ter Steege, H. Morgan, and M. Van Der Heijden. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51:335-380.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. Murray, London.

de Bello, F., M. Vandewalle, T. Reitalu, J. Leps, H. C. Prentice, S. Lavorel, and M. T. Sykes. 2013. Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. Journal of Ecology 101:1237-1244.

Elton, C. 1946. Competition and the structure of ecological communities. The Journal of Animal Ecology :54-68.

Fynn, R. W. S., C. D. Morris, and K. P. Kirkman. 2005. Plant strategies and trait trade-offs influence trends in competitive ability along gradients of soil fertility and disturbance. Journal of Ecology 93:384-394.

Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. Journal of Vegetation Science 17:255-260.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters 13:1085-1093.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in ecology & evolution 21:178-185.

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Sides, C. B., B. J. Enquist, J. J. Ebersole, M. N. Smith, A. N. Henderson, and L. L. Sloat. 2014. Revisiting Darwin's hypothesis: Does greater intraspecific variability increase species' ecological breadth? American Journal of Botany 101:56-62.

Silvertown, J., M. E. Dodd, D. J. Gowing, and J. O. Mountford. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400:61-63.

Silvertown, J., M. Dodd, D. Gowing, C. Lawson, and K. McConway. 2006. Phylogeny and the hierarchical organization of plant diversity. Ecology 87:S39-S49.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33:475-505.

Weiher, E., and P. A. Keddy. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos :159-164.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199:213-227.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. Cornelissen, and M. Diemer. 2004. The worldwide leaf economics spectrum. Nature 428:821-827.