Increased competition does not lead to increased phylogenetic overdispersion in a native grassland

Abstract

That competition is stronger among closely related species and leads to phylogenetic overdispersion is a common assumption in community ecology. However, tests of this assumption are rare and field-based experiments lacking. We tested the relationship between competition, the degree of relatedness, and overdispersion among plants experimentally and using a field survey in a native grassland. Relatedness did not affect competition, nor was competition associated with phylogenetic overdispersion. Further, there was only weak evidence for increased overdispersion at spatial scales where plants are likely to compete. These results challenge traditional theory, but are consistent with recent theories regarding the mechanisms of plant competition and its potential effect on phylogenetic structure. We suggest that specific conditions related to the form of competition and trait conservatism must be met for competition to cause phylogenetic overdispersion. Consequently, overdispersion as a result of competition is likely to be rare in natural communities.

Keywords
coeexistence, community phylogenetics, competitive exclusion, diffuse competition, limiting similarity, niche conservatism, phylogenetic clustering, phylogenetic evenness, plant competition, resource competition.

INTRODUCTION

Though competition is common in natural systems, its role in community assembly, and the methods used to detect its influence remain issues of substantial debate. For example, ecologists have long searched for a ‘signature’ of competition in patterns of species co-occurrence. Traditionally, negative co-occurrence patterns (check-erboards) suggest competition has played a role in structuring the community (Diamond 1975; Gotelli & McCabe 2002). Such approaches are still used (e.g. Maestre et al. 2008), and can include patterns in species traits (e.g. Wilson & Stubbs 2012) and their phylogenetic relationships (e.g. Butterfield et al. 2013), with both phylogenetic and trait-based approaches assuming that competition causes increased dispersion. However, particularly for phylogenetic approaches, support for the assumption is typically conceptual (Webb et al. 2002; Mouquet et al. 2012), with tests limited to constructed communities (e.g. Viole et al. 2011) or observational studies (e.g. Cavender-Bares et al. 2006; Kraft & Ackerly 2010). Here, we test the relationship between competition and phylogenetic community structure using both an observational approach across multiple spatial scales and the first direct experimental test conducted in a natural system.

A core theoretical justification behind the search for a phylo-genetic signature of competition dates at least to Darwin (1859), where he states that related species should be more similar and thus compete more strongly with each other than with less closely related species (the ‘competition-relatedness hypothesis’ sensu Cahill et al. 2008). Central to the competition-relatedness hypothesis is the assumption that there is trait conservatism within a phylogeny, such that more closely related species will also be more functionally similar (Webb et al. 2002). A related idea, the theory of limiting similarity (MacArthur & Levins 1967), holds that niche differences are necessary for coexistence and that if species are too similar, the inferior competitor will be competitively excluded. Combined, these tenets of modern community ecology suggest that in a community in which competition is strong, there should be non-random exclusion of some species, such that those which persist will be ecologically distinct and the community will be overdispersed in both niche space (MacArthur & Levins 1967) and with respect to phylo-geny (Webb et al. 2002). Thus, if competition structures communities, co-occurring species should be less similar, or less related, than expected by chance (Weiher et al. 1998; Webb et al. 2002).

The value of phylogenetic overdispersion as an indicator of competition’s role in community assembly has recently been challenged. For example, whether competition leaves, or does not leave, a signature of overdispersion may be contingent upon how competitive and niche differences are related to phylogeny (Mayfield & Levine 2010). Facilitation (Valiente-Banuet & Verdú 2007) and herbivory (Webb et al. 2006) can also result in phylogenetic overdispersion among species within a community. This later issue relates directly to Connell’s (1980) invocation of ‘the ghost of competition past’; without evidence that competition is driving the observed patterns, then the pattern does not support any particular process. Following these challenges, we suggest that understanding whether competition affects phylogenetic community structure requires a more direct measurement of competition itself in natural systems.

Following from the idea that the effects of competition are most pronounced at small scales where co-occurring species share a
resource pool (Huston 1999), overdispersion is predicted to be most common at smaller spatial scales (Cavender-Bares et al. 2009). As such, phylogenetic community structure should change from overdispersed to clustered with increasing spatial scale, as the importance of competition wanes and environmental filtering becomes more important. For plant communities, existing tests of the relationship between spatial scale and phylogenetic community structure have largely been within forests (Cavender-Bares et al. 2006; Kraft & Ackerly 2010), with little consideration in herbaceous communities (e.g. Soliveres et al. 2012). Here, we use a spatial survey of plant community structure to test whether overdispersion increases at smaller spatial scales in native grassland. If there is no consistent evidence of overdispersion at the scales where plants compete, then it would suggest that overdispersion as a signature of competition is either rare or that competition is unimportant in community assembly.

Recently, the component assumptions of the competition–overdispersion relationship have also been questioned. Empirical support for the competition-relatedness hypothesis in plants is mixed and even when significant, the relationship is weak (Cahill et al. 2008; Burns & Strauss 2011). Furthermore, it has been suggested that competitive outcomes may be tied to specific character states, rather than mean or maximum values; such character states are plastic, varying as a function of the environment and not necessarily heritable (Cahill 2013) or conserved (Grime 2006). Competition in natural systems can also be diffuse, occurring among many different individuals of multiple species, both closely and distantly related. Such diffuse competition can dilute the effects of individual neighbours (Thorpe et al. 2011) and it remains unclear what the expected effect of mean relatedness should be on the outcome of diffuse competition.

Here, we test the competition–overdispersion relationship using two approaches, a competition experiment and a spatially explicit survey, both in a native grassland community. First, we manipulated competition and compared the strength of competition with the degree of overdispersion in the community, providing the first direct test of whether overdispersion increases with increased competition in natural communities. Second, we test for phylogenetic overdispersion in observational data at a variety of scales, ranging from scales where we expect grassland plants to compete (0.01–0.25 m²), to those where competitive interactions among all individuals are not possible (2500–10 000 m²). Finally, we examine the component assumptions of the competition–overdispersion relationship and integrate phylogenetic community ecology theory with plant competition theory to predict when competition should lead to overdispersion.

MATERIALS AND METHODS

Study site

The study occurred in a 50 ha section of native prairie at the University of Alberta research ranch at Kinsella, Alberta, Canada (53°05′ N, 111°33′ W). The field site is a savannah type habitat with mixed grass prairie interspersed with stands of aspen (Populus tremuloides Michx.). Graminoids comprise most of the biomass at the site and eudicots comprise > 70% of the diversity (Lamb & Cahill 2008). Primary productivity at the site is co-limited by water and nitrogen (Lamb et al. 2007), although competitive intensity is more closely linked to water availability (Lamb & Cahill 2008). Competition is generally intense and can reduce plant growth on average by 90% during seedling establishment (Lamb et al. 2007; Bennett & Cahill 2012) and 30% in established plants (Lamb & Cahill 2008). However, there is substantial variation in the actual strength of competition experienced at any particular location, including substantial evidence for facilitation (Lamb & Cahill 2008; Bennett & Cahill 2012).

Phylogeny construction

To construct the molecular phylogeny, we included 146 species across 35 families found at the study site. A 1400 bp section of the ribulose-biphosphate carboxylase gene (rbcL) was amplified and sequenced to construct the phylogeny (see Appendix S1). Phylogenetic relationships among focal taxa were inferred using Bayesian inference and maximum likelihood. Although we only sampled one gene, sequence variation in rbcL was sufficient to resolve relationships such that the topology was consistent with published angiosperm phylogenies with strong support (see Appendix S1 for further details). We pruned tips from the larger phylogeny if they were not present in the current community data set. This resulted in phylogenies containing 89 species for the field survey and 53 species for the competition experiment (experimental details below). Both phylogenies were well resolved and contained few polytomies. Of the polytomies present, all were near the tips and should have little effect on our analyses (Swenson 2009). For the four species for which we had no phylogenetic information, we substituted congeners otherwise absent from the data set. Some species were cryptic unless flowering, making differentiation among congeners difficult. These congeners (three pairs of species) were pooled and assigned the identity of the most common species for phylogenetic analyses. All subsumed species were rare (< 1% occurrence rates).

Competition experiment

We used the data from Lamb & Cahill (2008) to experimentally test whether phylogenetic overdispersion increases with the strength of competition. The strength of competition was assessed using 20 pairs of established plants for each of the 12 most abundant species at the site. Plant pairs were selected as similarly sized plants of the same species separated by c. 1 m. Neighbours were removed around one plant in each pair. The relative strengths of root and shoot competition (Cahill 1999), and the total intensity of competition can vary with resource availability (Bennett & Cahill 2012; Rees 2013). As different forms of competition can have different effects on community structure (Hautier et al. 2009; Lamb et al. 2009) half of the pairs were fertilised with nitrogen at a rate of 5.4 g NH₄NO₃ m⁻²; the remaining plots were left unfertilised. Competition was estimated as the log response ratio (Cahill 1999) comparing the relative growth rate of plants grown with neighbours to plants grown without neighbours. More detailed methods on the experiment can be found in the original manuscript (Lamb & Cahill 2008).

Competition-overdispersion

To estimate phylogenetic community structure, we calculated the net relatedness (NRI) and nearest taxon (NTI) indices (Webb et al.
From these measurements, we extracted two principal components structure (see Lamb & Cahill 2008 for measurement methods details). Environmental filtering is also predicted to have strong effects on phylogenetic community structure, we ran a series of separate mixed models with NRI and NTI as response variables. Each model included a factorial combination of competition intensity and nitrogen treatment as fixed factors and focal species as a random factor in SPSS (v. 20.0; IBM Corp., Armonk, NY, USA).

Out of concern for the potential to obtain Type II errors if competition is mild in most plots, we ran a second set of analyses. Here, we binned plots into quartiles based on the strength of competition, with quartiles varying from strong competition (mean growth reduced > 75%), to facilitation (growth increased > 200%). Given that the predictions for both increasing competition (Webb et al. 2002) and facilitation (Valiente-Banuet & Verdú 2007) are increased overdispersion, we tested for differences between the quartiles with the strongest competition and the weakest (mean growth reduced < 20%) using bootstrapped t-tests, based on 1000 bootstrap samples.

Environmental filtering is also predicted to have strong effects on phylogenetic structure (Cavender-Bares et al. 2009; Mayfield & Levine 2010). Therefore, we tested whether total soil nitrogen, soil moisture, estimated annual incident radiation, and light penetration to the soil composition at two smaller spatial scales where we would expect the effects of competition to be most intense. For each plot, we assessed species composition in fifteen randomly placed 0.01 m² quadrats and in one central 0.25 m² quadrat. Species composition for the whole plot (4 m²) was assessed as the presence or absence of species in any of the smaller quadrats. To create larger sized areas, where we expected environmental filtering to be operating, we grouped neighbouring plots based on their spatial proximity. For example, when we paired plots, we created pairs between plots that were separated by 35.3 m at most (the hypotenuse of a 25 m by 25 m plot), such that each plot pairing was said to represent 625 m². We repeated this process such that a group of three plots represented 50 × 50 m or 2500 m² and a group of four plots 100 × 100 m or 10 000 m². For these larger areas, we determined community composition as all species present within each plot within that group. From these measures of community composition, we estimated NRI and NTI using the picante package (Kembel et al. 2010) in R following the same procedure as outlined above. We used bootstrapped one-sample t-tests to determine if the average phylogenetic community structure differed from zero at each spatial scale for NRI and NTI separately in spss (v.20.0). Due to the sample size disparity between the 0.01 m² scale and the other spatial scales, we conducted a second set of analyses where we created random subsamples containing only 100 plots from the larger data set (N = 1462), and ran t-tests on each of these subsamples. This subsampling procedure was repeated 100 times.

As many processes can affect phylogenetic community structure, we also measured nitrate, ammonium, phosphate, soil pH, soil texture, soil moisture and slope within each of the 4 m² plots (see Appendix S1). Similar to the competition experiment, we extracted three principal components from these variables and used them to explain variation in NRI and NTI at the individual plot scale (4 m²) using general linear models.

**Results**

**Competition–overdispersion**

On average, competition reduced growth rates by 30%. However, neighbour effects were highly variable, ranging from strong facilitation (growth rates increased by a maximum of > 300 times) to strong competition (growth rates reduced by a maximum of > 98%). However, we found no evidence that competition left a ‘signature’ of phylogenetic overdispersion. Increased competition between the quartile representing strong competition and the one representing mild competition using bootstrapped t-tests. If competition is greater among related species, we should expect lower scores of MPD.t in the quartile with stronger competition. We repeated both tests with an abundance weighted index of MPD.t (MPD.t.a), but the results did not differ and thus we only present only the results using unweighted indices (see Figs S3 and S4; Tables S2 and S4).
was not associated with increased phylogenetic overdispersion, nor did this relationship vary as a function of nitrogen addition. This result was found when using either the net relatedness index (NRI) or the nearest taxon index (NTI; Fig. 1, see Table S1). There were also no differences in phylogenetic community structure between the 25% of plots in which competition was strongest and the 25% in which it was weakest, despite a fourfold average increase in the strength of competition (see Fig. S3; Table S2).

Though overdispersion was not associated with competition, communities tended to become more overdispersed along principal component 1 (Fig. 2a). This axis was correlated with low incident radiation and low light penetration (see Appendix S1) and suggests that light limitation may be associated with phylogenetic overdispersion, even if the combined effects of root and shoot competition are not. However, caution is warranted in this result, as the relationship explained relatively little of the total variation and was only significant for NRI ($R^2 = 0.038$, $F_{1,189} = 7.048$, $P = 0.009$; see Table S3 for full results).

**Competition relatedness**

We found no evidence that competition increased in intensity with higher mean relatedness between target plants and their neighbours (MPD.t), nor was this relationship altered by nitrogen addition (Fig. 3; see Table S4). This result is supported by our analysis using only strong and weak competition quartiles, where we found no difference in mean relatedness (see Table S2; Fig. S3).

**Phylogenetic signature and spatial scale**

We found mixed results regarding the relationship between phylogenetic structure and spatial scale of observation. At the smallest scale (0.01 m$^2$), where we expect competitive interactions among co-occurring plants to be the most intense, communities were not overdispersed for NTI, but were for NRI (Fig. 4; Table 1). Interestingly, NTI, not NRI, is thought to be the statistic best able to detect the effects of competition on phylogenetic structure (Kraft et al. 2007). Further, even for NRI at 0.01 m$^2$, the mean value was quite small ($> -0.1$), and we did not detect significant phylogenetic structure for any individual plots at that scale (Table 1). This finding of significant overdispersion remained marginally significant after random subsampling (see Table S5). There was no significant phylogenetic overdispersion at other scales where we may expect plants to interact (0.25 or 4 m$^2$; Table 1).

Phylogenetic clustering increased with spatial scale for both NRI and NTI, although clustering was only significant at the 4 m$^2$ scale (Fig. 4; Table 1). However, each spatial scale was quite variable and showed evidence of both clustering and overdispersion (Table 1). At the 4 m$^2$ scale, principal component 2 explained some of this variation for both NRI ($R^2 = 0.066$, $F_{1,92} = 4.167$, $P = 0.044$) and NTI ($R^2 = 0.060$, $F_{1,92} = 4.577$, $P = 0.035$; see Table S3 for full results). Communities became more phylogenetically clustered along the component (Fig. 2b,c), which was associated with clay content, water retention and pH (see Appendix S1). This suggests that niche conservatism in response to poorly drained, high-clay, basic soils may have led to phylogenetic clustering.

**DISCUSSION**

Competition is often inferred as the mechanism causing overdispersion in species co-occurrence patterns (Maestre et al. 2008), trait distributions (Wilson & Stubbs 2012) or phylogenetic relationships (Webb et al. 2002; Cavender-Bares et al. 2009). Despite strong competition in this system (Lamb & Cahill 2008; Bennett & Cahill 2012), we found no evidence that competition caused phylogenetic overdispersion, nor did we find strong evidence for phylogenetic overdispersion at any spatial scale. While we do not imply that competition cannot cause phylogenetic overdispersion in communities, our data suggest that overdispersion is not a necessary outcome of competition, con-
consistent with the predictions of Mayfield & Levine (2010). Given that this is the first experimental field test of the competition-overdispersion hypotheses, we suggest that more tests are needed to assess whether there are any situations in which competition causes phylogenetic overdispersion in natural systems. For example, competitive effects on seedlings may increase overdispersion, but we are limited to data on adult plants in this study and this remains an important avenue of inquiry. Until then, current understanding of plant competition and coexistence theory may offer some insight into when overdispersion is more, or less, likely an outcome of competition. From these theories, overdispersion should depend on (1) the form of competition, (2) the importance of relatedness and (3) the nature of trait conservatism (Fig. 5).

The form of competition

The form of competition varies depending on whether plants are competing aboveground for light, belowground for soil resources (Casper & Jackson 1997; Schwinning & Weiner 1998), or both (Cahill 1999). When competing for light, larger plants pre-empt light interception, making light competition size asymmetric—the benefit of being large is disproportional to the size difference (Schwinning & Weiner 1998). Conversely, belowground competition is size symmetric and resource capture is proportional to size (Cahill & Casper 2000). Due to these differences, light competition is generally more intense and has a greater impact on community structure than root competition (Hautier et al. 2009; Lamb et al. 2009). For competition to leave a phylogenetic signature, it must alter community structure, either through competitive exclusion or abundance reductions. Further, its effects must be stronger than other factors influencing community structure for the signature to be detectable among multiple factors (Mayfield & Levine 2010). In systems where root competition dominates, such as this one (Lamb & Cahill 2008) and many others (Casper & Jackson 1997), competition is unlikely to leave a strong signature because it has little effect on community structure (Fig. 5). However, we did find increased phylogenetic dispersion with light limitation, which is consistent with light competition affecting community structure (Hautier et al. 2009; Lamb et al. 2009) and thus promoting overdispersion (Mayfield & Levine 2010). We suggest that a significant competition–overdispersion relationship is most likely when size asymmetric competition dominates (Fig. 5; Lamb et al. 2009); however, experimental tests are needed.

The importance of relatedness

For competition to cause overdispersion, competition must be stronger among closely related species than among less related
systems with a dominant species, relatedness to the dominant should be important, but when a dominant is lacking, diffuse competition should reduce the importance of relatedness (Thorpe et al. 2011). Within natural communities, many interactions reduce the importance of relatedness in competition (Beltrán et al. 2012); suppression of a shared competitor can lead to indirect facilitation (Levine 1999) and shared mycorrhizae can influence competitive outcomes (Moora & Zobel 1996). Such interactions are common and likely reduce the importance of relatedness in competition, thereby reducing or eliminating any potential phylogenetic signature of competition. Thus, in communities where diffuse competition dominates, we should not expect competition to leave a measurable phylogenetic signature, regardless of whether competition is stronger among close relatives (Fig. 5).

The nature of trait conservatism

Recent theoretical advances suggest that the conservatism of niches and competitive abilities is important in determining the phylogenetic signature of competition (Fig. 5; Mayfield & Levine 2010). If strong competitive abilities are conserved within a lineage, and niche differences do not promote coexistence of less competitive lineages (niche differences not conserved), then competition should cause clustering. Conversely, if niche differences are conserved, but competitive abilities are not, then close relatives with similar niches will compete more strongly and competition will cause overdispersion. If both niche and competitive abilities are conserved, then the signature of competition depends on the relative importance of competitive ability and niche differences (Fig. 5; Mayfield & Levine 2010). If there is no clear dominance of niche or competitive processes in determining community structure, then phylogenetic signature is likely to be random (Soliveres et al. 2012). Experimental evidence from plant communities is lacking; however, niche differences are expected to be conserved, while competitive ability differences are likely convergent (Grime 2006), which should lead to competition causing overdispersion (Mayfield & Levine 2010). However, despite strong competition and the conservatism of multiple functional traits (Kembel & Cahill 2011), we found only weak evidence of overdispersion at the site and no evidence that competition was related to overdispersion.

**Table 1** Results of bootstrapped one-way $t$-tests determining whether phylogenetic community structure deviates from zero

<table>
<thead>
<tr>
<th>Index*</th>
<th>Area ($m^2$)</th>
<th>N</th>
<th>Est. Mean</th>
<th>Est. SE</th>
<th>$t^p$</th>
<th>Minimum</th>
<th>Maximum</th>
<th>$-\beta^p$</th>
<th>$+\beta^p$</th>
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<td>NRI</td>
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<td>-0.097</td>
<td>0.010</td>
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<td>-0.92</td>
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<td></td>
<td>0.25</td>
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<td>-0.011</td>
<td>0.036</td>
<td>0.781</td>
<td>-0.84</td>
<td>0.94</td>
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<td>0.108</td>
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<td>0.004</td>
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<td>0.171</td>
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<td>0.175</td>
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*a*NRI denotes the net relatedness index and NTI the nearest taxon index (Webb et al. 2002).
+Values in bold are significant at $\alpha = 0.05$.
†(+) represents the percentage of cases exhibiting significant clustering and (−) significant overdispersion at $\alpha = 0.05$. 

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In addition, significant phylogenetic overdispersion was found only when the conditions that must be met for competition to lead to a detectable phylogenetic signature of overdispersion. The conditions are shown in boxes and predicted phylogenetic signatures in bubbles. Competition must be size asymmetric and pairwise, while niches, but not competitive abilities, must be conserved for overdispersion to occur. However, if competitive abilities are conserved, the influence of niches on community structure must be stronger than competition. Pathways dealing with the conservation of competitive abilities and niches are modelled after the predictions of Mayfield & Levine (2010).

Figure 5 The hypothesised model showing the conditions that must be met for competition to yield a detectable phylogenetic signature of overdispersion. The conditions are shown in boxes and predicted phylogenetic signatures in bubbles. Competition must be size asymmetric and pairwise, while niches, but not competitive abilities, must be conserved for overdispersion to occur. However, if competitive abilities are conserved, the influence of niches on community structure must be stronger than competition. Pathways dealing with the conservatism of competitive abilities and niches are modelled after the predictions of Mayfield & Levine (2010).

Often overlooked in phylogenetic community ecology is the fact that it is the differences in trait states and not mean or maximum trait values that influence competitive outcomes (Cahill 2013). An individual’s height relative to neighbours will determine the outcome of light competition, not its maximum potential height. Further, many traits will vary as a function of the environment; such plasticity can obscure patterns of trait conservatism (Burns & Strauss 2012). Thus, conservatism of mean or maximum trait values does not necessarily impact the phylogenetic signature within communities, as it is the expressed trait state that determines competitive outcomes.

Spatial scale and signature detection

Given that we found no evidence that competition increased overdispersion, it seems unlikely that the weak evidence we found for overdispersion at the 0.01 m² scale is an outcome of competition. In addition, significant phylogenetic overdispersion was found only at the 0.01 m² scale and for the net relatedness index (NRI), which measures relatedness across the community. Yet, the nearest taxon index (NTI), which measures distances to the closest relative, is expected to be the more powerful statistic for detecting limiting similarity (Kraft et al. 2007). This suggests that competitive interactions may not be driving overdispersion at this scale. However, the relative power of NTI and NRI varies as a function of multiple variables, making it difficult to specify why results differed between the two statistics (Kraft et al. 2007; Kraft & Ackerly 2010).

Our spatial survey results were consistent with the prediction that overdispersion should be more common at small spatial scales with clustering more common at larger scales (Cavender-Bares et al. 2006, 2009; Vamosi et al. 2009; Kraft & Ackerly 2010). This suggests that theory may be able to predict the overall pattern. However, at each spatial scale, plots varied from overdispersed to clustered, suggesting spatial heterogeneity in the factors affecting phylogenetic community structure. Further, when coupled with our finding of no relationship between competition and overdispersion, it suggests that the proposed mechanisms driving this pattern, competition causing overdispersion at small spatial scales and environmental filtering causing overdispersion at larger scales (Cavender-Bares et al. 2006, 2009), may need to be reevaluated.

Synthesis

Although competition is widely assumed to cause phylogenetic overdispersion, tests of this assumption are rare and this study is the first to experimentally test this relationship in the field. Despite strong competition in this system, we found little evidence that competition drives phylogenetic overdispersion. We suggest that this system is similar to other plant communities where competition is primarily diffuse (Wilson & Keddy 1986) and belowground (Casper & Jackson 1997). Therefore, we think it unlikely that competition will often lead to a detectable signature of overdispersion. Adding to the predictions laid out by Mayfield & Levine (2010), we suggest extra conditions that must be met for competition to lead to a detectable signature of overdispersion (Fig. 5). Our data suggest that competition-driven overdispersion is spatially heterogeneous and often obscured by other processes. Given the small proportion (2–12%) of plots with significant phylogenetic structure in our and other studies (e.g. Kembel & Hubbell 2006; Kraft & Ackerly 2010), we suggest that studies focus on experimentally determining the factors driving this heterogeneity (e.g. Soliveres et al. 2012), rather than searching for general trends.

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AUTHORSHIP

JFC originated the idea to empirically test the competition–overdispersion relationship. JAB and JFC developed the fuller concepts here, including the integration of the spatial scale survey. Competi-
tion data were collected in a study conducted by EGL, designed by JFC and EGL. JAB and JFC designed the spatial scale survey, with data collection by JAB. JCH and WMCH conducted the molecular phylogeny and wrote the related methods. JAB performed the statistical and phylogenetic analyses; JAB and JFC interpreted the data; JAB wrote the initial manuscript; JAB and JFC edited subsequent versions of the manuscript.

REFERENCES


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