

IDEA AND PERSPECTIVE

Opposing effects of competitive exclusion on the phylogenetic structure of communities

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Abstract

Though many processes are involved in determining which species coexist and assemble into communities, competition is among the best studied. One hypothesis about competition's contribution to community assembly is that more closely related species are less likely to coexist. Though empirical evidence for this hypothesis is mixed, it remains a common assumption in certain phylogenetic approaches for inferring the effects of environmental filtering and competitive exclusion. Here, we relate modern coexistence theory to phylogenetic community assembly approaches to refine expectations for how species relatedness influences the outcome of competition. We argue that two types of species differences determine competitive exclusion with opposing effects on relatedness patterns. Importantly, this means that competition can sometimes eliminate more different and less related taxa, even when the traits underlying the relevant species differences are phylogenetically conserved. Our argument leads to a reinterpretation of the assembly processes inferred from community phylogenetic structure.

Keywords

Coexistence, community assembly, competitive ability/fitness differences, competitive exclusion, niches, phylogenetics, regional species pool.

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INTRODUCTION

The complex processes involved in species coexistence and community assembly have long-fascinated ecologists and evolutionary biologists. Competition is among the most important and best studied of these processes (Schoener 1983; Goldberg & Barton 1992). A common hypothesis about competition's role in community assembly is that closely related taxa compete more intensely than their distantly related counterparts, limiting their ability to coexist (Webb *et al.* 2002; as discussed in Silvertown *et al.* 2001; Slingsby & Verboom 2006; Prinzing *et al.* 2008; and reviewed in Dayan & Simberloff 2005; Cavender-Bares *et al.* 2009). This hypothesis has been termed the 'competition-relatedness hypothesis' (Cahill *et al.* 2008).

The hypothesis is usually attributed to Darwin (1859), who noted that species of the same genus tend to be more ecologically similar, and should thus compete more severely than species of distinct genera. The hypothesis has received renewed attention of late due to its importance for interpreting phylogenetic patterns in the study of commu-

nity assembly (Webb 2000; Swenson *et al.* 2006; Helmus *et al.* 2007; Maherali & Klironomos 2007; Jiang *et al.* 2010). Most notably, it has been proposed that when traits are sufficiently conserved across phylogenies, competitive exclusion will cause closely related species to co-occur less frequently than expected by chance (Webb *et al.* 2002; Davies 2006; Swenson *et al.* 2006; Cavender-Bares *et al.* 2009). It is the theoretical ecological foundation for this proposition that we revisit in this paper.

To explain our criticism fully, we start by highlighting two of the central premises of the competition-relatedness hypothesis. First, an organism's niche is determined in part by its phylogenetic history (Wiens & Graham 2005). The frequent association of ecological traits with species' position in a phylogeny supports this notion (Elton 1946; Webb *et al.* 2002; Ackerly 2003; Wiens & Graham 2005; niche conservatism is also the subject of recent debate: Losos 2008a,b; Wiens 2008). The second premise is that niche differences between taxa are important for their coexistence. This principle originates from classic ecological theory and has been illustrated in evolutionary studies of

trait divergence between co-occurring species (Harper *et al.* 1961; MacArthur & Levins 1964, 1967; tested in Silvertown *et al.* 2001; and reviewed in Losos 1994; Dayan & Simberloff 2005).

Despite the classic underpinnings of the competition-relatedness hypothesis, empirical support has been mixed at best. Even the originator of the idea, Darwin (1859), commented on the coexistence of closely related species, suggesting a causative process analogous to environmental filtering. Numerous studies have subsequently used genus: species ratios (Elton 1946; Harper *et al.* 1961; Simberloff 1970; Lawton & Strong 1981; Colwell & Winkler 1984; Silvertown *et al.* 2001) and the co-occurrence of species pairs (Losos 1994; Gotelli *et al.* 1997; Tofts & Silvertown 2002; Silvertown *et al.* 2006; Slingsby & Verboom 2006) to examine this hypothesis quantitatively in real communities. In reviewing historical debate on genus: species ratios, Jarvinen (1982) noted the rarity of statistically robust empirical evidence for congeneric species' coexisting less often than more distantly related taxa. More recently, Cahill *et al.*'s (2008) meta-analysis of competition experiments revealed little evidence that more closely related plant species compete more strongly than distantly related taxa (but see Maherali & Klironomos 2007; Jiang *et al.* 2010 for support of the hypothesis from non-plant systems). Further evidence against the competition-relatedness hypothesis comes from recent studies of biological invasions, the subject that motivated Darwin's original hypothesis. For example, Duncan & Williams (2002) and Diez *et al.* (2008) found that exotic species more closely related to the native taxa in a given region are more likely to invade that region successfully.

Despite ample empirical evidence against the competition-relatedness hypothesis, most studies explain this counter evidence as resulting from either a lack of phylogenetic trait conservatism or a weak influence of competition on the assembly of the examined system (recent uses of these interpretations in Cahill *et al.* 2008 and Cavender-Bares *et al.* 2009). While these potential explanations are certainly reasonable, the literature largely ignores the possibility that when competition is an important assembly process, it may differentially exclude distantly related species, even when traits have strong phylogenetic signal. In this article, we explore how Chesson's (2000) framework for how species differences influence coexistence changes our expectations for how relatedness influences competitive exclusion. With this updated view of coexistence, we reinterpret phylogenetic evidence for the impacts of environmental filtering and competitive exclusion on community assembly. We begin this discussion with a brief summary of the relationship between classical niche theory and phylogenetic approaches to community assembly. We then argue against the use of community

phylogenetics for inferring environmental filtering and competitive exclusion. Specifically, we propose that the approach rests on an ecologically outdated expectation about how competitive exclusion influences patterns of relatedness in communities.

MODERN PHYLOGENETIC TOOLS AND COMMUNITY ASSEMBLY THEORY

Phylogenetic tools are increasingly used to study community assembly (Brown *et al.* 2000; Gillespie 2004; Melville *et al.* 2006; Emerson & Gillespie 2008; Cavender-Bares *et al.* 2009; Moen & Wiens 2009; Moen *et al.* 2009; Stephens & Wiens 2009), and the approach and conclusions of many of these studies do not involve the competition-relatedness hypothesis (Brown *et al.* 2000; Gillespie 2004; Melville *et al.* 2006; Moen & Wiens 2009; Moen *et al.* 2009; Stephens & Wiens 2009). Our paper specifically focuses on 'null community' phylogenetic studies (such as Webb 2000; reviewed in Emerson & Gillespie 2008 and Cavender-Bares *et al.* 2009), which aim to separate the effects of competitive exclusion and environmental filtering by assuming the validity of the competition-relatedness hypothesis.

In these 'null community' studies, the relatedness of species in an observed community is compared to the relatedness in randomly assembled null communities compiled from a 'regional species pool' (Webb *et al.* 2002; Cavender-Bares *et al.* 2006; Slingsby & Verboom 2006; Swenson *et al.* 2006; Prinzing *et al.* 2008). Depending on the question, there is variation in how these species pools are constructed (Slingsby & Verboom 2006; Swenson *et al.* 2006), but they usually include all species found within a study landscape or region (Gotelli & Graves 1996; Webb 2000; Cavender-Bares *et al.* 2009). This type of pool is considered a proxy for the set of species within dispersal range of the focal community and has recently been shown to relate to the evolutionary history of lineages in the relevant region (Gerhold *et al.* 2008). Comparison of the patterns of relatedness in the pool and the local community has been used to evaluate competition, environmental filtering, facilitation, and other factors important to community assembly, though we focus here on the 'null community' approach for studying the first two processes (Weiher & Keddy 1995; Webb 2000; Webb *et al.* 2002).

In this approach, and following from the competition-relatedness hypothesis, if co-occurring species are less closely related than expected by chance, competitive exclusion is suggested to play a structuring role (Fig. 1). By contrast, phylogenetic clustering, where species are more closely related than expected, is interpreted as evidence for environmental filtering (Weiher & Keddy 1995; Webb 2000). Though its definition varies, environmental filtering is typically considered the process through which species fail

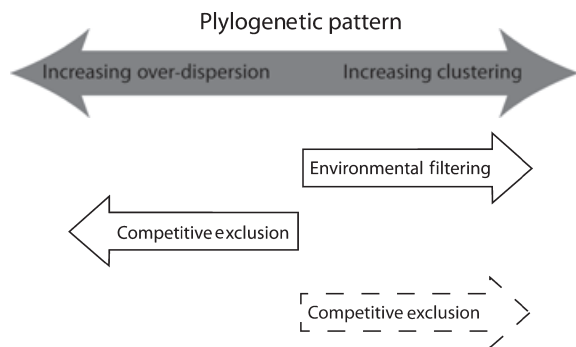


Figure 1 Theoretical ecological processes (assuming that involved traits are sufficiently conserved) influencing the pattern of relatedness between species in a community. Phylogenetic over-dispersion means that species are less related than expected by chance, while clustering means the opposite. The dashed competitive exclusion arrow is the contribution of advances in coexistence theory, coupled with empirical evidence.

to establish in a community due to incompatibility with relevant environmental factors. This process is assumed to drive clustering when relevant traits are sufficiently conserved and closely related taxa share similar environmental tolerances, allowing them to colonize the community (Webb *et al.* 2002; Swenson *et al.* 2006; Donoghue 2008; Emerson & Gillespie 2008; Prinzing *et al.* 2008; Cavender-Bares *et al.* 2009).

Putting the different assembly processes together, if environmental filtering prevents the establishment of species that cannot physiologically tolerate a habitat, it is likely to be the first restriction on species colonizing a community, followed by further restriction via competitive exclusion (and undoubtedly other processes such as facilitation; Webb 2000; Valiente-Banuet & Verdu 2007; Cavender-Bares *et al.* 2009). Because of this, phylogenetic community patterns cannot readily reveal the separate, individual effects of environmental filtering and competitive exclusion. However, because these two processes are expected to have opposing effects on patterns of relatedness in communities (Fig. 1), these methods can, in theory, still reveal the balance of the two processes (Cavender-Bares *et al.* 2009). For example, phylogenetic clustering suggests that environmental filtering is stronger than competitive exclusion in determining community membership (Webb *et al.* 2002; Mayfield *et al.* 2005; Cavender-Bares *et al.* 2009).

The success of this approach rests on several important assumptions being met. Most importantly, for community assembly to affect the phylogenetic structure of a community, the traits involved in the assembly processes must be sufficiently phylogenetically conserved, or have detectable phylogenetic signal (Emerson & Gillespie 2008; Losos 2008a,b; Cavender-Bares *et al.* 2009). This does not mean

that all trait differences between species are positively correlated with phylogenetic distance, but those involved in determining the outcome of competitive exclusion or environmental filtering must be. Still, the traits regulating the various assembly processes may be convergent or have distinct histories and this complicates the interpretation of phylogenetic patterns (Cavender-Bares *et al.* 2004, 2009; Donoghue 2008). As a consequence, ecologists increasingly acknowledge that testing the phylogenetic signal in functional traits is a key step when conducting phylogenetic community assembly analyses (Webb *et al.* 2002; Ackerly 2003; Kraft *et al.* 2007; Cavender-Bares *et al.* 2009 to name a few).

Other assumptions include the requirement that local interactions modulate the phylogenetic structure of communities more than the reverse (Prinzing *et al.* 2008) and that strong negative interactions between species lead to species exclusion rather than character displacement (Silvertown *et al.* 2006). Finally, authors have noted that if neither competitive exclusion nor environmental filtering dominates, or if other assembly processes overwhelm these two, it can be difficult to tease apart their contrasting effects (Mayfield *et al.* 2005; Cavender-Bares *et al.* 2006; Swenson *et al.* 2006; Helmus *et al.* 2007).

The almost certain violation of at least some of these underlying assumptions has raised questions about certain uses of phylogenies to make inferences about the processes involved in community assembly (Silvertown 2004; Losos 2008a). However, no critiques have challenged the fundamental ecological basis for expecting competition to be more intense between more closely related taxa. As a likely consequence, the competition-relatedness hypothesis still underlies numerous phylogeny-based analyses of the roles that competition and environmental factors play in regulating community assembly (Slingsby & Verboom 2006; Swenson *et al.* 2006; Prinzing *et al.* 2008; Cavender-Bares *et al.* 2009).

A MORE COMPLETE VIEW OF COEXISTENCE

Recently, advances in our understanding of coexistence (Chesson 2000; Leibold & McPeck 2006; Adler *et al.* 2007) have revised our expectations about the role that species differences play in influencing the outcomes of competitive interactions. The conclusion of this emerging framework is that coexistence in competitive communities is driven by the interaction of two types of species differences: niche differences and competitive ability differences. Importantly, the latter make coexistence harder to achieve, promoting competitive exclusion. As we will show, this changes the expectations of both the competition-relatedness hypothesis and current phylogenetic approaches to the study of competition's role in community assembly. We note that

both niche and competitive ability differences are manifestations of trait value differences between species, which may or may not have phylogenetic signal. Furthermore, how these traits influence coexistence depends on their interaction with the factors limiting growth in the environment.

The niche is well appreciated to have a variety of definitions (Grinnell 1917; Gause 1934; Elton 1946; Hutchinson 1957), which, in turn, dominate different applications of the concept in ecology. In Chesson's coexistence framework, niche differences include all species trait differences that cause species to limit themselves more than their competitors (causing intraspecific effects to exceed interspecific effects; Chesson 2000). As a simple example, consider a community of two competing plant species, where one best exploits well drained, rocky soil (species A), while the other favours fine clays with greater organic matter content (species B) (for empirical examples, see Pantastico-Caldas & Venable 1993; Gram *et al.* 2004). Also assume that the environment presents an equal fraction of these two soil types. Under these conditions, species differences in their soil texture affinity will segregate the competitors across soil types and cause individuals of species A to limit other individuals of species A more than they limit individuals of species B and *vice versa*. Such differential limitation can also arise from species-specific interactions with resources, specialist consumers, pathogens, mutualists or temporal environmental heterogeneity (Chesson 2000; Chesson & Kuang 2008).

All these niche differences facilitate coexistence by favouring species when they drop to low density and are threatened with extinction (frequency-dependent regulation; Adler *et al.* 2007). Niche differences in Chesson's framework are therefore the key processes stabilizing species coexistence. In line with classical niche theory (which has often been debated), 'limiting similarity' emerges when competitive exclusion limits the coexistence of taxa that are too similar in their traits (MacArthur & Levins 1964, 1967; Abrams 1983; Davies 2006).

In contrast to niche differences, competitive ability differences (termed 'fitness differences' in Chesson's framework) drive competitive exclusion. Examples include differences in species' abilities to draw down common limiting resources (Tilman 1987), differences in susceptibility to predation by generalist consumers (Chesson & Kuang 2008), and variation in the number of viable offspring produced per parent (Franco & Silvertown 2004). A well-studied plant competition example includes species differences in plant height in a light-limited system (Harper 1977; Mitchley & Grubb 1986; Goldberg & Miller 1990). Such differences advantage one species over competitors regardless of commonness or rarity (frequency-independent advantages), and have no influence on the degree to which species limit themselves vs. competitors. Although competi-

itive ability differences have always operated in ecological models of competing species, Chesson (2000) showed how the determinants of coexistence could be explicitly decomposed into niche and competitive ability differences. In the absence of niche differences, the species that is the best competitor, on average, displaces the others.

Chesson's framework for niche and competitive ability differences is most useful when all focal species can tolerate the environment in the absence of neighbours (they are not filtered out by abiotic factors), and that species interactions mediated via shared resources or consumers limit persistence. It is worth noting that taken to an extreme, species with poor enough competitive ability will simply not survive the abiotic environment. Although environmental filtering, not competition eliminates such species, the distinction between these processes in empirical studies can be fuzzy.

While competitive ability differences drive some species to dominance and others to elimination, niche differences favour species when they drop to low densities. The outcome of competition therefore depends on the relative strength of these two types of species differences (Fig. 2). A more technical and extensive explanation of this relationship can be found in Adler *et al.* (2007) and Chesson (2000). In Fig. 2, the coexistence of the two competitors (A and B in the figure) occurs in the region below the 1 : 1 line,

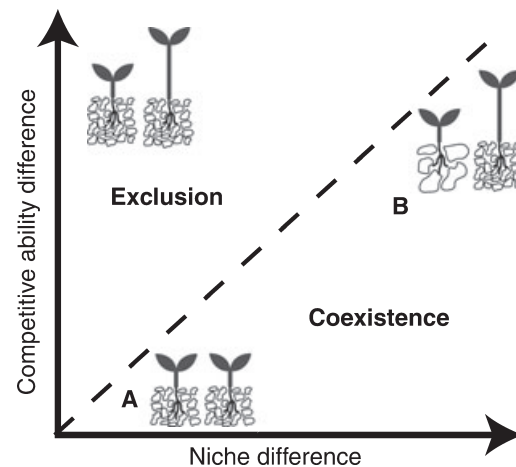


Figure 2 Coexistence occurs when niche differences exceed competitive ability differences among competitors, the region below the dashed 1 : 1 line (the line shows where growth rates when rare are zero). Variation in soil texture preference is presented as a niche difference, while variation in height is presented as a competitive ability difference. Letters A and B indicate different coexistence scenarios. Species can coexist when they are relatively similar when subtle niche differences overcome small competitive ability differences (location A). They can also coexist when they are quite different when large niche differences overcome large competitive ability differences (location B).

where species growth rates when rare are positive. Coexistence can thus arise from subtle niche differences overcoming slight competitive ability differences (Fig. 2, point A) or strong niche differences overcoming large differences in competitive ability (Fig. 2, point B). With competitive ability differences, but no niche differences (communities falling along the y -axis), species cannot coexist. By contrast, with niche differences, but no competitive ability differences (communities falling along the x -axis), species do coexist. When there are no species differences, the community exhibits neutral dynamics (the origin in Fig. 2; Hubbell 2001; Adler *et al.* 2007). The key point is that species differences are involved in both enhancing (niche differences) and limiting (competitive ability differences) coexistence, and this is true regardless of the details of Chesson's formalization of this point (Münkemüller *et al.* 2009). Of course, when processes other than competition limit species in communities, such as facilitation (Valiente-Banuet & Verdu 2007), then it is these processes that will determine the phylogenetic structure of communities.

We use a simple example to illustrate why competitive exclusion might preferentially eliminate more similar or more different taxa depending on the strength of niche and fitness differences. We continue with the same hypothetical system we mentioned above, in which different species favour coarse vs. fine soils – a niche difference in an environment with a range of soil textures (Fig. 3a, ignoring the phylogeny). In this example, competitive exclusion preferentially eliminates taxa that overlap too much in their soil texture preferences, leaving species that are less similar in this trait. Now consider a hypothetical light-limited system where the main difference between species is their height, in this case a competitive ability difference (Fig. 3b, ignoring the phylogeny). In this scenario, competitive

exclusion preferentially eliminates taxa that are too short, leaving their taller competitors and a more narrow range of traits.

Of course, real communities will contain species with both niche and competitive ability differences, with individual traits having different effects depending on the limiting factors in the community (Chesson 2000). But unlike classical niche theory and the competition-relatedness hypothesis, contemporary thinking about the role of competition in community assembly generates no expectation that trait similarity necessarily favours competitive exclusion. Additionally, other processes, including facilitation (Valiente-Banuet & Verdu 2007) and demographic stochasticity (Hubbell 2001), may further modify patterns of relatedness in communities.

IMPLICATIONS FOR PHYLOGENETIC STUDIES OF COMMUNITY ASSEMBLY

An updated view of coexistence, involving both niche and competitive ability differences, predicts that the competition-relatedness hypothesis may hold in some circumstances (Maherali & Klironomos 2007; Jiang *et al.* 2010). But consistent with mounting evidence against this hypothesis, our updated view leads to the central prediction of our paper, that competition (when occurring) will sometimes be more intense and coexistence less likely between ecologically dissimilar, distantly related taxa (Fig. 2). We illustrate this prediction by adding a phylogenetic context to our plant competition example (Fig. 3). If competitive exclusion preferentially eliminates taxa that overlap too greatly in their soil texture preferences, and how different species are in this trait is positively related to phylogenetic distance, competition will drive phylogenetic over-dispersion (Fig. 3a). By contrast, if species differ greatly in height,

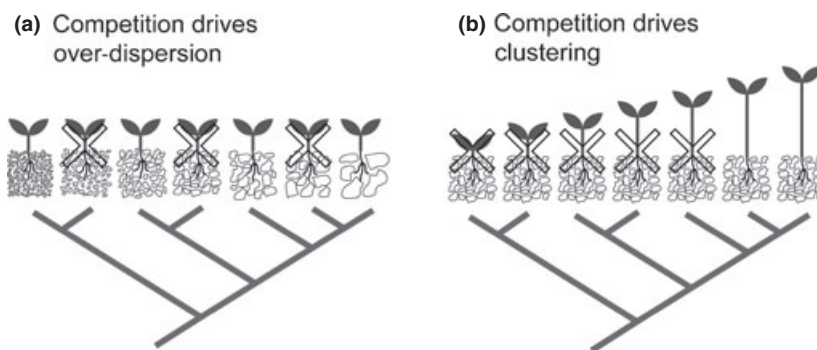


Figure 3 Competitive exclusion can drive either phylogenetic over-dispersion or clustering. (a) Competitors differ primarily in their preference for different soil textures, and this niche difference is phylogenetically conserved in this example. Species overlapping in their preferred soil type will compete most intensely, and competitive exclusion will eliminate species that are too closely related. (b) Competitors differ primarily in their height, a competitive ability difference when light is limiting. Competitive exclusion eliminates all but the tallest competitors. More closely related taxa have more similar heights, and competitive exclusion drives clustering.

and this difference is correlated with phylogenetic distance and determines competitive dominance, competition will drive phylogenetic clustering (Fig. 3b). Of course, one's ability to detect such results depends on having a sufficiently large number of sampled species, strong phylogenetic patterns, and a system in which competition is a dominant assembly factor.

Unlike our simplified example, species in real communities have traits contributing to both niche and competitive ability differences. Thus, depending on their relative strength, competitive exclusion may drive over-dispersion or clustering (solid vs. dashed arrow in Fig. 1). The influence of competitive exclusion on patterns of relatedness also depends on the phylogenetic signal of traits contributing to niche and competitive ability differences (Fig. 4; Cavender-Bares *et al.* 2004). For example, regardless of the importance of niche and competitive ability differences, if neither is related to phylogeny, we expect no phylogenetic pattern to result from competitive exclusion (upper left box of Fig. 4). Conversely, if both niche and competitive ability differences are important, but only the latter are positively correlated with phylogenetic distance, we expect competition to drive clustering (lower left box of Fig. 4). Of course, added complications arise when traits are convergent or co-occurring congeners evolve in response to one another (Cavender-Bares *et al.* 2004, 2009; Emerson & Gillespie 2008). Most generally, Fig. 4 illustrates that even with a more complete view of coexistence, testing the

		Niche differences	
		Unimportant or unrelated to phylogeny	Important and positively correlated with phylogenetic distance
Competitive ability differences	Unimportant or unrelated to phylogeny	Competitive exclusion is random with respect to phylogeny	Competitive exclusion favors overdispersion
	Important and positively correlated with phylogenetic distance	Competitive exclusion favors clustering	Competitive exclusion can favor clustering or overdispersion

Figure 4 The influence of competitive exclusion on the pattern of relatedness among community members depends on both the strength of niche and competitive ability differences and their phylogenetic signal. In the lower right box, competitive exclusion can drive clustering, over-dispersion, or neither, depending on the relative strength of niche and competitive ability differences and the relative strength of their phylogenetic signal.

phylogenetic signal in important ecological traits is key to considering how competition influences patterns of relatedness.

The importance of distinguishing niche and fitness differences in phylogenetic community analyses is exemplified by Cahill *et al.*'s (2008) meta-analysis of how relatedness influences the strength of plant competition. They found that eudicots suffered greater competitive reductions from other eudicots than from monocots, suggestive of conserved niche differences between the groups. However, the authors found that monocots also grew better with other monocots than with eudicots, causing Cahill *et al.* (2008) to conclude that eudicots were simply better competitors than monocots (in the greenhouse settings of their study). In the context of our argument, what was phylogenetically conserved was not a niche difference, but a competitive ability difference. Although the underlying traits were not explored, this finding makes mechanistic sense, because light was generally the limiting resource (Cahill *et al.* 2008), and species differences in light acquisition tend to favour one competitor over the other (Mitchley & Grubb 1986).

The fact that competitive exclusion can drive over-dispersion, clustering or no pattern is consistent with empirical evidence against the competition-relatedness hypothesis (e.g. Jarvinen 1982; Silvertown *et al.* 2001; Cahill *et al.* 2008). However, it complicates efforts to use the relatedness of species within communities to distinguish between environmental filtering and competitive exclusion (Fig. 1 including dashed arrow). Both processes can drive phylogenetic clustering, and thus past evidence for environmental filtering may also reflect the influence of competitive exclusion. Although over-dispersion can still only result from competitive exclusion, such a phylogenetic pattern is not simply a function of strong competition. In contrast to what we described in the introduction, over-dispersion results when competitive exclusion based on limiting similarity (niche differences, as in Fig. 3a) overwhelms the collective influence of environmental filtering and competitive exclusion of poor competitors (Fig. 3b), a more nuanced interpretation.

One solution to these complicating issues might be to broaden the definition of environmental filtering to include competitive exclusion based on competitive ability differences. This may seem appealing because if the excluded species are found elsewhere in the landscape, they could, under this definition, be viewed as competitively inferior under the environmental conditions of the focal site. However, such a revised meaning of environmental filtering lumps together competition and abiotic environmental filters, two processes that the 'null community' phylogenetic approach often aims to separate (but this may be acceptable for some research aims). In sum, even if all evolutionary assumptions for the 'null community' phylogeny approach

are met, modern coexistence theory predicts that competitive exclusion may not leave a consistent signature in phylogenies.

CONCLUSIONS

In this article, we have provided a theoretical framework based on established coexistence theory to provide an ecological explanation for why more distantly related competitors may be less likely to coexist (Harper *et al.* 1961; Losos 1994; Duncan & Williams 2002; Tofts & Silvertown 2002; Davies 2006; Leibold & McPeck 2006; Slingsby & Verboom 2006; Cahill *et al.* 2008; Diez *et al.* 2008). The competition-relatedness hypothesis proves to be a special case within a range of outcomes predicted by coexistence theory (Chesson 2000). We therefore conclude that competitive exclusion should only sometimes eliminate more closely related taxa, a prediction consistent with the mixed empirical evidence in this research area (e.g. Cahill *et al.* 2008).

Coupled with this mixed evidence, the absence of strong theoretical support for the competition-relatedness hypothesis should lead to reinterpretations of past phylogenetic evidence for environmental filtering and competitive exclusion. Still, the more general question of how species differences influence the outcome of competition, independent of phylogeny, remains a fundamental empirical problem, central to debate between niche and neutral theory (Adler *et al.* 2007). Based on the arguments presented here, answering this question will require separating the influence of niche and competitive ability differences, the details of which are explained in several recent papers (Chesson 2000; Leibold & McPeck 2006; Adler *et al.* 2007; Levine & HilleRisLambers 2009).

Quantifying trait values in various systems and identifying those important for niche and competitive ability differences will be an important step forward in the study of competition and its role in community assembly. Results from such trait-based empirical studies may inform the next generation of community assembly questions answerable with phylogenetic approaches. Some of these questions arise from the coexistence perspective we have outlined here. For example, does the likelihood of coexistence via similar competitive abilities rather than niche differences depend on the patterns of relatedness in the species pool? Do niche or competitive ability differences increase more rapidly with phylogenetic distance? Or from a more evolutionary perspective, does adaptive radiation depend on the degree to which coexistence relies on similar competitive ability rather than niche differences? Answering these questions will provide fresh insights into the importance of species differences and relatedness for coexistence.

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