

# REVIEWS

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## Why phylogenies do not always predict ecological differences

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**Abstract.** The merger of phylogenies with ecology has given rise to the field of “community phylogenetics,” predicated on the assumption that ecological differences among species can be estimated from phylogenetic relationships (the phylogenetic distance/ecological difference, or PDED, hypothesis). A number of studies have failed to find strong support for this assumption, thus challenging the utility of phylogenetic approaches. This gap might highlight the fact that the PDED relationship is not useful for community assembly, but it is difficult to know because the lack of a relationship might also be due to a number of biological or methodological reasons, including inappropriate phylogenies, skewed distributions of phylogenetic distances, the lack of consideration of models of trait evolution, or the absence of sufficient niche space in experimental and observational venues. Each of these limitations, separately or combined, may confound recent experimental or observational results that examine relationships between phylogenetic distance and ecological differences. Notably, common evolutionary models can support alternative conclusions about the relationship between evolutionary distances and ecological differences than typically assumed and can change interpretations of community-based phylogenetic analyses. Here we review a number of issues that may lead to confounded effects in community phylogenetic analyses. In light of these potential pitfalls, we provide a number of guidelines for researchers to follow and stress that they need to address methodological shortcomings before concluding that ecological differences are unrelated to phylogenetic distances.

**Key words:** biodiversity; Brownian motion model; coexistence; competition; ecophylogenetics; evolution; experiments; niche differences.

### INTRODUCTION

Explaining the rules by which species assemble into communities has a long and somewhat acrimonious history in ecology (e.g., Hutchinson’s size ratios [Hutchinson 1959], Diamond’s assembly rules and the null model wars [see Gotelli and Graves 1996]), yet it is one of the most active fields of ecological research today. The theory of limiting similarity (Gause 1934, Hardin 1960) dictates that no two species can coexist indefinitely when competing for the same limiting resource. There has thus been a

search for patterns of species differences that link to ecological differences or separation in niche space and the ability to coexist (HilleRisLambers et al. 2012, Kraft et al. 2015b). Recently, the quest to understand and predict coexistence has been reinvigorated by a new appreciation of the importance of niche and fitness differences for coexistence and competitive exclusion (Chesson 2000, Adler et al. 2007, HilleRisLambers et al. 2012).

Extrapolating from his theory on descent with modification, Charles Darwin inferred that competition should be more intense between close relatives: “as species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them.” Evolutionary theory thus suggests

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that we might be able to infer the strength of competition by simply measuring the phylogenetic distances (or some function of these distances) between co-occurring species. This basic premise has given rise to the field of community phylogenetics (Webb 2000, Webb et al. 2002, Cavender-Bares et al. 2004), and over the past two decades, ecologists have increasingly used phylogenetic relationships as a proxy for ecological differences among species (Cavender-Bares et al. 2009, Burns and Strauss 2011, Mouquet et al. 2012, Srivastava et al. 2012, Verdu et al. 2012, Cadotte et al. 2013) to evaluate how the evolution of fitness and niche differences allow for coexistence (Narwani et al. 2013, Godoy et al. 2014, Germain et al. 2016). With advances in gene sequencing and availability of phylogenetic data, incorporating phylogenetic information in the interpretation of ecological patterns is now becoming standard.

The origin of ecological differences rests upon a simple assertion: that species evolve. The assembly of ecological communities and the coexistence of, for example, ecologically different species then reflects the selection of evolutionarily divergent species from a larger species pool to coexist (Connell 1980, Vellend 2010). However, species divergence can result from one of two major biogeographical processes. First, this divergence might be the product of past or ongoing selection pressures driven by the fact that closely related species have been in sympatry, and current species coexistence and responses to abiotic conditions might thus reflect this selection history (e.g., Grant 1972, Schluter et al. 1985, Clarke et al. 2015, Nuismer and Harmon 2015). The alternative is that trait differences arise in allopatry (adaptive or not) or via neutral processes, and a certain amount of time is required for sufficient ecological differences to emerge before species can coexist (Davies et al. 2007, Anacker and Strauss 2014). Regardless of the actual mechanisms by which local species differences are produced, the basic point is that they reflect evolved differences, and it is thus reasonable to hypothesize that the phylogenetic distances separating species should have some relationship to their ecological differences and associated patterns of coexistence, though perhaps not always in the ways that ecologists have assumed. In many studies the articulated hypothesis is most often that there should be a (generally) monotonic relationship between phylogenetic distances and ecological differences (Gerhold et al. 2015), but the relationship between the two can take many forms, depending on how ecological differences have actually evolved (i.e., the evolutionary models underlying the evolution of traits implicated in ecological differences).

There is now an accumulation of evidence from observational studies showing phylogenetically non-random communities and species co-occurrence patterns (Slingsby and Verboom 2006, Davies et al. 2007, Helmus et al. 2010, e.g., Cardillo 2012, Andújar et al. 2015, Li et al. 2015a). There are relatively fewer studies, however, that report weak or random phylogenetic community patterns (Cahill et al. 2008, CaraDonna and Inouye 2015), likely

suggesting either a publication bias toward positive results or a biologically interesting reality: that evolutionary history matters. In explaining such nonrandom patterns, researchers have often looked to the environment or competition for causation (but see Gerhold et al. [2015] for a thoughtful discussion about the problems with viewing these two mechanisms as mutually exclusive). For example, in a study of the seedling mortality in a pristine rainforest in French Guiana, Paine et al. (2012) show that mortality is negatively related to seedling height, but that the reduction in mortality with increased height is less for seedlings near close relatives than for those near distant relatives. Similarly, Li et al. 2015b show that germination appeared to benefit from the presence of close relatives, but individuals suffered more intense competition from these same relatives as they grew larger. At a larger scale, Davies et al. (2007) examined carnivore geographic overlap among sister species and found greater range overlap among more distantly related species, which was explained by their greater difference in carnassial tooth length, an indicator of preferred prey size. In these examples, increased competition between close relatives translates into nonrandom occurrence patterns, where we should see a higher probability of distantly related species, or those with greater trait differences, co-occurring together (Cavender-Bares and Wilczek 2003). Such interpretations assume that competitive ability is independent from environment (but see Cadotte and Tucker 2017), or that the environment over which species compete is relatively homogeneous, which might not always be the case.

The fundamental link among these types of studies is the relationship between evolutionary distance and ecological similarity (i.e., the mapping of evolutionary history to niche differences). Researchers often assume that niche differences are reflected in patterns of relatedness and that the strength of competition is a product of the degree of niche overlap. Yet competition and coexistence are influenced by both niche overlap and the relative fitness differences among species, and evolution might shape both of these, making the link between phylogeny and competition/coexistence more complex (Godoy et al. 2014). In their seminal 2002 paper, Webb et al. (2002) recognized these limitations; however more recent critiques have challenged both the linkages between phylogeny and ecological similarity (Narwani et al. 2013), and between ecological similarity and competition (Gerhold et al. 2015). Perhaps more fundamental, however, is the fact that the relationship between trait evolution, environmental filtering, and species interactions is inherently complex (Cavender-Bares et al. 2004), but this complexity is ignored in most studies (e.g., disregarding of models of evolution that result in non-linear scaling between phylogenies and niche differences).

Despite the substantial number of studies revealing phylogenetically nonrandom community patterns (Vamosi et al. 2009), there are many untested assumptions that can limit (1) the interpretability of the relationship between phylogenetic distance and ecological

differences (hereon referred to as the PDED hypothesis), (2) the power to detect such a relationship, and (3) the ability to distinguish among alternative mechanisms generating community patterns (Mayfield and Levine 2010, Gerhold et al. 2015). To move from post hoc conjecture about the links between pattern and process inferred from observational studies to robust hypotheses testing how phylogenetic relationships influence community assembly, experiments provide perhaps the most robust approach (Gravel et al. 2012, Mouquet et al. 2012, Godoy et al. 2014, Kraft et al. 2015a).

The relationship between phylogenetic distance and intensity of competition has been evaluated experimentally. Interestingly, small scale experiments using plants have often failed to show an effect of phylogenetic distances on the strength of competition, as measured by individual growth and size (Dostal 2011, Bennett et al. 2013). It is important to recognize, however, that coexistence and competition are not opposite sides of the same coin. In other words, species that do not compete for the same resources are highly likely to be able to coexist (assuming other dimensions of their niche requirements are similar), but at the same time, species that have high niche overlap and compete intensively can also coexist if fitness differences are small enough (Adler et al. 2007). We might also predict that competition and coexistence might be more strongly associated with phylogenetic distances if species have evolved allopatrically and their differences follow simple models that describe trait divergence (Cadotte and Jin 2014, Germain et al. 2016). Whereas for sympatric species, competition might be unrelated to phylogenetic distances simply because species occurring together have evolved the necessary differences to coexist, even if they are closely related (Davies et al. 2007, Staples et al. 2016).

Several controlled multigenerational experiments that assess species coexistence and that vary the relatedness of co-occurring species have been published recently (Violle et al. 2011, Narwani et al. 2013, Godoy et al. 2014) and some of these have also cast doubt on the PDED hypothesis. This, coupled with criticisms of some of the basic theoretical assumptions of the PDED hypothesis (Mayfield and Levine 2010, Gerhold et al. 2015), has led to a debate on the generality of PDED relationships and thus questioned the usefulness of phylogenetic structure for informing our understanding of species interactions. In many ways, this debate parallels that on the integration of phylogenetic methods in ecology from the mid 1990s (Harvey et al. 1995, Westoby et al. 1995). There are two broad explanations for why studies often fail to support a PDED relationship: the theoretical expectations might be wrong or experimental tests might be insufficient. Here we review seven reasons (divided between these two broad explanations) why studies may fail to support a PDED relationship, and show that investigators need to carefully consider each of these alternatives before drawing conclusions from PDED analyses. First we briefly review the three

biological reasons for why we may not always observe a PDED relationship at all and then follow this with four potential methodological shortcomings. Although some of the points presented here have been raised previously, given literature trends (i.e., increase in simplistic community phylogenetic studies), it is apparent that many ecologists are not taking these issues into account. We hope that by systematically reviewing and providing a summary of these issues we can (1) increase our ability to provide in-depth interpretations about negative results when linking phylogenies to ecological patterns and (2) improve on methodological (including experimental setups and analytics) weaknesses of previous analyses.

#### A BRIEF INTRODUCTION TO EVOLUTIONARY MODELS IN COMMUNITY PHYLOGENETIC CONTEXT

Underlying the PDED relationship is the model describing the evolution of functional traits and how they lead to species differences. Models of trait evolution are often overlooked in most ecophylogenetic studies (but see Letten and Cornwell 2014). Before discussing PDED relationships, we thus need to understand the expectations under these models. Perhaps the simplest (in terms of fewest parameters) and most commonly assumed evolutionary model describing change in traits over time is Brownian motion (BM; Felsenstein 1985). In Brownian motion models, trait change occurs as a random walk over time from some initial trait value  $X$ , with the temporal deviation sampled from a normal distribution (Felsenstein 1985, Harvey and Pagel 1991). The change in  $X$  through a given period of time  $t$  is

$$dX(t) = \sigma dB(t) \quad (1)$$

where,  $dB(t)$  represents a random change in time  $t$  that is normally distributed  $N(X, t)$  and  $\sigma$  scales the magnitude of fluctuations. For multiple lineages, total trait variation depends on the length of time ( $t$ ) that the process operates, such that greater  $t$  results in greater trait dispersion (Fig. 1). With BM evolution, it is important to note that the expected mean trait value of a clade stays constant across a large number of independently evolving species,  $\bar{X}_{t-1} = \bar{X}_{t-2}$  (Fig. 1) and if two lineages start with identical trait values,  $\bar{X}_{1t-0} = \bar{X}_{2t-0}$ , then  $\bar{X}_{1t} = \bar{X}_{2t}$  even if  $\sigma_1 \neq \sigma_2$ .

BM evolution assumes that species drift over evolutionary time and/or selection coefficients fluctuate randomly, and there are plenty of cases where this is not likely to be true. Strong directional selection (e.g., rising temperatures), divergent evolution (e.g., competitively reinforced character displacement), and strong stabilizing selection all violate the assumption of BM. Further, any single trait could show evolutionary patterns that do not conform to BM expectations, even if evolving under a BM process. However, if analyses include large numbers of species and combine multiple traits, which have been subject to different selection regimes, then the

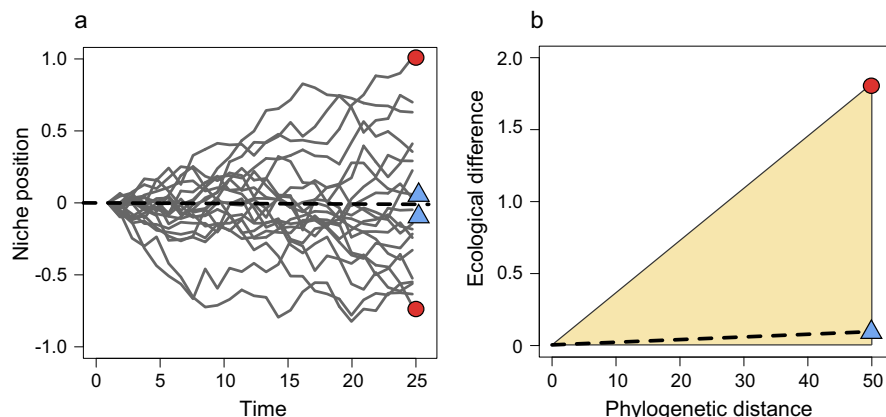


FIG. 1. (a) Brownian motion evolution models trait change as a random walk over time, with traits evolving independently from one another. (b) This random walk process generates species differences for a single trait that increase in variance (large triangle) with time and exhibiting only a weak relationship between the mean (dashed line) and evolutionary time (or phylogenetic distance). Blue triangles represent species that remain ecologically similar, and red circles represent species that diverge ecologically over evolution.

pattern of evolution is likely to be indistinguishable from BM (Cooper and Purvis 2010), but we lose information on the evolutionary processes structuring individual traits, which could bias the detection of patterns, a point to which we return later.

However, if coexistence is structured on a single trait, for example, body size or tooth size (e.g., Davies et al. 2007), then the evolutionary trajectory of that particular trait is rather important because it is unlikely that the evolved trait differences will scale well with phylogenetic distances (Peres-Neto et al. 2012; see below). It is now relatively straightforward to compare between alternative models of trait evolution, for example, using Akaike information and other types of criteria (Butler and King 2004, O'Meara et al. 2006, Boettiger et al. 2011, Beaulieu et al. 2012). One common alternative model to BM is the Ornstein-Uhlenbeck (OU) model (Hansen 1997, Butler and King 2004), which approximates stabilizing selection toward an optimum value. The OU model is the same as the BM model, but with an added term, shown in Eq. 2

$$dX(t) = \alpha(\theta - X(t)) + \sigma dB(t) \quad (2)$$

where  $\alpha$  is the strength of selection driving the trait to the optimal trait value  $\theta$  (Butler and King 2004).

More complex models are possible, for example, allowing for multiple optima, rate variation, and differences in the strength of stabilizing selection (Beaulieu et al. 2012). It is worth noting, however, that there have been a paucity of models that explicitly incorporate species interactions, including competition, although recent work is attempting to fill this gap (Clarke et al. 2015, Nuismer and Harmon 2015). Importantly, once the correct model (or an approximation of it) has been identified, it is then possible to rescale the branch lengths of the phylogeny such that expectations of trait differences can be scaled according to expected evolutionary model

underlying trait evolution (Pagel 1999). However, it is not yet clear whether a similar transformation can be employed for models of competitive character displacement. Moreover, it is likely that more than one but perhaps not a very large number of traits influence species ecological differences (Díaz et al. 2015) and it is not clear either how one single re-scaling of phylogeny would be able to accommodate other traits evolving under different models of evolution (or differences in their parameters; e.g., selection strength). Finally, these models underlie average expected differences and even traits that are negatively correlated can in principle evolve under the same model, though leading to different interpretations about their roles in determining ecological differences.

The reason for introducing evolutionary models is to make clear the need to think carefully about how traits and niches correlate with phylogenetic distances and make their associations more accurate so that phylogenies serve as better proxies of ecological differences. Translating a phylogeny into expected ecological differences is not a straightforward exercise, and evolutionary models provide a powerful opportunity to develop alternative hypotheses about PDED relationships.

While generating expectations from evolutionary models is obviously advantageous, the evolution of traits might be even more complex than current models allow, thus biasing interpretation of phylogenetic patterns within communities in ways that might result in the incorrect inference of assembly mechanisms (Cavender-Bares et al. 2004, Mayfield and Levine 2010, Gerhold et al. 2015). For example, conserved traits are often evoked for concluding that phylogenetically clustered communities result from environmental filtering. However, conserved traits may also give a clade of species a competitive advantage and result in clustering because they exclude more distantly related species (Mayfield and Levine 2010). Further complicating interpretations,



phylogenetic overdispersion can result from environmental filtering acting on convergent traits, where distantly related species are most similar, though, again, in order for species to coexist, they likely differ along other trait axes (Cavender-Bares et al. 2004).

### *Intraspecific variation*

Phylogenetic analyses of coexistence typically assume species are fixed entities, and there is little consideration of how trait variation within species might respond to local environmental conditions or indeed competition from other species (Bolnick et al. 2011, Albert et al. 2012, Burns and Strauss 2012). However, a significant proportion of the trait differences between plant communities are explained by intraspecific variation, although interspecific differences tend to be greater (Siefert et al. 2015). Individuals routinely show different phenotypes in response to genetic differences, environmental conditions, and the genotype  $\times$  environment interaction; these differences have implications for competition and other types of interactions (Miner et al. 2005, Bolnick et al. 2011, Burns and Strauss 2012). For example, it has been suggested that flowering plants partition the temporal niche by shifting flowering phenology to reduce competition (Parrish and Bazzaz 1979), though phenological differences are also necessary for reproductive isolation and may be intimately related to speciation. However, while species phenological responses to environmental cues and mean flowering phenology have significant phylogenetic patterning, day of year of flowering is largely environmentally determined (Davies et al. 2013, Li et al. 2016). Thus species tend to show large inter-annual and spatial variation in flowering phenology. As such, phylogenetic structure can be uninformative as to how species partition the temporal niche space and access to resources across the growing season (but see Li et al. 2016), especially in cases where intra-specific differences across populations overlap to a large degree with inter-specific differences (Violle et al. 2012, Dwyer et al. 2014).

Intraspecific variability (due to plasticity or genetic variation), therefore, has the potential to overshadow average trait differences between species, and thus any phylogenetic signal in their interactions, though this may not be the case for all taxa (e.g., plants vs. vertebrates). With sufficient niche variation, ecologically similar or closely related species can coexist because divergent phenotypes are selected locally, reducing niche overlap (e.g., Violle et al. 2012; Fig. 2), or because with highly multi-dimensional niche axes, individual variation can allow species coexistence especially if individuals vary along different axes (Clark et al. 2010). Burns and Strauss (2012) found that responses to competition were strongest when competitors were closely related and they surmised that such variability (in their case, likely plasticity) increases the coexistence of closely related species, resulting in a weakening of the relationship between phylogenetic diversity and competitive exclusion.

Intraspecific trait variation and phenotypic plasticity can thus facilitate co-existence of otherwise very competitive species (Bolnick et al. 2011, Violle et al. 2012), which could explain why some studies fail to find evidence of competitive exclusion (Gerhold et al. 2015). Given this, researchers should determine if the major trait axes that influence the strength of competition are plastic and if coexistence is influenced (facilitated or not) by this plasticity, before assuming any straightforward relationship between phylogenetic distance and ecological difference.

### *Tempo of evolution*

Under the commonly assumed Brownian motion model of evolution, phylogenetic signal (the expected covariation between trait differences and phylogenetic distances) is independent from the rate of evolution (the speed with which traits change over time; Revell et al. 2008), but the magnitude of species differences can still be influenced by evolutionary rates, thus influencing their ecological niche overlap and ability to coexist.

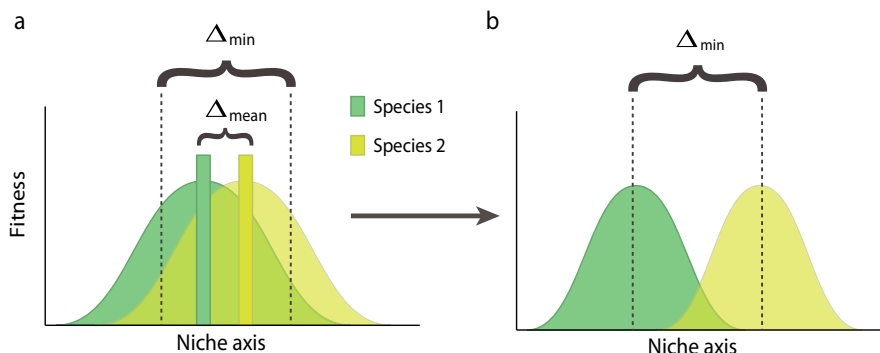


FIG. 2. (a) Niche breadths for two ecologically similar species. If species' mean niche positions are known or estimated ( $\Delta_{\text{mean}}$ ), species may not be predicted to coexist since this distance is less than the minimum required for coexistence ( $\Delta_{\text{min}}$ ). (b) However, each species obtains higher fitness beyond the bounds of  $\Delta_{\text{min}}$ , and thus divergent phenotypes are selected, reducing niche overlap, and increasing coexistence within local communities.

Further, under alternative models of evolution, such as evolution with constraints, fluctuating selection or where traits evolve with a central tendency (e.g., as represented by an Ornstein-Uhlenbeck process discussed earlier), the relationship between trait divergence and phylogenetic distance can also become obscured when evolutionary rates are rapid (Revell et al. 2008). For example, the observation that phylogenetic signal tends to decrease with clade age (Ackerly 2009) is consistent with a model of niche filling (i.e., bounded evolution). Under a model of niche filling, the evolution of the traits influencing species' ecological differences might deviate sufficiently to reduce phylogenetic signal, and so phylogenetic relationships will appear to offer little insight into species' differences and coexistence. In general, we might expect phylogeny to be less informative of niche differences when traits evolve under an OU process and evolutionary rates are rapid; however, even slow rates under an OU process might mask the PDED relationship if taxa have had a long time to diverge.

There are various reasons why some lineages (and traits) might have different rates of evolution, such as the geography of speciation or adaption to new environments during evolutionary times (e.g., Martínez-Cabrera and Peres-Neto 2013). Ecologically similar species that have evolved in allopatry might be expected to accumulate ecological differences slowly through random drift. However, sympatric species may have rapidly diverged so that even closely related species differ substantially

(Schluter 1994, Coyne and Orr 2004, Clarke et al. 2015, Nuismer and Harmon 2015). Thus, in aggregate, the relationship between phylogenetic distance and ecological difference becomes non-monotonic and non-stationary, with different clades having different correlations. Nonetheless, we might still detect a significant PDED relationship even with in an adaptive radiation because incipient species not only interact with their close relatives, but also with other species in the assemblage (Futuyma 2010). Interacting species may thus exhibit concomitant niche shifts as new species fit into niche space (Clarke et al. 2015, Nuismer and Harmon 2015) and more distantly related species are pushed further away in niche space (Fig. 3).

Ecologists might be inclined to conclude that non-significant PDED relationships are the result of rapid evolution, but more analyses are required to support this. As discussed above, the influence of evolutionary rates on niche or trait differences depends on the evolutionary model. In our review of the literature, we have not found any papers that conclusively link rates of evolution to current community phylogenetics patterns.

In the cases discussed above, evolution has generated species differences, but the ways in which ecologists currently examine ecophylogenetic patterns might limit insights within some contexts. For example, one common and potentially problematic assumption is that ecological differences across species accumulated at similar

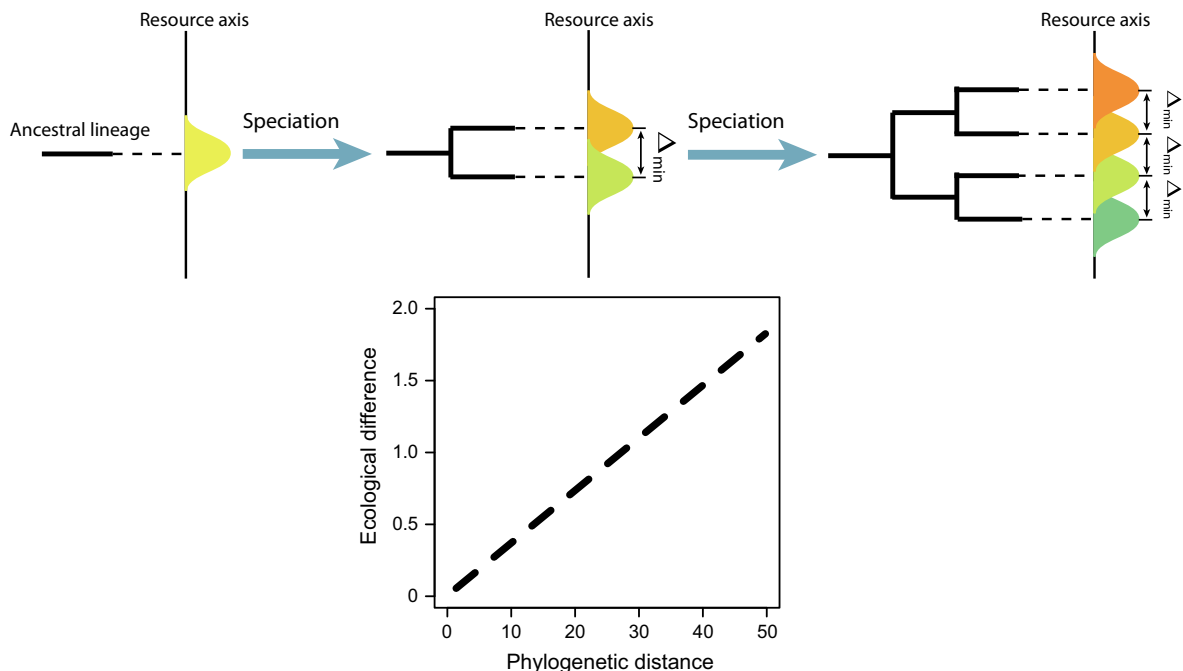


FIG. 3. A schematic representation of the speciation-niche partitioning model. Every successful speciation event results in species adjusting their relative niche optima to some minimum distance to ensure coexistence ( $\rho$ ). The result is that close relatives are more similar than distantly related species and that the phylogenetic distance/ecological difference (PDED) relationship is a linear one (Nuismer and Harmon 2015).

evolutionary rates. As the phylogenetic coverage of species trait differences increase in breadth, this assumption is not likely to hold (Revell et al. 2012) because, as we have shown, different process might drive evolutionary divergence in different clades or places. One potential solution here is to develop methods that change phylogenetic distances in a non-homogenous way across the phylogeny to account for potential non-stationary evolutionary rates while estimating ecophylogenetic links (see *A brief introduction to evolutionary models*). The latter would be akin to estimating the rate of evolution of traits underlying ecological interactions on the tree but without actually having these traits at hand (see Peres-Neto et al. 2012).

*Competition and niche differences are  
only part of the story*

Ecophylogenetic analyses have been heavily influenced by two opposing hypotheses: that coexistence patterns are driven by competitive interactions *or* environmental filtering. This duality is over-simplistic, and the real mechanisms driving community patterns are much more complex, particularly when community assembly is the result of multiple processes occurring at different spatial scales (Cavender-Bares et al. 2004), including neutral processes, predator–prey interactions, or non-equilibrium dynamics. It is well understood that these hypotheses are not mutually exclusive (Gerhold et al. 2015, Kraft et al. 2015a, Cadotte and Tucker 2017) and that both mechanisms can result in similar community patterns (Mayfield and Levine 2010) or shift with the spatial and taxonomic scale of analyses (Cavender-Bares et al. 2006, Swenson et al. 2006, 2007). For instance, imagine a set of species that appear together across a large number of local communities and which are phylogenetically overdispersed relative to some regional species pool (see *Inappropriate species pool*). For instance, consider a set of species that are overdispersed according to one particular trait (or sets of traits) but that they always appear together in local communities; it is likely then that another trait (or set) will be important in explaining why they always appear together, which is in line with environmental filtering (i.e., trait underdispersion) (Cavender-Bares et al. 2004). In this case, the relevant question is not whether they appear over or underdispersed, but which traits are associated to which patterns, and use this to help identify the various processes shaping community composition. Indeed, one particular issue that has not been well studied is whether underdispersed vs. overdispersed communities tend to have greater or lower beta-diversity (i.e., differences in species composition). We would expect regions with large species pools and dominated by underdispersed communities to have higher beta-diversity given that there is likely high turnover in species composition among sites (Grman and Brudvig 2014). For overdispersed communities with lower beta-diversity, it is likely that some other traits could explain why certain

species repeatedly co-occur across local communities (again, consistent with the environmental filtering hypothesis). Note, however, that phylogenetic approaches alone will be limited in their ability to disentangle such complex patterns, and it is thus important to search for the relevant traits, particularly in cases where the phylogenetic relationships with these traits are weak and they are negatively correlated (thus explaining both over and underdispersion patterns, e.g., Bässler et al. 2014). Further, species interactions other than direct competition, such as pathogen spread among close relatives (Liu et al. 2012), can also produce phylogenetic overdispersion, and experiments testing for competition might not be able to recover the phylogenetically correlated mechanism.

Since competition is likely one of a number of processes structuring local communities, and because different processes can give rise to similar community structures, inferring interspecific competition from community structure alone may be misleading, and the importance of competition as the force determining community patterns should be tested and not assumed (Chave 2004, Gerhold et al. 2015). In some cases, competition could be the dominant mechanism, in others it may be partially responsible for some patterns (as in the hypothetical example), and in others still, such as in very dynamic or non-equilibrium systems, it may not be important at all. As results from empirical and experimental studies accumulate, we will be able to generate a set of comparisons across taxa and environmental types to understand when and how phylogenetic relationships are informative of competitive interactions.

*Inappropriate species pool*

The species pool used in community phylogenetic analyses can greatly influence the likelihood of detecting nonrandom phylogenetic patterns in ecological communities (Cadotte and Davies 2016). The number of species, taxonomic resolution, and the evolutionary depth of the species pool are all well understood to influence the statistical power of tests (Cavender-Bares et al. 2006, Kraft et al. 2007, Lessard et al. 2012). When calculating mean distances or random expectations, the topology of the species pool phylogeny can also greatly bias the detection of nonrandom patterns, for example by including a small number of distantly related species (Cadotte 2014).

Using an inappropriate taxonomic scale or evolutionary depth for the pool phylogeny can alter the nature of the pattern detected (Cavender-Bares et al. 2006), and taxonomic scale needs to be thought about carefully. For example, should we include ferns and gymnosperms in the analysis of phylogenetic patterns of plant communities that are dominated by angiosperms? Is it legitimate to include monotremes or marsupials when analyzing mammal communities if placental mammals dominate them? There is no easy answer to these types of questions.

The reason why it is so difficult to answer these questions is because our consideration needs to move beyond

just the biasing of mean or null estimations, but goes to the heart of our assumptions about the PDED relationship. We might expect that traits or ED correspond to species relatedness in the species pool, but this expectation might be problematic for three reasons. First, if our pool is too small (e.g., <25 species), we have difficulty detecting a phylogenetic signal (Blomberg et al. 2003) because of the lack of statistical power. The second issue is that the evolutionary depth or taxonomic scale might be too large to reasonably correspond to trait or niche differences. While it might seem reasonable to make the assumption that PD correlates with ED among closely related species (say within a single family), we should be skeptical when extrapolating to distantly related species. Given enough evolutionary time, lineages can diverge, converge, and change trait states multiple times. Thus, very distantly related species might be ecologically different, but they could also demonstrate convergences, for example, the thylacine of Australia and coyote of North America, which may be more or less likely depending on the particular model under which traits evolved (see also following sections).

One final reason for why the species pool might introduce problems for understanding the PDED relationship is that the size of the pool often co-varies with spatial scale. If we are studying meadow plants across a large landscape, we are confronted with the problem of how to construct the regional species pool. Do we include all plant species that occur in the landscape, or only those we observe in our meadows? If we include all species we would undoubtedly include species occurring in other habitat types within our landscape, especially forest and wetland species. These species will have very different life history attributes and come from different evolutionary clades, and would thus fundamentally change our interpretation of observed patterns and the strength of the phylogenetic signal in niche differences or traits. Our meadow communities would appear phylogenetically clustered and the product of conserved traits. If we build our pool from species only found in meadows, then we would likely change our estimation of the phylogenetic signal and the relative relatedness of species in our meadows. In essence we have pre-filtered on a set of conserved traits by limiting the species pool, potentially biasing our analyses toward overdispersion.

The fix for the first issue (the pool is too small for robust statistical analyses) seems obvious: increase our spatial or taxonomic scale so that more species are included. However, doing this increases the likelihood that our second and third issues (evolutionary depth and spatial scale too large) become significant problems (if we indeed perceive these as problems). One way forward would be to start with the largest, most taxonomically expansive, species pool and then repeat analyses with nested pool subsets. If patterns of statistical significance changes, then we can link patterns to particular scales, potentially making it easier to infer process. Similar approaches have been taken by building species pools

using ecological and evolutionary constraints to understand patterns of species co-existence (Peres-Neto et al. 2001, Lessard et al. 2016).

### *Lacking evolutionary models and identifying the number of relevant traits*

A critical step in testing the PDED hypothesis is translating the phylogeny into expected niche differences (Letten and Cornwell 2014). In *Tempo of evolution* above, we argued that non-significant results could be explained by the fact that lineages might have evolved at different rates. However, non-significant PDED relationships might also result from the fact that the stated PDED hypothesis was not compared to expectations from the correct evolutionary models or that the number of underlying traits are too small to be well represented by the phylogeny even if the correct model is identified. The commonly articulated expectation (and occasionally tested hypothesis) is that there is a positive (usually monotonic) relationship between ecological differences and phylogenetic distances (Fig. 4). Studies that assume this expectation (e.g., Cadotte et al. 2008, Kelly et al. 2014), implicitly adopt the notion that greater evolutionary distances necessarily indicate that species have accumulated more ecological differences. This expectation follows naturally from Darwin's original hypothesis, that competition should be more intense among close relatives, however, it assumes a very particular evolutionary model, where traits continue to diverge linearly over time and convergence is rare (e.g., Fig. 3). This type of model is actually not commonly seen in comparative phylogenetic comparative datasets, which more often assume a Brownian motion process (Kelly et al. 2014), though a wide range of alternative models are available (see *A brief introduction to evolutionary models*). Yet, despite extensive discussion in the comparative methods literature on models underlying trait evolution (O'Meara 2012), they are only rarely considered within studies examining species coexistence (Peres-Neto et al. 2012, Letten and Cornwell 2014).

Several papers have called for ecophylogenetic analyses to consider more explicitly models of evolution in their analyses (Mouquet et al. 2012, Peres-Neto et al. 2012, Srivastava et al. 2012, Letten and Cornwell 2014). If we assume that a trait relating species' ecological position in niche space evolves under Brownian motion evolution, we would expect the mean niche position across all tips to remain unchanged from the ancestral value for a clade, but the average difference between species to increase with time (Fig. 1). However, as we have discussed, even after ample time for evolutionary change, some species remain very similar, while some species appear quite divergent from one another. Therefore, we also expect increasing variance in the pairwise differences in species' trait values through time (Felsenstein 1985) as some lineages drift apart (diverge) while others drift together (converge), resulting in a triangular PDED relationship (Fig. 1). Thus when considering just a few traits, the



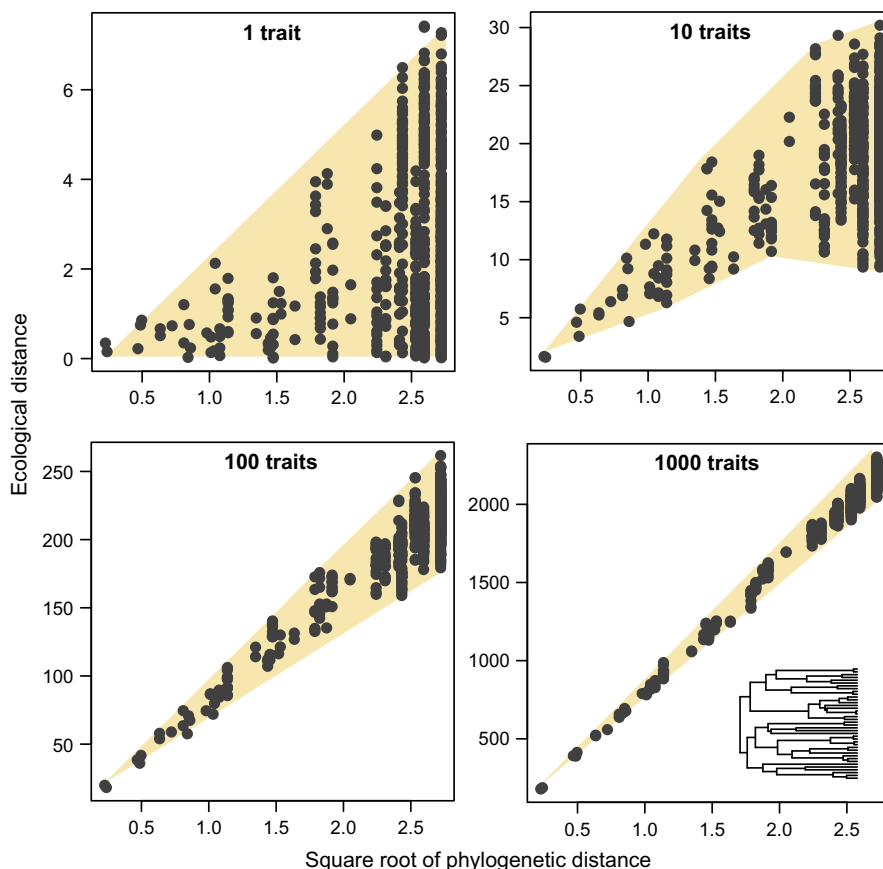


FIG. 4. A simple Brownian motion model of trait evolution for 20 independently evolving lineages showing final species niche position for 1, 10, 100, and 1,000 independently evolving traits. By taking the pairwise difference between any two species' niche values,  $\eta_i$ , as a measure of ecological difference ( $ED_{ij} = |\eta_i - \eta_j|$ ), the relationship between ED and phylogenetic distance is triangular when  $\eta$  is influenced by few traits, and close to linear, with the square root of the divergence time, when many traits are involved.

PDED relationship is expected to be relatively weak but the overall variance in trait values should increase through time. Conversely, if a large number of traits influence niche differences, and are modeled independently, then the expected PDED relationship converges on a linear form (or linear with the square root of the phylogenetic distance under Brownian motion [Letten and Cornwell 2014]; Fig. 4). The main issue here is that if only a few key traits mediate species coexistence, then phylogenetic distances will likely not be a robust measure of their ecological differences, at least under many commonly used quantitative frameworks in community phylogenetics (Ives and Helmus 2011; for robust approaches when only a few traits are involved, see Peres-Neto et al. [2012]). In this case, we may assume the correct model of evolution but, depending on the number of traits involved, we may not be able to detect ecophylogenetic relationships simply because the underlying traits are not strongly correlated with the phylogeny (Fig. 4).

If the strength of competition were determined by a few key traits that approximate a BM model of evolution, then we would expect co-occurrence patterns to follow the triangular data envelope shown in Figs. 1 and 4 rather

than a linear correlation frequently assumed in the literature. Such triangular relationships are indeed commonly reported in observational studies. Cavender-Bares et al. (2004) plotted the relationship between co-occurrence and relatedness of oaks in Florida and their results are analogous to that shown in the first panel in Fig. 4. In an examination of co-occurrence patterns within a subclade of Schoenoid sedges (Cyperaceae) in South Africa, Slingsby and Verboom (2006) discuss the absence of data in the upper left (similar to that shown in the first panel of Fig. 4), and use a quantile regression, to show a positive relationship for upper quantiles. A similar approach was adopted by Cardillo (2012) in an analysis of species co-occurrence in southwestern Australian shrublands. Quantile regression can detect changes in data boundaries, and is thus a useful approach for analyzing triangular data, but it ignores underlying models that might provide mechanistic underpinnings, and alternative statistical approaches, such as those that model mean and variance simultaneously (e.g., Aitken 1987), will be more powerful.

We thus suggest that the observed strength of the PDED relationship in many instances might say more about the number of traits that determine species niche

relationships or our ability to correctly characterize the model of evolution in which these traits evolved than whether or not phylogeny provides a good proxy for species differences. More powerful than simply correlating ecological differences to phylogenetic distances could be to link trait simulations to phylogenetic evolutionary models and quantifying the relationship between these traits (not the phylogeny itself) on ecophylogenetic patterns (Peres-Neto et al. 2012). Thus researchers could compute different expectations from evolutionary models, scale phylogenies accordingly (i.e., phylogenetic distances and topologies) and then determine which model best describes the observed pattern of ecological differences. From this model, we could then learn the selective forces structuring the community.

Again, we argue that experiments are ultimately needed to assess if PDED relationships can explain patterns of

co-occurrence, but their interpretation also additionally requires consideration of the underlying evolutionary process. Experiments that assess species coexistence over multiple generations look for evidence that some sort of niche partitioning or ecological difference is correlated with phylogenetic distance. Below we briefly discuss examples of such studies in light of simple evolutionary models, following on from the examples mentioned above.

In a carefully designed protozoan microcosm experiment, Violle et al. (2011) showed that competitive exclusion was more common in trials with close relatives. Further, they quantified species performance by measuring how far inferior competitors were from their monoculture population sizes when grown with a competitor (Fig. 5a), and showed that inferior competitors maintained higher population sizes when paired with distantly related species. However, in addition to a clear mean effect, variance was

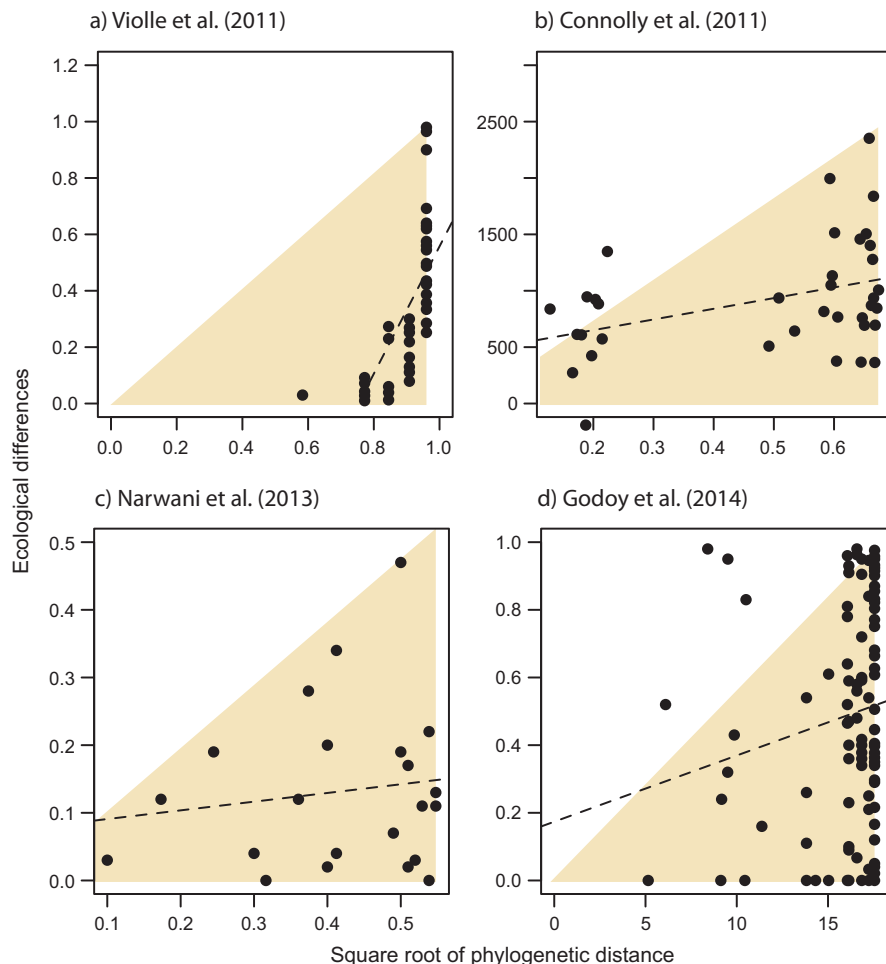


FIG. 5. Examples of experiments assessing the relationship between ecological differentiation (ED) and phylogenetic distance, including (a) protozoan microcosms (Violle et al. 2011), where ED is measured as the competitive effect on an inferior species; (b) a long-term plant competition experiment (Connolly et al. 2011), where ED is the pairwise species additional contribution to biomass beyond the expectation from monoculture; (c) a laboratory algal experiment (Narwani et al. 2013), where ED is measured as the abundances of species under competition; and (d) an annual plant experiment (Godoy et al. 2014), where ED is calculated from intra- and interspecific competition coefficients. Yellow shaded area illustrates average expected area of ecological differences evolving under Brownian motion evolution.

also higher among distantly related species pairs, consistent with a scenario in which ecological differences reflect the influence of a moderate number of independently evolving traits under a BM model.

In a multigenerational grassland biodiversity experiment, Connolly et al. (2011) estimated species niche complementarity as the pairwise species contributions to polyculture biomass production beyond monoculture expectations. Though not shown in the main body of the manuscript, the relationship between phylogenetic distance and complementarity is again consistent with BM evolution of a few underlying interaction traits, demonstrating the distinctive triangular relationship between phylogenetic distance and, in this case, biomass production or overyielding (Fig. 5b).

In two more recent experiments, Narwani et al. (2013) and Godoy et al. (2014) use the coexistence framework of Chesson (2000) to assess niche and fitness differences to explain competitive exclusion and coexistence. In the first, Narwani et al. (2013) tested the hypothesis that niche differences in algae increased with phylogenetic distance, but here they concluded that evolutionary relationships were not informative based on the results of a linear regression. Nonetheless, their results (Fig. 5c) again appear consistent with BM expectations. In the second experiment, Godoy et al. (2014), assessed competitive interactions between pairs of annual plant species. They quantified both fitness and niche differences, with the latter shown in Fig. 5d. Of all the studies reviewed in this paper, this was the only one to explicitly compare results to expectations from BM evolution, though they fit a quadratic equation and do not model variance. While their results also seem to fit a BM model (Fig. 5d), they concluded that phylogenetic history failed to represent niche differences sufficiently to explain coexistence. In some of these examples above (e.g., Fig. 5b, c), the intercepts of the regression lines are all greater than zero, which might reflect intraspecific variability or measurement error (Hardy and Pavoine 2012), nonetheless the triangular PDED relationship, predicted from a BM evolutionary model is clear in all cases. We focus solely on BM expectations here, but more research is needed to predict how other models would predict PDED relationships.

#### *Shortcomings with experimental designs*

Researchers make decisions about which species to include in experiments based on a number of theoretical and practical considerations, and one critical consideration for PDED experiments must be the phylogeny itself. In a meta-analysis of the relationship between phylogenetic diversity and biomass production in plant assemblages, Cadotte et al. (2008) noted that many studies tended to have few close relatives, making it difficult to test phylogenetic hypotheses. Further, observational studies are subject to using species that actually co-occur together, and natural assembly mechanisms can limit

the number of closely related pairs, influencing local community phylogenetic patterns (Gerhold et al. 2015). Thus experiments need to ensure that they sample a range of phylogenetic distances, for example, by including very closely related species, as the lack of close relatives can hamper the power to detect relationships with phylogenetic distance. For example, in a meta-analysis of plant competition experiments, Cahill et al. (2008) found that there was substantial variation in the strength of the correlation between competition and phylogenetic distance. Their results indicated that phylogenetic distance does not predict the strength of competition very well; we suggest that this observation might be deceptive because they lacked data on competition between close relatives (e.g., pairs of species that diverged less than 25 million years ago).

However, ensuring that there are closely related species is not in itself sufficient for robust analyses. There are two more subtle issues that researchers need to also recognize. First is the non-independence of internal phylogenetic edges. The extreme problematic case would be where the strength of competition was assessed on a single species pitted against competitors of increasing phylogenetic distances (Fig. 6a). In this case, the treatments would be resampling the same edges, while the analyses used likely assume independence. Further, the evolutionary trajectory leading to any single species, e.g., species A in Fig. 6a, may follow a particular evolutionary path not broadly representative of other evolutionary lineages. Similar issues have been raised in different contexts such as experiments that investigate how species complementarity affects ecosystem functioning and the way species complementarities are mixed within experimental replicates (Petchey 2003). In addition to the non-independence introduced by examining the same evolutionary pathways multiple times, researchers need also to consider other sources of non-independence. For example, the biogeographical origins of species might influence their responses, as might local growing conditions.

Second, pairwise phylogenetic measures generate an additional important problem: an uneven distribution of distances (Fig. 6b). A fully resolved phylogenetic tree is a hierarchical bifurcating graph and as such the first (deepest) split is traversed by the greatest number of pairwise distances between taxa. If there are only one or two pairs of closely related species, then there could be more than an order of magnitude difference in the number of pairwise distances considered in an experiment and this imbalance can affect the power of analyses (Cadotte and Davies 2016). The graphs in Fig. 5 show this inequality, with greater numbers of data points at higher phylogenetic distances. This is problematic because parametric statistical tests assume that data are homoscedastic across the independent variable. The distribution of pairwise distances is greatly influenced by tree topology and stemminess with the variance in pairwise distances increasing with stemminess and the mean

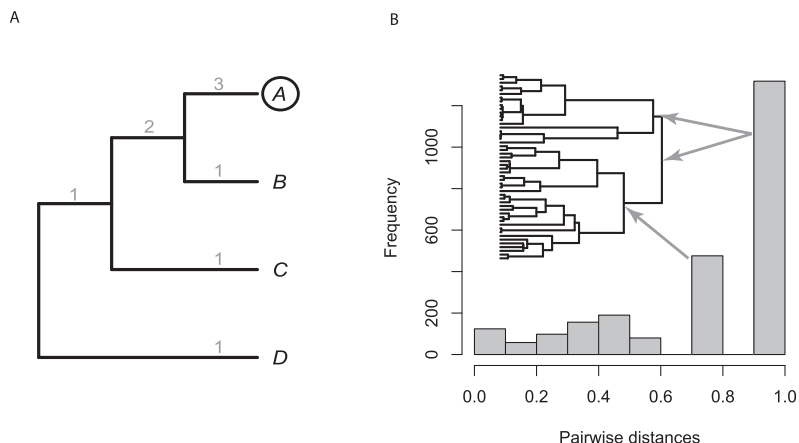


FIG. 6. Phylogenetic limitations of experimental design. (a) Pairwise competition trials with a focal species (Sp. A) limit independence because internal edges will be repeatedly resampled (shown by the gray numbers). (b) Pairwise distances (PD) will be heavily biased toward large distances simply because deeper splits are more frequently traversed in pairwise combinations.

of pairwise distances decreasing with imbalance (Davies and Buckley 2012), therefore the unevenness in the distribution of pairwise distances will vary among alternative tree topologies, further complicating comparisons between studies.

#### *Experimental venues limit niches*

One further possible explanation for null findings in explorations of the PDED relationship is that the relatively homogeneous environments at the small spatial and temporal scales commonly used in experimental studies do not allow for evolved niche partitioning to be relevant (e.g., niche partitioning has occurred along a separate niche axis to the one considered) or that the abiotic environment is a more important determinant of fitness than competition in these systems (Bennett et al. 2013). This becomes an issue in experiments in laboratory or other highly controlled settings, where the spatial and temporal heterogeneity that is important for coexistence in nature is absent, making it difficult to test coexistence mechanisms (Kraft et al. 2015b). Species have evolved all sorts of innovative strategies to deal with environmental challenges and to reduce the negative consequences of interspecific interactions. If the experimental setting lacks these axes of environmental heterogeneity or niche opportunities that species have evolved to, and which promote coexistence, then we should not expect to observe a significant PDED relationship. We might then infer from such experiments that phylogenetic relationships are not important for understanding species interactions, but it could be that the analyses simply miss the important niche differences that co-vary with phylogeny. Within experiments, some species may appear more competitive in the venue conditions and competitive exclusion might appear more important than stabilizing coexistence (Kraft et al. 2015b), but these might not reflect potential for coexistence in natural communities (McGill 2012).

#### WHY CERTAIN TYPES OF STUDIES WORK WITHOUT EVOLUTIONARY MODELS

When many traits determine niche position, ecological differences may more often correlate with phylogenetic distance, and so expectations and model align. However, there are cases where phylogenetic distance appears to be a good predictor of ecology regardless of the underlying evolutionary model (Cadotte 2015). This appears to occur under some circumstances, but especially when we sum phylogenetic distances into a community-wide measure of phylogenetic diversity (e.g., Faith's PD). When we sum phylogenetic distances, we capture the expected variance among species (assuming a BM or similar model) and this may reflect the total niche space occupied by the set. Even though a model directly relating PD to niche space would be helpful, analyses using PD do not seem to be as sensitive to the lack of an explicit evolutionary model because, in this instance, our response variable also represents the variance in species traits (total volume of niche space occupied) and not their differences. The relationship between summed phylogenetic distances and niche volume occupied is perhaps most clearly seen in ecosystem function analyses, where PD has been shown to be a powerful predictor of quantitative measures of ecosystem functioning (Cadotte et al. 2008, Srivastava et al. 2012, Cadotte 2013, Pu et al. 2014).

One outstanding question is that, if competition or niche differences are often poorly correlated to phylogenetic distances, why have community assembly analyses so consistently found nonrandom phylogenetic patterns (Cavender-Bares et al. 2009, Vamossi et al. 2009, Mouquet et al. 2012)? In part, the answer is that community assembly mechanisms operate directly on species' ecologies and under most models of evolution, very closely related species will always tend to be more ecologically similar (Kelly et al. 2014). Thus, under competitive exclusion, we see overdispersion, since those species that are different will



most likely be distantly related (and the similar but distantly related species will be filtered out of the local assemblage). However, this logic fails to explain phylogenetic clustering, for example, due to environmental filtering or competition (*sensu* Mayfield and Levine 2010), since distantly related species could also be ecologically similar due to strong niche conservatism or convergence (Cavender-Bares et al. 2004). In fact, Cavender-Bares et al. (2004) showed convincingly in their Floridian oak system that conserved traits tend to be over-dispersed in communities and convergent traits tend to be clustered. Yet phylogenetic underdispersion is reported frequently in the literature (Vamosi et al. 2009). It is possible that clustering relies on niche conservatism that is stricter than BM, where convergence is rare, or, environmental filtering might be more often influenced by multiple traits, and therefore phylogenetic distance will tend to better represent ecological differences. Alternatively, clustering might simply reflect biogeographic processes that influence regional species pools, and their related history of speciation, extinction, and migration (Pigot and Etienne 2015). There may also be a scale effect where clustering is more obvious at larger scales and observational studies may be biased at detecting clustering because they tend to occur at larger

spatial scales and clustering is easier to detect statistically (Parmentier et al. 2014).

### CONCLUSIONS

Interspecific interactions and species coexistence are among the most complex natural phenomena, and no simple mechanism will fully explain them. However, evolutionary relationships have become a popular approach for assessing the candidate mechanisms that influence competitive interactions and patterns of species co-occurrence. While ecological phylogenetic approaches are attractive, it should not be forgotten that in many situations traits could be more informative (Baraloto et al. 2012, Best et al. 2013, Cadotte et al. 2013), even when they are phylogenetically correlated. However, approaches that combine both trait and phylogenetic data can be even more powerful (Cadotte et al. 2013, Bässler et al. 2016, Thorn et al. 2016), for example, when candidate traits are well known, a good approach is to develop evolutionarily informed models of trait distributions (Davies et al. 2012) in order to assess the role of traits and evolution in assembling extant communities. Moreover, one could assess whether traits that evolved under different rates or modes

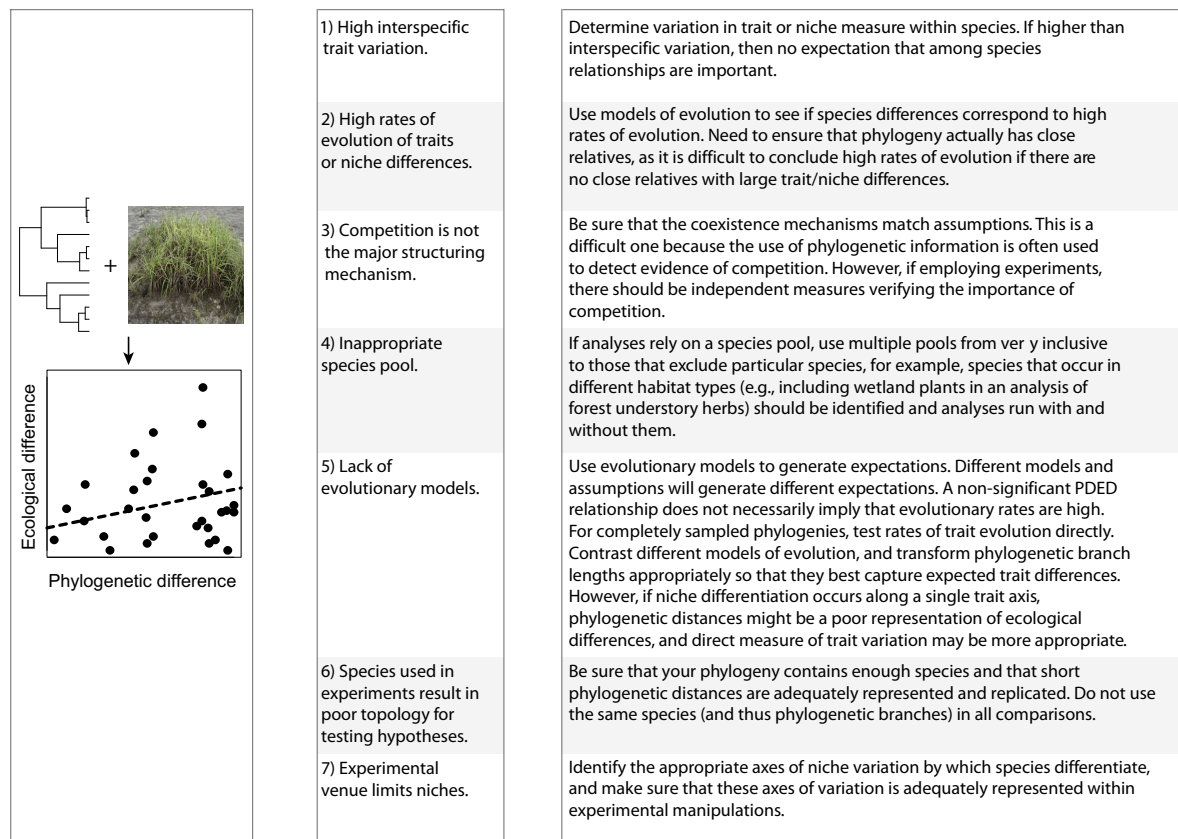


FIG. 7. Seven guidelines (corresponding to the seven reasons why phylogenetic distance does not predict ecological difference [PDED]) for ensuring that inferences from PDED relationships are robust.

could have different roles in mediating species coexistence. Nonetheless, in many cases, key traits are either unknown or hard to measure, and we have only information on evolutionary relationships. Phylogeny alone can still be informative, yet many ecological studies that examine community phylogenetic patterns are not fully cognizant of the evolutionary processes that they represent and how these impact predictions and interpretation of ecophylogenetic patterns (see Fig. 7).

In this paper, we highlight seven reasons why studies might not find a relationship between phylogenetic distance and ecological difference, the first three are evolutionary or ecological reasons, and the last four are shortcomings of the experimental design and analysis. We suggest that there is a major gap in our interpretation of statistically non-significant PDED relationships and our understanding evolutionary dynamics. Studies reporting null PDED relationships often cite some combination of our first three mechanisms without actually testing them. In Fig. 7, we provide a set of guidelines to ensure that inferences are robust. If researchers show that null results were indeed caused by high intraspecific variability rather than high evolutionary rates and convergences, for example, then we have gained a key insight into how evolution influences contemporary coexistence. Rejecting the PDED relationship rejects a particular hypothesis about how evolution has shaped ecological differences and not the fact that ecological differences have evolved. Future studies would advance the field by moving beyond single dichotomous hypotheses about how evolution influences ecology, and instead compare alternative hypotheses based on evolutionary models and number of traits. There is a desperate need for more research on the expectations about the PDED relationship from different evolutionary models. Studies that fail to find a PDED relationship need to ensure that results reflect biological reality and that methodological decisions do not lead to erroneous conclusions.

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