A new framework for inferring community assembly processes using phylogenetic information, relevant traits and environmental gradients

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Abstract

Background

Functional and phylogenetic diversity are increasingly used to infer the important community assembly processes that have structured local communities, which is one of the most fundamental issues in ecology. However, there are critical assumptions and pitfalls associated with these analyses, which can create ambiguity in interpreting results.

New information

Here, we present a conceptual framework which integrates three approaches to reduce the likelihood of drawing incorrect conclusions from analyses of functional and phylogenetic diversity (FD and PD, respectively):

1. testing hypotheses for how diversity measures and ecological processes vary along an environmental gradient;
2. analysis of both FD and PD in concert; and

3.   careful selection of traits related to processes of interest for inclusion in FD analyses.

We describe the utility of each of these recommendations and show, using hypothetical examples, how combining these approaches can strengthen one's ability to correctly infer community assembly. We present this framework in the context of identifying the signatures of interspecific competition and environmental filtering, important processes that operate in many systems across different taxa and are most often referred to in the FD and PD literature. We provide examples showing how our framework can be used to test general hypotheses such as the Stress-Dominance Hypothesis, which predicts a shift in the relative importance of environmental filtering and competition along a gradient of environmental stress, using PD and FD calculated separately for alpha (competition-related) traits and beta (environmental filtering-related) traits. Our approach can be applied to other processes besides competition and environmental filtering. This framework has the potential to enhance comparability between studies, allow for testing of alternative hypotheses regarding changes in community assembly processes along gradients, and improve interpretations of FD and PD analyses.

Keywords

Introduction

A long-standing goal in ecology has been to document patterns in natural community structure and connect these patterns to underlying processes such as environmental filtering, disturbance, competition, and predation (i.e. community assembly processes). Over the last decade, ecologists have increasingly attempted to infer community assembly processes from observed species composition by calculating communities' functional and phylogenetic diversity (hereafter "FD" and "PD", respectively), measures that describe the distributions of functional traits or the degree of phylogenetic relatedness among co-occurring species (Petchey and Gaston 2006, Cavender-Bares et al. 2009). Unlike diversity measures that are based solely on species' identities, FD and PD can describe important differences between species, such as in the ways that they use resources, respond to and influence the local environment, and otherwise function in the community (Weiher and Keddy 1995, Lavorel and Garnier 2002, Swenson 2013).

The approach of inferring processes from these measures is based on the idea that deterministic community assembly processes produce consistent patterns in trait distributions or the phylogenetic relationships within communities, by creating communities of species that are either more similar or dissimilar than expected by chance (Cavender-Bares et al. 2009, Kraft and Ackerly 2010). FD and PD have therefore been used to infer whether a particular community assembly process, such as interspecific

competition (hereafter "competition") or environmental filtering, has been most important for structuring a community or set of communities. Competition is often expected to exclude species with a large degree of niche overlap (Macarthur and Levins 1967), producing a community with high FD or PD compared to a randomly assembled community ("overdispersion" [Kraft and Ackerly 2010]), while environmental filtering often limits community membership to species with similar adaptations to local environmental conditions (Kotowski and Diggelen 2004), resulting in low FD or PD compared to the null expectation of random assembly ("clustering" [Kraft and Ackerly 2010]).

Recently, several authors have cautioned that care must be taken when using FD and PD, since inappropriate choice of traits, diversity metrics, or null models can produce ambiguous results and even lead to incorrect conclusions about the processes underlying community assembly (e.g. Petchey and Gaston 2006, Kraft et al. 2007, de Bello 2011, Swenson 2013). However, even when these considerations are taken into account, most studies that use FD and PD to infer community assembly processes rely on a set of problematic assumptions (see Gerhold et al. 2015 for a review of the assumptions of PD studies).

First, FD and PD have often been treated as interchangeable, based on the assumption that functional traits (and, more generally, ecologically important aspects of the niche) are phylogenetically conserved, so that closely related species share similar traits (Wiens and Graham 2005). Second, it is generally assumed that competition and environmental filtering are the most important processes structuring communities. The former is considered as the primary cause of overdispersion of FD and PD while the latter is associated with clustering patterns of FD and PD.

While there are indeed cases in which these assumptions are supported, there are also many cases where they are not: many ecologically important traits do not show strong phylogenetic signal (Losos 2008); processes other than competition and environmental filtering are often important, and can produce overdispersion and clustering of PD and FD (Sargent and Ackerly 2008, Cavender-Bares et al. 2009); and the patterns of PD and FD produced by competition and environmental filtering can be difficult to distinguish from one another. In particular, environmental filtering may actually cause high FD or PD if there is high environmental heterogeneity within the observed community and filtering occurs at a finer scale than the one used in the study (Adler et al. 2013, Kraft et al. 2014), while competition can cause clustered FD or PD when species with certain traits or from certain clades outcompete others (Grime 2006, Mayfield and Levine 2010, Goberna et al. 2014). Based on species coexistence theory (Chesson 2000), recent manipulative experiments have shown that the pattern of FD that is produced by competition actually depends on whether traits confer niche differences that allow species to coexist or fitness differences that cause some species to competitively displace others (Kraft et al. 2014, Kraft et al. 2015). These complex factors show that the potential for correctly inferring processes from FD and PD patterns is limited by our ability to confidently discern which community assembly process caused a particular pattern.

The growing recognition that the common assumptions of FD and PD studies are not always valid has not diminished the prevalence of these studies (as evidenced by a number of published studies in 2016, e.g. Arnan et al. 2016, Saito et al. 2016, Strauß et al. 2016), nor does it suggest that they necessarily should be abandoned altogether (although some have argued as much; e.g. Gerhold et al. 2015). While it is clear that experimental approaches that manipulate individual processes and examine their effects on FD and PD are still needed, there is still utility in using observational data sets to infer community assembly processes, particularly for drawing inference at spatial and temporal scales for which manipulative experiments are infeasible. However, in order to draw meaningful inference from studies of FD and PD, it is necessary to move beyond the commonly used assumptions of the relationships between community assembly processes and community structure and adopt more rigorous approaches for linking FD and PD patterns to underlying processes.

Here, we review three of these approaches and describe their utility: 1) consideration of how diversity measures and ecological processes vary along an environmental gradient; 2) analysis of both FD and PD, and explicit testing for phylogenetic signal of traits; and 3) careful selection of traits related to processes of interest for inclusion in FD analyses. We then go a step further by presenting a framework that integrates all three, and use hypothetical examples to show how combining these approaches can strengthen one's ability to correctly infer community assembly processes. We consider three major benefits of this framework over the ways that FD and PD analyses have typically been done: it requires that authors explicitly recognize the assumptions that go into choosing traits and predicting the responses of FD and PD to community assembly processes; it involves comparison of multiple lines of evidence to draw conclusions, allowing for tests of multiple alternative hypotheses for how community structure responds to community assembly processes; and it can be applied to multiple taxa and ecosystems, thus promoting comparison across studies.

Here we focus on using this framework to detect the effects of competition and environmental filtering, two community assembly processes that are most commonly discussed in the literature. Substantial work has been done to identify the functional traits most relevant to these processes for a variety of systems (e.g. Gómez et al. 2010, Bernard-Verdier et al. 2013), and we point to an existing but underutilized conceptual framework for evaluating those traits. Although we focus on competition and environmental filtering, we also highlight how this framework could be used to identify the effects of other community assembly processes.

Testing hypotheses that predict changes in diversity metrics along environmental gradients

One way to improve confidence in interpreting community assembly processes from FD and/or PD is to examine changes in these measures along an environmental gradient (e.g. Graham et al. 2012, Bryant et al. 2012, Coyle et al. 2014, Cisneros et al. 2014,

Dreiss et al. 2015). This approach is used to detect changes in the relative importance of community assembly processes in response to environmental conditions, rather than identifying the absolute importance of competition or environmental filtering to the structuring of communities. In addition, changes in community structure along environmental gradients can be used to make predictions for other communities and ecosystems (e.g. Fortunel et al. 2014), therefore increasing our understanding of commonalities and distinct features across ecosystems and potentially improving our ability to predict changes in community structure in response to global environmental change (McGill et al. 2006, May et al. 2013).

What are often lacking in studies that use PD and FD to detect community assembly processes are forthright hypotheses for how community assembly processes, and thus FD and/or PD patterns, are expected to change along the focal environmental gradient. Instead, these studies tend to rely on post hoc interpretations of patterns based on the assumption that competition causes over-dispersion and environmental filtering creates clustering. Hypothesis testing would create more transparent, and therefore more robust and comparable, interpretations of results. Considering changes in FD and/or PD along environmental gradients lends itself to hypothesis testing, because there are a number of general ecological hypotheses that predict changes of the relative importance of community assembly processes along resource, disturbance, and/or stress gradients. One example is the Stress-Dominance Hypothesis ("SDH"; Coyle et al. 2014, adapted from Swenson and Enquist 2007), which predicts that in stressful environments, strong environmental filters limit community membership, while in more benign environments this filter weakens and competition becomes more important for structuring communities (Weiher and Keddy 1995).

Although rarely explicitly referenced, the SDH has been posed in many studies that use FD and PD to infer community assembly processes (e.g. Kluge and Kessler 2011, Bryant et al. 2012, Coyle et al. 2014). Because this hypothesis predicts changes in the importance of competition and environmental filtering in response to environmental stress rather than a particular environmental gradient, it can be applied to many different environmental gradients, provided that they cause varying stress for the focal taxon. Examples include gradients of elevation (Graham et al. 2009, Kluge and Kessler 2011, Machac et al. 2011), soil fertility (Anderson et al. 2011, Coyle et al. 2014), and dissolved oxygen content (Bryant et al. 2012). FD and PD can thus be used to test the generality of the SDH and other hypotheses that predict changes in community assembly processes across environmental conditions or scales (Kraft and Ackerly 2010, Meynard et al. 2011, Coyle et al. 2014), therefore increasing the potential for synthesis across studies and improvement of our ability to predict changes in community structure in response to global environmental change (McGill et al. 2006, May et al. 2013).

Incorporating both trait- and phylogenetic information to gain greater insight

PD and FD are often used essentially interchangeably, because when the traits used to calculate FD are highly phylogenetically conserved (i.e. closely related species share similar traits), PD and FD analyses will theoretically produce similar results (Webb et al. 2002). However, while phylogenetic niche conservatism is common (Wiens and Graham 2005, Wiens et al. 2010), not all ecologically relevant traits are phylogenetically conserved (reviewed by Losos 2008). Examples of relatively labile traits include habitat use and activity time in *Anolis* lizards (Losos et al. 2003), habitat preference and body coloration in ants (Blaimer et al. 2015), and habitat affinity in Florida oaks (Cavender-Bares et al. 2004). Indeed, depending on the mechanism and trajectory of evolution, traits may show varying amounts of phylogenetic signal (Revell et al. 2008, Graham et al. 2012). This means that FD and PD often provide different information.

Furthermore, each of these measures has its own benefits and drawbacks (reviewed in Swenson 2013). Some have suggested that FD is the more useful measure for inferring community assembly processes because species' traits both reflect and shape their interactions with the environment and other species (Lavorel and Garnier 2002, McGill et al. 2006). The drawback to FD is that identifying which traits will provide the most relevant information can be a challenge (Petchey and Gaston 2006, Swenson 2013, Lefcheck et al. 2015), particularly since the traits that are easiest to measure do not necessarily have clear or simple linkages to organismal function or community assembly processes (Petchey and Gaston 2006, Violle et al. 2007).

PD, on the other hand, has the advantage of integrating over multiple niche dimensions and may therefore capture subtle differences among niches better than a small set of traits can (Cadotte et al. 2009). However, PD patterns can be difficult to interpret without knowledge of the traits that underpin them (Cavender-Bares et al. 2009, Bernard-Verdier et al. 2013, Mason and Pavoine 2013). For example, phylogenetic overdispersion can result from the traditionally expected result of competition causing limiting similarity of phylogenetically conserved traits (Fig. 1), environmental filtering acting on convergent traits (Fig. 2; Webb et al. 2002), or other processes, such as facilitation between distantly related species (reviewed in Cavender-Bares et al. 2009). Likewise, clustering of PD could be generated by a number of different processes, including environmental filtering of closely related species with similar physiological tolerances (Webb et al. 2002), phylogenetically conserved defenses to predation (Fine 2004, Fine et al. 2006), shared mutualists (Sargent and Ackerly 2008), or recent adaptive radiation and trait lability (Grant and Grant 2006). Thus testing for phylogenetic signal in traits (and correctly interpreting the results of those tests) is crucial for interpreting PD patterns (Cavender-Bares et al. 2004, Cavender-Bares et al. 2009, Anderson et al. 2011, Crisp and Cook 2012). However, it is important to note that these tests do not always accurately predict whether PD will reflect underlying trait patterns (Revell et al. 2008, Graham et al. 2012,

Mason and Pavoine 2013), particularly when competition between closely related species within the same community drives trait differences between them (Burns and Strauss 2012, Graham et al. 2012).

When analyzed together, FD and PD can improve insight into underlying community assembly processes (Pavoine and Bonsall 2011, Stegen and Hurlbert 2011, Bernard-Verdier et al. 2013) because they often provide complementary information (Cadotte et al. 2013, Savage and Cavender-Bares 2012). While trait information may provide a clearer link between species and ecological processes acting at local scales, especially when traits are measured at the scale of the community with information about intraspecific trait variation (Carlucci et al. 2012), phylogenetic information reflects processes operating at larger spatial and temporal scales such as evolution, speciation, and migration, which shape species distributions and determine species' adaptations to environmental conditions (Ricklefs 1987, Webb et al. 2002, Cavender-Bares et al. 2009). Thus, understanding the phylogenetic basis for traits can reveal constraints on the relationship between traits and the environment, as well as correlations between different types of traits (Savage and Cavender-Bares 2012). In addition, PD patterns can reflect processes acting on aspects of a species' niche that are difficult to measure or relate to particular physiological traits, such as phylogenetically conserved habitat affinity (Savage and Cavender-Bares 2012), response to disturbance (Cavender-Bares and Reich 2012), or shared pathogens (Allan et al. 2013).

Choosing specific traits that relate to individual community assembly processes

The clearest way to connect community assembly processes to FD patterns is to calculate FD from traits with clear linkages to specific processes or particular aspects of a species' niche. For example, some traits provide stress tolerance (e.g. leaf size in plants; Spasojevic and Suding 2012), while others relate to resource acquisition (e.g. bill length in birds; Gómez et al. 2010, Graham et al. 2012), fire tolerance (e.g. re-sprouting and flammability in plants; Gagnon et al. 2010, Pausas et al. 2015), or reproductive ability (e.g. seed mass and seed number in plants; Moles and Westoby 2004; Table 1). Any examination of metrics that combine or correlate with multiple traits, such as PD or multivariate measures of FD, can therefore mask patterns that would be detectable if individual traits were considered separately (Cavender-Bares et al. 2004, Swenson and Enquist 2009, Spasojevic and Suding 2012). For example, if environmental filtering and limiting similarity caused by competition produce opposing effects on community structure, a community influenced by both processes would likely show both overdispersion in traits that are important for competition and clustering of traits related to environmental filtering. In this case, both PD and FD calculated from both types of traits could resemble a random pattern, potentially leading to the incorrect inference that neither competition nor environmental filtering was important processes in that system (Helmus et al. 2007, Anderson et al. 2011, García-Baquero and Crujeiras 2015, Saito et al. 2016). In contrast, calculating FD separately for traits influenced by competition and those

influenced by environmental filtering would reveal the respective influences of those processes on community assembly (Spasojevic and Suding 2012).

When trying to detect the signals of multiple community assembly processes, we recommend analyzing FD separately for traits that are related to each process (e.g. environmental filtering traits, competition traits, dispersal traits), which can be thought of as defining different axes of a species' niche. In the case of competition and environmental filtering, these traits are sometimes called "alpha traits" and "beta traits", respectively, corresponding to the alpha and beta niche (Whittaker 1975, Pickett and Bazzaz 1978). The alpha niche refers to the ways that species partition resources at the local scale, therefore determining species' responses to biotic interactions, while the beta niche refers to a species' environmental tolerances, and thus determines where a species will occur along an environmental gradient (Silvertown et al. 2006a, Silvertown et al. 2006b, Ackerly and Cornwell 2007). Alpha traits include those related to behavior, small-scale habitat preference or resource acquisition (Lovette and Hochachka 2006, Ingram and Shurin 2009, Bernard-Verdier et al. 2013). Within the context of coexistence theory (Chesson 2000), alpha traits are those that produce stabilizing niche differences by allowing species to partition available resources. It is important to note that these same traits sometimes create competitive hierarchies by endowing some species with higher fitness than others (HilleRisLambers et al. 2012, Kraft et al. 2015), so that competition could cause either overdispersion or clustering of alpha traits (Mayfield and Levine 2010). Examples of alpha traits are gill raker length and head length in fish, which relate to trophic position and feeding strategy, two important factors that determine resource acquisition (Ingram and Shurin 2009, Pease et al. 2012; see Table 1 for more examples). Beta traits are those that provide tolerance to environmental conditions or determine a species' position along an environmental gradient such as temperature, precipitation, or ocean depth (Ingram and Shurin 2009, Pease et al. 2012; see Table 1). For example, wood density in shrubs and trees relates to drought tolerance (Ackerly et al. 2006, Savage and Cavender-Bares 2012), while ability to form resistant structures is a form of stress tolerance in bacteria (Goberna et al. 2014).

Separately analyzing FD calculated from alpha traits and beta traits would not only prevent the problem of competition and environmental filtering masking one another when both types of traits are included in a single FD metric; it can also reduce the likelihood of confusing the effects of these two processes when unexpected or ambiguous patterns are generated, such as if competition causes clustering rather than overdispersion of FD (Mayfield and Levine 2010). Furthermore, connecting traits to particular processes can reduce the risk of interpreting a FD pattern as a signal of competition or environmental filtering when it is truly caused by a different process. A few studies have explicitly used alpha and beta traits to infer competition and environmental filtering (e.g. Silvertown et al. 2006a, Silvertown et al. 2006b, Ingram and Shurin 2009, Saito et al. 2016), while some others have used traits that are thought to primarily respond to either competition or environmental filtering without invoking the "alpha" and "beta" terms (e.g. Bryant et al. 2012, Pease et al. 2012, Goberna et al. 2014). However,

despite its ability to clarify interpretation of FD, the alpha and beta trait concept has been used surprisingly rarely in FD and PD studies.

One plausible reason is that identifying alpha and beta traits *a priori* can be challenging. Ideally, determining whether a trait mediates species' interactions with a particular community assembly process would be done using manipulative experiments that test relationships between species' resource use or environmental tolerances in relation to their traits (Adler et al. 2013, Kraft et al. 2014). However, it is more common to use observed relationships and information on species' natural histories to relate traits to species' abiotic and biotic interactions (Adler et al. 2013). A further issue is that there are undoubtedly cases where it is difficult to identify traits that are influenced by only a single process, since many traits provide multiple functions (Douma et al. 2012, Fortunel et al. 2014). To circumvent this problem, some have used alternative methods to detect the signal of multiple processes acting on the same traits, such as identifying orthogonal axes of trait variation that each correspond to one aspect of a species' niche (i.e. niche axes) using multivariate analysis (e.g. Westoby et al. 2002). Several authors have used this approach to define axes of variation in multiple traits that relate to competition and environmental filtering, respectively, to calculate two measures of FD, one relating to the alpha niche and one relating to the beta niche (Ingram and Shurin 2009, Gómez et al. 2010). Whether using traits that are relatively unambiguously related to one process, traits that appear to be more related to one process than the other, or multivariate combinations of traits that pertain to one process, analyzing FD calculated from only traits related to one niche axis has the potential to increase confidence of inference from observational data (Saito et al. 2016).

Combining environmental gradients, phylogenetic information and alpha and beta traits: hypothetical examples

We have argued that analyzing changes in community structure along environmental gradients, considering both phylogenetic and trait information, and choosing traits related to specific processes can all improve the inference of assembly processes. We now describe two simple hypothetical scenarios framed in the context of the Stress-Dominance Hypothesis (SDH), to show how combining these three approaches can strengthen inferences and clarify otherwise ambiguous or misleading results.

The SDH predicts that competition will become more important as the environmental filter weakens. Based on the two dominant assumptions, that PD and FD are essentially interchangeable and that competition causes overdispersion while environmental filtering causes clustering, the most common prediction of the SDH is: PD and FD calculated from both alpha and beta traits ("FD_{both}") will be clustered at the harsh end of a stress gradient and overdispersed at the benign end of the gradient (Fig. 3). However, analyzing alpha and beta traits separately would show a different pattern, because alpha traits are not strongly influenced by environmental filtering and beta traits are not strongly influenced by competition. Thus, FD calculated from one or more alpha traits ("$FD_{\alpha\text{-traits}}$")

and FD calculated from one or more beta traits ("FD$_{\beta\text{-traits}}$") would both increase with decreasing environmental stress, similar to the pattern expected for PD, but FD$_{\alpha\text{-traits}}$ would not show clustering at the harsh end of the gradient and FD$_{\beta\text{-traits}}$ would not show overdispersion at the benign end of the gradient (Fig. 3).

In the following examples we show that patterns of FD$_{\alpha\text{-traits}}$ and FD$_{\beta\text{-traits}}$ can more clearly distinguish the effects of competition and environmental filtering than either PD or FD$_{both}$, and that analyzing PD, FD$_{\alpha\text{-traits}}$, and FD$_{\beta\text{-traits}}$ in tandem can reveal which community assembly processes are operating. For simplicity, we consider two scenarios: one in which analyzing only PD or FD$_{both}$ would not show support for the SDH when in fact it is reflected in alpha and beta traits, and one in which the opposite is true and FD$_{\alpha\text{-traits}}$, and FD$_{\beta\text{-traits}}$ reveal that the SDH is not supported by the data. In all cases, testing for phylogenetic niche conservatism reveals whether FD$_{\alpha\text{-traits}}$ and FD$_{\beta\text{-traits}}$ will provide different information than PD.

Scenario 1: The SDH is supported by FD$_{\alpha\text{-traits}}$ and FD$_{\beta\text{-traits}}$, but PD shows unexpected pattern

Even when the conditions of the SDH are in place (i.e. there is a shift in relative importance from environmental filtering to competition with decreasing environmental stress), if either alpha or beta traits are not highly phylogenetically conserved, PD could show a number of different patterns along the stress gradient (dashed lines, Fig. 4). If alpha traits were labile across the phylogeny but beta traits were conserved (as is sometimes the case in plants; Silvertown et al. 2006a), PD would likely track the FD$_{\beta\text{-traits}}$ pattern and therefore not show evidence of competition (in this figure, shown as overdispersion) at the benign end of the gradient (gray line, Fig. 4A). In the opposite case, if alpha traits were conserved but beta traits were not, PD would likely track the FD$_{\alpha\text{-traits}}$ pattern and not show clustering consistent with environmental filtering at the stressful end of the gradient (black line, Fig. 4B). In a more extreme case, if neither type of trait were highly conserved on the phylogeny, PD could show any number of different patterns, but evidence for the SDH would still be reflected in FD$_{\alpha\text{-traits}}$ and FD$_{\beta\text{-traits}}$.

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highly conserved on the phylogeny, PD could show any number of different patterns, but evidence for the SDH would still be reflected in $FD_{\alpha\text{-traits}}$ and $FD_{\beta\text{-traits}}$.

Separating FD into $FD_{\alpha\text{-traits}}$ and $FD_{\beta\text{-traits}}$ can also clarify patterns when competition causes clustering rather than overdispersion (Mayfield and Levine 2010). In this case, the SDH could still be supported by a pattern of $FD_{\alpha\text{-traits}}$ that goes from random (or overdispersed) at the stressful end of the gradient to clustered at the benign end of the gradient, or a generally decreasing pattern of $FD_{\alpha\text{-traits}}$ with decreasing environmental stress (Fig. 4C). This could be driven by resource competition in benign environments causing those species with traits that allow them to use resources more efficiently to competitively exclude other species. In this case, the alpha traits that allow species to coexist in stressful environments also allow some species to outcompete others in benign environments.

Scenario 2: PD shows expected pattern, but the SDH is not supported by $FD_{\alpha\text{-traits}}$ and FD $_{\beta\text{-traits}}$

The PD pattern predicted by the SDH (Fig. 3) could also be caused by mechanisms other than a shift in the relative importance of environmental filtering and competition. For example, mutualism could be a more important driver of PD along the stress gradient than competition or environmental filtering. If communities are sampled along a gradient that is not a stress gradient for the study taxon but is for the mutualist taxa, and if obligate mutualism is phylogenetically conserved within the study taxon, then the pattern of PD predicted by the SDH could be driven by a higher diversity of the mutualistic taxa at the benign end of the gradient and a lack of these taxa at the harsh end, such that only species that do not require the mutualism survive in the "harsh" environments (Sargent and Ackerly 2008). In this case, neither $FD_{\alpha\text{-traits}}$ nor $FD_{\beta\text{-traits}}$ would likely show a strong pattern along the gradient, since there were no changes in the strength of competition or environmental filtering (Fig. 5A).

This PD pattern could also be created by one of the two processes acting on phylogenetically conserved traits. For example, this could arise if there was a shift from competition to facilitation as the environment becomes more stressful (the Stress Gradient Hypothesis; Bertness and Callaway 1994). This could produce a pattern of random (or overdispersed) $FD_{\alpha\text{-traits}}$ in stressful environments and overdispersed $FD_{\alpha\text{-traits}}$ in benign environments as a result of stronger competition in more benign environments. If alpha traits were phylogenetically conserved, this pattern would likely be reflected in PD. However, $FD_{\beta\text{-traits}}$ would likely not show any change along the gradient, indicating other processes besides environmental filtering were driving community structure at the stressful end of the gradient (e.g. facilitation, Fig. 5B).

Finally, this PD pattern could show the effects of competition and environmental filtering on alpha and beta traits that have phylogenetic signal, but in a way that is not consistent with the SDH. This could occur if competition for resources is actually stronger in harsh environments and causes competitive exclusion of some species (and thus clustered FD $_{\alpha\text{-traits}}$), which could be the case if competition for resources is a stronger force when

those resources are limiting (Fig. 5C). Environmental filtering could also create overdispersion of $FD_{\beta\text{-traits}}$ in benign environments if environmental heterogeneity occurs at a finer scale in those environments (Fig. 5C).

Discussion

The conceptual framework we have proposed here has potential to improve the inference of community assembly processes from trait and phylogenetic information by:

1. considering changes in diversity measures along an environmental gradient;
2. analyzing both PD and FD and explicitly testing for phylogenetic signal of traits; and
3. choosing traits for inclusion in FD analyses that directly relate to the processes of interest.

While each of these approaches has been used with some frequency, few studies have used all three (but see Spasojevic and Suding 2012, Graham et al. 2012, Goberna et al. 2014). We believe that these methods are complementary to one another, and that using all three together can significantly reduce uncertainty in interpreting results from FD and PD analyses. Specifically, we suggest that our framework has three major benefits over the typical methods of FD and PD analysis seen in the literature.

The first benefit is that our framework requires that the researcher explicitly hypothesize how the relative importance of community assembly processes changes along a gradient, make predictions of how FD and PD will change as a result, and choose traits that relate to the processes being examined. As we have described, relating the chosen traits to community assembly processes can aid in distinguishing the effects of those processes. Further, explicit statement of the predictions that are being tested and the assumptions underlying them will help in both interpreting results and weighing confidence in the interpretation.

Second, this framework can produce more robust inferences by comparing multiple lines of evidence to reach conclusions about which community assembly processes have driven community structure. As discussed above, analyzing FD and PD in tandem provides information on both ecological and evolutionary drivers of community structure, and testing for phylogenetic signal in traits can reveal constraints on the relationship between traits and the environment and correlations between different types of traits. Analyzing PD and traits related to each process means that three trends are compared to draw conclusions, reducing the risk of concluding support for a hypothesis that is supported by some, but not all, of the data. Comparing three different trends will also enhance researchers' ability to test multiple competing hypotheses for how the relative importance of community assembly processes changes along a gradient or how these processes will affect FD and PD patterns, because there is reduced likelihood that two competing hypotheses will produce the same expected patterns for three different diversity metrics.

The third benefit of this framework is that it can be adapted to apply to community assembly processes other than competition and environmental filtering. Although we have focused on environmental filtering and competition, this framework can be implemented more broadly by choosing specific traits (e.g. those that confer fire adaptation or predator resistance) that are related to the processes of interest (e.g. fire, predation) and considering gradients along which their relative importance could be expected to change (e.g. variation in disturbance frequency or predator density). For example, in riparian forests the effect of flooding is often more important in communities close to the riverbank (Giehl and Jarenkow 2015), while the relative importance of environmental filtering, namely drought, may increase away from the stream channel into upland forest types. Examining traits that relate specifically to ability to withstand and recover from floods, such as re-sprouting capacity (Giehl and Jarenkow 2015) and at traits that related specifically to drought-tolerance, such as leaf size (Spasojevic and Suding 2012) or wood density (Ackerly et al. 2006, Savage and Cavender-Bares 2012), would allow for increased inference of shifts in the relative importance of flooding to drought along a topographic gradient. We believe our framework can be extended in this way to improve synthesis across studies and help to reveal generalities about important community assembly processes other than competition and environmental filtering.

One possible limitation of this framework is that it hinges on the ability to identify traits related to individual community assembly processes, which can be difficult because many traits are influenced by a combination of processes (Douma et al. 2012, Fortunel et al. 2014). As we have discussed, there is a potential solution to this issue which can be incorporated into our framework: the calculation of orthogonal axes of trait variation that correspond to niche axes. We envision that the researcher can either use these axis values to calculate FD or choose traits that weigh more heavily on one axis or another to calculate FD values pertaining to each community assembly process of interest. Another solution for traits that are related to multiple processes is to assign variation in trait values to different components corresponding to each process (Ackerly and Cornwell 2007). Finally, when it is not possible to identify categories of traits that would help to distinguish between the effects of different processes, another useful approach is to utilize different null models that are specifically designed to test for the effects of each process of interest (Kraft et al. 2007, Lessard et al. 2016). For example, creating a null model that limits the species pool to those species that can establish in the local environmental conditions (or general habitat type) can make it much easier to detect the effects of competition on community structure (Helmus et al. 2007). Ultimately, however, significant overlap in the traits relevant to different assembly processes will pose problems for inference regardless of the particular framework or approach.

A promising way forward is to use information garnered from manipulative experiments that elucidate the relationships between individual community assembly processes and specific traits. For example, Kraft et al. (2015) quantified species' vital rates and pairwise competitive interactions for 18 species across a density gradient and examined whether fitness declined with increasing neighbor density. Experiments such as these should inform FD analyses using observational data, by helping to identify traits that respond to

given processes and testing whether the function assigned to a given trait is correct. A further step would be the development of research agendas that combine manipulative experiments and observational data analysis. For example, Fayle et al. (2015) observed that body size tended to be overdispersed within ant communities; they then carried out experiments that confirmed that species were less likely to successfully invade a community when it already contained a species with a similar body size. Another promising approach would be to first use manipulative experiments to determine how traits change with variation in environmental conditions or biotic interactions (HilleRisLambers et al. 2012) and then use this information to examine changes in these traits across larger spatial and temporal extents using the framework provided here.

Despite some limitations, we believe that our framework provides a useful advance beyond typical analytical approaches that use FD and PD and allows for more robust interpretations of patterns and enhanced potential for synthesis across studies. As with all studies using FD and PD, it is important that appropriate traits, environmental gradients, and null models are used, and that the assumptions involved in inferring community assembly processes from observed community patterns are explicitly recognized. We believe that this framework has the potential to increase confidence in inferences of community assembly processes from analyses of FD and PD, by allowing for comparison of results to predictions based in ecological theory.

Acknowledgements

Conflicts of interest

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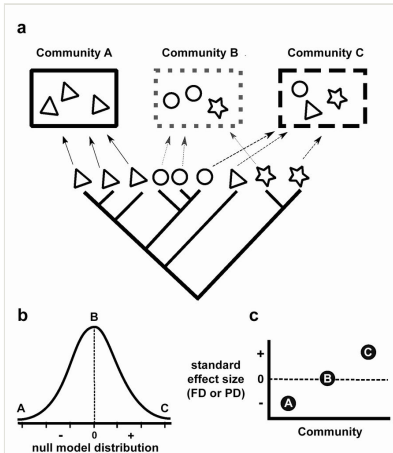
Figure 1.

Predicted effects of interspecific competition and environmental filtering on FD and PD.

In Figure 1A, individual species are represented by symbols at the tips of the phylogenetic tree, the shapes of the symbols indicate different trait states, and rectangles represent communities. In this example, the trait is conserved on the phylogeny, such that closely related species tend to have the same traits (shapes). Figure 1B shows the observed PD or FD for each community compared to the distribution of values predicted by the null model; this predicted value is then converted into a standard effect size (SES) relating to the mean of the null model distribution (Figure 1C). Environmental filtering selects for species with similar traits (Community A in Figure 1A), causing functional or phylogenetic clustering (point A in Figure 1C), while interspecific competition limits similarity between co-occurring species resulting in different trait states (Community C in Figure 1A) and functional or phylogenetic overdispersion (point C in Figure 1C). PD or FD that is no different from random expectation can also occur (Community B in Figure 1A, point B in Figure 1C).
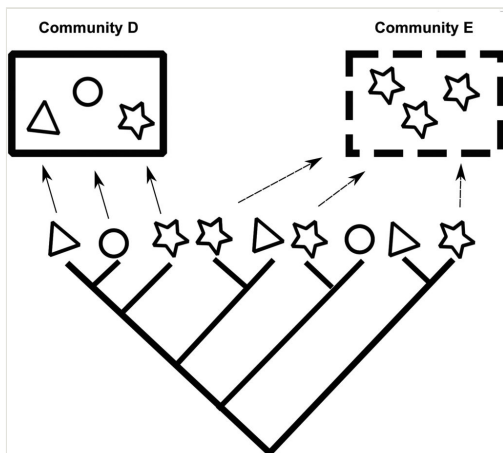
Figure 2.

An example highlighting the different interpretations of FD and PD patterns when traits are labile.

When traits used to calculate FD are not phylogenetically conserved, PD values will not necessarily reflect FD. In this example, the trait represented by shape is labile across the phylogeny. As a result, a community that is clustered in PD (Community D) is overdispersed in FD. Similarly, a community that is overdispersed in PD (Community E) could be clustered in FD.
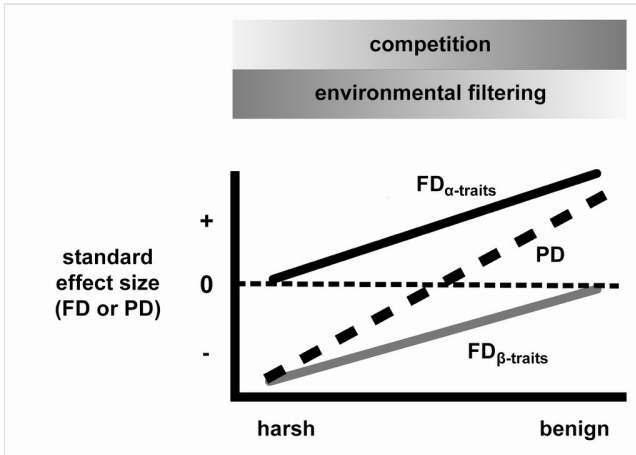
Figure 3.

Prediction of the Stress Dominance Hypothesis for $FD_{\alpha-traits}$, $FD_{\beta-traits}$, and PD.

Horizontal axis represents a gradient of environmental stress. At the harsh end of the gradient, environmental filtering is strongest, so PD is clustered (negative standard effect size). At the benign end of the gradient, competition becomes more important and results in coexistence of functionally and phylogenetically distinct taxa. Thus PD is overdispersed (positive standard effect size). Because it only reflects traits related to competition, $FD_{\alpha-traits}$ would not show clustering at the harsh end of the gradient; similarly, because it only includes traits related to environmental filtering, $FD_{\beta-traits}$ would not show overdispersion at the benign end of the gradient.
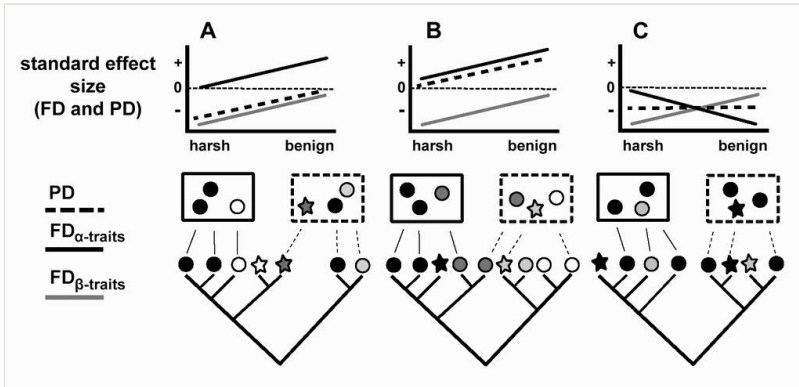
Figure 4.

Hypothetical examples of how examining FD $_{\alpha\text{-traits}}$ and FD$_{\beta\text{-traits}}$ shows support for the SDH, even when PD shows an unexpected pattern.

For each example (**A-C**), individual species are represented by symbols at the tips of the phylogenetic tree; the shape of the symbols represents beta traits, the color of the symbols represents alpha traits, and communities are represented by rectangles. In each example, we show two communities, one at the stressful and one at the benign end of the stress gradient. In case **A**, the alpha traits are labile while the beta traits are conserved; therefore PD tracks the pattern observed for FD$_{\beta\text{-traits}}$, so that competition is not evident from the PD pattern at the benign end of the gradient. In the opposite case (**B**), alpha traits are conserved but beta traits are not; therefore PD tracks the alpha trait pattern and does not show clustering consistent with environmental filtering at the stressful end of the gradient. In case **C**, PD shows an unexpected pattern because neither alpha nor beta traits have strong phylogenetic signal and competition shows a different pattern than the one that is generally expected, with strong competition causing competitive exclusion at the benign end of the gradient.
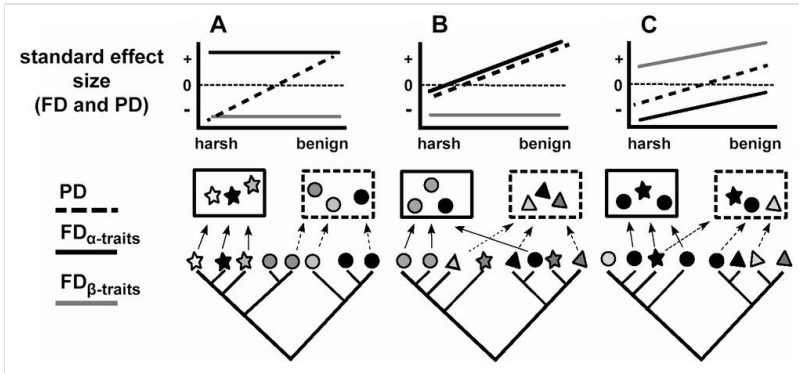
Figure 5.

Hypothetical examples where PD shows the pattern predicted by the SDH, but FDα-traits and FDβ-traits show that the SDH is not supported.

For each example (A-B), individual species are represented by symbols at the tips of the phylogenetic tree; the shape of the symbols represents beta traits, the color of the symbols represents alpha traits, and communities are represented by rectangles. In each example, we show two communities, one at the stressful and one at the benign end of the stress gradient. In case A, both alpha and beta traits are labile on the phylogeny, and looking at these traits would suggest that there is not a shift from environmental filtering to competition along the stress gradient. In case B, the alpha trait is phylogenetically conserved but the beta trait is not, so while the PD pattern appears to support the SDH, the beta trait pattern shows that there is no change in the importance of environmental filtering along the gradient. In case C, the expected PD pattern is generated from strong competition causing competitive exclusion and clustering of FDα-traits at the harsh end of the gradient and environmental heterogeneity and fine-scale environmental filtering causing overdispersion of FDβ-traits at the benign end of the gradient.

Table 1.

Examples of alpha (competition) and beta (environmental filtering) traits from the literature.

Trait	Role or function	Taxon	References
Alpha traits			
Height	Competitive ability	Plants	Spasojevic and Suding 2012, Bernard-Verdier et al. 2013, Giehl and Jarenkow 2015, Kraft et al. 2015
Lateral spread	Competitive ability	Plants	Klimeš and Klimešová 2000
Rooting depth	Resource capture	Plants	Kraft et al. 2015
Head length, depth	Feeding strategy	Fish	Pease et al. 2012
Gill raker length	Feeding strategy	Fish	Ingram and Shurin 2009
Bite rate	Foraging behavior	Fish	Adam et al. 2015
Bill length	Feeding strategy	Birds	Gómez et al. 2010, Graham et al. 2012
Foraging stratum	Feeding strategy	Birds	Gómez et al. 2010
Trophic position	Feeding strategy	Aquatic insects	Saito et al. 2016
Organic carbon consumption	Resource capture	Bacteria	Goberna et al. 2014
Nitrogen fixation	Resource capture	Bacteria	Goberna et al. 2014
Beta traits			
Leaf size	Stress tolerance	Plants	Spasojevic and Suding 2012
Wood density	Drought tolerance	Plants	Ackerly et al. 2006, Savage and Cavender-Bares 2012
Pectoral and pelvic fin length	Habitat use and locomotion	Fish	Pease et al. 2012
Eye size	Depth habitat	Fish	Ingram and Shurin 2009
Wing chord	Temperature constraints	Birds	Graham et al. 2012
Body coloration	Camouflage and habitat use	Ants	Blaimer et al. 2015
Respiration mode	Oxygen constraints	Aquatic insects	Saito et al. 2016
Ability to form resistant structures	Stress tolerance	Bacteria	Goberna et al. 2014