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# The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity[1]

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Patterns of biodiversity are ultimately the product of speciation and extinction. Speciation serves as the biodiversity pump while extinction serves as the agent that culls global to local levels of biodiversity. Linking these central processes to global and local patterns of biodiversity is a key challenge in both ecology and evolution. This challenge necessarily requires a simultaneous consideration of the species, phylogenetic, and functional diversity across space and the tree of life. In this review, I outline a research framework for biodiversity science that considers the evolutionary and ecological processes that generate and cull levels of biodiversity and that influence the inter-relationships between species, phylogenetic, and functional diversity. I argue that a biodiversity synthesis must begin with a consideration of the inherently ecological process of speciation and end with how global biodiversity is filtered into local-scale plant communities. The review ends with a brief outlook on future challenges for those studying biodiversity, including outstanding hypotheses that need testing and key data limitations.

The production and distribution of biodiversity is a major focus of evolutionary biologists and ecologists. Ecologists are often concerned with spatial or temporal trends in levels of biodiversity within a particular study region or across the planet (e.g., Kreft and Jetz, 2007). Evolutionary biologists are often concerned with levels of biodiversity within and across clades (e.g., Magallon and Castillo, 2009). Despite their differing foci and research approaches, both groups are studying biodiversity patterns that result from a shared set of ecological and evolutionary processes. Here, I argue that this fundamental connection creates the framework for a biodiversity synthesis. By considering the influences of ecological and evolutionary processes on biodiversity across space and across the tree of life simultaneously, we can achieve an understanding of biodiversity that spans from its global production to its filtering into local-scale communities (Webb et al., 2002; McGill et al., 2006).

The study of biodiversity has traditionally focused on quantifying patterns of species diversity and determining the ecological and evolutionary processes that have produced the observed patterns (e.g., Rosenzweig, 1995). This work has been fundamental to our understanding of large-scale patterns of biodiversity. While great progress has been made by studying patterns of species diversity, there are limitations to a species-diversity-centered approach, two of which I will highlight here. First, biodiversity is not simply species diversity. Two regions could have the same exact species diversity but wildly different levels of phylogenetic and functional diversity and, therefore, wildly different biodiversities (Faith, 1992; Petchey and Gaston, 2006). Thus, we cannot determine the processes that produce biodiversity by examining only one of its components. Second, and perhaps more importantly, species names are relatively information-poor. They convey little to no information regarding the function or evolutionary history of species—information vital for determining the ecological and evolutionary processes that have combined to produce the observed levels of biodiversity. These inherent limitations of a species-diversity-centered approach suggest that a more pluralistic approach to studying biodiversity is needed to obtain a mechanistic understanding of how patterns of biodiversity are formed (e.g., Webb et al., 2002; McGill et al., 2006). In particular, a biodiversity synthesis will necessarily require consideration of the interrelationships between the three primary components of biodiversity—species diversity, functional diversity, and phylogenetic diversity (Fig. 1).

Implementing a more pluralistic approach in studying biodiversity across the globe and the tree of life is no small feat. Ideally it would require a complete tree of life, a complete map of life, and detailed information regarding the functional ecology of all life. Such an idealized data set does not yet exist, but researchers are making considerable progress by analyzing the three biodiversity components within and across local communities and by analyzing the distribution of functional strategies across the tree of life. Specifically, plant community ecologists are increasingly comparing the levels of species, phylogenetic, and functional diversity in communities in an attempt to identify the relative strengths of the ecological interactions that determine how regional diversity is filtered into local communities. This work has been conducted in species-rich tropical communities (e.g., Swenson et al., 2007; Kraft et al., 2008; Swenson and Enquist, 2009) and in less species-rich temperate communities (e.g., Thompson et al., 1996; Weiher et al., 1998). An interesting finding of this initial work is that the results are generally not system-specific and that plant function is often filtered in predictable ways. Our understanding of patterns of biodiversity has also been spurred by the mapping of plant traits that indicate plant ecological strategies onto very large phylogenetic trees (e.g., Moles et al., 2005). This work has often shown that while there is a considerable degree of global variation in plant traits, closely related species often tend to share similar trait values (Moles et al., 2005; Chave et al., 2006;

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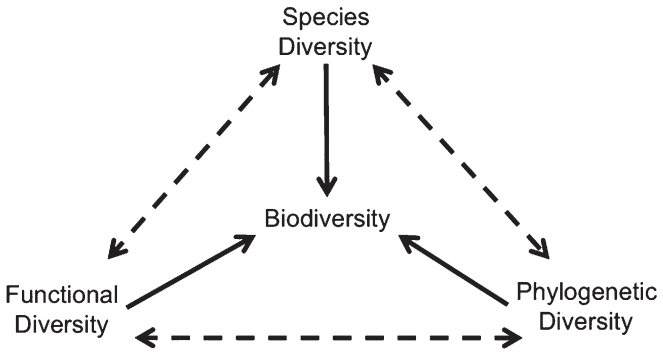


Fig. 1. A triangle representing the three main components of biodiversity. The majority of investigations into the structure of biodiversity have focused on species diversity. Increasingly, investigators have quantified the relationship between two of the triangle's vertices, but few studies have simultaneously quantified all three vertices.

Swenson and Enquist, 2007). Further large divergences in trait values between sister clades occur infrequently on the phylogeny, and they are often clustered within a few regions of the phylogeny (Moles et al., 2005; Swenson and Enquist, 2007). Other work on reproductive traits, such as floral color, that are likely more closely linked with speciation, has found little phylogenetic signal (Sargent and Ackerly, 2008; McEwen and Vamosi, 2010).

Work that considers the filtering of biodiversity from regional pools to local communities and the evolution of function needs to be expanded in scale and scope. In particular, while there is some consistency in results among the studies highlighted above, many more studies are needed to identify any actual generalities. The research should also be expanded to more explicitly link the production of biodiversity to speciation and the role of ecological divergence during and after speciation—in other words, the degree to which species niches are phylogenetically conserved.

The goal of the present review is to begin to outline a framework for how global production of biodiversity is linked to local levels of biodiversity. I will start by discussing the production of biodiversity through the process of speciation and the role of ecology during this process. Specifically, I will outline the linkage between net diversification rates, species diversity, and phylogenetic diversity. I will also present the argument, made by speciation researchers past and present, that speciation generally does not occur in an ecological vacuum and that this has a central role in how we understand the generation of functional diversity.

In the second section, I will discuss how the degree of ecological divergence during and after speciation may vary and how this is expected to influence the interrelationships between species, phylogenetic, and functional diversity. Specifically, ecological divergence between sister taxa can occur along one to many niche dimensions. The degree of that divergence and the identity of those dimensions is critical for our understanding of patterns of biodiversity.

The third section will focus on how regional levels of biodiversity are filtered into local communities and how different filtering processes will influence the interrelationships of species, phylogenetic, and functional diversity across space. Specifically, this section will argue that although regional and local levels of diversity are strongly linked, gradients in the relative importance of different ecological processes or filters across space can alter the relationships among the three components of biodiversity.

The review will conclude with a section that outlines outstanding questions, goals, and key data limitations. In particular, I will focus on fundamental observational and experimental research, yet to be conducted, that could greatly influence how we perceive patterns of biodiversity. I will end by arguing that the generation of global-scale plant biodiversity data sets is critical for a biodiversity synthesis and holds the potential to transform how we study and perceive biodiversity.

## II. NET DIVERSIFICATION, ECOLOGY, AND THE PRODUCTION OF SPECIES, PHYLOGENTIC, AND FUNCTIONAL DIVERSITY

Species and phylogenetic diversity are ultimately produced via the evolutionary process of speciation and tempered via extinction. This net diversification rate (speciation rate − extinction rate) sets the level of species diversity and phylogenetic diversity across space and the tree of life. For example, the latitudinal diversity gradient in its most basic sense is the result of large-scale geographic differences in the rates of speciation and/or extinction (Mittelbach et al., 2007; Weir and Schluter, 2007), but the robustness of the methods used to infer those rates remains heavily debated (e.g., Quental and Marshall, 2009; Rabosky, 2010). Patterns of biodiversity ultimately cannot be understood without a consideration of patterns of speciation and extinction. Net diversification rates determine the raw levels of species and phylogenetic diversity, but they also determine the relationship between species and phylogenetic diversity. Specifically, accelerated net diversification rates will cause species diversity to increase at a faster rate than phylogenetic diversity, and decelerating net diversification rates will cause species diversity to increase at a slower rate than phylognetic diversity.

The production of functional diversity via speciation and extinction is less straightforward than the production of species and phylogenetic diversity. Extinction will limit functional diversity, but whether extinction events are functionally random or not (Nee and May, 1997; Heard and Mooers, 2000; Vamosi and Wilson, 2008) will dictate the degree to which global functional diversity is culled. Speciation may increase global functional diversity, but this is entirely dependent on whether sister species ecologically diverge during and after speciation and by how much. Thus, it is worth considering the degree of ecological divergence during and after the evolutionary process of speciation or, in other words, the degree to which there is phyogenetic niche conservatism.

Before we examine ecological divergence and speciation, I would like to address the term "phylogenetic niche conservatism." In the statistical sense or methodologically, this term is generally used to reflect the degree to which closely related species are more similar than expected given some model, usually Brownian motion, of niche or trait evolution. Thus, sister species can be divergent in their traits or niches but still similar enough to produce a pattern of phylogenetic niche conservatism. This may confuse those unfamiliar with the methods used to quantify phylogenetic niche conservatism, because many view the term as representing an absence of differentiation in niches or traits between sister species or even closely related

species. Thus, the same term is often used interchangeably to describe two very distinct evolutionary patterns. I therefore suggest that "phylogenetic niche similarity" or "phylogenetic trait similarity" be used in the former instance and that "strict phylogenetic niche conservatism" or "strict phylogenetic trait conservatism" be used in the latter instance. It is critical that these distinctions be highlighted and defined before moving on. This review is not the first to discuss alternative perspectives on what "phylogenetic niche conservatism" means; Blomberg and Garland (2002) and Losos (2008) have provided perhaps the best extended discussions on the topic.

Let's begin by considering ecological and nonecological speciation models. Some researchers make the distinction between these two models of speciation (Schluter, 2009) whereas others largely dismiss the notion of nonecological speciation (Mayr, 1947; Sobel et al., 2010). Nonetheless, a consideration of nonecological speciation whereby sister species do not diverge ecologically during speciation is warranted. This results in a pattern of strict phylogenetic niche conservatism so long as sister species do not diverge ecologically after speciation. Strict phylogenetic niche conservatism should result in no increase in functional diversity with speciation and time since species divergence, or there should be a stepwise increase in functional diversity, with step increases in functional diversity arising when "key innovations" (Donoghue, 2005) are evolved or new adaptive zones are invaded (Ricklefs, 2006). A proposed sympatric mechanism of nonecological speciation is polyploid speciation, and proposed allopatric mechanisms are genetic drift and uniform selection between populations. It is important to reiterate that nonecological speciation followed by trait or niche evolution within one or both lineages would not produce a pattern of strict phylogenetic niche conservatism and would result in a pattern of phylogenetic niche or trait similarity.

An ecological speciation model posits that ecological divergence between populations and reproductive isolation are fundamentally intertwined during the speciation process. Sister species, in this model, should be ecologically divergent, and a pattern of strict phylogenetic niche conservatism is rejected in favor of a pattern of phylogenetic niche similarity. Therefore, the only way to support a model of nonecological speciation followed by stabilizing selection on the ancestral niche is to find a pattern of strict niche conservatism, while patterns of phylogenetic niche similarity cannot be used to infer whether speciation was ecological or nonecological.

Ultimately, ecological speciation and postspeciation adaptive divergence produce functional diversity, and the rate of that production depends on the speciation rate and the degree and rate of ecological divergence. This suggests that species, phylogenetic, and functional diversity must be loosely coupled and are likely tightly coupled. In other words, speciation is a functional diversity pump as well as a species and phylogenetic diversity pump, but the magnitude of functional diversity produced in relation to species and phylogenetic diversity critically relies on the degree and rate of niche or trait divergences between sister lineages.

## III. ECOLOGICAL DIVERGENCE, DISPERSAL, AND THE INTERRELATIONSHIPS OF BIODIVERSITY COMPONENTS

In the previous section, I discussed the linkage between functional diversity and species and phylogenetic diversity. These three components of biodiversity are not likely to increase at the same rate through space or through time. In this section, I will discuss how different ecological and evolutionary processes should alter the relative levels of the three biodiversity components along the tree of life and in a region.

The first relationship I will examine is between species and phylogenetic diversity. I will generically define species diversity as the number of lineages at a certain time slice on the phylogeny or the number of species represented in a given region, and phylogenetic diversity as the total length of the phylogenetic branches prior to a certain time slice on the phylogeny or represented in a given region. The relative acceleration or deceleration of the net diversification rate determines the relationship between species (or lineage) and phylogenetic diversities (Fig. 2). Thus, in two regions with equal numbers of species, phylogenetic diversity should be lower in a region with recent speciation events and/or accelerating extinction rates and higher in a region with older speciation events and/or decelerating extinction rates. Of course not all members of a clade are found only in one region, regions vary in their levels of species diversity, and net diversification rates vary across the tree of life, but the general relationships between diversification rates and the species diversity–phylogenetic diversity relationship provide a basic framework for understanding patterns of species and phylogenetic diversity.

Ecological divergence between sister species during and after speciation dictates that species and functional diversity are positively associated. The positive relationship between ecological divergence and levels of reproductive isolation (e.g., Funk et al., 2006) shows that strict phylogenetic niche conservatism is generally the exception and not the rule. Given the importance of this suggestion and the general interest in phylogenetic niche conservatism and phylogenetic niche similarity in ecology (e.g., Wiens and Graham, 2005; Wiens et al., 2010), it is worthwhile here to quickly make some qualifying statements regarding ecological divergence, strict phylogenetic niche conservatism, and the similarity of closely related species. First, it is important to note that although strict phylogenetic niche conservatism is generally unlikely and unsupported, closely related species in the coarse sense are still likely more similar to one another than distantly related species (Moles et al., 2005; Swenson and Enquist, 2007). Indeed, two sister species of palm are likely much more ecologically similar to one another than they are to a sunflower, but this is not strict phylogenetic niche conservatism as defined above, because the two sister species of palm are ecologically divergent. Second, what is important is the degree to which closely related species have ecologically diversified and along which niche axis or axes. Many sister species may have ecologically diversified only slightly, particularly if speciation occurred during allopatry. For example, sister species may have diversified with respect to their flower color (Sargent and Ackerly, 2008; McEwen and Vamosi, 2010) while in allopatry as a result of different biotic interaction matrices. This diversification could have fundamentally altered the pollination or reproductive ecologies of the sister species, but it may have little influence on how the sister species respond to broad-scale temperature and precipitation gradients. Thus, these once allopatric species may disperse, experience secondary contact, and, ultimately, coexist at the same location along a resource gradient, but this does not mean that their ecological niches are strictly conserved in their entirety or that strict phylogenetic niche conservatism explains their distributions. It is important to note that a key trait or series of key traits linked to

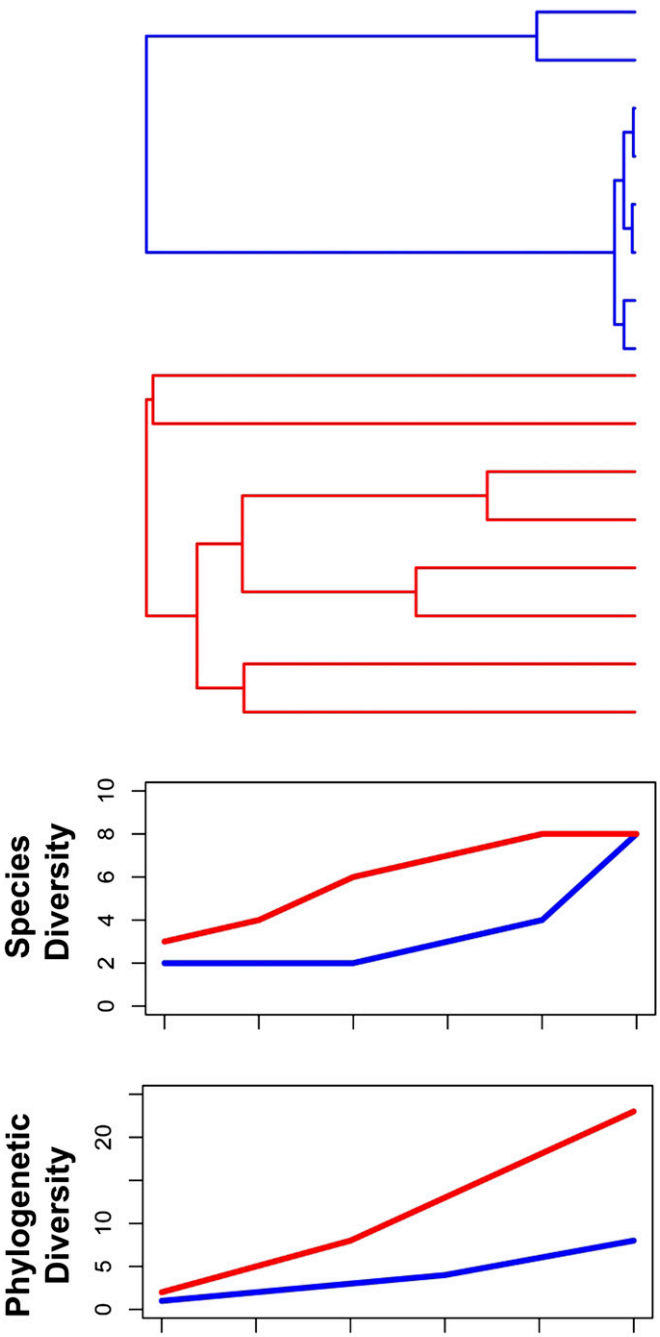


Fig. 2. The accumulation of lineages and phylogenetic diversity through time in two phylogenies. The blue phylogeny represents an acceleration of net diversification, and the red phylogeny represents a deceleration. Both phylogenies ultimately produce the same number of species, but the accumulated branch lengths (i.e., phylogenetic diversity) in the red phylogeny is much higher because of early diversification.

the broad-scale distribution of a species may have a pattern of strict trait conservatism, whereas a key trait or series of key traits linked to local-scale distributions and coexistence may not have a pattern of strict phylogenetic trait conservatism or even phylogenetic trait similarity. Such a scenario is directly linked to the concept of alpha and beta niches or alpha and beta traits and their evolution (Ackerly et al., 2006; Ackerly and Cornwell, 2007). Beta traits are linked to the distribution and fitness of species along broader-scale environmental gradients, whereas alpha traits are linked to the distribution and fitness of species within a particular assemblage. A prediction from an allopatric speciation model may be that beta traits and niches have strict phylogenetic conservatism whereas alpha traits and niches diverge, thereby allowing the coexistence of sister species. In sum, while sister species are generally ecologically divergent and strict phylogenetic niche conservatism is rare or absent, the degree of ecological divergence between sister species may be slight compared with the global range of ecological strategies, producing a pattern of phylogenetic niche or trait similarity. Thus, a consideration of which niche axes have diverged is critical for understanding broad- and fine-scale patterns of biodiversity.

Although species and functional diversity must be positively related, identifying the degree of ecological divergence is important, not only for understanding the distribution and coexistence of related species, but also more generally with respect to the species diversity–functional diversity relationship. Specifically, the degree and rate of ecological divergence determine the relationship between functional diversity and species diversity in much the same way that the net diversification rate influences the species diversity–phylogenetic diversity relationship. For example, an initial adaptive radiation of a clade followed by a finer partitioning of a confined niche space (i.e., a decelerating rate of ecological disparity) or convergence will ultimately lead to species diversity accumulating at a faster overall rate than functional diversity. Thus, the overall volume of niches occupied or functional diversity in a species-rich region is expected to be the same as that found in a less species-rich region (Fig. 3) . Conversely, if speciation results in a continual expansion of ecological niche space (i.e., the rate of ecological disparity is consistent through time), then functional diversity will accumulate at a rate similar to that of species diversity. In this scenario, the overall volume of niches occupied or functional diversity in a species-rich region is expected to be larger than that found in a species-poor region (Fig. 3).

The influence of ecological divergence on the functional diversity–phylogenetic diversity relationship is similar to its influence on the functional diversity–species diversity relationship, with one exception. Rates of functional evolution may vary along the length of branches in the phylogenetic tree, and commonly used measures of phylogenetic signal in trait data test the degree to which the observed rate of trait evolution differs from that expected under Brownian motion (e.g., Blomberg et al., 2003). Accelerating rates of trait evolution in relation to branch lengths will generate a general increase in functional diversity in relation to phylogenetic diversity. Decelerating rates of trait evolution in relation to branch lengths will generate a decrease in functional diversity in relation to phylogenetic diversity.

The interrelationships between species, phylogenetic, and functional diversity described above assume that species are not limited by dispersal and that speciation is sympatric. These are flawed assumptions—generally, species are dispersal-limited and the majority of speciation events likely occur in allopatry. Thus, a consideration of dispersal limitation is required. In general, dispersal limitation should be expected to increase the species and phylogenetic diversity via allopatric speciation. Conversely, dispersal limitation is not necessarily expected to increase the functional diversity of an area at the same rate of increase as species and phylogenetic diversity. This is because

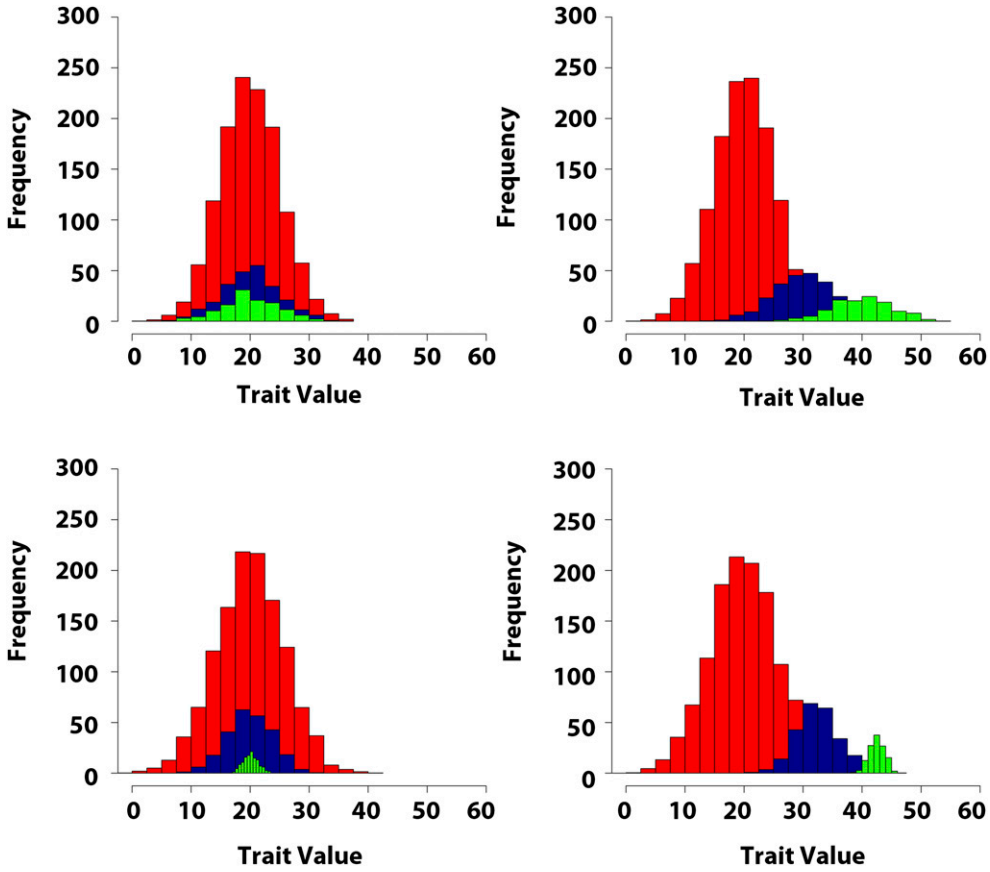


Fig. 3. The trait distribution in three hypothetical communities that have varying levels of species richness. In the top panels, the community morphological volume increases with species richness. In the bottom panels, species are packed more tightly into a constrained morphological volume as species richness increases. This figure is used here to introduce the general idea of trait packing versus volume filling, but note that both likely occur simultaneously along species richness gradients.

ecological divergences between sister species can be expected to be lower, on average, when speciation is allopatric. Dispersal limitation should also increase the degree of niche similarity and, therefore, not increase the global functional diversity. Thus, in areas where species are more dispersal-limited, we can expect a level of species and phylogenetic diversity that is relatively higher than the functional diversity.

The above suggests that phylogenetic diversity will be maximized in situations in which an early burst is followed by a deceleration of net diversification and in which dispersal limitation is high, and functional diversity will be maximized in relation to species diversity. These processes set the global pool of species, phylogenetic, and functional diversity that is eventually filtered into local plant communities. The next section will discuss possible filtering processes and how they influence the regional–local biodiversity relationship.

## IV. ECOLOGICAL FILTERING, DISPERSAL, AND THE REGIONAL–LOCAL BIODIVERSITY RELATIONSHIP

Regional biodiversity is ultimately the result of three processes—speciation, extinction, and dispersal. Quantifying how these three processes vary across regions provides the foundation for our understanding of how broad-scale gradients in biodiversity are produced. The strong relationship between regional and local biodiversity and biodiversity disparities between assemblages in similar climates on different continents suggest that regional biodiversity and historical contingency play a large role in setting local biodiversity levels (see Ricklefs, 2004).

Despite the reality that regional diversity explains a large amount of the variability in local diversity, there is a considerable amount of variation in local diversity within regions, and previous work suggests that regional biodiversity can be filtered into local assemblages disproportionately within and across regions. This differential filtering will influence the interrelationships between species, phylogenetic, and functional diversity in local assemblages. In this section, I will focus first on the filtering of regional biodiversity into local communities generically and then on the possibility of differential filtering along intra- and interregional gradients.

The biodiversity of a region plays a central role in setting local community diversity, but a tremendous debate has formed around whether local communities are simply a random sampling of the regional pool. Much of this early debate concerned taxonomic ratios (i.e., genus-to-species ratios) and null models (e.g., Elton, 1946; Simberloff, 1970; Jarvinen, 1982). This taxonomic-ratio literature grew into the phylogenetic community-ecology literature (Webb, 2000; Webb et al., 2002), which refined taxonomic ratios by using phylogenetic branch lengths. Both approaches generally ask the same question: is the local

phylogenetic diversity higher or lower than expected given the species diversity and a random draw from some larger pool.

The evidence to date primarily shows that regional phylogenetic diversity is filtered nonrandomly into local communities: in meso-scale assemblages, phylogenetic diversity is less than expected given the species diversity, whereas in very localized assemblages there is often higher-than-expected phylogenetic diversity given the species diversity (e.g., Cavender-Bares et al., 2006; Swenson et al., 2006, 2007; Vamosi et al., 2009; Kraft and Ackerly 2010). There are exceptions to these emergent patterns, but they are fairly rare. The degree to which the total results from the community phylogenetics literature indicate whether coexisting species are ecologically similar or dissimilar critically depends on the degree to which closely related species are ecologically similar, or, in other words, the degree to which there is phylogenetic niche similarity (Webb et al., 2002). It can also be difficult to strongly infer ecological processes from these phylogenetic patterns even if closely related species are ecologically similar, because multiple mechanisms could result in the same pattern (Cavender-Bares et al., 2009; Swenson and Enquist, 2009). What can be concluded from this work, though, is that the phylogenetic diversity of local communities is not simply an equivalent proportion of the regional phylogenetic diversity and that it is typically a smaller-than-expected fraction of the regional phylogenetic diversity.

The filtering of regional functional diversity into local communities has proved to be much more difficult to quantify than the filtering of phylogenetic diversity. The studies that have been published to date, though, have found evidence somewhat similar to that found for phylogenetic diversity. Specifically, the local functional diversity is generally lower than expected given the regional functional diversity at meso-scales (e.g., Thompson et al., 1996; Swenson and Enquist, 2007, 2009; Kraft et al., 2008). The fine-scale patterns of functional diversity are not necessarily consistent, and part of this may be that researchers often examine individual trait diversities and have found that locally some traits have higher-than-expected diversity whereas others have lower-than-expected diversity. Interestingly, these opposing patterns are somewhat consistent across the few studies that have examined similar types of traits (Swenson and Enquist, 2009). In particular, traits indicative of light and regeneration niches (i.e., maximum height, seed mass) often express higher-than-expected diversity locally, and traits indicative of resource acquisition rates (i.e., the leaf economics spectrum, wood density) often express lower-than-expected diversity locally. It is likely that these results reflect differential partitioning of broad- and fine-scale abiotic gradients whereby traits related to light and regeneration niches partition fine-scale gradients and resource-acquisition-related traits partition broader-scale gradients (Swenson and Enquist, 2009). This prediction seems to be supported by stronger global scale trait–climate relationships for leaf economics and wood density than those found for seed mass and maximum height (Wright et al., 2004; Moles et al., 2007; Swenson and Enquist, 2007; Chave et al., 2009; Moles et al., 2009). Thus, the preliminary evidence suggests that not only is local functional diversity a nonrandom and constrained subset of the regional functional diversity, but the diversity of individual traits is differentially influenced across scales and communities.

The above studies are generally consistent in their finding that regional diversity is typically nonrandomly filtered into local communities. Fewer studies have been able to quantify the strength of the filtering across significant ecological gradients within and across regions. A stress-gradient hypothesis (Weiher and Keddy, 1995) has typically been proposed as a potential mechanism for intraregional differential filtering of phylogenetic and functional diversity. A stress-gradient hypothesis predicts that regional phylogenetic or functional diversity is filtered to a greater degree in local communities that occur in abiotically harsher habitats and is less filtered in benign habitats. The few detailed tests of this hypothesis have found mixed results, with some rejecting the stress-gradient hypothesis (e.g., Bryant et al., 2008) and others finding stronger support (e.g., Cornwell and Ackerly, 2009). Thus, the generality of the stress-gradient hypothesis with regard to patterns of functional and phylogenetic diversity filtering along gradients within regions is still unclear, and we await the results from more investigations from a broader variety of regions.

A stress-gradient hypothesis has also been proposed in comparing the differential filtering of regional functional diversity across different regions. Specifically, it has been proposed that in less climatically benign temperate environments, functional diversity should be more filtered than in more climatically benign tropical regions. To date, only one published study has clearly tested this hypothesis in plant communities, and it used only a single plant trait (Swenson and Enquist, 2007). Specifically, Swenson and Enquist (2007) found general support for a stress-gradient hypothesis when examining the filtering of wood density in tree communities along a latitudinal gradient. Additional work on several other often-measured plant functional traits suggests that a stress-gradient hypothesis is generally supported when comparing assemblages across latitudes (Swenson et al. unpublished data). The above suggests that although differential filtering of functional and phylogenetic diversity occurs within and across regions, patterns within regions have been mixed. Evidence for a stress gradient across regions is stronger, but the number of studies is quite low. More broad-scale comparative analyses will be needed to determine whether any generality, and perhaps mechanism, can be found that would help explain why differential patterns of functional and phylogenetic filtering occur.

## V. OUTSTANDING QUESTIONS, GOALS, AND KEY DATA LIMITATIONS

The general goal of identifying the causal mechanism underlying biodiversity patterns on Earth will be difficult to achieve. Seemingly simple tasks such as building a comprehensive list of the world's plant species will prove daunting, and even large-scale observational and experimental studies of plant communities have been a challenge. For example, we lack an answer to the fundamental question of whether species-rich tropical plant communities simply pack more functionally similar species into a confined functional volume or whether tropical communities house a greater range of functions (Fig. 3). Limiting similarity (MacArthur and Levins, 1967) would predict that tropical communities should have a greater functional volume than temperate communities, but this has been tested only rarely in animals, and with mixed results (e.g., Shepherd, 1998: Roy et al., 2000; Ricklefs, 2009). Answering this question would provide strong baseline information regarding the ecological and evolutionary processes that structure plant communities across latitudes, and it would allow robust tests of whether the relative rate of increase in functional diversity from the temperate zone to the tropics is faster or slower than the rate of increase in

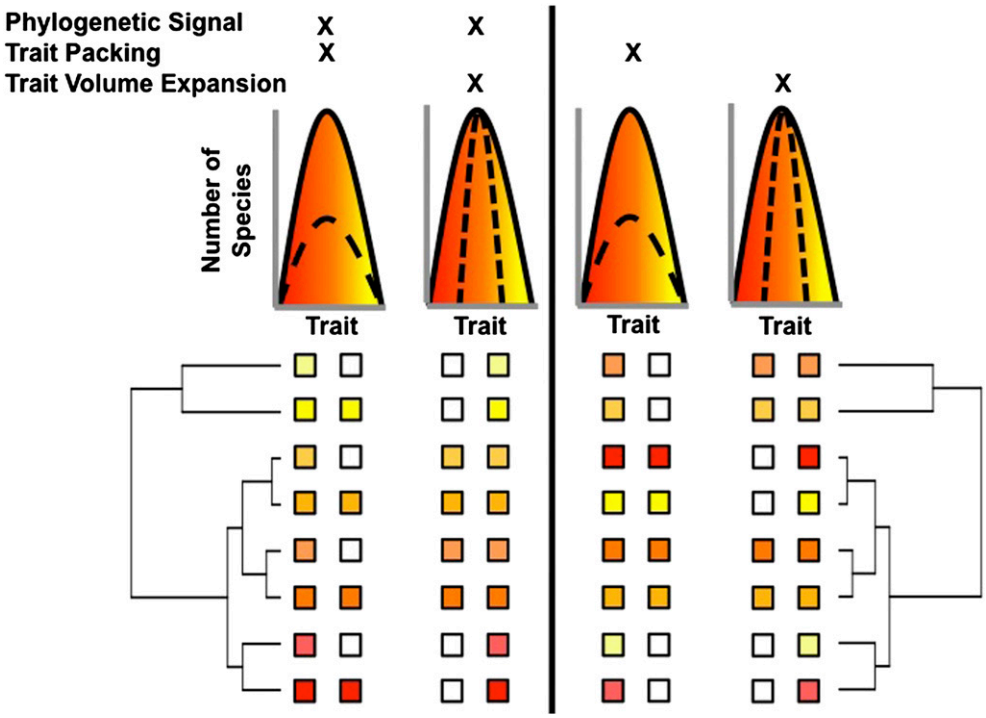


Fig. 4. This figure depicts the potential ways in which trait packing versus volume expansion could be influenced by the presence of novel clades. In the phylogeny on the left, there is phylogenetic signal in the trait data (i.e., closely related species are functionally similar, but not identical). In the phylogeny on the right, there is no phylogenetic signal in the trait data. On the left, functional volume expansion or packing is mirrored by phylogenetic volume expansion or packing. On the right, functional packing or volume expansion is not mirrored phylogenetically.

species diversity. Lastly, examining these patterns in the light of a phylogenetic tree would allow one to determine how much the presence of novel clades influences the packing or expansion of functional volumes in tropical communities (Fig. 4).

Another goal for the study of biodiversity should be broad-scale experimental investigations. Experimental studies would allow for stronger inferences regarding the mechanisms that produce gradients in biodiversity and the linkages between species, phylogenetic, and functional communities. In some cases, such as tree communities, experimentation may be difficult, but "natural" experiments such as studying latitudinal gradients in biodiversity in successional forests with known histories may yield important insights into how regional diversity is filtered during community assembly.

Finally, quantifying the degree and type of ecological divergence between sets of sister species pairs across latitude would provide the most basic building blocks for a synthesis of species, phylogenetic, and functional diversity patterns. For example, is there a latitudinal gradient in ecological divergence size between sister species? Do tropical species tend to differentiate along niche axes that are more related to biotic interactions? Do sister species tend to differentiate along niche axes that are related to broad-scale climatic gradients, fine-scale gradients, biotic interactions? Answering these seemingly simple questions could be tremendously powerful and beneficial to both ecologists and evolutionary biologists studying biodiversity patterns.

Quantifying patterns in biodiversity has been a major research objective for plant ecologists and evolutionary biologists for quite some time, but in many ways the study of plant biodiversity is still in its infancy. Indeed, we are only now beginning to generate estimates of the global distribution of species diversity (Kreft and Jetz, 2007). Such estimates are undoubtedly destined for major revisions, and we have even less information regarding the geographic distribution of functional and phylogenetic diversity. This data limitation, particularly in the tropics, has hindered our ability to generate a biodiversity synthesis, but these obstacles are increasingly being eroded through large-scale data collection and compilation (e.g., Wright et al., 2004; Moles et al., 2005; Kraft et al., 2008; Chave et al., 2009; Kress et al., 2009; Swenson and Enquist, 2009) and novel methods for generating large phylogenetic trees (e.g., Smith et al., 2009). Ultimately, to understand the evolutionary and ecological processes underlying biodiversity patterns and to predict the fate of biodiversity in the future, we must first inventory our biodiversity and map it onto the tree of life and onto the globe.

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