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IDEA AND PERSPECTIVE

Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time

Catherine H. Graham[1*†] **and Paul V. A. Fine**[2†]
[1] *Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY, USA*
[2] *Department of Integrative Biology, University of California, Berkeley, CA, USA*
**Correspondence: E-mail: cgraham@life.bio.sunysb.edu*
† Both the authors contributed equally.

Abstract

A key challenge in ecological research is to integrate data from different scales to evaluate the ecological and evolutionary mechanisms that influence current patterns of biological diversity. We build on recent attempts to incorporate phylogenetic information into traditional diversity analyses and on existing research on beta diversity and phylogenetic community ecology. Phylogenetic beta diversity (phylobetadiversity) measures the phylogenetic distance among communities and as such allows us to connect local processes, such as biotic interactions and environmental filtering, with more regional processes including trait evolution and speciation. When combined with traditional measures of beta diversity, environmental gradient analyses or ecological niche modelling, phylobetadiversity can provide significant and novel insights into the mechanisms underlying current patterns of biological diversity.

Keywords

Alpha diversity, beta diversity, community phylogenetics, ecological niche modelling, phylobetadiversity, phylogenetic beta diversity.

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INTRODUCTION

The mechanisms that generate and maintain species diversity vary depending on the taxonomic, spatial and temporal scale over which they are quantified. For instance, at regional scales, diversity gradients are strongly influenced by both evolutionary factors, such as variation in the timing and rate of lineage diversification, and ecological factors, including current and past expanse of suitable habitat (Wiens & Donoghue 2004; Cardillo *et al.* 2005; Graham *et al.* 2006; Ricklefs 2006; Weir & Schluter 2007). At local scales, research integrating community ecology and phylogenetics has emphasized the importance of biotic interactions and trait evolution in community assembly (Webb *et al.* 2002, 2006; Cavender-Bares *et al.* 2004; Kembel & Hubbell 2006; Maherali & Klironomos 2007). A key challenge is to elucidate how processes at these different scales interact to connect local processes (e.g. coexistence, environmental filtering) with more regional, evolutionary processes (e.g. trait evolution, habitat specialization, and speciation). Phylogenetic beta diversity (phylobetadiversity) measures how phylogenetic relatedness changes across space in much the same way that beta diversity measures how species composition changes across space. As such, it provides an evolutionary approach to evaluate how community structure and the associated traits of species in a community change as a function of both spatial and environmental gradients (Chave *et al.* 2007). We show how applying this framework to a series of topics in ecology and evolution promises to substantially advance our understanding of the mechanisms underlying the origin and maintenance of biodiversity patterns.

The use of phylogenies is increasingly common in community ecology to understand the origins and histories of species within a community (i.e. alpha diversity) and explore theories about the influence of historical and ecological factors in structuring communities (e.g. Ricklefs & Schluter 1993; Losos 1996; Webb *et al.* 2002). In a seminal paper, Webb *et al.* (2002) developed the field of community phylogenetics, which uses a phylogenetic framework to evaluate how different ecological processes (ecological filtering, competition, dispersal) interact with evolutionary processes (speciation and extinction) to influence the distribution of species and traits in communities. The central idea is that given a phylogeny of available lineages and a rate of evolution for functional traits, we expect different patterns of phylogenetic and phenotypic community structure depending on whether competition or ecological filtering is the primary driver influencing community assembly (Webb *et al.* 2002). For example, co-occurring oaks in Florida are phylogenetically overdispersed, suggesting that competition among close relatives (and/or ecological speciation) restricts close relatives from inhabiting the same local communities (Cavender-Bares *et al.* 2004, 2006).

Beta diversity (often referred to as turnover) is the change in species composition across geographic space (Whittaker 1960, 1972) and can be calculated many different ways (Koleff *et al.* 2003). The concept has been used extensively in ecology to study a variety of phenomenon such as the relationship between local and regional diversity, or the relative importance of current or historical environmental factors influencing species turnover (e.g. Tuomisto *et al.* 2003; Qian *et al.* 2005; Graham *et al.* 2006; Qian & Ricklefs 2007). While beta diversity effectively captures the amount of overlap in species composition between sites (habitats, geographic regions), it does not provide information about how deep in evolutionary time these lineages have been separated, which can provide very different insights about the ecological, historical and evolutionary processes that structure communities (Chave *et al.* 2007; Hardy & Senterre 2007). For example, the temperate tree floras of East Asia, western North America, eastern North America and Europe have almost no tree species in common, and thus each has a beta diversity of one compared with the other three (i.e. the maximum amount of species turnover between regions if compositional dissimilarity is calculated). However, from a more evolutionary perspective, the regions are not equally dissimilar, and can be compared in terms of their relative phylogenetic similarity which is dependent on connectivity among regions combined with speciation and extinction within each of the four regions (Latham & Ricklefs 1993; Qian 2001; Donoghue & Smith 2004). Comparing the regional phylogenies of each of these four tree floras affords the opportunity to address additional questions beyond simply how many genera or families overlap between two different regions. For example, phylobetadiversity can elucidate which lineages are driving turnover patterns between regions and during which time periods, or provide insight regarding the relative importance of *in situ* diversification vs. differential extinction in driving patterns of extant diversity and species compositions.

Research in community phylogenetics and beta diversity provides a fundamental advance in our understanding of how evolutionary and ecological factors interact to influence current patterns of diversity across broad spatial scales. We believe that extending these fields to include a phylogenetic component of beta diversity will allow us to rigorously evaluate how biotic interactions, phylogenetic constraints, current and past geographic isolation and environmental gradients interact to produce observed patterns of diversity, effectively unravelling the relative importance of processes acting across spatial scales. In this essay, we describe how to measure phylobetadiversity and explore how phylobetadiversity extends current approaches in community ecology and phylogenetics. We then show how current topics in ecology and evolution, such as ecological neutral theory, community structure and speciation could benefit from considering the phylogenetic component of beta diversity. The greater availability of well-resolved, and comprehensive phylogenetic data for many organisms will continue to afford a more rigorous examination of the phylogenetic basis of turnover of species composition across space and time, an approach that we argue, will provide many new insights into fundamental questions about the distribution of diversity.

PHYLOBETADIVERSITY: DEFINITION, MEASUREMENT AND COMPARISON TO CURRENT APPROACHES

Phylobetadiversity can expand on two dimensions of biodiversity research, time and space, which are important foci of macroecological and biogeographical theory. Phylobetadiversity is beta diversity with a temporal dimension; defined as the phylogenetic distance (branch lengths) between samples of individual organisms between any two sites on the planet. The beta diversity and phylobetadiversity between two sites would be exactly the same if every species in the regional pool were equally related to every other one (a giant star-phylogeny). However, this is not likely given that populations and species have different ages of common ancestry and divergent histories. Moreover, in analogy with beta (change in species composition across space) diversity, phylobetadiversity quantifies how phylogenetic relationships among species change across space. As such, phylobetadiversity extends research on phylogenetic community assembly (i.e. Webb *et al.* 2002) and geographic mapping of phylogenetic diversity (e.g. Soutullo *et al.* 2005; Davies *et al.* 2007; Forest *et al.* 2007) by explicitly quantifying the change in phylogenetic patterns across geographic space, often as a function of environmental gradients and geographic barriers.

A hypothetical example

Imagine two islands, each of which contains two habitat types, wet and dry forest (Fig. 1a) where samples of palm community composition are taken from each habitat type in each region. By exploring the different combinations of dispersal limitation and niche conservatism or lability at the extremes, we present five hypothetical clade types which reflect the relative influence of geographical and ecological (habitat) factors that drive patterns of phylobetadiversity

(Fig. 1b). Note that clade type 5 is not structured by geography or habitat, and thus represents a null expectation. If lineages are structured by geography (dispersal limitation) there should be large phylobetadiversity values between islands regardless of habitat affinity (Fig. 1c, clade types 1–3), whereas lineages with high dispersal abilities should have low or random phylobetadiversity between islands (Fig. 1b, clade types 4 and 5). If lineages exhibit phylogenetic niche conservatism we expect species to sort by habitat (Fig. 1b clade types 1, 2, and 4), whereas if niches are labile, closely-related species are predicted to exist in different habitats (Fig. 1b clade type 3). We acknowledge that clades in nature are not likely to be as clearly diagnosable as the five clade types depicted in Fig. 1b, nonetheless, the extent to which phylobetadiversity patterns differ from clade type 5 with increasing geographic scale (the *y*-axes in Fig. 1c) and increasing environmental heterogeneity (the difference between within-habitat and between-habitat lines along the *x*-axes in Fig. 1c) allows one to investigate the extent to which niche conservatism vs. lability, and dispersal limitation are operating within the region of interest.

Our example is simplistic: only two habitats exist, geographic regions (island) are isolated, no species are found in more than one habitat or more than one island, and no samples were taken along more subtle gradients (i.e. along an elevation gradient in the mountain). In nature we are confronted with difficult-to-delineate communities that interact in complex ways across environmental gradients and geographic distance. Because of this complexity, as we will argue in the next section, measures of phylobetadiversity offer additional insight into community assembly beyond what are offered by traditional approaches that incorporate only beta diversity, phylogenies or community phylogenetic structure.

Phylobetadiversity and related approaches in phylogenetics and community ecology

Phylobetadiversity and phylogenetic community ecology

Phylogenetic community ecology explores how historical and ecological factors interact to structure local communities (Webb *et al.* 2002, 2006). Nonrandom patterns of phylogenetic structure can result from environmental filtering (phylogenetic clustering when traits are conserved) or biotic interactions, including competitive exclusion as well as attack from natural enemies (phylogenetic overdispersion when traits are conserved). In Fig. 1, one could imagine that communities within habitat types might be experiencing competitive interactions, such that close relatives would not be found in the same community. Yet, this pattern of overdispersion would only be apparent if the null model was based on a narrowly defined species pool (i.e. only the palms from one island and/or one of the habitat types) – using a reference pool of all of the palms found on island 1 and island 2 obscures this pattern. If one is interested in investigating whether competitive interactions are causing phylogenetic overdispersion at the local scale, it is critical that an appropriate species pool be used (Cavender-Bares *et al.* 2006; Swenson *et al.* 2006). This highlights the scale problem inherent in community phylogenetic structure studies. Researchers have overcome this difficulty by evaluating the influence of scale on patterns of clustering vs. overdispersion at progressively larger spatial extents (i.e. based on some neighbourhood around a given community) and evaluating variation in phylogenetic community structure across these extents (Cavender-Bares *et al.* 2006; Kembel & Hubbell 2006; Kraft *et al.* 2007).

Phylobetadiversity offers a complementary approach to phylogenetic community assembly. Investigating phylobetadiversity comparisons along a continuous spatial scale will remove the subjectivity that is introduced when investigators define their communities by steadily increasing spatial scales. For example, at a small spatial scale, competitive exclusion (or attack by natural enemies) that limits coexistence by close relatives within a community should result in low phylobetadiversity measures coupled with high beta diversity measures between communities of a similar habitat type. When studying how species composition changes across space either from a species or phylogenetic perspective a researcher can choose communities to explicitly control for the distance among communities and the type of environmental conditions within and between communities (see Quantifying phylobetadiversity below). By capturing how relatedness of communities varies from point to point across a specific landscape, the study of phylobetadiversity allows one to ask 'where in geographic space is there signal in phylogenetic turnover?' rather than the more abstract 'what is an appropriate community size and do we have clustering or overdispersion in that community?' What is unique about phylobetadiversity is that, by retaining pairwise information, it allows one to pinpoint in space where patterns of community structure change. As a result, changes correlated with geographical features, or environmental gradients, are more readily identified than when communities are simply pooled across multiple spatial extents.

Phylobetadiversity in relation to spatial and taxonomic scale

It is well established that ecological and evolutionary processes may influence community composition at different scales. For example, phylogenetic structure is often hierarchically nested (clustering at the plot level, overdispersion at the community level and clustering again at the regional level, Cavender-Bares *et al.* 2006). As discussed above, this structure can be detected by conducting phylobetadiversity comparisons at increasing spatial scales, and by including a wide variety of environmental variables. To be effective, such analyses should cover a spatial scale appropriate for the research question at hand. For example, many comparisons within small spatial scales are unlikely to be informative for studying mechanisms such as speciation, because for most organisms (but not all) speciation and extinction are a result of regional, not local, processes (Ricklefs & Schluter 1993; Ricklefs 2004). In the study of such processes, sampling should limit the overlap in species composition between all the communities sampled (i.e. maximize beta diversity). It is also possible to use phylobetadiversity analyses to determine the scale (either spatial or environmental) where patterns change from being clustered to being overdispersed. Thus, phylobetadiversity analyses allow one to investigate the specific geographic scale where changes in patterns of community phylogenetic structure occur for any group of lineages, or a range of environmental variation in a region.

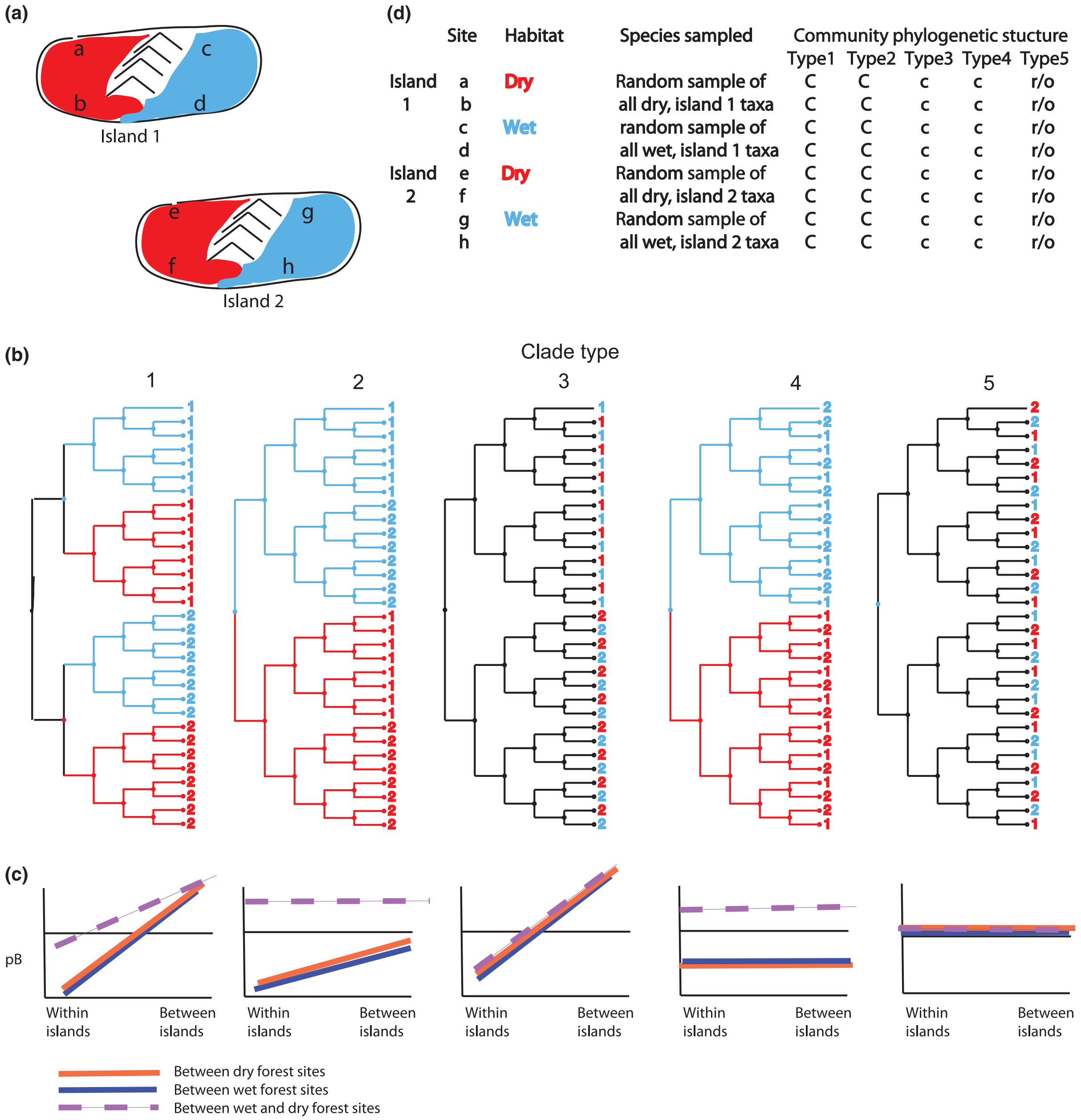
Phylobetadiversity approaches are particularly powerful if there are concordant patterns of geographic structuring or niche conservatism that result in ecological structuring among the *many clades* within the two communities being sampled. Strong concordance within distantly related lineages may indicate a common mechanism of community assembly and/or speciation at a regional scale (Avise 2000; Carstens *et al.* 2005). Alternatively, it is possible that if some of the clades have geographic structure and others have ecological structure, then a random pattern of phylogenetic diversity could result that will mirror the null expectation that geography and ecology play no role in phylogenetic relatedness. This random result may be caused by the taxonomic scale of the analyses and should be further explored by narrowing the taxonomic scale of analysis by picking focal clades from the community-wide sample (Cavender-Bares *et al.* 2006; Kembel & Hubbell 2006; Swenson *et al.* 2006). More broadly, studies of focal clades will be more likely to identify the influence of recent speciation, but will suffer from low statistical power if there are only a few species sampled. In contrast, large clades (encompassing larger numbers of species) are less likely to be well-resolved and as a result will not yield insight into patterns of recent speciation, but instead are likely to provide information about regional speciation, extinction, and biogeographical patterns from older time periods.

Phylobetadiversity and mapping habitat characteristics onto phylogenies

A phylobetadiversity approach can complement phylogenetic analyses of niche conservatism vs. lability and dispersal limitation. In phylogenetic analyses a trait is generally assigned a single value (i.e. a mean) and mapped onto a phylogeny (but see Felsenstein 2008). While this approach is straightforward and may provide sufficient

Figure 1 (a) Two islands, separated by 100 km of open ocean. Each island has a small mountain range in its centre, creating a rain shadow. Red areas represent dry forest, blue areas represent wet forest. In each island, community samples of all palm trees have been conducted at four one-hectare sites, two in each habitat type, separated by 25 km. Island 1 has been sampled four times, site a and site b in dry forest, and site c and site d in wet forest. Island 2 has been sampled four times, site e and site f in dry forest, and site g and site h in wet forest. (b) Hypothetical phylogenies of the palms from Island 1 and Island 2, exploring different combinations of geographical and ecological (habitat) structure. For simplicity, all species are restricted to only one habitat type and only one island, so all five of the phylogenies exhibit some degree of dispersal limitation and niche conservatism at the level of species. Clade type 1 is primarily structured by geography, and secondarily structured by habitat. Clade type 2 is primarily structured by habitat and secondarily structured by geography. Both of these clades exhibit niche conservatism with respect to wet and dry forest, and dispersal limitation with respect to island. Clade type 3 is structured by geography but not habitat and exhibits niche lability and dispersal limitation. Clade type 4 is structured by habitat but not by geography and exhibits niche conservatism but no dispersal limitation. Clade type 5 exhibits random structure with respect to geography and habitat and is the basis for the null expectation for the phylobetadiversity graphs in part C. For each hypothetical phylogeny, see Table in part D to see what pattern of community phylogenetic structure would arise in each site, and the graphs in part C for phylobetadiversity measures among sites of similar habitat type and between habitats, within and between islands. (c) Phylobetadiversity measures among sites of similar habitat type (red lines indicate comparisons among dry forest sites, blue lines indicate comparisons among wet forest sites) and among divergent habitat types (purple dashed lines indicate comparisons among wet and dry forest sites). The x-axes represent spatial scale, and smaller values on this axis represent within island comparisons. The horizontal line in the graphs are the null expectation of phylobetadiversity among sites given no geographic or ecological structure (see clade type 5). Points below the line indicate lower than expected phylobetadiversity and points above the line indicate higher than expected phylobetadiversity. For this example, site comparisons are presented as either between habitat types or within habitat types, but this kind of analysis could also be undertaken comparing sites with low vs. high variance in a particular environmental variable (with respect to region-wide sampling). (d) A Table showing for each site, a–h, the habitat type and the species of palms sampled in each site. For example, site 'a' contains a random sample of all dry forest palms found in Island 1 (see part B). On the right, the table shows what the pattern of community phylogenetic structure within each site, depending on what clade type the palms belonged to (see part B). Big 'C', strong phylogenetic clustering (the sample of species is more closely related than a random expectation); little 'c', weak phylogenetic clustering; r/o, random patterns and/or phylogenetic overdispersion (the sample of species within a community is less closely related than a random expectation; see Webb *et al.* 2002). Note that for clade types 1–4, all community samples are predicted to exhibit phylogenetic clustering.

insight into the trait in question, it can also be misleading. For example, a species with a broad range of environmental tolerances could have an average trait value similar to that of the species possessing a narrow range of tolerance leading to the conclusion that the niches inhabited by the two species are similar. As an example, in a study of Burseraceae trees and habitat specialization in the Western Amazon, Fine *et al.* (2005) found that about three quarters of the species were restricted to a single soil type, while the rest could be found in two different soil types. When soil type (or a continuous trait such as the range of nutrient availabilities in which a tree species grows) is mapped onto a phylogeny, only a single summary value is used and the potential variation around that average is ignored. Phylobetadiversity analyses performed across relevant environmental gradients within the geographic range of a clade can accommodate all of the within lineage variation. Trait conservatism can then be assessed in finer detail where lineages differ in the range of soil types (or nutrient availabilities) in which they are found. Phylobetadiversity comparisons between sites with different nutrient availabilities (i.e. comparing the dashed line and the solid lines in Fig. 1c) will be divergent if trait conservatism



	Site	Habitat	Species sampled	Community phylogenetic stucture				
				Type1	Type2	Type3	Type4	Type5
Island	a	Dry	Random sample of	C	C	c	c	r/o
1	b		all dry, island 1 taxa	C	C	c	c	r/o
	c	Wet	random sample of	C	C	c	c	r/o
	d		all wet, island 1 taxa	C	C	c	c	r/o
Island	e	Dry	Random sample of	C	C	c	c	r/o
2	f		all dry, island 2 taxa	C	C	c	c	r/o
	g	Wet	Random sample of	C	C	c	c	r/o
	h		all wet, island 2 taxa	C	C	c	c	r/o

Table 1 Expected variation in beta diversity and phylobetadiversity values resulting from different range sizes and ages of species across two communities at two sites

	Lower beta diversity	Null beta diversity	Higher beta diversity
Lower phyβ diversity	Widespread species (similar species composition between sites)	Random pattern of geographic distributions with respect to species composition	High proportion of small ranged species, most of them Neoendemics (lower-than expected average divergence times)
Null phyβ diversity	Random pattern in phylogeny with respect to geographic structure	Random pattern of geographic distribution with respect to species composition and phylogenetic relatedness	Random pattern in phylogeny with respect to geographic structure
Higher phyβ diversity	Probably impossible Given a low B, phyβ should always be low	No spatial pattern in species distributions	High proportion of small ranged species, most of those are Paleoendemics (higher than expected average divergence times)

Sites are separated by a relatively large geographic distance such that widespread species may be found in both sites, but those with small distributions (i.e. endemics) are only in one site. A null expectation of beta diversity can be generated by using species composition data from many sites within the region where the two sites are located. The null expectation for phylobetadiverisity requires a phylogeny of the larger regional species list from which subtrees are generated that reflect the species composition at a give site.
Phyβ diversity, phylogenetic beta diversity.

with respect to nutrient availability is common in these trees, and will be similar if these traits are labile.

Beta diversity and phylobetadiversity

Beta diversity and phylobetadiversity considered in tandem can allow us to better detect the processes structuring communities. Table 1 demonstrates how the two measures can be combined to make inferences about what processes influence variation in communities across geographic space. If most species that occur at the two sites are wide-ranging, indicating ample opportunity for dispersal, we expect both beta diversity and phylobetadiversity to be lower then the null expectation (see Table 1). In the case that the species composition exactly matches between the two sites, phylobetadiversity values will match beta diversity values. In contrast, when there is little or no opportunity for dispersal between two sites and/or differential extinction resulting in entire clades disappearing from one region, both the high beta diversity and high phylobetadiversity is expected. This pattern indicates that the communities found in two sites contain species that come from lineages with long-standing and disparate evolutionary histories. This could occur if the two sites encompass such different abiotic environments that species and their close relatives (perhaps even whole lineages) have evolved traits that preclude them from occurring in both sites. Alternatively, if the sites have a high proportion of small-ranged species, most of which are neoendemics (lower-than expected average divergence times) phylobetadiversity should be low and beta diversity relatively high with respect to the null model. This could occur if traits that confer habitat specialization are evolutionarily labile, and neoendemics are habitat specialists that have close relatives in divergent environments within a region.

Quantifying phylobetadiversity

Metrics to calculate phylobetadiversity

Phylobetadiversity can be calculated in different ways. Two recent studies have used analogous population genetic measures, such as F_{st}, which estimate the amount of allelic diversity within and among populations (Chave *et al.* 2007; Hardy & Senterre 2007). Hardy & Senterre (2007) and Chave *et al.* 2007 extended additive partitioning methods developed using species data to evaluate phylogenetic diversity in terms of both alpha-diversity and beta-diversity components. Both of these methods calculate the divergence time (branch lengths) between each pair of taxa and sum this difference among all possible pairs and use this continuous variable in the Simpson index, a traditional index for calculating beta diversity. Classic metrics to measure similarity between communities, such as the Jaccard or Sorenson's index also could be explored (Magurran 2004). These metrics are calculated as the ratio of shared species to total species. In phylogenetic terms, this metric could be calculated as the total branch length covered by shared species relative to the total branch length covered by all species in both communities (Ferrier *et al.* 2007; Bryant *et al.* in press). In addition, Phylocom (Software for the Analysis of Phylogenetic Community Structure and Character Evolution, with Phylomatic; Webb *et al.* 2007, 2008) provides metrics to measure phylogenetic distance between samples by calculating either the mean branch-length distance for all possible pairs of taxa in one sample to the other or the nearest neighbour distance among samples. Future simulation studies are required to compare the relative utility of each of these approaches and the influence of a variety of different phylogenetic patterns. For instance, a community that included species from a phylogeny that had both very old and young species could result in uneven branch lengths in a community phylogeny pool a in higher probabilities of finding phylogenetic clustering at local scales (Kraft *et al.* 2007). This phenomenon should increase phylobetadiversity measures among sites as spatial scale increases.

Testing for significance and environmental variables

There are various ways to construct a null model to determine if patterns of phylobetadiversity are different than a random expectation. Null models will be subject to the many caveats inherent in studies of phylogenetic structure of local communities because differences in individual abundances, and spatial and taxonomic scale can affect the statistical power of the analyses (Gotelli 2000; Cavender-Bares *et al.* 2006; Kembel & Hubbell 2006; Kraft *et al.* 2007). Further, models will vary in complexity to account for a range of factors that can limit the species composition of a particular community. The simplest null model first produces a distribution for community composition based on 1000 random draws from an overall species pool, and then calculates a matrix of pair-wise phylogenetic distances among communities. Such models may be overly simplistic because spatial autocorrelation in species ranges is not accounted for. A distance decay null model, similar to that formulated for beta diversity by (Condit *et al.* 2002) accounts for dispersal limitation but assumes that species are functionally equivalent with respect to changes in environmental variables. Thus, according to this null model, communities that are closer together in space should be more similar phylogenetically than those that are further apart.

The distance decay null model can be further developed by incorporating environmental heterogeneity or topographic barriers which may supercede distance decay. This ecological decay null model is analogous to distance decay but species range limits would be correlated with environmental variables, which are expected if traits corresponding to that particular environmental variable are phylogenetically conserved. Alternatively, barriers such as mountains or rivers my influence range limits instead of, or in addition to, geographic distance (Chave *et al.* 2007). These types of null models are especially important if organisms are restricted in their ecology to some environmental (abiotic and biotic) conditions or in their dispersal as a result of geographic barriers. There are situations where we expect environmental heterogeneity to have a strong spatial structure, such as discrete habitat types arranged as islands with either water or non-suitable habitat in intervening areas. In these cases the influence of distance vs. ecological decay might be scale dependent since we expect both to influence phylobetadiversity between habitat types, but distance decay should influence turnover within habitat types. Organisms that exhibit significant departure from an ecological decay null model can be considered to exhibit trait lability with respect to that particular environmental variable.

To evaluate the correlation between phylobetadiversity and environmental suitability or geographic factors either a Mantel test or generalized dissimilarity model (GDM) can be used (Legendre & Legendre 1998; Ferrier *et al.* 2007). In both these methods a site X site matrices of phylogenetic distance are correlated with geographic distance, current or historic environmental variables. Generalized dissimilarity modelling (Legendre & Legendre 1998; Ferrier *et al.* 2002, 2007; Ferrier & Guisan 2006) should theoretically be more informative than a Mantel test because it can capture nonlinear responses to the environment that represent ecologically realistic relationships between dissimilarity and ecological distance (Ferrier *et al.* 2007). Species environment interactions are more often unimodal than linear (Gauch 1982). Further, a linear model assumes that the rate of turnover in species composition or phylogenetic distance is constant along an environmental gradient, while a nonlinear method allows for non-constant rates of turnover, a pattern more common in empirical studies (e.g. Oksanen & Tonteri 1995; Simmons & Cowling 1996). For example, a Mantel test would fit a linear relationship between phylogenetic dissimilarity and rainfall, which assumes a change in precipitation of 200 to 500 mm year^{-1} is the same as 4000 to 4300 mm (where in reality the former is likely a much larger change from an ecological perspective), but a generalized dissimilarity model would capture this variation by fitting a nonlinear relationship. While this example is demonstrative and simplistic (a log transformation could clearly be applied to linearize the data), there are many cases in ecological research where it is not possible to linearize data and recent work focused on modelling species environment interactions indicate that nonlinear methods, such as general additive models, perform better than linear models (i.e. general linear models; e.g. Quinn & Keough 2002; Elith *et al.* 2006). To evaluate significance for either type of matrix regression test randomizations can be conducted by shuffling the species in the reference phylogeny, shuffling the sites that the species are found in, and by shuffling the environmental variables of the sites.

APPLICATIONS OF PHYLOBETADIVERSITY TO BIODIVERSITY SCIENCE

Adding phylogenetic information into the study of beta diversity should advance studies across an array of questions in ecology and evolution. Phylobetadiversity research provides a link between present spatial variation in community composition and evolutionary mechanisms that influence this variation, such as speciation and trait evolution. Here we develop a series of research areas where quantifying phylobetadiversity could provide significant insight into what mechanisms influence observed patterns of diversity. What follows is not exhaustive; our goal is to develop a diverse set of examples in order to stimulate further use of phylobetadiversity in ecological and evolutionary studies.

Phylobetadiversity and speciation

Using a framework such as the GDM described above, a series of correlates could be explored to evaluate what types of environmental gradients or barriers influence turnover for different species groups (Chave *et al.* 2007). This sort of analysis has been undertaken for studies of beta diversity and has shown that both current and historic factors can influence beta diversity patterns with pronounced differences depending on the dispersal abilities of the taxonomic group being examined (e.g. Graham *et al.* 2006). Extending such analyses to explore correlates of phylobetadiversity will allow us to more rigorously quantify connectivity among communities, and hence the potential for allopatric speciation, and the strength of environmental gradients and potential for ecological speciation.

For example, at a regional scale, such as a mountain range, we can explore how beta diversity and phylobetadiversity vary across two different types of gradients: space at the same elevation (Fig. 2, line A & C) and elevation (Fig. 2, line B). In the former, we expect species at higher elevations (line A) to currently be more isolated than species at lower elevations (line C) given that high elevation climates are less likely to be continuous in rugged mountain terrain than lower elevations. This general pattern, isolation of mountain top species relative to mid-elevation species, is likely even given cooler or warmer historic climate conditions. If organisms' traits are generally conserved with respect to their environmental niches, this should promote isolation between high elevation habitats and hence increase the potential for allopatric speciation (Wiens 2004). As a result, close relatives should be found in similar climatic regions, such as mountain tops, separated by regions of low niche suitability (Kozak & Wiens 2006). Empirical studies of sister-taxa of Appalachian salamanders indicate that high elevation sister-taxa have similar climatic niches, especially in comparison to lower elevation congeneric species suggesting that niche conservatism and climatic isolation resulted in allopatric speciation (Kozak & Wiens 2006). Extending this rational to an entire community we expect a relatively low phylobetadiversity (and potentially higher beta diversity) across high elevation regions (line A) if allopatric speciation were prevalent across the clade.

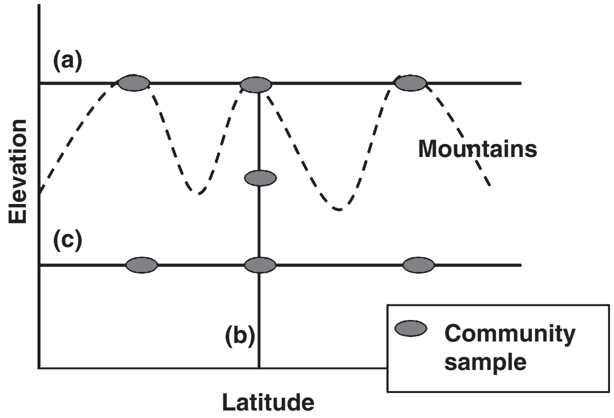


Figure 2 A schema of different types of environmental gradients that may influence patterns of species turnover through time and space.

Evaluation of how phylobetadiversity patterns change in a given region is particularly informative in comparison to gradients or potential barriers within the same region (i.e. Fig. 2, line B & C). For example, if niches were conserved we would expect a higher phylobetadiversity along an altitudinal (i.e. climatic) gradient. An alternative to niche conservatism is that traits that confer survival and fitness in a particular niche are evolutionarily labile, and that divergent selection across environmental gradients can lead to ecological speciation, which can occur allopatrically or parapatrically (Moritz *et al.* 2000; Schluter 2000; Kozak & Wiens 2007). In this case, we would expect lower phylobetadiversity across gradient B than if niches were conserved. Alternatively, different types of environmental variables, such as current environment and historic isolation or habitat stability, can be used to evaluate what factors might influence patterns of both beta diversity and phylobetadiversity. For example, Graham *et al.* (2006) evaluated how beta diversity was influenced by current and historic environmental variables. This type of study could be extended to evaluate how these variables correlated with phylobetadiversity where we might expect a stronger influence of those variables that drive speciation.

The above-mentioned approaches would be strengthened by evaluating if patterns were consistent across multiple groups. In addition, research could focus on explicit traits, such as frost tolerance in plants or flight physiology in hummingbirds where specific hypotheses can be generated to better understand what factors influence range limits and how these in turn interact with existing environmental variables to promote isolation (i.e. Wiens *et al.* 2006). The pattern of trait variation across geography or environmental gradients and as a function of phylogenetic distance should

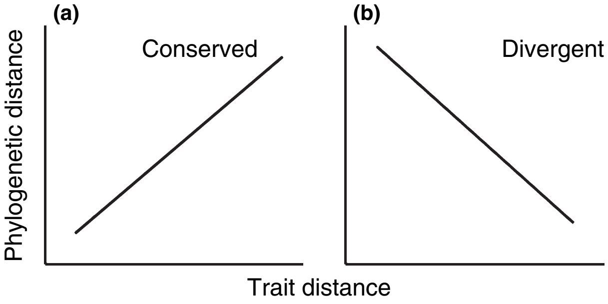


Figure 3 Changes in within-community traits across spaces as a function of phylogenetic distance.

provide additional information on trait lability. If trait distance is positively correlated with phylogenetic distance then these traits are phylogenetically conserved (Fig. 3a). Conservation of traits, coupled with limited dispersal abilities, might lead to lower local species richness and potentially empty niches. In contrast, if the traits that exhibit variation within a local community are divergent among sister taxa this suggests that such traits are labile and this lability may allow closely related species to coexist (Fig. 3b). Hence, evaluating the relationship between trait and phylogenetic distance across space provides additional insight into the forces that govern species richness at local scales. Integrating studies of traits together with phylobetadiversity measures will provide a more complete picture of the role of geographic isolation and ecological speciation in driving diversity patterns in different regions of the world.

Phylobetadiversity and ecological niche modelling (ENM)

Exploring why particular species are not found in all habitats that are physiologically suitable should allow us to evaluate the relative importance of factors such as dispersal limitation, biogeographic barriers and biotic interactions (competition, natural enemies) affecting patterns of both beta diversity and phylobetadiversity. Combining ecological niche modelling (ENM) with patterns of species occurrence provides a method to better understand the specific mechanisms influencing patterns of both beta diversity and phylobetadiversity. For instance, Anderson *et al.* (2002) used ENM to show that species replacements along an elevational gradient are likely caused by competition. Svenning & Skov (2004) used ENM to demonstrate that some tree species in Europe had not moved as far north as predicted by their ENM suggesting that diversity patterns from southern to northern Europe might be a result of dispersal limitation.

To integrate ENM with phylobetadiversity, one can compare the phylogenetic and trait similarity among species that exist in a given community with those of species that are predicted to exist in it (Fig. 4). If a species is predicted to exist in a community but does not then a series of alternative hypotheses can be evaluated. For example, if competition was important in structuring communities then we might predict that if a target species does not occur where it is predicted to a phenotypically similar and potentially closely related species might exist there in its place. The potential role of competition in limiting the target species could be evaluated by comparing traits and phylogenetic relationships of the species that is most similar (with respect to physiology or other traits that allow survival at that particular climate or soil type) to the target species where it does and does not exist (Fig. 4). Alternatively, a species might not exist where it is predicted to because of a large barrier between two communities that a given species (or suite of species) is unlikely to cross. Essentially, integrating ENM with phylobetadiversity allows us to determine what species can exist in a given community and then to start to investigate alternative hypotheses about why a given species might be absent. Such investigations could include evaluating if absent species are dispersal limited or the extent to which biotic interactions influence community assembly (e.g. manipulative experiments to investigate the role of interspecific competition and natural enemies).

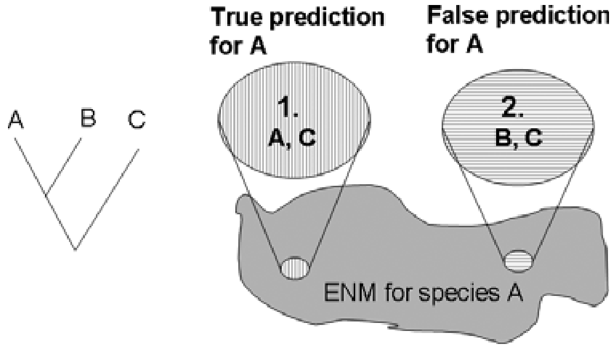


Figure 4 Depicted are two communities and an ecological niche model prediction (ENM) for species A. In this example species B is excluding species A because of their phylogenetic proximity and the more distant C was able to coexist with both. In community 1 species A is predicted to be present and is present. In community 2 species A is predicted to be present but is not present. The closest relative to species A in community 1 (species C) is more distant than the closest relative in community 2 (species B).

Phylobetadiversity and neutral models

The unified neutral theory posits that species–neutral interactions structure ecological communities more strongly than deterministic forces such as niche and habitat specialization, competition and density-dependent enemy attack (Hubbell 2001, 2003; Kembel & Hubbell 2006). Theoretically, tests of phylogenetic community structure could quantify the relative importance of species-neutral vs. deterministic forces, and if communities represented random assemblages of the regional reference pool this would be consistent with the unified neutral theory (Kembel & Hubbell 2006). Unfortunately, scale dependence and uncertainty of appropriate null models can prevent clear tests of neutral theory, because changing the geographic scale and taxonomic scale often influences whether local communities exhibit random, clustered or overdispersed phylogenetic structure (Kembel & Hubbell 2006; Swenson *et al.* 2006; Kraft *et al.* 2007). Phylobetadiversity analyses, however, may provide a more rigorous test of the influence of neutral process in community structure, because one can explicitly compare communities along a continuum of geographic distances and incorporate different habitat types. For example, if dispersal limitation is important for a group of organisms (i.e. trees, Hubbell *et al.* 1999), neutral processes should result in phylogenetic trees that have strong patterns of geographic structure. Deterministic forces such as habitat specialization are hypothesized to be unimportant, thus neutral theory should predict clades with random ecological structuring. Thus, phylogenies of organisms structured by species-neutral forces should resemble Fig. 1b, clade type 3, and phylobetadiversity comparisons between and within habitats are predicted to resemble Fig. 1c, clade type 3, with measures of phyobetadiversity increasing with increasing spatial scale.

Phylobetadiversity and global biodiversity patterns

Phylobetadiversity can provide insight into environmental and historical factors that influence variation in species richness across biomes. For instance, evaluating how phylobetadiversity varies across a series of environmental and historical gradients can be used to explore species generation on mountain ranges across different biomes since the climatic zonation of mountains has a strong latitudinal component (Janzen 1967). Janzen (1967) suggested that selection for reproductive isolation between similar elevational habitats should be more prevalent in tropical mountains. Smaller seasonal variation in tropical mountains should result in greater climatic stratification along an elevational gradient, promoting selection of organisms with narrow temperature tolerances and an increase in beta diversity along altitudinal gradients. In contrast, temperature seasonality in temperate mountains would be comparatively large, selecting for species with broader physiological tolerances (Ghalambor *et al.* 2006) and hence, causing less potential for climate-associated allopatric isolation and parapatric speciation along altitudinal gradients (Janzen 1967). This hypothesis could be tested by quantifying the degree of phylobetadiversity in temperate and tropical montane regions and determining the relative importance of climatic factors on influencing patterns of biodiversity. Based on Janzen's hypothesis, we expect the difference in total annual temperature between lowlands and highlands to influence phylobetadiversity in tropical mountains more than in temperate mountains. While phylogenies of a focal clade (i.e. salamanders, Kozak & Wiens 2007) could be used to address this hypothesis, phylobetadiversity analyses would allow a test at the community level, i.e. all vertebrates.

Temperate and tropical biomes differ in other factors besides climate that may influence the degree to which environmental gradients influence speciation rates. For example, biotic interactions are considered to be stronger in tropical than in extra-tropical systems (Dobzhansky 1950; Coley & Barone 1996; Mittelbach *et al.* 2007). Biotic interactions can interact with abiotic gradients to promote habitat specialization, and over time this phenomenon could lead to habitat-mediated speciation (Fine *et al.* 2004). The hypothesis that tropical biomes should have stronger patterns of habitat specialization than temperate biomes can be tested by comparing phylobetadiversity across a similar range of environmental variables (i.e. soil chemistry, elevation) between temperate and tropical regions, in conjunction with quantifying the strength of biotic interactions (herbivory, diseases, parasitism). Ultimately, we can use analyses of phylobetadiversity to determine the relative frequency of niche conservatism vs. divergent selection and trait lability in diverse lineages across the biomes of the world, and connect this to mechanistic processes that produce large-scale patterns such as the latitudinal gradient in biodiversity. If high biodiversity in the tropics is largely due to niche conservatism in tropical lineages preventing invasion of extratropical regions as hypothesized by Wiens & Donoghue (2004), than comparisons of sites straddling the frost line should look like the phylobetadiversity comparisons in Fig. 1b and c, clade type 2.

Like the examples presented above, historical biogeography would benefit from evaluating the degree of phylobetadiversity across different gradients and barriers. Historical biogeography attempts to discover connections among different regions as a way to quantify the influence of dispersal vs. *in situ* radiations at different times across large temporal and spatial scales (Lomolino *et al.* 2006). Quantifying phylobetadiversity among regions should elucidate the degree of connectivity that has existed as well as the directionality of patterns of dispersal. This type of analysis might be particularly useful if conducted across various taxonomic levels or species with different dispersal abilities (i.e. frogs vs. birds). Species- and family-level analyses might show different patterns; indeed one can partition the strength of phylobetadiversity patterns at different times (deeper vs. shallower nodes within the community phylogeny, Hardy & Senterre 2007). For instance, if dispersal limitation is a strong force then phylobetadiversity at the species level may be more influenced by within-region environmental gradients and topography while patterns at deeper levels in the phylogeny (corresponding to Linnean families, perhaps) could be influenced by connectivity among regions. Along the same lines, we expect patterns to vary by taxonomic groups depending on dispersal ability (Pennington *et al.* 2006). Those clades with low dispersal ability should have high geographic clustering (Fig. 1b, clade types 1–3), while those with high dispersal/vagility should exhibit low geographic clustering (Fig. 1b, clade types 4–5). Finally, phylobetadiversity should provide information about the age and duration of geographic barriers. If barriers are relatively new, or short-lived we expect less phylobetadiversity between sites on both sides of the barrier compared to old or long-standing barriers which should produce greater levels of phylobetadiversity.

CONCLUSIONS AND PERSPECTIVES

Theoretical attempts to explain species diversity traditionally have been studied at distinct spatial and temporal scales. Those founded in evolutionary biology and biogeography posit that diversity is a result of evolutionary diversification across regional or continental scales over long periods of time. In contrast, those elaborated in community ecology have focused on biotic interactions such as competition or predation, played out within small areas and over shorter time periods (Ricklefs 2004; Helmus *et al.* 2007). While this disparity is increasingly recognized it remains a challenge to combine information from different spatial and temporal scales; a necessary step towards a more mechanistic explanation of diversity patterns. As more and more phylogenetic data are accumulated, we can begin to elucidate the true relationships among organisms as well as the timing of their origination. In this essay we have attempted to integrate the spatial and temporal component of diversity into a single heuristic measure: phylobetadiversity. Phylobetadiversity can be combined with other data (local richness, environmental gradients, historical barriers, species-specific traits) and other methodologies (mapping traits and geography onto phylogenies, community phylogenetic structure) to evaluate how mechanisms, such as dispersal limitation or niche conservatism, combine to cause variation in biodiversity across space.

Understanding the interaction between local and regional controls on biodiversity is not only important for theoretical studies but will allow us to better predict how patterns of biodiversity will be influenced by human-induced climate and land use changes. For instance, if community-wide patterns of phylobetadiversity at large scales indicate that species are in general dispersal limited and highly conserved, we can predict what regions or clades might be negatively influenced by environmental changes. Likewise, linking phylobetadiversity (and beta diversity) to specific gradients or barriers will allow us to predict the influence of environmental changes on community structure. The more we understand the processes underlying current patterns of diversity the more likely we are to be able to mitigate the effects of environmental change.

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