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REVIEW AND
SYNTHESIS

The merging of community ecology and phylogenetic biology

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Abstract

The increasing availability of phylogenetic data, computing power and informatics tools has facilitated a rapid expansion of studies that apply phylogenetic data and methods to community ecology. Several key areas are reviewed in which phylogenetic information helps to resolve long-standing controversies in community ecology, challenges previous assumptions, and opens new areas of investigation. In particular, studies in phylogenetic community ecology have helped to reveal the multitude of processes driving community assembly and have demonstrated the importance of evolution in the assembly process. Phylogenetic approaches have also increased understanding of the consequences of community interactions for speciation, adaptation and extinction. Finally, phylogenetic community structure and composition holds promise for predicting ecosystem processes and impacts of global change. Major challenges to advancing these areas remain. In particular, determining the extent to which ecologically relevant traits are phylogenetically conserved or convergent, and over what temporal scale, is critical to understanding the causes of community phylogenetic structure and its evolutionary and ecosystem consequences. Harnessing phylogenetic information to understand and forecast changes in diversity and dynamics of communities is a critical step in managing and restoring the Earth's biota in a time of rapid global change.

Keywords

Community assembly, deterministic vs. neutral processes, ecosystem processes, experimental approaches, functional traits, phylogenetic community ecology, phylogenetic diversity, spatial and phylogenetic scale.

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INTRODUCTION

Community ecology investigates the nature of organismal interactions, their origins, and their ecological and evolutionary consequences. Community dynamics form the link between uniquely evolved species and ecosystem functions that affect global processes. In the face of habitat destruction worldwide, understanding how communities assemble and the forces that influence their dynamics, diversity and ecosystem function will prove critical to managing and restoring the Earth's biota. Consequently, the study of communities is of paramount importance in the 21st century.

Recently, there has been a rapidly increasing effort to bring information about the evolutionary history and genealogical relationships of species to bear on questions of community assembly and diversity (e.g. Webb *et al.* 2002; Ackerly 2004; Cavender-Bares *et al.* 2004a; Gillespie 2004;

Fine *et al.* 2006; Strauss *et al.* 2006; Davies *et al.* 2007; Vamosi *et al.* 2008). Such approaches now allow community ecologists to link short-term local processes to continental and global processes that occur over deep evolutionary time scales (Losos 1996; Ackerly 2003; Ricklefs 2004; Pennington *et al.* 2006; Mittelbach *et al.* 2007; Swenson *et al.* 2007; Donoghue 2008; Emerson & Gillespie 2008; Graham & Fine 2008). This effort has been facilitated by the rapid rise in phylogenetic information, computing power and computational tools. Our goal here is to review how phylogenetic information contributes to community ecology in terms of the long-standing questions it helps answer, the assumptions it challenges and the new questions it invites. In particular, we focus on the insights gained from applying phylogenetic approaches to explore the ecological and evolutionary factors that underlie the assembly of communities, and how the interactions among species within them ultimately influence evolutionary and ecosystem processes.

There are three perspectives on the dominant factors that influence community assembly, composition and diversity. First is the classic perspective that communities assemble according to niche-related processes, following fundamental 'rules' dictated by local environmental filters and the principle of competitive exclusion (e.g. Diamond 1975; Tilman 1982; Bazzaz 1991; Weiher & Keddy 1999). An alternative perspective is that community assembly is largely a neutral process in which species are ecologically equivalent (e.g. Hubbell 2001). A third perspective emphasizes the role of historical factors in dictating how communities assemble (Ricklefs 1987; Ricklefs & Schluter 1993). In the latter view, the starting conditions and historical patterns of speciation and dispersal matter more than local processes. The relative influence of niche-related, neutral and historical processes is at the core of current debates on the assembly of communities and the coexistence of species (Hubbell 2001; Chase & Leibold 2003; Fargione *et al.* 2004; Ricklefs 2004; Tilman 2004). This debate falls within the larger historic controversy about the nature of communities and the extent to which they represent associations of tightly interconnected species shaped over long periods of interaction or are the result of chance co-occurrences of individually dispersed and distributed organisms (Clements 1916; Gleason 1926; Davis 1981; Brooks & McLennan 1991; Callaway 1997; DiMichele *et al.* 2004; Ricklefs 2008).

Here we review how the merging of community ecology and phylogenetic biology advances these debates and allows new areas of enquiry to be addressed. First, phylogenetics helps to resolve the long-standing controversy about the relative roles of neutral vs. niche-related processes in community assembly and facilitates identification of the kinds of processes that underlie community assembly. Second, insights from phylogenetic approaches present strong challenges to the classical idea that the species pool (and the traits of species within it) is static on the time scale over which communities are assembled. These approaches are also beginning to demonstrate that community interactions might strongly influence how the pool itself evolves and changes across space and time. Finally, phylogenetic diversity and composition is relevant to predicting ecosystem properties that impact global processes.

We argue that ongoing efforts to integrate knowledge of phylogenetic relationships of organisms with their functional attributes will enhance understanding of the distribution and function of the Earth's biota at multiple scales, increasing our ability to predict outcomes of species interactions as well as the consequences of these outcomes for ecosystem and evolutionary processes. Progress towards this end will require consideration of

both phylogenetic and spatial scale in the interpretation of ecological and evolutionary patterns (Box 1, Figs 1 and 2) and cognizance of the multiplicity of processes that underlie patterns. Observational, experimental and theoretical studies aimed at deciphering the mechanisms involved in community assembly and how they shift with scale are paving the way for phylogenetic approaches to large-scale prediction of ecosystem dynamics in response to global change.

We first discuss the historical origins of the classic debates in community ecology that phylogenetics helps to address. We then turn to specific examples in the general areas highlighted above and review contributions made possible by integrating community ecology and phylogenetic biology. In doing so, we discuss the challenges involved in further progress. We close with a summary of the major advances, challenges and prospects for the emerging field of phylogenetic community ecology. We include illustrative examples from animals, plants and other organisms in discussing the contributions of phylogenetic information to understanding community assembly and the feedbacks to evolutionary processes. However, we focus largely on the plant literature in discussing the ecosystem and global consequences of community assembly, reflecting the plant orientation of much of the relevant literature.

HISTORICAL OVERVIEW

Niche-related processes and assembly rules

Early ecologists, including Darwin, recognized that specific attributes of species could influence their interactions with other species and with the environment in predictable ways. In particular, Darwin noted a paradox inherent in phenotypic similarity of species with shared ancestry. On the one hand, if closely related species are ecologically similar, they should share similar environmental requirements and may thus be expected to co-occur. On the other hand, closely related species should experience strong competitive interactions due to their ecological similarity, thereby limiting coexistence and thus driving selection for divergent traits.

The idea that similar phenotypes should share habitat affinities was championed by the Danish plant ecologist, Eugenius Warming (1895), who emphasized differences in the physiological abilities of plants to adjust to some environments but not others. The core idea was that similar physiological attributes would be selected for by similar environments in different regions and that plant phenotypes should match their environments in predictable ways (Collins *et al.* 1986). These ideas were important in the development of niche theory (e.g. Grinnell 1924; Elton

Box 1 Scale dependency of phylogenetic community structure

Spatial and temporal scale

The processes that influence species diversity shift with spatial scale (e.g. Davies *et al.* 2005; Silvertown *et al.* 2006; Diez *et al.* 2008) and phylogenetic patterns of species assemblages are likely to reflect those shifts. We might expect at the neighbourhood scale that density-dependent interactions will be strongest giving way to environmental filtering at the habitat scale, mediated by organismal dispersal, and finally to biogeographical processes (Ricklefs 2004; Wiens & Donoghue 2004) at larger spatial scales (Fig. 1). Similarly, viewed over longer temporal scales, biogeographical processes also dominate as drivers of species distributions. Empirically, phylogenetic clustering has been shown to increase with spatial scale in plant communities (Cavender-Bares *et al.* 2006; Swenson *et al.* 2006, 2007; reviewed in Vamosi *et al.* 2008). The proposed explanation is that as the spatial extent of the analysis increases, greater environmental heterogeneity is encompassed, and groups of closely related species with shared environmental requirements sort across contrasting environments. At larger spatial scales, phylogenetic clustering may continue to increase, depending on the vagility of clades, as the signature of biogeographical processes comes into focus (Box 1, Fig. 2b).

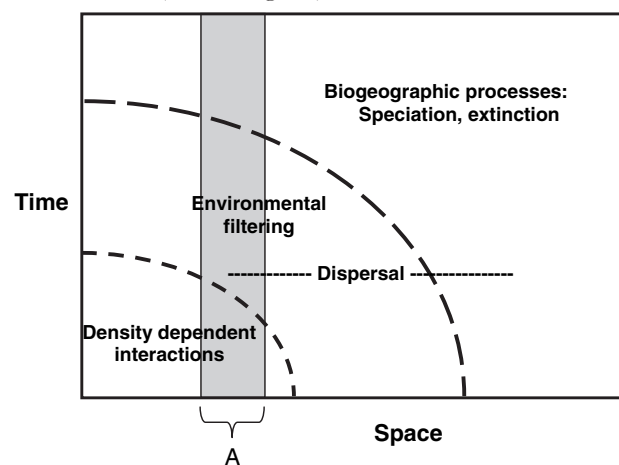


Figure 1 The processes that drive the organization of species in a focal area operate over varying temporal scales and depend fundamentally on the spatial scale of analysis. At the broadest spatial scale, species distributions are determined largely by biogeographical processes that involve speciation, extinction and dispersal. These processes occur over long temporal scales. Dispersal varies with the mobility of the organism and can alter patterns of species distributions established through ecological sorting processes (Vamosi *et al.* 2008). At decreasing spatial scales, the environment filters out species lacking the physiological tolerances that permit persistence, given the climate or local environmental conditions. The environment can include both abiotic factors (temperature, soil moisture, light availability, pH) or biotic factors (symbionts, pollinators, hosts, prey). Density-dependent processes are likely to operate most intensively at neighbourhood scales. These processes may include competition, disease, herbivory, interspecific gene flow, facilitation, mutualism, and may interact with the abiotic environment to reinforce or diminish habitat filtering. At a given spatial scale (e.g., A), species distributions depend on multiple factors, which may be difficult to tease apart. Methods that can partition the variance among causal factors driving community assembly facilitate understanding of mechanism. This figure was adapted from figures in Weiher & Keddy (1999) and Swenson *et al.* (2007).

Phylogenetic scale

Several studies have demonstrated that community phylogenetic structure also depends on the taxonomic or phylogenetic scale in terrestrial plant (Cavender-Bares *et al.* 2006; Swenson *et al.* 2006, 2007) and aquatic microbial communities (Newton *et al.* 2007). One hypothesis is that competition and other density-dependent interactions are most predictably intense among close relatives. Hence if competition drives ecological character displacement or competitive exclusion, the consequences for phylogenetic structure should be observable within clades but become more diffuse in community assemblages that span diverse taxa. At the same time, as a greater diversity of taxa are included in the analysis, the range of possible trait values and niches is likely to expand. Whereas traits may be labile within a clade, at larger taxonomic scales, the ranges of possible trait values for the clade may often be limited relative to a more phylogenetically diverse group of species (Box 1, Fig. 2). Hence, patterns reflective of processes within narrowly defined communities are likely to be missed in analyses that include broad taxonomic diversity.

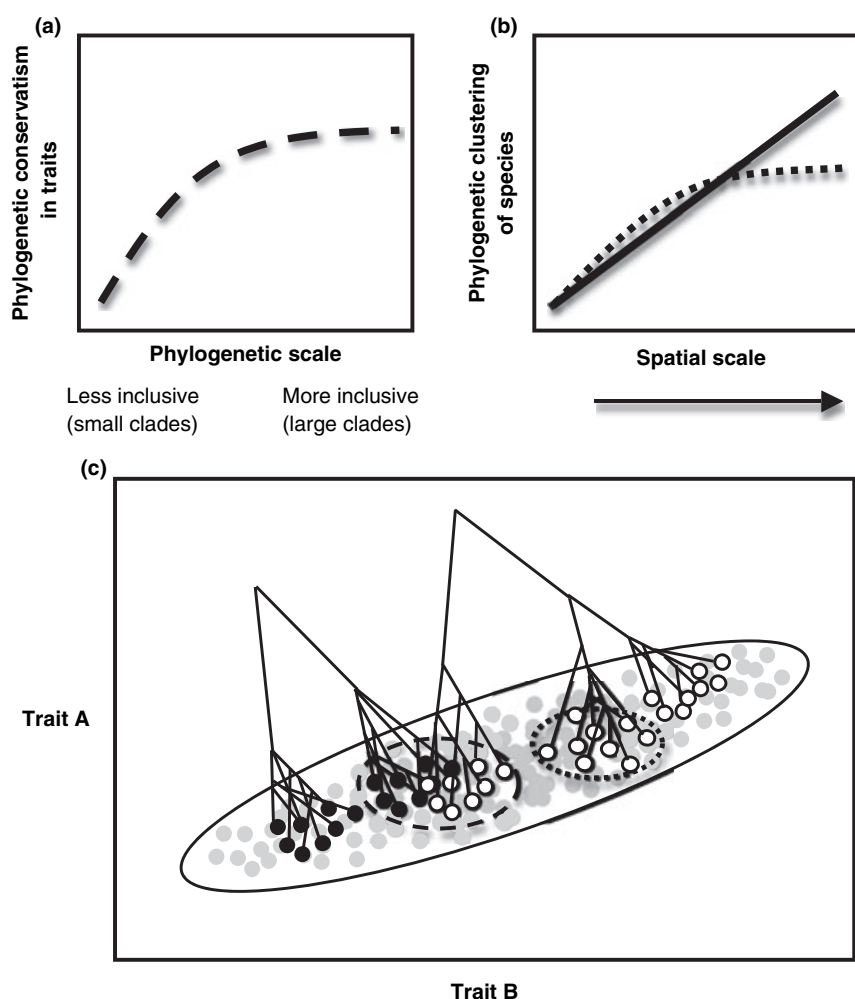
Box 1 *continued*

Figure 2 *Hypothesized variation in phylogenetic clustering and trait conservatism with phylogenetic scale* (a) Phylogenetic conservatism of traits and phylogenetic clustering of species in communities varies as more of the tree of life is encompassed in an analysis. Ecologically relevant traits may be labile towards the tips of the phylogeny (less inclusive phylogenetic scale) because close relatives often have divergent or labile traits as a result of character displacement and/or adaptive radiation or due to drift and/or divergent selection following allopatric speciation. At increasing phylogenetic scales (as more of the tree of life is encompassed), we expect traits (dashed line) to show increasing conservatism because traits within clades are less variable than traits among clades. However, conservatism of traits deeper in the phylogeny may diminish due to homoplasy, particularly if lineages in different geographical regions have converged towards similar trait values as a result of similar selective regimes, for example. (b) Phylogenetic clustering (solid line), or the spatial aggregation of related species, also tends to increase with phylogenetic scale (data not shown) and with spatial extent. Competition and other density-dependent mechanisms are predicted to be strongest at small spatial scales and may prevent close relatives from co-occurring. Once the spatial scale at which species interactions are strongest is surpassed, the similar habitat affinities of more recently diverged species will cause spatial clustering. Phylogenetic clustering continues to increase with increasing phylogenetic scale due to biogeographical history (i.e. most species from a clade tend to be concentrated in the region in which the clade originated). The strength of this trend should depend on dispersal ability. Highly mobile species (dotted line) are less likely to show a signature of their biogeographical history, whereas clades that contain species with more limited vagility (solid line) are likely to be clustered spatially at the largest spatial extent. (c) Organisms often show trait trade-offs or correlations as a result of selection for specialization or due to biochemical, architectural or other constraints (e.g. Reich *et al.* 2003; Wright *et al.* 2004) that can be represented in two dimensional 'trait space'. Often, trait variation represented by members of an individual clade may be limited due to common ancestry, as shown here. Thus, while traits can be labile *within* clades (shown by random arrangement in trait space of tips descended from a common ancestor), the range of variation represented by an individual clade is likely to be limited (indicated by the dotted circle) at some phylogenetic scale relative to the global trait space occupied by organisms drawn from

Box 1 *continued*

across the tree of life (small grey circles). This highlights the possibility that the range of clade-wide values for a given trait can be reasonably predicted from a small number of individuals within the clade. At broad phylogenetic scales, convergence of traits between distantly related clades (shown by close proximity in trait space of tips from two unrelated clades within the dashed circle) may occur due to similar selective pressures on different continents or islands, for example. This explains the decrease in trait conservatism (dashed line) in (a).

1927; Hutchinson 1959) in which similarities and differences among species in their resource and habitat requirements as well as their impacts on the environment were understood to be important in determining the outcomes of species interactions (reviewed in Chase & Leibold 2003).

While early naturalists seamlessly integrated ecological and evolutionary thinking, theoretical developments starting in the 1920s (reviewed in Ricklefs 1987; Schluter & Ricklefs 1993), and critical experiments by Gause led to the adoption of the 'competitive exclusion principle' and the notion of limiting similarity (Hutchinson 1959; MacArthur & Levins 1967) which posited that species that are too similar ecologically could not coexist. This became one of the central paradigms of community ecology and led to a growing separation between ecology and evolutionary biology, reinforcing the convenient assumption that evolutionary processes were not relevant at the time scales of ecological processes. The competitive exclusion paradigm precipitated the view within ecology that new species could not join a community without the compensating disappearance of others, and that there are 'assembly rules' guiding the assembly of communities (Diamond 1975; Weiher & Keddy 1999). The importance of evolutionary process in ecology was still recognized by ecologists, however; empirical studies and theoretical models indicated the presence of evolved trade-offs that prevent all species from occurring in all environments, thus permitting coexistence (Tilman 1982; Bazzaz 1996; Chesson 2000; Reich *et al.* 2003). Darwin's paradox led to the conclusion that shared ancestry should result in non-random ecological associations of taxa with respect to relatedness, resulting in contrasting patterns of species coexistence depending on the relative importance of competition or physiological tolerances in driving species distributions (Elton 1946; Williams 1947; Simberloff 1970; Webb *et al.* 2002). More recently, patterns of phylogenetic relatedness of species within and across communities, or 'phylogenetic community structure', have been used to explore the processes underlying them and the scale at which they operate (Webb *et al.* 2002; Cavender-Bares *et al.* 2006; Swenson *et al.* 2006; Emerson & Gillespie 2008; Vamosi *et al.* 2008).

Neutral processes

The roles of dispersal, disturbance and stochastic processes in community assembly, which played a central role in the

theory of island biogeography (MacArthur & Wilson 1967), were clearly recognized by early ecologists (e.g. Braun 1928) and paleobiologists (Davis 1981). These processes were given new prominence by Hubbell (2001) in his Unified Neutral Theory of biodiversity. Hubbell challenged the perspective that deterministic niche processes influence community assembly asserting that ecological communities are open, continuously changing, non-equilibrium assemblages of species whose presence, absence and relative abundance are governed by random speciation and extinction, dispersal limitation and ecological drift. According to this view, species differences do not predict outcomes of competition, species do not specialize for specific habitats, and interactions between species and with the environment are not relevant to community assembly. Tests of phylogenetic community structure have attempted to quantify the relative importance of species-neutral forces vs. those driven by species differences (Kembel & Hubbell 2006; Kelly *et al.* 2008; Jabot & Chave 2009), and this an area of increasing interest for the application of phylogenetic tools (Box 2).

Historical processes

Ricklefs (1987) brought to the ecological debate a focus on the importance of historical processes in influencing local diversity, inviting incorporation of 'historical, systematic and biogeographical information into the phenomenology of community ecology'. He reminded ecologists that the equilibrium theory of island biogeography (MacArthur & Wilson 1967) was based on a balance of regional processes (those that increase colonization) and local processes (those that cause local extinction). He argued that limiting similarity was in most cases a weaker force than regional processes in community assembly, and specifically, that local diversity, rather than being determined solely by local environmental factors and limiting similarity, was consistently dependent on regional species diversity. According to this view, which gained support from empirical studies (e.g. Cornell & Washburn 1979; Sax *et al.* 2002), communities were rarely saturated because local species respond to larger species pools by reducing their niche breadths through increased specialization. The historical perspective thus re-opened the door to bring an evolutionary perspective into community ecology, and emphasized the shifting nature of the species pool and the ecological and

Box 2 Quantifying phylogenetic community structure

In addition to the difficulties in ascribing phylogenetic signal in communities to any one process or cause in the absence of detailed information on the interactions and traits of species, a further barrier to the synthesis of existing studies of community phylogenetic structure has been the wide variety of methods employed. While many studies have used the same terminology of phylogenetic overdispersion and clustering to describe patterns of relatedness relative to some null model, it is important to note that the underlying methods used to measure phylogenetic community structure have varied a great deal. Vamosi *et al.* (2008) provide a recent review of some of the most commonly used phylogenetic diversity metrics and software.

Most measures of community phylogenetic structure can be divided into two broad categories: those that measure the relatedness of species occurring together in a community or sample, and those that measure the concordance of phylogenetic and ecological dissimilarities among species. To date there has been little quantitative evaluation of the relative strengths and weaknesses of these different approaches (but see Hardy 2008).

Measures of phylogenetic relatedness within communities are in many ways similar to earlier measures of taxonomic similarity within communities (Elton 1946). Faith (1992) proposed perhaps the first quantitative measure of phylogenetic diversity (PD) based on the evolutionary branch length spanned by a given set of species, and this metric has been widely applied in ecology and conservation biology (Redding *et al.* 2008). The net relatedness index and nearest taxon index (Webb 2000) measure average branch lengths separating taxa within communities, allowing comparison with the patterns expected under some null model of community assembly. Other measures based on tree balance (Heard & Cox 2007; Redding *et al.* 2008) use the shape of phylogenetic trees rather than relatedness *per se* to understand phylogenetic diversity. Several measures of phylogenetic diversity within communities can take species abundances and evenness into account (Chave *et al.* 2007; Helmus 2007a), and methods to partition variation in phylogenetic diversity into components attributable to spatial and environmental variation (Helmus 2007b) or to measure relationships between trait and phylogenetic diversity (Prinzing *et al.* 2008) are increasingly common. Phylogenetic beta diversity measures (Graham & Fine 2008) such as UniFrac (Lozupone & Knight 2008), PD dissimilarity (Ferrier *et al.* 2007) and the phylogenetic Sørensen index (Bryant *et al.* 2008) measure the total branch lengths separating taxa within individual communities relative to the shared or total tree length for taxa in multiple communities. Other measures of phylogenetic beta diversity such as the phylogenetic depth of species turnover between communities could provide a means of quantifying the phylogenetic nature of changes in community structure in space and time.

Measures of the concordance between phylogenetic and ecological dissimilarities of species are also widely used. These methods compare pairwise phylogenetic distances (or phylogenetic covariances) among species to some measure of the ecological similarity of those species. Concordance among these dissimilarities has been measured in several ways including Mantel tests (Cavender-Bares *et al.* 2004a; Kozak *et al.* 2005) and logistic regression approaches (Helmus 2007b) based on linear correlations (Cavender-Bares *et al.* 2004a; Kozak *et al.* 2005) or quantile regression (Slingsby & Verboom 2006).

To determine whether communities are phylogenetically clustered or overdispersed, observed results from all of these approaches are compared to the patterns expected under some null model of phylogenetic relatedness or community assembly. Many of these null models are based on a conceptual model of randomization of species labels across the tips of the phylogeny, or of community assembly from some larger pool of species that might potentially colonize each local community (Gotelli & Graves 1996). The choice of species pool and null model can strongly influence the outcome of the results, highlighting the importance of choosing methods and defining the species pool in a way that is appropriate to the hypothesis being tested (Kembel & Hubbell 2006; Hardy 2008). Kraft *et al.* (2007) used simulation studies to demonstrate that the size of local communities and the regional species pool from which communities are assembled both influence the ability of different methods to detect a phylogenetic signal in community structure. The effects of regional pool size on phylogenetic community structure varied depending on the assembly process that was operating. Swenson *et al.* (2006) compared the phylogenetic structure of local assemblages to species pools drawn from increasingly larger geographical scales and found an increasing signal of local phylogenetic clustering, which they attributed to environmental filtering.

Our understanding of the relative strengths and weakness of these different methods is poorly developed. Quantitative comparisons of these different measures and null models when applied to studies of community phylogenetic structure are only beginning to be conducted, with mixed results. Recent studies have found that different null models differ in their Type I error rates (Kembel & Hubbell 2006; Hardy 2008) and that measures of similarity within communities differ in their ability to detect different community assembly processes (Kraft *et al.* 2007). More generally, there is a need for model-based

Box 2 *continued*

simulations and tests of the ability of these methods to detect the signature of different ecological and evolutionary processes that may give rise to phylogenetic signal in community structure, and recent studies have begun to address this need (Jabot & Chave 2009). Quantitative comparisons of metrics of co-occurrence (Gotelli 2000) and trait similarity within communities (Collwell & Winkler 1984) were instrumental in providing a sounder theoretical framework to support research in these areas, and will be required as studies of community phylogenetic structure continue to increase in popularity.

We note that a variety of underlying processes might cause closely related species to be more ecologically similar than distantly related species. For example, both random (e.g. drift through ecological space, also known as Brownian motion) and deterministic evolutionary processes (e.g. stabilizing selection) can result in a positive relationship between phylogenetic divergence and ecological divergence (Blomberg *et al.* 2001; Losos 2008; Revell *et al.* 2008; Wiens 2008). Nevertheless, so long as close relatives exhibit greater ecological similarity than distant relatives, phylogeny can have important consequences for community assembly. Therefore, we imply no specific causal process when using the term 'trait conservatism' throughout this review, although we acknowledge that developing metrics to quantify the degree of trait conservatism and rate of trait change relative to various models of evolution is an important area for future research.

evolutionary forces at play at different temporal and spatial scales (Box 1, Fig. 2).

The nature of communities

Relevant to the importance of historical processes in community assembly are the roles of speciation and adaptation in community assembly. This issue is connected to one of the earliest debates in community ecology, which focused on the nature of communities. Frederick Clements (1916) viewed a community as a group of interdependent and inextricably linked species, or as a 'superorganism', in contrast to Henry Gleason (1926), who defined communities as chance assemblages of individually distributed species. Clements' Lamarkian views not withstanding, these perspectives can be viewed as opposite ends of the spectrum of the kinds of real communities that exist in nature. Consider at one extreme, assemblages of species that evolved together over long time periods and developed tightly woven interdependencies, and at the other extreme, assemblages of recently colonizing species drawn from disparate sources following major disturbances (such as temperate regions that were heavily impacted by glacial cycles). While the individualistic perspective has largely been adopted by ecologists (but see Callaway 1997), evolutionary studies have continued to demonstrate the importance of evolutionary dynamics between interacting species (Ehrlich & Raven 1964; Thompson 2005; Bascompte & Jordano 2007; Jablonski 2008; Ricklefs 2008; Roderick & Percy 2008).

An integrated perspective on the nature of communities emerged with the introduction of historical ecology (Brooks & McLennan 1991). Brooks and McLennan argued that community development involves both evolutionary processes, including speciation and adaptation, as well as dispersal and colonization, resulting in both recent and historical elements in most communities. They emphasized

a conservative homeostatic element that is composed of species that evolved *in situ* through the persistence of ancestral associations, a perspective supported by fossil evidence (DiMichele *et al.* 2004). Reminiscent of the Clementsian view, they argued that this portion of any community is 'characterized by a stable relationship across evolutionary time' and may thus 'act as a stabilizing selective force on other members of the community by resisting the colonization of competing species'. They also saw a strong role for adaptive processes in which either old residents or new arrivals adapt to changing interactions or novel conditions. This contrasted other contemporary views that communities assemble by 'ecological fitting' in which new members that evolved elsewhere fit themselves into existing communities without adaptive shifts, like 'asymmetrical pegs in square holes' (Janzen 1985). An important advance represented by phylogenetic community ecology is to incorporate data and methods to examine the role of evolution in community assembly, and in turn, to examine the influence of community interactions on processes of speciation and adaptation (Fig. 3).

These historical debates in community ecology encompass fundamental questions about the relative importance of deterministic, neutral and historical processes in community assembly, as well as the relative roles of speciation, adaptation, extinction and dispersal. Several recent advances have enabled ecologists to re-examine these debates from a phylogenetic perspective, including (1) the availability of comprehensive phylogenetic information for many lineages, (2) the availability of abundance and geographical occurrence data and associated environmental data, (3) computing power for null model analysis and (4) the rapid rise of new statistical and informatics tools for statistical testing. In the next sections, we review how phylogenetics has been applied to discern the processes driving community assembly (e.g. Webb *et al.* 2002), to examine the role of *in situ* evolution relative to

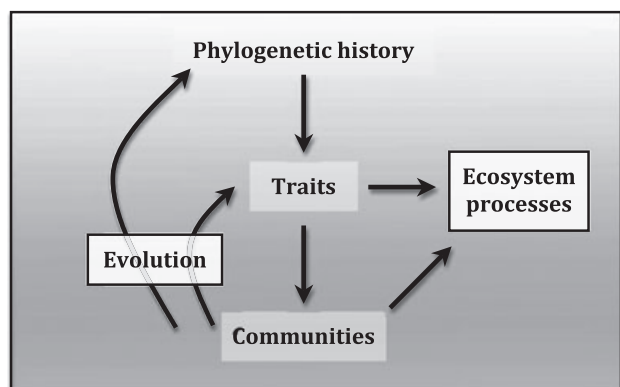


Figure 3 Traits arise as innovations along the tree of life, often reflecting their biogeographical origins, and tend to be shared by species that have common ancestry (phylogenetic history). Traits, in turn, play a central role in ecological processes that influence the distribution of organisms and the organization of communities. For plants, in particular, physiological traits and the organization of species with different traits in communities influence processes and emergent properties of ecosystems. Hence, plant functional traits are an important mechanistic link by which phylogenetic history influences ecological processes. Interactions within communities also influence traits and evolutionary processes, causing a feedback loop between ecological and evolutionary processes.

dispersal in community assembly (e.g. Losos 1996; Gillespie 2005) and to investigate the macroevolutionary responses of organisms to interspecific interactions (e.g. Jablonski 2008; Phillimore & Price 2008; Roderick & Percy 2008). We then turn to the ecosystem consequences of community phylogenetic structure and the potential for phylogenetics to facilitate a more predictive framework for understanding the links between traits, species composition and ecosystem or even global processes (Chave *et al.* 2006; Edwards *et al.* 2007; Cadotte *et al.* 2008).

PHYLOGENETIC COMMUNITY STRUCTURE, NEUTRAL PROCESSES AND ASSEMBLY RULES

Weiher & Keddy (1999) clarify that an important goal of community ecology is to determine the rules that govern the assembly process in order to predict the composition of ecological communities from species pools. One contribution of phylogenetic community ecology relates to whether communities are largely shaped by niche-based assembly rules or by neutral processes (Webb *et al.* 2002). A central distinction between the two perspectives is that the neutral theory assumes that species differences do not matter, while the niche assembly theory assumes that they do. Under the niche assembly theory, the phylogenetic distance between species can serve as a proxy for the evolved ecological differences between them, assuming close relatives are

ecologically more similar to each other than more distantly related species. This relatively simple measure can then be diagnostic, if the assumption holds.

There is a burgeoning literature that takes advantage of phylogenetic distances between species (or phylogenetic community structure) to test whether differences among species are important in community assembly. Phylogenetic community structure is the pattern of phylogenetic relatedness of species distributions within and among communities. It is subjected to statistical tests by examining the extent to which species are more closely related (phylogenetically clustered) or less closely related (phylogenetically overdispersed or 'even') than expected in relation to null models in which species distributions are randomized (see Box 2 on *Quantifying phylogenetic community structure*). Patterns of phylogenetic community structure (including diversity and dispersion patterns) are not meaningful in their own right, but they serve as a means to infer processes and shifts in processes with scale, in concert with other evidence, and to eliminate competing hypotheses. They also have consequences for ecosystem function (Cadotte *et al.* 2008) and conservation (Faith 1992), which we discuss in the last section.

Webb *et al.* (2002) laid out a heuristic framework for using community phylogenetic structure to uncover deterministic processes, or assembly rules, in community assembly. This framework made the simplifying assumption that ecological sorting processes due to trait-environment matching (environmental filtering) and interspecific competition are the two dominant forces structuring communities and that they cause non-random species assemblages with respect to phylogenetic relatedness. Specifically, Webb *et al.* (2002) suggested that when close relatives occur together more than expected (phylogenetic clustering), the underlying cause was environmental filtering on shared physiological tolerances (trait conservatism). In contrast, when species in communities are less related than expected (phylogenetic overdispersion), Webb *et al.* (2002) suggested that this could result either from competition causing overdispersion of conserved traits or environmental filtering on ecologically important convergent traits. This simple framework is consistent with the niche-assembly perspective of community ecology, which posits that ecological communities are limited membership assemblages of species that coexist due to partitioning of limiting resources (Chase & Leibold 2003).

This framework has stimulated much research demonstrating significant non-random phylogenetic structure in communities at multiple spatial and taxonomic scales across diverse taxa (e.g. Losos *et al.* 2003; Cavender-Bares *et al.* 2004a; Kozak *et al.* 2005; Horner-Devine & Bohanan 2006; Kembel & Hubbell 2006; Lovette & Hochachka 2006; Slingsby & Verboom 2006; Swenson

et al. 2006; Davies *et al.* 2007; Hardy & Senterre 2007; Helmus 2007b; Verdu & Pausas 2007), including recent reviews focused on insular communities (Emerson & Gillespie 2008) and emerging patterns across spatial scales (Vamosi *et al.* 2008). In particular, community phylogenetic structure has been used as a means to quantify the relative importance of species-neutral processes vs. deterministic processes (e.g. Kembel & Hubbell 2006; Hardy & Senterre 2007; Kelly *et al.* 2008). Using the lack of phylogenetic community structure to provide support for neutral processes, however, has proved challenging because of the difficulty in ruling out contrasting niche-based processes that operate at different spatial, temporal or phylogenetic scales (Box 1). Uncertainty of appropriate null models for such tests and how to circumscribe the species pool are further challenges (Box 2). A related but alternative approach has been proposed using phylogenetic beta diversity – a measure of the geographical turnover in phylogenetic diversity – in relation to geographical distance and environmental gradients to tease apart neutral processes, such as dispersal limitation, from niche-based processes, such as environmental filtering (Graham & Fine 2008). This provides the possibility of identifying the scale and conditions under which neutral vs. niche-based processes predominate.

Environmental filtering

Studies of phylogenetic community structure have been successful in providing evidence for and revealing the mechanisms underlying deterministic processes. At local spatial scales, the co-occurrence of closely related species (phylogenetic clustering) is often interpreted as evidence for environmental filtering (or habitat filtering) on phylogenetically conserved traits (Webb 2000; Cavender-Bares *et al.* 2006; Kembel & Hubbell 2006; Lovette & Hochachka 2006; Swenson *et al.* 2007). Shared physiological tolerances and habitat affinities within lineages are widespread, such as the hygrophilic habit of willows (*Salix*) and the xerophytic habit of cacti (*Cactaceae*). Hence, ecological similarity of closely related species, in the absence of strong biotic interactions, should cause closely related species to occupy similar environments, and hence to cluster spatially (Wiens & Graham 2005). However, ecological similarity of closely related species cannot be assumed without specifically testing for it (Losos 2008) because ecological niches and their underlying traits can be labile (Losos *et al.* 2003; Cavender-Bares *et al.* 2004a; Pearman *et al.* 2008).

Examining the conservatism in ecologically relevant functional traits in relation to the spatial distribution of traits or their distributions across environmental gradients can help decipher the processes that cause phylogenetic

structure in communities (Cavender-Bares & Wilczek 2003). For example, in Mediterranean woody plant communities, frequent fire disturbance drives the phylogenetic clustering of species in communities because fire protection of seeds is highly conserved (Verdu & Pausas 2007). At the same time, environmental filtering can also cause phylogenetic overdispersion if traits important for habitat specialization are labile and close relatives specialize for different niches (Losos *et al.* 2003; Cavender-Bares *et al.* 2004a; Fine *et al.* 2005; Ackerly *et al.* 2006). Gradients in water availability and fire frequency thus drive phylogenetic overdispersion in Florida oak communities because traits related to fire and drought resistance are convergent (Cavender-Bares *et al.* 2004a,b). Ecological divergence of close relatives, or character displacement, may be the expected outcome of natural selection (Schluter 2000).

Competitive interactions

Darwin's hypothesis that similarity in resource use due to shared ancestry would cause closely related species to compete more strongly than distantly related species inspired an examination of the frequency of co-occurring congeneric species (Elton 1946; Williams 1947), species-to-genus ratios (e.g. Simberloff 1970), and more recently, of phylogenetic diversity, (Webb 2000; Webb *et al.* 2002) in natural communities. Several studies have implicated competition as the likely causal mechanism for phylogenetic overdispersion in communities, including the fynbos shrub communities in South Africa (Slingsby & Verboom 2006), sunfish communities in Wisconsin (Helmus 2007b), mammalian carnivores (Davies *et al.* 2007), monkey, squirrel and possum assemblages (Cooper *et al.* 2008), eastern North American salamanders (Kozak *et al.* 2005), warblers (Lovette & Hochachka 2006) and bacteria (Horner-Devine & Bohannan 2006) (Table 1). However, we note that competitive interactions and character displacement might also cause trait divergence between close relatives (Schluter 2000; Grant & Grant 2006) that permits their coexistence, resulting in phylogenetic clustering of species within a community (e.g. a benthic stickleback is more closely related to a limnetic stickleback from the same lake, than it is to benthic stickleback from a different lake).

Direct evidence for an increase in competitive interactions with phylogenetic relatedness comes from experiments with plants in controlled environments (Cahill *et al.* 2008). In a meta-analysis of plant competition experiments, Cahill *et al.* (2008) compared the relative competitive ability of 50 vascular plant species competing against 92 competitor species measured in five multi-species experiments. Within the eudicots, competition was more intense among closer relatives. Within the monocots, however, relatedness was not predictive of interaction strength.

Table 1 Causes and consequences of phylogenetic community structure

| A. Processes inferred to cause phylogenetic community structure | | | | |
|---|------------|---|--|---------------------------|
| Ecological mechanisms | Dispersion | | Representative studies | |
| Density dependent mechanisms: | | | | |
| Competition/limiting similarity | + | | Slingsby & Vrboom 2005, Kozak <i>et al.</i> 2005, Horner-Devine & Bohannen 2006, Davies <i>et al.</i> 2007, Helmus <i>et al.</i> 2007, Cahill <i>et al.</i> 2008 | |
| Herbivore/Pathogen specificity | + | | Webb <i>et al.</i> 2006, Gilbert & Webb 2007 | |
| Herbivore facilitated ecological sorting | + | – | Fine <i>et al.</i> 2004, 2006, Fig. 4 | |
| Facilitation of nurse plants | + | | Valiente-Banuet & Verdú 2007 | |
| Pollinator-plant interactions | + | – | Sargent & Ackerly 2008 | |
| Temporal niche dynamics | + | – | Cavender-Bares <i>et al.</i> 2004a, Kelly <i>et al.</i> 2008; | |
| Environmental filtering | + | – | Webb 2000, Ackerly <i>et al.</i> 2004, Cavender-Bares <i>et al.</i> 2004a,b, Cavender-Bares <i>et al.</i> 2006, Verdú & Pausas 2007, Kraft <i>et al.</i> 2007 | |
| Facilitation by mutualists | | – | Sargent & Ackerly 2008 | |
| Plant-pollinator interactions | + | – | Sargent & Ackerly 2008 | |
| Neutral processes | | x | Hubbel 2001, Kembel & Hubbel 2006 | |
| Combinations of processes | | x | Lovette & Hochachka 2006, Cavender-Bares <i>et al.</i> 2006 | |
| Dispersal | ? | ? | x | Vamosi <i>et al.</i> 2008 |
| Evolutionary/genetic mechanisms | | | | |
| Biogeographic history | | | Ricklefs 2004, Wiens & Donoghue 2004, Vamosi <i>et al.</i> 2008 | |
| Allopatric speciation (depends on scale) | + | | Johnson & Stinchcombe 2007 | |
| Sympatric speciation | | – | Johnson & Stinchcombe 2007 | |
| Character displacement | | – | Schluter 2000, Grant & Grant 2006 | |
| Convergent evolution | + | | Cavender-Bares <i>et al.</i> 2004a, Kraft <i>et al.</i> 2007 | |
| Mimicry | | – | Brower 1996 | |
| Gene flow and local hybridization | + | | Dobzhansky 1937, Mayr 1942, Losos 1990, Levin 2006, Grant & Grant 2008, Fig. 5 | |
| B. Consequences of phylogenetic community structure and composition | | | | |
| Feedbacks to evolutionary processes | | | Representative studies | |
| Density dependent diversification rates | | | Gillespie 2004, Ruber & Zardoy 2005, Kozak <i>et al.</i> 2006, Phillmore & Price 2008, Rabosky & Lovette 2008, Williams & Duda 2008 | |
| Evolution of increased host specialization | | | Roderick & Percy 2008 | |
| Co-evolutionary arms races | | | Ehrlich & Raven 1964, Farell 1998, Thompson 2005, Hoberg & Brooks 2008 | |
| Ecosystem properties and processes | | | | |
| Productivity | | | Maherali & Klironomos 2007, Partel <i>et al.</i> 2007, Cadotte <i>et al.</i> 2008 | |
| Capacity to respond to environmental change | | | Knapp <i>et al.</i> 2008 | |
| Invasion resistance | | | Strauss <i>et al.</i> 2006, Diez <i>et al.</i> 2008 | |
| Decomposition, nutrient cycling | | | Kerkhoff <i>et al.</i> 2006, Swenson <i>et al.</i> 2007, Weedon <i>et al.</i> 2009 | |
| Temperature sensitivity/Response to global change | | | Edwards <i>et al.</i> 2007, Edwards & Still 2008, Willis <i>et al.</i> 2008 | |
| Conservation value | | | Faith 1992, Gerhold <i>et al.</i> 2008 | |

Phylogenetic community structure has been used to infer ecological and evolutionary processes that influence community assembly, in concert with other evidence, and to predict consequences for ecosystems and evolutionary processes. (A) Processes that have been shown or hypothesized to influence community phylogenetic structure including both ecological and evolutionary mechanisms (a plus (+) indicates that the process increases a tendency towards phylogenetic overdispersion/evenness; a minus (–) indicates that it decreases phylogenetic dispersion towards clustering; an x indicates that the process(es) is (are) predicted to generate random patterns; and a ? indicates that the directionality cannot be predicted. (B) Hypothesized and empirically determined consequences of phylogenetic community structure, in terms of diversity and composition. For brevity, only representative studies are listed; patterns of phylogenetic community structure are reviewed elsewhere (Vamosi *et al.* 2008, Emerson & Gillespie 2008). Studies that propose hypotheses versus those that test them empirically are not distinguished.

Determining the generality of increased competitiveness among close relatives has important consequences for using niche-based assembly rules to understand and predict the outcomes of community interactions. For example, the hypothesis that the strength of species interference increases with phylogenetic similarity has been used to predict the invasiveness of exotics in California grasslands. Strauss *et al.* (2006) showed that highly invasive grass species are, on average, significantly less related to native grasses than are introduced but noninvasive grasses. They reasoned that matches between characteristics of the exotic and those of members of the existing native community limited invasion success. In a related study of plant communities in the Auckland region of New Zealand, Diez *et al.* (2008) found that the relationship between exotic invasion and presence of congeneric natives depended on the spatial scale. Within habitats, there was correlative evidence that native species limited invasion of closely related exotics. At larger spatial scales, a positive association between congeneric and native

abundances suggested that congeneric native and exotic species respond similarly to broad-scale environmental variation.

The extent to which phylogenetic relatedness can predict invasion success across a range of systems remains to be explored. An experimental approach that introduces species into model communities with a range of phylogenetic distances from resident species would test whether phylogenetically similar species are less likely to become established. Ideally, such experiments would be established at nested spatial scales given the dependency of invasion processes on scale (Davies *et al.* 2005; Diez *et al.* 2008) and in contexts that do not introduce exotic species to a region. Positive results at the neighbourhood scale would provide strong support for a scale-dependent link between species interference and species relatedness (Strauss *et al.* 2006). Experiments with well-characterized micro-organisms (e.g. *Dictyostelid* cellular slime moulds; Schaap *et al.* 2006) are likely to be informative. The

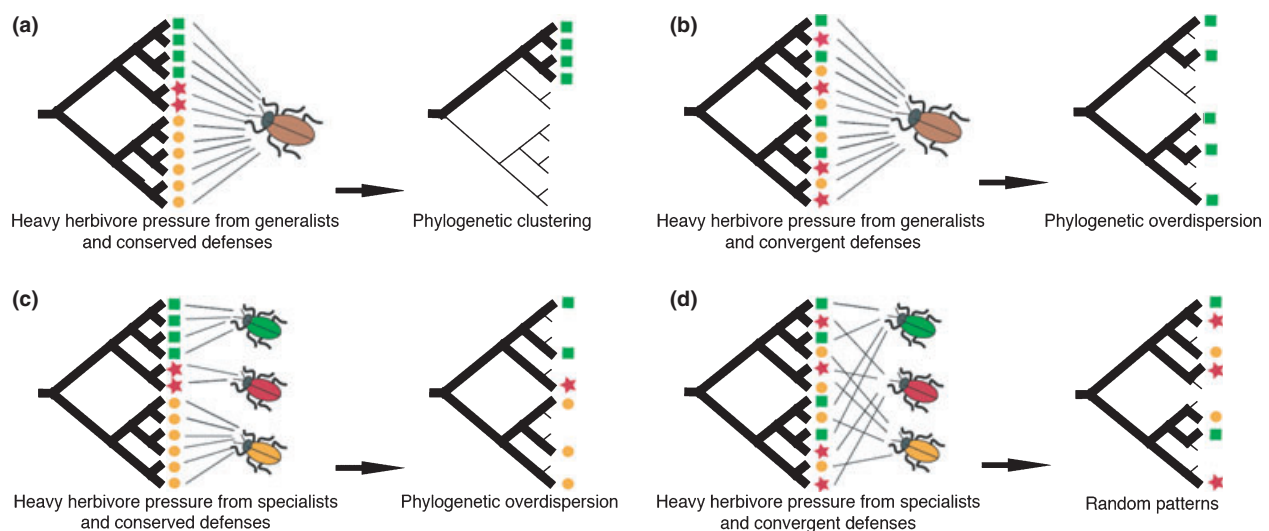


Figure 4 If most herbivores are generalists, and only a subset of the plant species pool can defend or tolerate the dominant enemies, then plant species composition will shift to become dominated by those species that share these defence and tolerance traits. In this figure, green squares, red stars and orange circles represent different defence traits that confer tolerance of herbivory in plants within a community, and thin lines indicate a species has been eliminated from a community by the herbivore. If defence traits are conserved (a), heavy herbivore pressure will drive phylogenetic clustering within the community. For example, large mammalian herbivores consume a wide variety of plants, yet grasses are able to tolerate high herbivory pressure and in the presence of these large herbivores, quickly dominate communities. If herbivores are excluded, plant composition changes, and trees or forbs can take over (McNaughton 1985, Pringle *et al.* 2007). However, if such traits that confer tolerance or defence are convergent, generalist enemies will drive the phylogenetic community structure towards overdispersion (b). If specialists exert a large proportion effect on plant fitness within a community, this will result in strong patterns of density dependence (Janzen 1970, Connell 1971). This should increase local diversity by favouring rare species which can escape their natural enemies more often than more abundant species. Furthermore, if related plants have qualitatively similar defence strategies (trait conservatism) (c), strong Janzen–Connell regulation in a community could limit the co-occurrence of closely related species and promote the co-occurrence of distantly related species at neighbourhood scales, causing community phylogenetic overdispersion (Webb *et al.* 2006). In this figure, ‘specialist enemies’ can eat only plants from the pool that have similar defence traits, similar to Becerra (1997). (d) If plants’ defence traits are convergent, however, Janzen–Connell regulation by specialist enemies will promote random patterns in plant community phylogenetic structure.

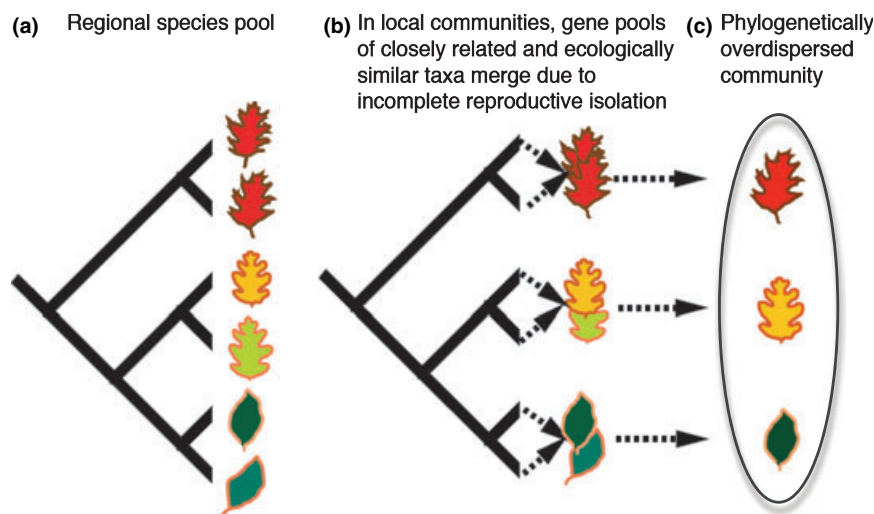


Figure 5 In clades where the degree of reproductive isolation between species is associated with their time since divergence, interspecific gene flow may have consequences for community assembly and resulting patterns of phylogenetic community structure. Shown here is an example in which closely related lineages that are ecologically similar merge into a single gene pool where they come into contact locally. As only lineages that are reproductively isolated can coexist without merging, local communities tend to be comprised of taxa that are more distantly related (and ecologically divergent) than expected by chance. An expected outcome of this process is the assembly of communities that exhibit phylogenetic overdispersion. (a) Phylogenetic relationships of species in the regional pool. These species maintain their genetic integrity in other portions of their geographical ranges where they do not come into contact. (b) Closely related and ecologically similar lineages that lack reproductive isolating mechanisms merge into a single gene pool where they come into contact, thereby preventing their long-term coexistence in local communities. (c) Close relatives thus occur less than expected in communities relative to the regional species pool (phylogenetic overdispersion). These influences are likely to be important only in communities dominated by a single clade (e.g. oaks) in which hybridization occurs among close relatives.

breadth of species distributions across environmental gradients may also be important to consider in interpreting relationships between phylogenetic relatedness and invasion success, given the theoretical and counterintuitive relationship between species coexistence and niche breadth (Scheffer & van Nes 2006).

While competition is one possible mechanism for phylogenetic overdispersion, again, it cannot be assumed. In addition to environmental filtering on convergent traits, other density-dependent interactions such as host–pathogen interactions or plant–insect interactions (Fig. 4) (Webb *et al.* 2006), and facilitation during succession (Valiente-Banuet & Verdú 2007; see below), have also been shown or hypothesized to cause phylogenetic overdispersion. We also suggest that a lack of reproductive isolation between closely related and ecologically similar species could prevent their long-term coexistence and cause phylogenetic overdispersion (Fig. 5) through mechanisms difficult to distinguish from competitive exclusion (Losos 1990; Levin 2006) (see Section *Gene flow and lack of reproductive isolation*). The multiplicity of processes that can cause the same pattern (Table 1) highlights the importance of understanding the functional biology of species and the nature of their interactions.

MOVING BEYOND THE ENVIRONMENTAL FILTERING – COMPETITIVE EXCLUSION PARADIGM

Janzen–Connell mechanisms, natural enemies and trophic interactions

In observational studies of the spatial association of species (e.g. Uriarte *et al.* 2004) competitive effects between close relatives may be difficult to distinguish from other density-dependent effects without experimental tests. Closely related species are likely to share pests and pathogens (Gilbert & Webb 2007). Adult harbouring of pathogens and pests may reduce recruitment and competitive ability of species in proximity to close relatives, promoting phylogenetic overdispersion (Webb *et al.* 2006). Here we focus on plant–herbivore and plant–pathogen communities to illustrate how trophic interactions may influence phylogenetic community structure. There are three variables that together interact to determine the directionality of trophic interactions on phylogenetic community structure and whether this will lead to overdispersion, clustering or random patterns (Fig. 4). These are: (1) the strength of the interactions, (2) the degree of specialization of the interactions and (3) the amount of trait conservatism or

convergence found in prey or host defences against higher trophic levels.

Some plant communities experience much greater herbivory, disease and predation than others; for example, many authors have proposed that there is a latitudinal gradient in the strength of enemy attack (Coley & Barone 1996; Mittelbach *et al.* 2007). Communities that have a low degree of trophic complexity may be more likely to be governed by environmental filtering or plant–plant competition than by trophic interactions. Yet, most plant communities support abundant and diverse communities of natural enemies, and many studies have documented that natural enemies are often the most dominant factors influencing plant community dynamics; indeed they are often much stronger forces than environmental factors or plant–plant competition (McNaughton 1985; Carson & Root 2000).

In addition, attack from natural enemies can result in selection for plant traits that are an advantage in one habitat type but are a disadvantage in other habitats. This interaction of herbivory with abiotic gradients can amplify the effect of environmental filtering, because plant strategies for each habitat include trait trade-offs that become more divergent with more herbivore pressure, resulting in stronger patterns of habitat specialization, influencing community assembly within a region. Two examples are the trade-off between competitive ability and defence investment across resource gradients such as white-sand and clay forest (Fine *et al.* 2004, 2006) and shaded understorey and light gaps (Coley *et al.* 1985).

Whether enemies are mostly specialists or generalists within a community of hosts causes large effects in the phylogenetic structure of host communities, with phylogenetic clustering becoming less likely with increasing specialization (Fig. 4). Herbivores and pathogens are not always specialists in the sense of a one-host-one-plant relationship, but in many communities the dominant herbivores tend to display a strong phylogenetic signal in their diet (Agrawal & Fishbein 2006). Yet, in some communities, like grasslands, the most important herbivores are large ungulates that eat a wide variety of plants (McNaughton 1985). The implication of the degree of specialization by natural enemies for plant community structure, in turn, depends on whether the plants' defence traits are phylogenetically conserved or convergent (Fig. 4).

There is strong circumstantial evidence that at least some of the defensive compounds in plants are conserved (Fig. 4a,c). Detailed analyses of insects and fungal pathogens feeding on their host plants in tropical and temperate forest communities reveal that many enemies feed only within narrow subsets of the angiosperm phylogeny (generally within families or genera) (Berenbaum 1990; Coley *et al.* 2005; Novotny & Basset 2005; Weiblen *et al.* 2006; Dyer *et al.* 2007). In the few cases that defence chemistry has been measured in multiple plant species within a lineage, there is

evidence for trait conservatism in the qualitative type of defence, with patterns of trait convergence in the quantitative amount of defence investment and/or specific chemical structure within a broad category of defence type (i.e. terpenes) (Berenbaum 1990; Becerra 1997; Coley *et al.* 2005; Fine *et al.* 2006).

In general, while trophic interactions influence community structure in complex ways, there is a predictable framework in which to investigate the directionality of these effects on community structure, and phylogenetic information plays an important role. Interpreting patterns of phylogenetic community structure and evaluating the role of trophic interactions in producing these patterns will be facilitated by paying attention to the strength and specificity of these interactions, as well as to the amount of convergence and conservatism in defence traits.

Mutualism and facilitation

While negative interactions, such as competition and Janzen–Connell mechanisms, are often emphasized in structuring communities, facilitation and mutualisms tend to be underemphasized despite their known importance (e.g. Stachowicz 2001; Callaway *et al.* 2002; Bascompte & Jordano 2007; Maherali & Klironomos 2007). Mutualisms can influence phylogenetic community structure in either direction (clustering or overdispersion), depending on the nature of the interactions (Sargent & Ackerly 2008). Plant–pollinator interactions have been hypothesized to increase phylogenetic clustering due to the benefits accrued to congeners through shared pollinators (Moeller 2005; Sargent & Ackerly 2008). It stands to reason that mutualisms and other positive interactions should promote phylogenetic clustering any time that mutualists are spatially aggregated and specialized enough that they enhance the survival of phylogenetically similar species. While positive interactions may promote phylogenetic clustering when they enhance fitness of phylogenetically similar species, they may promote high phylogenetic diversity (overdispersion) if they increase the co-occurrence of distantly related species. For example, early residents in Mexican plant communities facilitated establishment of a diverse assemblage of species by creating protected microhabitats for regeneration (Valiente-Banuet & Verdú 2007). Positive interactions tended to occur between these early 'nurse plants' and distantly related benefactors. Hence, in this case, facilitation caused overdispersion of communities.

Gene flow and lack of reproductive isolation

A lack of reproductive isolation might also have consequences for community assembly and phylogenetic community structure, particularly in communities dominated by

a single clade. For example, in clades where the evolution of reproductive isolation is positively associated with both divergence time and the extent of ecological divergence between species (Funk *et al.* 2006), gene exchange may preclude the long-term coexistence of closely related lineages in local communities (Losos 1990; Levin 2006) causing phylogenetic overdispersion (Fig. 5). This can occur if gene pools of two lineages merge within local communities even though they may maintain their genetic integrity in other parts of their geographical ranges. Alternatively, sympatry of close relatives may be limited by hybridization and production of hybrid offspring with reduced fitness. In such 'tension zones' the lack of reproductive isolation between taxa, coupled with selection against hybrid individuals, prevents both the merger of the hybridizing lineages and their establishment within each other's ranges (Burke & Arnold 2001). Under both of these models, coexistence would be limited for close relatives, but not for distantly related ones causing a tendency towards phylogenetic overdispersion (assuming that the degree of reproductive isolation increases with time since divergence). Gene exchange can also increase genetic variation and evolutionary change in populations, potentially promoting divergence (Arnold 1992; Grant & Grant 2008). Adaptive divergence enabled by low-level gene exchange between lineages could enhance a tendency for close relatives to occur in contrasting habitats causing phylogenetic overdispersion.

The challenge of linking pattern to process

Ecologists learned in past decades that attempts to infer community assembly rules from community patterns (e.g. Diamond 1975) could not replace experimental and other classical methods for determining ecological processes (e.g. Connell 1980; Strong & Simberloff 1981). The difficulty of interpreting process from pattern again confronts us now that data and tools for phylogenetic analysis are widely available, presenting a challenge to phylogenetic community ecology. We argue that novel insights arise when patterns of phylogenetic relatedness are used in conjunction with an understanding of the functional biology of organisms in the context of their ecological interactions and evolutionary history, bearing in mind the importance of scale (Box 1). In particular, it is important to understand the nature and strength of interactions between organisms and their environment, the strength and specificity of biotic interactions, as well as the amount of convergence and conservatism in traits that influence these interactions. Finally, we argue that controlled experiments that make use of phylogenies in their design (e.g. Agrawal & Fishbein 2008) can play an important role in determining the strength and specificity of these kinds of interactions.

THE EVOLUTIONARY COMPONENT OF COMMUNITY ASSEMBLY

An expanding area of phylogenetic community ecology challenges the classical assumption in ecology that the species pool is static at time scales relevant to ecological processes. Ecologists have often agreed explicitly (e.g. Weiher & Keddy 1999) or implicitly to leave to evolutionary biologists and paleobiologists the roles of speciation, extinction and biogeographical dispersal in generating the species pool. However, the availability of time-calibrated phylogenies and their application to studies of community assembly have revealed the dynamic nature of the species pool and demonstrated that generation of the pool, as well as evolution of species traits within the pool, must be considered part of the assembly process (Fig. 3) (e.g. Brooks & McLennan 1991; Losos *et al.* 1998a; Ackerly 2004; Gillespie 2004; Pennington *et al.* 2006; Givnish *et al.* 2008). As we discuss below, interspecific interactions within communities can feed back to evolutionary processes (Haloian & Strauss 2008) causing, for example, *in situ* speciation and adaptive radiation (e.g. Schluter 2000) that add species to the regional pool. Such feedbacks are likely to operate differently on islands where many species are descended from a small number of ancestors compared to continental settings where there is a pool of species from surrounding areas (Losos 1996). Investigations of this kind shed light on early controversies about the nature of communities and provide insight into the biogeographical and evolutionary processes that influence community assembly, answering Ricklefs (1987) plea from two decades ago.

Community assembly through dispersal vs. *in situ* evolution

By providing a temporal dimension to community ecology, phylogenetic information allows community ecologists to assess when and where traits of ecological significance originated, and consequently, whether communities are primarily assembled through *in situ* evolution or through dispersal and habitat tracking (e.g. Brooks & McLennan 1991; Spironello & Brooks 2003; Ackerly *et al.* 2006). The assembly process has thus been characterized as a race between adaptation and colonization (Urban *et al.* 2008). Evidence that ecologically relevant traits are phylogenetically conserved has lent support to the hypothesis that it is easier for organisms to move than to evolve (Donoghue 2008). Chaparral communities in Mediterranean California provide an important example of using phylogenies to determine the relative roles of *in situ* evolution and migration in community assembly. Plant species with sclerophyllous leaves and low specific leaf area were long thought to have acquired

these traits through convergent evolution in response to Mediterranean climates (Cody & Mooney 1978). However, Ackerly (2004) found that these traits evolved prior to the Mediterranean climate in most lineages, providing evidence that these species tracked the climates to which they were previously adapted. Far from being an example of *in situ* convergent evolution, Mediterranean chaparral communities were shown to represent an example of dispersal and ecological sorting on phylogenetically conserved traits that evolved elsewhere. Nevertheless, other studies demonstrate a strong role for convergent evolution in community assembly. For example, *Anolis* lizard communities on different islands and iguanian lizard communities on different continents were assembled through *in situ* convergence of ecomorphs (Losos *et al.* 1998a; Melville *et al.* 2006).

The shifting role of evolution in community assembly through time

Phylogenetic approaches have also revealed that communities assembled through dispersal vs. those assembled through *in situ* evolution represent two extremes of a continuum. Evidence suggests that available ecological space is filled either by adaptation of early occupants or by dispersal of conserved ecological types, depending on which occurs first (Stoks & McPeck 2006). Hawaiian *Tetragnatha* spiders provide a striking example of this pattern where communities on different islands have formed by both *in situ* evolution of adaptive phenotypes as well as by colonization of pre-adapted phenotypes (Gillespie 2004). In particular, some species colonized new islands without changing their ecological niche and conserving their ecomorph. For the spiders that arrived on islands where their old niche was already filled, these species then diversified after colonizing a new island, switching ecological niches and thus changing ecomorphs. Prinzing *et al.* (2008) found a similar pattern in the Dutch flora. They showed that vascular plant communities are either comprised of many lineages that are nested within different clades with low functional trait diversity or few lineages that evolved with high functional trait diversity, where functional trait diversity is determined by the variance in traits found to be important in defining ecological niches. They interpreted this as evidence that there are suites of available niches that can be filled either by *in situ* evolution in which one lineage radiates generating high functional diversity, or through colonization by many different lineages such that species from diverse lineages generate similar functional diversity within communities.

Phylogenetic studies of the assembly process in island adaptive radiations reveal that the extent to which a community acquires its species through dispersal and

in situ evolution changes as it is assembled (Emerson & Gillespie 2008). Phylogenetic community ecology has thus raised a key question at the intersection of ecology and evolutionary biology: When does dispersal or *in situ* evolution predominate in the assembly process? Relative rates of dispersal and diversification are likely to be critical. In island studies where dispersal is slower than speciation, early species that are pre-adapted to existing ecological conditions arrive via dispersal, but *in situ* speciation and adaptive divergence subsequently take over as the predominant process by which species assemble in the community (Emerson & Gillespie 2008).

FEEDBACKS TO EVOLUTIONARY PROCESSES

Community-level interactions feed back to influence evolutionary process of speciation and adaptation (Fig. 3) (Antonovics 1992; Bascompte & Jordano 2007; Johnson & Stinchcombe 2007; Haloin & Strauss 2008; Hoberg & Brooks 2008; Jablonski 2008). Classical community ecologists have generally focused on the interactions among members of communities and have been reluctant to consider how they might impact the evolutionary processes that generate the regional species pool from which communities are assembled (Fig. 3). An important area in which phylogenetic community ecology can advance classical community ecology is the investigation of how interactions among species within communities feed back to influence the evolutionary processes that impact species ecological roles and ultimately the diversity of traits and species in the regional pool.

Plant–insect interactions provide well-known examples of how evolutionary innovations that emerge at one trophic level can influence evolutionary processes at higher trophic levels as a result of co-evolutionary arms races (Ehrlich & Raven 1964; Farrell 1998). Insects feeding on host plants drive divergent selection for new defences which, in turn, drive selection in insects to evolve strategies to circumvent these novel defences (Kawecki 1998). These novel strategies can have the effect of increasing the amount of specialization in the herbivore (especially if they incur a cost) – further strengthening selection in the plant for more defence investment (and/or novelty).

The ecological roles of insect herbivores and selection pressures on host plants can change over time and space, altering species interactions and selection patterns (Thompson 2005). For example, isolated islands often have limited subsets of both mainland plants and their specialist enemies, especially soon after colonization. Planthoppers from the genus *Nesosydne* (Hemiptera: Delpaciidae) are recent colonists to the Hawaiian islands (Roderick & Percy 2008). On the mainland, this genus is generally always associated with monocot lineages like grasses and sedges.

In contrast, on Hawaii this lineage has expanded its host breadth to cover more than 25 plant families, mostly eudicot lineages. This ecological release is probably due to both selection for increased host breadth in the insects due to less competition from other herbivores and selection in the plant lineages for lower levels of defences due to their own escape from their specialist enemies after arriving in Hawaii. Yet within these newly arrived planthopper lineages, *Nesoydne* species are already beginning to re-specialize on the Hawaiian lineages, with 77% of the species monophagous, feeding on only a single plant species (Roderick & Percy 2008). This illustrates how changing phylogenetic community structure influences evolution of herbivore-host specialization.

Evolutionary feedbacks have important consequences for the temporal dynamics and diversity of the species pool. In general, phylogenetic studies of species with a deep history of coexistence indicate that rates of ecological and morphological diversification tend to be greatest during the early phases of a clade's radiation (when ecological opportunity is abundant) and then decline as niches are filled and ecological interactions among co-occurring species constrain further opportunities for diversification (Kozak *et al.* 2005; Harmon *et al.* 2008; Wellborn & Broughton 2008). Several recent studies on birds, fishes and salamanders suggest that as lineages spread through a geographical area to form communities, the rate at which new species accumulate in the regional pool declines as geographical space is filled and as ecological niches are filled with competing species (Ruber & Zardoya 2005; Kozak *et al.* 2006; Phillimore & Price 2008; Rabosky & Lovette 2008; Williams & Duda 2008).

Although the potential links between community ecology and macroevolution are exciting, a variety of challenges must be overcome to fully understand the extent to which community interactions shape long-term evolutionary processes (Johnson & Stinchcombe 2007). Perhaps the biggest hurdle is reconciling mismatches of evolutionary and ecological patterns that emerge at different spatial and temporal scales (Jablonski 2008). Focused comparative studies using well-resolved phylogenies between interacting species on islands of different ages hold promise for disentangling the relative strengths of historical contingency, deterministic ecological interactions, speciation and dispersal (Losos *et al.* 1998b; Emerson & Gillespie 2008).

CONSEQUENCES OF PHYLOGENETIC COMMUNITY STRUCTURE AND TRAIT CONSERVATISM FOR COMMUNITY DYNAMICS AND ECOSYSTEM PROCESSES

While considerable effort has been placed on using phylogenetic community structure to infer causal processes in community assembly, much less work has

focused on the consequences of phylogenetic history and phylogenetic community structure for ecosystems and their responses to global change (Table 1). As outlined in Fig. 3, phylogenetic history influences both traits of species, as well as the organization of communities, both of which influence ecosystem properties. Here we focus on the plant literature, reflecting the general orientation of ecosystem-level research. We know that important functional attributes of plants, such as leaf traits (Ackerly & Reich 1999) wood density (Chave *et al.* 2006; Swenson & Enquist 2007), allocation patterns (McCarthy *et al.* 2007) and element concentrations and their stoichiometric ratios (Kerkhoff *et al.* 2006), show evidence of trait conservatism as inferred from phylogenetic or taxonomically based variance partitioning. These and related studies highlight the possibility of predicting clade-level ranges of trait values from a subset of individuals within a clade (Box 1, Fig. 2). Such traits can have important consequences for ecosystem functions, including decomposition rates, nutrient cycling and carbon sequestration (Vitousek 2004; Weedon *et al.* 2009). It follows that both phylogenetic community structure and composition may influence ecosystem-level processes and that phylogenetic information can thus help predict ecosystem properties and responses to changing environments. An important emerging area of investigation focuses on using phylogenetics to understand and predict long-term community dynamics (Willis *et al.* 2008), ecosystem processes (Cadotte *et al.* 2008) and responses of ecosystems to global change (Edwards *et al.* 2007).

Predicting ecosystem function from community phylogenetic diversity

The phylogenetic structure of communities shows promise for predicting ecosystem processes. Two recent studies of links between phylogenetic diversity and ecosystem function in plants (Cadotte *et al.* 2008) and plant-mycorrhizal communities (Maherali & Klironomos 2007) have demonstrated that phylogenetic diversity can predict community productivity better than species richness or functional group diversity. While biodiversity experiments, such as those analysed by Cadotte *et al.* (2008) may not be truly representative of natural communities because they are often artificially assembled and weeded, they provide support for the hypothesis that phylogenetically diverse communities can maximize resource partitioning and hence use greater total resources. This is based on the evidence that the more differentiated species are the greater their resource exploitation (Finke & Snyder 2008). If phylogenetic relatedness predicts ecological similarity, phylogenetic diversity should enhance complementarity and increase ecosystem productivity by maximizing total resource uptake. By the same logic, high phylogenetic

diversity may be predicted to increase ecosystem stability by ensuring that sufficient ecological strategies are represented in an assemblage to ensure persistence of the ecosystem in the face of changing conditions. Knapp *et al.* (2008) found an uncoupling between species richness and phylogenetic or functional diversity in urban areas in Germany. They hypothesized that despite high species richness in these areas, low phylogenetic and functional diversity in urban ecosystems should limit their capacity to respond to environmental changes. Similarly, phylogenetic diversity may be linked to nutrient cycling, resistance to invasion, soil carbon accumulation and other ecosystem processes, goods and services. Such links, if they continue to be substantiated, lend support to the argument that phylogenetic diversity has higher utility than species richness as a conservation criterion for management decisions (Faith 1992; Gerhold *et al.* 2008).

Deterministic models of community dynamics using ecologically important traits – is there a role for phylogeny?

Theoretical approaches to understanding communities have been successful in accurately predicting the transient dynamics and outcome of species interactions based on fundamental ecological properties of organisms in low diversity systems (Dybzinski & Tilman 2007; Purves *et al.* 2008). In a test of the resource ratio hypothesis (Tilman 1982), Dybzinski & Tilman (2007) accurately predicted the outcome of species competition from minimum resource concentrations in monocultures (R^*). Purves *et al.* (2008) used a mathematical model that relies on a small number of species-level parameters, including canopy join heights (Z^* , a measure of shade tolerance) as well as understory and overstory mortality rates to predict long-term community dynamics in forests of the Upper Midwestern United States. Extending such models to predict the future of vegetative communities globally faces many challenges, including encapsulation of the extreme diversity in tropical forests. Phylogenetics may allow species to be parameterized by lineage, reducing the number of parameters in the model and the data required, and by linking phylogenetically similar species in a predictive framework. A recent study demonstrates that phylogenetic conservatism in the ability of species to adjust their flowering time phenology to climatic warming in New England underlies a phylogenetically biased pattern of local extinction and is thus predictive of long-term community dynamics (Willis *et al.* 2008).

Perhaps the biggest challenge facing this emerging area of phylogenetic community ecology is to determine whether ecological traits that are most predictive in ecological and dynamic global vegetation models are evolutionarily labile, and are therefore not well predicted by phylogeny.

Theoretical studies have indicated, for example, that alternative designs of equal fitness in the same environment are likely to evolve (Marks & Lechowicz 2006), and empirical studies have shown evidence for many-to-one mapping of critical ecological traits, such that the same ecological function can evolve through more than one pathway (Wainwright *et al.* 2005). As a result, close relatives may not necessarily be more ecologically similar than distant relatives. Nevertheless, there is increasing evidence that ecologically relevant traits are likely to show as much phylogenetic conservatism as reproductive and other taxonomically relevant traits (Prinzing *et al.* 2001; Donoghue 2008). This presents us with the challenge to understand the extent and phylogenetic scale of conservatism in ecological traits – a challenge that will require both experimental manipulations and analytical surveys within and across a broad range of taxa.

Phylogenetic vs. functional group approaches in dynamic global vegetation models

Dynamic global vegetation models are increasingly using a functional trait-based approach to predict responses of biomes to climate change (e.g. Bonan *et al.* 2003). Edwards *et al.* (2007) argue that phylogenetic information provides a powerful means to scale from organism physiology to global processes. They reason that physiological traits used to scale between individuals and ecosystems vary among different groups of organisms, and these differences originated as evolutionary innovations along the branches of the tree of life. For example, C_3 and C_4 grasses are commonly used functional groups in ecological experiments and in global vegetation models (e.g. Bonan *et al.* 2003). However, variations of the C_4 photosynthetic pathway have evolved multiple times, and it turns out that the response of species to temperature depends more on the phylogenetic lineage than on the qualitative delineation of the photosynthetic apparatus as C_3 or C_4 (Edwards and Still, 2008). Thus phylogenetic information may be more useful than functional group classification schemes in dynamic global vegetation models that predict responses of the Earth's biota to climate change (Edwards *et al.* 2007).

We hypothesize that the power of phylogeny to predict ecologically relevant traits is likely to increase with the phylogenetic scale of the analysis up to a point (Box 1, Fig. 2). However, at the largest phylogenetic scales, the probability of trait convergence may be high due to the presence of similar selective regimes in geographically disjunct regions of the globe. Phylogenetically based functional groups may thus be most useful at intermediate phylogenetic scales, and are likely to be most useful in cases where trait data are incomplete and diversity is high.

CONCLUSION

The merging of community ecology and phylogenetic biology now allows community ecologists to consider phenomena occurring over broader temporal and spatial scales than was previously possible. The rapidly expanding field of phylogenetic community ecology is thus poised to resolve long-standing controversies in classical community ecology and to open new areas of enquiry. Studies in this emerging field have addressed fundamental questions about the role of niche-based vs. neutral processes in community assembly, challenged the assumption that evolutionary processes are not relevant to community assembly, revealed influences of community interactions on evolutionary processes, and begun to provide predictive information about the responses of communities and ecosystems to global change.

A large number of studies have analysed the phylogenetic structure of communities to examine the evidence for neutral or niche-based processes in community assembly. The most convincing of these are studies that examine the functional ecology of organisms and test for conservatism in traits and niches. These have revealed many different processes that cause non-random phylogenetic community structure (Table 1). Two challenges facing this area of study are determining the extent and scale of phylogenetic conservatism in ecologically important traits, rather than assuming it, and drawing on functional biological information to interpret phylogenetic patterns in communities. The merging of phylogenetics and community ecology will continue to advance the debate about the roles of neutral vs. niche-related processes by working at multiple spatial scales and investigating turnover in phylogenetic diversity of organisms across environments over distances greater than dispersal distances. Such studies can provide evidence for or against ecological sorting and evolution of habitat specialization, not predicted under neutral theory. In general, we argue that there is a need for greater emphasis on experimental and modelling approaches (cf. Kraft *et al.* 2007) in a phylogenetic context that examine the conditions under which specific processes are important in community assembly. Such approaches would be useful, for example, to determine whether close relatives are generally expected to show stronger competitive interactions than distant relatives and at what temporal and spatial scale such interactions are likely to influence community assembly.

One of the most important contributions phylogenetic community ecology has made is a greater appreciation for the role of evolution in community assembly. Ecologists are now challenged to consider broader temporal and spatial scales in explaining coexistence, diversity and community

composition. In particular, phylogenetic community ecology offers insight into the conditions under which it has been easier to move than to evolve. Time-calibrated phylogenies allow the possibility to test not only the extent to which communities assemble through dispersal vs. *in situ* evolution, but also the relative timing of the arrival of species and the evolution of functional traits, providing insight into the conditions under which evolution is favoured over dispersal. An important area of investigation is the influence of community interactions on processes of speciation, adaptation and extinction. A challenge in this area is reconciling macroevolutionary trends with results from microevolutionary studies (Jablonski 2008), but it is one that can be overcome with focused studies integrating well-resolved phylogenies, functional traits and interactions among species.

Finally, the application of phylogenetic information to predicting community dynamics, ecosystem function and responses to global change shows increasing promise. An important challenge involves the comprehensive examination of the extent to which ecologically important traits useful in predictive models are phylogenetically conserved. To the extent that they are, phylogenetic biology will offer increased predictive power in ecology.

The questions that phylogenetic community ecology addresses are fundamental to understanding the nature of biological communities. With the increasing rate of global change – including land use change, habitat loss, species invasions, alterations in element cycling and global climate change – basic understanding of the causes and consequences of community structure has never been more important. Protecting our biological resources requires continued commitment to understanding how communities assemble and how they respond to forces of change.

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