

# PHYLOGENIES AND COMMUNITY ECOLOGY

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■ **Abstract** As better phylogenetic hypotheses become available for many groups of organisms, studies in community ecology can be informed by knowledge of the evolutionary relationships among coexisting species. We note three primary approaches to integrating phylogenetic information into studies of community organization: 1. examining the phylogenetic structure of community assemblages, 2. exploring the phylogenetic basis of community niche structure, and 3. adding a community context to studies of trait evolution and biogeography. We recognize a common pattern of phylogenetic conservatism in ecological character and highlight the challenges of using phylogenies of partial lineages. We also review phylogenetic approaches to three emergent properties of communities: species diversity, relative abundance distributions, and range sizes. Methodological advances in phylogenetic supertree construction, character reconstruction, null models for community assembly and character evolution, and metrics of community phylogenetic structure underlie the recent progress in these areas. We highlight the potential for community ecologists to benefit from phylogenetic knowledge and suggest several avenues for future research.

## INTRODUCTION

The differences among species that co-occur in an ecological community are the result of modifications to a common ancestor that the species all ultimately share. As molecular and analytical methods make the elucidation of phylogenetic relationships easier and more reliable, ecologists have an invaluable new dimension of information available with which to make sense of these differences among species. However, despite recognition of the potential for using phylogenies in community ecology (Brooks & McLennan 1991, Losos 1996, Thompson et al. 2001), and increasing interest in the role of history in ecology (Ricklefs 1987, Ricklefs & Schluter 1993a), integration of evolutionary biology and community

ecology remains elusive. This is due partly to the conceptual and methodological difficulties of bridging gaps of temporal and spatial scale and partly to poor communication: many ecologists are either unaware of the potential benefits of knowing about the phylogenetic relationships in their communities or are deterred by the unfamiliarity of molecular techniques and phylogenetic methods and the accompanying terminology. Similarly, many systematists are unaware of the fascinating ecological questions that can be addressed using the phylogenies they produce or the ways in which knowledge of community composition might bear on studies of character evolution, diversification rate, and historical biogeography. Our intention in this review is to introduce to both parties the various approaches that have already been taken to incorporate phylogenetic information into community ecology.

Phylogenies are being used extensively in the larger field of evolutionary ecology (see Miles & Dunham 1993, Miller & Wenzel 1995, Ackerly et al. 2000), so we limit our review to studies and concepts explicitly relating to the phylogenetic and taxonomic structure of local communities. We do not explicitly review character displacement in species pairs (Schluter 2000a), adaptive radiation in particular clades (Schluter 2000b), "host-client" coevolution (host-parasite, plant-herbivore, and host-pathogen), general historical biogeography, or the uses of microbial phylogenies. Previous reviews and discussions of the interaction of phylogeny with community ecology include Wanntorp et al. (1990), Brooks & McLennan (1991, 2002), Eggleton & Vane-Wright (1994), Losos (1996), McPeck & Miller (1996), Grandcolas (1998), and Nel et al. (1998).

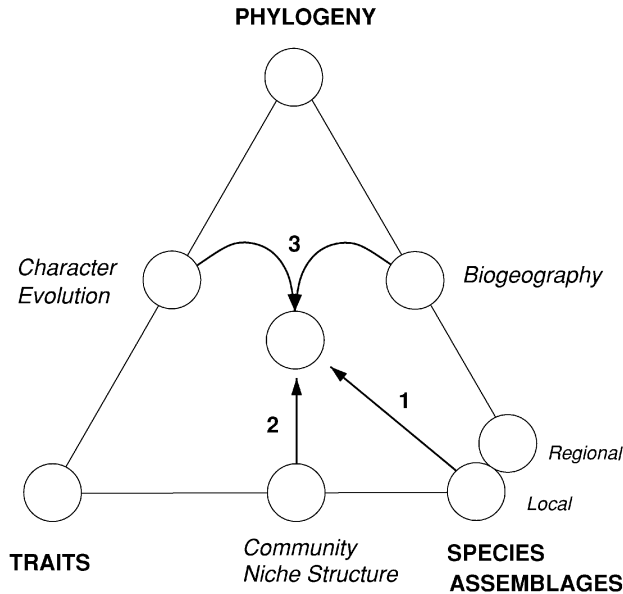
Empirically, phylogenies and community ecology have been put together predominantly in studies of community assembly, organization, and species co-occurrence, and we identify in this literature three major approaches (Figure 1). Other questions of community ecology, relating to relative abundance, range size distributions, and species richness have received less attention from a phylogenetic perspective, but we cover the work that has been done so far. We then review recent methodological advances and conclude with suggested directions for further work.

## COMMUNITY STRUCTURE AND COEXISTENCE

Even though phylogenetic methods were developed fairly recently, a connection between taxonomy and community ecology has long been recognized:

As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera (Darwin 1859).

Darwin's statement already contains what we see to be the essential elements of an evolutionary understanding of community organization: that species interact



**Figure 1** Schematic summary of various approaches to the integration of phylogeny, traits, and communities. (1) Examining the phylogenetic structure of community assemblages; (2) exploring the phylogenetic basis of community niche structure; (3) adding community context to studies of trait evolution and biogeography.

in communities, that species interact based on their phenotypic differences and similarities, and that phenotypic variation has a basis in evolutionary history. In a synthetic understanding of the origin and maintenance of community composition, three elements are drawn together: phylogeny, community composition, and trait information (Figure 1). Researchers have tended to approach this synthesis using one (or more) of three methods: 1. analyzing community taxonomic or phylogenetic structure, 2. exploring the phylogenetic basis of niche differentiation, and 3. adding community context to character evolution and biogeography. We discuss these approaches below, in order of increasing information requirements and increasing potential to reveal both ecology and evolution in the past and present.

## The Phylogenetic Structure of Community Assemblages

*Key question: Is the distribution of species among habitats (or samples) in a community nonrandom with respect to phylogeny? (Using: species list of local community + distribution of species among community samples + phylogeny of community species list)*

Since the advent of formal classification, natural historians have asked why different areas are dominated by different species, genera, and families (e.g., Gentry

1982). The quantitative taxonomic structure of communities was first addressed by Elton (1946), who reasoned that the lower number of species per genus observed in local areas than in the whole of Britain was evidence for competitive exclusion of ecologically similar congeners in local habitats. Interest continued in species/genus ratios for a number of years (Moreau 1948, Williams 1964, Simberloff 1970, Tokeshi 1991) and was notable as the context for the first use of null models in ecology (Gotelli & Graves 1996). Implicit in these analyses was the same three-part interaction discussed above (Figure 1): community organization (i.e., the role of competition) can be deduced from the (assumed) ecological similarity within a genus, and the taxonomic structure of a community (i.e., the significant departure of species/genus ratios in community samples relative to a regional species pool). More recently, the global consistency of taxonomic structure in forest communities has been examined by Enquist et al. (2002), who compared the species/genus and species/family ratios across many standardized 0.1 ha plots. They found an exponential relationship between numbers of genera or families and the numbers of species, across two orders of magnitude of species number, and suggest that this result indicates the existence of forces acting to constrain phylogenetic structure.

The availability of phylogenies, along with methods for the construction of supertrees and for assembling the phylogenies of communities, now permits community structure to be assessed phylogenetically. A simple logical framework can then be employed to infer mechanisms of contemporary coexistence (Table 1, and see Figure 2 for terminology). A clumped phylogenetic distribution of taxa ("phylogenetic attraction") indicates that habitat-use is a conserved trait within the pool of species in the community, and that phenotypic attraction dominates over repulsion. However, phylogenetic overdispersion (repulsion) can result either when closely related taxa with the most similar niche-use are being locally excluded (phenotypically repulsed), such that there is minimum niche overlap of coexisting species, or when distantly related taxa have converged on similar niche-use and are phenotypically attracted. Note that the fourth possible interaction, phenotypic repulsion of traits that are convergent, will not tend to recreate phylogenetically clustered communities, but phylogenetically random ones.

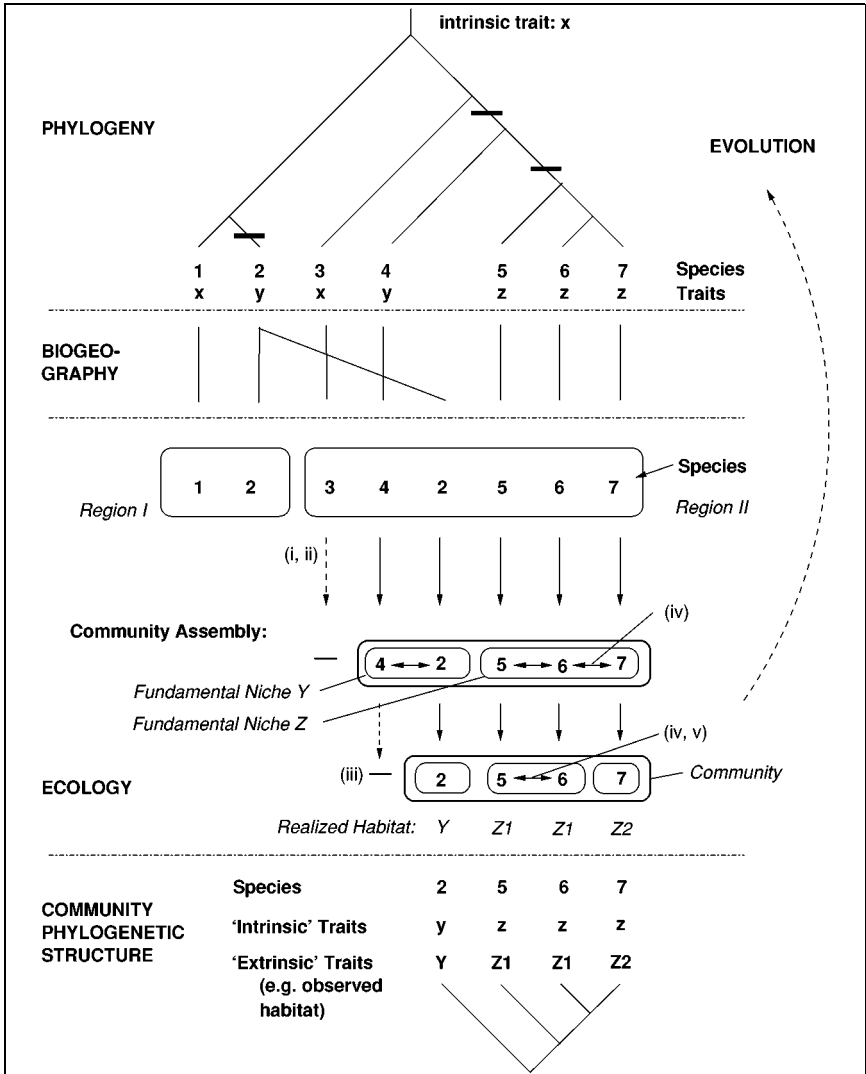
For example, Webb (2000) found that the tree taxa that co-occurred in 0.16 ha plots in Indonesian Borneo were more closely related than expected from a random sampling of the local species pool. Assuming that conservatism dominates in the phylogenetic distribution of ecological character, he interpreted this as evidence for the predominant role of habitat filtering (and phenotypic attraction), as opposed to local competitive exclusion (and phenotypic repulsion) of similar species. In a similar study, H. Steers (personal communication) determined that a measure of the frequency of co-occurrence of tree species pairs in a Mexican dry tropical forest was positively correlated with their phylogenetic proximity, again interpreting this as evidence of habitat selection for ecologically similar, phylogenetically related species. Kelly (1999) found that British plant taxa in extreme environments were more closely related than expected by chance, which was seen as evidence that these

**TABLE 1** The expected distribution of sample taxa on the phylogeny of a pool at a larger spatial scale, given various combinations of phylogenetic trait distribution and ecological process

	Ecological traits phylogenetically	
	Conserved	Convergent
<b>Dominant ecological force:</b>		
Habitat filtering (phenotypic attraction)	Clustered	Overdispersed
Competitive exclusion (phenotypic repulsion)	Overdispersed	Random

species were ecologically similar. Conversely, Graves & Gotelli (1993) showed that congeners seldom co-occur in the same mixed-species foraging flock in the Amazon, but that this “checkerboard” pattern breaks down at higher taxonomic levels. They interpreted this finding as the effect of intra-community competitive exclusion among ecologically similar species (i.e., phenotypic repulsion), with congeners being most similar. In Florida woodland communities dominated by oaks, J. Cavender-Bares (personal communication) also found that close relatives co-occurred less than expected by chance. In this case each plot generally had one species from each of three major *Quercus* clades (sections).

The spatial scale of samples used in studies of community phylogenetic structure is of great importance to the interpretation of the patterns found because the biological nature of phenotypic and phylogenetic attraction and repulsion depends upon the scale involved. At the largest, continental scales (e.g., 1,000–10,000 km), phylogenetic clustering of members of a regional sample on a global phylogeny reflects biogeographic rather than ecological processes, as clades diversify within the sample region, and cause many taxa in the region to be, on average, more related to each other than to taxa outside the region. Within a region (e.g., 10–1,000 km), phenotypic sorting might occur among communities that differ environmentally from one another (e.g., wetlands versus montane). Such phenotypic attraction might lead to phylogenetic attraction or repulsion of the community sample on the regional pool, depending on the phylogenetic distribution of important traits. Sustained phenotypic repulsion within a community might also lead to semipermanent exclusion of too-similar taxa from individual communities, with taxa maintained in the regional pool by low rates of dispersal among communities (e.g., Tilman 1994). At the community scale (e.g., 100 m–10 km), species should segregate into habitats based on the relative strengths of habitat filtering versus competition among similar species (see Figure 2). Finally, at the smallest, neighborhood scales (e.g., <100 m), one might observe the effect of individual-based interactions that lead to within-habitat filtering or “neighborhood exclusion.” Hence, a spatially nested analysis of community phylogenetic structure may detect different patterns of phylogenetic clustering or over-dispersion at different scales, providing more information about community processes than an analysis at just a single scale.



**Figure 2** Schematic of the general framework employed in this review, with associated terms. A lineage may diversify by the division of its ancestral range and allopatric speciation, such that sister clades are no longer coregional (ancestor of species 1 and 2 versus ancestor of species 3–7; *BIOGEOGRAPHY*). Alternatively, sympatric and parapatric or even allopatric speciation mechanisms may lead to the origination of new species that are coregional with their sister species (species 3–7). A phylogeny can be reconstructed for the lineage (*PHYLOGENY*) using molecular and morphological species traits. Species may appear in regions either through the geographical division of their area (vicariance) or by subsequent dispersal (species 2

**Figure 2** (*Continued*) dispersed into region II). The phylogenies of lineages and the distribution of taxa among regions can be used to infer the historical patterns of movement in the taxa and associated reconstruction of area connectedness (area cladograms), using biogeographic methods. Trait change occurs as the lineage diversifies, and ancestral state changes can be reconstructed (or traced) on a phylogeny using, for example, parsimony or maximum likelihood (x to y, y to z). Traits can usefully be divided into intrinsic (morphological or physiological traits that can be assessed validly when an organism is removed from its environment, e.g., skeletal structure, beak size, body size, plant sexual system) and extrinsic (traits that only have meaning in an external abiotic and biotic environment, e.g., swimming speed, maximum growth rate, drought tolerance, shade tolerance, prey choice, diet breadth). The “ecological character” of an organism is usually a complex set of correlated characters, but can often be directly related to simpler intrinsic morphological characters (e.g., Losos 1995).

The pattern of evolution of any trait can be characterized as conservative (more closely related taxa are more similar) or convergent (homoplasious, the independent evolution of similarity). Trait divergence is not intrinsically conservative or convergent, but because the greater the change in a trait, the more likely it is to resemble the value of a species in an independent lineage, divergence often results in convergence. Additionally, the rate of homoplasy increases with decreasing number of potential trait states (Donoghue & Ree 2000) and increasing number of ways for species to be functionally similar while intrinsically different (e.g., fleshy-fruitedness arises via a number of anatomical paths). When referring to ecological traits, the term “phylogenetic niche conservatism” has been used (Harvey & Pagel 1991, Lord et al. 1995). This conservatism may be due to active, stabilizing selection (Lord et al. 1995) or to a reduction in the potential range of ecological character evolution caused by the fixation of ancestral traits (i.e., developmental constraints; Westoby et al. 1995).

Species are assembled into communities from a regional species pool (the list of all species in an area at the next-highest spatial scale from the scale under consideration; e.g., species 2–7 form a species pool relative to the community) (e.g., Liebold 1998, Fox 1999, Blackburn & Gaston 2001) (*ECOLOGY*). In this review we consider a community to be more than two species in the same trophic level and the same guild (e.g. meadow plants, desert granivores) co-occurring spatially at a scale over which species might disperse within a few generations. Some species present in a region may fail to meet the ecological requirements to survive in any of the niches in a community, that is, they are filtered out, or simply fail to reach a particular community by chance (species 3 and process i or ii, respectively). Community species richness is often correlated with regional pool richness, suggesting that communities seldom saturate (Cornell & Lawton 1992). Species may persist (coexist for long periods) in the same community by occupying different niches, thus minimizing competition for resources

**Figure 2** (*Continued*) (“habitat partitioning”; species 2 and 4 versus species 5–7; Wisheu 1998). However, with enough species in the community, several species with similar niche requirements will tend to be filtered into the same niche (a phenotypic attraction). Simultaneously, negative interindividual interaction (phenotypic repulsion) is expected among species that occupy the same niche and/or habitat (process iv). This negative interaction is expected to be stronger among ecologically more similar species and may alter the realized niche/habitat distribution of taxa into sub-niches (or localities) within the fundamental niche (but never beyond the bounds of the fundamental niche; species 7 versus 5 and 6), or may lead to classic competitive exclusion (process iii on species 4). It may also lead to the exclusion of competing species on the most proximate, neighborhood scale (e.g., at the scale of individual interactions), without leading to community exclusion. Species may coexist within a habitat by non-niche-partitioning, equalizing (*sensu* Chesson 2000) processes (species 5, 6, and process v), or may be in the slow, nonequilibrium process of being excluded from the community. We use habitat to mean the spatial location where a combination of resource levels come together.

A phylogeny can be reconstructed for species sampled in a spatially defined area (region, community), rather than for all species in a lineage (*COMMUNITY PHYLOGENETIC STRUCTURE*). The occurrence of taxa in areas at a smaller spatial scale (community and habitat, respectively) can be indicated on the phylogeny of the larger pool of species. The distribution of these taxa can be phylogenetically clumped, random, or over-dispersed on the phylogeny of the entire pool (e.g., a sample containing species 6 and 7 is clustered on the phylogeny of the community of species 2, 5, 6, and 7).

Sustained selective pressure from individual competitors or environmental changes leads eventually to change in ecological character over evolutionary time, usually in the direction of reduced niche overlap (*EVOLUTION*). The community context may also cause stabilizing selection, especially in diverse systems in which interspecific interactions are unpredictable. Trait change may also be the result of drift, founder effects, or pleiotropy. Trait change resulting from ecological interactions may itself lead to ecological speciation within a region (McPeck 1996, Schluter 2001).

## The Phylogenetic Basis of Community Niche Structure

*Key question: How are niche differences in communities arrayed on a phylogeny? (Using: species list of local community + distribution of species within community + phylogeny of community species list + ecological character data for those species)*

Ecologists have long studied the distribution of ecological characters of species in communities to understand community organization (e.g., MacArthur & Levins 1967, Bowers & Brown 1982). An even dispersion of trait values along some



gradient (e.g., constant body-size ratios) has been held to be evidence for both contemporary competitive exclusion and the long-term evolutionary effect of such competition (Connell 1980), although the establishment of the significance of this overdispersion has been controversial (reviewed by Gotelli & Graves 1996).

The availability of data on the taxonomic or phylogenetic distribution of niche differences enables the allocation of contemporary niche structure to either contemporary ecological or historic evolutionary causes, or a combination thereof. For example, because Cavender-Bares (see above, personal communication) had assessed water-use trait data as well as water availability in sample plots (Cavender-Bares & Holbrook 2001), she was able to interpret the phylogenetic overdispersion of local plots as the result of contemporary habitat filtering mediated by characters that were phylogenetically convergent. Similarly, Webb & Peart (2000) assessed the species, genus, and family associations of rain forest trees with three habitat types and found both genera and families that had all of their species associated with a particular habitat. Although not phylogenetic, this pattern of ecological conservatism supports Webb's (2000) interpretation of the role of habitat filtering. In the same forests, Ashton (1988) has argued that too much emphasis has been placed on differences in habitat use among species and that in the Dipteroocarpaceae, genera and sections differ significantly in ecological character, with species within them differing mainly by minor morphological (particularly floral) changes. At a deeper phylogenetic level, Dimichele & Phillips (1996) showed consistent occupation of various habitats in Pennsylvanian-age fossil plant communities by different lineages (lycopsids, seed plants, ferns, and sphenopsids), and T. Feild and colleagues (personal communication) have inferred the maintenance of an ecological niche (disturbed understory) in several early angiosperm lineages.

Whereas clear cases of simple conservatism occur, it is likely that with a large community the phylogenetic distribution of traits is a complex mix of conservatism and convergence. A different phylogenetic scope of a study (e.g., a community of *Quercus* versus all angiosperms) might thus have a strong influence on the community phylogenetic structure observed. Silvertown et al. (1999) demonstrated for meadow plants that mean pairwise co-occurrence of species in a hydrologically defined niche-space was less than expected, indicating significant divergences in habitat use among species. Using the same methods, comparing just the species within a genus, they found a few cases of segregation of species, some cases with random overlap, and some examples of higher than expected niche overlap (Silvertown et al. 2001). This mixture of overlap and segregation was also seen at higher taxonomic levels, although the broadest comparison showed eudicots and monocots to be more segregated than expected. These results indicate that the underlying ecological traits exhibited varying patterns of divergence and stasis (i.e., convergence and conservatism) corresponding to the observation of segregation and overlap, respectively. In a related study of community assembly, Tofts & Silvertown (2000) assessed the effect of environmental filtering on grassland community membership, finding that trait values for species in a local community

were less variable than those in a regional pool, independent of phylogenetic effects; they used phylogenetic independent contrasts to remove the effect of phylogenetic trait conservatism.

The trait-phylogeny-community relationship may also appear to be random: Winston (1995) found no difference in co-occurrence rate between groups of phylogenetically closely related and more distantly related stream fish, even though co-occurrence was less among morphologically similar species than among less similar ones, a result he attributed to the effects of competition. Barraclough et al. (1999) tested whether species of tiger beetle that co-occurred in the same habitat at a locality had lower than expected similarity in various ecomorphological characters, using a phylogenetically based null model. They found no evidence for character divergence between co-regional or co-occurring species, or for habitat divergence in co-regional species. Divergence patterns were indistinguishable from random character change (see also McCallum et al. 2001).

Some studies perform the equivalent of phylogenetic independent contrast analysis (Felsenstein 1985) on the association between particular traits and community membership. For example, Chazdon et al. (2002) asked whether there were associations between reproductive traits and forest types for Costa Rican trees, and found that the significant associations found could be explained by the different phylogenetic composition of the forest types and the generally phylogenetically conservative nature of the reproductive traits. Ibarra-Manriquez et al. (2001) showed the same outcome for differences in seedling germination type among different forests. Other studies have looked primarily at the distribution of ecologically related traits of species from a species pool, without reference to community-level variation in species composition (Grandcolas 1993, Brandl et al. 1994). For example, Böhning-Gaese & Oberrath (1999) found little evidence of conservatism in ecological traits for 151 co-occurring bird species.

## Biogeographic History, Character Evolution, and Community Assembly

*Key question: Where and under what community conditions did patterns of niche-use originate? [Using: species list of local communities + distribution of species within communities + phylogeny of full lineage (and of other lineages) + ecological trait data for lineage members + biogeographic reconstruction of regional distribution of ancestral taxa]*

When phylogenetic and ecological information is available for all extant taxa in a lineage, including species in and outside of a particular community, ancestral character reconstruction of ecological traits and niche use can be examined (within limits of reconstruction methods; Cunningham et al. 1998). The questions of niche-use evolution described above can thus be answered more accurately (e.g., McPeck & Brown 2000).

Including all taxa in a lineage permits assessment of the contemporary geographic distribution of clades. Where all the members of a clade are currently

co-regional, and no members of other (closely related) clades are present, the region may be considered to be closed (without immigration), and character evolution methods can also be used to reconstruct the evolution of community structure. Furthermore, where there is evidence that (a) intra-community interactions occurred among all taxa in the region (often assumed) and (b) no major interactors in the historical communities came from other clades (e.g., ants versus rodents), trait changes can be interpreted as both cause and effect: The ancestral communities can be reconstructed and change in characters can be interpreted as the response to character states in other ancestral species. Work by Losos and colleagues (Losos 1992, 1995; Losos et al. 1998) on Greater Antillean *Anolis* lizards exemplifies this approach: the majority of species on each island result from intra-island radiations, and a similar pattern of habitat use (e.g., crown, trunk, twig) has evolved on each island within each radiation. This method also allowed the researchers to reconstruct the composition of ancestral communities and to infer that diversification in habitat use was a response to the habitats already occupied.

Most regions are, however, open (Losos 1996), i.e., they contain members of clades that can be inferred (using biogeographic methods) to have originated elsewhere and to have arrived in a region by dispersal. For example, McPeck & Brown (2000) reconstructed the phylogeny of all *Enallagma* (damselfly) species in eastern North America and were able to differentiate between a recent radiation in New England and an older diversification in the southeast United States; most eastern lakes from the Gulf of Mexico to Canada, however, contain members of both clades. Combining such biogeographic data with trait reconstructions permits the determination of whether traits and current niche-use evolved in situ or whether the traits were established elsewhere, outside the current region (Brown & Zeng 1989). Cadle & Greene (1993) analyzed the clade composition and size distribution of 15 Neotropical colubrid snake communities to test whether the overall distribution in sizes in any community was independent of the clade composition. They found that (a) the overall size distribution of a community bore a direct relationship to the clade composition, (b) different clades had different mean sizes (and size-associated differences in diet), and (c) the lineages appear to have originated and diversified in isolated areas. The work thus indicated the role of history in shaping the regional pool of species and did not support the hypothesis that snake communities are organized by processes that tend to maintain some overall distribution in size. In his study of Lesser Antillean *Anolis* species, Losos (1992) noted that the one or two species on each island are not generalists, as the ancestors of the Greater Antilles lizards are inferred to be, but show conservatism of niche-use and appear to have been ecologically sorted onto the islands according to the available habitats (see also Vitt & Zani 1996, Zimmerman & Simberloff 1996, Sturmbauer 1998, Barker & Mayhill 1999, Craig et al. 2001, Galassi 2001). Richman (1996) used phylogenies to suggest that Japanese and European assemblages of *Phylloscopus* warblers were formed by multiple invasions from mainland Asia, with only limited subsequent speciation and little associated morphological diversification. There was strong conservatism in body size throughout the genus, irrespective

of region, and no evidence of convergence in morphology or habitat-use in Europe and Japan. In addition (in contrast to previous analyses, e.g., Richman & Price 1992), habitat-use (low-elevation conifer versus high-elevation deciduous) divergence was shown to have mainly occurred early in the diversification of the lineage (although habitat-use was only inferred from morphology, not recorded directly).

It is often noted that the ecological character of species in today's plant communities reflects the biogeographic history of the species and their recent ancestors. For example, Lechowicz (1984) asked why temperate tree communities show a wide range in the time of leaf appearance in spring, using physiological, phylogenetic, and biogeographic data. There was no significant phylogenetic clustering of early versus late leafers (based on taxonomies available at the time), but early leafers were generally derived from cool temperate lineages, whereas late leafers were primarily of tropical lineage origin, reflecting evolutionary conservatism in physiological traits. Similarly, in subtropical montane forests of Mexico the evergreen understory is composed of tropical elements, while the deciduous overstory is composed primarily of species from temperate clades (Williams-Linera 1997; see also ter Steege & Hammond 2001).

Mediterranean-type ecosystems have been the subject of considerable study owing to the apparent convergences in plant and animal communities on five continents (Cody & Mooney 1978). Community-level convergence in distributions of ecological traits may arise by a combination of recent adaptive responses of the organisms to current environments and by sorting or assembly of lineages drawn from the regional species pools. Phylogenetic, biogeographic, and historical studies are key to evaluating these alternatives. In the plants of Andalusia, Spain, Herrera (1992) demonstrated that character syndromes differed between "old" and "new" lineages (distinguished by fossil records and intercontinental disjunctions). The persistence of ecological character in old lineages again emphasizes the importance of conservatism in traits contributing to community structure. Expanded and better resolved phylogenies now make it possible to evaluate such hypotheses with detailed studies of ancestral states in relation to community assembly. In California chaparral, D.D. Ackerly (unpublished) found that plants with similar leaf characteristics in the contemporary flora were derived from both subtropical and north-temperate lineages. In this case the subtropical lineages maintained ancestral traits that predated the mediterranean-type climate, while the temperate lineages exhibited more recent evolutionary shifts, presumably representing adaptations to changing climatic conditions compared with their biogeographic origins (see also Verdu et al. 2002).

Reconstructing ancestral communities and determining the causes of trait change is harder in open regions than in closed ones, but methods have been developed for this. When several lineages share the same area cladogram and can be assumed to have evolved in the same time frame, co-regionality can be inferred for ancestral species (co-speciation *sensu* Brooks & McLennan 1993). If community co-occurrence and biotic interaction can be reasonably assumed

between members of different lineages, patterns of trait change can be interpreted as co-adaptations (*sensu* Brooks & McLennan 1993). Co-adaptation may most reasonably be inferred where trait change in one lineage is associated with putative dispersal into a region by a species in another lineage (see figure 3 in Losos 1996). Brooks & McLennan (1991) reconstructed the influence of pre-adaptation and co-adaptation in helminth parasite communities in Neotropical stingrays, considering different host species as different niches at six different sites in South America. They showed that three contemporary communities came about primarily by vicariant division of ancestral communities, two originated by dispersal of parasites into a region without switching host species (or niches), whereas one represented a complicated assembly of vicariance and dispersal, with some host conservatism and some host switching (see also Poulin 1999, Sasal et al. 1999, Morand & Guegan 2000). Mayden (1987) used geological and fish phylogeny information to reconstruct the history of vicariance in Ozark river drainages. Gorman (1992) then added information about habitat use (position in water column) of contemporary species to reconstruct ancestral community composition and habitat occupancy and was able to infer which competitive interactions were leading to contemporary niche displacement, which he tested experimentally. Losos et al. (1997) also applied an experimental approach to test hypotheses derived from biogeographic and trait evolution data, finding that *Anolis* limb length evolved adaptively in populations established on small islands.

## Community Organization: Conclusions

A phylogenetic approach to studying community organization provides a new perspective on the perennial questions of the role of competition and the maintenance of diversity in communities, by highlighting the similarities of co-occurring species as well as the differences. A dominant perception in evolutionary ecology is that co-existing species must differ significantly and that most variation between closely related species is the adaptive response to past competition when species did not differ (e.g., Harvey & Rambaut 2000). The general prediction from this model of evolution is that divergence (and therefore homoplasy) in ecological character should be widespread. However, phylogenetic analysis reveals that many (possibly the majority of) lineages studied show evidence for conservatism of dominant ecological character, in both animal lineages (e.g., Richman 1996, Barraclough et al. 1999, Peterson et al. 1999, Lindeman 2000, McPeck & Brown 2000, Price et al. 2000, Forstmeier et al. 2001) and in plants (Grime 1984, Peat & Fitter 1994, Lord et al. 1995, Ackerly 1999, Prinzing et al. 2001). For plants this runs counter to a long-standing belief that functional and ecological strategies evolve rapidly, leading to widespread convergence and little correspondence between taxonomic and ecological groupings (e.g., Warming 1909, Cronquist 1988).

An associated insight arising from a phylogenetic perspective is that even if convergent evolution has occurred in a single trait (e.g., diet), other axes of ecological similarity (e.g., forest-type use) are often conserved. The more traits involved, the

more likely it is that a composite measure of “net ecological similarity” will be conserved in a lineage, especially if there are life-history trade-offs among traits. Change in such a composite measure would perhaps be best modeled by evolutionary drift. Ecologically, difference on one niche axis alone may be sufficient to reduce competition with other species under stable conditions, but it is more likely that the competitive environment shifts over time, with species experiencing intermittent interactions with other species on different niche axes (food, shelter, water, nutrients, space). Hence, when viewed across many traits, interactions that challenge the co-existence of closely related, ecologically similar species may be more frequent than recognized.

If conservatism of ecological traits is widespread, then the effect of contemporary competition can be assessed by the extent to which phylogenetically related, ecologically similar species co-occur: avoidance of closely related species by one another (e.g., Graves & Gotelli 1993) would be indicative of strong competition among similar species. Because the strength of negative interaction should generally be proportional to the phylogenetic proximity, a likely community outcome might be a hierarchical pattern of both phylogenetic clumping and overdispersion: Some conserved characters will determine the ability of taxa to occupy a fundamental niche (leading possibly to overall phylogenetic attraction of co-occurring taxa, e.g., taxa 5, 6, and 7 in Figure 2), whereas others will cause local competitive exclusion (leading to phylogenetic repulsion of co-occurring taxa within those attracted clades, e.g., taxa 6 and 7 in Figure 2). Where related, similar species do co-occur, attention must be given to mechanisms that permit the co-existence of similar rather than different organisms (e.g., Chesson & Warner 1981, McPeck & Brown 2000, Hubbell 2001).

The study of adaptive radiations on islands (e.g., Givnish 1998) may have led to an overemphasis on evolutionary character displacement and ecological niche partitioning. In diverse, continental communities (in which most species live), interactions may be more unpredictable over time, both on the timescale of individuals (because of the diversity of neighbors) (Connell 1980), and because species ranges may change more often. This would lead to weaker pairwise interactions among sister taxa, and species radiations might occur with little ecological differentiation (change being nonadaptive) (*sensu* McPeck & Brown 2000, e.g., Richardson et al. 2001). Local communities on continents may then represent a selective sampling of the regional pool to minimize ecological similarity or may only be able to contain species that are similar (over long periods of time, if not indefinitely). On islands, species must change or go extinct. A systematic review of the prevalence of conservatism and convergence in both island and continental systems would be very valuable.

Incorporating phylogenetic information offers important new perspectives but also brings additional challenges. Perhaps the most immediate challenge is to explicitly define the ecological, spatial, and taxonomic scales in a study because the processes that structure the assembly of regions, communities, and habitats differ (see *The Phylogenetic Structure of Community Assemblages*, above), and using

phylogenies only of taxa that co-occur at a particular spatial scale can confound inferences about ecological and evolutionary processes (see Jablonski & Sepkoski 1996). Although it is valid to assess the correlation between relatedness and similarity (i.e., the effective degree of conservatism) in any sample of species, it must be remembered that partial (community) phylogenies may not provide accurate inferences about character evolution or lineage-wide assessment of conservatism and homoplasy (the issue of “taxon sampling”; Ackerly 2000). An example is given in Figure 2, in which the taxa included in the community phylogeny would lead to an incorrect reconstruction of the evolution of traits *y* and *z*. We recognize that all phylogenies of extant taxa are only partial samples, owing to extinction, but phylogenies for co-occurring species are particularly egregious samples and are likely to introduce systematic bias in the study of trait evolution owing to the distribution of ecological characters in different communities.

Obtaining estimates of the absolute lengths of branches in a partial (community) phylogeny greatly increases the accuracy of inference about the correlation between relatedness and similarity. Estimates of relative branch lengths often come from rates of molecular evolution but ultimately depend upon the dating and phylogenetic placement of fossils. Age estimates are also vital for the accurate reconstruction of the species composition of ancestral communities. Congruence of the topologies of different lineages without age information cannot determine the order of arrival of taxa in an ancestral region or the temporal order of trait change in the lineages. Disentangling cause from effect requires temporal information (see Donoghue et al. 2001, Hunn & Upchurch 2001, Sanmartin et al. 2001).

A related challenge when using regional-scale biogeographic methods to reconstruct historical intra-community interactions is that community co-occurrence of ancestral taxa must be assumed. The spatial scale of the areas in an area cladogram is usually far larger than a single community (Grandcolas 1998), and coregional ancestral species may never have interacted, because they occurred only in different types of communities or because they were spatially segregated by chance while still sharing a region. However, phylogeographic methods (Avice 2000) may permit the use of intra-species genetic variation to reconstruct historical population movement and to indicate patterns of intra-region historical co-occurrence (e.g., Zink 1996, Comes & Kadereit 1998, Taberlet et al. 1998). Fossil communities (e.g., Wing et al. 1993, Hadly & Maurer 2001) might also be used to confirm community co-occurrence.

## EMERGENT PROPERTIES OF COMMUNITIES

Most work to date at the intersection of phylogenetics and community ecology has dealt with the presence and absence of species in a community, associated differences in traits, and the assembly of communities through time. Community ecology also deals with species diversity, the relative abundance of co-occurring

species, and the distribution of range sizes. There have been a number of creative uses of phylogeny in these areas.

## Species Diversity

*Key question: Why do different areas vary in the species richness of particular clades? (Using: species lists of local communities + local and global estimates of species richness of clades + phylogenetic relationships of local and global clades)*

One answer to the question “Why do similar habitats in different regions have different numbers of species?” is that differing histories of the areas have led to occupancy by different clades (Latham & Ricklefs 1993, Schluter & Ricklefs 1993, Qian & Ricklefs 1999, Ricklefs 2002) and that different clades have different potentials for diversification (Farrell et al. 1991, Sanderson & Donoghue 1996, Dodd et al. 1999, Gardezi & da Silva 1999) and thus different numbers of extant species. A second answer is that the areas differ in the length of time they have been occupied (Brown et al. 2000, Ricklefs 2002). For example, a latitudinal gradient in diversity may reflect the relative ages of major climate regions (and the challenges of adapting to temperate climates) as much as the effect of local ecological processes (Blondel & Vigne 1993, Latham & Ricklefs 1993). Phylogenetic analyses and age inferences are central to testing such hypotheses: For example, Ricklefs & Schluter (1993b) found that the clades of passerine birds in Panamanian forest were on average 2.6 times the age of the clades in forests in Illinois.

The dominant hypothesis for why islands differ in species richness is MacArthur & Wilson's (1967) equilibrium theory of island biogeography. Phylogenies are playing a major role in testing the applicability of this hypothesis. Using molecular estimates of species age, Ricklefs & Bermingham (2001) were able to reject the assumption of constant rates of immigration and extinction in Antillean birds. Using island species lists and a phylogeny, Losos & Schluter (2000) were able to differentiate between in situ speciation of *Anolis* lizards on Caribbean islands, and immigrants from other islands. They showed that on islands larger than 3,000 km<sup>2</sup>, in situ speciation overtakes immigration as a source.

## Relative Abundance

*Key question: How does the relative abundance of taxa vary across a community phylogeny? (Using: species list of local community + relative abundance structure of local community + phylogeny of species in local community)*

The distribution of relative abundance in communities has long been the subject of attention by ecologists. Whereas there are many ways to statistically characterize the shape of abundance-distribution curves (e.g., log-series, log-normal), satisfactory explanatory models have been few (but see MacArthur 1960). Fewer still make predictions about the relation of phylogeny to relative abundance. The most comprehensive model of community abundance (Hubbell 2001) predicts that older species should be more abundant and widespread than younger species (in itself, an old idea; Willis 1922). Methods exist to date nodes in a phylogeny, but



the pruning of phylogenies by extinction means the time since divergence from the most closely related extant taxon may often be a poor predictor of species age (Box 2 in Chown & Gaston 2000).

An increasing number of studies have asked if there is a relation between characters of a taxonomic group and the mean abundance of its members (Farrell et al. 1991; see also Heard & Hauser 1995, Edwards & Westoby 2000, Murray & Westoby 2000). Schwartz & Simberloff (2001) found that vascular plant families with few species tended to have fewer than expected rare species. Such analyses will benefit from an explicit phylogenetic framework: Webb & Pitman (2002) found that a rank-based association between common species and diverse families of rain forest trees disappeared when considered phylogenetically.

Another approach to relative abundance is illustrated by the work on bird size and abundance (e.g., Cotgreave & Harvey 1994, Harvey & Nee 1994). In Britain, overall bird population size is negatively related to body size (Nee et al. 1991), but within a tribe the relationship is often positive. If ecological similarity and competition are correlated, and if larger bodied birds attain higher densities under competition than smaller birds, then those clades that contain the most ecologically similar species should show the strongest positive association of body size and abundance. Nee et al. (1991) found that the branch length (using taxonomic levels) from the base of a tribe's clade to the rest of the birds was a good predictor of the strength of the positive relationship, longer branches being associated with more complete guilds.

Examining relative abundance structure from a phylogenetic standpoint will surely be an exciting avenue of research. Finding any association between abundance and relatedness could indicate that local abundance is actively influenced by phylogenetically conserved characters.

## Geographical Range

*Key question: How do the sizes and spatial arrangement of species ranges vary across a phylogeny? (Using: species lists of local community or region + range information for these species + phylogeny for these species)*

Range size can be treated as a continuous character, and its evolution and association with other characters assessed. The community context of the species in such analyses is generally not addressed. In the few cases studied, closely related species tend to have more similar range sizes than distantly related species (Jablonski 1987, Ricklefs & Latham 1992, Brown 1995). This might appear to imply that (a) some ecological traits are responsible for range size and (b) there is some conservatism in these traits. However, an alternative explanation for such a pattern is that related species tend to be of a more similar age than less related species, and if age is correlated with area (Willis 1922, Fjeldsa & Lovett 1997), then area would appear as a phylogenetically conserved attribute of species. Kelly & Woodward (1996) investigated the correlation between life-form and range size in British plants, using a phylogeny, and found that trees have larger ranges than nontrees, and that wind-pollinated species have larger ranges than related

non-wind-pollinated species. Gregory (1995) found that phylogenetic conservatism did not explain the relationship between range size and body size in British birds. Gotelli & Taylor (1999) used phylogenetic independent contrasts in an analysis correlating the probability of stream colonization by fish with body size, population size, range size, and distance from range center. They found that the importance of removing phylogenetic effects to detecting the effect of distance-from-range-center was substantial.

Range information has also been used to investigate modes of speciation, reasoning in the "opposite direction" from most work reviewed here (Lynch 1989, Barraclough & Nee 2001, Gimaret-Carpentier et al. 2002). Species range size is likely to be closely linked to the probability of further diversification under any model of allopatric speciation (Barraclough & Vogler 2000, Chown & Gaston 2000). Barraclough et al. (1998) used the range overlap of clades as an indicator of the mode of speciation in tiger beetles. If allopatric speciation and subsequent range movement dominated, the degree of range overlap between sister clades should start low for two sister species and increase as more taxa are included in both clades. However, sympatric speciation and subsequent range movement should start with high range overlap of sister species and decrease as more taxa are included. The authors found that overlap started low and increased with increasing clade inclusiveness and inferred allopatric speciation.

## METHODOLOGICAL ADVANCES

### Community Phylogenies

Phylogenetic methods are in a sustained phase of rapid development, with new maximum-likelihood (Lewis 2001) and Bayesian (Huelsenbeck et al. 2001) approaches being explored. Phylogenies from separate studies can now be joined to form "supertrees" (Sanderson et al. 1998, Bininda-Emonds et al. 1999), either being assembled "by hand" (e.g., Donoghue et al. 1998) or using algorithms to resolve conflict among trees (Semple & Steel 2000, Salamin et al. 2002, Bininda-Emonds et al. 2002). From these supertrees, phylogenies of community species lists can be prepared (e.g., Tofts & Silvertown 2000, Webb 2000); tools are now available to facilitate this process (Webb & Donoghue 2002). Community phylogenies constructed from supertrees usually lack information about branch length, but there are supertree methods that yield branch lengths (Lapointe & Cucumel 1997), and we anticipate that branch lengths based on absolute age estimates will soon be available for many groups (e.g., Magallon & Sanderson 2001).

### Tests for Phylogenetic Conservatism

As we have emphasized, predictions and interpretation of patterns of phylogenetic community structure depend on patterns of ecological similarity and divergence among related species. Using taxonomic information, these patterns have been evaluated with hierarchical analysis of variance, partitioning interspecific variation

into different levels: species within genera, genera within families, families within orders, etc. (e.g., Mazer & Wheelwright 1993, Peat & Fitter 1994, Lord et al. 1995). With the development of well-resolved phylogenies, a variety of quantitative methods have been proposed to examine the extent to which ecological traits are conserved or convergent on a phylogeny. For discrete characters, randomization-based tests of the number of reconstructed character changes have been used (Maddison & Slatkin 1991, Barraclough et al. 1999); a conserved character has fewer changes, or “steps,” than expected based on the number of occurrences in the terminal taxa. Such tests are easily modified to handle ordered or continuous characters (the Quantitative Convergence Index; Ackerly & Donoghue 1998, Prinzing et al. 2001). An alternative method for continuous traits is based on regressions of trait differences versus phylogenetic distance (Legendre et al. 1994); a positive correlation indicates that traits are conserved. The phylogenetic “neighborhood” over which trait conservatism is evident can be assessed with phylogenetic “autocorrelation” (Cheverud et al. 1985, Gittleman et al. 1998, Böhning-Gaese & Oberrath 1999). Owing to the nonparametric structure of phylogenetic data, significance testing often requires randomization methods or null model simulations (Legendre et al. 1994, Lapointe & Garland 2001).

Despite the proliferation of such tests, few comparisons have been conducted to evaluate their performance on common data sets. Morales (2000) conducted one such comparison, and Ackerly has reanalyzed his data with several additional methods (D. Ackerly, unpublished data). Ackerly found that hierarchical ANOVA, the quantitative convergence index, and phylogenetic correlation of distance matrices give parallel results across different traits; however, there was little correspondence between these methods and phylogenetic autocorrelation or eigenvector analyses. For applications to community data sets, we favor methods based on phylogenetic distance (regression or autocorrelation) rather than parsimony-based trait mapping, to avoid the suggestion of inferring patterns of historical trait evolution from just the community-based taxon sample. More work is needed to examine the statistical power of these methods and their sensitivity to different kinds of deviation from random patterns.

## Null Models for Community Phylogenies and for Community Assembly

There has been extensive work on the generation of random phylogenies (e.g., Raup et al. 1973, Losos & Adler 1995, Heard & Mooers 2000), but few studies have employed an explicitly ecological model (but see Maley 1998, Doebeli & Dieckmann 2000). Hubbell (2001) has claimed that a realistic null model for phylogenies must include information on a region’s biota (his “meta-community”), because the probability of a taxon’s extinction is inversely related to its population size, and the sum of all populations of all extant taxa is often limited (e.g., for canopy trees). The probability of extinction is therefore dependent on the number of species in the region because increasing species richness will tend to increase

the number of species with small populations. Hubbell's (2001) null models for phylogenies generate patterns of hierarchical diversity (e.g., frequency distributions of species per family) that fit observed data well. Jansen & Mulder (1999) incorporated speciation into a patch-dynamic model to simulate the evolution of lineages in an explicitly competitive environment.

The simplest null models for community phylogenies are generated by subsampling the taxa in a larger area, using existing phylogenies for the relationships among those taxa (e.g., Webb 2000). The large literature on null models for the assembly of communities used to detect nonrandom co-occurrence patterns and assembly rules (usually independent of phylogeny/taxonomy) is relevant here (e.g., Diamond 1975, Connor & Simberloff 1979; reviewed by Gotelli & Graves 1996). Null models also exist for the distribution of ecological traits expected in communities where competition is important (Colwell & Winkler 1984, Leibold 1998, Stevens & Willig 2000) and for the evolution of traits in lineages without effects of competition (e.g., Ackerly 2000); these approaches need to be combined in future models.

## Metrics of Community Phylogenetic Structure

Metrics that quantify the distribution of taxa in a sample relative to a pool have been developed by Webb (2000). The net relatedness index (NRI) is a standardized measure of the mean pairwise phylogenetic distance of taxa in a sample, relative to a phylogeny of an appropriate species pool, and quantifies overall clustering of taxa on a tree (similar to Clarke & Warwick's 1999 and von Euler & Svensson's 2001 metrics). It is calculated as  $-1 \cdot ((\text{mn}(X_{\text{obs}}) - \text{mn}X(n))/\text{sd}X(n))$ , where  $X_{\text{obs}}$  is the phylogenetic distance between two taxa (the sum of all intervening branch lengths) in the phylogeny of the pool,  $\text{mn}(X_{\text{obs}})$  is the mean of all possible pairs of  $n$  taxa, and  $\text{mn}X(n)$  and  $\text{sd}X(n)$  are the mean and standard deviation expected for  $n$  taxa randomly distributed on the phylogeny of the pool (found by multiple iteration; note that this formulation is slightly modified from Webb 2000). Where continuous branch length estimates are not available, phylogenetic distances can be based on the number of nodes separating two taxa (Farris 1969, Gittleman & Kot 1990). The nearest taxon index (NTI) is a standardized measure of the phylogenetic distance to the nearest taxon for each taxon in the sample and quantifies the extent of terminal clustering, independent of deep level clustering. NTI is calculated as  $-1 \cdot ((\text{mn}(Y_{\text{obs}}) - \text{mn}Y(n))/\text{sd}Y(n))$ , where  $Y_{\text{obs}}$  is the phylogenetic distance to the nearest taxon in the phylogeny of the pool;  $\text{mn}(Y_{\text{obs}})$ ,  $\text{mn}Y(n)$ , and  $\text{sd}Y(n)$  are calculated as for  $X$ .

These metrics share much in common with those developed to assess the phylogenetic uniqueness of taxa in a conservation area (e.g., Williams et al. 1991, Faith 1996, Crozier 1997, Nee & May 1997, Clarke & Warwick 1999, Sechrest et al. 2002). Both NRI and NTI increase with increasing clustering and become negative with overdispersion. The precise response of NRI and NTI in communities formed by phenotypic attraction (Table 1) depends upon the form the trait conservatism

takes. Maximum conservatism in traits, at a deep level (leading to a high consistency index), yields both high NRI and NTI. Conservatism at more terminal levels in the phylogeny causes NTI to increase in significance relative to NRI. Both NRI and NTI depend on the particular species pool, and further study is required to determine when and how these measures can be compared across different studies. A suitable null model of community assembly (see above) can be used to generate expectations for the distribution of relatedness indices with which the observed values can be compared. An alternative approach to assessing whether the taxa that co-occur in samples are more related than expected by chance is to correlate a metric of co-occurrence with phylogenetic distance for all possible pairs of taxa (H. Steers, personal communication).

## DIRECTIONS FOR FUTURE WORK

Beyond the directions already taken and reviewed in this paper, we have identified a number of areas that might be profitable to pursue.

### Dynamics of Community Phylogenetic Structure

The static patterns of community phylogenetic structure described above (Webb 2000; H. Steers personal communication, J. Cavender-Bares personal communication) result from differential mortality of species that vary in phylogenetic relatedness and ecological characteristics. Changes in phylogenetic structure could also be observed directly over time in the many existing long-term datasets of community composition. In age- and size-structured populations, comparing the community structure of different age- or size-classes at a single time can provide a (limited) proxy for the direct observation of change over time (e.g., Webb & Peart 1999). For example, increasing size classes of seedlings and trees in small plots in Bornean rain forest shows a monotonic increase in phylogenetic clustering (C.O. Webb, unpublished data). This pattern, at a single time, is consistent with the cumulative mortality of locally ill-suited species over time (if ecological suitability is phylogenetically conserved).

### Using Phylogenetic Information in Models of Neighborhood Performance

Most models of the performance response (growth, survival) of focal individuals to neighborhood density classify neighbors either as conspecifics or heterospecifics. This dichotomy hides a great range of ecological similarity between species and an expected range of magnitude of effect. Weighting the interaction by a measure of phylogenetic relatedness should greatly improve the performance of such models, if important parameters of ecological similarity are phylogenetically conserved. For instance, if (a) negative neighborhood interactions are mediated by pathogens or herbivores (e.g., Gilbert et al. 1994), (b) at least some of the pathogen species infect multiple host species, and (c) at least some of the polyphagous pathogens

have a phylogenetically restricted set of host species (Futuyma & Mitter 1996, Farrell 2001, Frenzel & Brandl 2001, Novotny et al. 2002), then the expected effect of neighbor density will be greater the more closely related it is to the focal individual. Analytical models of community stability, based on modified Lotka-Volterra competition models with phylogenetically structured interaction coefficients; may also be possible and would be expected to predict the maintenance of a phylogenetically diverse (or overdispersed) set of species.

## Comparative Surveys of Community Phylogenetic Structure

Understanding variation in community phylogenetic structure across known gradients (e.g., moisture regime and species richness) may yield important insights into community organization (Thompson et al. 2001). Including gradients that integrate change in both resources and predation (e.g., Leibold 1996) will be especially revealing. The basic analysis of community phylogenetic structure requires only plot-based samples and a species list (which can be converted into a community supertree), and can thus be rapidly conducted on preexisting data. Where phylogenies can be constructed for fossils (e.g., Upchurch 1995, Vermeij & Carlson 2000) and a stratigraphic turnover of communities can be reconstructed (e.g., Olszewski & Patzkowsky 2001, Jackson & Overpeck 2000), change in community phylogenetic structure could be assessed over time.

## Phylogenetic Ordination and Classification

Basing ordination and classification methods on intersample distances that reflect net phylogenetic dissimilarity rather than Euclidean distance in  $N$ -dimensional species space offers a means to display the phylogenetic relations among sample-plots. Such methods can reveal meaningful ecological relationships hidden by standard, nonphylogenetic methods: e.g., plots sharing many genera should still cluster even if they share none of the same species.

## Balance of Community Phylogenies

Tree balance (the degree to which sister clades differ in their number of taxa) provides another way to quantify the complex branching structure of community phylogenies (e.g., Heard & Mooers 2000). Models relating the phylogenetic distribution of niche space among taxa in a regional pool and the niche structure of local communities should generate predictions about the balance of local community phylogenies.

## CONCLUSIONS

We resist the temptation to declare that “phylogenetic community ecology” is a new field. Rather, we view phylogenetic information as a “glue” that can stick ecological and evolutionary studies together, where often they have slid past each

other, their practitioners speaking different languages. We want to emphasize, however, that despite its great utility, there is no simple, single way to apply phylogenetic information in community ecology, as is highlighted by the diversity of approaches reviewed here. Phylogenies must also be used with full knowledge of the assumptions and uncertainties that underlie them. There is a real danger that with the increasing ease of obtaining phylogenetic information, ecologists will forget that phylogenies are hypotheses to be further tested, and not the truth. This said, we genuinely believe that no ecological study can fail to benefit in some way from an understanding of the phylogenetic relationships of its taxa. Community ecologists and phylogenetic biologists should continue to engage in a discussion that will surely enrich and hopefully unite both disciplines.

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## LITERATURE CITED

- Ackerly DD. 1999. Comparative plant ecology and the role of phylogenetic information. In *Physiological Plant Ecology*, ed. M Press, JD Scholes, MG Barker, pp. 391–413. Oxford, UK: Blackwell Sci.
- Ackerly DD. 2000. Taxon sampling, correlated evolution, and independent contrasts. *Evolution* 54:1480–92
- Ackerly DD, Donoghue M. 1998. Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in maples (*Acer*). *Am. Nat.* 152:767–91
- Ackerly DD, Dudley SA, Sultan SE, Schmitt J, Coleman JS, et al. 2000. The evolution of plant ecophysiological traits: recent advances and future directions. *Bioscience* 50:979–95
- Ashton PS. 1988. Dipterocarp biology as a window to the understanding of tropical forest structure. *Annu. Rev. Ecol. Syst.* 19:347–70
- Avisé JC. 2000. *Phylogeography: the History and Formation of Species*. Cambridge, MA: Harvard Univ. Press
- Barker GM, Mayhill PC. 1999. Patterns of

- diversity and habitat relationships in terrestrial mollusc communities of the Pukeamaru ecological district, northeastern New Zealand. *J. Biogeogr.* 26:215–38
- Barraclough TG, Hogan JE, Vogler AP. 1999. Testing whether ecological factors promote cladogenesis in a group of tiger beetles (Coleoptera: Cicindelidae). *Proc. R. Soc. London Ser. B* 266:1061–67
- Barraclough TG, Nee S. 2001. Phylogenetics and speciation. *Trends Ecol. Evol.* 16:391–99
- Barraclough TG, Vogler AP. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. *Am. Nat.* 155:419–34
- Barraclough TG, Vogler AP, Harvey PH. 1998. Revealing the factors that promote speciation. *Philos. Trans. R. Soc. London Ser. B* 353:241–49
- Bininda-Emonds ORP, Gittleman JL, Purvis A. 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biol. Rev.* 74:143–75
- Bininda-Emonds ORP, Gittleman JL, Steel M. 2002. The (super)tree of life: procedures, problems, and prospects. *Annu. Rev. Ecol. Syst.* 33:265–89
- Blackburn TM, Gaston KJ. 2001. Local avian assemblages as random draws from regional pools. *Ecography* 24:50–58
- Blondel J, Vigne J-D. 1993. Space, time and man as determinants of diversity of birds and mammals in the Mediterranean region. See Ricklefs & Schluter 1993a, pp. 135–46
- Böhning-Gaese K, Oberrath R. 1999. Phylogenetic effects on morphological, life-history, behavioural and ecological traits of birds. *Evol. Ecol. Res.* 1:347–64
- Bowers MA, Brown JH. 1982. Body size and coexistence in desert rodents: chance or community structure? *Ecology* 63:391–400
- Brandl R, Kristin A, Leisler B. 1994. Dietary niche breadth in a local-community of passerine birds, an analysis using phylogenetic contrasts. *Oecologia* 98:109–16
- Brooks DR, McLennan DA. 1991. *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology*. Chicago: Univ. Chicago Press
- Brooks DR, McLennan DA. 1993. Historical ecology: examining phylogenetic components of community evolution. See Ricklefs & Schluter 1993a, pp. 267–80
- Brooks DR, McLennan DA. 2002. *The Nature of Diversity*. Chicago: Univ. Chicago Press
- Brown JH. 1995. *Macroecology*. Chicago: Univ. Chicago Press
- Brown JH, Zeng Z. 1989. Comparative population ecology of eleven species of rodents in the Chihuahuan desert. *Ecology* 70:1507–25
- Brown JM, McPeck MA, May ML. 2000. A phylogenetic perspective on habitat shifts and diversity in the North American *Enallagma* damselflies. *Syst. Biol.* 49:697–712
- Cadle JE, Greene HW. 1993. Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. See Ricklefs & Schluter 1993a, pp. 281–93
- Cavender-Bares J, Holbrook NM. 2001. Hydraulic properties and freezing-induced xylem cavitation in evergreen and deciduous oaks with contrasting habitats. *Plant, Cell Environ.* 24:1243–56
- Chazdon RL, Careaga S, Webb CO, Vargas O. 2002. Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests. *Ecol. Monogr.* In press
- Chesson P. 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31:343–66
- Chesson PL, Warner RR. 1981. Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.* 117:923–43
- Cheverud JM, Dow MM, Leutnegger W. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution* 39:1335–51
- Chown SL, Gaston KJ. 2000. Areas, cradles and museums: the latitudinal gradient in species richness. *Trends Ecol. Evol.* 15:311–15
- Clarke KR, Warwick RM. 1999. The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. *Mar. Ecol. Prog. Ser.* 184:21–29



- Cody ML, Mooney HA. 1978. Convergence versus non-convergence in Mediterranean-climate ecosystems. *Annu. Rev. Ecol. Syst.* 9:265–321
- Colwell RK, Winkler DW. 1984. A null model for null models in biogeography. In *Ecological Communities: Conceptual Issues and the Evidence*, ed. DR Strong, D Simberloff, LG Abele, AB Thistle, pp. 344–59. Princeton, NJ: Princeton Univ. Press
- Comes HP, Kadereit JW. 1998. The effects of Quaternary climatic changes on plant distribution and evolution. *Trends Plant Sci.* 3:432–38
- Connell JH. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–38
- Connor EF, Simberloff D. 1979. The assembly of species communities: chance or competition? *Ecology* 60:1132–40
- Cornell HV, Lawton JH. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *J. Anim. Ecol.* 61:1–12
- Cotgreave P, Harvey PH. 1994. Phylogeny and the relationship between body size and abundance in bird communities. *Funct. Ecol.* 8:219–28
- Craig DA, Currie DC, Joy DA. 2001. Geographical history of the central-western pacific black fly subgenus *Inseliellum* (Diptera: Simuliidae: *Simulium*) based on a reconstructed phylogeny of the species, hot-spot archipelagoes and hydrological considerations. *J. Biogeogr.* 28:1101–27
- Cronquist A. 1988. *The Evolution and Classification of Flowering Plants*. New York: NY Bot. Gard.
- Crozier RH. 1997. Preserving the information content of species: genetic diversity, phylogeny, and conservation worth. *Annu. Rev. Ecol. Syst.* 28:243–68
- Cunningham CW, Omland KE, Oakley TH. 1998. Reconstructing ancestral character states: a critical reappraisal. *Trends Ecol. Evol.* 13:361–66
- Darwin C. 1859. *The Origin of Species by Means of Natural Selection*. London: Murray
- Diamond JM. 1975. Assembly of species communities. In *Ecology and Evolution of Communities*, ed. ML Cody, JM Diamond, pp. 342–444. Cambridge, MA: Harvard Univ. Press
- Dimichele WA, Phillips TL. 1996. Clades, ecological amplitudes, and ecomorphs: phylogenetic effects and persistence of primitive plant communities in the Pennsylvanian-age tropical wetlands. *Palaeogeogr. Palaeoclim. Palaeoecol.* 127:83–105
- Dodd M, Silvertown J, Chase M. 1999. Phylogenetic analysis of trait evolution and species diversity variation among Angiosperm families. *Evolution* 53:732–44
- Doebeli M, Dieckmann U. 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *Am. Nat.* 156:S77–101
- Donoghue MJ, Bell CD, Li J. 2001. Phylogenetic patterns in Northern Hemisphere plant geography. *Int. J. Plant Sci.* 162:S41–52
- Donoghue MJ, Ree RH. 2000. Homoplasy and developmental constraint: a model and example from plants. *Am. Zool.* 40:759–69
- Donoghue MJ, Ree RH, Baum DA. 1998. Phylogeny and the evolution of flower symmetry in the Asteridae. *Trends Plant Sci.* 3:311–17
- Edwards W, Westoby M. 2000. Families with highest proportions of rare species are not consistent between floras. *J. Biogeogr.* 27:733–40
- Eggleton P, Vane-Wright RI, eds. 1994. *Phylogenetics and Ecology*. London: Academic
- Elton C. 1946. Competition and the structure of ecological communities. *J. Anim. Ecol.* 15:54–68
- Enquist BJ, Haskell JP, Tiffney BH. 2002. General patterns of taxonomic structure and biomass division within extant and fossil woody plant communities. *Nature*. In press
- Faith DP. 1996. Conservation priorities and phylogenetic pattern. *Conserv. Biol.* 10:1286–89
- Farrell BD. 2001. Evolutionary assembly of the milkweed fauna: cytochrome oxidase I and

- the age of *Tetraopes* beetles. *Mol. Phylogenet. Evol.* 18:467–78
- Farrell BD, Dussourd DE, Mitter C. 1991. Escalation of plant defense: Do latex and resin canals spur plant diversification? *Am. Nat.* 138:881–900
- Farris JS. 1969. A successive approximations approach to character weighting. *Syst. Zool.* 18:374–85
- Felsenstein J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1–15
- Fjelds J, Lovett JC. 1997. Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. *Biodivers. Conserv.* 6:325–46
- Forstmeier W, Bourski OV, Leisler B. 2001. Habitat choice in *Phylloscopus* warblers: the role of morphology, phylogeny and competition. *Oecologia* 128:566–76
- Fox BJ. 1999. The genesis and development of guild assembly rules. In *Ecological Assembly Rules: Perspectives, Advances, Retreats*, ed. E Weiher, P Keddy, pp. 23–57. Cambridge, UK: Cambridge Univ. Press
- Frenzel M, Brandl R. 2001. Hosts as habitats: faunal similarity of phytophagous insects between host plants. *Ecol. Entomol.* 26:594–601
- Futuyma DJ, Mitter C. 1996. Insect-plant interactions: the evolution of component communities. *Philos. Trans. R. Soc. London Ser. B* 351:1361–66
- Galassi DMP. 2001. Groundwater copepods: diversity patterns over ecological and evolutionary scales. *Hydrobiologia* 453:227–53
- Gardezi T, da Silva J. 1999. Diversity in relation to body size in mammals: a comparative study. *Am. Nat.* 153:110–23
- Gentry AH. 1982. Patterns of Neotropical plant species diversity. *Evol. Biol.* 15:1–84
- Gilbert GS, Hubbell SP, Foster RB. 1994. Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. *Oecologia* 98:100–8
- Gimaret-Carpentier C, Dray S, Pascal J-P. 2002. Broad-scale biodiversity pattern analyses of the endemic tree flora of the Western Ghats (India) using canonical correlation analysis of herbarium records. *Ecography*. In press
- Gittleman JL, Anderson CG, Cates SE, Luh H-K, Smith JD. 1998. Detecting ecological patterns in phylogenies. In *Biodiversity Dynamics: Turnover of Populations, Taxa, and Communities*, ed. ML McKinney, JA Drake, pp. 51–69. New York: Columbia Univ. Press
- Gittleman JL, Kot M. 1990. Adaptation: statistics and a null model for estimating phylogenetic effects. *Syst. Zool.* 39:227–41
- Givnish TJ. 1998. Adaptive radiation of plants on oceanic islands: classical patterns, molecular data, new insights. In *Evolution on Islands*, ed. P Grant, pp. 281–304. Oxford, UK: Oxford Univ. Press
- Gorman OT. 1992. Evolutionary ecology and historical ecology: assembly, structure, and organization of stream fish communities. In *Systematics, Historical Ecology, and North American Fresh Water Fishes*, ed. RL Mayden, pp. 659–88. Stanford, CA: Stanford Univ. Press
- Gotelli NJ, Graves GR. 1996. *Null Models in Ecology*. Washington, DC: Smithsonian Inst. Press
- Gotelli NJ, Taylor CM. 1999. Testing macroecological models with stream-fish assemblages. *Evol. Ecol. Res.* 1:847–58
- Grandcolas P. 1993. The origin of biological diversity in a tropical cockroach lineage: a phylogenetic analysis of habitat choice and biome occupancy. *Acta Oecol.* 14:259–70
- Grandcolas P. 1998. Phylogenetic analysis and the study of community structure. *Oikos* 82:397–400
- Graves GR, Gotelli NJ. 1993. Assembly of avian mixed-species flocks in Amazonia. *Proc. Natl. Acad. Sci. USA* 90:1388–91
- Gregory RD. 1995. Phylogeny and relations among abundance, geographical range and body size of British breeding birds. *Philos. Trans. R. Soc. London Ser. B* 349:345–51
- Grime JP. 1984. The ecology of species, families and communities of the contemporary British flora. *New Phytol.* 98:15–33
- Hadly EA, Maurer BA. 2001. Spatial and temporal patterns of species diversity in montane

- mammal communities of western North America. *Evol. Ecol. Res.* 3:477–86
- Harvey PH, Nee S. 1994. Comparing real with expected patterns from molecular phylogenies. See Eggleton & Vane-Wright 1994, pp. 659–88
- Harvey PH, Pagel MD. 1991. *The Comparative Method in Evolutionary Biology*. Oxford, UK: Oxford Univ. Press
- Harvey PH, Rambaut A. 2000. Comparative analyses for adaptive radiations. *Philos. Trans. R. Soc. London Ser. B* 355:1599–605
- Heard SB, Hauser DL. 1995. Key evolutionary innovations and their ecological mechanisms. *Hist. Biol.* 10:151–73
- Heard SB, Mooers AO. 2000. Phylogenetically patterned speciation rates and extinction risks change the loss of evolutionary history during extinctions. *Proc. R. Soc. London Ser. B* 267:613–20
- Herrera CM. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. *Am. Nat.* 140:421–46
- Hubbell SP. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton Univ. Press
- Huelsenbeck JP, Ronquist F, Nielsen R, Bollback JP. 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294:2310–14
- Hunn CA, Upchurch P. 2001. The importance of time/space in diagnosing the causality of phylogenetic events: towards a “chronobiogeographical” paradigm. *Syst. Biol.* 50:391–407
- Ibarra-Manríquez G, Martínez-Ramos M, Oyama K. 2001. Seedling functional types in a lowland rain forest in Mexico. *Am. J. Bot.* 88:1801–12
- Jablonski D. 1987. Heritability at the species level: analysis of geographic ranges of cretaceous mollusks. *Science* 238:360–63
- Jablonski D, Sepkoski JJ. 1996. Paleobiology, community ecology, and scales of ecological pattern. *Ecology* 77:1367–78
- Jackson ST, Overpeck JT. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiol.* 26:194–220
- Jansen VAA, Mulder GSEE. 1999. Evolving biodiversity. *Ecol. Lett.* 2:379–86
- Kelly CK. 1999. On the relationship between function and phylogenetic relatedness: environmental severity and community structure. *XVI Intl. Botan. Congr.* (Abstr.)
- Kelly CK, Woodward FI. 1996. Ecological correlates of plant range size: taxonomies and phylogenies in the study of plant commonness and rarity in great Britain. *Philos. Trans. R. Soc. London Ser. B* 351:1261–69
- Lapointe F-J, Cucumel G. 1997. The average consensus procedure: combination of weighted trees containing identical or overlapping sets of taxa. *Syst. Biol.* 46:306–12
- Lapointe F-J, Garland T. 2001. A generalized permutation model for the analysis of cross-species data. *J. Classif.* 18:109–27
- Latham RE, Ricklefs RE. 1993. Continental comparisons of temperate-zone tree species diversity. See Ricklefs & Schluter 1993a, pp. 294–314
- Lechowicz MJ. 1984. Why do temperate deciduous trees leaf out at different times? Adaptations and ecology of forest communities. *Am. Nat.* 124:821–42
- Legendre P, Lapointe F, Casgrain P. 1994. Modeling brain evolution from behavior: a permutation regression approach. *Evolution* 48:1487–99
- Leibold MA. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence and diversity patterns in communities. *Am. Nat.* 147:784–812
- Leibold MA. 1998. Similarity and local coexistence of species in regional biotas. *Evol. Ecol.* 12:95–110
- Lewis PO. 2001. Phylogenetic systematics turns over a new leaf. *Trends Ecol. Evol.* 18:30–37
- Lindeman PV. 2000. Resource use of five sympatric turtle species: effects of competition, phylogeny, and morphology. *Can. J. Zool.* 78:992–1008

- Lord J, Westoby M, Leishman M. 1995. Seed size and phylogeny in six temperate floras: constraints, niche conservatism, and adaptation. *Am. Nat.* 146:349–64
- Losos JB. 1992. The evolution of convergent structure in Caribbean *Anolis* communities. *Syst. Biol.* 41:403–20
- Losos JB. 1995. Community evolution in Greater Antillean *Anolis* lizards: phylogenetic patterns and experimental tests. *Philos. Trans. R. Soc. London Ser. B* 349:69–75
- Losos JB. 1996. Phylogenetic perspectives on community ecology. *Ecology* 77:1344–54
- Losos JB, Adler FR. 1995. Stumped by trees: a generalized null model for patterns of organismal diversity. *Am. Nat.* 145:329–42
- Losos JB, Jackman TR, Larson A, de Queiroz K, Rogriguez-Schettino L. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279:2115–18
- Losos JB, Schluter D. 2000. Analysis of an evolutionary species-area relationship. *Nature* 408:847–50
- Losos JB, Warheit KI, Schoener TW. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* 387:70–73
- Lynch JD. 1989. The gauge of speciation: on the frequency of modes of speciation. In *Speciation and Its Consequences*, ed. D Otte, JA Endler, pp. 527–53. Sunderland, MA: Sinauer
- MacArthur RH. 1960. On the relative abundance of species. *Am. Nat.* 94:25–36
- MacArthur RH, Levins R. 1967. The limiting similarity, convergence and divergence of co-existing species. *Am. Nat.* 101:377–85
- MacArthur RH, Wilson EO. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton Univ. Press
- Maddison WP, Slatkin M. 1991. Null models for the number of evolutionary steps in a character on a phylogenetic tree. *Evolution* 45:1184–97
- Magallon S, Sanderson MJ. 2001. Absolute diversification rates in angiosperm clades. *Evolution* 55:1762–80
- Maley CC. 1998. *The evolution of biodiversity: a simulation approach*. PhD thesis. Cambridge, MA: MIT
- Mayden RL. 1987. Historical ecology and North American highland fishes: a research program in community ecology. In *Community and Evolutionary Ecology of North American Stream Fishes*, ed. WJ Matthews, DC Heins, pp. 210–22. Norman, OK: Univ. Okla. Press
- Mazer SJ, Wheelwright NT. 1993. Fruit size and shape: allometry at different taxonomic levels in bird-dispersed plants. *Evol. Ecol.* 7:556–75
- McCallum DA, Gill FB, Gaunt SLL. 2001. Community assembly patterns of parids along an elevational gradient in western China. *Wilson Bull.* 113:53–64
- McPeck MA. 1996. Linking local species interactions to rates of speciation in communities. *Ecology* 77:1355–66
- McPeck MA, Brown JM. 2000. Building a regional species pool: diversification of the *Enallagma* damselflies in eastern North American waters. *Ecology* 81:904–20
- McPeck MA, Miller TE. 1996. Evolutionary biology and community ecology. *Ecology* 77:1319–20
- Miles DB, Dunham AE. 1993. Historical perspectives in ecology and evolutionary biology—the use of phylogenetic comparative analyses. *Annu. Rev. Ecol. Syst.* 25:587–619
- Miller JS, Wenzel JW. 1995. Ecological characters and phylogeny. *Annu. Rev. Entomol.* 40:389–415
- Morales E. 2000. Estimating phylogenetic inertia in *Tithonia* (Asteraceae): a comparative approach. *Evolution* 54:475–84
- Morand S, Guegan JF. 2000. Distribution and abundance of parasite nematodes: ecological specialisation, phylogenetic constraint or simply epidemiology? *Oikos* 88:563–73
- Moreau RE. 1948. Ecological isolation in a rich tropical avifauna. *J. Anim. Ecol.* 17:113–26
- Murray BR, Westoby M. 2000. Properties of species in the tail of rank-abundance curves:

- the potential for increase in abundance. *Evol. Ecol. Res.* 2:583–92
- Nee S, May RM. 1997. Extinction and loss of evolutionary history. *Science* 278:692–95
- Nee S, Read AF, Greenwood JJD, Harvey PH. 1991. Phylogeny and the relationship between abundance and body size in British birds. *Nature* 351:312–13
- Nel A, Nel J, Masselot G, Thomas A. 1998. An investigation into the application of the Wagner parsimony method in synecology. *Biol. J. Linn. Soc.* 65:165–89
- Novotny V, Basset Y, Miller SE, Weiblen G, Bremer B, et al. 2002. Low host specificity of herbivorous insects in a tropical forest. *Nature* 416:841–44
- Olszewski TD, Patzkowsky ME. 2001. Evaluating taxonomic turnover: Pennsylvanian-Permian brachiopods and bivalves of the North American midcontinent. *Paleobiology* 27:646–68
- Peat HJ, Fitter AH. 1994. Comparative analyses of ecological characteristics of British angiosperms. *Biol. Rev.* 69:95–115
- Peterson AT, Soberon J, Sanchez-Cordero V. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285:1265–67
- Poulin R. 1999. Speciation and diversification of parasite lineages: an analysis of congeneric parasite species in vertebrates. *Evol. Ecol.* 13:455–67
- Price T, Lovette IJ, Bermingham E, Gibbs HL, Richman AD. 2000. The imprint of history on communities of North American and Asian warblers. *Am. Nat.* 156:354–67
- Prinzinger A, Durka W, Klotz S, Brandl R. 2001. The niche of higher plants: evidence for phylogenetic conservatism. *Proc. R. Soc. London Ser. B* 268:2383–89
- Qian H, Ricklefs RE. 1999. A comparison of the taxonomic richness of vascular plants in China and the United States. *Am. Nat.* 154:160–81
- Raup DM, Gould SJ, Schopf TJM, Simberloff DS. 1973. Stochastic models of phylogeny and the evolution of diversity. *J. Geol.* 81:525–42
- Richardson JE, Pennington RT, Pennington TD, Hollingsworth PM. 2001. Rapid diversification of a species-rich genus of Neotropical rain forest trees. *Science* 293:2242–45
- Richman AD. 1996. Ecological diversification and community structure in the Old World leaf warblers (genus *Phylloscopus*): a phylogenetic perspective. *Evolution* 50:2461–70
- Richman AD, Price T. 1992. Evolution of ecological differences in the Old World leaf warblers. *Nature* 355:817–21
- Ricklefs RE. 1987. Community diversity: relative roles of local and regional processes. *Science* 235:167–71
- Ricklefs RE. 2002. Phylogenetic perspectives on patterns of regional and local species richness. In *Tropical Rainforests: Past and Future*, ed. C Moritz, E Bermingham. In press
- Ricklefs RE, Bermingham E. 2001. Nonequilibrium diversity dynamics of the Lesser Antillean avifauna. *Science* 294:1522–24
- Ricklefs RE, Latham RE. 1992. Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. *Am. Nat.* 139:1305–21
- Ricklefs RE, Schluter D, eds. 1993a. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. Chicago: Univ. Chicago Press
- Ricklefs RE, Schluter D. 1993b. Species diversity: regional and historical influences. See Ricklefs & Schluter 1993a, pp. 350–63
- Salamin N, Hodkinson TR, Savolainen V. 2002. Building supertrees: an empirical assessment using the grass family (Poaceae). *Syst. Biol.* 51:136–50
- Sanderson MJ, Donoghue MJ. 1996. Reconstructing shifts in diversification rates on phylogenetic trees. *Trends Ecol. Evol.* 11:15–20
- Sanderson MJ, Purvis A, Henze C. 1998. Phylogenetic supertrees: assembling the trees of life. *Trends Ecol. Evol.* 13:105–9
- Sanmartin I, Enghof H, Ronquist F. 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biol. J. Linn. Soc.* 73:345–90

- Sasal P, Niquil N, Bartoli P. 1999. Community structure of digenean parasites of sparid and labrid fishes of the Mediterranean sea: a new approach. *Parasitology* 119:635–48
- Schluter D. 2000a. Ecological character displacement in adaptive radiation. *Am. Nat.* 156:S4–16
- Schluter D. 2000b. *The Ecology of Adaptive Radiation*. Oxford, UK: Oxford Univ. Press
- Schluter D. 2001. Ecology and the origin of species. *Trends Ecol. Evol.* 16:372–80
- Schluter D, Ricklefs RE. 1993. Convergence and the regional component of species diversity. See Ricklefs & Schluter 1993a, pp. 230–41
- Schwarz MW, Simberloff D. 2001. Taxon size predicts rates of rarity in vascular plants. *Ecol. Lett.* 4:464–69
- Sechrest W, Brooks TM, da Fonseca GAB, Konstant WR, Mittermeier RA. 2002. Hotspots and the conservation of evolutionary history. *Proc. Natl. Acad. Sci. USA* 99: 2067–71
- Semple C, Steel M. 2000. A supertree method for rooted trees. *Discrete Appl. Math.* 105: 147–58
- Silvertown J, Dodd ME, Gowing DJG. 2001. Phylogeny and the niche structure of meadow plant communities. *J. Ecol.* 89:428–35
- Silvertown J, Dodd ME, Gowing DJG, Mountford JO. 1999. Hydrologically defined niches reveal a basis for species richness in communities. *Nature* 400:61–63
- Simberloff DS. 1970. Taxonomic diversity of island biotas. *Evolution* 24:23–47
- Stevens RD, Willig MR. 2000. Community structure, abundance, and morphology. *Oikos* 88:48–56
- Sturmbauer C. 1998. Explosive speciation in cichlid fishes of the African great lakes: a dynamic model of adaptive radiation. *J. Fish Biol.* 53:18–36
- Taberlet P, Fumagalli L, Wust-Saucy A, Cosson J. 1998. Comparative phylogeography and postglacial colonization routes in Europe. *Mol. Ecol.* 7:453–64
- ter Steege H, Hammond DS. 2001. Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology* 82:3197–212
- Thompson JN, Reichman OJ, Morin PJ, Polis GA, Power ME, et al. 2001. Frontiers of ecology. *Bioscience* 51:15–24
- Tilman D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16
- Tofts R, Silvertown J. 2000. A phylogenetic approach to community assembly from a local species pool. *Proc. R. Soc. London Ser. B* 267:363–69
- Tokeshi M. 1991. Faunal assembly in chironomids (Diptera): generic association and spread. *Biol. J. Linn. Soc.* 44:353–67
- Upchurch P. 1995. The evolutionary history of sauropod dinosaurs. *Philos. Trans. R. Soc. London Ser. B* 349:365–90
- Verdu M, Barron-Sevilla JA, Valiente-Banuet A, Flores-Hernandez N, Garcia-Fayos P. 2002. Mexican plant phenology: Is it similar to Mediterranean communities? *Bot. J. Linn. Soc.* 138:297–303
- Vermeij GJ, Carlson SJ. 2000. The muricid gastropod subfamily Rapaninae: phylogeny and ecological history. *Paleobiology* 26:19–46
- Vitt LJ, Zani PA. 1996. Organization of a taxonomically diverse lizard assemblage in Amazonian Ecuador. *Can. J. Zool.* 74:1313–35
- von Euler F, Svensson S. 2001. Taxonomic distinctness and species richness as measures of functional structure in bird assemblages. *Oecologia* 129:304–11
- Wanntorp HE, Brooks DR, Nilsson T, Nylin S, Ronquist F. 1990. Phylogenetic approaches in ecology. *Oikos* 57:119–32
- Warming E. 1909. *Oecology of Plants*. London: Oxford Univ. Press
- Webb CO. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *Am. Nat.* 156:145–55
- Webb CO, Donoghue MJ. 2002. *PhyloMatic: A Database for Applied Phylogenetics*. <http://www.phylodiversity.net/phyloMatic>
- Webb CO, Peart DR. 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology* 80:2006–17

- Webb CO, Peart DR. 2000. Habitat associations of trees and seedlings in a Bornean rain forest. *J. Ecol.* 88:464–78
- Webb CO, Pitman NC. 2002. Phylogenetic balance and ecological evenness. *Syst. Biol.* In press
- Westoby M, Leishman M, Lord J. 1995. On misinterpreting the “phylogenetic correction.” *J. Ecol.* 83:531–34
- Williams CB. 1964. *Patterns in the Balance of Nature*. New York: Academic
- Williams PH, Humphries CJ, Vane-Wright RI. 1991. Measuring biodiversity: taxonomic relatedness for conservation priorities. *Austr. Syst. Bot.* 4:665–79
- Williams-Linera G. 1997. Phenology of deciduous and broadleaved-evergreen tree species in a Mexican tropical lower montane forest. *Glob. Ecol. Biogeogr. Lett.* 6:115–27
- Willis JC. 1922. *Area and Age: A Study of Geographical Distribution and Origin in Species*. Cambridge, UK: Cambridge Univ. Press
- Wing SL, Hickey LJ, Swisher CC. 1993. Late Cretaceous vegetation. *Nature* 363:342–44
- Winston MR. 1995. Cooccurrence of morphologically similar species of stream fishes. *Am. Nat.* 145:527–45
- Wisheu IC. 1998. How organisms partition habitats: different types of community organization can produce identical patterns. *Oikos* 83:246–58
- Zimmerman BL, Simberloff D. 1996. An historical interpretation of habitat use by frogs in a Central Amazonian forest. *J. Biogeogr.* 23:27–46
- Zinc RM. 1996. Comparative phylogeography in North American birds. *Evolution* 50:308–17

