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Evolutionary Ecology of Communities

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Introduction

Ecological communities are composed of interacting or potentially interacting organisms. Communities do not evolve per se; rather, they shift in composition, diversity, and structure through time. The assembly of local communities is influenced by both regional factors and local processes, each of which can influence evolutionary patterns and processes within those communities. We start by discussing early ecological and evolutionary debates on the nature of communities and then consider regional-historical perspectives codified by later researchers. We then consider recent research on the phylogenetic structure of communities, considering the myriad local and long-term biogeographic and macroevolutionary processes that can affect it. On shorter evolutionary timescales, we briefly treat the literature in community genetics and eco-evolutionary dynamics, which shows how community interactions can exert evolutionary pressures that then have further consequences at the community and ecosystem scales. In these sections, we mostly draw from studies on plant communities, but we also consider trophic interactions, particularly plant-insect interactions, and animal community guilds, such as *Anolis* lizards and dragonflies. We discuss the importance of an evolutionary perspective on communities for understanding ecosystem processes, and its relevance for conservation and restoration. Finally, we discuss seminal methods to examine the consequences of evolutionary processes for community assembly.

Historical Perspectives on the Nature of Communities

The early 20th century saw many debates on the nature of ecological communities that have echoes in current discussions about how evolution operates in a community context. It has been known, since at least the time of Alexander von Humboldt, that the traits of species are linked to gradients in climate across major biomes; Darwin clarified how such gradients drive species differences. Although these broad patterns are well recognized, the manner in which communities assemble locally has been contested ever since, and evolutionary considerations have been brought into this debate almost from the start. Some researchers have emphasized the ways that species in communities evolve *in situ* as a result of their interactions, eventually becoming closely associated with one another. Others contend that species assemblages are transient products of historical contingency, and they are continually re-created as a consequence of environmental change. Moreover, debate is ongoing about whether current patterns of species composition and richness can be explained primarily in terms of present-day abiotic conditions and species interactions or whether biogeographic history leaves an imprint. In favor of the latter view, researchers have marshalled evidence that factors like long-term regional climatic stability or chance colonization events have had strong legacy effects on the composition and richness of present-day communities. In this section, we review these debates, and trace the first applications of explicitly evolutionary methods to understanding community assembly. Ecologists and evolutionary biologists tend to explain the assembly of communities in terms of factors that operate along different timescales, but a long tradition in natural history considers ecological and evolutionary processes to be inextricably linked.

The Nature and Origin of Communities

Historically, controversy has arisen about the nature of communities and the extent to which they represent associations of tightly interconnected species shaped either over long periods of interaction or as the result of chance co-occurrences of individually dispersed and distributed organisms. The perspectives of Frederick Clements and Henry Gleason represent opposite ends of the spectrum in terms of the nature of communities. Clements viewed a community as a group of interdependent and inextricably linked species (Clements 1916).

This perspective is relevant to assemblages of species composed of lineages that have undergone *in situ* diversification, evolving together over long time periods and developing intricate interdependencies. Gleason 1926 defines communities as chance assemblages of individually distributed species. This perspective is particularly relevant in the context of major environmental changes, e.g., interglacial cycles in temperate regions, where species may colonize from disparate sources, as later evidenced by Margaret Davis's seminal work on fossil pollen showing that species reassemble after glaciation following their own individual trajectories (Davis 1981; see also Dynamism). Braun 1938 and Braun 1967 recognize that assemblages are composed of different temporal elements that emerged (evolved) in different eras of geologic history with some degree of coherence among these elements, represented by identifiable climax vegetation types. The author thus provides a picture of continental scale community assembly that echoed elements of both the Gleasonian and Clementsian perspectives. This perspective reemerges in the paleontological work found in DiMichele, et al. 2004 (see Stasis), which clarifies that some components of communities can be identified in the fossil record that occur together consistently over long time periods. Complementary to these perspectives, Warming 1895 emphasizes differences in the physiological abilities of plants that allow them to adjust to some, but not all, environments. Warming stressed that similar physiological attributes would be selected for by similar environments in different regions, which is relevant when considering convergent evolution. Along similar lines, Janzen 1985 proposes the idea of ecological fitting, in which species can adjust and fit into new environments without being perfectly adapted to them. Also relevant to these early conceptions of communities is Brown and Wilson's concept of character displacement (Brown and Wilson 1956), in which they hypothesized that species interactions lead to evolutionary changes that cause similar species to have more pronounced character differences when they occur together than when they occur apart. In contrast, Connell 1980 argues that it is difficult to make inferences about species interactions in the past that shaped current communities because all we can observe are outcomes of past processes.

Braun, E. L. 1938. Deciduous forest climaxes. *Ecology* 19:515–542.

Geologic and biogeographic history, including past environmental conditions, climate instability, and disturbance regimes, have shaped the modern flora. Repeated climax assemblages can be identified from their constituent elements, which have emerged from different geologic periods and have combined to form the assemblages we see today.

Braun, E. L. 1967. *Deciduous forests of eastern North America*. New York: Hafner.

This seminal work integrates botanical, ecological, and geological thinking to document forest composition as distinct vegetation types across geographic space and traces through geologic time the development of present patterns of forest distribution. In doing so, the book brings to life a dynamic and deep-time perspective on the assembly of forest communities.

Brown, W. L., and E. O. Wilson. 1956. Character displacement. *Systematic Zoology* 5.2: 49–64.

Enhanced evolutionary differentiation in functional characters in the geographic region where similar, and closely related, species overlap, as a consequence of competitive interactions.

Clements, F. E. 1916. *Plant succession: An analysis of the development of vegetation*. Washington, DC: Carnegie Institution of Washington.

Communities consist of species that are inextricably linked due to (co)evolutionary processes, making them resemble "superorganisms."

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35.2: 131–138.

This classic paper explains how difficult it is to make inferences about the process of competition from patterns. The outcomes of competition leave signatures that do not necessarily reveal the nature of the competitive process, making it very difficult to infer that competition was even important.

Davis, M. B. 1981. Quaternary history and the stability of forest communities. In *Forest succession: Concepts and application*. Edited by D. C. West, H. H. Shugart, and D. B. Botkin, 132–153. New York: Springer-Verlag.

Davis used fossil pollen data to show that North American tree species followed different climatic trajectories post-glaciation, supporting Gleason's perspective on community structure.

Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 63:7–26.

Communities are merely the species that occur, by chance, in the same place at the same time based on their individual distributions. Thus, communities result from historical coincidence rather than constituting superorganisms.

Janzen, D. H. 1985. On ecological fitting. *Oikos* 45.3: 308–310.

This essay introduces the concept of "ecological fitting" whereby new members of communities that evolved elsewhere fit themselves into existing communities without adaptive shifts, "*like asymmetrical pegs in square holes*." The implication is that absolute fitness matters more than relative fitness: organisms just need to survive in a novel environment, not be optimally adapted to it.

Warming, E. 1895. *Plantesamfund: Grundtræk af den økologiske plantegeografi*. Copenhagen: P. G. Philipsens Forlag.

Warming's pioneering work promoted the idea that limits in the physiological tolerances of plants should cause plant phenotypes to match their environments in predictable ways, with the consequence that species with similar phenotypes share habitat affinities.

Regional Perspectives

During the 1960s and 1970s, it was common for ecologists to assume that local community structure and diversity were determined by local processes like competition and trophic interactions. These processes, it was presumed, caused diversity in many local communities to reach a saturated equilibrium independent of the slower historical processes that generate the regional species pool. Ricklefs 1987 argues forcefully against this view, reviewing evidence that the evolutionary history of a region and generation of the regional species pool can influence local communities as much, or more, than do local interactions. From this perspective, communities are not isolated systems in equilibrium; rather, they are snapshots in time and space that result from long-term regional and continental processes (Ricklefs 2004, Ricklefs 2008; but see Brooker, et al. 2009). We would argue this work was influenced by John Lawton's earlier attempts (Lawton 1999), though somewhat unsuccessful, to find generalities among communities and across scales. Explaining aspects of communities like species richness may require understanding deterministic ecological forces, but also historical biogeography (Latham and Ricklefs 1993). Consequently, biogeographic and systematic data can have great value in interpreting patterns of variation among communities. Holt and Gaines 1993 provides an empirical case study of how regional and local processes interact in a fragmented landscape.

Brooker, R. W., R. M. Callaway, and L. A. Cavieres. 2009. Don't diss integration: A comment on Ricklefs's disintegrating communities. *American Naturalist* 174.6: 919–927.

This comment counters Ricklefs 2008 in arguing that studies of local coexistence can be useful in understanding not just local diversity, but also the regional-scale consequences of local interactions.

Holt, R. D., and M. S. Gaines. 1993. The influence of regional processes on local communities: Examples from an experimentally fragmented landscape. In *Patch dynamics in marine and terrestrial environments*. Edited by T. Powell, S. Levin, and J. Steele, 260–276. Berlin: Springer-Verlag.

The chapter presents a case study of the interaction between regional-level controls of diversity and local-scale assembly in a fragmented landscape.

Latham, R. E., and R. E. Ricklefs. 1993. Global patterns of tree species richness in moist forests: Energy-diversity theory does not account for variation in species richness. *Oikos* 67.2: 325–333.

The authors use variation in tree species richness across climatically similar portions of separate continents to argue that species richness may have more to do with the unique histories of biogeographic regions than environmental factors.

Lawton, J. 1999. Are there general laws in ecology? *Oikos* 84.1: 177–192.

The paper is perhaps the most influential of a series of perspective pieces Lawton wrote and published in *Oikos* around that time. It is an all-encompassing review of many areas of ecology, focusing on generality (and a lack thereof) and integrating macro- and community ecology. Interestingly, Lawton suggests that "progress might be made . . . by drawing on knowledge of the dynamics of similar species (taxonomic relatives," p. 180), suggesting a potential role for phylogeny.

Ricklefs, R. E. 1987. Community diversity: Relative roles of local and regional processes. *Science* 235.4785:167–171.

This pivotal study advocates a "regional-historical" viewpoint to the problem of understanding variation in local community diversity. In this view, local diversity can be constrained not just by local processes, but also by historical factors that affect regional diversity, such as the history of dispersal and diversification in an area.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* 7.1: 1–15.

Ricklefs attempts to bridge the divide between local and regional explanations of patterns of biodiversity by proposing that dispersal causes local species interactions, and their consequences for population size, to play out over regional scales. The fact that populations interact over entire regions and equilibrate slowly, if at all, lessens the gap in temporal and spatial scales between regional-historical and local perspectives.

Ricklefs, R. E. 2008. Disintegration of the ecological community. *American Naturalist* 172.6: 741–750.

Here Ricklefs argues, with echoes of Gleason, that defining local communities places arbitrary bounds on ecological processes that are continuous in space and time. As a result, local communities tend to be poorly integrated, epiphenomenal combinations of species that result from the regional-historical processes that determine the origin and distribution of each species.

Early Phylogenetic Perspectives on Community Assembly

Although the author of Elton 1946 and others used species/genus ratios to understand competition decades ago, evolutionary biologists were among the first to carefully examine the evolutionary forces driving community assembly at different temporal and spatial scales. They harnessed emerging comparative methods (including those collated and developed in Harvey and Pagel 1991) to make inferences about the consequences of species interactions for trait evolution, including character displacement, and adaptive changes that accompany introduction to novel environments or niche shifts. In particular, Schluter and McPhail 1992 outlines the strict requirements necessary to provide evidence for character displacement, as defined in Brown and Wilson 1956 (cited under the Nature and Origin of Communities), to indicate the enhanced (genetically based) differentiation in functional characters related to resource use in the region where closely related competing species overlap. Losos 1992 embarks on long-term studies of the evolution and ecology of *Anolis* lizards, examining their functional evolution in the context of species interactions and the habitats they occupied. Brooks and McLennan 1991 offers a novel and integrative perspective on communities, considering the processes and elements that are influential over multiple timescales, including both ecological and evolutionary processes. The contributors to Ricklefs and Schluter 1993 were the first to expand these perspectives to consider the eco-evolutionary processes in the assembly of communities. With the development of phylogenetic methods and computational tools to construct phylogenies at scales appropriate for examination of community assembly, phylogenetic information could be harnessed for studies of community assembly (Losos 1996).

Brooks, D. R., D. A. McLennan. 1991. *Phylogeny, ecology, and behavior: A research program in comparative biology*. Chicago: Univ. of Chicago Press.

The authors provide an integrative perspective that community development involves both recent and historical elements and that both evolutionary processes, including speciation and adaptation, as well as dispersal and colonization are critical to assembly.

Elton, C. 1946. Competition and the structure of ecological communities. *Journal of Animal Ecology* 15.1: 54–68.

Elton conducts a cross-habitat synthesis of species composition that uses low species/genus ratios to posit that, at small scales, competition prevents co-occurrence of related species. The study is an important precursor to community phylogenetics, later developed by Campbell Webb and colleagues.

Harvey, P. H., and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford: Oxford Univ. Press.

The book provides an early canonical overview of phylogenetic comparative methods.

Ricklefs, R. E., and D. Schluter. 1993. *Species diversity in ecological communities: Historical and geographical perspectives*. Chicago: Univ. of Chicago Press.

This broad-ranging edited volume discusses the generation and maintenance of species richness across scales, from local to regional, and from a variety of perspectives.

Schluter, D., and J. D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. *American Naturalist* 140.1: 85–108.

This influential exposition provides an empirical application of six criteria for rigorously establishing the occurrence of character displacement in a community, with a discussion of the implications of character displacement for speciation.

Losos, J. B. 1992. The evolution of convergent structure in Caribbean *Anolis* communities. *Systematic Biology* 41.4: 403–420.

This is one of the first of Losos's classic papers on the convergent evolution of *Anolis* lizards and its consequence for the community assembly of these species.

Losos, J. B. 1996. Phylogenetic perspectives on community ecology. *Ecology* 77.5: 1344–1354.

Here Losos provides an overview of the various ways phylogenetic comparative methods could be applied in a community ecological context.

Linking Phylogenies and Community Ecology

The authors of a wide body of literature, conducted across many regions and taxa, have attempted to use phylogenies in conjunction with data describing the presence or abundance of species across communities to understand the processes that govern community assembly. A common approach is to map the species present in a community onto a phylogeny of species in a regional species pool and calculate metrics describing how the species in the community are distributed through the phylogeny, often in conjunction with analyses of trait evolution. The core intuition behind this approach comes from Charles Darwin, who recognized that specific attributes of species could influence their interactions with other species and with the environment in predictable ways. On the one hand, if closely related species are ecologically similar, they should share similar environmental requirements and may thus be expected to co-occur. On the other hand, closely related species should experience strong competitive interactions due to their ecological similarity, thereby limiting coexistence and thus driving selection for divergent traits. This argument, and approaches derived from it, have been popular but controversial due to the challenges of making robust inferences of process from pattern.

Phylogenetic Community Structure

To operationalize Darwin's ideas, Webb, et al. 2002 lays out a heuristic framework to use community phylogenetic structure to uncover deterministic processes, or assembly rules, in community assembly, building on an earlier publication (Webb 2000). Under the assumption that species' niches are conserved through evolutionary time (such that closely related species resemble one another), trait-environment matching (environmental filtering) should lead to communities of closely related species (phylogenetic clustering) and interspecific competition should lead to communities of distantly related species (phylogenetic overdispersion). The framework, followed by several seminal papers and a 2006 special issue in *Ecology* (see Swenson, et al. 2006) initiated a large body of work incorporating phylogenetics into community ecology. Losos, et al. 2003 clarifies that the functional traits underlying species niches are not always conserved. Cavender-Bares, et al. 2006 demonstrates that in assemblages of closely related species, some traits can be conserved and others convergent; the set of traits critical for habitat sorting drives community assembly and, hence, the pattern of phylogenetic community structure. In oaks, functional traits are convergent, causing overdispersion. Stephens and Wiens 2004 also highlights convergent evolution in turtles in their broader biogeographic context. Slingsby and Verboom 2006 finds evidence that close relatives (in South African sedges) did not co-occur because of limiting similarity (competitive or other density dependent processes). The issues of scale quickly became apparent as an explanation in the contrasting results that were emerging. Dealing with the issue of spatial and phylogenetic scale, Cavender-Bares, et al. 2006 and Swenson, et al. 2006 demonstrate that patterns of phylogenetic clustering and overdispersion depend on spatial extent and phylogenetic breadth under examination. The contributors to Kraft, et al. 2007 then tested the framework in Webb, et al. 2002 using a simulation approach in demonstrating that conserved or convergent evolution in traits important for ecological filtering or competitive exclusion would lead to the predicted patterns of phylogenetic community structure. The authors of Hardy, et al. 2012 use multiple approaches to examine the processes underlying phylogenetic structure at different scales.

Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* 163.6: 823–843.

This empirical study conducted within a single tree genus demonstrates convergent evolution of the functional traits that determine species' distributions across an environmental gradient to explain why close relatives co-occur less than expected. It is perhaps the first study to examine the phylogenetic structure of plant communities considering the evolution of functional traits in community assembly.

Cavender-Bares, J., A. Verboom, and B. Miles. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87.sp7: S109–S122.

The authors demonstrate in woody plant communities in Florida that both phylogenetic inclusiveness of communities and the spatial extent of the analysis influence that phylogenetic structure of communities and whether traits are statistically conserved or convergent.

Hardy, O. J., P. Couteron, F. Munoz, B. R. Ramesh, and R. Pélissier. 2012. Phylogenetic turnover in tropical tree communities: Impact of environmental filtering, biogeography and mesoclimate niche conservatism. *Global Ecology and Biogeography* 21.10: 1007–1016.

Patterns of phylogenetic relatedness of species within and across communities (phylogenetic community structure) were used to explore the processes underlying them and the scale at which they operate.

Kraft, N. J. B., W. K. Cornwell, C. O. Webb, and D. D. Ackerly. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist* 170.2: 271–283.

This pivotal paper tests they heuristic framework of Webb, et al. 2002 using simulations, but highlighting that dispersal has the potential to confound community phylogenetic patterns.

Losos, J. B., M. Leal, R. E. Glor, et al. 2003. Niche lability in the evolution of a Caribbean lizard community. *Nature* 424:542–545.

The traits underlying community assembly could be extremely labile, as shown in this classic paper.

Slingsby, J. A., and G. A. Verboom. 2006. Phylogenetic relatedness limits co-occurrence at fine spatial scales: Evidence from the schoenoid sedges (Cyperaceae: Schoeneae) of the Cape floristic region, South Africa. *American Naturalist* 168.1: 14–27.

The study provides a great example of the use of functional trait and phylogenetic information to examine a floristic system and the first to use quantile regression to examine phylogenetic community structure.

Stephens, P. R., and J. J. Wiens. 2004. Convergence, divergence, and homogenization in the ecological structure of emydid turtle communities: The effects of phylogeny and dispersal. *American Naturalist* 164.2: 244–254.

Stephens and Wiens provide an interesting example of convergence in turtles, focusing on the wider biogeographical context of trait evolution and community assembly.

Swenson, N. G., B. J. Enquist, J. Pither, J. Thompson, and J. K. Zimmerman. 2006. The problem and promise of scale dependency in community phylogenetics. *Ecology* 87.10: 2418–2424.

This related empirical study demonstrates how varying the taxonomic scope and geographic definition of the regional species pool could lead community phylogenetic methods to appear to detect differing ecological processes underlying community assembly.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *American Naturalist* 156.2: 145–155.

This paper was the first to introduce and apply metrics to formally test whether species in a community are more related than expected by chance. These metrics were later modified to be able to test for overdispersion in Webb, et al. 2002.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33:475–505.

A must-read framework for testing hypotheses about the evolution of species' niche-based community assembly.

Multiple Processes Contribute to Phylogenetic Community Structure

The popularity of community phylogenetics as a research program since Webb, et al. 2002 (cited under Phylogenetic Community Structure) led many researchers to identify factors that complicate a straightforward mapping of phylogenetic pattern onto ecological and evolutionary processes. Cavender-Bares, et al. 2009 points out that, for applications that seek to use phylogenetic distance as a proxy for functional differences, one must evaluate whether traits driving assembly are convergent or conserved. Furthermore, the authors note that patterns of phylogenetic dispersion can be caused not just by direct competition or environmental filtering, but also by facilitation (see Valiente-Banuet and Verdú 2007), apparent competition and Janzen-Connell mechanisms (see Gilbert and Webb 2007), or even lack of reproductive isolation among similar species (see Pollock, et al. 2015). Kembel 2009 finds that dispersal (even when species-neutral) could confound inferences about niche-based assembly processes, a problem that might be mitigated, in part, by choosing appropriate null models. Graham, et al. 2012 establishes the difficulty of reconciling inferences from phylogenetic and trait-based data even for conserved traits. Finally, from an explicitly evolutionary perspective, Losos 2011 discusses how limitations in comparative methods impede inference of process from phylogenies. Finally, Vamosi, et al. 2009 provides a useful review of general trends in the community phylogenetics literature up to that date, including lists of important considerations for future researchers.

Cavender-Bares, J., D. Ackerly, and K. Kozak. 2012. Integrating ecology and phylogenetics: The footprint of history in modern-day communities. *Ecology* 93.sp8: S1–S3.

This article introduces and provides an overview of a special issue in *Ecology* on integrating ecology and phylogenetics with a focus on the consequences of multiple macroevolutionary processes for community assembly.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12.7: 693–715.

This seminal review of the community phylogenetics literature outlines a variety of factors that can shape community phylogenetic structure, emphasizing the crucial challenge of linking pattern to process.

Gilbert, G. S., and C. O. Webb. 2007. Phylogenetic signal in plant pathogen-host range. *Proceedings of the National Academy of Sciences of the United States of America* 104.12: 4979–4983.

Density-dependent processes, such as disease, may also influence the phylogenetic structure of communities if close relatives are susceptible to the same pathogens.

Graham, C., J. L. Parra, B. A. Tinoco, F. G. Stiles, and J. A. McGuire. 2012. Untangling the influence of ecological and evolutionary factors on trait variation across hummingbird assemblages. *Ecology* 93.sp8: S99–S111.

Humming bird assemblages provide a case study that establishes the difficulty of predicting the trait structure of a community from phylogenetic dispersion even for conserved traits, given the complexity of trait evolution.

Kembel, S. W. 2009. Disentangling niche and neutral influences on community assembly: Assessing the performance of community phylogenetic structure tests. *Ecology Letters* 12.9: 949–960.

Picking up from Kraft, et al. 2007 (cited under Phylogenetic Community Structure), this metacommunity simulation-based study compares methods to measure community phylogenetic structure under scenarios of purely neutral or niche-based assembly processes. Even when communities are assembled through purely species-neutral dispersal, non-random patterns of phylogenetic dispersion can be observed, depending on the null model used.

Losos, J. B. 2011. Seeing the forest for the trees: The limitations of phylogenies in comparative biology. *American Naturalist* 177.6: 709–727.

Losos critiques the reliance of many research programs on phylogenetic information, given the limitations of present-day comparative methods and the fact that phylogenies represent patterns rather than causal mechanisms.

Pollock, L. J., M. J. Bayly, and P. A. Vesk. 2015. The roles of ecological and evolutionary processes in plant community assembly: The environment, hybridization, and introgression influence co-occurrence of *Eucalyptus*. *American Naturalist* 185.6: 784–796.

The study examines co-occurrence patterns in *Eucalyptus*, showing that lack of reproductive isolation, rather than competitive exclusion, keeps closely related species from co-occurring.

Valiente-Banuet, A., and M. Verdú. 2007. Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters* 10.11: 1029–1036.

This study of nurse plant facilitation shows that particular lineages often maintain the regeneration niche of distantly related lineages. Thus, facilitation can promote coexistence of distant lineages.

Vamosi, S. M., S. B. Heard, J. C. Vamosi, and C. O. Webb. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology* 18.4: 572–592.

This thorough review and meta-analysis of the community phylogenetic literature until 2009 shows general trends and highlights important considerations such as tree balance, spatial scale, and taxonomic bias.

Relatedness and Competitive Strength

A particular theme that emerges from the literature on the multiple processes affecting phylogenetic community structure is whether relatedness corresponds to the strength of competition among species. Strauss, et al. 2006 shows that highly invasive grass species are less related to the native community than less invasive introduced species. Along similar lines, Burns and Strauss 2011 shows that more closely related species were more ecologically similar and competed more strongly under field conditions. Maherali and Klironomos 2007 finds similar results in fungal communities. On the other hand, Cahill, et al. 2008 shows weak or negligible relationships between relatedness and competitive intensity. Mayfield and Levine 2010 and Godoy, et al. 2014 place these results in the context of modern (Chessonian) coexistence theory to critique the assumption that more related species compete more strongly. The authors argue that even if traits are conserved across a phylogeny, trait differences (or phylogenetic distance) can correspond to either niche differences (which promote coexistence) or fitness differences (which hinder coexistence). Along similar lines, Germain, et al. 2016 demonstrates the imprint of historical interactions on how niche and fitness differences relate to phylogenetic relatedness. Finally, Nuismer and Harmon 2015 develops methods to use phylogenies to predict rates of interspecific interactions.

Burns, J. H., and S. Y. Strauss. 2011. More closely related species are more ecologically similar in an experimental test. *Proceedings of the National Academy of Sciences of the United States of America* 108.13: 5302–5307.

This experimental test of competition shows that more related species have more similar germination and early survival niches. More related species compete more strongly under field soils, a trend that is reversed in potting soil.

Cahill, J. F., S. W. Kembel, E. G. Lamb, and P. A. Keddy. 2008. Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspectives on Ecology, Evolution and Systematics* 10.1: 41–50.

The authors conduct a long called for experimental test of the association between phylogenetic relatedness and competitive outcomes. Overall, the relationships between competition and phylogenetic relatedness are weak and masked by a competitive hierarchy in which monocots are suppressed by eudicots, and eudicots are mostly strongly suppressed by other eudicots.

Godoy, O., N. J. B. Kraft, and J. M. Levine. 2014. Phylogenetic relatedness and the determinants of competitive outcomes. *Ecology Letters* 17.7: 836–844.

This thoughtful empirical study examines whether phylogeny can predict species' competitive interactions and coexistence. The experimental results lead to the conclusion that phylogenetic distance is positively correlated with fitness differences and variance in fitness differences, but not niche differences, with the overall consequence that coexistence is unrelated to phylogenetic relatedness.

Germain, R. M., J. T. Weir, and B. Gilbert. 2016. Species coexistence: Macroevolutionary relationships and the contingency of historical interactions. *Proceedings of the Royal Society B: Biological Sciences* 283.1827:c20160047.

The authors conduct an experiment similar to Godoy, et al. 2014 but assay competitive interactions among both allopatric and sympatric species pairs. Among sympatric species pairs, fitness differences show no relation to relatedness, while among allopatric species pairs, fitness differences decrease with relatedness, making coexistence less likely among more distantly related species.

Maherali, H., and J. M. Klironomos. 2007. Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science* 316.5832: 1746–1748.

In this experimental test of plant-fungal interactions, plants are inoculated with mycorrhizal communities comprising species that were more or less related to one another. Lower initial phylogenetic relatedness yields higher final species richness and plant productivity.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13.9: 1085–1093.

This pivotal study integrates modern coexistence theory and community phylogenetic patterns and processes to contest a naive mapping of phylogenetic assemblage structure onto ecological processes.

Nuismer, S. L., and L. J. Harmon. 2015. Predicting rates of interspecific interaction from phylogenetic trees. *Ecology Letters* 18.1: 17–28.

This paper uses simple models of trait evolution and species interactions to determine whether phylogenies can be used to predict interaction rates within a community. The authors find that their success is dependent on the nature of the interaction, but that, in general, recently diverged species interact more strongly regardless of the model of trait evolution.

Strauss, S. Y., C. O. Webb, and N. Salamin. 2006. Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences of the United States of America* 103.15: 5841–5845.

This paper shows that in California, exotic grasses that become invasive are less related to the native community than exotic grasses that are not invasive. The authors conclude that phylogenetic distance may predict ecological novelty, which affects the likelihood of competitive success.

Order of Trait Evolution

One of the many themes that has emerged in the incorporation of phylogenetics in communities is the question of whether there are generalizations about the order of trait evolution with respect to α- or β-niches. Whittaker 1975 develops that concept of spatial hierarchies in diversity, such α-diversity is that within local habitats, β-diversity is due to turnover among habitats, and γ diversity is the total diversity in a region. Pickett and Bazzaz 1978 further develops these ideas to consider the concept that niches could also have α and β dimensions; α-niches run along niche axes that differ within a habitat, while β-niches segregate species across habitats. Silvertown, et al. 2006 poses the hypothesis that traits that define these hierarchical niches would also be hierarchical within the tree of life, such that α-niches would be labile, while those important for β- and γ-niches would be conservative. In other words, the traits that underlie γ-niches would be expected to evolve prior to β-niches, and the traits underlying α-niches would be most recent. Ackerly, et al. 2006 develops a method to test the order of trait evolution in adaptation radiations. There is mixed evidence for the pattern suggested in Silvertown, et al. 2006, although a meta-analysis has never been undertaken.

Ackerly, D. D., D. W. Schwilk, and C. O. Webb. 2006. Niche evolution and adaptive radiation: Testing the order of trait divergence. *Ecology* 87.sp7: S50–S61.

The study maps the concepts of environmental and competitive filtering on the basis of ecological traits onto the macro-evolutionary sequence of the evolution of traits.

Pickett, S. T. A, and F. A. Bazzaz. 1978. Organization of an assemblage of early successional species on a soil moisture gradient. *Ecology* 59.6: 1248–1255.

Following Whittaker's definitions, Pickett and Bazzaz develop the concept of α- and β-niches.

Silvertown, J., M. Dodd, D. Gowing, C. Lawson, and K. McConway. 2006. Phylogeny and the hierarchical organization of plant diversity. *Ecology* 87.sp7: S39–S49.

The authors posit that the order of trait divergence can have consequences for (and interact with) community assembly.

Silvertown, J., K. McConway, D. Gowing, et al. 2006. Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proceedings of the Royal Society B: Biological Sciences* 273:39–44.

Building on the concept of α- and β-niches, this study explicitly links sequential assembly of ecological communities, as a result of α- and β-traits, to the order of the macro-evolution of those traits. The study should be read in concert with Ackerly, et al. 2006.

Whittaker, R. H. 1975. *Communities and ecosystems*. New York: Macmillan.

This seminal book introduces and defines α-, β-, and γ-diversity.

Long-Term Perspectives on Community Assembly

Our discussion of the relationship between community assembly and macroevolutionary process is divided into two distinct, but strongly related themes. The first theme is the tension between perspectives that emphasize the tendency for assemblages of lineages to remain stable through macroevolutionary time and those that emphasize the contingency of species assemblages, which are seen as epiphenomena of the distinct responses of individual species to environmental conditions. The second theme is the relative extent to which assemblages of species are generated via *in situ* evolution, as opposed to ecological sorting of lineages that evolved elsewhere. Within each of these themes, the former perspective resembles a Clementsian super-organismal view of community boundaries, while the latter more closely resembles a Gleasonian individualistic view. Because these debates both require historical information, evidence from paleontology and comparative methods bear strongly on them. In particular, paleoecological evidence, like pollen and macrofossils, bear most directly on the question of stasis and dynamism, while phylogenetic approaches are more often used to understand *in situ* diversification and sorting.

Stasis

Recent research has emphasized the widespread tendency for species and lineages to maintain similar ecological traits over evolutionary time, a tendency called niche conservatism (Wiens and Graham 2005). Because niche conservatism ties lineages to particular sets of abiotic conditions, biome shifts tend to be less common than biome stasis (Crisp, et al. 2009). At the community scale, niche conservatism can cause entire assemblages of species to remain stably associated over time, a pattern corroborated by the fossil record (DiMichele, et al. 2004). Over long periods of association, interacting species may be expected to evolve together into integrated communities. Cavender-Bares and Reich 2012 and Stock and Verboom 2012 both document situations in which traits driving community assembly show strong niche conservatism, resulting in strong associations of particular lineages with abiotic conditions and with each other.

Cavender-Bares, J., and P. B. Reich. 2012. Shocks to the system: Community assembly of the oak savanna in a 40-year fire frequency experiment. *Ecology* 93.sp8: S52–S69.

A phylogenetic perspective on changes in plant community composition across a fire frequency gradient reveals that the traits driving community assembly evolved 80–140 million years ago and have remained relatively conserved among lineages since.

Crisp M., M. T. K. Arroyo, L. G. Cook, et al. 2009. Phylogenetic biome conservatism on a global scale. *Nature* 458:754–756.

Among Southern Hemisphere plant species, biome stasis has been much more common than biome shifts over tens of millions of years. As a result, present-day taxonomic composition of biomes is partly a legacy of where taxa originated.

DiMichele, W. A., A. K. Behrensmeyer, T. D. Olszewki, et al. 2004. Long-term stasis in ecological assemblages: Evidence from the fossil record. *Annual Review of Ecology, Evolution, and Systematics* 35:285–322.

Fossil evidence from marine plants and animals is used to support the notion that communities maintain a conservative homeostatic element. Variation in the composition of assemblages tends to be bounded due to the tendency for clades to track their physical environment.

Stock, W. D., and G. A. Verboom. 2012. Phylogenetic ecology of foliar N and P concentrations and N:P ratios across Mediterranean-type ecosystems. *Global Ecology and Biogeography* 21.12: 1147–1156.

Lineage conservatism is evident in foliar nutrient concentrations and stoichiometric ratios across Mediterranean-type ecosystems globally. Differences in nutrient-use strategies influence how species assemble across gradients of nutrient availability.

Wiens, J. J., D. D. Ackerly, A. P. Allen, et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13.10: 1310–1324.

This exposition of tests and evidence for niche conservatism discusses how niche conservatism can be used to explain the stability of interspecific interactions among lineages.

Wiens, J., and C. Graham. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology and Systematics* 36:519–539.

Conceptually, conservatism of species ecological niches should maintain some conservatism of assemblages if they similarly track the environment and maintain interactions.

Dynamism

In contrast to the niche conservatism perspective, other case studies reveal dynamism in long-term dynamics of community assembly. From this perspective, which has echoes of Gleason’s views on succession, species distributions reflect not a tight coupling of species within assemblages but rather a high degree of variation among species in migration rates and demographic responses to environmental change. As a result, community assembly is dynamic, and associations among species shift over long periods of time, as revealed, for example, in reconstruction of plant communities from pollen after the end of the Pleistocene glaciation in North America (Webb, et al. 1983; Davis and Shaw 2001) and Eurasia (Tarasov, et al. 2000).

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292.5517: 673–679.

This influential case study links past glaciation to present-day population genetic structure, emphasizing that species had complex and individual responses to climate change due to differences in tolerances to many climatic variables. In doing so, it largely overturns the Clementsian perspective of communities as superorganisms.

Tarasov, P. E., V. S. Volkova, T. Webb III, et al. 2000. Last glacial maximum biomes reconstructed from pollen and plant macrofossil data from northern Eurasia. *Journal of Biogeography* 27.3: 609–620.

The authors use pollen records to reconstruct vegetation at the last glacial maximum in northern Eurasia.

Webb, T., III, E. J. Cushing, H. E. Wright Jr. 1983. Holocene changes in the vegetation of the Midwest. In *Late-quaternary environments of the United States*. Vol. 2, *The Holocene*. Edited by S. C. Porter and H. E. Wright Jr., 142–165. Minneapolis: Univ. of Minnesota Press.

The authors use broad-scale palynological data to show that tree species varied in their responses to early Holocene climatic changes. Some assemblages found during that time no longer exist, even though their constitutive species do.

In Situ *Diversification*

Reflecting the early debate on the nature of communities, a long-standing issue in understanding communities has been the extent to which organisms evolve in the context of their environments and the species they co-occur with via *in situ* diversification, or alternatively, whether attributes that allow persistence in novel environments evolved in other contexts (exaptations) and now influence community assembly by ecological sorting. Evidence exists for both kinds of assembly, even in the same system (Gillespie 2004). We break this into two sections, one including studies that emphasize *in situ* diversification and one that emphasizes ecological sorting. Much of the work on *in situ* diversification is focused, detailed work on case studies: while this makes drawing generalities difficult, it reflects the complexities of the biology of this system. Kozak, et al. 2005 and Harmon, et al. 2008 focus on amphibian systems, while McPeek and Brown 2000 focuses on insects, and Becerra 2005; Verboom, et al. 2014; and Tanentzap, et al. 2015 focus on plants, respectively. Many studies, including Harmon, et al. 2008; Tanentzap, et al. 2015; and Gillespie 2004 are focused on islands, where *in situ* diversification may matter more because isolation can make it unlikely for frequent dispersal events to occur. This is a growing area of study where careful, detailed work by taxon experts is much needed.

Becerra, J. X. 2005. Timing the origin and expansion of the Mexican tropical dry forest. *Proceedings of the National Academy of Sciences of the United States of America* 102.31: 10919–10923.

Diversification of the Burseraceae is linked to the expansion of the tropical dry forest biome, using calibrated phylogenies of *Bursera* to provide time estimates of biome expansion in Mesoamerica. The paper develops the premise that the *Bursera* were able to expand only when the climatic conditions changed, creating a window for diversification of this lineage with synapomorphic traits adapted to these novel conditions.

Cavender-Bares, J., S. Kothari, J. E. Meireles, M. A. Kaproth, P. S. Manos, and A. L. Hipp. 2018. The role of diversification in community assembly of the oaks (*Quercus* L.) across the continental U.S. *American Journal of Botany* 105.3: 565–586.

The study provides a framework for explaining how the diversification process influences the assembly and phylogenetic structure of communities. The North American oaks are used as an example showing that parallel adaptive radiation of the genus into a range of habitats across the continent was a critical driver of community assembly of the lineage continent-wide.

Gillespie, R. G. 2004. Community assembly through adaptive radiation in Hawaiian spiders. *Science* 303.5656: 356–359.

Similar ecomorphs of spiders across the Hawaiian islands arise both through dispersal and species sorting and through convergent *in situ* evolution. Together, these processes are shown to cause similar sets of ecomorphs to be present on each island, demonstrating non-random community assembly.

Harmon, L. J., A. Larson, J. Melville, and J. B. Losos. 2008. The role of geography and ecological opportunity in the diversification of day geckos (*Phelsuma*). *Systematic Biology* 57.4: 562–573.

The study emphasizes the potential role of ecological opportunity, through island area, in driving diversification.

Kozak, K. H., A. Larson, R. M. Bonett, and L. J. Harmon. 2005. Phylogenetic analysis of ecomorphological divergence, community structure, and diversification rates in dusky salamanders (Plethodontidae: *Desmognathus*). *Evolution* 59.9: 2000–2016.

This thorough analysis of a model lineage links species diversification with the *in situ* evolution of habitat preferences.

McPeek, M. A., and J. M. Brown. 2000. Building a regional species pool: Diversification of the *Enallagma* damselflies in eastern North America. *Ecology* 81.4: 904–920.

Diversification in two clades of North American *Enallagma* damselflies appears to be driven less by ecological niche-filling than by sexual selection and reproductive isolation. Later work shows that species interactions in this genus tend to be neutral and dominated by ecological drift.

Tanentzap, A. J., A. J. Brandt, R. B. Smissen, P. B. Heenan, T. Fukami, and W. G. Lee. 2015. When do plant radiations influence community assembly? The importance of historical contingency in the race for niche space. *New Phytologist* 207.2: 468–479.

The importance of evolutionary priority effects are demonstrated in the community assembly of New Zealand vascular plant clades. Integrating phylogenies and paleoclimatic data, the authors find that genera that colonized earlier encountered more available niche space, which allowed them to diversify more and become more dominant in present-day flora. These radiations dampened the diversification of later-arriving genera.

Verboom, G. A., H. P. Linder, F. Forest, V. Hoffmann, N. G. Bergh, and R. M. Cowling. 2014. Cenozoic assembly of the Greater Cape flora. In *Fynbos: Ecology, evolution and conservation of a megadiverse region*. Edited by N. Allsopp, J. F. Colville, and G. A. Verboom, 93–118. Oxford: Oxford Univ. Press.

The origin of the hyperdiverse Greater Cape flora are explained as a consequence of both repeated dispersal and sorting from Australia and elsewhere in Africa and, for many clades, dramatic *in situ* diversification.

Sorting

Ecological sorting processes are often associated with niche conservatism and, hence, phylogenetic clustering, and they are considered one of the primary factors driving community assembly. Sorting processes are often discussed in terms of ecological filtering, whereby the only species that persist in a habitat are ones with attributes that allow them to tolerate the environment. Sorting processes are important regardless of whether functional attributes that influence the niche are conserved or convergent but do not include dispersal processes that influence whether species arrive at a local site. Conservatism, however, is widely observed, as evidenced by the phenomenon that related species occupy similar environments and sort into similar kinds of habitats or microenvironments even after arriving in new geographic locations or after the emergence of novel environments. Ackerly 2004 highlights the importance of plant species with the sclerophyllous leaf habitat sorting into the novel Mediterranean climate after its emergence. Horner-Devine and Bohannan 2006 notes the ecological sorting in bacterial communities in a series of empirical experiments. Willis, et al. 2008 demonstrates ecological filtering with global change using long-term herbarium records, documenting the loss of lineages that shared vulnerable phenologies. Filtering processes operate in urban areas in central Europe (Knapp, et al. 2008) as well as in the Amazonian rain forest (Kraft and Ackerly 2010), impacting the phylogenetic composition plant communities in these disparate environments.

Ackerly, D. D. 2004. Adaptation, niche conservatism, and convergence: Comparative studies of leaf evolution in the California chaparral. *American Naturalist* 163.5: 654–671.

Species that currently occupy the Mediterranean climate region in California evolved their leaf traits before the biome emerged in Earth history. Chaparral communities thus assembled by species sorting into a novel environment to which they were well suited.

Horner-Devine, M. C., and B. J. M. Bohannan. 2006. Phylogenetic clustering and overdispersion in bacterial communities. *Ecology* 87.sp7: S100–S108.

While it is frequently asserted that bacteria are "everywhere," the paper clarifies that this is not the case; the study demonstrates ecological sorting through the use of eco-phylogenetic tools.

Knapp, S., O. Schweiger, I. Kühn, and S. Klotz. 2008. Challenging urban species diversity: Contrasting phylogenetic patterns across plant functional groups in Germany. *Ecology Letters* 11.10: 1054–1064.

Urban areas harbor unusually high levels of species diversity, but this diversity is sorted down to a restricted pool of functional and phylogenetic diversity as a consequence of the urban environment.

Kraft, N. J. B, and D. D. Ackerly. 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological Monographs* 80.3: 401–422.

The study comprehensively investigates ecological sorting within a section of Amazonian forest.

Willis, C. G., B. Ruhfel, R. B. Primack, A. J. Miller-Rushing, and C. C. David. 2008. Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences of the United States of America* 105:17029–17033

Phylogenetically conserved phenological traits explain why, over time, certain plant lineages are lost from or maintained in woodland communities as climate has warmed and season length expanded.

Biogeographic Origins and Evolution of Components of Communities

The climate and environment in which organisms evolve shapes the functional attributes of lineages and descendent species through niche conservatism. Origins thus leave long-term legacies for habitat sorting, colonization of new geographic regions and environments, and how species partition microhabitats or temporal niches. Lechowicz 1984 first distinguishes biogeographic origins as distinct from phylogenetic conservatism. Wiens and Donoghue 2004 explains the consequences of biogeographic origins, in concert with climatic niche conservatism, for explaining the latitudinal gradient in diversity. Edwards and Still 2008 distinguishes niche conservatism from anatomical innovations (C4 anatomy) in grasses as possible confounding explanations for why C4 grasses occur in warmer places and have higher water use efficiency. Sedio, et al. 2013 provides evidence that biogeographic origins influence physiological traits that drive ecological sorting after migration in plant lineages across the Isthmus of Panama. Papers by Ackerly provide theoretical (Ackerly 2003) and empirical (Ackerly 2009) consideration of where past biogeographic processes can influence present-day community diversity and composition. Wiens 2012 is a broader plea for the relevance of historical biogeography in understanding patterns of species richness and trait diversity around the world. Cavender-Bares, et al. 2016 reviews the evidence for evolutionary legacy effects of biogeographic origins on communities and ecosystems, distinguishing these kinds of legacy effects from phylogenetic niche conservatism. Thus, biogeographic origins ultimately influence the ecosystem functions and services that impact humans.

Ackerly, D. D. 2003. Community assembly, niche conservatism and adaptive evolution in changing environments. *International Journal of Plant Sciences* 164.S3: S165–S184.

Ackerly conceptually treats the evolutionary and adaptive processes that accompany or facilitate species biome shifts and their importance for community assembly.

Ackerly, D. D. 2009. Evolution, origin and age of lineages in the Californian and Mediterranean floras. *Journal of Biogeography* 36.7: 1221–1233.

California's flora is complex and diverse, and this study examines how climate and species' tolerances of it have shaped diversification within the region.

Cavender-Bares, J., D. D. Ackerly, S. E. Hobbie, and P. A. Townsend. 2016. Evolutionary legacy effects on ecosystems: Biogeographic origins, plant traits, and implications for management in the era of global change. *Annual Review of Ecology, Evolution and Systematics* 47.1: 433–462.

The climatic and environmental conditions in which species evolved have lasting influence (legacy effects) through phylogenetic conservatism of traits that underlie community assembly and drive ecosystem processes. Evolutionary legacy effects include preemptive colonization and radiation into regions that open up after climate change, for example, before other lineages have the opportunity. The ecological patterns we observe today have been influenced by a series of evolutionary legacies.

Edwards, E. J., C. P. Osborne, C. A. Strömberg, S. A. Smith, and C4 Grasses Consortium. 2010. The origins of C4 grasslands: Integrating evolutionary and ecosystem science. *Science* 328.5978: 587–591.

Understanding the evolution of a critical aspect of plants' physiology—in this case C4 photosynthesis—can inform our understanding of how those plants assemble ecologically.

Edwards, E. J., and C. J. Still. 2008. Climate, phylogeny and the ecological distribution of C4 grasses. *Ecology Letters* 11.3: 266–276.

Evolutionary innovations in function (photosynthetic pathway) in response to historical environmental changes drive ecological sorting and community assembly.

Lechowicz, M. J. 1984. Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. *American Naturalist* 124.6: 821–842.

Phenological differences among co-occurring tree species are hypothesized to be linked to biogeographic origins, an explanation related to but distinct from phylogenetic conservatism. This paper is the first to clarify the distinction.

Sedio, B. E., J. R. Paul, C. M. Taylor, and C. W. Dick. 2013. Fine-scale niche structure of Neotropical forests reflects legacy of the Great American Biotic Interchange. *Nature Communications* 4:2317.

Important legacies of biogeographic origin are evident within two plant genera in their present-day hydraulic traits and soil moisture microhabitat. The study demonstrates the importance of ecological sorting and niche conservatism over millions of years.

Wiens, J. J. 2012. Why biogeography matters: Historical biogeography versus phylogeography and community phylogenetics for inferring evolutionary and ecological processes. *Frontiers of Biogeography* 4.3: 128–135.

This well-argued critique of the limitations of common community phylogenetic approaches explains how historical biogeography can complement them.

Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution* 19.12: 639–644.

This seminal paper contributes a niche conservatism hypothesis to explanations of the latitudinal gradient in diversity, perhaps the most widely documented and explained biological pattern on Earth. Given that that tropical biome is much older than the temperate biome, more species evolved in the tropics and then migrated into the temperate zone, which required a climatic niche shift. The authors argue that niche conservatism linked to biogeographic origins helps explain why there are fewer species in the temperate zone.

Is There Density Dependent Diversification?

It remains unclear whether there is a global “carrying capacity” to the total number of species on Earth. Evolutionary biologists have debated whether density-dependence in species’ diversification exists, and, if so, whether it would drive such a carrying capacity. Sepkoski 1981 is one of the first articles to address this issue in marine fauna. More recently, papers such as Phillimore and Price 2008 have revived the question. The debate in this field has been fierce; Wiens 2011 is a fantastic (if opinionated) entry point into the literature. The controversy is well summarized by two articles published following a debate at an American Society of Naturalists meeting: Rabosky and Hurlbert 2015 argues that there are ecological limits to continental-scale species diversity set by total resource availability, while Harmon and Harrison 2015 argues against the proposition. Ecological studies can do much to inform such studies, as the mechanisms by which density-dependence is assumed to operate are often implicitly ecological and often revolve around the evolution of communities. For example, Kozak and Wiens 2010 bears upon the question of how interactions among co-occurring clades affect the limits of diversification. McPeek 2008 provides a conceptual and empirical overview of the patterns as they relate to patterns of differentiation during speciation, and Pearse, et al. 2013 asks whether the structure of present-day communities can be linked to deep-time diversification of species.

Harmon, L. J., and S. Harrison. 2015. Species diversity is dynamic and unbounded at local and continental scales. *American Naturalist* 185.5: 584–593.

Presented at a meeting of the American Society of Naturalists, this study is to be read with Rabosky and Hurlbert 2015.

Kozak, K. H., and J. J. Wiens. 2010. Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters* 13.11: 1378–1389.

High diversification rates in the tropics are explained as a consequence of fast climatic niche evolution in places with stable climate. The study provides evidence for ecological limits on diversification, but these limits are dependent on overlap among coexisting clades, not clade area.

McPeek, M. A. 2008. The ecological dynamics of clade diversification and community assembly. *American Naturalist* 172.6: E270–E284.

McPeek describes a continuum of ways in which community interactions and ecological diversification can affect the dynamics of lineage accumulation over time. In clades where most speciation involves ecological differentiation, lineage accumulation tends to decelerate; in clades where speciation involves little ecological differentiation, lineage accumulation may even accelerate over time.

Pearse, W. D., F. A. Jones, and A. Purvis. 2013. Barro Colorado Island’s phylogenetic assemblage structure across fine spatial scales and among clades of different ages. *Ecology* 94.12: 2861–2872.

If density-dependent dynamics have an ecological basis, they should leave a signature in the present-day community structure of species. This paper finds evidence for such a signature: younger clades are more likely to co-occur, implying greater niche differentiation.

Phillimore, A. B., and T. D. Price. 2008. Density-dependent cladogenesis in birds. *PLoS Biology* 6.3: e71.

This classic paper provides early evidence for diversity-dependent diversification in bird evolution.

Rabosky, D. L., and A. H. Hurlbert. 2015. Species richness at continental scales is dominated by ecological limits. *American Naturalist* 185.5: 572–583.

Presented at a meeting of the American Society of Naturalists, this paper together with Harmon and Harrison 2015 discuss recent developments in this exciting debate on diversification and ecological limits to species richness. Both should be read, as they are companion pieces.

Sepkoski, J. J. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7.1: 36–53.

Changes in diversity in the marine fossil record are described as a series of logistic-like patterns of diversification, with multiple perturbations, in this early analysis.

Wiens, J. J. 2011. The causes of species richness patterns across space, time, and clades and the role of "ecological limits." *Quarterly Review of Biology* 86.2: 75–96.

This comprehensive review offers an opinionated critique of the role of ecological limits in determining the total number of species on Earth.

Community Genetics

First coined by Janis Antonovics in his seminal book chapter (Antonovics 1992), "community genetics" refers to the microevolutionary consequences of species interactions. While many of the papers cited in this article focus on the ecological assembly and evolution of *species*, they ignore variation within species. The field of community genetics addresses such variation and was the focus of a special feature in *Ecology* led by Anurag Agrawal in 2003. Neuhauser, et al. 2003; Whitham, et al. 2003; and Cavender-Bares and Wilczek 2003 provide overviews of various aspects of community genetics, its ecosystem-scale consequences, and its potential integration with macroevolution. Hersch-Green, et al. 2011 concludes another special issue on community genetics and traces out a path forward for the field, while Wade 2007 is a review focused on the genetics of close interspecific interactions. Schweitzer, et al. 2008 applies the community genetics perspective to plant-microbe symbioses, showing that genetic variation in plant genotypes can affect microbially mediated ecosystem processes. One allied topic of interest is the nascent field of "eco-evolutionary dynamics." This field documents the feedback process through which interactions between species can impose selective pressures on the genetic variation within a population, which, in turn, can further affect species interactions or ecosystem properties (Post and Palkovacs 2009; terHorst, et al. 2018). The literature in these fields overlaps with other well-investigated topics at the interface of ecology and evolution, such as character displacement. At a more general level, McPeek 2017 attempts a unification of community ecology and the quantitative genetics of trait evolution to try to understand how species coexist. Ultimately, the separation of the macro- and microevolution of communities reflects a broader separation between macro-evolutionary models and population-genetic models. It is likely that, in the future, this separation will cease to exist as the role of species interactions, and their microevolutionary consequences, in diversification comes to be better understood.

Antonovics, J. 1992. Towards community genetics. In *Ecology and evolution of plant resistance to herbivores and pathogens: Ecology, evolution, and genetics*. Edited by R. S. Fritz and E. L. Simms, 426–449. Chicago: Univ. of Chicago Press.

In this seminal work, Antonovics lays out the foundation of community genetics as the study of the genetics of species interactions. The author outlines both a reductionist and a holistic approach, the former concerned with consequences of genetic variation for dynamics of interacting populations and the latter concerned with the broader relationships between genetic diversity and community structure.

Cavender-Bares, J., and A. Wilczek. 2003. Integrating micro- and macroevolutionary processes in community ecology. *Ecology* 84.3: 592–597.

An integration of microevolutionary and phylogenetic approaches to understanding the evolutionary dynamics important for community assembly is proposed.

Hersch-Green, E. I., N. E. Turley, and M. T. J. Johnson. 2011. Community genetics: What have we accomplished and where should we be going? In *Special issue: Community genetics: At the crossroads of ecology and evolutionary genetics*. Edited by J. K. Rowntree, D. M. Shuker, and R. F. Preziosi. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366.1569: 1453–1460.

This article is the conclusion of a special issue on community genetics, suggesting key topics and experiments to close gaps in our understanding of the field.

McPeek, M. A. 2017. *Evolutionary community ecology*. Princeton, NJ: Princeton Univ. Press.

This monograph outlines an innovative synthesis of theory in community ecology and quantitative genetics with implications for the causes of ecological differentiation, coexistence, and many other topics.

Neuhauser, C., D. Andow, G. F. Heimpel, and S. Wagenius. 2003. Community genetics: Expanding the synthesis of ecology and genetics. *Ecology* 84.3: 545–558.

The role of community genetics in interpreting responses to anthropogenic changes is discussed using three case studies.

Post, D., and E. Palkovacs. 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: Interactions between the ecological theatre and the evolutionary play. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 364.1523: 1629–1640.

Five empirical case studies of feedbacks between microevolutionary adaptation and ecosystem processes are reviewed. In each system, species interactions impose a selective regime on one or more of the interacting species, which alters the distribution of traits through which those species modify their habitat through niche construction. The ecological consequences of alterations in niche construction then affect the selective regime further.

Schweitzer, J. A., J. K. Bailey, D. G. Fischer, et al. 2008. Plant-soil microorganism interactions: Heritable relationship between plant genotype and associated soil microorganisms. *Ecology* 89.3: 773–781.

This study examines plant-microbial associations in the context of community genetics. Genotypes of *Populus* are associated with variation in microbial biomass and composition, with the implication that these species interactions could, in turn, alter ecosystem-level processes.

terHorst, C. P., P. C. Zee, K. D. Heath, et al. 2018. Evolution in a community context: Trait responses to multiple species interactions. *American Naturalist* 191.3: 368–380.

The paper provides a review of stylized facts from the literature about how evolution operates in the context of species interactions.

Wade, M. J. 2007. The co-evolutionary genetics of ecological communities. *Nature Reviews Genetics* 8.3: 185–195.

This influential review focuses on the genetics and evolution of species' interactions.

Whitham, T. G., W. P. Young, G. D. Martinsen, et al. 2003. Community and ecosystem genetics: A consequence of the extended phenotype. *Ecology* 84.3: 559–573.

Microevolutionary processes involved in plant-insect interactions are linked to ecosystem processes.

Plant-Insect Interactions

Communities are almost always spatially, temporally, and taxonomically delimited, but there is no reason for them to be delimited to a single taxonomic group. Close species interactions often show phylogenetic host specificity (Weiblen, et al. 2006; Pearse and Hipp 2009), which may link the phylogenetic structure of two or more interacting taxonomic groups. Several studies have measured the evolution of associations between species and how they affect community assembly in both groups. The kind of association perhaps subject to the most research is plant-insect interactions, including pollination and herbivory. This section includes some key entry points into the literature of the evolution of herbivory and various mutualisms, an exciting but currently underexplored aspect of community evolution. These span both statistical advances (Ives and Godfray 2006, Rafferty and Ives 2013), results from manipulative experiments (Lind, et al. 2015), and results from long-term experiments and observational studies (Weiblen, et al. 2006; Becerra 2007; Fine, et al. 2004; Fine, et al. 2006). Agrawal, et al. 2006 includes a wide-ranging review of how the structure of vegetative communities influences the micro- and macroevolution of plant-insect interactions.

Agrawal, A. A., J. A. Lau, and P. A. Hamback. 2006. Community heterogeneity and the evolution of interactions between plants and insect herbivores. *Quarterly Review of Biology* 81.4: 349–376.

This insightful review provides broad coverage of how plant-insect herbivore interactions evolve.

Becerra, J. X. 1997. Insects on plants: Macroevolutionary chemical trends in host use. *Science* 276.5310: 253–256.

The study provides a critical empirical demonstration of the role that plant defense compounds can play in the evolution of insects.

Becerra, J. X. 2007. The impact of herbivore-plant coevolution on plant community structure. *Proceedings of the National Academy of Sciences of the United States of America* 104.18: 7483–7488.

The author notes that conserved chemical defenses can lead to phylogenetically overdispersed communities.

Fine, P. V. A., I. Mesones, and P. D. Coley. 2004. Herbivores promote habitat specialization by trees in Amazonian forests. *Science* 305.5684: 663–665.

This study is one of the few experimental demonstrations of expectations based on the theory that there are evolved trade-offs in growth and defense investment in plants. The paper posits that in tropical Amazonia, herbivores select for specialization of trees on different soil types because they prevent fast-growing, poorly defended species from inhabiting low resource environments.

Fine, P. V. A., Z. J. Miller, I. Mesones, et al. 2006. The growth-defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology* 87.sp7: S150–S162.

The study provides a validation and expansion of the results of Fine, et al. 2004. The authors measured defense-related traits to validate the growth-defense trade-off.

Ives, A. R., and H. C. J. Godfray. 2006. Phylogenetic analysis of trophic associations. *American Naturalist* 168.1: E1–E14.

The study presents one of the first statistical analyses of the macro-evolution of trophic interactions.

Lind, E. M., J. B. Vincent, G. D. Weiblen, J. Cavender-Bares, and F. T. Borer. 2015. Trophic phylogenetics: Evolutionary influences on body size, feeding, and species associations in grassland arthropods. *Ecology* 96.4: 998–1009.

This is one of the few studies examining the phylogenetic relationships of both insect assemblages and their plant hosts in a manipulated diversity experiment (Cedar Creek long term BioDIV experiment). Results shows conservatism in insect host preferences; thus, phylogenetic diversity of plant communities predicts the phylogenetic diversity of herbivore communities even after accounting for plant species richness.

Pearse, I. S., and A. L. Hipp. 2009. Phylogenetic and trait similarity to a native species predict herbivory on non-native oaks. *Proceedings of the National Academy of Sciences of the United States of America* 106.43: 18097–18102.

If phylogenetic distance can predict herbivory, this has implications for Janzen-Connell-type effects and the diversification of species. This excellent paper gives a thorough example of how such effects might operate.

Rafferty, N. E., and A. R. Ives. 2013. Phylogenetic trait-based analyses of ecological networks. *Ecology* 94.10: 2321–2333.

Phylogenetic generalized linear mixed models are applied to interaction network data, providing a coherent framework for measuring the macroevolution of species' traits and their interactions.

Weiblen, G. D., C. O. Webb, V. Novotay, Y. Basset, and S. E. Miller. 2006. Phylogenetic dispersion of host use in a tropical insect herbivore community. *Ecology* 87.sp7: S62–S75.

The authors quantified the host breadth of insect herbivores in a New Guinea rain forest using feeding trials. The study shows that similarity of herbivore faunal communities declines with phylogenetic distance between plant hosts, and a large proportion of insects show phylogenetic clustering in their plant associations, marking them as clade specialists.

Evolution in the Context of Metacommunities

A strong criticism of theories and approaches to understanding of much of the community assembly literature was the lack of explicit incorporation of spatial scale or consideration of dispersal processes. To some extent, these issues were addressed by the focus on regional processes. However, the concept of metacommunities—local communities linked by limited dispersal—emerged as a means to explicitly incorporate the role of space and dispersal in terms of both ecological and evolutionary processes. Robert Holt and others had long emphasized the importance of source-sink dispersal processes and the consequences for evolution in the context of populations and communities (Holt 1996). In 2004, Mathew Leibold and colleagues developed a metacommunity framework for considering the movement of species at large spatial scales and the consequences for local communities, arguing that local coexistence depends on the outcome of local species interactions and regional migration. The authors of Leibold, et al. 2010 use the metacommunity framework to address long-standing debates about the relative importance of local and historical processes in community phylogenetics. Mark Velland subsequently expanded on the framework to develop a new conceptualization of community ecology built around four higher-level forces: selection, drift, dispersal, and speciation (Vellend 2016). Urban and Skelly 2006 seeks to apply the spatial context of the metacommunity framework to understanding local adaptation and other consequences of genetic variation. The statistical advancement of approaches integrating evolution and metacommunity theory has not always kept pace with conceptual development. The authors of Pillar and Duarte 2010 (advanced in Peres-Neto, et al. 2012) generated a statistical framework to test these conceptual advances. Rosindell, et al. 2015 aims to use individual-based simulations to unify metacommunity ecology and macroevolution.

Holt, R. D. 1996. Adaptive evolution in source-sink environments: Direct and indirect effects of density-dependence on niche evolution. *Oikos* 75.2: 182–192.

Holt couples models of evolutionary and population dynamics to explore how density-dependence and dispersal behavior affect niche evolution.

Leibold, M. A., E. P. Economo, and P. Peres-Neto. 2010. Metacommunity phylogenetics: Separating the roles of environmental filters and historical biogeography. *Ecology Letters* 13.10: 1290–1299.

A comparative study of the phylogenetic metacommunity structure of two zooplankton taxa is presented. Distributions in one taxon are heavily constrained by historical biogeography, while the abiotic environment is more important for the other, more vagile taxon.

Peres-Neto, P. R., M. A. Leibold, and S. Leibold. 2012. Assessing the effects of spatial contingency and environmental filtering on metacommunity phylogenetics. *Ecology* 93.sp8: S14–S30.

The paper provides an advanced metacommunity phylogenetic framework accounting for processes and patterns operating across multiple spatial and temporal scales.

Pillar, V. D., and L. S. Duarte. 2010. A framework for metacommunity analysis of phylogenetic structure. *Ecology Letters* 13.5: 587–596.

The is the first empirical and statistical study to incorporate metacommunities into a phylogenetic context.

Rosindell, J., L. J. Harmon, and R. S. Etienne. 2015. Unifying ecology and macroevolution with individual‐based theory. *Ecology Letters* 18.5: 472–482.

An individual-based metacommunity model with weak selection and protracted (non-point) speciation is used to predict macroevolutionary and ecological patterns as emergent from community interactions.

Urban, M. C., and D. K. Skelly. 2006. Evolving metacommunities: Toward an evolutionary perspective on metacommunities. *Ecology* 87.7: 1616–1626.

Evolution shapes local species coexistence and exclusion within a multiscale and multispecies context.

Vellend, M. 2016. *The theory of ecological communities*. Princeton, NJ: Princeton Univ. Press.

In this book, Vellend argues that low-level processes that cause variation in community composition can be summarized into four high-level processes—selection, drift, dispersal, and speciation—defined by analogy to population genetics. Eco-evolutionary adaptation within communities can alter the regime of ecological selection within communities, while the macroevolutionary structure of present-day communities is a consequence of all four processes.

Communities, Phylogenetics, and Ecosystem Function

To what extent does phylogenetic diversity drive ecosystem processes, including productivity and stability? This debate has emerged from the biodiversity-ecosystem function (BEF) literature. Since Cadotte, et al. 2008 found that phylogenetic diversity was a better predictor of the productivity of experimental plant communities than species richness, debates have been ongoing about the role of phylogenetic diversity in mediating ecosystem functions. Much of this research has taken place in experimental grassland communities, most notably at Cedar Creek Ecosystem Science Reserve in Minnesota, and it has been focused on the stable production of plant biomass and associated ecosystem functions. Exceptions to this tendency include Thompson, et al. 2015 and Gravel, et al. 2012. One locus of the debate is whether (or when) phylogenetic diversity constitutes a better predictor of ecosystem function than species richness or functional diversity. Phylogenetic diversity is often interpreted as a proxy for functional diversity, and it may be superior if traits that drive ecosystem function are hard to measure well. Cadotte, et al. 2008; Cadotte, et al. 2009; and Cadotte, et al. 2012 find that at Cedar Creek, phylogenetic diversity is a strong predictor of productivity and stability, though these findings have been contradicted by a later meta-analysis, which found that phylogenetic diversity yielded no improvement over species richness alone (Venail, et al. 2015). A promising direction of research is to evaluate the context-dependence of these relationships. Gravel, et al. 2012 finds that imposing a strong selective regime on bacterial communities weakens the effect of lineage diversity on productivity. Davies, et al. 2016 urges a consideration of whether phylogenetic effects on overyielding are driven by broad-scale functional complementarity or by a few key innovations as a path toward a more nuanced understanding of why phylogenetic diversity matters.

Cadotte, M. W., B. J. Cardenale, and T. H. Oakley. 2008. Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences of the United States of America* 105.44: 17012–17017.

This paper is the first of several using the Cedar Creek long-term plant diversity experiment to examine linkages between phylogenetic diversity and ecosystem function. The analysis reveals that phylogenetic diversity is a stronger predictor of productivity than species richness.

Cadotte, M. W., J. Cavender-Bares, D. Tilman, and T. H. Oakley. 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS One* 4.5: e5695.

This paper provides an excellent introduction to the use of phylogenetic and functional trait information in analyses of biodiversity ecosystem-function (BEF) experiments. The authors find that the best model for explaining productivity at Cedar Creek involves phylogenetic diversity as well as a minimal set of functional traits (seed weight, presence of nitrogen fixers), and that phylogenetic diversity is often a better predictor than small sets of traits.

Cadotte, M. W., R. Dinnage, and D. Tilman. 2012. Phylogenetic diversity promotes ecosystem stability. *Ecology* 93.sp8: S223–S233.

This study builds on the incorporation of phylogenetic information into BEF experiments and shows that phylogenetic diversity is strongly linked to stability, again using the Cedar Creek long-term plant diversity experiment.

Davies, T. J., M. C. Urban, B. Rayfield, and P. R. Peres-Neto. 2016. Deconstructing the relationships between phylogenetic diversity and ecology: A case study on ecosystem functioning. *Ecology* 97.9: 2212–2222.

The authors revisit the Cedar Creek long-term plant biodiversity experiment and find no association between evolutionary distinctiveness and ecosystem functioning; rather, they identify phylogenetic elements (nitrogen fixers from the Fabaceae) with species of high functional contribution.

Gravel, D., T. Bell, C. Barbera, M. Combe, T. Pommier, and N. Mouquet. 2012. Phylogenetic constraints on ecosystem functioning. *Nature Communications* 3:1117.

Experimental tests manipulating phylogenetic diversity of ancestral and newly evolved lineages of marine bacteria in mesocosms demonstrate that phylogenetic diversity can influence ecosystem functions (productivity), but it depends on the evolutionary history of lineages. Only the phylogenetic diversity of ancestral lineages show strong relationships with productivity, not the evolved ones.

Thompson, P. L., T. J. Davies, and A. Gonzalez. 2015. Ecosystem functions across trophic levels are linked to functional and phylogenetic diversity. *PLoS One* 10.2: e0117595.

Experimental manipulations of zooplankton functional and phylogenetic diversity explain the functioning of twenty-three natural pond communities; strong correlations emerge between zooplankton diversity and ecosystem function, while local environmental conditions are less important. Diversity-ecosystem function relationships were more pronounced for measures of functional and phylogenetic diversity than for species richness.

Venail, P., K. Gross, T. H. Oakley, et al. 2015. Species richness, but not phylogenetic diversity, influences community biomass production and temporal stability in a re-examination of 16 grassland biodiversity studies. *Functional Ecology* 29.5: 615–626.

This meta-analysis shows that phylogenetic diversity has no positive effect on grassland productivity and stability after controlling for species richness. Cadotte contests the results in a response and Venail offers a rebuttal.

Integrating Evolutionary Thinking in Conservation and Restoration

Starting with Faith's early work bringing a phylogenetic perspective to conservation (Faith 1992), evolutionary perspectives on community assembly and the role of phylogenetic criteria in restoration and in setting conservation priorities have now become mainstream. Cavender-Bares and Cavender 2011 provides a framework for considering community assembly processes and phylogenetic community structure in restoration. Hendry, et al. 2010 explicitly brings evolutionary biology into the policy realm. Díaz, et al. 2013 highlights the importance of incorporating phylogenetic perspectives in risk assessment and conservation by considering the evolution and coupling of traits that respond to change and those that influence ecosystem function. Hipp, et al. 2015 provides a brief history of incorporating evolutionary perspectives into conservation and restoration, pondering the reasons for why phylogenetic information is not more widely used, while Barak, et al. 2016 takes a multitemporal approach considering evolutionary processes at multiple timescales and their possible importance in informing restoration. A special issue of *Philosophical Transactions of the Royal Society B* (Forest, et al. 2015) treats these issues from multiple perspectives, including extinction risk (Faith 2015), which echo themes emphasized in Isaac, et al. 2007. Finally, Larkin, et al. 2016 provides a framework for considering multiple factors that may trade off with evolutionary distinctiveness in setting priorities for conservation.

Barak, R., A. L. Hipp, J. Cavender-Bares, et al. 2016. Taking the long view: Integrating recorded, archeological, paleoecological, and evolutionary data into ecological restoration. *International Journal of Plant Sciences* 177.1: 90–102.

Barak, and colleagues review how diverse forms of history can be used to inform restoration actions and inform our definition of the historical baseline.

Cavender-Bares, J., and N. Cavender. 2011. Phylogenetic structure of plant communities provides guidelines for restoration. In *Restoration ecology*. Edited by S. Greipsson, 119–129. Sudbury, MA: Jones & Bartlett Learning.

The chapter (in a book edited by Greipsson on incorporating ecological principles into restoration) lays a foundation for considering phylogenetic community structure, phylogenetic composition, and metrics of phylogenetic diversity in restoration using empirical examples from prairie restoration experiments, among others.

Díaz, S., A. Purvis, J. H. C. Cornelissan, et al. 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* 3.9: 2958–2975.

This study reviews, with empirical case studies, how the evolution of species' *effect* and *response* traits can be used to generate a risk assessment for ecosystems under threat. Because response functions measure species tolerances to environmental change, and effect functions measure their consequences for ecosystem services, the extent to which these functions are correlated and evolve in tandem can influence assessments of risk to ecosystems and their services.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* 61.1: 1–10.

This landmark paper introduced the concept of phylogenetic diversity as a sum of branch lengths on a phylogeny.

Faith, D. P. 2015. Phylogenetic diversity, functional trait diversity and extinction: Avoiding tipping points and worst-case losses. In *Special issue: Phylogeny, extinction and conservation*. Edited by F. Forest, K. A. Crandall, M. W. Chase, and D. P. Faith. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370.1662: 20140011.

Part of a special issue, the study integrates phylogenetic perspectives on diversity with non-linearities and tipping points in the context of conservation.

Forest, F., K. A. Crandall, M. W. Chase, and D. P. Faith. 2015. Phylogeny, extinction and conservation: Embracing uncertainties in a time of urgency. In *Special issue: Phylogeny, extinction and conservation*. Edited by F. Forest, K. A. Crandall, M. W. Chase, and D. P. Faith. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370.1662: 20140002.

The paper provides an introduction to a series of articles describing recent advances in conservation prioritization based on phylogenetic diversity.

Hendry, A. P., L. G. Lohmann, E. Conti, et al. 2010. Evolutionary biology in biodiversity science, conservation, and policy: A call to action. *Evolution* 64.5: 1517–1528.

This study provides an overview of how evolutionary biology can inform the practice of conservation biology.

Hipp, A. L., D. J. Larkin, R. J. Barak, and E. Weiher. 2015. Phylogeny in the service of ecological restoration. *American Journal of Botany* 102.5: 647–648.

The article reviews how community phylogenetic approaches can inform ecosystem restoration.

Isaac, N. J., S. T. Turvey, B. Collen, C. Waterman, and J. E. M. Baillie. 2007. Mammals on the EDGE: Conservation priorities based on threat and phylogeny. *PLoS One* 2:e296.

This paper launched the Zoological Society of London’s “EDGE” program, the only global-scale phylogenetically informed conservation prioritization initiative in existence at the time of writing.

Larkin, D. J., S. K. Jacobi, A. L. Hipp, and A. T. Kramer. 2016. Keeping all the PIECES: Phylogenetically informed ex situ conservation of endangered species. *PLoS One* 11.6: e0156973.

In prioritizing species for *ex situ* collection, phylogenetic criteria, such as evolutionary distinctiveness, need to be weighed against other competing objectives, such as extinction threat. The PIECES index (Phylogenetically Informed *Ex situ* Conservation of Endangered Species) integrates phylogenetic considerations into a flexible framework for prioritizing species using multicriteria decision analysis.

Methods

The development of methods for integrating phylogenetics, comparative methods, and communities was critical to advances in understanding the importance of evolutionary forces in communities. We start with Felsenstein’s method for phylogenetically independent contrasts (Felsenstein 1985) and remind the reader of the importance of Harvey and Pagel’s comparative methods book (see Harvey and Pagel 1991, cited under Early Phylogenetic Perspectives on Community Assembly). We then highlight metrics for phylogenetic community structure, whose development began with Webb 2000 (cited under Phylogenetic Community Structure). The number of metrics that measure community phylogenetic structure is almost equaled by the number of reviews and syntheses of those metrics. Pearse, et al. 2014 provides a short introduction to metrics, models, and simulation of community phylogenetic structure that synthesizes all metrics into one of four categories. Another more detailed review focusing on metrics (Tucker, et al. 2016) sets the bar in terms of both simulation and estimation. Much early work focused on the mean phylogenetic distance separating species or individuals within a community; Helmus, et al. 2007 (see also Kembel, et al. 2010, cited under Software), and Cadotte, et al. 2010 define perhaps all of the commonly used metric families and are worth reading for insight into the limitations of the entire suite of approaches. Hardy and Senterre 2007 develops a family of community phylogenetic metrics inspired by population genetics. Miller, et al. 2017 compares the performance of many of these metrics and various null models in accurately detecting community assembly processes. Going beyond metrics, the phylogenetic generalized linear mixed model approach found in Ives and Helmus 2011 is a promising avenue of future work, given its generality. Cadotte and Davies 2016 provides a useful overview of methods in community phylogenetics with code examples. The phylogeny of a study is as important as its ecological data, and so those unfamiliar with building phylogenies should examine Webb, et al. 2008 or Pearse, et al. 2015 (both cited under Software), which are intended to aid non-specialists in building, finding, and/or manipulating phylogenies. Citations are separated into Methods papers or books and Software packages.

Cadotte, M. W., T. J. Davies, J. Regetz, J. W. Kembel, E. Cleland, and T. H. Oakley. 2010. Phylogenetic diversity metrics for ecological communities: Integrating species richness, abundance and evolutionary history. *Ecology Letters* 13.1: 96–105.

A highly influential series of metrics are presented. The paper is notable for its focus on how the abundance of individuals are distributed throughout a phylogeny.

Cadotte, M. W., and T. J. Davies. 2016. *Phylogenies in ecology*. Princeton, NJ: Princeton Univ. Press.

This book provides an approachable introduction to (and reference for) the use of phylogenies in ecology, relevant concepts, and their practical application in R language.

Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125.1: 1–15.

This pivotal paper explains the problem of the phylogenetic non-independence of species for interpreting ecological correlations and presents the method of phylogenetically independent contrasts to examine the direction and magnitude of correlated changes.

Hardy, O. J., and B. Senterre. 2007. Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. *Journal of Ecology* 95.3: 493–506.

The authors present methods for additively partitioning phylogenetic diversity across sites and regions using approaches inspired by the population genetics literature.

Helmus, M. R., T. S. Bland, C. K. Williams, and A. R. Ives. 2007. Phylogenetic measures of biodiversity. *American Naturalist* 169.3: E68–E83.

The paper introduces the influential “phylogenetic species variability” family of phylo-diversity metrics.

Ives, A. R., and M. R. Helmus. 2011. Generalized linear mixed models for phylogenetic analyses of community structure. *Ecological Monographs* 81.3: 511–525.

The first, if not only, comprehensive statistical framework for the measurement of phylogenetic structure, which can place species’ trait-environment relationships within the context of macro-evolution.

Miller, E. T., D. R. Farine, and C. H. Trisos. 2017. Phylogenetic community structure metrics and null models: A review with new methods and software. *Ecography* 40.4: 461–477.

The review provides a detailed comparison of community phylogenetic structure metrics and null models to assess low error rates in detecting processes.

Pearse, W. D., A. Purvis, J. Cavendish-Bares, and M. R. Helmus. 2014. Metrics and models of community phylogenetics. In *Modern phylogenetic comparative methods and their application in evolutionary biology: Concepts and practice*. Edited by L. Zsolt Garamszegi, 451–464. Berlin: Springer-Verlag.

The chapter reviews metrics and models in the assessment of community phylogenetic structure, splitting phylogenetic metrics on the basis of the underlying data they require for calculation.

Tucker, C. M., M. W. Cadotte, S. B. Carvalho, et al. 2016. A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews* 92.2: 698–715.

The authors give a comprehensive review of metrics for the measurement of community phylogenetic structure, identifying three major groupings of metrics on the basis of their performance in simulations and hypotheses that can be answered using them.

Software

The R language has more developed tools for community phylogenetics than any other language. Many R packages for phylogenetics are based on APE, which provides basic tools for handling and manipulating phylogenies (Paradis, et al. 2004). APE is a dependency for packages that implements community phylogenetic metrics, like Phylocom (Webb, et al. 2008), Picante (Kembel, et al. 2010), and *pez* (Pearse, et al. 2015). Many other R packages have been developed for implementing phylogenetic comparative methods useful for community phylogenetics (Pennell, et al. 2014; Revell 2012). Phylocom also implements Phylomatic, one of several tools to automatically generate phylogenies for a set of input taxa, with a source database of all seed plants.

Kembel, S. W., P. O. Cowan, M. R. Helmus, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26.11: 1463–1464.

Arguably the first community phylogenetic R package, containing methods that have driven the field.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* 20.2: 289–290.

The foundation for all R packages identified in this section.

Pearse, W. D., J. Cavender-Bares, M. W. Cadotte, and M. R. Helmus. 2015. *pez*: Phylogenetics for the environmental sciences. *Bioinformatics* 31.17: 2888–2890.

An R package capable of reproducing the results of Pearse, et al. 2014 and Tucker, et al. 2016 (both cited under Methods) and implementing the PGLMM approach of Ives and Helmus 2011 (cited under Methods).

Pennell, M. W., J. M. Eastman, G. J. Slater, and L. Harmon. 2014. Geiger v2. 0: An expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* 30.15: 2216–2218.

More focused on phylogenetic comparative methods, this package contains fast implementations of most common (and many uncommon) models of trait evolution.

Revell, L. J. 2012. Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3.2: 217–223.

phytools has become one of the de facto standard phylogenetic packages. A must-use tool.

Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: Software for the analysis of phylogenetic community structure and character evolution. *Bioinformatics* 24.18: 2098–2100.

A comprehensive toolkit for the construction of assemblage phylogenies and the analysis of their structures. Implements many of the methods and approaches outlined in Webb, et al. 2002 (cited under Phylogenetic Community Structure).

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