

## Review

# Evolution in a Community Context: On Integrating Ecological Interactions and Macroevolution

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**Despite a conceptual understanding that evolution and species interactions are inextricably linked, it remains challenging to study ecological and evolutionary dynamics together over long temporal scales. In this review, we argue that, despite inherent challenges associated with reconstructing historical processes, the interplay of ecology and evolution is central to our understanding of macroevolution and community coexistence, and cannot be safely ignored in community and comparative phylogenetic studies. We highlight new research avenues that foster greater consideration of both ecological and evolutionary dynamics as processes that occur along branches of phylogenetic trees. By promoting new ways forward using this perspective, we hope to inspire further integration that creatively co-utilizes phylogenies and ecological data to study eco-evolutionary dynamics over time and space.**

## Introduction

That patterns of diversity are shaped by the joint contributions of both ecology and evolution has been central to our theoretical understanding of biology since Darwin's tangled bank. However, while this connection is well accepted in principle, studying the long-term consequences of the interplay between ecological and evolutionary dynamics remains challenging [1,2]. As such, we still know relatively little about links between ecological dynamics and broad-scale patterns of diversity. At issue is whether our increasing knowledge of short-term eco-evolutionary processes, which typically involve one or two species over a few generations, informs our understanding of patterns across entire communities or clades. For example, short-term studies have demonstrated that rapid trait evolution can influence population dynamics, species interactions, and ecosystem functioning, and such effects can feed back to affect further evolutionary change [3–5]. But, does demonstrating such short-term eco-evolutionary dynamics help us explain the origins of species diversity and macroevolutionary patterns over larger temporal and spatial scales? One possibility is that such dynamics have negligible effects on longer-term patterns of phenotypic change and diversification, and leave no imprint on the information held by phylogenetic trees (e.g., patterns of trait evolution, speciation, and extinction). An alternative possibility, however, is that such dynamics are central to our interpretation of trait change and species diversity over deep timescales, and thus cannot be excluded when considering mechanistic hypotheses for the origin and maintenance of diversity. In this review, we consider reasons why this latter perspective might be the case, and highlight timely and promising research avenues towards merging ecological and macroevolutionary perspectives. We argue that eco-evolutionary thinking deserves a central role in the study of broad-scale and

## Trends

Ecology and evolution interact over deep time scales, and innovative new research from a variety of fields is expanding our ability to understand these interactions and their effects.

New developments in comparative phylogenetic methods incorporate species interactions in models of character change and lineage diversification, enabling direct tests of hypotheses concerning the impacts of ecological interactions on macroevolution.

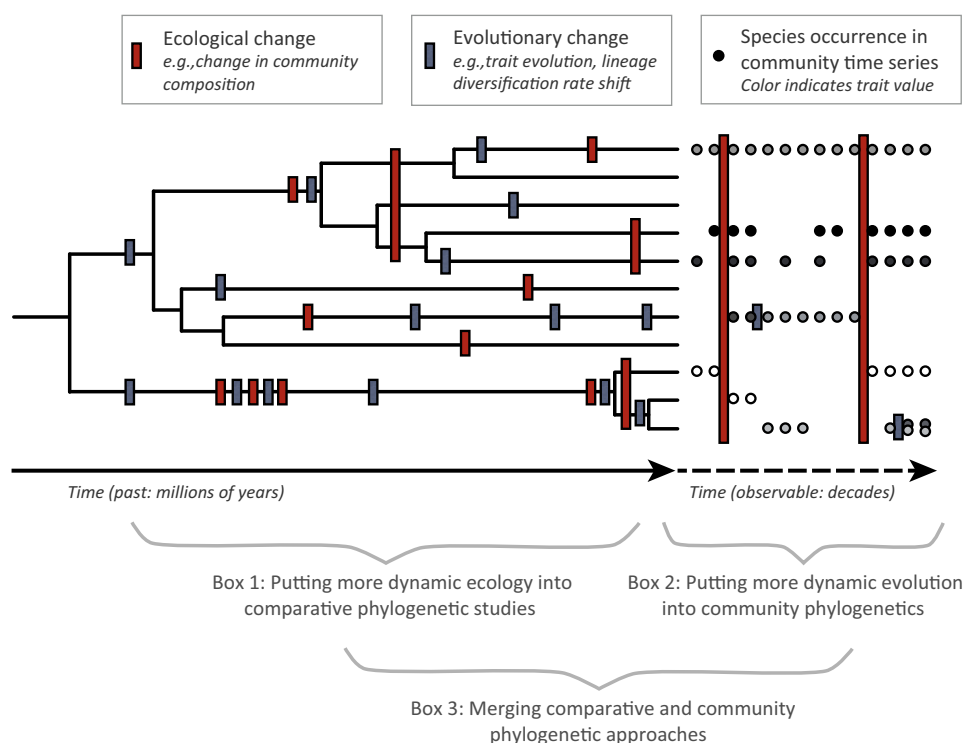
Advances in community phylogenetics improve the study of macroevolutionary constraints on coexistence by using null models that account for the geography of speciation.

Although links between ecology and macroevolutionary patterns are difficult to test using a single framework, the synthesis of multiple research approaches makes it increasingly apparent that reciprocal eco-evolutionary dynamics can influence rates of diversification, phenotypic evolution, and community coexistence patterns.

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#### Trends in Ecology & Evolution

**Figure 1. Ecological and Evolutionary Dynamics through Time: Processes That Occur along Branches of Phylogenetic Trees.** Evolutionary (blue bars) and ecological changes (red bars) occur throughout the history of a lineage as species evolve, shift their distributions, and encounter changing species interactions. These effects may impact resulting phylogenetic tree topology (increasing or decreasing speciation rates), trait evolution, and species' ecology. In Boxes 1–3, we highlight future directions that combine approaches from comparative phylogenetic methods and community ecology to suggest particularly promising avenues for making progress on merging these perspectives. These include the development of macroevolutionary models that incorporate ecological mechanisms (Box 1), the dynamic use of phylogenetic approaches in communities with rapid turnover and the potential for *in situ* evolution (Box 2), and the integration of comparative phylogenetic studies with community data (Box 3).

deep-time patterns of biodiversity, and propose that such patterns can be better understood by studying the interplay between ecological and evolutionary processes as phenomena that occur concomitantly along the branches of phylogenetic trees (Figure 1). By focusing specifically on synergies between comparative and community phylogenetic perspectives, we aim to provide a neontological perspective on these issues that is complementary to paleobiological work, where the impacts of ecological interactions on patterns of diversity in the fossil record are well studied (e.g., [1,6]). Integrating ecological dynamics and macroevolution is a fundamental challenge at the forefront of biodiversity research, and creative new approaches to tackle this problem are emerging that facilitate our study of this exciting frontier.

## Ecological Dynamics Alter Macroevolution

### Ecological Impacts on Phenotypic Evolution

A wide range of short-term, microevolutionary studies have produced abundant evidence that ecological dynamics can impact the rate and direction of phenotypic evolution. For example, species interactions can generate stabilizing or directional selection pressures that can contribute to patterns of evolutionary stasis, divergence, or convergent phenotypic evolution [7–10]. The challenge now lies in relating ecological selection on traits operating over one or a few generations to large-scale patterns of trait diversification involving whole clades over long

time periods [1,11,12]. The debate over whether short-term evolutionary fluctuations generally translate into long-term patterns of phenotypic change has a long history in evolutionary biology [11,13]. In essence, linking short-term studies of ecological selection on traits to patterns of evolution on a phylogeny is an extension of this challenge, but includes the major additional challenge of attempting to extend the study of impacts on community dynamics into the past, frequently with very limited and purely contemporary data available. However, current evidence supports an important role for ecology in shaping broad-scale patterns of trait evolution in several systems. We review these areas below, and the new approaches being developed to tackle this problem.

One classic approach to testing for ecological impacts on trait macroevolution has been to seek out island-like systems where ecological interactions are well-defined due to the discrete nature of communities. In these cases, the contribution of local community interactions to clade-level patterns is more easily inferred, largely because island isolation and replication allow for simultaneous and integrative study of these two processes. For example, in Caribbean anoles and Hawaiian spiders, studying individual island communities reveals the repeated evolution of distinct habitat specialist types, termed ecomorphs, and clade-level trait evolution analyses provide evidence that ecomorphs have evolved repeatedly in isolation of one another (e.g., [14,15]). This evidence suggests that phenotypic diversification within these clades was perceptibly shaped by the presence or absence of other species in the community.

Other researchers have studied community impacts on trait evolution in larger and less-discrete geographies, like continents. One approach uses contemporary range overlap as a proxy for the presence of historical species interactions. Recent studies in birds reveal patterns consistent with competition driving patterns of macroevolutionary divergence, namely that sympatric relatives have greater divergence in ecological traits [16] or in habitat use [17] than non-sympatric relatives. However, the degree of contemporary sympatry among clade members is not necessarily a good indicator of the presence or absence of community interactions over evolutionary history. Pairing experimental work on species interactions with comparative models that incorporate historical biogeography will help inform hypotheses about the effects of species interactions through time [18]. In addition, the development of methods that pair phylogenetic models of ecological trait evolution with information about species co-occurrence [19], or with models of historical range overlap, would aid efforts to link species interactions and patterns of trait evolution (Box 1).

While most paradigmatic studies linking ecological interactions to trait evolution have focused on groups of closely related species (e.g., congeners), interactions between distantly related species also have strong potential to shape patterns of trait macroevolution. For example, in both coevolution and mimicry research, interactions among very distantly related species in the community are hypothesized to be drivers of phenotypic divergence and convergence across phylogenies (e.g., [20]). In paleontological studies, interactions among divergent clades are commonly hypothesized to influence clade diversification (e.g., [21,22]). And, in the species interaction literature, ecological interactions between distantly related members of the same trophic guild have long been hypothesized to shape evolutionary trajectories (e.g., [23]). However, theory concerning how biotic selective pressures shape trait evolution has been slow to integrate into the macroevolutionary arena. For example, biotic adaptive peaks are hypothesized to move more frequently than abiotic adaptive peaks [24], and obligate mutualistic interactions are hypothesized to lead to stabilizing 'trait matching' scenarios more than facultative ones [25], but these types of hypotheses have rarely been investigated at the macroevolutionary scale despite translating into direct predictions for rates of trait diversification.

## Box 1. Including Ecological Dynamics in the Study of Macroevolutionary Patterns

Ecological interactions can shape species' population dynamics, alter natural selection, and impact trait evolution and lineage diversification. However, despite the abundant evidence for these effects, most phylogenetic comparative methods do not incorporate ecological interactions [70], and clade-based comparative studies often ignore community ecological processes and their influence on trait and species evolution [71]. Such deficiencies are partly due to inherent challenges in considering complex ecological dynamics in the context of species evolution on phylogenetic trees. Yet, both evolutionary history and ecological interactions are intrinsically important to understanding the diversity of communities and clades, and approaches that add ecological context to comparative phylogenetic studies of lineage diversification and trait evolution are sorely needed. Here we highlight gaps and suggested approaches that can guide fruitful research in integrating ecology into comparative phylogenetic thinking.

First, work is needed to connect trait evolution models to explicit ecological processes. A battery of phylogenetic comparative methods has grown over the last two decades to fit explicit evolutionary models to trait data on trees, most of which involve some alteration of the basic Brownian motion process. However, the disconnect between clade-level patterns of trait evolution and the local ecological mechanisms influencing evolutionary processes remains substantial. The actual ecological processes producing Brownian motion patterns of trait evolution are largely unidentifiable without explicit data on population size, heritability, and other parameters typically not considered in macroevolutionary comparative analyses [72]. This is largely due to limitations in inference from comparative data alone, which makes it difficult to link large-scale patterns with specific processes without directly considering microevolutionary models and parameters [73]. Additionally, macroevolutionary models explicitly designed to incorporate species interactions and community dynamics are strikingly rare. Two exceptions include a recent model by Nuismer and Harmon [40], which incorporates species interaction parameters into models of continuous trait evolution on phylogenies, and a new method by Drury [19], which accounts for competition and sympatry in trait evolution models. Other models exist in the literature on coevolution (e.g., [26]), but are typically not phylogenetic. Also, in newly developed models traits are generally assumed to have singular impacts on species interactions (e.g., trait similarity leads to increased competition for resources which are assumed to be limiting), but more sophisticated treatments of trait similarity–interaction relationships into models of trait evolution are needed. Future development of methods that connect coevolutionary models with comparative methods will not only directly incorporate species interactions into comparative analyses, but will also supply an explicit historical (phylogenetic) context to studies of coevolution.

Second, more work is needed to develop diversification models that include a mechanistic understanding of how ecological and evolutionary processes interactively influence speciation and extinction. Despite a plethora of concepts that link ecology and diversification, such as ecological opportunity, key innovations, and diversity-dependent diversification, inferring these processes from phylogenies is challenging. For example, the diversity-dependent diversification literature requires that we carefully consider an ecology-dependent view of diversification, where rates at any given timepoint are dependent upon current species diversity in the system. Explicit diversity-dependent models have been shown to provide good fits to diversification patterns in extant taxa, and to provide estimates of extinction more consistent with what is known from the fossil record [74]. However, perceived slowdowns can be the result of artifacts [56], or have alternative explanations [75]. Although some object to the idea that species richness could have clade-level 'limits' [76], other models, such as Cornell's damped increase hypothesis, do not rely on this assumption [77]. It should also be noted that diversity-dependent models frequently have equilibria well below the clade-level carrying capacity [78]. Developing these models is an active field of research, and one that provides promise for linking species diversification patterns to the ecological 'stage' upon which evolution occurs.

An additional issue is the incorporation of ecological mechanisms of speciation themselves into macroevolutionary methods. Previous theoretical models have investigated how different mechanisms thought to influence diversification can affect the shape of phylogenetic trees (e.g., [48,79]), but in such cases the speciation process itself is modeled as an input, rather than an output that emerges based on underlying ecological and evolutionary dynamics [80]. In the few cases where explicit ecological mechanisms of divergence, speciation, and/or species persistence have been considered, the conclusion has been that the ability of phylogenetic information to predict the history of species interactions or community assembly is highly contingent on landscape dynamics and resource distributions [80], as well as on the nature of species interactions [81,82]. Such studies suggest that modeling rates of diversification and ecological change over landscapes, and/or while incorporating specific ecological mechanisms, will prove insightful for understanding how ecological and evolutionary processes affect the phylogenetic structure of clades, communities, and traits. Ultimately, phylogenetic models of lineage diversification will be more realistic if they move towards incorporating those processes that we know to be important, such as genetic and community drift, selection, dispersal, and species interactions.

Three, more work is needed to develop comparative phylogenetic models incorporating multiple interacting clades. Currently, methods for evaluating multiple interacting phylogenies are limited to simple one-to-one trait or topology matching scenarios. However, many multiclade interactions that likely have strong impacts on macroevolutionary patterns are not hypothesized to fit these simple codiversification scenarios. Partner switching, extinction, and sweeps of a single species across a clade of partners are examples of situations that are common in coevolution frameworks yet are poorly accounted for in current methods. The development of new, creative methods that integrate dated phylogenies and interaction-network data are needed to test more nuanced hypotheses about how ecological interactions shape macroevolutionary patterns of interacting clades [83].

Given the evidence that ecological interactions are important drivers of macroevolutionary trait trajectories, how best do we move towards more effective approaches for studying the interplay between ecology and trait diversification? In the field of comparative phylogenetic methods development, a major research priority is to develop models that more realistically incorporate predictions for how and when ecological interactions leave detectable signatures on patterns in trait evolution across the tree of life (Box 1).

#### Ecological Impacts on Lineage Diversification

Decades of microevolutionary studies have compellingly shown that species interactions can directly impact factors such as genetic divergence [26], range/population size [27], hybridization [28], the evolution of reproductive isolation [29], and the persistence of young species [30]. However, do these dynamics translate into changes in the rates of speciation and extinction at the macroevolutionary scale?

Perhaps the best-known concept directly linking ecological interactions to macroevolutionary patterns of lineage diversification is the classic idea of 'ecological opportunity.' Defined as a 'wealth of evolutionarily accessible resources little used by competing taxa,' ecological opportunity has long been held as a primary driver of adaptive radiation [10]. In this framework, speciation rates may be expected to decline with increasing species richness due to niche-filling processes [10,31]. This question has long been investigated, for example when seeking to link traits to macroevolutionary patterns, often in the framework of asking about effects of 'key innovations' on clade diversity patterns [1,32]. However, the impact of ecological dynamics on macroevolutionary patterns of lineage diversification is not limited to competitive effects on niche availability. Antagonistic interactions, such as those between plants and their herbivores or predators and prey, are hypothesized to result in escalating radiations of interacting clades as they overcome counter-adaptations [20]. Mutualistic interactions are also implicated in driving patterns of diversification: traits facilitating mutually beneficial interactions correlate with increased lineage diversification rates repeatedly across different clades (e.g., [33]).

In many cases, the challenge of reconstructing interactions in deep time has been sidestepped using traits that mediate species interactions as proxies for the presence of actual interactions through time. For example, traits that mediate mutualisms between plants and arthropods, like extrafloral nectaries, have been used as a proxy for the existence of that mutualism [33]. However, these studies generally assume traits have singular, straightforward impacts on interactions, and tradeoffs, pleiotropy, or context dependency in trait impacts are rarely incorporated. An alternative approach applies a biogeographical framework rather than relying on traits, using coexistence as a proxy for species interactions. For example, Tanentzap *et al.* [34] found that plant clades which arrived earlier to a biogeographic region were more likely to diversify, whereas later arriving clades failed to radiate. This pattern is consistent with priority effects where early colonizers diversify to fill open niches, squelching the opportunity for further radiations [35].

While research on the ecological drivers of lineage diversification is a more developed subfield linking ecology and macroevolution, progress is limited by a lack of comparative tools available to test for the patterns predicted to arise from many types of ecological dynamics (Box 1).

#### Evolution Alters Ecological Dynamics and Community Coexistence

##### Phenotypic Evolution Impacts Ecological Dynamics

Just as ecology shapes evolution, evolution can modify species distributions, coexistence, and species interactions. Any ecological interaction mediated by a heritable trait can be altered by trait divergence, and ecological interactions impacting realized niche space can be shaped by traits under selection. While evolutionary studies have documented changes in many traits that

mediate ecological interactions at both macro- and micro-scales, community ecological studies generally assume that traits (and interactions) are fixed across populations and time, and that phenotypic evolution is slow enough that it can be modeled independently of ecological dynamics. However, ongoing evolution may be essential to explain ecological dynamics in many natural populations and communities [2,36], and ignoring the role of evolution in community studies may be inappropriate in many cases.

Coexistence dictated by limiting similarity is a classic example of a community interaction that is limited by the rate and amount of trait divergence necessary to decrease competition. While it is frequently studied in a microevolutionary framework (i.e., character displacement [10]), evolution-enabled coexistence can operate over a range of evolutionary scales. Multispecies comparisons of trait evolution support trait-mediated species interactions impacting, for example, the rate of return to sympatry among close relatives [37] and contemporary coexistence patterns among sister taxa [16,17]. More recent theory demonstrates that the evolution of traits underlying competitive interactions can enable coexistence [38], and that shifts in trait variation within species can modify the outcome of interspecific interactions in 'evolving metacommunities' [39]. Even recent theory suggests that the interpretation of trait distributions on phylogenies is sensitive to the presence and nature of ecological interactions [40], suggesting that any effects of trait evolution on ecology might influence the explanatory power of phylogenetic information to reflect ecological interactions. While 'the ghost of competition past' is often invoked in community assembly as a historical process explaining contemporary patterns [41], in some systems evolution has the potential to change the relationship between phylogenetic distance and species interaction strength in observable ways as well [12].

Despite this evidence, the ways in which we incorporate evolutionary perspectives into community ecology remain limited. In community ecology theory, species historically have been treated as units that do not change in phenotype over time, an assumption that modern theory generally continues to adopt [42]. This has also translated to community phylogenetics, where phylogenies are treated as static proxies of species differences, generally within and across spatially segregated sites. However, this limits our ability to connect statistical inferences from phylogenetic patterns to the ecological and evolutionary processes that jointly determine community assembly and function. Studies that test for patterns consistent with within-community phenotypic evolution and its potential to impact ecological interactions over many generations remain rare in community ecology [43], yet heritable phenotypes can be dynamic over a range of short and long timescales. In addition, combining data on evolutionary relationships, community composition, and individual or population-level traits in high-turnover systems can help disentangle the roles of ecological processes and their evolutionary dimensions (Box 2).

#### Lineage Diversification Impacts Ecological Dynamics

The number and similarity of species coexisting in a community have strong effects on the stability of ecosystem function [44] and composition (e.g. diversity effects on invasibility [45]). Thus, speciation and extinction dynamics, which alter the abundance of taxa in regional species pools, can have direct repercussions for ecological interactions within and across communities [46]. As key studies of community and phylogenetic structure have demonstrated, the potential for coexistence is also highly impacted by species traits [47]. As such, variation in lineage diversification rates has direct repercussions for coexistence patterns by altering both the number and type of available species in a region. Clades with higher net diversification rates might contribute disproportionately to regional species pools. If species from such rapidly radiating clades retain similarity in traits related to ecological coexistence [48], this could affect both the likelihood of coexistence and the strength of species interactions, both positively (e.g.,



via facilitation or environmental sorting) and negatively (e.g., via competition for limiting resources). More generally, both the mechanism and geography of speciation can also alter the distribution of, and niche partitioning among, close relatives. For example, sympatrically and allopatrically speciating lineages have different expectations regarding the timing of coexistence of close relatives, as well as their ecological similarity [49]. Aside from the geography, different mechanisms of speciation also produce sister taxa with very different potential for ecological coexistence. If intrinsic isolation mechanisms evolve first, reproductive isolation will exist prior to ecological divergence, whereas in ecological speciation, ecological divergence facilitating coexistence may exist prior to reproductive isolation [50]. Clades that frequently speciate via ecological mechanisms may therefore contribute disproportionately to the buildup of diversity compared to clades speciating via nonecological mechanisms [51]; however it is possible that these different mechanisms of speciation also have different implications for the persistence of species through time [50].

While phylogenetic comparative studies frequently evaluate patterns of diversification rates and divergence in traits thought to mediate speciation (e.g., traits involved in sexual selection or competition for limiting resources [15,52]), this work is still rarely integrated into ecological studies on coexistence. For example, community phylogenetic studies do not currently incorporate knowledge of the speciation rate or mode when evaluating the composition of

#### Box 2. Changing Imprints of Macroevolution in Dynamic Communities: Possibilities for Eco-Evolutionary Integration Using Long-Term Time-Series Data

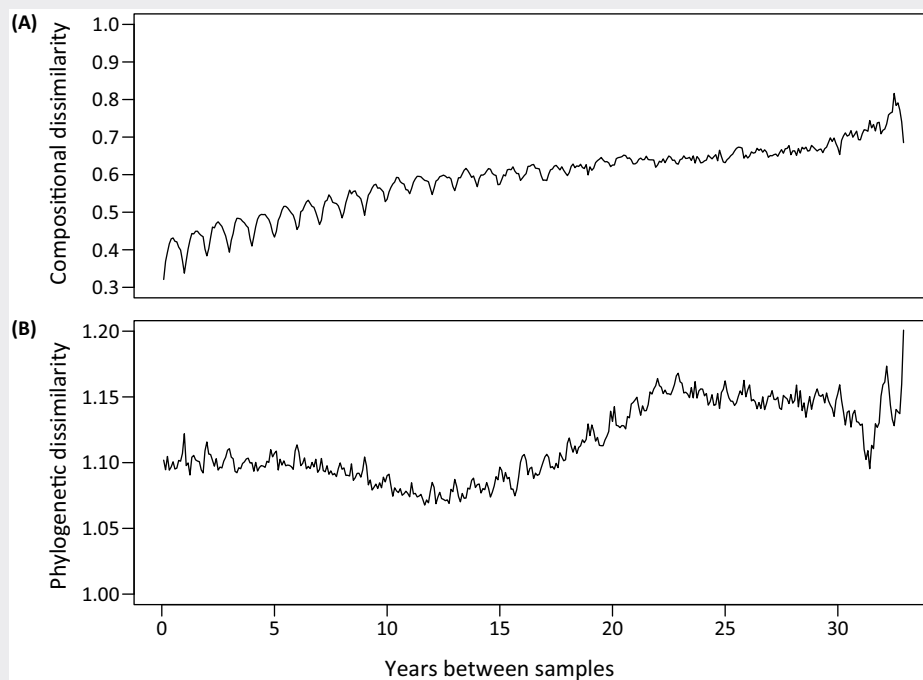
The joint analysis of community composition and phylogenetic relationships has become widespread in community ecology (known as phylogenetic community ecology), yet most phylogenetic community studies ignore the dynamic nature of community composition through time and focus instead on static snapshots of communities across space. This omission of an explicit temporal dimension from phylogenetic community ecology has compromised our ability to study the inherently dynamic nature of ecological processes in light of phylogenetic relatedness.

Directly studying community structure through time using long-term time-series data offers an exciting opportunity to link patterns of evolutionary relatedness with dynamic ecological processes. Such processes include shifts in the magnitude or direction of species interactions over seasonal timescales [84] and in long-term succession, changes in the relative importance of assembly mechanisms with time [85], and coexistence mechanisms that depend on temporal dynamics (e.g., storage effects [86]). In this way, datasets with the potential for changes in community membership over a range of timescales can help to disentangle connections between ecology and evolution.

Systems where seasonal dynamics or other disturbances result in the repeated reassembly of communities are particularly good opportunities to merge a dynamic approach to studying assembly processes with studying the contribution of short-term trait evolution relative to longer-term diversification processes in generating community functional diversity. For example, how does the importance of species turnover versus evolution within species in response to seasonal or long-term disturbance depend on the composition of the regional species pool, dispersal rates, disturbance characteristics, and genetic variation? What can we learn from asking not only about a series of snapshots of phylogenetic structure, but also about where on a phylogeny the relationship between evolutionary relatedness and ecological similarity is most likely to break down and how that factors into our null hypotheses for coexistence [49,87]?

As an example, take phytoplankton communities, which demonstrate remarkably predictable compositional fluctuations on an annual basis, as well as long-term turnover in community composition (Figure 1A). Examining the change in phylogenetic relatedness among community members reveals substantial changes in phylogenetic dissimilarity only at longer timescales (>25 years), which could align with recovery from eutrophication or response to long-term changes in thermal regimes (Figure 1B). Observations such as this can generate testable hypotheses about the timescale of interactions between ecological and evolutionary processes. This is because fluctuations in phylogenetic relatedness over time could reflect species with static trait values reacting to fluctuating environmental conditions and changing species interactions, or potentially also evolutionary dynamics wherein trait evolution alters species' abilities to persist under static ecological conditions. If the latter is happening, then phylogenetic structure of communities could change even if the rules of assembly do not. For example, *in situ* trait evolution over 30 years (over 1000 generations in phytoplankton) could progressively decouple species-level phylogenetic relationships from ecological similarity [88], changing the ability of species with a fixed level of evolutionary relatedness to tolerate environmental conditions or coexist with each other.

Replicating these types of phylogenetic time-series across space as well as time provides an even stronger approach. In the phytoplankton example, time-series of phylogenetic community composition could be examined for many discrete, replicated natural lake ecosystems across the globe. This would allow for robust tests for patterns consistent with community assembly mechanisms (e.g., deterministic versus priority or historical contingency effects on community composition [90]), varying micro-evolutionary trajectories in the same species across variable environments, and unique tests of the environmental- and community composition-dependence of trait evolution. Indeed, a handful of recent studies on community phylogenetic patterns through time have begun to demonstrate the power of this joint analysis of spatial and temporal variation in phylogenetic structure. These include changing phylogenetic community structure 20 years post-disturbance in zooplankton communities [91], several decades of post-disturbance succession in tropical tree communities [92], 40 years of fire response in oak savannah [93], and a 150-year time series of natural warming in woodland flowering plants [94]. Evidence from these diverse systems suggests that evolution affects community assembly via the conserved divergence of traits governing response to environmental disturbance or change, and argues for a careful look at the interplay between temporal change in habitat filters and their effects on close versus distant relatives.



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**Figure 1. Correlogram of Community Composition in the Lake Zurich Green Algae Dataset from 1976 to 2009.** The x-axis gives the lag time between observations, and the y-axis gives the average dissimilarity in community composition based on (a) species composition, or (b) phylogenetic relatedness. These response metrics are the two components of total phylogenetic community dissimilarity (PCD [89]), which is partitioned into a nonphylogenetic component due to species overlap among communities, and a phylogenetic component due to the relatedness of nonshared species (shown in panels (A) and (B), respectively). We calculated these metrics using the `pcd` function in the `picante` package of R.

communities, even though these factors shape null expectations for coexistence [53]. While the geography and rate of speciation may not always be relevant for understanding community assembly (e.g., at a very local scale or with no dispersal limitation) a more regional integration of ecological and evolutionary forces shaping species distributions will require null models that account for both of these processes [54]. Both theory and empirical evidence strongly support the idea that lineage diversification dynamics can shape ecological interactions, and future work should fill this gap by integrating community ecology studies with clade-level comparative work on the lineages that make up those communities (Box 3).



### Box 3. Integrating Clade-level Phylogenetic Comparative Studies with Contemporary Community Data

Integrating comparative phylogenetic information with data on species coexistence, traits, and interactions is both a useful and a necessary way forward in understanding community assembly, and the evolution of species and species traits. Integrating these areas more fully will provide useful information for parameterizing comparative phylogenetic models that incorporate ecology (see Box 1), and also for testing hypotheses at the community level derived from clade-level phylogenetic patterns. For example, evolutionary theory points to the role that species interactions can play in generating trait divergence (e.g., character displacement), or convergence (e.g., via facilitation, mimicry, or competition) between taxa in sympatry, whereas much ecological theory points to the role of interspecific competition in limiting coexistence. However, comparative phylogenetic work typically examines models of trait evolution without regard to the geographic distributions of clade members, and the potential role that interactions in sympatry, or lack thereof, have had on trait evolution. Likewise, community phylogenetic work rarely takes into account the broader history of the traits and species within their focal clade, including the role of historical biogeography in shaping community assembly patterns [53] and the evolutionary dynamics that shaped regional species pools [46]. By seeking to explicitly examine and compare the results of analyses at community and at clade levels, we create the potential to link community phylogenetic patterns with patterns of trait evolution and lineage diversification within clades [46] (Table I). Furthermore, ignoring these connections has the potential to create positively misleading conclusions in the interpretation of both community and clade level datasets.

Important work by Pigot and Etienne [54] is a clear example of how ignoring evolutionary processes of species formation may generate positively misleading inferences about community assembly processes. A frequent hypothesis in community phylogenetic studies is that phylogenetic overdispersion is the result of competition limiting coexistence between close relatives. Pigot and Etienne [54], however, show that patterns of geographical distribution generated by a null model assuming allopatric speciation can produce phylogenetic overdispersion in communities, without any community-level mechanisms limiting coexistence. Thus, phylogenetic overdispersion of local communities may result from the spatial signature of speciation itself.

Likewise, ignoring local community context gives us at best an incomplete picture of the factors influencing trait evolution in clades, and at worst can also be positively misleading. For example, convergent evolution is a pattern of longstanding interest to evolutionary biologists, and new analytical tools have recently heightened interest in testing for this pattern in clade-level phylogenies [95]. However, the mechanisms underlying convergence may differ widely depending on the distribution and coexistence of the clade members. If convergent forms are always found allopatrically, this suggests that similar selective pressures and/or resource distributions have led to the repeated evolution of similar ecotypes (e.g., [64]). In contrast, if convergent forms are found sympatrically, this could suggest that local interactions may be promoting the evolution of similar phenotypes. This is especially powerful if patterns of sympatry *per se* can be disentangled from specific shared abiotic conditions. By integrating clade- and community-based perspectives, we can move beyond pattern detection approaches, and towards evaluating the likelihood of different ecological mechanisms underlying clade-based patterns in trait evolution (see also Box 1).

Ideally, integration of clade and community perspectives would take a reciprocal implementation approach, whereby hypotheses are generated at one scale of study and tested and refined at the other. Although the reciprocal influence of these scales has long been appreciated [8,71], few studies use integrative approaches to bridge across these distinct subfields (see Table I for examples). Evaluating hypotheses generated at one scale (community-level) with data from the other scale (phylogenetic patterns), and vice versa, will require creatively integrating approaches traditionally used in either phylogenetic or ecological studies. In order to initially identify patterns of trait similarity and relatedness in communities, for example, studies must move beyond current practices of relying exclusively on simple tests of phylogenetic signal to describe patterns of trait variation on community phylogenies. A basic assumption of many community phylogenetic approaches is that functional traits important to community assembly have phylogenetic signal, and when this assumption breaks down, phylogeny is assumed to not provide useful information about community assembly, despite continued recognition of the importance of functional traits for community assembly processes [96]. As such, traits that do not conform to a strict Brownian motion (BM) model in community phylogenetic studies are often treated in a nonphylogenetic manner. However, traits within communities can display interesting phylogenetic patterns beyond a strict BM pattern and these patterns can generate hypotheses about the processes shaping a lineage's evolution and ecology. Indeed, many traits that are potentially ecologically relevant have shown complex patterns of evolution in clade-specific studies, so it is puzzling that the default hypothesis in community-based studies is that they should conform to simple BM on phylogenies where branches can span much larger time frames, allowing longer periods for evolutionary dynamics to intercede. Although this has long been recognized by phylogenetic community ecologists [70,97], there are still limited options for moving beyond this 'BM-or-bust' paradigm.

Some relatively new approaches in community phylogenetics provide promising alternatives that move in this direction. Approaches in community phylogenetics for scaling branch lengths relative to trait phylogenetic signal have been proposed [96], somewhat analogous to approaches introduced to studies of trait evolution 15 years ago (e.g., [98]). However, it remains unclear how rescaled fits to phylogenetic tests of community assembly relate to ecological mechanisms for community assembly, or what fitted trait models on local community data mean in terms of the

evolutionary history of the group. Likewise, rescaling approaches to compensate for differences in the importance of specific functional traits and phylogenetic history may provide better fits to community assembly metrics [96], yet relating these results back to understanding the mechanisms of ecological or evolutionary dynamics at play may be difficult. Other, more flexible modeling approaches, such as GLMM models incorporating phylogenetic information, provide another promising approach for using more realistic models that can be more specifically tied to ecological mechanisms [99].

Greater integration and tool-sharing between researchers working at the community versus clade perspectives is an important way to facilitate expanded capacity for alternate model testing, and we advocate increased work that truly crosses the boundaries between these fields, by incorporating community data into clade-level studies (Table 1, part 1), and by incorporating perspectives on clade-level evolution into studies of community assembly (Table 1, part 2). Other integrative work both combines these two areas and examines how the diversification process itself affects eco-evolutionary dynamics.

Table 1. Integrating Clade and Community Perspectives Requires Clade-Level Studies to Consider the Impacts of Community-Level Ecological Processes on Larger-Scale Macroevolutionary Patterns, and in Parallel Community-Level Studies to Examine Broader Phylogenetic Patterns in the Analysis of Local Community Structure. Although these connections have long been recognized [8,46], relatively few studies reach across these disciplinary barriers. We highlight exemplary studies below that succeed in reaching across the traditional disjunction between these fields.

| Integrative approach  | Refs    |
|---|---------|
| Clades  |         |
| Trait evolution   |         |
| Ecological competition models can be used in a phylogenetic context to fit process-based models to trait data on trees  | [40]    |
| Accounting for geographic overlap, and therefore the possibility for competition, between taxa produces better fits to models of clade-level trait evolution              | [19]    |
| Diversification   |         |
| Population-level models of competition can inform macroevolutionary models of clade diversification and diversity patterns invoking competition                           | [81,82] |
| Communities   |         |
| Range overlap among sister taxa is explained by ecological trait divergence   | [37]    |
| Divergence in habitat among sister taxa is driven by competitive interactions in sympatry   | [17]    |
| Range overlap among sister taxa is not explained by ecological or sexual trait divergence, and instead results from the geography of speciation                           | [100]   |
| Rapid trait evolution can break down a correlation between phylogenetic and ecological similarity, making phylogenetic structure a poor proxy for ecological interactions | [88]    |
| Accounting for the geography of speciation is crucial for generating appropriate null models of community assembly  | [54]    |

The Reciprocal Interplay between Species Interactions and Macroevolutionary Divergence and Diversification

The core idea behind eco-evolutionary studies is that ecological interactions, phenotypic evolution, and lineage diversification reciprocally impact one another. Due to methodological constraints and/or differences in the perceived rate of ecological versus evolutionary processes, most studies focus on very short-term outcomes of eco-evolutionary interactions [2]. However, theory strongly suggests that ecological and long-term evolutionary dynamics are reciprocally linked over deep-time. In adaptive radiations the rate of ecological change is hypothesized to be intrinsically and reciprocally linked to the rate of speciation [10] (although much work has questioned how frequently we robustly detect such patterns in radiating clades, both for morphological evolution [55], and for lineage diversification [56]). Similarly, theory on the adaptive dynamics of community structure suggests that evolution, via trait evolution or

speciation, can alter the strength of species interactions, modify community structure, and ultimately impact the fitness landscape to which organisms are adapting and on which new species are forming [57]. The challenge now is to simultaneously study both ecological and evolutionary processes as they interact in complex communities and over longer timescales.

Because of their tight coevolutionary coupling, studies of evolving interactions between hosts and parasites or pathogens are promising starting points. Viruses can modify their host environment, affecting transmission and selection pressures on subsequent generations [58]. Rapid evolution of diseases can have ecological effects on hosts (e.g. changing population size and connectivity) that directly change the likelihood of further diversification of associated parasites and pathogens. Experimental evolution in systems with short generation times has also made progress in testing theoretical feedbacks between ecology and lineage diversification. Recent experimental studies using the bacterium *Pseudomonas fluorescens* have revealed cases where evolutionary and ecological dynamics are reciprocally dependent, at least in a microbial system. Experiments in this system have demonstrated that inter- and intra-specific interactions can affect the buildup of phenotypic and genetic diversity of *Pseudomonas* through time [59]. In addition, recent experimental work suggests that variation in the strength of feedbacks between genotypes of *Pseudomonas* and environmental conditions influence the likelihood and extent of adaptive radiations [60]. Generally speaking, microbial experimental systems have elegantly demonstrated that ecological interactions can alter the pace and outcome of macroevolutionary change, and vice versa (reviewed in [61]).

Beyond microbial systems, and over longer timescales, evaluating the influence of eco-evolutionary dynamics on macroevolutionary patterns is more challenging. Phenotypic divergence in *Geospiza fortis* is a classic example of how rapid evolution can contribute to ecological dynamics [62]. That these taxa are part of an adaptive radiation makes it tempting to suggest that strong eco-evolutionary dynamics influenced rapid lineage diversification and/or trait evolution more broadly in this group. However, making such connections requires greater understanding of how eco-evolutionary feedbacks impact speciation dynamics. Although some traits under selection within populations may also affect species diversification rates, there is no necessary connection between rates of lineage-level evolution and diversification rate [32]. However, scenarios where speciation is tied to shifts in ecological resource use, and where resource availability mediates eco-evolutionary dynamics, are particularly strong candidates for detecting eco-evolutionary processes in lineage diversification.

One additional example where such processes may be occurring is Caribbean anoles, where competition among species for microhabitat (perches on tree branches) results in character displacement over short timescales [63]. In combination with evidence linking competition to patterns of divergent and convergent trait evolution throughout the Greater Antilles [64], the importance of interactions between ecology-dependent selection, geographic patterns of community occupation, and long-term macroevolutionary processes in this system are apparent. Uniting these different focal scales of study, and truly connecting local-scale eco-evolutionary interactions to clade-level patterns, is close at hand in this system. The remaining challenge is in understanding the extent to which eco-evolutionary dynamics versus other processes (e.g., historical contingency, local adaptation driven by extreme environments) have contributed to whole-clade diversity in species and in traits.

Finally, the influence of eco-evolutionary feedbacks on patterns of trait macroevolution may depend critically on the nature of selection. Processes involving consistent directional selection are more likely to influence long-term patterns, but evidence for such directional selection versus fluctuating selection is mixed [65]. An important ongoing challenge is therefore understanding whether generalities exist regarding the kinds of selective agents that tend to produce

long-term directional trends versus fluctuation, as the latter is more likely to contribute to macroevolutionary patterns. These differences could be in interaction strength [66], in geography [67], or in whether selection is driven by biotic or by abiotic forces [24]. If such generalities exist, and selective agents are consistent across multiple species in a clade, this could result in clade-level patterns of trait evolution that reflect eco-evolutionary dynamics (e.g., [68]). Furthermore, by better integrating short-term selection studies with macroevolutionary patterns in the fossil record [69], we can gain a more mechanistic understanding of diversity over truly deep timescales. Despite the challenges involved in simultaneously studying ecology and evolution together on phylogenies, both theory and empirical evidence suggest that eco-evolutionary interactions are a key part of the macroevolutionary process, and finding new ways to study them on deep timescales will further our understanding of the origin and evolution of biodiversity.

### Concluding Remarks

Fundamentally, both ecologists and evolutionary biologists seek to understand the processes that generate patterns of biological diversity. However, evolutionary biologists tend to focus on the processes generating diversity among populations, species, and clades, while ecologists tend to focus on the processes shaping communities of interacting species. Despite this divide, innovative new research approaches are demonstrating how community and evolutionary dynamics shape one another in observable ways. At the macroevolutionary scale, research on adaptive radiations, the role of ecological opportunity, diversification dynamics, and trait-based species interactions strongly support a role for ecology in shaping macroevolutionary patterns of speciation, extinction, and trait evolution. Because of this, the status quo of excluding species interactions from models of evolutionary change along phylogenies is beginning to change (Box 1). At community phylogenetic scales, a growing number of studies are disentangling how relatedness of species in a community shifts over complex spatial and temporal landscapes, linking these findings to ecological and evolutionary processes at play through time (Box 2). And finally, the way in which we study ecological and evolutionary dynamics is changing: barriers between phylogenetic comparative studies and community phylogenetic perspectives continue to fall (Box 3). Overall, innovative research is filling these important gaps, moving towards the simultaneous study of ecological interactions and evolutionary change along branches of the tree of life.

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### Outstanding Questions

How and when do species interactions within and across clades shape macroevolutionary patterns of species and trait diversity?

How and when do macroevolutionary dynamics (lineage diversification and trait evolution) shape community assembly patterns across space and time?

How and when do these processes interact, translating short-term eco-evolutionary dynamics into long-term and large-scale links between local communities and regional species pools?

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