

SYNTHESIS

What Can Evolutionary History Tell Us about the Functioning of Ecological Communities? The ASN Presidential Debate

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ABSTRACT: In January 2018, Sharon Strauss, then president of the American Society of Naturalists, organized a debate on the following topic: does evolutionary history inform the current functioning of ecological communities? The debaters—Ives, Lau, Mayfield, and Tobias—presented pro and con arguments, caricatured in standard debating format. Numerous examples show that both recent microevolutionary and longer-term macroevolutionary history are important to the ecological functioning of communities. On the other hand, many other examples illustrate that the evolutionary history of communities or community members does not influence ecological function, or at least not very much. This article aims to provide a provocative discussion of the consistent and conflicting patterns that emerge in the study of contemporary and historical evolutionary influences on community function, as well as to identify questions for further study. It is intended as a thought-provoking exercise to explore this complex field, specifically addressing (1) key assumptions and how they can lead us astray and (2) issues that need additional study. The debaters all agree that evolutionary history can inform us about at least some aspects of community function. The underlying question at the root of the debate, however, is how the fields of ecology and evolution can most profitably collaborate to provide a deeper and broader understanding of ecological communities.

Keywords: evolution, ecology, ecosystem functioning, community ecology, eco-evolutionary dynamics.

Introduction

The studies of evolution and ecology have a long-shared history, summarized famously by the title of G. E. Hutchinson's 1965 book, *The Ecological Theater and the Evolutionary Play*. We now appreciate that the converse is also critical: evolution sets the stage for ecological processes and their outcomes. On January 5, 2018, Sharon Strauss, then president of the American Society of Naturalists (ASN), convened a debate on whether evolutionary history can meaningfully inform how extant ecological communities' function as part of the ASN stand-alone meeting in Asilomar, California. The debaters, coauthors here, presented caricatures of their arguments. In this article, we first summarize the key points presented at the debate to bring out contrasting viewpoints. The opinions presented are purposefully extreme to provoke deeper explorations of the connections between ecology and evolution and reveal fertile directions for future research. We go beyond arguing about whether *evolutionary history* matters to discuss the more nuanced (and, we argue, more interesting) question of when considering evolutionary history is most important for understanding the functioning of ecological communities. Because our goal is to stimulate discussion, including among new members of this research community, we include as appendixes a glossary of key terms (supplemental PDF, sec. 1; all terms in sec. 1 of the supplemental PDF are in italic type when first introduced in the main text) and a collection of discussion questions we hope will be useful for journal clubs interested in discussing this topic in more depth (supplemental PDF, sec. 2).

For the purpose of debate, we consider *community function* to refer to any and all of the ecological properties

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ascribed to a *community*. This incorporates the diverse ways that community function has been used in the literature: from specific functions, such as energy transfer rates and nutrient cycling, to the role of communities and species interaction networks in maintaining ecosystem productivity and resilience. *Ecological functions* are typically performed by assemblages of species, and therefore questions involving community functioning focus on functions performed by the community in its broader sense as well as by particular species contributing to these functions.

Microevolution

In this section, we focus on whether and when we expect microevolutionary effects (including *adaptation* but not *speciation*) to be important for understanding the current and future ecological functioning of communities. Our arguments revolve around (i) the relative importance of *microevolution* compared with changes in the presence or abundance of species through *ecological sorting*, (ii) whether the effects of microevolution on communities are rapid and transitory or long term and self-perpetuating, and (iii) whether microevolution is more likely to maintain function or lead to novel functions in response to environmental change.

Within-Species Variation May Be as Important as Among-Species Variation When Explaining Community Functioning

PRO: Because the traits that species express determine their functions within communities, any genetic variation within or among populations of the same species may affect ecosystem function.

CON: When trait differences among species greatly exceed trait variation within species, intraspecific variation and microevolution will have more limited effects on ecosystem function compared with shifts in community composition.

Pro. A central goal of community genetics is to identify how intraspecific variation in species traits influences community properties and ecosystem functions (Hersch-Green et al. 2011). For microevolution to influence ecosystem or community function, there must be genetic variation for relevant traits. A surprise from the first *allozyme studies* was how much genetic variation is carried by species (Antonovics 1976), and continued work has shown that most ecologically important traits are genetically variable (Geber and Griffen 2003; Bolnick et al. 2011). Therefore, when a community experiences a perturbation, it is likely that populations of at least some species will undergo natural selection. This evolutionary process can affect

function in two ways. First, if selection is *hard* (i.e., affects per capita population growth; Reznick 2016), then evolution will change how species abundances respond to a perturbation. For example, after an initial population decline in response to a novel stress, evolution may *rescue* populations by the chance appearance of favorable mutations (*evolutionary rescue*; reviewed in Bell 2017) that allow species, and the functions they provide, to recover (Gomulkiewicz and Holt 1995). Thus, microevolution can play a role in the response of community functions to perturbations by promoting population persistence (Vasseur et al. 2011; Germain et al. 2022; Yamamichi et al. 2022).

Second, many examples illustrate how microevolutionary history influences the magnitude of ecological effects of species (reviewed in Strauss et al. 2008; Agrawal et al. 2012). As a result, evolution can influence community function, even if population density remains constant. For example, individual plant genotypes can attract different herbivore or microbial communities with clear ecosystem consequences (e.g., Crutsinger et al. 2006; Fitzpatrick et al. 2015; Gehring et al. 2017). Two meta-analyses compared the effects of within-species variation to among-species variation in plants on guilds of arthropods (Koricheva and Hayes 2018) and on a variety of ecosystem functions (Des Roches et al. 2018). Both analyses found that while within-species variation explained less ecological function than among-species variation, it still explained a sizable fraction of ecological function. As a result, any evolutionary shifts in genotype frequency can affect community functions (Whitham et al. 2003; Johnson et al. 2006; Fitzpatrick et al. 2015). For example, rhizobia (nitrogen-fixing bacterial plant mutualists) evolved reduced cooperation with plant hosts in response to 20 years of experimental nitrogen addition. *Rhizobium* evolution affects soil nitrogen availability, and these effects are as strong, and sometimes stronger, than the presence or abundance of rhizobia (Lau et al. 2022). Thus, ignoring evolutionary history may lead to an incomplete, or even erroneous, understanding of modern communities.

Species in communities that experience large, novel abiotic or biotic disturbances may adapt and, in doing so, may mediate the impact of disturbances on ecological function (Kennedy 2013). For example, invasive species can have large impacts on native communities and drive evolutionary changes of native species throughout the community; these changes, in turn, may lessen invasive impacts (Shine 2011; Lankau 2012). In addition, changes in the traits of *keystone species*, which are known to have disproportionate effects on ecosystem function, will also likely have a large impact on community function (Whitham et al. 2003). Similarly, species involved in keystone (or other ecologically important) interactions in communities, such as mycorrhizal associations with trees, often have strongly coevolved

traits (Fritz and Simms 1992; Phillips et al. 2013); evolutionary changes in these traits will likely affect ecosystem functions by changing the interaction.

Con. Changes in species composition will often have much greater effects on community function than changes in the genetic composition of individual species. This is true whenever a diverse collection of species spans more trait variation and a greater range of ecological functions than a single species; when there is greater among- than within-species trait variation, then changes in species composition should be more important in determining ecological function than trait changes within any one species. This result is demonstrated in a model by de Mazancourt et al. (2008) of phenotypic evolution within changing environments. When new niches arise in communities due to environmental change, existing species largely preadapted to the novel niche rapidly fill it, quashing within-species evolution (*adaptation*) to the novel niche by other, less suited species (Lewontin 1974; Wallace 1975; Reznick 2016). In general, we thus might expect that evolution within species will be relatively more important to ecological function in communities composed of few species while less important in diverse communities.

Moreover, *phenotypic variation* within species by itself is not sufficient to conclude that within-species variation is as important as among-species variation for community function. In the Koricheva and Hayes (2018) analysis, even though the within- and among-species effects on arthropod communities were similar in size, these authors point out that most studies measured arthropod responses on only one plant species, often in a dominant species. By focusing on a single plant species and ignoring the full diversity of arthropods across all plant species in a community, these studies likely overestimate the effects of within-species variation on ecosystem function (Koricheva and Hayes 2018). Furthermore, while some studies have documented that phenotypic variation of within-species traits can be on the same order of magnitude as the same traits measured among species (Albert et al. 2010), few have shown that this within-species trait variation is genetically based and subject to microevolution. Therefore, comparisons of within-versus among-species phenotypic variation cannot be used to gauge the importance of microevolution within species for overall community functioning without greater study of the source of variation (Snell-Rood and Ehlman 2021).

In summary, changes in species composition (*ecological sorting*) are expected to have greater impacts on ecological function than the evolution of traits within species for large and diverse communities and for functions that involve diverse species. Despite this, we expect effects of within-species evolution on ecological function to be important in cases when single species have large ecological impacts, such as a keystone species or invaders (Fritz and

Simms 1992), or in low-diversity communities, where changes in one species can have major effects on others.

The Effects of Microevolution on Ecological Function Are Rapid and Important

PRO: Ecological and evolutionary dynamics can occur on the same rapid timescale, suggesting that ecological dynamics can only be understood considering evolutionary dynamics.

CON: While evolution can occur rapidly and affect ecological dynamics in the short term, what stops *rapid evolution* from eating up available genetic variation and stalling longer-term evolution? If genetic variation is not maintained in a natural system, then self-sustained eco-evolutionary dynamics can be limited.

Pro. Rapid evolution occurring on the same timescale of ecological dynamics is common and unsurprising (Pimentel 1961; Yoshida et al. 2003; Fussmann et al. 2007; Rudman et al. 2022). For example, dichlorodiphenyltrichloroethane (DDT) was first used to control *Aedes* mosquito vectors of malaria in 1946, and resistance in *Aedes* was first identified in 1947 (Brown 1986), the year before Paul Hermann Muller received the Nobel Prize for discovering the insecticidal properties of DDT. When selection is strong and genetic variants exist that increase fitness in the *novel environment*, rapid evolution necessarily occurs. Such rapid evolution can then feed back on ecological properties of the system. Trivially, the adaptation of mosquitoes to DDT increased mosquito per capita population growth rates—an altered ecological function—in the presence of DDT. Less trivially, the rebound in the mosquito population following resistance to DDT reduced malaria control, leading to increased human death and consequent changes to the ecological properties of the ecosystems in which humans were embedded.

Rapid evolution is likely to be important for any species or community experiencing a large perturbation (Antonovics 1992; Leibold et al. 2022). In a classic example, when tropical guppies colonize new low-predation streams, the subsequent increases in guppy density cause reduced food availability, which in turn causes selection on size at maturity, among other traits (Reznick et al. 2019). The suite of traits differing between high- and low-density-adapted guppies in turn affects nutrient cycling in streams (El-Sabaawi et al. 2015), thus showing how trait evolution within species contributes to altered ecological function. Similarly, the rapid evolution of invasive species in novel colonized communities may be responsible for their successful invasion, which in turn causes changes in community function (Lee 2002; Eales et al. 2010; Lavergne et al. 2010; Stern and Lee

2020). These evolutionary effects on ecological function are likely to persist because the selection pressure persists and may influence many ecological dynamics (French and Holmes 2020; Pastore et al. 2021; Germain et al. 2022) and result in alternative ecological states (Kefi et al. 2008; Strauss 2014).

Con. Rapid evolution is undoubtedly important. However, if selection is strong and directional, we expect a shift in traits. Also, simple population genetic models predict a depletion of genetic variation for such traits and eventual *fixation* (Haldane 1927; Crow and Kimura 1970). If genetic variation is depleted in nature, then evolution will stop, barring new mutations or immigration of novel variants. Thus, the research challenge is to understand what maintains genetic diversity, thereby allowing rapid evolution to be an ever-present influence on ecological dynamics (Byers 2005).

The con side argues that the conditions under which rapid evolution is long term are restrictive, raising the question of how common eco-evolutionary dynamics are in natural systems. Here, we are using eco-evolutionary dynamics in a narrow sense to refer to the situation in which ecological dynamics cannot be understood separately from evolutionary dynamics. For eco-evolutionary change to be self-perpetuating and pervasive in community function, the evolutionary change must generate ecological change that then changes the selective regime to drive further evolutionary change. An example involves predator-prey dynamics (Ives et al. 2020). Resistance of pea aphids to their dominant parasitoid, *Aphidius ervi*, comes with a trade-off; resistant pea aphid clones have lower population growth rates. Parasitoid abundance, and hence selection pressure on resistance in aphid hosts, varies greatly not only through time but also through space due to the interaction between predator-prey cyclic dynamics and disturbances (harvesting) in the agricultural system. Thus, there is a spatiotemporal mosaic of selection for resistance that can lead to *self-perpetuating eco-evolutionary dynamics* (Byers 2005). A key difference between this example and many cases of rapid evolution is that changes in selection are generated by the internal dynamics of the system, rather than solely by an external perturbation.

Self-perpetuating eco-evolutionary dynamics have been found in very simple ecosystems, such as laboratory algal-rotifer cycles (Yoshida et al. 2003), low-diversity lakes or streams (Duffy and Sivars-Becker 2007), agricultural ecosystems (Ives et al. 2020), and exotic species with relatively few herbivore interactors (Lankau and Strauss 2007). They require strong interactions among species that affect each other's abundances and traits. Such conditions may be rare in diverse natural communities, as the presence of other species can dilute strong interactions and selection (Vellend and Geber 2005). Diverse communities might provide complex selection trade-offs (such as is seen in Schaffner et al.

2019; Ives et al. 2020; Brans et al. 2022) that maintain high levels of genetic variation in many traits across interacting species. Nonetheless, the same complex selective trade-offs will make strong selection and rapid evolution unlikely to drive ecological dynamics. Thus, self-perpetuating eco-evolutionary dynamics may be rare.

In summary, the pro argument asserts that rapid evolution can be important for community functioning when communities experience external perturbations. The con argument concedes this point but redirects focus on eco-evolutionary dynamics that are maintained by the inherent internal forces of species interactions (Schaffner et al. 2019; Ives et al. 2020; Brans et al. 2022). Self-perpetuating eco-evolutionary dynamics require mechanisms to maintain genetic variation underlying evolution despite the possibility of genetic fixation. We need a greater understanding of what maintains genetic variation before we can guess the extent to which eco-evolutionary dynamics are important for community function.

Microevolutionary Processes Can Be Used to Predict Future Ecosystem Function

PRO: When species experiencing novel ecological conditions like extreme climatic events evolve in response to these changes, understanding evolutionary responses is important for predicting future ecosystem functions.

CON: Local adaptation is common and acts to preserve species functions. The ubiquity of local adaptation implies that evolution is a strong force maintaining ecological stasis. While this recognition does not mean that evolution is unimportant, it does mean that ecologists do not necessarily need to study evolution, as we expect it will act in future environments as it does currently.

Pro. Evolution may decrease the effects of environmental change on community functions if evolution allows species to adapt and maintain their functions (e.g., through evolutionary rescue). However, evolution may also increase changes in community function, thereby supporting the argument that future functions cannot be predicted without understanding evolution. One example is when evolutionary responses to climate change involve the *coevolution* (Ehrlich and Raven 1964) of interacting species. For example, interspecific competition can cause *positive feedback loops* that amplify the response of species to environmental change (Northfield and Ives 2013); environmental changes that give one species a competitive edge will be amplified by the competitive suppression of other species (MacArthur and Levins 1967). When there is also coevolution of traits that affect the competitive interactions among species,

whether coevolution adds to or counteracts the positive feedback depends on the mode of competition (Northfield and Ives 2013). Other likely scenarios involve evolutionary changes in the driver of environmental change itself; natural selection on invaders in the novel range can sometimes cause shifts in invader traits that increase growth and competitive ability, increasing the likelihood of successful invasion and invader impacts on ecosystem function (Blossey and Notzold 1995; Lee 2002; Eales et al. 2010; Lavergne et al. 2010). Additional hypotheses to explain invasibility suggest that prior history with competitors in the native range (Fridley and Sax 2014) or adaptation to human disturbance and high resource availability (Vellend et al. 2007; Hufbauer et al. 2012) have selected for invader traits that are advantageous in the novel range. In these cases, evolution of invaders either in native or novel ranges increases their impacts on community functions, supporting the pro argument.

Con. Local adaptation provides evidence for the power of evolution to shape species and communities (Kawecki and Ebert 2004). It also supports the argument that evolution should maintain communities and the roles of species they contain in the face of future environmental change. For example, consider the response of a key ecosystem function, net primary production, to global changes in atmospheric CO₂ concentrations. Plants evolving under elevated CO₂ treatments in a long-term field CO₂ enrichment experiment subsequently responded much less to elevated CO₂ than genotypes originating from ambient CO₂ plots (Lau et al. 2008). These rapid evolutionary responses (or possibly *maternal effects*) reduced the magnitude of the CO₂ fertilization effect.

The con argument extends this idea. If evolution consistently acts to mitigate the effects of environmental changes, then studying evolution is unnecessary to forecast broad ecological changes in the future; in most cases evolution is likely to dampen the ecological response to environmental changes rather than generate an unexpected response. In the example of plant responses to elevated CO₂ concentration, evolution will counteract the effects of global changes in CO₂ concentration on net primary production. Similarly, when invaders evolve to be more competitive, there are often cases in which counter-adaptations by native species reduce invader impacts or success, thus buffering ecological function (Leger 2008). In Australia, native predators have adapted to the presence of toxic cane toad prey, which initially decimated their populations, by evolving smaller mouths and different feeding behaviors (among other traits) to ingest less toad toxin (Phillips and Shine 2006; Shine 2011). If such buffering effects of evolution are common, then one might simply assume that evolution reduces the mag-

nitude of ecological impacts while maintaining the ecosystem function status quo, limiting the added value of explicitly considering evolutionary responses.

Evolution and the ecological process of species sorting can act simultaneously, thereby linking the debate point here with the microevolution debate point 1 above. For example, Fischer et al. (2001) compared the evolutionary (local adaptation) and ecological (species composition) responses among three zooplankton communities from three lakes ranging from high to low pH by experimentally subjecting the communities to low pH. The study showed that communities from low pH lakes were resistant to experimental acidification due to both changes in species composition and local adaptation by the species that persisted. In this example, both ecological and evolutionary processes led to reduced sensitivity of communities to experimental change in pH: species sensitive to low pH dropped out of communities, and those species that remained adapted to low pH.

In summary, both the pro and con sides argue that evolution can alter function but differ in perspective on how useful the study of evolutionary responses is to predict future community function. Ultimately, that answer depends on how often evolution reduces or exacerbates the response of community functions to environmental change.

Macroevolution and Phylogenetic Relationships

The composition of species found in a given ecosystem reflects *biogeographic processes* and macroevolutionary history (Wiens and Donoghue 2004; HilleRisLambers et al. 2012); thus, we expect *macroevolution* to affect community function through the traits of species present. But what type of information—information about traits, evolution, or both—is best for understanding the function of communities (Johnson and Stinchcombe 2007)?

In this section we explore the extent to which incorporating evolutionary history and phylogenetic relationships among species in communities is important to understanding the ecological functioning of those communities. We explore arguments revolving around (i) phylogenies and their relationship to traits, (ii) trait *convergence* and *divergence*, and (iii) the role of history in understanding the response of communities to novel environments.

Phylogenies Are Useful Tools for Understanding Community Function

PRO: Phylogenies are a proxy for similarities of *functional traits* among species and capture unique information owing to *phylogenetic constraints* in the absence of trait data. Even when trait data are available, phylogenies can reflect similarity in additional

unmeasured traits or functions. They thereby offer many insights into the ecological functioning of communities.

CON: Analyses using information only about traits tell us most of what we need to know about community functions. Phylogenies provide largely redundant information to measured traits known to influence function. Only when ecologically important traits are unknown or unmeasured do phylogenies offer additional, nonredundant information about how communities' function.

Pro. In theory, all that is needed for phylogenies to be informative about the functioning of ecological communities is for niches to be on average more similar among closely related species than among distantly related species (Webb 2000). In simple terms, it makes sense that two species of hummingbirds will have more similar dietary niches than will a hummingbird and a duck. The phylogenetic history of diversity is widely considered useful in that it can account for the effects of unmeasured or unique functional traits and offer unique insights about community function beyond what can be gleaned from the study of traits alone (Webb 2000; Ackerly 2003; Cavender-Bares et al. 2009; Losos 2011).

Phylogenies are useful for understanding species interactions, especially trophic interactions, which are hard to decipher. The trophic structure of natural communities is statistically predictable because food webs have *phylogenetic signal*, not so much in their "fine wiring" but in the way species are embedded in the network of interactions (Cattin et al. 2004; Eklöf et al. 2012; Stouffer et al. 2012; Dalla Riva and Stouffer 2016). That is, closely related species tend to have similar specializations and to interact with a similar set of species (Cattin et al. 2004; Bersier and Kehrli 2008; Peralta 2016). Indeed, examples of phylogenies providing a quantitative structure for the ecology of species interactions, such as herbivory, parasitism, pollination, and seed dispersal, have been reported from multiple clades and kingdoms and are pervasive across interaction types (Gomez et al. 2010). For example, cophylogenetic signal is detectable in pollination interactions from local to global scales (Rafferty and Ives 2013; Hadfield et al. 2014; Hutchinson et al. 2017). The connections in seed dispersal networks are more diffuse and tend to be governed more by *trait matching* and correlations of phylogenetic uniqueness between fruit-bearing plants and frugivorous animals (Jordano 1995; Schleuning et al. 2015; Pigot et al. 2016). The need to think in terms of interaction networks, or pairwise interactions among species, is highlighted by studies showing that trait matching and thus potential phylogenetic matching between pollinators and crops are better predictors of crop pollination effectiveness than trait-based metrics of func-

tion (Garibaldi et al. 2015). Similarly, phylogenetic relationships often perform better than the most widely available organismal traits in predicting food web structure (e.g., Eklöf and Stouffer 2015), perhaps because the phylogenetic distance between taxa provides an estimate of similarity in a more complete spectrum of unmeasured traits, including physiology, life history, and behavior (Mouquet et al. 2012).

Con. Although it is undeniable that phylogenetic patterns offer insights into community function in certain cases, in other cases phylogenetic patterns are largely redundant with trait analyses (Cadotte et al. 2019), offering few unique insights that cannot be gained through the study of traits alone. This is particularly true for communities of organisms within a single trophic level (e.g., plant communities or insect communities) rather than food webs or cross-trophic mutualisms.

One of the original arguments for using phylogenetic analyses as a proxy for functional traits was that we do not know or have measurements of all important traits for most species. In many cases, however, we do know which traits are important, especially if we are focused on specific ecological functions, at least for plants and microbes (Kraft and Ackerly 2010; Flynn et al. 2011; Martiny et al. 2015; Le Bagousse-Pinguet et al. 2019). Laughlin (2014) made a compelling case that data on traits are very important for studying plant community function and noted that we need not look at all traits (or even many traits) to gain substantive understanding. Rather, Laughlin (2014) showed that including as few as seven traits—one from each of seven orthogonal axes of plant properties—is all that is necessary to answer many questions about how plant communities function. This study, although focused only on plants, is useful for making us think about the types of questions that can be answered by studying a few traits of known functional importance without additional phylogenetic analyses.

The concept that phylogenetic information reflects all traits is often pitched as an advantage, yet it also represents a drawback because phylogenies provide no mechanistic information about which traits contribute to ecological function, limiting what we can learn from analyses based on phylogenetic patterns alone. Li et al. (2017), for instance, present a statistical method to incorporate both trait variation and phylogenies in the analysis of community composition. When high-quality data on functional traits were available, these authors found that phylogeny did not add significant amounts of explanatory power for community composition.

The use of phylogenetic relationships to assess ecological function is also largely based on the assumption that most functionally important traits are conserved (Webb 2000). This assumption has recently been challenged for some taxa. For instance, Martiny et al. (2015) found that

many functionally important microbial traits, such as the ability to use simple carbon substrates, are not deeply conserved. In plants, Sedio et al. (2018) found that for tropical (but not temperate) plants, metabolomic compounds involved in plant defense showed no phylogenetic signal, with similarity among plant congeners extremely low. This finding suggests that important functional traits are not always conserved.

The strength of phylogenetic signal is also highly variable among traits. Blomberg et al. (2003), for example, found that although phylogenetic signal is ubiquitous across a wide range of plant and animal taxa, on average most traits have less phylogenetic signal than expected under *Brownian motion evolution*. They also found that traits varied significantly in how much phylogenetic signal they had, with behavioral traits more evolutionarily labile than physiological, body size, and life history traits.

In summary, phylogenetic approaches may be particularly useful for understanding difficult-to-measure but highly conserved and coevolved interactions like food webs and mutualisms or in large sets of species for which particular traits are either not available or incompletely sampled. Trait-based approaches may be more appropriate for functions mediated by less conserved traits, extremely well measured traits, or sets of species interacting within trophic levels.

Convergence Does Not Undermine the Use of Phylogenies to Understand Community Function

PRO: Convergence mainly occurs in biogeographic isolation, so convergence does not undermine the use of phylogenies to understand community function, particularly at local or regional scales.

CON: Convergence is widespread at the trait level, and in modern times biological invasions have led to increased co-occurrence of convergent species. Thus, convergence is likely to confound phylogenetic analyses of community functions more often than suggested by the pro argument.

Pro. Evolutionary convergence is the evolution of similar features or traits in species with distinct *evolutionary histories* (Losos 2017). Convergence as a process has been well studied (Mahler et al. 2017). However, there is little direct evidence that convergence causes problems for measuring niche similarity or ecological function across communities using phylogenetic tools. There are two main reasons for this. First, although convergent evolution is widespread, it is relatively uncommon compared with trait differentiation, reducing the extent to which it erases the phylogenetic signal of niches and associated

functions in whole communities. Second, when convergent evolution does occur, it most often involves species that are separated in different biogeographic regions and continents (Pigot et al. 2020), making even strong convergence unimportant for the study of local communities and their function.

Many impressive examples of convergence exist in geographically isolated lineages. The convergent evolution of the *Euphorbias* of South Africa and the Cactaceae (cacti) of North and Central America is associated with shared functions in their respective communities, yet they occur in distant biogeographic regions (Bennici 2003). Similarly, the convergence of Arctic auks and Antarctic penguins happened in the context of ecological opportunity and biogeographic isolation (Pigot et al. 2020). Except in gardens and zoos, members of these taxa do not live in the same communities. Thus, unless studies are using phylogenies to infer ecological or functional information at global scales, this type of convergence rarely confounds the relationship between phylogeny and ecological function in a community context.

Co-occurrence of convergent forms remains the exception rather than the rule, and the extent to which even these cases undermine phylogenetic approaches is debatable. Examples of within-community convergence do exist, such as the swifts (Apodidae), which are convergent in body form and diet with the swallows (Hirundinidae), another distantly related aerial insectivore (Videler 2006; Pigot et al. 2020). Multiple members of both families often occur together in the same avian communities, but despite their co-occurrence and similar niches and morphology, phylogeny is still informative about ecological function. Any tip in the community phylogeny connected to a swift by a very short branch length will be another swift, occupying the same dietary niche. Conversely, longer branch lengths will be, on average, associated with a range of different ecological niches. Unlike the shortest branch lengths, the likelihood that these longer branch lengths lead to a species with a similar dietary niche is low, despite unrelated aerial insectivores (swallows) being present in the community. Thus, overall, evolutionary convergence is unlikely to greatly reduce the utility of phylogenies to understand the ecological function of local communities.

Con. Through most of the history of life on this planet, biogeographic isolation has provided the most common conditions for convergence to occur (Losos 2017). In the modern world, human-induced transport of species (i.e., biological invasions) has resulted in extensive mixing of species with completely distinct biogeographical and evolutionary histories. Convergent traits between invaders and native residents are common, reflecting the need for exotic species to fit ecologically in order to effectively invade (Sax and Gaines 2008; Lai et al. 2015; Sol et al. 2022). Distantly

related invaders can have completely novel roles in their invaded communities (e.g., cane toads as toxic prey; Shine 2011) or replace natives that once filled similar ecological roles (e.g., exotic annual grass invasion of low-elevation Californian habitats; Seabloom et al. 2003). Thus, while convergence may be relatively rare on a global scale historically, biological invasions make it much more common for species with convergent traits to be found in the same communities. Thus, convergence is no longer a special case, having become fairly common in many invaded systems around the world (Cleland et al. 2011; Drenovsky et al. 2012; Lai et al. 2015). Modern invaded communities therefore exemplify common scenarios for which phylogenetic information is unlikely to predict ecological function, owing to convergence on function by native and nonnative community members or simply due to novel functions of multiple invaders originating from disparate evolutionary origins.

In summary, across the history of this planet, convergence has largely occurred when evolution has led to similar strategies to the same challenges in distinct geographic locations. The prevalence of biological invasions worldwide in modern times, however, has changed how often convergent lineages now co-occur and thus how likely convergent lineages are to have major impacts on community function. Thus, we might expect that phylogenies are more informative for increasingly uncommon pristine, intact native communities, in contrast to communities that have experienced extensive resorting of species through biological invasions.

Macroevolutionary History Can Be Used to Predict Community Function in the Future

PRO: Phylogenies have been useful for ecological forecasting, including projections of range shifts in response to biological invasions and changing climates.

CON: The novel communities of the Anthropocene are developing at an unprecedented speed and in ways that have not been experienced in the past. The dominance of *transient* and *novel environments* means that past adaptations are unlikely to provide sufficient information to predict responses to novel future conditions.

Pro. Evidence for the importance of phylogenetic history for understanding modern community responses to future environmental change comes from studies of range shifts and range overlaps at biogeographic scales. A combination of ecological trait divergence and phylogenetic distance can predict the extent of geographical range overlap among related species (Pigot and Tobias 2013). This is in line with Jordan's (1908) rule, which states that

closely related forms of species tend to occupy adjacent but nonoverlapping ranges, at least in groups where *allopatric speciation* predominates, but it also reflects competitive exclusion among ecologically similar forms (Grether et al. 2017). Using phylogeny and traits to quantify biotic interactions, including the probability of coexistence among related species, is an important step toward refining range shift models (Lavergne et al. 2010; Grether et al. 2017). Thus, phylogenetic information can increase the predictive power of models forecasting changes in future community composition, particularly in animal systems (Tobias et al. 2020).

Phylogenetic tools have also been widely used for forecasting invasion success and biodiversity loss. In some cases, communities comprising species from phylogenetically distinct lineages have been shown to be less likely to experience alien establishment (i.e., invasion) compared with communities composed of closely related species (Gerhold et al. 2011). Competitive exclusion among closely related territorial bird species has been shown to drive non-random declines or local extinctions in habitat fragments (Bregman et al. 2015; Ulrich et al. 2017). These and hundreds of similar findings suggest that phylogeny—particularly in conjunction with functional traits—provides valuable insights about the potential for future biodiversity loss, biological invasions, and the impacts of climate and land use change on ecological communities.

Con. Human activities over the last century have led to unprecedented changes in our environment, both in the speed with which environmental conditions are changing and in the creation of no-analog *novel conditions* around the globe (Williams and Jackson 2007; Williams et al. 2007; Hobbs et al. 2009). Schimel et al. (2013) further point out that much of our understanding of how species interact with the environment is based on *steady state*, not rapidly changing or *transient conditions*. Many drivers of current global change are tipping systems out of steady-state dynamics and into *transient states* (Trisos et al. 2020). Thus, we lack a robust theoretical framework for how we expect phylogeny to relate to function in such transient systems. There is no reason to expect that past evolution in traits will be useful for predicting which traits will be prevalent in future environments because of the expectation that current and near future environments will differ markedly from the past (Chapin et al. 2000; Dakos et al. 2019).

In summary, our future undoubtedly comes with uncertainty relating to the novel changes that humans are imposing on the natural world. Although evolutionary history may help us understand certain questions about community climate adaptation, particularly those relating to large-scale processes like geographical range shifts, there are many questions about smaller-scale local community-scale changes in response to novel and transient communities that history may not help much for finding answers.

Synthesis

The Contextual Importance of Evolutionary History for Community Function

The debate presented above is intentionally highly caricatured. It is intended as an exercise in exploration of the different perspectives of ecologists and evolutionary biologists working on community function. The pro and con arguments force us to think beyond absolutes. While micro- and macroevolutionary processes clearly can and often do affect the functioning of ecological communities, the question is under what conditions is evolutionary history essential to include and when can it be comfortably ignored? What is clear is that the contributions of micro- and macroevolution depend tremendously on ecological and evolutionary context. For instance, phylogenetic signal in interaction networks varies with taxonomic and spatial scale (Mouquet et al. 2012; Peralta 2016). Moreover, the extent to which phylogeny predicts interacting partners, module composition, species roles, and nested patterns in interaction networks varies across clades and interaction types (Peralta 2016; e.g., in rodents and their ectoparasites [Hafner and Nadler 1988] but not in bird hosts and avian malaria [Fecchio et al. 2018]). The richness of natural communities requires that we consider context to understand the contributions of evolution to ecological function.

Figure 1 provides a broad overview of the aspects of organisms and environments that might influence the relative importance of evolutionary history to ecological function. Meta-analyses exploring each of these qualities are generally lacking but could provide us with greater confidence in identifying contexts under which evolutionary processes are more or less important than ecological function. Box 1 goes deeper into some specific hypotheses about these contexts to nurture further debate and discussion, but again it is not exhaustive. Space precludes our delving into all of the areas we have outlined as important (fig. 1; box 1), so we focus on a selection of these, including a mixture of essential points and those that have received less attention previously in the literature.

Habitat. Habitat types and characteristics likely influence the importance of micro- and macroevolution to ecological function. We expect most readers to say they know this already. Despite that general understanding, no study, to our knowledge, has synthesized or reviewed this in depth. A valuable contribution to future literature would be a study of whether macroevolutionary history is better at explaining variation in community function in some habitats than others. For example, does macroevolutionary history explain function in habitats with persistent niche construction by sessile species, as in long-lived corals or trees that modify

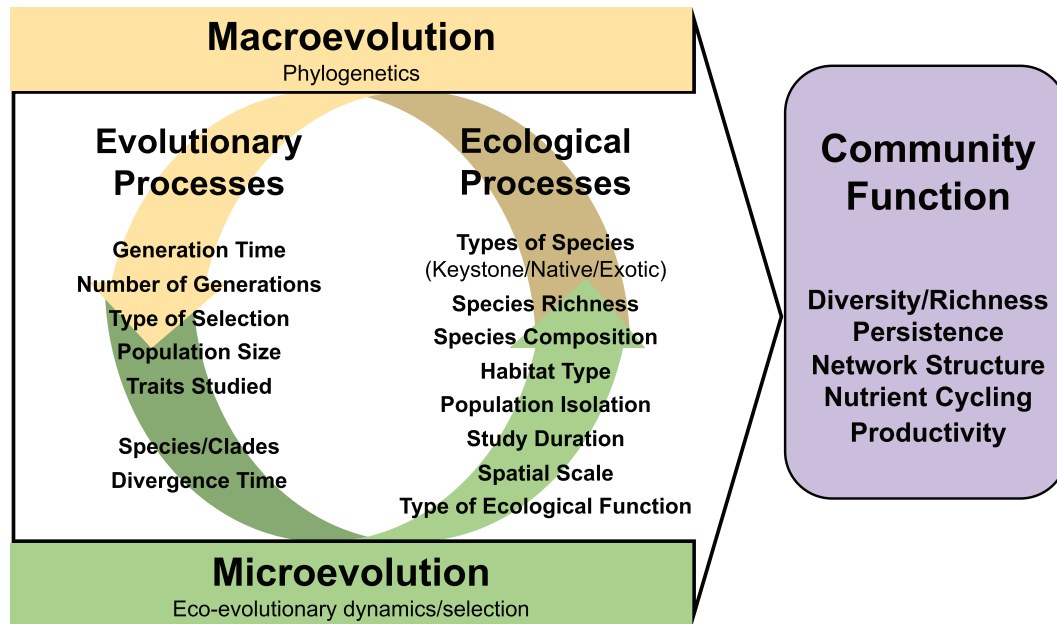


Figure 1: Conceptual diagram showing the complex relationship between the evolutionary and ecological processes involved in determining how communities' function. Each of the functions in the box on the right result from a combination of micro- and macroevolutionary processes. Both average values and variation in functions are important for community functioning and are impacted by evolutionary processes.

Box 1: Contextualizing when, and how much, evolutionary history informs ecological function

We present below hypotheses and associated questions that could be explored by synthesizing the existing literature to provide deeper insight into when and how much evolutionary history affects the functioning of ecological communities. Some of these hypotheses have already been addressed in the literature, but many have not.

1. **Which ecological function?** *Hypothesis:* Numerous ecological functions are measured within communities (e.g., ecological resilience, productivity, and species interaction networks). These functions may differ systematically in how much they are affected by evolutionary history. *Question:* Which ecological functions are more or less affected by macro- or microevolutionary history?
2. **Which organisms?** *Hypotheses:* Short-lived organisms, such as microbes, may respond more rapidly to environmental changes than longer-lived organisms because of short generation times and large population sizes. Longer-lived, larger organisms may construct their niches with lasting impacts, potentially affecting ecological function over long time periods. *Questions:* (a) Do short-lived species perform ecological functions more influenced by rapid eco-evo dynamics than organisms with longer life spans? (b) Do organisms that modify their environment through extensive niche construction (e.g., forest trees) have a greater tendency to perform ecological functions influenced by macroevolutionary history? (c) Are the ecological functions of sessile versus mobile organisms more influenced by macroevolutionary history for the same reasons?
3. **Which temporal scale of evolution?** *Hypothesis:* We know that the importance of macroevolution to ecological function depends on the swath of evolutionary history sampled. Even within a particular clade, sampling across deep nodes may increase the predictive power of evolutionary history to explain ecological function. *Question:* How do we explicitly consider the magnitude of divergence time between species in assessing the importance of macroevolutionary history to understanding community function?
4. **Which traits?** *Hypothesis:* Traits linked to different functions (e.g., resource acquisition, edaphic tolerance) are not equally likely to reflect long-term versus short-term evolutionary history. *Questions:* (a) For which types of traits does evolutionary history contribute most to predicting ecological function? (b) Are traits that can be measured over huge swathes of evolutionary history (e.g., millions of years), like specific leaf area, more or less likely to inform ecological function than traits that are specific to younger clades, like orchid floral structures? (c) Is evolutionary history more or less informative in traits with specific trophic functions (e.g., mammal teeth and bird beaks)? (d) Can the *response-effect trait framework* inform which traits and functions are most affected by evolutionary history?
5. **What population size?** *Hypothesis:* Small populations are subject to random effects of *genetic drift* and extinction. *Question:* Does population size and isolation increase or decrease the importance of eco-evo dynamics or macroevolution to community function by limiting the genotypes/species present and the rate and direction of evolution?
6. **What type of selection?** *Hypothesis:* The nature of selection may determine whether eco-evo dynamics are long or short term. Directional selection may cause rapid eco-evo dynamics but then stasis, if genetic variation is depleted; in contrast, frequency-density-dependent or fluctuating selection all maintain genetic variation within populations and may result in oscillating, longer-term eco-evo dynamics. *Question:* Does directional selection lead to persistent changes in ecosystem function or are microevolutionary effects on ecological function maintained only in cases of persistent, self-sustaining eco-evolutionary dynamics or fluctuating selection?
7. **How much intra- versus interspecific trait variation?** *Hypothesis:* When the magnitude of functional trait differences is much greater among versus within species, this distinctiveness should increase the importance of deeper macroevolutionary history but may simultaneously decrease the importance of microevolution, as changes in genotype frequencies (evolution) will have little effect compared with species sorting. *Question:* How does the relative magnitude of intra- and interspecific trait variation influence the relative importance of macro- and microevolution in predicting ecological function?
8. **Which habitats?** *Hypothesis:* Some types of habitats are inherently more stable than others. The stability of habitat patchiness in space or time may increase the importance of evolutionary history to ecological

Box 1 (Continued)

- function. *Question:* Does the degree to which evolutionary history affects ecological community function vary according to the temporal and spatial scales of habitat heterogeneity and transience?
9. **How diverse?** *Hypothesis:* Microevolutionary effects and eco-evo dynamics may be stronger in smaller, simpler communities, with fewer species exerting conflicting selection on traits and with less ecological redundancy among species. *Question:* Do simple, less diverse communities exhibit stronger effects of micro- and macroevolutionary history, possibly because there is less ecological redundancy?
 10. **Study duration?** *Hypothesis:* Studies with longer duration over which ecological function is measured may reveal a greater role for micro- and macroevolutionary history than shorter-term studies. This may occur because a wider range of ecological conditions is sampled, like wet and dry years, in which different clades thrive, thus increasing the importance of phylogeny in explaining ecosystem function over time. *Question:* Does evolutionary history provide the greatest insights about ecological function when studies are long term?
 11. **Which spatial scale?** *Hypothesis:* Several syntheses have already shown that spatial scale is important in how much evolutionary history influences ecological function. Spatial scale of the community studied will determine habitat heterogeneity, species pools, the relative importance of local interactions versus habitat changes, and the number of ecological opportunities for specialized clades. *Question:* Over what spatial scales does evolutionary history provide the greatest insights into ecological function, and about which specific functions?

habitats and accumulate mutualists and enemies over decades? A synthesis of micro- and macroevolutionary impacts on ecosystem functions across different habitat types and characteristics could determine whether there are commonalities in evolutionary impact across Earth's diverse habitats.

Organisms, Traits, and Functions. Variance in the relative importance of evolutionary processes to contemporary community function may also stem from inherent properties of organisms and traits (which are related to evolutionary history) and the ecological functions measured. In the macroevolution portion of the debate, we presented arguments for and against the importance of using phylogenetic analyses in addition to functional traits to understand community function, and most evidence points to the use of both traits and phylogeny as the best option in most cases (Rezende et al. 2007; Weber et al. 2017). Seemingly conflicting perspectives on the relative importance of traits versus macroevolutionary history may reflect the types of traits and community functions selected for studies of different taxonomic groups, as well as varying definitions of community. For example, most studies of plant community function look at within-trophic-level aspects of function, like productivity, while animal studies are more likely to focus on cross-trophic functions, like food web structure or predator-prey dynamics, or interactions within trophic levels, like competition. As a result of the focus on different functions, studies of plant communities typically measure

traits linked to physiological function, like specific leaf area (SLA; Pérez-Harguindeguy et al. 2013), while those measured in animal communities tend to reflect the acquisition of specific resources (beak size, teeth structure, etc.; Tobias et al. 2020). SLA can be measured across a huge evolutionary swathe of the plant kingdom. In contrast, animal studies often focus on clade-specific traits (Schluter et al. 1985; Navalón et al. 2019), like incisor size and shape (Dayan and Simberloff 1994; Kohli and Rowe 2019), that are intimately linked to the acquisition of specific resources (Schluter et al. 1985; Dayan and Simberloff 1994; Rico-Guevara et al. 2019) and are typically studied across less diverged taxa and shorter evolutionary timescales. Thus, the choice of ecological function affects both which traits are measured and the likelihood that evolutionary history is important for understanding community function. Traits involved in the outcomes of species interactions (one type of ecological function) typically have strong phylogenetic contributions (Pigot and Tobias 2013; Weber et al. 2017). In contrast, traits associated with productivity, like SLA, can have low (e.g., Li et al. 2017) or more variable (e.g., Scher et al. 2020) phylogenetic signal. Syntheses comparing the influence of micro- or macroevolutionary history across traits associated with different functions are needed.

Spatial and Temporal Scale. We have long known that spatial and temporal scale affects the strength and importance of evolutionary history in explaining the functioning

of ecological communities (Webb et al. 2002; Kembel and Hubbell 2006; Backhaus et al. 2021; Leibold et al. 2022). While we do not want to rehash old results, we wish to re-emphasize how crucial scale is in interpreting the importance of evolutionary history to ecological function. Generally, communities sampled at smaller spatial scales exhibit weaker phylogenetic influence on function compared with those sampled at large scales, and they often show different patterns of evolutionary relationships: small-scale communities often have low levels of co-occurrence among close relatives, while at larger spatial scales closely related lineages or clades co-occur often. For small communities or patches, habitat heterogeneity, stochasticity (Shoemaker et al. 2019), and dispersal (Backhaus et al. 2021) can overwhelm lineage effects, and competition might result in exclusion of closely related species (e.g., plants [Jin et al. 2020] and bats [Patrick and Stevens 2016]). In contrast, sampling large spatial scales that include diverse habitats and cross biogeographic boundaries capture deeper phylogenetic divergences, which increase macroevolutionary contributions to ecosystem function. The magnitude of microevolutionary eco-evolutionary feedbacks will also be affected by spatial scale, as dispersal distances of individuals will affect frequency- and density-dependent processes and gene flow (Govaert et al. 2022).

In addition to spatial scale, temporal scale is also key, as it reflects the amount of time that evolution has had available to work on a trait or community. Paleoecological studies using soil, lake, or ice cores are extremely valuable for studying the combined ecological and evolutionary processes structuring communities over time, as they allow us to look at cross sections of evolutionary history at community scales (Orson 1999; Pandolfi et al. 2020; Fletcher et al. 2021; Wu and Colautti 2022). The duration of studies of contemporary communities is also important and plays an often-underappreciated role in the detection of evolutionary forces influencing ecological function. We hypothesize that the longer the duration of a study, the greater the importance is likely to be of both micro- and macroevolution to ecological function. Studies spanning many years will capture greater interannual environmental variation than short-term studies. We might therefore expect different clades to contribute to ecological function under average versus extreme years, thereby contributing to ecosystem function through something like a *portfolio effect*. We might also expect extreme events to exert strong selection on populations within communities, leading to populations with different trait distributions from those preselection, again possibly altering ecological function through eco-evolutionary feedbacks (e.g., Fitzpatrick et al. 2015). Testing these hypotheses requires long-term datasets that capture extensive interannual variation in a wide range of systems.

Conclusions

Reconstructing the evolutionary and ecological histories that have together given rise to extant communities will help us understand both the small-scale and the large-scale processes that explain how ecological communities operate. This understanding is particularly important in today's world, where we are seeing the creation of novel no-analog environmental conditions and associated communities. Yet sometimes we can safely ignore both micro- and macroevolutionary history. In sum, it is time to explore how, when, and to what extent—rather than whether—evolutionary processes affect the function of extant ecological communities.

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Statement of Authorship

S.Y.S. proposed the debate topic that forms the basis of this article. The authors initially took primary responsibility for developing the ideas for and writing the following sections: microevolution pro (J.A.L.), microevolution con (A.R.I.), macroevolution pro (J.A.T.), and macroevolution con (M.M.M.). S.Y.S. and M.M.M. took primary responsibility for the introduction and synthesis section and for editing to create a cohesive voice; all authors contributed to editing all parts.

Data and Code Availability

No data were used in this article.

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