

Ecological Interactions and Macroevolution: A New Field with Old Roots

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Abstract

Linking interspecific interactions (e.g., mutualism, competition, predation, parasitism) to macroevolution (evolutionary change on deep timescales) is a key goal in biology. The role of species interactions in shaping macroevolutionary trajectories has been studied for centuries and remains a cutting-edge topic of current research. However, despite its deep historical roots, classic and current approaches to this topic are highly diverse. Here, we combine historical and contemporary perspectives on the study of ecological interactions in macroevolution, synthesizing ideas across eras to build a zoomed-out picture of the big questions at the nexus of ecology and macroevolution. We discuss the trajectory of this important and challenging field, dividing research into work done before the 1970s, research between 1970 and 2005, and work done since 2005. We argue that in response to long-standing questions in paleobiology, evidence accumulated to date has demonstrated that biotic interactions (including mutualism) can influence lineage diversification and trait evolution over macroevolutionary timescales, and we outline major open questions for future research in the field.

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1. INTRODUCTION

Ecological interactions between species are ubiquitous in nature. The major classes of interactions (mutualism, competition, predation, herbivory, and parasitism) are globally distributed and can have major impacts on population dynamics, natural selection, and short-term evolution. However, despite extensive empirical and theoretical evidence that ecological interactions drive microevolution, understanding the role of ecological interactions in shaping patterns of evolution over geologic timescales has remained a central challenge. Links between ecological interactions and macroevolution (speciation, extinction, and long-term phenotypic evolution) have been notoriously difficult to test. Yet, research questions at this intersection remain fundamental to our understanding of biology. As a result, researchers have been asking whether interactions are a force driving macroevolution and investigating the evolution of interactions themselves over macroevolutionary timescales for over a century, with the field progressing through major changes in research questions, theoretical advances, methods development, and data availability.

Because the study of ecological interactions and macroevolution (see the sidebar titled *Macroevolution and Ecological Interactions*) has spanned multiple research disciplines over a century and has used an array of methodologies, conceptual threads and innovative insights are easily lost. Here, we take a deep historical perspective on the study of ecological interactions using a macroevolutionary approach. We begin with a historical overview, discussing the trajectory of this important and challenging field through time. We divide research into work done before the 1970s (dominated by ideas from Darwin and the Modern Synthesis), research between 1970 and 2005 (the flourishing of macroevolutionary research using fossil data, as well as concepts from evolutionary ecology), and work done after 2005 (marked by an increase in the use of neontological data to study macroevolution alongside paleobiology). Specifically, we ask the following questions:

1. What are the major hypotheses linking species interactions and macroevolution across historical eras of research?
2. How has our understanding of the role of biotic interactions in macroevolution changed over time?

MACROEVOLUTION AND ECOLOGICAL INTERACTIONS

The term macroevolution was coined simultaneously with microevolution by Filipchenko¹ (Philipschenko 1927). Since the mid-twentieth century, it has been widely defined as all evolution above the species level (e.g., Rensch 1959, Stebbins 1974, Stanley 1975, Eldredge 1988, Jablonski 2017); we use this definition here. Macroevolution comprises multiple distinct research traditions, including paleobiology (which uses fossil data to understand long-term evolution) and neontological research on long-term evolution (which uses contemporary species trait data and phylogenies to model evolutionary history). While these approaches are historically connected and ask similar questions, they differ in their inherent limitations and have progressed relatively independently (Jablonski 2008a).

Here, ecological interactions refer to interactions (both pairwise and diffuse) among different species within communities, including interspecific competition (interactions that decrease the fitness of both participants), antagonism (interactions that increase the fitness of one participant while decreasing the fitness of the other), mutualism (interactions that increase fitness for both participants), and commensalism and amensalism (interactions that are neutral for one participant). Ecological interactions also comprise networks of interacting species, and the term is synonymous with the terms biotic interactions and species interactions in this article. We do not consider intraspecific interactions, nor do we consider hybridization, despite their importance for evolution.

¹Different spellings of the author's name reflect English and German transliterations from the Cyrillic.

3. What new questions are we asking now that could not be asked or answered previously? What historical questions, if any, have been recently neglected and deserve to be revisited? Conversely, what questions have researchers largely answered?

Our goal is to synthesize questions and hypotheses across eras, demonstrating the continuities and changes in our understanding of the role of ecological interactions in macroevolution since the early twentieth century. We argue that, in resolution to early debates, research over the last 50 years has unequivocally demonstrated that biotic interactions contribute to shaping macroevolution; abiotic processes alone cannot explain patterns of diversity and processes of diversification for all taxa. Furthermore, research has demonstrated that not only competition and antagonism (parasitism, predation, and herbivory) but also mutualism can play an important role in driving long-term patterns of evolution. Additionally, we identify several major questions that are either current areas of cutting-edge research or that have the potential to be foci in the field going forward. Some of these questions have had a continuous progression of attention from evolutionary biologists since the mid-twentieth century, whereas others have been relatively neglected or are new.

What does it mean to ask if ecological interactions are important or play a role in macroevolution? Researchers have considered links between broad-scale evolutionary dynamics and ecological interactions for over a century, but different thinkers have described this interface in a variety of ways. For example, for Jablonski (2008a, p. 715), “[c]lades are said to interact when interactions between their constituent organisms, populations, or species impinge significantly on speciation, extinction, morphological variety, and/or spatial deployment on one or more of these clades.” Demonstrating that interactions are responsible for macroevolutionary change requires showing that, as Jablonski writes, they have an “overriding role at large spatial and temporal scales, or in molding species- and clade-level dynamics. . . . In short, we lack a powerful theory for how lower-level processes cascade upwards to clade-level dynamics, and vice versa.” Weber and colleagues (2017, p. 291) more broadly refer to “the long-term consequences of the interplay between ecological and evolutionary dynamics,” noting, like Jablonski (2008a), that

One possibility is that such [ecological] dynamics have negligible effects on longer-term patterns of ecological change and diversification. . . . An alternative possibility, 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.

Most recently, Harmon et al. (2019, p. 770) echo these definitions, while adding that “[m]any prominent theories of macroevolution. . . include species interaction as a primary factor.” All of these authors recognize that demonstrating an effect of biotic interactions in macroevolution involves demonstrating the effect of species interactions on lineage diversification (speciation and extinction) and/or trait evolution, the two phenomena centrally emphasized in macroevolution research since the 1970s (e.g., Stanley 1979, Gould 2002).

However, in addition to these two phenomena, integrating ecological interactions into our understanding of macroevolution also requires asking questions about the macroevolutionary dynamics of ecological interactions themselves. How frequently species and clades acquire, lose, or shift their interactions with other taxa and how readily different interaction outcomes change over evolutionary time are the focus of much recent interest; changes not only in pairwise interactions but also in larger interaction networks are of interest, as Harmon et al. (2019) point out. This broader formulation of changes is encompassed within Weber et al.’s (2017, p. 291) “long-term consequences of the interplay between ecological and evolutionary dynamics,” a sort of eco-evolutionary dynamics extending over deep time. Consequently, we consider that demonstrating a role for ecological interactions in macroevolution encompasses either

Diversification: net changes in the species richness of clades over time due to the combined effects of speciation and extinction

Neontologist: an evolutionary biologist who works with extant species data rather than fossils, in contrast to a paleontologist, who works with fossils

(a) evidence consistent with ecological interactions having an effect on trait evolution or lineage diversification (including lineage turnover) or (b) the quantitative assessment of changes in species or clade interactions themselves over geologic timescales.

Within these broad themes, the specific questions that evolutionary biologists have emphasized in studying the role of ecological interactions in macroevolution have varied over time. Major questions have included the following: Do ecological interactions play any substantial role in macroevolution, or is macroevolution driven primarily by abiotic factors? If biotic interactions shape macroevolution, how do biotic and abiotic factors interact to influence trait evolution and diversification over deep time? How do the microevolutionary effects of species interactions scale upward to affect macroevolutionary processes? What effects on diversification and trait evolution do different types of interactions have? How do these processes and patterns vary across different regions of the biosphere? Finally, how easily do species and clades acquire, switch, and escape their interactions with other taxa? In taking a historical approach to this field, our goals are to synthesize research over the last century, highlight the many connections between paleobiological and neontological approaches to these questions, and suggest avenues for future work.

2. ECOLOGICAL INTERACTIONS AND MACROEVOLUTION BEFORE 1970

The idea that interactions among species drive evolutionary change is an old one. In *On the Origin of Species*, Charles Darwin's (1859) descriptions of how natural selection works often explicitly use examples involving predation and competition. For generations of biologists, Darwin's metaphor of the tangled bank has symbolized the profound and myriad ways in which ecology and diversification are intertwined. Darwin envisioned lineage diversification patterns (what we would now call clade replacement dynamics) as driven largely by competition. In his later monograph on orchids, Darwin (1877) anticipated much twentieth-century work on mutualism and coevolution. Around this same time, Bates (1862) and Müller (1879) documented mimicry as an early example of macroevolutionary patterns of convergence in response to selection imposed by biotic interactions.

Moving forward, most of the participants in the Modern Synthesis recognized but rarely acknowledged the evolutionary significance of ecological interactions, devoting only a few pages in each of their books to this topic. Among the most macroevolution-focused of the Modern Synthesis founders, however, the American paleontologist George Gaylord Simpson (1902–1984) and the German neontologist Bernhard Rensch (1900–1990) described the potential for biotic interactions to influence macroevolution. Simpson and Rensch were contemporaries who wrote their initial synthesis works (Simpson 1944, Rensch 1947) during World War II while unable to obtain each other's recent publications (Rensch 1959). Following the war, they were able to read each other's work and correspond directly (Rensch 1959). Their revised postwar syntheses of macroevolution, *The Major Features of Evolution* (Simpson 1953) and *Evolution Above the Species Level* (Rensch 1959; originally published in German in 1954), come to similar conclusions about many evolutionary phenomena, including the role of biotic interactions in evolution over geologic time. Both Simpson and Rensch, while acknowledging the role of abiotic forces, argued that competition and trophic interactions shape the diversification and extinction of clades, drawing examples primarily from the waxing and waning of vertebrate clades in the Cenozoic. Rensch (1959, p. 239) downplayed abiotic processes and argued in particular that extinction due to phyletic competition (what we would now call clade replacement) is “by far the most frequent” kind of extinction. Simpson proposed the subsequently influential concept of adaptive zones (corresponding to clade-level niches) into which clades diversify. He was clear that such zones could be defined by

biotic interactions, giving the example of how the adaptive zone of certain horses may have been formed by the diversification of grasses in the Tertiary. At the same time, Simpson also warned that even if interactions do govern such adaptive zones, it can be hard for paleontologists to prove this rigorously. Rensch's (1947) work strongly influenced Simpson, who read the first edition in German. *Major Features of Evolution* (Simpson 1953) would later inspire twenty-first-century work on adaptive radiation and macroevolution.

Other participants in the Modern Synthesis were also thinking and writing about the potential for ecological interactions to affect evolution, although often from microevolutionary perspectives. Competition—both intra- and interspecific—was recognized as a driver of adaptive radiation not only by Simpson but also by his contemporaries, including David Lack (1947). Ronald Fisher (1930), Ernst Mayr (1942), Ivan I. Schmalhausen (1949), and Theodosius Dobzhansky (1950) acknowledged that competition, predation, and parasitism could drive natural selection and speciation. In his biotic interactions hypothesis, Dobzhansky (1950) also suggested that an increased relative importance of biotic interactions (including competition, predation, and symbiosis) in the tropics could be responsible for the latitudinal gradient in species diversity seen across many clades. In another example, Fisher (1930) made links between biotic selection and the evolution of mimicry. However, it was the botanists of the era who most clearly emphasized a role for ecological interactions in evolution. The work of Verne and Karen Grant (Grant & Grant 1965) elucidated the role of pollinators in plant speciation. G. Ledyard Stebbins (1974), synthesizing the work of the Grants and others on tabulating shifts among pollination syndromes, anticipated the kinds of large comparative analyses of interactions that would flourish many decades later. However, while ecological interactions were recognized as evolutionary forces, most research in this period focused on other, unrelated aspects of evolution. Even those biologists who thought interactions were important generally discussed them relatively little compared to abiotic factors (e.g., Fisher 1930, Schmalhausen 1949, Simpson 1953, Rensch 1959).

In the 1960s, interest increased in biotic interactions as drivers of macroevolutionary patterns. It was during this time period that evolutionary ecologists began to hypothesize about how species coevolve over short and long timescales. For example, Ehrlich & Raven's (1964) groundbreaking paper on butterflies and their host plants suggested that interactions between plants and herbivores led to increased lineage diversification rates via a process termed escape-and-radiate coevolution, inspiring decades of subsequent research in coevolution, macroevolution, and plant-insect ecology. Additionally, groundbreaking studies on character displacement (Brown & Wilson 1956), niche partitioning (MacArthur 1958), and trade-offs in organismal trait allocation (e.g., Cody 1966) were building to form an exciting foundation for linking ecological interactions to phenotypic divergence among species. The post-Modern Synthesis focus of evolutionary ecologists on species interactions thus set the stage for the burst of macroevolutionary thought focused on such interactions in the 1970s.

3. ECOLOGICAL INTERACTIONS IN MACROEVOLUTION FROM 1970 TO 2005

For some biologists today, the term macroevolution harkens to a body of research in paleobiology that flourished during the 1970s and 1980s. This era of research is most commonly associated with a group of American paleobiologists that included Steven Stanley (1941–), Niles Eldredge (1943–), David Raup (1933–2015), J. John Sepkoski Jr. (1948–1999), Elisabeth Vrba (1942–), and Stephen Jay Gould (1941–2002), although many other researchers in many countries also published in this tradition during that era and more recently. Macroevolutionary research in this era primarily utilized data from fossils and focused on questions relating to the evolution of

Origination:

the origin of new taxa, whether species (speciation) or higher categories such as genera or families

organisms' traits as well as taxonomic diversity over geologic timescales. Macroevolutionists during this era were explicit in thinking of diversity and diversification as net consequences of speciation and extinction, with a focus on the insights that could be derived through the statistical examination of paleontological data over deep time (Stanley 1979, Eldredge 1988). Major questions discussed during this period included how speciation and extinction have shaped the diversity of organisms through geologic time, how such rates vary with external factors, whether morphological evolution is primarily directional or stochastic, how to reconcile microevolutionary change with macroevolutionary patterns, and whether macroevolutionary change is gradual or saltational (Stanley 1979, Eldredge 1988, Gould 2002). Much paleobiological research in macroevolution during this era focused on hard-skeletoned marine invertebrates (mollusks, corals, bryozoans, trilobites, and brachiopods) since these taxa are fossilized at high rates at many localities, facilitating large sample sizes for statistical analyses, but important work was also done on other groups, including terrestrial plants and vertebrates, during this period as well.

With regard to the nature of macroevolutionary change, some paleobiologists (e.g., Eldredge 1971; Eldredge & Gould 1972; Stanley 1975, 1979; Gould 2002) considered speciation to be very rapid, with new species then changing little morphologically over long periods of time. This emphasis on brief periods of morphological change followed by morphological stasis as the tempo and mode of evolution (the punctuated equilibrium of Eldredge & Gould 1972) implied that most macroevolutionary change is tied to differential speciation (origination) and/or differential extinction (e.g., Gould 1982), while most microevolution can proceed without impacting long-term trajectories. In this view, new species arise as a result of allopatric speciation, and a macroevolutionary process called species selection (Stanley 1975) governs which lineages survive and which go extinct. Proponents of species selection suggested that organismal traits (which can be heritable and thus can be shared among clade-mates) can affect origination and extinction rates (Jablonski 2008b). Some aspects of this formulation of how macroevolution proceeds were anticipated by Soviet paleontologists in the 1960s, such as Lidiya A. Nevesskaya (1923–2009), Vasilii Ye. Ruzhentsev (1899–1978), and Valeriya N. Ovcharenko, who argued that new species arise rapidly in the fossil record via allopatric speciation and then undergo little morphological change (Ruzhentsev 1964, Nevesskaya 1967, Ovcharenko 1969; for an overview in English of Nevesskaya's career, see Rozanov et al. 2010). American paleobiologists independently came to similar conclusions and further synthesized the hypothesized connections between allopatry, speciation, and macroevolutionary change, becoming aware of the Soviet work only around 1975 (Eldredge 1971; Stanley 1975; N. Eldredge & S.M. Stanley, personal communication). The species selection perspective promoted both new statistical approaches in paleontology and neontology (e.g., Stanley 1979, Rabosky & McCune 2010) and the formulation of new hypotheses about how biotic interactions might affect diversification over geologic timescales.

3.1. Biotic and Abiotic Interactions in Macroevolution from 1970 to 2005

For paleobiologists during this period, biotic interactions were a subject of keen interest but also of disagreement and controversy. Although many paleobiologists, like many of their Modern Synthesis predecessors, focused primarily on abiotic drivers of macroevolutionary patterns, they also conducted groundbreaking work on the potential role of biotic interactions in shaping their systems. Disagreement revolved around two primary questions:

1. Have biotic interactions had a considerable role in shaping macroevolutionary patterns, or instead, has evolution over geologic timescales been driven primarily by abiotic (geologic, climatic, extraterrestrial) processes?

2. Since most interest in biotic interactions and macroevolution focused on competition and antagonism, are the macroevolutionary effects of mutualistic interactions detectable in the fossil record?

We discuss these in turn.

3.2. The Importance of Biotic Drivers of Macroevolutionary Patterns Relative to Abiotic Factors

Several of the founders of modern macroevolutionary research argued vigorously that biotic interactions were highly influential in shaping macroevolutionary signatures. For example, based in part on her empirical work on Tertiary cockle radiations in the Paratethys Sea, Nevesskaya² (Nevesskaya 1967, Nevesskaya et al. 2001) articulated her view that “in the evolution of all groups the scale of environmental variation, both abiotic and biotic [variation], . . . must also have played a great part” (Nevesskaya 1967, p. 12). Ovcharenko (1969) identified rapid speciation in brachiopods, which she argued was driven by selection from predators. In another example, in his first paper on macroevolution and species selection, Stanley (1975, pp. 648–49) argued that much of the macroevolutionary dynamics of clades was driven by biotic interactions:

Differential survival [of lineages] is in response to the basic agents of nonaccidental extinction: predation, competition, and habitat alteration. . . . Even many aspects of the latter are biological in nature. *We must conclude that biological interactions play a major role in governing large-scale evolutionary trends. Critical factors will vary from taxon to taxon.* Predator-limited groups will tend to shift toward efficient predator avoidance and food-limited groups, toward efficient food capture. Adaptive breakthroughs in the form of morphologic innovations will improve chances for survival in certain clades and may also accelerate rates of speciation by increasing the incidence of survival of peripheral isolates. (emphasis added)

Stanley continued to emphasize the potential role for biotic interactions in macroevolution in his subsequent work, rejecting abiotic or other stochastic processes in support of species selection (and the biotic interaction drivers thereof) as a major driver of clade replacement (e.g., Stanley 1979, 2008).

The hypothesis that competitors and predators together comprise a major selective force on the evolution of lineages and clades attracted a great deal of subsequent empirical attention. Interest in the macroevolutionary effects of these interactions primarily took two forms. First, competition appeared in some cases to prevent diversification. Diverse and ecologically dominant incumbent clades could, by having preempted ecological opportunities, prevent other clades from diversifying into the same niches. The sudden extinction of an incumbent clade—such as in a mass extinction—would then allow diversification of a new clade into the same adaptive zones. The classic example of this phenomenon is the diversification of mammals following the extinction of nonavian dinosaurs at the end of the Cretaceous (Simpson 1953, Jablonski 2008a); such a role for competitive incumbency in macroevolution was not contested among paleobiologists of this era. Second, quantitative paleobiologists such as Sepkoski endeavored to test the hypothesis that clades measurably affect each other’s diversification dynamics via competition. Going back to Darwin (1859), many candidate examples of such clades replacing each other had been proposed, but in this era, few stood up to scientific scrutiny (Benton 1987). Some replacements that appeared to be at least partially driven by competition included the diversification of bivalves versus

²Many of Nevesskaya’s works have been translated into English, but her name has been transliterated in two different ways.

brachiopods (Miller & Sepkoski 1988, Sepkoski 1996), cheilostome bryozoans versus cyclostome bryozoans (McKinney 1995, Jablonski et al. 1997, Sepkoski et al. 2000), and a series of ecological replacements among clades of terrestrial vascular plants (Knoll 1984). Bryozoans are particularly interesting because they overgrow each other when they compete for substrates, and this overgrowth is then fossilized, revealing a consistent competitive advantage of cheilostomes over cyclostomes over the past 100 Myr (McKinney 1995). Using pairs of coupled logistic equations that model speciation and extinction rates in relation to a carrying capacity, Sepkoski found that it was possible to generate diversity through time curves that resembled empirical curves for cheilostome and cyclostome bryozoans (Sepkoski et al. 2000) and for bivalves and brachiopods (Sepkoski 1996). Despite evidence consistent with a hypothesis of competition, Sepkoski and others noted that abiotic processes (e.g., mass extinctions) have unequivocally affected diversity dynamics in bryozoans, bivalves, and brachiopods. Furthermore, it was difficult to assess the effects of predation—as well as poorly fossilizing competitor taxa—on any of these clades.

Although antagonism and competition are challenging to disentangle empirically in the fossil record, some paleobiologists have heavily emphasized the importance of both interactions. One of the most prominent of these investigators, Geerat Vermeij (1946–), argued strongly for a role for biotic interactions in shaping macroevolution. In a wide-ranging series of books and papers (e.g., Vermeij 1977, 1978, 1987, 1994, 2013), Vermeij argued for a pervasive history of escalation (enemy-driven evolution, i.e., continuous increases in offense and defensive adaptations among certain clades) in biotic interactions throughout much of the Phanerozoic. He noted an increasing frequency of defensive and offensive armature and predation damage in fossil marine faunas, variation in these traits among ocean basins today, and the evolution of poorly defended marine lineages into refugial habitats. Based on these observations, Vermeij proposed that competition and predation have played a fundamental role in trait evolution, lineage diversification, and community assembly during the past 500 million years. Vermeij also extensively discussed the interplay of biotic and abiotic factors (e.g., Vermeij 1978). Although Vermeij's work has received a great deal of attention among neontologists, many other paleobiologists of this era have argued for a role for varied antagonistic interactions in macroevolution, including the bioturbation of sediments by mobile marine invertebrates negatively affecting certain others in the Paleozoic (e.g., Thayer 1983), predation in driving the Cambrian explosion (e.g., Stanley 1976, Marshall 2006), and herbivory in the evolution of insects and herbivorous mammals (e.g., Stebbins 1981, Labandeira 1998, Strömberg 2006).

The paleobiologist Leigh Van Valen (1935–2010) advocated a unique view of how biotic interactions might be important in macroevolution. His Red Queen hypothesis (Van Valen 1973) [named after a fictional character in Lewis Carroll's (1872) novel *Through the Looking-Glass*] argues, based on empirical data (a compiled collection of taxonomic survivorship curves through time from clades across the tree of life), that taxa within fossil clades show a constant rate of extinction. For Van Valen, the main mechanism that might produce such a pattern would be a constant rate of environmental change (echoing Fisher 1930), and the main mechanism that can account for such environmental deterioration would be a never-ending coevolutionary arms race between every species and all of its competitors, predators, pathogens, and parasites.

In contrast, many other paleobiologists put forth compelling arguments for the primacy or exclusivity of abiotic processes—climatic changes, plate tectonics, volcanism, mountain formation, erosion, sea-level changes, glaciation, and impacts of extraterrestrial objects with the earth—in governing macroevolutionary dynamics. For some of these paleobiologists, macroevolution is essentially driven by abiotic processes, with the role of biotic factors being largely limited to microevolutionary change. There is indeed a massive amount of evidence for geologic and climatic changes in Earth's history, as well as mass extinctions. Evolutionary biologists have

recognized mass extinctions as being important in evolution since at least the Modern Synthesis (Mayr 1942) and have generally considered them to be the result of abiotic events, even if the particulars remain unclear (Raup 1991, Gould 2002). The Modern Synthesis had found ample evidence for climatic and geologic processes driving allopatric speciation (Mayr 1942). Additional evidence from the fossil record was invoked to argue for a primary role for abiotic processes in diversification. Vrba, for example, drew from her empirical work on temporally coordinated patterns of species turnover in mammal faunas in east Africa to propose that most extinction—and therefore most macroevolutionary patterns—are driven by abiotic factors such as climate change, reasoning that biotic factors would not be expected to result in temporally coordinated patterns of local extinction (Vrba 1985, 1993). Eldredge (2003, p. 28) stated “nothing much in the way of adaptive evolutionary change takes place unless and until physical disturbance impacts ecosystems.” In support of this conclusion, he cited evidence for coordinated turnover within mammal and trilobite faunas and the role of mass extinctions in lineage turnover (Eldredge 1988, 1999, 2003). He also pointed out that extrapolating the importance of competition from local scales—where it is easily studied as an ecological and microevolutionary process—to explain the macroevolutionary dynamics of clades over deep time is an unsupported assumption (Eldredge 1988). Gould (2002), going farther, proposed that focusing on competition as a macroevolutionary force is a lingering unhelpful consequence of Darwin’s (1859) use of competition as a rhetorically plausible, noncreationist explanation for evolutionary change. Gould and Raup (Raup & Gould 1974, Gould 2002) also proposed the hypothesis that species drift or phylogenetic drift is common in clade dynamics. According to this hypothesis, many clades are species poor at any given time due to random chance; their disappearance (or shift among areas of morphospace) is the result of the cumulative effects of localized and idiosyncratic abiotic or biotic factors. In this way, they argued, larger-scale patterns of lineage diversification may be effectively decoupled from any particular deterministic factor.

Subsequently, other paleobiologists came to similar conclusions: Different external factors operate at different scales in evolution, and the role of ecological interactions among organisms in evolution is largely confined to microevolution (e.g., Barnosky 2001; for a review, see Benton 2009). Lieberman (2012), interestingly, acknowledged that several model adaptive radiations (anole lizards, sticklebacks) are indeed biotically driven but argued that they are exceptional among clades in this regard. A subset of the literature advocating for abiotically driven macroevolution has focused on testing the Red Queen hypothesis as a general hypothesis of biotically driven macroevolution (in an allusion to the Red Queen, such hypotheses are referred to by some as Court Jester hypotheses) (Vrba 1993, Eldredge 1988, Barnosky 2001; for a review, see Voje et al. 2015). However, it should be emphasized that some advocates for a prominent role for biotic interactions—Vermeij, Sepkoski, and others—conducted their work independently of the Red Queen framework, focusing on other mechanisms by which biotic interactions might drive macroevolution. Subsequent empirical reanalysis of taxon durations in the fossil record has also cast doubt on the rates of extinction cited by Van Valen (see summary in Finnegan et al. 2008). Perhaps the most intriguing of abiotic explanations for macroevolutionary dynamics came from Raup (1991) and Gould (2002), who proposed an underappreciated role for impacts of extraterrestrial objects with the Earth as a fundamental driver of extinction, and therefore of macroevolution, over deep time.

The debate over the relative importance of biotic interactions was never fully resolved within paleontology (for a review, see Voje et al. 2015). Although some macroevolutionists took strong views in favor of or against biotic interactions in driving speciation, extinction, and morphological change, many investigators were more concerned about understanding the relative importance of biotic and abiotic factors and whether they reinforce or are orthogonal to each other in particular clades. Indeed, the view that macroevolution is driven primarily by abiotic processes continues

to be widely advocated in paleontology (e.g., Benton 2009, Myers & Saupe 2013), while others have continued to advocate for a strong driving role of biotic interactions in tandem with abiotic interactions (Jablonski 2008a, 2017; Liow et al. 2016). Ultimately, the debate about the relative importance of biotic and abiotic drivers of macroevolution in different contexts continues in part because of the difference in our ability to test hypotheses related to biotic versus abiotic drivers of temporal patterns in fossil data. Abiotic processes unquestionably have a strong effect on evolution. However, reconstructing past interactions from fossil data was (and remains) a challenge (Stanley 2008). Paleontological studies of biotic interactions must rely primarily on evidence such as the assessment of predation and competition based on feeding morphology (Vermeij 1987), comparisons to extant communities (Vermeij 1978), or, more rarely, direct fossil evidence for predation, parasitism (including insect herbivory), or competition (Vermeij 1978, 1987; Labandeira & Currano 2013; Liow et al. 2017; Gao et al. 2019). Accordingly, even some of those who argued for ecological interactions as an important driver of macroevolution (Schmalhausen 1949, Rensch 1959, Van Valen 1973) presented little evidence to support this contention.

We also note briefly the literature from this era on biotically induced indirect effects on the global ecosystem affecting subsequent macroevolutionary trajectories of clades. For instance, as mentioned above, the diversification of mobile, bioturbating benthic marine invertebrates likely led to a permanent change in benthic marine environments, affecting the subsequent macroevolution of certain sessile marine invertebrate clades that depended on undisturbed sediment for habitat (Thayer 1983). Similarly, Bambach (1999) proposed that the colonization of land by terrestrial plants in the Ordovician and the subsequent diversification of angiosperms in the Cretaceous increased nutrient runoff to oceans, facilitating the diversification of some predatory marine animal clades.

3.3. If Biotic Interactions Have Left Consistent Macroevolutionary Signatures, Do All Forms of Interactions Have Similar Effects?

Although much interest in biotic interactions during this era focused on competition and antagonism, and at least one paleobiologist explicitly discounted mutualism as a macroevolutionary agent (Van Valen 1973), a number of paleobiologists took a keen interest in whether mutualisms are important in affecting long-term phenotypic evolution, speciation, or extinction. Paleobiologists interested in mutualism focused particularly on photosymbioses (involving scleractinian corals and bivalves, including Cenozoic *Tridacna* giant clams, Permian alatoconchids, and Jurassic-Cretaceous rudists, with symbiotic algae) and pollination (particularly by insects of angiosperms but also of seed ferns and gymnosperms). Much of this research focused on documenting the origin of mutualisms in the fossil record, mutualism-relevant traits (Cowen 1983, Crepet 1984, Crepet & Friis 1987, Seilacher 1990, Labandeira 1998, Ren 1998, Friis et al. 2006, Ren et al. 2009), and transitions between mutualism (e.g., insect pollination) and free-living status (e.g., wind pollination) (Zavada & Crepet 1981, Crane et al. 1989). A few investigators hypothesized about the relationship between mutualism and diversification dynamics. Anticipating problems that would later occupy the attention of many evolutionary ecologists, opinions on the long-term consequences of mutualism were varied. Some paleobotanists explicitly argued, based on fossil flowers with recognizable suites of traits that in the Holocene are associated with specialization to particular pollinator guilds, that pollinators not only were responsible for floral-trait evolution but also in part promoted the Cretaceous-Tertiary diversification of angiosperms (e.g., Crepet 1984). Vermeij (1978) extended his ideas of escalation to mutualism, suggesting that the same resource-rich tropical ecosystems that promote antagonistic and competitive escalation also promote the evolution of highly specialized, mutually dependent, and species-rich mutualisms. In contrast to the views

of paleobotanists, some researchers focusing on marine photosymbioses hypothesized that mutualistic symbiosis might make invertebrate clades more vulnerable to extinction (Seilacher 1990, Jablonski 2008a). In particular, analyses of extinction rates in scleractinian corals showed that putatively photosymbiotic lineages had higher extinction rates across the Cretaceous-Tertiary mass extinction than did putatively nonsymbiotic lineages (Rosen & Turnšek 1989, Kiessling & Baron-Szabo 2004). While not resolved in this era, the question of the role of mutualism in macroevolution found renewed interest several decades later using neontological approaches.

3.4. The Rise of Evolutionary Ecology

While paleobiologists were constructing a novel and exciting framework for understanding evolution over geologic time, neontologists were also making exciting progress on the problem of how ecological interactions affect trait evolution and lineage diversification using extant organisms. Like paleontologists, neontological researchers of this time period were approaching questions about the role of biotic interactions in shaping biodiversity using a wide range of taxa and interactions. Their work resulted in the flourishing of the field of evolutionary ecology, born out of the foundations laid by researchers such as Brown & Wilson (1956), MacArthur (1958), and Ehrlich & Raven (1964). New research in this era included work on topics such as coevolution (Thompson 1994) and endosymbiosis (Margulis 1970) and a renewal of interest in adaptive radiation (Schluter 2000), parasite evolution (Price 1980), and mutualism (Boucher et al. 1982). Around the same time, several prominent books were published laying out the phylogenetic neontological research model as a path for young biologists. These included Harvey & Pagel's (1991) *The Comparative Method in Evolutionary Biology* and Brooks & McLennan's (1991) *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology*. For many of the taxa considered by neontologists of this time, data from the fossil record were considered somewhat limited relative to those available for groups such as bivalves and mammals that were commonly studied by paleobiologists, resulting in these two approaches being complementary in driving the research forward.

Despite their use of different methods, evolutionary ecologists and paleobiologists of the time were certainly well aware of, and inspired by, each other's work. For example, neontological research on adaptive radiation and parallel evolution was influenced by Simpson and Gould (Losos et al. 1998, Schluter 2000, Harmon et al. 2003). Paleobotanists, entomologists, and neontological botanists collaborated to investigate the origins of pollination of angiosperms by insects (for a review, see Pellmyr 1992). Paleobiologists, most notably Vermeij (1978, 1987, 1994) but also Stanley (1979), integrated neontological developments in the study of coevolution into their work, and Jablonski frequently cited the neontological literature in his work on macroevolution (e.g., Jablonski 2008a, 2017).

Despite interest in evolution over geologic timescales, most evolutionary ecology research of this period heavily emphasized ecological interactions as a microevolutionary rather than macroevolutionary process. In part, this was due to the difficulty of testing existing hypotheses about the macroevolution of species interactions using extant clades at a time when molecular phylogenetics and phylogenetic comparative methods (PCMs) (see the sidebar titled Phylogenetic Comparative Methods) were in their infancy (Losos 2011). One important challenge that became clear during this era was the difficulty of linking microevolutionary processes to macroevolutionary patterns. The view that macroevolutionary change is essentially decoupled from microevolutionary processes within populations and over shorter timescales implies that much of what is studied by neontologists—microevolution at the level of populations and recent speciation events—reveals little about macroevolution (Stanley 1979, Eldredge 1988, Gould 2002). In the

PHYLOGENETIC COMPARATIVE METHODS

Phylogenetic comparative methods (PCMs) are a suite of statistical tools for modeling macroevolutionary patterns on molecular phylogenies. These methods include phenotypic diversification models, which quantify the rates and direction of phenotypic change through time on a phylogeny, as well as lineage diversification models, which quantify patterns of net speciation and extinction dynamics over time (O'Meara 2012, Pennell & Harmon 2013, Harmon 2019). The development of new PCMs is a rapid (and sometime contentious) area of contemporary research in evolutionary biology. While most PCMs use purely neontological data (e.g., molecular phylogenies built using DNA alignments and contemporary trait data for estimating phenotypic evolution), some methods are also able to incorporate paleontological data (Hunt & Slater 2016).

realm of ecological interactions in macroevolution, this perspective would imply that the microevolutionary effects of species interactions (which were the focus of so much research during this period and subsequently) do not necessarily tell us anything about the impact of those same interactions over macroevolutionary timescales (Jablonksi 2008a). On the contrary, a number of studies during this period began to link interactions in the present day to macroevolutionary patterns (e.g., Schluter 2000, Eldredge et al. 2005); some have argued subsequently that we cannot understand evolution over deep time without such observations made in shallower time scales (Losos 2011).

Regardless, during this period, innovative and exciting advances in our understanding of ecological interactions as a driver of evolutionary processes came from microevolutionary approaches in evolutionary ecology, from theory in evolutionary ecology, and from paleontological perspectives. Furthermore, many investigators working in the macroevolutionary tradition today were trained in evolutionary ecology during this exciting time period.

4. ECOLOGICAL INTERACTIONS IN MACROEVOLUTION FROM 2005 TO THE PRESENT

By the early 2000s, the groundwork was set for a burst of neontological research into the role of biotic interactions in driving long-term patterns of phenotypic evolution, speciation, and extinction. The primary questions posed by previous eras have remained largely open. However, over the past several decades, the field of macroevolution has undergone a massive increase in PCM-based neontological research. This increase has coincided with a shift toward a focus on more pattern-based, rather than process-focused, research and heightened attention among neontologists on quantifying the magnitude and direction of macroevolutionary responses to different biotic interactions in different evolutionary contexts.

While the neontological approach has drawbacks and limitations (some of which are not present in fossil-based approaches), its development in previous decades opened the door for modern neontologists to study biotic interactions that were previously difficult to trace using fossil data alone. For example, there has been a recent surge of studies focused on reconstructing historical biotic interactions from traits of contemporary species, either directly or via proxies with clear function. These include suites of traits correlated with specialization to particular interaction guilds [e.g., pollinators (Kay et al. 2005, Okuyama et al. 2008, Martén-Rodríguez et al. 2010, Lagomarsino et al. 2017), diet types (Burin et al. 2016)], traits that have clear associations with the presence or absence of particular interactions [e.g., defensive traits (Weber et al. 2012, Weber & Agrawal 2014, Foisy et al. 2019), floral traits (Sargent 2004, Davis et al.

2014), fruit traits (Nascimento et al. 2020)], or the presence or absence of interactions themselves (Friedman & Barrett 2008, Chomicki & Renner 2017, Werner et al. 2018, Sato & Toju 2019). Phylogenies have also been used to infer the composition of past communities of co-occurring species (e.g., Mahler et al. 2010) and to test the hypothesis that interacting clades have diversified in parallel (de Vienne et al. 2013, Hembry et al. 2013, Clayton et al. 2016, Wang et al. 2019).

The recent burst of neontological studies has also opened the door for more direct integration of phylogenetic and trait data with field and laboratory studies. In this approach, tests of the presence and selective effects of interactions between extant species that have been chosen carefully from the phylogeny are used to bolster our understanding of the macroevolutionary trajectories of lineages (Losos 2007, Weber & Agrawal 2012, Clayton et al. 2016, Harmon et al. 2019). For example, in neontological adaptive radiation research, ecological studies of competition in the field have been used to interpret phylogenetic patterns (Losos 2009). Field studies can be used to assess the ecological significance of traits that function within biotic interactions, and those traits can then be reconstructed as character states, allowing biotic interactions in the evolutionary past to be inferred. As we describe in Section 5, this trait-based work has revealed compelling evidence of macroevolutionary patterns consistent with biotic interactions shifting lineage diversification rates and influencing trait evolution and such interactions themselves undergoing transitions among lineages within a clade.

Despite advances in our ability to use neontological data to address hypotheses about the macroevolutionary effects of species interactions, in many cases the mechanisms by which species interactions shape macroevolution remain unclear. For instance, the gain of mutualism is associated with increased diversification rates in a number of studies, but macroevolutionary approaches alone cannot distinguish among the multiple hypotheses about how this may occur mechanistically (Hembry et al. 2014). One strength of the macroevolutionary framework is that it can be agnostic to microevolutionary processes while revealing aspects of evolutionary history, such as diversification, turnover, or trait evolution. However, the difficulty of linking microevolutionary processes to macroevolutionary patterns is a major challenge for the field going forward and a reason why this topic has been historically so difficult to study. As such, alongside massively increasing the popularity of the neontological, PCM-based approaches, modern work on ecological interactions and macroevolution has undergone a shift toward focusing more on quantifying patterns and away from testing hypotheses about process (Losos 2011). While it is prudent for neontologists to be cautious about interpretations of macroevolutionary data, testing fundamental questions about process remains central to our understanding of biology.

One approach to overcoming the limitations of neontological approaches is to link these studies with other approaches, including paleontological perspectives (Losos 2011). While neontological approaches using PCMs are much more common now than in previous eras, macroevolutionary research using fossil data or combinations of fossil and neontological data sets continues to be an active and innovative area of the field (e.g., Slater 2013, 2015; Silvestro et al. 2015; Bapst et al. 2016; Hunt & Slater 2016; Lloyd 2016; Voje 2018) and includes statistical approaches designed to test the hypothesis that competition between clades influenced their diversification dynamics (Slater 2013, 2015; Silvestro et al. 2015; Pires et al. 2017). Such methods allow researchers to ask fundamental questions about the history of biotic interactions while minimizing the limitations of either approach. Interestingly, however, paleontological and neontological research programs still largely progress independently of one another, despite their shared historical roots and their similarities in questions and theories. Regardless, advances in both traditions over the past several decades potentially represent great improvements in our ability to study past biotic interactions, allowing us to test hypotheses about the role of biotic interactions in macroevolution (Harmon et al. 2019).

5. CLASSIC HYPOTHESES REVISITED IN LIGHT OF CONTEMPORARY STUDIES

After two decades of using phylogenetic comparative methods to study the role of ecological interactions in macroevolution, what have we learned?

Contemporary macroevolutionists have largely shifted away from the historical debate about whether biotic interactions indeed shape macroevolutionary change over deep time. As we have noted, this debate was never really fully resolved within paleobiology. We agree with Eldredge (2003), Barnosky (2001), and Lieberman (2012), for instance, that the evidence for geologic and climatic factors affecting macroevolution is ample and incontrovertible. Neontological macroevolutionists have continued to demonstrate the role of abiotic processes in macroevolution (e.g., Rolland & Condamine 2019). Yet whether or not biotic interactions substantially affect diversification and trait evolution over macroevolutionary time remains a question of fundamental relevance to our understanding of evolution, as does the question of how macroevolutionary processes themselves affect interactions among organisms.

The evidence that has accumulated over the past two decades through the use of fossils, PCMs, and other evolutionary ecological approaches in a phylogenetic framework supports the hypothesis that ecological interactions can be important factors in macroevolution. There is ample evidence that species interactions can influence diversification rates and trait evolution. There is a large and growing body of research demonstrating that interactions themselves change over macroevolutionary time, in some cases linking these changes to shifts in diversification and trait evolution. In the next section, we provide more detail on examples that support these claims.

5.1. Ecological Interactions Can Influence Diversification Rates and Trait Evolution

In our view, particularly compelling evidence for a role of ecological interactions in affecting diversification is provided by those studies in which ecological interactions are reconstructed as traits, studies that use island-like systems to reconstruct the coexistence of interacting species, and studies demonstrating the role of competition in adaptive radiation. For example, multiple studies have shown that the repeated evolution of traits (or suites of traits) is associated with a given interaction within a single clade. For instance, in the Neotropical plant genus *Costus*, ancestral character state reconstruction of morphological and color traits that predict pollinator guilds (i.e., orchid bees or hummingbirds) indicates that hummingbird pollination syndromes have evolved repeatedly (Kay & Schemske 2003, Kay et al. 2005). Trait-interaction correlations and the repeated transition of pollination syndromes provide strong evidence that interactions with hummingbird pollinators have driven not only trait evolution but even some of the speciation events within *Costus* (Kay et al. 2005). Similar examples of trait changes associated with changes in interactions have been documented using PCMs in other mutualisms, particularly pollination (Sargent 2004, Okuyama et al. 2008, Martén-Rodríguez et al. 2010, Lagomarsino et al. 2017, Tripp & Tsai 2017) but also plant defense mutualisms (Weber et al. 2012), as hypothesized by Modern Synthesis botanists (Grant & Grant 1965, Stebbins 1974). Extensive research on adaptive radiation, particularly tests of the ecological theory of adaptive radiation, have found that resource competition is associated with trait and lineage divergence in model adaptive radiations (Schluter 2000), particularly those on islands [e.g., Galápagos finches (Grant & Grant 2008), anoles (Losos 2009)] and lakes [e.g., sticklebacks (Schluter 2000)]. Furthermore, correlations between host defense traits, parasite traits, and parasite and host phylogenies suggest macroevolutionary relationships between interactions and trait evolution in plant-herbivore and vertebrate-ectoparasite systems (Clayton et al. 2016, Endara et al. 2018).

We also now have evidence that interactions can influence lineage diversification rates. For example, extrafloral nectaries, which attract predatory arthropods that then defend plants from herbivores, have evolved repeatedly in angiosperms and are associated with increased diversification rates in the plant lineages that have them (Weber & Agrawal 2014). As with examples involving parallel evolution of traits functionally associated with certain interactions, the strong trait–interaction correlation and repeated association between the trait and diversification rates constitute evidence that plants’ interactions with both herbivores and protective mutualists have affected both their trait evolution and their lineage diversification. Other studies have found increases in diversification associated with the gain of mutualism in varied taxa (Lengyel et al. 2009, Marazzi & Sanderson 2010, Gómez & Verdú 2012), herbivory in insects (Wiens et al. 2015), and defensive traits in animals (Blanchard & Moreau 2017). We also consider some of the asserted examples of incumbency effects—in which an ecologically dominant clade prevents the diversification of ecologically similar clades until the dominant clade is removed (Schluter 2000, Nevesskaja et al. 2001, Jablonski 2008a)—to be compelling, providing evidence for a second mechanism by which competition can shape macroevolutionary trajectories. Alongside these studies, we consider the growing interest in ways to assess competition’s effects on diversity over deep time using fossils and molecular phylogenies to be a promising trend that may provide additional examples of biotic interactions shaping macroevolutionary patterns. In addition to these examples combining ecological and phylogenetic data, we note the literature on the role of biotic interactions in driving speciation (e.g., Smith & Benkman 2007, Hosoi et al. 2010, van der Niet & Johnson 2012).

As anticipated by paleobiologists studying flowering plants and photosymbiotic marine invertebrates in the late twentieth century, many good examples of ecological interactions shaping macroevolution involve mutualistic associations such as defensive mutualism (including associations in which plants or corals provide shelter or food to predatory arthropods who then protect their hosts from herbivores or grazers) and pollination. In part, this abundance of examples from mutualism is due to the ability to treat biotic specializations within certain mutualisms as traits that can be examined in a PCM framework. However, these studies also highlight the macroevolutionary importance of an interaction type that is ecologically pervasive but was difficult to access via fossil data alone in many cases. The finding that mutualism can play this kind of role in shaping macroevolution also underscores the taxonomic differences in emphasis between paleobiology and neontology. Many paleobiologists in this field have focused on competitive or trophic interactions, primarily among hard-skeletoned marine invertebrates or terrestrial mammals, since they leave ample fossil records. In contrast, neontological macroevolutionists interested in interactions work on a broader range of taxa, including mutualism-rich plant–animal interactions, as they are able to use molecular phylogenies to work with taxa that fossilize less readily.

5.2. Ecological Interactions Themselves Evolve Over Geologic Timescales

An extensive number of studies, involving reconstructing host taxa or interaction guilds as traits and inferring ancestral character states in a PCM framework, have documented changes in interactions within clades over macroevolutionary time. This work has shown that some interactions are highly conserved over evolutionary time (Sachs & Simms 2006, Luo et al. 2018, Lutzoni et al. 2018), whereas others are surprisingly labile. Further, interactions may be labile at certain phylogenetic or biogeographic scales but conservative in others (e.g., Hembry et al. 2013, Chomicki et al. 2015). Some highly specialized interacting clades diversify asynchronously (Ramírez et al. 2011). Furthermore, clades can undergo repeated independent shifts onto the same partner taxa, such as multiple independent transitions to bird or bat pollination within an angiosperm clade or to ectomycorrhizal symbiosis with angiosperms within Boletales fungi (Kay et al. 2005, Lagomarsino et al. 2017, Sato & Toju 2019). In addition, such approaches can reveal

transitions among interaction types themselves (such as the gain and loss of mutualism) within a clade (Sachs & Simms 2006, Barbeitos et al. 2010). A smaller number of studies have documented changes in the links between taxa within species interaction networks over evolutionary time by integrating network and phylogenetic approaches (e.g., Hembry et al. 2018). Although changes in interactions over macroevolutionary time are traditionally not considered to be evidence of interactions shaping macroevolution, we argue that an understanding of this phenomenon is essential to a complete integration of ecological interactions into the field of macroevolution.

The evidence for biotic interactions shaping macroevolution in certain ways does not mean that biotic interactions govern all aspects of macroevolution. The best evidence we have comes from only a few kinds of interactions: relatively specialized mutualisms, parasitic associations, and competition within the early stages of adaptively radiating clades. Some neontological studies that looked for macroevolutionary impacts of interactions have not found evidence for them (Smith et al. 2008, Afkhami et al. 2018, Nelsen et al. 2018, Foisy et al. 2019, Kaur et al. 2019), just as microevolutionary studies do not always find evidence of local adaptation associated with biotic interactions even when interactions affect fitness (Hargreaves et al. 2020). Furthermore, aside from a few well-studied adaptive radiations and a few clear incumbency examples, demonstrating that competition within a clade or between two clades has shaped either of their diversification dynamics remains challenging. Does this total body of research provide evidence that, generally, most kinds of biotic interactions are pervasive in driving trait and lineage diversification patterns over deep time? Or are mutualism and parasitism often drivers of macroevolutionary change, while competition and predation are rarely so (except perhaps in the early stages of adaptive radiation), as many paleobiologists (Benton 1987, Eldredge 1988, Vrba 1993, Gould 2002, Lieberman 2012) have argued? Currently, the available evidence does not allow us to determine the answer to this question. Simpson's (1953) warning that the effects of biotic and other factors can be difficult to distinguish in the fossil record remains true for many interactions and for both paleontological and neontological approaches alike.

Ultimately, however, the total body of work on interactions and macroevolution up to this point provides rigorous evidence to support the views of Nevesskaya (1967), Stanley (1975, 1979), Vermeij (1987, 1994), Van Valen (1973), and Sepkoski (1996, Sepkoski et al. 2000) that biotic interactions play a role in driving macroevolutionary change—although they do not specifically endorse the Red Queen, escalation, or clade-competition hypotheses per se. Neontological work over the last two decades has provided a set of well-developed examples, and recent paleontological studies support our conclusions that ecological interactions can influence diversification and trait evolution alongside abiotic factors and that the interplay between the two can be assessed using fossil data (for reviews, see Jablonski 2008a, 2017).

6. MAJOR QUESTIONS ABOUT ECOLOGICAL INTERACTIONS IN MACROEVOLUTION FROM 2005 TO THE PRESENT

Over the past 15 years, biologists have diversified and refined the questions that they ask at the nexus of species interactions and macroevolution. Some of these questions remain open from earlier debates; others are novel. Below are key outstanding questions that are actively receiving attention in this field.

6.1. What Are the Relative Roles of Abiotic Environmental Processes and Biotic Interactions in the Macroeolution of Clades?

Although we have argued that available evidence makes it clear that both biotic interactions and abiotic processes can shape the course of macroevolution, it remains unclear how the two interact

to drive the evolution of clades and what their relative importance is in different contexts. This question is inherently difficult to test. PCMs as well as historical biogeographic methods (analytical methods that allow the biogeographic histories of clades and lineages to be reconstructed over geologic timescales) allow the relative strength of correlations between abiotic and biotic factors, lineage diversification dynamics, and trait evolution to be assessed for individual clades. Numerous studies have tested for patterns consistent with the macroevolutionary effects of abiotic and biotic factors in the diversification of individual clades (e.g., Wagner et al. 2012, 2014; Lagomarsino et al. 2016; Tripp & Tsai 2017) and have shown that both can predict clade diversification. A suite of models is available to test for correlations between abiotic or biotic variables and macroevolutionary phenomena such as shifts in lineage diversification rates [e.g., hidden state speciation and extinction (HiSSE) (Beaulieu & O'Meara 2016)] or trait divergence/convergence (e.g., Drury et al. 2016, 2018b). The development of methods that can address this question is an active area of research, and many creative opportunities exist for evaluating the relative effects of biotic and abiotic factors on macroevolutionary patterns in the future.

6.2. Does Competition for Resources Drive Trait Divergence? What Are the Limits to This Process?

These questions, dating back to Simpson (1953) and Schmalhausen (1949), have been continuously pursued by evolutionary ecologists and have inspired a great deal of postmillennial macroevolutionary research (e.g., Schluter 2000; Harmon et al. 2003; Mahler et al. 2010; Wagner et al. 2012, 2014). Although character displacement driven by competition has been widely demonstrated neontologically within closely related populations and species (Schluter 2000), it is considerably more challenging to demonstrate a role for competition over a macroevolutionary timescale, as witnessed by disagreements among paleobiologists about this topic (Stanley 1975, Eldredge 1988, Sepkoski 1996, Gould 2002). Currently, these questions are being addressed via simulations or reconstructions of past communities based on phylogenetic data. In such simulations, communities of co-occurring, potentially competitive taxa are reconstructed over time, either from molecular phylogenies (Mahler et al. 2010) or fossil data (Silvestro et al. 2015). This approach is particularly useful for island-like systems that have undergone recent radiation (Losos 2009, Mahler et al. 2010, Wagner et al. 2014), in which assumptions about past biogeographic history can be made more rigorously, and competition can be assessed neontologically via field studies. Other studies of this type have aimed to link lineage accumulation dynamics to the ecological effects of competition (Rabosky 2013, Pires et al. 2017). Adding to the challenge, adaptive radiations seem to pass through different phases of trait evolution and disparity (Schluter 2000). Competition may indeed drive diversification and trait disparity during the early stages of a radiation, but following this initial stage, subsequent diversification may be driven by noncompetitive processes (such as climatic fluctuations or interisland dispersal). Such a sequence of stages raises the possibility that the microevolution we observe today is not representative of other phases of the diversification process.

New models of trait evolution and diversification that explicitly incorporate the ecological divergence of coexisting species with similar traits have also recently been developed (e.g., Drury et al. 2016, Nuismer & Harmon 2015). These contributions are a promising step toward directly testing for patterns consistent with competition-based divergence across species in deep time. Competition is invoked not only as a driver of divergence (and thus diversification) but also, via incumbency, as a constraint on trait and lineage diversification, both within and between clades, dating back to Simpson's (1953) vision of adaptive zones (Jablonski 2008a). The longstanding hypothesis that most extinction is driven by competition (Rensch 1959, Van Valen 1973) may

in part be testable via ecological studies on how frequently invasive species extirpate native taxa (Gurevitch & Padilla 2004, Bellard et al. 2016). Under what circumstances competition drives diversification, and under what circumstances it impedes it, remains an open question. We also note that distinguishing the effects of competition and predation remains challenging, although studies that examine increases in diversification associated with defensive traits (Blanchard & Moreau 2017, Foisy et al. 2019) or trends in these traits themselves (Agrawal et al. 2009) may represent one way to detect the macroevolutionary signatures of antagonistic interactions.

6.3. What Is the Role of Mutualism in Trait and Lineage Diversification?

While there has been simmering interest in mutualisms (especially pollination) as drivers of macroevolutionary patterns since Darwin, mutualism traditionally received relatively little attention from many paleobiologists (as described in Section 3.3). However, the macroevolutionary effects of mutualism have received a great deal of attention from evolutionary ecologists since the early 2000s. Some studies have shown increases in net diversification rates associated with mutualisms or traits involved in mutualism (Lengyel et al. 2009, Gómez & Verdú 2012, Weber & Agrawal 2014), while others have not (e.g., Smith et al. 2008, Afkhami et al. 2018). These studies largely model associations between evolutionary states of traits associated with mutualism and diversification rates. How mutualism actually spurs diversification remains an open question; in fact, theoretical and empirical work suggest that mutualism may instead restrict diversification (Yoder & Nuismer 2010, Hembry et al. 2014), while paleontological studies suggest that some obligate mutualisms increase extinction rates (e.g., Kiessling & Baron-Szabo 2004). One potential explanation is merely that the acquisition of mutualism represents the gain of ecological opportunity that permits a greater net lineage accumulation rate than would otherwise be possible (Chomicki et al. 2019). In other cases, mutualism may control the trajectories of morphological or other trait change or diversification through shifts among partner guilds (Kay et al. 2005, Okuyama et al. 2008, Martén-Rodríguez et al. 2010, Lagomarsino et al. 2017). Mutualisms can vary considerably from one another and over space and time, varying in their degree of specialization, obligacy, and mutual benefit (Bronstein 2015). Thus, mutualism in general is unlikely to have a one-size-fits-all effect on macroevolutionary dynamics. A future goal in this field is to merge theory and empirical studies to build a more nuanced framework in which to investigate if and how different types of mutualism affect macroevolutionary dynamics. The accumulation of more empirical studies, and ultimately meta-analyses and comparisons across mutualism types, will facilitate this exciting work. Given the ubiquity of mutualisms in the natural world, continuing to build research focused on the role of mutualism in macroevolution may help reveal how these interactions have come to be so ecologically ubiquitous on earth today.

6.4. How Evolutionarily Labile or Conserved Are Interactions?

The last several decades of research have seen a surge of new studies investigating the extent to which extant lineages of interacting clades are phylogenetically conservative or labile. In particular, a recent increase in the use of molecular phylogenetic and PCM methods to study relatively specialized interactions, especially mutualistic and parasitic ones, has highlighted a range of questions about the phylogenetic lability and conservatism of certain species interactions that were previously less accessible (e.g., Price 1980, Thompson 1994). Evidence for the conservatism and lability of species interactions is interesting in light of how repeated glacial and interglacial cycles must have disrupted many species interactions through the individualistic shifts of species ranges over the past 2 Ma, both in the oceans and on land (Jablonski 2008a). There are

opportunities to test existing hypotheses concerning which types of interactions are labile and which are conserved over macroevolutionary time, as well as to test for the effect of changes in interactions on diversification rates, as some studies have done (Smith et al. 2008, Lengyel et al. 2009, Marazzi & Sanderson 2010, Gómez & Verdú 2012, Weber & Agrawal 2014, Wiens et al. 2015, Tripp & Tsai 2017, Afkhami et al. 2018, Nelsen et al. 2018, Foisy et al. 2019, Kaur et al. 2019). We draw particular attention to the growing interest among evolutionary ecologists in the dynamics of species interaction networks over evolutionary time (via the gain and loss of species and their interactions) (Hembry et al. 2018, Harmon et al. 2019, Ponisio et al. 2019).

6.5. Does the Importance of Interactions for Driving Macroevolutionary Patterns Vary from the Tropics to Colder Climates?

Recent ecological studies and some disagreement have revolved around the question of whether species interactions are stronger and/or more specialized in tropical climates than in temperate zones (Schemske et al. 2009, Moles & Ollerton 2016, Baskett et al. 2020). This research follows from Dobzhansky's (1950) and Vermeij's (1978) hypotheses about latitudinal gradients and the importance of biotic interactions relative to abiotic factors in driving evolution. Recent studies have also asked whether speciation rates are higher in tropical or temperate/boreal latitudes, in some cases questioning the hypothesized importance of tropical biotic interactions for generating higher speciation rates (e.g., Schluter 2016). In light of recent interest in how latitudinal gradients fit within major ecological and evolutionary patterns, there is great potential for further research assessing the role of ecological interactions in macroevolution across latitudes, including research that integrates paleontological data (e.g., Collins et al. 2019). The development of phylogenetic comparative models to test specific predictions about the links between trait evolution, lineage diversification, and biogeography is an active area of modern research (e.g., Drury et al. 2018a).

6.6. How Important Is Coevolution at Macroevolutionary Scales?

Some of the earliest concepts of coevolution—such as Ehrlich & Raven's (1964) hypothesis of escape-and-radiate coevolution and Van Valen's (1973) Red Queen hypothesis—are explicitly macroevolutionary in that they describe the effects of coevolution on species origination and extinction over deep time. More recently, researchers have proposed that coevolution may promote diversification by promoting speciation, with clade-level consequences for diversity (Thompson 1994, 2005; Althoff et al. 2014), and that, in such scenarios, coevolutionary diversification (diversification in which coevolution plays some role) is unlikely to produce pairs of matching phylogenies (Thompson 2005). Coevolution might also operate to determine which lineages persist and go extinct in interacting clades without affecting the process of speciation itself (Hembry et al. 2014). Despite the clear potential for coevolution to shape diversification or trait evolution over deep time, the majority of coevolutionary research has focused at the level of microevolution. Part of the challenge in studying coevolution's role in macroevolution is that we lack an understanding of how coevolution and its effects could be identified using the phylogenetic and trait data used by popular PCM approaches. Many studies have attempted to test escape-and-radiate coevolution by looking for bursts in diversification associated with the gain of defensive or counter-defensive traits, but most have been able to test only one or a few components of this multifaceted hypothesis (Futuyama & Agrawal 2009, Althoff et al. 2014; but see Endara et al. 2017). Some researchers have argued that coevolution is not necessary to explain observed patterns of diversification (Althoff et al. 2012). Future work should extend existing coevolutionary theory to macroevolutionary scales via a phylogenetic framework, so as to develop hypotheses for what macroevolutionary patterns

would be produced by the process of coevolution (Nuismer & Harmon 2015). Ultimately, the questions of if, when, and how coevolution has an impact on macroevolutionary dynamics remain open challenges.

6.7. Can We Develop a Predictive Theory for How Biotic Interactions Affect Macroevolution?

Research to date suggests that the effects of ecological interactions on macroevolution are varied—in some cases promoting diversification or trait disparity, while in other cases, restricting diversification or disparity or even causing extinction. Several authors have proposed that there are general patterns in which the effects of interactions on macroevolution or diversification may vary in consistent ways for particular interaction types or particular phylogenetic scales (sensu Graham et al. 2018). For instance, as described in Section 6.2, competition can drive trait disparity and promote diversification in young clades, but it is also believed by many to restrict diversification (either within or between clades) over longer timescales. In another example described in Section 6.3, neontological studies suggest that mutualism increases the diversification rate in some groups but not in others, while paleontological studies suggest that obligate mutualism might increase extinction rates. Jablonski (2008a, 2017) pointed out that effects may vary at different taxonomic scales and that mismatches across scales are to be expected; others have noted that mutualism, competition, and different types of antagonism may have different effects on speciation depending on whether they promote stabilizing, diversifying, or directional selection (Yoder & Nuismer 2010, Hembry et al. 2014). There may also be differences in these effects for different taxa, as Knoll (1984) suggested for the role of competition in plant versus animal macroevolution. We view this topic as an especially promising area for further synthesis on interactions and macroevolution.

6.8. Should Macroevolutionists Be Investigating Pattern or Process?

Since the mid-twentieth century, there has been a shift in macroevolutionary research from an emphasis on uncovering process to an emphasis on uncovering pattern. Macroevolution as a field has its origin in an effort to understand evolutionary processes at temporal and phylogenetic scales well above those that were directly observable [Stanley even subtitled his 1979 book *Pattern and Process* (Stanley 1979)]. We note that there has been a shift in recent neontological literature toward describing macroevolution in terms of pattern instead of process. Stark warnings about the dangers of overinterpreting the processes behind macroevolutionary results have undoubtedly shaped the approaches of many modern evolutionary biology students (Revell et al. 2008, Losos 2011, Louca & Pennell 2020). The increased use of PCMs over the last decades perhaps inherently promoted this shift, as the fitting and interpretation of parameter estimates for macroevolutionary models become a central venture in many research studies, and often a given parameter estimate can be explained equally well by several different evolutionary processes. The limitations inherent in this many-to-one mapping problem of pattern to process certainly make the emphasis on patterns in the current literature defensible. However, process remains central to answering fundamental questions at the heart of ecological interactions and macroevolution. Pattern can be linked to process by integrating additional lines of evidence in some but not all cases. We encourage researchers in this field to consider more generally whether we are seeking to uncover pattern alone in studying macroevolution, or whether our true goal is to reveal macroevolutionary processes. If we conclude that process is important, then a future goal in this field is to find creative ways to overcome the limitations inherent in pattern-only approaches in order to address fundamental questions about how species interactions have or have not shaped biodiversity on our planet.

7. CONCLUSIONS

Evolutionary biologists have been interested in the role of ecological interactions in macroevolution for over a century, and this topic has been the source of some of the longest-standing debates in evolution. At the same time, the study of interactions and macroevolution today is a rapidly evolving field that has changed enormously in the past decade.

Despite this new ferment of methods, data sets, and ideas, there is great value for macroevolutionists today in understanding the historical context of the field in which we work. Just as the development of new neontological approaches to macroevolution has benefited from the ideas and questions proposed by Simpson, Raup, Sepkoski, Gould, and Stanley during the twentieth century, we have endeavored to show here the utility of examining the history of hypotheses about ecological interactions in macroevolution. Taking this historical view reveals what this new field with old roots has accomplished in the past few decades—demonstrating, in answer to a long-running debate in paleobiology, that ecological interactions can indeed shape macroevolution alongside geologic and climatic processes and that mutualism can play this role alongside competition and antagonism. At the same time, we note that some of the challenges the field faces are not new, and some of the big picture hypotheses and open questions put forth by investigators over the past half century can continue to guide new advances.

Looking ahead, we urge consideration of three additional issues central to the continued development of this field.

First, concern continues within the study of macroevolution as to whether the field is limited more by methods or data. Several recent papers and conference symposia have drawn attention to the limitations of current PCMs (e.g., Rabosky & Goldberg 2015, Cooper et al. 2016, Voje 2018, Louca & Pennell 2020), which are of course used for a wide variety of types of research questions beyond studying the effects of ecological interactions. At the same time, despite the growth of publicly available data, obtaining high-quality data sets that contain real information about interactions and relevant traits is still a time-consuming enterprise. Alongside the creative use of preexisting data and museum collections, we emphasize that there is still a role for gathering new, targeted data on particular interactions and clades. Additionally, fossilized evidence of biotic interactions, historical biogeography, and sets of species interaction networks across biogeographic gradients all hold promise for answering questions about the macroevolution of interactions. As Weber et al. (2017) point out, there is no single PCM that by itself allows all investigators to test whether or not ecological interactions have played some role in driving lineage diversification or trait evolution in a clade of interest. Rather, there is a diversity of methods and types of data, only some of which are applicable to any given system, and creative approaches are required to make progress in this field.

Second, beyond methodological concerns related to current PCMs and despite recent successes in this field, many past ecological interactions remain difficult to rigorously infer or reconstruct. Many apparently coadapted interactions, including those involving invasive species, have shallow evolutionary histories (Thompson 1994). Ultimately, our inability to go back in time and confirm species interactions in the deep past (Simpson 1996) will remain a limitation in this field. We urge investigators to keep this fundamental limitation in mind, even as we predict that this area of research is ripe for many new and exciting advances over the next decades.

Finally, what Jablonski (2008a, p. 715) said over a decade ago remains true: We still “lack a powerful theory for how lower-level processes cascade upwards to clade-level dynamics, and vice versa.” Some hypotheses about the macroevolutionary effects of biotic interactions, such as those involving competition and antagonism among clades, remain as difficult to rigorously test as they were fifty years ago. In other cases, such as in some mutualisms, the effects of interactions seem

clear, but general patterns across systems and process-based explanations for observed patterns remain elusive. The search for general patterns, as a first step to developing such a “powerful theory” for the interplay of ecological interactions and macroevolution over deep time, should be a priority for future work.

We hope that alongside methodological advances, further examination of the history of ideas in this field will continue to lead to more insights into the ways in which biotic interactions influence evolution over long timescales. There are undoubtedly many more historical studies that we have failed to include, or that are largely forgotten altogether, that can bring inspiration and insight if uncovered. To borrow a metaphor from *The Major Features of Evolution* (Simpson 1953), it is as if the field has passed from one adaptive zone into a new one and is beginning to radiate into many new niches. Simpson makes clear in his formulation that the boundaries of adaptive zones can change over time, and we are confident that we have now entered a zone whose boundaries are widening as the field continues to diversify.

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