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Review

Investigating Biotic Interactions in Deep Time

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Recent renewed interest in using fossil data to understand how biotic interactions have shaped the evolution of life is challenging the widely held assumption that long-term climate changes are the primary drivers of biodiversity change. New approaches go beyond traditional richness and co-occurrence studies to explicitly model biotic interactions using data on fossil and modern biodiversity. Important developments in three primary areas of research include analysis of (i) macroevolutionary rates, (ii) the impacts of and recovery from extinction events, and (iii) how humans (*Homo sapiens*) affected interactions among non-human species. We present multiple lines of evidence for an important and measurable role of biotic interactions in shaping the evolution of communities and lineages on long timescales.

Biotic Interactions in the Fossil Record

Biotic interactions occur when organisms living in the same community directly or indirectly influence one another. Biotic interactions can occur within or among species, be positive or negative, and cover a wide range of interactions including predation, commensalism, mutualism, resource competition, and parasitism [1]. Biotic interactions play an important role in structuring modern communities (e.g., [2]). Understanding their importance in the past therefore has the potential to shed light on their role in shaping ancient and recent diversity patterns. Historically, however, the study of biotic interactions in the fossil record has largely focused on direct physical evidence of interactions such as bore holes in shells, plant damage by insects, patterns of bryozoan encrustation, rare occurrences of gut contents, and carnivore damage on bones (e.g., [3,4]). Analysis of unusually well-preserved fossil assemblages allows reconstruction of trophic relationships among diverse organisms (e.g., [5]) and earlier work documented long-term trends in **ecospace** (see Glossary) occupation [6]. However, temporally continuous evidence for biotic interactions (traditionally thought to structure biodiversity on only very limited spatiotemporal scales [7]) with appropriate temporal resolution (i.e., high-resolution stratigraphic sequences) is only rarely preserved. Consequently, paleontologists have focused primarily on the more accessible long-term trends in climate as important regulators of biodiversity and the differential success of species (e.g., [8]); only short-term ecological phenomena or long-term patterns that cannot be explained by climate have typically been attributed to the outcome of biotic interactions (e.g., [9], but see [6]). However, as the only source of sufficiently long-term data, and in light of several recent methodological advances, the fossil record is now uniquely positioned to answer many of the questions at the core of the evolutionary and ecological sciences. Herein, we address important recent advances in understanding the role of biotic interactions in shaping macroevolutionary and macroecological phenomena in the fossil record (Figure 1) and highlight areas of future research we believe will be illuminating. In this review, we exclude studies of physical evidence for interactions, except where they are used to contextualize large-scale biodiversity patterns.

Highlights

Challenging the widespread perspective that long-term diversity patterns are shaped primarily by climate is not possible without using fossil record data to understand the role of biotic interactions.

Important recent development and application of models that utilize data of both living and extinct species have enabled analyses to move beyond simply excluding potential abiotic drivers to explicitly modeling biotic drivers for the first time.

Analyses of paleontological data show that biotic interactions shape the temporal diversity trajectories and rates of origination and extinction for numerous taxa.

Extinction of keystone species has disproportionate impacts on biotic interactions among surviving species.

Recovery from extinction events can be sped up or slowed down by biotic interactions among surviving species.

Historically, humans (*Homo sapiens*) have acted as large, generalist predators, disrupting interaction networks among non-human species.

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Biotic Interactions on Large Spatiotemporal Scales

Interactions among individuals operate on timescales shorter than the typical temporal resolution of the fossil record (i.e., thousands to millions of years). The effects of biotic interactions do not scale up from individuals to species and clades in straightforward ways, but result from a multitude of interactions occurring among large assemblages of individuals, some of which may have opposing or multiplicative outcomes [7,10]. However, if interspecific and intraspecific interactions impact the ecological and reproductive success of individuals over large spatiotemporal scales, they can have effects on entire species and clades that are measurable on macroevolutionary and macroecological scales (Box 1 and Figure 1) [7,11–13]. Such emergent patterns include, but are not limited to, shifts in species abundances, diversity, and spatial distributions (e.g., [14–16]), partitioning of trait and phylogenetic space (e.g., [17,18]), change in rates of diversification and morphological change (e.g., [19–23]), and the success or failure of biological invasion (e.g., [20,24,25]). Although a significant body of theory has been developed to address the cumulative effects of biotic interactions (Box 1; [7,11,12,26–29]), empirical tests of models that account for the complexity of paleontological data have lagged behind theory.

The development of comprehensive phylogenetic and occurrence-based data sets that include extant and extinct species (Table 1) (e.g., [30]) have begun to close this gap by enabling empirical testing of hypotheses relating biotic interactions to emergent biodiversity patterns (Figure 1). Models of evolutionary processes have increased in sophistication to allow explicit inclusion of interactions among clades (Table 1) [31–33]. There have been concurrent advances in analyses for understanding the role of biotic interactions in shaping macroecological patterns (e.g., [34]) and trophic networks (e.g., [5]; Figure 1).

Biotic Interactions as Drivers of Macroevolution

Identifying how to quantitatively test for the impacts of biotic interactions on diversification has remained a ‘holy grail’ of macroevolutionary biology [10,35]. An exciting advantage of recent methodological developments is that they go beyond simply excluding potential abiotic drivers to explicitly model biotic drivers (Table 1 and Figure 1). After new phylogenetic comparative approaches showed limitations when applied to extant-only data [36,37], the major advance of the last 5 years was the development of process-based models of diversification [38–41], some of which can incorporate data from living and fossil organisms (Table 1). Within this flexible modeling framework, the goodness of fit of models that include parameters representing biotic interactions (e.g., intraclade diversity) is estimated and compared with the fit of purely abiotic models (e.g., [42]; Table 1). In tandem, phylogenetic comparative approaches have been applied to construct specific hypotheses relating biotic interactions to macroevolutionary patterns (e.g., [19]). Such new approaches have been applied primarily to three important phenomena: interclade diversity dynamics, intraclade diversity limitation, and morphological evolution.

The fossil record includes many instances of the contemporaneous diversification of one clade and decline of another [12,23]. These **‘double-wedge’ diversity patterns** are inferred to result from **clade competition** manifesting over long timescales (Box 1) [12]. An archetypal case of the double-wedge pattern is the post-Permian decline of brachiopods and rise of bivalves [23]. Earlier quantitative studies indicated that the double wedge was a coincidence [43] or did not result from clade competition [44]. However, application of stochastic differential equations [23,45] (Table 1) showed that, from the Ordovician to recent, brachiopods experienced higher origination rates when bivalve extinction rates increased, indicating **competitive release**. Climate did not show a statistically significant relationship with origination rate for either clade, suggesting a more

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important role for biotic interactions [23]. Similar double-wedge diversity patterns have been observed for clades of carnivorous mammals [42,46]. Clade-level competition may, therefore, have been important in shaping the diversity of both marine and terrestrial taxa. We note, however, that comparatively short-term covariation between climate and diversity could be obscured, except in the unusual scenario of a diversity record with the finer temporal resolution common of climate records (e.g., [47]). It is important to avoid mismatches in temporal resolution, but improvement in sampling of the fossil record or artificial time averaging of climate records should continue to ameliorate these analytical issues.

Some extinct clades show **equilibrial** or **unimodal diversity patterns**, implying the presence of ecological limits to species richness (i.e., **carrying capacity**; Box 1) [21,48–50]. Even if no absolute carrying capacity exists, equilibrial diversity patterns imply limits to either niche or physical space that must be set, at least partly, by biotic interactions among species (e.g., **limiting similarity**). Recent studies of Phanerozoic (i.e., Paleozoic through Cenozoic) global vertebrate richness show effectively 'flat' diversity curves, after accounting for variable preservation and sampling (Table 1). Flat diversity curves may relate to earlier formation of stable food webs [51]; the precise cause is not yet known. There is, however, evidence for global, regional, and locality-scale limits to vertebrate species richness over many millions of years, which implies the operation of biotic interactions [48–50,52,53]. Earlier diversification periods such as the **Great Ordovician Biodiversification Event**, however, provide evidence for relaxation of such ecological limits [54].

Unimodal diversity patterns through time have been observed for a number of extinct taxa (e.g., zooplankton, large-bodied mammals). Recent paleobiological studies suggest that abiotic and biotic factors drive biodiversity change during different phases of clade evolution. As diversity accumulates and niche overlap increases, a clade reaches its apparent maximum richness, and biotic interactions become the primary factor limiting further accumulation of new species (i.e., **negative diversity dependence** is operating; Box 1) [55,56]. During the diversification and decline phases, abiotic forcing is the primary factor controlling the loss and accumulation of species [55]. Further studies have similarly suggested that diversification rate is limited by within-clade diversity (and, by extension, intra-clade biotic interactions), while extinction rate may, most often, be set by abiotic factors [21,42,57,58].

Inferring the importance of biotic interactions on the basis of statistical rejection of abiotic factors is the most common approach employed by recent publications [24,42,46,58,59]. There are potential limitations to these modeling approaches (Table 1), and continued characterization of their statistical behavior will be important to assess validity. New methods that go a step further to explicitly model biotic interactions have been developed [31–33] (Table 1), but their application is not yet commonplace.

Patterns and models of diversification can be strongly indicative of within- or among-clade competition (Box 1) but do not incorporate information about whether the taxa involved could reasonably be expected to interact. Trait-based methods are built on existing ecological theory relating morphological similarity to ecological similarity and patterns of trait space occupation that suggest the operation of biotic interactions (e.g., limiting similarity and **character displacement**). By including this information, trait-based approaches may have an advantage over strictly diversity-based approaches [60]. Models that include trait evolution are necessarily more parameter rich, but may provide more powerful tests of predictions relating rate and mode of morphological differentiation to clade-level biotic interactions (e.g., [32]).

Glossary

'Big Five' mass extinctions: Accelerations in extinction rates with respect to origination rates such that 75% or more of standing species-level diversity is lost in a relatively short period, usually less than 2 million years. These include the End Ordovician (~443 Ma), End Devonian (~359 Ma), PT (252 Ma), Triassic–Jurassic (200 Ma), and Cretaceous–Paleogene (66 Ma) mass extinctions. While other intervals of elevated extinction rate or depressed origination rate have been identified and debated, the 'Big Five' have been generally accepted since this pattern was first described nearly four decades ago.

Carrying capacity: Originally defined as the maximum stable size of a population in an ecosystem, the term has been expanded in macroecological and paleobiological contexts to refer to ecological limits on the number of species that can co-occur in a community. This occurs when a limit is reached in the number of resources available such that origination and immigration rates equal extinction and extirpation rates, and net growth in species richness is zero.

Character displacement: refers to competition-driven evolution of divergent traits in which the strength of selection increases with the phenotypic similarity between competitors.

Clade competition: an emergent phenomenon resulting from negative interactions among populations of species (e.g., exploitation of common resources, interference) at the local scale, which lead to decreases in population growth rate and/or population size for the least competitive population. If populations interact frequently and over large enough spatial scales, competition may eventually lead to **competitive exclusion** and the extinction of the least competitive clade. Sepkoski [12] preferred the term 'clade displacement'.

Competitive exclusion: species competing for the same resource in the exact same way cannot co-exist.

Cretaceous–Paleogene (KPg) mass extinction: the extinction of around 76% of species and 40% of genera 66.02 million years ago after the impact of a bolide in the Yucatan Peninsula. Most notably, this extinction wiped out the non-avian dinosaurs.

High rates of diversification and trait evolution may coincide with periods of biotic interchange, which suggests that species and trait diversity are limited prior to invasion of new ecological space [20,61]. However, some clades show no evidence of within-clade diversity-dependent rates of morphological evolution (e.g., canids [19]). Predictions from models of trait change and diversification may therefore not be universally applicable. Existing studies are limited primarily to terrestrial mammals, leaving much room for further investigation. Although traits have been collated for a number of other extinct taxa (e.g., invertebrates) [60,62,63], similar analyses have, to our knowledge, not been conducted. Collation of body size and dietary data for additional extinct groups, further development of trait-based approaches, and formalization of appropriate predictions could further our understanding across multiple clades to provide evidence for the larger role of biotic interactions in shaping macroevolutionary patterns.

Biotic Interactions and Extinction Events

Extinctions are among the most prominent ecological events. When species disappear, their biotic interactions also disappear, potentially disrupting the ecological networks of which they were part [64,65]. In particular, the loss of keystone species – those that interact with a wide range of other species through alteration and modulation of ecosystem processes – has broad implications for the rest of the biota and can lead to fundamental, permanent changes to the functioning of postextinction ecosystems [66–69]. The study of extinction events has long been a focus of the paleobiological sciences. Now, examination of the interplay between biotic interactions and extinction is burgeoning due to the application of approaches for inferring biotic connections among species, such as trophic and network analyses (Figure 1), as well as methods for assessing species' functional roles in ecosystems (Figure 2 and Table 1). These approaches are used in two primary research areas: how biotic interactions buffer, amplify, and shape the trajectory of extinction events, and how they influence the process of postextinction recovery.

Centuries of research into the **'Big Five' Mass Extinctions** has unequivocally demonstrated their significant and often long-term effects on ecological diversity. The **Permo–Triassic (PT)** and **Cretaceous–Paleogene (KPg) mass extinctions**, for example, had the greatest effects on species networks, implying significant shifts in the numbers and types of interacting species [70,71]. Recent work, however, has shown that biotic interactions (e.g., guild structure) can buffer communities of organisms against extinction events by reducing the number of direct interactions, thereby promoting species coexistence and survival in times of high environmental stress. During the terrestrial PT extinction event, for example, guild structure persisted within tetrapod communities through the first two extinction pulses [65]. Maintenance of trophic interactions among large-bodied species resulted in local stability of interaction networks [5]. The addition of new species, such as that which occurred during the Early Triassic, which was characterized by an archosauromorpha-dominated disaster fauna [16], can, however, lead to ecological restructuring (Figure 2) [65].

Certain types of biotic interactions (i.e., those maintained by keystone species) may also decrease the resilience of communities to extinctions. These destabilizing effects can be either 'top down' (i.e., consumer extinction impacts producers) or 'bottom up' (i.e., producer evolution or extinction impacts consumers). For example, the PT extinction on land was amplified by the loss of herbivorous taxa that resulted in an **extinction cascade** among the previously diverse and abundant predator guild [72]. Similarly, the post-KPg collapse of primary productivity amplified loss of suspension-feeding mollusks, producing a long-term shift toward deposit feeders and predators [71]. Outside the context of mass extinctions, evolution among phytoplankton that

Double-Wedge Diversity Pattern: contemporaneous decline of one clade and diversification of another. An emergent phenomenon attributed to *clade competition*.

Ecological or competitive release: niche expansion observed when species from highly competitive environments invade habitats with fewer competitors or when competitors become extinct.

Ecospace: multidimensional ecological space defined by various ecological traits that influence modes of life in an ecosystem.

Environmental filtering: a process whereby species are sorted along abiotic gradients according to their environmental tolerances. Under a strong environmental filter, such as a latitudinal or altitudinal climate gradient, species may meet the limits of their environmental tolerances and be excluded from communities.

Extinction cascade: the loss of multiple interdependent species following the extinction of a keystone species or guild in the ecosystem.

Functional diversity: herein used as the value and range of organisms' traits possessed by members of a community or assemblage of species.

Great Ordovician Biodiversification Event: the dramatic sustained increase in both diversity and disparity within almost all marine animal lineages during the first 30 million years of the Ordovician, that is, from the Tremadocian to the Sandbian (ca. 485–455 Ma), is known as the Great Ordovician Biodiversification Event (GOBE).

Limiting similarity: a mathematical model that describes the minimum niche difference between competing species that is required for their co-existence.

Negative diversity dependence: a model wherein higher standing diversity tends to suppress origination (or to increase extinction, though typically the former).

Niche incumbency: one or more resident species preventing new species with similar niches from colonizing otherwise suitable habitats.

Permo–Triassic (PT) mass extinction: the extinction of approximately 90% of marine species and almost 70% of terrestrial vertebrates at the end of the Permian, 252 million years ago. It is now generally accepted that volcanism in the Siberian Traps sparked the environmental changes that resulted in this extinction.

form the base of the marine food web drove the extinction of over 100 species of benthic foraminifera during the mid-Pleistocene [73]. Similarly, loss of herbivorous mammalian megafauna at the end of the Pleistocene, many of which were keystone species, dramatically reduced dispersal distances among herbivore-dispersed plants, creating population and genetic discontinuities [74–76].

Following major extinction events, communities of species undergo variable durations of recovery. During these periods of ecological reorganization, **functional diversity** may play important roles in determining the time it takes to reach a new dynamically stable state (Figure 2). Recovery of the marine biological nutrient pump post-KPg was accelerated relative to increase in species richness, suggesting that functional roles of species were more important in shaping whole ecosystem recovery [77–79]. Conversely, reassembly of tetrapod communities following the PT mass extinction was marked by the recovery of species richness prior to substantial ecomorphological diversification [16], suggesting that the importance of functional diversity in recovery vary with ecological and environmental setting.

Unimodal Diversity Pattern: A hump-shaped diversity curve consisting of three distinct phases: richness accumulation (growth), equilibrium diversity or maximum richness, and decline to extinction. Attributed to negative diversity dependence and to abiotic factors during the accumulation and decline phases (described in [55]).

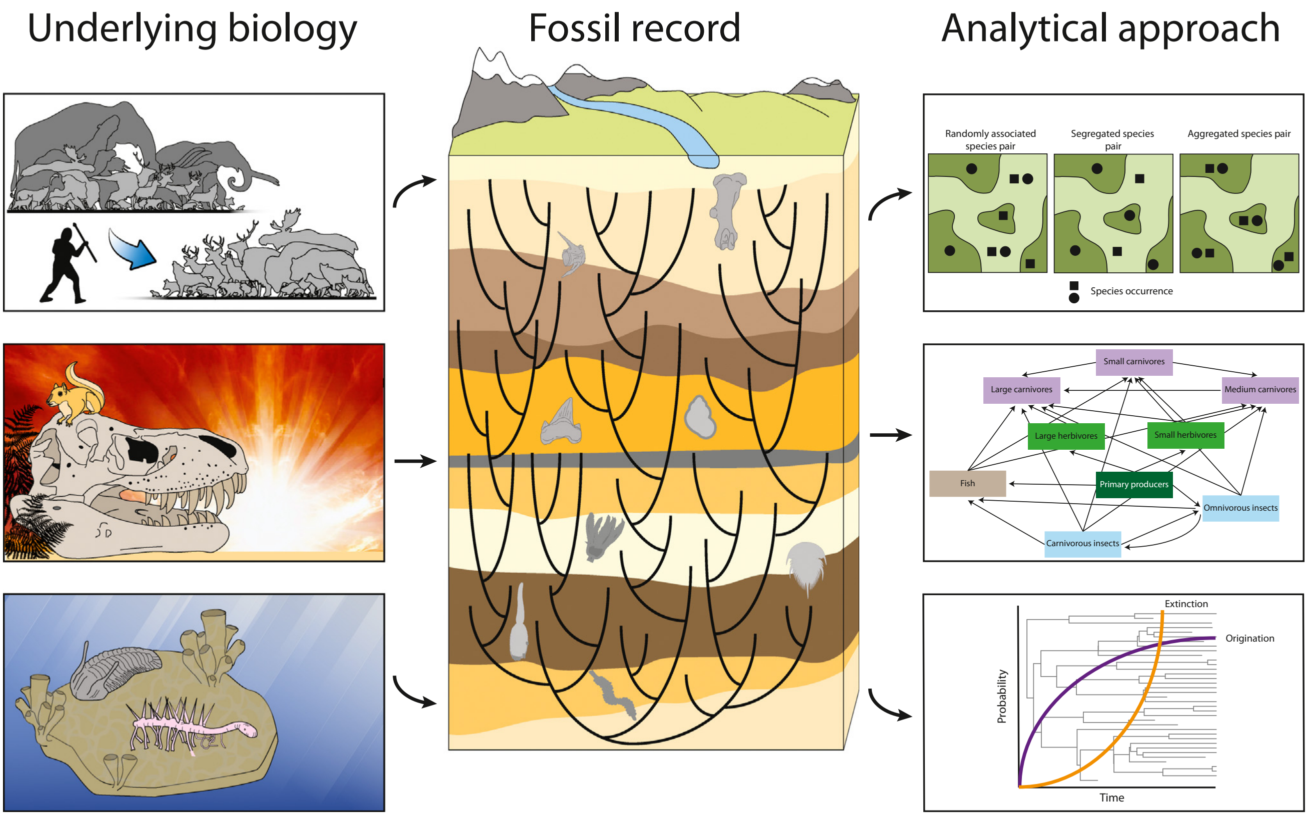

Figure 1. Substantial Evidence That Biotic Interactions Play a Role in Structuring Biodiversity Patterns over Large Spatiotemporal Scales. Biotic interactions play a role in, from bottom left to top left, shaping patterns of diversification such as that which occurred early in the history of life (e.g., the Cambrian Explosion), responses to and recovery from extinction events (e.g. the KPg mass extinction), and the response of non-human organisms to human (*Homo sapiens*) ecological disturbance (e.g., human overhunting of the mammal megafauna during the latest Pleistocene). Biotic interactions that help to shape patterns of organismal diversity (left column) are filtered through the processes of fossilization (middle column), which introduce myriad analytical complexities that have, until recently, proven difficult to account for. However, there are now a range of analytical methods available to paleobiologists (Table 1) that enable inference of the operation of biotic interactions and account for differential preservation and sampling of the fossil record or are relatively robust to such biases. Some of these methods include, from bottom to top right, process-based models of origination and extinction rates (e.g., [39]), trophic and food web analyses (e.g., [5]), and macroecological analyses of species co-occurrence (e.g., [34]). Figure elements were created by D. Fraser, M. Gilbert, S. Rufolo, and E. Tóth.

Box 1. A Summary of the Basis for Attributing of Macroevolutionary and Macroecological Patterns to Biotic Interactions.

Theory of Island Biogeography

The Theory of Island Biogeography (TIB; [28,29]) proposed ecological rules governing species richness and macroevolution on islands. TIB has been extended to explain continental macroecological and temporal diversity patterns in the fossil record. Much of the theory for **equilibrial** and unimodal patterns of diversity draw upon TIB.

Species Richness

There is a positive relationship between island size and species richness, which is attributed to elevated extinction among small populations on small islands and enhanced origination among large populations on large islands. Species–area relationships are found in both neontological and paleontological contexts (e.g., [109]). TIB predicts greater richness over larger spatiotemporal scales (e.g., [53,110]) and enhanced origination during dispersal (e.g., [20,24]).

Equilibrial or Equilibrium Diversity

As richness nears the carrying capacity of an island, species accumulation (immigration and origination) will slow due to niche saturation and **niche incumbency**. This is the basis for the concept of negative diversity dependence, wherein higher diversity suppresses origination (or increases extinction) on evolutionary timescales [21,55,58,59].

Red Queen Hypothesis

The Red Queen Hypothesis (RQH; [13]) is based on the observation that species are equally likely to go extinct at any time, given an unvarying environment (age-independent extinction) [111]. RQH forms the basis for understanding how biotic interactions shape patterns of species coexistence and diversification in the fossil record. RQH remains controversial due to its focus on abiotic factors as the primary drivers of long-term biodiversity patterns [26].

Ecosystem Energy

Competition for available ecosystem energy is mediated by biotic interactions that structure the division of niche space and set limits to diversity (i.e., equilibrium diversity; e.g., [50,53]). As a community reaches equilibrium, speciation and invasion decrease (or extinction increases), as the number of ways to divide the niche space decrease. RQH predicts richness be greater in environments or during periods of higher ecosystem energy (e.g., [8]) as well as negative diversity dependence and unimodal diversity-through-time patterns (e.g., [21,55]).

Zero-Sum Game

Evolutionary change in one species that improves the overall fitness of its members results in a negative effect of equal magnitude among coexisting species. An increase in abundance or diversity of one species also results in an energetically equivalent decrease in the abundance or diversity of other species (e.g., [42]). Without environmental change, equilibrium diversity is stable, despite fluctuations in the relative abundances and taxonomic identity of constituent species (e.g., [50]).

Recovery often involves the incorporation of new species into communities and new biotic interactions through the processes of origination and immigration (Figure 2). Ecological release has been invoked to explain the diversification of post-KPg mammals for decades but is now being studied in ways that more explicitly invoke biotic interactions. Analysis of niche occupation and morphological disparity among Mesozoic and early Cenozoic mammals shows an expansion of niche diversity post-KPg [18]. It remains unclear, however, whether the true driving mechanism of mammal diversification in the wake of the KPg mass extinction was ecological release or increased plant biodiversity. A recent study found a positive correlation between plant standing richness and diversification in the Juglandaceae, a potentially energy-rich food source for mammals, and mammal morphological diversity [80]. In a similar vein, recovery of the marine gastropod communities of South America following the mid-Pliocene extinction of 61–76% of mollusk species was characterized by enhanced taxonomic diversity among grazers and suspension feeders, due to a reduction in predation pressure [81]. Recovery of benthic marine communities, post-PT mass extinction, however, may have been comparatively slowed by a reduction in interspecific competition [82]. The effects of biotic interactions on extinction recovery may therefore take on different forms and rates across the marine and terrestrial realms as well as among higher taxa (e.g., mammals and marine benthos).

Table 1. Approaches Recently Used to Quantify or Model the Macroevolutionary Effects of Biotic Interactions Using Fossil Occurrence or Trait Data (Some Are Novel, While Others Are Extensions of Previously Applied Methods)[a]

Method	Approach	How it is used to detect biotic interactions from fossil evidence	Advantages	Limitations	Example applications
Birth–death process with fossil occurrences	A birth–death-sampling (BDS) model is one that describes a phylogenetic tree of living taxa and fossil occurrences, parameterized with rates of character change, origination, extinction, and fossil sampling. Bayesian Markov Chain Monte Carlo algorithms are used to estimate the probability density of possible phylogenies based on the data.	Interclade and intraclade diversity dependence and abiotic factors can be explicitly included in the modeling framework to estimate their relative contribution. If the inclusion of diversity dependence or interaction between the diversity trajectories of two clades in the model leads to more probable phylogenies, then biotic effects can be inferred to be important.	The process of biotic interactions contributing to evolution is directly modeled, which eliminates the ambiguity inherent in modeling the resulting pattern of evolution (rather than the process) common in other approaches, where one pattern can be generated by a number of different possible processes.	Models are often highly complex and in combination with a paucity of data they can be difficult to fit reliably. The behavior of estimation algorithms has not yet been well characterized in a breadth of macroevolutionary scenarios to understand possible biases. Some BDS models assume complete species sampling. The method does not inherently consider whether specific taxa could reasonably be expected to be interacting with one another.	**[46]*** (canids), [24] (carnivores); **[42]*** (carnivores), **[59]*** (sharks); **[57]*** (ferns); **[58]*** (crocodiles); [39]; [33]; [101]
Phylogenetic methods	Several extensions of pre-existing approaches that use Hansen models of morphological evolution on a phylogeny (e.g., Brownian motion, Ornstein–Uhlenbeck, Early Burst), which are applied in this context by combining them with estimates of diversification rate.	Hypotheses are constructed of each unique study system, of how the rate of diversification of the clade, and the rate or mode of morphological evolution of the clade would be expected to relate to one another through time in the presence or absence of the influence of biotic interactions.	Modeling morphological change is a more robust test than simple identification of diversity dependence and can be used to make links to functional roles, paleoecology, or dispersal.	Different mechanisms can generate the same observed pattern, making isolation of biotic interactions as the main driver difficult. These approaches infer the role or mechanism of biotic interactions but cannot currently explicitly test for it.	[20] (equids); [19] (canids); [75] (palms)
Richness or diversification	A variety of ways to measure diversity, richness, or diversification rate through time for one or more groups, and model diversity trajectories to establish whether they reach equilibrium. Some approaches compare patterns to other clades, to changes in geographic overlap, or test for correlations between diversity and other biotic or abiotic factors.	Asymptotic growth in clade diversity through time implies a carrying capacity in species diversity (i.e., biotic interactions place a limit on diversity). Diversification rates that negatively correlate with standing diversity, or alternatively an explicit test of correlation between the richness or diversity trajectories of two clades through time, are used as evidence for the effect of biotic interactions.	Richness and diversity can be calculated from occurrence, spatial presence/absence, or abundance data, making this approach suitable in a majority of extinct clades for which we have fossils.	Carrying capacity approaches rely on the assumption that diversity dependence is itself evidence for biotic interactions. Where there is a relationship between the diversity trajectories of two clades, it can be difficult to eliminate joint abiotic drivers. The method does not inherently consider whether specific taxa could reasonably be expected to be interacting with one another. Diversity metrics are sensitive to spatial sampling and a variety of preservation biases.	**[55]*** (mammals); **[21]*** (zooplankton); [9] (mammals); [17] (mammals); [48] (tetrapods); [49] (vertebrates); [50] (tetrapods); [52] (benthic invertebrates); **[102]*** (planktonic foraminifera); [20] (equids); **[63]*** (marine invertebrates); **[60]*** (fish)

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Table 1. (continued)

Method	Approach	How it is used to detect biotic interactions from fossil evidence	Advantages	Limitations	Example applications
Detecting causality with time series analysis	Stochastic differential equations (SDEs) are used to establish the presence of causal relationships between time series data of origination, extinction, and sampling rates. The time series can be from different clades and/or climate variables.	If there is a causal relationship between combinations of origination and/or extinction rates within or between clades, this indicates that biotic interactions are influencing macroevolutionary patterns.	SDEs are a strong test of whether a variable in one time series is driving patterns in a second time series, rather than a correlation which could be driven by a third unmeasured (abiotic) variable.	The time continuity and resolution of fossil occurrences required for this approach to have statistical power are uncommon in the fossil record, so it is not yet broadly applicable.	**[23]*** (clams and brachiopods); **[45]*** (birds, hares and lynx, brachiopods and bivalves)
Trophic networks	Trophic networks have been used in a variety of new approaches, starting from inferring the network within communities of extinct (and extant) species, followed by applying stability analyses, modeling, and simulation of networks through time as well as across space, or incorporating traits to understand how they relate to the network.	By calculating network metrics through time, the broad-scale effects of large events that include the removal or addition of particular species (e.g., during mass extinctions or the loss of the mammalian megafauna) on interactions between other species can be assessed. These approaches are primarily used to infer stability resulting from the cumulative effect of biotic interactions.	With these approaches it is possible to characterize and sometimes predict the effects of removal of species (including humans) in different functional or trophic roles, or to predict the resilience of an ecosystem based on its current network of biotic interactions.	It is difficult to reliably infer the nature of links between fossil taxa in the network, and the presence or absence of particular links. In particular, taphonomic and other sampling biases affect recovery of portions of the network, and some fossil assemblages; therefore, these may be subject to a high degree of missing data.	[5] (terrestrial vertebrates); **[72]*** (terrestrial vertebrates); [70] (marine animals); **[95]*** (humans and marine organisms)
Co-occurrence analysis	Co-occurrence analysis in this context builds upon existing methods that use a null model to classify co-occurrence patterns as significantly aggregated, segregated, or random, or measure them on a continuous scale from negatively to positively associated. New approaches then investigate how these classifications change through time, or in relation to traits.	Deviation from the expectation of co-occurrence patterns under a null model, or under the effects of **environmental filtering** or dispersal, or under functionally uniform environmental conditions, especially in relevant extents (e.g., where the range of a species pair overlaps), is inferred to indicate biotic interactions shaping community assembly.	These methods can be used to assess the effect of biotic interactions on community assembly and composition across landscapes, without requiring information on the evolutionary relationships between species.	By itself, co-occurrence analysis cannot currently be used to explicitly quantify the contribution of biotic interactions or the type of interaction, but only to exclude what we understand to be all other potential drivers.	[86] (terrestrial organisms), [34] (mammals); [96] (mammals)
Species distribution or niche models	Forecasting the expected niche of a species in a subsequent time interval, and computing deviations of the actual fossil occurrences from that expectation, in periods with novel biotic factors	If real occurrence distributions deviate significantly from the expected distribution based on earlier occurrences and given a climate model, at a point in time when novel biotic factors were introduced, then biotic interactions are inferred to be important in shaping the species distribution in that period	Abiotic factors can be eliminated within the analytical framework because they are used to estimate the species niche with the species distribution model.	It is difficult to eliminate taphonomic biases as an alternative explanation, and the approach could therefore only be used in scenarios for which there is a rich fossil record and a clear case for how interaction between two taxa could occur.	[15] (canids); **[112]*** (mammals and plants); **[67]*** (mammals and plants)

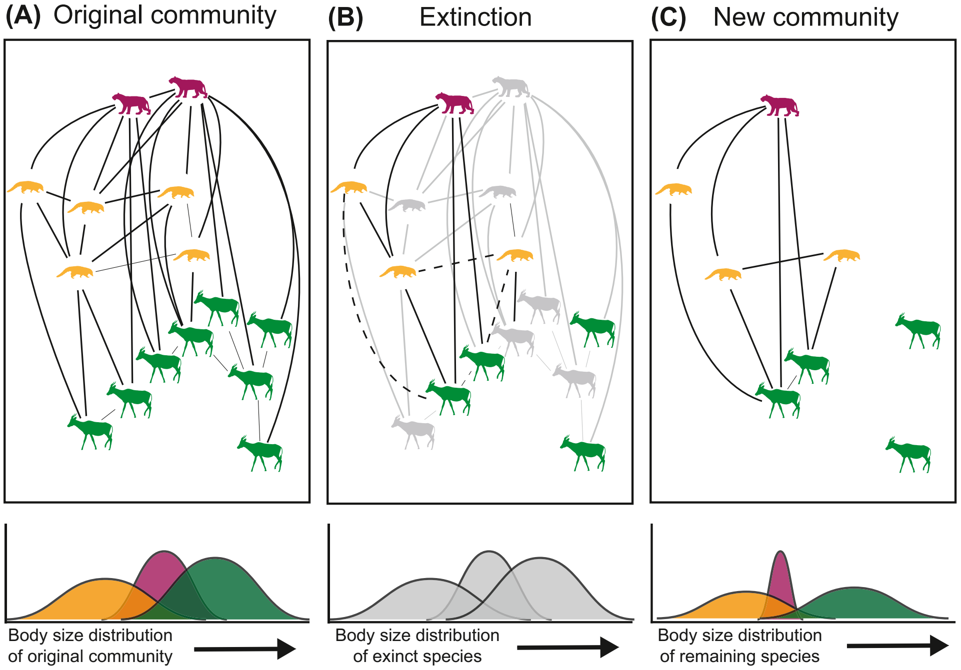
Table 1. (continued)

Method	Approach	How it is used to detect biotic interactions from fossil evidence	Advantages	Limitations	Example applications
Trait spaces	Traits are used to map morphospace or ecospace occupation, which can then be linked to functional roles within communities or clades, and measured through time.	Changes in occupation of trait spaces through time are measured, sometimes used in combination with phylogenetic comparative approaches. These changes are then compared with measured diversity dependence or with contemporaneous changes in other clades or within ecosystems.	The analysis of traits, especially within paleocommunities, provides specific information on functional roles and putative species interactions and can therefore be used to test for possible mechanisms of diversity dependence.	Biotic interactions are almost always inferred in this context through comparing patterns and showing concurrent changes in different clade-level diversity and morphology statistics, rather than through an explicit test or modeling approach.	**[72]*** (vertebrates); [60] (reef fishes); [18] (mammals, dinosaurs, plants); [17] (mammals); [71] (marine mollusks); [81] (marine gastropods)
Abundance within communities	Data on community composition, including raw or relative abundance, are combined with models or expectations of change through time under different macroevolutionary scenarios.	Linear models showing positive or negative correlation between abundance of two or more species through time, or a lack of relationship to other (abiotic) factors, are inferred as evidence for the importance of biotic factors.	Analysis of abundance data allows for a richer understanding of the relative success of different species or groups, and community-level analysis allows inference of which taxa might reasonably be interacting.	Reliable abundance data are uncommon in the fossil record, with the exception of pollen, microfossils preserved in drill cores, some other marine invertebrates, and well-sampled mammals. These approaches therefore cannot currently be broadly applied without further collecting effort.	[82] (marine invertebrates); [78] (marine invertebrates); **[55]*** (mammals)
Agent-based models	Distributions generated by agent-based model simulations are compared with real fossil distributions, and biotic changes can be introduced into the simulations to generate expectations for different scenarios.	Expected distributions of fossil occurrences are simulated under a scenario that includes diversification and abiotic drivers (e.g., climate niche) to generate a null model. These expectations are then either compared with real distributions of fossil occurrences through a period that includes a major biotic event (e.g., extinction of mammalian megafauna), or compared with simulations that include a change in a biotic factor, to identify whether biotic factors were important in generating observed patterns.	In certain scenarios, this approach allows investigation of how behavior of individuals might scale up to signals that can be observed as patterns in the fossil record.	This is not a direct test of the influence of biotic interactions but relies on the assumption that other important factors have been adequately included in the null model simulations.	**[74]*** (mammals and plants)

[a]Relevant methods papers are included in 'Example applications', even if they do not contain an empirical application of the method they propose. Where there is an empirical application, the focal taxa are in parentheses. Papers that include an explicit test of or model the effect of biotic interactions (rather than inferring their effect by eliminating other factors) are bolded and starred.

Human Impacts on Biotic Interactions

Modern humans (*Homo sapiens*) left Africa and began their global dispersal before 50 ka [83]. Humans interact with numerous species, thus their ecological impacts and effects on biotic interactions have been diverse [84,85]. New integrative studies suggest that human alteration of ecosystems extends thousands of years into the past [83,86,87]. It is therefore increasingly



Original, intact community and *direct* biotic interactions. Thicker lines represent negative interactions, thinner lines represent positive interactions. Ways to model this are discussed in *Biotic interactions and extinctions*. We show an example of three indices, composition, trophic interactions, and body size distributions, as a community undergoes an extinciton event.

Extinction event (grayed-out lines and silhouettes) and reorganization (dotted lines) of community. Extinctions can be cascading where the extinction of a prey species directly impacts the predator and leads to its extinction. Removal of certain species can also lead to changes in vegetation via reduced ecosystem engineering and affect habitat suitability for the remaining species.

New community with ‘open’ niche space. There are many possible new states:
(H_0) The community stays reduced with accompyaning changes in abundance of remaining species;
(H_1) Species diversification and/or invasion of new species leading to changes in guild proportions and/or body size distributions;
(H_2) Complete community turn over.

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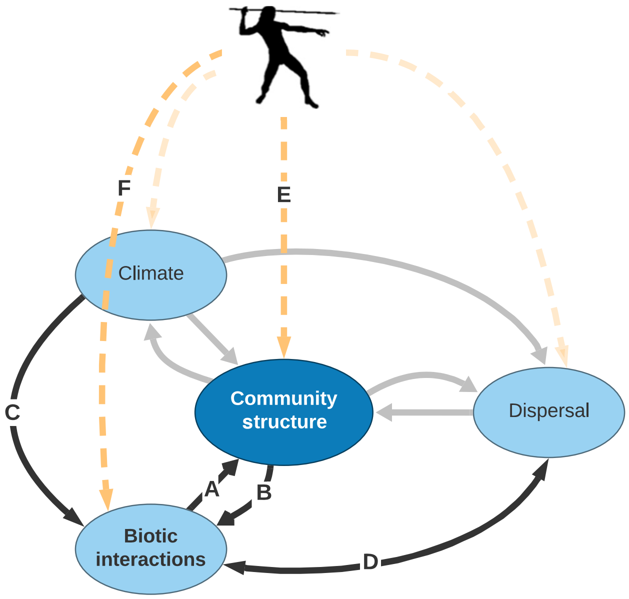
Figure 2. An Example of Change in Community Composition with Direct Biotic Interations (Top Three Panels) and Body Size Distributions (Middle Three Graphs), as a Community Changes from its Original State (A) through an Extinction Scenario (B) to an New State (C). The new community (C) can may look different than what the hypothesis (H_0) depicted. These indices can be tracked in both the fossil and modern record. Each silhouette represents a species within a guild (red = carnivores, gold = herbivores, green = herbivores), and we are showing an example of what ‘raw’ data may look like. There are many approaches that model the effects and underlying processes of extinction on the community, such as network analysis, co-occurrence analysis, and food webs.

clear that the ecological consequences of human migration and colonization are not adequately captured by contemporary ecological studies. Recent studies examine changes in continental and global patterns of mammal diversity [64,88,89], animal and plant species composition on islands [90], and the large-scale human domestication of plant species in regions previously considered pristine [91] (Figure 3). Herein, we focus explicitly on anthropogenic impacts on biotic interactions among non-human species, excluding studies of human–environment and human–non-human interactions (Figure 3F). The studies we review use trophic network analysis [92], macroecological analyses of species co-occurrence [34,86], and species distribution modeling [15] to show that human activities (e.g., species translocation, agriculture, extinctions) have



Trends in Ecology & Evolution

Figure 3. A Conceptual Diagram of Controls on Community Assembly (Blue Bubbles) and Anthropogenic Impacts on Those Controls (Yellow Broken Lines). The complex nature of community assembly is due, in part, to the existence of feedbacks (gray arrows) among community structure (used here to refer to observed aspects of communities such as richness, composition, taxonomic diversity, and evenness) and its primary driving mechanisms. In the last few thousand years, humans have altered patterns of community structure directly by removing or shifting species and indirectly by altering the natural mechanisms that underlie observed community structure (yellow arrows). Herein, we focus on the role of biotic interactions in this system (arrows A–F). We do not cover relationships between other aspects of the system (unlabeled arrows). Much empirical evidence for mechanistic feedbacks derives directly from the paleontological literature (A: [55]; B: [34]; C: [4]; D: [74]). Humans directly influence community structure (E: i.e., hunting/extermination, introduced species, agriculture; [84]), but our activities also act on the biotic interactions among species, thereby indirectly influencing community structure (F: [15,92,95], for instance in the form of resource concentration or appropriation). Paleontological research on human influence has focused primarily on changes in community structure via human interactions with other species (E: e.g., [90,91]), but researchers seldom make the additional step (B) to examine what this means for biotic interactions and how those effects may percolate through the system.

altered the diversity and types of biotic interactions among non-human species over periods extending to many thousands of years.

As large-bodied predators, humans increase average connectivity of trophic networks, due to their exploitation of wide arrays of prey items and tendency to feed at multiple trophic levels [92,93]. Human global migration during the late Pleistocene (16–14 ka) and Holocene (11.7 ka to modern) was therefore particularly destabilizing to terrestrial mammal trophic networks, leading to extinction cascades, loss of functional redundancy, and reduction in resilience to further environmental change [92,94]. In marine systems consisting of mammals and non-mammals, however, these effects were mitigated by seasonal shifts in the focus of human foraging efforts based on resource availability [95]. Combined, these studies indicate that, historically, humans have had divergent effects in different realms and continents.

Application of null models for identifying statistically significantly associated pairs of species (Table 1) indicates that humans have also had pervasive, spatially extensive impacts on the ways in which communities of species assemble and, by extension, the ways in which species interact (Figure 3). By the Pleistocene–Holocene transition (11.7 ka), humans had altered the pattern of a preponderance of positive associations (statistically significant rates of coexistence) that had persisted for 300 million years [86]. This shift could not be explained by non-anthropogenic factors (e.g., climate) [86,96]. Application of new methods for differentiating between abiotic and biotic controls on species associations (Table 1) shows that the loss of positive species associations reflects a breakdown in the frequency and importance of biotic interactions [34], such as those between carnivores and their prey [96]. Weakening of biotic interactions may have resulted from the spread of generalist life strategies in the wake of the loss of large-bodied, ecosystem engineering mammals that followed human colonization [34,96]. Similarly, species distribution modeling shows that human introduction of the domestic dog (*Canis familiaris*) induced shifts away from shared niche space among extant wild canids [15], potentially driving at least some of the observed change in the frequency of positive species associations.

In the face of ongoing, rapid anthropogenic global change, ensuring functioning ecosystems in the future will require a paradigm shift toward facilitating their adaptive and functional capacities, even as individual species populations ebb and flow. Developing effective strategies under this new paradigm will require deeper understanding of the long-term dynamics that govern ecosystem function and persistence (e.g., [34,96]), including biotic interactions among non-human species (Figure 3). The aim of future research into human impacts should therefore continue to make use of large data sets and new analytical tools to understand how biodiversity has changed in the past, why conservation efforts need to take prehistory into account, and what thresholds and tipping points are characteristic of socioecological systems (Figure 3) [97–99].

Concluding Remarks and Future Perspectives

The paleontological record represents natural experiments that contain a wealth of information on evolutionary and ecological change (Figure 1) [98]. Established analytical approaches, combined with decades of data collection, have allowed successful separation of real evolutionary and ecological signals from sampling heterogeneity in fossil preservation (e.g., [53,100]). Parsing these signals to understand their driving mechanisms has, until recently, proved more challenging, especially as they pertain to biotic interactions. Recent developments now allow rigorous quantitative assessment of macroevolutionary and macroecological change (Figure 1 and Table 1) [101]. Collectively, the studies we review provide multiple lines of evidence for an important and measurable role of biotic interactions in shaping the evolution of communities and lineages on long timescales.

Phylogenetic and ecological models that explicitly include parameters representing biotic interactions are important recent developments (e.g., [21,23,38,45,46,55,57–59,72,95,102]). Further growth of new and existing models and careful assessment of how and when they can be applied to the fossil record, given differential preservation and sampling, are important next steps (e.g., [41]). Statistically coherent birth–death-sampling models have been used to explicitly model extinct and extant species character evolution and diversification [40,41,103] and could be extended to model biotic interactions. New individual-based modeling simulations include population growth, species diversification, biogeographic distributions, and morphological change [104–106]. These and other models [31,32,36,106,107] could be extended for application to the fossil record.

Fossil data about Earth system responses to past extinctions and the roles of biotic interactions in resilience and recovery provide unique and valuable analogues for species responses to modern global change. Although we identified a small set of studies, there has been limited effort to characterize changes in biotic interactions between non-human species during human dispersal. Biotic interactions of humans with other species have been more extensively studied (e.g., [83,84,87]). Co-occurrence analysis of fossil data is increasingly common, but recent null model frameworks that explicitly test for the relative contributions of biotic factors (e.g., [108]) have not been widely applied in the fossil record (but see [34]). Fossil time series data could be used to infer probable diversity and extinction trajectories of modern groups and to identify strategies for maintaining important ecosystem functions. Research that makes use of the rich eco-evolutionary data sets of the fossil record provide a powerful way to untangle the shifting influence of biotic interactions on the fate of species, clades, and communities (see Outstanding Questions).

Outstanding Questions

Which metrics (e.g., intraclade diversity, morphological similarity) best approximate the intensity of biotic interactions? Which are the most easily measured and most informative for fossil data?

How does ecospace occupation change during the different phases of clade evolution (i.e., species accumulation, equilibrium, decline)?

Are differences in equilibrium diversity among clades related to divergent levels of ecomorphological differentiation?

How do biotic interactions among organisms in the terrestrial and marine realms (or across the body size, latitudinal, and phylogenetic spectra) result in differences or similarities in ecological responses to extinctions?

Did variability in the timing of human dispersals to new continents and islands during the late Pleistocene drive differential changes in the pre-existing biotic interactions among organisms on each land mass?

How do changes in community structure (e.g., extinction of an entire functional groups) induced by anthropogenic impacts influence or change biotic interactions?

Can new models be used to detect character displacement as an evolutionary response to novel biotic interactions among non-human species (e.g., how are invasive species influencing the ways in which resident species share niche space)?

Can synthesis of diversity, morphological, and distribution data under flexible modeling frameworks be leveraged to build predictive models for future changes in networks of biotic interactions among resident species in the invaded community?

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