

## Review

Phylogenetic Paleoecology:  
Tree-Thinking and Ecology in  
Deep Time

James C. Lamsdell,<sup>1,2,\*</sup> Curtis R. Congreve,<sup>3</sup>  
Melanie J. Hopkins,<sup>2</sup> Andrew Z. Krug,<sup>3</sup> and  
Mark E. Patzkowsky<sup>3</sup>

The new and emerging field of phylogenetic paleoecology leverages the evolutionary relationships among species to explain temporal and spatial changes in species diversity, abundance, and distribution in deep time. This field is poised for rapid progress as knowledge of the evolutionary relationships among fossil species continues to expand. In particular, this approach will lend new insights to many of the longstanding questions in evolutionary biology, such as: the relationships among character change, ecology, and evolutionary rates; the processes that determine the evolutionary relationships among species within communities and along environmental gradients; and the phylogenetic signal underlying ecological selectivity in background and mass extinctions and in major evolutionary radiations.

## Combining Tree-Thinking and Ecology in Deep Time

Over the past 50 years, the field of **paleoecology** (see [Glossary](#)) has offered important insights into ecological determinants for survival across mass extinctions [1,2], intrinsic environmental controls on the distributions and abundance of species [3–5], and how ecosystems form and change [6,7]. However, much of this work has been done with little consideration of organism relationships or phylogenetic history. Incorporating phylogenetic hypotheses with the fossil record is integral to resolving longstanding ecological questions, such as the nature of niche conservation [8], by providing a finer-scale understanding of organism relationships and expanding the repertoire of questions that these data can answer ([Box 1](#)). Ecologists and conservation biologists use standardized phylogenetic metrics to compare different studies [12], and there are numerous metrics and protocols available for quantifying phylogenetic tree robustness and handling multiple conflicting hypotheses ([Box 2](#)). Paleoecological data combined with **tree-based methods** can test whether ecological patterns recovered from modern studies are ubiquitous across space and deep time.

**Phylogenetic paleoecology** represents a synthesis between phylogenetic theory and quantitative paleoecology, with the goal of better understanding how historical and environmental processes shape the evolution of life. As such, phylogenetic paleoecology combines the fields of paleobiology, stratigraphy, geochemistry, phylogenetics, **macroevolution**, and **macroecology** to explain temporal and spatial changes in species distributions and ecological occupation in deep time. Here, we explore how phylogenetic paleoecology has the potential to make major advances in our understanding of the interplay between ecology and evolutionary rates [21,22,24,29,30], further our existing knowledge of community evolution and

## Trends

Phylogenetic paleoecology is a new research paradigm that promotes the explicit incorporation of ‘tree-thinking’ in studies of deep-time ecological processes.

Evolutionary relationships are vital to answering priority paleoecological questions because they allow paleoecologists to distinguish biological changes that are due to similar environmental interactions (convergent responses) from those that are due to shared ancestry (contingent responses).

Not only does the fossil record contain evidence of past environmental crises and biotic recovery, it is also a huge resource of ecological data spanning the history of life.

A better understanding of ecosystem recovery from past environmental crises is essential for predicting responses of modern biotas to current climate change.

<sup>1</sup>Department of Geology and Geography, West Virginia University, 98 Beechurst Avenue, Brooks Hall, Morgantown, WV 26506, USA

<sup>2</sup>Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA

<sup>3</sup>Department of Geosciences, Pennsylvania State University, University Park, PA 16802, USA

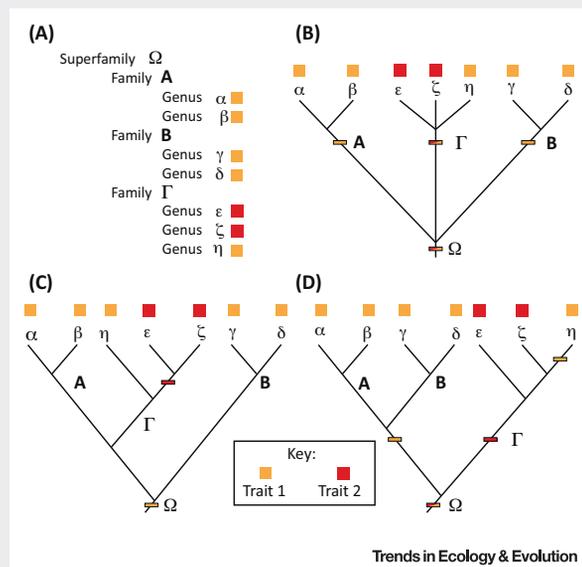
\*Correspondence: [james.lamsdell@mail.wvu.edu](mailto:james.lamsdell@mail.wvu.edu) (J.C. Lamsdell).

## Box 1. Phylogenetic versus Taxonomic Methods: Different Data Sets for Different Questions

Taxonomic hierarchies are commonly used in paleoecological studies that do not demand detailed knowledge of evolutionary history. For example, global diversity analyses, studies of evolutionary rates of major groups, and gradient analyses of local fossil assemblages can all be done without knowing how taxa are related. However, paleoecologists are increasingly interested in investigating questions that demand some knowledge of evolutionary relationships, such as whether mass extinctions have eliminated species that are closely related or spread randomly across the evolutionary tree.

Given that most extinct clades are still lacking robust evolutionary trees, recent studies have used taxonomic classifications as proxies for phylogenies [9]. This approach should be especially robust for groups with well-studied, stable taxonomies and good fossil records. For example, in mammals and bivalves, most morphologically defined genera are monophyletic as determined from molecular phylogenies [10]. A comparison of taxonomy-based trees to cladistics-based phylogenies in 52 animal clades indicated that the two approaches produce similar results for well-sampled clades when analyzed with phylogenetic comparative methods [11]. This is good news for paleoecologists, because it means that many questions requiring knowledge of evolutionary history can be addressed currently in groups that have not received formal phylogenetic analysis [11].

Nonetheless, taxonomic approaches may not be adequate for some evolutionary questions. Taxonomy-based trees are less informative than phylogenetic trees because the relationships of co-ranked taxonomic units resolve as polytomies (Figure I). This is especially problematic for groups with poor fossil records where stratigraphic information of first occurrences may not be reliable indicators of evolutionary origins. Phylogenetic trees provide a hypothesis of evolutionary relationships among all lineages permitting analyses of character evolution (Figure IC,D), which are not possible with taxonomy-based trees (Figure IB).



**Figure I. Demonstration of the Different Degrees of Information Contained within Purely Taxonomic and Phylogenetic Frameworks, and How This Disparity in Information Affects Inferences of Macroevolutionary and Macroecological Trends..** (A) Example taxonomy with genera assigned one of two ecological traits. (B) Tree of evolutionary relationships as indicated solely by the taxonomy. While the three families are reconstructed as clades, there is no indication as to the relationships of the three genera within  $\Gamma$  and the interrelationships of the three families are equivocal. As such, it is impossible to determine the ancestral trait condition for  $\Gamma$  and, in turn, the overall ancestral trait condition for  $\Omega$ . (C) Hypothetical phylogeny. The increased resolution of relationships indicated by the phylogeny allows for the ancestral trait condition to be reconstructed in  $\Omega$ ; as such, trait 1 is the ancestral trait condition for  $\Omega$ , as it is for  $\Gamma$ . (D) A hypothetical alternative phylogeny demonstrating how different tree topologies and, therefore, different reconstructions of evolutionary trends can be accommodated within the taxonomy. In this topology, the ancestral trait condition for  $\eta$  is trait 2, resulting in a reversal for  $\eta$  and the ancestral trait condition for  $\Omega$  being equivocal. It should be noted that the recovered ancestral trait conditions are dependent on branch lengths and the optimization criterion used.

## Glossary

**Contingency:** a nonrepeatable response to an event, whereby the outcome is dependent in part on the evolutionary history of the impacted organisms as manifested by the structure of ecosystems and populations at the time of the event and, as such, responses to the same pressure will likely be different in the future; evolutionary changes with long-term historical impacts that are the result of chance survivorship as opposed to the result of strong selective pressures.

**Convergence:** concerted evolutionary responses among distantly related groups in response to an external stimulus; the historical evolutionary signal of preferential loss or survivorship due to a widespread selective pressure. This definition is similar to the traditional phylogenetic definition, which refers to the phenomenon of functionally similar characteristics that evolved independently and, therefore, are shared among distantly related groups, but applied more generally to both ecological and evolutionary traits.

**Ecological hierarchy:** a nested biological hierarchy of organization through which energy flow occurs, ranging from enzymes through to cells, organisms, populations, communities, and the biosphere.

**Ecological traits:** characteristics of organisms that have bearing on the interaction between those organisms and the biotic and abiotic environment around them (e.g., trophic level, reproductive and/or life-history traits, and mobility). Ecological traits may also be emergent at the population or species level (e.g., geographic range size or abundance). Some morphological traits may be used as proxies for ecological traits (e.g., the size of the pallial sinus is indicative of burial depth in bivalves).

**Evolutionary Fauna:** a set of higher-level taxonomic groups that exhibit shared diversification histories, recognized by similar distributions in geological time.

**Functional diversity:** variation in performance of a function or activity among organisms within a clade, geographic region, and/or interval of time (e.g., bite force in jawed fishes). Although sets of morphological traits are often used as proxies for

### Box 2. Quantifying Phylogenetic Uncertainty

Quantifying **uncertainty** is an integral component of generating phylogenetic hypotheses. Spurious relationships retrieved from the source trees can impact the results of downstream analyses using phylogenetic hypotheses of tree topology as frameworks for estimations of evolutionary rates, ancestral state reconstruction, temporal shifts in phylogenetic diversity, and phylogenetic clustering of origination and extinction [13]. There are two primary sources of uncertainty in estimating phylogenetic relationships: incomplete sampling of taxa and conflicting data, which are both factors present in any analysis of modern or fossil taxa. Uncertainty can result in either low statistical support for hypothesized relationships or multiple conflicting topologies, which are summarized using a variety of metrics. Statistical support for relationship pairs within a phylogenetic tree is regularly expressed through a measure of branch support. Among likelihood and parsimony analyses, branch support is generated through jackknife resampling or nonparametric bootstrapping. The resulting statistics are not true probabilities, and there is ongoing debate as to whether Bayesian posterior probabilities encapsulate probability distributions [14] and how posterior probabilities relate to bootstrap values. Further work is needed to establish suitable thresholds of bootstrap, jackknife, and posterior probability branch support for determining the reliability of phylogenetic hypotheses incorporating morphological data.

#### Handling Conflicting Hypotheses

Results of phylogenetic analyses derived through Bayesian, maximum likelihood, and parsimony optimization are summarized through consensus of the retrieved tree topologies. Strict consensus (where conflicting topologies are resolved by collapsing the contradicting bifurcating relationships into polytomies) and majority rule consensus (where the most common of the conflicting relationships among the retrieved trees is selected) are the most common protocols used. For parsimony analyses, majority rule consensus results in the *ad hoc* selection of relationships based on their frequency among equally parsimonious trees [15]; however, majority rule consensus of Bayesian analyses represents the optimal summary of phylogenetic relationships given the available data [16].

Macroevolutionary and ecological meta-analyses resolve conflicting topologies either by using one of the multiple trees [17–19], the strict consensus tree including polytomies [20–23] or the strict consensus tree with randomly resolved polytomies [24], or by performing the analysis on every retrieved tree topology and either comparing the results directly for similarities or selecting a subset of those results through model fitting [25,26]. While some studies have shown anecdotally that selecting a single topology through picking one of multiple trees or randomly resolving polytomies tends to yield comparable results irrespective of tree topology used [17], empirical studies have also suggested that some such methods break down patterns imparted by phylogenetic structure [27]. Use of polytomies results in more conservative hypotheses of relationships and has been shown to result in more accurate representations of known phylogenetic trees using modeled data [15,28]; it seems likely that meta-analyses will continue to move towards conservative strict consensus or multi-tree model-fitting approaches.

historical biogeography [31–34], and provide important insights into the role of ecological selectivity in mass extinctions and subsequent radiations [22,23,35–37]. Finally, we set out a series of future avenues for research to which phylogenetic paleoecology is poised to make novel contributions.

While the focus of our review is on deep-time analyses, phylogenetic paleoecology has practical applications in modern biological systems. For example, ecologists are interested in predicting biotic responses to future climate change [38–41]. Given that the modern record comprises only the smallest fraction of species that have existed, it is necessary to look into the past for a more complete view of the general patterns and processes underlying biotic responses [42]. However, extinction and recent radiations obscure past evolutionary rates and ancestral ecological occupation, so that deep-time macroevolutionary and macroecological patterns cannot be reconstructed fully from extant data alone [43,44]. The fossil record is detailed and robust enough to make well-supported statements regarding the distribution of many fossil organisms, their ecologies, and the timings of radiation and extinction (Box 3). Some ancient marine extinctions exhibit environmental trends predicted for future scenarios [53] and demonstrate the importance of the loss of ecological interactions in terms of extinction impact [54–57]. Only through studying the fossil record can long-term biotic responses to climate change be observed [58–60]. There is now general agreement between ecologists [58,61] and paleoecologists [59,62,63] about the need to incorporate deep-time paleontological data into macroecological analyses [64].

functional diversity, multiple morphological solutions may exist for a single functional requirement.

**Genealogical hierarchy:** a nested biological hierarchy of organization through which historical information flow occurs, ranging from codons through to genes, organisms, demes, species, and monophyletic taxa.

**Ghost ranges:** the inferred temporal occurrence of a lineage for which there is no direct record implied from the occurrence of a longer-ranging sister taxon. Given that ghost ranges are informed by minimum divergence times from sister taxa, they only extend points of origin backwards in time and cannot alter the inferred timing of extinction. Ghost ranges are one type of adjustment made to stratigraphic or temporal ranges to account or correct for stratigraphic uncertainty, incompleteness, or inconsistency.

**Macroecology:** the study of relationships between organisms and their environment for the purpose of explaining patterns of abundance, distribution, and diversity at large spatial scales.

**Macroevolution:** the study of broad evolutionary trends across geological time; evolutionary patterns associated with the birth, death, and persistence of species and clades.

**Morphological disparity:** net morphological differences, usually within a group of organisms sharing a common ancestor; may be assessed within the clade, geographic region, and/or interval of time.

**Morphospace:** a multidimensional space defined by a set of morphological descriptors, such as morphometric or character data. The positioning of taxa relative to one another in the morphospace reflects their degree of morphological similarity. Morphospace analysis comprises the description of the relative distribution of subsets of taxa that may be grouped by taxonomic, ecological, spatial, or temporal association, and how that distribution relates to other groups, often in the context of the original morphological descriptors.

**Niche conservatism:** the phenomenon by which species and closely related taxa maintain similar environmental tolerances; inheritance by a daughter species of the niche

### Box 3. The Structure and Fidelity of the Fossil Record

The fossil record is the primary source of information on the ecology and evolution of extinct taxa. Many taxonomic groups with easily preserved skeletons (bone, shell, or cuticle) have both a rich source of characters for phylogenetic analysis and multiple occurrences necessary for robust inference of environmental distributions and **stratigraphic ranges**.

#### The Fidelity of the Fossil Record

The ecology of fossil taxa is often preserved with high fidelity [45], but inferences of organismal interactions and assessments of community composition are sometimes obscured by **time-averaging**. Thus, paleoecologists have devoted considerable effort to understanding how time-averaging affects different richness and abundance indices. Comparisons of the taxa living in an area with the remains of taxa accumulating on the ocean floor ('dead assemblages') reveal that relative abundance relationships and spatial gradients of living communities are well represented in the dead assemblages, whereas the richness of dead assemblages exceeds the richness estimated from surveys of living taxa [45]. Nonetheless, some studies of richness benefit because time-averaging is effectively filtering short-term fluctuations in richness and, thus, is a better representation of the species pool occupying a site over longer timescales. Numerous approaches are available for estimating ecological parameters of species, such as preferred environment, environmental tolerance, and peak abundance, including multivariate ordination of fossil assemblages [46], ecological niche modeling [47], and probability-based approaches that also account for variation in sampling [48].

#### The Structure of the Fossil Record

The spatial and temporal distribution of fossil occurrences are nonuniform and determined largely by how sedimentary basins accumulate fossiliferous deposits and by processes of erosion and tectonics (uplift and subsidence) that determine the formation and preservation of sedimentary basins [49]. This leads to two types of uncertainty in age data extracted from the fossil record. First, stratigraphic range end-points (first and last occurrences) are always underestimated because of sampling issues. Many early methods used to estimate uncertainty around first or last appearances assumed a uniform distribution of sampled occurrences through time, which is far from reality. In the meantime, many attempts to date trees of extinct groups have taken first appearances at face value. More recent methods have demonstrated the utility of using varying sampling rates over time, space, and taxa in estimating divergence times [50]. These approaches are distinct from the use of **ghost ranges** to extend first appearances back in time, which are inferred from a time-scaled tree.

Second, even accurately determined fossil occurrences are resolved almost exclusively to intervals of time rather than to precise points in time, complicating any application that uses point estimates of age. Most studies that have used first occurrences to scale trees including fossil taxa have simply used the median of the time interval from which that occurrence was sampled. However, it is straightforward to incorporate age imprecision, for example, by, repeatedly scaling the same topology with ages sampled from the intervals bounding first occurrences [51]. Critical assessment of different approaches for scaling trees both simultaneously with, and *a posteriori* to, topological inference continues to be a priority for all tree-based paleobiological studies [52].

## Ecology and Evolutionary Rates

### Character Change, Diversification, and Disparity

Documentation of changes in **morphological disparity** through time is one of the major contributions that paleobiologists have made to evolutionary biology. In particular, an early peak in disparity characterizes the evolutionary history of most clades, and disparity often peaks before **taxonomic diversity** does [65,66]. This pattern is consistent with early adaptive radiation into new ecological niche space. However, it is difficult to link changes in disparity with particular ecological innovations because disparity estimates alone do not indicate what aspects of morphology are changing.

Combining **morphospace** with phylogenetic analyses can be particularly informative about the potential connection between ecological occupation and morphological novelty. For example, in horseshoe crabs, repeated invasions into non-marine habitats drove the evolution of new morphologies and associated increases in disparity [22]. In post-Paleozoic echinoids, rates of character change were particularly high during two periods of time, and the majority of the changes that occurred could be linked directly to ecology, specifically the evolution of new feeding structures [24]. However, high rates and habitat shifts do not necessarily lead to

or part thereof from its parent species.

**Paleoecology:** the study of the fossil record to reconstruct the life habits of past organisms, their association in communities, and their interactions with the biotic and abiotic components of the environments in which they lived.

**Phylogenetic paleoecology:** an emerging branch of paleoecology that combines tree-based methodologies with habitat, abundance, and biogeographic data of fossil taxa to study the interplay of historical and environmental processes in shaping the evolution of life.

**Richness:** the raw count of taxonomic units, usually species or genera, in a fossil assemblage. Typically richness is a property of communities, but the term 'species richness' has been used synonymously with taxonomic diversity, for example, the number of species in a genus.

**Stratigraphic range:** the temporal interval over which a taxon has been sampled from the fossil record. The stratigraphic range is bounded by the oldest ('first') and youngest ('last') sampled occurrences of specimens, and is an estimate of the true duration of the taxon. First and last occurrences can be assigned absolute ages with varying precision based on the association of radiometric dates with sediments from which that taxon was sampled.

**Taxonomic diversity:** the raw count of taxonomic units, often species but frequently higher taxa, such as genera or families, within a clade, geographical region, and/or interval of time.

**Time-averaging:** a property of fossil assemblages that reflects the degree to which they contain individuals that lived at different times. Time-averaging occurs because rates of population turnover typically exceed rates of net sediment accumulation; time-averaging is increased by low sediment accumulation rates or reworking of sediments. In marine environments, time-averaging is typically in the range of decades or millennia.

**Tree-based methods:** methods applied to studies of ecology and evolution that incorporate trees of hypothesized relationships between taxa.

increases in disparity: clades that shift in morphospace may be evolving rapidly without any increase in overall disparity [67]. Studying the heritability of characteristics such as evolutionary rate and ecological occupation would permit observations of how repeated patterns in the history of life (e.g., mass extinction, adaptive radiations, ecological invasion, and clade origination) result in similar evolutionary responses.

### Shifts in Ecology and Shifts in Rates

Species diversification and longevity have been correlated with ecological traits, such as geographic range size and niche breadth [53,68,69]. Different marine environments are characterized by different rates of diversification, but this pattern may be due, in part, to differential distribution of clades diversifying at different rates [4]. To determine the extent to which such patterns are due to ecological or historical processes, it is necessary to integrate phylogenetic and geographic methods into studies of ecological and evolutionary rate shifts [29].

Time-scaled phylogenetic trees allow for the analysis of rates of origination and extinction alongside rates of morphological evolution calculated along branch lengths [17]. This has allowed for trends in the rate of morphological evolution to be studied directly, and reveals a complicated signal. For example, the early radiations of closely related clades often demonstrate distinct patterns of morphological evolution. Morphological rates in early tetrapods decreased through time along the phylogeny [17], while a general decrease in rates through time among Early Cretaceous birds is complicated by high rates within derived ornithomorph clades [26]. Tree-based methods can be used to test for underlying environmental causes of these complex patterns of diversification. By mapping paleoecological data onto phylogenetic topologies, it is possible to determine whether differential rates of morphological evolution, origination, and extinction are linked to ecological occupation, and discover instances where changes in ecological occupation resulted in rate shifts.

Using tree-based methods, studies of adaptive radiations in modern and fossil ants have revealed broad congruence between lineage and phenotypic diversification mediated by ecological opportunity [19], while, among extant birds, different dietary guilds have been associated with differential rates of origination and extinction [70]. Examination of ichthyosaurs also revealed increases in extinction rates as environmental volatility increased, with rates of origination and morphological change both decreasing before their extinction in the Cenomanian [21]. However, analysis of extant sea snakes has shown that ecological invasion is not tied to immediate diversification, but rather that diversification came later through extreme dietary specialization and partitioning of a single group nested within sea snakes [71]. This serves as a strong reminder of the two evolutionary hierarchies that define macroevolutionary trends and responses [72], and that it is through the interaction of these twin **genealogical** and **ecological hierarchies** that evolutionary history is shaped. Intrinsic developmental processes within the genealogical hierarchy can mediate morphological disparity and rates of taxonomic diversification, with morphological innovations influencing the potential for successful expansion of ecological occupation (equivalent to the realized niche). Conversely, pressures from the ecological hierarchy can affect rates of diversification through population dynamics, shape trends in morphological disparity through natural selection, and impact ecological occupation directly through incumbency, resource partitioning, and competition. This suggests that evolutionary change and ecological occupation are interacting, but not necessarily correlative, properties of biological systems.

Further evidence of the quasi-independence of the genealogical and ecological hierarchies is the frequent disconnect between morphology (disparity) and diversity, because disparity may correlate more closely with ecological occupation. The cause of these disconnects vary. Disparity has been shown to become decoupled from diversity during and after mass

**Uncertainty:** uncertainty applies to any assertion for which data or precision are lacking. For example, phylogenetic uncertainty can be the result of inability to resolve relationships between taxa or by the occurrence of conflicting phylogenetic hypotheses. Stratigraphic uncertainty refers to the level of temporal accuracy and/or precision that can be applied to the occurrence of a specimen in the fossil record.

extinctions [73]. Disparity also exhibits clade- and biogeography-specific trends [74] that result in the potential for major shifts in trajectory as a result of selective extinctions or radiations. Indeed, disparity was shown to increase in plesiosaurs as diversity decreased in one dominant clade and other clades underwent minor radiations [20]. The directionality of this decoupling is nonspecific, because disparity may remain constant both as diversity declines [75] or increases [18]. As such, it is important that evolutionary studies consider both genealogical and ecological hierarchies when examining evolutionary rates and trends in disparity and diversity.

### Community Evolution and Historical Biogeography

Both modern and ancient biogeographic studies reveal that diversity is clustered into 'hotspots' [76–79] or localized in specific environments [29]. Phylogenies that include extinct taxa can reveal the historical processes of origination, extinction, and dispersal that determine community structure and that shape geographic and environmental gradients in diversity.

#### Biogeography and Community Structure

The **richness** and composition of communities varies across the planet, the result of both the response of taxa to biological and environmental variables and the temporal patterns of extinction and origination within the region. The fossil record allows for these patterns of variable diversification to be analyzed not only geographically, but also temporally. Global climate varies through time, and large-scale climatic shifts can result in changes in the distribution of evolutionary hotspots, effectively modifying the spatial patterns of diversification through time. For example, studies using phylogenetic biogeographic methods and ecological niche modeling have demonstrated that early diversification and adaptation within fossil horses was correlated with Miocene climatic variations, which fragmented available habitat space and promoted an increase in speciation [80,81]. These variable climatic conditions disappeared after the Miocene, and diversification rates within equids plummeted.

Similar to origination, extinction risk is also unevenly distributed spatially and temporally and is responsible for large-scale patterns of regional community structure. For example, the striking difference between faunas of the Arctic and Antarctic suggest a deep evolutionary divergence that precludes simple models of taxa following their preferred environment during global cooling [82]. Investigation of the evolutionary relationships of fossil bivalves demonstrated that differential extinction patterns during the early Cenozoic, rather than more recent climatic change, are likely the primary reason for this dramatic difference in faunal composition [31]. These historical patterns of extinction are often missed in studies that focus strictly on modern data and, therefore, necessitate the incorporation of fossil taxa.

Differential origination and extinction patterns through time can also have long-lasting effects on the evolutionary structure of community assemblages [83]. Phylogenetic overdispersion of taxa within a community (i.e., taxa are more distantly related than expected by chance) suggests that competition for resources has prevented closely related species from coexisting. By contrast, phylogenetic clustering of taxa within communities (i.e., taxa are more closely related than expected by chance) suggests that habitat sorting, substrate preference, or other climatic variables drove the coexistence of taxa [84]. The fossil record allows for the direct study of the role that differential origination and extinction has in shaping regional species pools. For example, patterns of extinction and origination in response to long-term climate change can affect the phylogenetic pattern from which communities are drawn. Phylogenetically clustered extinctions through time can create a more dispersed regional species pool [85], leading to incorrect conclusions about the role of habitat sorting versus competition in assembling the community. Thus, phylogenetic paleoecology can be used to directly inform the historical processes that underlie modern community structure.

### Diversity Gradients through Time

In marine environments, onshore–offshore variation in the origin of evolutionary novelty and the assembly of communities explains the ecological structure of marine communities over geological time. Clades with similar diversification histories (**‘Evolutionary Faunas’**) show similar large-scale dispersal patterns: members of these Faunas assembled onshore during the early Paleozoic, then spread offshore by the end of the Paleozoic [86]. These patterns exist despite the fact that Evolutionary Faunas comprise disparate groups both phylogenetically and ecologically. Early work indicated that the pattern of onshore assembly and offshore spread of community types could be explained by an extinction gradient with higher extinction rate onshore. Clades with high extinction rates were then replaced by clades with lower extinction rates, which then spread offshore [3]. The importance of *in situ* differential rates of origination and extinction has been further supported by recent analysis of **niche conservatism** within genera during this time [58], but the role of niche evolution through migration or expansion remains unknown. Post-Paleozoic clades show a propensity for the earliest species to arise in onshore environments and then spread offshore [87]. This suggests that evolutionary novelties appear more frequently in some environments than others, a hypothesis that could be tested throughout deep time using evolutionary trees to correct for potential sampling issues (Box 3). Phylogenetic paleoecology also offers a means to test whether this pattern of differential origination and extinction holds across multiple clades through time.

The latitudinal diversity gradient (LDG) is a well-known modern pattern that has deep evolutionary roots [76,77,79]. Analyses of the fossil record of marine bivalves demonstrated that the modern LDG is driven by higher origination and lower extinction in the tropics compared with extratropical regions, and by migration of some clades out of the tropics [77,79]. However, this modern LDG may have only originated 30 million years ago, and may not have been a persistent feature through time. Instead, icehouse and greenhouse regimes appear to be characterized by different LDG patterns [88]. Resolving whether there are evolutionary drivers to LDG formation, and whether these mechanisms are consistent irrespective of the latitudinal position of the diversity peaks, requires combining the spatial and temporal patterns of origination and extinction from the fossil record with the phylogenetic relationships of extinct taxa.

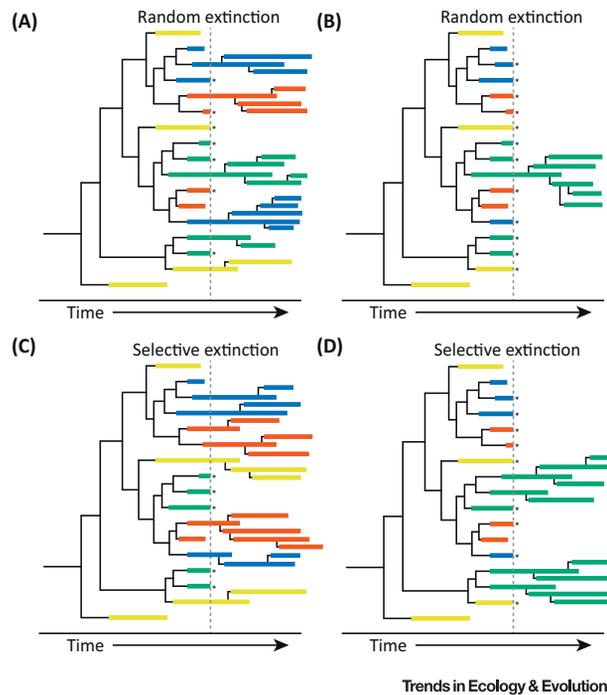
Many questions remain about the development of diversity gradients through time that require knowledge of the evolutionary relationships. For example, how do rates of character evolution vary along environmental gradients, and are rates highest in environments with highest diversity? Does offshore expansion occur primarily by occupation and diversification of new subclades in new environments, or does environmental expansion occur within multiple subclades across the tree? Given that evolutionary trees are still lacking for most marine groups with an extensive fossil record, community paleoecology is bound to yield many insights into the origin and maintenance of diversity gradients as evolutionary trees become more common.

### Selectivity in Extinction and Radiation

Mass extinctions and their recoveries can have a disproportionate effect on specific ecologies, an observation supported by analyses of both fossil [89] and modern [90] data. By incorporating phylogenetic hypotheses into these studies, it is possible to distinguish whether these ecological shifts are the result of **contingent** (chance) or selective processes (Figure 1). Given current concerns about the modern biotic crisis and mass extinctions [90], it is this aspect of phylogenetic paleoecology that is most directly relevant to conservation biology (Box 4).

### Differential Responses to Extinction Events

Mass extinctions have varied widely in their severity and ecological and evolutionary consequences [53,94], due in part to differences in the dynamics of the pre-extinction ecosystems.



**Figure 1.** Representations of Contingent and Convergent Responses to Random and Selective Extinction Pressures among Species Exhibiting a Variety of Ecological Traits (Denoted by Yellow, Red, Blue, or Green Range Bars). Species that go extinct in response to the extinction event are shown with an asterisk (\*). These examples consider only one ecological trait, and other properties of the organisms (such as biogeography, life history, or other ecological traits) may also be selected upon. (A) A random extinction with contingent response in respect to the observed ecological traits. (B) A random extinction with contingent response in respect to the observed ecological traits, resulting in the persistence and proliferation of the green ecological trait through the chance survival of a species that has this trait. (C) A selective extinction that selects against the green ecological trait, resulting in a convergent response across disparate clades. (D) A selective extinction that selects for the green ecological trait, resulting in a convergent response across distantly related clades. This is distinguishable from the contingent response to the random extinction shown in (B) because the survivors belong to two disparate clades. Phylogenetic hypotheses of relationships allow researchers to determine these patterns of selectivity at a finer scale than would be seen using taxonomy-based approaches (Box 1, main text).

Major extinction events have been shown to permanently alter prevailing evolutionary dynamics [77], resulting in new ecological associations with patterns of diversification that are distinct from the pre-extinction communities. The cause of a given mass extinction event also impacts its outcome, with protracted events resulting in delayed biotic recovery long after the initial extinction pulse [95]. Extinction severity has also been documented to vary spatially and between environments during mass extinction events, although the degree of this variation is not consistent between events. For example, different biogeographic provinces exhibited different shifts in rate in response to the end-Cretaceous mass extinction [77], and differential extinction rates consistently prevailed in epicontinental seas and open marine settings across multiple mass extinctions [96]. One major outcome of these regional variations is that changes in alpha and beta diversity during mass extinctions become decoupled [97]. These differential responses are likely the result of a combination of historical and contingent factors. However, to separate these factors, it is necessary to understand the evolutionary relationships of organisms along with their temporal and spatial distributions, because spatial cohorts may be unequally distributed on the phylogenetic tree. As such, ecologically random extinctions (Figure 1A,B) may be due to biogeographic selection, while ecologically selective extinctions (Figure 1C,D) may appear random when viewed solely through the lens of biogeography.

#### Box 4. The Natural Synthesis of Phylogenetic Paleoecology and Conservation Biology

As environmental change accelerates and ecosystems become increasingly threatened, focusing conservation efforts on important aspects of biodiversity is paramount [53]. To maintain the tree of life, focus has increasingly turned to preserving the evolutionary processes that maintain that tree today. The evolutionary history recorded by species is represented as the branch lengths of a phylogeny, and is calculated as phylogenetic diversity (PD; [91]), which measures the length of those branches globally, regionally, or within communities. While correlated with richness, certain communities can harbor more phylogenetic diversity than expected given the species diversity in that area, making these crucibles of evolution important foci for conservation efforts. If extinctions are random, 95% of the modern tree of life will be preserved even with species-level extinction rates as high as 80% [92]. However, modern extinctions are nonrandom, and conserving PD requires understanding how it is accumulated within communities. This means communities must be studied in their natural state before human interference.

The fossil record offers an undisturbed baseline for community assembly before anthropogenic activities [60,62]. Paleocommunities have many advantages for guiding conservation efforts. First, because they are time-averaged, they preserve a complete sample of species that coexisted within a region, including relative abundance. Additionally, paleocommunities record the response of species to environmental changes through time, allowing researchers to differentiate real biotic responses to disturbance from natural variation in community structures or geographical ranges that occur on annual to decadal timescales. This is necessary if we are to predict the response of species to future climate shifts. Analyses of living communities can only analyze the snapshot of the diversity within a region today, and must reconstruct ancestral niches or geographical ranges using the phylogenetic relationships of living taxa [8]. However, paleocommunities allow a direct window into niches occupied by ancient species and how those change [93]. Paleocommunities also allow us to determine extinction rates within communities. Combined, this information can focus conservation efforts on regions that harbor the most threatened portions of the tree of life, allowing for the preservation of phylogenetic diversity and the recovery of communities as they respond to climate shifts.

#### The Phylogenetic Distribution of Extinction and Recovery

Using taxonomic clustering of brachiopods as a proxy for phylogenetic selectivity demonstrated that significant shifts in the strength of phylogenetic selectivity occurred following the Late Ordovician mass extinction [9]. Extinction was taxonomically random or weakly clustered during the Ordovician, including the Late Ordovician mass extinction, but shifted to be significantly clustered after the mass extinction. A phylogenetic framework would bolster these analyses by explicitly testing whether the taxonomic groups used are monophyletic (thereby reducing the noise caused by the pseudoextinction of paraphyletic groups or the duplicated loss of a polyphyletic lineage) and by allowing for phylogenetic clumping to be assessed directly. Furthermore, these patterns of extinction and radiation can be evaluated in concert with both morphological (see **functional diversity**) and **ecological traits** to determine whether changes in diversification rates across these events significantly correlate with ecological occupation or morphological evolutionary shifts.

Ecological severity is known to be decoupled from taxonomic selectivity at mass extinctions [54], suggesting that different forcing mechanisms will frequently leave a different ecological signature [55]. However, outside of a phylogenetic framework, it cannot be determined whether the outcomes of extinctions and subsequent recoveries are due to selection for particular ecological traits across disparate clades, which would require smaller extinction intensities to bring about large ecological shifts, or whether ecological traits rise to dominance through chance survival and radiation of a single group, requiring larger extinction intensities to remove whole clades (Figure 1). For example, eurypterids exhibit extreme gigantism in two disparate clades over different time periods. One clade comprises large marine predators and the other large freshwater sweep-feeders, indicating that gigantism has arisen independently in each clade but has subsequently been phylogenetically conserved within them [98]. Only two eurypterid clades persist past the end of the Devonian, both showing affinities to freshwater. Both freshwater clades are only distantly related phylogenetically, yet both are able to weather the biotic crisis that defines the late Devonian due to their **convergent** ecological occupation [23]. The late Devonian extinctions in particular exhibit great ecological changes compared with earlier Paleozoic extinctions [55]. Phylogenetic study of fossil terebratulide brachiopods

showed that, both organismal (body size) and emergent (geographic range size) ecological traits tend to be phylogenetically conserved within the group [99]. Therefore, even a small extinction event focused within specific clades could cause an extreme ecological shift. Any event that preferentially selected against these characteristics could present an example of ecologically selective extinction processes. Even during the extreme taxonomic loss of the end-Permian mass extinction, ecologically selective trends are apparent in the therapsid phylogeny, where distantly related taxa that show convergent development of earlier sexual maturity preferentially survived the extinction [36].

### Concluding Remarks

The burgeoning synthesis of phylogenetic and paleoecological data expands the analytical toolset of deep-time macroevolutionary and macroecological studies. Deep-time, temporal data derived from the fossil record is also of direct relevance to analyses of modern systems, because it contextualizes results, permits the observation of large-scale trends, and allows for the formulation of predictive hypotheses based on past events [58,59,61–63]. Phylogenetic paleoecological analyses can have direct bearing on several major evolutionary questions concerning controls on disparity, the nature of mass extinctions, details of community construction, and the influence of scale and hierarchy on emergent trends (see Outstanding Questions). Phylogenetic trees incorporating fossil taxa are an urgent priority. In particular, efforts to identify phylogenetically informative morphological characters must continue for traditionally ‘problematic’ fossil groups (e.g., ammonites, brachiopods, or gastropods). Continuing developments in phylogenetic analysis and range reconstruction will further increase the accuracy and obtainability of phylogenetic trees. Finally, there remains a need for increased accessibility to the primary data of the fossil record; in this case, more collections with detailed locality (geographic, stratigraphic, and taxonomic) data.

Further understanding of the role of ecological processes in shaping the history of life will develop as new methods are applied to the vast paleontological resource and synthesized with data derived from extant organisms and ecosystems. Collaborations between taxonomists and paleoecologists with detailed knowledge of the morphology, distribution, life habit, and range of these groups alongside phylogeneticists with knowledge of the appropriate analytical methods are crucial to the accomplishment of this goal.

### Acknowledgments

J.C.L. was supported by a Lerner Gray Postdoctoral Fellowship at the American Museum of Natural History. A.Z.K. and M.E.P. were funded by NASA Astrobiology grant number 11-EXO11-0070. The authors thank Peter Wagner and three anonymous referees for useful comments in the review process.

### References

1. Raup, D.M. and Sepkoski, J.J. (1982) Mass extinctions and the marine fossil record. *Science* 215, 1501–1503
2. Jablonski, D. (1987) Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science* 238, 360–363
3. Sepkoski, J.J., Jr (1991) A model of onshore-offshore change in faunal diversity. *Paleobiology* 17, 58–77
4. Kiessling, W. and Aberhan, M. (2007) Environmental determinants of marine benthic biodiversity. *Paleobiology* 33, 414–434
5. Jablonski, D. et al. (2013) Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proc. Natl. Acad. Sci. U. S. A.* 110, 10487–10494
6. Vrba, E.S. (1980) Evolution, species and fossils: how does life evolve? *S. Afr. J. Sci.* 76, 61–84
7. Tomašových, A. et al. (2014) Onshore-offshore gradient in metacommunity turnover emerges only over macroevolutionary time-scales. *Proc. R. Soc. Lond. B* 281, 20141533
8. Lawing, A.M. and Matzke, N.J. (2014) Conservation paleobiology needs phylogenetic methods. *Ecography* 37, 1109–1122
9. Krug, A.Z. and Patzkowsky, M.E. (2015) Phylogenetic clustering of origination and extinction across the Late Ordovician mass extinction. *PLoS ONE* 10, E0144354
10. Jablonski, D. and Finarelli, J.A. (2009) Congruence of morphologically-defined genera with molecular phylogenies. *Proc. Natl. Acad. Sci. U. S. A.* 106, 8262–8266
11. Soul, L.C. and Friedman, M. (2015) Taxonomy and phylogeny can yield comparable results in comparative paleontological analyses. *Syst. Biol.* 64, 608–620
12. Tucker, C.M. et al. (2016) A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biol. Rev. Camb. Philos. Soc.* Published online January 20, 2016. <http://dx.doi.org/10.1111/brv.12252>
13. Rangel, T.F. et al. (2015) Phylogenetic uncertainty revisited: implications for ecological analyses. *Evolution* 69, 1301–1312

### Outstanding Questions

In 2012, a workshop was convened at Oxford University, the goal of which was to identify priority research questions in paleoecology [100]. A subset of those identified focused on better understanding the emergence of novel ecosystems and processes driving biodiversity over deep time, but there was little discussion of the utility of phylogenetic frameworks in future investigations of these topics. Outstanding questions that would benefit from such an approach include:

Is occupation of new ecological niches driven by evolutionary innovation, and are such events linked to increases in evolutionary rates?

Are there particular environments or biogeographic regions that have favored species diversification, and has this changed over the Phanerozoic?

Have communities been more frequently altered by *in situ* diversification or by biotic invasions?

What is the relationship between niche occupation and phylogenetic distance?

Are mass extinctions individualistic, unique events, or do different forcing mechanisms result in predictable ecological outcomes?

Does the extent of morphological disparity within a clade correlate with its chances of survivorship during extinction events?

How does the use of different taxonomic levels in macroevolutionary and macroecological studies impact observed trends, and are there distinct emergent trends at both the clade and species levels?

14. Cummings, M.P. *et al.* (2003) Comparing bootstrap and posterior probability values in the four-taxon case. *Syst. Biol.* 52, 477–487
15. Congreve, C.R. and Lamsdell, J.C. (2016) Implied weighting and its utility in palaeontological datasets: a study using modelled phylogenetic matrices. *Palaeontology* 59, 447–462
16. Holder, M.T. *et al.* (2008) A justification for reporting the majority-rule consensus tree in Bayesian phylogenetics. *Syst. Biol.* 57, 814–821
17. Ruta, M. *et al.* (2006) Evolutionary patterns in early tetrapods. I. Rapid initial diversification followed by decrease in rates of character change. *Proc. R. Soc. Lond. B* 273, 2107–2111
18. Ruta, M. *et al.* (2013) Decoupling of morphological disparity and taxic diversity during the adaptive radiation of anamniote therapsids. *Proc. R. Soc. Lond. B* 280, 20131071
19. Price, S.L. *et al.* (2016) Tightly congruent bursts of lineage and phenotypic diversification identified in a continental ant radiation. *Evolution* 70, 903–912
20. Benson, R.B.J. *et al.* (2012) High diversity, low disparity and small body size in Plesiosaurs (Reptilia, Sauropterygia) from the Triassic–Jurassic boundary. *PLoS ONE* 7, e31838
21. Fischer, V. *et al.* (2016) Extinction of fish-shaped marine reptiles associated with reduced evolutionary rates and global environmental volatility. *Nat. Commun.* 7, 10825
22. Lamsdell, J.C. (2016) Horseshoe crab phylogeny and independent colonizations of fresh water: ecological invasion as a driver for morphological innovation. *Palaeontology* 59, 181–194
23. Lamsdell, J.C. and Selden, P.A. (2017) From success to persistence: identifying an evolutionary regime shift in the diverse Paleozoic aquatic arthropod group Euryptera, driven by the Devonian biotic crisis. *Evolution* 71, 95–110
24. Hopkins, M.J. and Smith, A.B. (2015) Dynamic evolutionary change in post-Paleozoic echinoids and the importance of scale when interpreting changes in rates of evolution. *Proc. Natl. Acad. Sci. U. S. A.* 112, 3758–3763
25. Benson, R.B.J. *et al.* (2014) Rates of dinosaur body mass evolution indicate 170 million years of sustained ecological innovation on the avian stem lineage. *PLoS Biol.* 12, e1001853
26. Wang, M. and Lloyd, G.T. (2016) Rates of morphological evolution are heterogeneous in Early Cretaceous birds. *Proc. R. Soc. Lond. B* 283, 20160214
27. Rabosky, D.L. (2015) No substitute for real data: a cautionary note on the use of phylogenies from birth-death polytomy resolvers for downstream comparative analyses. *Evolution* 69, 3207–3216
28. O'Reilly, J.E. *et al.* (2016) Bayesian methods outperform parsimony but at the expense of precision in estimation of phylogeny from discrete morphological data. *Biol. Lett.* 12, 20160081
29. Ricklefs, R.E. (2006) Evolutionary diversification and the origin of the diversity–environment relationship. *Ecology* 87, S3–S13
30. Hunt, G. *et al.* (2015) Simple versus complex models of trait evolution and stasis as a response to environmental change. *Proc. Natl. Acad. Sci. U. S. A.* 112, 4885–4890
31. Krug, A.Z. *et al.* (2010) Differential extinction and the contrasting structure of polar marine faunas. *PLoS ONE* 5, e15362
32. Raia, P. (2010) Phylogenetic community assembly over time in Eurasian Plio-Pleistocene mammals. *Palaïos* 25, 327–338
33. Wright, D.F. and Stigall, A.L. (2013) Geologic drivers of Late Ordovician faunal change in Laurentia: investigating links between tectonics, speciation, and biotic invasions. *PLoS ONE* 8, e68353
34. Villalobos, F. *et al.* (2016) Phylogenetic fields through time: temporal dynamics of geographical co-occurrence and phylogenetic structure within species ranges. *Proc. R. Soc. Lond. B* 371, 20150220
35. Congreve, C.R. (2013) Cladal turnover: the end-Ordovician as a large-scale analogue of species turnover. *Palaeontology* 56, 1285–1296
36. Botha-Brink, J. *et al.* (2016) Breeding young as a survival strategy during Earth's greatest mass extinction. *Sci. Rep.* 6, 24053
37. Bromham, L. *et al.* (2016) Detecting macroevolutionary self-destruction from phylogenies. *Syst. Biol.* 65, 109–127
38. Colles, A. *et al.* (2009) Are specialists at risk under environmental change? Neoeological, paleoecological and phylogenetic approaches. *Ecol. Lett.* 12, 849–863
39. Pyron, R.A. and Burbrink, F.T. (2013) Phylogenetic estimates of speciation and extinction rates for testing ecological and evolutionary hypotheses. *Trends Ecol. Evol.* 28, 729–736
40. Moen, D. and Morlon, H. (2014) Why does diversification slow down? *Trends Ecol. Evol.* 29, 190–197
41. Day, E.H. *et al.* (2016) Is specialization an evolutionary dead-end? Testing for differences in speciation, extinction and trait transition rates across diverse phylogenies of specialists and generalists. *J. Evol. Biol.* 29, 1257–1267
42. Fritz, S.A. *et al.* (2013) Diversity in time and space: wanted dead and alive. *Trends Ecol. Evol.* 28, 509–516
43. Betancur-R, R. *et al.* (2015) Fossil-based comparative analyses reveal ancient marine ancestry erased by extinction in ray-finned fishes. *Ecol. Lett.* 18, 441–450
44. Mitchell, J.S. (2015) Extant-only comparative methods fail to recover the disparity preserved in the bird fossil record. *Evolution* 69, 2414–2424
45. Patzkowsky, M.E. and Holland, S.M. (2012) *Stratigraphic Paleobiology: Understanding the Distribution of Fossil Taxa in Time and Space*, University of Chicago Press
46. Holland, S.M. and Zaffos, A. (2011) Niche conservatism along an onshore-offshore gradient. *Paleobiology* 37, 270–286
47. Saupe, E.E. *et al.* (2014) Macroevolutionary consequences of profound climate change on niche evolution in marine molluscs over the past three million years. *Proc. R. Soc. B* 281, 20141995
48. Hopkins, M.J. (2014) The environmental structure of trilobite morphological disparity. *Paleobiology* 40, 352–373
49. Holland, S.M. (2016) The non-uniformity of fossil preservation. *Phil. Trans. R. Soc. B* 371, 20150130
50. Wagner, P.J. and Marcot, J.D. (2013) Modelling distributions of fossil sampling rates over time, space and taxa: assessment and implications for macroevolutionary studies. *Methods Ecol. Evol.* 4, 703–713
51. Lloyd, G.T. *et al.* (2012) Identifying heterogeneity in rates of morphological evolution: discrete character change in the evolution of lungfish (Sarcopterygii; Dipnoi). *Evolution* 66, 330–348
52. Bapst, D.W. *et al.* (2016) Topology, divergence dates, and macroevolutionary inferences vary between different tip-dating approaches applied to fossil theropods (Dinosauria). *Biol. Lett.* 12, 20160237
53. Harnik, P.G. *et al.* (2012) Extinctions in ancient and modern seas. *Trends Ecol. Evol.* 27, 608–617
54. McGhee, G.R., Jr (2013) A new ecological-severity ranking of major Phanerozoic biodiversity crises. *Palaeogeogr. Palaeoecol. Palaeoecol.* 370, 260–270
55. Christie, M. *et al.* (2013) Contrasting the ecological and taxonomic consequences of extinction. *Paleobiology* 39, 538–559
56. Valiente-Banuet, A. (2015) Beyond species loss: the extinction of ecological interactions in a changing world. *Funct. Ecol.* 29, 299–307
57. Hull, P.M. *et al.* (2015) Rarity in mass extinctions and the future of ecosystems. *Nature* 528, 345–351
58. Yasuhara, M. *et al.* (2016) Combining marine macroecology and palaeoecology in understanding biodiversity: microfossils as a model. *Biol. Rev. Camb. Philos. Soc.* 92, 199–215
59. Dietl, G.P. (2013) The great opportunity to view stasis with an ecological lens. *Palaeontology* 56, 1239–1245
60. Kosnik, M.A. and Kowalewski, M. (2016) Understanding modern extinctions in marine ecosystems: the role of palaeoecological data. *Biol. Lett.* 12, 20150951
61. Beck, J. *et al.* (2012) What's on the horizon for macroecology? *Ecography* 35, 673–683
62. Dietl, G.P. *et al.* (2015) Conservation paleobiology: leveraging knowledge of the past to inform conservation and restoration. *Annu. Rev. Earth Planet Sci.* 43, 79–103
63. Benton, M.J. (2015) Exploring macroevolution using modern and fossil data. *Proc. R. Soc. Lond. B* 282, 20150569

64. Weber, M.G. *et al.* (2017) Evolution in a community context: on integrating ecological interactions and macroevolution. *Trends Ecol. Evol.* 32, 291–304
65. Erwin, D.H. (2007) Disparity: morphological pattern and developmental context. *Palaeontology* 50, 57–73
66. Hughes, M. *et al.* (2013) Clades reach highest morphological disparity early in their evolution. *Proc. Natl. Acad. Sci. U. S. A.* 110, 13875–13879
67. Hopkins, M.J. (2016) Magnitude versus direction of change and the contribution of macroevolutionary trends to morphological disparity. *Biol. J. Linnean. Soc.* 118, 116–130
68. Kammer, T.W. *et al.* (1997) Species longevity as a function of niche breadth: evidence from fossil crinoids. *Geology* 25, 219–222
69. Crampton, J.S. *et al.* (2010) Biotic influences on species duration: interactions between traits in marine molluscs. *Paleobiology* 36, 204–223
70. Burin, G. *et al.* (2016) Omnivory in birds is a macroevolutionary sink. *Nat. Commun.* 7, 11250
71. Sanders, K.L. *et al.* (2010) Uncoupling ecological innovation and speciation in sea snakes (Elapidae, Hydrophiinae, Hydrophiini). *J. Evol. Biol.* 23, 2685–2693
72. Eldredge, N.I. and Salthe, S.N. (1984) Hierarchy and evolution. *Oxf. Surv. Evol. Biol.* 1, 184–208
73. Bapst, D.W. *et al.* (2012) Graptoloid diversity and disparity became decoupled during the Ordovician mass extinction. *Proc. Natl. Acad. Sci. U. S. A.* 109, 3428–3433
74. Brusatte, S.L. *et al.* (2012) Dinosaur morphological diversity and the end-Cretaceous extinction. *Nat. Commun.* 3, 804
75. Hopkins, M.J. (2013) Decoupling of taxonomic diversity and morphological disparity during decline of the Cambrian trilobite family Pteroccephaliidae. *J. Evol. Biol.* 26, 1665–1676
76. Crame, J.A. (2002) Evolution of taxonomic diversity gradients in the marine realm: a comparison of Late Jurassic and Recent bivalve faunas. *Paleobiology* 28, 184–207
77. Krug, A.Z. *et al.* (2009) Signature of the end-Cretaceous mass extinction in the modern biota. *Science* 323, 767–771
78. Floeter, S.R. *et al.* (2014) Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. *J. Fish Biol.* 64, 1680–1699
79. Jablonski, D. *et al.* (2017) Shaping the latitudinal diversity gradient: new perspectives from a synthesis of paleobiology and biogeography. *Am. Nat.* 189, 1–12
80. Maguire, K.C. and Stigall, A.L. (2008) Paleobiogeography of Miocene Equinae of North America: a phylogenetic biogeographic analysis of the relative roles of climate, vicariance, and dispersal. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 267, 175–184
81. Maguire, K.C. and Stigall, A.L. (2009) Using ecological niche modeling for quantitative biogeographic analysis: a case study of Miocene and Pliocene Equinae in the Great Plains. *Paleobiology* 35, 587–611
82. Clarke, A. (2008) Antarctic marine benthic diversity: patterns and processes. *J. Exp. Mar. Biol. Ecol.* 366, 48–55
83. Ricklefs, R.E. (2007) Estimating diversification rates from phylogenetic information. *Trends Ecol. Evol.* 22, 601–610
84. Webb, C.O. *et al.* (2002) Phylogenies and community ecology. *Annu. Rev. Ecol. Evol. Syst.* 33, 475–505
85. Fraser, D. *et al.* (2015) Macroevolution and climate change influence phylogenetic community assembly of North American hoofed mammals. *Biol. J. Linnean. Soc.* 114, 485–494
86. Sepkoski, J.J., Jr and Miller, A.I. (1985) Evolutionary faunas and the distribution of Paleozoic marine communities in space and time. In *Phanerozoic Diversity Patterns: Profiles in Macroevolution* (Valentine, J.W., ed.), pp. 153–190, Princeton Press
87. Jablonski, D. (2007) Scale and hierarchy in macroevolution. *Palaeontology* 50, 87–109
88. Mannion, P.D. *et al.* (2014) The latitudinal biodiversity gradient through deep time. *Trends Ecol. Evol.* 29, 42–50
89. Wagner, P.J. and Estabrook, G.F. (2014) Trait-based diversification shifts reflect differential extinction among fossil taxa. *Proc. Natl. Acad. Sci.* 111, 16419–16424
90. Payne, J.L. *et al.* (2016) Ecological selectivity of the emerging mass extinction in the oceans. *Science* 353, 1284–1286
91. Faith, D.P. *et al.* (2004) Integrating phylogenetic diversity, complementarity, and endemism for conservation assessment. *Conserv. Biol.* 18, 255–261
92. Nee, S. and May, R.M. (1997) Extinction and the loss of evolutionary history. *Science* 278, 692–694
93. Patzkowsky, M.E. and Holland, S.M. (2016) Biotic invasion, niche stability, and the assembly of regional biotas in deep time: comparison between faunal provinces. *Paleobiology* 42, 359–379
94. Payne, J.L. and Finnegan, S. (2007) The effect of geographic range on extinction risk during background and mass extinction. *Proc. Natl. Acad. Sci. U. S. A.* 104, 10506–10511
95. Thibodeau, A.M. *et al.* (2016) Mercury anomalies and the timing of biotic recovery following the end-Triassic mass extinction. *Nat. Commun.* 7, 11147
96. Miller, A.I. and Foote, M. (2009) Epicontinental seas versus open-ocean settings: the kinetics of mass extinction and origination. *Science* 326, 1106–1109
97. Darroch, S.A.F. and Wagner, P.J. (2015) Response of beta diversity to pulses of Ordovician-Silurian mass extinction. *Ecology* 92, 532–549
98. Lamsdell, J.C. and Braddy, S.J. (2010) Cope's rule and Romer's theory: patterns of diversity and gigantism in eurypterids and Palaeozoic vertebrates. *Biol. Lett.* 6, 265–269
99. Harnik, P.G. *et al.* (2014) Phylogenetic signal in extinction selectivity in Devonian terebratulide brachiopods. *Paleobiology* 40, 675–692
100. Seddon, A.W.R. *et al.* (2014) Looking forward through the past: identification of 50 priority research questions in palaeoecology. *J. Ecol.* 102, 256–267