

Extinction as the loss of evolutionary history

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Current plant and animal diversity preserves at most 1–2% of the species that have existed over the past 600 million years. But understanding the evolutionary impact of these extinctions requires a variety of metrics. The traditional measurement is loss of taxa (species or a higher category) but in the absence of phylogenetic information it is difficult to distinguish the evolutionary depth of different patterns of extinction: the same species loss can encompass very different losses of evolutionary history. Furthermore, both taxic and phylogenetic measures are poor metrics of morphologic disparity. Other measures of lost diversity include: functional diversity, architectural components, behavioral and social repertoires, and developmental strategies. The canonical five mass extinctions of the Phanerozoic reveals the loss of different, albeit sometimes overlapping, aspects of loss of evolutionary history. The end-Permian mass extinction (252 Ma) reduced all measures of diversity. The same was not true of other episodes, differences that may reflect their duration and structure. The construction of biodiversity reflects similarly uneven contributions to each of these metrics. Unraveling these contributions requires greater attention to feedbacks on biodiversity and the temporal variability in their contribution to evolutionary history. Taxic diversity increases after mass extinctions, but the response by other aspects of evolutionary history is less well studied. Earlier views of postextinction biotic recovery as the refilling of empty ecospace fail to capture the dynamics of this diversity increase.

biodiversity | morphologic disparity | ecosystem engineering

Extinction is the inevitable fate of organisms, although there is considerable variance in both rates of extinction through time and the duration of particular species or clades. By some estimates, extant multicellular biodiversity is but 1–2% of all multicellular species that have existed over the past 600 Ma (1, 2). Paleontologists have long recognized that the relatively regular overturn of species is occasionally punctuated by more severe biotic crises, including at least five events recognized as mass extinctions. Some have claimed that rates of current species loss exceed those of past mass extinctions. Perhaps the most valuable contribution that paleontologists can make to understanding the current biodiversity crisis is to identify the relationship between attributes of the loss of past evolutionary history and both the depth of past crises and the speed and structure of subsequent biotic recovery. Given that conservation biologists increasingly face a problem of triage, where not all species can be saved, can paleontological data provide any insights into the species, communities, or structures that should have the highest priority for support? Paleontological data are unlikely to be decisive in such decisions, but the unique perspective provided by the fossil record may provide a useful input.

Here, I discuss a range of potential metrics for the impact of extinction on the loss of evolutionary history and provide a preliminary application of them to the five canonical mass extinctions (see also ref. 3). There are, however, relatively few applications of these metrics to understanding the processes of postextinction biotic recovery.

Metrics for the Loss of Evolutionary History

The traditional accounting method for the loss of evolutionary history is taxa: populations and species for biologists, often genera or families for paleontologists because the vagaries of

preservation and correlation make species-level compilations impractical. Conservation biologists have long focused on species, an approach enshrined in the U.S. Endangered Species Act. This reliance on taxa tends to assume, implicitly, that taxonomic entities are a reliable metric to the impact of extinction on ecosystem structure and function, morphological variability, behavior complexity, and developmental processes. This assumption is often far from true. Consequently, conservation biologists have proposed other metrics for identifying critical targets for conservation (4), including biogeographic centers of endemic taxa, or hotspots (5), and the characterization of phylogenetic diversity (6, 7) and evolutionary distinctiveness (8). There is, however, a more important reason for considering the loss of other aspects of evolutionary history, and that is the search for mechanisms underlying patterns of extinction and construction of biodiversity. Ecologists increasingly recognize the importance of a network of interactions in generating biodiversity, including positive feedback relationships among biodiversity, productivity, and stability (9, 10).

Although paleontologists are aware of the diversity of effects on evolutionary history caused by past extinctions, particularly mass extinctions, we have been slow to develop and apply comparative metrics beyond taxic compilations and estimates of geographic range. Enough work has been done to suggest a range of alternative metrics. Biogeographic structure is an important aspect of evolutionary history that has been considered elsewhere (11).

Taxic Diversity. The divisions of the geologic time scale are framed by biotic crises recognized by early geologists as “revolutions” triggering wholesale changes in the biota. Paleontologists have since compiled records of fluctuations in taxonomic diversity for marine taxa (12, 13), terrestrial plants (14), vertebrates (15), and various microfossil groups (16). Patterns of extinction and origination have received considerable attention, particularly the decline in “background” extinction rates through the Phanerozoic for marine families and genera (17) and episodic events of increased extinction. Curiously, as the English geologist John Phillips understood as long ago as the 1840s, extinctions within geologic stages appears pulsed, rather than spread out through the stage (18). Within clades paleontologists have also identified intriguing patterns of replacement where successive subclades replaced earlier clades. For higher-resolution analyses statistical techniques have been developed to account for sampling problems (see ref. 19 for an application to the end-Permian mass extinction).

Several general lessons emerge from these compilations. First, the persistent decline in extinction rates suggests an increased stability in younger taxa, although this may be a statistical artifact of increased species/genus and species/family ratios (17). It would be of considerable interest to know whether this apparent

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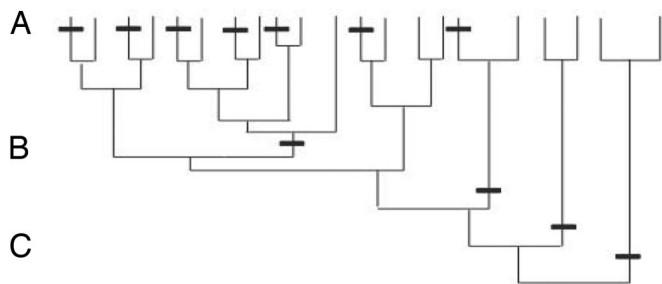


Fig. 1. Similar losses of taxic diversity have very different implications for the loss of evolutionary history depending on the phylogenetic distribution of the extinctions. Three different scenarios are shown, at levels A, B, and C. (A) Seven taxa are lost (33% extinction) but the overall structure of the phylogeny is preserved. (B) An entire clade of seven taxa is pruned, but the remaining structure is preserved. (C) Six taxa are lost but this eliminates the deepest branching clades.

increased robustness is real and whether it translates into some of the other metrics described below. Second, patterns of subclade replacement can suggest adaptive improvement within the activities of the larger clade, a pattern confirmed by the power of incumbency (20). Third, as demonstrated by a recent analysis of Cenozoic mollusks from New Zealand, species and genera exhibit a limited interval of peak abundance, followed by a long decline to extinction. In this system at least, the species at greatest risk of extinction are those already in decline (21), although this does not appear to hold true during mass extinctions that may truncate ranges (22). Fourth, mass extinction events periodically upset these patterns, and particularly at the end-Permian mass extinction, trigger pervasive changes in patterns of ecological and evolutionary dominance. Thus over evolutionary time, episodic extinctions has been an important driver for evolution.

Understanding the processes controlling long-term changes in diversity requires identifying and correcting for biases in the fossil record that can be introduced by preservation and sampling. Consequently paleontologists have developed new approaches designed to identify and correct for such biases (23–27). These techniques have been applied to correct for biases in our record of the end-Ordovician mass extinction (28). As discussed by Alroy (3), the diversity patterns produced by this intensive compilation of taxic diversity largely follow those of Sepkoski's earlier work (29–31). This effort identifies at least three of the five canonical mass extinctions below. However, like other work (32, 33) it raises questions about the magnitude of other extinction events.

Finally, counting taxa, whether species, genera, or families, assumes that each taxon is equivalent, which is far from true when one considers the differences in diversity or abundance within different groups, much less their evolutionary distinctiveness, morphologic disparity, ecological function, or evolutionary potential.

Phylogenetic Diversity. The two remaining species of tuatara are the sister clade to the $\approx 6,200$ snakes and lizards of the Order Squamata, as the few remaining onychophorans are to the Phylum Arthropoda. Both onychophorans and tuataras are far more evolutionarily distinct than any two members of their sister clade, a fact not captured by a simple taxic approach. A simple exercise illustrates that identical levels of species loss can conceal very effects on evolutionary history (Fig. 1). In each case roughly the same total number of species has been lost. In alternative A, however, there is little loss of the overall structure of the tree, whereas in alternative B, an entire clade has been pruned. Alternative C removes the most basal clades, each of which represents unique units with long evolutionary history. This

simple example demonstrates how knowledge of the phylogenetic structure is essential to evaluating the amount of evolutionary history lost or at risk, and not surprisingly conservation biologists have proposed several different metrics for measuring phylogenetic diversity (6–8). Although some have argued that taxic diversity is a reliable proxy for phylogenetic diversity, empirical studies have convincingly demonstrated the need for phylogenetic analyses. A study of the plants of the fynbos of South Africa, for example, showed that generic richness is strongly decoupled from phylogenetic diversity (34). The most direct demonstration of the importance of a phylogenetic framework was a study showing that some 80% of the structure of the underlying phylogeny can survive even a 95% loss of species (35), if the extinctions are random. When the phylogenetic structure of an extinction is highly clustered, the effects on evolutionary history can be more severe (36).

Paleontologists have long recognized the unequal impact of past biotic crises on the disappearance of particular clades, including archaeocyathid sponges in the Early Cambrian; many trilobite clades and numerous problematica during the various Cambrian crises; trilobites, blastoids and many smaller clades during the end-Permian mass extinction; conodonts at the end-Triassic event; and nonavian dinosaurs, ammonoids, and rudist bivalves during the end-Cretaceous mass extinction. Each such disappearance removed clades of considerable evolutionary distinctiveness. The application of phylogenetic analyses remains sufficiently new that although some studies have addressed phylogenetic patterns across mass extinction boundaries, many of these are at high taxonomic level and broad temporal scope. Several studies have addressed the issue of whether phylogenetic analyses to “correct” ranges using ghost lineages provide a better estimate of diversity than a purely taxic approach (compare ref. 37 with refs. 38 and 39), but this is a different issue from using phylogenetic analysis to understand the structure of an extinction. No studies have explicitly addressed the impact of mass extinctions on phylogenetic diversity to my knowledge. Could one develop a metric of the severity of past extinction crises based on the extent of phylogenetic diversity lost? Identifying a reliable standard of comparison will be challenging, but is likely to provide a very different perspective from taxic studies.

Morphologic Disparity. Every paleontologist is familiar with lost, unique morphologies: the “weird wonders” of the Middle Cambrian Burgess Shale fauna, or *Arthropleura*, the immense, 20-cm-wide, several-meter-long millipede of the Carboniferous. Paleontologists have characterized such morphological distinctiveness as disparity (reviewed in refs. 40 and 41). Although paleontologists have long used ranks of the Linnean hierarchy as a proxy for disparity, quantitative analyses of form have demonstrated that neither taxonomic rank nor taxic diversity is a reliable proxy for disparity (42). A host of quantitative methods has been proposed to analyze different aspects of morphology, and the occupation of morphospace by particular clades, with the appropriate techniques dependent on the question being addressed, and whether continuously variable characters or meristic characters are being used (43). In almost every case examined, morphometric studies of disparity have demonstrated overwhelmingly that morphospace is rapidly constructed early in the evolutionary history of major clades, with taxonomic diversification often lagging behind (41).

Patterns of disparity have been analyzed across a number of mass extinctions, principally to understand the patterns and processes involved in the re-establishment of ecospace after these crises. Despite significant reductions in disparity in the immediate aftermath of a mass extinction, studies of brachiopods, crinoids, blastozoans, and ammonoids generally demonstrate rapid re-expansion of morphospace, although often in a different region than was occupied before the extinction (refs.

44–48 and discussion in ref. 41). Even in clades that experience almost catastrophic decreases in diversity and disparity, such as echinoids and ammonoids during the end-Permian mass extinction, disparity can rebound to even greater levels (e.g., ref. 46 for ammonoids). Critically, these studies suggest that at least within broad body plans, the developmental process does not become so increasingly constrained with time as to limit the exploration of morphospace.

Functional Diversity or Ecospace. Holling (49) defined resilience as the magnitude of disturbance that a system can absorb before shifting to an alternative state. Ecological studies have demonstrated that the loss of biodiversity can imperil ecosystem services and functions (50–55), potentially leading to a negative feedback loop further reducing diversity. An assessment of experiments on grassland biodiversity (56) demonstrated a positive relationship between the number of species considered and the overall functioning of multifunctional ecosystems. These results contradict claims of ecological redundancy in ecosystem function (57) and suggest that many, if not most, species do play important roles in ecosystems.

The challenge in analyzing functional diversity is to establish appropriate metrics. For ecological studies Petchey and Gaston (58) conclude that tabulating the number of functional groups or types is not reliable. Paleontologists thus face significant, although not unsurmountable, problems in identifying the ecological services and functions because the most straightforward paleontological approach is to categorize taxa of interest into different functional groups, such as carnivores, herbivores, suspension feeders, etc. Such categories can often readily be identified in fossils and can be consistent across larger taxonomic groups. Paleontologists have long discussed the selective impact of mass extinctions on trophic groups, such as the pervasive extinction of epifaunal, suspension-feeding marine taxa during the end-Permian mass extinction (59).

Macroecological guilds were developed as an extension to ecological guilds, encompassing a suite of species (not necessarily related) competing for a similar resource (60). The concept has primarily been applied to large-scale paleoecological trends, rather than more intensive studies of extinction episodes. One limitation of the guild approach, however, lies in identifying the critical limiting resources that define the members of a guild. A more operational concept is ecospace, which focuses on general modes of life and can be defined independently of species. For marine animals these modes of life are defined in terms of motility, or ability to respond to disturbance; tiering or relationship to the substrate (burrowers versus swimmers), and feeding strategy, or means of acquiring energy (61). The six possibilities along each of these axes define a 3D grid of 216 possibilities, of which only 92 appear to be occupied (62). As with marine guilds, many different taxa can occupy each of these different modes of life, so identifying which modes are occupied across a mass extinction may not be particularly informative. One could imagine a more intensive study in which this framework was used to chronicle across mass extinction both how many modes of life were exhibited by various clades and the changing density of occupation by various clades of particular modes of life. Such a study would be particularly informative if it revealed differences in extinction intensity between different functional groups.

In some cases it may be possible to apply more rigorous analyses to the problem, such as the comparison of food web structures. Ecologists have developed a rich toolkit for studying the network properties of food webs (63), and with a working group at the Santa Fe Institute we have recently shown that such methods can be applied to Cambrian fossil communities. Although ecologists have access to direct feeding observations and gut contents in practice they often rely on morphology and other data also available to the paleoecologist. Our results demon-

strate that ancient food webs can be reliably reconstructed, opening up the potential to study changes in the network properties of ecosystems across mass extinctions.

Modeling changes in functional diversity, trophic complexity, and food web structure in the search for patterns that can be observed in the fossil record is another approach. We developed a simple model in which extinction was simulated by the collapse of primary productivity, triggering reductions in the diversity of higher trophic levels (64). The results imply that the trophic structure of extinction may influence the tempo and pattern of recovery. More detailed computer simulations of the effects of both productivity loss and resulting secondary extinctions through a food web further emphasizes the importance of the network structure in the pattern of extinction (65, 66). Although the significance of these results is limited because of the lack of empirical input into the food web structure, it suggests something of the insights that may eventually result.

An additional area that could prove important in understanding the loss of functional diversity is the correlation between scaling relationships and ecological networks, particularly as biodiversity collapses. For example, metabolic scaling theory posits linkages across metabolic activity, form, population size, species diversity, and other variables (67–69). The apparent relationship between metabolic activity and some mass extinctions (33, 70), suggests that the relationship between scaling theory and extinction is worth exploring, as are species-energy relationships (71, 72).

Ecological networks also provide a host of services to the community, ranging from clean water to fine-scale modification of climate (microhabitats). These ecological services have been a subject of considerable interest among conservation biologists, but have not been addressed in deep time. For example, what was the impact on the water quality in shallow marine ecosystems as a consequence of the loss of so many articulate brachiopods, crinoids, bryozoans, and other filter feeders during the end-Permian mass extinction? This issue is probably best investigated through stable isotope studies of nutrient flow or geochemical cycling (73) or where the services leave a tangible fossil record.

Architectural Diversity and Ecosystem Engineering. The framework of modern reefs is generated by scleractinian corals, with a significant contribution from coralline algae and early diagenetic cements. Architecturally similar structures, at least at a gross scale, have been built by microbial communities, sponges and archaeocyathids, tabulate and rugose corals, stomatopods, bryozoans, brachiopods and rudist bivalves. Reefs are a specific example of the provisioning of architectural diversity, which can provide a positive feedback on biodiversity. Such ecosystem engineering allows species to modify the environment in ways that can affect, either positively or negatively, resource availability for other species (74). A related concept is niche construction, in which species modify their own environment in a way that influences the fitness of the population and, through ecological inheritance, the fitness of subsequent generations (75). Although ecosystem engineering can be recognized in the fossil record, identifying niche construction requires an understanding of selection pressures that is generally more difficult for paleontologists. Both niche construction and ecosystem engineering are currently the subject of considerable investigation and appear to have significant implications for macroevolution (76).

Reef ecosystems provide a clear example where the loss of the 3D complexity of the reef has a strong negative impact on biodiversity. Kiessling (77) showed that over million-year periods high biodiversity on reefs is related to stability, as measured by the density of skeletal organisms, the style of reef building and the types of biotic reefs. Some mass extinction events destroy this buffering from environmental fluctuations. The composition and consequent fabric of reefs has undergone considerable

variation during the 543 Ma of the Phanerozoic (78, 79). The structure of Early Cambrian to Early Ordovician reefs was dominantly microbial. From the Middle Ordovician radiation through the Late Devonian mass extinctions, stromatoporoids (coralline sponges) and corals were the primary reef builders, with important contributions from other sponges in the early part of the interval. Latest Devonian through Early Permian reefs are often described as “mud mounds” because of the absence of abundant framework builders in these primarily algal and microbial systems. In the Early to Middle Permian, between five and seven different reef types have been described with sponges, brachiopods, corals, and bryozoans being prominent components of different types. Scleractinian corals become the major reef builders in the Late Triassic, with significant contributions from bivalves during some intervals. Indeed, post-Aptian Cretaceous reefs were built largely by rudist bivalves. Cenozoic reefs were constructed by scleractinian corals and coralline red algae. These gross patterns obscure Phanerozoic trends of changing ecology, including higher nutrient requirements toward the recent (79). An important issue for further exploration is the extent to which these different reef types were ecosystem builders that enhanced the diversity of other groups. For example, the phylloid algal mounds of the Lower Permian of West Texas apparently were so dense that they excluded many other organisms (80), whereas later scleractinian reefs appear to have enhanced diversity. On land, trees and forests often provide a similar architectural structure to reefs in the ocean.

Behavioral and Social Complexity. The social and behavioral complexity of extinct animals might seem irretrievably lost, (other than what might be inferred from morphology or the known history of social clades). In fact, the preservation of tracks, trails, and burrows provides insights into behavior, with the constraint that such trace fossils can rarely be uniquely associated with particular species (81). More commonly, particular trace fossils could be produced by many distantly related species. Worms of several different phyla can produce similar burrows. Nonetheless, trace fossils can provide considerable insight into the complex behavioral repertoires of their makers. Vertebrate trace fossils on land provide similar insights, for example, into herding behavior among some dinosaurs, or burrowing among Late Permian dicynodonts in South Africa (personal observation). Other evidence of behavioral complexity comes from the characteristic patterns preserved in fossil leaves by herbivorous insects reflecting both the behavior and mouthpart morphology of various herbivorous insect groups (82). One means to track changes in behavioral complexity during a mass extinction is by documenting changes in trace fossil abundance and diversity.

Developmental Diversity. The great morphologic disparity of Cambrian and Ordovician trilobites might appear to be a paradigmatic example where we can infer the loss of great developmental diversity. Comparative studies of the genes involved in development have now demonstrated that many developmental processes are highly conserved across all bilaterian animals and some originated even deeper in time, as shown by genes with the same developmental role in cnidarians and vertebrates (summarized in ref. 83; see also ref. 84). This pattern of extreme conservation of developmental patterning suggests that the loss of developmental diversity caused by extinction may be less extensive than it might otherwise appear. Studies of other arthropods, coupled with detailed studies of the patterns of morphologic evolution of trilobites (including developmental information retrieved from fossilized representatives of larval stages), have demonstrated that information on developmental patterning can be recovered (85). Although patterns of gene expression, much less the network of gene regulatory interactions, cannot be identified, Hughes (85) has compared the

restructuring of the cephalic and trunk regions during the Cambrian and Ordovician diversifications of trilobites. His analysis shows that the Cambrian radiation of the group involved fundamental changes in various parts of the body plan: the number of body segments, how they were formed and in the articulations between them. In contrast, the Ordovician radiation involved morphological “embellishments” of trilobite subclades whose architectures had already stabilized.

The deep conservation of developmental processes across many clades is consistent with recent comparative studies of the evolution of gene regulatory networks suggesting that the evolution of regional patterning systems during the initial diversification of animal body plans generated a hierarchical structure (86, 87). Studies from echinoderm endomesoderm formation and arthropod and vertebrate heart development have revealed a network of highly conserved regulatory genes at the core of these systems whose interaction is required for development of the relevant body parts. Surrounding this kernel of conserved regulatory interactions, however, is a network of other interactions, and downstream a set of structural genes whose activity is controlled by the network. Elements of this surrounding network are less refractory (to varying degrees) to evolutionary modification, and of course the structural genes are the locus of adaptive evolution.

If this result is generally true of metazoan developmental evolution, one implication is that although the loss of biodiversity will result in the loss of downstream elements of the regulatory hierarchy, these elements are also the most labile to evolutionary change. In contrast, kernels appear to be broadly conserved within major body plans, and in some cases across disparate groups. Consequently loss of these kernels was likely only occurred during the infrequent loss of clades the equivalent of the Linnean rank of phylum or class. For marine animals this loss would have been largely during the Cambrian and again during the end-Permian mass extinctions. The loss of major clades of insects during the end-Permian might have caused a loss of some developmental diversity, but it is less clear whether unique developmental processes at the level of kernels were present. Among vertebrates there are many extinct groups of fish and early tetrapods, such as the armored fish of the Devonian and the mammal-like reptiles of the Permo-Triassic, that could have harbored now vanished developmental strategies. But as with insects, it is far from clear they were unique at the level of kernels.

Our understanding of plant developmental biology, although expanding rapidly, is less advanced than for animals, and we do not know whether a similar highly structured regulatory hierarchy exists within plants. Morphologic evidence has revealed the diversity of tree-like forms that evolved repeatedly, with many now-extinct clades using very different developmental and structural strategies to achieve a similar end. All trees need to solve the same basic problem of providing structural support while distributing nutrients vertically. Both modern pines and other flowering trees such as dogwood or oaks are constructed with an inner, woody, secondary xylem produced by the vascular cambium and surrounded by phellem. But cycads are constructed of an inner pith and an outer cortex, with much of the structural support on the outside from persistent leaf bases. Arborescent lycopsids, horsetails in the Carboniferous, tree palms, and tree ferns each have distinct ways of forming trees. Yet each of these different types of trees was adapted to a particular suite of environmental conditions, which influenced the nature of the resulting communities (88, 89). Thus it seems likely that major developmental strategies of plants have disappeared, particularly during the late Paleozoic.

Table 1. The effect on different measures of diversity for marine organisms during the five canonical mass extinction episodes of the Phanerozoic

Diversity	Ordovician	Devonian	Permian	Triassic	Cretaceous
Taxic	60/26%	57/22%	82/52%	53/22%	47/16%
Phylogenetic	?	?	High	?	? Medium
Morphologic	High	Medium	High	?	? Medium
Functional	Medium	High	High	Low	Medium
Architectural	Medium	High	High	Medium	Low
Behavioral	?	?	High	Medium	Medium
Developmental	Low	?	Medium	?	?

Taxic diversity drops are shown for genera and families from ref. 90. Estimates of loss of phylogenetic diversity are based on the loss of major clades, as documented by phylogenetic analyses; morphologic disparity is assessed within particular clades, and the loss of major clades; functional diversity was assessed based on published paleoecological studies. Loss of architectural diversity measured by changes in reef volume and the diversity of reef ecosystems (78, 94). Changes in behavioral diversity were assessed by changes in the complexity of trace fossil assemblages. Developmental diversity was assessed as described. Question marks indicate an absence of sufficient data.

Application to Past Biotic Crises

Applying some of these different aspects of diversity to past mass extinctions is difficult because of both lack of data and difficulties in establishing appropriate criteria and reproducible metrics, but identifying these different measures of diversity is the first step toward building a more robust and quantifiable approach. Table 1 provides a preliminary, somewhat impressionistic, application of these metrics for marine animals across the five classic mass extinction intervals. In the absence of more comprehensive tools, proxies are used for some categories such as reefs for architectural diversity and trace fossils for behavioral complexity. Estimates of the loss of family and generic diversity are from ref. 90.

One perplexing aspect of the end-Ordovician mass extinction (490 Ma) is that although it is the second largest loss of taxic diversity of marine organisms it had relatively little ecological impact in most groups (91). Limited phylogenetic analyses have been produced, mostly for graptolites and gastropods, although some broader studies do span the boundary. The loss of morphologic disparity during this event appears to have been high, whether as measured by the major losses among graptolites, conodonts, brachiopods, and possibly nautiloids or by more quantitative studies of disparity within major clades (44, 45, 92, 93). Using reefs as our measure of architectural complexity, there is a major loss of both reef types and carbonate production although there is little ecological impact (78, 94), hence the medium ranking in Table 1. Twitchett and Barras (95) record only a single study of trace fossils through this interval, too little to estimate the impact on behavioral complexity. Finally, as no major clades completely disappeared the loss of developmental diversity at this time appears to have been fairly low. What developmental complexity was lost was likely in the terminal portions of the networks rather than the highly conserved cores.

The Late Devonian mass extinctions were a series of events best expressed in rocks of Europe (96). The loss of morphologic disparity seems to have been intermediate, both in terms of the loss of major clades and for the few clades where disparity has been quantitatively assessed. Reef builders were heavily impacted by this episode, with colonial tabulate corals virtually disappearing as significant constructors. Together with the significant loss of stromatoporoids, this extinction caused a major shift in reef types that persisted into the Permian (78, 94). There are too few studies of this event on which to assess its impact on phylogenetic, behavioral, or developmental diversity.

Two major extinction episodes close out the Permian, one at the end of the Guadalupian, of which much less is known, and the most severe mass extinction of the Phanerozoic at the close of the Permian (97). The loss of taxonomic diversity during this

interval was higher than during any other event, some 82% of marine genera and 54% of marine families (90). Phylogenetic analyses of articulate brachiopods, bryozoans, and gastropods reveal a considerable loss of diversity. The impact on morphological disparity is apparent from the large number of clades lost (trilobites, blastoids, and the tabulate and rugose corals) or severely affected (articulate brachiopods, echinoids, ammonoids, radiolarians, bryozoans, and foraminifera). The loss of disparity is confirmed by quantitative studies of disparity among brachiopods (45), ammonoids (46), and crinoids and blastoids (48, 98). Carbon isotopes indicate a significant loss of primary productivity (19) that persisted for ≈ 2 million years (99, 100). The most pervasive indication of the functional and ecological impact of this extinction was that the marine communities of the Ordovician-Permian, dominated by epifaunal, suspension feeding brachiopods, bryozoans, and pelmatozoan echinoderms, simply vanished (97). A large suite of reef types had developed by the Middle Permian, virtually all of which disappeared, leaving a gap in metazoan-constructed reefs during the Early Triassic (78, 94). Detailed investigations of trace fossils have revealed a significant loss of diversity with only a few types of shallow burrows occurring in earliest Triassic sections (95, 101). I have ranked the loss of developmental diversity as moderate because of both the loss of major clades and major subclasses.

In the Late Triassic ammonites and bivalves experienced the greatest extinction. There are few studies on which to assess the extent of loss of phylogenetic or developmental diversity or morphologic disparity. Although there are few studies of paleoecological patterns across this boundary, much less studies of food web structure, there is little evidence for major disruptions of functional diversity except among reefs, where a major drop in sea level triggered a substantial decline in reef volume and a somewhat less substantial drop in diversity (94). Trace fossils have been studied in different regions, but the impact of the extinction varies between localities, in part because of shifts in the environments of deposition at the same time as the biotic crises. There is, however, evidence of some decrease in the complexity of trace fossil assemblages that cannot be attributed simply to changes in the sedimentary environment in which they were deposited.

The end-Cretaceous mass extinction led to the disappearance of significant numbers of foraminifera and other plankton and a significant drop in primary productivity (102). Ammonoids finally disappeared, as did belemnites and rudist bivalves. The loss of rudists was the major loss among reef biota, and Flugel and Kiessling (94) record few other impacts among reef ecosystems. Studies of the complexity of trace fossils across this interval

are relatively few and suggest only moderate impact by the mass extinction (95).

Although not one of the canonical five mass extinction episodes, extinction rates measured by taxic diversity were high during a number of stages of the Cambrian, sorting out the winners and losers among the Cambrian diversification of animals. Indeed by some metrics, particularly morphologic disparity and developmental diversity, these events may have winnowed a greater degree of evolutionary history than any of the subsequent biodiversity crises of the Phanerozoic.

The (Re)-Construction of Diversity

Empty ecological space has long been considered a key factor in evolutionary innovations, as an unexploited opportunity opened by new adaptations, a new geographic region with underexploited resources, or an environment opened up through environmental change. Recoveries from mass extinctions have been viewed as encompassing each of these possibilities, as the removal of previously dominant clades provides opportunities for expansion, including by migration, of minor groups and the origin of new clades, as an increased likelihood for success of adaptations that might have been blocked, and as an instigator of environmental change that might favor new groups. What the economist Joseph Schumpeter described as “creative destruction” is true of evolution: continuing biotic overturn and more comprehensive biodiversity crises have been a normal part of the history of life, and perhaps essential to the success of evolutionary innovations.

Two principal classes of models have been applied to understanding the underlying processes of taxic diversity (103). The first class includes global-level correlates of population growth models that invoke logistic growth models and either global carrying capacities (104, 105) or coupled logistic models. One example is Sepkoski's description of the diversity patterns of the Cambrian, Paleozoic, and Modern evolutionary marine faunas (12); see ref. 106 for a critique. The alternative class was labeled expansionist by Benton and Emerson (103) as it does not invoke an explicit carrying capacity, or it suggests that it may never have been reached, possibly because of recurrent disturbances (107–109). The utility of a global carrying capacity is extremely doubtful (103, 109, 110).

The critical question for understanding biotic recoveries is in understanding how the network of ecological and environmental interactions facilitates the construction of biodiversity, which is a network issue, not one that is properly addressed by borrowing models of population demography. Thus understanding the growth of taxic diversity after mass extinctions requires understanding the ecological relationships that build these networks, including both the positive feedbacks (such as niche construction and environmental engineering) and the more commonly invoked negative feedbacks such as competition. At present we have no theoretical models applicable to this problem.

Our knowledge of the response of most of the other metrics during postextinction biotic recoveries is generally even more fragmentary than our knowledge of their behavior during the extinctions. The highly uneven branching structure of most phylogenetic trees reflects uneven rates of diversification along different branches of a tree and the loss of some branches through extinction (35). With the exception of the substantial literature on the relationship of the bird and placental mammals across the Cretaceous-Tertiary boundary, there are relatively

few large-scale phylogenetic studies of postmass extinction biotic recoveries. Despite this absence, many evolutionary radiations of single clades are well studied during biotic recoveries. Examples include trilobites in the Late Cambrian, ammonoids after the Late Devonian, end-Permian, and end-Triassic episodes, and quillworts in the Early Triassic. As discussed above, where it has been studied among marine taxa, morphologic disparity rapidly expands after mass extinctions (41). Significantly for the structure of these recoveries, disparity often expands into different dimensions than were occupied by the preextinction taxa, demonstrating that recoveries have their own dynamic and are not simply the refilling of previously occupied morphospace. Without detailed studies, my impression is that architectural diversity as measured by the reappearance of framework-bound reefs is often one of the last segments of diversity to rebound, and in almost all cases (the Early Jurassic is a possible exception) does so by the appearance of new groups. This apparent delay could reflect the fact that a considerable ecological network needs to be constructed, in appropriate environmental settings, before such architectural diversity can succeed.

Although there are a growing number of case studies of biotic recoveries after mass extinctions and some smaller biotic crises, our theoretical understanding of increases in taxic diversity remains lacking, as does our knowledge of the response of some of the other diversity metrics described here and the factors underlying them. One hesitates to suggest that there is a considerable empty niche here for future research.

Conclusion

This survey of mass extinction episodes illustrates that different metrics capture different dimensions of the loss of evolutionary history. Although these extinction events have been defined by loss of taxic diversity, this metric often captures only one perspective on the loss of biodiversity and evolutionary history. Indeed, debates continue among paleontologists about whether some of these episodes (particularly the Late Devonian and end-Triassic) actually constitute mass extinctions on the scale of the end-Permian and end-Cretaceous events. Fully appreciating the extent of the loss of evolutionary history during any biodiversity crisis requires a more complete accounting of other dimensions of biodiversity, a task that is in its infancy for some of the metrics discussed here.

The metrics of past loss of evolutionary history may provide some insights into more recent events. Although this survey illustrates that the available data on these various metrics are often meager, enough information is available to suggest that the loss of different aspects of evolutionary history may portend very different outcomes for recovery. For example, if architectural diversity is lost early in a biodiversity crisis one might expect greater loss of other aspects of diversity than if architectural diversity remains high. Empirical investigations of such effects will require very high-resolution studies, but may be possible in the Cenozoic. This is clearly an area where well designed modeling studies may prove useful.

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