

Life in the Aftermath of Mass Extinctions

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<http://dx.doi.org/10.1016/j.cub.2015.08.053>

The vast majority of species that have ever lived went extinct sometime other than during one of the great mass extinction events. In spite of this, mass extinctions are thought to have outsized effects on the evolutionary history of life. While part of this effect is certainly due to the extinction itself, I here consider how the aftermaths of mass extinctions might contribute to the evolutionary importance of such events. Following the mass loss of taxa from the fossil record are prolonged intervals of ecological upheaval that create a selective regime unique to those times. The pacing and duration of ecosystem change during extinction aftermaths suggests strong ties between the biosphere and geosphere, and a previously undescribed macroevolutionary driver — earth system succession. Earth system succession occurs when global environmental or biotic change, as occurs across extinction boundaries, pushes the biosphere and geosphere out of equilibrium. As species and ecosystems re-evolve in the aftermath, they change global biogeochemical cycles — and in turn, species and ecosystems — over timescales typical of the geosphere, often many thousands to millions of years. Earth system succession provides a general explanation for the pattern and timing of ecological and evolutionary change in the fossil record. Importantly, it also suggests that a speed limit might exist for the pace of global biotic change after massive disturbance — a limit set by geosphere–biosphere interactions. For mass extinctions, earth system succession may drive the ever-changing ecological stage on which species evolve, restructuring ecosystems and setting long-term evolutionary trajectories as they do.

Introduction

Extinction rates are not constant over the long history of life. Instead, bursts of extinction and subsequent speciation punctuate long intervals of relatively moderate taxonomic turnover [1,2]. Rather than a plodding tortoise, extinction is a hare — racing in fits and starts above some background level of attrition [1]. The largest of these events are known as mass extinctions.

Mass extinctions are topics of intense interest because of their ecological and evolutionary effects [3–5]. From a macroevolutionary perspective, they have a twofold importance [5] (Figure 1). First, mass extinctions have profoundly influenced the history of life through death [3]. The largest mass extinctions, referred to as the ‘Big Five’ (Box 1), are thought to have killed more than 75% of species alive at the time [6]. Because extinctions are typically selective, the mass death of species results in entire branches being trimmed from the tree of life [7]. In addition, selectivity during mass extinctions often differs from that in surrounding time periods (Box 2) [5,8]. Changed selectivity means that once diverse clades, such as the non-avian dinosaurs of the late Cretaceous, can be lost in a sudden swoop across extinction boundaries [9,10]. Second, mass extinctions have influenced the history of life through their long-reaching effects on the life that survives [11–13] (Figure 2).

Although extinction intervals are so brief as to appear geologically instantaneous [14], strange ecosystems dominate for up to millions of years in their aftermath (Figure 3) [15–17]. Multiple lines of evidence suggest that post-extinction ecosystems function differently than those before and long-after the event [18]. Extinction boundaries typically coincide with excursions in geochemical markers and with changes in the formation and composition of the rocks themselves [19–21]. Generally speaking, these changes in geochemical and geological records

indicate global scale upheaval in various components of the earth system, such as the carbon cycle, coincident with the extinction [22,23]. As such, mass extinctions are not step-events but rather a step into a prolonged alternative global ecosystem state [18].

In addition, survivors of extinctions are an unusual lot, exhibiting morphological, physiological and ecological characteristics biased by the selectivity of the extinction [24–26]. This also has important implications for ecosystems in the aftermath. For instance, the loss of large bodied taxa across mass extinction boundaries is so characteristic that it is known as the ‘Lilliput effect’ after the diminutive Lilliputians in Swift’s *Gulliver’s Travels* [27]. Body size is a key ecological trait, and widespread dwarfing can change, for instance, the efficiency of energy use within and among taxa [28]. The preferential loss of certain clades, morphologies, trophic levels and functional types (including habitat providing taxa) can also reduce the number of possible life history strategies in the immediate aftermath of an extinction. Such a reduction leaves the re-evolution of some ecological strategies dependent on the evolution of others and can allow entirely new ecological strategies, and interactions, to evolve [29–31]. Reptiles in the aftermath of the largest mass extinction of all, the Permian-Triassic (PT) extinction, provide an example of the latter, as they evolved from sprawled into upright predators on land [32] and invaded the sea [33], all in the Early Triassic. These innovations were not presaged by evolutionary trends in the Permian and are instead attributed to the effects of the aftermath of the PT mass extinction [33,34]. In short, it is in the unusual world of extinction aftermaths that species radiate and, in doing so, rebuild species-rich clades and geologically stable ecosystems [13,35].

In this review, I consider the potential of mass extinctions to influence the history of life through their long-lasting influence on

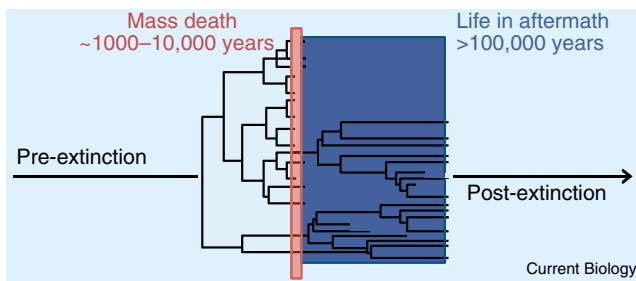


Figure 1. The impacts of mass extinctions.

Mass extinctions effect macroevolution through extinction and through the evolution of life in the aftermath. Mass extinctions coincide with the abrupt disappearance of taxa from the fossil record (red) and are followed by rapid, often stepped, rediversification in surviving taxa (blue) during interval characterized by strange ecosystems globally. The time spans are approximate and based on order of magnitude estimations for the duration of the last three of the Big Five mass extinctions and their aftermaths.

life. In particular, I focus on the unusual ecosystems in the aftermath and their role in macroevolution — a period during which diversity rapidly rebounds to pre-extinction levels [36]. Rapid evolution in a world emptied of ecological incumbents is expected if interspecific interactions are assumed to affect speciation rates [4,12,37], but multiple factors might set the pattern and pace of evolution, including the extent and duration of ecological collapse [38]. Mass extinctions are often discussed as if they are instantaneous point-events, characterized by the abrupt, selective loss of some taxa and the subsequent radiation of others. But this is far from true: whether and how the prolonged aftermath of mass extinctions matters in the history of life is the primary question that I seek to address.

First, I briefly review key aspects of what is known about life in the immediate aftermath of mass extinctions. This section is deliberately selective. I focus primarily on a single extinction event (the Permian-Triassic: PT) and a single realm (marine) in order to highlight typical aspects of life in the aftermath of extinctions, the types of records and data used to make such inferences and the pertinence of these intervals to (macro-) evolution. Over the last decades, widespread evidence has accrued for a long-pacing of post-extinction community turnover and eventual ecosystem stabilization. I then use a second mass extinction (the Cretaceous-Paleogene; KPg) to consider whether biosphere–geosphere feedbacks might account for this pattern and timing of biotic change. Biosphere–geosphere feedbacks are intriguing, because they provide a means for global ecosystems to drive directional changes in the environment over many 10,000s to 1,000,000s of years. I end by briefly considering the relative importance of the aftermaths of mass extinction in the history of life by comparing the evolutionary events of aftermaths with the times in-between.

Ecological Flux in the Aftermath

The change in ecosystems across extinction boundaries is arguably as dramatic as the loss of taxa (Figure 3) [5]. In the wake of mass extinctions, complex biotic structures, such as coral reefs, can be lost for hundreds of thousands to millions of years [18]. At the same time, the composition and geochemistry of the rocks being formed often indicate a prolonged interval of earth system change [16,18]. On the re-establishment of pre-extinction-like

complexity in ecosystems, the fundamental organization (structure) and function of ecosystems is often permanently changed (Figure 2B) [13,39–41]. How do we know that ecosystems changed, and what does it mean for understanding the evolution of life in the aftermath?

The PT extinction, the greatest mass extinction of the last half billion years (Box 1), provides a classic example of the prolonged existence of strange ecosystems in the aftermath of extinction [16]. The PT mass extinction was likely triggered by a single massive pulse of flood basalt volcanism in Siberia ~252 million years ago [42]. Erupting through thick carbon- and sulfur-bearing sediments [43,44], this pulse of volcanism released enormous volumes of gases that led to an increased atmospheric CO₂ concentration, global warming, acid rain and terrestrial erosion, and ocean acidification [16,19]. At the same time, marine sediments across the PT mass extinction evidence widespread anoxic, and sometimes also sulphidic, conditions in the open ocean [16,19], likely to be due to some combination of increased nutrient input from land and slower ocean circulation [45]. In the ocean, the extinction selected against taxa with poorly buffered respiratory physiologies and calcareous shells [25,46]. This selectivity has been attributed to factors including oxygen stress (hypoxia), CO₂ poisoning (hypercapnia) and carbonate undersaturation [25] — all physiological factors tied to various environmental perturbations suggested by the rock record and earth system models. Extinction survivors were also typically small bodied [47,48]. Estimates for loss of species across the PT boundary reach as high as more than 90% of well-fossilized marine species alive at the time [49,50], although strong selectivity complicates such estimates.

To step back for a moment, just consider how remarkable this hypothesis is — to argue that we can trace the trigger of mass extinction a quarter of billion years ago to a single pulse of volcanism in Siberia and its cascade of environmental effects. It is astounding and relies on dramatic improvements in our ability to precisely date the geological time scale, to discern the relative amount of time captured in very thin layers of rock and to measure various aspects of the environment with geochemistry. For instance, in the case of PT mass extinction, recent dating estimates that it occurred ~242 million years ago over a period of 60,000 years (+/- 48,000) [42]. 60,000 years is quite short relative to the estimated full eruption duration of the Siberian Traps of 1–2 million years, the generally recognized trigger of the extinction [50,51], and suggests that a single, outsized pulse of volcanism triggered the extinction [42]. Similar improvements in constraining the timing, causality, and importance of triggers and feedbacks have been made across many major extinction events and have resulted in real progress in our understanding of extinctions and their aftermaths [52].

Various lines of evidence suggest the existence of a long, multi-million year interval characterized by highly altered ecosystems in the aftermath of the PT mass extinction [16]. Coral and metazoan reef systems were replaced by microbial carbonate mounds for up to six million years [16]. Key marine functional types including macroalgae, metazoan suspension feeders, mobile predators and deposit feeders were lost or rare for at least the first million years [16]. Complex burrowing of benthic sediments remained relatively rare for yet another ~4 million years

Box 1. What is a mass extinction?

A mass extinction is any interval of time with global extinction rates above background levels for a large portion of clades (Figure 2A) [2,18,126]. How this definition is applied varies in practice, but is typically determined using the record of abundant shelly marine metazoans [127]. The largest marine mass extinctions coincide with comparable events in terrestrial fauna but some terrestrial extinctions do not have marine analogs [128]. One recent authoritative estimate placed the total number of mass extinction events in the last half billion years at 18 [2], with earlier estimates ranging from nearly thirty to more than sixty events [126,129]. However, the very largest mass extinction events, which may have killed more than 75% of the species globally [6], are clear regardless of the approach [1,2]. The first family-level Phanerozoic diversity curve of shelly marine metazoans brought immediate attention to five intervals of remarkable low diversity [1,123]. An overview of these five events is provided below along with the leading hypothesized trigger, the losers (total extinction or heavy losses) and the winners (radiating or increasing in abundance or importance):

Event	Trigger	Losers	Winners
Ordovician-Silurian (OS)	Glaciation	Strophomenid & rhynchonellid brachiopods, nautiloids, trilobites, crinoids, conodonts, graptolites	Siliceous sponges, tabulate corals
Late Devonian (F/F)	Glaciation	Stromatoporoids, tabulate corals, trilobites, crinoids, eurypterids, brachiopods, ammonoids, agnathans, placoderms	Chondrichthyans, actinopterygians (ray-finned fishes)
Permian-Triassic (PT)	Volcanism	Brachiopods, crinoids, ammonoids trilobites, tabulate and rugose corals, basal tetrapods	Bivalves, gastropods, malacostracans, echinoids, scleractinian corals, archosaurs
Triassic-Jurassic (TJ)	Volcanism	Calcareous sponges, scleractinian corals, brachiopods, nautiloids, ammonites	Siliceous sponges, dinosaurs
Cretaceous-Paleogene (KPg)	Impact	Non-avian dinosaurs, ammonites, calcareous plankton, mosasaurs, pterosaurs, rudist bivalves	Birds, mammals, spiny-rayed fishes

Table based on [2,16,18,120,130–133].

Dubbed the ‘Big Five’, these events are by far the best studied mass extinctions — with most of the attention devoted to the Permian-Triassic and Cretaceous-Paleogene mass extinctions [18]. Of the Big Five, the Late Devonian is probably not a mass extinction at all, but rather a mass depletion of biodiversity driven by low speciation rates [134]. In spite of the unceremonious down-grading of the Late Devonian, the ‘Big Five’ remains in common usage in the scientific community, accounting for the evocative, albeit speculative, label ‘The Sixth Mass Extinction’ for the current biotic crisis.

The vast majority of individuals are born and die without leaving a trace [135]. Thus, the window into the history of life provided by the fossils has a rather particular view. Mass extinctions are, perhaps surprisingly, identified through diversity compilations at the family or genus level [1,136], with extrapolated species-level losses [49], in order to minimize issues related to taxonomic standardization and sampling. Geographic [137], physiological [25,46] and ecological selectivity [24] all ensure that global-scale species-level extrapolations are best estimates, rather than precisely known quantities. Within-clade studies often reach much finer temporal resolution (thousands rather than millions of years) and directly assess species level changes [17], but cannot resolve rates globally or in rarely to never fossilized clades. Even in well-fossilized clades, it can be difficult to assess whether a species is extinct or just rare, as rare species have a low chance of being discovered as fossils [14]. Consequently, at a global scale all that is known for certain is that past mass extinctions are events that trim once-dominant branches in the tree of life from view and coincide with widespread evidence for prolonged ecological upheaval.

In any given clade, the most important extinction event may or may not be a global mass extinction. For instance, the Late Quaternary (from 50,000 to ~11,000 years ago) saw the global extinction of roughly 90 genera of mammalian megafauna [138,139]. In North and South America and Australia, more than 70% of all mammalian megafauna genera were lost [139]. Although this was a mass extinction of mammalian megafauna, it is not considered a ‘mass extinction’ because it primarily affected one clade.

[16,48], a decrease otherwise not observed outside of extinction intervals [18,53,54]. In the aftermath of the PT extinction, certain features were preserved in rocks that had not occurred since abundant metazoans fully colonized the soft sediments of the seafloor [55]. These features, and other anachronistic structures [56], are important because they imply that certain ecological strategies were so rare (or even absent) that they no longer had a readily observable effect on ecosystems. Evidence on

land is relatively limited by comparison due to the availability of records, but a gap in the formation of coal suggests broad-scale changes in terrestrial systems as well [16].

The rate at which species re-diversified and complex ecosystems were re-established from this altered ecosystem state differed across taxa, environments, habitats and locations. For instance, the re-evolution of pre-extinction like burrowing in deep sea sediments (bioturbation) in benthic communities varied

Box 2. Distinct patterns of extinction selectivity influence macroevolution

There is now widespread support for the importance of selectivity in mass extinctions and their aftermaths [5]. Mass extinctions can have distinct patterns of selectivity relative to surrounding time intervals [8] with regards to factors like geographic range, body size, ecology, and physiology.

For instance, geographic range is a major predictor of background extinction risk, with small ranges generally coinciding with higher extinction risk [140], but during the end-Ordovician and KPg extinction geographic location was key [137,141]. Large bodied taxa can also be preferentially lost at extinction boundaries [18], as happened in PT ecosystems [47,142,143] and KPg terrestrial faunas [144], but there are exceptions [145,146]. Ecological and physiological selectivity, in turn, depends on the extinction drivers. Examples include the selective loss of carnivores and herbivores relative to detritivores across the KPg [24], the heavy losses of marine predators in the PT and KPg [16,26], preferential loss of calcifiers during the PT, TJ, and KPg [22,25,147], and preferential loss of physiologically unbuffered taxa during the PT [46]. The important commonality is that selectivity across mass extinctions can be distinct from the selectivity of surrounding intervals. Because of this, once abundant lineages can go abruptly extinct across extinction boundaries or suffer very high levels of extinctions.

What's more, selectivity during the extinction determines the phylogenetic, ecological, and biogeographic character of the surviving fauna, and this can have long-term effects [11]. For instance, the extinction of the once-diverse fusulinid foraminiferans during the PT mass extinction coincided with a change in the relationship between body size in foraminifera and atmospheric CO₂ concentration (coupled before, decoupled after) [148]. Perhaps most importantly, the chance filling of emptied niches in the aftermath of mass extinctions often allows taxa with previously circumscribed diversity or abundance to radiate or increase in abundance (see 'winners' in Box 1 for examples).

between localities by up to millions of years and followed closely on the amelioration of low oxygen or high temperature conditions [57,58]. Such variation in the spatial distribution of change is common across many large biotic events. Patterns vary by habitat as well. Although ammonites suffered very high levels of extinction during the end-Permian, they diversified within the first 2 million years after the extinction [59,60]. Conodonts and marine tetrapods, also pelagic groups, likewise radiated in the earliest Triassic [33,61–63]. Benthic taxa, by contrast, generally took more than 5 million years to fully recover pre-extinction levels of diversity and community complexity — perhaps due to ongoing, environment-specific disturbance like periodic oxygen stress [57,58]. Alternatively, rapid radiations in groups such as ammonites and conodonts might also partially reflect higher than average speciation rates at all times [62]. Regardless of the cause, variation in diversification rates amongst taxa is typical of mass extinction aftermaths more generally. On land, some ecological strategies lost at the extinction boundary re-evolved immediately while others, like small-bodied insectivory and large bodied herbivory, took more than 15-million years to reappear [64], resulting in distinct Early Triassic food-web structures in the meantime [65].

The existence of, and variability in, post-extinction ecosystems can be critical for interpreting the cause of macroevolutionary patterns. For instance, after the PT, diversification rates cannot be reasonably interpreted without considering how environmental and ecological conditions varied across clades and sites. Following a one-million year long post-PT low, ammonite diversity increased rapidly, recovering within two million years of the Triassic [59]. If just the extinction is considered, a reasonable explanation for this explosive diversification is that low species richness released taxa from the pressures of interspecific competition and led to rapid diversification and niche space filling until a new equilibrium was reached [4]. However, the importance of interspecific competition in pacing the recovery is called in to question by tracers of environmental change [66]. These show that ammonite diversification began precisely

as the carbon cycle stabilized [60]. A leading hypothesis for the dynamics of the carbon cycle in the aftermath of the PT extinction is that it reflects ongoing Siberian trap eruptions [19]. If this is the case, we might interpret ammonite diversification as being held back, at least at the start, by environmental conditions. Yet another hypothesis combines biological and environmental drivers of diversification to posit that ammonites and conodonts are inherently more dynamic than most benthic taxa. This is due to higher background rates of origination and extinction, enabling them to more closely track environmental conditions [62]. In short, the key to a comprehensive theory of macroevolution may really lie in understanding the balance in evolution between factors intrinsic to the system, such as intraspecific competition, and extrinsic to it [16], such as environmental disturbance from volcanoes. In this regard, mass extinctions dynamics may be particularly unique.

Understanding how it is possible for unusual ecosystems to persist in the aftermath of extinctions can offer insights into the balance and relative importance of intrinsic and extrinsic drivers of macroevolution. Extensive research has documented the existence of unusual ecosystems in the aftermath of extinctions, but how and why these intervals occur is still in question. One possibility is that evolving ecosystems lead to the re-diversification of species, with increased ecosystem complexity providing more niches and opportunities for ever more species. If this is generally true, then the slow pace of ecosystem change (thousands to millions of years) has yet to be explained. Alternatively, it could be the other way around — species re-diversification leading to changes in ecosystem structure and function — but the pattern and timing of change suggest otherwise.

Earth System Succession

In the period before geologically stable ecosystems are re-established, post-extinction communities and biogeochemical cycles are often highly dynamic, in a fashion seldom observed outside of such times. In some cases, the extinction-causing perturbation is thought to be on-going throughout the entirety

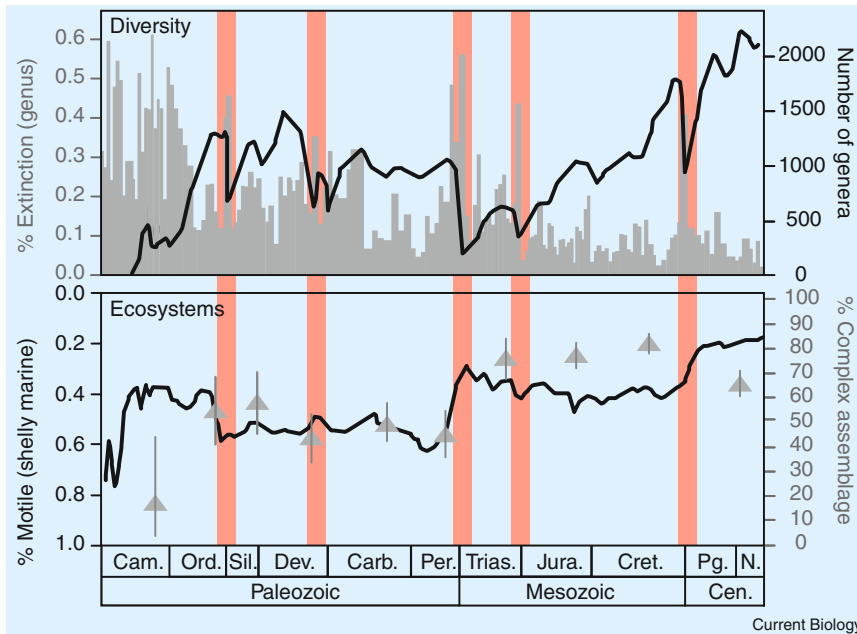


Figure 2. Extinctions and ecological change.

Mass extinctions are characterized by elevated extinction rates relative to background (upper panel) and long-lasting ecosystem change (lower panel). Over the Phanerozoic, background rates of extinction in shelly marine invertebrates have generally declined (grey bars, upper panel), with the Big Five mass extinctions (red bars) standing out as relative lows in standing diversity (black line). Step changes in community structure (one exemplar, black line, lower panel) and complexity (grey triangles, lower panel) coincide with the largest of the Big Five mass extinctions. This figure is a composite of information from previously published papers: % extinction [2], number of genera [149], % motility [13], % complex assemblage [35].

turnover is unclear, as many successive communities appear functionally identical to the level that can be resolved in fossils.

A second strange aspect of the sequential community turnover is the timing — both the total duration of the low complexity interval and the frequency of

of the strange aftermath interval, such that both the mass extinction and the dynamic post-extinction world have the same driver. This may be the case for the PT mass extinction. After the PT, multiple lines of evidence tie on-going Siberian trap volcanism to environmental disturbance [16,19]. For instance, some of the same factors thought to be involved in the extinction, such as volcanic outgassing, erosion, productivity and anoxia, are observed for millions of years after the extinction [19,23,67,68]. Because the re-evolution of pre-extinction-like complexity in ecosystems occurs once these environmental disturbances disappear [16,57,58], this suggests that the strange aftermath of the PT, like the extinction, was driven by volcanism. However, the timing of eruptions relative to environmental and ecological dynamics is still in question [42], leading others to argue that the strange PT aftermath is instead driven by the unusual structure and function of the low diversity, post-extinction ecosystems [60,69].

For extinctions where the trigger is short-lived compared to the duration of the aftermath, the role of ecological drivers in the aftermath is relatively uncontested. For instance, the KPg mass extinction is tied to the impact of a massive bolide, likely an asteroid, into the Yucatan Peninsula [70] — a geologically instantaneous event. Across the KPg boundary, the two main calcifying clades in the open ocean, coccolithophores (marine algae) and planktonic foraminifera (heterotrophic protists), suffered high levels of extinction with more than 90% of species lost [71,72]. In the roughly million years after the KPg impact, both groups were characterized by a succession of short-lived, low-diversity communities [73,74]. In each successive community, a single species dominated the assemblage, accounting for the vast majority of fossils. Surprisingly, turnover between the dominance of one species to the next appears unrelated to their evolutionary first appearance 10s–100s of thousands of years earlier [17]. Instead, community turnover is simply a shift in the relative abundance of taxa — one rising to dominance, while the other falls [74,75]. What leads these communities to

turnover occur on very long-time scales compared to ecological mechanisms. On much shorter time scales of days to centuries, the sequential replacement of communities after disturbance is a well-known ecological phenomenon, known as ‘succession’ [76]. A classic example of ecological succession occurs in forests. When a gap is created by a fallen tree, a sequential replacement of plant communities ensues from the early arriving opportunists with characteristics like high dispersal, rapid growth and high-light needs to the slow growing canopy-forming trees of mature forests [77]. In succession, sequential replacement is driven by the interactions among taxa — at any one stage, conditions favor a certain subset of taxa due to some combination of intra- and inter-specific interactions (directly favoring or disfavoring certain species) and environmental tolerance for the conditions created by earlier communities [77].

Succession occurs on time scales of days to centuries, depending on the system and disturbance in question. After extinctions, the serial replacement of fossil communities looks like classic ecological succession but on time scales that are much longer — tens to hundreds of thousands of years. With turnover and eventual stabilization on such protracted time scales after extinctions, the communities alive during any given period lived and thrived in conditions that would have appeared permanent from one generation to the next. In other words, serial community replacement in the aftermath of mass extinctions cannot be classic ecological succession. So what then causes communities to change on these very-long time scales? And why is this dynamic of community turnover often found in intervals of low fossil diversity?

Perhaps a new type of succession needs to be considered for these times, that of earth system succession. On a global scale, the structure and function of ecosystems affects key earth-system processes, such as rates of weathering, soil formation, organic carbon sequestration, nutrient availability and recycling, and the availability of key substrates such as soils and reefs [78–80]. These processes move various elements between earth

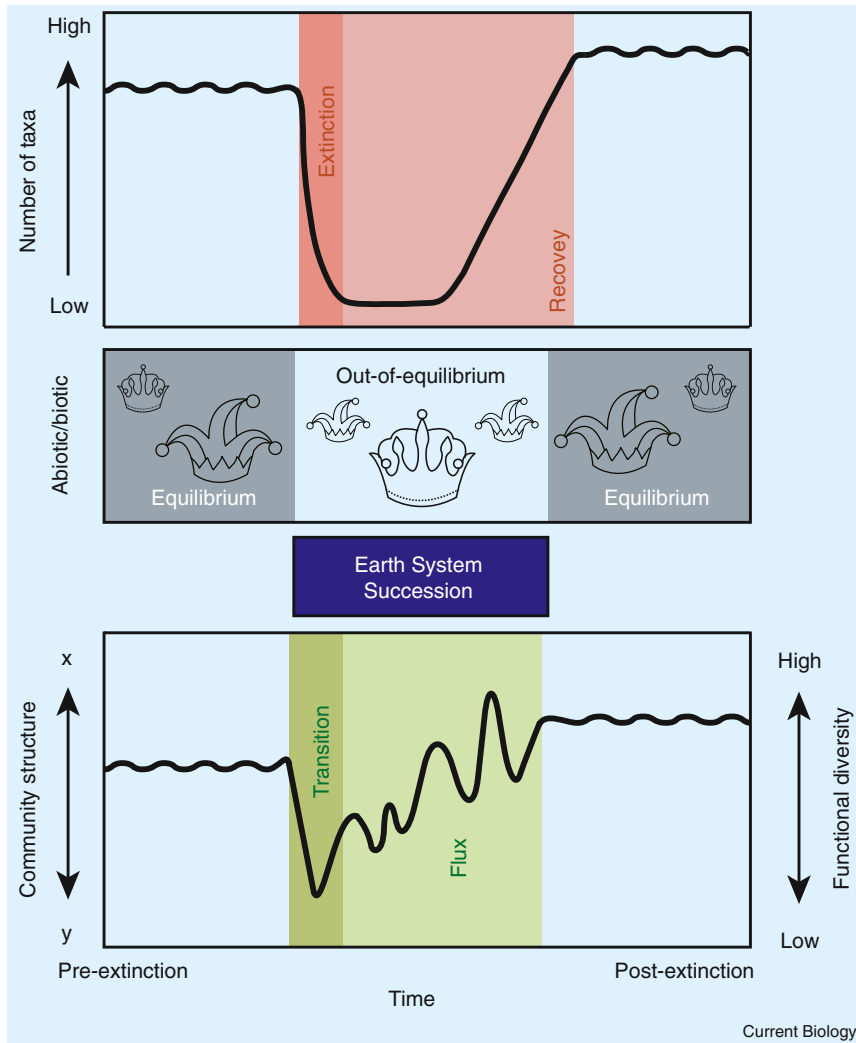


Figure 3. Re-diversification in altered ecosystems.

Re-diversification in the aftermath of mass extinctions coincides with widespread changes in global ecosystems. Environmental disturbance and ecological change during the extinction (top and bottom) perturbs the dynamic equilibrium of the earth system (middle). As species and ecosystems re-evolve, earth system feedbacks (i.e., earth system succession) pace the direction, nature, and timing of ecosystem turnover (bottom). Biotic forcing (also referred to as Red Queen dynamics) is thus particularly apparent during earth system succession because it is the ultimate driver of ecosystem evolution. This contrasts with other intervals during which environmental change is physically forced and drives biotic change (also referred to as ‘court jester dynamics’) [150]. Note, all lines are schematics; functional diversity curve (bottom) refers to local scale communities (which exhibit greater change) rather than global scale compilations. Panels after [18] used with permission from the Paleontological Society.

long-term equilibrium. Returning to a geological stable equilibrium would be an inherently protracted process, and would result in subtle shifts in environmental conditions likely to favor different taxa through time. For instance, earth system sequestration of CO₂ after the Paleocene-Eocene Thermal Maximum took somewhere between 120,000 and 220,000 years [84], during which temperatures were warmer [85], ocean carbonate saturation state briefly dropped [86], and the structure and function of ecosystems changed [84,87]. After extinctions, assuming that low-diversity communities would also be likely to lack some functional redundancy, dynamic turnover of

system reservoirs, for instance from the ocean to the atmosphere or from soils to streams. On a global scale, the time it takes for various elements to move, on average, between reservoirs can be quite long (100 years to 10 million years) [81]. As various earth-system reservoirs and fluxes change, they have the scope to, in turn, affect ecosystems on a global scale, because they alter the prevailing nutrient availability and environmental conditions [80,82]. The effect that any given change will have depends on the relative size of the change, the amount of those elements in the system, and how they are distributed between various reservoirs. The term ‘earth system succession’ is used here to describe the sequential change in global ecosystems that occurs as biogeochemical reservoirs and fluxes return to equilibrium after perturbation.

Earth system succession after mass extinctions and other large biotic perturbations might naturally be expected if taxa responsible for key ecosystem functions were affected, as they sometimes are [38,83], or if the perturbation itself significantly changed a biogeochemical reservoir. Even if the ecological functions could be quickly replaced, the cycling among various components of the earth system would be altered and out of

communities and geochemical proxies (as is observed) would be one expectation of the mechanism.

Earth system succession may be occurring in post-extinction aftermaths. First, mass extinctions generally perturb a major component of the geosphere (or biogeosphere) directly and/or cause a lasting change to ecosystem function. Many extinctions are accompanied by evidence for direct perturbations of the (bio-)geochemical reservoirs, and most depend on some change in these systems to drive the extinction [18,19]. The structure and function of ecosystems is likewise often changed in the aftermath of mass extinctions [18,39]. Second, some biogeochemical perturbations or ecosystem changes appear to have a global effect on environmental conditions. After the KPg extinction, the reduction of pelagic carbonate producers, particularly of the coccolithophores, led to a very high carbonate saturation state throughout the ocean [88]. The post-extinction interval after the Triassic-Jurassic mass extinction (Box 1), by contrast, coincides with a silica deposition boom, perhaps driven by a combination of increased weathering of new basalts and siliceous sponges out-competing carbonate corals in the aftermath of an ocean acidification event [15,89]. Third, there is the suggestion that

long-term changes in community composition and functionality may be, in turn, shifting global environmental conditions. This third component has yet to be vetted with coupled ecological and earth system models — although it is notable that such feedbacks have been suggested to sometimes cause mass extinctions [90,91]. Together, the rough correspondence between the stabilization of environmental proxies, the re-establishment of geologically stable ecosystems, and the recovery of diversity suggests that earth system succession might drive post-extinction dynamics.

Although I have named earth system succession in analogy to ecological succession, there are important differences. Earth system succession occurs when a change in the biosphere or the geosphere (that is, a disturbance or innovation) results in disequilibrium between the various components of the earth system. In contrast to ecological succession, the final composition of communities is not known at the start, as new species and ecological strategies evolve during the course of earth system succession. Similarly, there is no expected final community in earth system succession. Although the earth system is unlikely to ever be in true geochemical equilibrium, earth system succession might be considered ‘over’ when the rate and amplitude of change is indistinguishable from times long-outside of extinction intervals (Figure 3). Finally, whereas ecological succession implies some predictability of the timing of community turnover and their likely composition, earth system succession is unpredictable outside of the recognition that high turnover is expected after disturbance until a biogeochemical equilibrium is re-established.

Earth system succession might also prove relevant for understanding the effects of environmental change, such as long-term cooling, that alter biogeochemical reservoirs in the absence of extinctions, or the effects and rise of key innovations, such as the evolution of oxygenic photosynthesis (see Primer by Patrick Shih in this issue) [92], the evolution of pelagic calcifiers [93], and the evolution of grasses [94]. In each case, as the innovative clade increased in abundance, often in fits and starts and over many of millions of years, biogeochemical cycles were fundamentally changed. From an ecosystem perspective, the possibility of earth system succession is important because it means there may be inherent speed limits on the re-establishment of geologically stable ecosystems after global biotic disturbances. These speed limits would be set by the size of biogeochemical reservoirs and exchange rates between different biogeochemical reservoirs, and the extent to which they were out of equilibrium.

It is important to note that earth system succession is closely related to the concept of ecosystem engineering [95,96] but differs in scale and end effect. Ecosystem engineering describes how the activities of a given species affect the success of others [96]. Ecosystem engineering is often used to describe local effects, although it can and has been used at the global scale of earth system succession [96,97]. Earth system succession is characterized by three important aspects beyond those of global ecosystem engineering: it is paced by interactions among various components of the earth system (global); it leads from less to more stable earth system dynamics (directional); it occurs during times of earth system disequilibrium (constrained). In other words, earth system succession describes the process

by which the sum effect of numerous local scale changes (including ecosystem engineering) leads to an ecological succession-like turnover in global ecosystems on very long (roughly >1000 year) timescales.

From a macroevolutionary perspective, processes related to earth system succession might better explain the apparent timing of radiations, and the ecosystems they give rise to, than explanations relying on ecological or evolutionary processes alone. Earth system succession provides an ultimately ecological means to account for sustained ecological and evolutionary trends on very long time scales, a problem that has long interested paleontologists [98]. In doing so, earth system succession may provide a general explanation for why and how some ecological and evolutionary changes take so long to occur.

Innovation and Radiation during Other Times

The abundant evidence for strange ecosystems in the aftermath of mass extinctions, including strong feedback between the geosphere and biosphere, raises the question of whether extinction aftermaths exert a unique influence on the evolution of life. In other words, aside from the rapid re-diversification of lineages, is evolution in the aftermath of extinctions qualitatively different than during the intervals between extinctions? The answer is decidedly less clear, as two examples illustrate.

The most recent global mass extinction is the Eocene-Oligocene Transition (EOT) ~34 million years ago, which is marked by the onset of Antarctic glaciation [2]. The glaciation of the Antarctic changed the world from one without large continental ice sheets — a greenhouse world — to one with large continental ice sheets — an icehouse world. This fundamentally altered oceanographic and climatic dynamics and is considered the largest climatic transition of the last 66 million years [99,100]. A relatively minor extinction event overall (~15% loss of shelly marine invertebrates [2]), the EOT also showed strange ecosystems within the first million years likely due to prevailing environmental conditions [101,102]. After the EOT many clades diversified that are still dominant today: diatoms radiated [103], ancient whales (archaeocetes) were replaced by modern whales (odontocetes and mysticetes) [104], and pinnipeds (i.e., seals, sea lions, and walruses) diverged from other mammalian carnivores [105].

Surprisingly, from a modern phylogenetic perspective, neither of the last two mass extinctions, the EOT or the KPg, stand out as having changed the rate of evolution in lineages leading up to extant mammals [106] or teleosts [107]. These two groups point to the Early Eocene Climate Optimum (EECO; ~52–50 Ma) as the time when rates of lineage diversification changed. For birds, the evidence from extant taxa is mixed. A recent species-level phylogeny also supports the EECO as the critical transition in rates of lineage diversification [108], and full-genome sequencing of 48 species supports both the KPg and the EECO in the same 10–15 million year window [109]. While the early Eocene is well-known as the warmest interval of the Cenozoic [110], it is strikingly unremarkable from an extinction rate perspective [71,111]. There are many other reasons that the early Eocene might stand out as a critical time for macroevolution [84], but the key point is that the EECO may have been more important for the macroevolution of modern taxa than either of the last two mass extinctions. This is not an isolated case, nor is the inference regarding the importance of intervals likely to be just

an artifact of using modern-phylogenetic inferences from extant taxa, as could be the case with the phylogenies discussed above.

The Cretaceous terrestrial revolution provides another example of the importance of the intervals that lie between mass extinctions, and one based entirely on fossils [112]. During the Cretaceous, angiosperm plants radiated on land and rose to dominance, coincident with periods of massive innovation in terrestrial vertebrates (dinosaurs, mammals, squamates) and insects [112–114]. At roughly the same time, near-coastal and open ocean marine ecosystems and species underwent an equally profound revolution in their structure and function [93,115].

This discussion is not meant to demote mass extinctions as important drivers of the evolution of life, but rather to question how truly unique they are in their evolutionary effects. There certainly is widespread paleontological evidence for rapid diversification in the aftermath of mass extinctions [36], including bursts of morphological innovations [26]. What's more, state changes in macroevolutionary dynamics, in origination and extinction rates, coincide with the largest extinction boundaries [116,117]. Within clades, important innovations can also appear in the aftermath of extinctions. For instance, tetrapods invaded and radiated in the marine realm after the PT and KPg mass extinctions, perhaps due to the preferential extinction of large bodied animals and the opening of ecospace after both extinctions [33,118]. Spiny-rayed fishes likewise showed a major wave of reef colonization after the KPg mass extinction [119], and increased their abundance and occupation of niche- and morpho-space relative to cartilaginous fishes at the same time [26,120]. However, these fishes provide the case in point, in that the macroevolutionary effects of the KPg mass extinction, as pronounced as they are, do not appear unique to the boundary interval. The first wave of reef colonization is likely to have taken place earlier in the Cretaceous [119] during a time of generally high diversification rates [107], and the largest change in diversification rates in lineages still extant today, a decline, occurred in the Eocene [107]. While the KPg mass extinction was certainly important in the macroevolutionary history of spiny-rayed fishes, other time periods were as well.

It is clear that mass extinctions have profound ecological and evolutionary effects through the mass death of taxa [3] and by allowing state changes in macroevolutionary dynamics [116,117] and ecosystem structure [13]. In their aftermaths, a large number of evolutionary events also occur over a relatively short time as clades re-diversify, but how important (or distinct) these times are for macroevolution relative to the intervals between them is still an outstanding issue. Does the unique selective regime suggested by earth system succession in the aftermath really matter for macroevolution? This is a question for future studies to address.

Conclusion

Macroevolution is shaped as much by those who survive as those who did not [3,121]; it is shaped as much by extinction, as by innovation and speciation [3,122]. More than 99% of all the species that have ever lived are now extinct [3], and the losses have often been distinctly non-random [7,8]. The largest biotic crises eliminate entire branches of the tree of life [1], drive the decline of once diverse clades [123], and lead to the radiation of

new species and ecosystems [13,124,125]. In the prolonged aftermath, ecosystem change across the globe exerts an evolutionary influence distinct from the extinction itself, with a timing characteristic of the earth system (i.e., earth system succession). As such, mass extinctions should not be considered as macroevolutionary point events, but rather as prolonged intervals of varying selection spanning the mass death and subsequent radiation of taxa.

Beyond this, a general macroevolutionary understanding of the importance of mass extinctions relative to other events in earth history will require an understanding of why innovations and radiations characterize the intervals in between extinctions perhaps even more so than the aftermaths of the extinctions themselves. This is an exciting area of research as detailed paleontological, geochemical, geological and phylogenetic datasets are just now becoming available to compare between them. Only an estimated 4% of species extinctions in the last half billion years of life coincided with one of the Big Five mass extinctions [3], but most species that have ever existed are now dead and those losses have shaped the history of life. An integrative understanding of the role of extinction and speciation in macroevolution has yet to be achieved but is central to understanding the evolution of life.

ACKNOWLEDGEMENTS

This manuscript was much improved by thoughtful feedback from J. Burke, D.H. Erwin, N.J. Planavsky, D.E. Penman, E.E. Saup, L.G. Tarhan, three anonymous reviewers, and the editor F. Maderspacher, and the ideas were encouraged by brief discussions with D.E.G. Briggs, M.J. Henehan, and S. Finnegan. L.E. Elder and A.Y. Hsiang are gratefully acknowledged for their help in constructing Figure 2 and illustrating the jester hat and crown in Figure 3, respectively.

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