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# Lessons from the past: Evolutionary impacts of mass extinctions

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Mass extinctions have played many evolutionary roles, involving differential survivorship or selectivity of taxa and traits, the disruption or preservation of evolutionary trends and ecosystem organization, and the promotion of taxonomic and morphological diversifications—often along unexpected trajectories—after the destruction or marginalization of once-dominant clades. The fossil record suggests that survivorship during mass extinctions is not strictly random, but it often fails to coincide with factors promoting survival during times of low extinction intensity. Although of very serious concern, present-day extinctions have not yet achieved the intensities seen in the Big Five mass extinctions of the geologic past, which each removed  $\geq 50\%$  of the subset of relatively abundant marine invertebrate genera. The best comparisons for predictive purposes therefore will involve factors such as differential extinction intensities among regions, clades, and functional groups, rules governing postextinction biotic interchanges and evolutionary dynamics, and analyses of the factors that cause taxa and evolutionary trends to continue unabated, to suffer setbacks but resume along the same trajectory, to survive only to fall into a marginal role or disappear (“dead clade walking”), or to undergo a burst of diversification. These issues need to be addressed in a spatially explicit framework, because the fossil record suggests regional differences in postextinction diversification dynamics and biotic interchanges. Postextinction diversifications lag far behind the initial taxonomic and morphological impoverishment and homogenization; they do not simply reoccupy vacated adaptive peaks, but explore opportunities as opened and constrained by intrinsic biotic factors and the ecological and evolutionary context of the radiation.

To the conservation biologist, there is little positive to be said about extinction. From an evolutionary perspective, however, extinction is a double-edged sword. By definition, extinction terminates lineages and thus removes unique genetic variation and adaptations. But over geological time scales, it can reshape the evolutionary landscape in more creative ways, via the differential survivorship of lineages and the evolutionary opportunities afforded by the demise of dominant groups and the postextinction sorting of survivors. The interplay between the destructive and generative aspects of extinction, and the very different time scales over which they appear to operate, remains a crucial but poorly understood component of the evolutionary process.

The fossil record is rich in extinction events at all intensities and spatial scales, and thus provides the essential raw material for an extremely important research objective: the comparative calibration of evolutionary responses, both positive and negative, to perturbation. Despite limits on direct comparisons to present-day and future events, discussed below, paleontological data afford the opportunity to test the evolutionary impact of such factors as the initial state of the system, the nature, duration, and magnitude of the perturbation, and postextinction physical and biotic conditions. Comparative analysis of the Big Five mass extinctions (1, 2) is just beginning, as is work on the myriad

smaller—and sometimes more localized—events manifest in the geologic record, and so this paper is as much a research agenda as a review. One approach to the problem is through the related issues of extinction selectivity and evolutionary continuity across mass extinction events in the geologic past. Recent work on the geographic fabric of extinction events and their aftermath suggests that the spatial dimension of diversity dynamics also will be an important component of a rigorous theory of extinction and its evolutionary consequences, and so although data are sparse I will raise some of these issues as well.

## Selectivity and Loss

Mass extinctions would be important evolutionary agents even if they simply intensified variations in clade survivorship seen in times of low extinction rates. For example, if mass extinctions primarily removed lineages in decline or in the early stages of diversification, truncating the time span available to those and other clades for the acquisition of evolutionary novelties, then they would significantly reinforce the stability of the status quo. The fossil record shows, however, that the major extinction events of the geologic past have played a larger and more complex role, by removing not just marginal players but also dominant incumbents, owing at least in part to extinction selectivities that are partly independent of those seen under “normal” extinction regimes. For example, factors such as local abundance, species richness, and species-level geographic ranges, all apparently significant during times of low extinction intensities (3), played little role in the survival of marine invertebrate clades during the end-Cretaceous (K-T) mass extinction, where the data are most extensive (2, 4, 5, †), and have been unimportant in at least some of the other mass extinction events as well (2, 6). At the same time, broad geographic distribution at the clade level, regardless of species-level ranges, significantly enhanced survivorship at all of the major extinction events (2, 4, 7) (note that this discordance across hierarchical levels means that surviving clades need not consist of generalized or opportunistic species, contrary to some oversimplifications of these results). These analyses suggest that clades or adaptations may be lost not because they are poorly adapted to the pre(or post) disturbance settings, but because they lack the broad geographic deployment or other traits that favor survival during the extinction bottleneck—a pattern of “nonconstructive selectivity” (8) that yields differential survival among clades without promoting the long-term adaptation of the biota (2, 6, 9).

This is not to say that traits favored under low extinction intensities were never advantageous during mass extinctions: resting stages in phytoplankton, occupation of unperturbed

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†Lockwood, R. (1997) *Geol. Soc. Am. Abstr. Programs* 29, A-404.

habitats or regions, physiological tolerances that happened to match the extinction-driving stresses, and perhaps particular ecological strategies, all might play a role in survivorship (10–12). Further, the broad correspondence between survivorship during mass extinction and long-term clade volatility (variance in standing diversity, i.e., net diversification rates rather than per-taxon origination or extinction rate) (13–15) suggest that other intrinsic biotic factors (6) carry over from low to high extinction-intensity regimes. Little has been done to explore this possibility, however, or the alternative that taxa with high per-taxon turnover rates have a lower threshold for crossing into the mass-extinction selectivity regime.

Given that some clades show consistently severe or mild responses to extinction events, which suggests that intrinsic biotic factors are important determinants of survivorship, why does the vulnerability of other clades appear to vary significantly among extinction events (6, 16)? This question bears critically on the evolutionary consequences of extinction events but has received little attention. Potential explanations range from long-term hardening of clades by the removal—and failure to re-evolve—extinction-prone constituents, to contrasting forcing mechanisms in the different extinction events, to fortuitous trait combinations evolved under “background” extinction regimes. Such analyses also are needed to make better biological sense out of apparent selectivity against major clades (e.g., ammonites, mosasaurs, dinosaurs etc. at the K-T boundary) when other selectivities appear indifferent to clade membership [e.g., widespread vs. restricted-range bivalves and other taxa at many extinction events (2, 4)].

I should note that the terms background and mass extinction should be used carefully: major extinction events stand out in geologic time series as maxima against a local background of lower rates, but the overall frequency distribution of extinction intensities is a highly skewed, unimodal continuum (9). Contrasts in selectivity between the major extinction events and times of relatively low extinction suggest a threshold effect (2, 5), but the position and taxonomic generality of that threshold is uncertain; comparative analyses that encompass smaller extinction episodes such as the Cenomanian-Turonian and Eocene-Oligocene events would be valuable.

The likelihood of clade- or ecosystem-specific thresholds for the onset of mass-extinction selectivities underscores the complexity underlying extinction time series in the fossil record, a point sometimes lost in the general focus on a few of the most massive events. The direct comparability of the Big Five mass extinctions to present-day biodiversity losses remains unclear. Although present-day losses are severe and appear to be accelerating (17), they have yet to approach the scale of the Big Five extinctions of the geologic past. For example, the K-T extinction removed 50% of the marine bivalve genera globally (4), and 97% of the photosymbiont-bearing coral species (and 83% of those genera) (18), and the sampling biases inherent to the fossil record virtually require that these victims were drawn from the more abundant and widespread components of the biota (2, 9). Viewed in this light, these are shocking statistics that exceed even the most severe estimates for present-day losses, although long-term projections eventually can approach such magnitudes. Further, over the past 2,000 yr species-poor clades and geographically restricted species have been the overwhelming majority of losses (19), corresponding to an intense version of the “background extinction” regime rather than the mass extinction selectivities of the fossil record.

This is neither to belittle the violence being wrought on today's biodiversity, nor to imply that the fossil record offers few insights regarding the future of evolution in the face of human activities and other stresses. It does suggest, however, that the most useful comparisons must go beyond absolute extinction intensities to involve such factors as: relative extinction intensities among

regions, clades and functional groups; long-term effects of geographic variation not only in extinction but also in postextinction biotic interchanges and evolutionary dynamics; patterns of biotic continuity, lag times, and innovation as reflected in postextinction evolutionary rates and patterns. Also important, of course, are the looming questions of what causes the transition to selectivities seen under paleontological mass-extinction regimes, and whether that threshold can be avoided in the near future. Still unknown, for example, is whether that threshold is simply a function of the spatial scale and intensity of the forcing perturbation, of the quality of the perturbation [see, for example, the apparently more severe biotic effects of increased seasonality as opposed to simple changes in mean annual temperature (20)] or whether feedbacks involving, for example, the compounding of perturbations (21), or the disruption of biotic interactions or community structures come into play.

In principle, threshold effects should be detectable in time series around mass extinction events, and this would be especially valuable in light of the cumulative extinction processes operating today. The demonstrable selectivity of extinctions raises the issue of weakening vs. hardening of the biota if unfavorable conditions are imposed over a protracted interval: as the most vulnerable taxa such as endemic species are lost, under what circumstances will the extinction-resistant residue withstand further stresses, and when will they give way to the mass-extinction regime? A hardening process may underlie the pulse of extinction near the onset of Pleistocene glaciation and the dearth of extinction thereafter (22) (the end-Pleistocene megafaunal extinction is probably a different issue), and we need a better understanding of exactly what separates such events from the major mass extinctions, and to what extent such hardening processes undermine linear projections of present-day extinction estimates to future losses. We can simply appeal again to the spatial scale, intensity, or quality of the perturbation, or to the quality of the perturbation, but this leads us back to the uncertain nature of the threshold, whether it is graded or a step-function, and its potential variation among taxa, communities, and regions.

### Spatial Patterns

Most paleontological analyses of mass extinctions have neglected the spatial dimension, tending to focus instead either on single stratigraphic sections or regions, or on synoptic global databases. Both scales have been extremely productive, but the global biota is spatially complex, with diversity gradients and hotspots (e.g., refs. 23–26) and concomitant variation in the generation and persistence of evolutionary novelties and higher taxa (27) [although the relation to species-level evolutionary dynamics is still unclear (28, 29)]. Paleontological analyses that contain a spatial component, for example regarding regional extinction events at all scales (30) or the biogeographic fabric of postextinction evolutionary patterns, therefore would be especially valuable with reference to present-day and future processes. Biotic interchanges in the paleontological record, such as the late Cenozoic responses to the joining of North and South America after the final uplift of the Panama Isthmus, or the opening of transpolar interchange between Pacific and Atlantic, clearly document asymmetries in biotic interchanges that correspond to regional differences in extinction intensities (31, 32). These paleontological findings that regions suffering greater losses were more heavily invaded is an important verification and extension into deep time of observations made in modern communities (33).

Geographical analyses of mass extinctions and their aftermath, however, show that more complex dynamics may sometimes operate. For example, although K-T extinction intensities were statistically homogeneous for marine mollusks on a global scale (except perhaps for shallow, clear-water tropical platforms), the evolutionary and biogeographic response was decid-

edly inhomogeneous. Of the four regions analyzed as time series (34), only the North American Gulf and Atlantic Coastal Plain showed a prolific but short-lived burst of diversification by several clades [termed “bloom taxa” (35)] that were quiescent elsewhere and was significantly more subject to postextinction biotic invasions. Although further analyses are desirable, particularly from a phylogenetic standpoint, these patterns are likely to be robust: they hold whether the bloom taxa are treated as a proportion of the biota or as raw species numbers when the K-T bottleneck is taken into account (34). Furthermore, neither burst nor excess invasion appears in an extensive new analysis of an important fauna in the earliest Tertiary of northern Europe (36), which is the region most likely to conform to North America by reason of proximity and climatic similarity.

Understanding these paleontological patterns is particularly pressing in light of the massive biotic interchanges that are currently being directly or indirectly mediated by human activities. Why was North America subject to more intense invasion after the K-T event despite its unexceptional (if severe) extinction intensities? This response implies a nonlinear between extinction and invasion intensities, or perhaps simply a threshold above which the relation breaks down. Another possibility is that when losses approach paleontological mass-extinction levels (that is, 50% of the relatively abundant and widespread genera) or are globally both severe and homogeneous, qualitative as well as quantitative losses determine the probability of the evolutionary excursions and invasions seen in North America: the identity of the victims and not just their numbers becomes particularly important. The functional role of taxa lost from each of the regional biotas will be difficult to assess rigorously, but divergent regional responses to homogeneous extinction intensities provide a natural experiment sufficiently rich in potential insights to demand further investigation. Lockwood’s analyses<sup>†</sup> showing no relation between abundance and survivorship in this fauna undermines one of the simplest hypotheses: that preferential removal of abundant and thus dominant taxa was masked by a strictly taxonomic approach (although a detailed parallel analysis of other regions is required for a definitive test, of course).

The evolutionary effects of biotic homogenization may depend in part on how it is achieved. Homogenization via elimination of endemics will leave a residue of already widespread taxa that may be relatively resistant to geographic isolation and rapid diversification, whereas homogenization via range expansion may more readily promote the origin and diversification of new endemic taxa. Invaders are not drawn randomly from the source biota, however (34, 37), and this bias could itself channel subsequent evolution into narrower pathways among regions than would otherwise be expected.

Spatial effects may be important in finer scales as well. For example, in North America within-habitat molluscan diversity appears to recover within a few million years after the K-T extinction (38), but total regional diversity evidently does not reach preextinction levels until roughly 10 million years after the event (34, 35). Although this result needs to be verified elsewhere, and tested more rigorously for sampling artifacts, it suggests that beta diversity, the differentiation of local faunas among habitats and along environmental gradients, takes longer to recover than alpha, i.e., local, diversity.

### Continuity and Creativity

Mass extinctions have never entirely reset the evolutionary clock: even the huge losses at the end of the Permian, which appear to have permanently restructured marine and terrestrial communities, left enough taxa and functional groups standing to seed the recovery process without the origin of new phyla (39). One key to understanding the past and future evolutionary role of extinctions will involve the factors that permit the persistence of

certain biological trends or patterns—e.g., net expansion or contraction of clades or directional shifts in morphology—in the face of extensive taxonomic loss and ecological disruption. Besides extinction, at least four evolutionary patterns can be seen in the fossil record. These are: (i) unbroken continuity, (ii) continuity with setbacks, (iii) survival without recovery (“dead clade walking”), and (v) unbridled diversification.

**Unbroken Continuity.** Some large-scale patterns withstood one or more of the Big Five extinctions with little disruption. These include the continued dominance of reefs by rugose and tabulate corals and stromatoporoid sponges across the Ordovician-Silurian boundary (40, 41), the escalation of morphological responses seen in molluscan shells to increased predation intensity across the K-T boundary (42), the prolonged Paleozoic decline of trilobites (43), and the onshore-offshore expansions and retreats of a number of post-Paleozoic marine orders (44).

**Continuity with Setbacks.** Other trends suffer setbacks—presumably owing to the contrast between mass extinction and “normal” selectivities—but then resume their long-term trajectories. These include rising cheilostome bryozoan dominance relative to cyclostomes (45), the ecological expansion of angiosperms (46, 47) although this may be more an ecological than an evolutionary setback, and the spread to greater burrowing depths by veneroid bivalves,<sup>‡</sup> all at the K-T boundary, the early Paleozoic spread of suspension-feeding bivalves to offshore shelf environments (48), and the overall Paleozoic increase in suture complexity in ammonoids (49). An important open question amenable to direct testing and simulation is whether such setbacks are generally a simple byproduct of high extinction intensities (if the extremes of the morphospace volume are sparsely occupied, for example, then random extinction could clear those portions), or represent selection against the traits being maximized under low extinction intensities.

**Dead Clade Walking.** Clade survival is no guarantee that preextinction trends will persist or be reasserted in the postextinction setting. Each extinction has examples of clades that survived the extinction event only to fall into a marginal role or eventually disappear (dead clade walking). These include bellerophonid snails (7) and prolecanitid ammonoids at the Permo-Triassic boundary (50), the brachiopod order Spiriferoida after the end-Triassic extinction (51), and the planktic foraminiferal *Zeauvigerina* lineage after the K-T event (52). Such lingering demises need to be tested against stochastic attrition, of course (43). My preliminary, unpublished analysis suggests that the intervals after mass extinctions tend to be significantly enriched in taxa that failed to cross the next stage boundary, relative to other intervals before the extinction event; in other words more clades that survived a mass extinction tend to dwindle or disappear shortly after the event than would be expected by chance. Also intriguing is the geographic variation in the proportion of dead clade walking taxa across the K-T boundary, with values highest not in North America (which makes an interesting statement on the impact of the greater influx of invaders there—they followed extinctions but did not drive them), but in the tropical Indian Ocean.

These diverse postextinction trajectories again demonstrate that analysis of the evolutionary role of extinctions must include much more than taxonomic survivorship at the event itself. We need to understand why some clades, and some polyphyletic trends such as escalation of antipredatory defenses, persist uninterrupted across the extinction event, why others stumble but recover their preextinction trajectory, and still others survive

<sup>†</sup>Lockwood, R. (1998) *Geol. Soc. Am. Abstr. Programs* 30, A-286.

but never recover. All of the patterns discussed so far strongly attest that postextinction evolutionary processes involve not simply unbridled radiation (see below), but a sorting of survivors in the postextinction world. At this early stage, many alternative hypotheses are feasible and the relative power of the alternatives may vary among different situations. The most obvious is the taxonomic breadth of the trend: all else being equal, any evolutionary trend that advances along a broad ecological or taxonomic front is less likely to be halted by extinction. Although this is surely a factor, it is unlikely to be sufficient in all cases, because many trends are fairly circumscribed phylogenetically, as in the bryozoan and veneroid examples given above.

Given the discordance in selectivity between times of high and low extinction intensities, another factor in the persistence of trends is likely to be the strength of association between traits involved in trends and those related to survivorship. The role of this macroevolutionary linkage in promoting the long-term persistence of trends is virtually unexplored. A final potential explanation is even more context-specific, that the differential persistence of trends depends less on the intrinsic traits of clades than on the strong variation recorded in postextinction recovery (*i*) among ecosystems, e.g., the more rapid recovery of diversity in oceanic plankton vs. marine benthos (53, 54) (with potentially important implications for the relative persistence of mineral and nutrient cycles); (*ii*) across ecological scales, e.g., discordances in the time to recovery of local vs. global diversity (as mentioned above, with potentially important implications for the accumulation of biological diversity and the development of spatial structure); and (*iii*) among regions in clade dynamics and biotic interchanges, e.g., the concentration of bloom taxa and postextinction invasions in particular areas (with potentially important implications for the persistence and recovery of local biotas and intraregional source-sink dynamics).

**Unbridled Diversification.** The most dramatic and creative evolutionary role of mass extinctions is the promotion of postextinction diversifications, typified most vividly by the exuberant radiation of the mammals after the demise of the dinosaurs and other reptilian clades at or near the K-T boundary. Postextinction bursts of diversification have been extensively discussed and documented for many extinction events, both morphologically and at several taxonomic levels (6, 39, 41, 55–58). Therefore, before returning to the need for further analysis of geographic variation in evolutionary dynamics, I will make only two further points, on predictability and time scales.

**Predictability.** Although the evolutionary response to mass extinction has sometimes been depicted simply in terms of the reoccupation of preextinction adaptive peaks (“reinventing the ecological wheel,” ref. 59), evolution is both too opportunistic and too constrained by inherited body plans for this to be wholly true. Striking convergences in form and habit are, of course, a major theme in evolution, but postextinction dynamics are complicated by near-simultaneous radiation of multiple clades [with the powerful incumbency advantage at stake (32)], the distinct ecological context of each postextinction interval, and the raw material provided by surviving lineages. These effects can be seen in the incomplete congruence of successive occupations of morphospace after extinction events (60, 61).

To drive home these important but somewhat abstract points on the long-term prospects for evolutionary replacements, consider the Cenozoic history of birds. The large, flightless phorusrhacid and diatrymid birds, probably the top carnivores of early Cenozoic terrestrial communities (62, 63), interfered with the triumphant mammalian ascent to center stage in the post-dinosaurian world, and probably were not replaced by an exact mammalian analog once they disappeared. Note also that these carnivorous birds opportunistically converged on theropod di-

nosaurus rather than adhering to the pterosaur models that might have been the most likely targets for convergence given a flying avian starting point (62). Over the course of Cenozoic diversification, other birds did assume modes of life similar to those vacated by pterosaurs: skimmers may roughly correspond to *Tropeognathus* with its keeled jaws, swallows and swifts to *Pterodactylus* with its similar size and wing proportions, flamingos to *Pterodaustro* with its bristling array of fringe-like teeth, and perhaps even condors to the enormous *Quetzlcoatlus* (64, 65). This does not mean, however, that birds—or even birds plus bats—managed to occupy the full range of pterosaur habits (66). Equally important, the granivorous habit so important in modern birds evidently represents a novel expansion of bird ecospace relative to their supposed pterosaur models (see ref. 66 on the avian trophic diversification). There may be good functional or ecological reasons for this (e.g., was the Mesozoic seed bank as rich and dependable a resource as in the angiosperm-dominated Cenozoic?), just as there seems to have been for the absence of baleen-like filter-feeding in Mesozoic marine reptiles (67), but such constraints and contingencies are precisely the factors that prevent a given set of clades at a given time from fully overlapping the evolutionary pathways of their predecessors. Attempts to predict evolutionary behavior after major extinction events can only operate in broad generalities, and always with the caveat, “expect the unexpected.”

**Time Scales.** The fossil record shows that destructive and generative aspects of extinction generally operate in different time frames, as many authors have pointed out (2, 41, 68). The biotic impoverishment and homogenization necessarily precedes the evolutionary response, and there is surprisingly little hard evidence for major evolutionary innovations within a major extinction episode. Even for apparently protracted or multistep extinctions that see origination within the extinction interval, such as the end-Ordovician or end-Permian episodes, “little biological innovation is apparent” (41).

Recoveries of different biomes, clades, or communities may have different postextinction lag times; for example, broadly defined “reef” systems lag behind oceanic plankton systems (see ref. 2 for discussion). Whether these lags reflect a general property of large-scale diversity dynamics (13, 69), sampling and other biases (6, 70), the duration or intensity of environmental stresses (71), a protracted process of assembling new ecological communities (2, 72), or evolutionary waiting times set by intrinsic diversification rates (73) awaits further comparative analysis.

**Geography.** The spatial dimension is important not only to extinction selectivity and postextinction interchange, but to long-term evolutionary dynamics in a postextinction world. Certain habitats and regions, such as onshore marine settings (44), and the tropics in both marine (27) and terrestrial (74–76) settings, appear to be important sources of postextinction evolutionary novelty, but the implications of this nonrandom creativity have only begun to be explored. On finer geographic scales, a systematic search for diversity hotspots in the geologic record to test for their long-term persistence and evolutionary significance would be valuable. For example, is the end-Ordovician extinction of brachiopods and other benthic taxa in North America a potential case study in the destruction and later refurbishment of a diversity hotspot? North America straddled the equator and harbored a rich biota of endemic taxa in the epicontinental sea that occupied the center of the continent. Oscillating climates and fluctuating sea levels virtually eliminated this and other interior seaways and their biotas, and the postextinction interval saw an invasion pulse as taxa from outside the region expanded to occupy the returning favorable habitats (77, 78).

Tracking such hotspots and other crucibles of biotic novelty

over evolutionary time might help to prioritize targets for both research and conservation efforts in the near future. Do relatively localized hotspots primarily contribute taxonomic richness to the global biotic inventory, or are they also important reservoirs of biodiversity, that is morphological richness? The evolutionary importance of the answer will depend in part on the mean lifetime of such hotspots, and the extent to which novelties that arise in hotspots tend to spread elsewhere, as has been documented for novelties that originated in onshore environments or within tropical latitudes (27, 44, 74–76). For these and many other questions, paleontology can be a rich source of natural experiments in macroevolutionary dynamics before, during, and after perturbations of widely varying intensities and durations.

## Conclusion

I would not go far wrong in saying that the most dramatic evolutionary effects of mass extinctions can be epitomized in just four words: they remove successful incumbents. But going beyond what amounts to a concession to contingency, what are the lessons of the past that transcend the specific mechanisms, intensities, and participants of earlier events?

(i) Mass extinctions happen. The fossil record provides ample evidence that even the more widespread and species-rich clades, ecosystems, and biogeographic provinces are not infinitely resilient. Biogeochemical and other data are accumulating on the concomitant breakdown of nutrient cycling and other ecosystem-level processes (53), and the links among the collapse and

recovery of taxonomic diversity, morphological, or functional disparity and ecosystem function should be a high priority.

(ii) Survivorship during mass extinctions need not be closely related to many aspects of biological success as measured during “background” times. An understanding of the evolutionary role of mass extinctions requires continued analysis of why well-established incumbents are lost, surely at least in part a function of the spatial scale of perturbations, and the long-term consequences of such losses.

(iii) Extinction itself promotes biotic interchange. Asymmetries in ancient biotic interchange generally appear to reflect geographic differences in extinction intensity. The K-T extinction shows, however, that although biotic interchanges pervade the postextinction world, simple linear relationships can break down to produce unexpected source-sink patterns.

(iv) The evolutionary response to mass extinction is slow on human time scales, difficult to predict owing to the contingencies of postextinction conditions including the identity and evolutionary dynamics of the survivors, and geographically heterogeneous. Each of these complications, however, is amenable to comparative paleontological analysis and modeling, with the attendant opportunities for detecting patterns, testing hypotheses, and drawing lessons relevant to the future of evolution.

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