

Mass extinctions and macroevolution

David Jablonski

Abstract.—Mass extinctions are important to macroevolution not only because they involve a sharp increase in extinction intensity over “background” levels, but also because they bring a change in extinction selectivity, and these quantitative and qualitative shifts set the stage for evolutionary recoveries. The set of extinction intensities for all stratigraphic stages appears to fall into a single right-skewed distribution, but this apparent continuity may derive from failure to factor out the well-known secular trend in background extinction: high early Paleozoic rates fill in the gap between later background extinction and the major mass extinctions. In any case, the failure of many organism-, species-, and clade-level traits to predict survivorship during mass extinctions is a more important challenge to the extrapolationist premise that all macroevolutionary processes are simply smooth extensions of microevolution. Although a variety of factors have been found to correlate with taxon survivorship for particular extinction events, the most pervasive effect involves geographic range at the clade level, an emergent property independent of the range sizes of constituent species. Such differential extinction would impose “nonconstructive selectivity,” in which survivorship is unrelated to many organismic traits but is not strictly random. It also implies that correlations among taxon attributes may obscure causation, and even the focal level of selection, in the survival of a trait or clade, for example when widespread taxa within a major group tend to have particular body sizes, trophic habits, or metabolic rates. Survivorship patterns will also be sensitive to the inexact correlations of taxonomic, morphological, and functional diversity, to phylogenetically nonrandom extinction, and to the topology of evolutionary trees. Evolutionary recoveries may be as important as the extinction events themselves in shaping the long-term trajectories of individual clades and permitting once-marginal groups to diversify, but we know little about sorting processes during recovery intervals. However, both empirical extrapolationism (where outcomes can be predicted from observation of pre- or post-extinction patterns) and theoretical extrapolationism (where mechanisms reside exclusively at the level of organisms within populations) evidently fail during mass extinctions and their evolutionary aftermath. This does not mean that conventional natural selection was inoperative during mass extinctions, but that many features that promoted survivorship during background times were superseded as predictive factors by higher-level attributes. Many intriguing issues remain, including the generality of survivorship rules across extinction events; the potential for gradational changes in selectivity patterns with extinction intensity or the volatility of target clades; the heritability of clade-level traits; the macroevolutionary consequences of the inexact correlations between taxonomic, morphological, and functional diversity; the factors governing the dynamics and outcome of recoveries; and the spatial fabric of extinctions and recoveries. The detection of general survivorship rules—including the disappearance of many patterns evident during background times—demonstrates that studies of mass extinctions and recovery can contribute substantially to evolutionary theory.

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Introduction

Mass extinctions and their causes have attracted enormous attention over the past two decades, but relatively few authors have focused on these events from a macroevolutionary standpoint. Steve Gould saw the major mass extinctions as a third evolutionary tier with its own “predominating causes and patterns.” The essential property of mass extinctions, he argued, is that these rare, intense events derail the evolutionary patterns shaped by organismic selection, speciation, and spe-

cies sorting during times of background extinction (operationally defined here simply as the intervals of lower extinction intensity between the “Big Five” extinction peaks of the Phanerozoic). Mass extinctions would thus represent another challenge—among several presented by Gould (2002) and others—to *extrapolationist*, non-hierarchical approaches to evolutionary theory, in which large-scale patterns are understood strictly in terms of “extrapolating from evolutionary change over ecological time frames in local populations” (Sterelny and Griffiths 1999: p. 305).

Here I will discuss mass extinctions from an evolutionary perspective, drawing mainly on the heavily studied end-Cretaceous (K/T) event but noting results from other extinctions where comparable analyses are available. I will argue that shifts in extinction selectivity are just as important as variations in intensity, and that the sorting of clades in post-extinction recoveries is also crucial to our understanding the evolutionary role of mass extinctions. I will conclude that simple extrapolationism fails at mass extinction events, whether defined as empirical predictability from background to mass extinction, or in more demanding terms as reducibility to exclusively organism-level processes.

Intensity

Mass extinctions are important episodes in the history of life regardless of their broader evolutionary implications, but they are difficult to study rigorously. The absolute magnitude and temporal fabric of extinctions and subsequent recoveries are almost certainly distorted by the incompleteness and bias of the stratigraphic record (see discussions of Sepkoski and Koch 1996; Kidwell and Holland 2002; Foote 2003). Nevertheless, many lines of evidence refute the extreme Darwin-Lyell claim that the major extinctions are essentially sampling artifacts. This evidence includes, most obviously, the permanent loss of abundant, well-sampled clades that persist until late in the pre-extinction interval (such as ammonoids, rudist bivalves, and globotruncanacean foraminifers at the K/T boundary), qualitative and long-standing shifts in biotic composition, and the temporal sharpening of the events with improved sampling and correlations (e.g., Sepkoski 1984, 1996; Jablonski 1986a, 1995; Hallam and Wignall 1997; Droser et al. 2000; Erwin et al. 2002; Steuber et al. 2002; Bambach et al. 2002; Benton and Twitchett 2003; Erwin 2003; see also the modeling results of Foote 2003, 2005). Taxonomic standardization tends to reduce the intensity of major events relative to estimates from synoptic databases (e.g., Smith and Jeffery 1998; Kiessling and Baron-Szabo 2004; for an exception see Adrain and Westrop 2000), but such revisions rarely encompass the target clade's

"background" extinction patterns and so the boundary-focused revisions lack a quantitative context (as also noted by Fara [2000] and Foote [2003]).

Some authors have argued that the apparent continuum of extinction intensities from the most placid stratigraphic intervals to the Big Five events, yielding a right-skewed unimodal distribution when all Phanerozoic stages are plotted as a single population (e.g., Raup 1991a,b, 1996; MacLeod 2003a,b; Wang 2003), undermines any claim for a significant macroevolutionary role for mass extinctions (e.g., Hoffman 1989; Lee and Doughty 2003; MacLeod 2003b). However, this seems an oversimplification, for several reasons.

Most importantly, the seemingly continuous distribution of extinction intensities may arise from grouping heterogeneous data. The high turnover rates of the early Paleozoic, which anchor the secular decline in background extinction intensities documented by Raup and Sepkoski (1982; see also Van Valen 1984; Gilinsky and Bambach 1987; Gilinsky 1994; Sepkoski 1996; Newman and Eble 1999; MacLeod 2003a; Foote 2003), generate a set of high-extinction intervals that bridge the gap between the bulk of background extinction stages and the most extreme of the mass extinctions. If the secular decline is factored out, by omitting the Cambrian-early Ordovician stages and/or by scaling extinction intensities as residuals to a line fit to the Phanerozoic decline, then at least three of the major extinction events form a statistically significant mode in the extinction-frequency distribution (Bambach and Knoll 2001; S. Peters personal communication 2002; Bambach et al. 2004). The end-Permian, end-Cretaceous, and end-Ordovician extinctions constitute that discrete mode in the Bambach et al. analysis, the same three events that emerged in Hubbard and Gilinsky's (1992) bootstrap analysis and in Foote's (2003) models, an outcome that underscores the peculiarity—at least in the synoptic Sepkoski databases—of the Late Devonian and end-Triassic extinctions. These two extinctions seem especially difficult to separate from the effects of facies changes, although the near-extirpation of ammonoids and other taxa and an apparently global upheaval of reef

communities lend credibility to some kind of exceptional biotic turnover in both the late Devonian and latest Triassic (McGhee 1996; Page 1996; Hallam and Wignall 1997; Balinski et al. 2002; Copper 2002; Flügel 2002; Racki and House 2002; Stanley 2003). Some of the lesser extinction pulses in the Phanerozoic record may truly reflect variations in preservation rather than true extinction events (e.g., Smith 2001; Peters and Foote 2001; Foote 2003, 2005; Erwin 2004), and removing such artifacts may also tend to set the mass extinctions apart, although this effect needs to be evaluated quantitatively. The apparent continuity of Phanerozoic extinction intensities is therefore debatable at best, and probably obscures more about extinction processes than it reveals.

Selectivity

More important than extinction intensity from a macroevolutionary standpoint is the question of selectivity. A slowly growing set of analyses has found that many traits correlated with extinction risk in today's biota, and with paleontological background extinction, tend to be poor predictors of survivorship during mass extinctions. Factors such as local abundance, reproductive mode, body size and inferred generation time, trophic strategy, life habit, geographic range at the species level, and species richness, which have all been hypothesized or shown to be significant under "normal" extinction intensities, had little effect on genus survivorship during the K/T extinction and were unimportant in one or more of the other mass extinctions as well (Jablonski 1986a,b, 1989, 1995; Jablonski and Raup 1995; Smith and Jeffery 1998, 2000a; Lockwood 2003). (The fact that many of the neontological and microevolutionary patterns are expressed at the species level, whereas most paleontological data are drawn from genus-level data, is a concern only if a hierarchical view is already preferred over an extrapolationist one; under an extrapolationist view patterns should be damped but not qualitatively different across the biological hierarchy.)

One example of this contrast can be seen in marine bivalves, where epifaunal suspension feeders such as scallops have significantly shorter genus durations than infaunal suspen-

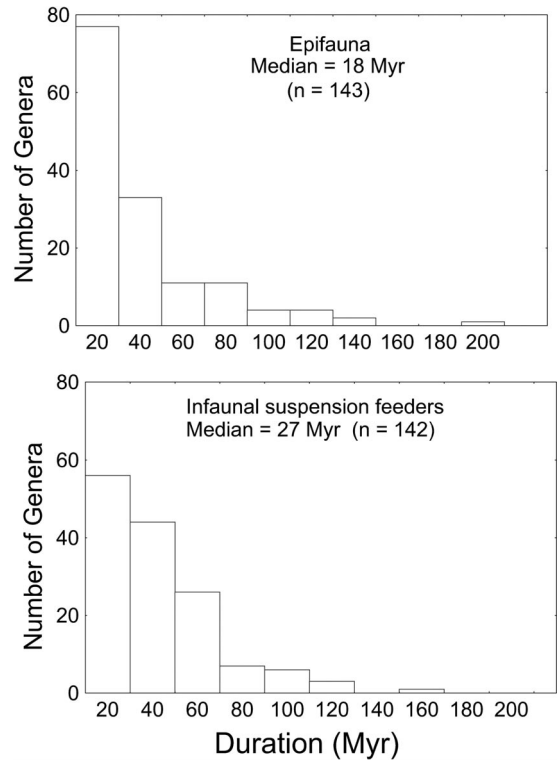


FIGURE 1. Epifaunal suspension-feeding bivalve genera (above) have significantly shorter genus durations than infaunal suspension-feeding bivalves (below) in the 140-Myr interval of background extinction leading up to the end-Cretaceous event (Mann-Whitney U -test: $P < 0.01$). As shown in Figure 2, this contrast disappears during each of the last three mass extinctions. (Data from the ongoing revision and ecological characterization of the bivalve portion of Sepkoski 2002 by D. Jablonski, K. Roy, and J. W. Valentine.)

sion feeders such as cockles in the 140-Myr interval between the end-Triassic extinction and the K/T boundary (Fig. 1). Although this is work in progress, the median durations differ by 50% and the frequency distributions differ significantly ($P < 0.01$), suggesting that the contrast is fairly robust (see also Aberhan and Baumiller 2003, and McRoberts' 2001 report of a smaller but equally significant difference in extinction rates between infauna and epifauna during the Triassic, albeit with a curious reversal in the Norian stage). These results should still be viewed cautiously, because the two functional groups differ mineralogically and thus in preservation potential: infaunal bivalves form less stable, exclusively aragonitic shells whereas the epifauna includes clades with more stable calcitic components. Poor

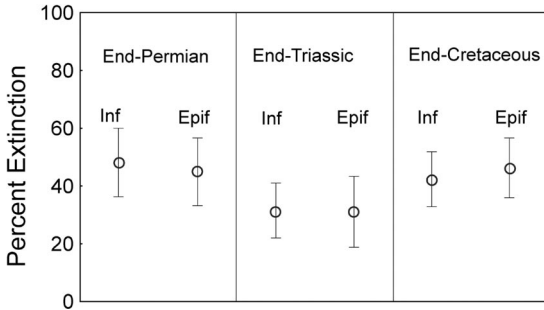


FIGURE 2. Genera of infaunal (Inf) and epifaunal (Epif) suspension-feeding bivalves do not differ significantly in extinction intensity during each of three extinctions: the end-Permian (Jablonski et al. unpublished), end-Triassic (McRoberts 2001), and end-Cretaceous (Jablonski and Raup 1995). (95% confidence intervals following Raup 1991c.)

preservation might impose lower taxonomic resolution on infauna and thus artificially inflate their durations. However, the contrast between mass extinction and background extinction times suggests that preservational effects do not overwhelm other factors (and see Kidwell 2005). The difference in durations disappears in the end-Permian, end-Triassic, and end-Cretaceous extinctions, where both functional groups suffer statistically indistinguishable extinction intensities (Jablonski and Raup 1995; McRoberts 2001; and a very preliminary analysis of end-Permian bivalve extinction) (Fig. 2).

A similar shift in genus survivorship patterns occurs in analyses of species richness, geographic range at the species level, and the interaction of these properties. For example, Late Cretaceous marine bivalve and gastropod genera that contained many, mainly widespread species tend to have significantly greater durations than genera consisting of few, spatially restricted species, and the other combinations tended to show intermediate values (Jablonski 1986a,b) (Fig. 3A). This makes intuitive sense and can readily be modeled in terms of clade demography (e.g., Raup 1985). However, these differences do not predict survivorship patterns during the end-Cretaceous extinction (Figs. 3B, 4) in the North American Coastal Plain (Jablonski 1986a,b) and elsewhere (Jablonski 1989). A partial list of analyses for other groups and events where

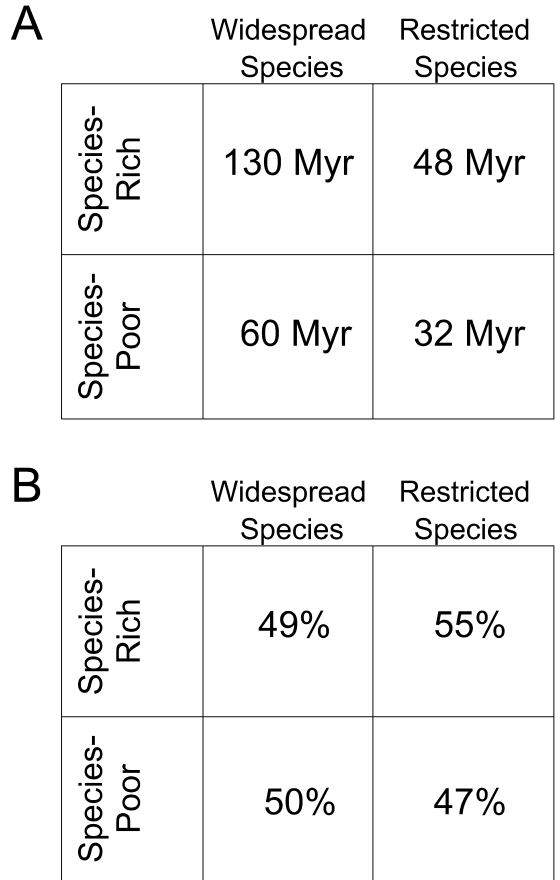


FIGURE 3. The interaction between species richness and geographic range at the species level in promoting genus survivorship, significant during (A) background times for marine bivalves and gastropods, is not apparent for (B) the end-Cretaceous mass extinction in the Gulf and Atlantic Coastal Plain. In A, values are median durations of genera; in B, values are extinction intensities. Species-rich defined as having three or more species in the study area; widespread as having at least 50% of species with geographic ranges >500 km in the study area; see Jablonski 1986b for details.

species richness was not a buffer against extinction is provided by Jablonski (1995).

Selectivity also shifts at the K/T boundary for developmental modes in marine invertebrates. The Late Cretaceous saw the independent evolution of nonplanktotrophic larvae in numerous gastropod lineages (Jablonski 1986c) and in five of the 14 orders of echinoids across a wide range of habitats and latitudes, presumably in response to pervasive changes in global climate or plankton communities (Jeffery 1997; Smith and Jeffery 2000a). However, the end-Cretaceous mass extinction was

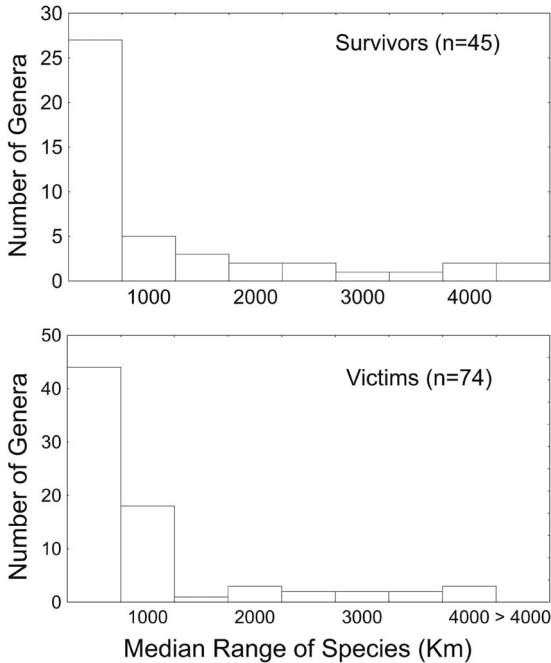


FIGURE 4. A new analysis of gastropods across the K/T boundary in the Gulf and Atlantic Coastal Plain shows no significant difference between the median geographic range of constituent species in victim and surviving genera; Mann-Whitney *U*-test: $P = 0.75$ (Jablonski unpublished).

nonselective with respect to larval types in both mollusks (Jablonski 1986b,c; Valentine and Jablonski 1986) and echinoids (Smith and Jeffery 1998, 2000a; Jeffery 2001). In this instance we can see that the selective regime operating immediately prior to the K/T event was inoperative across the boundary but re-

turned in its aftermath, judging by the early Cenozoic evolution of nonplanktotrophy in a diverse set of gastropod lineages and in at least three additional echinoid orders (Hansen 1982; Jeffery 1997; Smith and Jeffery 1998, 2000a). In contrast, trilobite genera inferred to undergo benthic development fared significantly better than those inferred to undergo planktic development during the end-Ordovician extinction (Chatterton and Speyer 1989), whereas Lerosey-Aubril and Feist (2003) suggested that planktic development favored trilobite survivorship in the late Devonian. This apparent inconsistency for trilobites at different extinction boundaries bears investigation, perhaps including further evaluation of the criteria for developmental modes.

Although these organism-, species-, and clade-level traits lose effectiveness as predictors of survivorship at mass extinction boundaries, survivorship is not completely random. Each event seems to exhibit some form of selectivity, but one factor that promoted survival for most major groups at each of the mass extinctions is broad geographic distribution at the clade level, regardless of species-level ranges (Table 1). Extinction intensities are significantly elevated even for widespread genera during mass extinctions but the differential between widespread and localized taxa remains (e.g., Jablonski and Raup 1995; Erwin 1996; Foote 2003). This provides, among other things, another line of evidence that extinction

TABLE 1. Extinction events and taxa in which broad geographic range at the genus level enhanced survivorship (updated from Jablonski 1995).

End-Ordovician bivalves	Bretsky 1973
End-Ordovician brachiopods	Sheehan and Coorough 1990; Sheehan et al. 1996; Brenchley et al. 2001; Harper and Rong 2001
End-Ordovician bryozoans	Anstey 1986; Anstey et al. 2003
End-Ordovician trilobites	Robertson et al. 1991
End-Ordovician marine invertebrates	Foote 2003
Late Devonian bivalves	Bretsky 1973*
End-Permian bivalves	Bretsky 1973
End-Permian gastropods	Erwin 1989, 1993, 1996†
End-Triassic bivalves	Bretsky 1973; Hallam 1981; Hallam and Wignall 1997: p. 148‡
End-Cretaceous bivalves and gastropods	Jablonski 1986a,b, 1989; Jablonski and Raup 1995
Exception: End-Cretaceous echinoids	Smith and Jeffery 1998, 2000a,b

* Rod and Lieberman (2004) found broad geographic range to promote species survivorship in the Late Devonian but did not provide genus-level analyses.

† Contrary to Smith and Jeffery's (2000b) misreading of these results.

‡ McRoberts and Newton (1995) report no effect of species-level geographic range on species survivorship for European end-Triassic bivalves, consistent with end-Cretaceous results, but they do not provide genus-level statistics.

events are not simply sampling artifacts involving the false disappearance of endemic taxa. It also suggests that McGhee's (1996: p. 125) statement that broad distribution had no effect on survivorship in the Late Devonian extinction(s) should be viewed cautiously: his only evidence is the severe losses suffered by major groups that had widespread members at the time, rather than a quantitative analysis of extinction intensities among geographic-range categories. On the other hand, Smith and Jeffery (1998, 2000a,b) failed to detect differential survivorship of K/T echinoid genera according to geographic range, an anomalous result perhaps deriving from their approach to translating cladistic analyses into a taxonomic classification. A spatially explicit version of Sepkoski and Kendrick's classic (1993) study is sorely needed, to explore how the protocol used to derive taxonomic structure from phylogenetic trees affects not only temporal but also spatial diversity patterns (see also Robeck et al. 2000).

Taken together, most analyses suggest that taxonomic survivorship during the Big Five mass extinctions approaches Raup's (1984) paradigm of "nonconstructive selectivity": not strictly random, but determined in many instances by features that are not tightly linked to traits honed during background times, and thus unlikely to reinforce or promote long-term adaptation of the biota ("wanton extinction" in Raup 1991b; see also Eble 1999; and Gould 2002: pp. 1035–1037, 1323–1324, and elsewhere). This injects what Gould (1985, 1989, 2002) would call a strong element of contingency into macroevolution: even well-established clades and adaptations could be lost during these episodes, simply because they were not associated with the features that enhanced survivorship during these unusual and geologically brief events. This removal of incumbents and the subsequent diversification of formerly marginal taxa is an essential element of the evolutionary role of the major extinctions (Jablonski 1986a,b,d, 2001; Benton 1987, 1991; Jablonski and Sepkoski 1996; Eldredge 1997, 2003; Erwin 1998, 2001, 2004; Gould 2002).

This emerging picture suggests that correlations may often masquerade as direct selec-

tivity. Because biological traits tend to covary, even across hierarchical levels, selection on one feature will tend to drag others along with it. For example, bryozoan taxa with complex colonies are generally more resistant than simple taxa to background levels of extinction but more extinction-prone during Paleozoic mass extinctions, an intriguing shift in apparent selectivity. However, colony complexity is also inversely related to genus-level geographic range, and so the actual basis for differential survival of bryozoan groups in the end-Ordovician extinction is unclear (see Anstey 1978, 1986; Anstey et al. 2003).

Even the often-cited claim for size-selectivity has proven to be questionable in many cases, and the potential examples that remain are complicated by (often nonlinear) covariation of body size with other organism- and species-level traits, from metabolic rate to local abundance to effective population size to genetic population structure to geographic range (Jablonski and Raup 1995; Jablonski 1996; Fara 2000; see also Brown 1995; Gaston and Blackburn 2000; Gaston 2003). For that matter, Fara (2000) argued that body size, diet, habitat, population size, and geographic range *all* covary in tetrapods, undermining attempts to pinpoint the key factor in taxonomic survivorship: was it modest body size, detritus-based food webs, freshwater habit, large population size, or broad geographic range? Large data sets that capture the full range of several variables, and multifactorial approaches that take into account polygonal and other nonlinear relationships, are required here.

Such correlations, whether via chance linkages or from well-tuned adaptive covariation, suggest that many selectivities apparent at the organismal level should be treated as possible indirect effects. For example, what was it about the end-Ordovician extinction that selected against broad apertural sinuses in snails (Wagner 1996) and multiple stipes in graptolites (Mitchell 1990; Melchen and Mitchell 1991); what aspect or driver of the end-Cretaceous extinction selected against schizodont hinges in bivalves, elongate rostra in echinoids, or complex sutures in cephalopods? All of these losses or severe declines

more likely represent correlations rather than direct causation, but they had long-term effects on the morphological breadth—and thus the future evolutionary raw material—of their respective clades, and additional examples are plentiful. Perhaps these phenotypes represent energy-intensive metabolisms (Vermeij 1995; Bambach et al. 2002) or taxa with narrow geographic ranges or physiological tolerances, but multifactorial analyses are needed to dissect cause from correlation. Novel methods for testing causation in observational data, developed mostly outside the biological sciences but with considerable potential wherever controlled experiments are impractical, should also be explored (e.g., Shipley 2000).

Part of the difficulty in understanding the role of extinction in macroevolution is that taxonomic extinction intensity need not map closely onto morphological or functional losses. Random species loss can leave considerable phylogenetic or morphological diversity, because evolutionary trees or morphospaces will tend to be thinned rather than truncated (e.g., Nee and May 1997; Foote 1993, 1996, 1997; Roy and Foote 1997; Wills 2001). Thus Smith and Jeffery (2000a: p. 192), finding no significant changes in morphological disparity of echinoids across the K/T boundary, argued that the extinction was neutral with respect to morphology, and Lupia (1999) made the same observation for angiosperm pollen. Of course, individual subclades may suffer selective extinction of certain morphologies even as their large clades show little overall pattern (e.g., Eble 2000 on K/T echinoids; Smith and Roy 1999 on Neogene scallops). Extreme taxonomic bottlenecks will also constrict morphospace occupation and functional variety, as in end-Paleozoic echinoderms (Foote 1999) and ammonoids (McGowan 2002, 2004a,b), if only by sampling error (e.g., Foote 1996, 1997; MacLeod 2002).

On the other hand, several analyses find strong selectivity, in the sense that more morphology, functional diversity, or higher-taxonomic diversity is lost than expected from purely random species removal in the fossil record (e.g., Roy 1996; McGhee 1999; Saunders et al. 1999; McGowan 2004a,b) and among endangered taxa today (Gaston and Blackburn

1995; Bennett and Owens 1997; McKinney 1997; Jernvall and Wright 1998; Russell et al. 1998; Purvis et al. 2000a,b; Cardillo and Bromham 2001; von Euler 2001; Lockwood et al. 2002; Petchey and Gaston 2002; Zavaleta and Hulvey 2004). These nonrandom patterns need not correspond to conventional taxonomic or functional groupings. For example, Triassic ammonoid extinctions are not selective with respect to the basic morphotypes within the clade, but they can leave survivors near the center or around the periphery of a multivariate morphospace, which is then filled in again during the evolutionary recovery phase (McGowan 2004a,b). In attempting to understand losses in morphospace or among higher taxa, indirect correlations with other selective targets such as geographic range again need to be tested (see also Roy et al. 2004). Such indirect selectivity can also arise via strongly unbalanced phylogenetic trees, in which random extinction can remove entire species-poor subclades while only thinning the more profuse ones (Heard and Mooers 2000, 2002; Purvis et al. 2000b). This general role of phylogenetic topology in survivorship patterns at mass extinctions, another form of nonconstructive selectivity, has barely been explored.

“Nonconstructive selectivity” implies survivorship that is indifferent, rather than antithetical, to many of the factors that promote success during background times. This indifference means that some “preadaptation,” or more properly exaptation, should occur by chance, when adaptations shaped during background times happen to improve a clade’s chances of surviving the particular stresses that triggered a given mass extinction. Statistically, selectivity patterns should not be entirely mutually exclusive during background and mass extinctions. For example, Kitchell et al. (1986) attributed the preferential survival of planktonic centric diatoms at the K/T boundary to the presence of a benthic resting phase selected for during background times by seasonal variations in light, nutrient levels, and other limiting factors (Griffis and Chapman 1988; see also P. Chambers *in* MacLeod et al. 1997, although these new data are averaged over 20 Myr of late Cretaceous–early Tertiary

time). Still needed is an analysis of diatom genus or species survivorship during background times relative to other plankton groups, and data on the relation of the resting spore habit to other aspects of diatom biology, including of course geographic range (for example, Barron [1995] noted that shelf species are more likely to have resting spores than are open-ocean species). The fact that no modern resting spores have been shown to remain viable for more than a few years (Hargraves and French 1983; Peters 1996; but see Lewis et al. 1999 for decadal viability) requires an especially sharp and short-lived K/T perturbation for this feature to have played a direct role in taxon survivorship (P. Chambers *in* MacLeod et al. 1997; see also Racki 1999: p. 113). On the other hand, early reports of preferential survivorship of marine detritivores at the K/T boundary, also thought to represent exaptation to an impact-driven productivity crash, have not been corroborated (see Hansen et al. 1993; Jablonski and Raup 1995; Smith and Jeffery 1998; Harries 1999; also Levinton's 1996 review of the coupling of marine planktic and detrital food webs).

Chance exaptation to extinction drivers, retention of morphological and functional breadth when extinction is random at the species level, and the persistence of diffuse ecological interactions such as predation and tiering are just a few of the factors that might explain why the evolutionary clock is not fully reset by mass extinctions. Many large-scale trends and higher taxa persist across the major boundaries, but pinpointing the reasons for that persistence or other aspects of cross-extinction evolutionary trajectories is difficult. For example, the setbacks suffered by many evolutionary trends that cross extinction boundaries (see Jablonski 2001) might be attributable to direct selectivity against the trait that was being maximized under low extinction intensities; to indirect selection owing to correlations with a disfavored trait such as narrow geographic range; or to high extinction intensities alone, with random extinction—relative to the focal trait—clearing recently invaded and thus sparsely occupied morphospace.

Recoveries

The evolutionary role of mass extinctions is not simply to knock the world into a new configuration. The extinction event does have its victims and survivors, and this raw material is crucial in shaping the post-extinction biota. However, the evolutionary novelties and ecological restructuring that typify post-extinction intervals, including the sorting of the survivors into winners and losers, may be as important as the extinction filter in determining the long-term trajectory of individual clades and the nature of the post-extinction world. Recovery intervals generally appear to be significantly longer than the extinction events that precede them (e.g., Erwin 1998, 2001, 2004; and see Sepkoski 1984, 1991a), and if this is true then the greater duration enhances the potential for sorting and biased origination to redirect evolutionary trajectories. But we still know little of the factors controlling recovery dynamics or the evolutionary directions they take.

The comparative study of recoveries is hampered by their notorious association with intervals of poor sampling and preservation. A few evolutionary systems, such as planktic foraminifera after the end-Cretaceous event, lend themselves to detailed analysis, but the fine structure of recoveries and even the timing of evolutionary pulses are generally difficult to retrieve from more than a few localized regions. As Erwin (2001) discussed, geochemical proxies and biomarkers can partially reconstruct short-term ecosystem dynamics (e.g., D'Hondt et al. 1998; Joachimski et al. 2002; and a host of stable-isotope studies), but in our present state of knowledge these tools are vague regarding the behavior of single clades.

Just as survivors of mass extinctions are difficult to predict from pre-extinction successes, long-term post-extinction successes are difficult to predict from the survivors of mass extinctions. Recovery intervals are famously important in opening opportunities for the diversification of once-marginal groups, the mammals and the dinosaurs being the classic example, but not all survivors are winners. Recoveries need not involve an across-the-

board expansion of a surviving clade in morphospace. They can instead involve only subregions of the occupied morphospace or be channeled in specific directions (e.g., Dommergues et al. 1996, 2001; Lockwood 2004; McGowan 2004a); in extreme cases, taxa can weather a mass extinction only to disappear a few million years later, or fall into marginal roles (Jablonski 2002). We lack predictive insight into why different clades or subclades follow different trajectories during the recovery phase, however. A simple probabilistic model would treat post-extinction success as a function of the severity of the clade's bottleneck at the boundary: the probability of avoiding stochastic extinction or marginalization in the post-extinction world should be positively related to the number of surviving subtaxa within the clade. However, the post-extinction persistence of the 182 Paleozoic marine invertebrate orders recognized by Benton (1993) is unrelated to the size of the bottleneck suffered by each order, measured in terms of the number of genera known or inferred to have survived a given extinction (Jablonski 2002). Sampling remains a concern for such an analysis, and of course direct or indirect selectivity on the morphological or functional diversity of clades need not be closely tied to raw numbers of survivors. Nonetheless, the data give no support to a model where the success or failure of surviving clades is set by how the clades fared at the extinction event itself. Much more is going on during the recovery phase.

Most analyses have been based on global compendia or local sections and single basins, but interregional comparisons have begun to explore the spatial fabric of recoveries. For example, the molluscan recovery from the end-Cretaceous extinction unfolds differently in North America relative to the other regions studied by Jablonski (1998). The short-lived evolutionary burst of what Hansen (1988) termed "bloom taxa" in North America cannot be seen in northern Europe, north Africa, or India and Pakistan (Fig. 5), and the relative roles of local diversification and invasion also varied among these regions (Jablonski 1998, 2003; see also Heinberg 1999; Stilwell 2003: p. 324; and see Wing 2004 for hints of spatial var-

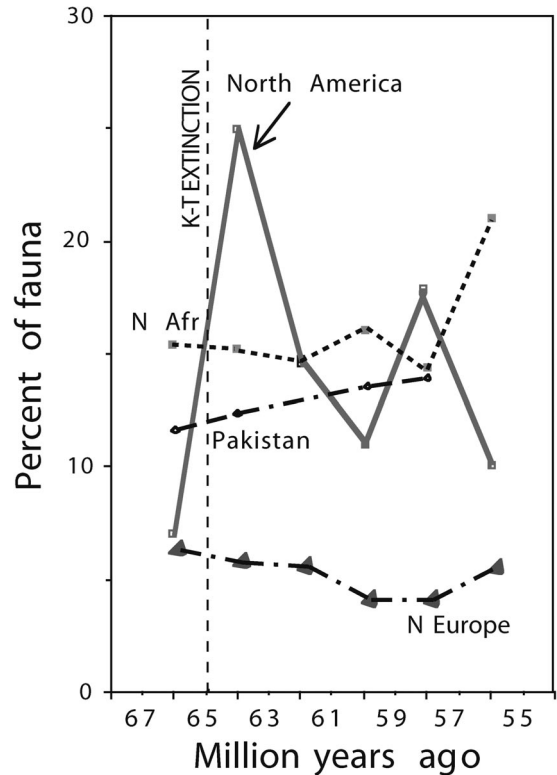


FIGURE 5. Geographic variation in the behavior of "bloom taxa" after the end-Cretaceous mass extinction. The molluscan groups that abruptly diversify and decline immediately after the extinction in North America show significantly less volatile evolutionary behavior in three other regions (North Africa, Pakistan-India, and northern Europe), as a proportion of species in each fauna as shown here, and in raw numbers. (From Jablonski 2003; for details and statistical confidence limits see Jablonski 1998.)

iation in the plant recovery). These regional differences open a host of new questions on the ecological, biogeographic, and evolutionary assembly of post-extinction biotas. Dissecting the spatial fabric of recoveries, as Miller and colleagues (Miller 1997a, 1998; Miller and Mao 1995, 1998; Novack-Gottshall and Miller 2003) have done so effectively for the Ordovician radiations, is a research direction likely to be full of surprises.

Net diversification rates accelerate for some clades after mass extinctions, providing ample evidence for the macroevolutionary role of incumbency effects and their removal (Sepkoski 1984; Van Valen 1985a; Benton 1987, 1991; Miller and Sepkoski 1988; Patzkowsky 1995; Jablonski and Sepkoski 1996; Erwin 1998,

2001; Jablonski 2001; Foote 1997, 1999, 2003). The extent of the evolutionary opportunities opened by extinction events must depend at least partly on the magnitude of the event (Sepkoski 1984, 1991a; Eldredge 1997, 2002; Solé et al. 2002), but this generalization derives mainly from end-member comparisons and rather simple models. As discussed above, the degree of phylogenetic, morphological, or functional clustering of losses should also be important in giving survivors scope for evolutionary diversification and innovation (e.g., Valentine 1980; Erwin et al. 1987; Valentine and Walker 1987; Brenchley et al. 2001; Sheehan 2001). However, we lack a well-developed calculus for such analyses, and a literal reading of patterns can be misleading or at least open to multiple interpretations. For example, diversification pulses might also be artificially heightened or depressed and smeared by sampling failure in post-extinction intervals (Foote 2003); comparative, spatially explicit analyses of clades having different post-extinction dynamics and different sampling regimens would help to evaluate this effect. The provocative finding that bivalves and mammals produce more new genera relative to estimated speciation rates during post-extinction recoveries than expected from background times (Patzkowsky 1995) should be tested from this sampling standpoint, but it also suggests a much-needed hierarchical, genealogical approach to the dynamics of morphospace occupation. Judging by the few data available, larger divergences or rates of apomorphy acquisition tend to be more clearly concentrated in initial radiations than in recoveries, but other authors have reported post-extinction shifts in the average magnitude of morphological divergence per branchpoint (Anstey and Pachut 1995; Wagner 1995, 1997; Foote 1999, Eble 2000).

Hierarchy

Mass extinctions do appear to disrupt “normal” sorting processes, rendering life’s trajectory difficult to predict from the patterns that prevail through the bulk of geologic time. Gould (1985, 2002) codified this view in terms of three evolutionary tiers; Raup (1984, 1991b; 1994) and Jablonski (1986a–d, 1995) were less

formal but explored these effects along similar lines, all undermining a purely extrapolationist approach to macroevolutionary patterns.

Some of the debate about the limits of the extrapolationist paradigm probably stems from the application of the term to two different concepts. Mass extinctions demonstrably challenge empirical extrapolationism, i.e., the predictability of long-term outcomes from observations over ecological and short-term geological timescales; mass extinctions so disrupt evolutionary processes that the fates of taxa cannot be predicted from the behavior of populations or species over 95% of geologic time. However, Sterelny and Griffiths (1999) discussed a “fall-back” position that might rescue another version of extrapolationism. If extrapolation simply requires that organism-level selection of any kind—along with the other canonical forces of microevolution—is the prime mover of evolution (a view that might be termed “theoretical extrapolationism,” as opposed to a hierarchical view of evolution operating on multiple levels simultaneously), then mass extinctions could still simply represent a relatively brief and intense change in the direction of selection. Under this fall-back position, which goes beyond predictability of outcome to continuity of process in the broadest sense, “Mass extinction by itself, however important, is no threat to the received view of evolution. Mass extinction only undercuts it if it provides crucial evidence for species selection or some other high-level mechanism” (Sterelny and Griffiths 1999: p. 306; see also Grantham 2004).

The most pervasive rule we have for mass extinction selectivity, namely the preferential survival of widespread genera, may be evidence for just such a high-level mechanism and thus support for the hierarchical view (Jablonski 1986a–d, 2000; Gould 2002). An extrapolationist approach to genus-level geographic ranges and survivorship would hold that widespread genera are simply collections of widespread, successful or ecologically generalized species, so that selectivity of genera according to their geographic ranges reflects the capabilities of their component parts.

Several lines of evidence falsify this extrapolation of organismic or species-level proper-

ties to the genus (clade) level in this context. As noted above, Jablonski (1986a,b) showed that molluscan genus survivorship at the K/T boundary was unrelated to the geographic ranges of the species within clades. That analysis found no significant difference between the frequency distributions of the geographic ranges, or the median geographic ranges, for all of the species within the surviving genera and those species within the victims (Figs. 3B, 4). The geographic ranges of species are subject to serious sampling problems and the recorded ranges are surely underestimates (Koch 1987; Jablonski 1987), but the nonparametric statistics used here, based on rank order among species ranges rather than absolute values, should be more robust to such sampling biases (Jablonski 1987; Jablonski and Valentine 1990; Gaston et al. 1996; see also Marshall 1991; and recall that Spearman's coefficient gives greater weight to pairs of ranks that are further apart and downplays the effects of ranks that are close together—see Sokal and Rohlf 1995: p. 600). Indirect evidence in the same direction also comes from recent findings that genus survivorship is unrelated to abundance at the K/T boundary for plants and marine bivalves (Hotton 2002; Lockwood 2003; Wing 2004), given the significant relation between species-level geographic range and abundance recorded for many extant groups (Gaston and Blackburn 2000 and references therein). Nor is the basic extrapolationist premise supported for living marine bivalves. For the best-documented marine molluscan biota in the world, on the eastern Pacific shelf from Point Barrow, Alaska, to Cape Horn, Chile, we find no significant relation between the geographic range of genera and the median geographic ranges of their constituent species (Fig. 6) (such analyses of nested taxa are not straightforward, owing to the autocorrelation imposed by the inability of species to be more widespread than their genera).

These paleontological data seem to be telling us, more generally, that the geographic ranges of genera are decoupled from the ranges or tolerances of their constituent species. A reasonable expectation might be that widespread genera consist mainly of environmen-

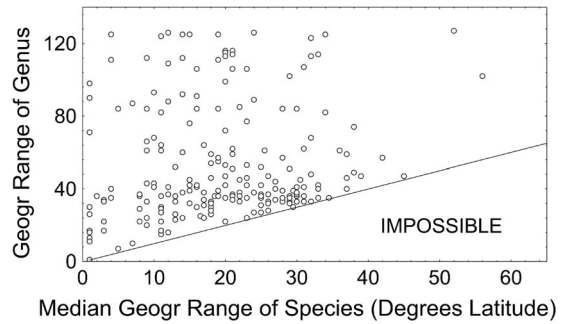


FIGURE 6. In living eastern Pacific marine bivalves, the geographic ranges of genera (in degrees latitude) cannot be predicted by the median geographic ranges of their constituent species ($n = 213$ genera, Spearman's $r = 0.17$; not significant). The lower right corner of the graph represents a field of impossible combinations: species cannot be more widespread than their genera (Jablonski, Roy, and Valentine, unpublished); statistical significance was assessed by resampling the data, using 10,000 repetitions where impossible combinations were discarded with replacement.

tally tolerant, high-dispersal, ecologically successful or generalized species that also have broad geographic ranges, so that selectivity of genera according to their geographic ranges simply occurs in the extrapolationist mode. But this does not appear to be the case: the paleontological evidence is not consistent with such an argument and a more direct analysis of present-day molluscan biogeography undermines the basic extrapolationist premise.

In this very concrete sense, geographic range at the genus level is an emergent property. Selectivity during mass extinctions evidently operates directly on the geographic range of the genus and is indifferent to the properties of the component parts at lower hierarchical levels (here, the geographic ranges of species and all of the organismic and species-level features that set those ranges). This difference across the hierarchy implies that geographic range can be an emergent property of clades, at least at the level traditionally ranked as genera, by the same criterion that suggests it can be an emergent property of species (Jablonski 2000, drawing on such related philosophical approaches as multiple-realizability, screening-off, and non-aggregativity; see Brandon 1982, 1988; Brandon et al. 1994; Wimsatt 2000). Such an argument raises the question: what actually determines geographic range at the clade level? If it was sim-

ply time since origination (Willis 1922; Gaston and Blackburn 1997; Miller 1997b), then we might expect a simple positive relation between taxon survivorship and taxon age rather than some form of Van Valen's Law (see Van Valen 1973, 1985b, 1987; Gilinsky 1994: p. 453). Dispersal ability and ecological strategies of constituent species must play some role, but interactions with biogeographic context, clade history, and other factors serve to decouple geographic range at the two levels. There are simply too many ways for a genus to become widespread—each apparently equivalent at a mass-extinction event, although this needs further exploration—for smooth extrapolation to apply.

None of these arguments require, or even suggest, that natural selection at the organismal level becomes inoperative during mass extinctions. Instead, they show that selectivity at a higher focal level yielded a predictable, coherent pattern whereas processes at the lower level often did not. Because geographic range at the clade level is probably not heritable as it is for species (Jablonski 1986b, 1987; Hunt et al. 2005—although the results and discussion of Miller and Foote [2003] could be taken to imply otherwise), mass extinctions may best be viewed as selective filters that are nonconstructive in part because they are noncumulative. Without heritability, clades will drift away from the biogeographic and other attributes that got their survivors through the mass extinction and thus become increasingly vulnerable again over time (an argument consistent with Stanley's [1990] "delayed recovery" hypothesis for extinction periodicity).

This is not to say that clade attributes related to extinction vulnerability cannot be stable over long intervals. One attractive explanation for the Phanerozoic decline in background extinction is that class- or order-level turnover rates are set early in the history of each group, so that the overall trend reflects sorting of higher taxa as the most volatile clades drop out of the biota (Sepkoski 1984, 1991a,b, 1999; Valentine 1990, 1992; Gilinsky 1994). The differential sensitivity of high-turnover, Paleozoic-fauna classes and low-turnover, Modern-fauna classes to the major extinction events (Sepkoski 1984, 1991a, 1999; Raup and Boya-

jian 1988) is another, little-explored selectivity pattern that, as Valentine (1990, 1992) stated, probably bears little relation to ecological adaptedness but nonetheless reflects coherent macroevolutionary processes. This leads to a fascinating set of observations of discordant behavior across hierarchical levels: (1) the relative volatility of class-level taxa during background times correlates with their respective losses during mass extinctions (Sepkoski 1984); (2) subtracting the median extinction rate for each class brings the mass extinction intensities of each to similar magnitudes, so that the most volatile classes do not actually suffer disproportionately, even though each class has a background extinction history more distinct from the others than expected by chance (Raup and Boyajian 1988); and (3) mass extinction selectivity *within* the classes is difficult to predict from background survivorship patterns, so that the evolutionary process at the species and genus level is disrupted and rechanneled by the major extinction events.

Conclusion and Outlook

Mass extinctions have evolutionary effects beyond a simple surge in extinction intensity: survivorship is not strictly random, and selectivity patterns change, so that the rules of extinction and survival are altered for a (geologically) brief time. Because the most pervasive selectivity pattern resides at the clade level, mass extinctions are a challenge to both empirical and theoretical extrapolationism. Evolutionary analyses of mass extinction therefore require a hierarchical framework that incorporates episodic shifts in the intensity and direction of selection at multiple hierarchical levels. Such an approach to the shaping of biological diversity would engender a macroevolutionary theory that is neither rigidly deterministic nor purely stochastic, and would yield a richer understanding of the long-term processes that have shaped clades and biotas.

Plenty of problems remain, of course, and these extend well beyond testing the generality of the patterns documented thus far. To list just a few:

1. The comparison of background and mass

extinction has very logically focused on single events and their immediately adjacent time bins. However, we do not know whether a fuller analysis across extinction events of differing intensities (mindful of the secular trend in background extinction mentioned earlier) would reveal a threshold effect for the shift in selectivity seen at mass extinction boundaries, or a more mixed or gradational change (see McKinney 1995 for a pioneering effort in this direction). Thresholds, if they exist, may be clade specific: volatile groups such as ammonoids might be pushed into a mass extinction selectivity regime while more phlegmatic groups such as bivalves and echinoids are relatively unfazed. This suggests that second-order extinction events, say the Eocene/Oligocene or the mid-Devonian extinctions, may prove to be a predictable, quantitative mix of background and mass extinction. Such an effect would not undermine a hierarchical view, as the differences in species-level and clade-level selectivity would still be a basic component of the evolutionary process, but we would have a deeper insight into how extinction intensity per se scales to the shift in extinction rules seen for the largest perturbations. Differences in survivorship between widespread and endemic genera have been recorded in second-order extinction events and probably hold even during background times (Jablonski 1995; Aberhan and Baumiller 2003). This suggests that the geographic-range factor is always at work at the clade level, but that it becomes most important and clearcut as the array of factors influencing genus duration during normal times dwindles in the face of heightened extinction intensities. More intense extinctions may prove, as a general rule, to be less selective (Jablonski 1986a,b,d, 1995; also Bannerjee and Boyajian 1996; Aguirre et al. 2000; Aberhan and Baumiller 2003), an argument that may also explain the failure of intrinsic factors to predict extinction risk in the most heavily stressed elements of the modern biota, such as freshwater fishes and Australian marsupials (Duncan and Lockwood 2001; Fisher et al. 2003).

2. The imperfect equivalency of taxonomic, morphologic, and functional diversities (see for example Foote 1996; Hulsey and Wainwright 2002; Valentine et al. 2002; Roy et al. 2001, 2004; Neige 2003) suggests that we have much to learn about the scope for indirect effects of extinction—i.e., the termination of genealogical units—on the array of adaptations that are lost or persist to be the springboard for the recovery process, and on the ecological impact of a given extinction intensity (e.g., Ives and Cardinale 2004; Solan et al. 2004; Wootton 2004; Zavaleta and Hulvey 2004). A deeper, predictive understanding of when these three aspects of diversity tend to correspond and when they diverge (see Foote 1996, 1997, 1999; Wills 2001, for a strong start) and the consequences of selectivity in one aspect on the extinction and recovery dynamics of the other two would shed fresh light on the role of contingency in evolution (Gould 2002).
3. We have barely begun to decipher the rules of successful recovery. As with the extinctions themselves, the emergence of winners from among the survivors might be stochastic, or governed by a set of recovery-specific rules, or dominated by processes prevalent during background times. The inordinate production of evolutionary novelties during recovery intervals suggests that post-extinction dynamics do not simply involve an immediate return to business as usual. This probably represents an especially fruitful area at the intersection of macroevolution and ecology (and see Foote 1999 for reasons to keep developmental biology in the mix). As with other diversifications—most famously the Cambrian explosion of metazoans—the cessation of the recovery phase, however defined (Erwin 1998, 2001, 2004), is potentially as interesting an area of inquiry as its onset.
4. The spatial fabric of extinctions and recoveries needs to be explored more rigorously, and in a comparative framework. If global analyses incorporate spatially explicit data, we will have a much better chance of distinguishing facies effects and regional variation in sample quality or density from bi-

otic pattern. Predictive models for the relative roles of local diversification and biotic interchange in the recovery of biodiversity (taxonomic, morphologic, and functional, as discussed above) may have more than academic interest as the present-day biota buckles under human pressure (see Jablonski 2001). The ongoing debate on whether Lazarus taxa represent sampling failure within local assemblages or localized persistence elsewhere (e.g., Jablonski 1986a; Wignall and Benton 1999; Fara 2001; Smith 2001; Twitchett 2001; Rickards and Wright 2002) is just one facet of the spatial dynamics of extinction and recovery.

Despite all of these unknowns and challenges, and I could list many more, the shared survivorship patterns among mass extinctions suggests that we are beginning to pinpoint general biological principles of survivorship and recovery. The K/T and Permo-Triassic events probably had different causes, but the similarities in biodiversity dynamics are all the more intriguing and biologically important for that reason. And as Gould (2002) forcefully argued, rare but intense extinction events under the “different rules” regime, imposed simultaneously on diverse clades, represent distinctive mechanisms operating on a distinctive scale across hierarchical levels. Mass extinctions and recoveries are far from being the entire evolutionary show, but they are vital as windows into the behavior of clades and ecosystems under extreme pressure and its aftermath. A more complete and effective understanding of the evolutionary process must incorporate these major episodes in the history of life.

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