PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 1989 **325**, 357-368
doi: 10.1098/rstb.1989.0093

Phil. Trans. R. Soc. Lond. B **325**, 357–368 (1989)
Printed in Great Britain

The biology of mass extinction: a palaeontological view

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Extinctions are not biologically random: certain taxa or functional/ecological groups are more extinction-prone than others. Analysis of molluscan survivorship patterns for the end-Cretaceous mass extinctions suggests that some traits that tend to confer extinction resistance during times of normal ('background') levels of extinction are ineffectual during mass extinction. For genera, high species-richness and possession of widespread individual species imparted extinction-resistance during background times but not during the mass extinction, when overall distribution of the genus was an important factor. Reanalysis of Hoffman's (1986) data (*Neues Jb. Geol. Paläont. Abh.* **172**, 219) on European bivalves, and preliminary analysis of a new northern European data set, reveals a similar change in survivorship rules, as do data scattered among other taxa and extinction events. Thus taxa and adaptations can be lost not because they were poorly adapted by the standards of the background processes that constitute the bulk of geological time, but because they lacked – or were not linked to – the organismic, species-level or clade-level traits favoured under mass-extinction conditions. Mass extinctions can break the hegemony of species-rich, well-adapted clades and thereby permit radiation of taxa that had previously been minor faunal elements; no net increase in the adaptation of the biota need ensue. Although some large-scale evolutionary trends transcend mass extinctions, post-extinction evolutionary pathways are often channelled in directions not predictable from evolutionary patterns during background times.

INTRODUCTION

Extinction has long been recognized as an integral part of the Darwinian equation. Mass extinctions are the most spectacular manifestations of this process, but for many reasons they are particularly problematical as evolutionary factors. Our knowledge of victims and survivors is still painfully sketchy, in terms of taxonomic composition, biological attributes or phylogenetic histories. The details of the timing and magnitudes of mass extinction events are still uncertain, and sampling and preservation can obscure or artificially generate patterns around critical extinction intervals (see Raup, this symposium). Even the definition of mass extinction, and thus the number and distribution of events through the Phanerozoic, is controversial. Nevertheless, the study of extinction has advanced greatly over the past decade, and some generalizations and suggestions for further research are feasible. Here, I focus on the five major mass extinctions of the Phanerozoic fossil record, which are generally agreed upon as significant events in the history of life (see Jablonski (1986*a*), Flessa *et al.* (1986) and Sepkoski (1986) for overviews), and will say little about driving mechanisms. Instead, I discuss evidence suggesting that mass extinctions remove taxa generally not at risk during times of low ('background') extinction intensity. Taxa or traits that are successful and extinction resistant during most of geological time thus may be lost during mass extinctions, and evolution channelled in directions not predictable from patterns prevalent during background times.

Patterns of extinction and survival

Neither background nor mass extinction is random. Palaeontologists have long argued, on empirical or theoretical grounds, that certain taxa are relatively extinction resistant (usually to background extinction) because of one set or another of functional, ecological or biogeographical attributes. For example, Alexander (1977) found that Palaeozoic brachiopod genera that cemented to the substratum were geologically longer lived than those attached by a pedicle; Levinton (1974) found that genera of deposit-feeding bivalves were geologically longer lived than suspension-feeders; Hansen (1980) and Jablonski (1986*c*) found that gastropod species with high larval dispersal capability were geologically longer lived than species with low dispersal. (See Ward & Signor (1983) for an excellent demonstration, in this case for ammonites, that observed differences in extinction rates need not be attributable to differences in morphological complexity, as has sometimes been suggested.) Studies such as these, although valuable, commonly combine background and mass extinctions without checking for differences between the two (exceptions are discussed below). In such instances it is tempting to regard observed patterns as typical of the background times that constitute the bulk of geological record, but explicit analyses are clearly needed.

Recently, some workers have compared mass and background extinctions and found differences not only in numbers of taxa lost, but in kinds of taxa lost. For late Cretaceous molluscs of the North American Coastal Plain, Jablonski (1986*b*) found that in background times, high species richness (defined as having three or more species in the last 6 Ma of the late Cretaceous of the area) and broad geographical range at the species level enhanced survivorship at the genus level. These observations are not surprising: genera whose species are many or widespread will be more likely to avoid total extinction in the face of most environmental perturbations than will genera with few species or whose species are each restricted to small areas. The relation between geographical range and duration at the species level has been repeatedly documented (see, for example, Jackson 1974; Hansen 1980; Jackson *et al.* 1985; Hoffman 1986; Jablonski 1986*b*, *c*, 1987), and this might be expected to translate into greater survival at the genus level as well (as shown by Jablonski (1986*b*, figure 2B): overall, genera composed mainly of widespread species have significantly greater median durations than genera composed mainly of restricted species).

Species-level relations between geographical range and geological duration might be an artefact of preservation and sampling (see, for example, Koch (1987); Russell & Lindberg (1988)), but for this particular assemblage of Cretaceous species, a comparison of patterns among taxa with different preservation and collection potential suggests that the relation is not artefactual (Jablonski 1988). If the apparent relation was simply an artefact, then the slope of the regression between range and duration should progressively decrease with increasing robustness and abundance of taxa; that is, a perfect fossil record would yield zero slope, and the worse the record, the steeper the slope. This null expectation was not met for Coastal Plain molluscs.

In contrast to background patterns, neither geographical range of constitutent species nor species richness played a significant role in the survival of genera during the end-Cretaceous mass extinction. The frequency distribution for geographical ranges of species within surviving genera was statistically indistinguishable from that of species within extinct genera: genera were not saved by the magnitudes of individual species ranges (see Jablonski 1986*b*, figure 2E, F).

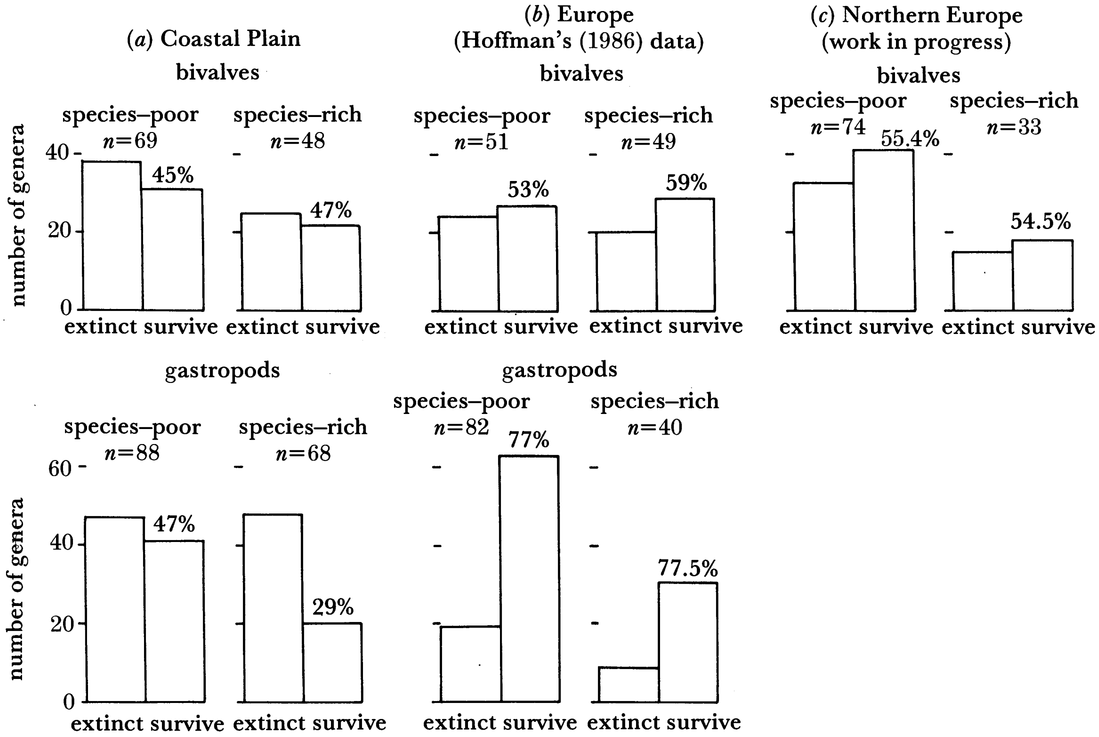

Figure 1. Species richness did not play a significant role in survival of genera during the end-Cretaceous mass extinction, for bivalves and gastropods of the North American Coastal Plain, Europe (re-analysing Hoffman's (1986) data), and Northern Europe (new analysis, still in progress). For example, 45 % of the 69 species-poor Coastal Plain bivalve genera, and 47 % of 48 species-poor genera, survived. Note that the only statistically significant difference between species-rich and species-poor groups, for the Coastal Plain gastropods, is in the opposite sense to expectations during background extinction.

Further, for bivalves, about 47 % of the species-rich genera and 45 % of the species-poor genera survived (viewed another way, 40 % of the victims and 42 % of the survivors were species rich) (see figure 1*a* and table 1). Even more strikingly, significantly fewer species-rich gastropod genera survived than did species-poor genera, reversing the survivorship pattern seen for the preceding 16 Ma (binomial probability = 0.0018).

A synergistic interaction between species richness and geographical range of constituent species occurs during background times. Thus, for North American molluscs, species-rich genera composed mainly of widespread species have significantly lower extinction rates than species-poor genera composed of geographically restricted species, and the other combinations exhibit intermediate values (Jablonski 1986*b*). This interaction is also lost during the end-Cretaceous mass extinction: 59 % of the ordinarily most durable group became extinct, as did 56 % of the ordinarily most vulnerable group (Jablonski 1986*b*).

Hoffman (1986) attempted a similar analysis for European molluscs, based on the compilation of Nevesskaya & Solovyev (1981), and failed to find the change in survival patterns. There are problems with these data: for example, the Soviet authors synonymized many genera considered to be useful by other workers. For example, species commonly placed within the scallop genera *Aequipecten*, *Camptonectes*, *Merklinia*, and *Mimachlamys* were all relegated to *Chlamys* (*Camptonectes perlucidus* Sobetski does appear in the list, but this species is repeated under *Chlamys*). Nevertheless, I reanalysed these Campanian–Maastrichtian data with only two modifications: (1) because species richness per genus tends to be a highly skewed

Table 1. Species-rich genera were equally represented among victims and survivors of the end-Cretaceous extinction

(Note that the statistically significant result for Coastal Plain gastropods is in the opposite sense to expectations during background extinction.)

	species-rich genera		
	victims	survivors	significance (binomial)
Coastal Plain (Jablonski 1986*b*)			
bivalves	40 %	42 %	n.s. ($0.30 < p < 0.40$)
gastropods	50 %	33 %	$p < 0.005$
Europe (Hoffman 1986)			
Campanian & Maastrichtian species			
bivalves	45 %	52 %	n.s. ($0.30 < p < 0.40$)
gastropods	32 %	33 %	n.s. ($0.40 < p < 0.50$)
Maastrichtian species only			
bivalves	46 %	44 %	n.s. ($0.30 < p < 0.40$)
gastropods	29 %	31 %	n.s. ($0.30 < p < 0.40$)
northern Europe			
bivalves	31.25 %	30.50 %	n.s. ($0.40 < p < 0.50$)

distribution, I avoided comparisons of mean values, which can be deceptive; (2) I excluded 'wastebasket' *sensu lato* (s.l.) genera, broadly defined taxonomic categories with little phylogenetic significance (e.g. *Lucina* s.l., *Cardium* s.l., '*Turbo*' s.l., '*Natica*' s.l. (their quotes)). Following these conventions, I found no significant difference between survivorship of species-rich and species-poor marine genera (see figure 1*b* and table 1). About 53 % of the species-poor bivalves and 59 % of the species-rich bivalves survived (not significant, binomial probability = 0.30). Among gastropods, 76.8 % species-poor genera and 77.5 species-rich genera survived (not significant (n.s.), binomial probability = 0.40). Finally, the frequency distributions of species richnesses of victims against survivors were not significantly different (Kolmogorov–Smirnov tests, $p > 0.50$). The same results obtain if only Maastrichtian species are used: for bivalves (96 genera) 59.3 % of the species-poor genera and 59.5 % of the species-rich genera survived, and for gastropods (85 genera) 79.7 % of the species-poor genera and 80.8 % of the species-rich genera. Hoffman's (1986) data for European molluscs, then, actually corroborate the North American results.

Preliminary analysis of my own compilation of northern European bivalve species also supports the North American results rather than Hoffman's conclusions. Of the 107 genera for which I have data so far (figure 1*c* and table 1), 55.4 % of the species-poor genera survived, and 54.5 % of the species-rich genera survived, again not a significant difference.

Despite the failure of formerly extinction-resistant features such as species richness, the end-Cretaceous extinction was not simply random. For North American molluscs, genera distributed outside the Coastal Plain study area had significantly higher probability of surviving than did genera endemic to that region. For bivalves, 55 % of the widespread genera but only 9 % of the endemic genera survived; for gastropods 50 % of the widespread genera survived but only 11 % of the endemic genera survived (see Jablonski (1986*b*) for details and statistical treatments). As noted above, geographical range at the species level played no role in survivorship, but geographical range at the clade level did: a selectivity manifested at a different hierarchical level from those characteristic of background times. Clade geographic range may indeed be a hedge against background extinction as well (this is difficult to demonstrate, because most studies average background and mass extinction situations), but this factor becomes tantamount during the mass extinctions.

The role of endemism cannot yet be assessed in the northern European data, simply because only 5 of 107 bivalve genera analysed so far were endemic to the area in the latest Cretaceous. The scarcity of endemics in north European molluscs (or conversely, the relatively large number of Coastal Plain endemics) may be an artefact of the relatively poor preservation typical of most north European localities relative to those of North America, or it could be a genuine reflection of the nature of the biogeographical barriers defining the respective provinces. Further investigations should clarify these matters, and a quantitative rather than binary biogeographical treatment should be useful.

The vulnerability of endemic genera during mass extinctions has been recorded for other groups and extinction events. Bretsky (1973) found that endemic bivalve genera diversified during background times but suffered disproportionately during the end-Ordovician, late Devonian, end-Permian and end-Triassic events. According to Fortey (1983) and Westrop & Ludvigsen (1987), trilobite extinction events that define the early Palaeozoic biomere boundaries also preferentially removed endemics.

Anstey's (1978, 1986) results for Palaeozoic bryozoans provide some intriguing parallels with end-Cretaceous molluscs. Morphologically simple bryozoan genera (interpreted as ecological generalists, and tending to be species-poor; see also Jablonski (1986*b*, p. 131)) exhibit fairly steady extinction rates through the Palaeozoic; in contrast, morphologically complex genera (inferred specialists that tend to be species rich) have lower background extinction rates but suffer greater losses during the mass extinctions. As with the end-Cretaceous, these Palaeozoic mass extinctions tended to remove endemics, and Anstey (1986, p. 49) concludes 'The differential loss of long-surviving morphologically complex bryozoans suggests that the terminal Ordovician extinction was both qualitatively and quantitatively different from preceding levels of background extinction'.

Latitudinal patterns in extinction represent another aspect of selectivity that may be evolutionarily important. The tropics are the most diverse regions of the globe, and so they might be expected to lose the greatest number of taxa during a mass extinction, even if tropical losses were no more severe on a percentage basis than those at high latitudes. The sparse data suggest, to some authors at least, that tropical marine organisms suffered disproportionately during mass extinctions (see, for example, Boucot (1983), Sheehan (1985), Jablonski (1986*a*), Stanley (1988*a*, *b*), all on benthic organisms; House (1985) on ammonoids), although Raup & Boyajian (1988) found extinction magnitudes for reef dwellers to be comparable to other invertebrates. Little is known on background origination or extinction rates for tropical marine organisms (see Jablonski & Bottjer (1989*a*) for review), but several of the authors cited above hold that per-taxon rates are low except in association with mass extinctions, whatever the role of disturbance, environmental mosaics, and other diversity-generating factors over ecological timescales. Tropical distribution, then, may yield extinction resistance during background times yet may be a liability during mass extinctions. Such results – which are in great need of rigorous study – have been taken to implicate global cooling as the cause of mass extinctions (see especially Stanley (1988*a*, *b*)). This may be true, but Jablonski (1986*d*) notes alternative explanations that should also be considered, ranging from potential fragility of the web of interactions among reef and other tropical organisms, so that perturbations similar in magnitude to those at high latitudes could bring more extensive extinctions, to the biogeographical structure of the tropical biota, enriched in endemics and hence more extinction prone in the face of any major perturbation, climatic or otherwise.

This is not to say that natural selection at the individual level was wholly ineffective or random during mass extinction, or that traits can never be of value during both background and mass extinctions. Kitchell *et al.* (1986) attributed the high survivorship of planktonic diatoms across the Cretaceous–Tertiary boundary to the presence a non-planktonic stage in the life cycle, which had already been selected during background times as a response to stressful surface-water conditions. (Unfortunately, they provide no comparative data on background extinction rates in these diatoms.) Sheehan & Hansen (1986) argue that deposit-feeding molluscs show greater end-Cretaceous survivorship than do suspension-feeding molluscs, an echo of Levinton's (1974) more general findings averaging background and mass extinction. Both molluscan and plankton results, however, may reflect instances of pre-adaptations to peculiar end-Cretaceous conditions (inferred disruption and collapse of planktonic food chains, etc.) rather than continuity of selective régimes from background to mass extinction. In any case, results from the end-Cretaceous and other extinction events do suggest a significant loss of effectiveness in at least some of the traits conferring resistance to background extinction. Rather than simply accelerating or emphasizing 'normal' extinction patterns, then, mass extinctions impose a different régime of selectivity that can have unpredictable and lasting effects on the course of evolution.

Evolutionary consequences

Because the traits that enhance survival during mass extinctions (e.g. broad geographical range at the clade level) need have little correlation with those that enhance survival and diversification during background times, mass extinctions are unlikely to promote the long-term adaptation of the biota. Such 'nonconstructive selectivity' (Raup 1984) can profoundly disrupt both short- and long-term evolutionary processes and remove taxa that are well adapted to background régimes. Taxa or morphologies could be lost not because they are maladaptive as measured under background conditions (which evidently constitute the bulk of evolutionary time), but because they happened to lack the appropriate biogeographic deployment or other traits necessary to weather the mass extinction. Mass extinction patterns will be complicated by the removal of taxa that were already dwindling or 'endangered' (cf. Kauffman 1984), but even expanding clades can be lost if they are endemics or if their centres of distribution lie within vulnerable regions (e.g. the tropical areas discussed above).

One vivid, if inexact, approach to the cost of mass extinctions in terms of lost adaptations involves iterative evolutionary patterns: certain traits are lost during mass extinctions that not only intuitively have adaptive value, but ultimately recur later in the history of the group to great success. Many features, of course, are lost once and for all during mass extinctions, but those that originate again to good effect in another branch of the same clade provide some sense of their evolutionary potential under background conditions. For example, one branch of the naticacean gastropods apparently evolved the ability to drill through the shells of their prey in the late Triassic, but this adaptation disappeared soon thereafter, despite the expansion of available resources that this innovation undoubtedly entailed at the organismic level (Fürsich & Jablonski 1984). More work is needed on late Triassic gastropod systematics, but Fürsich & Jablonski (1984) attribute the loss of the drilling ability to extinction of this innovative lineage in the end-Triassic event. Another naticacean line reoriginated the drilling ability some 120 Ma later, and the group has been expanding in diversity and abundance since that time. Similarly, the ability to bore into hard substrata was first achieved among the mytiloid bivalves late in the Ordovician (Pojeta & Palmer 1976; Wilson & Palmer 1988), and this habit surely opened up new living space and refuges from disturbance and predation. However, this lineage was lost in the end-Ordovician extinction, and bivalve borers do not appear again until the Triassic, some 200 Ma later. Examples probably exist in most higher taxa of invertebrates and vertebrates.

More commonly recognized are lasting effects of evolutionary bottlenecks imposed by mass extinctions. For example, it was the survival of the miocidarid echinoids during the Permo-Triassic extinction that fixed the standard pattern of plating in the echinoid test (Paul 1988); this must have imposed structural constraints on post-Palaeozoic echinoid evolution, but few would argue that it was the plating of the miocidarids that enabled them to survive the end-Permian crisis. Similarly, Aldridge (1988, p. 239) argues that conodont evolution was channelled by an extinction at the end of the early Silurian, which 'eliminated most, if not all, of the innovative ... stocks that might otherwise have gone on to enrich later faunas.' Although plant evolution at high taxonomic levels shows little response to the faunal mass extinctions (see, for example, Boulter *et al.* 1988), Wolfe (1987) argued that the end-Cretaceous event left a 'lasting imprint' on Northern Hemisphere vegetation in terms of distribution and relative abundances of deciduous habit and lower taxa.

Mass extinctions do not simply remove adaptations honed under background régimes, they create opportunities for faunal change by removing dominant taxa and enabling other groups to radiate in the aftermath of the event. As Benton (1987), among others, has pointed out, several radiations that had once been regarded as the triumph of adaptively superior taxa now appear to have been preceded and presumably triggered by the extinction of an earlier group. As Hallam (1987) argues, interactions among major groups seem to involve 'pre-emptive rather than displacive' competition. Removal of a major group sets the stage for diversifications of taxa – often minor components of the pre-extinction biota – that chanced to have traits enhancing survivorship during mass extinctions. Examples of extinction-mediated faunal replacements (reviewed by Benton (1987); see also Jablonski (1986*b*, *d*)) include the replacement of therapsids ('mammal-like reptiles') by dinosaurs, dinosaurs by mammals, and archaic carnivorous mammals by the modern order Carnivora. Among marine invertebrates, Sheehan (1982) found that rapid evolution in the 3–5 Ma after the end-Ordovician extinction 'produced most of the important new brachiopod groups that dominated for the following 85 million years', an interval in turn terminated by the late Devonian extinction. The sweeping changes in reef community composition through the Phanerozoic (see Sheehan 1985; Fagerstrom 1987; Stanley 1988*a*, *b*), producing a succession of what Copper (1988) terms 'six major evolutionary reef faunas', were also mediated by mass extinctions rather than by progressive competitive exclusion of a dominant group by a new taxon (the scleractinian coral – rudist bivalve interaction in the Cretaceous may be an exception, and deserves further attention; see Scott (1988)).

Some long-term faunal changes transcend individual mass extinction events. Examples include the decline of the trilobites or of Sepkoski's Palaeozoic fauna relative to the post-Palaeozoic fauna (protracted changes that Sepkoski (1984) argues would have unfolded even without mass extinctions), and the 'Mesozoic Revolution' of marine organisms involving escalation of shell-penetrating predators and their increasingly more armoured prey (see Vermeij 1987). However, even here mass extinctions may have played a role. For example, the rather steady pattern of bivalve diversification is broken by diversity drops followed by bursts of origination at the end-Permian and end-Cretaceous extinctions (Hallam & Miller 1988; Miller & Sepkoski 1988). If these bursts represent times of radiation in the absence of dampening interactions with other clades as suggested by Miller & Sepkoski (1988), rather than sampling artefacts around regressive intervals as implied by Bambach & Gilinsky (1988), then mass extinctions become significant at the level of clades and evolutionary novelties. Rebound intervals provide settings of unbridled radiation in which innovations can be captured and new adaptive zones occupied in relative freedom from the pre-emptive competition that typifies clade interactions during background times (see Jablonski & Bottjer (1989*a*) for a review of theories of clade-level interactions).

Another long-term evolutionary pattern that appears to transcend mass extinctions involves onshore–offshore shifts in marine invertebrate clades (see Bottjer & Jablonski (1988) and Jablonski & Bottjer (1989*b*) for reviews). Here too, however, extinctions can interrupt trends, and perhaps hasten or delay their progress by millions of years. For example, Frey (1987) and Miller (1988) found that the end-Ordovician extinction eliminated inroads made into offshore shelf environments by suspension-feeding bivalves that had begun diversifying onshore. The bivalves as a group eventually did spread across the shelf, but some of the pathfinding taxa reduced during the end-Ordovician event never recovered.

The rise to dominance of previously unimportant groups therefore does not require an adaptive breakthrough and competitive superiority. As outlined by Jablonski (1986*c*), a group might have suffered losses along with the rest of its contemporaries during a mass extinction, but undergone a more rapid pre-emptive diversification than the other survivors. On the other hand, new radiations might be seeded from those taxa relatively unscathed by the mass extinction, as appears to have been the case for the placental mammals after the demise of the dinosaurs and the near-extirpation of (North American) marsupials. The most persistent and diverse clades may be those in which major new adaptations and other traits favoured during background times happen to be associated with traits that favour survival during mass extinctions. Such accidental linkages could be extremely important during the rare but far-reaching mass extinction events.

Because mass extinctions are so wide-spaced in evolutionary time, clades are unlikely to remain static in the traits that allowed them to weather those events. Endemism is a liability during mass extinctions, for example, but cosmopolitan survivors will give often rise to new endemics in post-extinction times. At the same time, to the degree that they are heritable, individual-species-, or clade-level traits that confer resistance to background extinction will tend to increase during background times. During those times, loss or retention of traits helpful during mass extinctions will depend on their effects on background survivorship, and their chance linkages with other background-favoured traits. Thus during background times the number of species-rich clades could increase regardless of their geographical ranges relative to species-poor but widespread clades, and the vicissitudes of background extinction could remove those subgroups that represent a clade's best chances of surviving a mass extinction. Conversely, other groups could lose their most vulnerable members in one mass extinction and re-radiate from survivors that happen to retain their extinction resistance during subsequent background times, again altering extinction probabilities from extinction event to extinction event. This could explain, for example, severe extinction of the bivalve order Pholadomyoida during the end-Permian event but not during the end-Triassic event (Hallam & Miller 1988), or the severe end-Permian extinction and relatively mild end-Cretaceous extinction for the echinoderms (Paul 1988).

Threshold or continuum?

The change in rules of extinction and survival from background to mass extinction suggests that mass extinctions play a significant role in shaping the Earth's biota. As Jablonski (1986*b*, *d*) notes, however, the change in rules could represent two alternative selective régimes or endmembers of a continuum. Raup (1986) has shown that mass extinction magnitudes are not a separate class unto themselves, but the tail of a curve of extinction intensities when all Phanerozoic stages are surveyed. Threshold effects are of course still possible, but these and other results raise the possibility of a continuum of effects.

McKinney (1988) found echinoid extinction patterns to be similar to the Cretaceous molluscan patterns described above: species-rich clades were more resistant to background extinction, but enjoyed no advantage during mass extinctions. He found, however, a continuum of responses depending on the magnitude of the event. Similarly, Boyajian (1988) found that mass extinctions more severely affected geologically old clades than did background extinctions, and he suggests that clade age is a proxy for such hedges against background extinction as species richness. On examining the underlying age distribution of victims for all stratigraphic stages, he found the number of older clades lost during mass extinction events to be as expected statistically given the large overall extinction. Thus, in one sense, mass extinctions are simply background extinctions writ large. However, when viewed in terms of evolutionary consequences, or in terms of what clades experience over the course of their histories, the change in extinction rules is still a factor. As Raup (1986) shows, most time intervals exhibit low extinction rates, so that, for example, species-rich clades will be buffered against extinction for most of their histories; but those clades will suffer a relatively rapid erasure of that trait's effectiveness as a hedge against extinction when one of the rare, major perturbations arises. The size of the excursion from the small extinction probabilities that typify most of geological time in Raup's (1986) plot may determine how completely the background extinction rules are undermined, but the fact remains that successive time intervals can bring significant shifts in the nature of extinction-resistant traits.

Changes in the rules of extinction and survival, then, need involve no unique forcing mechanism. The failure of species richness and species' geographical ranges to protect clades from mass extinction is probably telling us more about the magnitude and pervasiveness of the perturbation than about which of the many hypothesized causes have come into play. Survival probabilities for the end-Cretaceous event were greatest for clades spread over many provinces, presumably because refugia were few and far between. For tens of millions of years previously, individual species widespread in a single province, or large numbers of species within a single province, were sufficient to enhance clade survivorship, because at any one time perturbations were comfortably below the provincial scale. This changed during the end-Cretaceous mass extinction (and for the other major extinctions, as far as is known), with lasting and unpredictable evolutionary consequences.

Conclusions

In terms of evolutionary effects, mass extinctions tend to remove not only more clades, but different clades from those lost during the times of background extinction. Clades cannot be viewed as static, however: a clade's ability to resist mass extinction can itself change through time. The relative proportion of taxa bearing traits that confer resistance to mass extinction almost certainly changes during the history of major groups. Furthermore, the traits that influence survivorship during mass extinctions vary at relatively low taxonomic levels: multi-province geographical range at the genus level, or extratropical distributions, to name two likely examples. Consequently, analyses of mass extinction selectivity among orders or classes will tend to yield mixed or ambiguous results. Even ammonites, one of the most notoriously volatile invertebrate groups in the fossil record, contain low-diversity, long-lived lineages. Not coincidentally, these low-diversity ammonite clades survive or are the last to disappear at mass extinction boundaries, and tend to be geographically widespread (see Ward & Signor 1983; House 1985).

Whenever traits that confer extinction resistance during mass extinctions (e.g. broad geographical range at the clade level) are poorly correlated with traits that enhance survival and diversification during background times, mass extinctions will disrupt evolutionary patterns and faunal dominance patterns established during background times. By removing or reducing dominant groups, mass extinctions provide opportunities for diversification of taxa that had been minor constituents of the pre-extinction biota. At the same time, mass extinctions can eliminate evolutionary innovations of high selective value if those traits are captured by clades that happen to lack extinction-resistant traits. For many reasons, then, evolution can be channelled in directions not predictable from situations established during background times. A broader range of hypotheses must be considered in analysing the histories of higher taxa and major adaptations, hypotheses that recognize the potential role of extinction processes that may not be congruent during mass extinctions and background times, or across levels in the biological hierarchy.

I thank N. J. Morris and R. J. Cleevely, British Museum (Natural History), for their generous advice and hospitality during my first foray into European Cretaceous bivalves. D. H. Erwin, A. Hoffman, S. M. Kidwell, D. M. Raup and S. Suter provided valuable reviews and discussions. This work was supported by NSF Grants EAR84-17011 and INT86-2045.

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Note added in proof – 29 *April* 1989

Becker (1986) argues for differences in background and mass extinction patterns among ammonoids at the late Devonian extinction. In their study of Palaeozoic seastars, Blakes & Guensburg (1988) discuss adaptations related to a predatory mode of life that were evidently lost to the group at the end of the Ordovician, and re-evolved in the Mesozoic some 250 Ma later. Seilacher (1988) concludes his morphogenetic comparison of nautiloids and ammonites: 'There was certainly nothing wrong about ammonite shell construction. Still only the less perfect design of the *Nautilus* shell did survive the catastrophe. Can there be a better example to illustrate that other criteria matter in mass extinctions than in normal selection?'

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