
Extinctions in the Fossil Record [and Discussion]

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Extinctions in the fossil record

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SUMMARY

Direct comparison of ancient extinctions to the present-day situation is difficult, because quantitative palaeontological data come primarily from marine invertebrates, fossilized species are usually drawn from the more abundant and widespread taxa, and time resolution is rarely better than 10^3 – 10^4 years. A growing array of techniques permits quantitative error estimates on some of these potential biases, and allows calculation of species extinction intensities from genus-level data, which are more robust. Extensive as today's species losses probably are, they have yet to equal any of the Big Five mass extinctions. Background extinction patterns are potential sources of insight regarding present-day biotic losses; over 90% of past species extinction has occurred at times other than the Big Five mass extinctions. Mean durations of fossil species vary by more than an order of magnitude even within clades, rendering uninformative any global average for background extinction. Taxon-specific variation is evidently related to intrinsic biotic factors such as geographic range and population size. Approaches to extinction analysis and prediction based on morphological variety or biodiversity should be explored as an adjunct or alternative to taxon inventories or phylogenetic metrics. Rebounds from mass extinctions are geologically rapid but ecologically slow; biodiversity recovery and the re-establishment of some communities typically requires 5–10 million years.

1. GLOBAL COMPILATIONS

The fossil record provides an enormous database on extinctions, and in this paper I will briefly review how the fossil record of extinction is quantified and discuss some implications for today's biota (see Jablonski (1994) for an expanded discussion).

Most large-scale analyses of extinction in the fossil record rely on synoptic compilations of geologic ranges for genera and families. The fossil record at the species level is very incomplete and most subject to sampling and preservational biases, and so more inclusive taxa are nearly always used for work at the global scale, particularly over large blocks of geological time. These synoptic time series are most useful for recognizing intervals of unusual extinction intensity, and for quantifying overall biotic losses. They are less effective in resolving the details of timing or geography for any given extinction event, a research problem requiring an intricate interplay between detailed, local time series and global compilations (not discussed here; see Raup 1989; Koch 1991; Marshall 1991; Sepkoski & Koch 1994).

As many authors have noted, the fossil record of shelly marine invertebrates is the most complete and reliable for global biodiversity analysis (Benton 1989; Signor 1990). Accordingly, Sepkoski's Compendium of Marine Animal Families has been a boon to all interested in such analyses (see also Benton (1989) and Maxwell & Benton (1990) on terrestrial vertebrates and Niklas *et al.* (1985) on the plant record).

Synoptic compendia have supported many in-

triguing analyses, but here I concentrate on the five major mass extinctions detected for marine invertebrates (table 1). Mass extinctions can be taken as substantial biodiversity losses that are global in extent, taxonomically broad, and rapid relative to the average duration of the taxa involved (Jablonski 1986*a*). The 'Big Five' extinctions have been confirmed in several generations of family- and genus-level databases (see Sepkoski 1994). The past decade of particularly intensive work, with many additions, corrections and reinterpretations of taxonomy and stratigraphy have served only to sharpen these events as seen both in Sepkoski's revised database (Sepkoski 1993) and in a semi-independent compendium by Benton (1993; with an army of taxonomic experts). A host of lesser extinction events are also known, but only a few of these are presently documented as global events (Sepkoski 1994).

Many taxonomic problems remain in those databases, of course; discussion has focused mainly on the inclusion of paraphyletic taxa and the problem of comparability of taxonomic ranks (e.g. Smith & Patterson 1988; Doyle & Donoghue 1993). However, even with arbitrary ranks, paraphyletic taxa turn out to be adequate proxies for species-level dynamics, and in fact under realistic sampling conditions for most groups, can provide a more robust portrait of biodiversity changes than will any tabulation of the relatively short-lived and undersampled species themselves (see Valentine 1990; Gilinsky 1991; Sepkoski 1987*a*, 1989; Fisher 1991; Sepkoski & Kendrick 1993).

Table 1. *Extinction intensities (percent extinction, $E/D \times 100$) at the five major mass extinctions in the fossil record*

(Genus- and family-level values based on Sepkoski's Compendia (Sepkoski 1994), with binomial standard errors calculated following Raup (1991a); species-level estimates based on Raup's (1979b) reverse rarefaction technique. Note the agreement between the two estimates of species losses for each extinction episode. Ma = million years ago, ages from Harland *et al.* (1990).)

mass extinction	families		genera	
	observed extinction (%)	calculated species loss (%)	observed extinction (%)	calculated species loss (%)
End-Ordovician (439 Ma)	26 ± 1.9	84 ± 7	60 ± 4.4	85 ± 3
Late Devonian (367 Ma)	22 ± 1.7	79 ± 9	57 ± 3.3	83 ± 4
End-Permian (245 Ma)	51 ± 2.3	95 ± 2	82 ± 3.8	95 ± 2
End-Triassic (208 Ma)	22 ± 2.2	79 ± 9	53 ± 4.4	80 ± 4
End-Cretaceous (65 Ma)	16 ± 1.5	70 ± 13	47 ± 4.1	76 ± 5

2. EXTINCTION METRICS

Quantifying extinction intensity has other pitfalls, however, and each of the standard extinction metrics has drawbacks (see Sepkoski & Raup 1986; Raup & Boyajian 1988; Gilinsky 1991; Sepkoski & Koch 1994; Foote 1994). For example, the raw number of extinctions in a time interval, E , has a simple error term but does not take into account the number of taxa at risk: the loss of 100 families is clearly a more significant event when global diversity (D) totals 200 rather than 600 families. The proportion of taxa becoming extinct (E/D) is intuitively a more satisfying metric but introduces additional uncertainty because estimates of global diversity also have an associated error (Gilinsky 1991).

Extinction rates (E/t) have often been used to take into account the possibility that longer intervals can accumulate more extinctions, but distortions enter owing to uncertainties in geologic time estimates (Sepkoski & Raup 1986; Raup & Boyajian 1988; Gilinsky 1991). For example, the Coniacian, the shortest stage of the Cretaceous, may exhibit an extinction peak in time series analyses depending on the timescale used, but exhibits unexceptional turnover under detailed study. More generally, Sepkoski & Koch (1994) show that recent estimates for the duration of stratigraphic stages in the Devonian differ by 26–33% of mean stage length; this uncertainty in the denominator yields alarmingly large error terms. In a simulation study, Foote (1994) found that rate metrics tend to be negatively correlated with interval length under the majority of realistic extinction models. Further, rate metrics assume that extinctions are evenly or randomly distributed through the time interval, which seems not to be true for several of the stratigraphic stages associated with mass extinctions. Per-taxon rates ($E/D/t$) may have the strongest theoretical appeal (Gilinsky 1991), but they compound these uncertainties and thus yield even larger potential error.

The statistical properties of the extinction metrics are still poorly understood. Consequently, the principal analytical strategies are: (i) use several metrics to test for sensitivity of features of interest to different error sources (e.g. Van Valen 1984, 1985; Sepkoski &

Raup 1986); or (ii) use stratigraphic intervals of approximately equal length, combining short intervals and subdividing long ones to reduce variance (e.g. Sepkoski 1989; Sepkoski & Koch 1994). Confidence intervals are calculated as binomial standard errors; these assume random sampling and thus are inexact, but are useful as measures of relative uncertainty (Raup 1991a; Sepkoski & Koch 1994).

3. ESTIMATING SPECIES-LEVEL EXTINCTION

Extinction intensities at the species level are estimated from the distribution of species within present-day families and genera ('reverse rarefaction'; Raup 1979), by assuming (i) that extinctions are temporally concentrated and not spread through a geologic stage or longer interval, and (ii) that the distribution of species within genera and families of present-day echinoids are representative of the biota as a whole. The latter may seem a particularly risky assumption (e.g. Valentine 1974; Van Valen 1985), but convergent estimates of species losses from both generic or familial data suggests that Raup's (1979) echinoid data do provide a reasonably good proxy (see table 1).

Reverse rarefaction also assumes that species survival is uncorrelated with membership in a particular higher taxon. However, related species tend to be clumped ecologically, and in some instances at least, e.g. reef dwellers, their shared risk probably exceeds the random expectation. Species losses would then be overestimated, because it would take fewer non-random species extinctions to remove a given number of genera (see Simberloff 1986, p. 170; Raup 1991b, p. 73). The assumption of random species loss relative to higher taxa also implies that species-poor genera and families should be at greater risk than species-rich ones, which was evidently not the case for many mass extinctions (see in Jablonski 1991a,b). This implies that the loss of a genus or family is more likely to involve a species-rich taxon than the random expectation, so that reverse rarefaction might then underestimate species loss. A conservative interpretation is that genus-level extinction data provides an empirical lower bound for percent species loss for each event; the

loss of a greater proportion of genera than species is unlikely under realistic conditions (D. M. Raup, personal communication, 1993). However, unusual circumstances could confound such an estimate: imagine losing nine monospecific genera but allow one ten-species genus to survive unscathed, and genus extinction is 90% but species extinction is 47%.

4. COMPARISONS TO PRESENT-DAY EXTINCTION

Palaeontological extinction data are extremely difficult to compare to present-day extinction rates. As already noted, the most robust palaeontological data, and most analyses on ancient extinction intensities and selectivities, deal with marine invertebrates. The conservation status of today's marine biodiversity is woefully underdocumented compared even to our incomplete knowledge of most terrestrial organisms, and only a handful of extinctions are known, reflecting perhaps both our ignorance and the greater inertia of marine systems. However, human impacts are increasingly severe, from overexploitation to introduction of exotics, and clearly the marine fossil record can provide useful insights for conservation. The larger problem, however, is how to generalize from the marine-biased history of global biodiversity to today's situation, where most data and the most rapid and extensive species losses are terrestrial.

Even in the marine record, fossil species and higher taxa are not random samples of the biota, or even of the biota with durable skeletons. The taxa in palaeontological databases – marine and terrestrial alike – are skewed towards the more abundant, widespread, and geologically long-lived species, which will have the greatest total number of individuals and occur in the greatest number of localities and rock types, and so are most likely to be preserved and recorded (see Koch 1991). It is therefore not at all clear that the majority of tropical species whose losses are inferred by extrapolation of local surveys – mainly rare, extreme endemics – would be palaeontologically detectable (Jablonski 1991a). Moreover, the best time resolution consistently achievable in the pre-Pleistocene fossil record is *ca.* 10^3 – 10^4 years, due to gaps in the record and time-averaging of successive populations (Kidwell & Behrensmeier 1993). This does not mean that the relative abundances, geographic ranges and geologic durations of fossil taxa are irretrievable or hopelessly distorted: quantitative analyses of sampling densities and preservation biases have verified that a strong biological signal is often present (e.g. Paul 1989; Marshall 1991; Kidwell & Bosence 1991). But the very nature of the fossil record suggests that palaeontological estimates should be applied to present-day situations with extreme caution.

Present-day extinction is usually expressed as a simple rate (E/t) rather than as a proportion (E/D). However, given the enormous differences in sampled or estimated diversities for extant and fossilized biotas, comparisons are only feasible after normalization according to the size of the taxon pool. Smith *et al.* (1993a) tabulated the percent species loss recorded for

different animal and plant groups since 1600, and found none greater than 1.3%. Species threatened by extinction in well-known groups, however, constitute a significantly higher proportion, e.g. 32% for gymnosperms. With some assumptions about extinction probabilities of such groups, these data imply 50% extinction within 50–100 years (Smith *et al.* 1993b). This approaches the intensities required to generate a genus-level extinction on the scale of the Big Five mass extinctions. Still uncertain, of course, is whether these numbers are representative of the biota as a whole, and how they should be scaled against palaeontological data. The next step might be to develop correction factors for more rigorous comparisons to the fossil record, by estimating for each group the proportion of species whose original abundance and distribution was on a scale commensurate with potential fossilization and discovery. This can be done directly using taxa with well-studied fossil records; for example more than 77% of shelled mollusc species off the California coast occur as Pleistocene fossils (Valentine 1989), and comparable figures could be probably obtained for temperate plant and arthropod species.

5. TAXON-SPECIFIC RATES

In the fossil record, species or genus durations within higher taxa vary by more than an order of magnitude even during times of background extinction away from the Big Five mass extinctions, so that computation of a grand mean is not very informative (although broad rate differences do exist among major groups; cf. Stanley 1979; Valentine 1990). Not only is the variance enormous, it is strongly right-skewed: most taxa within a major group tend to be geologically short-lived but the frequency distribution usually includes a tail of long-lived taxa (e.g. Stanley 1979). Some of the observed variation is due to sampling and other artefacts, but data on a wide variety of higher taxa show biological factors to be important in determining extinction rates for species and genera in the fossil record (for a review, see Stanley 1990a). For example, molluscan species durations are positively correlated with geographic ranges (Jablonski 1986b, 1987; Marshall 1991; also Jackson *et al.* (1985) on corals and bryozoans). Stanley (1990a) attributes the inverse relation between body size and species survival to differences in population size, but this needs to be tested more directly, because body size is a very poor predictor of species abundance (Blackburn *et al.* 1993).

Whatever the precise causal links or focal level of selection, the clear differentials in species survivorship detected in many fossil groups are a rich source of empirical data on variations in extinction risk among taxa (from protozoans (e.g. Norris 1991) to mammals (e.g. Van Valkenburgh & Janis 1993)). In fact, regions, habitats and taxa should be targeted for palaeobiological studies designed explicitly to address conservation issues. It may be surprising that I advocate palaeontological analyses of background extinction as a tool in assessing present-day extinction risk, given data suggesting that background rules of survivorship are disrupted during the major mass

extinctions (e.g. Jablonski 1986*b*, 1989, 1991*a*, and references therein). I am not belittling the magnitude of today's problems, nor do I deny the potential for long-term losses of similar scope and evolutionary impact to the major mass extinctions of the fossil record (cf. Simberloff 1986). Background extinction patterns may nevertheless provide clues to how the present-day biota will respond to anthropogenic disturbances, for at least three reasons.

1. It is not clear that present-day disturbances, although extensive relative to the quietest times of Earth history, are on a par with those that drove the major mass extinctions. If we could apply all the appropriate correctives, present and near-future extinctions may or may not fall quantitatively within palaeontological background rates but there is little evidence that the qualitative change in survivorship such as seen at the Cretaceous–Tertiary boundary has occurred today. So far as they are known, today's extinction patterns conform mainly to intensified versions of background expectations, with losses concentrated in endemic species and subspecies. The major mass extinctions operated on a different scale: genera endemic to single subcontinental provinces were lost preferentially, regardless of the geographic ranges of their constituent species (Jablonski 1986*a*, 1989, 1991*a,b*, and references on many groups and extinction events).

2. Even if selectivities of present-day extinctions were congruent with those seen during the ancient mass extinctions, not all background patterns of survival are overturned under the mass extinction régime, and some evolutionary continuity exists even across the most severe events (Jablonski 1986*c*, 1989). The persistence of survival advantages may be clade- or event-specific, such as a resting cyst in the life cycles of high-latitude phytoplankton during the end-Cretaceous event (Kitchell *et al.* 1986). In other instances, enhanced survivorship under both mass and background régimes may represent the long-term effects of previous mass extinctions. For example, severe extinction in the bivalve order Pholadomyoidea during the end-Permian extinction but not during the succeeding end-Triassic event may reflect the purging of vulnerable members of the clade followed by re-radiation from survivors that happened to retain extinction-resistant features. Similarly, the remarkably low extinction rates in shallow-water molluscs during the huge Pleistocene climate and sea-level fluctuations (references in Valentine & Jablonski 1993) have been linked to Pliocene turnover events that may have already eliminated the most vulnerable species (Stanley 1990*b*; see Jackson, this symposium). Because we are just beginning to explore the factors that allow clades or trends to prevail under both background and mass extinction régimes, the limits to the relevancy of background extinction patterns to perturbations of various magnitudes – particularly those short of the Big Five events – are still unclear.

3. The great majority, probably more than 90%, of species extinctions in the fossil record occur outside the five major extinction events (Raup 1991*c*): mass extinctions have such profound biological conse-

quences because they bite deep into standing diversity and disrupt background selection régimes, not because they account for most species terminations. In fact, extinction magnitudes for the stratigraphic stages of the Phanerozoic form a continuous distribution. Some impressive extinction pulses fail to stand significantly above background variance, and data from those intervals should be used to advantage as long-term records of taxon selectivity.

6. BIODIVERSITY AND BIODISPARIETY

Other palaeontological approaches can be used to explore the effects of extinction, such as quantifying the loss of morphological variety rather than taxonomic diversity per se. The ecological or evolutionary impact of an extinction event resides not simply in the number of taxa lost, but in the loss of what could be termed (with some trepidation) biodisparity, the range of morphologies or other attributes within a clade or within a local or regional subsample of a clade. A variety of methods are available for quantifying biodisparity, ranging from ecomorphological studies that test for convergence or displacement of species morphologies within and among communities to the construction of theoretical or empirical morphospaces used to track clades through geologic time (reviewed by McGhee 1991; Foote 1991, 1993). Most of the palaeobiological work has focused on radiations, particularly the relation between taxonomic and morphologic diversification during the Cambrian Explosion, but background and mass extinction could be analysed in the same fashion. At present we know little of how taxonomic losses impinge on patterns of morphospace occupation in ancient or present-day biotas. As Foote (1992) points out, if extinction is effectively random with respect to morphology, a disproportionately large number of extinctions is required to reduce morphological variety substantially. On the other hand, extinctions might be selective in morphospace just as they are taxonomically. This has not been explored, however, and we do not know if taxa lying in different regions or densities of morphospace vary predictably in risk.

7. REBOUNDS

Evolutionary rebounds after mass extinctions are an important component of macroevolution (reviews by Jablonski 1986*b,c*; Benton 1987). The recovery of both biodiversity and biodisparity in the aftermath of mass extinctions is rapid by geological timescales, often accompanied by significantly accelerated evolutionary rates (Hallam 1987; Miller & Sepkoski 1988; Sheehan & Coorough 1990), but it is extremely slow by human timescales. For example, one of the most striking biogeographic patterns in mass extinctions is the disruption of reef and related communities on tropical carbonate shelves: each mass extinction brings a major reorganization of these taxon-rich habitats. Refurbished reef communities, however, emerge only after a 5–10 million year lag following each of the major mass extinctions (Copper 1989). Talent (1988) argues that

this delay far exceeds the offset of the environmental stresses that eliminated the preceding community. This has significant implications for restoration ecology, as it implies some other constraint on the evolution of species or the assembly of communities capable of occupying these habitats; the community ecology of rebounds from past extinction events should be a focus for future research. In addition, recoveries from global events need not be geographically homogeneous. For example, the post-Cretaceous rebounds in molluscan faunas differ significantly in Europe and North America despite the lack of geographic variation in end-Cretaceous extinction intensities (see references in Jablonski 1991b; Raup & Jablonski 1993).

8. CONCLUSION

The mass extinctions of the fossil record are, if nothing else, cautionary tales. They show unequivocally that marine and terrestrial biotas are not infinitely resilient, but have breaking points that have been exceeded repeatedly in the past, with extreme and long-lasting biological consequences. The fossil record of extinction can yield more specific insights, however, even though estimates of present-day extinction are difficult to compare directly with those calculated for past mass extinctions. Raw numbers aside, the fossil record provides our only empirical data on what happens when biological communities collapse or disassemble, when increased extinction rates impinge on taxa of different relative vulnerabilities, when global warming or cooling occurs faster than species can adjust to local conditions, when ecological stresses ameliorate after prolonged or severe episodes, and so on. All of these are situations that we may face in the coming century, and it is in these more circumscribed questions that the fossil record may provide the most insight and has the greatest predictive power.

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Discussion

W. G. CHALONER (*Biology Department, Royal Holloway University of London, U.K.*). I was interested in Professor Jablonski's suggestion that in the marine invertebrate fossils that he had studied, extinction is seemingly scattered through the population randomly, and independently of the higher taxa to which they belong. Does he believe that this randomness of extinction extends outside the groups that he describes? Niklas *et al.* (*Nature, Lond.* **303**, June 1983, 614–616) showed that in vascular plant groups, 'species longevity' appears to be highly taxon-dependent. Does Professor Jablonski believe that their observations can be attributed to some basic difference between plant and animal evolutionary processes? Or does it, perhaps, link with the correlation that he described between mobility and resistance to extinction? It might be argued, for example, that early vascular plants with their homosporous reproduction have maximum dispersal potential, whereas seed plants have an increasingly

K-strategy reproductive biology, with diminished mobility. Would he care to comment on whether he believes that there are fundamental differences in the probability of extinction between plants and animals, and indeed between other groups?

D. JABLONSKI. I don't think that extinction is taxonomically random, but the differences among higher taxa depend on which groups are studied and whether the context is one of background or mass extinction. In times of background extinction, invertebrate higher taxa, like the plants, do exhibit broad differences in species- (and genus- and family) longevities: trilobites turn over more rapidly than bivalves. However, the variance is large and the distribution right-skewed, with within-group variance evidently related to biological characteristics such as geographic range, physiological tolerance, population sizes or growth parameters.

These factors may partly explain among-group differences as well, according to the relative proportion or degree of, say, widespread or tolerant species within a given higher taxon. During mass extinctions, no significant differences have been detected at the class level, and many taxa vary through time in their relative losses; but the cephalopods generally seem to suffer more than the gastropods during each event. Such apparent inconsistencies may well reflect the nature of the selectivity, focusing on a few aspects of geographical or ecological distribution. If plants have a tighter covariance between phylogeny and rate-influencing biological traits like reproductive features, then high taxa may have tighter modal values in turnover rates. I'm not sure if this is a fundamental difference, but plants and animals differ evolutionarily in other ways as well (see J. W. Valentine *et al.*, *Palaeos* **6**, 81–88).