



Crisis and Response: Current Trends and Future Prospects

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ABSTRACT - New technologies have continuously expanded the questions palaeontologists and other geologists can explore about mass extinctions, biodiversity crises and the subsequent biotic rebounds. From international correlations in the 1950s, to stable isotopes, high-resolution geochronology and modeling efforts, mass extinctions have been revealed as more sudden in timing and often more catastrophic in extent than had been recognised. These and other tools are now being applied to understanding the dynamics of recovery after mass extinctions, which have been revealed to be quite complex. As the spatial and temporal resolution increases palaeontologists have increasingly been able to interrogate the ecological dynamics of these events, a trend that seems likely to expand in the future.

RIASSUNTO - [Crisi e risposte: tendenze attuali e prospettive future] - Le nuove tecnologie hanno progressivamente ampliato i temi che paleontologi e geologi possono esplorare riguardo le estinzioni di massa, le crisi della biodiversità ed i successivi recuperi biotici. Dalle correlazioni internazionali degli anni '50, all'utilizzo degli isotopi stabili, alla geocronologia ad alta risoluzione ed agli sforzi di modellizzazione, le estinzioni di massa si sono rivelate come più improvvise (in termini temporali) e spesso più catastrofiche di quanto non fosse stato riconosciuto in passato. Questi e altri strumenti possono ora essere utilizzati per meglio comprendere le dinamiche di recupero che seguono le estinzioni di massa, più complesse di quanto ipotizzato in precedenza. Con l'aumentare della risoluzione spaziale e temporale, i paleontologi sono sempre più in grado di interrogare le dinamiche ecologiche che caratterizzano queste fasi, una tendenza che sembra destinata ad espandersi in futuro.

INTRODUCTION

On 6 June 1980 Luis and Walter Alvarez, Frank Asaro and Helen Michel published a paper in *Science* with evidence from sections in Italy and Denmark for enrichment of iridium at the Cretaceous-Palaeogene (K/Pg) boundary which they suggested was best explained “as indicating an abnormal influx of extra-terrestrial material” (Alvarez et al., 1980, p. 1102). This was neither first study of a mass extinction, nor was it the first study to posit an extra-terrestrial trigger for mass extinctions: Schindewolf (1963) had invoked cosmic rays as a cause of the end-Permian mass extinction largely because the boundary was placed within a single facies during his field work in Pakistan. This led Newell (1967) to advance a very different view of mass extinctions. In his Presidential Address to the Paleontological Society, McLaren (1970) evaluated a number of proposed causes of mass extinction and developed the hypothesis that extra-terrestrial impact was a plausible hypothesis for the Late Devonian Frasnian/Famennian crisis. It is hard to imagine a sustained research program on mass extinctions much earlier, as global efforts to improve international stratigraphic correlations and define stratigraphic boundaries only really began in the 1950s.

But mass extinctions have captured the attention of palaeontologists, geologists and the general public not simply because of their catastrophic nature, but because they may lead to the origin of new clades, the expansion of previously minor clades and the generation of entirely new ecosystems (Sepkoski et al., 1981; Bambach et al., 2002, 2004; Wagner et al., 2006; Erwin, 2008; Hull & Darroch, 2013; McGhee et al., 2013). The pivotal nature of these events continues to attract attention, particularly as interest grows in post-extinction recoveries (Erwin, 2001; Hull, 2015; Wood & Erwin, 2018).

Papers and discussions at the 1948 and 1952 International Geological Congress resulted in establishment of the International Stratigraphic Commission and eventually the elucidation of the concept of a Global Stratotype Section and Point (Walsh et al., 2004). But as McLaren emphasised in his remarks, even in 1970 the nature of boundaries was an active topic of debate, with Newell arguing that globally significant stratigraphic horizons did exist and could serve as the basis of correlation. Since the 1970s collaborations among hundreds of geologists has generated a remarkably refined stratigraphic framework for the Phanerozoic (although often not without some contention!), which is now being extended through the Ediacaran into the Cryogenian and Tonian periods. These efforts yielded sufficiently precise frameworks for considering the nature and causes of mass extinctions.

The generation and development of an increasingly highly resolved global stratigraphic framework is just one of many technologies adopted by geologists and others with interests in mass extinctions and subsequent biotic recoveries. Rather than produce yet another overview of the various extinction events, here I will focus on how the introduction of new technologies ranging from correlation to geochronology and databases has influenced the ability of palaeontologists to address new questions. I will focus largely on mass extinction events, rather than recoveries, but will close with some thoughts about the impact of mass extinctions on the course of evolution.

DATA

Interests in diversity patterns in general and mass extinctions more specifically have spurred the development of global databases of Phanerozoic marine families and

genera, and later plants, vertebrates, various marine microfossil groups and insects. Global databases have encouraged a broad-scale view of mass extinctions and debates about the number of events that properly qualify as mass extinctions (Bambach et al., 2004; Bambach, 2006). During the 1980s and 1990s the family and then generic database compiled by the late Jack Sepkoski of the University of Chicago (Sepkoski, 1997, 1981, 1984) featured in dozens of studies of diversity patterns. Arriving shortly after the Alvarez papers, Raup & Sepkoski proposed a cyclical pattern of mass extinctions through the post-Palaeozoic (Raup & Sepkoski, 1984, 1986; Sepkoski, 1987), generating great excitement about a possible general theory of mass extinctions. Sepkoski's three-phase logistic model of Phanerozoic diversity (Sepkoski, 1984) encouraged the then widespread view that the recoveries after mass extinction were largely an exponential expansion into "empty ecospace".

The inadequacies of the fossil record have required the generation of new methods to test the reliability of this data and correct for deficiencies. Sepkoski only recorded the global first and last appearances of taxa, and this limited the range of corrections that could be applied to the data. A group of younger palaeontologists generated a more comprehensive database based on lists of fossil occurrences at individual localities (www.paleobiodb.org) (Alroy et al., 2008; Alroy, 2010) which revealed a more complex pattern of biotic crises, and has enabled a broader array of analyses than was possible with Sepkoski's data set.

While global databases can aid in identifying general patterns, the 19th Century British palaeontologist John Phillips knew of the P/Tr and K/Pg extinctions (Phillips, 1860). They were, after all, the basis of his divisions of the Palaeozoic, Mesozoic and Cenozoic eras (although Phillips credited them to independent creations of life). The tradeoff between synoptic coverage and temporal resolution has meant that global compendia can only provide relatively coarse pictures of diversity, only rarely achieving the resolution required for analyzing the rates, selectivity or causes of these episodes. This requires detailed studies of individual sections across the globe, precise regional and global correlations using bio-, chemo- and magnetostratigraphy as well as integration with other data including radiometric dates, and stable isotopes. This of course requires field work, and the interest in mass extinctions spurred extensive field studies of many sections not only for the "big five" mass extinctions, but also for significant but smaller biodiversity crises. The spread of interest in mass extinctions coincided with increased interest in the quality and reliability of the fossil record for inferring the history of past events, and the generation of statistical techniques for assessing the record. For mass extinctions, the most important of these was recognition that less abundant taxa (usually genera or species) would disappear earlier simply because they were less likely to be sampled than more abundant taxa. Such range truncations make even an abrupt event appear gradual without correction for this "backward-smearing" (Signor & Lipps, 1982). The introduction of confidence interval analyses of taxon last appearances provided more robust estimates for actual extinction patterns for the K/Pg (Marshall, 1990; Marshall & Ward, 1996) and

then P/Tr events (Jin et al., 2000). Later we extended the approach to multiple P/Tr sections across south China (Shen et al., 2011; Wang et al., 2014) and the technique has been applied elsewhere. Such sampling effects are not the only bias imposed by geology on apparent extinction patterns. Sequence architecture also influences apparent extinction patterns (Holland & Patzkowsky, 2015; Nawrot et al., 2018).

Such integrated studies quickly revealed that we lacked, and indeed continue to lack, the tools to integrate diverse datasets at sufficiently high temporal and spatial resolution to address many pressing questions: Did the rate of extinction differ across the globe? Between high and low latitudes? Or between the oceans and land? Abrupt shifts in carbon isotopes occur at many extinction horizons, but do they lead the extinction, suggesting something about the initial causes, or are they a consequence of the event? The variable ecologic and evolutionary impact of the primary extinction episodes is also found in other groups. For example, although there was extensive ecological disruption of terrestrial plants associated with the Tr/J and K/Pg events, only during the P/Tr did the plant record parallel that of marine taxa (Cascales-Minana et al., 2018).

THE IMPACT OF NEW TECHNOLOGY

The comprehensive database of family and generic ranges compiled by Sepkoski was critical to research on biodiversity crises from the early 1980s onward, but it was hardly the only technological advance that played a significant role in advancing research on extinction episodes and subsequent biotic responses. Other advances have occurred in correlation methods, from quantitative stratigraphy to palaeomagnetism and chemostratigraphy; the spread of carbon and oxygen stable isotopes, followed more recently by other isotopic systems; the development of increasingly high-resolution geochronology, which has been vital for establishing rates of extinction and recovery; a remarkable range of modeling efforts, from impact models of the K/Pg extinction to ecological dynamics of extinction and recovery; and the increasing spread of phylogenetic analysis as a tool to understanding the breadth of both mass extinctions and recoveries. The excitement over the possibility of an extra-terrestrial trigger for the K/Pg event brought many other scientists into studies of mass extinctions and greatly enriched our understanding of the causes of these events. I will not discuss all of these areas, but will focus on stable isotopes, geochronology and phylogenetics before suggesting some future directions.

Stable Isotopes

In the case of the P/Tr extinction there was considerable global evidence for the abrupt shift in $\delta^{13}\text{C}$ isotopes coincident with the extinction, but we also knew that the nature of the recorded shift differs between different P/Tr boundary sections (Cao et al., 2010; Korte & Kozur, 2010). My colleagues at the Nanjing Institute of Geology and Palaeontology (NIGPAS) and I have spent much of the past two decades building increasingly high-resolution data sets from several localities in south China to address

the problem of isotopic shifts and their precise relationship to growing evidence for a very abrupt extinction (Jin et al., 2000; Shen et al., 2011; Burgess et al., 2014; Chen et al., 2016; Shen et al., 2018). In this case, a gradual decline in $\delta^{13}\text{C}$ begins well before the extinction horizon, with a sharp excursion coincident with the extinction pulse. We recently described a section from near Penglaitan in Guangxi Province with greatly enhanced thickness (and thus temporal duration) and a complex pattern of changes, with the isotopic shift beginning before the extinction interval. In the absence of quantitative estimates of species abundances, however, we still cannot determine whether this early decline in $\delta^{13}\text{C}$ marks a prelude to the extinction.

Detailed signatures of carbon and oxygen isotopes have been published for most major mass extinction intervals, documenting fluctuations in the carbon cycle, but newer isotopic systems have been introduced as well. For example, boron isotopes can reveal changing patterns of pH (Clarkson et al., 2015), variation in nitrogen fixation by nitrogen isotopes (Luo et al., 2016; Schoepfer et al., 2016), as well as anoxia from sulfur and other isotopic systems.

High-resolution Geochronology

“No dates, no rates.” The mantra of my colleague Sam Bowring of MIT captures the importance of high-resolution radiometric dating for establishing a temporal framework for extinctions and recoveries, and, most critically, for evaluating associated rates. This is not a matter of dating the boundary or the extinction. Absent sufficient dates above and below the interval of interest it is impossible to generate a temporal framework, but this requires datable volcanic material, ideally ash beds. As the precision and accuracy of radiometric dating improved through the 2000s, differences between different laboratories and between different isotopic systems became increasingly obvious and began to hinder comparison of results. This led to the establishment of an international consortium of geochronologists, palaeontologists and others working to reduce problems of inter-laboratory analytical differences and improve the application of geochronology to problems like mass extinctions and recoveries (Bowring & Erwin, 1998; Erwin, 2006) (www.earth-time.org).

The P/Tr boundary turned out to be particularly auspicious interval to explore the promise of high-resolution geochronology because of the frequent ash beds found through Upper Permian and Lower Triassic rocks. In our first paper we estimated the duration of the extinction at < 1 Ma with an analytical uncertainty on the dated ash beds of ~ 300 k.y. (Bowring et al., 1998). Improvement in analytical methods steadily reduced the analytical uncertainties and with additional ash beds estimates of the extinction duration fell to 60 ± 48 k.y. (Burgess et al., 2014) and more recently to 31 k.y. ± 31 k.y. years (with an uncertainty on the radiometric dates of ± 31 k.y.) (Shen et al., 2018). This allows us not simply to evaluate the rates of biotic extinction, but related events such as changes in stable isotopes. We examined regional differences across south China in extinction patterns at very high resolution for the P/Tr (Wang et al., 2014) and this approach can readily be expanded to extend studies of biogeographic patterns of extinction (Jablonski & Raup, 1995; Jablonski, 2017; Kocsis et al., 2018).

High-resolution geochronology has also resolved a remarkable rapidity for other mass extinction intervals. The end-Triassic mass extinction was coincident with the generation of the Central Atlantic magmatic province and may have lasted as little as < 5 k.y. based on integration of geochronology with an astrochronologic timescale (Whiteside et al., 2007; Blackburn et al., 2013). $^{40}\text{Ar}/^{39}\text{Ar}$ dating of Late Cretaceous ash beds from the Hell Creek region of Montana indicates that the K/Pg extinction, not surprisingly, transpired over a few thousand years (Renne et al., 2013), and the close timing between the extinction and timing of the eruption of the Deccan volcanics has been explored (Schoene et al., 2015). Each of these mass extinctions was so rapid that despite evidently different causes (eruption of flood basalts for the P/Tr and end-Triassic, and impact for the K/Pg) the common factor may be how ecosystems collapse once an extinction begins (Erwin, 2014). Pursuing this idea requires peering into the internal dynamics of mass extinctions and other biodiversity crises, rather than being content with comparisons of before and after, and integrating detailed, very high-resolution palaeoecological studies with models of network collapse. Such a research effort would be enormously challenging, but could address some fascinating questions: Do collapses propagate from collapse of primary productivity, or is there a more widespread phenomenon? Do the dynamics of mass extinctions differ fundamentally from those of smaller crises, or do differences lie more in the extent of network disruption? Of immediate applicability is the issue of whether extinctions, once begun, can be reduced in severity. An indication of the complexity of the problem comes from a comparison of the impact of the end-Ordovician mass extinction on alpha, beta and gamma brachiopod diversity which documented the importance of changes in range size (Darroch & Wagner, 2015).

Phylogenetics

Counting taxa provides information about changes in taxonomic diversity, but a very limited view of the dynamics of extinctions or recoveries. Extinctions of equivalent magnitude can have very different effects on a clade depending on how they prune an evolutionary tree. For example, elimination of 50% of species could have relatively little impact on broader diversity by removing species within otherwise speciose clades. But the same 50% extinction could also eliminate entire clades (Erwin, 2001). Phylogenetic perspectives on extinctions can also reveal missing lineages crossing extinction boundaries. For decades echinoids were not known to appear until the Late Triassic (Norian), but phylogenetic analysis showed that they must have split from the cidaroid echinoids during the Permian, as later confirmed by fossil evidence (Smith & Hollingworth, 1990; Thompson et al., 2015). Simple counting of extinct and surviving taxa can be misleading, however, when there is phylogenetic correlation of the factors controlling extinction or survival. Friedman examined the selectivity of extinction among teleost fish during the K/Pg event, examining the impact of body size and jaw mechanics with both taxic and comparative phylogenetic approaches (Friedman, 2009). Using phylogenetic contrasts he showed that jaw mechanics was the dominant factor influencing extinction,

probably reflecting increased pressure on groups high in marine food webs. This approach is also valuable in highlighting regions of morphology vacated by extinctions which may be accessible during subsequent recovery periods. Phylogenetic studies have long played a role in understanding the relationship of the diversification of birds and placental mammals to the K/Pg extinction (Halliday et al., 2017; Ksepka et al., 2017), but have also proven critical to evaluating the effects of mass extinctions in other clades (Friedman, 2009; Hopkins & Smith, 2015). Character analysis provides the best way of analysing selective factors behind both extinction and survival during these events.

CONCLUSIONS

The remarkable advances in technologies will continue to open up new opportunities to understand the rates, causes, dynamics and implications of biodiversity crises, and equivalent properties of the subsequent biotic recoveries. But understanding the dynamics of biotic recoveries is perhaps an even more promising area for future developments, in part because it lagged so far behind work on mass extinctions. The technologies discussed here, and others as well, are just as vital for understanding diversification events after these biotic crises. But, if I could hazard a guess, I would suggest that network analysis may have the greatest future impact. Derived from studies in statistical physics, network analysis is now being used to study problems from finance and economics to social systems and the interactions of gene regulatory networks.

When my colleague Sam Bowring and I first collected volcanic ash beds from the P/Tr boundary sections at Meishan we skipped several beds because Sam “knew” that we would never be able to generate sufficiently accurate dates to discriminate the ages of those beds from overlying ash beds. I have never tired of reminding Sam that only a few years later we made a special trip back to China just to collect the ash beds we skipped. With our colleagues at NIGPAS, led at first by Professor Jin Yugan and then since Lao Jin’s death in 2006 by Shen Shuzhong, our estimates of the duration of the extinction have dropped by two orders of magnitude. If most biotic crises occurred more rapidly than we can pry apart with field studies this should not render them immune to modeling efforts to understand the dynamics of collapse in ecological time: Is collapse distributed across a network, or does it begin with reductions in primary productivity? Can we apportion the direct effects on extinction from extra-terrestrial impact or volcanic eruptions from the indirect effects of the collapse of ecological networks? How does extinction propagate between ecological networks in different regions or between sea and land? Network dynamics has increasingly powerful tools to address such questions, and their application promises ongoing insights. Puzzles also remain about the fundamental evolutionary questions about mass extinctions, including how different they are from “background”, and how they have influenced subsequent evolutionary trajectories.

All scientific understanding is provisional. In the early 1970s papers by Valentine & Moores implicating

changing continental configurations and regression as the primary causes of the P/Tr mass extinction left many with the unfortunate view that the problem had been “solved” (Valentine & Moores, 1970, 1973). Consequently, the P/Tr event largely disappeared as a research question from the early 1970s until the late 1980s. As a young graduate student of his, I queried Jim Valentine about these papers, and his only, typically enigmatic (and maddening), response was that they were “not correct”. He left it to me to figure out just how they were wrong (enlightenment took about 18 months). Sam Bowring’s certainty about dating those ash beds at Meishan was misplaced as well, and some of what we are certain about mass extinctions and biotic rebounds will turn out to be similarly “not correct”. We can only hope that as new results illuminate the dynamics of these events, they will continue to reveal new understanding of their evolutionary impact.

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