

Temporal acuity and the rate and dynamics of mass extinctions

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In the excitement over the discovery of high levels of the element iridium at the Cretaceous-Paleogene (KPg) boundary and the high likelihood that the KPg mass extinction (66 Ma) was caused by the collision of an extraterrestrial object with Earth (1),

many envisioned a general theory of mass extinctions driven by impacts (2). Others favored an endogenous process, identifying correlations between the eruption of massive flood basalts and mass extinctions (3). A general model of mass extinctions and other biodiversity crises seemed to be supported by time-series analyses of compilations of the marine fossil record, which revealed a periodic pattern to extinctions over the past 250 million y (4). Over the past decade or so, evidence has grown for distinctive causes for the Permo-Triassic (PT) and the KPg mass extinctions, belying any general mechanism. However, in PNAS, the Burgess et al. (5) paper regarding very high-resolution radiometric dates for the PT event suggests that the similarities may lie not with the triggering mechanisms but in how the Earth's biota responds to environmental insults.

The PT boundary sections near the village of Meishan in Zhejiang Province, China, are the most intensively studied in the world. Easily accessible from Nanjing and Shanghai, they serve as the global reference sections for the boundary. More importantly, the mudstones and carbonates that outcrop along several kilometers of an old phosphate mine are interbedded with numerous layers of volcanic ash. For more than a decade geochronologic dating of the radiometric minerals in such ash beds have been producing dates of progressively higher resolution. In 1988, before the direct dating of these ash beds, the uncertainty on the age of the PT boundary was ± 4 Myr (6) and there was no data on the duration of the extinction. By 1998 uncertainties on U-Pb dating of these ash beds at Meishan were ± 300 ky and it was clear that the extinction was rapid (7). Now the uncertainties have improved to 31 ky (5), showing that the extinction was rapid indeed. [Astronomical (Milankovitch) cyclicity has also been used to evaluate the timing of this extinction (8), but has been difficult to test.] This improved temporal resolution has been driven by the need to distinguish the

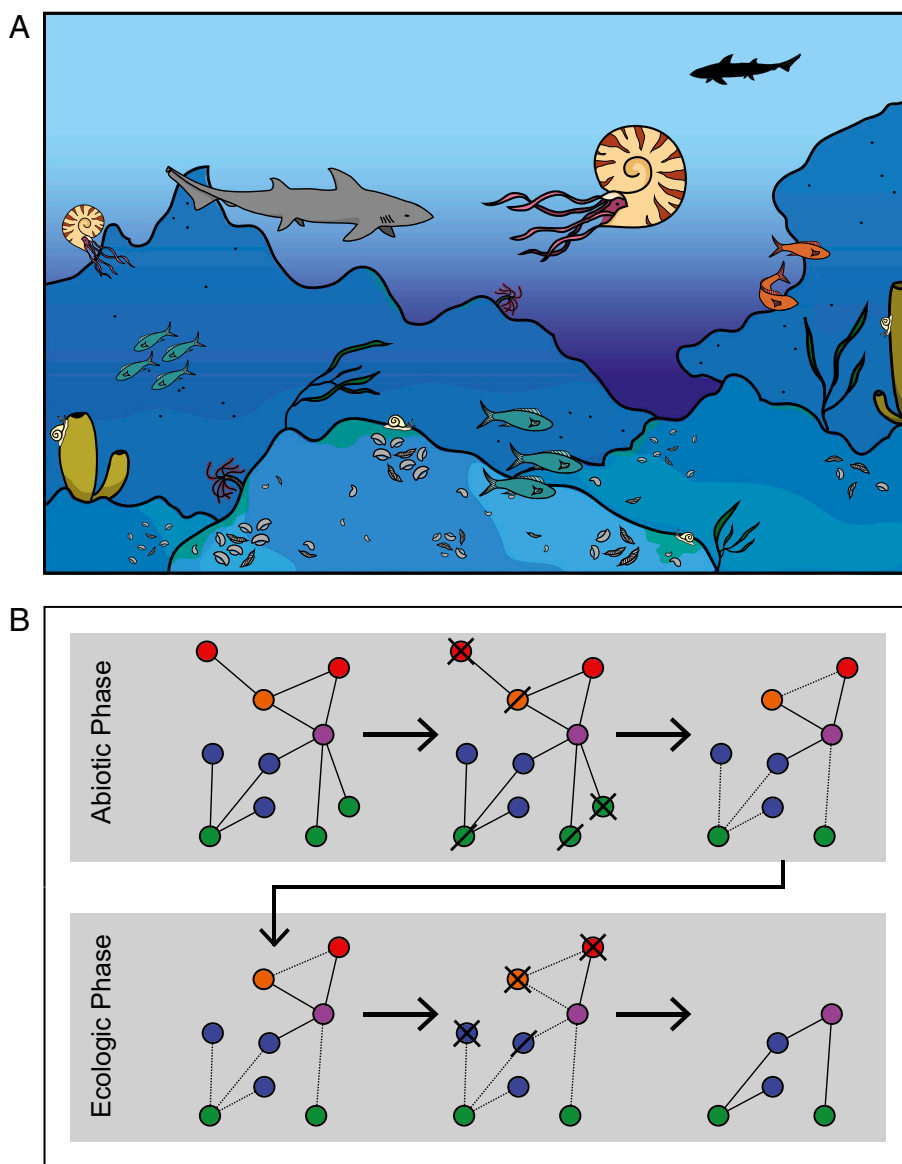


Fig. 1. (A) Reconstruction of a late Paleozoic reefal ecosystem. (B) Network effects of the abiotic and ecologic phases of a mass extinction on an ecological web. In the abiotic phase nodes with an "X" go extinct and those with a "/" experience reduced abundance, resulting in weakened ecological links (shown by dotted lines) in the reduced web to right. In the ecologic phase further extinctions occur, resulting in the postextinction web at right. (Image courtesy of Sarah Tweedt.)

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sequence of physical and biological events: Did a shift in carbon isotopes happen before, simultaneously, or after a mass extinction? What is the coincidence in timing between an extinction horizon and volcanic eruptions? Was a rapid increase in temperature associated with extinction, or did it occur during the aftermath? These and similar questions can only be investigated with very high resolution dates of the sort reported here (5).

Several of the implications of Burgess et al. (5) provide a new temporal framework for the Meishan section and for the PT mass extinction, and several of their findings are worth noting. The authors establish the maximum duration of the extinction was 61 ± 48 ky. In fact, the fossil data from Meishan (9, 10) suggests that the bulk of the extinctions happened even more rapidly than the interval identified by Burgess et al. (5), which would further shorten the duration of the extinction. The negative $\delta^{13}\text{C}$ shift began before the onset of extinction and was very brief, <20 ky, with the overall perturbations in the carbon cycle lasting <500 ky. An approximately 10°C temperature increase was coincident with the extinction interval (11, 12), as was an increase in ocean acidification (13). The Meishan PT section is highly condensed, making the ability of Burgess et al. (5) to resolve the sequence of events all the more remarkable. Applying this highly improved temporal resolution to less-condensed boundary sequences should further clarify the relationship between these changes and the extinction.

Several other recent studies have shown how high-resolution geochronologic analyses can help dissect the dynamics of extinction. Last year high-resolution $^{40}\text{Ar}/^{39}\text{Ar}$ dating of volcanic ash beds from the Hell Creek region of Montana and of tektites (impact melt droplets) from Haiti associated with the Chicxulub impact debris established that the two events coincided within 5 ± 27 ky (14), contrary to earlier claims that the impact preceded the KPg mass extinction by 180–300 ky. These results also show the associated $\delta^{13}\text{C}$ anomaly lasted 5 ± 3 ky, and the initial, postextinction basal Puercan mammalian fauna had a duration of only 53 ± 34 ky. The end-Triassic mass extinction, another of the “Big 5” mass extinctions, was synchronous with the earliest phase of the eruption of flood basalts associated with the Central Atlantic Magmatic Province (15). In this case, integration with a previously constructed astrochronologic timescale (16) suggests that the extinction duration was <5 ky. Many other smaller

biodiversity crises have also been identified in the fossil record (17). The duration of one of these, the late Devonian Hangenberg event, has also been determined by high-resolution geochronology. This episode of global cooling and biodiversity crisis lasted <90 ky based on U-Pb dating of ash beds in Poland that bracket the event (18).

In each case these durations are likely maximum durations, limited by geochronologic techniques and linear interpolation of sediment deposition between dated ash beds. The durations reflect a temporal acuity far finer than paleontologists and stratigraphers could contemplate even a few years ago. Achieving such resolution is a credit to the EARTHTIME initiative (earth-time.org), an international consortium of geochronologists and others who have spent the past decade refining radiometric dating methods, improving laboratory standards, and addressing interlaboratory correlation.

The geochronologists have done their job, and now it is time for paleobiologists to further explore the dynamics of mass extinctions. The rapidity of these events suggests that the biosphere may collapse at a similar rate, and perhaps in a similar fashion, independent of the ultimate cause of the event. In other words, a general theory of biotic crises should focus on the dynamics of extinction rather than the triggering events. In the past paleontologists have not been able to achieve sufficiently high resolution during a mass extinction event to deconvolve taxa that disappeared because of the primary, abiotic effects of the crisis (blast effects, rapid climatic change, anoxia, loss of habitat, and so forth) from the secondary and largely

biotic effects associated with the collapse of ecological interactions (both trophic and nontrophic interactions) (Fig. 1), instead evaluating patterns of selectivity after an extinction.

We really do not have a sense for the relative importance of these two aspects of extinction dynamics. Paleontologists have often assumed that mass extinctions wiped out primary productivity at the base of ecosystems, with the effects percolating upward through herbivores and the species that feed upon them. An equally compelling alternative is that the abiotic extinctions are distributed throughout ecological networks, triggering cascades of secondary extinction through collapse of ecological interactions, much as a small power outage can ripple across large areas. Consider a network where the nodes are species and the vertices trophic and nontrophic interactions between them (in contrast to a food web, which considers only trophic interactions). Primary extinction effects will remove some percentage of nodes and trigger secondary extinctions of other nodes that will cascade through the network. One could evaluate a plausible range of network structures with differing proportions of primary and secondary extinctions to ask what sort of extinction and what sorts of network structures, will cause a total extinction of magnitude x when some number of nodes are removed because of the primary extinction. Studies of network dynamics have already addressed closely related questions (19) and extending this work to mass extinctions may prove enlightening about past events, and cautionary about our immediate future.

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