Extinction: past and present

The fossil record, together with modern data, can provide a deeper understanding of biological extinction and its consequences.

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Extinction is a fundamental part of nature — more than 99% of all species that ever lived are now extinct. Whereas the loss of 'redundant' species may be barely perceptible, more extensive losses of whole populations, groups of related species (clades) or those that share particular morphologies (for example, large body sizes) or functional attributes such as feeding mechanisms, can have profound effects, leading to the collapse of entire ecosystems and the extermination of great evolutionary dynasties. The challenge is to understand both the causes — particularly the biological attributes that govern species' vulnerability — and the consequences of extinction.

These challenges are of more than academic interest. Today's biota is beset by many stresses, such as habitat destruction and fragmentation, over-exploitation and invasive species. In addition, species are susceptible to chain reactions that can destabilize them from the top down (by removing predators and other consumers) or from the bottom up (by removing or replacing primary producers). The most daunting obstacle to assessing and responding to these problems is the lack of anything close to a full accounting of present-day biodiversity: the 1.75 million known species probably represent less than 10% of the true inventory, and the figure is surely less than 1% for genetically distinct populations. Attempts to estimate global extinction from rates of habitat loss may eventually be verified, but a more effective strategy has been to analyse extinction in groups where the (approximate) size of the species pool is known, as in North American birds, tropical palms or Australian mammals. Such analyses have generally found, first, that the extinction or endangerment of species and populations is proceeding at an alarming pace, and second, that selectivity of extinction or decline tends to match theoretical expectations. For example, species with slow population growth rates, low population densities, or narrow geographic ranges tend to be more extinction-prone.

However, empirical data on extinction risk do not always follow neat theoretical lines. For example, large body size is associated with vulnerability in primates and birds, but is unimportant in carnivores, reptiles and marine mollusks. What emerges as an important issue is the covariation among the many traits that affect extinction risk — species with high population densities tend

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Loss and gain: the extinction of the dinosaurs allowed the diversification of the mammals.

to have short generation times, small body sizes and so on — so that indirect effects may underlie apparent patterns. Further, this covariation is complex, with relationships among traits often defining polygonal fields rather than linear trends (for example, small-bodied forms may be widespread or spatially restricted). And the impact of different factors may depend on the extinction mechanism, such as habitat loss versus introduced predators. We are only beginning to get to grips with such problems.

The fossil record is a spectacular archive of extinction, and provides a vital deep-time perspective on factors governing extinction patterns. Analyses of present-day biodiversity often can only measure the net outcome of past extinction and origination, whereas the fossil record is a direct window onto raw rates of taxonomic survival or extinction. Despite differences in scale and taxonomic coverage, palaeontological analyses of extinction tend to corroborate theory and present-day data, and extend them to evolutionary timescales in important ways.

The major mass extinctions are a different story. These rare events (five over the past half-billion years, each estimated to have removed more than 60% of marine species) bring not only surges in extinction intensity, but often shifts in selectivity as well. Factors that are apparently significant for 'normal' extinctions (such as local abundance, reproductive mode, body size, feeding strategy, geographic range at the species level and species richness) had little effect on the survival of clades during the mass extinction at the end of the Cretaceous period of 65 million years ago, and were unimportant in one or more of the other mass extinctions as well. The 'big five' mass extinctions appear to fit a model of 'non-constructive selectivity' — not strictly random, but often selecting on features such as clade-level geographic range that are not tightly linked to traits favoured during 'normal' times, and thus are unlikely to reinforce or promote long-term adaptation. Perhaps intrinsic factors diminish in importance with increasing perturbation, as also seen in today's freshwater fishes and Australian marsupials. Those shifts in selectivity, along with the sheer magnitude of the 'big five' events, may explain why post-extinction periods are famously important in opening opportunities for once-marginal groups, for example the expansion of mammals after the dinosaurs' demise.

In assessing extinction and the diversity of the remaining biota it is important to look at more than just the number of species lost. This is because the random loss of taxa generally has a weak impact on morphological diversity, whereas extinctions of clades can have far greater impact. Thus, the same taxonomic extinction intensity can have different effects on the morphological variety of the survivors, and significant adaptations can be lost simply because they belonged to a taxon that lacked other features, such as broad geographic range, that promoted extinction-resistance.

We still do not know how directly relevant the ancient mass extinctions will be to the present-day situation. But even excluding the 'big five' events, the fossil record contains a multitude of natural experiments on, for example, global warming or cooling episodes that exceed the ability of species to cope with local conditions, the disassembly of ecological communities, the extinction of formerly robust taxa and the colonization of previously sparsely populated habitats. All of these experiments are relevant to present-day systems. The comparative calibration of extinction magnitudes and effects, and how they relate to the initial state of the system, to the nature of the driving mechanisms, and to post-extinction physical and biotic conditions, will all be important components of a fuller theory of biodiversity dynamics. ■

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FURTHER READING

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