

Abrupt global shifts in ecosystem states

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On the face of it, deep-time paleoecology—trying to reconstruct species interactions and the flow of matter and energy in a complex ecosystem using nothing more than the remains of long-extinct organisms—seems like folly. Fossil data are biased, time-averaged residues of once-living systems in which it is impossible to directly observe or experimentally manipulate organism interactions. This is simply the nature of historical data; what happened in the past is done and history cannot be rerun. However, just as the study of human history provides examples

to understand political, social, and economic dynamics in the present day, the fossil record provides examples that have much to teach us about how modern ecosystems work. In PNAS, Aberhan and Kiessling (1) use the response of benthic marine molluscan assemblages to a severe global perturbation (the end-Cretaceous mass extinction 66 million years ago) to shed light on the complex dynamics of ecological systems.

Aberhan and Kiessling (1) focus on the functional ecology of mollusks from four sites

that span half the globe. To have a basis for comparing the fossil assemblages to each other in their pre- and postextinction states, the authors classified all species according to mode of life (e.g., mobile vs. sessile, infaunal vs. epifaunal, carnivorous vs. herbivorous, and so forth). Before the end-Cretaceous extinction, the proportions of species in different modes of life differed among all four sites but were relatively stable for several million years. After the Earth system recovered from the immediate and extreme effects of the extinction-causing event, communities at all four sites displayed decreased taxonomic diversity and changes in the proportions of different modes of life relative to their preextinction states. This is not surprising following a global-scale disruption that resulted in the loss of up to 75% of marine invertebrate species. The surprise is that communities at all four sites appear to have changed in the same way—they all show an increase in the abundance of mobile, infaunal, and deposit-feeding organisms and a decrease in suspension-feeding organisms—and the changes persisted for millions of years after the immediate environmental effects of the end-Cretaceous event.

This finding is significant because several other possible outcomes with different implications for how ecosystems work can easily be imagined. For example, the communities at each site could simply have returned to their original functional ecological structure despite substantial loss of taxonomic diversity (Fig. 1A). Such a result would be consistent with the idea that ecosystems contain a great deal of functional redundancy and that the role played by any one species in the community can be readily filled by others. In this scenario, the way an ecosystem functions would be a reflection of the environment it occupies rather than its particular species membership.

Alternatively, selective loss of particular modes of life could have resulted in much more similar functional ecological structure across the four sites (Fig. 1B). In this scenario, loss of taxonomic diversity results in a loss of functional diversity but not stability. Another

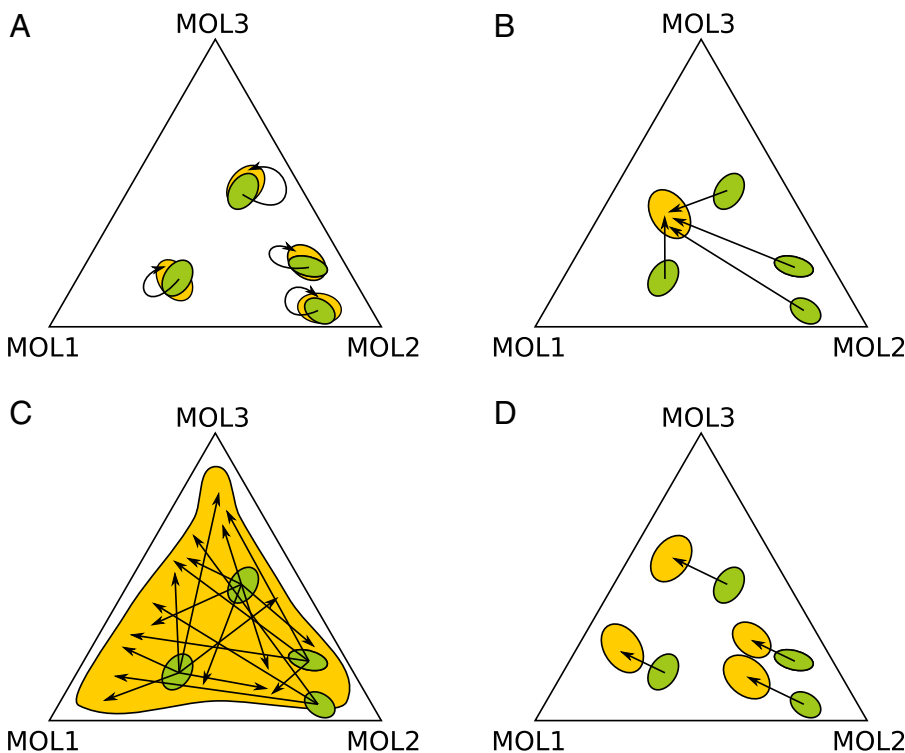


Fig. 1. Possible changes in functional ecology of benthic molluscan assemblages across the Cretaceous–Paleogene boundary. The apices of the ternary or simplex plots of functional ecology each represent a mode of life (MOL). Any individual ecological assemblage can be plotted as a point based on the proportion of species or specimens in each of the three modes of life. (Additional modes of life can be accommodated by increasing the number of apices/dimensions of the simplex.) Green areas cover the range of community variation among samples at each of four sites before the end-Cretaceous event; orange areas cover the range of community variation at each site after the end-Cretaceous event. (A) Ecosystems return to their pre-extinction state. (B) Ecosystems converge on a single postextinction state. (C) Ecosystem disruption results in loss of stability and increase in variation, including states dominated by a single mode of life. (D) Aberhan and Kiessling’s (1) result: despite starting in significantly different functional ecological states, all four sites shifted to new states in the same direction.

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alternative would be for the functional ecology of communities to have become much less stable, shifting rapidly from dominance by one mode of life to another (Fig. 1C). This kind of postextinction shift would suggest that functional stability is dependent on taxonomic diversity. In both of these scenarios, recovery to the relatively stable and functionally distinct community states seen before the perturbation event would require sufficient timescales for evolution to replace the functional as well as taxonomic losses suffered during the extinction.

Instead of any of these outcomes, Aberhan and Kiessling (1) find that the communities they analyzed recovered functional stability long before they recovered taxonomic diversity after the end-Cretaceous mass extinction, but that they had all moved to a new functional state (Fig. 1D). If this shift had been observed at just one site or in only a restricted geographic area, then it could easily be interpreted as a community-level response to a change in local environmental conditions. The fact that four communities from very different parts of the globe and starting from different functional states exhibit similar changes suggests that something more fundamental is being detected in the fossil record. The ecological shift could represent a response to a change in a global Earth system parameter that influenced all of the analyzed communities in a similar way, but Aberhan and Kiessling found little or no evidence for this. Instead, they interpret their results to represent a hysteretic shift (2) in the state of benthic marine ecosystems. In other words, the end-Cretaceous event was such an extreme perturbation that it pushed the global ecosystem beyond a point from which it could return to its previous functional configuration, and it instead settled into an alternative func-

tional state when similar environmental conditions were restored.

The idea that modern ecological systems can shift between alternative states abruptly is well established (2, 3), but the implications for fossil ecosystems are only beginning to be explored. In a pioneering study modeling terrestrial vertebrate communities from the Karoo Basin of South Africa before and after the end-Permian mass extinction, Roopnarine et al. (4) found that primary extinctions

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beyond a threshold magnitude resulted in a cascade of secondary extinctions and that postextinction communities composed of the surviving lineages differed fundamentally in structure from—and were much less stable (Fig. 1C) than—their pre-extinction predecessors.

Alternatively, ecological models of brachiopod assemblages from the Permian Reef in west Texas (5) indicate that high-diversity systems can settle into a pseudosteady transient state (not a true equilibrium) that can

last for millions of generations (i.e., geologic timescales), and when perturbed return to a state that is functionally similar but has significantly different relative abundances of the same lineages (Fig. 1A). In this case, ecological systems can move from one apparently stable state to another without requiring true hysteretic shifts.

What both of these studies (4, 5) share with Aberhan and Kiessling's (1) work is the idea that processes understood by ecologists studying living organisms in the present can successfully be extrapolated over geologic timescales to make surprising predictions that are only testable using fossil data. Importantly, defining what is stable and what is not requires information about ecosystems that is not readily available through experimentation and observation over human timescales but that can be studied through judicious use of the fossil record, despite its inherent limitations.

The global-scale ecological shift documented by Aberhan and Kiessling (1), based on fossil data, provides a lesson that is analogous to the warning of climate scientists regarding the effects increasing atmospheric pCO₂: although the increase may be gradual, the response of the Earth's climate system may result in an abrupt shift to a different state that is not reversible over human timescales. Similarly, sufficient perturbation of the global ecosystem in Earth's past has resulted in effectively irreversible shifts in how it functions, and if it happened then, it can happen again.

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4 Roopnarine PD, Angielczyk KD, Wang SC, Hertog R (2007) Trophic network models explain instability of Early Triassic terrestrial communities. *Proc Biol Sci* 274(1622): 2077–2086.

5 Olszewski TD (2012) Persistence of high diversity in non-equilibrium ecological communities: Implications for modern and fossil ecosystems. *Proc Biol Sci* 279(1727): 230–236.