

Diversity of Life Through Time

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Global diversity can be defined as the number of taxa extant in the present day or at any given time in the geological past. Using data collected from the fossil record, palaeontologists have reconstructed the trajectory of global biodiversity throughout the history of life. Documentation of this trajectory has fuelled a vigorous research agenda focusing on the causes of major diversity increases (radiations), decreases (extinctions) biotic transitions and the relationship between diversification in the marine and terrestrial realms.

Diversification of Life

Over the past quarter century, palaeontologists have calibrated and interpreted historical trends in the global number of taxa (i.e. global biodiversity) through geological time. While this research has been accelerated by technological advances that permit compilation and analyses of large sets of data, the prime motivation for this work emanates from two scientific themes:

1. Global diversity increases (radiations), decreases (extinctions), and changes in taxonomic composition through geological time reflect a variety of evolutionary processes. While the task of unravelling these processes is difficult, successful attempts reveal much about the role of evolution in mediating the history of life.
2. Global biodiversity trends in the past may help us to understand fate of biodiversity in the face of human-induced changes to the planet. The fossil record is the only source available for understanding the long-term consequences to biodiversity of physical perturbations to the Earth at local, regional and global scales. Because many human-induced changes to the Earth have natural analogues in the geological past (e.g. intervals of global warming), analyses of biodiversity in the face of these changes can be revealing. Researchers seeking to determine whether the Earth is currently experiencing a mass extinction of species have looked to the history of biodiversity for insights into levels of diversification and extinction expected 'naturally', in a world not influenced unduly by *Homo sapiens*.

Introductory article

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Patterns – Marine, Nonmarine, Vertebrates, Plants

Calibrating global diversity trends

The documentation of global diversity trends through time is simple conceptually. All that is needed is a table of how many fossil species lived on the planet during successive intervals of geological time.

That said, creating well-calibrated global diversity curves is actually very difficult in practice. First, no single researcher can possibly visit all of the world's fossiliferous strata to collect the data required for a depiction of global diversity throughout geological time. Thus, researchers have sought to construct compendia of fossil occurrences based on fossil occurrences at outcrops documented in the palaeontological literature. Typically, these compendia depict the oldest and youngest known global occurrences of individual taxa, which can then be used for diversity tabulations, with the assumption that each taxon was extant for the entire interval between its first and last occurrences.

Second, experience has shown that it is usually not practical to determine directly the number of species preserved globally throughout the history of life: there is too much uncertainty about species-level identification in many cases, and the sheer number of fossil species catalogued in the literature is daunting. While there have been attempts to construct global diversity curves at the species level, these are based either on random subsampling of the fossil record or on other means of statistical estimation (plants are exceptions; see below). Thus, global diversity compendia and curves have usually been constructed at the higher taxonomic levels of family or genus, with the inference that their most salient features would also have been observed at the species level.

Third, any pattern of taxonomic diversity through the entire Phanerozoic eon might be an artefact of changes in the quality of the fossil record. Most notably, researchers interested in the fossil record of marine (ocean dwelling) organisms have long worried that changes through time in the volume of sedimentary strata – the kinds of strata likely to contain fossils – are correlated directly with perceived levels of biodiversity. All else being equal, stratigraphic intervals containing larger volumes of sedimentary rock would be expected to contain more fossils and, therefore, a greater number of fossil taxa. This problem was noted as far back as 1860 by John Phillips, who is widely credited with publishing the first Phanerozoic diversity curve (**Figure 1a**). Interestingly, Phillips' diversity trajectory, which was limited in scope to the fossiliferous strata of Great Britain, would have exhibited maximum diversity in the Palaeozoic era had he not adjusted his values to account for the overwhelming volumetric dominance in British strata of Palaeozoic rocks. In global compilations, however, David Raup showed in 1976 that the Phanerozoic sedimentary rock record exhibits a pattern that is nearly the reverse of Britain by itself. Globally, a much greater volume of sediment is preserved for intervals of the Cenozoic era than for comparable intervals of the preceding Mesozoic and Palaeozoic eras. This has led to the suspicion that raw, uncorrected depictions of Phaner-

ozoic diversity, which all exhibit major increases during the Cenozoic (**Figure 2**), may similarly reflect increases in the available volume of the fossil record, rather than a genuine increase in biological diversity.

These and other concerns must be taken seriously, and remain as active avenues of investigation. Nevertheless, comparative analyses of global diversity compilations for marine organisms have revealed that the broad outlines of Phanerozoic diversification are probably not affected unduly by any of them. Nearly the same diversity trajectory has been recognized by researchers working independently, and with their own predilections, on: compilations at the taxonomic levels of family and genus; a compilation for species based on a statistical subsampling of published species records; and species-level compilations for skeletonized organisms and for trace fossils based on the median numbers of species contained within individual fossil assemblages drawn from each stratigraphic interval. Because it relies on determination of a median, this latter means of compilation is not governed directly by the actual number of assemblages or specimens preserved in each interval and, thus, is thought to avoid the problem of rock volume.

These issues have not been settled entirely and, in fact, a major effort is now under way to standardize the global marine trajectory with respect to sampling variation.

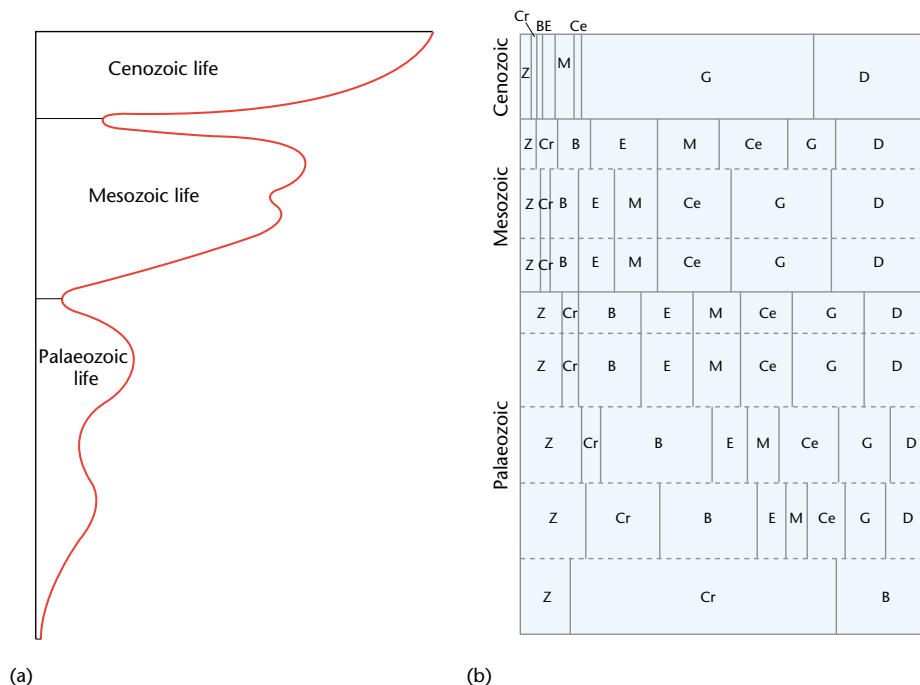


Figure 1 (a) John Phillips' 1860 depiction of the changing number of species throughout geological time, based on a compendium of fossil data from Great Britain (redrawn from Figure 1 of Phillips, 1860). (b) Phillips' rendition of the changing composition of marine invertebrate biotas through the Phanerozoic (redrawn from Figure 6 of Phillips 1860; taxonomic designations and spellings, some of which are outdated, are those of Phillips). Z, Zoophyta; Cr, Crustacea; B, Brachiopoda; E, Echinodermata; M, Monomyaria; Ce, Cephalopoda; G, Gasteropoda; D, Dimyaria.

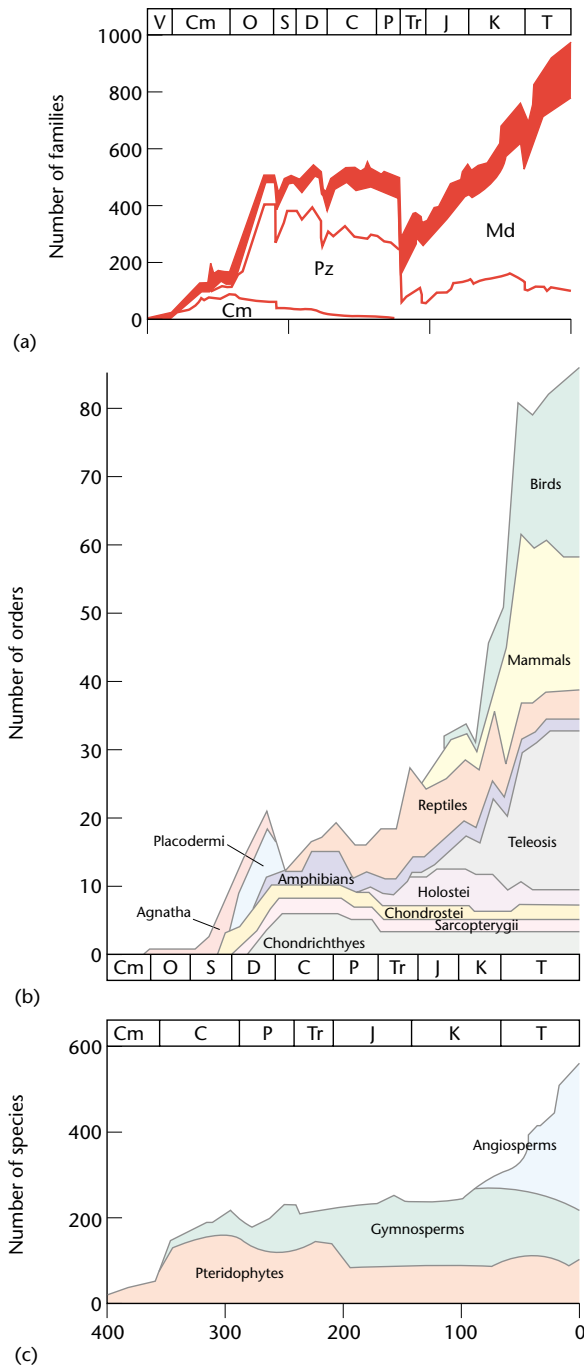


Figure 2 Illustrations of global Phanerozoic diversity trajectories for (a) marine families (based on an updated version of Figure 5 in Sepkoski, 1981; darkened region depicts poorly preserved taxa), (b) marine and terrestrial vertebrate orders (redrawn from Figure 3 of Padian and Clemens, 1985), and (c) terrestrial plant species (redrawn from Figure 8.15 in Niklas, 1997). Abbreviations in 2a denote the Cambrian (Cm), Palaeozoic (Pz) and Modern (Md) evolutionary faunas of Sepkoski. Timescale abbreviations include: V, Vendian; Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary.

However, it has been assumed conventionally by palaeobiologists that the raw patterns described are biologically meaningful.

Marine diversity

Because the likelihood of burial by sediments after death is greater in marine than in nonmarine settings, the fossil record is dominated overwhelmingly by marine organisms, and these provide the most comprehensive Phanerozoic diversity trajectories. While there have been several efforts to compile marine diversity trajectories since the 1960s, perhaps the best known depiction was presented by J. John Sepkoski, Jr, initially in 1981 (**Figure 2a**). It was constructed at the family level using a compendium of some 5000 fossil marine families that Sepkoski published in 1982 and updated regularly thereafter. Subsequent curves constructed at the genus level by Sepkoski in 1996, and at the family level by Michael Benton in 1995, share several major features with Sepkoski's earlier effort: an initial increase in the Cambrian (the 'Cambrian explosion'), followed by a more extensive diversification in the Ordovician (the 'Ordovician radiation'). For most of the remaining Palaeozoic, diversity apparently stabilized, only to increase anew through the Mesozoic and, especially, the Cenozoic. This trajectory was punctuated by a series of mass extinctions including the so-called 'big five': the Late Ordovician, Late Devonian, Late Permian, Late Triassic and Late Cretaceous (K/T) events.

While it is thought that broadly similar patterns would also be observed in a species-level compilation, the same is not true of marine diversity trajectories at taxonomic levels above that of family. At those higher levels, diversification is clearly 'front-loaded' in the Cambro-Ordovician or even earlier, and diversity trajectories for these higher taxa appear to stabilize well before the end of the Palaeozoic. In fact, based on the exquisite preservation of soft-bodied organisms in the Middle Cambrian Burgess Shale, Stephen Jay Gould and others have suggested that the Cambrian explosion was characterized by an unrepeated burst of diversification of basic phylum-level body plans, several of which subsequently became extinct. While this view remains controversial, it is clear that Phanerozoic diversity at the phylum level would not be expected to increase significantly, and might even decrease, towards the present day.

Underlying the diversity trajectory recognized at the family and genus levels are several significant transitions in the taxonomic compositions of marine biotas; a snorkelling excursion over a Palaeozoic seafloor would have revealed a seemingly alien world. Sepkoski recognized three Phanerozoic 'evolutionary faunas', each characterized by distinct taxonomic classes: the trilobite-rich Cambrian fauna, which dominated Cambrian seas, but declined in diversity thereafter; the Palaeozoic fauna, rich

in articulate brachiopods, stalked crinoids, stenolaemate bryozoans, and tabulate and rugose corals, which diversified dramatically during the Ordovician radiation and characterized seafloors for the remainder of the Palaeozoic; and the Modern fauna, dominated by gastropods, bivalves, echinoids and gymnolaemate bryozoans, which also underwent an initial radiation early in the Palaeozoic, but diversified much more appreciably in the post-Palaeozoic, far outstripping the diversity levels of earlier evolutionary faunas.

Vertebrate diversity

In 1985, Kevin Padian and William Clemens prepared a comprehensive overview of the Phanerozoic diversity trajectory for marine and nonmarine vertebrate orders (**Figure 2b**). Subsequent analyses at the family level have corroborated the major features exhibited by this trajectory, which is highlighted by several notable transitions: among fish, a Palaeozoic biota gave way in the late Mesozoic and Cenozoic to an assemblage dominated by teleosts; in the terrestrial realm, the initial, mid-Palaeozoic domination by amphibians was followed in the late Palaeozoic and, especially, the Mesozoic by an increased diversity of reptiles; the Cenozoic was highlighted by significant radiations of mammals and birds, which achieved diversity levels far in excess of other vertebrate classes.

Terrestrial plant diversity

The broad outlines of Phanerozoic floral diversity, described in a series of publications by Karl Niklas, reveal that the majority of Phanerozoic plant species can be classified into three sequential groups (**Figure 2c**): pteridophytes (e.g. ferns, lycopods and sphenopsids), which dominated floral assemblages of the Palaeozoic; gymnosperms (e.g. pines and conifers), which became increasingly diverse during the Mesozoic; and angiosperms (flowering plants), which first radiated during the Cretaceous period and became the most diverse of the three groups during the Cenozoic.

What causes global-scale biotic transitions?

The three graphs depicted in **Figure 2** all exhibit a broadly similar pattern: sequential domination by different groups during each of the three Phanerozoic eras, with younger faunas and floras achieving higher levels of standing diversity than their predecessors. Even if the dramatic Cenozoic increases depicted in these graphs result partly from the kinds of sampling artefacts described earlier, the underlying transitions in biotic composition exhibited in all three cases are surely real and motivate the obvious question: what caused them? A complete review of the vast

literature on this contentious question is beyond the scope of this essay. At one end of the spectrum are explanations that invoke global-scale competition among groups, with one group outcompeting another over the long term and ultimately supplanting it. At the other end of the spectrum are suggestions that global-scale transitions have little to do with long-term competitive advantages but, rather, result from 'chance' events that induce mass extinctions and decimate incumbent groups, thereby emptying eco-space worldwide and providing opportunities for the diversification of new groups. While a dispassionate look at the geometries of diversity increase and decrease exhibited by two groups under comparison should differentiate between such alternatives, in reality nearly every major biotic transition remains contentious. Two classic examples are the marine transition from articulate brachiopods (major elements of the Palaeozoic evolutionary fauna) to bivalve molluscs ('clams'; important constituents of the Modern evolutionary fauna), and the terrestrial transition from dinosaurs to mammals. In both cases, arguments continue about whether clams were competitively superior to brachiopods or mammals to dinosaurs. That each transition is closely associated in time with a mass extinction – the End Permian event in the case of brachiopods versus clams and the Late Cretaceous extinction in the case of dinosaurs versus mammals – has obviously motivated the counterargument that mass extinctions played more than passing roles in both transitions.

Equilibrium and Expansion Models

Dovetailing on the discussion of biotic transitions is another fundamental question: what governs the shape of the overall diversity trajectory throughout the Phanerozoic? Early in the history of diversification for all three biotas, there was an initial phase during which diversity increased rapidly (**Figure 2**). However, this was followed by an interval during which diversity stabilized. It is perhaps not surprising that this should be the case: the Earth offers a finite amount of ecospace, and it is logical that the world should eventually fill up with organisms, thereby inhibiting further diversification. In fact, the body of theory related to the colonization and eventual biological saturation of newly emergent islands supports this view. As diversity increases, the rate of origination of new species should decrease and the rate of extinction of existing species should increase; eventually the two rates should counter-balance one another, resulting in the achievement of equilibrium diversity.

Further investigation of the empirical record suggests a more complex picture, however, in that the marine and nonmarine realms did not simply become saturated with taxa: in all three examples in **Figure 2**, the stable interval was

ephemeral, and diversification began anew, apparently continuing to the present day. The role, if any, of equilibrium models in producing this pattern has been contentious, with three different models figuring prominently.

In several investigations that culminated in 1984, Sepkoski argued that equilibrium models played central roles in mediating Phanerozoic marine diversity, but that each of the three evolutionary faunas was characterized by its own level of equilibrium, owing to significant differences among them in average rates of origination and extinction. To accommodate these differences, Sepkoski developed a model in which diversity of each of the three evolutionary faunas was governed by a separate equation, or 'phase'; the model was 'coupled' in that the three phases interacted numerically with one another. The diversity of any one of the phases was affected during a modelled time interval by that of the other two phases, and changes in the levels of diversity through time were driven by these interactions. When Sepkoski simulated the major mass extinctions of the Phanerozoic as part of the model, he produced an outcome that closely matched the empirical pattern of Phanerozoic marine diversification (**Figure 3a**). From this perspective, equilibrium diversity has not yet been achieved because the equilibrium level for the now-dominant Modern fauna lies in the future. Moreover, the incorporation of mass extinctions was shown to affect diversity only temporarily, and trajectories predicted by the model in the absence of mass extinctions were simply resumed following the extinction 'events'. Thus, Sepkoski suggested that mass extinctions had little long-term effect on the Phanerozoic history of biotic transitions.

As shown by Richard Bambach in 1985, there is palaeoecological support for the claim that each successive evolutionary fauna should have achieved a higher level of equilibrium diversity than its predecessor: taxa comprising the Palaeozoic fauna occupied a larger number of habitats than those of the Cambrian fauna, and members of the Modern fauna, in turn, occupied a broader spectrum of habitats than the Palaeozoic fauna. Thus, the effective 'size' of the world available to each fauna increased, which would have permitted a greater level of equilibrium diversity.

In 1995, Benton countered with an argument that equilibrium diversity models are not supported by the empirical pattern. Instead, he suggested that the Phanerozoic diversity trajectory in both the marine and terrestrial realms best matches the expectation of a still-unfolding exponential diversification (**Figure 3b,c**): the logarithm of diversity provides a significant statistical fit to a straight line, suggesting that the per-taxon rate of diversification has been constant throughout the Phanerozoic. Subsequently, Benton conceded that, despite the statistical support for the pattern, a simple exponential diversification is an unsatisfying descriptor of marine diversification: this problem is easily observed in **Figure 3c**, in that the slope

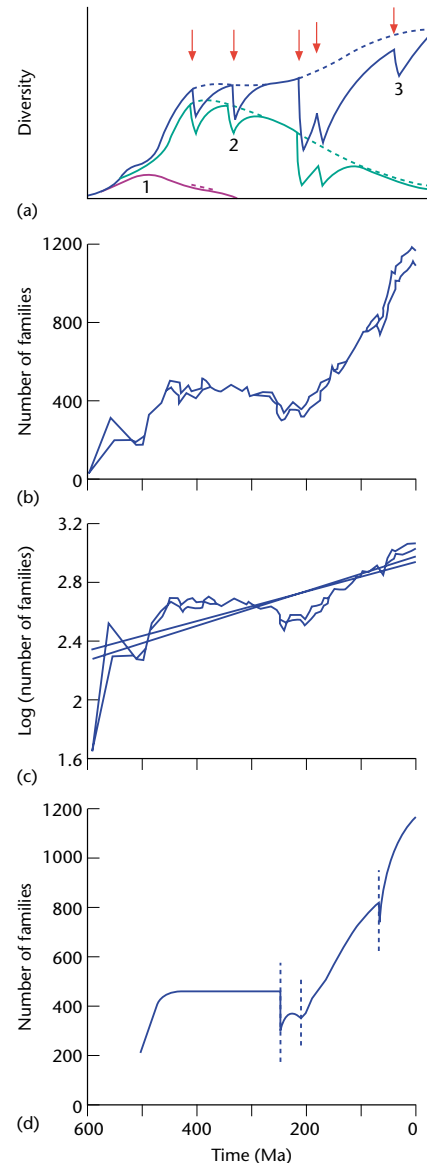


Figure 3 Alternative interpretations of global Phanerozoic marine diversity trajectories. (a) Sepkoski's three-phase coupled logistic model, depicting the modelled trajectories of the three evolutionary faunas. Five mass extinctions were incorporated (arrows) at simulated times, and with magnitudes, corresponding to their occurrences in the empirical record (**Figure 2a**). The dotted lines depict the trajectories in a simulation without mass extinctions (redrawn from Figure 8C of Sepkoski, 1984). (b) and (c) Benton's depictions of familial diversity using arithmetic (b) and logarithmic (c) diversity axes. In each case, two curves depict maximum and minimum estimates, based on inclusion or exclusion of families that could not be assigned definitively to a stratigraphic stage or the marine realm. In the semilogarithmic graph, best-fit exponential trajectories for the two curves are superimposed (redrawn from Figures 1C and 2C of Benton, 1995). (d) Courtillot and Gaudemer's representation of Phanerozoic diversity from the Ordovician to the Recent as a composite of four successive, simple logistic curves, demarcated by mass extinctions (dotted lines). Each of the four curves had unique diversification parameters (after Figure 1 of Courtillot and Gaudemer, 1996).

of the diversity trajectory rarely, if ever, parallels the best-fit line. Instead, diversity appears rather stable for an extended interval of the Palaeozoic, as noted previously by Sepkoski. On the other hand, Benton continues to observe that the terrestrial pattern is best described as a simple exponential diversification.

An interesting alternative to Sepkoski's coupled logistic model was provided in 1996 by Vincent Courtillot and Yves Gaudemer, who argued that equilibrium diversity was, indeed, operative as a mediating agent in the Phanerozoic of marine diversity, but that the entire system is most appropriately modelled with a single logistic curve, rather than with three curves diversifying simultaneously. In their formulation, mass extinctions played pivotal, rather than incidental, roles in diversification by selectively removing some taxa and permitting the radiation of others. These sudden changes in global biotic composition, in turn, are thought to have been responsible for resetting the attainable levels of equilibrium, permitting the substantial changes to overall levels of diversity exhibited in their wakes.

Thus, the 'causes' of biotic transitions and changes in diversity exhibited throughout the Phanerozoic are still under debate. In part, this reflects continuing uncertainty, highlighted earlier, about the biological validity of raw, uncorrected diversity trajectories. In fact, the recognition of an apparent correlation between species diversity and sedimentary rock volume motivated David Raup to note that one cannot rule out the possibility that species diversity has actually maintained a fairly constant, equilibrium diversity since the Palaeozoic.

Even if we accept, as most researchers have, that raw trajectories accurately depict the history of global biodiversity, ambiguities remain regarding the mechanisms that caused them in the most basic sense: are the patterns observed in global-scale compilations actually caused by processes operating at the global level? During major mass extinctions, global mediation is clearly evident. The Late Cretaceous (K/T) event, for example, was a global-scale phenomenon, the effects of which can be recognized in K/T boundary strata around the world. However, region-to-region comparisons of diversity trends during the protracted intervals between global mass extinctions have shown that regional transitions in biotic composition are highly episodic, with rapid intervals of biotic turnover fuelled by local perturbations and transitions to the physical environment. Because each region is affected by its own physical geologic peculiarities, the timing of biotic transitions in one region might not match those in another. When the records of biotic transitions for individual regions are combined to produce the global composites illustrated in **Figure 2**, one consequence may be a misrepresentation of the rates at which most transitions actually occur in any given venue: transitions that are almost always episodic when evaluated at the scale of their occurrences may, instead, appear gradual in synoptic,

global-scale compilations. This, in turn, would favour the invocation of causal mechanisms, such as competitive interactions, that require extended intervals to transpire, even though there is little evidence that these interactions produce gradual diversity transitions at regional levels.

Additional insight into Phanerozoic diversity trends has been provided by considering biotic transitions in morphological and ecological contexts, rather than strictly in taxonomic terms. A classic example of this approach was presented by Geerat Vermeij, who showed that morphological attributes of gastropod molluscs ('snails') were affected dramatically by the diversification of shell-crushing predators in the Mesozoic and Cenozoic eras. Vermeij subsequently broadened his arguments to include a host of interactions among predators and prey, and their consequences for diversity trends, in marine and non-marine settings. To the extent that these and related mechanisms are important components of global biotic change, they remind us that ecology often transcends taxonomy as an agent of evolution.

Radiations

There are several intervals of global diversity increase depicted in **Figure 2** that could rightly be viewed as radiations. These include: the so-called 'Cambrian explosion' and 'Ordovician radiation' of marine animals, which are most appropriately viewed as two unique intervals, rather than as a single early Palaeozoic diversification; the post-Palaeozoic expansion of the Modern evolutionary fauna following the Late Permian mass extinction; the first major diversification of land plants in the Devonian; the subsequent radiations of gymnosperms in the mid to late Palaeozoic and angiosperms in the Cretaceous and Cenozoic; the diversification of several different kinds of fish in the Devonian and the later, more extensive, radiation of teleosts; the colonization of land by vertebrates, followed by a major radiation of tetrapods; and the Cenozoic radiations of mammals and birds, which achieved diversity levels far in excess of their Mesozoic numbers.

Each of these radiations was characterized by, and contingent on, certain unique parameters. For example, while the precise reason(s) for the Cambrian explosion remain open to debate, the palette of likely explanations (e.g. the crossing of a threshold level of oxygen in the atmosphere or a sudden increase in the complexity of *Hox* genes) were important uniquely to the biological and physical attributes of the Neoproterozoic through Early Cambrian interval, and probably had little relevance, say, to the Cenozoic radiations of birds and mammals.

Nevertheless, this review suggests that there are macro-evolutionary themes relevant to all global radiations. These include a spectrum of possible prerequisites to

radiation: the evolutionary advent of key morphological innovations; the competitive superiority of the diversifying biota relative to the incumbents that were supplanted or replaced; the removal of incumbents through extinction and the resultant emptying of ecospace; and 'random chance'. In a given case, any, all, or none of these factors may prove to be of importance. In the end, we may discover that every radiation is too unique to delineate a set of overarching principles that governs all or most of them.

Perhaps more than anything, these themes remind us that, in reconstructing the history of life, it is important to look beyond what is unique to single events and to search for general macroevolutionary 'laws'. Perhaps more than anything else, the study of the diversity of life through time is emblematic of this quest.

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