Diversity of Life through Time

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Introductory article

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Global diversity is the total number of taxa living in the present day or at any time in the geological past. Reconstructing the trajectory of global diversity by compiling data from the fossil record has been a major research agenda for palaeontologists for decades. The goal is to produce an accurate reconstruction of the pattern of global diversity that will ultimately allow us to understand the causes of diversity increases, decreases and transitions in the composition of the biota. The Paleobiology Database, a new large-scale database based on individual collections of fossil taxa, allows palaeontologists to standardise sampling, thereby controlling for vagaries of the fossil record. Collection-level data also allows researchers to identify any asynchrony of changes in diversity among regions of the globe, with the ultimate goal of identifying the habitats or environments that support biodiversity growth.

Diversification of Life

For decades, palaeontologists have worked hard to reconstruct the pattern of global diversity through geological time. This endeavour, when it produces biologically meaningful trajectories, offers a plethora of insights not only about the history of life but also about evolutionary processes. 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 of this, understanding the causes of biodiversity changes in the past will help us to understand fate of biodiversity in the face of human-induced changes to the planet. Many human-induced changes to the Earth have natural analogues in the geological past (e.g. intervals of global warming or ocean acidification); analyses of past biodiversity during times of known environmental change can help us predict how diversity will be affected by current environmental changes. Researchers seeking to determine whether the Earth is currently experiencing a mass extinction of species have looked at the history of biodiversity for insights into levels of diversification and extinction expected 'naturally', in a world not influenced unduly by *Homo sapiens*. Palaeontologists unravel these processes by focusing on how global diversity changed over time and applying statistical methods of sampling standardisation. **See also**: Adaptive Radiation; Conservation Biology and Biodiversity; Extinction; History of Biogeography; Macroevolution: Overview

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Calibrating Global Diversity Trends

Sampling global diversity past and present

Global diversity is a simple number to wrap our minds around. Arriving at this number, however, is challenging, even for taxa alive today. There is no way to count all species without identifying each one; therefore, current biodiversity estimates are done by extrapolating from well-sampled collections. Estimating biodiversity in the past has similar problems as well as others that come from the fossil record itself. Up to the end of the twentieth century, palaeontologists have largely taken the fossil record at face value and relied on compendia of the oldest and youngest known global occurrences of individual taxa to construct diversity curves. The results from these compilations have shaped our view on the history of diversification and mass extinctions, which are depicted in most textbooks on evolution. It has long been realised that a database of individual fossil occurrences and their geological context would offer superior opportunities to elucidate biologically meaningful diversity trajectories. But the task is huge. The Paleobiology Database (PaleoDB, http://paleodb.org) was founded in 2000 to get a more reliable picture of diversity through time as well as answer other questions that were previously impossible to address. The PaleoDB is currently being developed by the joint effort of approximately 240 palaeontologists from 20 countries. The primary data used to construct diversity curves with the Paleobiology Database are the number of times a fossil taxon is sampled in each time interval. This occurrence-based approach is a powerful way to evaluate and control for any biases in sampling and led to a more robust estimate of global diversity. **See also**: Geological Time: Dating Techniques; Geological Time: Principles; History of Palaeontology

Experience has shown that it is usually not practical to assess ancient diversity at the species level: 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. Although there have been attempts to construct global diversity curves at the species level (e.g. Janevski and Baumiller, 2009), these are currently not deemed reliable because they are based on either extrapolation or raw counts. 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. However, in the new occurrence-based databases, all taxonomic information is recorded for each collection, and therefore, the diversity can be analysed at any taxonomic level. As the information contained in the PaleoDB grows, our ability to obtain an accurate estimate of species-level diversity will increase.

The fossil record does not record always a high-fidelity sample of taxa alive in the past. Because the pattern of taxonomic diversity through the Phanerozoic eon is derived from the fossil record, the quality of the fossil record itself can influence our estimates of diversity. Most notably, researchers interested in the diversity 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. David Raup showed in 1976 that the Phanerozoic sedimentary rock record exhibits a much greater volume of preserved sediment 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 Phanerozoic diversity, which all exhibit major increases during the Cenozoic (**Figure 1** and **Figure 2**), may similarly reflect increases in the available volume of the fossil record, rather than a genuine increase in biological diversity. This theme is currently under scrutiny (Peters and Foote, 2001; Smith and McGowan, 2007). **See also**: Fossil Record; Speciation and the Fossil Record

Counting methods and sampling standardisation

The method used to count taxa in each time interval can drastically influence the pattern of diversity. The role of counting methods in diversity curves was not fully appreciated until occurrence-based data sets allowed a comparison of methods. Early compendia – which recorded only the oldest and youngest known global occurrences of individual taxa – assume that each taxon was extant for the entire interval between its first and last occurrences. With this data structure, a simple tabulation of the number of taxa alive in each interval will be strongly affected by what palaeontologists know as the 'Pull of the Recent' (Raup, 1979). The record of extant taxa is many times better than in any time of the past. Thus, all extant taxa with any fossil record, if only found in exceptionally preserved sites, will contribute to the cumulative diversity after their oldest occurrence, whereas extinct taxa can only contribute if both their oldest and youngest occurrences are known. The overprint of the Pull of the Recent can mask important changes in global diversity, so that even if diversity is truly unchanging or even declining, apparent diversity would seem to increase only due to the Pull of the Recent. A primary concern in the development of counting methods has been the elimination of these types of methodological biases.

How global diversity patterns are tabulated depends on the basic data recorded for each taxon. With occurrence-based data, diversity in a time interval is simply the number of taxa that have actually been sampled, a method known as 'sampled-in-bin' (Alroy *et al.*, 2008). This counting method produces diversity curves with high short-term variation, because taxa that actually lived during the interval but not sampled are not counted. Therefore, a small correction is usually added; by counting taxa that are found in the interval immediately before and after an interval but not inside it, we can account for those taxa that can be reliably inferred to be present in that time. Other sampling issues, like variation in rock volume and research intensity, can be controlled for by using sample standardised sampled-in-bin counts.

In order to compare diversity counts between different time intervals, the amount of sampling in each interval must be comparable. This is because the number of taxa found in a sample is not a linear function of sampling intensity. A curve can be constructed by plotting the number of collections on the x-axis and the cumulative number of taxa found on the y-axis. Early on, as the first samples are made, lots of new taxa are found and the curve steeply increases. Eventually, as more sampling is done, fewer undiscovered taxa are left to be found. At the limit, no new taxa will be discovered no matter how hard we look for them. As the limit is approached, the curve will flatten out. The raw diversity counts of two intervals can be confidently compared only if both have flat sampling curves, which is rare. Sampling standardisation involves repeatedly pulling a random subsample of a comparable number

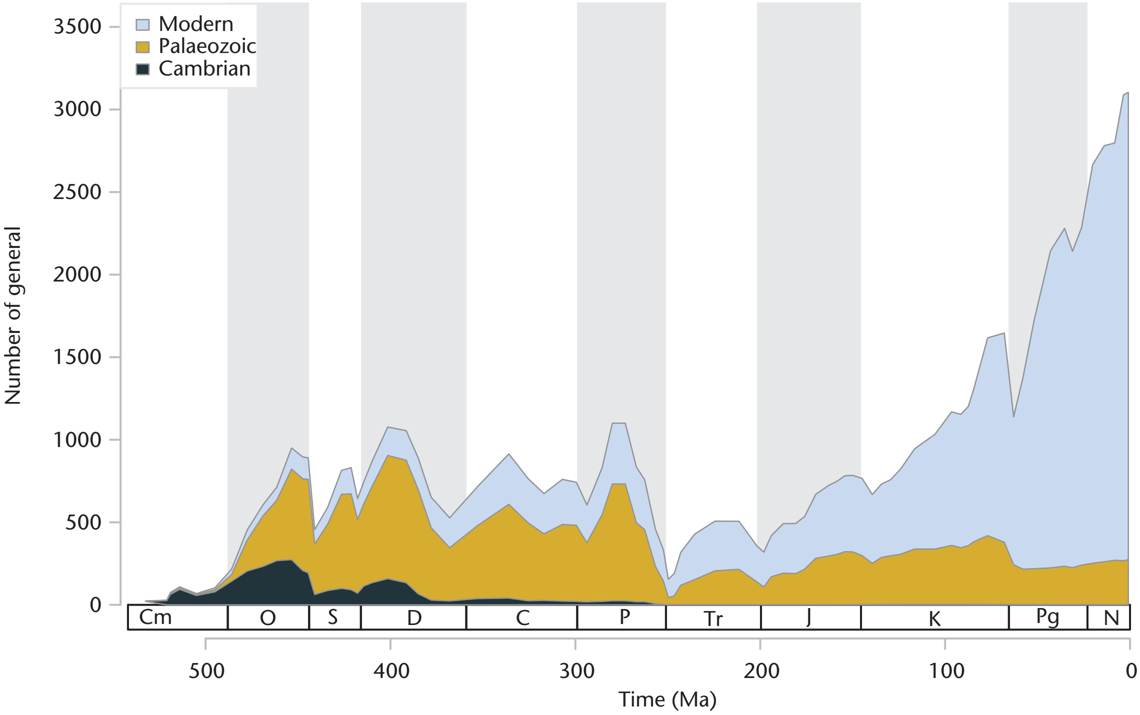

Figure 1 Global Phanerozoic diversity for marine genera (based on Sepkoski, 2002) showing the trajectories of the three evolutionary faunas. Only genera of the most representative groups of each evolutionary fauna are shown. Grey boxes indicate periods. Time scale abbreviations are: Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; N, Neogene.

of collections or occurrences in each interval. There are many methods for subsampling, and no one is clearly preferable. The development of these methods is an area of active research (Alroy, 2008, 2009; Alroy *et al.*, 2008). What palaeontologists do agree on, however, is the need for sampling standardisation for constructing biologically meaningful diversity curves.

Patterns – Marine and Terrestrial

Marine diversity

Most fossils are of marine organisms because they live predominantly where sediments get deposited. As a consequence, the most work on compiling global diversity curves has been done with marine organisms. Although there have been several efforts to compile marine diversity trajectories since the 1960s, the best known depiction was presented by John Sepkoski, initially in 1981 (Sepkoski, 1981). It was constructed at the family level using a compendium of some 5000 fossil marine families that Sepkoski published in 1982 and updated thereafter (Sepkoski, 1992). Subsequent curves constructed at the genus level by Sepkoski in 1996 (**Figure 1**), and at the family level by Michael Benton in 1995 (**Figure 2a**), share several major features with Sepkoski's earlier effort: an initial increase in the Cambrian, followed by a more extensive diversification in the Ordovician. For most of the remaining Palaeozoic, diversity apparently stabilised, 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 (Raup and Sepkoski, 1986): the Late Ordovician, Late Devonian, end-Permian, end-Triassic and end-Cretaceous 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 stabilise 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 (Gould, 1989, 1991) and others (Valentine *et al.*, 1999) have suggested that the Cambrian explosion was characterised by an unrepeated burst of diversification of basic phylum-level body plans, several of which subsequently became extinct. Whereas 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, toward the present day. **See also**: Burgess Shale

At the genus level, the most recent marine diversity curve derived from the Paleobiology Database (Alroy *et al.*, 2008) shows many of the same patterns as Sepkoski's curve but also some important differences (**Figure 3**). Importantly, the 'Big Five' mass extinctions are still observed in the

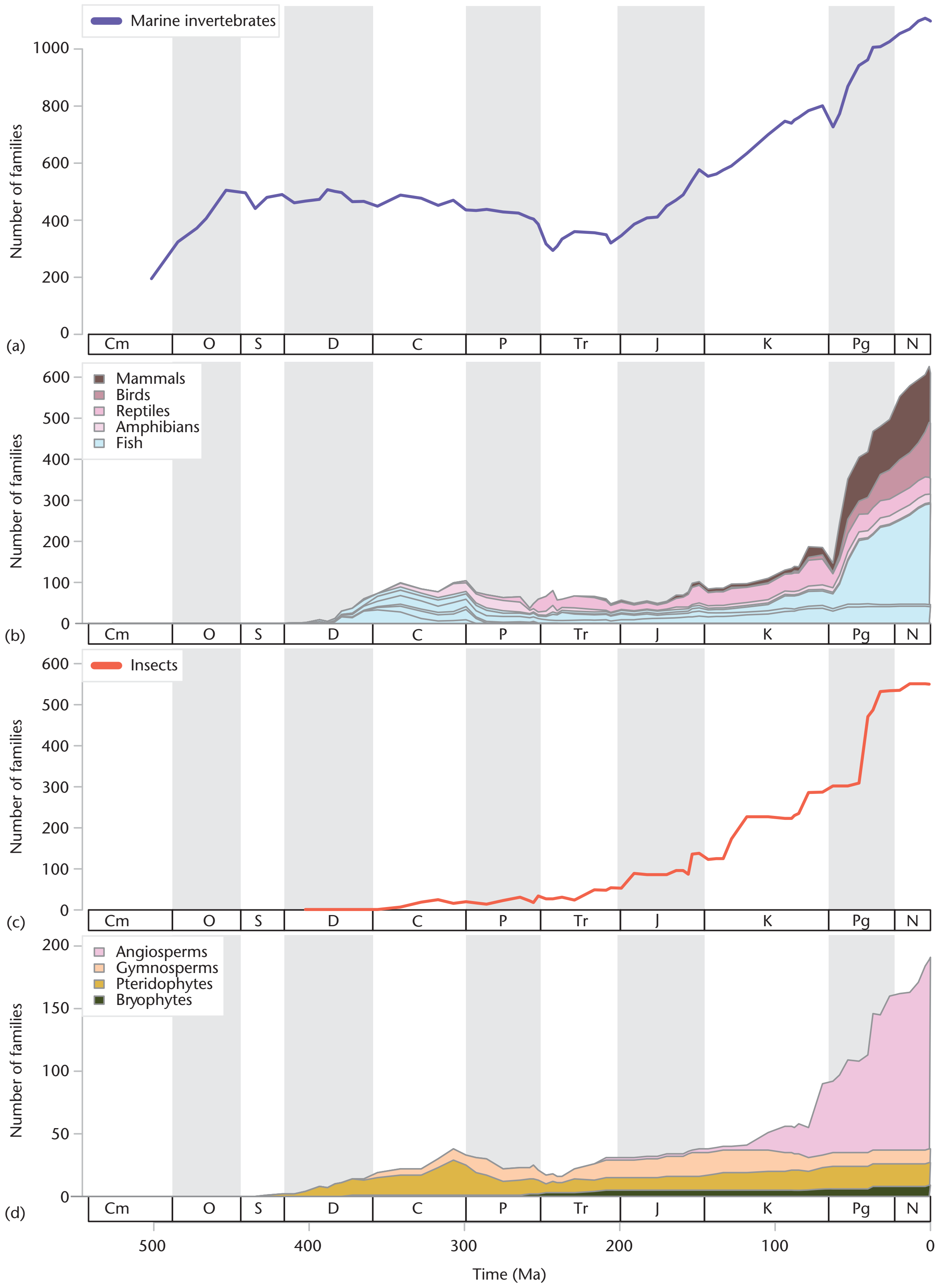

Figure 2 Global Phanerozoic diversity trajectories for (a) marine families, (b) marine and terrestrial vertebrate families, (c) insect families and (d) terrestrial plant families. Data are from Benton (1993). Grey boxes indicate periods. Time scale abbreviations are: Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; N, Neogene.

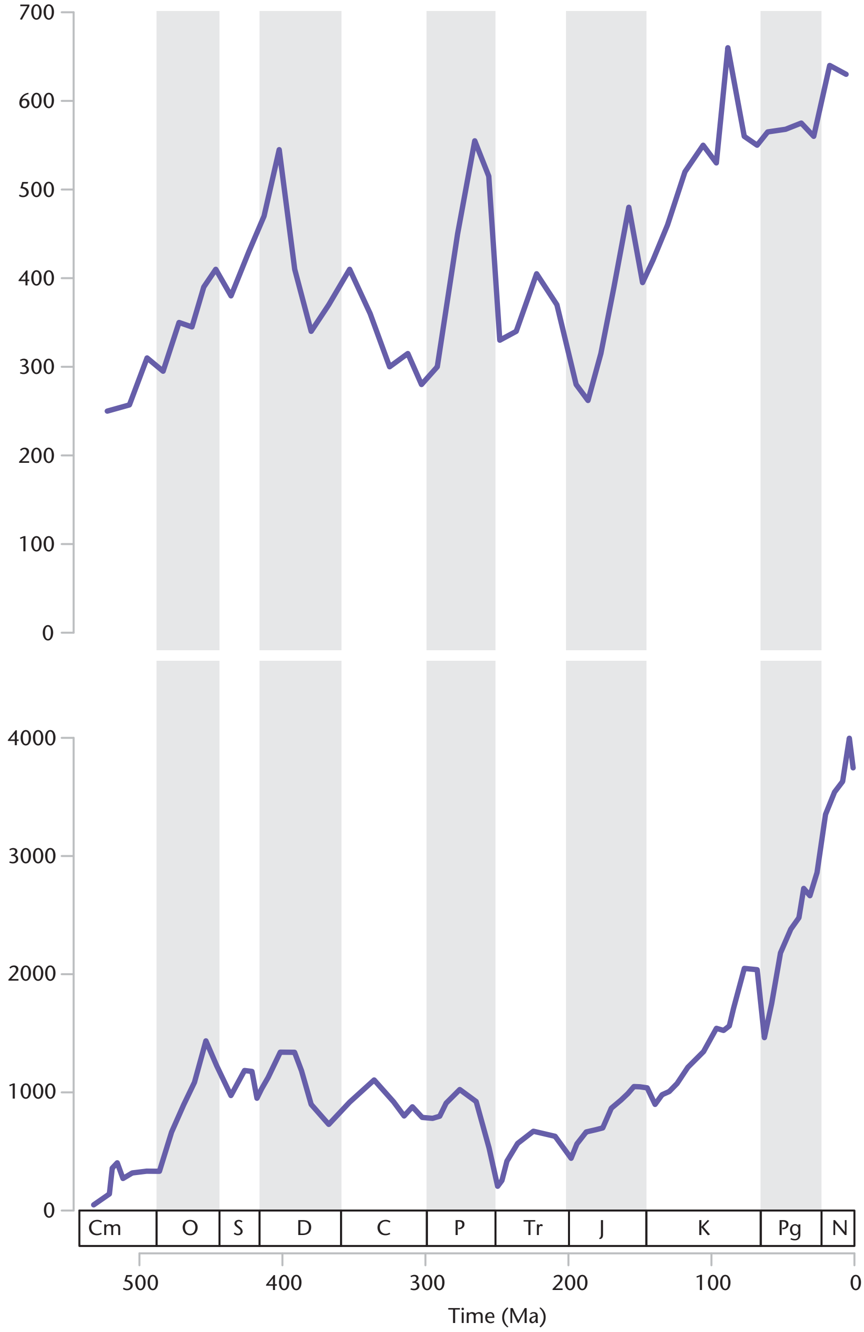

Figure 3 Comparison of global Phanerozoic diversity trajectories for marine genera. The top curve depicts sampling-standardised diversity from the Paleobiology Database (Alroy *et al.*, 2008). The data for the lower curve come from Sepkoski (2002). Grey boxes denote alternating periods. Time scale abbreviations are: Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; N, Neogene.

current data (Kiessling and Simpson, 2010), as are the diversity patterns of higher taxa. The major difference is in the pattern of diversity increase in the Cenozoic. After controlling for variation in sampling over time, the diversity curve presented by Alroy *et al.* (2008) shows only a less than 50% increase in diversity from the mid-Palaeozoic peaks to the Neogene.

Underlying the diversity trajectory 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. Applying multivariate statistical analyses of diversity patterns within clades, Sepkoski (1981) recognised three Phanerozoic ‘evolutionary faunas’, each characterised by distinct taxonomic classes (**Figure 1**): 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 characterised seafloors for the remainder of the Palaeozoic; and the Modern fauna, dominated by gastropods, bivalves, crustaceans, echinoids, gymnolaemate bryozoans and fish, 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. **See also**: Cambrian Radiation; Extinction: End-Permian Mass Extinction; Extinction: K–T Mass Extinction; Extinction: Late Devonian Mass Extinction; Extinction: Late Ordovician Mass Extinction; Mesozoic Marine Revolution; Post-Permian Radiation; The End Triassic Mass Extinction

Terrestrial diversity

Extreme estimates of modern terrestrial diversity can be up to 25 times greater than estimates of current marine diversity (Benton, 2001). The bulk of this diversity is made up of insects, nematodes and plants, but also important are vertebrates. Early on, patterns of terrestrial diversity where tabulated in much the same way as it is in the marine realm – by counting up the number of taxa that occurred in each interval in the past. More recently, however, terrestrial diversity has been estimated largely using phylogenetic methods. This works largely by extending ranges back in time from the observed fossil occurrences to the maximum extent predicted by phylogenetic relationships, assuming that sister taxa have the same time of origin (Norell and Novacek, 1992).

Benton (Benton, 2001; Benton and Emerson, 2007) maintains that patterns of terrestrial diversity are distinctly different from the marine realm. On land, diversity increases considerably faster than in the sea; diversification begins much later in history on land and possibly a larger number of species exist there today. This is undoubtedly true, but in addition, he finds this pattern sufficient evidence for unconstrained diversification in terrestrial organisms. If we consider the lessons learned about the influence of the Pull of the Recent in the marine taxa, there is reason not to take the long-term exponential increase observed in terrestrial datasets at face value. Logistic growth with maximum diversification early and flattening thereafter is also expected on land when counting and sampling methods are applied rigorously.

Diversity patterns of major groups

Vertebrates

Vertebrate diversity analyses at the family level 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 (**Figure 2b**).

Most vertebrate-wide diversity data are restricted to raw data of age ranges for families. Sampling-standardised diversity patterns have been constructed for mammals and dinosaurs. As in the marine diversity curve, the major biological signal in John Alroy's mammalian curve is its only modest increase in diversity over time (Alroy, 2009). The subsampled diversity curve of dinosaurs (Lloyd *et al.*, 2008) is also quite stable over time. However, if dinosaur diversity is instead measured phylogenetically a 7-fold increase in species richness is observed, but most of the change in diversity is concentrated early in dinosaur history. **See also**: Vertebrata (Vertebrates)

Insects

There are a shockingly large number of beetle species today. And they are just a part of the approximately 9 000 000 insect species estimated to be extant (Benton, 2001). The family-level diversity curve for insects (Benton, 1993) shows their remarkable diversification (**Figure 2c**). Interestingly, it is the low extinction rates of insect families that underpin their high diversity (Labandeira and Sepkoski, 1993). **See also**: Insecta (Insects)

Plants

The broad outlines of Phanerozoic floral diversity, described in a series of publications by Karl Niklas (e.g. Niklas, 1997), reveal that the majority of Phanerozoic plant species can be classified into three sequential groups: 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. Unfortunately, there is a dearth of recent work on patterns of plant diversity. In **Figure 2d**, we plot family-level diversity for land plants, based on the compilation of Benton (1993). **See also**: Angiosperms; Evolution of Ecosystems: Terrestrial; Gymnosperms; Plant Biodiversity; Pteridophytes (Ferns)

What Causes Global-Scale Biotic Transitions?

One aspect common to marine and terrestrial diversity curves is the sequential domination by different groups over time. Even if the dramatic Cenozoic increases depicted in the vertebrate and plant graphs prove to be due to similar sampling artefacts that influence the shape of the marine curve, the underlying transitions in biotic composition exhibited in all three cases are probably real. The obvious question is, what caused them? Most proposed answers lie somewhere on a continuum between purely abiotic and purely biotic causes. At one end of this spectrum are explanations that invoke global-scale competition among groups, with one group out-competing another over the long term and ultimately supplanting it. At the other end 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 ecospace worldwide and providing opportunities for the diversification of new groups. Although 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 end-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. **See also**: Tiering in the Sea – Reefs and Burrows (Late Palaeozoic); Tiering on Land – Trees and Forests (Late Palaeozoic)

Limits to Diversity – Equilibrium and Expansion Models

What governs the shape of the overall diversity trajectory throughout the Phanerozoic? Early in the history of diversification of marine organisms, there was an initial phase during which diversity increased rapidly (**Figure 1**, **Figure 2a**, and **Figure 3**). This was followed by an interval during which diversity stabilised. 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 unless major evolutionary innovations allow conquering new ecospace. In fact, the body of theory related to the colonisation and eventual biological saturation of newly emergent islands supports this view (e.g. MacArthur and Wilson, 1967). As diversity increases, the rate of origination should decrease and the rate of extinction should increase; eventually, the two rates should counterbalance one another, resulting in the achievement of equilibrium diversity. Under these conditions, the pattern of diversity over time can be modelled with a logistic equation. After an initial phase of exponential growth, diversity will slow down as an upper limit of diversity is reached. The final diversity pattern has a sigmoidal shape. The role, if any, of equilibrium models in producing the observed diversity pattern has been contentious, with three different models figuring prominently.

Analyses of raw data have been used to variously argue for equilibrium and expansion models. Publication of the Paleobiology Database diversity curve (Alroy *et al*., 2008) and the associated development of counting methods and sampling-standardised analyses require revisiting these issues. The new curve, with its 2-fold increase in diversity over time, has rekindled efforts to find equilibrium dynamics and any diversity dependence that could generate them (Alroy, 2008; Aberhan and Kiessling, 2010). Alroy found that diversity in an interval of time is positively correlated with extinction rates in the next interval and that a high extinction rate in one interval is often followed by a high origination rate in the next interval.

Additional insight into the relative frequency of equilibrium and expansion models has come out of recent work on time-calibrated molecular phylogenies (McPeek, 2008; Rabosky, 2009a, b; Rabosky and Lovette, 2008). McPeek showed that out of 245 molecular phylogenies ranging across various taxa of plants, vertebrates, insects and molluscs, a majority show evidence for a decline in diversification. Only a small minority of cases show accelerating lineage diversification. If these results turn out to be robust, then this new evidence – independent from the fossil record – clearly favours some form of equilibrium model. As John Alroy (2009) puts it 'Thus, the open issue is not whether limits exist, but rather whether they are approached quickly on a geological time scale'.

Local and Regional Patterns

Any variation in global diversity must be manifested at smaller scales, either in variations of diversity on the level of communities or in biogeographic regions. For example, an increase of global diversity could be achieved by higher species packing within communities, greater differences in taxonomic composition along environmental gradients or a greater number of or greater difference among biogeographic regions. Several studies of long-term trajectories of marine within-community (alpha) diversity have established that there is evidence for increase. The earliest such study by Richard Bambach (1977) used raw species numbers and concluded that alpha diversity has increased 3-fold since the Early Palaeozoic in open marine environments. A more rigorous approach was forwarded by Wagner and colleagues in 2006. Rather than analysing simple diversity metrics, the authors looked at rank-abundance distributions and found that there was just one major change in the community structure during the Phanerozoic, coinciding with the end-Permian mass extinction. Wagner *et al*. (2006) distinguished ecologically simple communities that follow a geometric series in a rank-abundance plot from ecologically complex communities, which exhibit a log-normal distribution. They found that simple and complex communities were about equally common in the Palaeozoic but complex communities dominated by far in younger communities. Because complex communities can maintain much greater species packing than simple communities, there is now good evidence for an abrupt increase of alpha diversity in the Triassic period.

Patterns of between-community (beta) diversity are less well constrained. There are indications that increasing specialisation of taxa during the Ordovician radiation led to greater beta diversity along environmental gradients (Sepkoski, 1988), but there was apparently little net increase thereafter. A recent analysis of beta diversity through the entire Phanerozoic has shown great variability without an underlying trend (Aberhan and Kiessling, 2010). A similar pattern is evident at the level of biogeographic disparity. Arnold Miller *et al.* (2009) have shown that there is no evidence for increasing marine provincialism through time. Faunal differences among equal-distance grids were as pronounced in the Early Palaeozoic as they are today.

Sources of Biodiversity

New taxa are thought to first evolve in fairly localised regions because speciation is largely a process involving the subdivision of the ancestral species. Jablonski and others (Jablonski, 1993; Jablonski and Bottjer, 1991; Jablonski *et al.*, 1983) first described the pattern that new orders tend to originate nearshore and in the tropics. At lower taxonomic levels, Jablonski *et al.* (2006) showed that new genera of marine bivalves tend to originate in the tropics before expanding out to higher latitudes. The causes of these geographical patterns are thought to be caused by physical disturbance, energy availability and biotic interactions (Jablonski *et al.*, 2006; Valentine *et al.*, 2008; Willig *et al.*, 2003). Recently, Kiessling *et al.* (2010) explicitly tested several possible hypotheses about the environmental location of the biodiversity cradle. They found that nearshore, tropical and carbonate environments are all common cradles. But more importantly, it was reef habitats, which are a combination of all three environmental parameters, where the origin of genera was concentrated.

Radiations

There are several intervals of global diversity increase depicted in **Figure 1**, **Figure 2** and **Figure 3** 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 end-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 colonisation 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. **See also**: Cambrian Radiation; Mesozoic Marine Revolution; Post-Permian Radiation

Each of these radiations was characterised 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. **See also**: Palaeoclimatology; Palaeoenvironments

Nevertheless, this review suggests that there are macroevolutionary 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.

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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