The History of the Biosphere: Equilibrium and Non-equilibrium Models of Global Diversity

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Species diversity on the earth has increased through time. The fossil record suggests that the increase may have occurred in several stages, with perturbations caused by mass extinctions and widespread radiations. Various models for global taxonomic diversification have been proposed: equilibrium models where there is a fixed number of species that the earth can support at any time; and non-equilibrium models of two kinds, in which either an equilibrium level exists, but is never reached, or in which there is no equilibrium number at all. At present, all three models can explain the data, although the equilibrium models have been heavily criticized. Detailed reassessments of the fossil record may indicate which models are more probably correct.

Two of the largest questions facing biologists and palaeontologists are: how many species are there living today, and how many have there been altogether during the whole of the history of life? There are no simple answers to these questions, but several current lines of research point towards ways in which estimates can be made of total global diversity and its changes during the many millions of years of life on earth. First, we must attempt to assess the present diversity of life, and then try to work backwards in time.

The total number of living species

Present estimates of the number of living species of plants and animals are remarkably varied, ranging from 1.5 to 30 million[1]. This order of uncertainty may seem inexplicable at first. An examination of the published taxonomic literature yields a total of over one million described species. New species are being found and described all the time, and the rate of discovery could be used to give a general estimate of the actual total number of living species.

For example, we know that there are about 8700 species of living birds, and about 4060 species of living mammals. New forms are discovered at a relatively low rate. Diamond[2] has estimated that 134 new species of birds have been found since 1934, but only nine new

genera. The rate of discovery has fallen since the early years of the 20th century, to give an average rate of about three new species per year since 1941. Most of the new species have come from the neotropics and Africa, and there have been bursts of discoveries when new areas have been explored by biologists.

For mammals, Diamond[2] found that 134 new genera had been described since 1900, but the rate of discovery has fallen to about one genus per annum since 1940. Again, most of the new forms are neotropical or African, with fairly high numbers from the orient and from New Guinea. The present modest rates of discovery of new species of birds and mammals would seem to suggest that we can expect increases of less than 5% on the total numbers quoted above. Traditionally, then, biologists have increased the known total number of species (~ one million) by only modest amounts to give an overall figure of 1.5–3.0 million.

However, new studies by Erwin[3] on the present diversity of tropical insects suggests a marked upwards shift in these estimates. Insects are

the most diverse group of multicellular organisms, and they make up most of the present total of one million described species. Tropical insects make up the largest part of this group, so Erwin attempted to estimate their total numbers more accurately. He generated an insecticidal fog in the canopy of specific trees in Panama over several seasons, and counted the numbers of species of arthropods, and of beetles (the largest group) in particular, that were knocked down. One species of tree, Luehea seemannii, yielded 1100 species of canopy-dwelling beetles. Erwin estimated that 160 of these beetles were 'host-specific', and that the remaining 940 species could live on at least one other type of tree.

Erwin then argued that each tropical tree species supports, on average, 160 unique beetle species, and 400 unique arthropod species (beetles make up about 40% of all known arthropod species). Next, he argued that this canopy fauna is at least twice as diverse as the forest-floor fauna, which would give a total arthropod diversity of 600 species associated with each tree species. There are an estimated 50 000
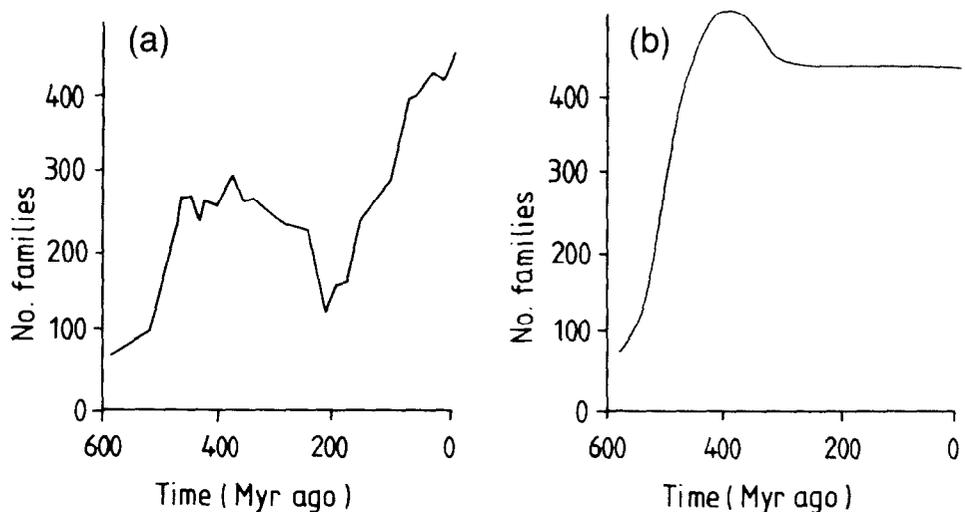

Fig. 1. The total diversity of families of benthic marine invertebrates over the past 600 million years. There are two models: (a) the 'empirical model', in which the data from the fossil record are plotted directly; and (b) the 'bias simulation model', in which 'corrections' are made for the supposedly very poor fossil record of the more ancient rocks. (After Refs 7 and 9.)

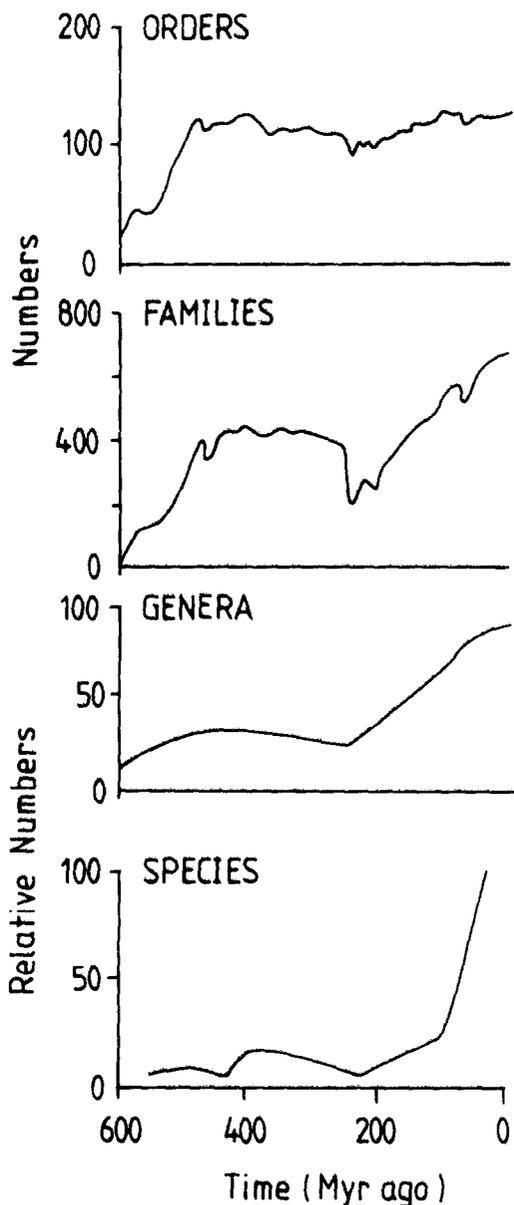Michael Benton is at the Department of Geology, The Queen's University of Belfast, Belfast BT7 1NN, UK.

Fig. 2. Trends in total marine diversity through time for different taxonomic categories. Note that the present-day total number of orders was established early on, whereas numbers of genera and species seem to have risen steeply only in the past 50–100 million years. The data for genera and species are estimated in various ways. (Based on several sources, after Ref. 14.)

species of tropical trees, which would give an ultimate total of 30 million living species of arthropods in the tropics, and that is only a part (albeit a large one) of the total present-day diversity of life.

Erwin's argument rests on a number of broad assumptions, as May[1] has noted. The estimate that 40% of arthropods are beetles is based on present knowledge, but this proportion could be much higher if virtually all arthropods are canopy-dwelling beetles. The estimates of 'host-specificity' are also tenuous. Nevertheless, May[1] argues that Erwin's estimate is of the correct order of magnitude, even if the final total figure is scaled down to, say, ten million.

The total number of extinct species

Since there is so little certainty in our estimates of total present-day species diversity, it might seem futile to proceed to estimate the total number of species that have ever lived. Nevertheless, estimates have been made. Teichert[4] tried to take account of the relative preservability of different plant and animal groups (many soft-bodied forms are most unlikely ever to be preserved). He arrived at a total of 569 000 living species that would be potentially 'preservable' as fossils, and extrapolated this to reach a figure of ten million discoverable fossil species.

Newell[5] used the idea of rates of discovery of new species of fossils in order to reach his estimate. He noted that, for many groups, the rate of description of new species was increasing all the time, and this led him to a tentative estimate that 'the known |fossil| record may represent not more than one per cent of the potentially knowable record', thus implying a total number of more than 50 million fossil organisms.

Valentine[6] surveyed the evidence on marine invertebrates, and he proposed a total of up to 5–6 million species since the origin of life. He also gave an overall maximum estimate for the total diversity of all of life, on land and in the sea, living and extinct, of less than 100 million species.

These kinds of estimate are subject to a large number of sources of error, and palaeobiologists have therefore shifted their focus recently to more tractable questions. For two practical reasons, it is believed that diversity estimates improve at higher taxonomic ranks – in other words, it is assumed that estimates of the diversity of families, orders or classes are better than estimates for species. This is firstly because there are fewer families and orders than there are species and, even if the fossil record is as much as 90% incomplete, a higher proportion of families and orders will be known. Thus, if there have been 100 million species, we might ultimately find only 10 million (10%). But, 100 million species could represent 20 million genera, 5 million families, 1 million orders, and so on. At 10% completeness for species, one might hope to find 30% of genera,

40% of families, 60% of orders and 70% of classes. These very crude estimates are confirmed by the studies cited earlier for the rates of discovery of new birds and mammals: 134 new species of birds have been discovered since 1934, but only nine new genera[2].

The second reason that palaeobiologists have focused on higher taxa is to do with the accuracy of geological dating. It is generally assumed that the family category is the best compromise since family durations tend to exceed the order of magnitude of error in absolute geological ages (typically ± 2–10 million years). Species and generic durations would tend to be 'lost' in these errors.

The history of global diversity

The first attempt to plot total diversity through time, by Valentine[7], showed a low initial level at the beginning of the Phanerozoic ('abundant life', from 600 million years ago to the present); this rose rapidly, plunged at the Permo-Triassic boundary (245 million years ago) and then rose steadily to the present day (Fig. 1a). He argued that the pattern was generally accurate and that it reflected changes in the physical environment, especially continental drift. For example, the massive drop in diversity at the Permo-Triassic boundary was ascribed to the coalescence of continents, and continental shelf seas, into a single super-continent at that time, and the concomitant decline in habitat diversity[8].

Raup[9] criticized the empirical model of Valentine, and others, and suggested that much of the pattern was produced by systematic sources of error. Various unavoidable physical factors, such as the volume of sedimentary rock and the area of exposed sedimentary rock, can determine our knowledge of the fossils of a particular age. These errors generally become worse in older rocks. There are also the avoidable human sources of error. Palaeontologists devote more time and attention to more recent fossils, and measurable 'Palaeontologist Interest Units' can be assigned to each geological age. These Units decline as one goes back in time. Raup[9] presented an alternative model of diversity change through time that attemp-

ted to correct for these, and other, biases. This model (Fig. 1b) shows an early rapid increase to maximum diversity, and a fall-back to an equilibrium level that has remained roughly constant ever since.

Valentine argued[10] that many of the sources of error identified by Raup might apply at the species level, but that these biases would be greatly reduced at the family level. Sepkoski et al.[11] compared global diversity curves based on several sets of data that are, to some extent, independent of each other:

(1) marine trace fossil species: burrows, tracks and trails;
(2) invertebrate species per million years, based on sampling from the Zoological Record;
(3) species richness in well-preserved marine benthic communities;
(4) generic diversity from compilations in the Treatise on Invertebrate Paleontology;
(5) family diversity of marine Metazoa.

These data sets all yielded very similar patterns and confirmed the general correctness of Valentine's model. All five graphs showed low levels at the start of the Phanerozoic, a higher 'plateau' from 500 to 245 million years ago, a sharp drop at the Permo-Triassic boundary, and a rising curve after that. Later compilations of data on species diversity of vascular land plants[12] and family diversity of non-marine tetrapods[13] gave further semi-independent confirmation of this pattern.

Signor[14] came to a similar conclusion by a different route. He made estimates of the various sources of error noted by Raup[9] and others, and removed them as far as possible, by computer modelling, from the data. He found that the empirical model still held up after correction, and that this was true for orders, families, genera and species (Fig. 2).

Equilibrium models

Palaeobiologists have developed equilibrium models for total global diversity based on extensions of the island biogeography theory of Macarthur and Wilson[15]. All of the parameters were scaled up from the ecological scale to the

evolutionary: the island became the world (or world shallow seas) etc., rates of immigration and local extinction became rates of global taxon origination and extinction, and the equilibrium level was for families or species globally rather than for species on an island. This scaling-up was explored by a number of authors, including Webb[16] and Rosenzweig[17].

Sepkoski[18-20] applied these models to a new compilation of Phanerozoic marine families. He developed a two-phase logistic model (Fig. 3) in which two global equilibrium levels were attained, the first in the Cambrian period (600–505 million years ago), and a second higher level in the later Palaeozoic (505–245 million years ago) which was terminated by the great mass extinction at the Permo-Triassic boundary. He later[21] extended this model by adding a third phase to explain the post-Permian rediversification (Fig. 4).

This three-phase model was interpreted as having been produced by the successive rise, attainment of equilibrium diversity, and subsequent decline, of three major 'evolutionary faunas'. Thus, the first fauna in the sea (trilobites and other primitive groups) reached its maximum diversity level of 100 families or so. It was then replaced by the second fauna (brachiopods, corals, cephalopods, crinoids, graptolites) which reached an equilibrium level of about 350 families. The third, 'modern fauna' of bivalves, gastropods, malacostracans, echinoids and vertebrates is apparently still increasing past 1800 or so families towards a new equilibrium level. It has been assumed[21,22] that these three great 'faunas' are cohesive units that were able to compete with each

other on the large scale.

Hoffman[23-25] has strongly criticized the equilibrium models of total global diversity, partly because of problems in extrapolating from the island biogeographic level to the global level. For example, it is hard to correlate local species immigration rates with global speciation or family origination rates. Species splitting in phylogeny is very different from the local addition of species to an otherwise unchanged island fauna. Speciation is a complex evolutionary phenomenon that depends on more than present taxic diversity. In an equilibrium model, extinction rate would be expected to increase with increasing global diversity. In fact, the findings of Raup and Sepkoski[26] and Van Valen[27] have shown that the exact opposite occurs.

Non-equilibrium models

Kitchell and Carr[28] have developed a non-equilibrium model for total global diversification. They accept the assumption of diversity
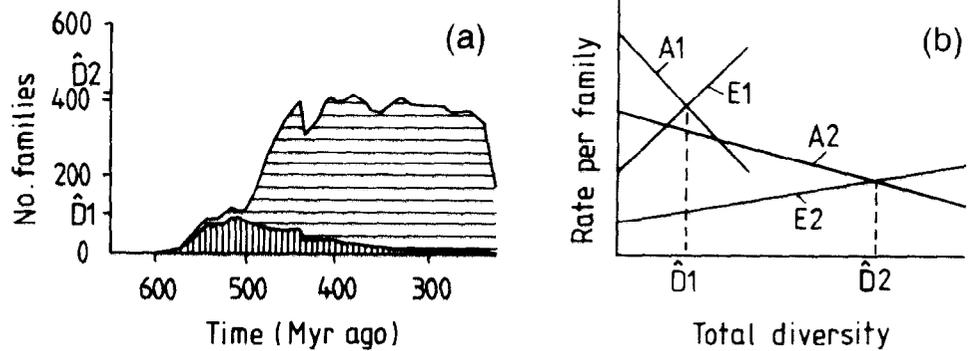

Fig. 3. The two-phase diversification model for marine animal families. The two phases are shaded differently in (a). The first-phase 'evolutionary fauna' reached its equilibrium diversity $(\hat{D}1)$, according to this model, about 550 million years ago, when the rate of origination of new families $(A1)$ matched the rate of extinction $(E1)$ (see b). Then the second-phase 'evolutionary fauna' took over, and total diversity moved up to its equilibrium level $(\hat{D}2)$ when its origination rate $(A2)$ matched its extinction rate $(E2)$. (After Refs 18–20.)
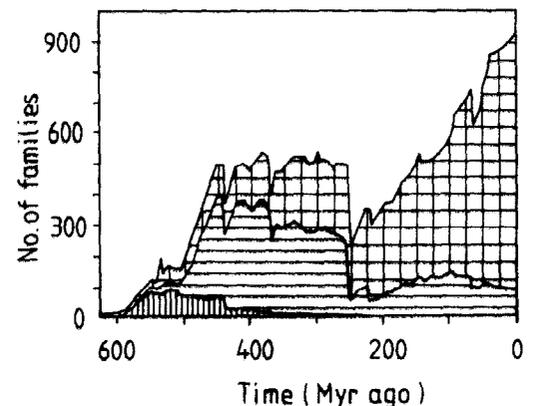

Fig. 4. The three-phase diversification model for marine animal families. The post-Cambrian history of marine diversification is divided into two phases, and the third phase 'evolutionary fauna' is still apparently diversifying towards a new higher equilibrium level. (After Ref. 21.)

dependence of the rates of origination and extinction within each evolutionary fauna, but argue that the system is kept away from reaching an equilibrium level by evolutionary innovations and mass extinctions. Their model matches the empirical data, but it retains the diversity-dependent assumption.

This assumption of diversity dependence of speciation and extinction rates has been questioned[23,25,29,30]. For example, Walker and Valentine[30] argued that a diversity-dependent model for speciation assumes that there is a fixed number of available niches, and that new species generally arise by displacing pre-existing species. They suggest that there is no evidence for either assumption, and they point to the ability of species, and higher taxa, to invade empty adaptive zones, and to increase overall species numbers on a global scale.

Hoffman[31,32] has developed a non-equilibrium, non-diversity-dependent 'neutral model' for total global diversification. He assumes that both origination and extinction rates are independent of total diversity and of each other, and he models each as a random walk. The only assumptions are that, over the entire Phanerozoic, the average probability of speciation exceeds the average probability of extinction, and that the system was perturbed by one major radiation event (at the end of the Cambrian) and one major mass extinction event (at the end of the Permian). A number of computer simulations
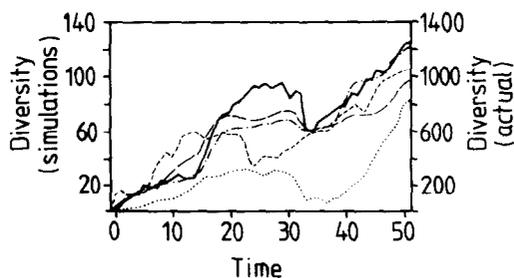
of this quasi-stochastic double random walk model gave graphs (Fig. 5) that matched the empirical patterns just as well as the equilibrium model of Sepkoski[18-21] and the non-equilibrium, diversity-dependent model of Kitchell and Carr[28].

Conclusion

There are, no doubt, parallels in this controversy over equilibrium theory and diversity dependence between palaeobiology and community ecology[25,33,34]. It seems to be clear that there are too many theoretical difficulties in the simple scaling up of island biogeographical theory from the ecological to the macroevolutionary level[25], and that a sounder theoretical base is needed in support of equilibrium models of global diversification.

However, the non-equilibrium models can also only be said to fit the empirical data, as far as we can tell. The notion of an ultimate, but unattainable, equilibrium number of species on the global scale is clearly of great significance[28] but hard to test. The search for an entirely stochastic model to explain the pattern of biotic diversification is subject to the same problems as are similar null models in ecology[35]. It is hard to exclude all biological factors, and many so-called 'null models' have turned out to be biased in one way or another. Furthermore, if the data fit a null stochastic model, the deterministic models are not thereby disproved. In the present case, there are arguments about the nature and rate of speciation, the interdependence of global speciation and extinction rates, and the randomness, or otherwise, of peaks and troughs in these rates, that will point to the correct model.

The problems in palaeobiology are further outlined by Hoffman[31]: 'Given the notorious limitations of the fossil record, the null model may in fact be too null to be rejected, at least at the present state of knowledge. For it is beyond the resolution potential of paleontology to provide a good estimate of global diversification at the species level and at a time scale of no more than about one million years, which would be necessary to test the model rigorously.'

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Fig. 5. Simulations of the diversification of marine animal families according to the neutral, non-equilibrium model. Four simulations are shown, and they appear to match the empirical pattern (solid line) scaled on the right-hand side. Time is divided into 50 equal steps, and the simulations proceed at random, except for two perturbations: a major radiation event early on, and a major mass extinction event about half-way through. (After Ref. 32.)