

Biodiversity on land and in the sea

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Life on land today is as much as 25 times as diverse as life in the sea. Paradoxically, this extraordinarily high level of continental biodiversity has been achieved in a shorter time and it occupies a much smaller area of the Earth's surface than does marine biodiversity. Raw palaeontological data suggest very different models for the diversification of life on land and in the sea. The well-studied marine fossil record appears to show evidence for an equilibrium model of diversification, with phases of rapid radiation, followed by plateaux that may indicate times of equilibrium diversity. The continental fossil record shows exponential diversification from the Silurian to the present. These differences appear to be real: the continental fossil record is unlikely to be so poor that all evidence for a high initial equilibrium diversity has been lost. In addition, it is not clear that the apparently equilibrium marine model is correct, since it is founded on studies at familial level. At species level, a logistic family-level curve probably breaks down to an exponential. The rocketing diversification rates of flowering plants, insects, and other land life are evidently hugely different from the more sluggish rates of diversification of life in the sea, perhaps as a result of greater endemism and habitat complexity on land. Copyright © 2001 John Wiley & Sons, Ltd.

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1. INTRODUCTION

Current concepts of the diversification of life are dominated by an equilibrium viewpoint that stems from the work of the late Jack Sepkoski. His plot of the pattern of diversification of families of skeletonized marine animals (Figure 1) is probably the most reproduced palaeontological illustration of recent times, perhaps rivalling images of the Berlin specimen of *Archaeopteryx*. The iconic image, derived from Sepkoski (1984), shows a three-phase pattern of diversification, an initial rise in the Vendian and Early Cambrian to a lowish Mid-Cambrian plateau, then a major rise in the Early Ordovician that initiated the famous Palaeozoic plateau. After the end-Permian mass extinction, diversity levels have risen steadily over the past 250 million years, with perhaps a hint of levelling off from the Late Miocene/Pliocene onwards, or perhaps not.

This image, and the ecological–evolutionary modelling behind it, are so pervasive that it is hard to consider an alternative view. Indeed, most discussion of the diversification of life through time has focused on the intensely studied fossil record of skeletonized invertebrates, such as sponges, corals, brachiopods, molluscs, arthropods and echinoderms, of the shallow marine shelf. The diversification of life on land has been virtually ignored, sometimes with a casual wave of the hand and an assertion that the continental fossil record is so hopelessly incomplete that it is not worth even contemplating it. However, life on land today may be as much as 25 times more diverse than life in the sea (Briggs 1994). Perhaps it is time to consider global diversification patterns from both realms on a more equal footing.

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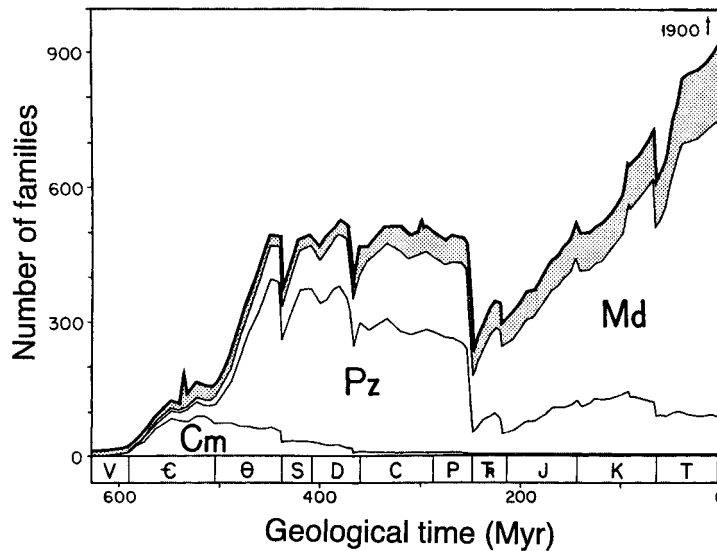


Figure 1. Diversification of marine skeletonized (white) and poorly skeletonized (stippled) animals through the Phanerozoic. The figure '1900' indicates the number of described families of animals in modern seas. The three evolutionary 'faunas' are indicated, the Cambrian (Cm), the Paleozoic (Pz) and the Modern (Md). Abbreviations: C, Carboniferous; Ɛ, Cambrian; D, Devonian; J, Jurassic; K, Cretaceous; Ɖ, Ordovician; P, Permian; S, Silurian; T, Tertiary; Ƨ, Triassic; V, Vendian. Based on Sepkoski (1984), reproduced by permission of the Paleontological Society.

In this paper, I discuss the different diversification patterns that have been published, I consider the critical point that has been made so often that the continental fossil record is too poor for any kind of meaningful comparison with the marine fossil record, and I discuss equilibrium and non-equilibrium interpretations for the patterns.

2. DEFINITIONS

It may be useful to define some terms, not least because protagonists of different viewpoints may use certain words in different ways, sometimes to the extent that the debate can end in confusion. This should not happen since there is a world of difference between an equilibrium view and a non-equilibrium view of global biodiversity.

In biology, the word *diversity* has many meanings, some of which include aspects of relative abundance, genetic variety, ecosystem complexity or morphological disparity. Palaeontologists tend to use the term in its simplest formulation, meaning the number of species, genera, families or other taxic units alive at any particular time, and it can refer to the global, continental or local geographic levels, and it can describe taxa within any particular clade or all of life. Diversity is commonly divided into alpha (α), beta (β) and gamma (γ) diversity, these meaning, respectively, diversity at the local, neighbouring and regional scales (Whittaker 1972). Alpha diversity is the number of species in a small area of essentially uniform habitat; beta diversity refers to the turnover of species from one habitat to the next, and gamma diversity is the number of species at a regional scale (an island, a major suite of habitats on a continent, or even a whole continent).

Following from the above definition of diversity, *diversification* is the achievement of diversity at a particular time through former time, and it can refer to both the patterns and processes of how that diversity was achieved. The viewing point is often the present day, but it can equally be any other point in the past, so one can refer to the diversification of trilobites up to the end of the Ordovician, or of all of life up to the present day. The popular buzz word *biodiversity* is a contraction of 'biological diversity' or 'biotic diversity', and it really means no more than diversity, but it is now such a familiar term that it can serve a useful purpose in communicating to a wider audience.

The process terms, equilibrium and non-equilibrium, are more complex. An *equilibrium* view of a biological process is that a dynamic equilibrium is reached at some point after some process of competition, in particular

diversity-dependent reduction of rates of origin (birth) or diversity-dependent increase of rates of extinction (death). A *dynamic equilibrium* is a steady level that is maintained through time despite the arrival and disappearance of components of that equilibrium level. In biology, *competition* is an interaction between individuals or species that depend on the same limiting resource, where one competitor benefits while at the same time harming the other. *Limiting resources* are entities necessary for life, such as food or space, that may be competed over.

The ideas of equilibrium modelling were formulated in the 1930s after the first controlled experiments with populations of competitor species. Typically, under controlled conditions, where two species were competing for a single limiting resource (usually food or space), both would reproduce rapidly at first. Then, as their closed world (a petri dish or a glass vessel) filled up, one species would outcompete the other and usually drive it rapidly to extinction. This was a *diversity-dependent process* where the extinction or origination rate of one species depended on the overall abundance or diversity of the other: the higher the diversity, the greater the depressing effect. The successful species would then continue at a fairly steady population level provided that the supply of space or food remained constant. Individuals would die and reproduce, but the global population size within the closed 'world' would remain constant. In other words, this was a dynamic equilibrium representing the *carrying capacity* of the system. The mathematics of such competitive interactions are highly tractable, taking the form of the well-known Lotka-Volterra equations. Classic competition theory is well summarized by Sepkoski (1996).

Famously, MacArthur and Wilson (1967) scaled these classic competitive/equilibrium observations up to the geographic level in their *theory of island biogeography*. Here, the closed system was an island which could support a number of species. Instead of simply documenting the interaction of two competitor species, they proposed that the whole ecosystem of an island was maintained in balance by similar processes. Each island had a fixed carrying capacity that depended on geographic area, distance from the nearest land, topographic complexity, climatic zone, and so on. They imagined a virgin island, newly emerged from the sea. Sooner or later, spores, insects, birds and other airborne organisms would land on the island by chance. At first, the rate of accretion of species might be fairly rapid since there were no competitors. After a time, however, as the early arrivals became established, new arrivals might face competition: some might be repulsed by sitting tenants, while others would outcompete the natives. So, even though the rate of arrival of wandering organisms would not necessarily change, the rate of successful establishment of species would decline, and the rate of local extinction would increase. At some point, the carrying capacity would be reached, the dynamic equilibrium, where the curves of establishment and local extinction rates crossed. The 'islands' of MacArthur and Wilson (1967) can clearly be the classic tropical islands everyone imagines, but also islands on land, such as forests or ponds, or even larger-scale islands, such as whole continents.

The theory of island biogeography has been hugely influential, becoming a central plank of evolutionary ecology, even though it has been hard to substantiate. A current view might be that the theory is so elegant and obvious that it clearly underlies large-scale biogeographic processes, but there are so many other local factors involved that it can rarely be demonstrated. An alternative view might be that the 'local' factors actually outweigh the deep-lying equilibrial expectations to the extent that they can barely be detected. According to this *non-equilibrial* viewpoint, every 'island' is different, local conditions determine what happens, and there is no predictable equilibrium level (Simberloff 1983; Williamson 1983; Price *et al.* 1984; Simberloff and Boecklen 1991; Wiggins and Møller 1997). Obviously, broadly speaking, a large island will hold more species than a small island, but the non-equilibrist would argue that the number of species on an island can vary greatly through time, without any sign of a predictable carrying capacity. Of course no island in nature is a closed system: nutrients, sunlight and organisms arrive at different rates. Also, importantly, organisms themselves create habitats. Every species of animal and plant has its parasites and symbionts. One tropical tree can harbour hundreds of endemic arthropods and epiphytic plants. So, if the history of an island is re-run, the early arrivers might be very different each time, and these first colonists could shape the entire future history of the island. If a particular tree seed washes up, habitats for hundreds of species might be supplied. If no such tree seed arrives, but only grasses and scrub, the animal population of the island could be halved for ever more.

Ecologists were keen to extend the island biogeography model to continental and global scales (e.g. Rosenzweig 1975, 1995; Whittaker 1977). Sepkoski (1978, 1979, 1984) further extended this approach, and developed an

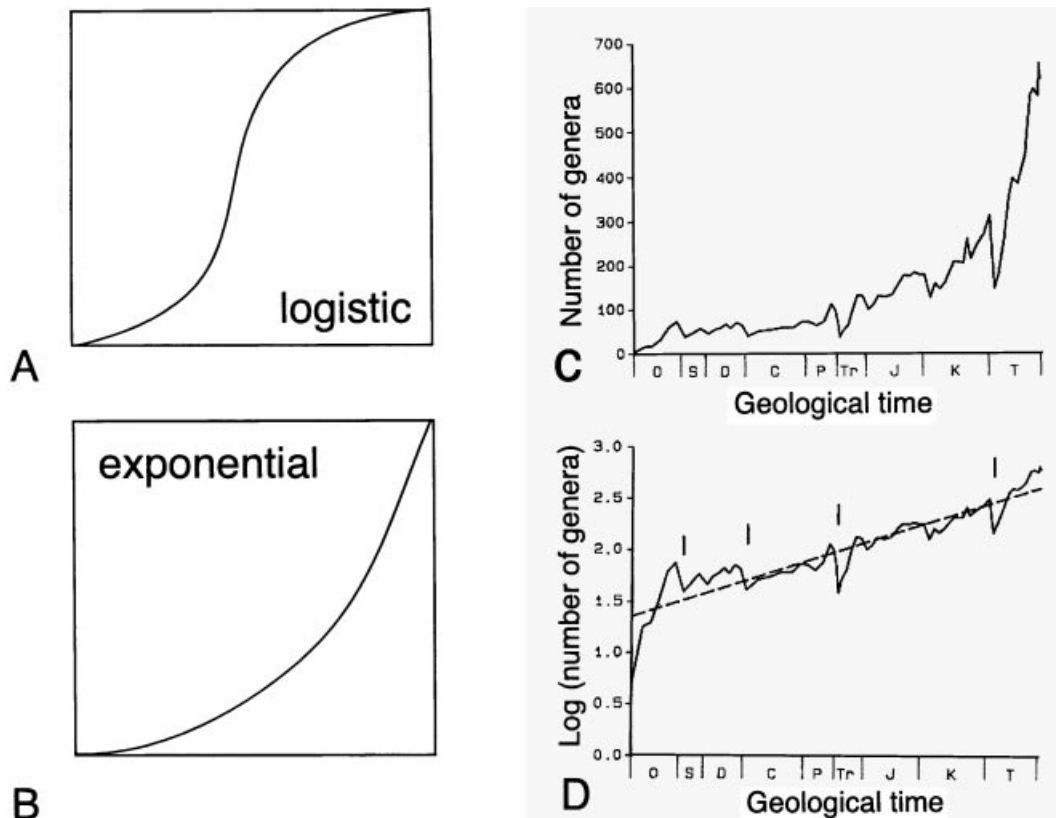


Figure 2. Diversification curves. Classic logistic (A) and exponential (B) curves. The diversification of bivalve genera through the Phanerozoic (C) follows an exponential curve. When the exponential curve is plotted as log (no. of genera) against geological time (D), it is close to a straight line. The gradient of the straight line (0.0025) is roughly one-tenth of the gradient of the post-Ordovician, post-Permian and post-KT rebounds in diversity (0.02–0.03). The post-Devonian rebound was apparently much slower. (C) and (D) are based on Miller and Sepkoski (1988), reproduced by permission of the Paleontological Society.

equilibrial model for diversification in the sea (see next section). The island was scaled up to the world, or at least the world's oceans, and local establishment and local extinction of species were scaled up to global origination and global extinction of species, genera or families. Evidence was presented that, as the global carrying capacity was approached, diversity-dependent processes came into play, and global origination rates were depressed, leading to the establishment of a global equilibrium. This I might term the *classic equilibrium model* which is represented by a logistic, or S-shaped, curve (Figure 2A): a rapid, essentially exponential diversification is followed by a slow-down (when diversity-dependent processes begin to act), leading to a plateau (when diversity-dependent processes hold the natural rate of diversification down and maintain a dynamic equilibrium). The plateau is interpreted as representing the global carrying capacity for species, genera or families.

Expectations of a non-equilibrial viewpoint can be various. At an extreme, what could be termed the *expansion model* is an exponential increase (Figure 2B) where diversification rates never slow down. There is no hint of a plateau. An exponential curve based on constant doubling is a normal expectation of many reproductive processes, as originally observed by Thomas Malthus: everyone knows that rabbits could entirely carpet the surface of the Earth within a hundred years of unfettered breeding. Likewise, splitting in phylogeny produces a simple exponential curve for numbers of species ($1 \rightarrow 2 \rightarrow 4 \rightarrow 8 \rightarrow 16 \rightarrow 32 \rightarrow 64 \rightarrow 128 \rightarrow 256$ *et seq.*) if there is no extinction. With extinction, the line is still an exponential curve, but with a lower exponent, unless the rate of extinction equals the rate of origination, when it becomes a straight line (linear curve). If the rate of extinction exceeds the rate of

origination, the curve becomes a negative exponential. The non-equilibrial expansionist would expect an overall damped exponential or straight-line pattern for the diversification of life.

This is where the terminology, and the debate, become tangled. The non-equilibrist would clearly suggest that an exponential or a straight line could not be equilibrial: without a plateau, there is no evidence for a predictable carrying capacity of the system, and that is that. However, a curve that accelerates at a rate less than doubling can be interpreted as a *damped exponential*, and such a curve could be produced by competition which produces a diversity-dependent effect (it need not of course: the extinctions that result in damping could be entirely unconnected with the origin of new species, but caused by physical catastrophes, parasites or predation). This case was made by Miller and Sepkoski (1988), who presented a competitive model for the diversification of bivalves through the Phanerozoic. The diversification curve for bivalve genera is exponential (Figure 2C), but Miller and Sepkoski (1988) argued that it was a damped exponential, citing as evidence the rapid rebounds after mass extinctions (Figure 2D). In other words, those rapid post-extinction rates represented the true potential rate of diversification of bivalves, and the normal rate (roughly one-tenth of the post-extinction rate) was heavily damped by interaction with other competitor groups.

There could, however, be another explanation for the 'rebounds' after extinction events: that perhaps they are merely artefacts (Gale *et al.* 2000). If extinction events are associated with physical upheavals of various kinds, for example major rises in sea-level, the apparent magnitude and duration of the event may be masked. Particular environments, geographical areas and biotas might not be preserved. The 'rebound' could then be merely a recovery to normal conditions of preservation.

So the equilibrium/non-equilibrium divide is clearly different from the competition/non-competition divide, a fact that has not always been made clear (e.g. Benton 1987, 1991, 1995). A supporter of the equilibrial viewpoint clearly must demonstrate an equilibrium at some point: a plateau, and evidence for diversity-dependent control on origination or extinction rates. A supporter of a non-equilibrial interpretation would deny such phenomena, or would seek to explain any plateau either as an artefact of the data, or as the result of physical processes, parasites, predators or indeed anything other than competition, or a combination of factors, perhaps including competition. The fact that Miller and Sepkoski (1988) could present a convincing competitive, diversity-dependent model for the exponential expansion of bivalve diversity through time, shows the need to separate ideas of equilibrium from competition. Their model clearly fitted a competitive, interactive world view, but there was no hint of an equilibrium. Everyone accepts that bivalves have diversified exponentially for 540 million years, and there is, and has been, no hint of a final equilibrium level. Rapid rebounds after extinction events are evidence for damping of a natural rate of increase, perhaps evidence for competitive release (but see below), but they are not evidence for equilibrium.

The continuing popularity of the equilibrium approach in macroevolution (e.g. chapters in McKinney and Drake 1998) is striking, especially in view of the fact that so little evidence has been found by evolutionary ecologists for the existence of equilibria in nature, for example, in the theory of island biogeography. Current evidence shows that there is abundant evidence for interspecific competition and effects such as character displacement, character release and improvements in competitive ability (Arthur 1980; Schluter 1994), but that there is little support for competition as a major, or sole, force that shapes community structure. As Cracraft (1985) pointed out, analysts who seek to apply diversity-dependent equilibrial models to patterns of diversity change through time read both patterns and processes in those terms and in no others. 'Metaphorically speaking, the biosphere is viewed as a large *Tribolium* population bottle, in which space and resources are assumed to be limited' (Cracraft 1985, p. 798). Equilibrium and competition as a major structuring agent of ecosystems should not be axiomatic; they should be open to test and refutation.

3. PATTERNS AND PROCESSES OF DIVERSIFICATION

Sepkoski's (1984) explanation for the pattern of diversification of marine skeletonized animals was a three-phase kinetic model. He argued that the pattern in Figure 1 was real, and that it could be best understood as the result of three successive bursts of diversification, each of which followed a logistic pattern. The exponential phase was

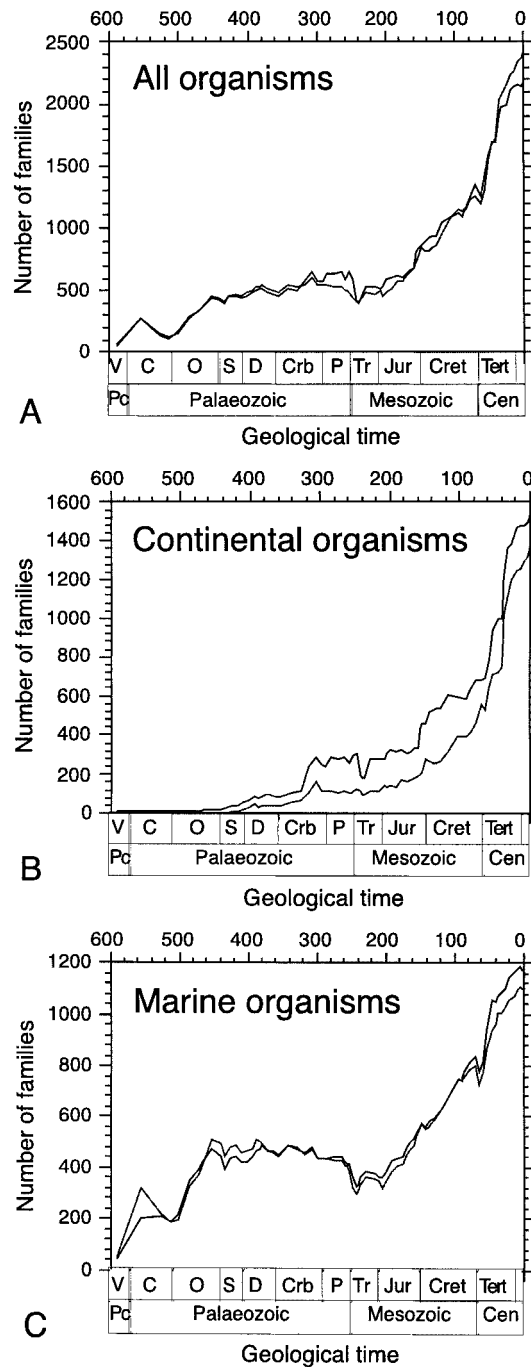


Figure 3. Patterns of the diversification of life through time, plotted for all organisms (A), continental organisms (B) and marine organisms (C), in terms of changes in numbers of families extant per stratigraphical stage. In each graph, a maximum and minimum is shown, based on a combination of stratigraphical and habitat-preference information (see Benton 1995). Abbreviations: C, Cambrian; Cen, Cenozoic; Crb, Carboniferous; Cret, Cretaceous; D, Devonian; Jur, Jurassic; O, Ordovician; P, Permian; Pc, Precambrian; S, Silurian; Tert, Tertiary; Tr, Triassic; V, Vendian. Based on data from Benton (1993).

explained as corresponding to a time when new forms of life were able to conquer new habitats, and to diversify fast, exploiting new habitats and empty niches. Then, as diversity approached the global carrying capacity, diversity-dependent processes slowed down the rate of origination. At the equilibrium diversity level, the rate of origination of new groups matched the rate of extinction of established groups, hence maintaining a dynamic equilibrium. Switches from one logistic/equilibrium phase to the next were triggered by mass extinctions (the Late Cambrian series of events and the end-Permian mass extinction respectively). It is interesting that only these extinction events seemed to have had such major restructuring effects: the end-Permian mass extinction was, of course, on a different scale from the others, but the Late Cambrian events were no more or less important than several other extinction phases.

In the three-phase logistic model, each successive assemblage of organisms was able to achieve a higher equilibrium diversity level than the previous one because of the greater cumulative versatility, or adaptive capacity, of those organisms. Hence, the Cambrian hyolithids, archaeocyathids and inarticulate brachiopods were able to conquer a limited range of living modes. The replacing Palaeozoic 'fauna', consisting of trilobites, articulate brachiopods, crinoids, corals, nautiloids, and others, were able to burrow deeper and exploit new resources by tiering, develop more varied reefs, and swim more actively in the nektonic zones. The 'modern' marine fauna of bivalves, gastropods, decapods (crabs, lobsters), echinoids, fishes, and marine reptiles and mammals are able to extend the potential range of niches in the sea even further, producing more complex ecosystems, and hence pushing global diversity higher than was ever possible in the Palaeozoic.

A plot of the diversification of all continental organisms was not attempted in the 1980s. However, overviews of individual continental groups, such as vascular plants (Niklas *et al.* 1985), tetrapods (Benton 1985) and insects (Labandeira and Sepkoski 1993), were interpreted along the lines of a succession of global assemblages replacing each other within an equilibrium world view.

On the basis of an independent data set (Benton 1993), plots of the diversification of families of all organisms (Figure 3A) continental organisms (Figure 3B) and marine organisms (Figure 3C) were presented by Benton (1995). He made the startling suggestion that the continental curve might be best understood in terms of an exponential model, not least because it looked exponential. In other words, life on land had apparently diversified continuously since the Silurian with no sign of any plateau; the global carrying capacity for life on land has yet to be achieved. Benton (1995) also cheekily suggested that the 'all-life' curve (Figure 3A) looked as much exponential as logistic, but of course the Palaeozoic bulge above the best-fitting exponential curve is hard to explain in such a model (Hewzulla *et al.* 1999).

There are three ways to interpret the differences between the marine and continental familial diversification curves (Figure 3B, C). First, the continental curve could be so overlaid by error that it is incorrect. Second, the shape of the continental curve could be accepted as essentially correct, but an equilibrium explanation could be sought in which, somehow, what looks like an exponential curve actually is not, and is controlled by diversity-dependent processes. Third, it could be argued that the curve is exponential, and that it is under the influence only of ever-accelerating diversification through time, and that the marine situation is not a good model for understanding of the diversification of the bulk of life.

4. QUALITY OF THE CONTINENTAL FOSSIL RECORD

4.1. Confusion of scale

It is widely accepted that the continental fossil record is poorer than the marine. This seems so obvious that it surely could not be challenged. After all, continental fossils include all kinds of flying and tree-living creatures that rarely fall into sediment, and the nature of continental sedimentary deposition (in lakes, rivers, in soils, under glaciers) is patchy and sporadic. The poor quality of the continental fossil record is a key element of every lecture on 'preservation of fossils' delivered to first-year palaeontology students around the world. It is as much a truism as the observation that the fossil record becomes worse the further back in time one goes.

But neither observation is universally true.

Everyone who has spoken or written on these two observations (and that includes the author) has committed the logical fallacy of confusion of scale. Practical field geologists clearly justify the relatively poor continental fossil record, and the diminution of quality back in time, by their first-hand observations. Marine fossil beds are packed with thousands of specimens, while continental beds of the same age may contain only rare fossils. Likewise, a Miocene or Jurassic fossil bed is almost certain to be richer than one from the Cambrian or Ordovician, not only in the numbers of specimens, but also in their completeness and lack of distortion. These field observations are clearly true, but it is a non-sequitur then to apply them to the global macroevolutionary scene. Macroevolutionary discussions are generally framed at the stratigraphical level of the zone, stage or epoch, at the geographic level of the continent or ocean, and at the taxonomic level of the genus or family or higher. Field palaeontologists work with time intervals of individual sedimentary horizons and short sequences, in single quarries or restricted geographic areas, and the material they examine is individual specimens and species.

In day-to-day life, it is commonplace to fall foul of the fallacy of confusion of scale: 'This rugby player drinks too much beer, so all sportsmen are drunks'; 'My dog stinks, so I think I'll buy a cat instead'. These are common bar-room assertions, but it is unusual to find such a fallacy of confusion of scale at the core of a modern science. The fallacy is the assumption that local-scale observations of the quality of the fossil record scale up to the global level.

4.2. *Constant fossil record quality through time*

The assertion that the quality of the fossil record declines with age (Raup 1972) has been challenged by a large-scale empirical study (Benton *et al.* 2000) that shows no hint of such a phenomenon. The approach in this study was to compare the shapes of cladograms (founded on morphological and molecular characters) with the sequence of fossils in the rocks. A sample of 1000 cladograms of all groups of organisms, culled from the published literature, showed no evidence of changes in the quality of matching between trees and the order of fossils in the rocks through time (Figure 4). The comparisons were founded on three age versus clade congruence metrics: the relative completeness index (RCI; Benton and Storrs 1994), the stratigraphical consistency index (SCI; Huelsenbeck 1994), and the gap excess ratio (GER; Wills 1999). In all cases, higher values of the metrics indicate better congruence between stratigraphical and cladistic data. The expectation was that Palaeozoic groups would show poorer matching of cladograms and stratigraphy than post-Palaeozoic groups. Whether assessed period-by-period (Figure 4A) or by larger time divisions (Figure 4B–D), there is only limited evidence for improvement of the scores through geological time. So, clearly, it is true to say that the Cambrian fossil record is worse than the Cenozoic, if one wants to compare species-level analyses of evolutionary rates, or palaeoecology. But, for studies of the sequence of major groups through time, and of the patterns of diversification and extinction of genera and families on a global scale, the fossil record is of essentially constant quality through the last 540 million years of the Phanerozoic.

4.3. *Equivalence of marine and continental fossil records*

The assumption that the marine fossil record is self-evidently better than the continental has also been challenged, this time in two ways. One approach was to consider the absolute stratigraphical completeness of individual sections using a simple formula (Strauss and Sadler 1989; Marshall 1990). The formula compares fixed time spans determined by radiometric dating with the sum of the time represented by sedimentary beds, calculated using mean sedimentation rates from modern observations, lying between the two radiometric dates. In most sedimentary sequences, it turns out that there is much more gap than section. Indeed, a typical sedimentary sequence of 100 m might represent less than 1% of the time span, since the preserved sediments were deposited relatively rapidly, and deposition phases are separated by disconformities that represent long times of erosion or non-deposition. When calculated for a range of fossiliferous sedimentary sections, Schindel (1982) found that, among the case studies he sampled, the most complete were continental sections: Plio-Pleistocene lacustrine/volcanic successions in the African Rift Valley, Eocene fluvial/palaeosol successions in the mid-western United States,

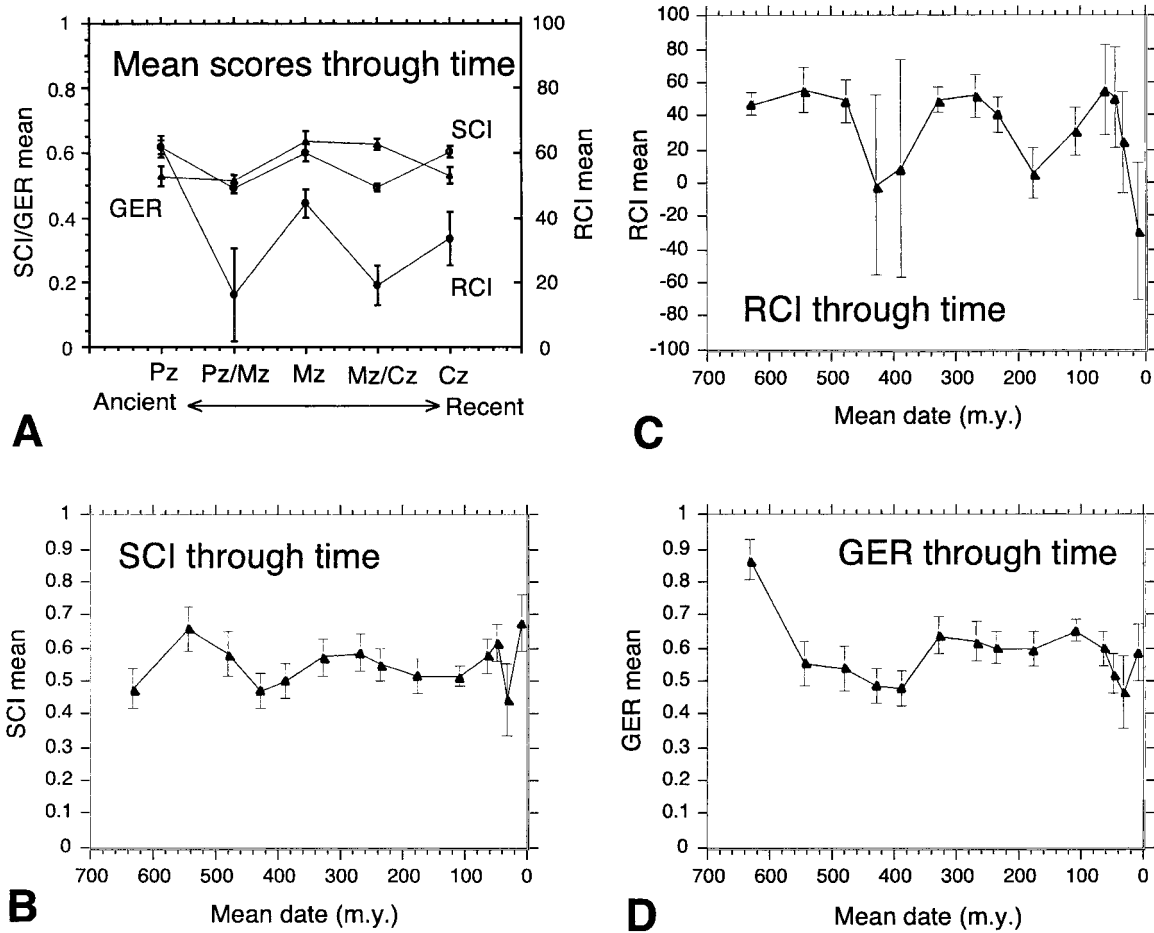


Figure 4. Mean scores of the age versus clade metrics for finer-scale divisions of geological time. (A) Stratigraphical consistency index (SCI), the relative completeness index (RCI), and the gap excess ratio (GER) for five time partitions of the data set of 1000 cladograms, namely cladograms with origins solely in the Palaeozoic (Pz), cladograms with origins spanning the Palaeozoic and Mesozoic (Pz/Mz), cladograms with origins solely in the Mesozoic (Mz), cladograms with origins spanning the Mesozoic and Cenozoic (Mz/Cz), and cladograms with origins solely in the Cenozoic (Cz). (B–D) Age versus clade metrics for cladograms partitioned into geological periods and epochs (see Figure 3 for the time divisions used), showing temporal variations in the SCI (B), RCI (C) and GER (D). The age versus clade metrics are explained in Benton *et al.* (1999, 2000). There is no statistically significant secular trend for the broad-scale time divisions (A), nor for the period-by-period assessments by the SCI (B) or RCI (C). The GER values (D) do improve through time ($0.5 > p > 0.025$), but the regression becomes non-significant if the low Vendian value (based on 34 trees) is omitted.

and deltaic/lacustrine successions in the Pennsylvanian of North America. In his synthesis of thousands of modern sedimentation rates, Sadler (1981) found that terrestrial/fluviatile sections show higher sedimentation rates than marine shelf and abyssal sediments over time intervals up to 100 years.

Such studies give pause for thought: continental sedimentary sections can be as good as, or better than, marine sections in terms of completeness. However, these are merely case studies, and it could still be asserted that they are not representative of the normal situation. The clade versus age congruence approach offers another view, and could be said to be more comprehensive. In an initial study of 63 cladograms and molecular phylogenies of echinoderms and 63 cladograms of continental tetrapods (Benton and Simms 1995), the echinoderms apparently had a poorer fossil record. This could have been a chance result, perhaps reflecting some other phenomenon such as the propensity for fragmentation of echinoderm specimens, or the fact that many more palaeontologists study continental tetrapods than echinoderms (Donovan 1996). However, more comprehensive studies by Benton and Hitchin

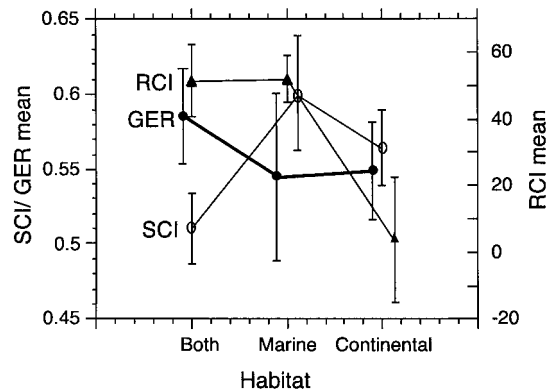


Figure 5. Variations in age versus clade metrics with broad habitat for a data set of 1000 cladograms. There is no discernible difference between the quality of the fossil records of marine, continental, or mixed (i.e. continental plus marine) groups of organisms. The continental groups score significantly worse than the marine for the RCI (relative completeness index), and worse, but not significantly so, for the SCI (stratigraphical consistency index). According to the GER (gap excess ratio), both major habitat types have fossil records of equal quality. The low value of the continental RCI is probably an artefact stemming from the fact that most cladograms of marine organisms date from the Palaeozoic, while most cladograms of continental organisms are post-Palaeozoic in age; long known time spans enhance the RCI value. Error bars encompass 95% of variation about the means of each sample.

(1996), who had incorporated fishes into the data base, and by Benton *et al.* (1999), who had added further groups, confirmed that there was no evident difference between marine and continental groups.

This can now be assessed from the larger data base of 1000 cladograms. Of these 1000 trees, 374 were founded on clades which included organisms that occupy both land and sea (e.g. Arthropoda, Vertebrata, Tetrapoda, Mammalia, Carnivora), 193 were founded on entirely marine clades, and 433 on entirely continental (i.e. land + freshwater) clades. Mean measures of the RCI, SCI and GER metrics (Figure 5) show that entirely marine groups have broadly better clade versus age congruence than entirely continental groups for the RCI measure, but not for the SCI or GER. For SCI, the marine-only clades score a higher mean value than the continental-only clades, but the distributions of values overlap substantially. The mixed marine/continental clades do, however, show significantly lower values. For RCI, the mixed marine/continental clades score virtually identical values to the marine-only clades, and these are significantly higher than for the continental clades. For GER, all three data partitions have statistically indistinguishable ranges of values, with virtually identical values for the marine-only and continental-only categories.

This seems to be clear evidence that, at the taxic and stratigraphical levels of the cladograms (broadly supra-generic and stages), the quality of marine and continental fossil records cannot be distinguished. The exception is the RCI metric. The continental cladograms scored markedly lower RCI values than the marine cladograms and the mixed-habitat cladograms. This is readily explicable, however, by a particular property of the RCI, which is improved by long known ranges, in comparison to ghost ranges. Extant groups with origins in the Palaeozoic inevitably will have better RCI values than groups originating after the Palaeozoic, all other things being equal. In the study sample, marine cladograms dominate the Palaeozoic interval (39% of Palaeozoic cladograms are for marine-only taxa, compared to 9% for the post-Palaeozoic interval), and this could then artificially elevate the mean RCI value for marine cladograms.

Wagner (2000) sought to maintain the classic view that marine fossil records are better than continental by suggesting that the congruence results are artificial. He suggested that the cladograms of echinoderms and fishes are probably more accurate than are those for continental tetrapods, hence explaining marginally better congruence with stratigraphy of marine than continental cladograms. This suggestion is contrary to a common assumption that tetrapod cladograms are better than those of fishes and invertebrates since they have been much more intensively studied and revised by systematists (Gaston and May 1992; Benton *et al.* 1999), and perhaps there are more characters available. Indeed, Wagner's (2000) view would imply that cladogram quality of *all* continental organisms

(e.g. vascular plants, insects, reptiles, birds, mammals) was broadly inferior to that of *all* marine organisms (e.g. coelenterates, trilobites, crustaceans, brachiopods, echinoderms, fishes), an unlikely proposition.

At the global, long-term, familial level there is no evidence for any difference in the quality of the marine and continental fossil records. Hence, the first proposal, that the difference in shape between the marine and continental global diversification curves (Figure 3B, C) can be explained by the poor quality of the continental fossil record, is apparently not tenable.

5. EQUILIBRIAL AND NON-EQUILIBRIAL MODELS

This is not the place to enter into a long discussion about the relative merits of equilibrational and non-equibrational (expansion) models for the diversification of life on Earth. The issue was debated actively in the 1980s by proponents of the equilibrational approach (Carr and Kitchell 1980; Sepkoski 1984; Miller and Sepkoski 1988) and of the non-equibrational approach (Walker and Valentine 1984; Cracraft 1985; Hoffman 1986; Benton 1987), and more recent position statements have been made by Sepkoski (1996), Sepkoski *et al.* (2000) and Benton (1991, 1996b).

The equilibrium model still dominates thinking about diversification by many palaeobiologists, although it has been abandoned in its simple form by many evolutionary ecologists. It is assumed that there is a limited global carrying capacity for species, and that this limit acts as a diversity-dependent control, either on origination or extinction rates, or on both. There is, however, no evidence for a global carrying capacity of species (Walker and Valentine 1984; the pre-Darwinian 'principle of plenitude': Rieppel 1984), nor for predictable regional or 'island'-level carrying capacities (Simberloff 1983; Williamson 1983; Simberloff and Boecklen 1991; Wiggins and Møller 1997), nor for the inevitability of post-invasion extinction of either invaders or incumbents (Marshall *et al.* 1982), and evidence for diversity-dependent controls on origination rates are not as strong as has been assumed (Cowen and Stockton 1978). Coupled logistic equations, a useful approach to modelling the interactions of clades through time, can only suggest that data are consistent with competitive/equilibrational models, and they cannot reject alternative non-interactive, non-equibrational models (Sepkoski 1996).

Sepkoski (1996, p. 222) referred to three pieces of evidence that pointed to the appropriateness of the equilibrium modelling approach in studying the diversification of marine life.

- (1) There was an evolutionary explosion of marine animals during the early Cambrian, and diversification rates slowed after this initial exponential rise (Sepkoski 1984).
- (2) There were rapid rebounds after mass extinctions, in which local and global diversity recovered to pre-extinction levels during relatively short spans of time. This suggests that ecospace that had been vacated as a result of an extinction event could refill at a higher rate than entry into new ecospace (Miller and Sepkoski 1988).
- (3) The Palaeozoic plateau in marine animal diversity, lasting for some 200 million years, is strong evidence for equilibrium (Sepkoski 1984, 1996; Rosenzweig 1995).

All three propositions require further assessment. Alternative explanations exist for these aspects of the marine record, and it has been hard to find similarly convincing evidence of equilibrium for other sectors of the fossil record.

(1) *The Cambro-Ordovician logistic.* The dramatic slow-down after the rapid Cambrian/Ordovician diversification is very clear in familial-level plots (Figure 3C). In a non-equibrational world, this part of the marine curve could be explained as an exponential rise in diversity during the Cambrian that shows the appearance of damping at higher taxic levels as major new Baupläne cease to arise. However, it is not clear that the relative rate of this rise, and its levelling off, are replicated at the species level (see below). It is necessary to consider whether the Cambro-Ordovician families become, on average, more speciose at the same time, which could turn a logistic curve into an exponential. It is also necessary to consider the effect of extinction events. The slow-down coincides with a series of extinction events in the Late Cambrian and a further major event in the Late Ordovician. Extinction events, induced by physical causes, reduce diversity whether one lives in an equilibrational or a non-equibrational world.

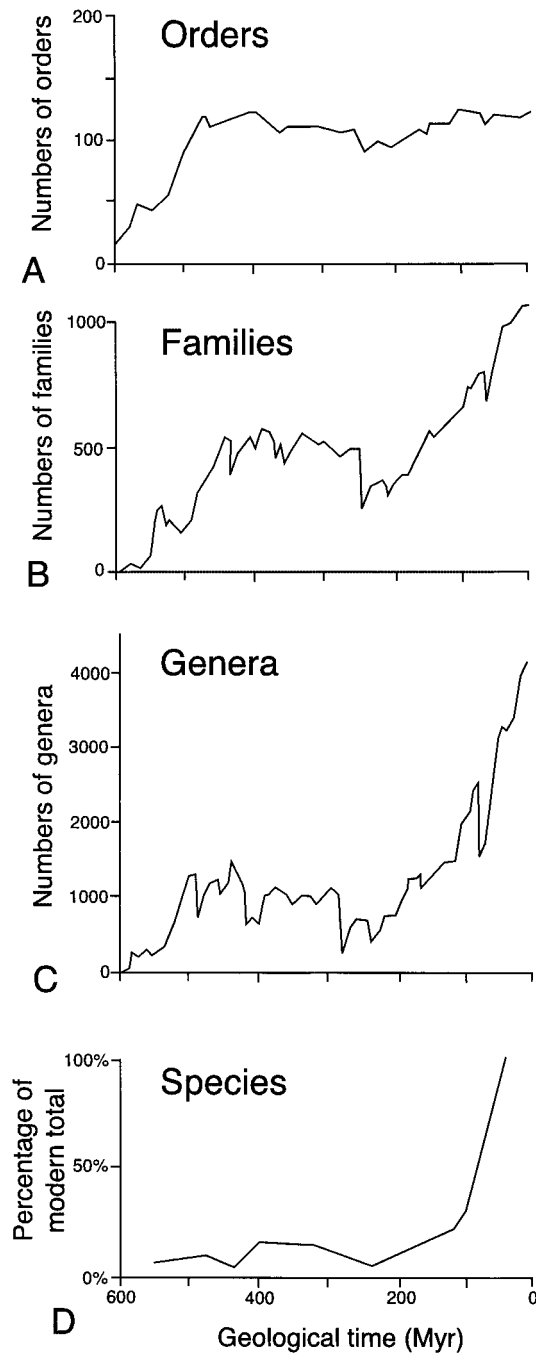


Figure 6. Patterns of diversification of well-skeletonized marine animals, counted as orders (A), families (B), genera (C) and species (D). The ordinal, familial and generic counts are based on empirical data, while the species curve is based on real counts and on simulations. The Phanerozoic plateau at ordinal level (A) decays to a Palaeozoic plateau at familial (B) and generic (C) levels, and may disappear at specific (D) level. Figure reproduced from Benton (1997), with permission from Elsevier Science, based on Sepkoski (1984, 1993, 1996) and Signor (1985), respectively.

(2) *Rapid rebounds*. If the rebounds after extinction events are as rapid as they seem, this is good evidence for damping, possibly by some competitive mechanism, as argued by Miller and Sepkoski (1988). These authors found that diversification rates were some ten times normal values in the intervals following extinctions. This phenomenon has to be estimated at the species level to see whether there are some artefacts of taxic scale (e.g. rapid establishment of genera associated with slower addition of new species), or whether there are fossil record artefacts, such as unrecorded Lazarus taxa, or human artefacts, such as the way in which originations and extinctions are summed within time spans, that might sharpen the post-extinction drops and rises in diversity. The discovery of 10 Ma time lags after background and mass extinctions (Kirchner and Weil 2000) is not a prediction of the logistic model (Erwin 2000), and indeed it argues actively against it. It seems that new taxa perhaps do not evolve soon after an extinction event, as if rebounding rapidly towards an ideal carrying capacity. Species loss during an extinction event causes profound damage to ecosystems. It is only after a long time lag that some new species appear and, in doing so, they create opportunities for further species to become established, generating a positive feedback process.

(3) *The Palaeozoic plateau*. The Palaeozoic plateau is the most telling evidence for a global equilibrium. According to the accepted viewpoint (Sepkoski 1984), the Palaeozoic plateau is sustained at a total level of about 550 families, composed mainly of the equilibrium diversity of the 350 families of the Palaeozoic evolutionary 'fauna'. Other analysts have interpreted the plateau as real, but not as an indicator of equilibrium. According to this interpretation, perturbations have kept communities well below any resource limitation (Whittaker 1977; Levinton 1979; Kitchell and Carr 1985; Valentine 1985; Hoffman 1986). A number of kinds of models have been proposed, some that are broadly diversity-dependent (Kitchell and Carr 1985), others in which speciation is diversity-dependent but extinction is diversity-independent (Walker 1985; Walker and Valentine 1984; Valentine 1985), and finally a neutral model that assumes random and independent variation in rates of speciation and extinction (Hoffman 1986). A third suggestion (Benton 1997) is that the Palaeozoic plateau may be an artefact of taxic level, and that it did not exist at species level. The plateau lasts for most of the Phanerozoic at ordinal level (Figure 6A). At familial level (Figure 6B), the plateau contracts to the Palaeozoic, and generic plots (Figure 6C) show a lower and less convincing plateau. For reasons mentioned below, empirical species-level curves are not available, and would probably be meaningless. However, an independently modelled species diversification curve (Figure 6D) is pretty well exponential. If the Palaeozoic plateau, and the two or three logistic curves behind the marine familial diversification curves, are an artefact of the shape of phylogenetic trees, then the equilibrium versus exponential model debate rather fizzles out.

6. CURVE FITTING AND MODELS

6.1. Curve fitting

Curves of various kinds—linear, logistic, exponential, parabolic, hyperbolic—may be fitted to plots of real data in an attempt to find out what processes lie behind those data. Modern software allows the analyst to try curves of various shapes and slopes to find the best-fitting one (i.e. the curve that gives the highest correlation coefficient, r ; the closer r approaches 1.00, the better the positive fit). In order to optimize the result, the analyst may attempt to fit curves to different subdivisions of the data. So, for example, Sepkoski (1979, 1984) found that he achieved a better fit of logistic curves to his marine diversification data by splitting the data points at the Cambrian–Ordovician and the Permian–Triassic boundaries. In an independent exercise, Courtillot and Gaudemer (1996) found that they achieved a better fit of logistic curves to the 'all-life' plot of Benton (1995) by inserting the same Permo-Triassic split, but also a Triassic–Jurassic division. They did not recognize the Cambrian as a separate division. Following this kind of logic, one could repeat the curve-fitting exercise *ad infinitum*, making endless modifications to the data divisions in order to improve the correlation coefficients. Presumably also, after each revision of the data sets, the divisions and the curves might change.

In terms of the evolutionary models behind the curves, it is important to be cautious in curve-fitting. The differences between Sepkoski's (1984) and Courtillot and Gaudemer's (1996) conclusions are more than simply

statistical. The latter authors were essentially saying that there was no such thing as a separate Cambrian 'fauna', but there was a separate Triassic 'fauna' that behaved largely independently of the Palaeozoic and the Modern faunas before and after it.

6.2. *Species-level curves*

It is important to note that most of the debate about equilibrium versus exponential models has focused on the classic family-level curves. However, evolution takes place at the species level. In an ideal world, of course, one would simply plot a species-level curve and discuss that. However, the reality is that such a curve would be so full of error that it could well be worse than useless. The scaling issue is important here. At high taxonomic levels, the fossil record is much more complete than at lower taxonomic levels (Sepkoski 1990; Benton *et al.* 2000), for both palaeontological and human reasons. At species level, a global compilation would be hugely incomplete and misleading, first because a larger proportion of species than of genera or families is unknown (it takes one specimen to identify the presence of a family, but that specimen represents only one of perhaps 100 species in the family). Human factors also conspire against the species: species lists are far less stable than lists of genera or families because new discoveries and observations can make profound changes at the more detailed levels.

As suggested above, the equilibrium plateau that is so evident at ordinal and familial levels appears to break down at generic and specific levels (Figure 6). There are two reasons that demand that this happens: the shape of trees, and increasing specioseness of families. First, phylogenetic trees branch from older to younger portions. The taxonomic categories—phyla, classes, orders, families, genera and species—are determined retrospectively once a phylogenetic tree has been branching for some time. It is inevitable then that the highest taxa—phyla, classes and orders—became established early in Phanerozoic history (Hennig 1966; Valentine 1969; Sepkoski 1978; Holman 1996), and very few have arisen subsequently. On the other hand, families, genera and species, as ever-smaller divisions of the phylogenetic tree, originated at all times through the Phanerozoic, although the points of origin of extant families are clearly older than those of extant genera, and the points of origin of extant genera are older than those of extant species. The geometry of a phylogenetic tree forces this phenomenon.

A plateau could be retained at species level if families behaved in a diversity-dependent manner, and families were equally speciose through time. They apparently are not. Censuses of a range of marine families show dramatic increases in numbers of species through time (Flessa and Jablonski 1985) by a factor of perhaps five times. So, relatively constant numbers of families through the Palaeozoic may say very little about evolution at the species level. Presumably, life was becoming ever more diverse as species branched and insinuated into new modes of life and new habitats. It just so happens that major new Baupläne (i.e. new families) in the sea arose at a rate equal to the rate of extinction of other families, hence rendering a family-level global equilibrium that masked what was really happening.

Could an exponential family-level curve be founded on a logistic species-level curve? It would be virtually impossible to imagine such a situation, where families appeared at a modestly accelerating rate through the Phanerozoic, but speciosity of those families was increasingly suppressed through time. However, following the logic of Miller and Sepkoski (1988), an exponential curve can be explained by a competitive model if there is evidence of damping of the natural rate of increase. In the case of the exponential continental curve (Figure 3B), however, it is not clear which other groups were interacting with all the continental organisms in order to suppress their natural rate of increase. One could cite only competition among the continental organisms that held down their natural rate of diversification. But equilibrium modelling is meaningless in such a situation.

7. EXPONENTIAL DIVERSIFICATION OF LIFE ON LAND

Strong evidence for an exponential increase in the diversity of life on land comes from two areas: studies of the origins of clades, and comparisons of modern biodiversities.

Although there is no evident logistic curve in the continental diversification pattern (Figure 3B), there could be evidence for interaction of major groups, perhaps times when diversification rates were heavily damped because of intense levels of competition. Such times should be indicated by a switch in the nature of group originations, from origins in unoccupied ecospace to competitive displacement of pre-existing taxa. An outline study of the origins of all 840 families of tetrapods that are represented by more than one species (Benton 1996a, b) has provided no evidence for the approach of equilibrium at any point. Only 13–26% of tetrapod familial origins *could* be (but need not be) explained by competitive interaction with a pre-existing family. The distribution of these candidate competitive displacements is largely random with respect to time.

Modern levels of biodiversity on land and in the sea are also telling. Of the 1.8 million described species, only 15% are marine and 85% are continental (May 1994; Reaka-Kudla 1997). Estimating true biodiversities is problematic since one must add multipliers to these figures to account for the biodiversity that has yet to be described. Indeed, this is a disputed issue for both the marine and the continental realms. Current estimates of total global biodiversity range from 5 to 120 million, the higher figures reflecting the view that certain groups, such as insects, fungi, marine meiofauna and microbes, are so vastly diverse that systematists have barely begun to sample the true range of their species. The figures in Table 1 represent a relatively conservative consensus viewpoint (May 1992, 1994; Briggs 1994; Stork 1997), where continental diversity (especially that of insects) is pulled back from the wilder conjectures of 50–100 million species.

True marine biodiversity is hotly debated, with estimates ranging from a modest 178,000 species (Briggs 1994) to 10 million species or more. Grassle and Maciolek (1992) suggested that the marine benthic macrofauna, primarily molluscs, crustaceans and polychaete worms, might number 10 million species. Poore and Wilson (1993) and Snelgrove (1998) preferred a somewhat lower figure of about 5 million species of marine organisms alive today. However, critics of such estimates, including May (1992, 1994) and Briggs (1994), argued that figures of 5–10 million species in the sea are huge extrapolations from small-scale sampling exercises. After all, Grassle and Maciolek (1992) sampled a 21 m² area of the continental slope of the northwestern Atlantic, and extrapolated from the 798 species found within that area to the global total of 10 million in the 300 million km² of the modern oceans. May's (1992, 1994) estimate of 500,000 marine species is used herein (Table 1).

Life in the sea is less diverse than life on land, whichever estimate is preferred. Using the conservative figures in Table 1, marine biodiversity is only 4.1% (= 0.5/12.34) of the total. When it is recalled that Phanerozoic continental diversity was achieved in less time than marine diversity (essentially through the past 400–440 million years, since the Silurian and Devonian, rather than through the past 600–540 million years, since the Vendian and Cambrian), it is clear that, geometrically, a different and faster diversification curve is necessary.

In this discussion, microscopic organisms have been excluded since it seems almost impossible to establish meaningful approaches to estimating their modern biodiversity (Embley *et al.* 1994). Exceptional diversity has been claimed for microbes (Ward *et al.* 1990; Hawksworth 1992), but Stork (1997) estimated less than 1 million species for protozoans, bacteria and viruses combined.

Table 1. Estimated diversities of species of plants and animals on land and in the sea (modified from Briggs 1994, with upward estimates of marine groups from May 1994 and Stork 1997)

Marine	Estimated species numbers	Continental	Estimated species numbers
Porifera	9 000	Fungi	1 000 000
Cnidaria	9 000	Plants	300 000
Nematoda	35 000	Nematoda	1 000 000
Annelida	15 000	Mites	750 000
Arthropoda	200 000	Spiders	170 000
Mollusca	190 000	Mollusca	20 000
Bryozoa	15 000	Insects	9 000 000
Chordata	15 000	Chordata	25 000
Others	12 000	Others	75 000
Totals	500 000		12 340 000

The seemingly low species-level diversity of marine life is countered by high diversity at higher taxonomic levels. While 28 phyla of macroscopic organisms are terrestrial, 43 are marine. The contrast is even greater for animals alone: there are 32 marine phyla compared to 12 terrestrial. Ninety per cent of all known taxonomic classes are marine (May 1994; Reaka-Kudla 1997). The high diversity of marine phyla and classes could simply reflect the fact that marine animals have had a longer history than continental animals. In 600 million years or more, marine animals have had time to evolve major differences in their body plans, and functional and biochemical diversity. Alternatively, this phenomenon could be an artefact. Perhaps taxonomists have been comfortable to identify major clades that date back to the Cambrian as phyla, while groups dating from the Devonian cannot achieve that status. A part of the artefactual argument could also be the difficulty in arguing that phyla, classes and other taxonomic categories are meaningfully comparable across phylogenetic trees.

In view of the difficulties with higher taxa, it is best to focus on the species level, and to consider why life on land has achieved such a huge diversity when compared to the more ancient life of the sea. There are three possible explanations: (1) there are more opportunities for endemism on land; (2) habitats are more varied on land; or (3) the size of primary producers plays a key role. These will be considered in turn.

(1) *Higher endemism on land.* Through geological time, continental masses have moved, fusing and splitting apart, and sometimes moving through major climatic zones. During the past 200 million years, from the Triassic to the present, the split-up of Pangaea has been paralleled by the evolution of many groups of plants and animals. The endemism of marsupials in South America and in Australia is one of thousands of examples where individual clades have been isolated geographically, and have evolved independently. Such cases are harder to establish in the sea, where, despite the opening and closing of barriers, most taxa are free to migrate, or be swept, over large areas, whether as adults or as larvae. Such mixing must reduce the possibilities for endemism and hence limit diversification.

(2) *More varied habitats on land.* Habitats on land are seemingly more heterogenous than those in the sea in terms of temperature ranges from pole to equator, temperature fluctuations through a typical day and a typical year, and architectural elaboration. However, topography and patchiness of food supplies may be rather comparable (May 1994). Coral reefs are as architecturally complex, and as rich in species, as any forest, but there are forests of very different kinds at different latitudes on land, while coral reefs are restricted latitudinally. The environmental heterogeneity on land is perhaps even more marked if one considers geological time. Climates have changed dramatically, often on time scales of tens or hundreds of thousands of years, but such fluctuations probably did not have such a profound effect on the sea. Marine ecosystems have probably experienced remarkable stability when compared to most continental ecosystems.

(3) *Primary producers on land are big.* Primary production in the sea occurs in the phytoplankton, minute single-celled organisms that are generally smaller than the herbivores, the zooplankton. On land, primary producers are plants, which are typically macroscopic rather than microscopic, and which are often very large indeed. In fact, primary producers on land are larger than their commonest herbivores, insects (Briggs 1994). May (1994) also noted differences in grazing efficiency: while zooplankton typically graze only 1–5% of primary productivity per day, terrestrial herbivores consume 5–70% (typically 5–20%). The higher efficiency presumably means that more biomass of herbivores can be sustained on the same volume of plant matter on land than in the sea. The large size of terrestrial primary producers, and the fact that they are not killed in huge numbers by herbivores, means that they provide diverse habitats in addition to supplying food. Complex coevolutionary relationships between plants and insects, for example, probably account for huge ranges of biodiversity that are not matched by any comparable phenomenon in the sea.

8. IMPLICATIONS OF AN EXPANSION MODEL

The idea of unconstrained expansion of life on land (or of all life) is somewhat bewildering. Non-equilibrium models seem much more appropriate than equilibrium models for describing an open system such as the biosphere, where energy is fed in continuously from the Sun. Biological systems have become ever more complex through

time, and it is not clear what purpose there is in trying to place an equilibrium cap over such systems. Equally, in the face of an exponential curve for the diversification of life on land (Figure 3B), it is rather weak of the equilibrium modellers simply to argue that it is merely an illustration of our ignorance of the continental fossil record.

Cracraft (1985) presented a non-equilibrium theory of lithospheric (geomorphological) complexity as the driving force behind global species diversification. He argued that the dominant mode of speciation is by the allopatric (geographic) model, where physical barriers divide populations within a species from each other, and in time promote species splitting. Through time, with short-term changes in topography, climate and vegetation distribution, species split repeatedly and adapt to smaller and smaller niches. Such habitat complexification is non-equilibrium, and may continue without limit, and so the diversification of species can also proceed without limit. He applied the model to life in the sea and on land, although the most convincing evidence came from examples of terrestrial plants and animals.

Unconstrained expansion certainly seems to characterize some clades, such as insects, angiosperms, birds and mammals, which continue radiating linearly or exponentially for many tens or hundreds of millions of years. Such ever-expanding patterns imply that these groups are highly successful and adaptable. The overall patterns of diversification incorporate the numerous constituent clades, some expanding, others diminishing, and yet others remaining at constant diversity at any particular time. From an expansionist viewpoint, there is no prediction of how the individual clades affect each other. New global diversity levels may be achieved by combinations of new adaptations, habitat changes and extinction events. In the past 250 million years, the diversification of life has been dominated by the spectacular radiations of certain clades, both in the sea (decapods, gastropods, teleost fishes) and on land (insects, arachnids, angiosperms, birds, mammals). There is little evidence that these major clades have run out of steam, and nothing to indicate that they will not continue to expand into new ecospace. Nor is there any hint that new radiations will not occur at any time (note the vast radiations of species of murine rodents and passerine birds in the past 5–10 million years).

Exponential increase could imply that diversification would last forever. Presumably there is a limit to the numbers of families, or other taxa, that can inhabit the Earth at any time: such a limit would be imposed not least by the amount of standing room on the Ark. If a limit of living space were approached, ever-smaller organisms would presumably be favoured by selection. Equally, as has happened so many times during evolution, organisms would take unexpected measures to survive, for example, by occupying the air, burrowing into sediments and, in the case of some bacteria, living deep within the Earth's crust. With size reduction, the ultimate limit to the diversification of life might then become the availability of the chemical components of life, principally carbon.

The volume of carbon may not in fact be a simple ultimate limiting factor on the potential diversity of life. Since the biosphere is an open thermodynamic system, with the influx of energy and matter from space, and since the rates and effectiveness of cycling essential elements through biological systems may well have improved through time, it is likely that total global biomass has increased through time, and will continue to increase (Cracraft 1985).

This thought, that life will continue to expand into the future, should not lead to complacency, however. It is important to note that, although biomass and biodiversity have increased through time, and will continue to increase into the future, the rate of species destruction by human activity is much more rapid than any natural propensity of life to diversify.

9. CONCLUSIONS

The prevalence of competitive/equilibrium thinking among palaeobiologists is striking. It stems from a strong focus on the fossil record of well-skeletonized marine invertebrates, and on an assumption that competition and equilibrium models dominate modern evolutionary ecological thinking. Both points are misleading.

The majority of species today, from 85 to 96%, live on land, and hence their patterns of diversification are worthy of consideration in attempting to understand how life as a whole has diversified. All the evidence points to exponential patterns of increase in the numbers of continental families. This implies an expansion model, not an equilibrium model, of increase. In addition, it is evident that at least part of the classic marine diversification

pattern is artefactual: below the ordinal and familial levels, the famous Palaeozoic plateau breaks down, and the curve of species diversification in the sea was probably exponential too.

The assumption that competition and equilibrium rule nature today has not been confirmed. The theory of island biogeography, while elegant and mathematically tractable, has been hard to demonstrate. In fact, many experimental and natural studies so far have rejected it. It is also not surprising then that such an approach, derived from the classic competition experiments of the 1930s in closed laboratory systems, does not work in the open system of the real world. Interspecific competition is important in producing local effects, but it is only one of many agencies that affect diversity, such as predation, parasitism, mutualism, climate change, asteroid impact, volcanic eruption and the rest. The theory of island biogeography was expected to provide a predictive framework for a new science of evolutionary ecology, but it did not (Hall 1988; Keddy 1989; Grimm 1994; Shradefrechette and McCoy 1994; Trepl 1994; Weiner 1995). If it were true, repeated histories of islands should be identical, but this does not seem to be the case. Identical patches of land may be colonized in many different ways, and they may end up with very different diversities, which depend more on the chances of history (which species arrived first, whether there was a huge storm that washed the soil away, whether there was an epidemic, levels of parasites and epiphytes, whether ants arrive or not, and so on) than on the reality of a fixed number of species/niches in a fixed area of territory. Palaeobiologists, therefore, need not feel obliged to force the expectations of such equilibrium models on to the vaster canvas of the history of life.

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