

# 18. The causes of the diversification of life

M. J. BENTON

*Department of Geology, University of Bristol, Bristol, UK*

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## Abstract

Diversification on the large scale has been explained in many different ways. Equilibrium and non-equilibrium models of various kinds have been proposed, but both kinds suffer from unsupported assumptions. More specific explanations of diversification fall into four main categories: (1) the patterns are artefacts of a biased fossil record; (2) the patterns are real and caused mainly by physical perturbation; (3) the patterns are real and caused mainly by biotic factors; or (4) the patterns are real but stochastic. At least 14 specific explanations have been given, but most of these fail to explain long-term global patterns. Three main candidate models for large-scale diversification are tested with data from the fossil record of tetrapods, and the strongest seems to be expansion of adaptive space, followed by subdivision of niches and specialization, and then by provinciality caused by topographic and climatic change. These tests illustrate some of the complexities of disentangling the different explanations for diversification, but they point to ways in which such tests may be quantified.

## Introduction

Life has diversified massively during the course of geological time. It should be possible to establish the broad pattern of the global diversification of life since its origin some 3.7 billion years ago, and to determine the causes of that diversification. Further, if all organisms are related to each other in a great phylogenetic tree that derives from a simple common ancestor, the causes of diversification will describe major phylogenetic processes affecting a single clade.

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So far, palaeobiologists have approached this problem by a piecemeal approach, plotting the patterns of diversification of relatively well preserved segments of the fossil record. An early attempt by Valentine (1969) showed the diversification of benthic marine invertebrates over the past 600 Ma (Fig. 18.1(a)). An initial low level of 50 or so families in the Early Cambrian was followed by a rapid rise to 250 or so in the Late Ordovician, a sudden drop at the end of the Permian, and a continuing climb ever since. Valentine (1969) argued that this pattern was essentially real, and that it reflected changes in the physical environment, such as continental drift. Valentine and Moores (1972) argued, for example, that the great extinction at the end of the Permian was caused by the coalescence of continents, and continental shelf seas, into a single supercontinent, Pangaea. The consequent loss of shelf habitats supposedly led to widespread extinction.

Raup (1972) challenged Valentine's model, and suggested that much of the pattern of diversification in the Phanerozoic was produced by systematic sources of error. For example, he argued, the volume of sedimentary rock preserved, and its area of exposure today, diminish the further back one goes in time. Hence, early Palaeozoic floras and faunas are less well represented than are more recent ones, and their global diversity appears depressed. There are also human factors involved. It is a well known fact that more palaeontologists devote their efforts to describing Mesozoic and Cainozoic fossils than Palaeozoic ones. 'Palaeontologist Interest Units' can be assigned to each geological period, and these show a systematic bias against earlier faunas which

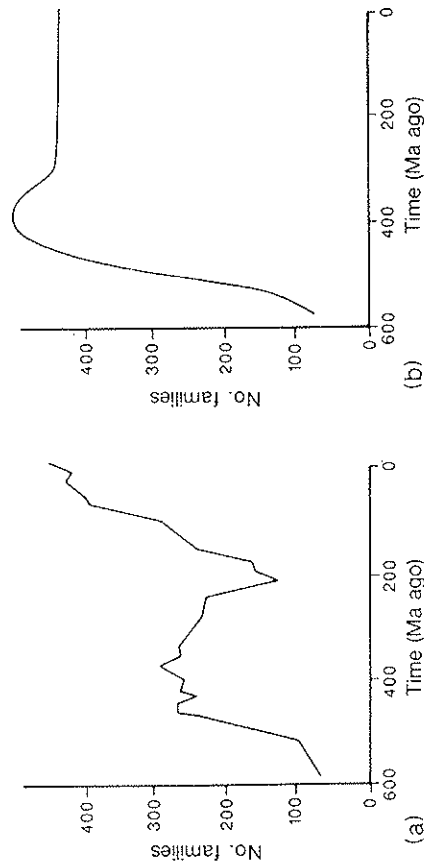


Fig. 18.1. Two views of the pattern of diversification of marine invertebrates during the Phanerozoic (the past 600 Ma): (a) the empirical model (after Valentine 1969); and (b) the bias simulation model, in which estimated systematic biases have been removed (after Raup 1972).

will thus appear less diverse (Sheehan 1977). Raup (1972) presented a 'bias simulation model' (Fig. 18.1(b)) which was meant to represent the true pattern of diversification of marine benthic organisms through time, after the various systematic sources of error had been accounted for. This model shows a rapid rise to a peak in the Cambrian and Ordovician, followed by an equilibrium level.

Gould *et al.* (1977) and Sepkoski (1978) supported Raup's (1972) model, but later studies have tended to confirm Valentine's (1969) empirical model (Fig. 18.1(a)). For example, Sepkoski's (1981, 1984) and Sepkoski *et al.*'s (1981) detailed studies of the diversification of marine animals have produced essentially the same pattern (see below), as have the compilations by Niklas *et al.* (1983) on the species diversity of vascular land plants, and Benton (1985a) on the family diversity of non-marine tetrapods (Fig. 18.2(a)-(c)).

The aims of this chapter are to look at the broad patterns of the

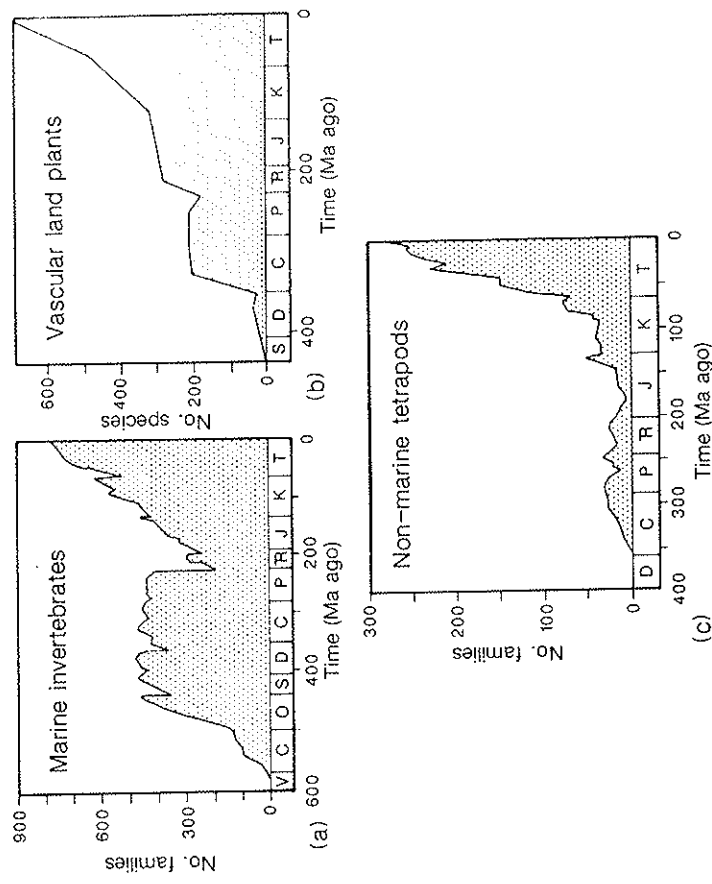


Fig. 18.2. The diversification of three groups of multicellular organisms during the Phanerozoic: (a) marine invertebrates (after Erwin *et al.* 1987); (b) vascular land plants (after Niklas *et al.* 1980); and (c) non-marine tetrapods (after Benton 1985a). Standard stratigraphic abbreviations are used for the geological periods.

diversification of life, to review the numerous available explanations for diversification, and to apply tests of these postulated causes to some examples of the diversification of tetrapods. First, a comparison of the two broad ways of viewing diversification, by means of equilibrium and non-equilibrium models, will be given.

### Equilibrium and non-equilibrium models

#### 1. Equilibrium models

Many palaeobiologists assumed that the appropriate approach to understanding global diversification would be within an equilibrium framework. The models were developed as extensions of logistic models from the ecological literature, of which MacArthur and Wilson's (1967) theory of island biogeography is an example. All of the parameters were scaled up from the ecological scale to the evolutionary: the island

became the world (or world shallow seas); 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. Sepkoski (1978, 1979, 1981) applied these models to the record of marine animal ordinal and family diversification. He determined first that the Palaeozoic faunas fell into two major 'evolutionary faunas', the first in the Cambrian of under 100 families, and the second in the Ordovician of about 350 families (Fig. 18.3(a)). The model (Fig. 18.3(b)) seeks to explain how each 'evolutionary fauna' had different overall rates of origination and extinction, and hence different equilibrium levels. The model was later extended (Sepkoski 1984) to include a third 'evolutionary fauna' which rose to importance after the end-Permian extinction event. The third 'fauna' has already risen past 1800 families, and it has not yet apparently reached its equilibrium level (Fig. 18.3(c)).

Hoffman (1981, 1983, 1985, 1989), Cracraft (1985), and others, have criticized these kinds of equilibrium models, partly because of problems in extrapolating from the ecological level to the global level. For example, local species immigration rates are very different from global speciation or family origination rates: species splitting in phylogeny cannot simply be equated with the local addition of existing species to an otherwise unchanged fauna. A further criticism is that, in island biogeography theory, local extinction rate increases with increasing species diversity, whereas the opposite appears to have been the case, at least for families, during the global diversification of marine animals (Raup and Sepkoski 1982; Van Valen 1984).

#### 2. Non-equilibrium models

Various kinds of non-equilibrium models for total global diversification have been developed recently. For example, Kitchell and Carr (1985) argued that their modelled ecological system never reaches an equilibrium level because of evolutionary innovations and mass extinctions. Their model matches the empirical data, but they retained an assumption that rates of origination and extinction are diversity-dependent.

This diversity-dependent assumption has been questioned by Hoffman (1981, 1985), Walker and Valentine (1984), and Cracraft (1985). These authors argue 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. This idea that there is an equilibrium level of species diversity, a level of saturation with species, has also been criticized by Gould and Calloway (1980), Rieppel (1984), and Benton (1987a), who note that species, and higher taxa, can invade empty adaptive zones,

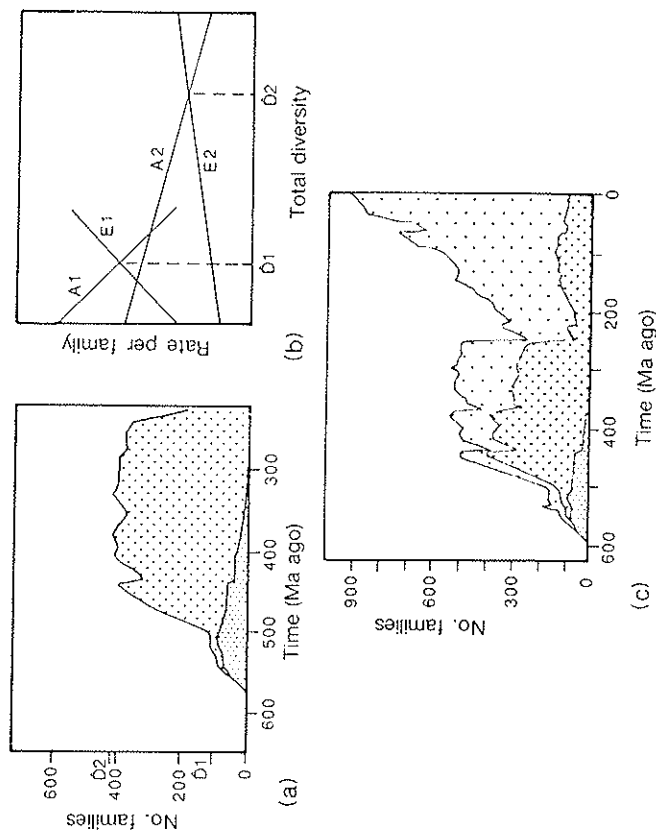


Fig. 18.3. The kinetic equilibrium model for the Phanerozoic diversification of marine metazoans: (a) two faunal phases for the Palaeozoic part of the pattern (after Sepkoski 1978); (b) the equilibrium model in which faunal phase (1, 2) has a characteristic rate of origin (A1, A2), extinction (E1, E2), and equilibrium diversity (D1, D2) (after Sepkoski 1978); (c) three faunal phases for the whole Phanerozoic record (after Sepkoski 1984). (See text for discussion).

and increase overall species numbers on a global scale.

Hoffman (1986, 1989) and Hoffman and Fenster (1986) have developed a non-equilibrium, non-diversity-dependent 'neutral model' for total global diversification. Here, both origination and extinction rates are assumed to be independent of total diversity, and of each other, and each is modelled as a random walk. Computer simulations of this 'neutral', or null, model produced graphs that appeared to match the empirical patterns just as well as the equilibrium model of Sepkoski (1984) or the non-equilibrium diversity-dependent model of Kitchell and Carr (1985), but the models were not truly null (see below).

### 3. Resolution?

It is hard at present to choose between the equilibrium and the non-equilibrium approaches to modelling global biotic diversification. There are clear parallels in this debate with the controversy over equilibrium theory and diversity dependence in community ecology (e.g. Harvey *et al.* 1983; Strong *et al.* 1984; Diamond and Case 1986; Benton 1987a). The criticisms of the equilibrium approach, especially those concerning its theoretical basis, require answering. Sounder justification is needed in support of equilibrium models of global diversification than a mere scaling-up of the concepts of community ecology (Webb 1969; Rosenzweig 1975).

The non-equilibrium models are also problematical. Is there an ultimate, but unattainable, equilibrium number of species on a global scale (Kitchell and Carr 1985)? Is it possible to develop an entirely stochastic null model, as Hoffman (1986) has attempted? It may be that, as in modern ecological examples, most so-called 'null models' still include some biological factors or biases (Harvey *et al.* 1983). In any case, if the data fit a null model, the deterministic models are not thereby disproved.

### The causes of global biotic diversification

#### 1. Suggested explanations

Many explanations have been advanced for the patterns of apparent diversity increase observed in the fossil records of most groups of organisms (Figs 18.1, 18.2). These suggestions are listed below under four main headings that include proposals that the patterns are: (1) artefactual; (2) real and caused primarily by physical factors; (3) real and caused primarily by biotic factors; and (4) real, but neutral in cause. The proposed explanations are summarized briefly, and key references are given, as appropriate. They are then discussed in more detail, and tests are proposed.

#### 18. Causes of diversification

*Artefact* The pattern of increase is an artefact of the patchy quality of the fossil record and the way in which we study it (Raup 1972, 1976a, b).

1. The volume of unmetamorphosed sedimentary rock increases towards the present.
2. The area of exposure of such fossiliferous rock increases towards the present.
3. Palaeontologists devote more attention to younger faunas and floras and hence name more species, genera, and families.
4. The 'pull of the recent', in which our knowledge of modern species enhances our knowledge of close relatives of the recent geological past.

#### Real and caused by physical factors

5. Increased endemism (provinciality), as a result of global changes in topography or climate, such as the break-up of Pangaea, changing patterns of ocean circulation, and global climatic gradients (Valentice and Moores 1972; Valentine *et al.* 1978; Valentine 1980; Benton 1985b).
6. Fragmentation of physical habitats, by changes in topography or climatic zones, for example, and associated fragmentation of faunas.
7. Continuous change in the physical environment maintains a level of biotic turnover and diversification—'lithospheric complexity' (geographic and climatic barriers to migration, global climatic gradients, topography) is in constant flux and stimulates constant diversification (Cracraft 1985).

#### Real and caused by biological factors

8. Increased endemism, and increased speciation rate, as a result of genetic, physiological, or behavioural changes that reduced gene flow.
9. Reduction in the probability of extinction by:
  - (a) optimization of fitness (Raup and Sepkoski 1982);
  - (b) reduction in levels of diffuse competition (Van Valen 1984);

- (c) increase in the species: family ratio through time (Flessa and Jablonski 1985);
  - (d) increase in mean extinction resistance as the set of families increases in mean age (Boyajian 1986).
10. Increase in the overall adaptive space occupied by a clade.
  11. Subdivision of niches, so that later forms occupy narrower niches and have more specialized adaptations than their forebears.
  12. The 'progressive' quality of lineages which leads to increased diversity by:
    - (a) an internal motor of improvement;
    - (b) escalation (Vermeij 1987), or a Red Queen model (Van Valen 1973), in which all lineages specialize in order to remain in evolutionary equilibrium;
    - (c) 'stepping up' of the recovery time and scope following mass extinctions—surviving clades of each event are able to radiate faster and further than those surviving earlier events;
    - (d) large-scale competition between 'evolutionary faunas' and attainment of ever-higher intrinsic equilibrium levels after each major replacement (Sepkoski 1984).

*Real, but neutral in cause*

13. 'Cladistic inevitability'—a clade must have one ancestor by definition and, if the clade survives for long, its diversity is more likely to increase than to remain constant at one (it cannot decrease, or the clade would have disappeared and would not be the subject of a study of diversification): a geometric argument.
14. Null, neutral, or stochastic, model—the increase in biotic diversity is the sum of untold numbers of microevolutionary processes acting on all species, and has nothing to do with grand unifying processes (Hoffman 1986, 1989).

2. *Critique*

I shall survey the 14 proposed explanations for the increase in the diversity of life in order, and select those for testing that seem most likely to have played a significant part.

The suggestion (Raup 1972) that much of the pattern is an artefact of

the incompleteness of the fossil record, and of our biased methods of palaeontological study (points 1–4), has been widely discounted. The sources of error are not denied, but they do not seem to be the main determinants of the pattern established from the fossil record. Valentine (1973) argued that many of the sources of error identified by Raup (1972) might indeed apply at the species level, but that these biases would be greatly reduced when genera or families were used, the normal practical analytical level. In other words, one species record, out of the dozens possible, is enough to establish the presence of a family in rocks of a particular age. Analyses at these higher taxic levels are robust enough to withstand a rather poor-quality fossil record without being seriously distorted.

Two further specific tests were applied to the data of Valentine (1969) and Raup (1972) in order to determine who was correct. Sepkoski *et al.* (1981) 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 (1969) model. All five graphs showed low levels at the start of the Cambrian, a higher 'plateau' during the rest of the Palaeozoic, a sharp drop in the Late Permian, and a rising curve thereafter. Signor (1982) came to a similar conclusion by a different route. He made estimates of the various sources of error noted by Raup (1972) 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.

Of the abiotic factors, increasing endemism caused by continental drift, changes in patterns of ocean circulation, or global climatic change (point 5) are possible factors and they are testable (see below), but habitat fragmentation on a smaller scale (point 6), although testable, is unlikely to be a major factor in overall global biotic diversification. It is hard to envisage any form of habitat fragmentation that would have

acted in a single direction in a relatively constant way through Phanerozoic time, and that would have affected the ecologically diverse tetrapods in similar ways. Cracraft's (1985) suggestion of the constant flux in the physical environment as a stimulus for biotic diversification (point 7) deliberately minimizes the role of biological interactions, and it is hard to see how it could be quantified and tested.

Of the biotic factors, increased endemicity caused by genetic or physiological change (point 8) would probably be impossible to test in fossil taxa, and it suffers from the same criticism as point 6: although it could be a factor that would produce local increases in diversity, it is hard to see how such a phenomenon could produce sustained unidirectional change on a global and long-term scale.

Reduced probability of extinction of families (point 9) is an empirical observation from the fossil record of marine animals (Raup and Sepkoski 1982; Van Valen 1984, 1985). Boyajian's (1986) model in which reduced extinction rates are tied to a net increase through time of extinction-resistant families, and Flessa and Jablonski's (1985) explanation in terms of increase in the species: family ratio through time have to be considered before the other two, rather vague, biological explanations given by Raup and Sepkoski (1982) and Van Valen (1984). Both of these imply a progressive and competitive element to the history of life, which has been disputed (see below). However, a declining probability of extinction is not true of all fossil records, since Benton (1985a) found a rising trend in total extinction rates and a constant probability of extinction for non-marine tetrapods, and Niklas *et al.* (1983) reported a complex pattern of changing extinction rates for vascular land plants: declining within particular major plant groups, but increasing from group to group through time. The suggestion that the probability of extinction has declined through time must be further tested for all groups of plants and animals, and the significance of Flessa and Jablonski's (1985) and Boyajian's (1986) models must be assessed. The explanation of increased biotic diversification by a reduced probability of extinction will not be considered further here for the reasons noted, and because it is not necessarily in itself an explanation, but merely another way of saying the same thing. It does not explain, for example, the magnitude of biotic diversification, nor the appearance of new body plans and new modes of life.

Increases in overall adaptive space occupied (point 10) and subdivision of niches (point 11) are possible explanations of increasing diversity, and they will be further discussed and tested below.

The 'progressive' models for diversification (point 12) all suffer from at least some of the problems of the 'Whig interpretation of history' (Schoopf 1979)—they can only be identified as progressive *after* the

event, and the explanations of improvement given by evolutionists may have no relation to what was really going on at the time—many of the models tread perilously close to teleology. Gould (1985), Benton (1987a), and others have argued that there is very little evidence for progress in a law-like or broad way in the history of life, and that the concept of progress does not sit comfortably in modern evolutionary theory. Four models of a progressive quality of lineages have been noted above (point 12, a-d), of which (a) is pure teleology and would not now be accepted by evolutionists. Progress by escalation, or by the Red Queen model (b) both suffer from the problems of scale: it has yet to be demonstrated how either model could act in a global long-term way that would set it above the vicissitudes of large environmental changes and extinction events. As Vermeij (1989) notes, biotic factors may be significant at low taxic levels, but physical factors predominate in affecting the biosphere globally. Explanations (c) and (d), improvements in recovery rates after extinction events and large-scale competition, are both assumptions rather than independently supported theories. They take the form 'group A radiated faster than group B and replaced it, so group A must have been competitively superior'. They are *post hoc* explanations, they involve beliefs that certain clades are overwhelmingly better than others, and that interclade competition is possible globally and over millions of years, and they suffer from all of the other problems of such scenarios outlined by Benton (1987a): confusion of pattern and mechanism; oversimplification; lack of proof; and incoherent scaling of concepts. Indeed, Erwin *et al.* (1987) gave evidence that might contradict explanation (c); the early Palaeozoic radiation of marine metazoans went further in terms of morphological innovation and per-taxon rate of family appearances than did the Mesozoic radiation. I suggest that the 'progressive' explanations (point 12) are either teleological or statements of faith, and they are untestable and will not be considered further.

The final group of models, the neutral or null models, have a certain attraction for palaeobiologists who believe that the antidote to competitive macroevolution is stochastic macroevolution. Gladistic inevitability (point 13) must take a part in all patterns of diversification, and stochastic branching patterns can apparently produce 'clades' that match the empirical pattern (Gould *et al.* 1977). However, Stanley *et al.* (1981) argued that the model was incorrectly scaled and that a truly null model of stochastic species splitting did not match reality. Proper account had to be taken of times of varying origination and extinction rates, and of the intervention of particular biotic and physical factors. Random splitting may explain parts of a pattern of diversification, but by no means the bulk of it. It is unclear also whether such a model can

explain the overall diversification of the biosphere, and the appearance of major new body plans.

The second neutral explanation (point 14), that of Hoffman (1986, 1989) and Hoffman and Fenster (1986), suffers from similar problems. These authors had to maintain the rate of origination higher than the rate of extinction permanently in order to produce a realistic curve. A straightforward random walk model with no such constraint would be as likely to decline as to increase. In addition, they inserted and removed high numbers of clades at times equivalent to the Cambro-Ordovician radiation and the Late Permian extinction.

This leaves three explanations of diversification for testing: increasing endemism (point 5); increase in adaptive space occupied (point 10); and subdivision of niches (point 11). These are all testable, and some preliminary analyses (Benton and Blacker, manuscript) suggest that all three factors have played a role in the diversification of the tetrapods — especially the last two.

### Tests of postulated causes of diversification

#### 1. The data and methods

The data used in this study were based on the fossil record of marine and non-marine tetrapods. This group was chosen since it is a well-established clade, much of its phylogeny is relatively well worked out by cladistic analysis (e.g. Benton 1988*b*), it is known over a long span of time (the past 400 Ma, since the Late Devonian), it is ecologically diverse, and ecologies of extinct and living forms can be discriminated into many categories (Benton 1988*a*, 1989*a,b*). The data on family names and stratigraphic durations are given by Benton (1987*b*, 1988*a*), and these were updated for the purposes of the present study. Data on basic ecological divisions, body size, and geographic distribution were added to the data base for this study, and a second parallel data base on well-preserved faunas (fossil Lagerstätten) was also constructed (Benton and Blacker, manuscript).

#### 2. The role of physical change and endemism

It was expected that the break-up of Pangaea after the Triassic would have led to increased endemism of terrestrial tetrapod families at least. Earlier, Benton (1985*b*) established this in a preliminary study of Mesozoic tetrapods: whereas Triassic families had nearly world-wide distributions, those that arose in the Cretaceous were generally restricted to a single modern continental area. The present study, based on a larger and updated data set, did not support this finding (Fig. 18.4). All the major changes in levels of continental endemism

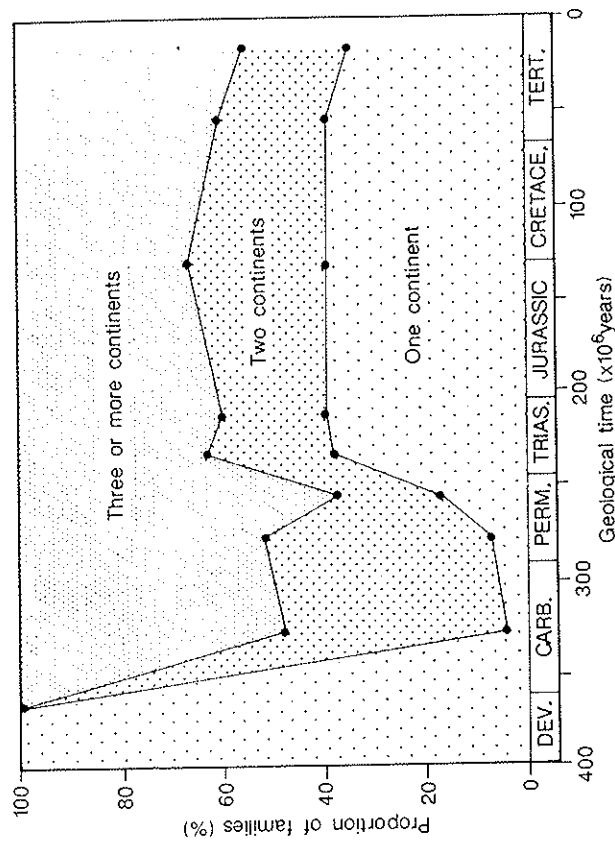


Fig. 18.4. Variations in the ultimate geographic distribution of non-marine tetrapod families that arose during each time interval. Family data were recorded by stratigraphic stage, and were then grouped into broad time intervals in order to provide large enough samples throughout ( $n = 44-360$ ; mean = 146 families per time interval).

took place in the Carboniferous and Permian when tetrapod families became more restricted in their geographic distribution, possibly as a result of increasing north-south climatic differentiation. From the Triassic to the present, about 35 per cent of families spread to become nearly global in distribution (present in three or more continents), about 25 per cent spread to two continents, and about 40 per cent were endemic to one continent for their entire existence.

These results are no doubt affected by a number of factors that may require further consideration before a definitive test can be made. First, the left-hand side of the graph, in the Devonian and Carboniferous in particular, is based on relatively small numbers of families (1-30 families present per stratigraphic stage). In addition, this older fossil record may give poorer distributional data than later fossil records, and may underestimate the numbers of continents ultimately reached by each family. In addition, the ultimate distribution of a family may depend on its stratigraphic duration, and durations that are underestimated either by gaps in the fossil record, or by the cut-off line

of the present day, may underestimate the final number of continents that members of a particular family will reach. Of course, the effect of the 'pull of the recent', noted above, will also distort records of familial distributions in more recent parts of the Cainozoic in the opposite direction, by expanding their distributions relative to families known only as fossils.

Valentine and co-workers (1978; Valentine 1980) developed a model of marine bioprovinces through time that depended upon continental drift, patterns of ocean circulation, and global climatic gradients. They argued that the diversification of marine life was controlled by the numbers of available marine bioprovinces which were determined by purely physical factors of the environment. Bakker (1977) provided a comparable model for diversification and extinction of terrestrial vertebrates.

### 3. The role of increases in adaptive space

Increases in the breadth of the adaptive space occupied by a clade would seem to be an obvious candidate for an explanation of diversification. In the case of the tetrapods, the earliest representatives, the two or three species of ichthyostegids and acanthostegids of the Late Devonian (Famennian) were semi-aquatic piscivores that lived in and close to fresh waters. During the Carboniferous and Permian, many lineages of tetrapods became more fully terrestrial in habits, and various gliding and flying forms appeared in the Permian and Triassic. Fully marine forms rose in the Permian (mesosaurs), Triassic (ichthyosaurs, nothosaurs, placodonts), Jurassic (crocodilians, plesiosaurs), Cretaceous (mosasaurs), Eocene (whales), and Oligocene (seals). Fliers became more diverse after the evolution of birds in the Jurassic and bats in the Eocene. These qualitative observations translate into quantitative data (Fig. 18.5(a)). The proportion of families remaining in the ancestral freshwater habitat declined from 100 per cent to a steady 10–15 per cent after the Late Permian. Tetrapods expanded first into terrestrial habitats in the Carboniferous and Permian, into flying, arboreal, and marine habitats in the Permian, and into burrowing habitats in the Jurassic. Occupancy of all of these additional zones of adaptive space has varied in proportion through time, and also in the precise nature of the occupants. Once conquered, however, it seems that these additional adaptive zones have been reconquered successively

or the majority of, species within a family (full details in Benton and Blacker, manuscript). Families were grouped into broader time units than stages, as in Fig. 18.4.

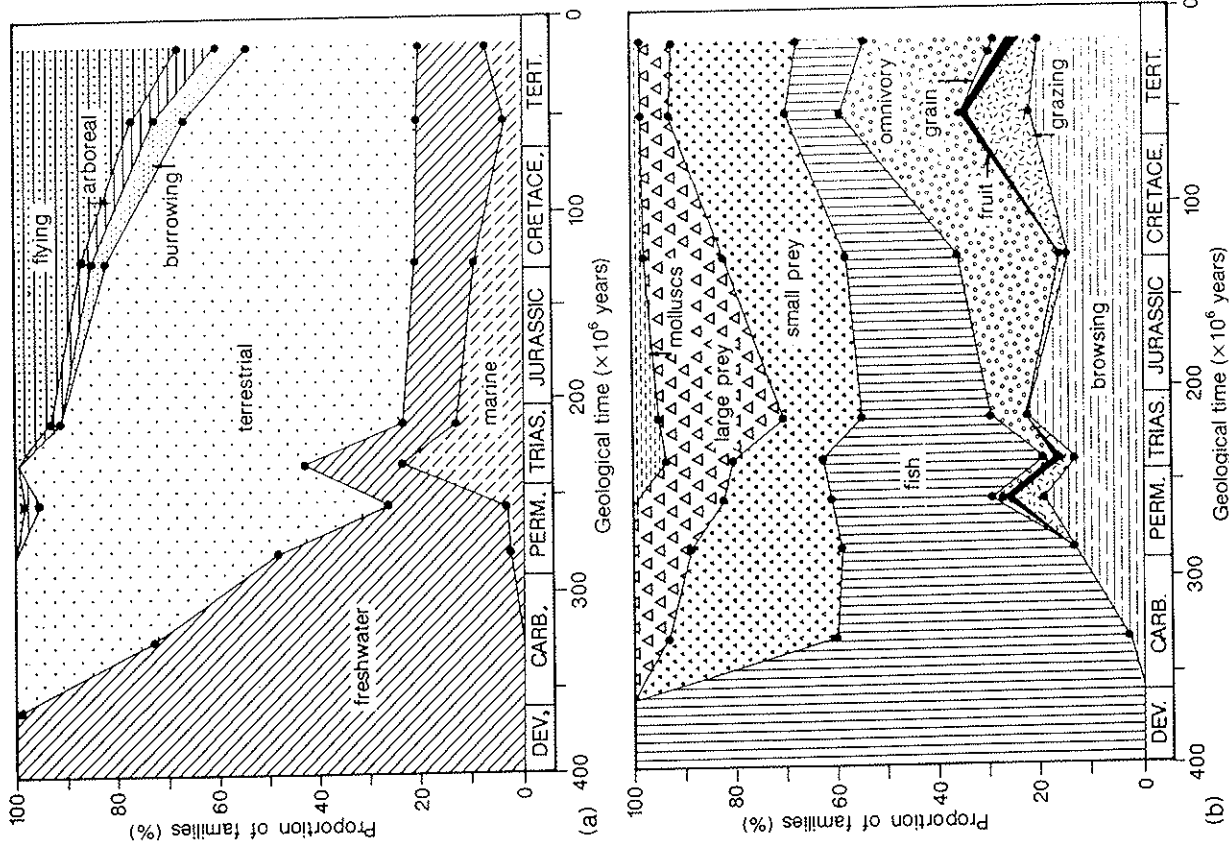


Fig. 18.5. Proportions of (a) broad habitat types and (b) diets of terrestrial and maritime tetrapod families through time. The habitats and diets were determined from the primary literature, and they represent the activities of all,



and independently, and a tetrapod presence has been maintained for all but relatively short intervals following major extinction events.

The expansion of adaptive space can also be documented in terms of diets (Fig. 18.5(b)). Fish-eating has fallen from 100 per cent dominance of tetrapod diets in the Late Devonian and Early Carboniferous to about 15 per cent in the Tertiary. Diets broadened to include insectivory and carnivory in the Carboniferous, broadly adapted browsing herbivory in the Permian, omnivory after the Late Permian, and ever-more specialized herbivorous or carnivorous modes after that (e.g. grazing, fruit, grain, molluscs).

These analyses suffer from some of the problems noted above for the study of endemicity, and especially from the fact that the earlier fossil record had yielded a relatively low number of tetrapod families. In addition, it is probably harder to determine the diets and habitat preferences of early tetrapods that have no close living analogues than those of Tertiary tetrapods. However, many of the usual problems of the fossil record are avoided in a study of this kind since the palaeobiologist needs only one or two well-preserved taxa in an extinct family in order to study their ecology and biology, and there are exquisitely preserved Devonian and Carboniferous tetrapods, just as there are excellent complete skeletons in the Tertiary.

Expansions of adaptive space have been proposed as a cause of the diversification of marine invertebrates (e.g. Bambach 1977, 1985; Ausich and Bottjer 1985) and of vascular land plants (e.g. Niklas *et al.* 1980). In the first case, marine invertebrates adopted entirely new life styles after the Cambrian, such as pelagic carnivory (cephalopods, vertebrates), benthic mobile suspension feeding (bivalves), carnivory (cephalopods, eurypterids, crabs, starfishes), deep infaunal deposit-feeding (bivalves), and shallow passive infaunal suspension feeding (bivalves, rostroconchs). New habitats conquered in the Mesozoic included pelagic herbivory (vertebrates), shallow infaunal passive deposit feeding and carnivory (bivalves), deep infaunal suspension feeding (bivalves, polychaetes, crabs), and deep infaunal active carnivory (polychaetes). Ausich and Bottjer (1985) focus on the expansion in adaptive space occupied by benthic marine invertebrates in terms of increases in tiering, that is, the vertical division of space above and below the sediment-water interface. The invention of invertebrate 'trees', such as long-stemmed crinoids, allowed these organisms, and a host of others that lived upon them, to occupy and feed in water up to 1 m from the sediment level from Silurian times onwards. In the other direction, the ability to burrow allowed invertebrates to occupy progressively deeper levels in the sediment, from maximum depths of 60 mm in the early Palaeozoic, to 120 mm in the Early

Devonian (bivalves), and 1 m from the Early Permian onwards (bivalves, arthropods). Similarly, in a comparison of the early Palaeozoic and the Mesozoic radiations of marine metazoans, Erwin *et al.* (1987) argued that filling of empty adaptive space was the main force behind diversification.

For vascular land plants, major jumps in diversity are linked to the evolution of heterospory and the seed habit, the origin of trees, the herbaceous habit in angiosperms, and other shifts into new adaptive space (Niklas *et al.* 1980).

#### 4. *The role of subdivision of niches*

The story of the evolution of many clades includes as much specialization, or niche subdivision, as it does expansion of adaptive space. For example, the early tetrapods had generalized dentitions, and it is assumed that many of them could have eaten a mixed diet of fish, insects, worms, small tetrapods, and even fruit and other nutritive plant parts. There is little evidence for highly specialized diets and other habits as are seen today in many groups. This argument is far too weak, however, without some firmer quantitative evidence.

An attempt has been made to test the idea of niche subdivision by comparing typical faunas through time, in a test analogous to that applied by Bambach (1977, 1985) to marine faunas. It is valid to compare an individual exceptionally-preserved fauna (Lagerstätte) from the Carboniferous with one from the Eocene, say, since levels of preservation appear to be equivalent. In other words, Lagerstätten of all ages can show preservation of tiny animals, soft parts such as skin, scales, and hair, and wholly soft-bodied organisms. A measure of the subdivision of niches can be obtained by counting the numbers of species in comparable faunas, that is, groups of tetrapods found in a single deposit in a single locality or small sedimentary basin. A preliminary survey of 100 such faunas, spanning the past 350 Ma in Europe and North America (Benton and Blacker, manuscript) shows a marked increase in mean faunal diversities from 18 in the Carboniferous to 35–51 in the Miocene and Pliocene (Fig. 18.6). The maximum figures rose from 25 in the Carboniferous to 80–100 in the Late Cretaceous and Tertiary.

This test requires refinement since a part of the increase in mean and maximum faunal diversities is almost certainly the result of the conquest of new adaptive space. Tertiary faunas typically include arboreal mammals and birds, for example. However, a preliminary survey on the present data set of the relative influences of niche subdivision and adaptive space expansion suggests that most of the increase in faunal diversity is caused by the former factor.

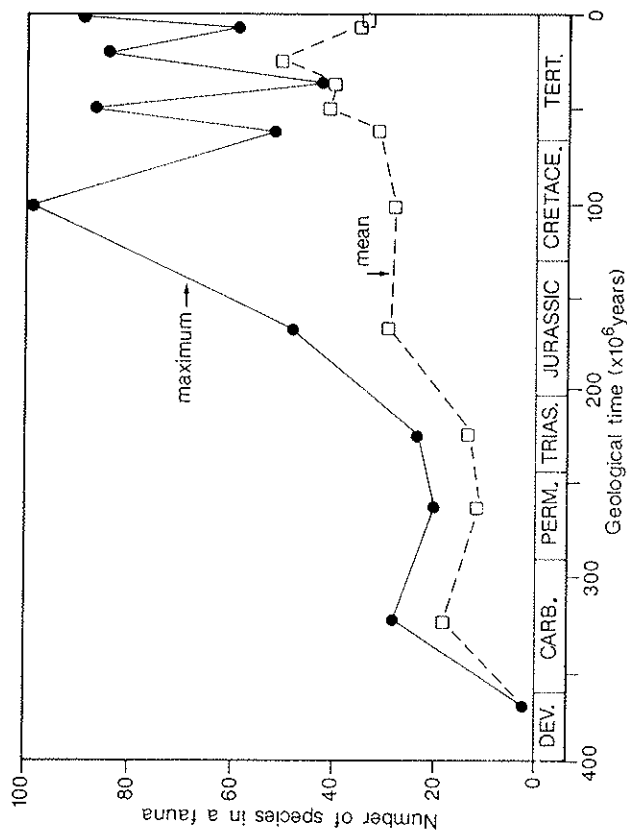


Fig. 18.6. Maximum and minimum mean numbers of tetrapod species in well-preserved terrestrial faunas. This graph is based on a sample of 100 faunas (details in Benton and Blacker, manuscript), with 1–20 faunas sampled per stratigraphic period (or epoch in the Cainozoic). Each 'fauna' is the species list of a single quarry or restricted sedimentary basin. Note the overall rise, with fluctuations in the maximum curve probably largely the result of variations in preservation quality.

### Conclusion

What are the relative roles of major physical change, adaptive space expansion, and specialization in producing diversification? Cracraft (1985) has argued that most macroevolutionary patterns can be tied to changes in the physical environment. However, the present study suggests that certain long-term physical changes that might have been expected to produce major effects (e.g. continental drift, climatic differentiation) are not adequate agents of diversification, for tetrapods at least. Doubt has also been cast on the role of continental drift and sea-level change in the history of marine invertebrates. Amalgamations of continents, such as occurred during the Permian, may indeed produce reductions in the circumcontinental shelf seas and global marine regressions (Valentine and Moores 1972), but the area of shallow water around oceanic islands increases. Nearly 90 per cent of marine families today are represented around oceanic islands, and these would survive a

major regression (Jablonski and Flessa 1986). The global effects of continental drift and marine regression on terrestrial faunas, argued eloquently by Bakker (1977), are even harder to confirm.

The relative roles of increased adaptive space and increased specialization in producing diversification are hard to determine, but the former may have had the main influence in tetrapod radiations. Bambach (1977, 1985) also found evidence that marine invertebrates have increased their diversity mainly by expansions of utilized adaptive space. Sepkoski (1988) has tested the relationship between increases in within-community, or alpha, diversity and between-region, or gamma, diversity. He found that the increases in alpha diversity detected by Bambach (1977, 1985) in offshore-shelf marine communities of 50–70 per cent during the Ordovician were insufficient to account for the total global increases in generic diversity of 300 per cent. The majority of the increase was probably explained by increases in between-community, or beta, diversity, in other words, by increases in the numbers of broad habitat types occupied, a conclusion that appears to correspond to the findings from the present study of terrestrial tetrapods.

Certain aspects of diversification patterns may of course be 'one-off' phenomena, dependent on specific historical circumstances, such as the break-up of Pangaea, latitudinal climatic diversification, the diversification of fishes (hence providing new adaptive space for predators), and other environmental changes. However, biological and ecological factors, such as increases in the overall adaptive space occupied by a clade, and subdivision of niches, seem to lie behind the long-term patterns of net increasing diversity. There is certainly no evidence for an inevitable motor of change that drives diversity ever upwards.

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