

## Why Is Life So Diverse?

### EXTENDED ABSTRACT

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**Abstract.** The present huge diversity of life—amounting to some 30 million species according to some estimates—has been explained as the result of a variety of processes, many of them incompatible. Specific explanations of diversification fall into four main categories: (a) that the patterns are artefacts of a biased fossil record, (b) that the patterns are real and caused mainly by physical perturbation, (c) that the patterns are real and caused mainly by biotic factors, or (d) that the patterns are real but stochastic. Three out of 14 proposed 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.

### INTRODUCTION

Life has diversified extensively during the course of geological time, ultimately from a single species to the present total of 30 million, according to recent estimates. 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.

Paleobiologists have plotted the patterns of diversification of relatively well preserved segments of the fossil record, especially benthic marine invertebrates (e.g., Valentine, 1969; Raup, 1972; Sepkoski, 1984). The literal plots of diversification of families and orders generally show low levels in the early Cambrian, a rise during the Cambrian and then a second larger rise during the Ordovician. The level of diversity then remained at a plateau for the rest of the Paleozoic, terminated by a massive decline at the end of the Permian. Since the early Triassic, diversity levels have risen with no sign of a leveling-off. Early debates about the accuracy of the literal plots of diversification have been resolved in favour of the view that they are broadly accurate representations of reality, and that the numerous sources of error do not have an overwhelming effect (Sepkoski et al., 1981).

The aims of this paper are to look at the broad patterns of the diversification of life, to review the numerous available explanations for diversification, and to summarise tests of these postulated causes. This paper is an extended abstract of a fuller account that has been published recently (Benton, 1990). Fuller explanations, and references, may be found there. A critique of adaptive radiation models presented here is not to be found in the longer account.

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## THE CAUSES OF GLOBAL BIOTIC DIVERSIFICATION

### Critique of Adaptive Radiation Stories

Typical explanations for diversification are ad hoc models that refer to individual radiation events, such as the radiation of the mammals at the beginning of the Tertiary. Such models may be termed story-like, or narrative, explanations, and they are hard to match with the larger-scale explanations needed for overall biotic increase. The story-like approach has been to describe the pattern and rate of radiation, and to seek adaptive explanations for the success of a group, whether it is supposed to have competitively replaced another group, or to have radiated opportunistically into empty ecospace (Cracraft, 1985; Benton, 1987a).

This kind of approach suffers from numerous difficulties, not the least being problems of simplification, assumptions of adaptation and competition, and untestability. In the case of the mammalian radiation 65 million years ago, the explanations cover most of the mammalian attributes, ranging over endothermy, the possession of hair, lactation, long gestation, parental care, large brains, and adaptable dentitions. The possession of one or more of these 'key adaptations' is said to explain the magnitude, rate, and adaptive variety of the radiation of placental mammals. Five criticisms may be levelled at such a mode of explanation.

1. The ideas are untestable. How is one to determine which one, or more, of the characteristics was important? It is not valid to compare contemporary groups that lack the character or characters in question since these features may not be viewed in isolation in the paleontological record. Can we perform experiments today, by placing mice and lizards in a box in order to test which is the best competitor? Can we test the value of hair by pitting an intact mouse against a half-shaved mouse?
2. Even if a case can be made for the value of a 'key adaptation' in terms of survival, this does not automatically make the link to stating that that was the feature that drove the radiation so successfully.
3. Further, the postulation of a 'key adaptation' does not explain why the radiation of mammals proceeded at such a high rate, why the mammals were able to achieve ten times the diversity of their ecological predecessors, the dinosaurs, nor why the mammals were able to enter so many adaptive zones not exploited by the dinosaurs. Each of these elements of the model involves further assumptions.
4. The 'key adaptation' types of explanations for radiations assume that the mammals were cyphers, or *tabulae rasae*, devoid of biological novelties except for the feature or features of interest. Organisms are complexes of interconnected homeostatic mechanisms, and it is probably impossible to extract one, or a small number of, features to which to ascribe their success.
5. Finally, simplistic 'key adaptation' models refer to individual events, and they allow few generalisations to the higher levels of explanation. Even if mammals radiated in the Paleocene because they had efficient teeth or hair, this does not go further to explain why tetrapods as a whole are ten times as diverse today as they were in the Mesozoic, why life as a whole is so diverse, nor why a particular broad pattern of increase has been followed through time.

### Explanations for Global Biotic Diversification

Many explanations have been advanced for the patterns of apparent diversity increase observed in the fossil records of most groups of organisms. These suggestions are listed below under four main headings.

**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):

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. paleontologists 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 (Valentine, 1980);
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:
  - i. optimization of fitness;
  - ii. reduction in levels of diffuse competition;
  - iii. increase in the species: family ratio through time;
  - iv. increase in mean extinction resistance as the set of families increases in mean age;
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:
  - i. an internal motor of improvement;
  - ii. escalation, or a Red Queen model, in which all lineages specialize in order to remain in evolutionary equilibrium;
  - iii. '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;
  - iv. 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, that 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, 1989).

### Critique

Few palaeontologists now subscribe to the idea that diversification is artefactual (nos. 1–4) after the tests by Sepkoski et al. (1981) and others. The abiotic and biotic models (nos. 6–8) are unlikely to apply to the global long-term level, and they are all hard to test. Explanation 9, that increases in diversity are the result of reductions in the extinction rate, is really another way of saying the same thing. In most cases, the observed decline in extinction rates is insufficient to explain the rate of diversification on its own, and for tetrapods at least, extinction rates remain constant, or increase marginally, while diversification proceeds apace. The 'progressive' explanations (no. 12) tend to be teleological, or to involve post hoc assumptions, or to be untestable assumptions (Benton, 1987a). The neutral or null models (no. 13) have been disputed, and none proposed yet is entirely neutral.

This leaves three explanations of diversification for testing, increasing endemism (no. 5), increase in adaptive space occupied (no. 10), and subdivision of niches (no. 11). These are all testable, and some preliminary analyses (Benton, 1990) suggest that all three factors have played a role in the diversification of the tetrapods, and especially the last two.

### Tests of Postulated Causes of Diversification

The data used in this study were based on the fossil record of marine and non-marine tetrapods (Benton, 1987b), with the addition of data on basic ecological divisions, body size, and geographic distribution. A second data base on well-preserved faunas (fossil Lagerstätten) was also constructed.

It was expected that the break-up of Pangaea after the Triassic would have led to increased endemism of terrestrial tetrapod families at least (explanation no. 5). However, the present study (Fig. 1) did not support this idea: after some major changes in the Devonian, Carboniferous, and Permian, levels of endemism remained roughly constant throughout the Mesozoic and Cenozoic, which witnessed the breakup of Pangaea. Hence, tetrapod diversification cannot be ascribed to continental drift.

Increases in the breadth of the adaptive space occupied by a clade would seem to be an obvious candidate for an explanation of diversification (no. 10). Indeed, this appears to have been the case (Figs. 2, 3): the relative significance of the mode of life of the earliest tetrapods—freshwater piscivory—declined from 100% in the late Devonian and early Carboniferous to levels of 10–15% in the Tertiary. The addition of diversity since those early times seems to have been mediated largely by the addition of broad new dietary types—insectivory, carnivory, herbivory, omnivory, as well as specialised diets of molluscs, grain, fruit, and so on—and new habitat ranges—terrestrial, marine, burrowing, arboreal, and flying.

The evolution of many tetrapod clades includes as much specialisation, or niche subdivision (no. 11), as it does expansion of adaptive space. An attempt has been made to test the idea of niche subdivision by comparing typical faunas through time. It is valid to compare, for example, an individual, exceptionally well-preserved fauna (Lagerstätte) from the Carboniferous with one from the Eocene, since levels of preservation appear to be equivalent. 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 million years in Europe and North America (Benton, 1990) shows a marked increase in mean faunal diversities from 18 in the Carboniferous to 35–51

in the Miocene and Pliocene (Fig. 4). 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, but most of the increase does appear to relate to niche subdivision.

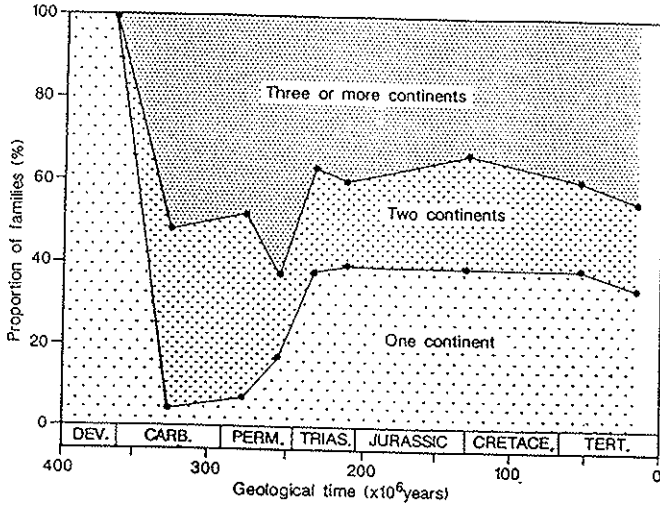


Figure 1. Variations in the ultimate geographic distribution of non-marine tetrapod families that arose during each time interval. Family data were recorded by stratigraphic stage, and were then grouped into broad time intervals in order to provide large enough samples throughout ( $n = 44-360$ ; mean = 146 families per time interval).

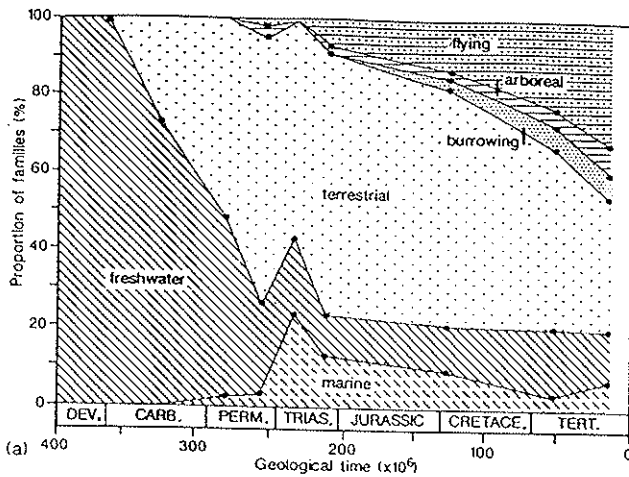


Figure 2. Proportions of broad habitat types of terrestrial and marine tetrapod families through time. The habitats were determined from the primary literature, and they represent the activities of all, or the majority of, species within a family (full details in Benton and Blacker, MS). Families were grouped into broader time units than stages, as in Fig. 1.

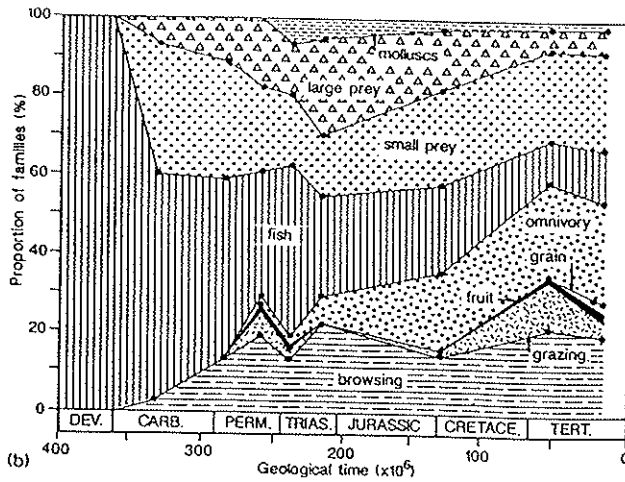


Figure 3. Proportions of broad dietary types of terrestrial and marine tetrapod families through time. The details and implications are as for Fig. 2.

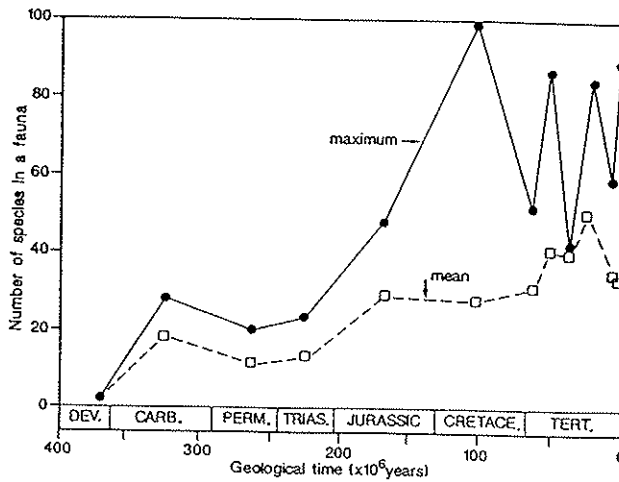


Figure 4. Maximum and minimum mean numbers of tetrapod species in well-preserved terrestrial faunas. This graph is based on a sample of 100 faunas (details in Benton and Blacker, MS), with 1–20 faunas sampled per stratigraphic period (or epoch in the Cenozoic). Each "fauna" is the species list of a single 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

Most of the diversification of the tetrapods seems to result from the conquest of new adaptive space and the subdivision of niches. Changes in the physical environment seem to have had a smaller effect, in contrast to the view of Cracraft (1985). 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 (Jablonski and Flessa, 1986). The global effects of continental drift

and marine regression on terrestrial faunas, argued 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. This supports the findings of Bambach (1985), who argued that marine invertebrates have increased their diversity mainly by expansions of utilized adaptive space. Sepkoski (1988) also finds that most of the increase in global diversity of marine life was produced by increases in the numbers of broad habitat types occupied.

Certain aspects of diversification patterns may of course be 'on-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. There is certainly no evidence for an inevitable motor of change that drives diversity ever upwards.

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