

remains >1000 years old have been sexed using a similar technique²) at ambient temperatures.

All of these are important considerations for the molecular ecologist who may not have access to specialized means of sample collection and storage while in the field, or who may have collected samples for other purposes, but now wishes to determine the sex of those individuals. Moreover, in this specific case a universal protocol for avian sexing involving only PCR and electrophoresis is likely to be available soon³⁻⁵.

In contrast, flow cytometry is only applicable to bird species in which the sex chromosomes differ significantly in size, and even in these cases requires calibration using fairly large samples of individuals of known sex. This would, for instance, limit the value of the technique in studies of endangered species⁶. Finally, an attractive feature of PCR techniques is that in addition to information about sex, the investigator will easily have access to DNA sequence information which might be valuable in evolutionary or population studies⁷.

We believe that our recommendation of PCR-based techniques for avian sexing was based on objective criteria which would be most useful to ecologists embarking on such a project. The reader may assess our objectivity by examining their nearest laboratory for the presence of a PCR instrument or a flow cytometer. If neither is available, but a means for reliable sexing of birds is required, the choice may be between purchasing a flow cytometer which may or may not be able to reveal the sex of the species of interest, or, for about one tenth of the cost, a PCR instrument that almost certainly will be able to and which will also be useful for microsatellite genotyping, RAPD, mtDNA, MHC, SSCP and sequence analysis, and numerous other applications in molecular ecology.

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References

1. Taberlet, P. et al. (1997) *Mol. Ecol.* 6, 869-876
2. Faerman, M. et al. (1997) *Nature* 385, 212-213
3. Griffiths, R. and Tiwari, B. (1993) *Proc. Natl. Acad. Sci. U. S. A.* 90, 8324-8326
4. Griffiths, R., Daan, S. and Dijkstra, C. (1996) *Proc. R. Soc. London Ser. B* 263, 1251-1256
5. Ellegren, H. (1996) *Proc. R. Soc. London Ser. B* 263, 1635-1641
6. Griffiths, R. and Tiwari, B. (1995) *Nature* 375, 454
7. Ellegren, H. and Fridolfsson, A.K. *Nat. Genet.* (in press)

Models for the diversification of life

Michael J. Benton

The diversification of life through geological time suggests a rise from presumably one species to many millions today. The diversification of marine families in the past 600 million years (Myr) appears to have followed two or three logistic curves, with equilibrium levels that lasted for up to 200 Myr. In contrast, continental organisms clearly show an exponential pattern of diversification, and although it is not clear whether the empirical diversification patterns are real or are artefacts of a poor fossil record, the latter explanation seems unlikely. Perhaps marine and continental organisms diversified in different ways, or perhaps the appearance of equilibrium patterns for marine organisms is an artefact of taxonomic structures.

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Life today is hugely diverse, with current estimates ranging from three million to 50 million species¹. It is likely that all known organisms originated from a single common ancestor, and it is of interest to know how this huge diversification happened. In an ideal world, the best approach to establishing the pattern of the diversification of life would be to collect data from a comprehensive fossil record and to read off the empirical pattern as documented by the fossils. The world, however, is not ideal, and this approach entails many problems of interpretation, not least the quality of the fossil record.

A critic of the fossil record might assert that fossils are, by definition, less knowable than extant organisms, and hence should be accorded a secondary role in interpreting patterns of evolution. This has

been a criticism particularly of the use of fossils in phylogeny reconstruction^{2,3}. The enthusiastic palaeontologist might assert that fossils add information not available in extant taxa, that they offer morphologies and modes of life that are entirely unpredictable from modern forms, and that they fill gaping holes in phylogenies⁴. Fossils also are datable, and they add the unique dimension of time to all phylogenies and diversification patterns⁵. Can these opposing viewpoints be resolved?

The quality of the fossil record

In studying patterns of diversification, palaeontologists typically focus on the past 550 million years (Myr), the Phanerozoic (literally, 'abundant life'), or the Vendian (610-550 Myr ago) plus the Phanerozoic. During this time, multicellular

animals are well represented, whereas earlier parts of the Precambrian fossil record are incompletely known.

A key criticism of the fossil record is that it probably becomes worse the further back in time one goes⁶. Comparisons of independent data sets, and error modelling, suggested that the fossil record is not statistically significantly biased, at least at higher taxonomic levels (i.e. genera, families)⁷. In a third approach, comparing changes in knowledge of the fossil record through research time^{8,9}, biases have turned out to be distributed randomly with respect to geological time.

Two further approaches, one geological and the other phylogenetic, have suggested that the fossil record is adequate as a representation of true patterns of global-scale diversification. First, comparisons of exceptionally well preserved fossil deposits, in which soft-bodied as well as hard-bodied organisms are retained, reveal no diminution in quality back through the Phanerozoic¹⁰. The same is true of winnowed concentrations of marine shells (coquina :))¹¹. Secondly, and contrary to expectation, comparisons of fossil record data with morphological and molecular phylogenies^{5,12-18} have shown good agreement by taxonomic group, habitat and geological age^{19,20}.

The fossil record is good enough to document aspects of the evolution of life, and it can be assumed that errors and gaps are randomly distributed with respect to time. Following normal practice in palaeontology, 'diversity' is assessed simply as numbers of species, genera or families, as indicated, and generally on a global scale.

Models of diversification

There are many ways to go from one species to many (Fig. 1), and these include three simple mathematical models, linear, exponential and logistic, each of which has attracted some attention. These are shown first as ideal uninterrupted models (Fig. 1a), and second with some mass extinctions superimposed (Fig. 1b).

The linear model^{21,22} represents net additive increase, simply the addition of a fixed number of new species in each unit of time. In terms of an evolutionary branching model, additive increase would mean that, through time, speciation rates have declined, or that extinction rates have increased regularly at a rate sufficient to mop up the excess speciations. The exponential model^{23,24} is more understandable in terms of a branching model of evolution. If speciation and extinction rates remain roughly constant, then there will be regular doubling of diversity within fixed units of time. The logistic model^{25–29} involves one or more classic S-shaped curves, each consisting of an initial period of slow diversity increase, a rapid rise, a slowing of the rate of increase as a result of diversity-dependent damping factors, and then a plateau corresponding to a limiting or equilibrium value.

There is no consensus on which model best explains the diversification of major

sectors of life through time, nor on whether all patterns of diversification adhere to the same model of increase. However, the choice of model is important since each makes profoundly different claims about evolution.

Do marine and continental records show different patterns?

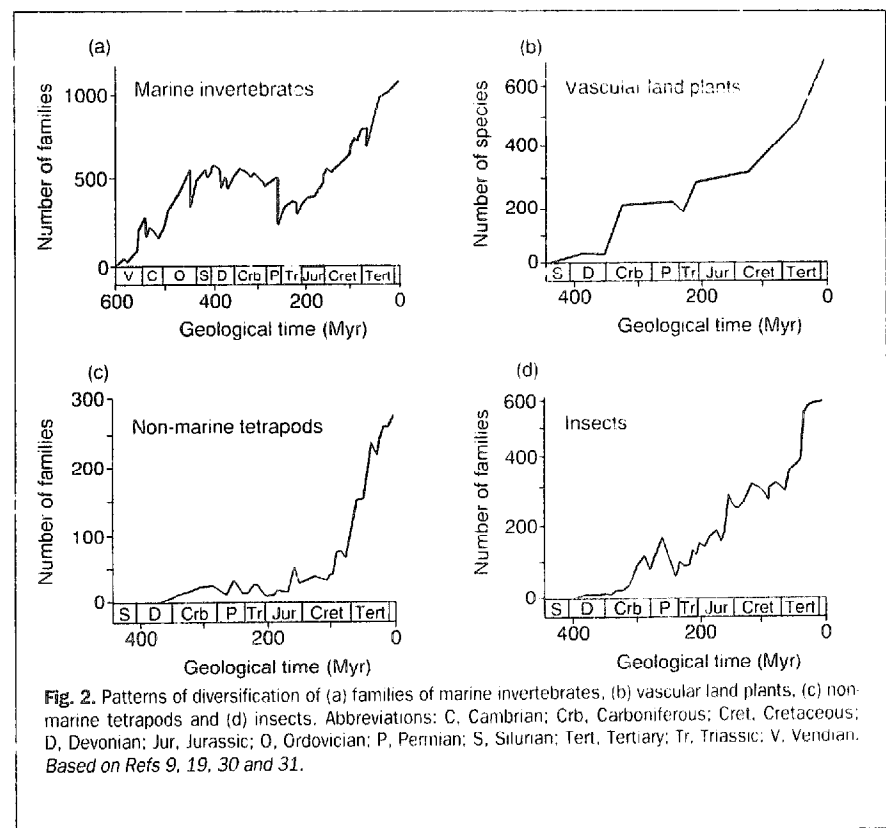
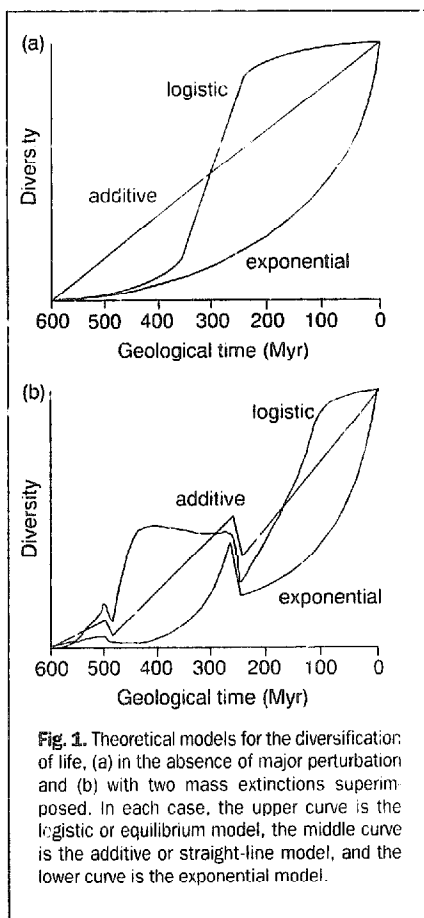
The pattern of diversification of marine invertebrate families (Fig. 2a) shows a short plateau in the Cambrian (c. 40 Myr), and a longer one from the Ordovician to the Permian (c. 250 Myr)²⁵. This is followed by a long phase (250 Myr) of near-exponential increase in diversity through the Mesozoic and Cenozoic, the rising element of a third logistic curve, which shows a hint of a slow-down in the last 25 Myr or so, suggesting that a third plateau level may be achieved 125 Myr in the future²⁵.

The diversification of species of vascular plants (Fig. 2b) has been interpreted in a similar way^{29,30} with a model that involves the successive rise of new major baupläne of plant types – early vascular plants in the Devonian, lycopods, ferns, conifers and others in the Carboniferous to Permian, gymnosperms in the Triassic to Jurassic, and angiosperms from the Cretaceous onwards. The initial segment of the curve is logistic, but the later segment is fit equally by a linear or exponential curve. The diversification of continental tetrapod families (Fig. 2c) is best explained by an exponential curve. The pattern of diversification may

be dissected into successive radiations of major tetrapod groups^{1,3} – basal tetrapods and synapsids, dinosaurs, and birds and mammals – but none of them shows a logistic pattern. The pattern of diversification of insects (Fig. 2d) is also largely exponential, especially in the last 100 Myr, but could be said to be approaching an equilibrium level now³¹.

Recent plots of the diversification of families of marine, continental and 'all' life (Fig. 3), founded on a new data base³², confirm these varying models for diversification. The continental curve (Fig. 3b), dominated by tetrapods, insects and land plants, is exponential. The marine curve (Fig. 3c) has been explained²⁸ by two logistic curves, one in the Palaeozoic, and the second in the post-Palaeozoic, with the beginning of a plateau phase in the Late Miocene or Pliocene, some 5–10 Myr ago. The combination of all marine and continental families (Fig. 3a) can be explained by a single poorly fitting exponential curve.

There may be fundamental differences between marine and continental life. Rates of taxonomic turnover in marine invertebrates declined through the Phanerozoic after the initial rapid Cambrian radiation, while vascular land plants show increasing rates of turnover through time³³. Terrestrial vertebrates show intermediate patterns. Perhaps adaptive space was filled early on in the sea, while land plants (and possibly vertebrates) have continued to conquer new ecospace, and may still be



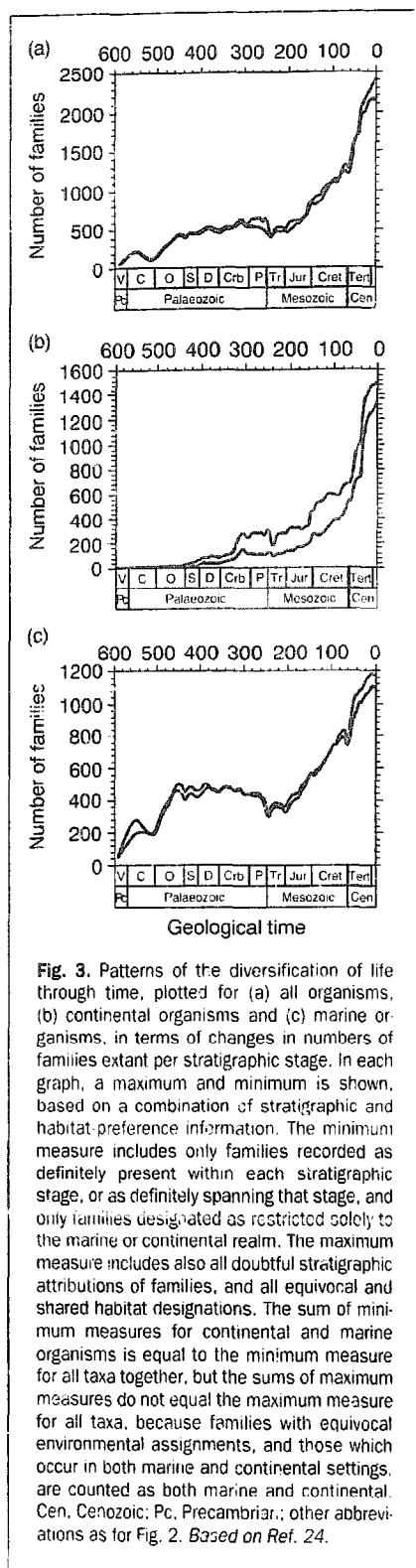


Fig. 3. Patterns of the diversification of life through time, plotted for (a) all organisms, (b) continental organisms and (c) marine organisms, in terms of changes in numbers of families extant per stratigraphic stage. In each graph, a maximum and minimum is shown, based on a combination of stratigraphic and habitat-preference information. The minimum measure includes only families recorded as definitely present within each stratigraphic stage, or as definitely spanning that stage, and only families designated as restricted solely to the marine or continental realm. The maximum measure includes also all doubtful stratigraphic attributions of families, and all equivocal and shared habitat designations. The sum of minimum measures for continental and marine organisms is equal to the minimum measure for all taxa together, but the sums of maximum measures do not equal the maximum measure for all taxa, because families with equivocal environmental assignments, and those which occur in both marine and continental settings, are counted as both marine and continental. Cen. Cenozoic; Pr. Precambrian; other abbreviations as for Fig. 2. Based on Ref. 24.

continuing to do so. Diversification on land began later than in the sea, and new groups of plants invaded unstable habitats and modified them³³.

Implications of equilibrium and expansion models

Logistic models for the diversification of life could be compared solely with ex-

ponential models; however, this would be restrictive, not least since the early phase of a logistic curve is typically exponential. The key distinction is between equilibrium and non-equilibrium (expansion) models. Equilibrium models imply the existence of global equilibria in diversity, while expansion models assume that there is no ceiling to the diversity of life, or at least that such a ceiling has yet to be reached.

Equilibrium models

Equilibrium models for the expansion of the diversity of life developed from an influential body of ecological theory that explained species assembly in confined patches of living space³⁴. This island-scale model was extended^{25,35} to regional and global scales, so that the island became the world, and local rates of colonization and extinction became global rates of origination and extinction of species. Time-scales moved from tens or hundreds of years to millions.

Logistic modelling of global-scale data on diversification implies (1) interactions among species within clades, (2) interactions between clades and (3) global equilibrium levels. Many studies show that clades may radiate initially at exponential rates, and then the rate of diversification slows at a certain point as a result of some diversity-dependent phenomenon, such as competitive exclusion, increased species packing or reduction of species ranges²⁷. This style of reasoning follows explicitly from classical experiments in competition where the increase of one population suppresses another population that depends on the same limiting resource.

The pattern of diversification of marine families (Fig. 2a) has been interpreted²⁵ in terms of a three-phase logistic model which represents the behaviour of three evolutionary 'faunas' (Fig. 3): Cambrian, Palaeozoic and Modern. The Cambrian fauna consisted of organisms with broad habitat and trophic requirements, while the later Palaeozoic groups included more specialized forms. The Cambrian generalists were able to radiate rapidly at first into empty ecospace, but because of their lack of specialization could not reach high diversities. New more-specialist forms could subdivide the ecospace more finely, and hence achieve higher diversities. The Modern evolutionary fauna, characterized by new predatory groups and new defence strategies, was apparently able to achieve yet higher diversity.

There are two views of the evolutionary interactions of species and higher taxa. One view is that clades compete in a broad-scale way. In other words, a newly arising clade, or an invading group, is regarded as competitively superior to another and can thereby replace it wholesale. Such inter-

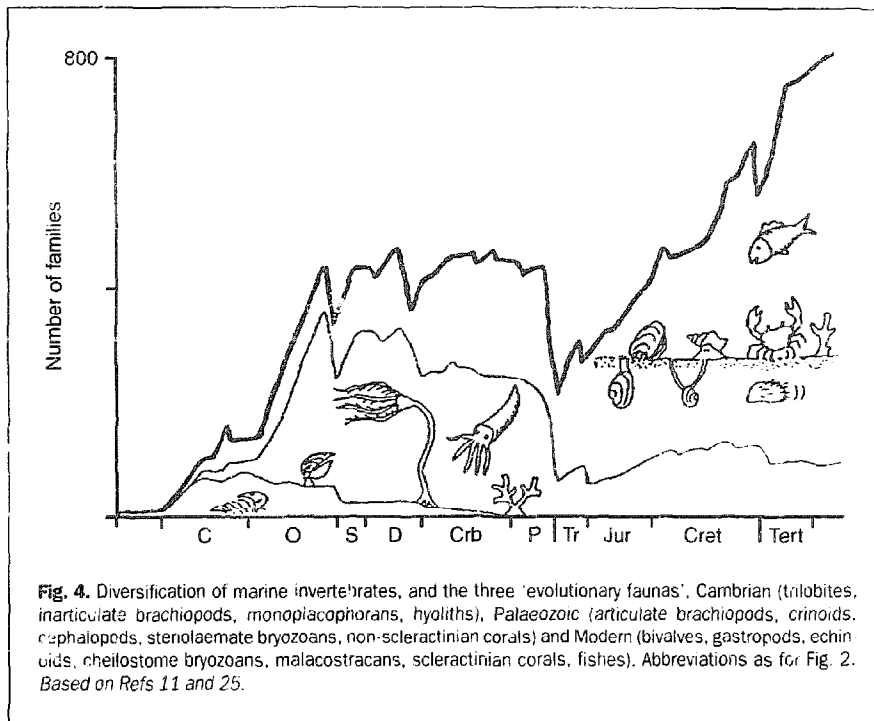
clade competition has often been assumed, without being precisely defined, but this viewpoint has been questioned^{27,36-40}. A second view is that interspecific competition can scale up to be expressed at higher levels²⁷. Patterns of waxing and waning of the clades are attributed to diffuse competition between members of species belonging to the different clades, where species in clade A are generally competitively superior to their ecological analogues in clade B.

A critical assumption of logistic models is that equilibrium levels exist – steady-state diversities at which speciation and extinction rates are balanced^{25,27,34,35}. In the case of global diversification patterns, these limiting processes could affect both extinction and origination rates⁴¹, but origination rates may be more diversity-dependent²⁷. However, there is no independent evidence for equilibria (i.e. for fixed carrying capacities)^{42,43}. In evolutionary terms, equilibrium diversities imply that all available resources are in use. However, with enough time, and with normal rates of origination and extinction, certain new species can surely insinuate, that is, find new things to do, and thereby increase species diversity with almost no limit^{44,45}.

Expansion models

Clades do not all diversify in the same way. Some radiate rapidly, reach a maximum size, and remain at that diversity level until they become extinct. Others continue for long spans of time at low diversity levels, and some, such as insects, angiosperms, birds and mammals, seem to continue radiating linearly or exponentially for many tens or hundreds of millions of years. Perhaps life diversifies in this way, with communities maintained well below any resource limitation^{42,45,46}.

The overall pattern consists of the sum of diversification behaviours of numerous unrelated clades. In the past 250 Myr, 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). The rate of increase has been exponential in the case of families of continental organisms, and perhaps linear in the case of marine families (Figs 2–4). Such expanding, even exponential, long-term diversification patterns may be understood intuitively. For example, the evolution of tetrapods (Fig. 5a) was characterized by repeated, but unpredictable, expansions of ecospace⁴⁷ from fresh waters to land, trees, the air, burrowing underground, occupying human habitations ... Who is to say what new habitats or modes of life vertebrates may adopt in the future which will drive their diversity ever higher?



Exponential increase could imply that diversification would last for ever. Presumably there is an ultimate limit to the numbers of families, or other taxa, that can inhabit the Earth at any time⁴¹: such a limit would be caused not least by the amount of standing room on the Ark, and ultimately the availability of the chemical components of life, principally carbon.

Equilibrium versus expansion: tests and explanations

The five following observations may provide test cases for distinguishing between equilibrium and expansion models of the diversification of life:

(1) There was an evolutionary explosion of marine animals during the early Cambrian, and diversification rates slowed

after this initial exponential rise²⁵. This strongly suggests a logistic/equilibrium explanation.

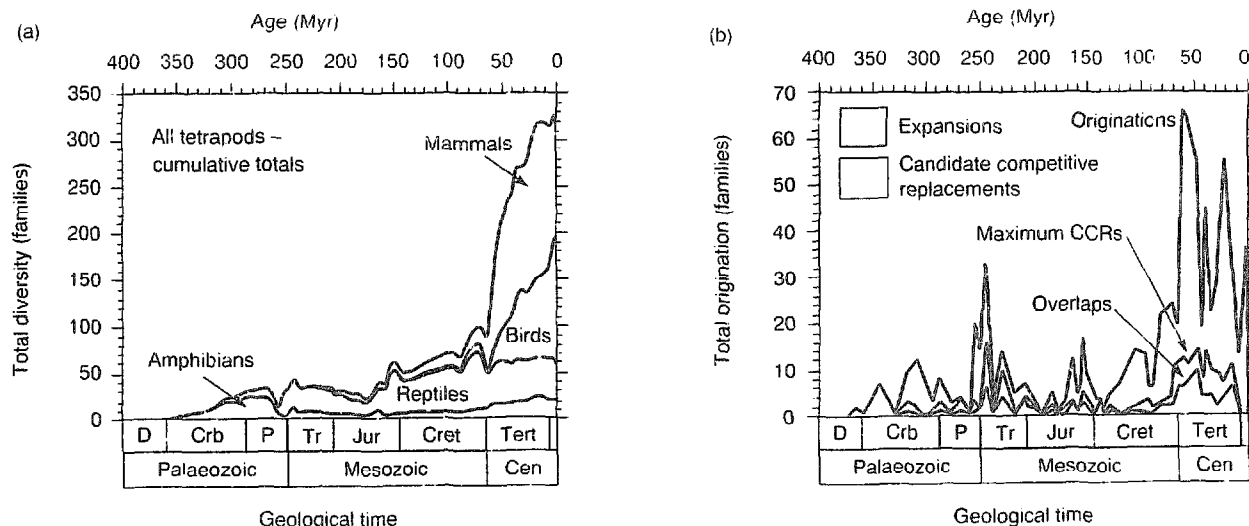
(2) The radiation of life on land, and of certain major marine and continental clades, appears to have followed an exponential pattern, and there is no sign of slowing down in the rate of increase, nor of the occurrence of any equilibrium levels. These radiations strongly suggest patterns of unfettered expansion.

(3) 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. Such rapid rebounds suggest a logistic/equilibrium model of diversification²⁷. They could also be understood in a world of unfettered expansion, especially since most rebounds reached levels that were higher than pre-extinction.

(4) Late phases of diversification cycles are associated with declining rates of origination and increasing rates of extinction, as the logistic curve approaches the equilibrium level. The marine record generally confirms such expectations, and provides evidence for the logistic model²⁵.

(5) The Palaeozoic plateau in marine animal diversity is strong evidence for equilibrium^{25,27,35}.

All five points require further study, but only the last two will be explored further



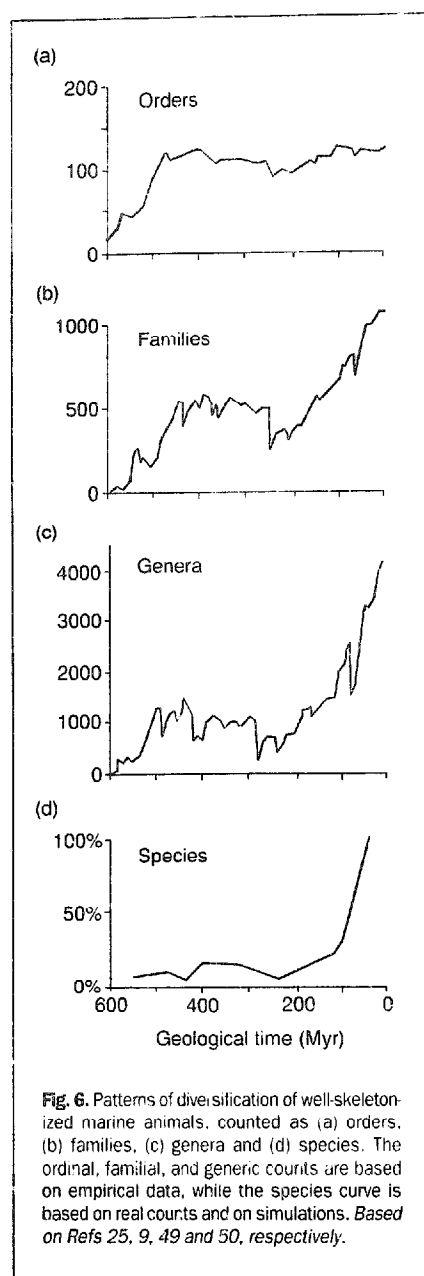


Fig. 6. Patterns of diversification of well-skeletonized marine animals, counted as (a) orders, (b) families, (c) genera and (d) species. The ordinal, familial, and generic counts are based on empirical data, while the species curve is based on real counts and on simulations. Based on Refs 25, 9, 49 and 50, respectively.

here. The slow-down in diversification rates as the asymptote is approached (point 4) is critical to the logistic model. At this time, there should be a switch in the nature of group originations, from origins in unoccupied ecospace, to more and more competitive displacement of pre-existing taxa. An outline study of familial originations of tetrapods^{40,48} has provided no evidence for the approach of equilibrium at any point (Fig. 5b). For all 840 families of tetrapods that have a fossil record, 13–26% of familial origins could be (but need not be) explained by competitive interaction with a pre-existing family. However, the distribution of peaks is random with respect to time. There is no evidence for a rise in candidate competitive replacements in the late Palaeozoic or the late Cenozoic, and hence no suggestion that

tetrapod niches were filling up at either of those times.

The most telling evidence for equilibrium models of the long-term diversification of life is the Palaeozoic 'plateau' in marine invertebrate diversity (Figs 2a, 3c, 4). This has been interpreted in a number of ways.

(1) 'It is real and indicates a global limit to diversity'. According to this view^{25,27,35}, the plateau is sustained at a total level of about 550 families, composed mainly of the equilibrium diversity of 350 families of the Palaeozoic evolutionary fauna.

(2) 'It is real but was maintained below any maximum carrying capacity by perturbations'. According to this view, perturbations have kept communities well below any resource limitation^{22,26,42,43,45,46}, and the quality of fit of some of the models to the data is claimed to be as good as for logistic models²⁶. A number of kinds of non-equilibrium models have been proposed, some that are broadly diversity-dependent²⁶, others in which speciation is diversity-dependent, but extinction is diversity-independent^{21,42,43}, and finally a neutral model that assumes random and independent variation in rates of speciation and extinction^{22,46}.

(3) 'It is an artefact of taxonomic levels'. A final view could be that the plateau is an artefact of analyses carried out at high taxonomic level. A comparison of plots of the diversity of marine life through time at ordinal, familial, generic and specific level (Fig. 6) shows how the logistic pattern appears to decay into an exponential pattern. At ordinal level, there is a single long plateau, at familial level, the shorter Palaeozoic plateau. At generic level, the Palaeozoic plateau is present⁴⁹, but it is relatively lower than the familial plateau, and the post-Palaeozoic diversification of genera is more exponential in appearance. For species, there is no available empirical curve, but a suggested consensus plot⁵⁰ retains indications of a two-phase Palaeozoic diversification pattern, but the pattern on the whole is exponential. Perhaps real diversification patterns are damped as one ascends the Linnean hierarchy^{49,50}. If damping is the explanation, then a focus on species-level evolution might indicate that exponential models are more appropriate than logistic, for the diversification of marine animals.

Conclusion

There is no doubt that competition occurs between individuals in populations of microbes in enclosed laboratory vessels, and between individuals in populations on islands³⁴. However, it is not clear whether such modelling can be extended to regional and global scales. The biosphere is essentially a closed system, but it is not

obvious whether life has yet reached the global taxic carrying capacity.

References

- May, R.M. (1990) How many species? *Philos. Trans. R. Soc. London Ser. B* 330, 293–304.
- Patterson, C. (1981) Significance of fossils in determining evolutionary relationships. *Annu. Rev. Ecol. Syst.* 12, 195–223.
- Goodman, M. (1989) Emerging alliance of phylogenetic systematics and molecular biology: A new age of exploration, in: *The Hierarchy of Life* (Fernholm, B., Bremer, K. and Jornvall, H., eds), pp. 43–61, Elsevier.
- Smith, A.B. (1994) *Systematics and the Fossil Record*, Blackwell Scientific.
- Benton, M.J. (1995) Testing the time axis of phylogenies, *Philos. Trans. R. Soc. London Ser. B* 348, 5–10.
- Raup, D.M. (1972) Taxonomic diversity during the Phanerozoic, *Science* 177, 1065–1071.
- Benton, M.J. (1987) The history of the biosphere: equilibrium and non-equilibrium models of global diversity, *Trends Ecol. Evol.* 2, 153–156.
- Maxwell, W.D. and Benton, M.J. (1990) Historical tests of the absolute completeness of the fossil record of tetrapods, *Paleobiology* 16, 322–335.
- Sepkoski, J.J., Jr (1993) Ten years in the library: how changes in taxonomic data bases affect perception of macroevolutionary pattern, *Paleobiology* 19, 43–51.
- Alison, P.A. and Briggs, D.E.G. (1993) Exceptional fossil record: distribution of soft-tissue preservation through the Phanerozoic, *Geology* 21, 527–530.
- Edwell, S.M. and Branchley, P.J. (1996) Evolution of the fossil record: thickness trends in marine skeletal accumulations and their implications, in *Evolutionary Paleobiology* (Jablonski, D., Erwin, D.H. and Lipps, J.H., eds), pp. 290–336, University of Chicago Press.
- Norell, M.A. and Novacek, M.J. (1992) The fossil record and evolution: comparing cladistic and paleontologic evidence for vertebrate history, *Science* 255, 1690–1693.
- Benton, M.J. (1994) Palaeontological data, and identifying mass extinctions, *Trends Ecol. Evol.* 9, 181–185.
- Huelsenbeck, J.P. (1994) Comparing the stratigraphic record to estimates of phylogeny, *Paleobiology* 20, 470–483.
- Benton, M.J. and Storrs, G.W. (1994) Testing the quality of the fossil record: paleontological knowledge is improving, *Geology* 22, 111–114.
- Benton, M.J. and Simms, M.J. (1995) Testing the marine and continental fossil records, *Geology* 23, 601–604.
- Benton, M.J. and Hitchin, R. (1996) Testing the quality of the fossil record by groups and by major habitats, *Hist. Biol.* 12, 111–157.
- Benton, M.J. and Hitchin, R. Congruence between phylogenetic and stratigraphic data on the history of life, *Proc. R. Soc. London Ser. B* (in press).
- Benton, M.J. (1985) Mass extinction among non-marine tetrapods, *Nature* 316, 811–814.
- Jablonski, D. (1991) Extinctions: a paleontological perspective, *Science* 253, 754–757.

- 21 Walker, T.D. (1985) **Diversification functions and the rate of taxonomic evolution**, in *Phanerozoic Diversity Patterns: Profiles in Macroevolution* (Valentine, J.W., ed.), pp. 311–334. Princeton University Press
- 22 Hoffmann, A. (1986) **Neutral model of Phanerozoic diversification: implications for macroevolution**, *N. Jb. Geol. Paläont. Abh.* 172, 219–244
- 23 Cailleux, A. (1954) **How many species?** *Evolution* 8, 83–84
- 24 Benton, M.J. (1995) **Diversification and extinction in the history of life**, *Science* 268, 52–58
- 25 Sepkoski, J.J., Jr (1984) **A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions**, *Paleobiology* 10, 246–267
- 26 Kitchell, J.A. and Carr, T.R. (1985) **Nonequilibrium model of diversification: faunal turnover dynamics**, in *Phanerozoic Diversity Patterns: Profiles in Macroevolution* (Valentine, J.W., ed.), pp. 277–309. Princeton University Press
- 27 Sepkoski, J.J., Jr (1996) **Competition in macroevolution: the double wedge revisited**, in *Evolutionary Paleobiology* (Jablonski, D., Erwin, D.H. and Lipps, J.H., eds), pp. 211–255. University of Chicago Press
- 28 Courtillot, V. and Gaudemer, Y. (1996) **Effects of mass extinctions on biodiversity**, *Nature* 381, 146–148
- 29 Knoll, A.H. (1984) **Patterns of extinction in the fossil record of vascular plants**, in *Extinctions* (Nitecki, M.H., ed.), pp. 21–68. University of Chicago Press
- 30 Niklas, K.J., Tiffney, B.H. and Knoll, A.H. (1985) **Patterns in vascular land plant diversification: a factor analysis at the species level**, in *Phanerozoic Diversity Patterns: Profiles in Macroevolution* (Valentine, J.W., ed.), pp. 97–128. Princeton University Press
- 31 Labandeira, C.C. and Sepkoski, J.J., Jr (1993) **Insect diversity in the fossil record**, *Science* 261, 310–315
- 32 Benton, M.J. (1993) *The Fossil Record 2*. Chapman & Hall
- 33 Valentine, J.W., Tiffney, B.H. and Sepkoski, J.J., Jr (1991) **Evolutionary dynamics of plants and animals**, *Palaos* 6, 81–88
- 34 MacArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press
- 35 Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press
- 36 Gould, S.J. and Calloway, C.B. (1980) **Clams and brachiopods – ships that pass in the night**, *Paleobiology* 6, 383–396
- 37 Benton, M.J. (1987) **Progress and competition in macroevolution**, *Biol. Rev.* 62, 395–338
- 38 Benton, M.J. (1991) **Extinction, biotic replacements, and clade interactions**, in *The Unity of Evolutionary Biology* (Dudley, E.C., ed.), pp. 89–102. Dioscorides Press
- 39 Lidgard, S., McKinney, F.K. and Taylor, P.D. (1993) **Competition, clade replacement, and a history of cyclostome and cheilostome bryozoan diversity**, *Paleobiology* 19, 352–371
- 40 Benton, M.J. (1996) **On the nonprevalence of competitive replacement in the evolution of tetrapods**, in *Evolutionary Paleobiology* (Jablonski, D., Erwin, D.H. and Lipps, J.H., eds), pp. 185–210. University of Chicago Press
- 41 Levinton, J.S. (1979) **A theory of diversity equilibrium and morphological evolution**, *Science* 204, 335–336
- 42 Walker, T.D. and Valentine, J.W. (1984) **Equilibrium models of evolutionary species diversity and the number of empty niches**, *Am. Nat.* 124, 887–899
- 43 Valentine, J.W. (1985) **A theory of origination and extinction**, in *Phanerozoic Diversity Patterns: Profiles in Macroevolution* (Valentine, J.W., ed.), pp. 419–424. Princeton University Press
- 44 Wilson, E.O. (1969) **The species equilibrium**, *Brookhaven Symp. Biol.* 22, 38–47
- 45 Whittaker, R.H. (1977) **Evolution of species diversity in land communities**, *Evol. Biol.* 10, 1–67
- 46 Hoffmann, A. (1985) **Island biogeography and palaeobiology: in search for evolutionary equilibria**, *Biol. Rev.* 60, 455–471
- 47 Benton, M.J. (1990) **The causes of the diversification of life**, in *Major Evolutionary Radiations* (Taylor, P.D. and Larwood, G.P., eds), pp. 409–430. Clarendon Press
- 48 Benton, M.J. (1996) **Testing the roles of competition and expansion in tetrapod evolution**, *Proc. R. Soc. London Ser. B* 263, 641–646
- 49 Sepkoski, J.J., Jr (1996) **Patterns of Phanerozoic extinction: a perspective from global data bases**, in *Global Events and Event Stratigraphy* (Walliser, O.H., ed.), pp. 35–51. Springer
- 50 Signor, P.W. (1985) **Real and apparent trends in species richness through time**, in *Phanerozoic Diversity Patterns: Profiles in Macroevolution* (Valentine, J.W., ed.), pp. 129–150. Princeton University Press

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£19.95/\$44.95 hbk (ix + 202 pages)

ISBN 0 632 03634 6

The rationale for any model in ecology (or anywhere else) is the scientific desire to capture the essence and to remove or reduce the redundant aspects of the system under study. What is essential and what is redundant and thereby what level of reduction is required, to a large degree depends on the questions being asked. The result is a 'model' of reality that is realistic to varying degrees.

A second reason for modelling is the fact that the abstraction obtained of the real world is much easier to handle and that we can ask of the model true Kantian 'what if...' questions by changing the assumptions and

comparing and possibly testing the predictions to see whether indeed the essence is captured in the model.

The best way to achieve a clear and unambiguous formulation of the assumed essence of ecological phenomena is to phrase these in mathematical language not in the least because of great power to manipulate the model once it has been framed in mathematical terms. Because the mathematical model can easily be translated into computer language, this opens a wide field of manipulative/interactive exploration of the consequences of the formulated ideas.

If one accepts this role for mathematics as the lingua franca of science then there is no alternative: ecologists should learn to speak the language to better communicate their science. This is not to say that the logic of the language is a guarantee for the quality of the communication. As pointed out by de Roos and Sabelis 'spatial' models have been shown to produce a bewildering variety of dynamical phenomena to the extent that almost every conceivable pattern can be generated by an appropriate model. Even worse, the assumptions of these models cannot immediately be discarded as biolog-

ically unrealistic. Grammar is a prerequisite not a guarantee for literature.

As Gillman and Hails clearly state, they wished to teach the grammar while introducing the literature. They have chosen to present the mathematics piecemeal on a need to know basis and to use the didactic success formula of presenting separate issues in boxes. Together they form a small 25-page primer in mathematics where, step by step, the tools are developed; this can be read separately if so desired. They succeed admirably in anticipating the mathematical problems and explaining them before they form a problem in following the ecological argument. I have not seen a book in which this is done as carefully and as clearly as here. No need for students to be scared of maths in ecology any more! It is only towards the end that the tight coupling between the ecological and mathematical argument begins to get lost.

Given the wide variety of topics in ecology that are phrased in mathematical terms, the authors had to select from the available models. Their choice seems reasonable: they choose for models with a high level of generality (i.e. high degree of reduction) and