

HOW DID LIFE BECOME SO DIVERSE? THE DYNAMICS OF DIVERSIFICATION ACCORDING TO THE FOSSIL RECORD AND MOLECULAR PHYLOGENETICS

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Abstract: The long-term diversification of life probably cannot be modelled as a simple equilibrational process: the time scales are too long, the potential for exploring new ecospace is too large and it is unlikely that ecological controls can act at global scales. The sum of many clade expansions and reductions, each of which happens according to its own dynamic, probably approximates more a damped exponential curve when translated into a global-scale species diversification curve. Unfortunately, it is not possible to plot such a meaningful global-scale species diversification curve through time, but curves at higher taxonomic levels have been produced. These curves are subject to the vagaries of the fossil record, but it is unlikely that the sources of error entirely overwhelm the biological signal. Clades radiate when the external and internal conditions are right: a new territory or ecospace becomes available, and the lineage has acquired a number of characters that open up a new diet or mode of life. Modern high levels of diversity in certain speciose clades may depend on such ancient opportunities taken. Dramatic climatic changes through the Quaternary must have driven extinctions and originations, but many species responded simply by moving to more favourable locations. Ecological communities appear to be no more than merely chance associations of species, but there may be real interactions among species. Ironically, high species diversity may lead to more speciation, not, as

had been assumed, less: more species create more opportunities and selective pressures for other species to respond to, rather than capping diversity at a fixed equilibrium level. Studies from the scale of modern ecosystems to global long-term patterns in the fossil record support a model for the exponential diversification of life, and one explanation for a pattern of exponential diversification is that as diversity increases, new forms become ever more refinements of existing forms. In a sense the world becomes increasingly divided into finer niche space. Organisms have a propensity to speciate freely, species richness within ecosystems appears to generate opportunities for more speciation, clades show all kinds of patterns from sluggish speciation rates and constant diversity through time to apparently explosive speciation, and there is no evidence that rapidly speciating clades have reached a limit, nor that they are driving other clades to extinction. A corollary of this view is that current biodiversity must be higher than it has ever been. Limits to infinite growth are clearly local, regional, and global turnover and extinction events, when climate change and physical catastrophes knock out species and whole clades, and push the rising exponential curve down a notch or two.

Key words: diversity, diversification, biodiversity, speciation, phylogeography, molecular phylogeny.

LIFE today, as Darwin noted, is extraordinarily diverse. Whereas 200 years ago, naturalists thought there were perhaps five or ten thousand species on the Earth, current estimates (May 1990; Wilson 1992) place the figure at ten or 20 million. It is usually assumed that life has never been more diverse than it is today. There could be three interpretations of this assumption: (1) evolution causes organisms to adapt and subdivide niches by ever-increasing specialization; (2) new groups of organisms conquer

previously unoccupied ecospace, or find new ways to speed energy and carbon through the ecosystem; or (3) it is an illusion brought about by a fossil record that diminishes in quality back in time, so a pattern of static diversity over hundreds of millions of years looks as if it is rising towards the present day as the quality of sampling improves.

Darwin's other key insight about the broad pattern of diversity today, and in the past, was that all life could be

organized in a single great tree of life, tracking back to a single ancestral species. His insight has been confirmed by the subsequent discovery of shared derived characters of all life (the genetic code, translational machinery, handedness of molecules). Fossil and molecular evidence indicate that the common ancestor, the single species/bacterial clone that gave rise to all of life, existed some 3000–3800 myr ago. Biodiversity has expanded in some way through geological time from one species to some 10–20 million species.

Although the disciplines of palaeobiology and evolutionary ecology may at first seem to be largely non-overlapping, there are a number of linking concepts. For example, the equilibrium, or logistic, model of global diversity accumulation has its roots in MacArthur and Wilson's (1963, 1967) equilibrium theory of island biogeography, which involved modelling colonization dynamics, competition and evolution on islands. The connection between palaeobiology and evolutionary ecology has been developed recently by Barnosky *et al.* (2005). The species-area curve is one of the best understood relationships in ecology, predicting how many species are expected as the geographical area of sampling increases (Godron 1971; Brown 1995; Rosenzweig 1995, 2001; Scheiner 2003), and Barnosky *et al.* (2005) concluded that the species-area effect markedly influences counts of fossil species. Perhaps the most useful connection between the disciplines of palaeobiology and evolutionary ecology is in molecular phylogenetic methodology. Molecular phylogenetics provides a means of dating the tree of life, generating an additional and complementary data source to the fossil record, although the task of reconciling differences between DNA sequences and fossils is not straightforward (Benton and Ayala 2003). However, there is a further potential use for molecular phylogenetic methodology: to explore the connection between palaeobiological and evolutionary ecological pattern and process. This has not received much attention, but there are interesting parallels between the two disciplines, with both seeking to understand the origin and nature of the accumulation of species diversity through time.

In this paper we proceed from the large to the small scale, exploring current debates about how life as a whole diversified through geological time, how individual clades diversify, convergence and diversity estimation, evolutionary opportunity, potential and success, the influence of climate on diversification, and community complexity and diversification. Molecular approaches, notably phylogeography, allow biologists to study small-scale processes happening today, but also to extend studies back into the Pleistocene, and then into deeper geological time. Furthermore, many debates, such as those between competition-driven ecosystem and diversification models and models in which communities are chance associations

that are buffeted by external forces and diversifications are unlimited, occur at all levels from the local to the global, and over time-scales from months and years to millions of years.

LARGE-SCALE PATTERNS AND MODELS OF DIVERSIFICATION

Species diversity has increased over time, but the nature of that increase is a topic of debate that has led to two conflicting theories. The first theory sees global diversity increasing to an equilibrium point (e.g. Raup 1972; Carr and Kitchell 1980; Alroy 1998), and the logistic models of Sepkoski (1978, 1979, 1984) have been the most prominent, culminating in the three-phase, coupled logistic model to describe Phanerozoic diversification of marine animals at the family level. The alternative theory sees diversity as having followed an expansionist growth pattern (e.g. Valentine 1969; Walker and Valentine 1984; Signor 1985; Benton 1995, 1997), and exponential models of diversification have been used to describe the diversification of families of both marine and terrestrial organisms of the last 600 myr (e.g. Hewzulla *et al.* 1997; Lane and Benton 2003).

We will outline the implications of the two models and the empirical data briefly, and then consider why the debate has been hard to resolve so far for three reasons: (1) the data sets are incomplete and possibly biased, (2) the record is beset by perturbations and (3) there are problems of scaling. In the final part of this section, we consider auxiliary evidence that speaks for equilibrium and expansion models of global diversification.

Implications of the models

Equilibrium models for the expansion of the diversity of life were based on an influential body of ecological theory, including classical experiments in competition where the increase of one population suppresses another that depends on the same limiting resource. In particular, Sepkoski (1978, 1979, 1984, 1996c) based his logistic models on the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967), seeing the Earth's oceans as an island, arrival rates as evolutionary origination rates, and local extinction rates as global extinction rates. Like a Petri dish, or an island, the world's oceans are thereby assumed to have a fixed carrying capacity, a level that marks the limit of global species richness. Some equilibrium supporters (e.g. Levinton 1979) are happy to accept the idea of a carrying capacity in terms of the sum of ecospace that can be occupied, but to assume that

biodiversity can continue to rise by increasing specialization and subdivision of ecospace.

Critics have queried many of the assumptions of the equilibrium model for the expansion of life.

1. There is no evidence for a global carrying capacity for species (Walker and Valentine 1984).
2. Coupled logistic equations, a useful approach to modelling the interactions of clades through time, can only suggest that data are consistent with competitive/equilibrium models, and they cannot reject alternative non-interactive, non-equilibrium models (Sepkoski 1996a).
3. The fact that there is apparently not a single equilibrium level, as Raup (1972) predicted, and Alroy *et al.* (2001) suggested, but several, causes problems: somehow life must re-jig itself several times so that it can hit higher levels, or the carrying capacity of the Earth at any time might change to allow more biodiversity or more biomass. It is unclear how many such equilibrium levels can be allowed before we accept that the pattern is really one of continual expansion (Benton 1997).
4. Furthermore, Benton (1997) pointed out that the Palaeozoic plateau, strong evidence for equilibrium, might be an artefact of taxonomic level that is not seen in a species-level curve (see below).
5. A core aspect of Sepkoski's logistic/equilibrium models, the three great clade assemblages (his 'evolutionary faunas') that dominated the oceans in the Cambrian, Palaeozoic and post-Palaeozoic, is not cohesive and they do not hand over one to the other as expected (Alroy 2004). Most notably, the 'modern fauna' radiated dramatically over the last 100 myr and shows no sign of reaching an equilibrium level (Benton 1996, 1997); this is a weakness of any equilibrium model as the last 100 myr represent the best-sampled part of the fossil record and might be expected to show something closer to the biological pattern than earlier records.
6. Finally, it is uncertain how a global logistic curve for the diversity of life, or even just the diversity of life in the sea (Benton 2001), could be achieved. Evolution happens at the level of species, and species react and interact in ever-changing ways. Individual clades adopt many shapes from long and thin to short and fat; some last for a short time, others for a long time; some reach a particular size and do not expand further, others keep on diversifying by adding species. There is no explanation for why the sum of all clades should approximate a logistic curve; the opportunistic and expansive nature of evolution suggests that the sum is more likely to approximate a damped exponential. Miller and Sepkoski (1988) and Sepkoski (1996c) argued that individual clades diversified as damped exponentials, but did not extend that model to the clade of 'all life'.

The alternative to equilibrium then is *expansion*, where there is no carrying capacity for the Earth, or that carry-

ing capacity has not yet been reached. The overall pattern of diversification of life of course incorporates the numerous constituent clades, some expanding, others diminishing, and yet others remaining at constant diversity at any particular time. From an expansionist viewpoint, there is no prediction of how the individual clades affect each other, whereas an equilibrist would see clades expanding and contracting to some extent in response to each other (Darwin's barrel of apples). Global diversity may expand repeatedly by the evolution of new adaptations, habitat changes and recovery following extinction events. 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). There is little evidence that these major clades have run out of steam, and nothing to indicate that they will not continue to expand into new ecospace.

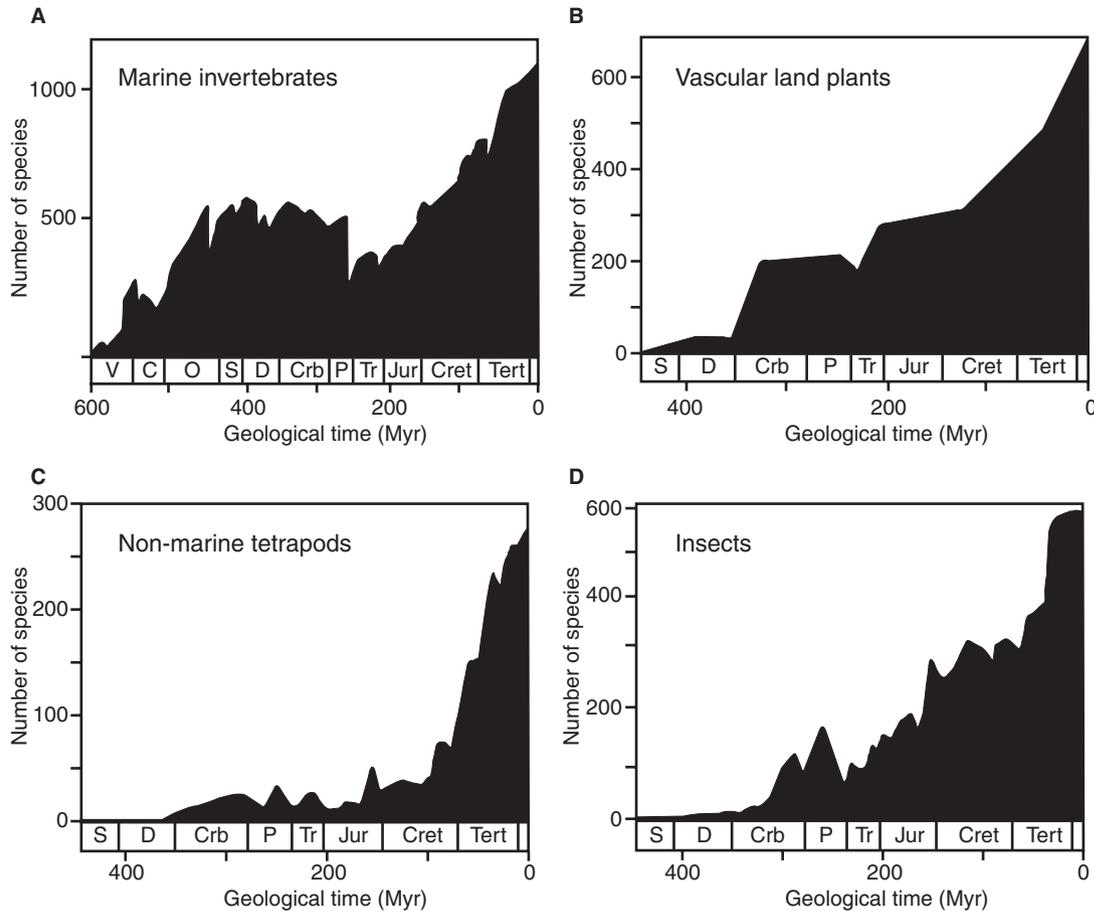
Exponential increase could imply that diversification would last forever. Presumably there is a limit to the numbers of families, or other taxa, that can inhabit the Earth at any time: such a limit would be caused not least by the amount of standing room on the Ark. If a limit of living space were approached,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

Global diversification patterns

Many studies of global diversification of certain ecological and phylogenetic sectors of life, and of all macroscopic life, have been published. Classic studies (Text-fig. 1) include the plots of diversification of marine animals by Sepkoski (1984), of vascular land plants by Niklas *et al.* (1985), of non-marine vertebrates by Benton (1985) and of insects by Labandeira and Sepkoski (1993).

These empirical plots may be compared with theoretical patterns for global diversification, most notably the logistic and exponential patterns (Text-fig. 2). At first sight, the curves for marine animals and for vascular land plants (Text-fig. 1A–B) could be interpreted as a series of steps, and so perhaps two or more logistic curves. The curve for non-marine vertebrates (Text-fig. 1C) is exponential, and the curve for insects (Text-fig. 1D) is somewhere in between, being close to a straight line.

Benton (1995) suggested that his plots of family-level diversification for all non-marine life looked entirely



TEXT-FIG. 1. Patterns of diversification of: A, families of marine invertebrates; B, species of vascular land plants; C, families of non-marine tetrapods; and D, families of insects (based on Sepkoski 1984; Benton 1985; Niklas *et al.* 1985; Labandeira and Sepkoski 1993).

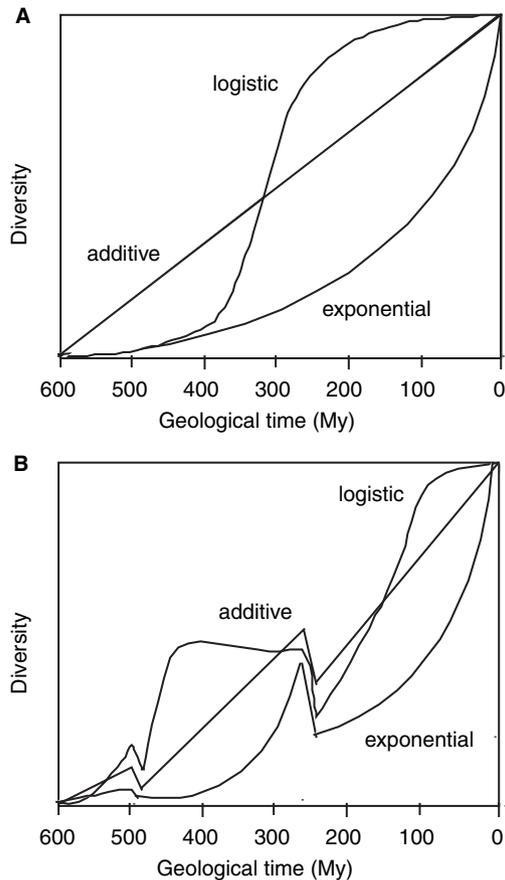
exponential, while the marine record retained the multiple-logistic appearance seen before. It could be that the whole record of the diversification of life is entirely exponential (Benton 1995), or that the marine and non-marine records are rather different, with some evidence for a global carrying capacity in the oceans, but not on land (Benton 2001).

Incompleteness of the record

It has long been understood that the fossil record is incomplete (Darwin 1859), and there are numerous biological and geological reasons why every organism cannot be preserved, nor even a small sample of every species. Most palaeontologists have implicitly accepted that the record is nonetheless complete enough to reveal the broad outlines of the history of life (Sepkoski *et al.* 1981). However, a strong case has been made that there is at least one major preservation bias, that older fossils are less well represented than younger fossils because geological agents

overwrite and obscure ever more ancient fossil records (Raup 1972). It has been urged, however (Sepkoski 1996b; Benton *et al.* 2000), that this bias, although obvious at low focal levels (e.g. individual specimens or species and individual fossil localities or geological formations) is to a large extent swamped at coarser sampling levels (e.g. genera or families sampled at the level of stratigraphic stages or substages) and that these coarser-level studies may represent something of biological reality.

A further suggested preservation bias is more complex, that the apparent diversity of fossils follows either the volume of sedimentary rocks deposited and preserved (Peters and Foote 2002) or the sea-level curve (Smith 2001). Both suggestions have been questioned. Peters (2005) found a correlation between fossil diversity and the number of named geological formations, but suggested that neither controlled the other, and that both might be following a third external driver, the *common cause hypothesis* (Peters 2005). That driver is likely to relate to plate tectonic movements and long-term rises and falls in sea-level: per-



TEXT-FIG. 2. Theoretical models for the diversification of life: A, in the absence of major perturbation; and B, with two mass extinctions superimposed. In each case, the upper curve is the logistic or equilibrium model, the middle curve is the additive or linear model, and the lower curve is the exponential model.

haps marine diversity is high at times of high sea-level, and low at times of low sea-level. Perhaps the opposite would be true of terrestrial faunas: at times of low sea-level, land areas were largest and so terrestrial biodiversity might be highest. Smith (2001) showed that global marine biodiversity only follows the sea-level curve up to 100 Ma, and then diverges: from the Late Cretaceous to the present-day sea-levels fell and yet marine biodiversity increased. Peters and Foote (2002) and Peters (2005) invoked the 'pull of the Recent', the combination of factors that allow palaeontologists to recognize more species in ever more recent rocks where there are many extant species, to explain the detachment of the marine diversity curve from the sea-level curve; Jablonski *et al.* (2003), by contrast, showed that the pull of the Recent is trivial for bivalves, and the same seems to be true for some other groups. Furthermore, terrestrial biodiversity through the same time interval does not in any way correspond to the inverse of the sea-level curve (Fara 2002).

The common cause hypothesis seems to be a better explanation of the apparent correlation between the rock and fossil records (Benton 2003; Peters 2005) than the preservation bias hypothesis (Raup 1972; Smith 2001; Peters and Foote 2002). As Peters (2005) noted, there is no clear test to distinguish between the two views, but his study of the time series of rock formations and fossil genera through time tends to favour the common cause hypothesis. This confirms the long-held assumption of palaeontologists and others (Darwin 1859; Newell 1952; Sepkoski *et al.* 1981) that the fossil record tells the history of life in its broad outlines, and clearly does not discount the obvious confounding factors of local- and regional-scale gaps and unusual fossiliferous horizons. In a thorough review of the marine generic fossil record, taking account of preservation bias, Foote (2003) confirmed the broad patterns of origination and extinction and the mass extinctions, thereby refuting his more extreme claims in Peters and Foote (2002).

Times of crisis in the geological record provide good tests of the common cause and preservation bias hypotheses. Generally, as Peters and Foote (2002) showed, the numbers of marine geological formations decline after major extinction events. So, for example, there are many fossiliferous geological formations before the Permo/Triassic boundary (PTB) and Cretaceous/Tertiary (KT) mass extinctions, and fossils are abundant and diverse. After both events, the numbers of formations plummet, as do the numbers of fossils. Does this indicate common cause or preservation bias? It is often hard to decide, especially as the post-extinction formations may represent different conditions of rock deposition. Most would accept though that the rock signal is reflecting some physical environmental crisis (e.g. major temperature change, asteroid impact, anoxia) that matches the crisis that killed life, and so the common cause model is assumed.

During times of crisis, the linkage between rock record and fossil record can break down, and this weakens the preservation bias hypothesis. While fossil diversity and abundance plummet through a mass extinction event, sampling may be constant (i.e. equal numbers of fossiliferous localities in similar rock facies across a time interval). In such cases, the preservation bias hypothesis would predict that fossil abundance and diversity would rise and fall with numbers of localities or formations sampled. To find the opposite, that fossil diversity falls, while fossil abundance and numbers of localities remain constant, or even rise, suggests that the fossil signal is robust (Wignall and Benton 1999; Benton *et al.* 2004). Furthermore, when good sampling returns after the KT mass extinction for example, the dinosaurs or ammonites do not reappear; this further

suggests that their disappearance was real and not a result of sampling bias.

This debate could be interpreted as a debate about sampling or about drivers of diversification. Palaeontologists are generally an apologetic breed and enjoy nothing better than a spot of navel gazing. A common assumption then is that evidence for an environmental driver of diversity patterns shows that there is sampling bias, and that the observed patterns of fossil occurrence are unreliable because they have been produced by extraneous factors. The common cause hypothesis is perhaps more appropriate, that physical and biological factors interact; as sea-levels rise and fall, biodiversity responds, and the record of linked waxing and waning is both a biological and a geological signal.

Perturbations

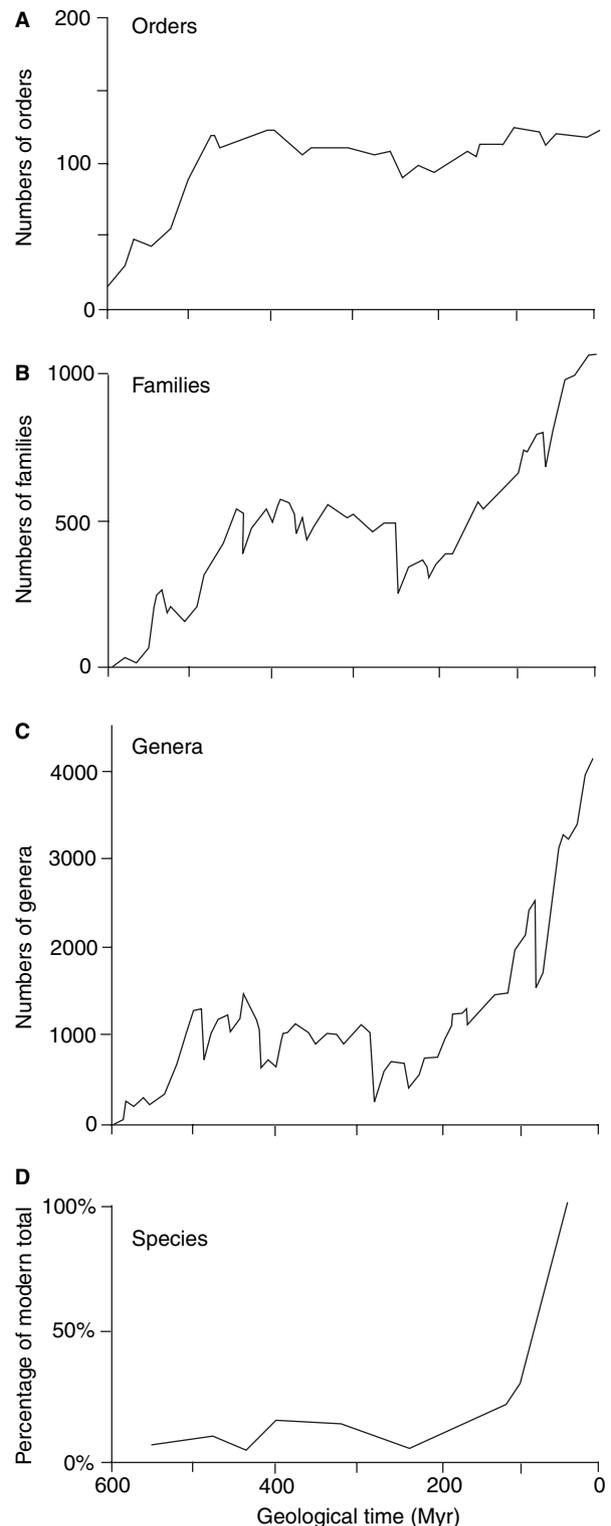
When Sepkoski (1978, 1979, 1984) and Hoffman (1985) debated the true shape of the diversification of life, they presented some clear-cut curves for logistic and exponential models (Text-fig. 2). Surely, it was argued, careful compilations of data from the fossil record should reveal which, if either, of these patterns was correct? Similar polarized predictions were made for resolution of the punctuated equilibrium vs. phyletic gradualism debate (Eldredge and Gould 1972) and the Red Queen vs. Stationary models of evolution (Stenseth and Maynard Smith 1984). In all cases, when perturbations are added to the distinctive graphs, the appearance of the plots converges.

In the case of comparisons between global-scale logistic and exponential curves, the main perturbation is extinction events. These re-set the diversification curve downwards and stimulate a renewed bout of diversification. With many perturbations, it becomes impossible to distinguish a logistic curve with a genuine equilibrium plateau from a damped exponential curve. Because of extinctions, the equilibrium global carrying capacity might never be reached (logistic model) or the rise in diversity is constantly slowed and reversed (exponential model).

The effect of perturbations appears to increase at lower taxonomic levels. Classes and orders can take a lot of punishment before they disappear, essentially because of their species richness, but families, and especially genera and species, may be hit hard by physical environmental crises. This is evident if one compares the family and genus-level curves (Text-fig. 3).

Scaling

Palaeontologists have traditionally used counts of families (Sepkoski 1978, 1979, 1984; Benton 1995) or genera



TEXT-FIG. 3. 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, and the curve is plotted as percentages of the modern total, set at 100 per cent (based on Benton 1997).

(e.g. Sepkoski 1996*b*; Peters and Foote 2002; Peters 2005) to indicate palaeontological patterns of diversification. The assumption was that the family or genus curves approximated the species-level curve, and they were then practical proxies at least within particular clades (e.g. Roy *et al.* 1996). Palaeontologists have avoided collating data on species for global-level studies for several reasons: (1) it would take far longer to compile global-scale lists of fossil species than genera or families; (2) a global-scale list of species would contain more errors (e.g. omitted synonyms, incorrect synonyms) than a comparable list of genera or families; (3) scaling the temporal precision is harder (species should be listed against geological zones or subepochs with durations of 1–3 myr, rather than geological stages with durations of 4–10 myr as for genera or families; the stratigraphic precision has to match typical durations of the taxa); and (4) scaling the geographical and facies precision is also harder; at species level, the records are very dependent on the efforts of individual palaeontologists and these might seriously skew the plots by locality, country or particular rock type. Forey *et al.* (2004) discussed these themes in more detail.

Families and genera may act as reasonable proxies for species in certain kinds of studies, especially of ecological attributes within clades. The assumption, however, that family- or genus-level curves match species-level curves at the global scale has been queried. Hoffman (1985) pointed out that families are arbitrary categories and their definition might vary between major groups, and that the family/species relationship varies through geological time. It could also be noted that small-scale rises and falls in a species-level curve are smoothed at higher taxonomic levels, because local-scale geographical, facies and temporal vicissitudes do not impinge; this could be seen as both good and bad.

The patterns of diversification of classes and orders may differ substantially from those of genera and species for both biological and geometric reasons. The fundamental divisions in the tree of life represent major bauplan differentiation, and major clades often acquired their unique morphological characters early in their history. So, plots of diversification of higher-category levels say a great deal about fundamental divergences in the history of life. Some of the difference in pattern between a plot of the diversification of classes and species, however, is geometric (Signor 1985; Benton 1997), depending on the architecture of the tree of life. The most recent twigs on the tree are species, deeper twigs genera, yet-deeper twigs families, and so on. As clades radiate, the numbers of genera and species must increase faster than the number of families, unless each clade remained monospecific.

This combination of the different biological meanings of classes and species, as well as the geometric imperative of

tree shape, underlies the remarkable transformation of the iconic Sepkoski (1978, 1979, 1984) diversification curves (Text-fig. 3), as Benton (1997) and Lane and Benton (2003) stressed. The logistic curve collapses to an exponential curve as one descends the taxonomic hierarchy. Sepkoski (1978) showed a single logistic curve for orders of marine animals in which modern diversity levels were achieved early in the Palaeozoic. His family-level plots (Sepkoski 1979, 1984) are more complex, with a short Cambrian and a long Palaeozoic plateau of family diversity, a drop, and then an inexorable rise to the present, which he interpreted as possibly heading for a third plateau. The generic-level plots (Sepkoski 1996*b*) show a merging and collapse of the Cambrian and Palaeozoic plateaux, and a more marked rise in marine animal diversity since the Palaeozoic. There is no global-scale species-level curve, but Valentine (1970) and Signor (1985) provided modelled versions, and these are pretty much single exponential curves. So, is the logistic model for the diversification of life in the sea an artefact of taxonomic scaling?

Auxiliary evidence for equilibrium and expansion in the diversification of life

It is surely rather sterile to attempt to determine the most appropriate model for the global diversification of life based on the shape of the plots (Text-fig. 1), and such an approach is fraught with all the difficulties outlined above. Five observations might provide tests for distinguishing 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 rise. 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 any slowing in the rate of increase, nor of the occurrence of any equilibrium levels. These radiations strongly suggest patterns of unfettered expansion (Benton 1985, 1995, 2001).
3. There were rapid rebounds after mass extinctions when 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 faster than new ecospace. Such rapid rebounds might suggest a logistic/equilibrium model of diversification (Sepkoski 1996*a*). Arguably, they could also be understood in a world of expansion, especially as most rebounds (mid-Cambrian, post-Ordovician, post-Permian, post-Triassic, post-Cretaceous) were associated with overall rises in global diversity to levels higher than those prior to the extinction.

4. Late phases of diversification are associated with an increase in competition, evidenced by declining rates of origination and increasing rates of extinction. This corresponds to the slowing down of diversification rates as the logistic curve approaches the equilibrium level (asymptote). The marine record generally confirms such expectations, but not entirely. For marine orders, total origination rates decline as a function of diversity, but total extinction rates do not increase as expected. A similar mismatch was discovered for families of marine animals; total origination rates of the Cambrian evolutionary fauna did not show the expected decline in the late Cambrian, nor did total extinction rates of the Palaeozoic evolutionary fauna clearly increase through the Palaeozoic (Sepkoski 1996a). These mismatches could indicate serious weaknesses of the equilibrium interpretation, or they could be the result of additional evolutionary factors that were overlaid on a three-phase logistic model (Sepkoski 1984).

5. The Palaeozoic plateau in marine animal diversity (Text-fig. 1A) is generally taken as strong evidence for equilibrium (Sepkoski 1984, 1996a). A second view, however, is that the Palaeozoic plateau is real, but was maintained below any maximum carrying capacity by perturbations, i.e. extinction events of varying magnitude. A third view is that the plateau is an artefact of analyses carried out at high taxonomic level (Benton 1997; Lane and Benton 2003). A comparison of plots of the diversity of marine life through time, shown at ordinal, familial, generic and specific level (Text-fig. 3), shows how a simple logistic pattern becomes more complex. At ordinal level, there is a single logistic curve, reaching a plateau that lasts for over 450 myr. At familial level, the plateau has shortened to extend for 200 myr of the Palaeozoic, and is followed by a rising curve through the last 250 myr, with no plateau. At generic level, the Palaeozoic plateau is lower and more irregular, and the post-Palaeozoic diversification of genera is exponential. For species, there is no available empirical curve; a suggested consensus plot retains indications of a two-phase Palaeozoic diversification pattern, but the pattern of diversification on the whole is exponential.

Patterns and processes

Whether life has diversified according to a logistic or an exponential pattern overall could fit with a variety of patterns and processes of individual clade diversification. A logistic global model could still allow explosive exponential expansion of certain clades, such as neogastropods or insects, but other clades would have to diminish in diversity dramatically to accommodate such expansions under the lid of a fixed global carrying capacity. More modestly

variable clade expansions and reductions, however, might be seen to chime better with the logistic global model; no one has yet identified a clear example of a dramatic clade contraction that has been forced by an explosively expanding clade. The relatively common phenomenon of rapid radiation at the base of many clades, and the fact that certain groups have apparently radiated to huge biodiversity and show little sign of a slow-down, fit the global expansion model better.

Twenty or 30 years ago it was hard to make a connection between such large-scale, long-term patterns and the day-to-day field and laboratory observations of biologists. There was a sort of 'dead zone' in time that could not be addressed effectively by palaeontologists or biologists, times greater than perhaps 100 years, but less than 1 myr. New molecular approaches have allowed biologists to extend their studies back to thousands and even millions of years, and palaeontologists, armed with ever-better radiometric and other time scales, can also talk about time spans of less than 1 myr. This allows biologists to address some of the larger questions about process that have been raised by palaeontological macroevolutionary work in the past 30 years. The new genetic and molecular approaches allow us to determine the patterns of species in time and space to a finer degree of resolution than is usually possible with fossils.

Stepping back from the global and long-term picture that has emerged from palaeontological work, one key question is why some modern groups are diverse and others are not. It is common to observe that sister taxa may show dramatically different evolutionary fates: *Sphenodon*, the tuatara, is a single genus and two species of a clade that was perhaps never diverse, but its sister-clade, Squamata, has expanded to 7390 species in the past 200 myr. Why should that be? Did the first lizard pioneer some extraordinary 'key adaptation' that ensured the rip-roaring success of Squamata, while Sphenodontia languished gloomily in New Zealand? Were the lizards and snakes favoured by ecology or biogeography? Do they have some genetic driver that forces them to speciate in ways that the sphenodontids never did? Were they just lucky in some other way? Or is there some innate principle that causes already speciose groups to become even more speciose?

SMALL-SCALE PATTERNS AND MEASURES OF DIVERSIFICATION

Morphological convergence and the underestimation of diversity

In measuring species diversity as a cumulative value through time, it is possible to underestimate the total value because of convergence, the repeated evolution of

the same evolutionary form. This may compromise the comparison of estimates of diversity between two areas at a given time, or between two time points for the same area. A textbook example of the independent evolution of similar forms is the mammalian sabre-tooth *Smilodon* from the upper Pleistocene, and the sabre-toothed marsupial *Thylacosmilus* from the upper Miocene–lower Pliocene. While for cases such as the sabre-tooths, evolutionary convergence (or multiple evolutionary events leading to the same morphology) have been identified, the possibility remains that other cases may perhaps go unnoticed, and recent molecular phylogenetic studies reinforce this idea.

But just how prevalent is convergence? If it is more prevalent at lower taxonomic levels then this is likely to contribute to a dampening of any exponential pattern of diversification. A recent study of the lizard *Anolis* on Caribbean islands suggests convergence is more common than had been assumed. On each of the greater Antillean islands of Cuba, Hispaniola, Jamaica and Puerto Rico, assemblages of *Anolis* lizard species are composed of species that differ in habitat use, and with a few exceptions each island has the same set of ‘ecomorphs’. Losos *et al.* (1998) undertook a morphometric and molecular phylogenetic analysis of this group to test between two competing hypotheses: (1) the single evolution hypothesis that each ecomorph has evolved only once and subsequently colonized all islands; (2) the recurring evolution hypothesis that none of the ecomorph classes forms a monophyletic group and that 17–19 evolutionary transitions among ecomorph classes have occurred. Although morphometric data clearly grouped individuals of the same ecomorph together, regardless of geographical affinity, molecular phylogenetic data revealed that island isolation and natural selection have resulted in at least 17 evolutionary transitions among ecomorph classes. In short, there has been substantially more evolutionary change on these islands than one would infer from morphology and ecology alone.

It had been assumed by many that such patterns of convergence are restricted to island biotas, rather than those of the continents. Melville *et al.* (2005) undertook a molecular phylogenetic comparative analysis of the evolutionary patterns of structural ecology and morphology of 42 species of iguanian lizards from two continental areas, Australia and North America. They found that evolutionary convergence of ecology and morphology occurs both in overall, community-wide patterns and in terms of highly similar pairs of intercontinental species. While the *Anolis* study of Losos *et al.* (1998) indicates evolutionary convergence among species within a genus, the study of Melville *et al.* (2005) demonstrates convergence between species from different reptilian families. Although many studies that have sought to document community-level

convergence in other organisms (e.g. Pianka 1986; Ricklefs 1987; Winemiller and Pianka 1990; Wiens 1991; Cadle and Greene 1993; Latham and Ricklefs 1993) found that the differences often outweigh the similarities, the results of Losos *et al.* (1998) and Melville *et al.* (2005) indicate that morphological convergence may contribute to the underestimation of evolutionary change.

Evolutionary opportunity, evolutionary potential and evolutionary success

Is modern diversity in speciose groups the result of current competition or can it be tracked to deeper divergences and adaptations? A global molecular phylogenetic analysis of lizards (Vitt and Pianka 2005) suggests that some adaptive events very deep in the tree are still influencing modern squamate biodiversity. Lizards and snakes arose somewhere between the late Triassic and early Jurassic, and they have diversified on all major continents and now occupy many different ecological niches. A combination of phylogenetic and ecological data for 184 lizard species in 12 families from four continents points to dietary shifts in major clades so that some lizard clades gained access to new resources, which in turn led to much of the biodiversity seen today. The most striking dietary divergence was that in the late Triassic between the iguanian and scleroglossan lineages. Scleroglossans appear to have gained access to sedentary and hidden prey through the acquisition of chemical prey discrimination, jaw prehension and wide foraging, and this may have had profound influences on subsequent diversification. Vitt and Pianka (2005) contended that the acquisition of chemosensory-based searching behaviour by the ancestral scleroglossan must have provided access to a set of resources that were relatively untapped by diurnal vertebrates. The implication is that this key evolutionary innovation in prey detection may have strongly influenced much of the squamate biodiversity observed today.

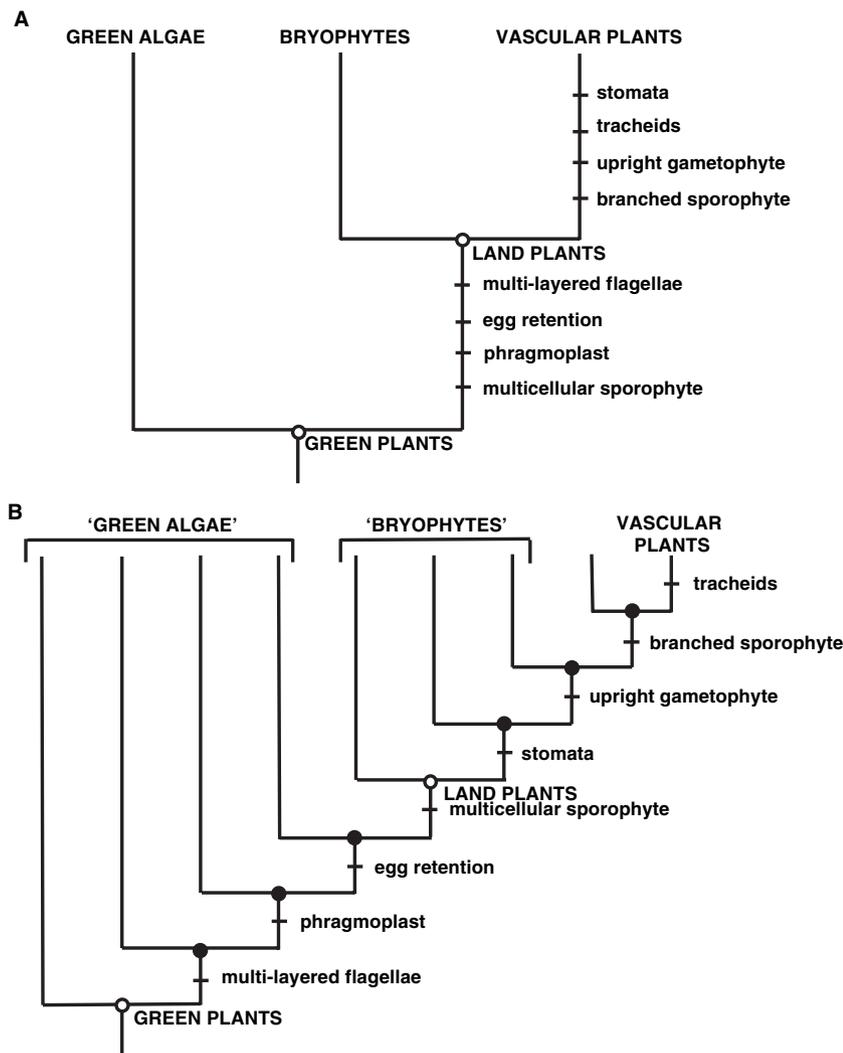
There are many classic cases of clade diversifications, sometimes in response to a morphological innovation and/or ecological opportunity. These kinds of diversifications have traditionally been called *adaptive radiations*, and they are frequently linked to a so-called *key adaptation* that is the key to the burst of evolution. Evolutionary biologists and palaeontologists generally avoid such terms now as they are more than merely descriptive, but imply a baggage of theory. Molecular phylogenetic studies suggest that radiations may be step-like, with acquisition of several characters that allow the organisms to adapt to new conditions.

Among land plants there are two notable events, the first being the radiation of terrestrial plants from an aquatic ancestor in the early Devonian at approximately

400 Ma. Early terrestrial plants evolved the morphological and life-history traits that characterize contemporary species (Bateman *et al.* 1998) and it is these innovations that are associated with the subsequent diversification of land plants. The second notable diversification event was that of the flowering plants in the Cretaceous at approximately 110 Ma, and it is thought that the flower, through its ability to make pollination so efficient, was the catalyst for this. In both of these cases it appears that ecological opportunity was either created or capitalized upon through the evolution of specific traits. However, recently Donoghue (2005) has pointed out that our notion of the relationship between these specific traits, or key innovations, and diversification is being refined by modern molecular phylogenetics. Considering the first of the two plant examples, the transition from water to land (Text-fig. 4), under the traditional view of monophyly of green algae and bryophytes, this transition involved a number of evolutionary steps that cannot be placed in any partic-

ular order (Text-fig. 4A). Donoghue (2005) pointed out that now we know that green algae and bryophytes are paraphyletic groupings, we can gain some insight into the sequence of events from the origin of the first green plants through to their movement on to land (Text-fig. 4B). But more generally, Donoghue (2005) noted that molecular phylogenetic results such as these challenge the very notion of key innovations. In terms of how we view the link between character evolution and success, instead of localizing key innovations it may be more correct to think in terms of causal links between characters. It seems then that the sequential evolution of characters culminates in traits that in combination facilitate diversification, and there is no single character that acts as a driver of diversification.

Diversification of an evolutionary lineage obviously requires both the extrinsic opportunity and the intrinsic potential for diversification to occur. For example, while the terrestrial environment of the Devonian provided the



TEXT-FIG. 4. Modern molecular phylogenetics forces a shift in understanding regarding character evolution. A, the traditional view of green algae and bryophytes as monophyletic groups resulted in a set of temporally unordered characters at a few nodes associated with the transition to land and the origin of vascular plants, which may be interpreted as temporally coincident. B, modern molecular phylogenetics now provides a sequence of character changes that clarify the temporal sequence for the evolution of the characters in relation to the transition to land and the origin of vascular plants (from Donoghue 2005).

extrinsic stage upon which plants could diversify, plants first required certain intrinsic genetically based changes to occur for the evolution of such things as a waxy cuticle and stomata. Irrespective of the sequence of evolution of these changes, why some lineages diversify and others do not may simply arise from a lack of synchrony between extrinsic and intrinsic variables. Here again, molecular phylogenetics can provide some insight into the interplay between evolutionary opportunity, evolutionary potential and evolutionary success. The silversword alliance (Compositae) of the Hawaiian archipelago has been regarded as 'one of the most remarkable examples of adaptive radiation in plants' (Raven *et al.* 2004, p. 210), comprising a single lineage with 28 Hawaiian-endemic species in the genera *Argyroxiphium*, *Dubautia* and *Wilkesia*. Early molecular phylogenetic studies based on chloroplast DNA pointed to a North American origin for the group (Baldwin *et al.* 1991), and subsequent studies using nuclear loci (Barrier *et al.* 1999) gave some indication as to why the North American common ancestor was able to capitalize on the ecological opportunity offered by the Hawaiian archipelago. A phylogenetic analysis using two floral homeotic genes (Barrier *et al.* 1999) revealed the tetraploid ancestor of the silversword alliance to be the product of a hybridization event between two ancestral tarweed species of the *Madia*/Raillardiopsis group. More specifically, this hybridization was determined to have involved members of the lineages that include *Raillardiopsis muirii* and *R. scabrida*. The simplest explanation for this is that a continental allopolyploid formed by the two tarweed species colonized the Hawaiian archipelago. The alternative and much less plausible hypothesis is that both tarweed species colonized the archipelago independently, hybridization occurred there and the two diploid progenitors subsequently went extinct. The conclusion reached by Barrier *et al.* (1999) is that, despite the phenomenal evolutionary success of the silversword alliance ancestor in the Hawaiian Islands, the same allopolyploid lineage in North America was an evolutionary dead end. In fact the very success of the silversword lineage may have been promoted by its hybrid constitution. The presence of two divergent genomes in the colonizing ancestor may have conferred more genetic variation (evolutionary potential) and a greater ability to respond (evolutionary success) to selection (evolutionary opportunity).

The implications of genome duplication for diversification are receiving increasing attention, with the feeling that they may underpin some of the major diversification events in the history of life (although see Donoghue and Purnell 2005 for an alternative view). Genome duplications have been credited with providing the genetic raw material necessary for major transitions such as the evolution of multicellularity, bilateral symmetry and the evolution of vertebrates (Ohno 1970; Sidow 1996; Holland

1999; Lundin 1999; Patel 2000). Recent evidence suggests an additional entire genome duplication in the ancestor of the ray finned fish, with the genome duplication and the diversification of the fish lineage possibly coinciding in time. There are approximately 25,000 species of fishes, almost half the total number of vertebrates on Earth, suggesting a possible cause-effect relationship between gene copy number and species diversity (Amores *et al.* 1998; Meyer and Schartl 1999). Supporting the hypothesis that tetraploidy promotes speciation, Taylor *et al.* (2001) have noted that the polyploid Salmonidae includes many more species (*c.* 70) than its diploid sister taxon, Osmeridae, which contains only about ten species. However, as has been pointed out by Donoghue and Purnell (2005), hypotheses linking genome duplications and the evolution of complexity in vertebrates, as currently formulated, are not really testable because they are defined too loosely for falsification.

Ohno (1970) proposed that it is much easier to make new genes by duplicating old ones than to create them *de novo*, and that genome duplication was a quick and easy way to produce vast numbers of duplicate genes, which in turn could then open the door to duplicating whole biochemical pathways. Polyploids often show novel phenotypes not present in their diploid progenitors or exceeding the ranges of the contributing species (Ramsay and Schemske 2002) that may allow them to enter new niches or enhance their competitive ability. These observations and the prominence of polyploidy in flowering plants imply some adaptive significance (Osborn 2002). Polyploidy can perhaps increase the evolutionary potential of a lineage in several ways: duplicated genes may have relaxed functional constraints, and thus be able to diverge, creating new phenotypes in polyploids (for a review, see Taylor *et al.* 2001). However, this does not explain the immediate effects often associated with polyploidy, and it is likely that these involve changes in gene expression (Osborn 2002). Lynch and Connery (2000) and Lynch and Force (2000) have presented a model that suggests gene loss or silencing may be more important to the evolution of species diversity than the evolution of new function or changes in expression in new genes. This model, named 'divergent resolution', describes how the loss of different copies of a duplicated gene in geographically separated populations could genetically isolate these populations should they become reunited.

Climate and diversification

Analysis of the fossil record has documented a number of cycles of mass extinction events that have been followed by subsequent diversification (Text-fig. 1). In an analogous

but less dramatic way, climatic changes through the Quaternary (2.4 Ma to the present) are believed to have had similar effects (e.g. Hewitt 2004; Turgeon *et al.* 2005). Through the Tertiary period (from 65 Ma) the Earth's climate became cooler with frequent oscillations that increased in amplitude and led to a series of major ice ages in the Quaternary. Glacial advances and retreats over the Pleistocene resulted in global cycles of contraction, expansion and fragmentation of species ranges resulting in species extinctions, population bottlenecks and differentiation. A consequence of this appears to be that many fossil assemblages from 20,000 to 10,000 years ago bear little resemblance to extant assemblages even though they consist of many of the same species (e.g. Holman 1993; Coope 1995; Graham *et al.* 1996; Elias 2000; Jackson and Overpeck 2000). Advances in our ability to obtain DNA sequence data from fossils are demonstrating that even when a fossil assemblage is the same as an extant assemblage, it may not necessarily be analogous. Barnes *et al.* (2002) have demonstrated that some brown bear fossil deposits in Beringia represent a different phylogenetic lineage from the extant form, suggesting regional extinction followed by recolonization.

While numerous phylogeographical studies attest to the intraspecific genetic and geographical consequences of climatic changes, there is perhaps less evidence for cycles of extinction followed by subsequent speciation. Referring to the abundance of insect remains in Quaternary deposits, Coope (2004) has pointed out that, although there is evidence of distributional change, there is remarkably little evidence for morphological change during this period of great climatic fluctuation. In fact, contrary to intuitive expectations, there is little evidence from the Quaternary invertebrate fossil record for large-scale extinctions and rapid evolution. However, it has been argued that this apparent stasis, with little recognizable influence of extinction or speciation, may be a reflection of the geographical bias of invertebrate fossils toward higher latitudes (Ribera and Vogler 2004). In western Europe most refugial areas appear to be at lower latitudes (Hewitt 2000), which is where we would expect differentiation and speciation to occur (Text-fig. 5). Ribera and Vogler (2004) argued that studies of European insect fossils have been conducted almost exclusively in northern latitudes, and these were affected more severely by the Pleistocene climatic changes and now have few narrow-range endemic taxa compared with southern Europe. Additional taxonomic bias has also been suggested by Turgeon *et al.* (2005), who pointed out that the use of genital characters alone to delineate species may mask significant diversification in other features. Both arguments may go some way towards explaining the discrepancy between the fossil record and several recent invertebrate molecular phylogenetic studies that suggest speciation is a consequence of

Quaternary climatic changes (e.g. Ribera and Vogler 2004; Turgeon *et al.* 2005).

It appears that we do not yet have a clear picture of what were the real consequences above the species level of Quaternary climate fluctuations. However, there are several features of the Quaternary that make it an informative geological time for understanding the interplay among climate fluctuation, extinction, speciation and intra-specific demographic change. In the same way that the fossil record becomes less complete the further we go back in time, the same can be said of molecular phylogenetic trees. This means that for both sources of data the Quaternary is relatively information-rich. Fossils suffer from many preservational biases that worsen with increasing time (see above), and this suggests that more recent geological episodes, such as the Neogene or Quaternary in particular, are likely to document a higher proportion of taxa, a key motivation for the work of Coope (2004), Elias and Matthews (2002), and others.

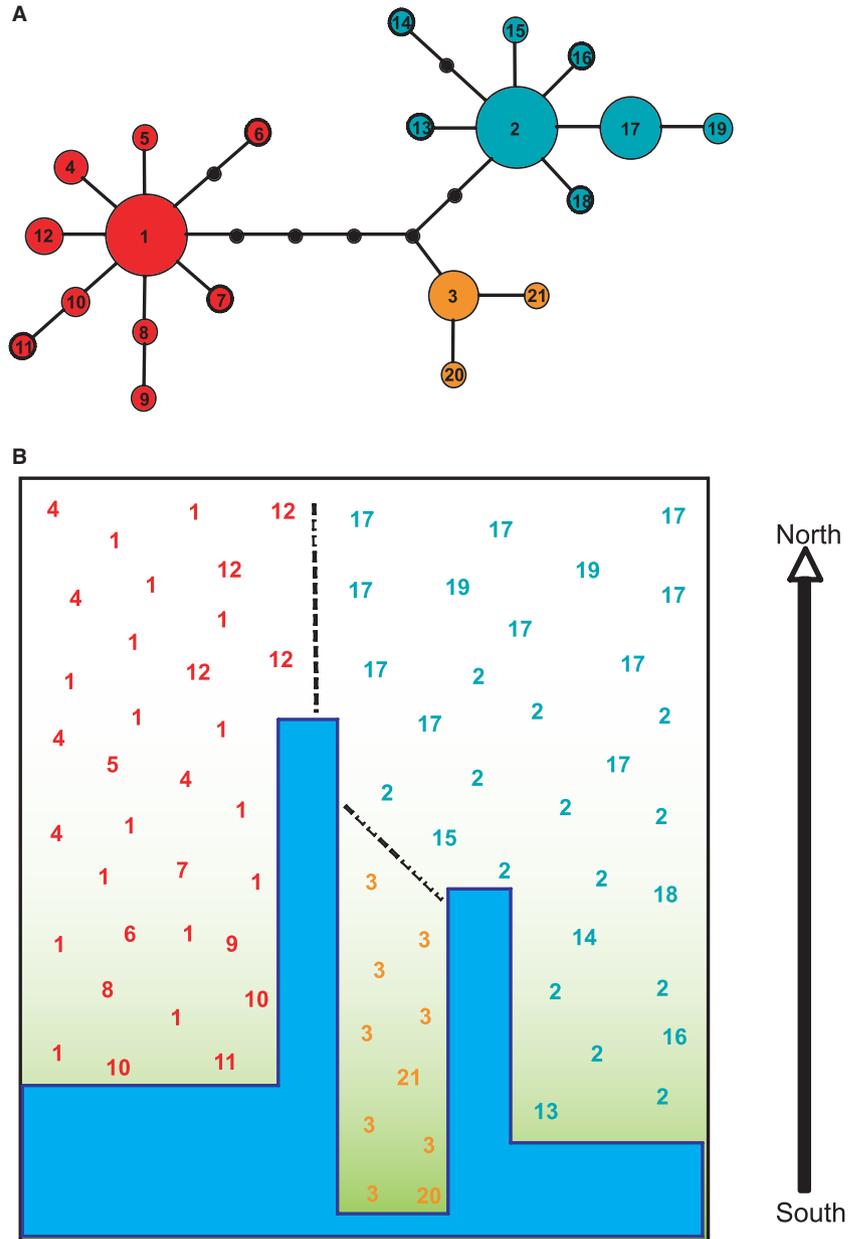
Molecular phylogenetics and palaeontology share the phenomenon of information loss with geological age. The older the most recent common ancestor (MRCA), the harder it is to infer the evolutionary history reliably (e.g. Emerson 2002; Emerson and Oromí 2005). In the same way that a fossil has a decreased probability of being represented in the fossil record with the passage of time, the same is true for the probability of a species being represented within a molecular phylogeny. Under a simple evolutionary scenario incorporating both speciation and extinction, but with an upper limit to species numbers, the older the MRCA, the larger will be the ratio of extant to extinct species.

The relatively new discipline of *phylogeography* (Avice *et al.* 1987) addresses the effects of Quaternary climate change on genetic differentiation and diversification within species (Text-fig. 5). At the core of this discipline is coalescent theory (Kingman 1982a, b) and its application to intraspecific genetic variation sampled across a geographical landscape. Such studies provide an insight into recent demographic and range changes that often reveal cryptic genetic structuring, differentiation and limitations to free gene flow underlying seemingly continuous geographical distributions (Hewitt 2000, 2004). In conjunction with pollen and ice core information, some of which extend back some 400 kyr (e.g. Reille *et al.* 1998; Stauffer 1999), phylogeographical methods address the causative links between climate fluctuation and diversification.

Community complexity and diversification

Understanding how communities of species assemble and evolve is a fundamental objective of evolutionary ecology,

TEXT-FIG. 5. A hypothetical network of DNA sequence haplotypes and their geographical distribution. A, a haplotype network in which each number represents a different haplotype, and the size of a circle is approximately proportional to the number of individuals sequenced containing that haplotype; solid circles represent haplotypes that were either not sampled, or are extinct; lines connecting haplotypes indicate single mutational differences; circles are coloured for reference to their geographical distribution. B, the geographical distributions of sampled haplotypes in a Northern Hemisphere continental setting, with southern glacial refugia indicated in green, and ocean barriers to dispersal in blue. Note: (1) the three coloured haplotype groups of A are associated with the three different refugial areas; (2) the most abundant haplotype within each group is also the most geographically widespread; (3) other haplotypes within each of the colour groups are derived from the most common haplotype; (4) star-like patterns consistent with population expansion in the red and green parts of the network; (5) genetic diversity is greatest in the south; (6) haplotype groups can form contact zones where gene flow may not be free (broken lines) (from Emerson and Hewitt 2005).



with implications for all branches of population and ecosystem biology. Historically, this research programme has been characterized by two viewpoints, the ‘Clementsian’ ideal that communities are repeatable and saturated assemblages of species structured by *in situ* competition, predation and resultant evolution (e.g. Hutchinson 1959; MacArthur 1972) vs. the ‘Gleasonian’ conception that communities are no more than terms of convenience for open and idiosyncratic groups of species assembled by chance immigration and extinction and ‘environmentally filtered’ by autecology (MacArthur and Wilson 1967; Hubbell 1979; Strong *et al.* 1984). The Gleasonian paradigm is dominant in modern community ecology (e.g. Hubbell 2001), and

this justifies, for example, the individualistic climate envelope approach to predicting species distributions as a function of climate change (e.g. Thomas 2004).

Studies capitalizing upon modern molecular phylogenetic techniques, however, now suggest a greater role for *in situ* speciation within communities (e.g. Losos *et al.* 1998; Gillespie 2004; Emerson and Oromí 2005), and the roles of both competition and predation have recently been highlighted as factors that can structure communities of species (Grant and Grant 2006; Nosil and Crespi 2006). Emerson and Kolm (2005) have suggested that species diversity itself may be implicated in much of the speciation that has occurred within the Canary and

Hawaiian island archipelagos. The rate of speciation on an island is positively related to species numbers, even after statistically controlling for physical features that could also contribute to species diversification rates (island age, area, altitude and proximity to the nearest neighbour island). In short, islands with more species seem to experience more evolution, which is strong evidence for the idea that *in situ* interactions and evolution can play a major role in creating and structuring communities.

Perhaps ironically, the theory of island biogeography (MacArthur and Wilson 1963, 1967) provides justification for this result. MacArthur and Wilson argued that islands with more species should exhibit increased competitive and predatory interactions, which would increase the extinction rate. However, rather than causing extinction, these increased negative interactions might instead drive adaptive evolution (e.g. Grant and Grant 2006; Nosil and Crespi 2006). Additionally, as species diversity in an area increases and average population size decreases, population genetic theory predicts that there will be an increased probability of divergence via genetic drift. Finally, increasing species diversity may lead to greater community structural complexity, and this has also been suggested as a possible evolutionary force driving speciation (see also Tokeshi 1999; Erwin 2005).

To date, and despite broad interest among ecologists and evolutionary biologists, few studies have sought to examine the relationship between competition and species coexistence within the context of a community assemblage of species (Rosenzweig 1995; Tokeshi 1999; Schluter 2000). However, Webb and colleagues (Webb 2000; Webb *et al.* 2002) have recently made a major theoretical advance by devising methods to combine phylogenies with community analysis, providing novel and deep insights into the evolutionary and ecological histories of entire communities. For example, in a landmark paper, Cavender-Bares *et al.* (2004) found that sympatric oak tree species in South Florida tend to be phylogenetically over-dispersed, meaning that closely related species are less likely to be found within the same 0.1-ha tree plots. Because further analysis also revealed that the main ecophysiological traits involved in coexistence are evolutionarily conserved, this suggests that local communities are assembled more via Gleasonian 'environmental filtering' rather than via the local evolution of niche divergence.

Whereas the forest tree analyses of Webb (2000) and Cavender-Bares *et al.* (2004) suggest a key role for environmental filtering, other studies suggest that inter-specific competition can mediate niche differences, contributing to the structure of ecological communities (Silvertown *et al.* 1999; Gotelli and McCabe 2002; Clark and McLachlan 2003; Fargione *et al.* 2003; McGill 2003;

Adler 2004). Recent work by Silvertown *et al.* (2006) on meadow plant communities characterized two levels of niche, β (habitat) and α (within habitat), and found that the β niche is evolutionarily conserved, whereas the α niche is evolutionarily labile. Silvertown *et al.* (2006) interpreted this as meaning that, although species must have similar β niches in order to occupy the same habitat, they must have sufficiently different α niches to be able to coexist. Although the results of Silvertown *et al.* (2006) are compatible with competition-mediated character/niche divergence, they do not directly demonstrate this. However, a recent demonstration of this for Darwin's finches does support the role of competition and character displacement in community assembly (Grant and Grant 2006), and poses some interesting questions. Has an evolutionary history of competition-mediated character/niche divergence contributed significantly to the biodiversity of today? It seems likely that this depends upon what regulates the number of α niches within a β niche, and one can imagine that this may be a function of the species both resident in, and entering, a given β niche.

The thought that species themselves are not just the products of diversification but also contribute to the process is a provocative one, and it will be interesting to explore the implications of this for models of diversification at both the macro- and the micro-evolutionary scale. For example, palaeontologists debate whether late phases of diversification are associated with an increase in competition, because total extinction rates do not seem to increase in these later phases as has been expected (see above). But if competition is a significant driver of diversification, then perhaps the absence of an increase in extinction rate is not unexpected, considering that competition has two outcomes: extinction or change. This also sits well with the comparison of plots for diversification over time from ordinal down to species level (Text-fig. 3). Text-figure 3 shows that diversification through geological time is marked by a trend toward change at lower taxonomic rank, and one possibility is that increasing competition at the macro-evolutionary scale led to smaller-scale species-level refinements in morphology rather than ordinal-level changes.

CONCLUSIONS

There are debates about whether life has diversified according to a logistic pattern, in which global diversity is capped at an equilibrium level, or whether diversification has followed a damped exponential pattern without reaching any limit. Current evidence favours the latter model, especially for life on land.

Individual clades diversify according to many patterns, some distinctly logistic, and the expansion of certain clades may indeed reach an equilibrium level. Others appear to continue finding new things to do. The sum of many clades, some ever-expanding, others not, is unlikely to be a single global logistic pattern.

Recent proposals that the fossil record is substantially flawed either by chronically poor sampling or that it mirrors the volume of rock appear to be exaggerations. Sampling clearly worsens in more ancient rocks but the broad outlines of phylogeny are equally well documented, and fossil Lagerstätten indicate that diversity is sampled reasonably well. At certain scales, fossil diversity and rock volume parallel each other, perhaps indicating that both are controlled by a third cause, such as changing sea-levels. However, diversity continued to rise through the last 100 myr even while sea-level fell. Evidence that the fossil record is purely an artefact of geological drivers is limited.

Convergence may mask true evolutionary diversity; molecular studies are revealing some cases of previously undetected convergence in morphology.

Clade radiations depend on a combination of extrinsic opportunity and intrinsic potential. Much of modern diversity in particular clades may be traced back to particular diversification events deep in time when an environmental opportunity became available and particular adaptations manifested themselves. There is little evidence for a simple key adaptation model of clade diversification: more often, a series of characters is acquired over time, and these open new ecospace for exploitation by a new mode of life. Genome duplication events may have opened further opportunities for rapid diversification by triggering major morphological change.

Studies of the dramatic climatic changes in the past 2 myr of the Quaternary have revealed less extinction and diversification than might have been expected. Changes from cold to warm climates seem to have driven species to migrate to more favourable zones, but more work is required to be sure that true patterns are not being masked by sampling artefacts.

Ecologists debate whether communities are real entities linked and controlled by complex interactions among species, or whether they are chance assemblages of species living side by side, but not controlling the fates of other species. New evidence suggests that there may be strong interactions that control biodiversity, but not in the limiting way predicted by equilibrium models such as the theory of island biogeography. Ironically, it seems that species-rich communities speciate more than species-poor communities. So, species interactions may drive speciation rather than acting as a density-dependent control that limits speciation.

Studies from the scale of modern ecosystems to global long-term patterns in the fossil record support a model for

the exponential diversification of life, in which the world becomes increasingly divided into finer niche space. Organisms have a propensity to speciate freely, species richness within ecosystems appears to generate opportunities for more speciation, clades show all kinds of patterns from sluggish speciation rates and constant diversity through time to apparently explosive speciation, and there is no evidence that rapidly speciating clades have reached a limit, nor that they are driving other clades to extinction.

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