

Review

The origins of modern biodiversity on land

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Comparative studies of large phylogenies of living and extinct groups have shown that most biodiversity arises from a small number of highly species-rich clades. To understand biodiversity, it is important to examine the history of these clades on geological time scales. This is part of a distinct ‘phylogenetic expansion’ view of macroevolution, and contrasts with the alternative, non-phylogenetic ‘equilibrium’ approach to the history of biodiversity. The latter viewpoint focuses on density-dependent models in which all life is described by a single global-scale model, and a case is made here that this approach may be less successful at representing the shape of the evolution of life than the phylogenetic expansion approach. The terrestrial fossil record is patchy, but is adequate for coarse-scale studies of groups such as vertebrates that possess fossilizable hard parts. New methods in phylogenetic analysis, morphometrics and the study of exceptional biotas allow new approaches. Models for diversity regulation through time range from the entirely biotic to the entirely physical, with many intermediates. Tetrapod diversity has risen as a result of the expansion of ecospace, rather than niche subdivision or regional-scale endemism resulting from continental break-up. Tetrapod communities on land have been remarkably stable and have changed only when there was a revolution in floras (such as the demise of the Carboniferous coal forests, or the Cretaceous radiation of angiosperms) or following particularly severe mass extinction events, such as that at the end of the Permian.

Keywords: diversity; biodiversity; tetrapods; Phanerozoic; phylogeny

1. INTRODUCTION

Life on land may represent 85 per cent of all species on Earth (May 1990; Vermeij & Grosberg *in press*), based on the huge diversity of insects, other arthropods, angiosperms and microbes, but figures are near impossible to establish accurately. There are currently numerous approaches to understanding the long-term history of modern biodiversity, and these may be characterized by two broad world views that may be termed broadly the ‘equilibrium’ and ‘phylogenetic expansion’ models, respectively: (i) the biosphere can be modelled according to density-dependent dynamics that incorporate all organisms as independent players that push and shove against each other but cannot exceed a global species-level carrying capacity (Raup 1972; Sepkoski 1984; Alroy *in press*), or (ii) global systems are too complex for any such descriptive model, and it is more fruitful to focus on episodic expansions in biodiversity as new sectors of ecospace were occupied through geological time following major crises and/or the acquisition of novel character sets (‘key innovations’) that enabled new life modes (Simpson 1944; Vermeij 1987; Bambach 1993; Gould 2002; Stanley 2007; Benton 2009).

The second world view is taken here, that global diversity at any time is a complex amalgam of

species-level and clade-level phenomena, and so change through time in global species diversity is unlikely to be captured by a single model (cf. Sepkoski 1984; Alroy *et al.* 2001, 2008; Alroy *in press*). Species-level phenomena include changes in abundance and geographical distribution resulting from interactions with competitors and predators, as well as short-term changes in climate and topography. Clade-level phenomena include radiations and extinctions resulting from innate factors such as ‘key adaptations’ that may or may not interact with larger-scale vicissitudes in climate and topography. Lineages and clades presumably have a fundamental propensity to diversify exponentially, but external pressures from other organisms and from unpredictable physical environmental changes may reduce the rate of expansion or reverse it. With these thoughts in mind (e.g. Stanley 1979, 2007; Barnosky 2000; Vermeij & Leighton 2003; Benton & Emerson 2007; Vermeij & Grosberg *in press*), the current paper approaches the topic from a non-model-based empirical point of view, seeking to identify the biotic and abiotic phenomena that are associated with major diversifications and phases of extinction.

The purpose of this paper is to explore what controls the diversity of life on land through long spans of time. The focus is on vertebrates, and new methods will be illustrated through recently published case studies that together seek to explore the interplay of biotic and abiotic factors in the evolution of terrestrial biodiversity. First, the broad approaches to

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understanding the long-term history of global biodiversity just outlined will be developed further, and the issues of completeness and adequacy of the fossil record will also be addressed.

2. HOW TO VIEW THE DEEP-TIME DIVERSIFICATION OF LIFE

There are currently wide disagreements in perceptions of the history of diversity, and these divide into a number of dichotomies that overlap in various ways: (i) the overall diversity of life on Earth at any time is diversity-dependent and its trajectory through time is best represented by one or more logistic curves (Raup 1972; Sepkoski 1984; Alroy *et al.* 2001, 2008; Alroy *in press*) or not (Walker & Valentine 1984; Benton 1995, 1997, 2009; Gould 2002; Stanley 2007; Vermeij & Grosberg *in press*); (ii) global diversity change through time may be modelled as a single equation, or series of equations for different episodes in deep time (Sepkoski 1984; Alroy *et al.* 2001, 2008; Alroy *in press*) or not (Benton 1995, 1997, 2009; Stanley 2007); (iii) the broad pattern of global diversity through time is the result largely of the summation of biotic processes such as competition and predation (the Red Queen viewpoint; Van Valen 1973) or has more to do with unpredictable changes in the abiotic environment such as climatic and topographic changes (the Court Jester viewpoint; Barnosky 2000; Benton 2009); and (iv) the fossil record is substantially biased, with quality declining back in time (Raup 1972; Alroy *et al.* 2001, 2008; Smith 2007; Alroy *in press*) or the fossil record gives an adequate representation of diversity change through time on a coarse scale (Sepkoski *et al.* 1981; Benton *et al.* 2000; Peters 2005).

It would be easy to link the diversity-dependent (logistic), model-based, Red Queen and fossil record bias viewpoints as a coordinated set, and the non-diversity-dependent, non-model-based, Court Jester and fossil record adequacy viewpoints as another. However, different authors have expressed different combinations of these pairs of positions, and here is not the place to dissect each and to seek to classify the wider literature on these themes.

The different viewpoints arise from real and substantial questions about the data and about the appropriateness of different kinds of models. Part of the distinction may reflect the broad interests of the researchers and the organisms they work on. It is notable, for example, that palaeontologists who are interested in palaeoecology and community evolution are often drawn to density-dependent viewpoints, whereas palaeontologists who study groups such as fishes, arthropods, tetrapods or plants that are amenable to large-scale phylogenetic approaches, such as cladistics or molecular analysis, see complexity and expansion in the history of biodiversity. The empirical data indicate an exponential trajectory for the diversification of life on land, whether for terrestrial life overall (Benton 1995; Kalmar & Currie 2010; Vermeij & Grosberg *in press*), angiosperms (Magallón & Castillo 2009), insects (Mayhew 2007) or tetrapods (figure 1; Benton 1985*a*, 1999), rather different from the

apparent multiple-logistic (Sepkoski 1984) or single-logistic (Raup 1972; Alroy *et al.* 2001, 2008) trajectories for diversification of life in the sea.

Of course, there may be differences in the diversification of life in the sea and on land (Eble 1999; Benton 2001). Perhaps the sea acts as a giant Petri dish in which species diversity has long been density-dependent (Benton 2001), or it could equally be that the logistic curves for marine diversification are an artefact of the coarse sampling level (families or genera) and would reduce to damped exponential curves at the species level (Benton 1997; Benton & Emerson 2007; Stanley 2007). However, it is worth noting that marine familial and generic diversity has followed an essentially exponential curve since the end of the Permian 250 Ma, and it has proved difficult to represent this as a logistic curve (Sepkoski 1984) or to explain it as simply the result of improved sampling (*cf.* Raup 1972; Alroy *et al.* 2001, 2008; Jablonski *et al.* 2003; Bambach *et al.* 2007). Further, following the Mesozoic Marine Revolution (Vermeij 1977), numerous marine groups, such as neogastropods, decapod crustaceans, stomatopods and teleost fishes (Alfaro *et al.* 2009), showed massive clade expansion and no sign that they were supplanting competitor taxa one-for-one, as would be expected in a density-dependent world.

The bulk of modern biodiversity is accounted for by relatively small numbers of clades, so it is worthwhile to focus on these speciose clades and to explore why they became so diverse. In a recent paper, for example, Alfaro *et al.* (2009) identified that 85 per cent of the modern biodiversity of species of jawed vertebrates is accounted for by six clades: Ostariophysi (catfishes and minnows), Euteleostei (the bulk of teleosts), Percomorpha (subclade within Euteleostei, including most of the coral reef associated fishes as well as cichlids and perches), non-gekkonid squamates (*i.e.* most lizards), Neoaves (most modern birds) and Boreoeutheria (most eutherian mammals). These six clades include collectively some 20 000 species of fishes (three clades) and 17 000 species of tetrapods (three clades), and there is no evidence that the marine fishes were in any way more constrained in their ability to speciate (a necessity in a density-dependent marine world) than the freshwater fishes or terrestrial tetrapods in these highly speciose clades.

3. DIVERSIFICATION OF LIFE ON LAND

(a) *Narrative of major events*

In one way, the terrestrial record can be documented more readily than the marine: the conquest of the land began long after that of the sea. The current understanding (Labandeira 2005) is that microbes, primarily cyanobacteria, may have expanded from shallow waters onto the immediate shores in the Precambrian, but substantial moves of plants and animals began perhaps in the Middle Ordovician, some 470 Ma. These records of early tentative steps onto land, and indeed some of the later terrestrial events, have been linked explicitly to abiotic drivers such as oxygen and carbon dioxide levels, as well as

global sea level and temperature change (figure 1; e.g. Ward 2006).

The oldest convincing evidence for life on land consists of spores from primitive liverworts, which are close relatives of vascular plants (Wellman *et al.* 2003). Molecular evidence for earlier phases of terrestrialization, most notably a putative date of 700 Ma for the first vascular land plants (Heckman *et al.* 2001), is still controversial, not being supported by fossil or biomarker evidence. Subsequent major steps in terrestrialization include the first small vascular plants and the first arthropods on land in the mid-Silurian (425 Ma), the first tetrapods in the Middle Devonian (400 Ma; Coates *et al.* 2008; Niedźwiedzki *et al.* 2010), the first trees and the first flying insects in the Late Devonian (375 Ma), the first gliding vertebrates in the Late Permian (260 Ma) and the first flying vertebrates in the Late Triassic (215 Ma). The narrative is continued through the ecosystem studies in §5c.

(b) *Quality and adequacy of the fossil record*

This narrative would be accepted by most palaeontologists, and yet the fossil record is patchy and incomplete, especially the terrestrial record. For example, Padian & Clemens (1985), Behrensmeier *et al.* (2000) and Smith (2001) note that the terrestrial fossil record is poorer than the marine because sedimentation is typically more sporadic, many organisms live in habitats such as deserts, forests and mountains where deposition is limited, and terrestrial rocks are harder to date than marine. These are valid points, and yet the important question is not whether the terrestrial fossil record is perfect, or even good, but whether it is *adequate* for the studies in hand.

Circumstantial evidence in favour of the likely adequacy of the terrestrial fossil record for broad-scale studies of macroevolution is that the overall picture has not changed much despite continuing efforts to find new fossils. Even much-heralded discoveries, such as the oldest tetrapod footprints, that move the record of the group back by 18 Myr (Niedźwiedzki *et al.* 2010), are not entirely unexpected: our experience is that fossils that are entirely out of place—such as a Miocene dinosaur or a Precambrian rabbit—are not being found. New discoveries extend temporal ranges (Benton & Storrs 1994). This intuition was borne out by a comparison of changing interpretations of the tetrapod fossil record (Maxwell & Benton 1990): whereas the diversity of tetrapods at the family level doubled between 1890 and 1987, and so the species-level diversity presumably increased by a factor of four or five, the overall pattern of diversifications and extinctions remained unchanged, except for a heightening and sharpening of mass extinctions.

New discoveries tend to fill gaps in an incomplete fossil record, but how well does this reflect former reality? Undoubtedly, whole groups of soft-bodied organisms are missing from the fossil record and will never be found. There are three responses to this point: (i) sites of exceptional fossil preservation, such as the Early Devonian Rhynie Chert of Scotland, or the Early Cretaceous Jehol Group of China, may

preserve all the life of their time, including such soft-bodied organisms, and so these sites act as periodic snapshots of a complete biota; (ii) there is generally good congruence between molecular phylogenies and the order of fossils in the rocks, thus confirming with independent evidence the broad pattern of the fossil record (Benton *et al.* 2000); and (iii) in considering an ancient terrestrial ecosystem, it is possible to include fungi and slugs even though they may not be known as fossils.

One approach to detecting, and perhaps mitigating for, inadequacies of the fossil record has been the use of *sampling proxies*, representations of some or all of the geological and human factors that introduce error. Two commonly used sampling proxies have been map area and number of formations, both reflecting aspects of available rock volume. Map area (= area of outcrop) identifies rocks that cover large areas of the landscape and so are likely to have been more sampled than those that do not. Studies of marine data sets show close correlation of diversity and map area, interpreted as evidence of a rock volume control on apparent diversity (e.g. Smith 2001, 2007; Smith & McGowan 2008), although a study of global map areas of terrestrial sediments found no such control on terrestrial diversity data (Kalmar & Currie 2010).

The alternative proxy for sampling, the number of geological formations, although widely used (e.g. Peters & Foote 2001, 2002; Fröbisch 2008; Barrett *et al.* 2009; Butler *et al.* 2009; Benson *et al.* 2010), may be less appropriate than map areas because of the arbitrariness of formation definitions, and the fact that they may reflect rock heterogeneity (Crampton *et al.* 2003; Smith 2007). The studies cited found tight correlations between number of formations and biodiversity, and this was interpreted as evidence for ‘geological megabiases’. This approach is problematic for a number of reasons: (i) the sampling proxy may be no more accurate than the palaeontological signal it seeks to correct; (ii) the correlation of formation numbers and diversity may reflect a kind of species–area effect (Marx & Uhen 2010) in which both metrics rise and fall together, perhaps driven by a third factor, a ‘common cause’ (Peters 2005) such as sea-level variation, and so the correlation is expected and not an indication of bias; (iii) counts of formations are redundant with the counts of genera in some cases, as ‘numbers of formations with fossil X’ rise and fall as ‘diversity of fossil X’ rises and falls (Wignall & Benton 1999).

The search for a *global* correction factor for sampling bias, whether map area, number of formations or estimates of human effort, is problematic. It may be more fruitful to carry out sampling standardization to seek to remove bias resulting from unequal preservation and collecting effort (e.g. Behrensmeier *et al.* 2000; Alroy *et al.* 2001, 2008; Rabosky & Sorhannus 2009). Some earlier methods overcompensated for bias (Bambach *et al.* 2007), and new approaches (Alroy *in press*) seek to reconstruct the relative size of each taxonomic sampling pool in proportion to ecological species richness. Another approach is to make study-scale investigations of completeness, such as measures of specimen quality and

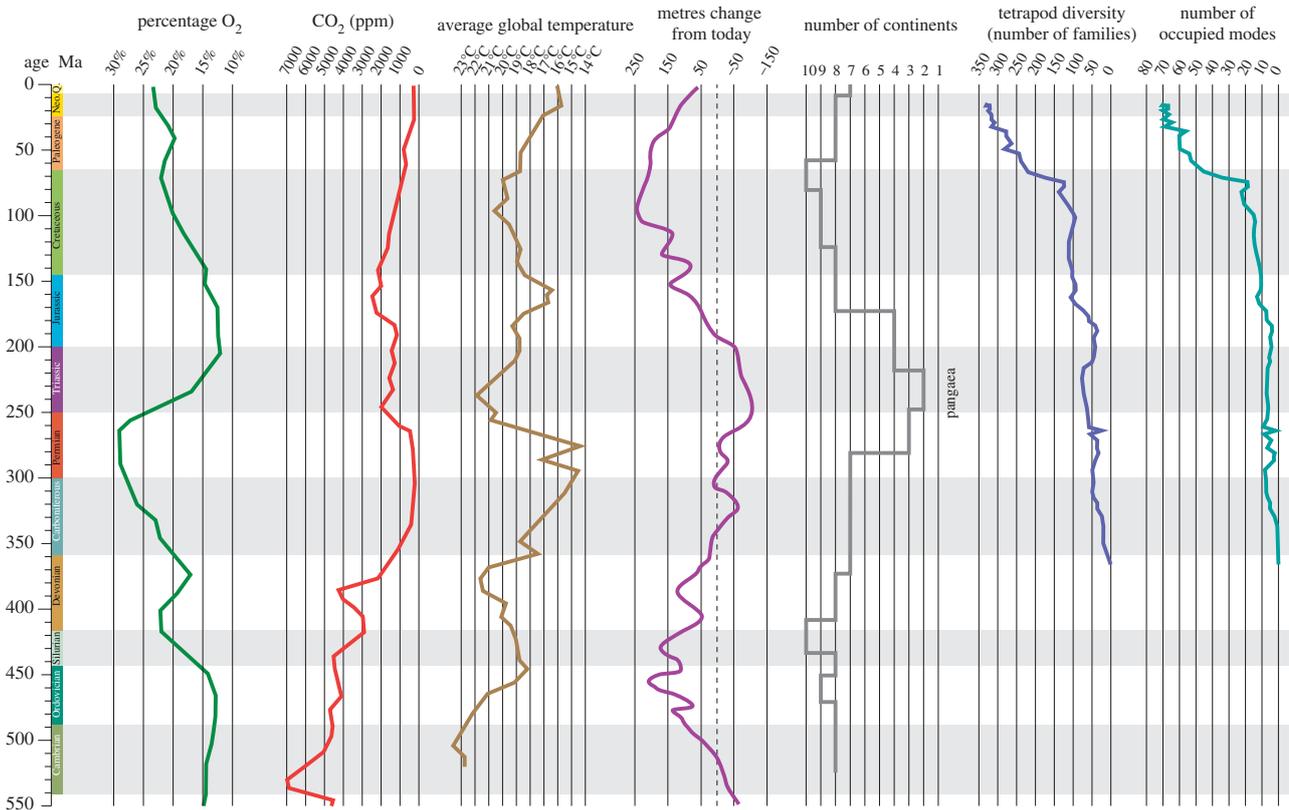


Figure 1. Changes through time in some key environmental parameters and in terrestrial tetrapod diversification. The curves, all plotted against the Phanerozoic time scale (left-hand side), show the percentage oxygen, carbon dioxide (in parts per million, ppm), the average global temperature (in degrees Celsius, °C), sea-level change (in metres difference above, or below, present levels) and the number of continents. Tetrapod diversification is documented as change in number of families and in number of major ecological modes ('guilds') documented in ecosystems. Sources of information: O₂ data from Berner (2003), CO₂ and temperature data from Royer *et al.* (2004), sea-level data from Haq & Schutter (2008), number of continents counted from the Scotese Paleomap website, <http://www.scotese.com/>, and tetrapod diversity and number of occupied niches from Sahney *et al.* (2010).

fossil abundance between bins, sample size standardization and matching samples of all available rock (e.g. Benton *et al.* 2004; Marx & Uhen 2010).

4. INCREASING BIODIVERSITY BY REGIONAL ENDEMICITY, EXPANSION OF ECOSPACE OR SPECIALIZATION

Today there are 27 000 species of tetrapods (4800 species of amphibians, 7900 species of reptiles, 9700 species of birds and 4600 species of mammals), and evolution from 1 to 27 000 species appears exponential (Benton 1985a, 1995; figure 1). Whatever the shape of the expansion, it would be interesting to determine any fundamental correlates of increasing species richness among tetrapods. Three candidates are (i) increasing regional-scale endemicity as the continents broke up through the past 200 Myr, (ii) increasing occupation of terrestrial ecospace, and (iii) increasing specialization. The latter two are aspects of how ecosystems are structured, incorporating alpha diversity, number of communities and whether terrestrial tetrapod communities have become more species-rich over the past 400 Myr, or whether numbers of communities regionally have increased.

Continental drift might be thought to drive at least a part of modern terrestrial tetrapod diversity. After all,

there was once a single global-scale supercontinent, Pangaea, through most of the Permian and Triassic, 290–200 Ma (figure 1), which divided into the current six continents by formation of the Atlantic and Indian oceans and various seaways and mountain ranges and other barriers to dispersal. The regionally endemic faunas of tetrapods in Australia, South America and Africa are obvious, as are the deep roots of presumably geographically determined clades among birds and mammals (e.g. Xenarthra, Afrotheria and Laurasiatheria). Yet there is little evidence that the break-up of continents through the past 200 Myr has had a major effect on global tetrapod familial biodiversity (Benton 1985b; Sahney *et al.* 2010): major increases in continental numbers in the Jurassic and Cretaceous (figure 1) are not marked by major jumps in diversity, and the slight decline in continental numbers through the past 100 Myr has corresponded to the most dramatic diversity increase. This might seem contrary, and yet alternative continental arrangements in the past, including Pangaea, exhibited regional-scale endemism: there were mountain chains and other barriers to dispersal, as well as major climate and habitat belts (e.g. Upchurch *et al.* 2002). Further, continental break-up was not simple—there were as many major continents as today, for example, in the Late Jurassic, and slightly more at the end of the

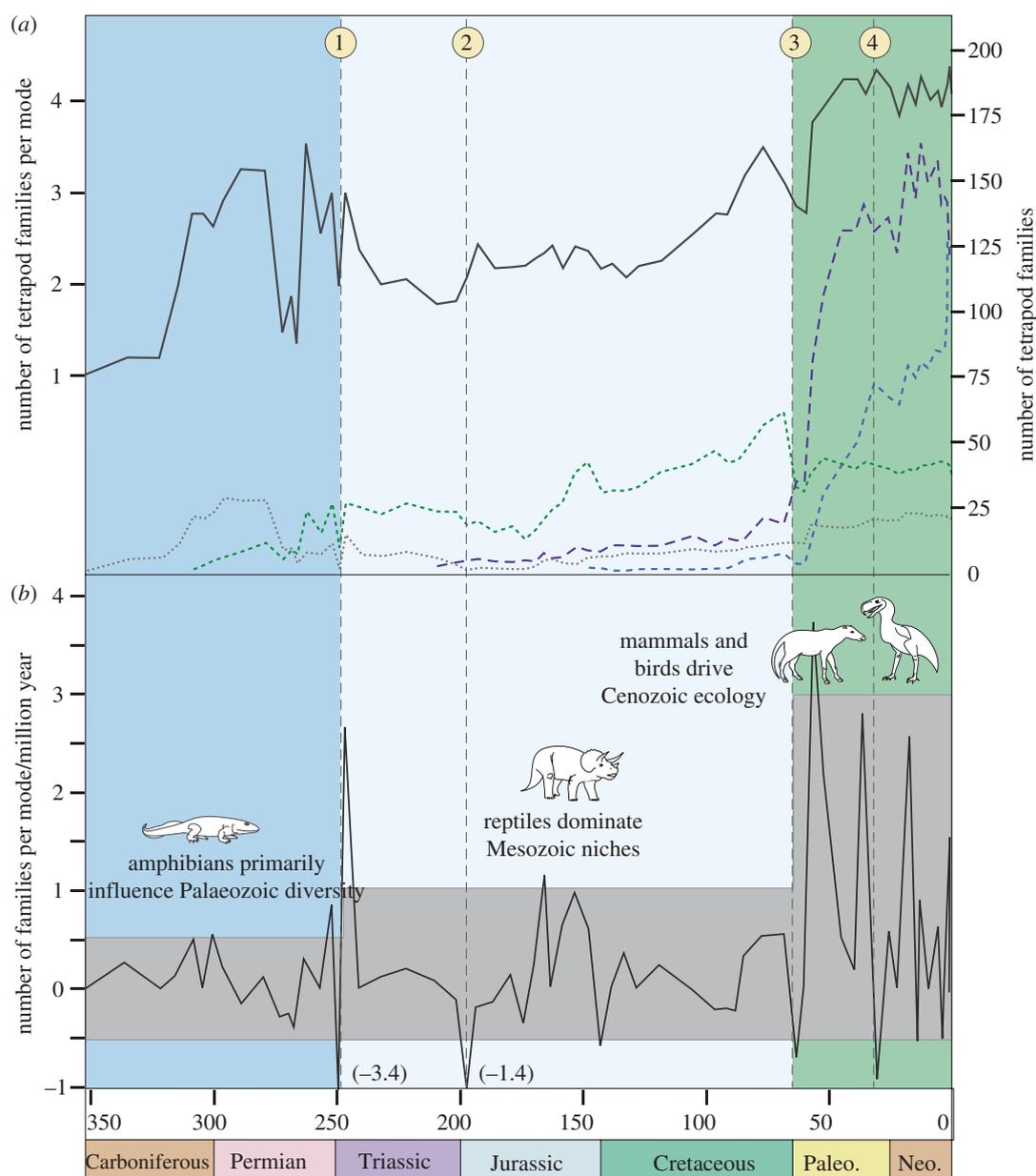


Figure 2. Ecological role of tetrapods through time. (a) The average number of tetrapod families occupying a single mode and the global taxonomic diversity of the different tetrapod classes. Black curve, families per mode; dashed dark blue curve, mammals; dashed light blue curve, birds; dotted green curve, reptiles; dotted grey curve, amphibians. (b) Rate of expansion/contraction of mode utilization and the general 'normal' range of this rate (shaded area) with the exception of troughs and peaks at major extinction events. Mass extinctions are labelled as (1) end-Permian mass extinction, (2) end-Triassic mass extinction, (3) end-Cretaceous mass extinction, and (4) Grande Coupure. Neo, Neogene; Paleo, Paleogene. Based on Sahney *et al.* (2010).

Cretaceous thanks to higher sea levels. At those times, for example, Europe and North America were divided into two or more blocks of land, respectively, by major seaways that have since disappeared.

As for ecospace use and specialization, Sahney *et al.* (2010) found that global diversity of tetrapod families rose in line with ecospace use, and that these patterns closely match the dominant classes of tetrapods (amphibians in the Palaeozoic, reptiles in the Mesozoic and birds and mammals in the Cenozoic; figure 2). These groups have driven ecological diversity by expansion and contraction of occupied ecospace rather than by direct competition within existing ecospace and each group has used ecospace at a greater rate than their predecessors. This was determined by

assigning the 1034 families of fossil tetrapods to major sectors of ecospace, defined by broad-scale body size (three divisions), diet (16 classes) and habitat (six), giving a total of 288 divisions of ecospace. Of these only 207 are feasible (excluding modes such as 'mollusc-eating in a desert ecospace', for example) and at most only 75 have been occupied. The closest correlations throughout were between global familial diversity and number of ecospace divisions occupied (Spearman's $\rho = 0.97$), much higher than had been expected. Thus, tetrapod families may have become more specialized by dividing diets or habitats, but most of their global expansion was mediated by occupation of new ecospace (Sahney *et al.* 2010). This is not a simple consequence of few families per mode,

where addition of a new family would demand a new mode—with 1034 families in 75 modes, the mean occupancy is 13.8 families per mode. This result confirms the earlier finding (Benton 1996*a,b*) that most new tetrapod bauplans (= families) arose by entering new ecospace or new geographical areas, and not by outcompeting previous incumbents. Note that these studies have been carried out at the family level and, assuming that the numbers of species reported per family have also increased through time (Flessa & Jablonski 1985), there may well have been considerable specialization and competition within families.

These studies confirm that continent-scale endemism and specialization have been less significant determinants of the current high species richness of tetrapods than the conquest of new ecospace through time. The fact that only 36 per cent (75 out of 207) feasible sectors of ecospace have been occupied by terrestrial tetrapods, compared with 78 per cent (92 out of 118) by animals in the sea (Bambach *et al.* 2007), might suggest that terrestrial tetrapods have not come close to saturation of ecospace. This could then be interpreted as good evidence for the previously postulated suggestion that there is still further to go in expansion of terrestrial species richness, but that marine species richness has reached an equilibrium (Benton 2001). However, this large difference in scores can only be seen as suggestive, because the sectors of ecospace defined by Sahney *et al.* (2010) are not comparable with each other in potential and scale, nor are they comparable with the arbitrarily bounded marine ecospace cells used by Bambach *et al.* (2007).

The diversification of angiosperms in the past 130 Myr may, on the other hand, represent a case of adaptation and specialization. Angiosperms today are remarkably diverse, consisting of over 250 000 species (Magallón & Castillo 2009), and that diversity is usually explained (Crepet & Niklas 2009) by either: (i) vegetative attributes, such as diverse organ morphology and anatomy, rapid growth rates coupled with high hydraulic conductivity and capacity for extensive phenotypic plasticity; (ii) reproductive features, including floral display and morphology, pollination syndromes employing non-destructive biotic as well as abiotic vectors, double fertilization, endosperm formation and rapid embryogenesis, and the benefits of broadcasting seeds by means of edible fruits; and (iii) multiple features of the unique structural or genetic and chemical attributes of the clade. Studies so far suggest that the correlates of angiosperm diversification are manifold, and that insect pollination, for example, is not an adequate driver on its own (Crepet & Niklas 2009). Combined fossil and molecular phylogenetic data show repeated bursts of diversification, associated with the evolutionary introduction of novel functional traits throughout the history of the flowering plants.

5. THE DETERMINANTS OF TERRESTRIAL TETRAPOD BIODIVERSITY

(a) *The Red Queen and the Court Jester*

Biologists and palaeobiologists have long debated the major determinants of species richness, whether

primarily biotic, primarily abiotic or a mixture of both (e.g. Darwin 1859; Stanley 1979; Wilson 1992; Benton 1995, 2009; Magurran 2004). The biotic and abiotic division is reflected in two previously described worldviews of macroevolution, the Red Queen and the Court Jester, that could be mutually exclusive or could operate at different scales.

Van Valen (1973) proposed the Red Queen model as a resolution of the paradox that organisms are currently well adapted to their environments, but are also under continuing natural selection and improvement of adaptation, both essential components of Darwinian evolution. The Red Queen model is that the environment within which an organism finds itself is constantly changing, and so the organism has to adapt constantly to remain sufficiently adapted. This model emerged from Van Valen's (1973) observation of a Law of Constant Extinction, as he called it: his assumption that species are equally likely to go extinct at any time, irrespective of their former duration—in other words, a long-lived species is on average no better at surviving the next increment of time than a newly evolved species. The Law of Constant Extinction has been criticized as ill-founded (McCune 1981; Pearson 1992), but the Red Queen still rules as a model of a broadly biotic driver of large-scale evolution, dependent on all aspects of the environment, but primarily the biotic components such as competition and predation.

Barnosky (2000) proposed the Court Jester model of evolution, which focused on the impacts of changes in the physical environment on large-scale evolution. The Court Jester was a capricious joker, licensed to behave unpredictably and irreverently and to take no account of a person's antecedents or position in society. In the Court Jester world of evolution, sudden fluctuations in climate, topography, continental position or ocean chemistry, and unpredictable crises such as volcanic eruptions, meteorite impacts or deep-sea methane releases reset evolution in minor to fundamental ways.

In contrasting these two models, the Red Queen allows for adaptive advantage and a feeding up of the day-to-day actions and consequences of evolution within populations to longer time scales—a broadly adapted or versatile (Vermeij 1973) group, perhaps with a high reproductive rate, is more likely to survive and flourish in the long term than a group of species with narrow habitat tolerances or narrow dietary requirements. The Court Jester allows none of this, and organisms that flourish during normal times might suffer as much as others when the crisis hits. During mass extinctions, the loss of a species is more a matter of bad luck than bad genes (Raup 1992). Blindness to selective advantage is likely a consequence of all kinds of rare, sudden changes in the physical environment because these are spaced far apart, and so no organism can adapt to survive through them. Large-scale evolution is most probably a mix of the Red Queen and the Court Jester (Barnosky 2000; Benton 2009, 2010), with the Red Queen dominating at local scales and over short time spans and the Court Jester on larger geographical and temporal scales (Jablonski 2008).

(b) Distinguishing abiotic and biotic factors

In distinguishing whether modern biodiversity has resulted from scaling up of community-level interactions, as in the Red Queen model, or whether these are constantly overwhelmed by larger scale drivers and events, as in the Court Jester model, requires careful compilation of data, with a view to sampling errors (Smith 2007), and careful consideration of the meaning of correlations or the apparent explanatory aspects of a model. There is an extensive literature on these themes (recent reviews include Stanley 2007; Erwin 2008, 2009; Jablonski 2008; Benton 2009), and no consensus has emerged about whether any sector of life is more or less susceptible to diversity change as a result of changes in climate, topography, continental position, food supply or other factors, nor of the proportional role in influencing future biodiversity, as viewed from any point in time, of former crises such as mass extinctions.

Climate and temperature change have already been noted as key drivers of biodiversity: there appears to be close tracking between temperature and biodiversity on the global scale for both marine and terrestrial organisms (Mayhew *et al.* 2008), where generic and familial richness were relatively low during warm 'greenhouse' phases of Earth history, coinciding with high origination and extinction rates. A key component of energy/temperature models for biodiversity is the latitudinal diversity gradient (LDG), reflected in the greater diversity of life in the tropics than in temperate or polar regions, both on land and in the sea. The LDG has existed throughout the past 500 Myr and may have been a major contributor to the generation and retention of high biodiversity (Jablonski *et al.* 2006; Mittelbach *et al.* 2007; Valentine *et al.* 2008).

It can be hard to distinguish biotic and abiotic drivers in evolution. For example, species diversities of marine plankton (e.g. Wei & Kennett 1986; Schmidt *et al.* 2004) and mammals (Barnosky 2000; Blois & Hadly 2009) through the past 50–100 Myr appear to have been heavily influenced by climate change. Other analysts (Alroy *et al.* 2000) found no correlations between diversity signals and measures of external environmental change for Cenozoic mammals, an unexpected result that may have arisen from mismatching of datasets, in which a global-scale temperature change record was compared with the diversity of mammals in North America alone (Barnosky 2000) or from exploring the effects in time bins of 1 Myr, perhaps too short to detect a climate signal (Blois & Hadly 2009). Whichever view is correct, even in well-documented fossil examples such as these, it may be hard to achieve a clear-cut result.

An alternative approach is to focus on living organisms alone and to identify the factors that correlate with high species richness. In a study of a broad cross-section of living mammals, Isaac *et al.* (2005) found that biotic factors such as body size, diet, colonizing ability or ecological specialization appeared to have little effect on diversity, whereas abundance and *r*-selected life-history characteristics (short gestation period, large litter size and short interbirth intervals) sometimes correlated with high species richness. In a similar study of birds, Phillimore *et al.* (2006) found

that high annual dispersal was the strongest predictor of high rates of diversification, followed by feeding generalization. Among certain birds, Seddon *et al.* (2008) found a strong correlation of sexually selected traits such as level of plumage dichromatism and complexity of song structure with species richness. Characteristics such as these, which ensure success through natural selection or sexual selection, should be reflected in higher species richness. A question then might be whether such correlates of high species richness are very widely distributed, and if not, why not. Other selective pressures presumably maintain the broad diversity of ecological characteristics, even if many do not link to increasing biodiversity.

The relative roles in maintaining and generating biodiversity of ecological characteristics and external drivers have rarely been assessed. Defining the limits of what can be measured, and then demonstrating convincingly the relative importance of different factors, would be statistically challenging. Techniques so far used in the ecological literature have focused on determining the ecological factors that correlate best with species-poor and species-rich clades. Establishing the relative influence of each factor is difficult, and then seeking to describe the nature of external drivers, and the way in which they influence diversity, is probably even harder.

One approach has been to seek to identify the simplest model comprising several factors that explains most of any diversity pattern. This approach at least allows combinations of different factors that may in any case interact and goes beyond a claim that diversity depends simply on breeding rate, sexually selected traits or regional climatic cycles. The weakness of this approach is that the range of models selected for comparison may not be exhaustive, and the data may be flawed if they span an interval of time.

An example is the study by Marx & Uhen (2010) of models for the diversification of whales (figure 3). They considered climate change (as measured by oxygen isotopes), diatom species diversity and nanoplankton species diversity, and factored in a measure of rock availability (number of marine rock formations) to control for sampling. They ran each putative external control separately and in various combinations, and used the secondary Akaike Information Criterion (AIC_c) to assess which model best explained the cetacean genus-level diversity curve through the past 25 Myr. The number of species of whales follows the combined diatom diversity/climate change model, and so the control came from changing temperatures and changes in food supply through simple food chains, such as diatoms → krill → baleen whales and diatoms → fish/squid → toothed whales. Marx & Uhen (2010) do not claim that they have identified the exact and complete explanation for modern whale biodiversity, but they show a way to manage the data, account for sampling and assess single and multiple drivers for goodness of fit.

(c) External factors and modern biodiversity: events

Four broad-scale events, out of many possible examples, are presented here, each of which appears

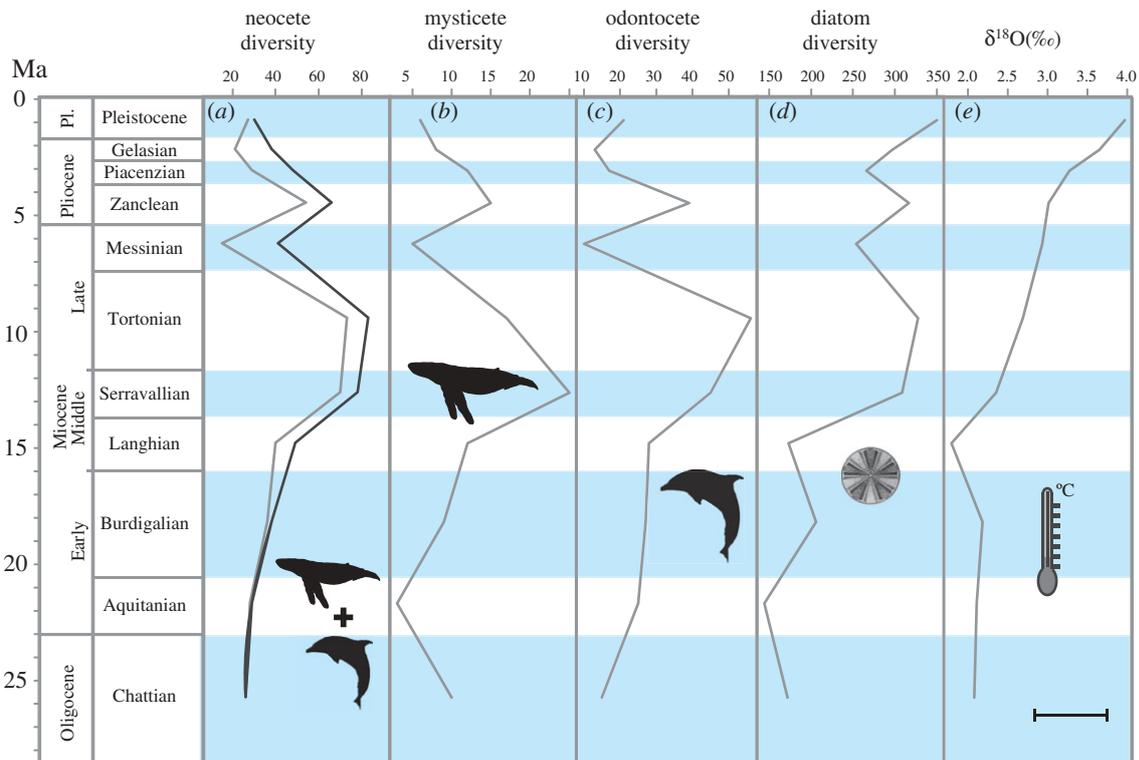


Figure 3. Comparison of (a) neocete, (b) mysticete and (c) odontocete (d) diversity with diatom diversity and (e) global $\delta^{18}\text{O}$ values through the past 30 Myr. Cetacean diversity is shown as sampled-in-bin data as downloaded from the Paleobiology Database (grey) and as a ranged-through estimate (black). Error for the $\delta^{18}\text{O}$ curve is shown as mean standard error (s.e.) multiplied by 100. Based on Marx & Uhen (2010), with permission from the American Association for the Advancement of Science.

to have had a substantial effect on expanding the diversity of tetrapods: (i) the collapse of the coal forests and rise of amniotes; (ii) the end-Permian mass extinction and subsequent recovery; (iii) the diversification of dinosaurs; and (iv) the Cretaceous Terrestrial Revolution (KTR). These examples illustrate aspects of the data and methods available for exploring clade expansions, phylogenetic aspects, changes in diversity (species or generic richness), changes in disparity (morphological variance) and changes in abundance (at the community level).

The *Late Carboniferous aridification event*, 305 Ma, is the change-over from damp, equatorial habitats of the Carboniferous coal forests with a lush clubmoss vegetation, giant insects and millipedes, and aquatic amphibians, to arid habitats of the latest Carboniferous and Early Permian, with xeric plants such as ferns, smaller arthropods and the first amniotes ('reptiles'). The vegetational shift was triggered by an abrupt change in climates in the equatorial belt, where most continents lay (Sahney *et al.* in press). A major glaciation in southern polar regions triggered cycles of sea-level change, and an intense glacial episode drained water from the seas, lowered sea levels and caused massive aridification. Coal forests fragmented, and they were further stressed when there was a reversal to greenhouse conditions 5–6 Myr later. Recent study (Sahney *et al.* in press) has shown that this event was marked by a peak in tetrapod extinction rate, a collapse of alpha diversity and regional-scale endemism for the first time. Rainforest collapse was accompanied by acquisition of new

feeding strategies (new kinds of predators, the first herbivorous tetrapods), consistent with tetrapod adaptation to the effects of habitat fragmentation and resource restriction. Effects on amphibians were particularly devastating, while amniotes fared much better, being ecologically adapted to the drier conditions that followed. Coal forest fragmentation profoundly influenced the ecology and evolution of terrestrial faunas and vegetation, climate and tetrapod trophic webs were evidently intimately connected.

Tetrapod communities continued to evolve, with rapid turnover of species and genera, and continuing establishment of high levels of complexity, through the Permian. Terminal Permian terrestrial faunas were the most complex yet seen, with typically 20 species ranging from aquatic fish-eating temnospondyls, through small insect and plant eaters, to the 1 tonne herbivorous dinocephalians and pareiasaurs, and their predators, the lion-sized sabre-toothed gorgonopsians (Benton *et al.* 2004). These complex communities, documented in the classic red bed successions of South Africa, Russia and China, apparently disappeared rapidly during the *end-Permian mass extinction*, 252 Ma, coincident with massive volcanic eruptions in Siberia which led to sustained and substantial global warming, acid rain and stagnation of the oceans (Benton 2003; Benton & Twitchett 2004). The Early Triassic, 252–248 Ma, was a time of continuing pulses of global warming, and life in the sea and on land did not recover; indeed there was a 'coal gap' on land and a 'coral gap' in the oceans, both spanning some 15 Myr, during which

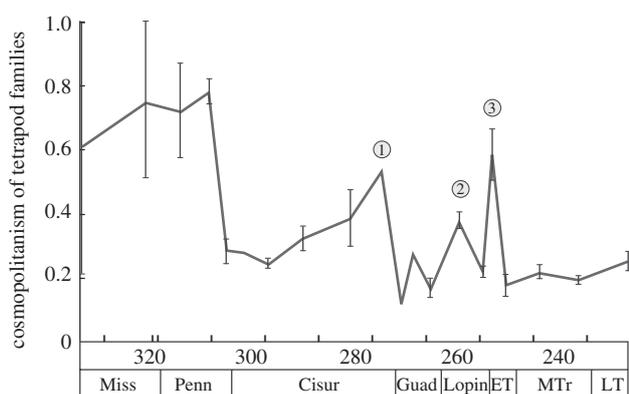


Figure 4. Cosmopolitanism of tetrapods through the Carboniferous, Permian and Triassic. Cosmopolitanism (C) is measured as mean alpha diversity (\bar{T}) divided by global diversity (Tt), according to the formula $C = \bar{T}/Tt$. The bars are total ranges of values for each time bin. Note the overall decline of cosmopolitanism through this time interval, perhaps related to increasing taxonomic and ecological diversity of tetrapods, but also note the coupled rises and falls in cosmopolitanism following major extinction events, especially Olson's extinction (1), the end-Guadalupian extinction (2), and the end-Permian extinction (3). Cisur, Cisuralian; ET, Early Triassic; Guad, Guadalupian; Lopin, Lopingian; LT, Late Triassic; Miss, Mississippian; MTr, Middle Triassic; Penn, Pennsylvanian. Based on Sahney & Benton (2008).

forests and coral reefs were absent (Benton & Twitchett 2004). Tetrapod faunas in the earliest Triassic were imbalanced, being dominated by *Lystrosaurus* in some places (sometimes approximately 90% of individuals), and by modest-sized aquatic tetrapods in others (Benton 1983). It took until the Late Triassic, perhaps 235–230 Ma, before terrestrial communities showed the range of ecological types that existed before the mass extinction, including large herbivores and carnivores (Benton *et al.* 2004). Alpha diversity remained relatively constant through this time, despite the mass extinction (Sahney & Benton 2008), but much of the rapid initial recovery seems to have been composed of 'disaster taxa', *r*-selected forms that survive in grim conditions and breed fast, but do not form the foundations of long-lasting ecosystems. Cosmopolitanism (figure 4) peaked immediately following the crisis, but then plummeted and remained surprisingly low during the Early and Middle Triassic. The interplay between cosmopolitanism (worldwide occurrence of species and genera) and endemism (regional-scale species and genus ranges) is a feature of crises in the history of life (e.g. Hallam & Wignall 1997), where global biotas apparently become massively simplified following environmental crises, but then have a propensity to diversify to endemic mode in times of less stress.

The *diversification of dinosaurs* in the Mid- to Late Triassic marked the first major step in the origin of modern terrestrial ecosystems, with the rise of classic Mesozoic groups such as dinosaurs and pterosaurs, but also the first turtles, lepidosaurs, crocodylomorphs and mammals (figure 5). The older view was that dinosaurs radiated in the Late Triassic, some 230 Ma, by competitively prevailing over their precursors, the crocodile-like crurotarsans and others,

because of superior adaptations, such as upright gait, bipedalism, superior feeding adaptations or endothermy. An earlier study (Benton 1983) suggested that the radiation of the dinosaurs was actually a two-stage event (figure 5*a,b*), with each step occurring after the extinction of crurotarsans and other taxa: first the dominant plant eaters died out 216.5 Ma, and the plant-eating sauropodomorph dinosaurs increased rapidly in diversity and abundance (figure 5*c*), and then further crurotarsans disappeared at the end of the Triassic, 199.6 Ma, and theropod dinosaurs and armoured ornithischians began to radiate. Recent phylogenetic and morphological studies (Brusatte *et al.* 2008, 2010*a,b*) show further that dinosaurs remained at moderate diversity and low disparity, and indeed at lower disparity than the crurotarsans they supposedly outcompeted, during the 17 Myr between the events (figure 5*b*). This is not decisive evidence, but it rejects a prediction of a broad-scale competition model that the successful group ought to show rises in diversity and morphological variance (disparity) as it occupies niches vacated by the less successful group it is supposedly replacing. The apparently coupled rises in diversity and disparity of crurotarsans and dinosaurs in the Late Triassic, and the continuing broad morphological range of crurotarsans (figure 5*d*) suggest that there was no insistent competition driving other groups to extinction but rather that the dinosaurs occupied new ecospace opportunistically, after it had been vacated. New evidence (Nesbitt *et al.* 2010) suggests that dinosaurian sister groups originated much earlier, perhaps by 240 Ma, and that the Dinosauromorpha (= dinosaurs and their closest stem-group relatives) existed at low diversity and low abundance for some 10–15 Myr before diversifying and rising in abundance at community level worldwide (Brusatte *et al.* 2010*b*).

The fourth event to be considered is the KTR (Lloyd *et al.* 2008), the upheaval in terrestrial floras caused by the replacement of ferns and gymnosperms by angiosperms (Dilcher 2000; Magallón & Castillo 2009). The explosive radiation of angiosperms from 125 to 80 Ma, during which they rose from 0 to 80 per cent of floral compositions, provided opportunities for pollinating insects, leaf-eating flies, as well as butterflies and moths, all of which diversified rapidly (Grimaldi 1999), and marked the point at which life on land became more diverse than life in the sea (Vermeij & Grosberg *in press*). Among vertebrates, squamates (lizards and snakes), crocodylians, and basal groups of placental mammals and modern birds all underwent major diversifications, although the timing of appearance of modern bird orders and modern mammal orders remains controversial. At the same time, dinosaur evolution was marked by the appearance of spectacular new forms, making Late Cretaceous faunas quite different from those that preceded. Qualitatively then, dinosaurs appear to have been part of the KTR, but only the radiation of two groups, Neoceratopsia and Euhadrosauria, count as statistically significant diversification shifts (Lloyd *et al.* 2008). Thus, dinosaurs apparently continued to diversify at pre-KTR rates and they plodded about experiencing the new scents and

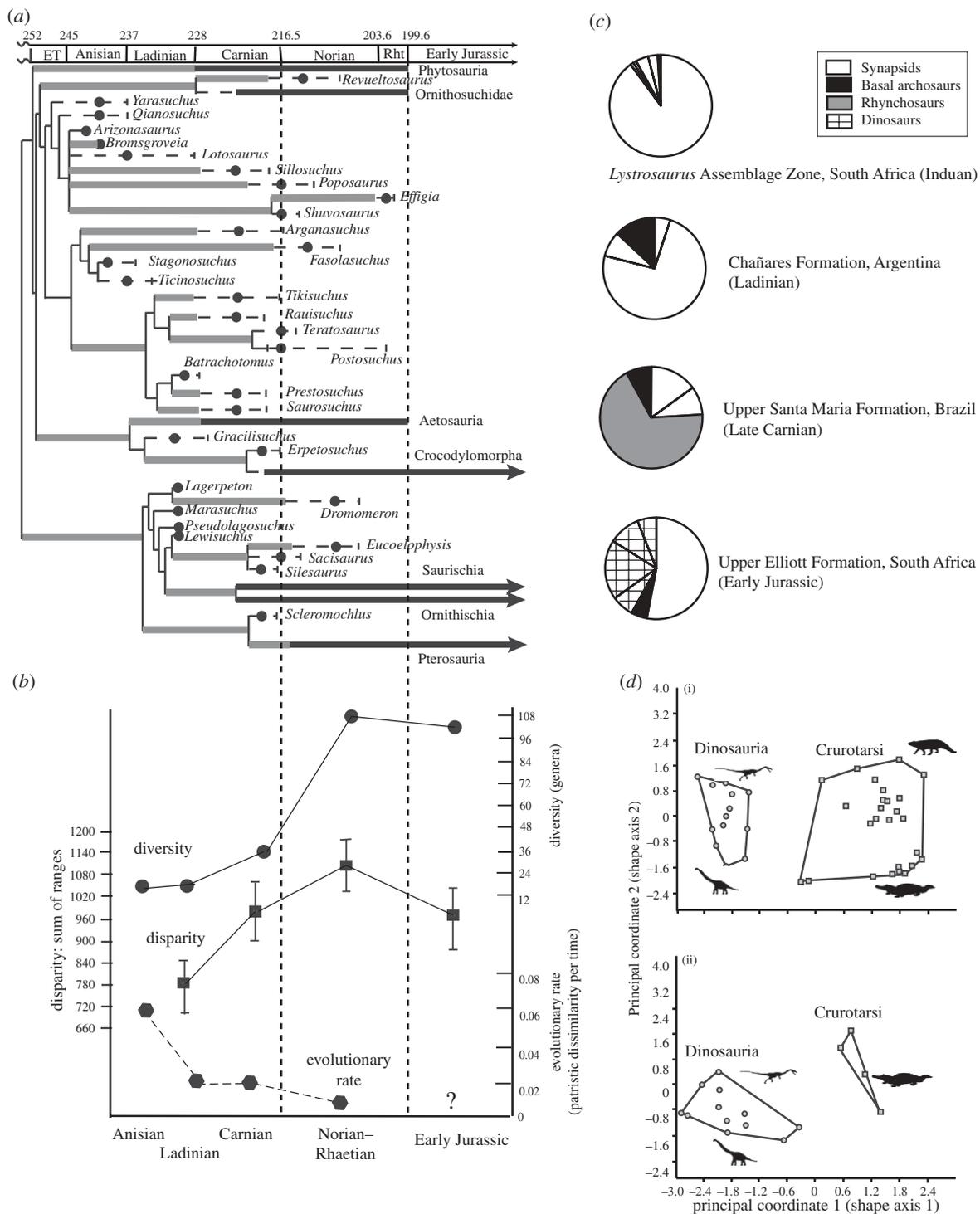


Figure 5. Phylogenetic study of dinosaurian origins, showing the interplay of diversity and disparity increase in an expanding clade, associated with changes in relative abundance. The phylogeny (a) shows much branching of major lineages in the Middle Triassic (Anisian, Ladinian) and Late Triassic (Carnian, Norian, Rhaetian). Vertical dashed lines mark the Carnian–Norian turnover, when many key tetrapods, especially herbivores, died out, and the end-Triassic mass extinction, and these extend through the comparison of key measures of evolutionary change among these archosaurs (b), namely diversity (counts of genera, phylogenetically corrected), disparity (sum of ranges) and morphological evolutionary rates (patristic dissimilarity per branch/time). Error bars on disparity values represent 95% bootstrap confidence intervals, and non-overlapping error bars indicate a significant difference between two time-bin comparisons. Question mark indicates uncertain rate measure for Early Jurassic archosaurs. Two patterns are shown: the major increase in archosaur disparity (Carnian) occurred before the main increase in diversity (Norian), and archosaur morphological rates were highest early in the Triassic, before the disparity and diversity spikes. (c) Relative abundance of four key groups in individual well-sampled faunas shows major changes in proportions through the Triassic, as synapsids are replaced by basal archosaurs and ultimately dinosaurs, as the dominant elements. (d) Morphospace plots for archosaurs in the (i) Late Triassic (Carnian–Norian) and (ii) Early Jurassic (Hettangian–Toarcian), showing the first two principal coordinates (shape axes). Crurotarsans had a larger morphospace than dinosaurs in the Late Triassic, but these roles were reversed in the Early Jurassic after crurotarsan morphospace occupation crashed. ET, Early Triassic; Rht, Rhaetian. Data modified from (a) Brusatte *et al.* (2010a), (b) Brusatte *et al.* (in press), (c) Benton (1983), and (d) Brusatte *et al.* (2010b).

colours of the flowers, but most of them presumably did not profit substantially from them.

Finally, the Cretaceous–Paleogene (KPg) mass extinction 65 Ma is often marked as the final step in the evolution of modern ecosystems. However, for life on land the KTR was the key event, and the disappearance of the dinosaurs did not lead to wholesale collapse of ecosystems, but allowed mammals and birds, and other modern groups, to continue their diversifications, which had already begun before the event (Dyke & Van Tuinen 2004; Bininda-Emonds *et al.* 2007).

6. CONCLUSION

Analytical approaches to large phylogenies of living (Alfaro *et al.* 2009) and extinct (e.g. Lloyd *et al.* 2008) vertebrate groups have shown that most biodiversity is accounted for by a few clades showing higher-than-normal rates of diversification. The four case studies mentioned in this paper suggest that major new clades (e.g. amniotes, dinosaurs and angiosperms) respond to the evolution of remarkable new adaptations, which may not emerge overnight but take some time to evolve. Further, the external conditions have to change, with the emergence of empty ecospace, whether this empty ecospace has been cleared by an extinction event, or has not previously been occupied and is available to any organisms with the right adaptations. Interdisciplinary work that crosses the boundary from the modern biota to the past, combining fossils with comparative phylogenetic methods, is essential if we are to disentangle the most substantial questions about evolution, not least the relative roles of biotic and physical factors (Benton 2009) and the nature and likely outcomes of the current biodiversity extinction threat (Davies *et al.* 2008).

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