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Palaeobiogeography and the Ordovician and Mesozoic–Cenozoic biotic radiations

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Abstract: Curves of taxonomic diversity through geological time consistently show major evolutionary radiations during the Ordovician Period and from the mid-Mesozoic to the present day. Both intervals were characterized by marked biotic provincialism, reflecting episodes of major continental break-up and global tectonism, and their later histories featured steep global climatic gradients. The Ordovician radiation can be recognized at a wide spectrum of taxonomic levels from species to class, and the biogeographical patterns associated with the radiation of individual clades reflect a complex combination of plate distribution, tectonic activity, sedimentary environment, sea-level rise and, ultimately, glaciation. The true scale of the mid-Mesozoic–Cenozoic biotic radiation is currently a topic of intense debate but there is no doubt that it affected plants and animals in both the marine and terrestrial realms. The role of land bridges and ocean gateways in controlling the formation of biodiversity patterns has been a persistent theme in Mesozoic–Cenozoic biogeography, and a complex set of Neogene tectonic events probably aided the development of both latitudinal and longitudinal provinces during the Cenozoic. The present volume highlights some of the successes across a spectrum of approaches to unravelling the Ordovician and Mesozoic–Cenozoic radiations within the context of palaeobiogeography.

> '... geologic history is the pacemaker of biologic diversity' (Schopf 1979, p.454)

Post-Cambrian curves of taxonomic diversity through geological time consistently show a major evolutionary radiation during the Ordovician Period, and a second, larger one from the mid-Mesozoic to the present day. Between these steep upward slopes the Silurian–Jurassic interval usually appears as a distinct plateau punctuated by mass extinctions and their recovery intervals (e.g. Sepkoski 1981, 1993, 1997; Niklas *et al.* 1985; Padian & Clemens 1985; Benton 1995, 2000, 2001; Conway Morris 1998). Although this general pattern seems to be robust, it is becoming increasingly clear that it may include biases introduced by both the quality of the fossil record and the sampling procedures employed. For example, Miller & Foote (1996) have shown how the use of more rigorous taxonomic and diversity metrics can alter the perception of the Ordovician radiation, and Alroy (2000; Alroy *et al.* 2001), using a technique that standardizes sampling to absolute time intervals, has cast doubt on the scale of the mid-Cretaceous–Recent one. Potential biases on a variety of spatial and temporal scales have been further highlighted by Smith (2000; Smith *et al.* 2001) and McCormick & Owen (2001).

Nevertheless, the general trends are still prominent across a wide range of faunal and floral groups (Benton 1999), and have been the focus of intense scientific debate. The Ordovician radiation reflects the rise of Sepkoski's (1981) Palaeozoic Evolutionary Fauna and the mid-Mesozoic to Recent one, at least in the marine realm, the full development of the Modern Evolutionary Fauna. Sheehan (2001*b*) has recently summarized the gross ecological changes associated with the rise of these Evolutionary Faunas. The mid-Mesozoic to Recent was also the time of spectacular radiation of major terrestrial groups such as the flowering plants (angiosperms), birds and mammals (Hallam 1994). Why have there been these two great pulses in the diversification of life? Are there any obvious similarities or differences between them that may provide clues as to what triggers biological diversification on a global scale? As both these intervals were characterized by marked biotic provincialism, reflecting episodes of major continental break-up and global tectonism, it has become particularly important to ask whether there may be a key link between palaeogeographical configuration and biotic radiations. This is especially so as the latter parts of both intervals featured steep global climatic gradients.

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In comparing the Vendian–Ordovician and Mesozoic marine diversifications, Erwin *et al.* (1987) highlighted the much lower number of taxonomically high level (order and above) originations in the later event. They attributed this to differences in the occupation of 'adaptive space' with the early Phanerozoic radiation reflecting the greater opportunity for the appearance of the novel morphologies used to diagnose higher level taxa. In the present volume, the accent is very much on diversification at lower taxonomic levels, and the Late Cenozoic–Recent interval in particular is characterized by the proliferation of species-rich clades (Crame 2001).

It is also clear that to make headway in the study of taxonomic diversity patterns, on either temporal or spatial scales, we have to be consistent in what is being measured and there is some confusion in terminology within the literature. Much of the rigorous definition of diversity measurement has been in relation to terrestrial environments. There are two basic categories of measurement: inventory diversity (*sensu* Whittaker 1977), that records the numbers of taxa per unit area (and may be weighted to take account of proportional abundances), and differentiation diversity that provides a measure of difference (or similarity) between levels of inventory diversity. Alpha (or within-habitat) diversity is the most common form of inventory diversity and records the number of taxa per area of homogenous habitat and so reflects species packing within a community. Beta (or between-habitat) diversity is the category of differentiation diversity that measures the variation in taxonomic composition between areas of alpha diversity (Magurran 1988). Whittaker (1977) used the terms 'gamma diversity' to reflect the number of taxa in an island or distinctive landscape and 'epsilon diversity' for the inventory diversity of a large biogeographic region. Using that terminological scheme, the term 'delta diversity' is used for the variation between areas of gamma diversity within an area of epsilon diversity (Magurran 1988). However, in palaeontological analyses of marine faunas, many workers (e.g. Sepkoski 1988 and references therein), have adopted a simpler scheme whereby gamma diversity is viewed as a measure of differentiation diversity at a larger spatial scale than beta, measuring taxonomic differentiation between geographical regions and thus a reflection of provinciality or endemicity.

Miller (e.g. 1997*a*, *b*, 1998, 2000) has consistently emphasized that it is essential to dissect the global diversity curves in order for them to be understood. If the patterns can be comprehended, then the processes that drive them can be addressed. Even understanding the partitioning of diversity change through the areal scales of its measurement is a significant challenge. Thus for the Ordovician, for example, the alpha diversities of a major clade may remain constant, in contrast to the global diversity change (e.g. Westrop & Adrain 1998; Adrain *et al.* 2000), increasing alpha diversities may be set against decreasing beta trends within a palaeogeographical region (e.g. Miller & Mao 1998) and measured increases in alpha and beta diversities may be insufficient to account for the scale of global biodiversity increase (Sepkoski 1988). To what extent therefore do gamma and delta diversity levels (i.e. provinciality) hold the key to understanding global diversity trends through time?

Biogeography and biodiversity change

Connections between biodiversity change and provinciality are well demonstrated in the literature (see Jablonski *et al.* 1985 for review). Boucot (1975, see also 1983) suggested that provincialism may be an important factor underlying diversity change in the Silurian and Devonian. Valentine (1973) and Schopf (1979) established a strong link between changes in endemism and the dramatic rise in taxa produced by the mid-Mesozoic–Cenozoic radiation. Valentine *et al.* (1978) attributed high marine species diversity in the Cenozoic to the marked rise in provinciality and simulated Phanerozoic marine diversity in terms of changing provincial patterns. They suggested as much as a five-fold increase in provinciality since the Late Palaeozoic, although this figure has been disputed (Bambach 1990). More recently, Smith (1988, fig. 8; see also Brenchley & Harper 1998, fig. 8.13) combined the schematic representation of the major continental plates and global marine familial diversity curve of Valentine & Moores (1970, 1972) to highlight the correspondence between diversity peaks and plate dispersal. Such a compilation would now be equally appropriate using Sepkoski's (1997) familial or genus-level curves.

Miller (1997*c*) drew attention to work by Jablonski (1987) on Cretaceous molluscs and other studies that show that geographical ranges were strongly correlated with stratigraphical durations, but these ranges were established very early in the histories of individual species. Miller showed a general increase in the longevity of Ordovician genera as well as an overall range expansion and suggested that by analogy with the Cretaceous mollusc data, the

Ordovician genera may have become more species-rich. Geographical range is also important in terms of differential survival during extinction events. Geographically widespread clades have a much higher probability of survival, as shown for example by Westrop (1991) for the latest Cambrian, Owen & Robertson (1995) and Sheehan *et al.* (1996) for the end-Ordovician and Jablonski (1986) for the end-Cretaceous extinction event.

Ordovician biogeography and biodiversity

In the introductory paper to the volume arising from the 1982 International Ordovician Symposium, Jaanusson (1984) highlighted three reasons why he considered the Ordovician to be 'so special': (i) extensive development of epicontinental seas, (ii) marked changes in the composition of skeleton-bearing faunas consequent on the appearance and diversification of major taxonomic groups, and (iii) pronounced biogeographical differentiation. The second of these has become the focus of considerable international attention in recent years, partially formalized under IGCP Project 410, 'The Great Ordovician Biodiversification Event' (see Webby *et al.* 1999). It is pertinent to assess the influence of the first and especially the third of Jaanusson's 'special' attributes of the Ordovician to that diversification.

The Ordovician radiation can be recognized at a wide spectrum of taxonomic levels from species to class. The major component of the diversification took place in clades that typified the Palaeozoic Fauna (Sepkoski 1981, 1995) both in groups that had a Cambrian history such as rhynchonelliformean ('articulate') brachiopods (e.g. Bassett *et al.* 2002) and vertebrates (e.g. Smith *et al.* 2002), and in groups that first appeared during the Period (e.g. bryozoans and some major echinoderm clades; Sepkoski 1995). Some elements of the Modern Fauna such as bivalve molluscs (e.g. Cope 2002) also radiated at this time as did clades within groups that characterize the Cambrian Fauna, in particular groups of 'inarticulated' brachiopods (Sepkoski 1995) and a substantial set of trilobite families constituting the so-called 'Whiterock Fauna' (Adrain *et al.* 1998).

Sepkoski (1988) argued that changes in alpha and beta diversities accounted for only about half of the increase in global genus-level diversity during the Ordovician and that much of the remaining increase was probably not attributable to changes reflecting provinciality or endemicity. Instead, he attributed much of the remaining diversity increase to 'hidden sources of beta diversity' such as the appearance and/or expansion of communities that were low in overall extent but rich in species, such as organic reefs, hardground communities, bryozoan thickets and crinoid gardens. This view was endorsed by Zhuravlev (2001) in a thoughtful comparison of the Cambrian and Ordovician radiations. Such communities reflect changes at a fairly high level in the ecological architecture of marine life (see Droser *et al.* 1997, 2000) but the lack of correlation between significant biodiversity change and palaeobiogeography during the Ordovician is surprising. Sepkoski considered that there was no change in the number of provinces from the Cambrian into the early Ordovician and that the degree of provinciality decreased during late Ordovician. However, his assessment did not take account of major palaeogeographical changes such as the fragmentation of the Gondwanan margin (Dalziel 1997; van Staal *et al.* 1998; Cocks 2001; McNamara *et al.* 2001, Bassett *et al.* 2002). Coupled with this, the plate tectonic dynamism of the Ordovician may have been crucial in generating hitherto unsuspected provinciality.

Miller (1997*b*) compared genus-level diversity curves from six palaeocontinents using both raw and rarefied (see Miller & Foote 1996) data. The extreme ends of the spectrum of palaeocontinental variation in diversity patterns were those of Laurentia and South China which both lay at low latitudes. Moreover, in terms of the partitioning of overall diversity change, Miller & Mao (1998) showed that whilst mean alpha diversities showed an overall slight increase from the Tremadoc to the Ashgill in both regions, there was a fall in mean beta diversity and this was much more marked in South China than in Laurentia. In itself, the fall in beta diversity shown in both regions set against rising alpha diversity is surprising, and was provisionally explained as reflecting the increasing environmental and geographical range of many genera throughout the Ordovician (see also Miller 1997*c*), possibly along with an increase in the species richness of these genera. This would reduce the beta diversity through time as measured at genus level as individual genera became more widespread causing a decrease in the distinction between assemblages at this taxonomic level. Miller & Mao (1998, p. 306) also argued that the increase in beta diversity recognized by Sepkoski (1988), largely on the basis of Laurentian data, represented a net change from the Cambrian to the Ordovician and was not in direct contradiction of the decreasing trend that they recorded through the Ordovician.

In a clever reversal of Sepkoski's (1988) question about the partitioning of diversity during the Ordovician biodiversification, Brenchley *et al.* (2001) recently addressed the issue of where the diversity was lost during the two phases of extinction at the end of that Period. They argued that the considerable reduction in alpha diversity had a significant impact on both beta diversity and provinciality. Given the speed of the extinctions, it was the major loss of endemic taxa that significantly reduced the number of provinces, rather than plate movements.

Emerging patterns

The biogeographical patterns associated with the radiation of individual clades during the Early Palaeozoic are only just starting to come to light and reflect a complex combination of plate distribution, tectonic activity, sedimentary environment, sea-level rise and, ultimately, climatic gradient. Smith *et al.* (2002) argue that the latest common ancestor of all 'ostracoderms' and jawed vertebrates was Laurentian but thereafter the early Palaeozoic diversification of the vertebrates reflected complex biogeographical patterns of dispersal, vicariance and tectonic convergence. In contrast, an 'out of Gondwana' radiation for many invertebrate groups is a recurring theme. However, the picture is complex as that continent extended from the south pole to north of the equator (Cocks 2001; Dalziel 1997) and encompassed both siliciclastic- and (at lower latitudes) carbonate-dominated shelf environments. Thus while Bassett *et al.* (2002) have shown that the mid-Cambrian precursors of the typical Palaeozoic Fauna rhynchonelliformean ('articulate') brachiopod communities first appeared in shallow-water carbonate settings in north and east Gondwana, the early Ordovician radiation of the bivalve molluscs took place in the shallow-water siliciclastic shelves of Gondwana (Babin 1995; Cope 2002) at all latitudes. Only late in the Ordovician did bivalves become established on the low latitude carbonate shelves of Laurentia and Baltica. Preliminary analysis suggests that the rise to dominance of the Whiterock Fauna of trilobite families (Adrain *et al.* 1998) took place a little earlier on the fairly high latitude siliciclastic margins of Gondwana (Owen & McCormick in press) than on low latitude Laurentia. A cladistic analysis by Turvey (2002) of one of the groups belonging to the Whiterock Fauna, the Reedocalymeninae (one of the archetypical Gondwanan groups), points to a series of biogeographical events affecting large areas of that plate during the early Ordovician.

The nature of the depositional environment clearly played a significant role in the diversification of clades during the Ordovician. Miller's (1997*b*) preliminary analysis of diversity curves from six palaeocontinents identified differences in the scale and timing of changes both in terms of total diversity and that of individual major clades representing all three Evolutionary Faunas. These differences were linked to the amount and timing of siliciclastic input, including the effects of uplift caused by orogeny and volcanism (see also Miller & Mao 1995, 1998), and therefore emphasize the importance of plate tectonic activity to the promotion of biodiversity change. Miller (1997*b*) suggested that the spread of siliciclastic sediment after the Taconic Orogeny triggered the flourishing of bivalves in Laurentia following their earlier radiation in siliciclastic sedimentary environments in Gondwana.

The Taconic Orogeny and the resultant increase in weathering of siliceous rocks in the late Ordovician may also have been responsible for the profound change in climate leading to the Hirnantian glaciation (Kump *et al.* 1999). This very short-lived glaciation during what was essentially a greenhouse world was the proximal cause of the complex series of events that produced the end-Ordovician mass extinctions (see reviews in Brenchley *et al.* 2001; Sheehan 2001*a*). The climatic decline (see Armstrong & Coe 1997; Kump *et al.* 1999) that led up to it may also have had some effect on biodiversity. Cope (2002) recognized an increase in bivalve endemicity as climatic gradients steepened during the late Ordovician. An analysis of conodont biofacies by Armstrong & Owen (2002) suggests that diversity fell in low latitude Laurentia coincident with the onset of ocean cooling in the early Ashgill, whereas on Avalonia the decline took place a little later when that microcontinent drifted northwards into tropical latitudes.

Plate tectonic activity clearly played a significant role in controlling biodiversity change during the Ordovician. On a local scale, but with possible wider consequence, Botting (2002) has provided a possible mechanism for diversification as a result of repeated volcanic activity whereby ash falls produce overturn of the stratified watermass. This overturn could cause blooms in the plankton and benthos and the generation of localized, temporary benthic 'islands' within the otherwise dysaerobic shelf which were the sites of high speciation rates. On a much larger scale, Bassett *et al.* (2002) link the early and mid-Ordovician spread and diversification of the rhynchonelliformean brachiopods typical of the Palaeozoic Evolutionary Fauna to a combination of global sea-level rise and fragmentation of the Gondwanan margin. Harper & MacNiocaill (2002) reach a similar conclusion and also demonstrate the importance of intra-oceanic sites in the development, divergence and survival of taxa.

Mesozoic–Cenozoic biogeography and biodiversity

The true scale of the mid-Mesozoic–Cenozoic biotic radiation is currently a topic of intense debate. Whereas a new compilation of generic rather than familial data suggests that it may not have been as marked as Sepkoski (1981, 1993) originally indicated (Alroy *et al.* 2001), a detailed taxonomic investigation of just one small part of the Late Cenozoic tropics suggests that it was considerably greater (Jackson & Johnson 2000, 2001). One thing that is beyond dispute about this radiation is that it affected plants and animals in both the marine and terrestrial realms. The spectacular radiation of the angiosperms, mammals and certain reptile groups (such as the snakes) on land is matched by that of the planktonic foraminifera, neogastropods, heteroconch bivalves, cheilostome bryozoans, decapod crustaceans and teleost fish in shallow seas (Hallam 1994). This co-radiation of such disparate taxa is often taken as strong evidence for a real evolutionary phenomenon (Signor 1990; Benton 1999). This was also the time when some of the largest (in terms of species richness) clades evolved. For example, some of the massive eudicot angiosperm clades have between 20 000 and 25 000 extant taxa, and both the neogastropod subfamily Coninae and the heteroconch bivalve family Veneridae have approximately 500 living species each (Crame 2001).

Some geographical constraints on the radiation

It now seems almost certain that the extant planktonic formainifera evolved from benthonic ancestors in Tethyan (i.e. tropical/subtropical) facies in the Early Jurassic (Toarcian) (Hart *et al.* 2002). A biostratigraphic analysis has indicated some expansion within the North Atlantic–European region in both the Bajoican–Bathonian and Aptian, but it was not until the latest Albian that a near-global distribution was achieved. There is a strong link here between phases of diversification as revealed by stratigraphic analysis, continental fragmentation, and the expansion of shelf seas. Interestingly enough, it would appear that latitudinal gradients in taxonomic diversity had been established by the Campanian–Maastrichtian (Huber 1988), and these have persisted through to the present day (Bé 1977).

The role of land bridges and ocean gateways in controlling the formation of biodiversity patterns has been a persistent theme in Mesozoic–Cenozoic biogeography (e.g. Hallam 1981). Have they, perhaps, created bottlenecks in the distribution of biotas that are large enough to be discernible in the fossil record? This forms the central theme in the papers by Aberhan (2002) and Cantrill & Poole (2002), and is discussed in a more general way by Crame & Rosen (2002).

In his study of Early Jurassic bivalve biodiversity, Aberhan (2002) has been particularly concerned with the role of the Hispanic Corridor, a putative narrow seaway across central Pangaea linking the eastern Pacific with western Tethys. Was there a preferential extinction of endemic South American taxa across the Pliensbachian–Toarcian boundary due to a sudden influx of cosmopolitan Tethyan forms, or was a renewed rise in late Toarcian–Aalenian species diversity in NW Europe attributable to an influx from Andean South America in the other direction? Using a comprehensive species-level database, Aberhan is able to demonstrate that, in fact, in both regions early Pliensbachian to Aalenian immigration rates through the corridor remained low. In comparison, the within-region origination of new species played a much more important role in the recovery of post-extinction faunas. The relative importance of immigration versus in situ radiation in the generation of large-scale biodiversity patterns throughout the fossil record is still a controversial issue (e.g. Vermeij 1993).

By the time of radiation of crown group angiosperms (flowering plants) in the Early Cretaceous, the major southern hemisphere continents had largely separated from one another and Antarctica was rapidly becoming isolated. It has long been thought that, by Aptian–Albian times, the only major terrestrial connection between western Gondwana (South America and Africa) and eastern Gondwana (India, Antarctica and Australasia) was the volcanic archipelago of the Antarctic Peninsula region. However, in a new analysis of southern, high latitude Cretaceous floras, Cantrill & Poole (2002) cast some doubt on this theory. Whereas the earliest known angiosperms from the Antarctic Peninsula are Early Albian in age, there are angiospermous pollen grains from Australia that are Early Aptian. Quite what the alternative immigration route may have been is uncertain, but Cantrill & Poole point to the proven existence of Turonian terrestrial sediments on the Kerguelen Plateau (Shipboard Scientific Party 2000) and Late Cretaceous dinosaur finds that link Madagascar, South America and India (Sampson *et al.* 1998). It is clear that the earliest Antarctic angiosperms occupied areas of disturbance and were understorey colonizers. Their major pulse of radiation in the Turonian was coincident with the acme of Cretaceous global warmth.

The relative importance of tectonics and climate

In a wide-ranging review, Crame & Rosen (2002) take as their starting point the major extant biodiversity patterns, and then work back through time. They address the reason for there being discrete tropical high-diversity foci in both the marine and terrestrial realms, with steep latitudinal diversity gradients leading away from them. Whatever the ultimate cause of tropical high diversity *per se*, it is clear that a critical sequence of Early Miocene (*c.* 20 Ma) tectonic events fractured a once homogeneous tropical biota into several distinct centres; the Indo-West Pacific (IWP) and the Atlantic–Caribbean–East Pacific (ACEP) are the most important of these in the marine realm. Together with the physical isolation of Antarctica, these same plate tectonic movements contributed significantly to the global reorganization of major ocean current systems and Cenozoic cooling. This in turn led to a marked increase in provincialism and biotic differentiation on a regional scale. Even so, something else may have been involved in the development of the steepest diversity gradients during the Late Cenozoic. Rates of origination may have been driven by an increase in Milankovitch cyclicity over the last 10–15 Ma and there may be some crucial links here between the geographical range of an organism and its propensity to allopatric speciation. However, the issue is a complex one and is yet to be fully resolved. The more frequent nature of climatic change in high latitude regions might mean that ecological isolates are less likely to persist or, alternatively, the more constant environment of the tropics could mean that ranges can be more easily split by slight temperature shifts (Chown & Gaston 2000; Dynesius & Jansson 2000).

The importance of databases in biodiversity studies

With the widespread availability of relational database and GIS software, it is now much easier to build a comprehensive biodiversity database on a desktop computer. However, in a methodological review of just how such a database should be constructed, Markwick & Lupia (2002) emphasize the need to take into account variations in scale, inconsistency in the data, and potential errors (inaccuracy). Scale is a particularly critical issue, for, whereas 'large-scale' to a biologist refers to a large area or duration, a 'large-scale map' is usually one of great detail but small area. As this can lead to confusion when using a GIS for biological or palaeobiological purposes, Markwick & Lupia advocate the adoption of two terms from landscape ecology. The first of these is 'grain', which is the minimum resolution or scale of an observation, and the second is 'extent', which is the total amount of space or time observed. Thus, a large-scale map is fine-grained but of limited extent. It is the heteorogeneities in scale (grain) in the fossil record that are potentially the major causes of problems in the construction of palaeontological databases.

Markwick (2002) goes on to show how a comprehensive database of Recent North American, European, South African and Australian non-avian tetrapods can be used to tackle some fundamental problems in the study of latitudinal diversity gradients. Pooling taxa from all these regions it can be shown that there is a strong, monotonic relationship with both absolute latitude and mean annual temperature (MAT); the highest diversities are clearly associated with the highest MATs and lowest latitudes. Nevertheless, it is clear that there are strong differences in the form of the latitudinal gradients between the ectotherms (reptiles and amphibians) and endotherms (mammals). Whereas the former show comparatively simple, steep gradients, reflecting their dependence on the immediate environment, the latter show a more complex pattern, based on an indirect dependence on the environment (through various feeding strategies). Markwick concludes that patterns of terrestrial species diversity are not simply a function of the amount of available energy, but how that energy is procured. As the proportion of ectotherms to endotherms shows a strong linear relationship to temperature, it can be used to retrodict MATs in the fossil record. An example is given for the Middle Eocene Messel fauna of Germany that shows close agreement with other palaeotemperature estimates.

Synopsis

The Ordovician Period witnessed the rise of Palaeozoic Evolutionary Fauna, comprising elements such as the rhynchonelliformean brachiopods, bryozoans, echinoderms, primitive vertebrates and many families of trilobites. The Mesozoic–Cenozoic radiation includes the rise of such groups as the flowering plants, birds, mammals, marine molluscs, teleost fish and decapod crustaceans. Full substantiation of these patterns remains a major task and will involve a massive coordinated effort in taxonomic palaeontology (Kerr 2001; Jackson & Johnson 2001).

If these two steep increases in taxonomic diversity are not artefacts of the fossil record, a challenge of equal dimensions is to establish what has been driving them. One of the simplest explanations to consider is that they represent two intervals in which there were fundamental increases in within-habitat species richness (i.e. alpha diversity). In a seminal study of Phanerozoic marine communities, Bambach (1977) suggested that there may well have been periodic expansion of available ecospace through the development of new or increased resource supplies (see also Bambach 1993). Rosenzweig (1995, p. 306), for example, has suggested that the Ordovician was the first time in Earth history that muddy bottoms were extensively colonized by marine organisms. Precisely why this may have been so is uncertain, but dissolved oxygen levels may have increased until they reached some sort of threshold and allowed widespread colonization. Similarly, Bambach (1977, 1993) linked the late Mesozoic–Cenozoic rise of both terrestrial and marine organisms to the blossoming of the angiosperms. Here was an abundant source of both new food and habitat space for a wide variety of organisms. In addition, Bambach (1977) pointed to both the late Ordovician and Cenozoic glaciations as a possible source of oceanic nutrient recycling. Changes in thermohaline circulation brought about by climate change could have led to substantial oceanic mixing, which in turn affected the food resources of shelf seas. In both instances though, the global diversity increase was well underway and in the case of the Ordovician may have already reached its plateau by the time such processes began.

In contrast to attempts to seek a limited number of global controls on biodiversity change, Miller (e.g. 2000) has argued that it is more realistic to try to understand the regional patterns and the processes likely to have driven them. None the less, some form of periodic increase in resource supply could lead to a rapid expansion in the numbers of taxa within some habitats and regions. Once an adaptive threshold has been breached it may be possible to pack more taxa into a locality or region within a comparatively short space of time. Patterns of alpha and gamma diversity could be expected to increase periodically rather than continuously. The concept of non-hierarchical, non-additive levels of ecological change introduced by Droser *et al.* (1997, see also 2000) promises to be a useful way of addressing step changes in biodiversity and/or the utilization of ecospace, the two not necessarily changing in tandem.

However, it is clear that something other than a sheer rise in numbers must be involved. There is abundant evidence that differentiation of biotas has occurred and on a variety of geographical scales. For example, in their review of the Cenozoic diversification event, Crame & Rosen (2002) indicate that a complex set of Neogene tectonic events probably aided the development of both latitudinal and longitudinal provinces. There are indications to suggest that between-habitat diversity (i.e. beta diversity) increases in tandem with alpha diversity but as well as this, between-community and between-province diversity must be increasing too. Similarly Harper & MacNiocaill (2002) argue that the break-up of the Gondwanan margin promoted a rise in between-province diversity amongst the rhynchonelliformean brachiopods and this break-up, together with sea-level rise that promoted migration over the continental shelves, also produced a rise in alpha diversities as established communities were augmented by immigrants. Subsequent to this, beta diversities rose as communities became increasingly developed in deeper water environments. This pattern of nearshore innovation and offshore expansion of communities at the expense of the existing community types during the Ordovician was documented by Jablonski *et al.* (1983; see also Bassett *et al.* 2002). However, Westrop & Adrain (1998) and Adrain *et al.* (2000) have also demonstrated that for the trilobites, alpha diversities remained remarkably constant across the shelf throughout the Period and so, whilst their diversity relative to the rapidly diversifying clades might have declined, they were not simply being displaced by them and 'pushed' into deeper water refuges. Jablonski & Bottjer (1991) also showed that the origins of post-Palaeozoic benthonic orders were largely in nearshore environments, but Jacobs & Lindberg (1998) have argued that this only applied prior to the Turonian after which offshore bottom waters became more widely oxic and amenable to originations. That change also marked the demise of dysoxic faunas, the expansion of deep burrowers into offshore environments and the offshore expansion of bryozoan diversity.

Coupled with any purely tectonic definition of provinces, it is clear that biotic differentiation was assisted by the steepened latitudinal temperature gradients that became established towards the end of each of these intervals. The studies by Cope (2002), Armstrong & Owen (2002), Harper & MacNiocall (2002), Crame & Rosen (2002), Cantrill & Poole (2002) and Markwick (2002) all emphasize that climate change has assisted range shifts into higher or lower latitudes. The differentiation of biotas along environmental gradients undoubtedly enhanced the process of global biodiversification during both the Ordovician and Mesozoic–Cenozoic. In the case of the latter, there are still areas of the Earth's surface, such as the very highest and lowest latitudes, about which very little is known, which must bias both the observed patterns and their interpretations. Tropical systems are particularly poorly known for many intervals in time, and one can only guess at how much 'hidden diversity' is locked up within them (Sepkoski 1988; Jackson & Johnson 2001).

Clearly, there is still a great deal to learn about the precise mechanisms underpinning the major biotic radiations and it is unlikely that they will be attributable to a single, simple cause. The palaeobiologist is uniquely placed to study the interaction of physical and biological forces that have shaped the major patterns of life on Earth and understanding the palaeobiogeographical context is crucial. It encompasses a multitude of controls on the distribution and ecology of organisms, from the location of continents, islands and oceans to the global climate. Importantly, especially from a geological perspective, it represents a series of very dynamic systems. The present volume reflects some of the wide spectrum of approaches to studying biodiversity change on a variety of spatial and temporal scales, from taxonomy to the analysis of large databases, and emphasizes their links to the components of these systems in the two most sustained episodes of overall biotic radiation in the Phanerozoic.

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