

The latitudinal biodiversity gradient through deep time

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Today, biodiversity decreases from equatorial to polar regions. This is a fundamental pattern governing the distribution of extant organisms, the understanding of which is critical to predicting climatically driven biodiversity loss. However, its causes remain unresolved. The fossil record offers a unique perspective on the evolution of this latitudinal biodiversity gradient (LBG), providing a dynamic system in which to explore spatiotemporal diversity fluctuations. Deep-time studies indicate that a tropical peak and poleward decline in species diversity has not been a persistent pattern throughout the Phanerozoic, but is restricted to intervals of the Palaeozoic and the past 30 million years. A tropical peak might characterise cold icehouse climatic regimes, whereas warmer greenhouse regimes display temperate diversity peaks or flattened gradients.

The modern-day latitudinal biodiversity gradient

The present-day decrease in biological diversity from equatorial to polar regions (Figure 1) is a pervasive pattern governing the distribution of life on Earth [1,2]. Attempts to explain this LBG have tended to ignore a deep-time perspective. Here, we redress this balance by bringing together data on the past distribution of biodiversity and examine what this reveals about the underlying causes of the LBG.

Before moving to a more palaeontological viewpoint, it is useful to summarise briefly what is known of the present-day LBG. This gradient describes most fauna and flora, in both terrestrial and marine realms, in both hemispheres, and across a range of spatial scales [1–3]. Some clades provide exceptions to this pattern [4,5], including temperate peaks in most salamander and frog families [6], as well as some aquatic birds and mammals [7–9], but contrarian groups are otherwise predominantly limited to aquatic floras and parasitic species [1]. Examples of hemispherical

asymmetry in biodiversity also exist, such as low ant biodiversity in the Northern Hemisphere, which tend to reflect either recent climatic differences, or evolutionary events, such as localised extinctions [10–13]. Most often in these instances, there is heightened overall diversity in one hemisphere, but it is rare that a tropical peak in species diversity exists in one hemisphere but not the other [10–13]. However, these are exceptions to the rule, and the LBG is regarded as the dominant first-order macroecological pattern on Earth today [14].

Understanding the causes and evolution of the LBG is critical to explaining present-day geographical variation in biodiversity and modelling biotic responses to climate change (e.g., [15–18]). Net diversification rates are higher in the tropics than elsewhere [19–23]. However, it is unclear whether this reflects relatively higher origination rates, lower extinction rates, or both (Box 1), and dispersal likely further complicates this picture [14,21,22,24–28]. Despite a long history of study, the causes of the LBG remain unresolved [1,2]. Most hypotheses can be rejected on the grounds of being circular, interlinked, or too specific to explain the ubiquity of the gradient, leaving three broad (although not necessarily mutually exclusive) themes for explaining higher tropical rates of net diversification and the modern-day LBG: (i) climatic (see below); (ii) geographical, pertaining to the greater areal extent of the tropics being able to support more species compared with other regions [29]; and (iii) historical, whereby the tropics have been less perturbed in the past by climatic events (e.g., the Pleistocene glaciations) and, thus, have accumulated species over a longer, uninterrupted time period compared with the extratropical regions [1,3,19,22].

Whereas geographical and historical hypotheses seem unlikely to be able to explain the LBG fully, climate is often regarded as the primary driver [1–3,12,30–34]. Direct, physiological effects result from low seasonality in the tropics, where annual variation in climatic variables is less than elsewhere. This low tropical seasonality potentially results in species with highly restricted environmental tolerances and limited dispersal ability across environmental barriers, leading to population fragmentation and speciation. Indirect climatic factors result from latitudinal variation in insolation, due to the angle of solar radiation, which becomes more oblique at high latitudes. Consequently, the tropics receive a greater concentration

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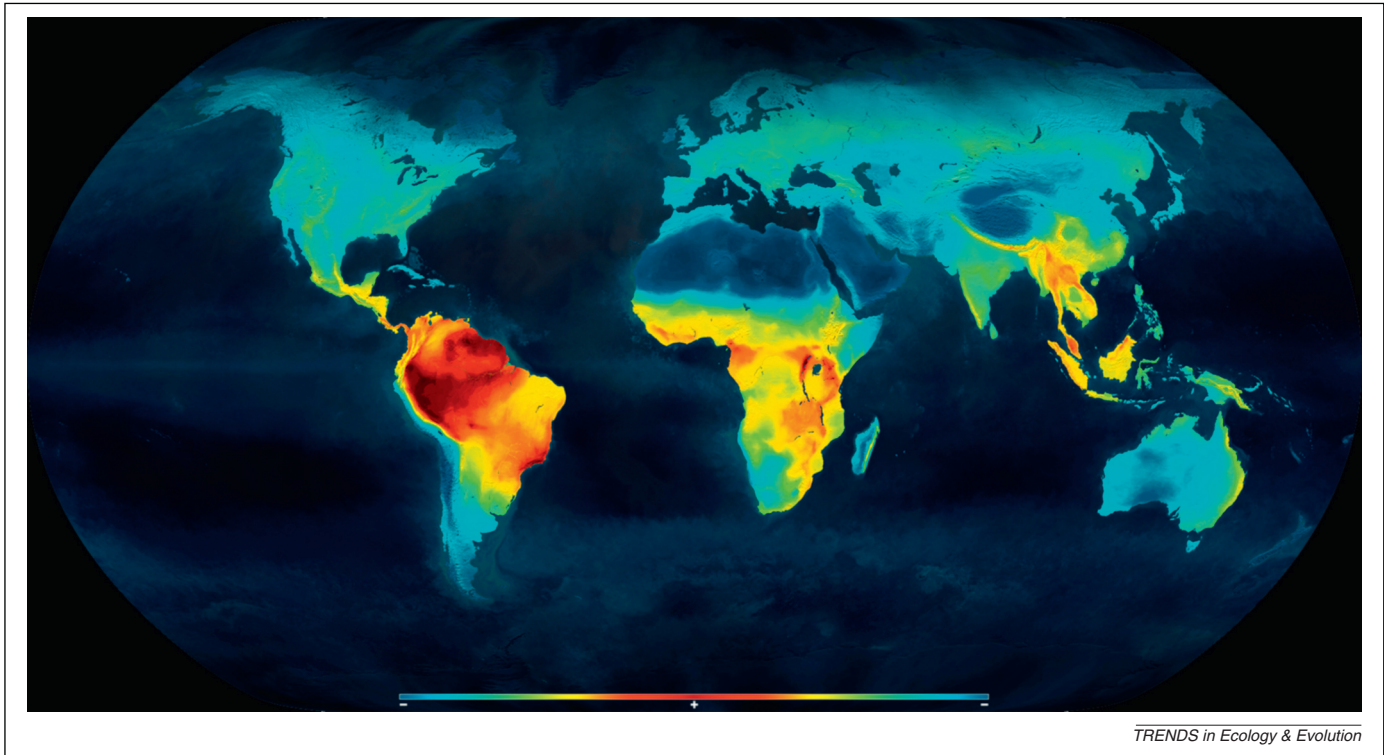


Figure 1. An example of the modern-day latitudinal biodiversity gradient. Distribution of extant terrestrial vertebrate species showing the high concentration of diversity in equatorial regions (closer to the red end of the colour spectrum), declining polewards (closer to the blue end of the colour spectrum) to form the modern-day latitudinal biodiversity gradient. Based on data from [18] and used with permission from Clinton Jenkins.

of solar energy, which promotes increased productivity. This might lead to larger viable population sizes of specialists and higher plant diversity, which in turn would support trophically dependent species, although there are several instances where these factors appear to be decoupled [12]. Seasonality has been regarded by some authors as the most important driver of the LBG [12,35]. However, most studies had difficulty teasing apart the effects of insolation from those of seasonality [3,32].

The fossil record offers an exceptional window onto the causes and evolution of the LBG, including responses to major climatic perturbations and evolutionary events [12,14,36]. Whereas climatic, geographical, and historical factors are broadly static in the present day, these variables fluctuated substantially over time spans of hundreds of millions of years. Furthermore, because the LBG ultimately arises from a complex combination of origination, extinction, and dispersal (Box 1), neontological data alone are not sufficient to understand its evolution: palaeontological data must also be integrated [28]. Whereas invertebrates and microorganisms provide the best fossil records in the oceans [14,21,28], extending back to the earliest records of complex animal life [31], vertebrates dominate our understanding of terrestrial ecosystems, with dinosaurs [36] during the Mesozoic [252–66 million years ago (Ma)] and mammals [37] during the Cenozoic [the past 66 million years (myr)] providing our best opportunities to study the deep-time LBG on land. Increasingly large fossil data sets, including the online open-access *Paleobiology Database* (www.paleodb.org), and new methods for mediating the effects of sampling biases (Box 2), enable the analysis of the evolution of the LBG and the testing of

competing hypotheses for its cause. Here, we review our current understanding of past LBGs, and show how the fossil record is starting to demonstrate that the distribution of biodiversity has a more complex evolutionary history than previously realised, which potentially reflects the history and strength of global climatic gradients.

A persistent pattern in deep time?

Numerous studies of the marine fossil record have detected a deep-time tropical peak and poleward decline in species diversity, suggesting that a ‘modern-type’ LBG has been present since approximately 500 Ma [14,31,38–41]. Although most authors recognise that the LBG only strengthened to form the steep, present-day gradient over the past 30 myr [12,38,39,42], in general it has been perceived that some form of the modern-type LBG has persisted throughout the Phanerozoic (the past 541 myr), even if the gradient was sometimes shallower (e.g., [22,38]). However, the strength of this conclusion is weakened by the methodological limitations of many previous studies (see [12,36,43]). These include: (i) the failure to correct for sampling bias (Box 2), which might produce artefactual peaks or gradients of diversity; (ii) the pooling of taxa from different environments, which are likely to show disparate sampling biases; and (iii) the use of higher-level taxonomic units (e.g., families), which are unsuitable because their content is arbitrary, with some families comprising a single species, whereas others are diverse with broad spatiotemporal ranges. Although genera could also be argued to constitute arbitrary units, palaeontological studies often use genera rather than species as the unit for estimating palaeobiodiversity because of inconsistent taxonomic

Box 1. Tropics as cradles, museums, or both?

Attempts to explain the 'modern-type' LBG as a product of latitudinal variation in evolutionary dynamics have focussed on differences in net diversification rates [22], with the species-rich tropics often regarded as either a 'cradle' (Figure 1A) that generates new species (i.e., origination rates are higher in tropical areas and extinction rates do not vary latitudinally), or a 'museum' (Figure 1B) that preserves existing species over time (i.e., origination rates are constant, but extinction rates are lower in the tropics) [14,22,79,80]. These two putative causal factors are not mutually exclusive. Indeed, many studies have found evidence for higher rates of speciation in the tropics [4,14,21,44,46,81–85], and a few analyses have demonstrated lower tropical rates of extinction [21,23,83]. It seems that the tropics might act as both a cradle and museum for biodiversity [21,22,83]: Jablonski *et al.* [21,28] proposed an 'out of the tropics' model (Figure 1C), in which origination rates are higher in the tropics and taxa disperse polewards without losing their tropical presence [14,86]. However, aspects of all of these models have been questioned: (i) Weir and Schluter [23] recovered elevated rates of origination at higher latitudes in recent birds and mammals; (ii) higher extinction

rates in the tropics were reported for marine invertebrates [24] and through simulations [87]; (iii) polar extinction rates in bivalves have been found to be lower than temperate rates [13]; and (iv) other authors have found no evidence for a correlation between diversification rates and latitude at all for a range of groups (e.g., birds, frogs, Foraminifera, and mammals) and through simulation studies [22,27,88–91].

Consequently, support for the cradle and museum hypotheses, or some combination of them, is controversial. It is possible that the timing of origination and extinction might have some role, including whether such events occurred during icehouse or greenhouse worlds, or at times of steep or shallow climatic gradients. Clade-specific events might also make a difference; for example, post-Eocene ants have suffered greater levels of extinction in the Northern than in the Southern Hemisphere [11]. Currently, most studies that have examined latitudinal patterns in diversification rates have been restricted to the past 30 myr: analyses extending further back in time might help tease apart the relative influence of these different factors.

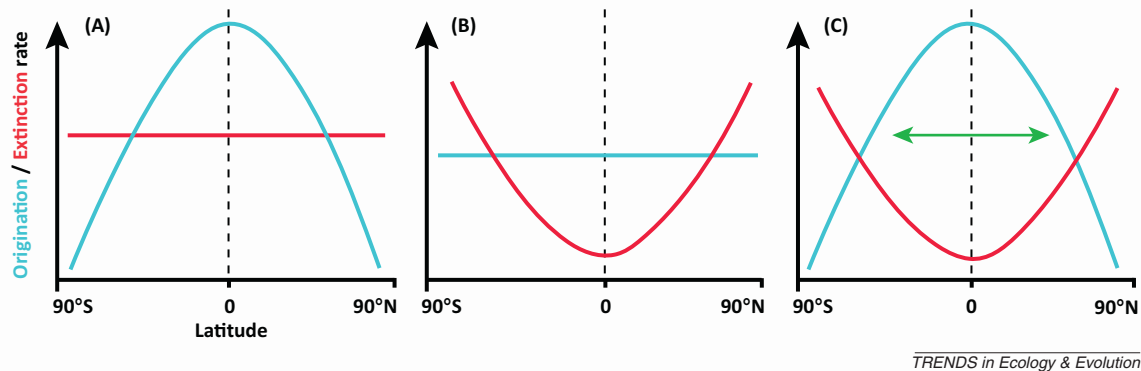


Figure 1. The three patterns proposed to explain declining polewards biodiversity and higher tropical diversification rates: (A) 'Tropics as cradle' model, whereby origination rates are higher in tropical areas and extinction rates do not vary with latitude [14,22,79,87]; (B) 'Tropics as museum' model, whereby origination rates are constant with latitude, but extinction rates are lower in the tropics [14,22,79,87]; (C) 'Out of the tropics' model, whereby origination rates are higher and extinction rates are lower in tropical areas, and species movement is higher from the tropics to the extratropical areas [21,28,87] (all figures based on [87]). Key: blue line, origination rate; red line, extinction rate; broken black line, Equator; green line, species dispersal out of the tropics, without losing their tropical presence.

treatment between different workers [14,36]. Studies that account for some, or all, of these factors suggest a different pattern in LBG evolution. It seems that, at certain times during the Phanerozoic, the gradient has weakened, flattened, or developed a palaeotemperate peak [5,12,14,31–33,38–41,44]. As such, strong evidence for a tropical peak and poleward decline in marine species richness is restricted to intervals of the Palaeozoic (approximately 458–423 Ma and possibly 330–270 Ma), and the past 30 myr [5,12,21,34,39,40,45,46]. Studies of the LBG in the terrestrial fossil record are less numerous, and extend back only to the Permian (299 Ma) [47]. Nevertheless, these studies are starting to reveal an equally complex and nonuniform evolutionary history for the LBG. Below, we focus on four recent sampling-mediated analyses of ancient marine and terrestrial LBGs, covering a wide range of organisms, that are shifting our understanding of how these ecological patterns have changed through time and which factors controlled their shape.

Late Ordovician–Early Silurian (458–423 Ma)

Krug and Patzkowsky [46] examined marine invertebrate diversity before and after the Late Ordovician mass extinction, when approximately 85% of marine species went

extinct during a transition from a greenhouse to an icehouse world. Before this extinction, sampling-mediated biodiversity was only slightly higher in palaeoequatorial Laurentia than in the palaeotemperate continents Baltica and Avalonia (Figure 2), and was lower for some taxonomic groups. This difference was magnified during the glaciation, because diversity declined at higher latitudes (Figure 2). Furthermore, postextinction diversity recovered more rapidly in Laurentia than elsewhere, and Laurentia exhibited higher postextinction origination and immigration rates. These authors [46] suggested that the tropical position of Laurentia might have buffered it from extreme cooling associated with the extinction event. Thus, it appears that a shallow, to flat, Equator-to-Pole diversity gradient occurred during the warmer portion of the Ordovician, and this gradient steepened during the subsequent glaciation.

Late Triassic–Cretaceous (237–66 Ma)

Early assessments of the Mesozoic plant and marine invertebrate fossil records recovered evidence for a modern-type LBG [38,48], whereas more recent work has suggested a palaeotemperate peak [31,49–51]. However, it should be noted that none of these studies took into account the

Box 2. The impact of sampling on reconstructions of past biodiversity

Early attempts to construct diversity curves through time and space were based on literal readings of the fossil record, with numbers of taxa summed for each temporal or spatial bin. However, it has become increasingly evident that such macroevolutionary patterns might be distorted or obscured by anthropogenic and geological sampling biases in the fossil record [92,93]. These biases include spatiotemporal fluctuations in the amount of available sedimentary rock outcrop and facies type (e.g., [92,94]), and variation in human collecting effort (e.g., [40,59,95]). These problems are of particular significance for any attempt to examine past LBGs because the preservation of fossil ecosystems is strongly biased towards intensive sampling of the North American and European fossil records [92], and by fluctuations in land distribution related to crosslatitudinal continental drift [14,36,43].

Three main approaches have been applied to help mediate the impact of sampling biases on reconstructions of past diversity: (i) subsampling; (ii) residuals; and (iii) phylogenetic diversity estimates. Subsampling methods enable comparisons of taxonomic richness between samples of different sizes through the simulation of uniform sample size (i.e., sample-based rarefaction; Figure 1A), or uniform

coverage (the sum of the frequencies of sampled species; i.e., shareholder quorum subsampling [40,59,95]). The residuals method works by producing a linear regression model of the relation between a sampling variable (e.g., numbers of collections) and diversity, after rank-ordering these two data series [92]. This model estimates predicted diversity if sampling entirely controls observed diversity. Predicted diversity is then subtracted from observed diversity to produce a residual that represents diversity that cannot be explained by sampling (Figure 1B). Thus, this residual can be interpreted as a measure of actual past biodiversity [92]. Phylogenetic diversity estimates utilise time-calibrated phylogenies, with ‘ghost’ ranges or lineages reflecting gaps in the fossil record [96,97]. A ghost lineage is estimated from the difference between the inferred origination time of a taxon (based on the age of its oldest-known sister taxon) and its earliest appearance in the fossil record [96] (Figure 1C). The numbers of lineages in each time bin are then summed to produce a diversity curve.

All three methods have their problems [59,93,95–98], but each captures different aspects of biases in sampling of the fossil record. Thus, a pluralistic approach to past diversity reconstruction is recommended [36,97,99].

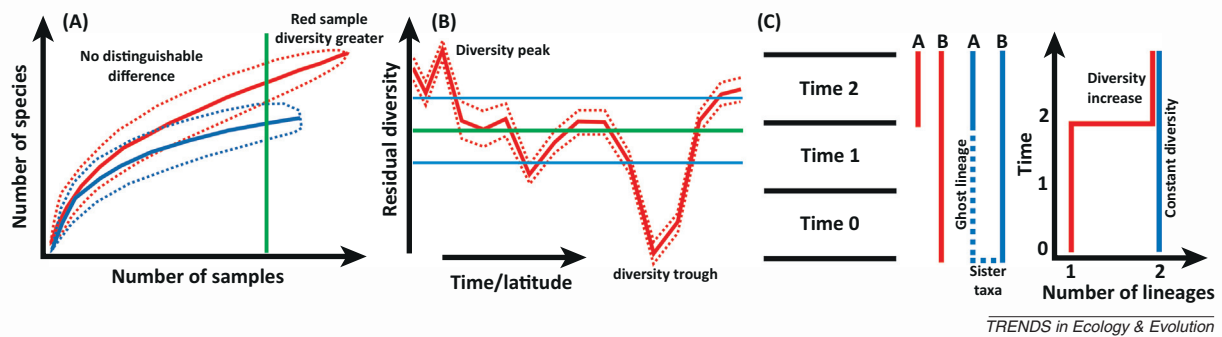


Figure 1. The three main methods for helping mediate the impact of sampling biases on reconstructions of past diversity: (A) subsampling, whereby the taxonomic diversity of two samples of different size (red and blue lines, with broken error margins) are compared through the simulation of uniform sampling size; left of the green line, the two samples cannot be distinguished, whereas to the right of the green line, diversity can be recognised as being higher in the red sample; (B) residuals, whereby predicted diversity (based on a sampling proxy) is subtracted from observed diversity, leaving a residual diversity curve (red line), with error margins (broken red line and blue lines) showing statistically significant deviation from the sampling model (green line); (C) phylogenetic diversity estimates, whereby species A is known only from time 2, whereas species B is known from time 0–2, meaning that diversity increases from one to two at time 2; however, if a sister taxon relation is recognised between the two species, then a ghost lineage for species A can be extended back into time 0, meaning that diversity is two throughout time 0–2.

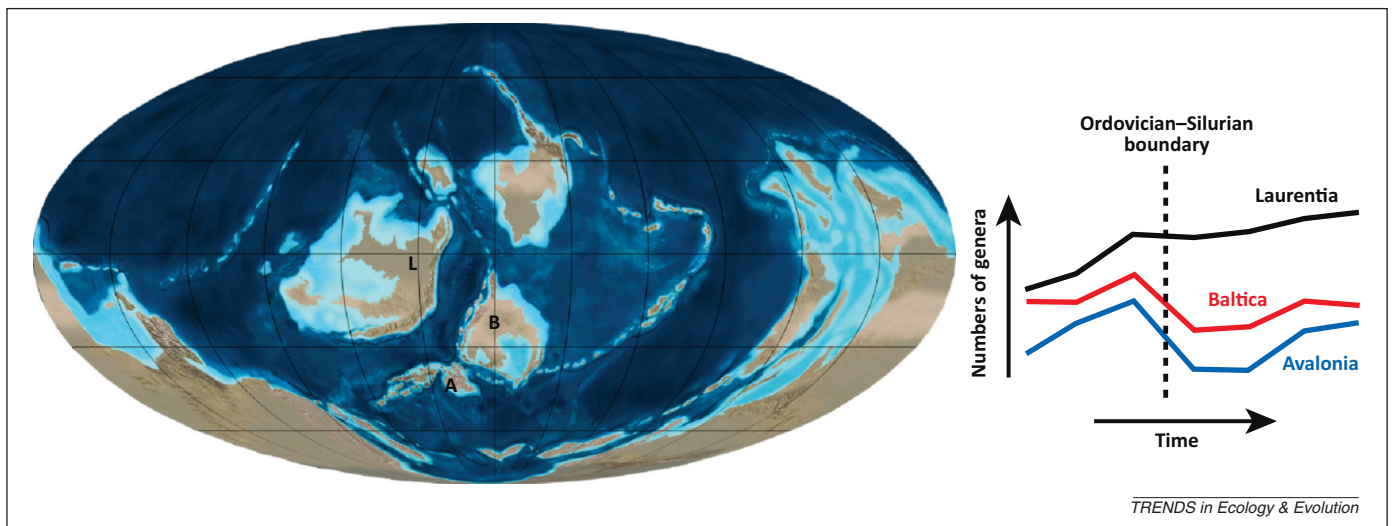


Figure 2. The latitudinal biodiversity gradient across the Ordovician–Silurian. Sampling-mediated diversity of Late Ordovician–Early Silurian invertebrate genera for three palaeocontinents (which existed before the formation of the supercontinent Pangaea, which later fragmented to form the present-day continents), shown on a Late Ordovician palaeogeographic reconstruction and plotted against geological time. These curves show a diversity decline across the ‘icehouse’ Ordovician–Silurian boundary at temperate latitudes [Baltica (B) and Avalonia (A)], but higher diversity and a more rapid recovery in equatorial Laurentia (L). Although Laurentia is more diverse than the other palaeocontinents both before and after the boundary, the magnitude of this difference is increased during the glaciation, as a result of higher origination rates and increased dispersal into tropically buffered Laurentia. Diversity values are relative, rather than absolute. Diversity curves based on [46] and palaeogeographic map used with permission from Ron Blakey.

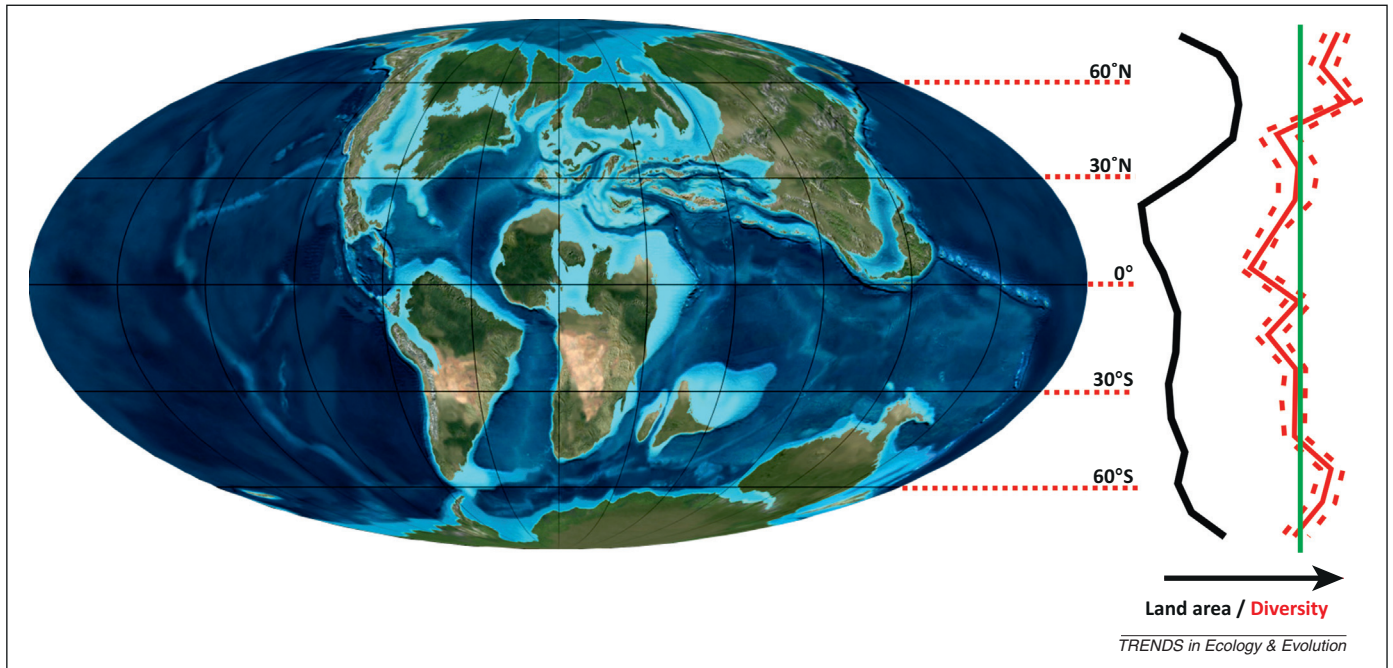


Figure 3. The Late Cretaceous dinosaur latitudinal biodiversity gradient (LBG). Late Cretaceous LBG for dinosaurs plotted against a palaeogeographic map, showing higher sampling-mediated diversity (red line, with broken lines for error margins) in the extratropics during a time of a weakened latitudinal climatic gradient, and a correlation with the distribution of land area (black line). The green line represents the sampling model (Box 2), with deviations either side of this representing peaks or troughs in diversity. Diversity values are relative, rather than absolute. Data redrawn from [36] and palaeogeographic map used with permission from Ron Blakey.

impact of sampling, including the strong bias against fossil plant localities in the palaeotropics [51]. Mannion *et al.* [36] found no evidence for a modern-type LBG in their global, sampling-mediated analyses of Mesozoic terrestrial dinosaurs (including birds). Instead, dinosaur diversity peaked at palaeotemperate latitudes (30–60°), and showed a strong correlation with the distribution of land area (Figure 3). These results are largely consistent across numerous time slices and in both hemispheres, despite crosslatitudinal continental drift during the study interval. Mannion *et al.* [36] proposed a diminished role for climate during the Mesozoic greenhouse interval, characterised by a weakened latitudinal climatic gradient [52–54]. Instead, the Mesozoic terrestrial LBG might have been driven by the distribution of land area. Similar palaeotemperate peaks in biodiversity have also been reported for Cretaceous to early Cenozoic crocodylomorphs (the group including the ancestors of modern crocodiles) [55,56].

Early Palaeocene (64–58 Ma)

Rose *et al.* [37] found no evidence for a modern-type LBG in early Palaeocene North American terrestrial mammals. Instead, they recovered a flat LBG between 35°N and 63°N that, despite falling entirely outside the palaeotropics, differs markedly from the ‘modern-type’ pattern observed in extant mammals for the same region. These authors [37] also found no evidence for a regionally flattened temperature gradient, and suggested an ancient decoupling of mean annual temperature and species distributions. They suggested that either: (i) early mammals responded to climatic gradients differently than extant mammals; or (ii) that diversity gradients had not had sufficient time to equilibrate following the Cretaceous/Palaeogene (K/Pg) mass extinction (66 Ma). A third possibility, not examined

by Rose *et al.* [37], is that a low Palaeocene seasonality gradient allowed a flattened LBG [35], despite latitudinal variation in temperature (e.g., [12]).

Early Eocene (53 Ma)

Archibald *et al.* [12] sampled fossil insect diversity at an early Eocene palaeotemperate (>50°N) site in Canada, using comparable methods to their sampling of localities from the present-day tropics of Costa Rica, and temperate Massachusetts, USA. Insect diversity was higher at the palaeotemperate site than the modern temperate locality, and comparable to the modern-day tropical locality. This was despite preservational and taxonomic biases that were likely to cause underestimated fossil diversity. Fossil plants of the same region exhibit a similar pattern [12,57], and polar Eocene plant diversity was comparable to that of the present-day temperate zone [58]. Archibald *et al.* [12] suggested that low, ‘tropics-like’ seasonality in the Eocene temperate zone enabled heightened diversity. Although these Palaeocene–Eocene studies [12,37,57,58] are consistent with an LBG in which extratropical diversity was higher than tropical diversity, it should be noted that none of these investigations sampled contemporaneous palaeotropical fossil localities. Therefore, it is conceivable that Palaeocene–Eocene biodiversity was globally higher than that of today (e.g., [59]), with the highest biodiversity still occurring in the palaeotropics, although Cretaceous analyses suggest that this is unlikely to have been the case [36].

Implications for the evolution of the LBG

A post-Eocene shift?

The emerging pattern from studies of the fossil record suggests a palaeotemperate peak in diversity for much

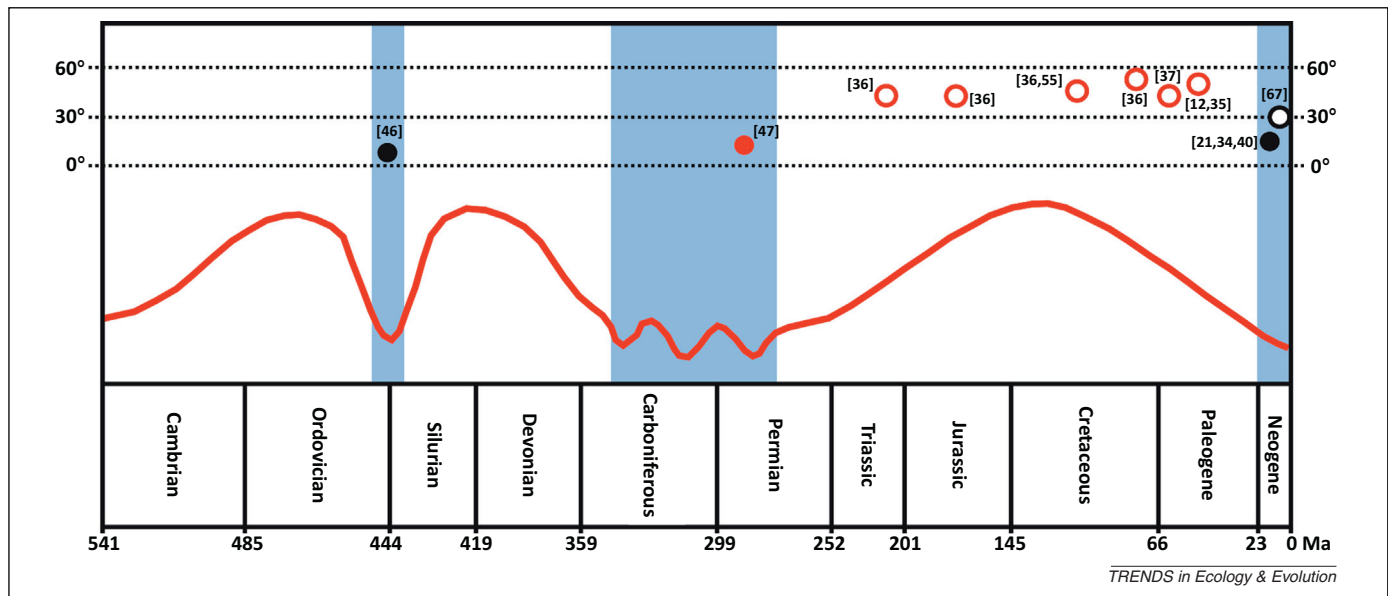


Figure 4. The latitudinal biodiversity gradient (LBG) through the Phanerozoic. Summary figure showing fluctuations in global smoothed-trend temperature (red line) through the Phanerozoic (past 541 million years), with icehouse world intervals marked with blue shading. The results of sampling-mediated studies exploring the LBG through time (including reference numbers) are marked on a simplified, single hemisphere palaeolatitudinal axis, separated into those supporting a poleward decline in species diversity (solid circles) and those supporting peaks in the palaeotemperate regions (open circles). Red indicates results from the terrestrial realm. Poleward declines in species richness seem to be restricted to icehouse worlds, whereas temperate peaks in diversity occur during warmer intervals [note that the one exception to this is during the Pleistocene (Neogene) interglacial [67], a short warming interval within an icehouse regime]. The temperature curve is based on [66,68], the timing of icehouse worlds is based on [68], and plotted diversity data are based on the results in [12,21,34–37,40,46,47,55,63,67]. Abbreviation: Ma, million years ago.

of the Phanerozoic (Figure 4). This is at odds with the prevalence of high tropical diversity in living species. For example, with the exception of some marine species [7], and an inverse gradient in the eastern USA [1], extant birds predominantly conform to the standard LBG [15,60], in contrast to their Mesozoic pattern [36]. Thus, at some point between the end-Cretaceous and the present day, there was a shift in the avian LBG from a palaeotemperate peak to the modern pattern in which biodiversity is highest in the tropics. Evidence from molecular analyses of avian phylogeny indicates that this change occurred after the Eocene [61], a view supported by similar temporal patterns in insect diversity [12]. If accurately dated, these shifts might coincide with the Eocene/Oligocene (34 Ma) boundary, which marks the onset of Antarctic glaciation, a transition to global cooling, a strengthened climatic gradient, and increased seasonality, especially outside of the tropics [12,62,63]. These changes might have resulted in the formation of a post-Eocene modern-type LBG, through: (i) increases in origination in, or dispersal into, the tropics; (ii) reduced extratropical speciation rates; and/or (iii) differential extinction rates [12,23,36,42,60,61,64] (Box 1).

Icehouse versus greenhouse worlds

Global biodiversity and temperature co-vary through time [65]. If biodiversity, temperature, and other climatic variables, such as seasonality, also co-varied spatially in deep time, then this might have driven a more specific correlation between global climatic regime and the nature of the LBG [66,67]. The Late Ordovician–Early Silurian, Late Carboniferous–Middle Permian, and past 30 myr all represent especially cold periods with steep climatic gradients ('icehouse' intervals), whereas the Earth was considerably warmer and more equable ('greenhouse' intervals) at other

times during the Phanerozoic [68] (Figure 4). Currently, evidence for a tropical peak and poleward decline in species richness, after mediating for sampling biases, only comes from icehouse intervals (e.g., [21,34,40,46,47]), whereas temperate peaks in biodiversity, or flattened gradients, are recovered from greenhouse intervals (e.g., [12,36,37,55]) and during interglacials (i.e., short periods of warming within icehouse regimes; e.g., [34,46,67]) (Figure 4). It is possible that icehouse worlds exhibit low tropical extinction rates and high dispersal rates into the tropics, which are less perturbed by glaciations than are the extratropics (e.g., [46]). For example, the tropics might have acted as a species refugium during the Pleistocene Ice Ages (1.8 Ma to approximately 11,000 years ago), and aridification caused by glacial sequestration of water might have resulted in rainforest fragmentation, leading to the isolation of populations and increased speciation (although see [12,69]). Conversely, during greenhouse or interglacial conditions (i.e., warmer, more equable time intervals), the tropics might simply have become too hot for many organisms (e.g., [70]), leading to increases in extinction rates and dispersal out of the tropics (e.g., [67]).

Based on their study of fossil insects and plants, and review of the modern ecological literature, Archibald *et al.* [12,35] argued that seasonality, not mean annual temperature, drives the LBG. Unfortunately, it is difficult to test the generality of this hypothesis beyond the Cenozoic because seasonality is poorly constrained in earlier time intervals for which there is strong, sampling-mediated evidence of a tropical peak and poleward decline in diversity. However, high seasonality might be characteristic of icehouse regimes and abrupt cooling intervals [31,63,71,72]. As such, it is conceivable that seasonality does have an important role in forming the LBG [12], but

that the timing of changes to both overall temperature and seasonality co-vary as part of the long-term icehouse–greenhouse climatic cycle [31].

Continental drift

The distribution of land area, although perhaps not the dominant driver, clearly has some influence on the distribution of biodiversity: terrestrial organisms cannot live where there is no land and it seems intuitive that a greater amount of land area has the potential to support higher terrestrial species richness [29]. Marine biodiversity is also affected by land distribution in that most marine life is restricted to the continental shelf (see [31] for an example in fossil invertebrates). The distribution of land area also affects climatic regimes (e.g., seasonality increases inland in large landmasses and continental positions affect oceanic currents). During the Early Palaeozoic, most continents were located in the Southern Hemisphere (Figure 2). However, a gradual northward shift produced an approximate hemispherical equilibrium by the Late Permian–Early Triassic [39], culminating in the pattern today whereby 70% of land area is within the Northern Hemisphere [12]. Teasing apart a possible ‘common cause’ mechanism, whereby the distribution of land area might drive both patterns in diversity and fossil record sampling, has yet to receive much attention [36,43], but is potentially important in any deep-time tests of geographical heterogeneity hypotheses. Most studies have ignored this aspect, or have taken these diversity patterns at face value (e.g., [66]), but there is some evidence that the distribution of land area might shape the LBG during times of a weakened climatic gradient [36].

Terrestrial versus marine realms

Distributional patterns of biodiversity on land and in the marine realm do not necessarily follow the same rules [25,28,44,73]. Even within the oceans, different environments show disparate patterns and varied responses to climatic fluctuations [9,33]. As well as numerous intrinsic and ecological differences between most terrestrial and marine organisms, barriers to dispersal might be more pronounced on land than in the sea [25]. Mittelbach *et al.* [22] noted that, whereas tropical conservatism seems common on land, it is less evident in the marine realm, where many groups span wide latitudinal ranges [21,28]. For example, during cooling intervals, marine organisms can descend the continental shelf or move towards the Equator, whereas terrestrial animals undergoing range shifts might instead be confronted with an impassable glacial barrier, leading to regional extinctions [44]. Additionally, latitudinal climatic zonation on land might preclude dispersal by introducing climatic barriers (e.g., arid-to-humid transitions) [61,64], leading to provincialism, whereby certain groups of organisms have a restricted geographic distribution [e.g., 56,74], making them especially vulnerable during climatic fluctuations.

Effect of mass extinction events on LBGs

Mass extinction events devastate life on Earth; thus, they have the potential to perturb LBGs greatly [75]. It is likely that their effects vary across taxonomic groups,

geographical regions, environments, latitudinal belts, and hemispheres. However, this issue has received little attention. Krug *et al.* [75] found evidence for heightened origination rates in marine bivalves after the K/Pg event, particularly in the tropics. Jablonski [76] reported high extinction rates of marine invertebrates in the time intervals immediately following mass extinctions, but noted regional variations after the K/Pg event. The absence of a modern-type gradient in early Palaeocene terrestrial mammals led Rose *et al.* [37] to suggest that disturbed ecosystems had yet to re-establish themselves following the K/Pg event. Thus, as well as profoundly affecting diversity and biogeographic distributions of taxa at regional scales, mass extinctions might cause short-term decoupling of latitudinal distributional patterns from their environmental drivers.

Summary and prospects

Although a latitudinal biodiversity gradient of a tropical peak and declining polewards species richness is a near-ubiquitous pattern in the present day, the fossil record suggests that this has not been a persistent feature in deep time. After mediating for biases in fossil record sampling, a tropical biodiversity peak is only recognised during intervals of the Palaeozoic and the past 30 myr (Figure 4), with the gradient steepening to form its present-day shape only in this latter period. There is evidence to suggest that these switches from tropical to temperate peaks in biodiversity correspond with transitions from icehouse to greenhouse worlds. The cause of the LBG remains obscure, but the fossil record presents a unique opportunity to explore these patterns in both time and space, and supports an important role for climate.

There are numerous avenues for further exploration of the evolution of the LBG. Studies should test all of the main hypotheses for the cause of the LBG: if there is a single driver, this should explain LBGs that do not conform to the modern pattern (including hemispherical asymmetries [12]), as well as those that do [4]. Many time intervals have received little attention, and most studies to date can be criticised for their failure to account for the effect of sampling biases on spatial patterns of diversity. Additionally, there have been few attempts to study the gradient along a single palaeolatitudinal transect, thereby removing any possible effects caused by longitudinal variation. Patterns on land have been understudied, and there are few time intervals for which sampling-mediated studies have compared distributions in diversity on land and in the sea. In all environments, many groups of taxa, especially vertebrates, have yet to be incorporated into analyses. Moreover, several ecological ‘rules’ established for extant taxa have yet to be tested thoroughly in the fossil record (e.g., Bergmann’s rule [77]). Pre-Cenozoic seasonality data, and testing of the hypothesis that the icehouse–greenhouse cycle controls shifts in seasonality, are needed. Lastly, the possible role of mass extinctions in shaping and disrupting the LBG has also been largely neglected [75].

Insights into drivers of the LBG from the fossil record will be crucial in understanding the threat to extant organisms from climate change. Many studies have

predicted the extratropical spread of tropical organisms as a result of global warming (e.g., [78]), but these models are primarily based on transitions between glacial and interglacial intervals of the Pleistocene icehouse world. Instead, the temporally more distant greenhouse world of the Cretaceous and early Cenozoic might represent a closer analogue to future climate patterns. One outcome of global warming might be a shallower climatic gradient; the future LBG might follow this climatic pattern, potentially producing a temperate biodiversity peak, but it remains unclear whether this flattening would reflect climatic changes and/or tropical decreases in biodiversity. Furthermore, a weakened climatic gradient might allow for an increased role for the distribution of land area. Although this might have contributed to palaeotemperature biodiversity peaks in the Mesozoic, today there is a greater tropical land area, which might support the maintenance of a steep LBG with a tropical peak, despite a weakened climatic gradient. As such, current predictions of climatically driven biodiversity change might be using the wrong model, and will need to consider the complex interactions of climate and geography if they are to make accurate forecasts about future dispersals and extinctions, with respect to latitude.

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References

- Willig, M.R. *et al.* (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* 34, 273–309
- Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *Am. Nat.* 163, 192–211
- Field, R. *et al.* (2009) Spatial species-richness gradients across scales: a meta-analysis. *J. Biogeogr.* 36, 132–147
- Krug, A.Z. *et al.* (2007) Contrarian clade confirms the ubiquity of spatial origination patterns in the production of latitudinal diversity gradients. *Proc. Natl. Acad. Sci. U.S.A.* 104, 18129–18134
- Kiel, S. and Nielson, S.N. (2012) Quaternary origin of the inverse latitudinal diversity gradient among southern Chilean mollusks. *Geology* 38, 955–958
- Wiens, J.J. (2007) Global patterns of diversification and species richness in amphibians. *Am. Nat.* 170, 86–106
- Chown, S.L. *et al.* (1998) Global patterns in species richness of pelagic seabirds: the Procellariiformes. *Ecography* 21, 342–350
- Proches, S. (2001) Back to the sea: secondary marine organisms from a biogeographical perspective. *Biol. J. Linn. Soc.* 74, 197–203
- Tittensor, D.P. *et al.* (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature* 466, 1098–1101
- Chown, S.L. *et al.* (2004) Hemispherical asymmetries in biodiversity: a serious matter for ecology. *PLoS Biol.* 2, e406
- Dunn, R.R. *et al.* (2009) Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecol. Lett.* 12, 324–333
- Archibald, S.B. *et al.* (2010) Seasonality, the latitudinal gradient of diversity, and Eocene insects. *Paleobiology* 36, 374–398
- Krug, A.Z. *et al.* (2010) Differential extinction and the contrasting structure of polar marine faunas. *PLoS ONE* 5, e15362
- Krug, A.Z. *et al.* (2009) Generation of Earth's first-order biodiversity pattern. *Astrobiology* 9, 113–124
- Orme, C.D.L. *et al.* (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436, 1016–1019
- Colwell, R.K. *et al.* (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322, 258–261
- Deutsch, C.A. *et al.* (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. U.S.A.* 105, 6668–6672
- Jenkins, C.N. *et al.* (2013) Global patterns of terrestrial vertebrate diversity and conservation. *Proc. Natl. Acad. Sci. U.S.A.* 110, 11457–11462
- Wiens, J.J. and Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends Ecol. Evol.* 19, 639–644
- Cardillo, M. *et al.* (2005) Testing for latitudinal bias in diversification rates: an example using New World birds. *Ecology* 86, 2278–2287
- Jablonski, D. *et al.* (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314, 102–106
- Mittelbach, G.G. *et al.* (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* 10, 315–331
- Weir, J.T. and Schluter, D. (2007) The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* 315, 1574–1576
- Martin, P.R. *et al.* (2007) Revisiting Jablonski (1993): cladogenesis and range expansion explain latitudinal variation in taxonomic richness. *J. Evol. Biol.* 20, 930–936
- Roy, K. and Goldberg, E.E. (2007) Origination, extinction and dispersal: integrative models for understanding present-day diversity gradients. *Am. Nat.* 170, 71–85
- Jocque, M. *et al.* (2010) Climatic control of dispersal–ecological specialization trade-offs: a metacommunity process at the heart of the latitudinal diversity gradient? *Global Ecol. Biogeogr.* 19, 244–252
- Soria-Carrasco, V. and Castresana, J. (2012) Diversification rates and the latitudinal gradient of diversity in mammals. *Proc. R. Soc. Lond. B: Biol. Sci.* 279, 4148–4155
- Jablonski, D. *et al.* (2013) Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proc. Natl. Acad. Sci. U.S.A.* 110, 10487–10494
- Rosenzweig, M.L. (ed.) (1995) *Species Diversity in Space and Time*, Cambridge University Press
- Hawkins, B.A. *et al.* (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84, 3105–3117
- Powell, M.G. (2007) Latitudinal diversity gradients for brachiopod genera during late Palaeozoic time: links between climate, biogeography and evolutionary rates. *Global Ecol. Biogeogr.* 16, 519–528
- Erwin, D.H. (2009) Climate as a driver of evolutionary change. *Curr. Biol.* 19, 575–583
- Yasuhara, M. *et al.* (2009) Temporal latitudinal-gradient dynamics and tropical instability of deep-sea species diversity. *Proc. Natl. Acad. Sci. U.S.A.* 106, 21717–21720
- Yasuhara, M. *et al.* (2012) Latitudinal species diversity gradient of marine zooplankton for the last three million years. *Ecol. Lett.* 15, 1174–1179
- Archibald, S.B. *et al.* (2013) Seasonality, montane beta diversity, and Eocene insects: testing Janzen's dispersal hypothesis in an equable world. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 371, 1–8
- Mannion, P.D. *et al.* (2012) A temperate palaeodiversity peak in Mesozoic dinosaurs and evidence for Late Cretaceous geographical partitioning. *Global Ecol. Biogeogr.* 21, 898–908
- Rose, P.J. *et al.* (2011) Flat latitudinal gradient in Paleocene mammal richness suggests decoupling of climate and biodiversity. *Geology* 39, 163–166
- Crame, J.A. (2001) Taxonomic diversity gradients through geological time. *Divers. Distrib.* 7, 175–189
- Powell, M.G. (2009) The latitudinal diversity gradient of brachiopods over the past 530 million years. *J. Geol.* 117, 585–594
- Alroy, J. *et al.* (2008) Phanerozoic trends in the global diversity of marine invertebrates. *Science* 321, 97–100
- Powell, M.G. *et al.* (2012) The latitudinal position of peak marine diversity in living and fossil biotas. *J. Biogeogr.* 39, 1687–1694
- Thomas, E. and Gooday, A.J. (1996) Cenozoic deep-sea benthic foraminifers: tracers for changes in oceanic productivity? *Geology* 24, 355–358
- Allison, P.A. and Briggs, D.E.G. (1993) Paleolatitudinal sampling bias, Phanerozoic species diversity, and the end-Permian extinction. *Geology* 21, 65–68
- Jablonski, D. (2008) Extinction and the spatial dynamics of biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* 105, 11528–11535

- 45 Fitzgerald, P.C. and Carlson, S.J. (2006) Examining the latitudinal diversity gradient in Paleozoic terebratulide brachiopods: should singleton data be removed? *Paleobiology* 32, 367–386
- 46 Krug, A.Z. and Patzkowsky, M.E. (2007) Geographic variation in turnover and recovery from the Late Ordovician mass extinction. *Paleobiology* 33, 435–454
- 47 Benson, R.B.J. and Upchurch, P. (2013) Diversity trends in the establishment of terrestrial vertebrate eco-systems: interactions between spatial and temporal sampling biases. *Geology* 41, 43–46
- 48 Crane, P.R. and Lidgard, S. (1989) Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. *Science* 246, 675–678
- 49 Rees, P.M. *et al.* (2004) Late Jurassic climates, vegetation, and dinosaur distributions. *J. Geol.* 112, 643–653
- 50 Coiffard, C. and Gomez, B. (2012) Influence of latitude and climate on spread, radiation and rise to dominance of early angiosperms during the Cretaceous in the Northern Hemisphere. *Geol. Acta* 10, 181–188
- 51 Peralta-Medina, E. and Falcon-Lang, H.J. (2012) Cretaceous forest composition and productivity inferred from a global fossil wood database. *Geology* 40, 219–222
- 52 Hay, W.W. (2008) Evolving ideas about the Cretaceous climate and ocean circulation. *Cret. Res.* 29, 725–753
- 53 Littler, K. *et al.* (2011) High sea-surface temperatures during the Early Cretaceous Epoch. *Nat. Geosci.* 4, 169–172
- 54 Jenkyns, H.C. *et al.* (2012) Warm Middle Jurassic–Early Cretaceous high-latitude sea-surface temperatures from the Southern Ocean. *Clim. Past* 8, 215–226
- 55 Markwick, P.J. (1998) Crocodylian diversity in space and time: the role of climate in paleoecology and its implication for understanding K/T extinctions. *Paleobiology* 24, 470–497
- 56 Carvalho, I.S. *et al.* (2010) Climate's role in the distribution of the Cretaceous terrestrial Crocodyliformes throughout Gondwana. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 297, 252–262
- 57 Smith, R.Y. *et al.* (2012) Early Eocene plant diversity and dynamics in the Falkland flora, Okanagan Highlands, British Columbia, Canada. *Palaeobiodivers. Palaeoenviron.* 92, 309–328
- 58 Harrington, G.J. *et al.* (2012) Arctic plant diversity in the Early Eocene greenhouse. *Proc. R. Soc. Lond. B: Biol. Sci.* 279, 1515–1521
- 59 Alroy, J. (2010) The shifting balance of diversity among major marine animal groups. *Science* 329, 1191–1194
- 60 Hawkins, B.A. *et al.* (2007) Climate, niche conservatism, and the global bird diversity gradient. *Am. Nat.* 170, 16–27
- 61 Hawkins, B.A. *et al.* (2006) Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of new World birds. *J. Biogeogr.* 33, 770–780
- 62 Bijl, P.K. *et al.* (2009) Early Palaeogene temperature evolution of the southwest Pacific Ocean. *Nature* 461, 776–779
- 63 Eldrett, J.S. *et al.* (2009) Increased seasonality through the Eocene to Oligocene transition in northern high latitudes. *Nature* 459, 969–973
- 64 Hawkins, B.A. *et al.* (2005) Water links the historical and contemporary components of the Australian bird diversity gradient. *J. Biogeogr.* 32, 1035–1042
- 65 Mayhew, P.J. *et al.* (2012) Biodiversity tracks temperature over time. *Proc. Natl. Acad. Sci. U.S.A.* 109, 15141–15145
- 66 Naimark, E.B. and Markov, A.V. (2011) Northward shift in faunal diversity: a general pattern of evolution of Phanerozoic marine biota. *Biol. Bull. Rev.* 1, 71–81
- 67 Kiessling, W. *et al.* (2012) Equatorial decline of reef corals during the last Pleistocene interglacial. *Proc. Natl. Acad. Sci. U.S.A.* 109, 21378–21383
- 68 Royer, D.L. *et al.* (2004) CO₂ as a primary driver of Phanerozoic climate. *GSA Today* 14, 4–10
- 69 Bennett, K.D. *et al.* (2012) Neotropical refugia. *Holocene* 22, 1207–1214
- 70 Sun, Y. *et al.* (2012) Lethally hot temperatures during the Early Triassic greenhouse. *Science* 338, 366–370
- 71 Crowley, T.J. *et al.* (1989) Seasonal cycle variations on the supercontinent of Pangaea. *Geology* 17, 457–460
- 72 Denton, G.H. *et al.* (2005) The role of seasonality in abrupt climate change. *Quat. Sci. Rev.* 24, 1159–1182
- 73 Sunday, J.M. *et al.* (2012) Thermal tolerance and the global redistribution of animals. *Nat. Clim. Change* 2, 686–690
- 74 Benson, R.B.J. *et al.* (2012) Theropod fauna from southern Australia indicates high polar diversity and climate-driven dinosaur provinciality. *PLoS ONE* 7, e37122
- 75 Krug, A.Z. *et al.* (2009) Signature of the end-Cretaceous mass extinction in the Modern Biota. *Science* 323, 767–771
- 76 Jablonski, D. (2002) Survival without recovery after mass extinctions. *Proc. Natl. Acad. Sci. U.S.A.* 99, 8139–8144
- 77 Zhang, Y. and Payne, J.L. (2012) Size-frequency distributions along a latitudinal gradient in Middle Permian fusulinoideans. *PLoS ONE* 7, e38603
- 78 Parmeson, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42
- 79 Chown, S.L. and Gaston, K.J. (2000) Areas, cradles and museums: the latitudinal gradient in species richness. *Trends Ecol. Evol.* 15, 311–315
- 80 Rull, V. (2011) Neotropical diversity: timing and potential drivers. *Trends Ecol. Evol.* 26, 508–513
- 81 Allen, A.P. and Gillooly, J.F. (2006) Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecol. Lett.* 9, 947–954
- 82 Allen, A.P. *et al.* (2006) Kinetic effects of temperature on rates of genetic divergence and speciation. *Proc. Natl. Acad. Sci. U.S.A.* 103, 9130–9135
- 83 McKenna, D.D. and Farrell, B.D. (2006) Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Proc. Natl. Acad. Sci. U.S.A.* 103, 10947–10951
- 84 Eo, S.H. *et al.* (2008) Population divergence in plant species reflects latitudinal diversity gradients. *Biol. Lett.* 4, 382–384
- 85 Kiessling, W. *et al.* (2010) Reefs as cradles of evolution and sources of biodiversity in the Phanerozoic. *Science* 327, 196–198
- 86 Valentine, J.W. *et al.* (2008) Incumbency, diversity and latitudinal gradients. *Paleobiology* 34, 169–178
- 87 Arita, H.T. and Vázquez-Domínguez, E. (2008) The tropics: cradle, museum or casino? A dynamic null model for latitudinal gradients of species diversity. *Ecol. Lett.* 11, 653–663
- 88 Wiens, J.J. *et al.* (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: tree frogs unearth the roots of high tropical diversity. *Am. Nat.* 168, 579–596
- 89 Escarguel, G. *et al.* (2008) Evolutionary rates do not drive latitudinal diversity gradients. *J. Zool. Syst. Evol. Res.* 46, 82–86
- 90 Buzas, M.A. and Culver, S.J. (2009) Geographic origin of species: the temperate-tropical interchange. *Geology* 37, 879–881
- 91 Jetz, W. *et al.* (2012) The global diversity of birds in space and time. *Nature* 491, 444–448
- 92 Smith, A.B. and McGowan, A.J. (2007) The shape of the Phanerozoic marine palaeodiversity curve: how much can be predicted from the sedimentary rock record of western Europe? *Palaeontology* 50, 765–774
- 93 Upchurch, P. *et al.* (2011) Geological and anthropogenic controls on the sampling of the terrestrial fossil record: a case study from the Dinosauria. *Geol. Soc. Lond. Spec. Publ.* 358, 209–240
- 94 Wall, P. *et al.* (2009) Revisiting Raup: exploring the influence of outcrop area on diversity in light of modern sample-standardization techniques. *Paleobiology* 35, 146–167
- 95 Alroy, J. (2010) Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology* 53, 1211–1235
- 96 Wagner, P.J. (2000) The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. *Syst. Biol.* 49, 65–86
- 97 Mannion, P.D. *et al.* (2011) Testing the effect of the rock record on diversity: a multidisciplinary approach to elucidating the generic richness of sauropodomorph dinosaurs through time. *Biol. Rev.* 86, 157–181
- 98 Benton, M.J. *et al.* (2011) Assessing the quality of the fossil record: insights from vertebrates. *Geol. Soc. Lond. Spec. Publ.* 358, 63–94
- 99 Smith, A.B. *et al.* (2012) Phanerozoic marine diversity: rock record modelling provides an independent test of large-scale trends. *Proc. R. Soc. Lond. B: Biol. Sci.* 279, 4489–4495