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Patterns in Palaeontology: The latitudinal biodiversity gradient

by Philip D. Mannion*1

Introduction:

Today, most living species are found in the tropics, the region of the Earth that surrounds the Equator. Species numbers, a measure of biodiversity, decline towards both the North and South poles (Fig. 1). This is known as the latitudinal biodiversity gradient (LBG), and it is the dominant ecological pattern on Earth today. Although there are exceptions to the rule, including high-latitude peaks in diversity of many marine or coastal vertebrates (including seals and albatrosses), the LBG describes the distribution of species diversity for the vast majority of animals and plants, both on land and in the sea, and in the Northern and Southern hemispheres. Understanding the causes and evolution of the LBG helps researchers to explain present-day geographical variation in biodiversity and to model the responses of species to climate change, for example by making forecasts of future dispersals and extinctions.

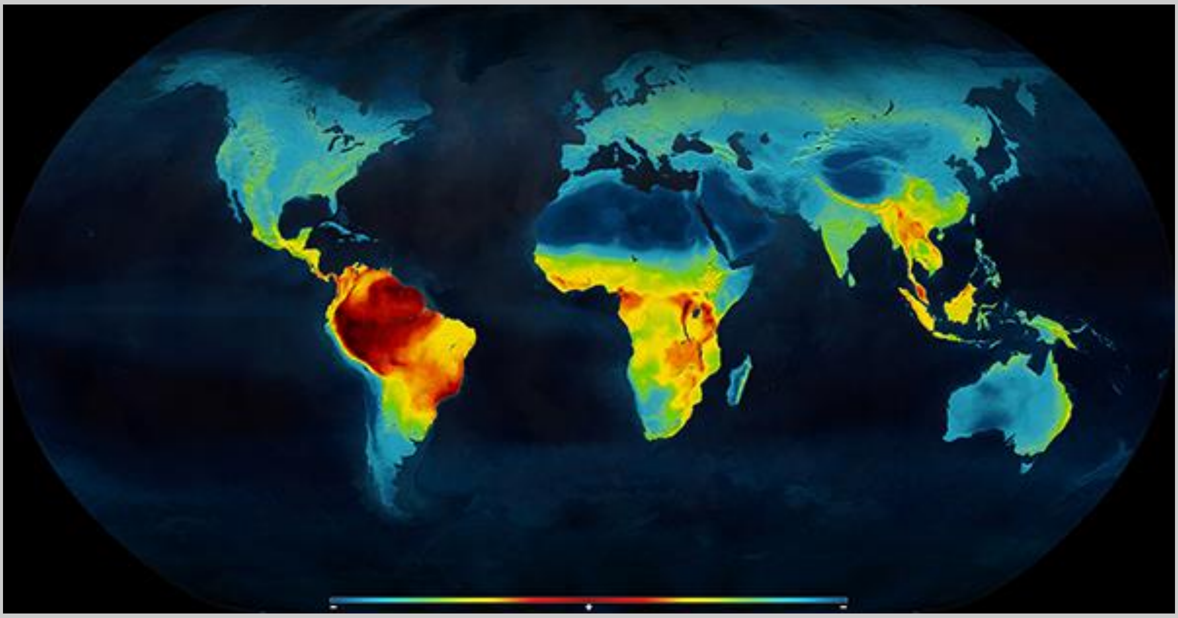

Figure 1 — An example of the modern latitudinal biodiversity gradient, showing the distribution of living terrestrial vertebrate species, with the highest concentration of diversity found in equatorial regions (red end of the colour spectrum) and declining polewards (blue end) to form the modern pattern. Source: Mannion et al. (2014), based on work by Clinton Jenkins.

Drivers of the latitudinal biodiversity gradient:

Net rates of diversification (calculated as the rates at which species originate minus the rates at which they go extinct) are higher in the tropics than elsewhere, but it is unclear whether this is because origination rates are higher in the tropics (the tropics are a 'cradle'), extinction rates are lower (the tropics are a 'museum') or both. Movement of species out of or into the tropics probably complicates this picture (Fig. 2). Although it was first recognized in the early part of the nineteenth century by the German polymath Alexander von Humboldt (Fig. 3), the underlying causes of the LBG are still not fully understood, and more than 100 hypotheses have been proposed to explain it. Most of these are circular, interlinked or too specific to one group of organisms and/or region of the world to explain the gradient, leaving three broad (although not necessarily mutually exclusive) themes that could explain it: historical hypotheses, geographical hypotheses and climatic hypotheses.

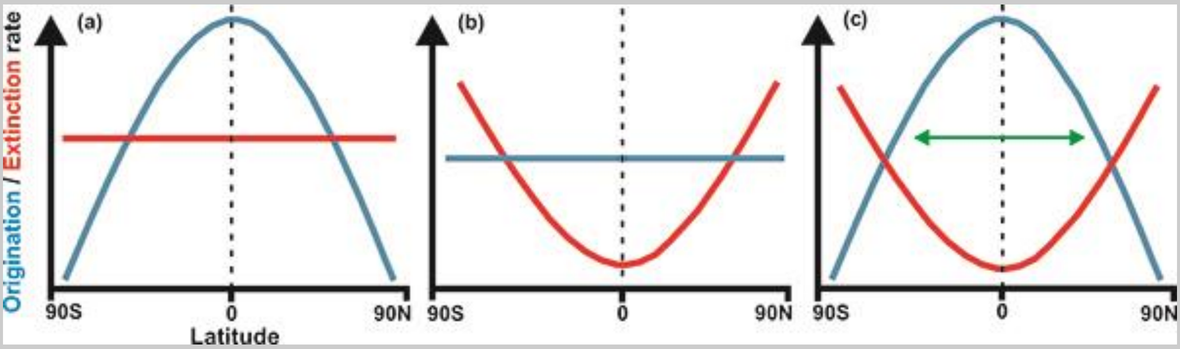

Figure 2 — The three patterns proposed to explain declining polewards biodiversity and higher tropical diversification rates: (a) 'Tropics as cradle' model, in which origination rates are higher in tropical areas and extinction rates do not vary with latitude; (b) 'Tropics as museum', in which origination rates do not vary with latitude but extinction rates are lower in the tropics; (c) 'Out of the tropics', in which origination rates are higher and extinction rates are lower in tropical areas, and species movement is higher from the tropics to the extratropical areas. Blue line, origination rate; red line, extinction rate; dashed black line, Equator; green line, species dispersal out of the tropics, without losing their tropical presence. Source: Mannion et al. (2014).

Historical hypotheses

The historical explanation for the LBG — the 'time and area' hypothesis — originates from the work of the British scientist Alfred Russel Wallace (Fig. 4) in the mid-nineteenth century. It suggests that the tropics have been less perturbed than regions outside the tropics (the extratropics) by past climate events such as the Pleistocene Ice Ages (between 1.8 million and 11,000 years ago), and have been able to accumulate species over a longer time. Related to this is the 'tropical conservatism hypothesis', in which factors intrinsic to the organism, such as the inability of tropical species to tolerate cooler temperatures, keep them from dispersing out of the tropics. However, historical hypotheses are problematic if the LBG has existed throughout deep time (see below), and the proposed mechanisms by which they might affect distributions of species have been heavily criticized.

Figure 3 — Alexander von Humboldt (1769–1859). Born in what is today Germany, Humboldt believed in the unification of the sciences and can be regarded as one of the founding fathers of the sciences of meteorology, biogeography and physical geography. He contributed to a wide range of disciplines, including the study of volcanoes and Earth's magnetic field, and during his travels around South America he discovered numerous species and geographical features that were previously unknown to Europeans. It was as a result of these travels that Humboldt first reported the LBG. Source: http://en.wikipedia.org/wiki/File:Alexandre_humboldt.jpg

Figure 4 — Alfred Russel Wallace (1823–1913). The Welsh naturalist, geologist, biologist, biogeographer, ecologist and explorer is best known for conceiving the evolutionary theory of natural selection independently from Charles Darwin. However, as that long list of titles indicates, Wallace can be credited with much more than that, including important contributions to our understanding of the distribution of organisms that remain an integral part of the field of biogeography. Source: http://en.wikipedia.org/wiki/File:Alfred_Russel_Wallace_1862_-_Project_Gutenberg_eText_15997.png

Geographical hypotheses

This model suggests that because the tropics are bigger than the extratropics, they are able to support more species. This is amplified by the fact that the tropics straddle the Equator, forming one continuous area, whereas the temperate and polar regions of each hemisphere are isolated from their counterparts.

Problems with the geographic hypothesis include the observations that the modern tundra, which has low species diversity, covers more area than other extratropical regions, and that 70% of land area is in the Northern Hemisphere (see Fig. 1), but its terrestrial species diversity is not consistently higher than in the Southern Hemisphere.

Climatic hypotheses

The historical and geographical hypotheses have been strongly criticized, but climate is widely regarded as the primary driver of the LBG. The tropics display much lower seasonal variability than the extratropics, which could result in tropical species being unable to cope with varied environments. As a consequence, they might not be capable of dispersing across newly formed environmental barriers such as mountains and sea inlets, leading populations to fragment and, ultimately, break up into different species. Additionally, the tropics receive more solar energy (insolation) than the extratropics, which promotes increased plant productivity. This might lead to larger viable populations of primary producers, which in turn would support species higher up in the food chain. Seasonality has been regarded by some authors as the most important driver of the LBG, but most studies have difficulty teasing apart the effects of geographical insolation from those of seasonality.

A deep-time view of the LBG:

The fossil record offers a unique window onto the causes and evolution of the LBG. Natural shifts in historical, geographical and climatic factors are typically too slow to detect in modern environments, but these factors are thought to have fluctuated substantially over time spans of thousands, millions or even hundreds of millions of years. Furthermore, because the LBG ultimately arose from a complex interplay of origination, extinction and dispersal, data on living species alone are not sufficient to understand it. Information from the fossil record is also necessary.

In general, it has been thought that some form of the modern LBG has persisted throughout the Phanaerozoic eon (the past 541 million years), even if it has not always been so pronounced. However, this picture changes if we take into account important biases in our sampling of the fossil record. Such factors include geological biases (for example, different areas might have different amounts of fossil-bearing rock) and biases associated with human collecting effort (for example, certain ‘key’ time intervals are more studied than others). These biases can produce false peaks in diversity when sampling is good (such as when we have lots of opportunity to collect fossils) and troughs for relatively poorly sampled time intervals (when we have few opportunities to collect fossils). This can produce a misleading picture of the fossil record. By using rigorous statistical methods to minimize these biases, we can infer that at certain times during the Phanaerozoic the LBG has weakened, flattened or even developed into a 'palaeotemperate peak' in which species numbers were highest at temperate latitudes, between 30° and 60° north and south of the Equator. Strong evidence for a modern-type LBG with a tropical peak and poleward decline in species numbers is restricted to the early Palaeozoic era (approximately 458 million to 423 million years ago), possibly the late Palaeozoic era (330 million to 270 million years ago), and the past 30 million years. In the remaining periods, the available evidence argues for palaeotemperate peaks in biodiversity, or flattened gradients. This evidence comes from a variety of fossil groups, including marine invertebrates, dinosaurs, early mammals, insects and coral reefs (Fig. 5).

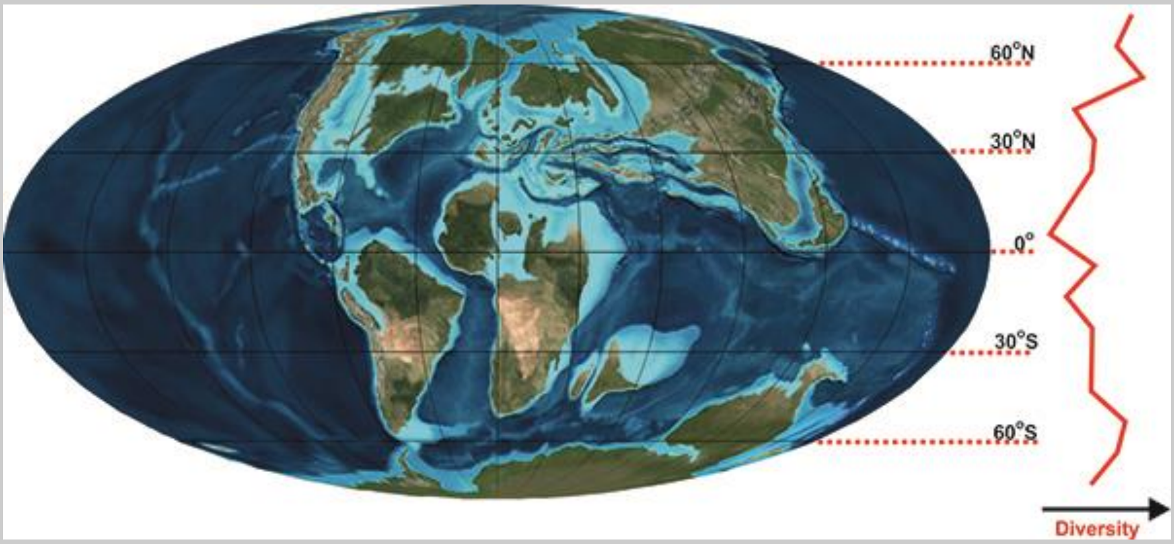

Figure 5 — The Late Cretaceous (100 million to 66 million years ago) LBG for dinosaurs plotted against a palaeogeographic map (showing the distribution of the continents at that time), demonstrating higher sampling-corrected diversity in the extratropics than in the tropics during a time of a weakened latitudinal climatic gradient. Source: Mannion et al. (2014).

The two intervals in deep time for which there is strong evidence of a modern-type LBG both represent periods of a much cooler Earth (icehouse worlds), whereas temperate peaks in biodiversity and flattened gradients occurred during hotter greenhouse intervals or interglacials (short periods of warming within icehouse regimes) (Fig. 6). It is likely that the tropics were less perturbed by glaciations than the extratropical regions; for example, the tropics might have acted as a refuge for species during the Pleistocene Ice Ages. Conversely, during warmer, more equable time intervals, the tropics might simply have become too hot for many organisms to survive. It seems that the present pattern developed only in the past 30 million years or so, coinciding with a transition to global cooling, a steepening of the climatic gradient (with a greater differentiation between tropical and extratropical climate), and the onset of Antarctic glaciation.

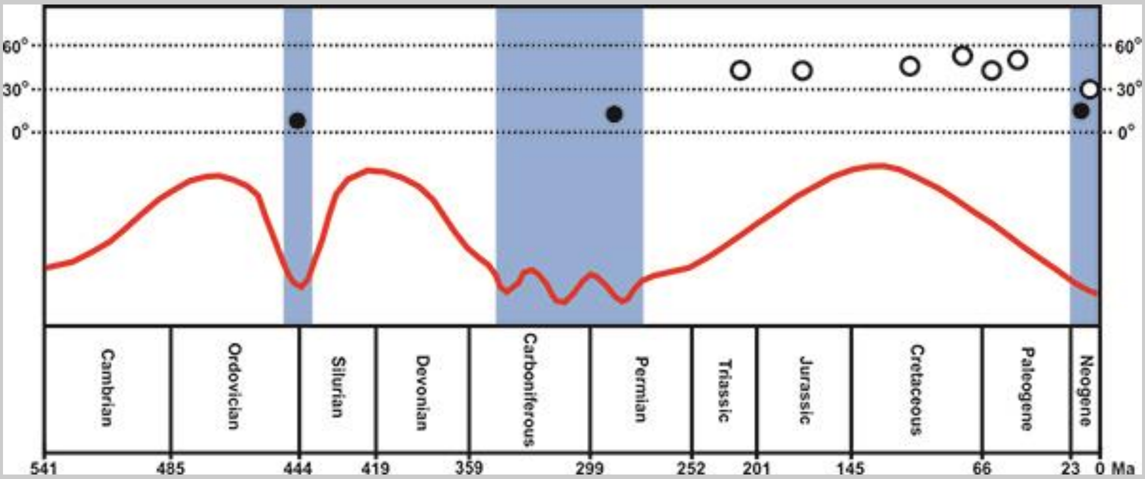

Figure 6 — Summary figure showing a comparison of the LBG with fluctuations in global temperature (red line) through the Phanaerozoic eon (the past 541 million years), with icehouse-world intervals marked in blue. Filled circles represent studies showing evidence of a poleward decline in species diversity; open circles represent studies that support peaks in the paleotemperate regions. Source: Mannion et al. (2014).

Prospects:

The causes of the LBG remain 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. Much more work needs to be done in examining the deep-time LBG, with many groups, regions, environments and time intervals currently neglected. Modern ecological 'rules' that seem to be correlated with the LBG, such as Bergmann's rule on organisms' body size, have yet to be thoroughly tested in the fossil record. Further insights into drivers of the LBG from the fossil record will be crucial in understanding the threat to extant organisms from ongoing climate change.

One outcome of global warming might be the development of a shallower climatic gradient (comparable to that of the time of the dinosaurs); the future LBG might follow this climatic pattern, with different levels of extinction and/or the dispersal of organisms out of the tropics potentially producing a temperate biodiversity peak. Current predictions of climatically driven biodiversity change will need to consider the complex interactions of climate and geography if they are to make accurate forecasts about future dispersals and extinctions. The fossil record, which includes instances of rapid global warming analogous to that generated by human activity today, is a vital resource for understanding and predicting what will happen to life on Earth in the coming years, decades and centuries.

Suggestions for further reading:

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