Explanations for latitudinal diversity gradients must invoke rate variation

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The latitudinal diversity gradient (LDG) describes the pattern of increasing numbers of species from the poles to the equator. Although recognized for over 200 years, the mechanisms responsible for the largest-scale and longest-known pattern in macroecology are still actively debated. I argue here that any explanation for the LDG must invoke differential rates of speciation, extinction, extirpation, or dispersal. These processes themselves may be governed by numerous abiotic or biotic factors. Hypotheses that claim not to invoke differential rates, such as 'age and area' or 'time for diversification', eschew focus from rate variation that is assumed by these explanations. There is still significant uncertainty in how rates of speciation, extinction, extirpation, and dispersal have varied regionally over Earth history. However, to better understand the development of LDGs, we need to better constrain this variation. Only then will the drivers of such rate variation – be they abiotic or biotic in nature – become clearer.

age and area hypothesis | tropics as older | tropics as stable | climate change | biodiversity gradient

The tropics teem with a diversity of life that dwindles toward the poles. This latitudinal gradient in species richness (LDG) has been studied intensively for over 200 years (1, 2). Despite concerted attention, significant debate still exists regarding the causal mechanisms behind a pattern that transcends clades, ecosystems, and continents (3).

Over 100 hypotheses have been proposed to explain the higher diversity observed at low versus high latitudes (3–11). Although explanations abound, here I contend that rate variation is inherent to all LDG hypotheses. That is, regional differences in species richness must be explained by one or more of the following four processes: speciation, extinction, local extirpation, or dispersal. These processes themselves may be controlled by a suite of abiotic and biotic factors that operate at different spatial and temporal scales (12), including spatiotemporal climate change (13–16), biotic interactions (17–20), and available resources and area (21–25).

Hypotheses that invoke differential rates have been traditionally classified as 'historical' hypotheses and are often contrasted with 'ecological' hypotheses that invoke constraints on the number of species that can occur together in any given location (8, 26). Differential rates, however, are implicated in both suites of hypotheses. For example, ecological hypotheses suppose that rates of speciation (incipient or not), extinction, extirpation, or dispersal change in association with the number of species in a region (27, 28). Rate variation is therefore inherent to both ecological and historical hypotheses, with the

'ecological' designation a reflection of a proposed mechanism that regulates this rate variation.

One hypothesis that purports not to invoke differential rates is the 'time for speciation' or 'time for diversification' hypothesis. Under this formulation, most clades originate at low latitudes and only later disperse to higher latitudes. The greater time that lineages spent equatorially would allow more diversity to accumulate there, even if diversification rates were similar across latitudes once these low-latitude lineages dispersed out of their ancestral home (6, 29–32). Rate variation, however, is still inherent to such an argument, even if somewhat fatuous: Diversification would have been higher at low latitudes simply due to its absence at higher latitudes. Whether the majority of clades have low-latitude origins is an open question that is both supported (33–35) and refuted (36–39) by empirical data. Regardless of where most groups originated, discussions around 'time for diversification' often implicitly assume that high-latitude regions were empty of life over much of Earth history. The fossil record, however, suggests these regions were never consistently devoid of life, even if most species were periodically eradicated due to large-scale climate perturbations (see below and Fig. 1).

The potential origin of many groups in tropical climates, in combination with strongly conserved physiological constraints, is often provided as a mechanism for maintaining LDGs (6, 30, 44–46). Conserved physiology, referred to as phylogenetic niche conservatism (47–49), would prohibit many species from dispersing out of low-latitude regions and would therefore retain higher diversity equatorially. Although physiological tolerances may be conserved within some lineages (50–52) and across some clades (40, 48, 53), fossil data suggest dispersal dynamics were variable, and more species may have dispersed from low to high latitudes than vice versa in many groups (54–58).

The 'time for speciation' hypothesis is sister to the 'age and area' hypothesis and often discussed concomitantly. The 'age and area' hypothesis posits the tropics were larger in extent
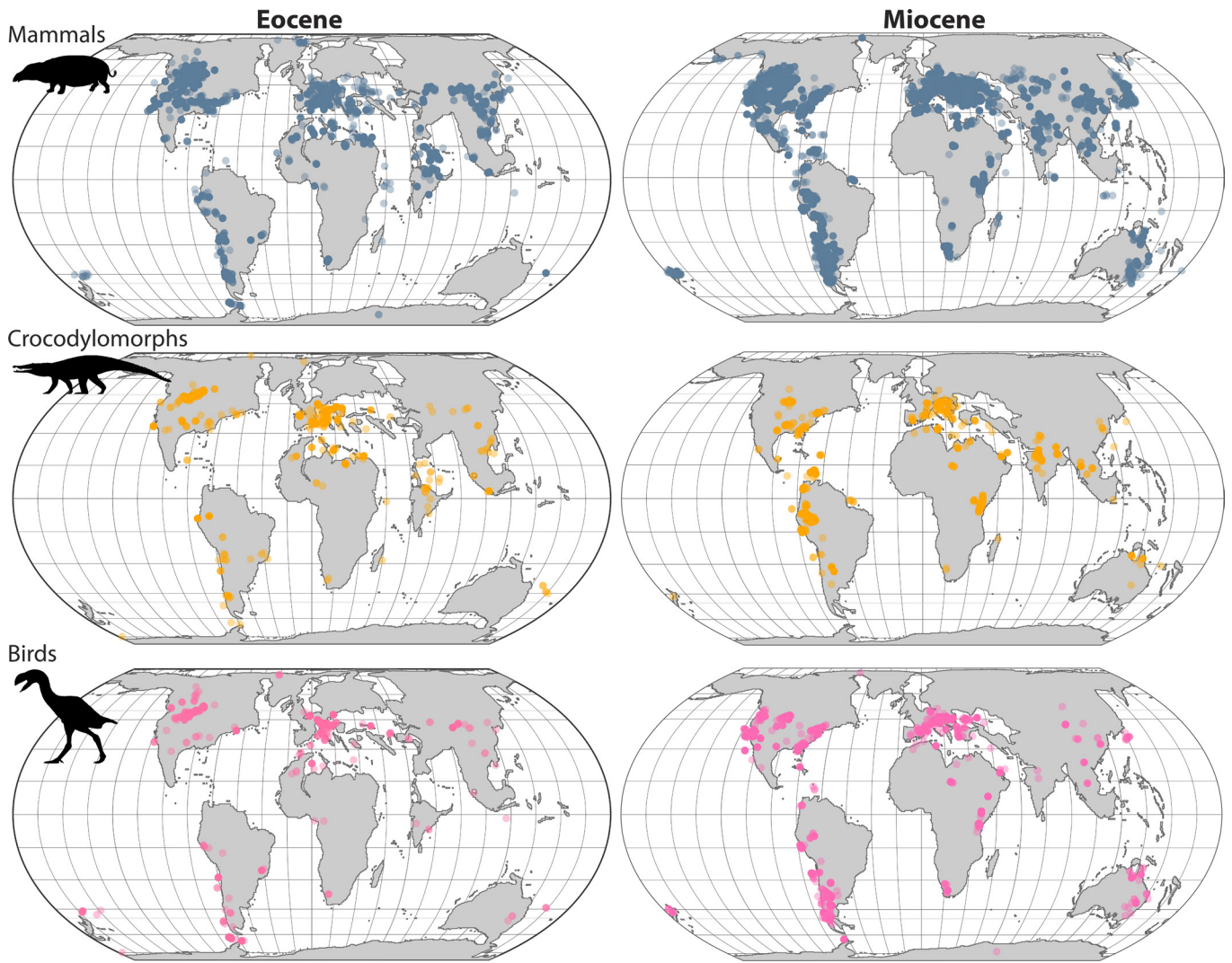
Fig. 1. Mammal, crocodylomorph, and bird occurrences during the Eocene (56 to 33.9 Ma) and Miocene (23.03 to 5.33 Ma),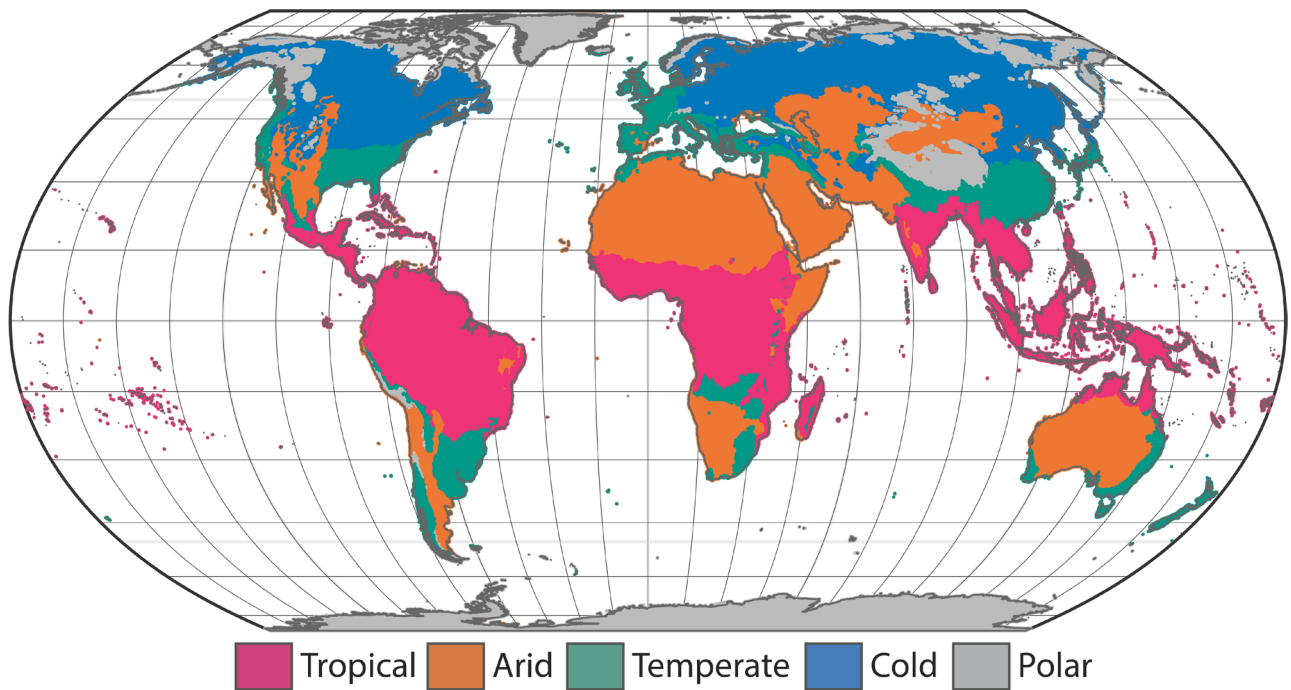 plotted on a Ypresian and Chattian paleogeography, respectively (40). Using two example time intervals, these maps show that clades were found at high latitudes millions of years ago. The disappearance of some of these groups from high-latitude regions points to broad-scale extinction, extirpation, or movement equatorward. Occurrences were rotated to their paleolatitudes and paleolongitudes in GPlates v.2.2.0 using Scotese's PALEOMAP PaleoAtlas (41). Fossil distributional data were downloaded from the Paleobiology Database on 22 February 2023 for the class Aves, class Mammalia, and unranked clade Crocodylmorpha. Animal silhouettes are from PhyloPic: *Moeritherium* from T. Michael Keesey (CC0 1.0), *Gastornis giganteus* from Scott Hartman (CC BY 3.0), and *Duerosuchus piscator* from Armin Reindl (CC BY 4.0). Maps were constructed in R v.4.2.1 using the sf package (42) and ggplot2 (43).

earlier in the Cenozoic (59–61), which fuelled higher equatorial diversity (30, 61, 62). Like all LDG hypotheses, the 'age and area' hypothesis cannot extricate itself from rate variation. The larger historical area of the tropics is thought to have elevated richness by potentially increasing the probability of population isolation and thus speciation, or by decreasing rates of extinction by increasing population size and access to resources (63–65). Environmental heterogeneity may also scale positively with area, further elevating rates of allopatric speciation. Regardless of whether—and why—larger tropical areas scale with richness, the 'age and area' hypothesis assumes that tropical-adapted taxa once occupying higher latitudes during warmer intervals have now been driven extinct, extirpated, or forced to migrate equatorward as warmer climates contracted (56, 66, 67). Thus, the historical effect of a once-larger tropical expanse involves differential rates: either through elevated extirpation/extinction at high latitudes, or greater dispersal from high to low latitudes.

Today, the larger areal extent of the tropics does not provide an explanation for high terrestrial richness at low latitudes, since tropical climate regions on land are no larger than extratropical ones (68–71) (Fig. 2). When examining historical patterns of richness and rate variation, care must be taken to quantify biodiversity dynamics by latitude, and to disentangle these dynamics from the potential drivers of latitudinal patterns, such as spatial climate variation over Earth history. The LDG is a pattern with respect to latitude, not with respect to climate regime. Climate and its variation throughout Earth history is one hypothesized driver of the LDG, but spatial variation in climate does not negate differences in diversification rates across latitudes, which may have occurred as climate changed over time.

The original formulation of the 'age and area' hypothesis likely dates to Wallace (1), who noted that equatorial regions have suffered less from climate change than temperate regions (6). Wallace's argument implicitly assumed higher

Fig. 2. Present-day Köppen-Geiger climate classifications for tropical, arid, temperate, cold, and polar regions. Tropical climate regimes are not larger in areal extent than extratropical climate regimes. However, individual 'tropical' climate classifications span larger areas, on average, than individual 'temperate' classifications, listed here. The individual climate categories are ranked from largest to smallest in area (km²) and were calculated using an equal area (Eckert 4) map projection at 10-km resolution from Beck et al. (70). Analyses relied on the R v.4.2.1 computing environment using the sf package (42) and ggplot2 (43).

Area 10⁴ km²	Köppen-Geiger climate classification	Area 10⁴ km²	Köppen-Geiger climate classification
2209.74	**A:** Desert, hot	261.22	**C:** Dry summer, cold summer
2108.25	**P:** Frost	202.23	**C:** No dry season, hot summer
1892.18	**C:** No dry season, cold summer	175.2	**T:** Dry winter, warm summer
1718.73	**Tr:** Savannah	153.46	**T:** Dry summer, hot summer
1138.9	**P:** Tundra	123.7	**C:** Dry winter, hot summer
902.53	**A:** Steppe, cold	120.39	**C:** Dry winter, warm summer
797.12	**A:** Steppe, hot	120.28	**C:** No dry season, very cold winter
772.2	**A:** Desert, cold	88.7	**T:** Dry summer, warm summer
758.87	**Tr:** Rainforest	56.68	**C:** Dry summer, warm summer
751.94	**C:** No dry season, warm summer	45.43	**C:** Dry winter, very cold winter
566.28	**T:** No dry season, hot summer	25.25	**C:** Dry summer, hot summer
530.95	**Tr:** Monsoon	11.66	**T:** No dry season, cold summer
422.95	**T:** Dry winter, hot summer	10.94	**C:** Dry summer, very cold winter
325.5	**C:** Dry winter, cold summer	0.26	**T:** Dry winter, cold summer
297.1	**T:** No dry season, warm summer	0.21	**T:** Dry summer, cold summer

rates of extinction/extirpation at high relative to low latitudes or greater high to low latitude dispersal (7, 71), and provides a corollary to the 'tropics are stable' hypothesis that implicates relatively low extinction rates at low latitudes (72).

There is little doubt that high-latitude cooling and glaciation instigated extinction, extirpation, or range shifts at high latitudes over Earth history [often defined as exclusive of 23.26° latitude, though see (68)]. Higher extinction rates at high latitudes have been reported for many clades, including vertebrates (40, 67, 73, 74), invertebrates (74, 75), and plants (76).

Comparisons of species' age distributions based on molecular phylogenies (73, 77) and fossil data (54, 75) additionally suggest a role for high latitude extinction, with greater variance in taxon age at low latitudes suggesting older taxa were preferentially lost at high latitudes (78).

Distributional patterns for groups also reveal a role for high latitude extinction or extirpation. For example, today, beetles with poorer dispersal abilities exhibit a steeper richness gradient across Europe compared to more vagile beetles better able to colonize regions once covered by ice (79). Fossil

data show similar evidence: high-latitude regions were richer in the past than they are today for many groups (80–82), particularly during warmer intervals such as the Eocene, around 55 to 45 million years ago (59, 60) (Fig. 1). During this time, the ancestors of bird clades now restricted to low latitudes were found as far north as ~47° paleolatitude, including the Anseranatidae, currently restricted to Australia and southern New Guinea, and the Coliidae, currently restricted to sub-Saharan Africa (40). Greater heat transport from the low to high latitudes in the Eocene warmed polar regions, allowing crocodylomorphs to roam Antarctica and to venture as far north as 73° in the Arctic circle (83). Indeed, many groups whose species are now restricted to lower latitudes today were found at higher latitudes during the Eocene, when temperatures were warmer. Consequently, LDGs may have been shallower during these warm intervals and steepened to their present-day configuration as climate cooled beginning around 34 to 15 million years ago (55, 66, 67, 84, 85).

Although Cenozoic cooling almost certainly drove high latitude extinction and extirpation, steepening the LDG (56, 67, 76, 79), these processes were likely not the only factors to have influenced the emergence of a modern-style LDG. Growing evidence suggests that low latitude speciation may have contributed to the formation of LDGs today, with perhaps even larger effects on LDG development than extinction dynamics (15, 54, 55, 84). Spatiotemporal climate change may instigate range fragmentation more readily at low latitudes, prompting higher rates of allopatric speciation and therefore piling up species equatorially (13, 14, 86, 87). This mechanism may operate in both the marine and terrestrial realm, with environmental heterogeneity possible across three dimensions (time, space, and depth) in the sea (55).

There is still much to be learned about variation in rates of speciation, extinction, extirpation, and dispersal regionally over Earth history. To better understand the development of LDGs, we need to better constrain this variation – only then will the mechanisms driving rate variation become clearer. This is no easy task. Direct inference from the fossil record can be challenged by gaps in spatial, temporal, and taxonomic coverage. Inferences from molecular phylogenies are similarly fraught: extinction is notoriously difficult to estimate (88, 89), and recent work suggests that any given extant timetree can be explained equally well by a large number of diversification scenarios (90). The latter represents a case of nonidentifiability, meaning that it is difficult to infer the true values of a given model's underlying parameters. Even approaches that combine fossil and molecular data to estimate evolutionary rates do not necessarily resolve issues of nonidentifiability (91).

Despite these difficulties, deeper insights on regional rate variation are still possible. New phylogenetic methods (92, 93) are providing means to examine whether diversification rate patterns are robust, despite issues of nonidentifiability. Geographic diversification models, such as GeoSSE (94) and ClaSSE (95), may help to elucidate spatial rate variation through time, especially when used in combination with fossil data. These methods should be employed to study new systems of relevance to LDGs, with focus on gathering empirical data for understudied groups, such as invertebrates. Paleontological models are also beginning to estimate rates of diversification regionally (96–98), with more work needed to develop our understanding of how spatial bias may affect rate parameters. Simulation models, such as mechanistic spatial algorithms, provide a new avenue to elucidate rate variation regionally over Earth history (15, 99–101), especially when forced with realistic estimates of how climate, continents, and topography have changed spatially and temporally over time (102). Even without realistic forcers, spatial models may provide null expectations for rate variation in silico (15).

Regional rate variation is best estimated using multiple approaches. This triangulation method echoes recent suggestions by Liow, Uyeda, and Hunt (103) and Meseguer and Condamine (67) to leverage diverse information, including phylogenetic estimates, fossils, developmental biology, and quantitative genetics, to better elucidate macroevolutionary history. For instance, more information on LDG dynamics may be provided when using phylogenetic and fossil data in a total-evidence framework (104) underpinned by several birth–death models that allow for rate variation through time and space. These diversification models can then be coupled to biogeographic analyses that estimate dispersal rates and local extinction rates in low and high latitudinal bands (56).

The richness of the tropics has long intrigued biologists. The pervasiveness of LDGs across ecosystems and clades rightfully deserves attention and begs a mechanistic explanation. Any explanation, however, must invoke differential rates of speciation, extinction, extirpation, or dispersal. Hypotheses that propose 'more time' for diversification over rate variation inadvertently eschew focus from the high latitude extinction or dispersal dynamics that are inherent to such arguments. Future work on LDGs should concentrate on better constraining variation in evolutionary rates across space and time using integrative, cross-disciplinary approaches (103, 105). The potential drivers of this rate variation, either biotic or abiotic in nature, will then become clearer.

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