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Opinion

The hierarchy of factors predicting the latitudinal diversity gradient

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The numerous explanations for why Earth's biodiversity is concentrated at low latitudes fail to explain variation in the strength and even direction of the gradient through deep time. Consequently, we do not know if today's gradient is representative of what might be expected on other planets or is merely an idiosyncrasy of Earth's history. We propose a hierarchy of factors driving the latitudinal distribution of diversity: (i) over geologically long time spans, diversity is largely predicted by climate; (ii) when climatic gradients are shallow, diversity tracks habitat area; and (iii) historical contingencies linked to niche conservatism have geologically short-term, transient influence at most. Thus, latitudinal diversity gradients, although variable in strength and direction, are largely predictable on our planet and possibly others.

Highlights

Myriad hypotheses try to explain the current latitudinal diversity gradient (LDG), with biodiversity concentrated in the tropics during a colder climate today than has been present for most of the history of complex life.

When Earth was hotter, however, LDGs were often flat or temperate-peaked.

Variation in the strength and direction of LDGs through deep time can be explained by the direct effects of climate, with habitat area becoming important when climatic gradients are shallow; less predictable factors such as organismal evolution to past climatic conditions – tropical conservatism – have short-term, transient influence at most.

Enhanced collaboration between ecologists and paleobiologists, bringing together data from both fields, is critical to better understand fundamental processes on our planet and possibly others.

The latitudinal diversity gradient and the test of time

The dramatic decline in biodiversity with increasing latitude is the most striking biological pattern on Earth. But would we expect to find a similar **latitudinal diversity gradient** (**LDG**; see Glossary) on other planets, or is the one here a feature of Earth's unique history and/or environmental idiosyncrasies? Robert May [1] speculated that if aliens visited our planet, the first question they would ask is how many species lived here. Would they also wonder why so many of these species were concentrated in our equatorial regions, or would they expect such a pattern based on other planets they had visited?

This question is about the predictability of the LDG. Numerous hypotheses posit broad **factors** that potentially drive the LDG, including climate, area, and history, with a variety of nonexclusive **hypotheses** for the specific mechanisms of influence [e.g., 2–6] (Box 1). These hypotheses include enhanced extinction rates [7] or reduced ecological carrying capacity [8] at high latitudes and latitudinal variation in dispersal capability [9,10]. Predicting LDGs on other planets or on Earth through deep time requires assessing the predictability of the factors themselves, as well as the predictability of the relationship between these factors and LDGs.

The factors vary considerably in their predictability. Climate is quite predictable – we can assess it reasonably well throughout the history of complex life on Earth (i.e., the **Phanerozoic**) [11], and we can even assess it remotely on other planets as a function of their position in the solar system and atmospheric chemistry (observable via Earth-orbiting satellites). Area is predictable as well, but less so – we have a good understanding of the distribution of land and shallow sea areas throughout the Phanerozoic here on Earth, but we will not be able to detect this on most other planets until probes or spacecraft actually approach them. Moreover, even on Earth, although we know that changing distributions of landmasses are driven by convective forces in the mantle, these forces themselves are somewhat of a black box. If we were to 'replay the tape' of Earth's history, it is not at all clear whether the shifting configurations of continents would have followed the same trajectory as played out this time. By contrast, given biogeochemical and solar energy

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Box 1. Comparing factors influencing LDGs

The LDG literature is replete with studies showing that diversity patterns are consistent with particular factors (hypotheses), but without rejecting others [2]. Important advances will include explicitly comparing support for different LDG factors and hypotheses. With additional data from past archives and methodological advances in ameliorating for spatiotemporal sampling heterogeneity, it will be possible to expand the quantification of the slope of the LDG (Figure I) to many more time periods throughout the Phanerozoic [22]. Meta-analyses could then assess LDG slope (response variable) as a function of paleoclimate, time-lagged paleoclimate, the proportion of habitat area at high versus low latitudes, and time-lagged habitat area, thereby explicitly comparing support for climate, niche conservatism, habitat area, and area.

As a side note, when we refer to 'flattened LDGs,' we mean with respect to the tropical and temperate zones, but not necessarily polar regions. Even during the hot Mesozoic, when LDGs for many taxa were flattened, groups such as sauropod dinosaurs were still unable to occupy very high latitudes [34,49], likely due to temperature rather than productivity constraints, so there were still polar diversity declines.

It might also be possible to compare these factors experimentally. Microcosm experiments on bacteria have greatly elucidated our understanding of evolution and fitness [e.g., 50,51]. Bacteria in experimental microcosms can also exhibit diversification; Zhang *et al.* [52] showed that temperature influenced divergence and coexistence among phenotypic ecomorphs. To the extent that these ecomorphs are useful proxies for genetic or ecological divergence, it might be possible to experimentally assess diversity as a function of temperature, energy availability, seasonality, available area, and history.

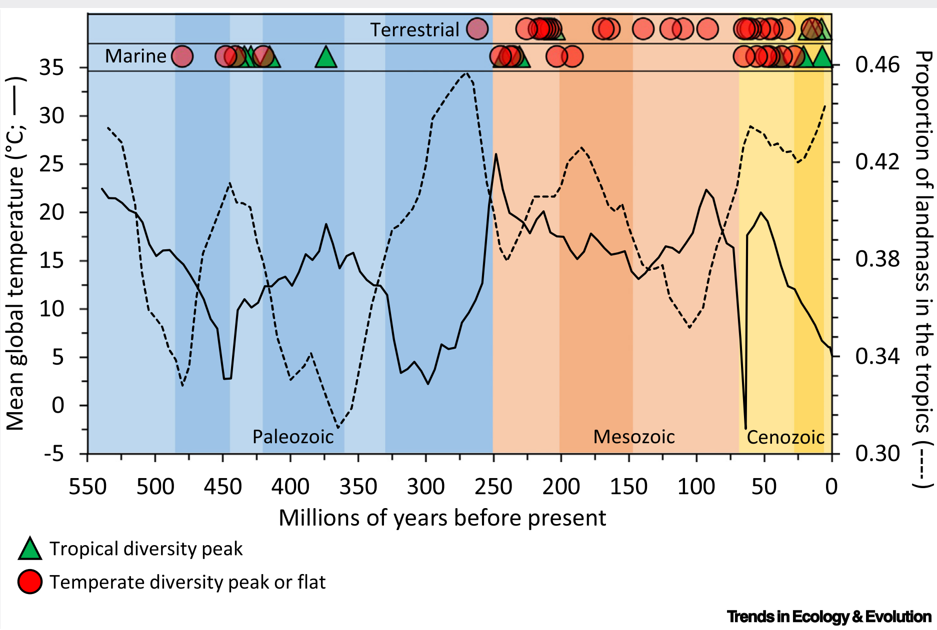

Figure I. Reconstructed latitudinal diversity gradients (LDGs), accounting for taphonomic and sampling biases, throughout the Phanerozoic. Periods (e.g., Cambrian, Ordovician) within each geological era are color banded but not labeled. Temperature and landmass data come from Scotese [11]; references for the LDG data are provided in the Supplementary Information.

parameters, we understand and can predict climate quite well [12]. Finally, historical contingencies as an LDG factor are, by definition, much less predictable. Many studies have argued that LDGs are products of organismal adaptation to conditions tens of millions of years earlier [e.g., 13–15] – parameters we cannot observe or predict on other planets.

Assessing the predictability of relationships between different factors and LDGs is the main focus of this opinion paper. A large and important body of literature continues to develop the theoretical underpinnings and ecoevolutionary mechanisms of different LDG hypotheses and factors

Glossary

Arctic conservatism: an implied (though never tested) corollary of the Tropical Conservatism Hypothesis whereby, following long periods of relatively cool conditions, most taxa would become cold-adapted. Following subsequent warming, biodiversity would become concentrated at high latitudes.
Ecological carrying capacity: the equilibrium number of species (or other taxa) that a given area is able to support based on finite ecological opportunity, diversity-dependent diversification, or a combination thereof.
Energetic Limits Hypothesis: posits that higher ecological carrying capacities are found in areas with greater per-unit-area energy available (e.g., the tropics) and/or larger areas with greater cumulative energy availability.
Enhanced Diversification Hypothesis: posits that the current LDG is driven by higher temperatures at low latitudes, leading to faster speciation, slower rates of extinction, or both.
Insolation: the amount of energy from the sun reaching a given portion of the planet.
Latitudinal diversity gradient (LDG): how the number of species or other taxa changes as a function of latitude. The current LDG on Earth is negative because diversity declines dramatically with latitude. But the LDG has had other shapes at different times.
LDG factors: general features that could affect the distribution of biodiversity across latitude, including climate, habitat area, and historical legacies.
LDG hypotheses: proposed processes by which a given factor influences the latitudinal distribution of diversity; for example, 'enhanced diversification' could be a way in which climate affects the LDG.
Phanerozoic: the last ~541 million years on Earth since the Cambrian 'explosion' of complex life.
Transient dynamics: geologically short-term (in this case, over thousands of years to a few million years) changes in diversity, following major climatic perturbations, where diversity is not at equilibrium.
Tropical Conservatism Hypothesis: posits that the current LDG is driven by most taxa having evolved megathermal conditions and become adapted to the warmth; because the world is currently very cool relative to most of its history, biodiversity is concentrated in the warmer, lower-latitude areas.

[6,8,16,17]. We complement this by comparing predictions of the different factors with LDG data through geological time. Indeed, combining ecological and paleobiological data can facilitate assessment of the predictability of the LDG on Earth by teasing apart the relative influences of the potential underlying factors. The LDG we observe today, with biodiversity highly concentrated in the tropics, has not always existed; a growing body of recent research reveals that the LDG has changed substantially over the Phanerozoic [18–25]. As currently formulated, most LDG hypotheses cannot explain temperate zone peaks in diversity or flattened gradients, as reconstructed for multiple taxonomic groups throughout much of the Phanerozoic (Table 1). We combine results and concepts from ecology and paleobiology to assess how a hierarchy of factors – climate, area, and historical contingencies – operating over different time scales could determine latitudinal distributions of diversity.

Factors driving the latitudinal distribution of diversity

Any planet with an axis of rotation outside its ecliptic will receive more cumulative **insolation** at lower latitudes. If latitudinal differences in abiotic conditions arising from this are responsible for diversity gradients, then planets harboring life might be expected to have LDGs. Several aspects of climate can affect diversity distributions, including temperature [6,22], precipitation [4,26], and seasonality [27]. Of these, temperature can be the most reliably estimated over deep time [11] and can influence diversity in multiple ways (discussed below); as such, we focus on this aspect

Table 1. Relative support from paleoecological data for climate and area as factors driving latitudinal diversity gradients

Time period	Global temperature (peak)	Relative proportion of landmass in tropics	Climate prediction for LDG peak	Area prediction for LDG peak	Observed LDG peak (Refs)
Evidence supporting a greater influence of climate than area					
Early Mesozoic (~250–220 Ma)	Hot	High	Temperate (The tropics were too hot for many taxa [33].)	Tropical	Temperate peak in synapsids [35], amphibians [23], dinosaurs [34], marine and terrestrial tetrapods [23], marine invertebrates [38]
Middle–Late Ordovician (~470–444 Ma)	Cool (tropical peak)	Low	Tropical	Temperate	Tropical in most marine invertebrates [22,36][a]
Short, early Cretaceous ‘cold-snap’ event (~145–133 Ma)	Hot (flat gradient) to cool (tropical peak), then back to hot	Consistently low	Temperate to tropical, then back to temperate	Consistently temperate	Temperate to tropical, then back to temperate for coral reefs [37]
Evidence supporting a greater influence of area than climate					
Neogene (~23–2.6 Ma) in North America only	Cool (tropical peak)	Low	Tropical	Temperate	Temperate peak in North American mammals [19]
Evidence agnostic about the relative influence of climate and area					
Mid–late Mesozoic (~220–66 Ma)	Hot (flat gradient)	Low	Temperate	Temperate	Temperate peaks in both the marine [20,23] and terrestrial [23,34,35] realms
Neogene (~23–2.6 Ma)	Cool (tropical peak)	High	Tropical	Tropical	Tropical peak in crocodilians [39,47] and marine plankton [10]
Quaternary (~2.6–0 Ma)	Cold (tropical peak)	High	Tropical	Tropical	Tropical peak in nearly all taxa [48]
Evidence inconsistent with current latitudinal diversity gradient hypotheses					
Cold intervals of the Permian (~299–280 Ma)	Cold (tropical peak)	High	Tropical	Tropical	Temperate peaks in some terrestrial taxa [44]

Abbreviation: LDG, latitudinal diversity gradient.
[a]Marine diversity is generally highest in shallow seas of continental shelves; therefore, an area-based explanation for LDGs would predict higher marine diversity in areas with larger landmasses.

of climate. Furthermore, at a coarse scale, global mean temperature is also thought to be negatively associated with seasonality [28] and can thus be a proxy for other aspects of climate. It is also important to note that throughout the Phanerozoic, when Earth was hot, temperatures have tended to vary less notably from low to high latitudes; only when Earth has been cooler have strong temperature gradients developed from the tropics to high latitudes, as we see today [11].

There are numerous hypotheses for how climate influences the LDG; we follow Mittelbach *et al.* [6] in grouping them into two broad categories. First, higher per-unit-area energy availability (i.e., higher insolation, assuming sufficient water and nutrients for plant growth) at low latitudes could lead to higher ecological carrying capacities there (the **Energetic Limits Hypothesis**) [e.g., 8,29]. Second, diversification (speciation minus extinction) rates could increase with temperature and/or decrease with seasonality (the **Enhanced Diversification Hypothesis**) [e.g., 27,30–32]. These hypotheses are clearly not exclusive (i.e., diversity 'limits') [17]. Climatic mechanisms would also operate via large-scale dispersal of taxa toward megathermal areas [10,22].

Peaks in diversity at temperate latitudes could arise for two reasons. First, during particularly extreme intervals within hothouse climate states, equatorial regions might be too hot for many organisms [33], and thus diversity becomes concentrated at higher latitudes [23]. Second, when mean global temperatures are high, there is generally an accompanying flattened latitudinal temperature gradient, such that diversity can track other factors such as habitat area.

Indeed, diversity could be higher in megathermal areas because they have been geographically larger than cold areas throughout most of the history of life and because larger areas support more species [16]. Positive relationships between present-day diversity and area are so ubiquitously observed that species–area relationships constitute one of ecology's few laws. But such relationships mostly apply within, not across, climatic zones; a 50-hectare research plot in tropical Borneo, for example, has more tree species than Earth's entire North Temperate Zone.

Other hypotheses propose that the LDG is due to historical contingencies that might not be duplicated on other planets, or if we could replay Earth's history with different abiotic conditions. For example, diversity might be associated with temperature or seasonality simply because most extant taxa happened to originate in warmer, less seasonal conditions [15] or to have adapted to aseasonal conditions such as those during the early–middle Eocene (~56–40 million years ago [Ma]), when many extant taxonomic families arose or diversified (the **Tropical Conservatism Hypothesis**). Such hypotheses clearly invoke climate, but in a much less predictable fashion than the 'climate' factor discussed in the preceding text, where current abiotic conditions directly drive the LDG in relatively predictable ways. (Global diversity will nearly always increase with temperature, for example.) Historical contingencies are different in that it is legacies of past climates that influence LDGs [13,14], and the relationship between temperature and diversity would not necessarily be positive, but would instead depend on past evolution. For example, tropical conservatism has an implied corollary, here termed '**Arctic Conservatism**,' positing that if Earth had been very cold throughout the Cenozoic and then warmed recently, we would expect to see diversity concentrated in polar regions – the climatic zone to which most taxa had adapted.

The hierarchy of LDG factors

Substantial research has assessed the theoretical underpinnings and ecoevolutionary mechanism of various LDG hypotheses [e.g., 6,17], but there has been little accompanying work to compare predictions from these hypotheses against paleoecological data. In qualitatively assessing the relative support for climate, area, and historical legacies based on paleolatitudinal diversity gradients, we find that LDGs are largely predictable based on their strong relationship to climatic conditions at the time. The relative importance of climate and habitat area could be distinguished via two scenarios where the factors would generate divergent predictions about the LDG. When the climate is relatively hot and a high proportion of the global landmass is in the tropics, the climate and area hypotheses would predict that the LDG would have temperate versus tropical peaks, respectively. When the climate is relatively cool and a low proportion of land is in the tropics, the climate and area hypotheses would predict that the LDG would have tropical versus temperate peaks, respectively. The first scenario is approximated by the early Mesozoic and the second by the Middle–Late Ordovician; most studies from these time periods recover temperate diversity peaks during the former [e.g., 23,34,35] and tropical peaks during the latter [22,36] – both consistent with climate being a stronger driver than habitat area of the LDG (Table 1). Some taxa in some areas buck this trend – Neogene North American mammal diversity was greater at higher than at lower latitudes [19], despite the world being generally cool, potentially reflecting the much greater land area at high than low latitudes in this continent at that time (Table 1). Further evidence supporting a stronger influence of climate than area comes from a natural experiment in which a geologically short-lived, relatively cool period (~145–133 Ma) developed during the otherwise warmhouse world of the Early Cretaceous [37], whereas the latitudinal distribution of continental area stayed essentially constant [11]. The LDG of coral reefs went from being relatively flat before the cooling to a tropical peak during the cooling, returning to a flattened gradient afterward [37].

Habitat area clearly has an important influence on the distribution of diversity, but the evidence outlined previously suggests that this effect is secondary to that of climate – modifying the impacts of climate or operating when spatial variation in climate is relatively low. Area seems to have primarily contributed to global diversity gradients when the world was hot and climate gradients were relatively flat across latitudes (Table 1); this is apparent during much of the Mesozoic in both the marine [20,23] and terrestrial [23,34,35] realms, though marine groups bucked this trend temporarily [38] and terrestrial crocodylomorphs for most of the era [35,39].

Available evidence suggests that historical legacies have relatively limited influence on LDGs (Table 2). Many tropical conservatism studies focus on the post-Eocene [e.g., 13,14,40], as the world has cooled substantially over the last ~34 million years. Tropical conservatism might be amplifying the current LDG if extant lineages have remained warm-adapted since the Eocene. But it remains difficult to explain why it would take >30 million years for organisms to adapt to altered temperature conditions (i.e., the much lower temperatures now than during the Eocene). Plant diversity, for example, rose extremely quickly (i.e., within ~20 000 years) during the acute spike in global temperatures during the Paleocene–Eocene Thermal Maximum (56.3 mya) [41]. Mirroring this, late Carboniferous cooling was associated with rapid declines in plant [42] and tetrapod [43] diversity. Arctic conservatism is likewise not supported by fossil data. The mid-Carboniferous through mid-Permian saw an ~70–million year stretch of some of the coldest temperatures of the Phanerozoic [11]; however, as the world warmed in the late Permian, diversity remained concentrated in the tropics [38] or temperate zone [23,44] rather than retreating to the poles. All of this is inconsistent with the tropical conservatism hypothesis's suggestion that the current tropical peak LDG is a holdover from climatic conditions of >30 Ma.

Historical legacies can best be described as **transient dynamics** in spatial biodiversity patterns (see Box 2). Over relatively short geological time periods – hundreds of thousands to potentially a few million years – global diversity patterns might be nonequilibrial and therefore unpredictable. For example, following a long cold period, rapid warming occurred in the late Permian, with global mean sea surface temperatures rising from ~28°C to ~32°C in just a few hundred thousand years; this led to the apparent extinction of tropical seed plants and equatorial marine algae

Table 2. General lack of support from paleoecological data for historical contingencies driving latitudinal diversity gradients

Conditions prior to climatic change	Climate change event	Historical legacy predictions for LDG	Evidence
Mid-Carboniferous through mid-Permian: an ~70 million year stretch of some of the coldest temperatures of the Phanerozoic [11]	Rapid warming in the late Permian over just a few hundred thousand years [38]	Retreat of diversity from the tropics to high latitudes	The apparent extinction of tropical seed plants and equatorial marine algae helped flatten the LDG [33], but equatorial marine algae began to reappear shortly thereafter (at even hotter temperatures than what drove the extinctions). This demonstrates that the absolute temperatures were not too hot for these organisms, suggesting that their cold adaptations could have contributed to their late Permian extinctions. Nevertheless, historical legacies ('arctic conservatism') did not shape the overall LDG in that diversity remained concentrated in the tropics [38] or temperate zone [23,44] rather than retreating to the poles.
Warm Late Cretaceous [11]	Dramatic cooling after the asteroid impact at the Cretaceous/Paleogene boundary (66 Ma)	Switch from flat LDG to tropical peak	Terrestrial tetrapod LDGs remained fairly constant from the Late Cretaceous to the early Paleogene [19,34]
Warm early Paleogene [11]	Acute spike in global temperature during the Paleocene–Eocene Thermal Maximum (56.3 mya) [41]	Flattening of LDG driven by extinction of tropical taxa not adapted to the new temperature regime	While there is little evidence for the shape of global LDGs at the time, Neotropical plant diversity rose extremely quickly (i.e., over ~20,000 years) rather than suffering major extinctions [41]

Abbreviation: LDG, latitudinal diversity gradient.

[33]. Temperatures then continued to rise, peaking at ~38°C or even >40°C in the Early Triassic. But equatorial marine algae began to reappear when sea surface temperatures cooled back to ~34°C (i.e., still hotter than what drove the initial extinctions). The group then persisted during a much more gradual (over ~1.5 million years) temperature rise to ~36°C and then, as temperatures held steady for another ~1.3 million years, began to slowly diversify [33]. In short, in assessing how temperature changes affect diversity, it is critical to consider all of the following: the rate at which temperatures change, the absolute magnitudes of the temperatures achieved, and the previous conditions to which the organisms had adapted. As a counterpoint, however, we note that terrestrial tetrapod LDGs remained fairly constant from the Late Cretaceous to the early

Box 2. Drivers of LDGs over different time scales

Historical legacies can modulate spatial patterns of diversity over short timescales, but they have limited impact on geologically long-term biodiversity patterns. If the present-day LDG were based on such historical legacies, fast-evolving taxa should have shallower or flatter LDGs than those of slower-evolving organisms because they have had many more generations to adapt to current climatic conditions. We are unaware of analyses that formally test this prediction, but a qualitative assessment of the literature suggests that some fast-evolving microbial groups display declining diversity with latitude [e.g., 53–55], though others show flat [56] or hump-shaped [57] relationships. (It is also worth noting here that patterns of micro-organism diversity are more related to local environmental conditions than to dispersal capabilities [57].)

By contrast to historical, legacy-based LDG hypotheses, it might be that evolution is often limited or constrained such that cold-tolerance traits are difficult or even impossible to achieve in many groups. Megathermal conditions, such as those in today's tropics, might simply support higher long-term fitness for more taxa than do colder conditions [58,59]. Indeed, global cooling is associated with diversity declines for plants [42] and tetrapods [43] at the Carboniferous–Permian transition and for plants from the middle Eocene to the Oligocene [60]. Although fitness might continue to increase indefinitely, the rate of increase becomes slower over time [61]. Therefore, overall diversity at high latitudes is unlikely to catch up to the levels observed in the tropics. This would suggest that the climatic history of the Cenozoic is irrelevant for explaining the current LDG. Diversity would be higher in the tropics today simply because more taxa are able to survive in megathermal conditions, rather than because lineages retain, for tens of millions of years, adaptations to the conditions in which their ancestors had evolved. This would also be consistent with alternate LDGs at different times in the past, such as when tetrapod diversity was flat across latitude during much of the Mesozoic [34,39]. Indeed, evolution is likely limited or constrained in most taxa. Although all animal phyla originated in the marine realm, 21 out of the ~32 of them have never adapted to land, despite having had ~540 million years of opportunity to do so (i.e., since the Cambrian explosion).

Paleogene [19,34], despite the devastating climatic changes wrought by the asteroid impact at the Cretaceous/Paleogene boundary (66 Ma), demonstrating that transient dynamics do not always affect LDGs.

The picture that emerges is that over hundreds of millions of years, the latitudinal distribution of diversity is driven primarily by geologically long-lasting global climatic states. Mannion *et al.* [18] argued that during coolhouse and icehouse climate states [sensu 45], such as we are in now, global diversity tends to be concentrated at low latitudes; by contrast, during warmhouse and hothouse climate states, which characterized Earth from the late Paleozoic until ~34 Ma, life can be more evenly distributed across latitudes or exhibit temperate peaks in diversity. Evidence accumulated since that publication continues to broadly support this pattern, though we now have a better appreciation of the nuances involved. For example, although LDGs of most tetrapod groups during the warm-to-hothouse Mesozoic were temperate-peaked or flat, many marine invertebrate groups show a tropical peak even during the very warm Middle Triassic [38]. Diversity patterns during the early–middle Permian also do not fully conform to the general pattern. This interval was relatively cold and had substantial tropical landmass, leading us to expect tropical diversity peaks. This appears to be the case for marine groups [38] but not for terrestrial tetrapods [44], though it remains possible that poor tropical sampling could be artificially flattening the tetrapod LDG [e.g., 24].

Concluding remarks

By looking at temporal changes over the Phanerozoic (see Outstanding questions), we can assess whether the LDG is likely to be predictable as a function of latitude. Over thousands to potentially millions of years, diversity distributions might exhibit some stochasticity, which might partly explain the low tropical diversity in the Early Triassic [38] following a geologically instantaneous major environmental perturbation [33]. Over periods of up to a few million years, diversity patterns can be influenced by historical legacies because organisms need time to adapt to current conditions. But over longer time scales – tens to hundreds of millions of years – the spatial distribution of diversity appears to be predictably based primarily on climate.

Factors beyond those addressed here might still play important roles as well – no currently formulated LDG hypothesis can explain, for example, temperate diversity peaks observed in some taxa during cold intervals of the early–middle Permian [44] or tropical-peaked marine LDGs during the hot Middle Triassic [38]. One issue could be that the LDG literature tends to assume that gradients are broadly the same for all taxa. But there could be important differences among groups [35,46] (Table 1), between marine and terrestrial realms [33,38], and between organisms with different sizes and dispersal capabilities [20,46].

Our findings have clear implications for a range of conceptual areas, from our basic understanding of ecology to our ability to predict ecological conditions on other planets. On planets near the cold end of their habitable zone, the diversity of living organisms (if roughly Earth-like in architecture) should tend to be highest in the equatorial regions, whereas planets near the hot end of their habitable zone should tend to have higher-latitude peaks in diversity. On hot planets, or at times with shallow latitudinal climate gradients, diversity should show a closer correspondence to habitat area. Enhanced collaboration between ecologists and paleobiologists, bringing together data from both fields, is critical to better understand the causes and variation of LDGs.

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Outstanding questions

What is the range of variation in the slope of the relationship between biodiversity and latitude over deep time and across taxa? Additional paleontological data are critically needed to address this, including from multiple taxonomic groups, environments, and time intervals.

What other factors, besides climate, habitat area, and historical legacies, could affect the strength and direction of latitudinal diversity gradients (LDGs)?

Although the LDG literature tends to assume that gradients are broadly the same for all taxa, more work is needed to understand what has driven differential LDGs across lineages through deep time.

Additional data and focus are needed on what happened to LDGs during the rapid mid-Carboniferous cooling, when temperatures were analogous with the Cenozoic but the proportions of land in tropical versus temperate zones were very different.

Do statistical models of diversity over deep time tend to support the existence of ecological carrying capacities and/or climate-dependent diversification rates?

Do the slopes of current LDGs across taxa vary as a function of evolutionary rate? If LDGs result from historical contingencies such as tropical conservatism, we would expect the slope of the diversity–latitude relationship to become shallower as evolutionary rate increases.

Across taxa, does the evolution of cold tolerance tend to be limited by standing genetic variation or constrained by genetic, biomechanical, or other life history trade-offs?

As data on rocky exoplanets accumulate, can we statistically predict the distribution of landmasses and seas? With knowledge about the present-day climate and distribution of habitat area, planetary LDGs could be predicted with some accuracy. But although the generalities of global climate can be predicted from planets' positions within their solar systems and atmospheric chemistry (both of

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which can be observed from afar), there is currently no way to predict or observe habitat area.

Declaration of interests

The authors declare no conflicts of interest.

Supplemental information

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