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News & views

Evolution

Tropical biodiversity linked to polar climate

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The rise in species diversity towards the tropics is a striking and unexplained global phenomenon. Ocean microfossil evidence suggests that this pattern arose as a result of ancient climate cooling and polar-climate dynamics.

The increase in the number of plant and animal species as one moves towards the Equator from higher latitudes is one of the most notable and consistent patterns on land and in the sea. Although the phenomenon has been known since the nineteenth century[1,2], the reasons for this latitudinal diversity gradient (LDG) are not fully understood[3]. The most commonly implicated suspect is an even more glaring and robust latitude-dependent pattern, namely, the rise in temperature from the poles to the Equator. The appeal of temperature-based explanations is bolstered by the role of temperature in innumerable biological processes. But decades of research have not closed the gap between correlation and causation, leaving biodiversity and climate dynamics as largely separate fields of study. Writing in *Nature*, Fenton *et al.*[4] and Woodhouse *et al.*[5] join some of the missing dots.

A key difficulty in understanding LDG dynamics is that we must rely on nature's own uncontrolled experiments conducted through Earth's history. These produce spectacularly different states of the system, but rarely provide more than a fragmentary record of the data that would be needed to reveal the causes and consequences. However, new tools and approaches, including massive data compilations and Earth-system models, are filling this gap. As Fenton *et al.* and Woodhouse *et al.* report, a new database (called Triton) of ocean fossils spanning the past 40 million years provides a tantalizing picture of how climate has altered the LDG.

The most abundant data for detecting changes to the LDG come from an unlikely source – microscopic fossils of shell-forming ocean plankton called foraminifera. These fossils are ubiquitous in marine sediments, and their species classifications (taxonomy) are well established. Evidence of the distributions of foraminifera over space and time has been compiled in the Triton database, which, as the authors report, enables the detection of changes in the LDG for the past tens of millions of years. Because planktonic foraminiferal diversity is correlated with overall biological diversity[6], this work might shed light on the mechanisms that underlie the LDG for other groups of organism, too.

Biodiversity patterns reconstructed by the authors from Triton's foraminifera data reveal surprising features. First, LDGs were much flatter roughly 40 million years ago than they are today. The climate then was warmer. Indeed, both studies report that the LDG gradually steepened and became more obvious during the ensuing period of global cooling, to emerge in its modern form and magnitude only around 15 million years ago as Fenton and colleagues indicate.

This finding complements other palaeobiological studies of LDGs, for example work showing that warming since the last ice age has shifted the maximum foraminiferal diversity away from the Equator towards higher latitudes[7]. Moreover, other research indicates that, for a broader set of marine animal groups, a relatively flat LDG followed the major warming-induced extinction that occurred at the transition between the Permian and Triassic periods approximately 252 million years ago[8], owing to poleward migration and a higher risk

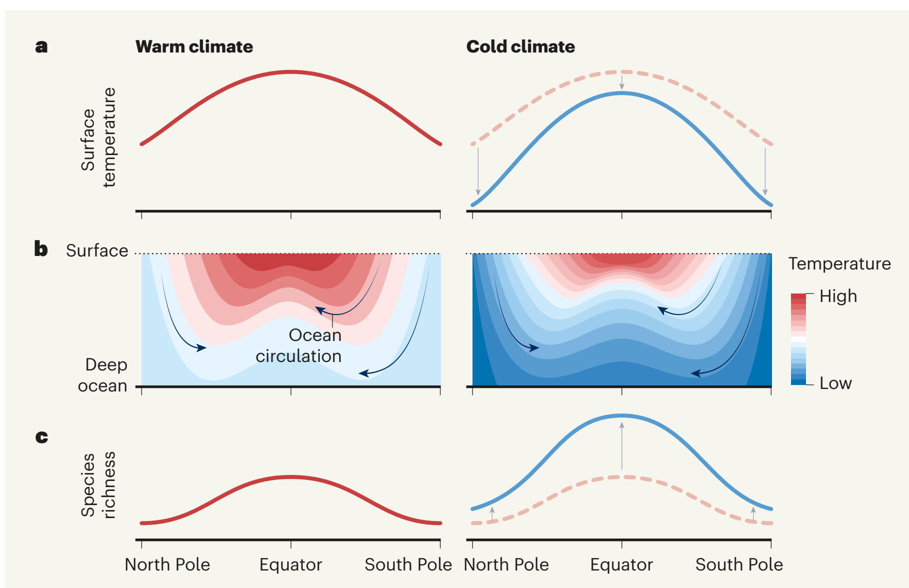

Figure 1 | A proposed link between climate and ocean biodiversity. Fenton *et al.*[4] and Woodhouse *et al.*[5] examined fossil records of ocean plankton to assess how species diversity changed as the climate varied over millions of years. **a**, When the climate cools, the change in ocean surface temperature between a warm (red dashed line) and a cold (blue line) climate is greatest near the poles – a phenomenon known as polar amplification. The conceptual model shown indicates how polar amplification might affect tropical (Equatorial) and global patterns of species diversity; these form what is known as the latitudinal diversity gradient. **b**, Ocean circulation (blue arrows) translates the gradient in surface temperatures into a vertical pattern of temperature zones that might harbour distinct species in given zones. A colder climate has more such zones spanning the ocean's depth, especially in the tropics, than does a warmer climate. **c**, The tropics in a colder climate thus have more biodiversity than in a warmer climate, resulting in a more obvious latitudinal diversity gradient pattern from the poles to the tropics.

of extinction for polar species[9]. Thus, a flatter LDG seems to have been a common feature of warmer climates.

The second revelation from the new Triton evidence concerns the cause for this trend. Why would global cooling have produced a strong rise in species richness in the tropics? At first glance, this observation seems counter-intuitive. If warmer climatic zones of the tropics are associated with greater diversity today, a warmer past would be expected to have had even more species, not less. This simplistic substitution of space for time does not explain the fossil record. Instead, both new analyses emphasize the importance of the 'vertical niche' — the layering of species across depth.

Using simulations of the global climate, Fenton and colleagues find that the diversity of tropical species is correlated with the vertical temperature variation in the water column. In short, enhanced tropical species richness follows an increased number of closely packed thermal niches from a steeper vertical temperature gradient in cold climates compared with that during warmer periods, an idea long advanced to explain terrestrial tropical diversity in relation to altitude[10]. If this vertical temperature gradient (tropical-ocean stratification) is enhanced in a cold climate, then species diversity should rise even as temperatures fall.

The suggestion that marine diversity across latitude reflects the thermal stratification of the ocean provides a simple and elegant link between biodiversity patterns and a well-established aspect of climate dynamics known as polar amplification. At equilibrium, both warming and cooling of surface climate are amplified near the poles, owing to climate feedback effects[11]. And because deep-ocean waters obtain their temperature from high-latitude surface waters, ocean circulation translates the global latitude gradient in sea surface temperature into the vertical temperature range of the tropics (Fig. 1).

Thus, a stronger Equator-to-pole gradient in the sea surface temperature in colder climates yields more-variable thermal niches across depth especially in the tropics. More thermal niches over depth could accommodate more species, with the effect being greatest in the tropics, consistent with the Triton data. The filling of these niches could occur through the evolution of new species, as indicated by Fenton *et al.*, or through the migration of species from the poles towards the Equator, as indicated by Woodhouse and colleagues, or both.

This intriguing link between polar amplification and tropical species diversity highlights key areas for future enquiry, which will be needed to close the gap between climatic correlation and its deeper biological causation. The concept of a thermal niche and the number of species that can fill it are central to developing mechanistic biodiversity models to help fill this gap, yet such efforts are often still poorly rooted in organismal biology and ecology.

Although the edges of species' geographical ranges align partly with temperature, their habitat boundaries are also strongly modulated by oxygen levels, not to mention species interactions. Because thermal stratification across water depth also tends to promote sharper oxygen gradients, the diversity–temperature correlations found by Fenton and colleagues might be jointly mediated by the availability of oxygenated habitats. A valuable test of the vertical-niche hypothesis would be to investigate whether the observed trends are consistent with thermal niches quantified from species thermal-tolerance traits[12].

Perhaps the greatest challenge will be in deciphering the degree to which this proposed mechanism might be responsible for the LDG for other plant and animal groups, such as those more familiar to casual observers or, indeed, to natural historians such as Alexander von Humboldt, who first articulated the LDG concept[2]. The tropical rainforests on land, or coral reefs in the ocean, are strikingly diverse but are not generally regions of strong temperature gradients, vertical or otherwise.

Whether the enigmatic global LDG and its relationship to climate variability turn out to arise from a diverse set of idiosyncratic causal chains with temperature as a major link, or instead rest on deeper mechanisms from thermal aspects of biology that operate across other domains of life, remains to be seen. Either way, rapidly growing global biogeographical data sets and their integration with Earth-system models linked to climate data are accelerating the pace of discovery and understanding of the past and future fate of Earth's biodiversity.

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1. Wallace, A. R. *Tropical Nature and Other Essays* (Macmillan, 1878).
2. von Humboldt, A. *Ansichten der Natur: mit wissenschaftlichen Erläuterungen* (Cotta, 1808).
3. Brown, J. H. *J. Biogeogr.* **41**, 8–22 (2014).
4. Fenton, I. S., Aze, T., Farnsworth, A., Valdes, P. & Saupe, E. E. *Nature* https://doi.org/10.1038/s41586-023-05712-6 (2023).
5. Woodhouse, A., Swain, A., Fagan, W. F., Fraass, A. J. & Lowery, C. M. *Nature* https://doi.org/10.1038/s41586-023-05694-5 (2023).
6. Yasuhara, M., Tittensor, D. P., Hillebrand, H. & Worm, B. *Biol. Rev.* **92**, 199–215 (2017).
7. Yasuhara, M. *et al. Proc. Natl Acad. Sci. USA* **117**, 12891–12896 (2020).
8. Song, H. *et al. Proc. Natl Acad. Sci. USA* **117**, 17578–17583 (2020).
9. Penn, J. L., Deutsch, C., Payne, J. L. & Sperling, E. A. *Science* **362**, eaat1327 (2018).
10. Janzen, D. H. *Am. Nat.* **101**, 233–249 (1967).
11. Hahn, L. C., Armour, K. C., Zelinka, M. D., Bitz, C. M. & Donohoe, A. *Front. Earth Sci.* **9**, 710036 (2021).
12. Penn, J. L. & Deutsch, C. *Science* **376**, 524–526 (2022).

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