Explanations for tropical diversity gradients are rooted in the deep past

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Species are distributed unevenly across the surface of the Earth. More species are found in the warm tropics than in cool temperate regions. This pattern was first recognized over two centuries ago by Alexander Von Humboldt, with his observation "*The nearer we approach the tropics, the greater the increase in the variety of structure, grace of form, and mixture of colors, as also in perpetual youth and vigor of organic life.*"

The incredible variety of form, color, and lifestyle found near the equator, and the relative paucity near the poles, is one of the most ubiquitous biological patterns on Earth, referred to as the latitudinal diversity gradient (LDG) (1). Biodiversity, however, not only varies latitudinally but also longitudinally. Even within the species-rich tropics, some regions house fewer species than others. Tropical rain forests, for example, are the most species-rich terrestrial ecosystem on the planet (2, 3), but they host comparably fewer species in Africa compared to the Neotropics and Indomalaya (3-5). In PNAS, Hagen et al. (6) use cutting-edge simulations to examine how and when differences in tropical diversity arose, which they term 'pantropical diversity disparity' (PDD). In doing so, the authors provide key insight into evolutionary mechanisms and ecosystem constraints.

Biodiversity gradients, including pantropical diversity disparity, can be explained only using combinations of differential speciation, extinction, and dispersal rates. That is, spatial diversity gradients emerge only from the generation of new species via speciation, the removal of existing species via extinction, or the movement of species into or out of regions via dispersal (7). Therefore, to explain diversity variation across the surface of the Earth, we must understand the levers that control rates of speciation, extinction, and/or dispersal. These three processes are thought to be initiated and inhibited by myriad abiotic and biotic events, such as climate change, mountain building, biotic invasions, and tectonic movement, to name only a few.

Hagen et al. (6) provide insight into the levers that may have instigated pantropical diversity disparity by directly modelling speciation, extinction, and dispersal over the last 110 million years. Their model uses virtual species that are assigned behavioral rules—essentially a model of their ecology and evolution. This eco-evolutionary model is then coupled to models for how the Earth system has changed in its climate, tectonic plate configuration, and mountain building over the last 110 million years.

The new model from Hagen et al. (6) begins with no pantropical diversity disparity and a single, widely distributed virtual species. Over the course of the simulation, this species responds to climate and other geohistorical changes that can—if the conditions are right—

instigate speciation, extinction, and dispersal. At the end of the simulation, a pattern of diversity emerges that can be compared to empirical diversity patterns today. If simulated and empirical diversity patterns match, the model tells us something important about what regulates speciation, extinction, and dispersal, and how their rates have varied across the surface of the Earth.

Interestingly, although previous work has suggested pantropical diversity disparity correlates closely with contemporary climate (5, 8), Hagen et al. (6) find virtually no support for this relationship. Although correlation does not indicate causation, the absence of correlation suggests present-day climate conditions do not structure spatial patterns of diversity in the tropics. Instead, the authors were able to simulate realistic-looking pantropical diversity gradients using historical estimates for how climate has changed, how mountain building has occurred, and how tectonic plates have moved. Hagen et al. (6) therefore suggest we must look to the deep past to understand the genesis of biodiversity.

In particular, Hagen et al.'s (6) model suggests mountain building has prompted high rates of speciation in the Neotropics and in Indomalaya, piling up species in these regions. Mountain building is thought to be particularly effective at generating new species because it creates a dynamic and complex landscape. This topographic, and therefore climatic, complexity can easily isolate populations and thus instigate allopatric speciation (9-11). In contrast to Indomalaya and the Neotropics, relatively little mountain building has occurred in Africa over the last 100 or so million years. This is because mountain building occurs when tectonic plate boundaries crash together, and Africa has had no such boundary over this period. Thus, African tropical forests did not receive the same injection of species from mountain building as did the Neotropics and Indomalaya.

Afrotropical diversity may also be low compared to other tropical hotspots due to high extinction rates. Hagen et al. (6) found that aridification in Africa from the Miocene onwards, ~23 million years ago, could have shrunk species' geographic ranges, leading to high extinction rates (12, 13). This result matches previous expectations that differences in extinction rates regulate pantropical diversity disparity (3, 13).

Not only do Hagen et al.'s (6) simulations reveal a historical origin for pantropical diversity disparity, but they also expose, more precisely, when this gradient may have developed. Was it only a few thousand years in the past, or do we need to invoke tens of millions of years of Earth system change to understand the full complement of processes causing differential pantropical diversity? The model seems to suggest a deeper time origin. Based on their simulations, the gradient formed as early as 35 million years ago, prior to the Eocene-Oligocene boundary. Again, this potential early origin suggests we cannot look only to modern-day to explain biodiversity patterns. Instead, we must invoke and understand the complex geological and climatic history of each region, which together have moulded present-day biodiversity (9). The dramatic and dizzying array of changes that have occurred in the distant past have pushed, pulled, and shaped tropical diversity to what it is today (10, 14).

Although many of the simulations run by Hagen et al. (6) produced pantropical diversity gradients, not all of them did. The occasional failure of their model to instigate a pantropical diversity gradient itself provides useful information. What conditions are needed to replicate the gradient? It turns out the simulations required an eco-evolutionary model that included niche conservatism. That is, the model needed to prohibit species from evolving their abiotic tolerances. Simulations that enforced a constraint of niche conservatism produced more realistic-looking gradients. This result is congruent with suggestions that niche conservatism is important in maintaining diversity gradients (15), and with previous simulation work in which global-scale diversity gradients emerged under the same constraint (16).

Niche conservatism may be crucial to generating diversity gradients for two reasons. First, niche conservatism may promote isolation when species' geographic ranges become fragmented by climatic or geographic barriers (e.g., mountains, rivers, ravines), eventually leading to allopatric speciation. Thus, niche conservatism is thought to facilitate allopatric speciation during periods of mountain building or when climate fluctuates across space and through time. Gradients begin to emerge when mountain building or climate change occurs at higher frequency in some regions than in others. The second reason that niche conservatism may be key to generating diversity gradients is because stable niches retain species and clades within biogeographic regions and prohibit broad-scale movement outside of specified climatic bounds. This constraint allows species to pile up in certain regions in the presence of a strong species pump, such as mountain building.

Computer simulations—which can be referred to as experiments *in silico*—have great potential to provide insight on the drivers of ecological and evolutionary processes (17, 18). The work of Hagen et al. (6) shows that we have much to learn from Earth history. Many of the patterns that biologists attempt to explain today have their likely origins in the deep past. A deeper origin to spatial patterns of biodiversity has been suggested by similar models that replicated larger-scale latitudinal gradients in diversity (16, 19). Together, *in silico* models support a role for topographic and climatic heterogeneity as primary levers on speciation, extinction, and dispersal rates, which have sculpted modern-day diversity gradients.

Although much has been learned, significant questions about diversity gradients remain. Chief among these is whether the same suite of processes can explain diversity gradients across taxa and ecosystems. As Hagen et al. (6) note, a natural next step in simulation studies is to determine the key ingredients necessary to maintain diversity gradients across ecosystems and regions. One way to identify potential common causal factors is to add or subtract different ecological and evolutionary components within *in silico* experiments and assess their effect on biodiversity patterns. By instigating higher rates of allopatric speciation, spatio-temporal environmental heterogeneity may be one common factor that explains spatial diversity differences, regardless if focus is on the pantropical diversity gradient (6) or the latitudinal diversity gradient on land (16) or in the sea (20).

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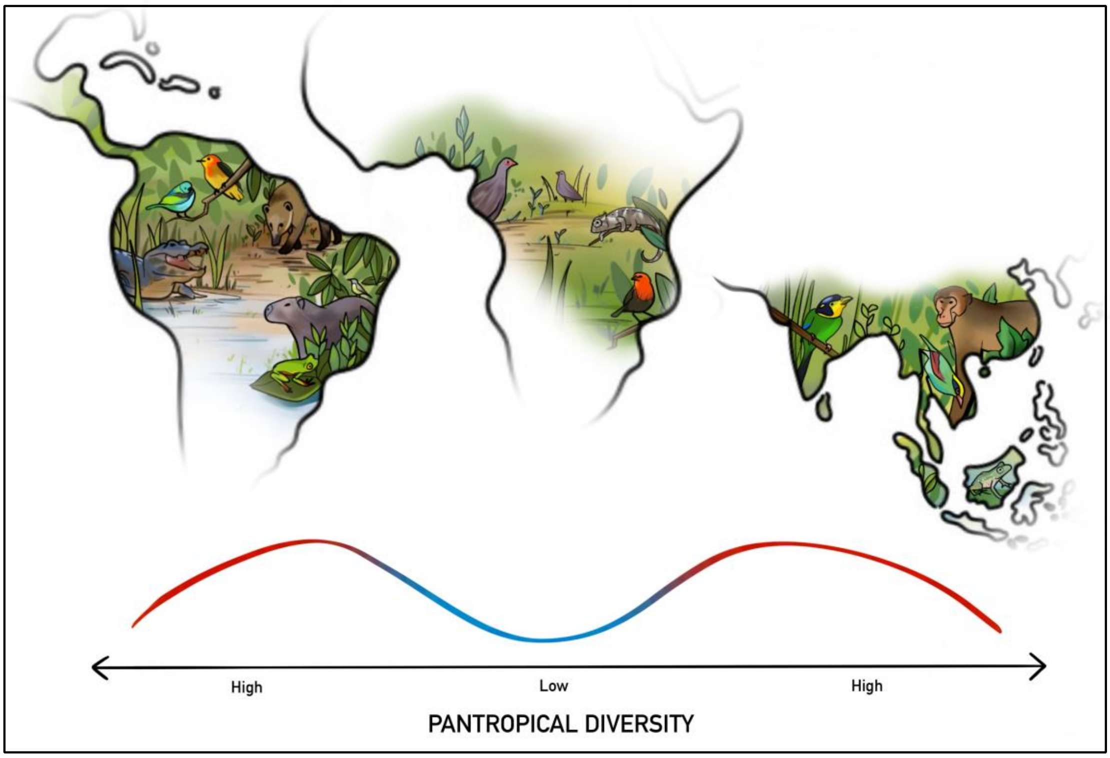

Fig. 1. Tropical and subtropical moist broadleaf forests are the most species-rich terrestrial ecosystems on the planet, located in three primary regions on Earth: continental Africa, the Neotropics, and Southeast Asia (2, 3). Although all three regions host an incredible array of diversity, African tropical forests are depauperate in species relative to forests in the Neotropics and Southeast Asia. In PNAS, Hagen et al. (6) refer to this pattern as 'pantropical diversity disparity' and use simulations to understand how this gradient may have arisen. The authors find pantropical diversity disparity may have emerged from distinct Earth system changes that occurred in each region, sometimes over tens of millions of years ago, which affected their rates of speciation, extinction, and dispersal.

References

1. H. Hillebrand, On the generality of the latitudinal diversity gradient. *The American Naturalist* **163**, 192-211 (2004).
2. A. H. Gentry, Tropical forest biodiversity: distributional patterns and their conservational significance. *Oikos* **63**, 19-28 (1992).
3. T. L. P. Couvreur, Odd man out: why are there fewer plant species in african rain forests? *Plant Syst Evol* **301**, 1299-1313 (2015).
4. P. W. Richards, "Africa, the "odd man out." " in Tropical forest ecosystems in Africa and South America: a comparative review, B. J. Meggers, E. S. Ayensu, W. D. Duckworth, Eds. (Smithsonian Institution Press, Washington, DC, 1973), pp. 21-26.
5. I. PARMENTIER *et al.*, The odd man out? Might climate explain the lower tree α-diversity of African rain forests relative to Amazonian rain forests? *Journal of Ecology* **95**, 1058-1071 (2007).
6. O. Hagen, A. Skeels, R. E. Onstein, W. Jetz, L. Pellissier, Earth history events shaped the evolution of uneven biodiversity across tropical moist forests. *Proceedings of the National Academy of Sciences* (2021).

7. R. E. Ricklefs, Community diversity: relative roles of local and regional processes. *Science* **235**, 167-171 (1987).
8. H. Kreft, W. Jetz, Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences* **104**, 5925-5930 (2007).
9. A. Antonelli *et al.*, Geological and climatic influences on mountain biodiversity. *Nature Geoscience* **11**, 718-725 (2018).
10. C. Hoorn *et al.*, Amazonia Through Time: Andean Uplift, Climate Change, Landscape Evolution, and Biodiversity. *Science* **330**, 927-931 (2010).
11. C. Rahbek *et al.*, Building mountain biodiversity: Geological and evolutionary processes. *Science* **365**, 1114-1119 (2019).
12. W. D. Kissling *et al.*, Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. *Proceedings of the National Academy of Sciences* **109**, 7379-7384 (2012).
13. P. Raven, D. I. Axelrod, Angiosperm biogeography and past continental movements. *Ann Mo Bot Gard* **61**, 539-673 (1974).
14. A. Blach-Overgaard, W. D. Kissling, J. Dransfield, H. Balslev, J. C. Svenning, Multimillion-year climatic effects on palm species diversity in africa. *Ecology* **94**, 2426-2435 (2013).
15. J. J. Wiens, C. H. Graham, Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution & Systematics* **36**, 519-539 (2005).
16. E. Saupe *et al.*, Spatio-temporal climate change contributes to latitudinal diversity gradients. *Nature Ecology & Evolution* **3**, 1419-1429 (2019).
17. M. Pontarp *et al.*, The Latitudinal Diversity Gradient: Novel Understanding through Mechanistic Eco-evolutionary Models. *Trends in Ecology & Evolution* **34**, 211-223 (2019).
18. N. J. Gotelli *et al.*, Patterns and causes of species richness: a general simulation model for macroecology. *Ecology Letters* **12**, 873-886 (2009).
19. T. F. Rangel *et al.*, Modeling the ecology and evolution of biodiversity: Biogeographical cradles, museums, and graves. *Science* **361**, eaar5452 (2018).
20. F. Leprieur *et al.*, Plate tectonics drive tropical reef biodiversity dynamics. *Nature Communications* **7**, 11461 (2016).