

MACROEVOLUTION

Biodiversity gradients emerge

A simulation of expansion, fragmentation and extirpation of species ranges over multiple glacial–interglacial cycles matches empirical biodiversity gradients and shows that high levels of biodiversity in the tropics can emerge from temporally variable but spatially patchy precipitation regimes, driven by allopatric speciation.

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The increase in the number of species that occurs from the poles to the tropics, the latitudinal diversity gradient (LDG), is a known pattern of biodiversity at the global scale; yet it is unclear at what spatial and temporal scales this pattern is formed. LDGs can be generated directly by mechanisms that regulate species diversification rates or total richness¹, such as temperature-dependent mutation, population turnover rates or competition for limited resources, but they can also emerge indirectly when range expansions and contractions redistribute diversity and maximize diversity at latitudes with the highest range overlap^{2,3}. Range disjunctions driven by long-term and persistent habitat fragmentation can also contribute to speciation if habitat fragmentation is not associated with a significant habitat loss, leading to novel

gradients in diversity not predicted by mechanisms occurring over shorter timescales^{4,5}. Spatially explicit models that incorporate the dynamic of species ranges over macroevolutionary timescales are therefore crucial in assessing the origin and maintenance of high species richness in the tropics^{6,7}. Writing in *Nature Ecology & Evolution*, Saupé et al.⁸ report simulations of range expansion, contraction and fragmentation under the influence of spatiotemporal changes in temperature and precipitation, showing that global patterns of vertebrate biodiversity can emerge in the absence of latitudinal gradients in diversity regulation and/or in net diversification rates directly determined by latitude-specific environmental conditions (for example, temperature).

In their simulations, lineages originate with equal likelihood at all

latitudes, the preferred habitat of initial lineages corresponds to temperature and precipitation conditions at the place of their origin, and their subsequent survival and range expansion largely depends on whether temporally changing climatic conditions at subsequent locations remain within the species' climatic niche.

A key aspect is that they model speciation as a gradual, drawn-out process that is determined by long-term variability in climatic suitability that controls the persistence of range disjunction. Because long-term variability in climate varies with latitude, it has a major role in determining the latitudinal gradient in the number of speciation events. Short-term variability can lead to species extinctions, but is not informative about changes in range disjunction occurring at a long enough timescale to allow speciation to take place.

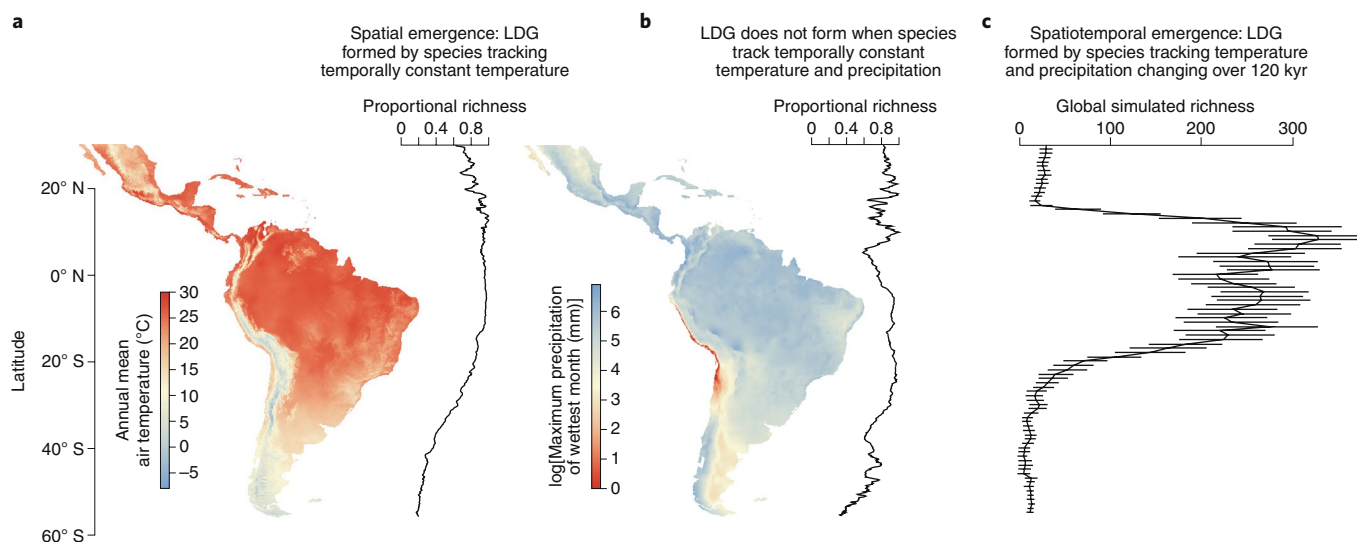


Fig. 1 | Emergence of an LDG illustrated for South America. **a**, An LDG can emerge from a historical spatial model where randomly placed virtual species expand their ranges according to their thermal tolerance (in this cartoon, set by thermal minima and maxima at the place of their origin, following refs. ^{5,13}). **b**, The addition of other environmental filters, such as maximum precipitation, that limit species distributions can degrade such spatial emergence. **c**, Saupé et al.⁸ show that historical spatiotemporal models of species distributions coupled with long-term temporal variability in climate over several glacial–interglacial cycles generate LDGs that emerge from precipitation-driven range fragmentation at low latitudes. The vertical line passes through mean richness and error bars refer to 95% confidence intervals.

Emergence refers to a phenomenon when LDGs cannot be predicted from mechanisms that limit richness or determine diversification rate at small spatial and temporal (seasonal–annual) scales. Spatial emergence can occur if the latitudinal extent of suitable habitat conditions changes with latitude. For example, in simulations that randomly seed species on the landscape with heterogeneity in temperature, species redistribute themselves so that low latitudes will have the highest richness because warm habitats generally have a broader latitudinal extent than cold habitats (Fig. 1a). However, this simplicity is misleading, because other important aspects of species niches, such as precipitation in terrestrial habitats, are incorporated into species distribution models, the strength of LDGs can significantly decrease (Fig. 1b). Spatiotemporal emergence can occur when long-term variability in habitat suitability that affects the dynamic of species ranges is added into spatial models^{9,10}, allowing range fragmentation followed by persistent range disjunction.

Saupe et al.⁸ found that spatiotemporal emergence produces the highest species richness in the tropics (Fig. 1c), which matches the shape of amphibian, bird and mammalian LDGs in terrestrial habitats, the shape of their range-size distributions, and the contributions of specialists and generalists to LDGs. These matches are primarily driven by a high frequency of speciation events at low latitudes that were subjected to habitat fragmentation but not to significant habitat loss over the past 120 kyr. This spatiotemporal emergence of LDGs is conceptually missed by models that explain LDGs by gradients in environment-specific diversification rates or by gradients in ecological limits, and is more realistic than simple spatial (ahistoric) emergence of LDGs that fails to incorporate speciation.

Changes in temperature and precipitation over several glacial–interglacial cycles allow for allopatric speciation as a gradual, long (protracted) process¹¹: speciation occurs once climatic effects fragment the geographic range of a given species into isolated populations and once this climatic isolation persists for at least 10,000 yr. Although the waxing and waning of ice sheets probably contributed to extinctions and delayed species accumulation at higher latitudes in the Northern Hemisphere, Saupe et al.⁸ show that temporal changes in precipitation regimes led preferentially to patchily distributed humid and arid regions at low latitudes. These conditions fragmented and isolated species ranges, thus boosting speciation rates in the tropics. This finding applies to simulations with and without ice sheets.

Although high latitudes were subjected to stronger changes in temperature than low latitudes, the magnitude of the temperature increase was relatively similar within individual latitudinal bands and did not translate into patchily distributed regions with low and high temperatures. The finding that the variability in precipitation was higher in the tropics is consistent with the notion that the greater climatic stability of tropics in the past had positive effects on diversification: changes in precipitation did not eliminate individual habitats and still allowed habitat specialization at low latitudes. The spatial heterogeneity in precipitation is more magnified in warm than in cold climates in terrestrial habitats, thus generating an overall tendency for higher habitat fragmentation at low latitudes.

These simulations open possibilities for assessing the effects of size of geographic ranges on speciation probabilities¹² by differentiating between rates of initial speciation and rates of speciation

completion. The rate of speciation completion is affected by the extinction probability under protracted speciation, and speciation-completion rate thus can be higher for species with broad ranges. Although it remains unclear how the predictive power of spatiotemporal models that account for range expansion and fragmentation compares with the power of explanations based on gradients in ecological limits, the approach of Saupe et al.⁸ can be extended to incorporate constraints on the total number of individuals, and thus can further illuminate the questions surrounding the origin of LDGs. □

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References

- Mittelbach, G. G. et al. *Ecol. Lett.* **10**, 315–331 (2007).
- Gotelli, N. J. et al. *Ecol. Lett.* **12**, 873–886 (2009).
- Tittensor, D. P. & Worm, B. *Glob. Ecol. Biogeogr.* **25**, 630–641 (2016).
- Jablonski, D. et al. *Proc. Natl Acad. Sci. USA* **110**, 10487–10494 (2013).
- Tomašových, A., Jablonski, D., Berke, S. H., Krug, A. Z. & Valentine, J. *Glob. Ecol. Biogeogr.* **24**, 157–167 (2015).
- Rangel, T. F. L. V. B., Diniz-Filho, J. A. F. & Colwell, R. K. *Am. Nat.* **170**, 602–616 (2007).
- Hurlbert, A. H. & Stegen, J. C. *Front. Genet.* **5**, 420 (2014).
- Saupe, E. et al. *Nat. Ecol. Evol.* <https://doi.org/10.1038/s41559-019-0962-7> (2019).
- Colwell, R. K. & Rangel, T. F. *Phil. Trans. R. Soc. B* **365**, 3695–3707 (2010).
- Leprieux, F. et al. *Nat. Commun.* **7**, 11461 (2016).
- Rosindell, J., Cornell, S. J., Hubbell, S. P. & Etienne, R. S. *Ecol. Lett.* **13**, 716–727 (2010).
- Birand, A., Vose, A. & Gavrillets, S. *Am. Nat.* **179**, 1–21 (2012).
- Leroy, B., Meynard, C. N., Bellard, C. & Courchamp, F. *Ecography* **39**, 599–607 (2016).

Competing interests

The author declares no competing interests.