

that were a fixture of central Hittite cities and construction of large-scale water infrastructure projects (Fig. 1), such as dams, that gained momentum during the thirteenth century BC.

What is uncommon, however, is a drought that lasts for more than two consecutive years, and which Manning *et al.* suggest is a serious enough event to create a tipping point in communities' efforts at adaptation and resilience. Although rightfully refraining from suggesting a direct causal relationship between this climate extreme and a sudden Hittite collapse, the authors highlight the 1198–1196 BC drought as being a key catalyst that might have caused the empire first to tap heavily into its landscapes for survival, inflicting long-lasting damage on its ecosystems, and ultimately to abandon its central cities, including Hattusa.

One of the many puzzles of Hittite studies is the abandonment of Hattusa during the final decades of the Hittite empire. This seems to have been meticulously planned, because all official buildings were emptied of their portable valuables, suggesting that the royal family moved to another city³. In the absence of archaeological evidence for the sacking of the city through warfare or conquest, the reasons for Hattusa's abandonment have been debated, with changes in climate and resulting droughts and famines considered among the candidates. Speculation could go only as far as a general correlation between favourable climatic conditions during the formation of the Hittite empire and adverse ones for its final centuries⁴.

Manning and colleagues' study is groundbreaking because it finally gives us a tangible clue to why Hattusa was abandoned. Future research might discover whether the extreme climate event of 1198–1196 BC was confined to central Anatolia or was a larger eastern Mediterranean phenomenon that can offer insight beyond the case of the Hittites.

Now that we know a major climate event might have tipped the Hittite empire beyond its point of no return, there are more questions to ask about climate change, its impact on states and society and, most crucially, what can be learnt from the past during our current climate crisis. The Hittite case makes one point abundantly clear: extended political and economic systems are especially fragile in the face of extreme climate events. When such systems collapse, large urban centres become unsustainable, begging the question of whether they were ever truly viable. Through urban decline, communities get another chance to live in smaller units, attempting to coexist with their landscapes and to draw more sustainably from a larger diversity of resources that are available in smaller quantities.

Archaeological perspectives on the past should make us think about possible alternative paths for human settlement, without romanticizing an idyllic rural life or

demonizing all urban conglomerates. Such exploration would not be new. The rapidly expanding and unsanitary urban environments of the Industrial Revolution and its aftermath triggered multiple responses, ranging from partially built models, such as English urban planner Ebenezer Howard's garden cities, to utopias such as US architect Frank Lloyd Wright's Broadacre City. Howard called for a marriage between town and country through small cities surrounded by green belts, agricultural zones and sustainable industry, whereas Lloyd Wright advocated a model of no absentee or corporate ownership, in which production would be centred on individual homesteads.

Although sustainable urban–rural systems have been discussed for centuries, these options have been superseded by the ever-expanding metropolises that trick us

into imagining a sense of stability there. Now is the time not only to dream creatively but also to generate cities that have lighter footprints, dispersed settlements and a balanced urban–rural divide.

Müge Durusu-Tanrıöver is in the Department of Art History, Tyler School of Art and Architecture, Temple University, Philadelphia, Pennsylvania 19122, USA.
e-mail: muggedurusu@temple.edu

1. Manning, S. W., Kocik, C., Lorentzen, B. & Sparks, J. P. *Nature* **614**, 719–724 (2023).
2. Cline, E. H. *1177 B.C.: The Year Civilization Collapsed* (Princeton Univ. Press, 2021).
3. de Martino, S. in *The End of Empires* (eds Gehler, M., Rollinger, R. & Strobl, P.) 82 (Springer, 2022).
4. Schachner, A. in *Handbook Hittite Empire: Power Structures* (ed. de Martino, S.) 167 (De Gruyter, 2022).

The author declares no competing interests.
This article was published online on 8 February 2023.

Evolution

Tropical biodiversity linked to polar climate

Moriaki Yasuhara & Curtis A. Deutsch

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. **See p.708 & p.713**

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 understood³. 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. Fenton *et al.*⁴ (page 708) and Woodhouse *et al.*⁵ (page 713) now 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 diversity⁶, 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 latitudes⁷. 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 ago⁸, owing to poleward migration and a higher risk of extinction for polar species⁹. 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 altitude¹⁰. 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 effects¹¹. And because deep-ocean waters obtain their temperature from high-latitude surface waters, ocean circulation translates the global latitude gradient in

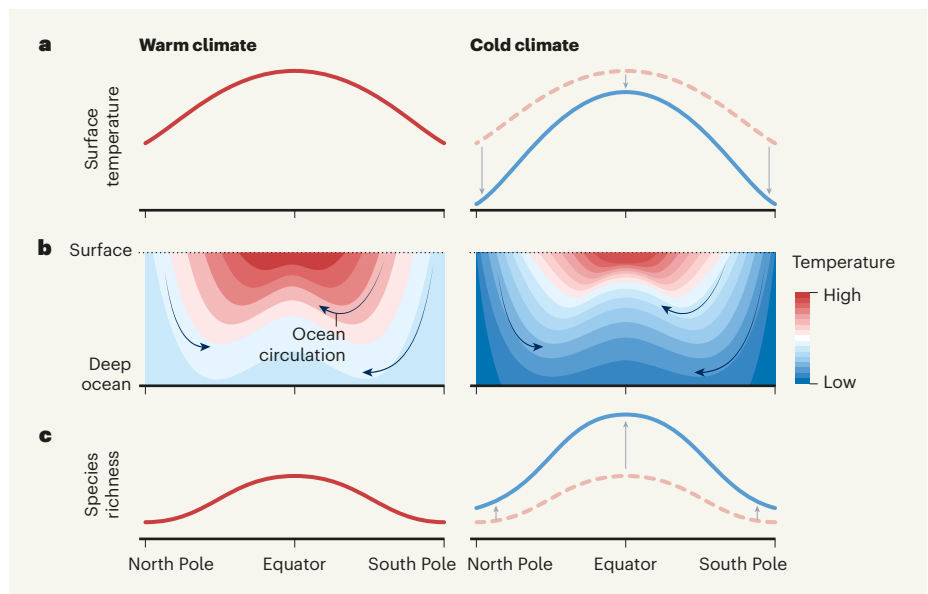


Figure 1 | A proposed link between climate and ocean biodiversity. Fenton *et al.*⁴ and Woodhouse *et al.*⁵ examined fossil records of ocean plankton to assess how species diversity changed as the climate varied over millions of years. **a**, When the climate cools, the change in ocean surface temperature 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.

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 traits¹².

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 concept². 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.

Moriaki Yasuhara is in the School of Biological Sciences, Area of Ecology and Biodiversity, and at the Swire Institute of Marine Science, Institute for Climate and Carbon Neutrality, and Musketeers Foundation Institute of Data Science, University of Hong Kong, and the State Key Laboratory of Marine Pollution, City University of Hong Kong, Hong Kong.

Curtis A. Deutsch is in the Department of Geosciences, and at the High Meadows Environmental Institute, Princeton University, Princeton, New Jersey 08544, USA.
e-mails: moriakiyasuhara@gmail.com;
cdeutsch@princeton.edu

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* **614**, 708–712 (2023).
5. Woodhouse, A., Swain, A., Fagan, W. F., Fraass, A. J. & Lowery, C. M. *Nature* **614**, 713–718 (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).

The authors declare no competing interests.

This article was published online on 15 February 2023.

Condensed-matter physics

A twist in the bid to probe electrons in solids

Rebeca Ribeiro-Palau

Two microscopy techniques have been merged into a tool for twisting ultrathin sheets of atoms relative to each other. The approach offers a new angle for studying the electronic properties of exotic layered materials. **See p.682**

In 2018, scientists took two sheets of single-atom-thick carbon, called graphene, twisted them relative to each other by a ‘magic’ angle and observed a remarkable thing: the system conducted electricity without any resistance¹. Efforts to characterize the properties of this intriguing twisted bilayer graphene began immediately, but the studies proved challenging². Although it’s tempting to imagine that the fabrication process is as easy as twisting two sheets of paper relative to each other, it’s actually highly complex, because the fully aligned configuration is more stable than a twisted one. On page 682, Inbar *et al.*³ report an exciting experimental technique for controlling the angular alignment of such layers *in situ* – perhaps the closest we’ll come to the ideal scenario, equivalent to twisting two sheets of paper.

The authors began by studying how charge carriers move from one layer to the other, and the twist angles at which this motion (conduction) is allowed. A simple way to explain this is by analogy with two trains that cross paths along their route. If the trains move in the same direction and at the same speed, it’s easy to jump from one train to the other. However, if they move at different speeds or in opposite directions, jumping from one to the other is almost impossible. This is because momentum is conserved – the person jumping needs to

have the same momentum before and after the jump.

The same thing happens to charge carriers: they can move easily between layers only when their momentum before the jump matches that after the jump^{4,5}. This simple but clever

concept of momentum matching allowed Inbar *et al.* to develop a microscopy technique that they named the quantum twisting microscope. The approach takes advantage of the structural properties of 2D materials with atomically flat surfaces to explore the most fundamental quantum-mechanical property of a material, its energy dispersion – the way in which the energy of the electrons depends on their momentum.

Practically, Inbar and colleagues’ technique is a merger of two existing microscopy tools: the atomic force microscope (AFM) and the scanning tunnelling microscope (STM), both of which involve scanning a sample using an extremely sharp tip. An AFM generates an image of the sample by measuring the forces between the tip and the sample, whereas an STM measures the current between the tip and the sample when a voltage is applied across them. The authors used these two capabilities to build a device that can control the angular alignment between thin sheets, and also measure the energy dispersion of the layered structure as it is manipulated *in situ*.

Inbar *et al.* first fabricated a pyramid-shaped AFM tip made from platinum, and deposited graphite and boron nitride on it. They then covered this tip with a layer of graphene so that it resembled a tent with a flat top. The authors installed the tip in an AFM and then brought the graphene into contact with another graphene layer; this had been placed on top of an angular rotator, which was used to control the angular alignment between layers (Fig. 1a). The contact area between the two layers was large (particularly compared with that in an STM), and this enabled the authors to investigate how the momentum matching between layers altered the charge-transport properties

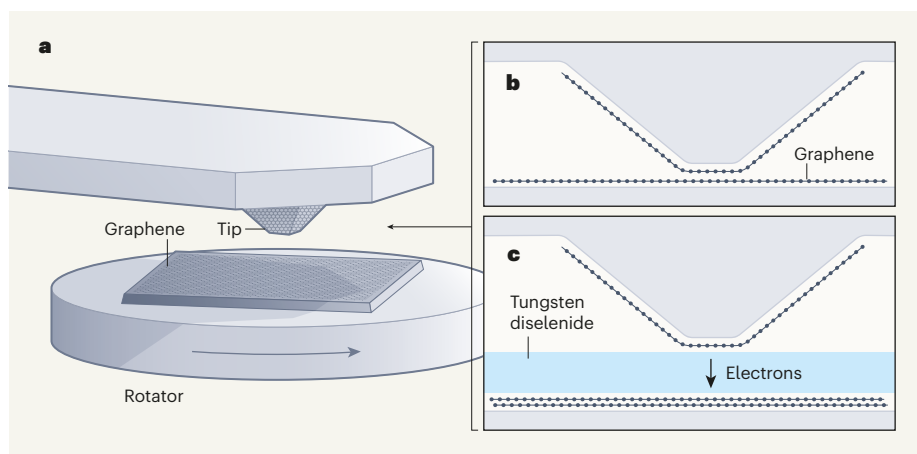


Figure 1 | The quantum twisting microscope. **a**, Inbar *et al.*³ developed a tool called a quantum twisting microscope, which can be used to control the angular alignment between one or more sheets comprising single layers of atoms – such as graphene, which is made of carbon. The microscope consists of a pyramid-shaped metal tip that is covered in one sheet (of graphene, for example), and brought into contact with a second sample on a rotator. **b**, In this way, the microscope can be used to control the angular alignment of such layers *in situ*. **c**, The device can also measure and change the way in which the energy of electrons in the multilayered structure depends on their momentum. In this mode, the electrons move through an added layer of tungsten diselenide.