2004 paper has had in condensed-matter physics and materials engineering. One easy metric is that it has more than 50,000 citations in the Web of Science database, making it one of the most cited physics papers in history, and reflecting the thousands of groups around the world that have embarked on 2D-materials research. These researchers include not only physicists, but also chemists, materials scientists, electrical engineers – and even physicians. What's the reason for this extraordinary interest? Part of it is that graphene's properties include many superlatives: it is the strongest and thinnest material, and the best conductor of heat and electricity. It's also not the only 2D material, which means that vastly different lines of research can all be traced back to Novoselov and colleagues' initial result.

The family of 2D materials now includes insulators, semiconductors, crystalline magnets, crystalline ferroelectrics (ferroelectrics are materials that show spontaneous electric polarization), superconductors (materials that have zero electrical resistance) – the list goes on. In many instances, the behaviour of these 2D crystals differs substantially from that of their 3D counterparts, and they are often much more easily 'tuned' (for example, by varying the number of layers or the density of charge carriers). As a result, researchers have predicted many potential scientific and technological applications of these 2D materials, some of which are beginning to be realized: ultrasensitive chemical and biological sensors and infrared cameras are among the first in line.

Another key aspect of 2D materials is that they can be stacked on top of each other to create 'heterostructures'[6], which are similar in some ways to structures built from children's Lego bricks. But Lego pieces have to be stacked in alignment or at right angles to each other, whereas 2D materials have no such restriction: they can be stacked with an arbitrary twist angle between their crystal lattices. And these twisted heterostructures have properties that can vary considerably from those of their constituent layers (Fig. 1b). For example, a twist angle of around 1 degree can turn stacked sheets of graphene (which is neither an insulator nor a superconductor) into a heterostructure that shows both insulating and superconducting behaviours, as a result of interactions between its electrons[7,8].

This field is often referred to as twistronics (or moiré quantum matter, because the superposition of the two crystal lattices forms a pattern of interference known as a moiré lattice) and it has become one of the most active areas of 2D materials research[9]. Remarkably, over the past six years, twistronics researchers have been able to realize nearly all the known phases of quantum matter, often with unconventional features. They have even discovered entirely new quantum phases and effects, including a phenomenon known as the fractional quantum anomalous Hall effect, which was realized in twisted moiré heterostructures last year[10–12].

The journey that started 20 years ago is far from over, and research on 2D materials continues to grow. Researchers studying these materials are making key discoveries about fundamental physics at a phenomenal rate, which is cause for genuine optimism. For example, chirality, or 'handedness', is a property that not only affects the behaviour of many physical systems, but also has crucial roles in chemistry and biology, and this property can be explored and carefully tuned in twisted heterostructures[13].

On the technological front, there are also reasons to be optimistic, albeit cautiously. Techniques for growing large, high-quality swathes of graphene and other 2D materials are improving rapidly, and engineers are increasingly open to the idea of incorporating these materials into platforms for fabricating devices. However, the quality of 2D samples must be increased still further, especially for materials other than graphene, and methods for fabricating miniature heterostructures with arbitrary twist angles must be automated. Such efforts will require substantial resources and the full ingenuity of physicists, chemists and engineers. But the pay-off could be huge and might pave the way for an entire generation of nanotechnologies in the decades to come.

Pablo Jarillo-Herrero is in the Department of Physics, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139, USA.
e-mail: pjarillo@mit.edu

1. Mermin, N. D. *Phys. Rev.* **176**, 250–254 (1968).
2. Novoselov, K. S. *et al. Science* **306**, 666–669 (2004).
3. Novoselov, K. S. *et al. Nature* **438**, 197–200 (2005).
4. Zhang, Y., Tan, Y.-W., Stormer, H. L. & Kim, P. *Nature* **438**, 201–204 (2005).
5. Novoselov, K. S. *et al. Proc. Natl. Acad. Sci. USA.* **102**, 10451–10453 (2005).
6. Dean, C. R. *et al. Nature Nanotechnol.* **5**, 722–726 (2010).
7. Cao, Y. *et al. Nature* **556**, 80–84 (2018).
8. Cao, Y. *et al. Nature* **556**, 43–50 (2018).
9. Andrei, E. Y. *et al. Nature Rev. Mater.* **6**, 201–206 (2021).
10. Cai, J. *et al. Nature* **622**, 63–68 (2023).
11. Zeng, Y. *et al. Nature* **622**, 69–73 (2023).
12. Park, H. *et al. Nature* **622**, 74–79 (2023).
13. Zhu, H. & Yakobson, B. I. *Nature Mater.* **23**, 316–322 (2024).

The author declares no competing interests.

Ecology

Global conservation goals for island plant diversity

Thomas J. Givnish

How much of Earth's plant diversity is distributed across islands, and how might this affect conservation efforts? It emerges that islands contain a disproportionately large share of global plant diversity and endangered species. **See p.868**

Islands provide homes for a wide variety of plant species, including some that are at risk of extinction. On page 868, Schrader *et al.*[1] present a catalogue of the plant species found on islands around the world. These data shed light on plant evolution and have implications for global conservation.

Oceanic islands have long had an outsized influence on our understanding of the biological world. Variation in the finches and tortoises of the Galapagos Islands inspired Charles Darwin to develop the theory of evolution by natural selection. Global patterns in the numbers of bird species on islands of different areas and distances from continents led Robert MacArthur and E. O. Wilson to develop their theory of island biogeography. This theory accounts for variation in species diversity by setting out how island size and distance from source areas affect the rates of local species extinction and colonization. It also laid the foundation for many advances in ecology, evolutionary biology and conservation biology[2].

Studies of the drivers of species number and functional diversity on islands have provided profound insights into the roles of dispersal, competition, adaptive radiation (ecological divergence among species derived from a common ancestor), reproductive strategies, speciation (the emergence of new species from ancestral colonists) and local extinction. Such work has also revealed how island-dwelling organisms – shaped by isolation and the resulting absence of many competitors, predators and other natural enemies; constrained by the small size of their island homes; and often occurring nowhere else in the world – are especially threatened by habitat destruction and the introduction of non-native species[3–7]. Schrader and colleagues shed light on how plant diversity is distributed across islands on Earth and what that means for global conservation efforts.

The authors provide a checklist that is the first comprehensive tally of vascular plant species (those that transport water in their tissues, such as flowering plants, gymnosperms and ferns) native to individual islands and archipelagos around the world. The authors also mapped geographical distributions, compiled data on the placement of each species in the evolutionary tree of life and assessed extinction risk on the basis of the Red List of Threatened Species from the International Union for Conservation of Nature. Remarkably, 31% of all vascular plant species are native to islands, even though islands represent only about 5% of global land area; 21% of all vascular plants are island endemics, meaning that they are found naturally only on islands. Of the 63,280 species that are island endemics, 70% are single-island endemics.

Most island endemics are native to a few large islands in the tropics. These islands are diverse because they retained some of the lineages of species found on the ancient Gondwanan supercontinent as the islands 'rafted' away through movements of tectonic plates (places such as Madagascar, New Zealand and New Caledonia), or are land-bridge islands that were previously connected to today's continents when glaciers lowered sea levels (New Guinea, Borneo, possibly Cuba). They are also diverse in terms of physical landscape (topography), soils, and thus habitats, and because their tropical position protected them from being overrun by ice sheets.

These tropical islands also have a high proportion of species that are endemic to them alone. Larger populations on larger islands should be more likely to survive than smaller populations on smaller islands, and thus to persist for long enough to diverge from the original colonists (with no local multiplication of species) or to spin off one or more new species. Speciation on larger islands should also be more likely than on smaller islands, given the wider range of habitats and barriers to dispersal, such as mountains or deserts.

Island isolation should also increase the proportion of endemism by reducing gene flow from ancestral populations and competition from new colonists, both of which could thwart the survival of existing species and their subsequent speciation. Globally, Schrader *et al.* find that 74% of the variation in the proportion of plant species endemic to individual islands can be explained by island (or archipelago) area and isolation, with 55% explained by island area alone. Islands at high latitudes that were glaciated over the past few thousand years (such as Ellesmere Island, part of Canada) are especially poor in both species and percentage endemism. The same is true for atolls at low latitudes: those rings of islands with low topographical relief have little habitat diversity and are susceptible to flooding when ocean levels are high. They also have few plant species[3] and a low share of species that are endemic to individual atolls.

PHOTO RESOURCE HAWAII/ALAMY

Figure 1 | ***Cyanea shipmanii*.** This rare plant species is found only in a small area of the island of Hawaii, and is a member of the largest plant genus that is naturally found only on the Hawaiian islands.

Schrader and colleagues report that isolated archipelagos with high endemism (such as Hawaii, the Canary Islands and the Mascarenes) accounted for only 21% of all island plant endemics. This is because they have fewer species overall than do land-bridge islands and archipelagos (such as the Greater Sunda Islands), which were previously connected to continents during lower ocean levels during glacial periods, or sites associated with continental rafts, including Madagascar. However, isolated archipelagos can support some highly diverse and ecologically divergent radiations, such as the Hawaiian lobeliads — the largest plant grouping, called a clade, that is restricted to any single oceanic island or archipelago[8] — and they do so on a tiny proportion of Earth's surface. Many members of such radiations, including the Hawaiian lobeliad *Cyanea shipmanii* (Fig. 1), are highly specialized and initially had extremely limited distributions; they have now become endangered through habitat destruction and the introduction of non-native animals and plants.

"Oceanic islands have long had an outsized influence on our understanding of the biological world."

Endemism of individual species, or species grouped by genus, is often greater at the scale of archipelagos compared with islands. This is probably because of the short distances between islands in an archipelago and the similar conditions that they share.

As has long been known, several plant families (such as the Asteraceae, Campanulaceae and Orchidaceae — the daisies and their relatives, bellflowers and orchids) excel at long-distance dispersal and are over-represented on islands compared with the entire global flora. Despite their dust-like seeds, orchid species are greatly under-represented on true oceanic islands (active or extinct volcanoes with short, above-water existences), probably because their highly specialized pollinators or fungal partners failed to co-disperse. Indeed, land-bridge islands and continental rafts — which guarantee co-dispersal — often support large numbers of orchid species from such genera as *Bulbophyllum* and *Dendrobium*[7].

Lineages of species with high seed dispersibility should be over-represented among colonists, but lower dispersibility should lead to greater genetic divergence among populations of a given species and subsequent speciation. Plants that have fleshy fruits might have the best of both worlds, combining high dispersibility across water, for colonization, with low dispersibility and high speciation rates if plants switch to the understorey layers of forests after arrival, given that forest-interior birds that eat fruits are often notoriously sedentary. In the Hawaiian flora, many of the largest genera are indeed fleshy-fruited plants of forest understoreys[8], and several of the largest plant genera of the Pacific Basin, such as *Psychotria* or *Melicope*, share the same characteristics.

Island endemics, especially single-island endemics, are at high risk of extinction, given their small ranges and consequent vulnerability to climate change, habitat destruction and the introduction of non-native species. Currently, 176 island endemics are considered extinct. These comprise 55% of all extinct plant species worldwide, highlighting the necessity of targeting island endemics for conservation.

Many large islands and archipelagos with large numbers of species found nowhere else on Earth have extremely little area set aside in biological reserves, and so should be high priorities for future conservation efforts. Overall, 94% of island endemics are native to areas of which less than 30% is protected. For some regions, such as dry forests on Hawaii or the Canary Islands, habitat destruction and the prevalence of invasive species are so great as to make conservation efforts highly challenging. There is a particular issue with invasive grasses that use a C_4 photosynthetic pathway, because they spread fires easily and catastrophically convert habitats[9].

Schrader *et al.* recommend that Indigenous peoples, as the long-term guardians of island biodiversity, be brought into conservation design and management to protect plant diversity and human cultural practices. Good starts to such community-based approaches include efforts to restore dry forest on Maui[10], and to inventory and study rainforest diversity on New Guinea[11].

The data provided by Schrader and colleagues offer many avenues for future research. One exciting possibility might be to analyse their data with a creative approach that used evolutionary trees (based on molecular phylogenies) for several hundred species of island birds to assess global patterns of bird dispersal, speciation, extinction, endemism, and species richness as affected by island area and isolation[12]. This could provide a framework for validating the MacArthur and Wilson theory of island biogeography applied to island plants worldwide. That theory has been used in many contexts to design conservation efforts in fragmented landscapes, and further insights could help to protect the large share of global plant diversity found on islands.

Schrader and colleagues' data might also be used to assess the importance of various plant characteristics for diversification on islands, and to evaluate the relative effects of island age, geographical proximity and environmental similarity in shaping the native floras of the world's oceanic islands and archipelagos.

Thomas J. Givnish is in the Department of Botany, University of Wisconsin–Madison, Madison, Wisconsin 53706, USA.
e-mail: givnish@wisc.edu

1. Schrader, J. *et al. Nature* **634**, 868–874 (2024).
2. Losos, J. B. & Ricklefs, R. E. (eds) *The Theory of Island Biogeography Revisited* (Princeton Univ. Press, 2009).
3. Kreft, H., Jetz, W., Mutke, J., Kier, G. & Barthlott, W. *Ecol. Lett.* **11**, 116–127 (2008).
4. Givnish, T. J. & Montgomery, R. A. *Proc. R. Soc. B* **281**, 20132944 (2014).
5. Enbody, E. D. *et al. Science* **381**, eadf6218 (2023).
6. Whittaker, R. J., Fernández-Palacios, J. M., Matthews, T. J., Borregaard, M. K. & Triantis, K. A. *Science* **357**, eaam8326 (2017).
7. Cámara-Leret, R. *et al. Nature* **584**, 579–583 (2020).
8. Givnish, T. J. *Taxon* **59**, 1326–1366 (2010).
9. Ellsworth, L. M., Litton, C. M., Dale, A. P. & Miura, T. *Applied Veg. Sci.* **17**, 680–689 (2014).
10. Medeiros, A. C., von Allmen, E. I. & Chimera, C. G. *Pac. Sci.* **68**, 33–45 (2014).
11. Novotny. V. & Molem, K. *Nature* **584**, 531–533 (2020).
12. Valente, L. *et al. Nature* **579**, 92–96 (2020).

The author declares no competing interests.

Developmental biology

An extra role for glucose in building bodies

Christian Schröter

An unexpected link has been found between the metabolic pathways that produce energy for embryo growth, and the cellular signalling systems that regulate cell specialization and movement during early development. **See p.919**

The transformation of a fertilized egg into an embryo requires cell growth, division and differentiation to create the diverse cell types that make up a multicellular organism. The conventional view is that the metabolic pathways that provide molecular building blocks and energy for cell growth operate mostly independently of the signalling systems that orchestrate cell differentiation over time and space. On page 919, Cao *et al.*[1] report a direct connection between these two facets, showing how the flow of nutrients through a metabolic pathway regulates cell-to-cell signalling in early development.

> **"Co-opting existing metabolic pathways might have been easier than evolving new mechanisms from scratch."**

Cao and colleagues focused on the relationship between cell signalling and metabolism during gastrulation, the process in which a tissue sheet made from cells of the same type is transformed into a 3D rudimentary body made of an array of specialized cell types. Gastrulation involves the differentiation and movement of cells in a precisely choreographed sequence, under the control of a small number of cell-to-cell signalling systems. One of the most crucial signals for gastrulation is transmitted by proteins called fibroblast growth factors (FGFs). When FGF signalling is genetically or pharmacologically perturbed, several specialized cell types do not differentiate, and cells fail to migrate to their target destinations.

FGFs cannot efficiently signal on their own. Instead, they require proteoglycans – proteins heavily decorated with sugars. Cells import the sugar glucose for the process of glycolysis, a central metabolic pathway for producing energy and chemical building blocks for growth. By diverting some imported glucose away from glycolysis and into another glucose metabolism pathway called the hexosamine biosynthetic pathway (HBP), cells can produce precursor molecules for proteoglycan synthesis. Although it is well established that proteoglycans are required for FGF signalling, it was not known whether cells can regulate proteoglycan synthesis through glucose metabolism as a strategy to modulate FGF signalling.

Cao and colleagues found the first hint that regulation of glucose metabolism could be tied to gastrulation when they looked at the dynamics of glucose uptake in developing