

between the layers (Fig. 1). Future studies should investigate stacked monocrystalline layers, in which each sheet consists of a single 2D lattice. This would enable a better understanding of the relationship between thermal anisotropy and the angle of rotation.

Twisted bilayer graphene, which consists of two stacked sheets of graphene twisted out of lattice alignment, becomes a superconductor⁵ at the ‘magic’ twist angle of 1.1°. Perhaps, in future, an analogous magic angle could be discovered for heat conduction, producing twisted layered systems that behave as superb thermal insulators or periodic heat-flux modulators (systems in which the anisotropic thermal conductivity alters in a regular spatial pattern across the layers). If so, Kim and colleagues’ findings could signify the start of a new area of study, analogous to twistrionics (the study of how the angle of rotation between layers of vertically stacked 2D structures triggers various electronic phenomena⁶).

Another follow-up to Kim and colleagues’ work could be to engineer twisted heterostructures – stacks composed of combinations of 2D materials. These could be used to investigate the limits of the heat-transport directionality that can be achieved by rotating 2D layers. Because there are many combinations of 2D materials that could be tested, it would be helpful to establish a general approach for predicting which twisted heterostructures are most likely to have the best thermal properties, rather than relying on a trial-and-error approach. Nevertheless, on the basis of the current findings, it seems possible that systems containing large crystalline monolayers of 2D materials, such as graphene and hexagonal boron nitride, could reach a thermal anisotropy factor of much greater than 1,000.

Finally, Kim *et al.* demonstrated a potential application of their anisotropic thermal conductors by coating nanoscale gold electrodes with a film of the layered MoS₂ material. The authors observed that the coated electrodes can carry a greater current without breaking than can bare electrodes. They attribute this effect to the remarkable ability of the MoS₂ film to dissipate heat – channelling it in only one desired direction (that is, through the layers of MoS₂), and not to the surface of the coated electrodes. If this idea can be implemented in microchips, it could make a big difference to the number of electronic components that can be incorporated into future devices, such as laptops.

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Ecology

Pollination advantage of rare plants unveiled

Marcelo A. Aizen

An analysis of plant–pollinator interactions reveals that the presence of abundant plant species favours the pollination of rare species. Such asymmetric facilitation might promote the coexistence of species in diverse plant communities. **See p.688**

Species diversification results from the balance between the formation of new species (speciation) and the loss of existing ones (extinction). The tremendous proliferation of different life forms on Earth can be attributed to both high rates of speciation and low rates of extinction. Flowering plants – a group called angiosperms – are one of the most diverse groups of non-mobile organism. There are approximately 352,000 plant species nearly 90% of which depend, to various extents, on insects and other animals for pollination and seed production¹. These animal pollinators have been key to the unstoppable diversification of the angiosperms, starting at least 120 million years ago, with pollinators promoting speciation by acting as potent selection agents for a plethora of flower traits^{2,3}. Pollinators also aid species persistence by enabling pollen transfer between relatively distant individuals in sparse plant populations⁴. Wei *et al.*⁵ report on page 688 that, for plant species that flower at the same time, pollinators mediate interactions that might facilitate species coexistence in diverse plant communities.

Plant species that flower at the same time can compete for flower visits by shared pollinators, resulting in reduced pollination. For example, flowers of one species might be visited less frequently when more-attractive or more-rewarding flowers are produced nearby by other species. Alternatively, limited pollinator availability can result in an overall reduction in flower visitation if flowers of different species open simultaneously and are similarly attractive or rewarding. By contrast, there are situations in which one or more species might benefit by overlapping their flowering time with that of other species. This could be the case when species producing flowers with plentiful nectar attract pollinators that then ‘spill over’ their visits to neighbouring species that offer comparatively less pollen or

nectar, or when multiple species of flowering plant clustered in the same patch attract more pollinators just by flowering together, thereby increasing flower visitation^{6,7}. The phenomenon of certain plant species positively affecting the pollination of other plant species, termed pollinator-mediated facilitation, seems to be more common than was previously thought^{6,8,9}.

Pollinator-mediated facilitation can promote species coexistence in diverse communities, particularly if rare plant species benefit from pollinators being attracted by common ‘co-flowering’ plants^{6,10} that act as pollinator ‘magnets’. However, although rare species might profit from such an effect, there are still lingering costs associated with pollinator sharing that might outweigh the benefits. First, the transfer of pollen between plants of a given species might be reduced through pollen losses during intervening visits to flowers of other species, which would result in reduced pollination success. Second, pollen-receiving flower structures called stigmas might become clogged with pollen from other species, hampering the performance of a species’ own pollen¹¹. Such costs are projected to be high for rare species because shared pollinators are expected to visit more flowers of abundant species than of rare ones during single foraging bouts. However, these costs are reduced if rare plant species specialize in a particular pollinator or pollinator group, by increasing the shape match (morphological fit) between flowers and pollinators, which can improve the effectiveness of pollen transfer⁷.

Wei and colleagues explored the benefits and costs of pollinator-mediated interactions in relation to plant abundance through plant–pollinator interactions (which pollinator species visit the flowers of which plant species), flower shape and quantitative patterns of pollen transfer within and between plant species. The authors studied pollination during the

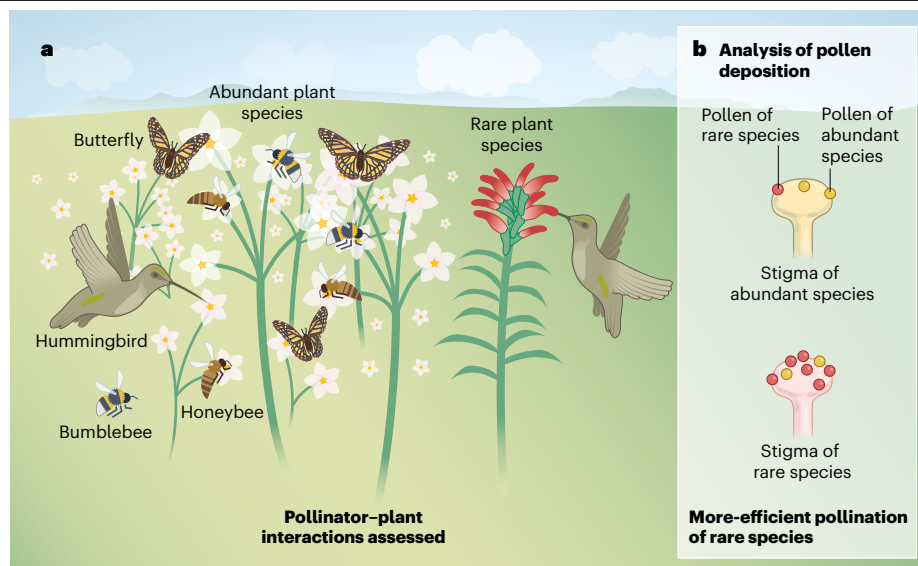


Figure 1 | Pollination and species coexistence. **a**, Wei *et al.*⁵ assessed pollination at grassland sites in California, tracking flower visits by a range of types of pollinator, including bees, butterflies and hummingbirds. Abundant species can act as ‘magnets’ for a high diversity of pollinators, and this can result in ‘spillover’, when pollinators visit flowers of other, neighbouring plant species. The flowers of rare neighbouring species typically have specialized shapes that are tailored to match the pollen-bearing structures of certain visitors, such as the beaks of hummingbirds. **b**, The authors assessed pollen deposited on the stigmas of flowers. This revealed that rare plant species are more successful in achieving pollinator-mediated transfer of pollen between flowers of their own species than are abundant plant species, which pay a larger cost in terms of pollen loss when their pollinators visit flowers of other species. As a consequence, rare plant species benefit more from the presence of the abundant species than abundant species gain from the presence of rare species.

peak flowering seasons of 2016 and 2017 at sites called serpentine seeps in California’s grassland and scrub habitats, which are a hotspot of global biodiversity. The plant community investigated included 79 plant species whose flowers were visited by more than 400 pollinator species, including myriad bee and fly species, several beetle, butterfly, moth, wasp and ant species, and one hummingbird species. Analysis of the authors’ unique data set revealed that, although the stigmas of rare plant species tend to receive slightly more foreign pollen than do the stigmas of abundant species, the rare species receive more pollen from flowers of their own species than abundant species receive from their own species.

Despite acting as pollinator magnets, abundant plant species seem to be penalized by losing more of their own pollen than do rare plants when pollinators visit flowers of other species. As the authors expected, the observed higher pollination efficiency of rare over abundant species was associated with more-complex flower morphologies and more-specialized (species-specific) plant–pollinator interactions (Fig. 1). Importantly, the authors discarded an alternative hypothesis that this more-efficient pollination might be explained by a mechanism ensuring reproduction that involves the autonomous transfer of self-pollen and self-fertilization of flowers.

The authors’ findings support the existence of a pollinator-mediated mechanism that differentially enhances the pollination of rare

species in diverse plant communities. This type of asymmetric facilitation has also been reported in a study conducted in a diverse grassland community in Brazil¹⁰. However, Wei and colleagues’ study goes deeper. It reaches a mechanistic understanding that addresses not only the pollination benefits but also the costs of pollinator sharing in terms of the loss of a species’ own pollen and receipt of foreign pollen. Furthermore, it assesses how pollinator specialization associated with distinctive flower shapes could alleviate these costs. The authors’ results were achieved by creatively linking data provided by tracking the network of plant–pollinator interactions and the network of pollen transfer.

Although Wei and colleagues’ study offers much both to praise and to learn from, the inference that pollinator-mediated facilitation is a process that favours the coexistence of plant species should be considered only as an intriguing proposal. This is because it is not known whether the pollination benefits for rare plants in the community studied result in an increase in seed production. As the authors recognize, other factors, such as available resources (light, water, nitrogen and phosphorus, among others) and the number of ovules to be fertilized, might be more relevant than pollination as factors that limit the number of seeds produced⁵. Furthermore, even if increasing pollinator attraction in diverse communities increases seed production by rare plants, the question remains whether

such a reproductive boost would enhance population growth. For many plant species, seed production above a certain level will have little or no effect on population growth, because either seedling establishment or the survival of already-established plants can be more-constraining factors¹².

Despite these limitations, Wei and colleagues’ study has broad implications for our understanding of some consequences of the ongoing global decline in pollinators¹³. Seed production is often chronically limited by pollinator availability¹⁴, so dwindling pollinator populations will further imperil plant reproduction, undoubtedly becoming a short- or long-term limiting factor in population survival. On the basis of Wei and colleagues’ work, we can predict that the local or regional decline in specialized pollinators, which are probably more susceptible to extinction, will impair the reproduction of rare plant species more than it will that of abundant ones. On a more positive note, this study has implications for the restoration of native plant communities, because it indicates that the propagation of common plants could help to rescue endangered plant species while also increasing pollinator diversity. More generally, asymmetric facilitation provides an overarching conceptual framework with which to develop management guidelines for the preservation of biodiversity.

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