if deficits in the TLE mice can be alleviated by activating MCs during learning.

Thus, Bui *et al.* provide some answers but also leave us with some questions. For example, how do MCs control only the duration of electrographic seizures? The reason may be similar to the reason MCs control convulsive seizures—in each case they terminate the seizure prematurely. It could be that activating surviving MCs might strengthen the DG inhibitory gate sufficiently to stop a seizure that has begun. However, how could a very small number of MCs stop a seizure that involves so many neurons in different brain regions? A possible explanation is that MCs that survive in the mouse model of TLE begin to grow additional connections (sprouting), which is known to happen in other cell types, such as GCs (*2*). Indeed, what would occur if all MCs survived in this model? Would MCs still inhibit GCs, or would they activate them? And would seizures be affected?

Other aspects of the DG that affect object location memory and convulsive seizures are also intriguing. For example, the DG is one of the few areas of the brain where GC neurogenesis occurs throughout life. Remarkably, new GCs influence the ability to distinguish novelty (*12*), which seems related to the functions of MCs to encode new object locations, identified by Bui *et al.* Reduction of new GCs in an adult mouse also enhances the susceptibility to convulsive seizures induced by systemic kainic acid injection (*13*). MCs make the first excitatory synapses on new GCs (*13*), so MC interactions with new GCs could play a role in spatial encoding and seizure susceptibility. Interestingly, GCs release peptides and even GABA, as well as undergoing many other changes, after seizures in mice (*14*). This might help explain why MC and GC manipulations had some different consequences in TLE mice. Further investigation should advance our understanding of how the DG contributes to memory and its role in epilepsy. ■

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ECOLOGY

The value of pollinator species diversity

Most crop-visiting species are needed to ensure high levels of crop pollination

By **Claire Kremen**

In a 1991 experiment that would be unlikely to pass a human-subject review today, eight intrepid adventurers were enclosed in a hermetically sealed structure (Biosphere 2), along with 3000 species of plants and animals and several habitats, including a coral reef, rainforest, mangrove, and wetland. However, most vertebrates and all pollinating insects went extinct, whereas ants and cockroaches multiplied. Carbon dioxide concentrations fluctuated wildly, and oxygen concentrations declined (*1*). The results highlighted how little we know about what it takes to maintain Earth's life-support system. On page 791 of this issue, Winfree *et al.* (*2*) investigate an important aspect of this problem: How many pollinators are needed to ensure crop pollination?

The question of how many species are needed to support ecosystem functioning has occupied an army of ecologists over the past 20 years (*3*). Experimental evidence is mainly based on randomly assembling grassland plant communities to comprise different numbers of species in small, replicated field plots. The results from these experiments increasingly suggest that large numbers of species are needed to support ecosystem functioning (*4, 5*). But it remains unclear whether the relationship between biodiversity and ecosystem functioning scales up from small plots to produce benefits to humans (or ecosystem services) in real, working landscapes, which are considerably more difficult to study (*5*).

In the experimental communities, species are picked randomly from a common species pool, and abundances are set to be similar from species to species (even). By contrast, natural communities are neither randomly assembled nor even. Instead, they typically consist of a few highly abundant (dominant) species and many rare ones. In the few studies that have looked at biodiversity–ecosystem functioning relationships in real-world settings, these dominant species were far more important for determining ecosystem functions than was the number of species (*6, 7*). Winfree *et al.* now take a fresh look at the role of dominance in ecosystem services, examining how many species are needed to supply crop pollination across a farming region.

High dominance (the presence of a few dominant species) tends to reduce the number of species needed to ensure ecosystem functioning (*7*), but species turnover (the replacement of one species for another across space or time) might increase it. When both properties occur in a real-world landscape, which one of them is more important in determining the relationship between biodiversity and ecosystem functioning? The answer will illuminate whether humanity's survival depends on a few or on many species. It will also help to resolve a longstanding conundrum (*8*): Should conservationists use ecosystem-service arguments to garner support from a broader array of people for biodiversity conservation, or would such an approach potentially undermine biodiversity conservation, if it turns out that relatively few species are needed to supply these services? Winfree *et al.*'s study helps to resolve these questions.

> ***"...understanding how much pollination a farmer would get at any point in the landscape is the relevant metric for assessing ecosystem services..."***

Pollinators are necessary to increase the production of 75% of our crop species. Honey bee colonies are often managed to supply crop-pollination services, but relying only on honey bees for pollination has become increasingly risky as beekeepers experience higher and higher rates of colony losses each year because of the combined effects of pesticides, diseases, and changes in habitat and climate. Native bee species can

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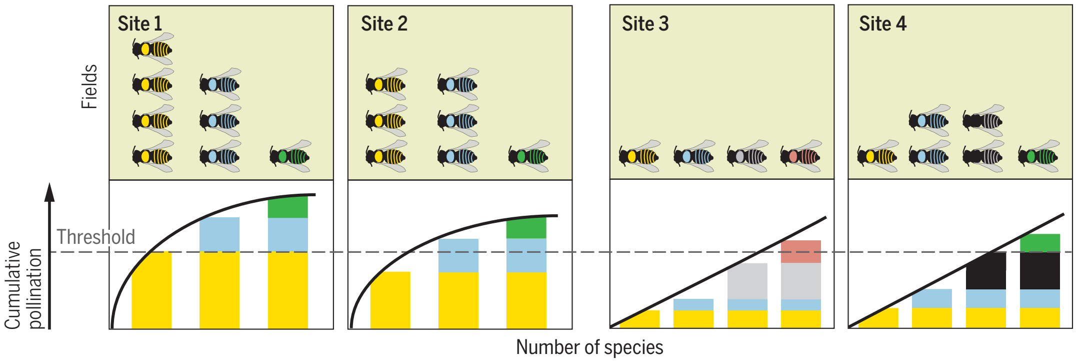
Bee diversity needed for pollination

Pollinating species vary from site to site; numbers of individuals indicate abundances at the site for each species type.



Dominant species contribute most to pollination function at sites 1 and 2, and only one or two species, respectively, are needed to surpass the threshold required for full pollination. Dominant species occur at all sites, but because of their low abundance at sites 3 and 4, most species are needed for pollination function. Species turnover between such sites means that most species in the species pool are needed to supply pollination function across the entire array of sites.

substitute for honey bees and often provide superior services (*9*). Of 20,000 bee species worldwide, 12% are estimated to contribute to crop-pollination services (*6*).

Winfree *et al.* elegantly disentangle the effects of species dominance from turnover in how different native bee species contribute to pollination of three crops (watermelon, blueberry, and cranberry) in the U.S. mid-Atlantic region. High functional dominance exists in the system, with just a few species supplying a large proportion of the pollination overall (*10*). The authors determine this by measuring both the typical amount of pollen that each species delivers on a single visit and the visit rate of each species at a given farm site, and then estimating the contribution of each species to the total amount of pollen delivered. However, as the team considered a larger and larger array of sites, they found that many more species were required to reach a threshold level of pollination (25, 50, or 75% of the mean total pollination per site).

Further, the authors quantified the relative importance of species turnover and species dominance with a null model that removed the effect of dominance. In this model, they effectively apportioned the pollination provided at a site evenly among all species present. The surprising result was that the effects of species turnover were, on average, 14 times more important than dominance effects for pollination function (at the largest scale of analysis), even though high levels of dominance occurred at individual sites and dominant species were widespread. Thus, achieving the 50% pollination threshold at a single farm site required, on average, 5.5 bee species, but 55 species were needed across the entire study region. At the 75% threshold, most bee species in the pool of crop-visiting species would be needed across all sites.

Why are these results so different from previous studies, including studies of crop pollination, which concluded that only a few dominant species are needed to supply ecosystem functions? A partial answer is that this is the first study to disentangle the contrasting effects of species dominance and turnover.

Equally important is how exactly the service was measured. Previous studies, including those by Winfree and co-workers (*6, 10*), looked at the relative contributions of functionally dominant and nondominant species to ecosystem function without considering the actual amount of pollination needed by farmers to reach critical pollination thresholds. In the current study, Winfree *et al.* instead looked at the magnitude of the service and whether a given threshold (25, 50, or 75%) is achieved at each site on the basis of the bee-community composition. Critically, at sites where the dominant, widespread pollinators are low in abundance, almost all or even all pollinator species may be needed (see the figure). At such sites, relatively rare species provide essential contributions to pollination function. Species turnover among such sites, then, is the reason why so many species are needed, regionally, to provide pollination.

Even though rare species make a small contribution overall across sites, identifying their contributions to reaching a threshold on a farm-by-farm basis shows how important they are. Arguably, understanding how much pollination a farmer would get at any point in the landscape is the relevant metric for assessing ecosystem services to real people in real landscapes (*11*).

The growing chorus, both from plot-based experimental studies (*3*) and now from a large-scale natural experiment (*2*), strongly supports the importance of maintaining a large amount of biodiversity to support human well-being sustainably. But maintaining this biodiversity in agricultural landscapes, both for pollination services and for other ecosystem functions and services that support crop production, is likely to require substantial changes in management. Specifically, it will require moving away from monocultures and fencerow-to-fencerow farming that rely extensively on external inputs of pesticides and fertilizers, as well as managed honey bees that may compete with wild bee species (*12*), and toward farms that generate much of the needed pest and disease control, soil fertility, and pollination services through crop and noncrop diversification and "ecological intensification" (increasing crop productivity through management practices that promote the organisms producing ecosystem services, rather than through increased use of pesticides and fertilizers) (*13, 14*). For example, planting diverse crops, flowering strips, and hedgerows can restore wild pollinator populations, enhance species turnover, and supply pollination services (*15*).

Winfree *et al.*'s study helps to show that there may be much more alignment than previously thought between ecosystem-service arguments for biodiversity conservation and intrinsic-value arguments (conserving biodiversity for its own sake). Given the key role of biodiversity for human well-being and sustainability, it is crucial that human societies better protect and restore biodiversity. ■

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