

model to the higher image velocities: the smaller the time constant, the higher the velocity the model is tuned to (Figure 1B,C). Both flight and octopamine agonist substantially reduced its value, consistent with the observed shifts in the H1 cell's velocity tuning [8].

An exciting parallel development is that the circuitry believed to generate the motion inputs corresponding to the Reichardt detector are, for the first time, becoming accessible to detailed studies, thanks to developments in genetics in the fruitfly, *Drosophila* [20]. Future studies will now be able to build on Jung *et al.*'s results to identify the mechanisms involved in detail. Already we know from intracellular recordings that locomotion alters the properties of the lobula plate tangential cells themselves, as well as the properties of their motion inputs [1,2]. It is certain that more signalling pathways than those using octopamine are involved, but how and where remains a mystery. Tying down the functional motivation for state-dependent vision in any model organism remains a big challenge, but based on current progress, work on the fly looks likely to succeed.

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The Circe Principle: Are Pollinators Waylaid by Attractive Habitats?

How do pollinators move across fragmented landscapes? Attractive habitats have been viewed as facilitating pollinator movement; however, they may actually be distracting the pollinators.

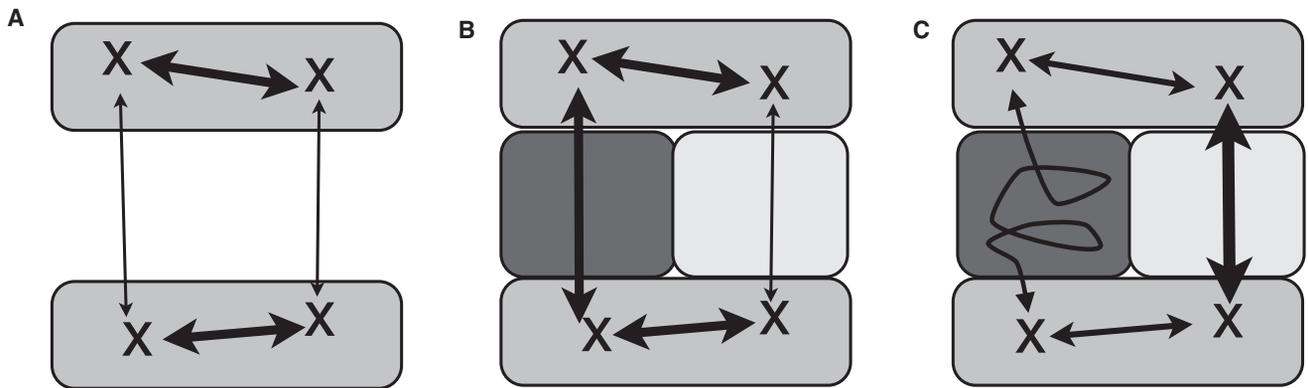
Ignasi Bartomeus
and Rachael Winfree

In order to understand vector-mediated ecological processes, we need to know how vector species move across landscapes. This is especially challenging when the vector species is an insect. Nevertheless, it is critical to understand the movement patterns of key insect functional groups — such as pollinators, which facilitate the reproduction of most of the world's plant species [1]. Several approaches have been used thus far to measure pollinator movement, but knowledge of how pollinators connect plants at the landscape scale remains elusive. The fundamental problem is

that large-scale approaches, which can inform us about how pollinators move among habitats, generally don't provide information on which individual plants are pollinated; whereas smaller-scale approaches that can measure pollinator movement among plants aren't feasible at the landscape scale. For example, capture–recapture methods can tell us how pollinators move among habitat types [2], but not about which plants are pollinated. Conversely, fluorescent dye techniques can identify the individual plants visited by pollinators [3], but such methods are generally not feasible for landscape-scale questions (but see [4] for an exception). Encouragingly,

recent technological innovations have made direct tracking of pollinators possible. However, direct tracking is still limited to species large enough to carry transmitters [5], or to species that move within reasonably open areas [6]. Perhaps the most promising technique estimates pollinator movements indirectly by using genetic methods on obligatory animal-pollinated plants [7]. These kinds of data are becoming easier and cheaper to obtain, and promise to greatly enhance the understanding of pollinator movement patterns at the landscape scale.

In a recent issue of *Current Biology*, Lander *et al.* [8] show that by mapping all of the individual trees in one population of a forest tree species and doing a paternity analysis, they can track pollination events between trees. The novel finding of the paper has to do with how habitat types in the larger landscape affect pollinator movements. The researchers use the data on pollination events, derived from the paternity analysis, to characterize



Current Biology

Figure 1. Pollination in fragmented habitats.

Schematic showing pollinator movements (arrows) between plants (x's) across habitat types (grey squares). The thicker the arrow, the more likely pollinator movement between two plants is to occur. Darker-colored habitats offer more floral resources to pollinators and thus are more attractive. (A) The classical view of a binary habitat versus non-habitat (matrix), in which matrix habitat composition is not considered. (B) Scenario in which different matrix habitats present different permeabilities, with the more pollinator-attractive habitat being more permeable. (C) Circe principle scenario in which attractive habitats can waylay pollinators, while unattractive habitats can enhance connectivity.

the habitat permeability between each pair of mated trees. The unintuitive finding is that for a given inter-tree distance, two trees growing in native forest were more likely to mate when separated by pine plantation, a habitat type relatively hostile to pollinators; whereas trees separated by agricultural fields, a pollinator-attractive habitat, were less likely to mate, although trees separately by an even more hostile habitat, clear-fell, as predicted did not mate as often. This contradicts current wisdom among pollination ecologists, and among landscape ecologists generally, that habitats hostile to an organism act exclusively as barriers to movement, whereas attractive habitats act as corridors [9,10] (Figure 1A,B).

Why might pollinator-attractive habitat serve as a barrier to pollination? Lander *et al.* propose a novel mechanism, which they term the Circe principle (Figure 1C). They suggest that in their study pollinators were waylaid by attractive habitats, and thus never delivered pollen to the female tree — much as Odysseus was waylaid on Circe's island, preventing his return to the waiting Penelope. Of course, ecology deviates from the Homeric metaphor in that the pollinators are not trying to move pollen among trees, but are rather looking for the best forage plants. Thus, what we see here is a conflict of interests between plants and pollinators. Intriguingly, smaller-scale studies in pollination ecology are consistent with the Circe

principle, as it is well-known that plants growing in the same habitat can compete with each other for pollinators [11]. The new work by Lander *et al.* [8] expands this concept to the landscape scale, with the competition for pollinators occurring among entire plant communities growing in different habitats.

In the context of global change, it is interesting that the 'good' habitat in the Lander *et al.* [8] study, which drew pollinators away from the forest tree species, was agricultural. This is not an anomaly: within naturally forested ecosystems, pollinator abundance is often higher in human-disturbed habitats [12]. Other researchers who have used genetic methods to measure the pollinator-mediated mating of native tropical trees likewise found that trees growing in human-disturbed areas were better pollinated either by native pollinators [13] or by exotic pollinators occurring mainly in the human-modified habitats [14]. However, in a temperate ecosystem, open areas and settlements do not seem to waylay pollinators, as pollen-mediated gene flow of an insect-pollinated tree occurring inside forest patches is enhanced when the patches are separated by human dominated lands [15]. These examples all show that disturbed habitats can affect the original plant-pollinator relationships in different ways. A final point is that genetic methods identify a pollination event from the plants' perspective; but we still lack

information about how differential responses of pollinators might modulate this effect.

The Lander *et al.* [8] paper contributes to a larger discussion within landscape ecology about the importance of including information about matrix habitat type in studies of animal movement. Until recently, most models of animal movement treated land cover as binary, with a given patch being either habitat or matrix (Figure 1A). Furthermore, matrix habitats were assumed not to provide resources, corresponding to the 'islands in a hostile sea' paradigm of island biogeography theory [16]. However, many animals in fact do use matrix habitats [17]; and the predictive ability of metapopulation and metacommunity models is improved when matrix habitats are included [18,19]. Previous large-scale experimental work on pollinator movements has been conducted using a binary matrix approach, in which the 'habitat' was early succession pollinator-attractive habitat and the 'matrix' a pine plantation [4]. The results do not agree with Lander *et al.*'s [8] hypothesis; rather, they showed that corridors facilitate both pollinator movement and pollination. More empirical studies are needed to determine whether the inconsistency between studies is due to pollinator taxon, landscape setting, or something else.

Lander *et al.*'s [8] work, while novel, leaves some loose ends and open

questions. Why, for example, did the two analytical approaches taken by Lander *et al.* [8] (a general linear model and a circuit model) come to opposing conclusions? Which mechanisms make one hostile habitat, clear-fells, act as a barrier, while the hostile pine plantations enhanced connectivity? And how might the Circe principle apply to the main pollinator taxon, bees (Hymenoptera: Apiformes), which differ fundamentally in their foraging and movement behavior from the syrphid flies (Diptera: Syrphidae) [20] studied by Lander *et al.* [8]? These questions leave plenty of scope for further research.

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Organelle Transport: Mitochondria Hitch a Ride on Dynamic Microtubules

In fission yeast, microtubules control mitochondrial position by a mechanism that is dependent on microtubule dynamics but not motor proteins. A new study now reveals the molecular basis for this novel mechanism of organelle movement.

Liza A. Pon

In 1985, Hirokawa, Bloom and Vallee [1] used quick-freeze, deep-etch electron microscopy to visualize crossbridges between microtubules and organelles in regions of the axon that are associated with fast axonal transport. This work provided the first direct evidence that organelles use microtubules for axonal transport. It also laid the foundation for establishing a role for kinesin and dynein in driving organelle movement along microtubule tracks in the neuronal axon, and for identifying adaptors that link motors to their cargos as well as mechanisms that regulate motor function in cargo binding and transport. In this issue

of *Current Biology*, Fu *et al.* [2] now identify a fundamentally different connection between mitochondria and microtubules in the fission yeast *Schizosaccharomyces pombe*.

During interphase, *S. pombe* cells contain dynamic bundles of microtubules that emerge from microtubule organizing centers in the center of the cell and extend toward the cell tips (Figure 1). Mitochondria in these cells are tubular structures that can interact with microtubule bundles. However, mitochondria do not exhibit track-dependent movement along microtubules. Rather, they bind to dynamic microtubule bundles and move to and from the cell tips as their associated microtubule bundle elongates and shortens [3,4].

Microtubules therefore control mitochondrial position and movement in fission yeast; however, they do so by a mechanism that is dependent on microtubule dynamics not motor proteins. Actin polymerization drives protrusion of the leading edge during cellular migration and intracellular movement of bacterial/viral pathogens, endosomes, and budding yeast mitochondria [5–9]. However, mitochondrial movement in fission yeast represents the first documented motility mechanism that is dependent on microtubule polymerization and dynamics.

In the new study, Fu *et al.* [2] identified a mitochondria-microtubule binder protein (*mmb1p*) in fission yeast. Deletion of *mmb1* results in aggregation of mitochondria and accumulation of the aggregated organelle at the cell tips. It also results in defects in mitochondrial inheritance and loss of cell viability. Thus, *mmb1p* has functional interactions with mitochondria that affect the distribution and inheritance of the organelle. Furthermore, they obtained evidence for a direct role for *mmb1p*