

Commentary

Mutualisms evolve in correlation across the plant tree of life

Mutualistic interactions occur throughout the plant body, from mycorrhizal symbioses in the roots (Tedersoo *et al.*, 2020) to mutualistic interactions with defending insects (Weber & Agrawal, 2014), animal pollinators (Dellinger, 2020), and animal seed dispersers (Janson, 1983). Animal pollination, in particular, is often considered a major driver of angiosperm trait diversity (Vamosi & Vamosi, 2010; Smith & Goldberg, 2015; Dellinger, 2020). However, these mutualisms and the plant organs involved are typically studied separately, under the assumption that the evolution of one organ or system is largely independent of the others. In an article published in this issue of *New Phytologist*, Yamawo & Ohno (2024; 1586–1599), challenge that assumption by proposing that population density serves as a unifying factor influencing the evolution of three major mutualistic interactions (type of mycorrhizal association, pollination mode, and seed dispersal mode), leading to macroevolutionary correlations between these mutualisms across broad swathes of plant diversity (Yamawo & Ohno). With impressive datasets on mycorrhizal type, pollination mode, and seed dispersal mode, Yamawo & Ohno find that arbuscular mycorrhizal (AM) associations lead to the evolution of biotic pollination and seed dispersal, while ectomycorrhizal (EcM) associations favor the evolution of abiotic pollination and seed dispersal.

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Can plant–soil feedbacks and population density mediate multiple mutualisms?

Yamawo & Ohno build on several recent studies suggesting that different types of mycorrhizal symbioses lead to high or low population densities of their plant hosts as a result of differing plant–soil feedbacks (Bennett *et al.*, 2017; Kadowaki *et al.*, 2018). In particular, trees with AM-type fungal associations tend to have negative plant–soil feedbacks which inhibit the growth of

conspecifics, leading to low population densities in plant hosts. By contrast, EcM-type fungal associations tend to produce positive plant–soil feedbacks which facilitate higher population densities among plant host species. As Yamawo & Ohno point out, this difference in population density among plant hosts engaged in mutualisms with AM- or EcM-type fungi may affect other mutualisms that also depend on population density.

One such mutualism occurs in pollination, where plants can be broadly categorized as having biotic pollination (where pollen is transported by animal vectors) or abiotic pollination (where pollen moves by wind). Wind is inefficient at transporting pollen large distances (Koenig & Ashley, 2003), such that when population densities are low, wind pollination may have poor fitness. Under such circumstances, animal pollination may evolve because animals are: (1) able to carry pollen farther distances; and (2) can selectively visit flowers of the same species, leading to greater pollination success. In high population densities, the opposite holds true: when individuals of the same species are spatially adjacent, wind pollination may be sufficient at accomplishing fertilization if enough pollen is released, and targeted pollination (via animals) may be less likely to evolve. Because wind pollen tends to be small and of lower density than pollen grains associated with animal pollination (Niklas, 1985), selection for wind pollination may occur under circumstances of high population densities.

Yamawo & Ohno extend this line of reasoning to seed dispersal. Seed dispersal can also be broadly categorized as biotic (where animals consume the fruits and transport the seeds away from the parent plant) or abiotic (where seeds are dispersed by wind, gravity, or occasionally other mechanisms). Animal dispersers can carry seeds farther distances than wind (or gravity) can, including beyond the spatial range of the negative plant–soil feedbacks experienced by AM-type trees. By contrast, under conditions of positive plant–soil feedbacks like those produced by EcM-type fungal associations, wind or gravity dispersal may be advantageous because those modes of dispersal would be more likely to deposit seeds in a beneficial soil environment. The evolutionary consequence of these plant–soil feedbacks leads to lower population densities in AM-type trees and higher population densities in EcM-type trees.

A macroevolutionary pattern

Yamawo & Ohno show that these hypothesized correlations occur not only within the handful of species that have been previously studied, but also emerge on a macroevolutionary scale: across more than 10 000 species, AM-type fungal associations are associated with both biotic pollination and biotic dispersal, while EcM-type fungal associations are associated with abiotic pollination and abiotic dispersal. Although the direction of causation in

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this study was largely assumed to be mycorrhizal type driving the evolution of pollination and seed dispersal modes, other directions of causation could hold true as well. For instance, long distance seed dispersal by animal vectors could result in low population densities as seeds are spread diffusely across the landscape, leading to evolution of biotic pollination and AM-type associations. Hypothetically, any factor that influences population density and/or plant–soil feedbacks could potentially tip the balance towards the AM/biotic/biotic or EcM/abiotic/abiotic states.

Beyond their empirical results, Yamawo & Ohno's results suggest that disparate organs of the plant body can evolve in correlation, and they offer a mechanism to explain the evolutionary pattern linking the evolution of those distinct organs. Although we often treat flowers, fruits, leaves, and roots as separate units whose traits evolve independently, that assumption may not always be true. For example, there is some evidence that flower and fruit traits may be correlated (such as flower size and seed number; Bawa *et al.*, 2019). There is also some evidence that the presence of mycorrhizal mutualists positively influences pollination (Gange & Smith, 2005). However, most such studies center on only a small number of species, and studies examining correlated evolution of traits across organs remain rare at the macroevolutionary and macroecological levels. At macroevolutionary and macroecological scales, it is especially important to assess whether correlations result from a shared factor that selects on multiple organs independently, or whether there is a mechanistic, biological link that could explain the observed patterns. Yamawo & Ohno present a compelling argument that the evolution of mutualistic interactions in disparate parts of the plant body may be linked via their influence on population density and positive or negative plant–soil feedbacks. Their results not only provide a biological mechanism for correlated evolution at macroevolutionary scales, but also add to the evidence that the evolution of the plant body cannot always be easily separated into its component parts.

Future directions

Yamawo & Ohno's results suggest several avenues of future research, both related directly to the mutualisms in their study as well as to the broader question of integrated and correlated evolution across the whole plant body. For instance, are the primary effects of mycorrhizal associations indirect (e.g. population density) or direct? Population density and plant–soil feedbacks may lead to evolution of particular combinations of mycorrhizal associations with biotic or abiotic pollination and seed dispersal. However, direct effects of mycorrhizal associations on floral and fruit traits could also influence the evolution of pollination and seed dispersal mode. In several fruit crops, inoculation with AM fungal partners was associated with larger, more colorful fruits (Mena-Violante *et al.*, 2006) and better seed germination (Copetta *et al.*, 2021). Similarly, in flowers of several species, inoculation with AM fungal partners increased visitation by animal pollinators likely through increasing flower size, number, or nectar sugar content (Gange & Smith, 2005).

Therefore, engaging in mutualistic interactions with AM-type mycorrhizas could provide additional resources for plants to produce flowers and fruits with traits that are more attractive to animal partners. Unfortunately, studies of such cross-organ effects of mutualisms have largely been restricted to AM-type fungi and to only a handful of species (Bennett & Meek, 2020). Whether and how such influences on floral and fruit traits may scale up to macroevolutionary or macroecological patterns remains unknown.

As Yamawo & Ohno's study suggests, our collective understanding of plant evolution would benefit from stepping back from the divide between organs, systems, and interactions and instead considering the mechanistic links that may jointly influence whole-plant evolution. After all, the correlated evolution of traits within organs to form syndromes is one of the main principles that is thought to structure the evolution of diverse organs including flowers, fruits, and leaves (Sinnott-Armstrong *et al.*, 2022). Similar correlated evolution across the whole plant body may be more widespread than previously appreciated and may underpin large-scale patterns in plant biodiversity.

ORCID

Miranda A. Sinnott-Armstrong  <https://orcid.org/0000-0002-1806-565X>

Miranda A. Sinnott-Armstrong^{1,2} 

¹Department of Sustainable Bio-inspired Materials, Max Planck Institute for Colloids and Interface, Potsdam, 14476, Germany;

²Department of Biology, Duke University, Durham, NC, 27708, USA
(email: miranda.sinnott-armstrong@duke.edu)

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