

A missing link: Connecting plant and pollinator population structure

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Plant–pollinator interactions are major drivers of flowering plant evolution. There are numerous examples of associations between floral traits and diversification rate and of parallel evolution of floral characters in unrelated groups that use similar pollinator types (Kay and Sargent, 2009). These macroevolutionary patterns highlight pollinators as selective agents driving floral trait variation, reproductive isolation, and diversification. However, the role of pollinators is even more fundamental to the plant life cycle than this adaptative framework suggests—pollinators are key dispersal agents. As dispersal agents, pollinators may also drive the distribution of neutral genetic variation and population connectivity within plant species. Population genetic studies of both plants and their pollinators can offer novel insight into how pollinators move across the environment, clarifying how pollinators affect plant evolution at the population scale.

CONNECTING POPULATION GENETIC STUDIES OF PLANTS AND THEIR POLLINATORS

Many plants rely on external vectors for pollen and seed dispersal. Data suggest that dispersal via seed is often limited, and the movement of pollen via pollinators represents a significant mechanism through which alleles move across the landscape (Ennos, 1994; Sork and Smouse, 2006; Browne and Karubian, 2018). Whether the distribution of genetic variation within a plant species reflects its pollinator's foraging characteristics has been of interest for decades (Loveless and Hamrick, 1984). Recent studies leverage sequence data to demonstrate that pollinator identity and mobility correlate with outcrossing rates, gene flow, and measures of genetic distance across plant lineages (Gamba and Muchhala, 2020; Wessinger, 2021). The notion that highly mobile pollinators carry pollen across long distances,

while less-mobile pollinators move pollen locally offers a mechanism to explain these correlations (Schmidt-Lebuhn et al., 2019). Known as the pollen dispersal-dependent speciation hypothesis, this framework posits that differences in pollinator mobility may scale up to affect the likelihood of speciation and extinction (Harvey et al., 2019; Wessinger, 2021). While evidence supporting this hypothesis is growing, the mechanisms that link pollinator identity to patterns of plant diversity are unclear. If variation in pollinator mobility explains the correlation between pollinator identity and plant diversification, then the genetic structure within a plant species will reflect the movement pattern of its pollinator(s) across space. Testing this hypothesis will bring deeper insight into the microevolutionary processes underlying recognized patterns of pollinator-mediated plant diversification.

MECHANISMS LINKING POLLINATOR MOVEMENT TO PLANT GENETIC STRUCTURE

Because pollinators are an important factor controlling gene dispersal in plants, an intuitive prediction is that plant population genetic structure will reflect pollinator movement patterns (Figure 1). Population genetic tools are useful to test this prediction because they can infer how pollinators are distributed across the landscape. The distribution of pollinators across a plant species' range is broadly important for pollen dispersal and subsequent gene flow. By pairing population genetic studies of plants and their pollinators, we can explore how plant population structure reflects (1) variation in pollinator visitation frequency, (2) the pattern of pollinator movement among populations, and (3) pollinator responses to the environment.

Differences in pollinator visitation frequency to each plant population will affect how genetic variation is distributed within

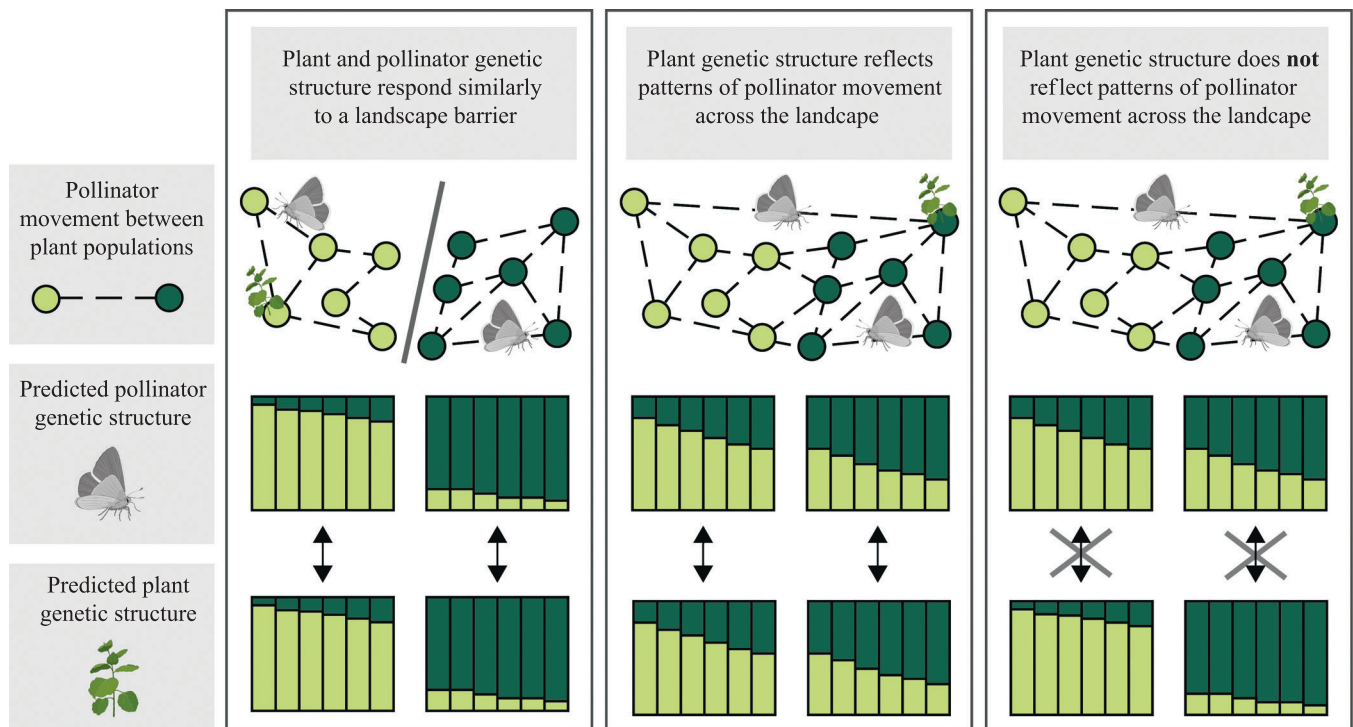


FIGURE 1 Predicted connections between pollinator and plant genetic structure. Green dots represent plant populations; dashed black lines indicate pollinator movement patterns. In the example in the left panel, pollinators are unable to cross a hypothetical landscape barrier resulting in structured genetic variation in the pollinator species. Because the landscape barrier also resists gene flow via pollen dispersal, plant genetic structure closely reflects pollinator genetic structure. In the middle panel, no barrier to movement predicts a pattern of isolation by distance in both plant and pollinator species. An alternative prediction is presented in the right panel. Broadly moving pollinators exchange genes freely across the landscape, driving a pattern of isolation by distance in the pollinator species. However, plant genetic variation does not reflect pollinator movement (or pollinator genetic structure) due to spatial variation in selection on plant genotypes and a variety of potential processes including pollinator behaviors that affect pollen dispersal such as pollen grooming or territoriality. Collecting population genetic data for both pollinators and plants in a given system will help clarify which of these predictions holds. Elements of the figure were drawn using [Biorender.com](https://biorender.com).

and between populations. Enhanced pollinator attraction will increase the likelihood of pollen movement between a wider number of individuals within and between populations (Harder and Barrett, 1996). For individuals in populations that receive relatively few pollinator visits (particularly from distant populations), the opportunity for diverse mating events is limited. As a result, inbreeding is more likely. Over time, inbreeding reduces the effective population size and can promote population differentiation (Charlesworth, 2003). Simultaneously, individuals in populations for which pollination events are rare will have infrequent opportunities for pollen receipt and/or export between individuals in other populations. Particularly when pollination occurs across short distances, these populations will tend to be more genetically isolated.

Additionally, the pattern of pollinator trips among populations will affect plant genetic structure. Because plants are sessile, we might assume that genetic structure reflects geographic location, therefore following a pattern of isolation by distance (Loveless and Hamrick, 1984; Cruzan and Hendrickson, 2020). However, when pollinators repeatedly move between spatially distant populations, these populations will be more genetically similar than predicted by geographic distance (Sork and Smouse, 2006). For example, land-use has fragmented populations of the prairie

endemic, *Oenothera harringtonii*, and yet, measures of genetic distance suggest that hawkmoth pollinators maintain population connectivity (Skogen et al., 2019). In this system, pollinator movement defines dispersal and contributes to plant genetic structure beyond isolation by distance.

Finally, patterns of pollinator response to the environment will affect pollen dispersal and plant population structure. Pollinators are distributed heterogeneously due to a variety of factors including territoriality and ecological adaptation. Landscape genetic distance/resistance approaches infer how environmental variables affect pollinator gene flow and can also identify landscape factors influencing pollen dispersal (Cruzan and Hendrickson, 2020; Emel et al., 2021). Whether landscape genetic factors affecting pollinator genetic structure in turn affect the structure of plant species remains unexplored.

Although these mechanisms intuitively link pollinator movement patterns to plant population structure, there are many reasons why plant structure may not reflect pollinator movement (Figure 1). Selection during the post-pollination and establishment phase may dominate in determining which alleles persist in a population and thus could obscure patterns of pollen flow. In some plant species,

seed/propagule dispersal may contribute more than pollen dispersal to population connectivity (Nazareno et al., 2021). For plant species using multiple pollinators (generalists), the individual impact of each pollinator may be swamped by a collective effect not attributable to any given pollinator. Alternatively, the effects of each pollinator type may be observable at different spatial scales or geographic regions. Pollinator behaviors including grooming or territoriality can impact pollen dispersal probabilities, breaking the connection between pollinator movement and realized pollen flow. Therefore, exploring the connection between plant and pollinator genetic structure remains an exciting future direction.

INVESTIGATING POLLINATORS AS DRIVERS OF PLANT POPULATION STRUCTURE

To determine whether and how plant population structure responds to pollinator movement in any specific biological system, two patterns must be described: (1) patterns of pollen movement by pollinators and (2) the distribution of genetic variation within the plant species. Pairing population genetic data of plants and their pollinators can achieve both goals.

Historical approaches for characterizing pollinator-mediated pollen dispersal include direct observations (e.g., Levin and Kerster, 1974), pollinator tagging, or the use of pollen grain analogues (e.g., fluorescing quantum dots), which have the additional advantage of incorporating variation in pollen pickup/deposition (e.g., Schmidt-Lebuhn et al., 2019).

Looking to the future, we advocate for studies using population genetics of pollinators to reveal their geographic distribution and infer movement patterns. While habitat and/or mating preferences likely also contribute to genetic structure, genetic measures of pollinator population connectivity infer how frequently individuals move between populations and across geography (Lowe and Allendorf, 2010). When these movements correlate with foraging, pollinator genetic structure will reveal potential patterns of pollen flow. Given the growing accessibility of genomic sequencing and advances in analytic methods, population genetic tools are increasingly tractable for exploring pollinator movement across the environment. However, population genetic studies remain rare for many pollinator types, with a notable dearth of data on insect pollinators. Particularly when paired with behavioral observations, population genetic data can be a powerful tool to connect pollinator movement, realized pollen flow, and plant population structure.

To explore the effect of pollinator movement on plant population structure, researchers can apply a variety of approaches using genetic data. Plant parentage analyses and assignment tests can reveal pollen movement within a reproductive season (Sork and Smouse, 2006; Bode et al., 2018).

Estimates of genetic distance between plant populations describe the cumulative impact of pollen dispersal and gene flow across generations (Cruzan and Hendrickson, 2020). Using pollinator movement patterns as an explanatory variable for plant genetic structure, researchers can then quantitatively test the prediction that pollinators affect the distribution of genetic variation within a plant species beyond isolation by distance (as is done with other environmental variables; e.g., Bradburd et al., 2013).

WHAT CAN WE LEARN ABOUT PLANT-POLLINATOR INTERACTIONS BY USING POPULATION GENETICS?

Quantifying the impact of pollinator movement on plant genetic structure will expand our understanding of the ecological and evolutionary consequences of plant-pollinator interactions and generate predictions that can inform species management. If pollinators provide key dispersal services, the predicted impacts of pollinator loss will affect not only plant reproductive output but also population connectivity. Environmental disturbances affecting pollinators will also affect plant population structure. Alternatively, if habitat disturbance fragments plant populations, mobile pollinators may maintain gene flow.

Emphasizing pollinators as dispersal vectors links patterns of pollinator driven diversification at the macroevolutionary scale to within species demographic processes (Harvey et al., 2019). When plant genetic structure reflects pollinator movement, pollinator-mediated gene flow may contribute to the likelihood of population isolation and species extinction, persistence, or divergence. Although the relationship between dispersal dynamics, metapopulation structure, and diversification is complex, growing evidence supports an association across diverse taxonomic groups (Harvey et al., 2019; Wessinger et al., 2019; Wessinger, 2021). While pollinator-mediated selection on adaptive floral traits is certainly important to flowering plant evolution, investigating pollinators as drivers of plant population structure can offer an additional path towards reconciling macroevolutionary patterns of floral diversity with microevolutionary processes.

AUTHOR CONTRIBUTIONS

G.B. and R.H. contributed equally to conceptualization, drafting, and writing.

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