Digest: Experimental evolution provides a window into the evolution of generalized pollination

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Do plants with multiple pollinators evolve unique trait combinations or intermediate phenotypes compared to plants with one pollinator? Using experimental evolution, Schiestl et al. (2018) found that plants pollinated by bumblebees and hoverflies evolved trait values not observed in plants pollinated by one taxon, which provides evidence for the existence of a unique generalized pollination phenotype.

While highly specialized plant-pollinator interactions like Darwin’s orchids, yucca moths, and fig wasps have captured the imagination of evolutionary biologists for centuries, a number of lines of research suggest that generalization, not specialization, may be more the rule than the exception, particularly in the northern hemisphere (see Johnson and Steiner 2000). For instance, network studies frequently find evidence for generalization (Oleson and Jordano 2002) or asymmetric specialization (Vázquez and Aizen 2004), and large scale analyses of floral phenotypes and pollinator visitation patterns provide mixed support for the idea that pollinators only visit plants with certain floral traits (Ollerton et al. 2009; Rosas-Guerrero et al. 2014).

Despite this evidence for the prevalence of generalization in plant–pollinator interactions, the ways in which pollination by multiple animals or types of animals affects floral trait evolution are relatively unknown. The “most effective pollinator principle” (Stebbins 1970) contends that pollinator-mediated selection is additive and determined by the most frequent or efficient visitor. However, recent studies have demonstrated that selection can be non-additive, such that visitation by multiple pollinators may generate selection for unique trait combinations rather than intermediate phenotypes (Sahli and Conner 2011; Brosi and Briggs 2013; Knauer and Schiestl 2017).

In this issue, Schiestl et al. (2018) utilized an experimental evolution approach to test key questions surrounding the evolution of generalized floral phenotypes. To determine if different pollinators generate different patterns of selection on floral morphology, scent, and rates of spontaneous selfing, they grew fast-cycling Brassica rapa (Brassicaceae; Wisconsin Fast Plants®) in a controlled environment and exposed seven generations of plants to one of three pollination treatments: bumblebees (Bombus terrestris), hoverflies (Episyrphus balteatus), and both insects together. At the end of the experiment, plants in the generalized pollination treatment exhibited lower floral scent production, greater height, and lower nectar production compared to one or both of the single-pollinator species treatment groups. Taken together, these results document the evolution of a unique generalized pollination phenotype that is not merely an average of the phenotypes produced by selection from each pollinator in isolation.

This study is only the third to estimate selection (using the Lande and Arnold (1983) method) via different pollinators on a plant within the same experiment (Figure 1). Across these studies, selection on some traits was consistent between pollinator treatments while patterns of selection on other traits varied. For instance, both bumblebees and cabbage butterflies exerted positive directional selection on floral morphology of B. rapa (Knauer and Schiestl 2017; Figure 1B), while bumblebees exerted positive selection on the positioning of reproductive parts, and honey bees exerted negative selection on Raphanus raphanistrum (Sahli and
Figure 1. Three studies have measured selection (using the Lande and Arnold (1983) method) under different pollination treatments that included single or multiple pollinator species during the same experiment: Sahli and Conner (2011) estimated selection on wild radish (*Raphanus raphanistrum*) by sweat bees, syrphid flies, cabbage butterflies, bumblebees, and honey bees, and the latter three taxa together (A); Knauer and Schiestl (2017) estimated selection on field mustard (*Brassica rapa*) by bumblebees, cabbage butterflies, and the two taxa together (B); and Schiestl et al. (2018) estimated selection on field mustard by bumblebees, hoverflies, and the two taxa together (C). The colors of the boxes around the images of the pollinators indicate the traits that the pollinators selected for: pink is floral morphology traits, blue is floral scent, purple is a negative correlation between floral morphology and floral scent, gold is flower number and/or plant height, and green is reproductive parts positioning or size. Rounded rectangles represent the treatments that contained multiple pollinators, while the single pollinator treatments are represented by square-cornered rectangles.

Photo credits: wild radish photo by James Lindsey (CC BY-SA 3.0); sweat bee photo by Aiwok (CC BY-SA 3.0); syrphid fly photo by Vengolis (CC BY-SA 4.0); cabbage butterfly photo by Richard Bartz (CC BY-SA 2.5); bumblebee photo by Katja Schultz (CC BY 2.0); honey bee photo by Ivar Leidus (CC BY-SA 4.0); field mustard photo by John Hilty, Illinois Wildflowers; hoverfly photo by Charles Sharp (CC BY-SA 3.0).
Conner 2011; Figure 1A). However, in line with the results of Schiestl et al. (2018), these studies also found unique patterns of selection in their generalized pollination treatments (two or more insect species; differences in color and line type of boxes around one pollinator vs. multiple pollinators within a column in Figure 1). This small body of literature indicates a potentially significant role for species interactions in determining patterns of selection that should be explored in a larger number of systems.

In addition to providing valuable insight into the evolution of generalized pollination, the work of Schiestl et al. (2018) highlights how experimental evolution can be used to address outstanding questions in the field of plant–pollinator interactions. While this approach will not be feasible in all systems, future studies can utilize the type of approach presented by Schiestl et al. (2018) to continue to disentangle the effects of different agents of selection and test how species interactions may affect patterns of selection.

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