

Digest: Shape-shifting in Solanaceae flowers: The influence of pollinators*

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Aside from climate, plant–pollinator interactions are thought to be one of the main drivers of diversification in tropical plant lineages (Fig. 1; Gentry 1982; Pérez-Escobar et al. 2017). It has been argued that the great variation in angiosperm flowers is largely influenced by pollinator-mediated selection (Sauquet et al. 2017), a force that has also been linked with diversification of large groups within the flowering plants, such as orchids (Pérez-Escobar et al. 2017). Micro-evolutionary studies aimed at understanding mechanisms underpinning changes in observed phenotypes have clearly demonstrated that pollinator shifts are strongly correlated with changes in floral traits (e.g., *Aquilegia*; Whittall and Hodges 2007). The importance of pollinator-mediated selection in driving divergence at a macro-evolutionary scale, however, remains unclear.

In this issue, Smith and Kriebel (2018) explore the question of pollinator-mediated selection at a macro-evolutionary scale in the Andean shrubs of the solanaceous tribe Iochrominae. To understand drivers of deep evolutionary shifts in floral traits, they used quantitative data in a phylogenetic context to test the Grant–Stebbins model, which predicts pollinator shifts will drive divergence and potentially speciation (Johnson 2006). In addition, the authors conducted corolla shape measurements based on geometric morphometrics and reconstructed a robust species-level phylogeny.

Pulling together the first such broad-scale dataset, Smith and Kriebel (2018) demonstrate that floral shape evolution within the Iochrominae, a clade that includes bird- and insect-pollinated species, has been largely pollinator mediated. Using statistical re-

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gression methods that account for phylogenetic relationships, they identify multiple shifts from narrow, tubular flowers to more open campanulate and bowl-shaped corollas. These shifts in flower shape are strongly correlated with shifts from hummingbirds, which pollinated the tubular flowers, to a variety of insect pollinators, which pollinate the more open flowers. Potentially, these shifts could also reflect a switch from specialist pollination systems to generalist strategies. Such shifts in pollination systems can occur several times even within genera, and are often associated with rapid processes of genomic and phenotypic change such as hybridization and polyploidization (e.g., McCarthy et al. 2016).

Smith and Kriebel (2018) also highlight reversibility and lability of floral shape and pollination system. Iochrominae are part of the Physalid clade within the Solanaceae, in which the flowers are thought to be ancestrally open and bee pollinated (Knapp 2010). In the Iochrominae, evolution from tubular flowers to these ancestral open flower shapes has occurred multiple times, with one clear reversal back to a tubular form. The authors suggest this switch might be enabled by tubular-flowered species maintaining some level of insect pollination, which would support previous notions that pollinator syndromes are not universal (e.g., Barrett 2013; Ollerton et al. 2015).

Smith and Kriebel's (2018) study shows that determining when and why a pollinator-shift model applies is important at macro-evolutionary scales, as not all evolutionary divergence is linked to floral trait shifts, nor are all trait shifts due to pollinator-mediated selection. They suggest that lability of floral traits and pollination systems may be linked to range expansion, opening a rich new seam of hypotheses for floral biologists to test at macro-evolutionary scales.

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family that includes important food crops (e.g., potatoes, tomatoes) but also a diversity of floral forms, including large flowers found in tropical lianas and epiphytes (Orejuela et al. 2017). (A) Brugmansia sanguinea. (B) Dunalia spinosa. (C) Browallia speciosa. (D) Deprea ecuatoriana. (E) Schultesianthus crosbianus. (F) Petunia patagonica. (G) Markea longiflora. (H) Nicotiana otophora. (I) Solanum whalenii. (J) Witheringia sp. (K) Physalis pruinosa. Photographs: A, B, Jhoana Castillo; C, D, Andrés Orejuela; E, Alex Monro; F, Steven Dodsworth; G, André Cardoso; H, I, K, Sandra Knapp; J, Oscar Alejandro Pérez-Escobar.

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