Digest: Trait variation in *Mimulus* provides new evidence for the joint action of ecological sorting and character displacement

Katherine E. Eisen

1Department of Ecology and Evolutionary Biology, Cornell University, New York 14850

2E-mail: kee39@cornell.edu

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Understanding how closely related species coexist in communities is one of the oldest goals of ecology and evolutionary biology. One long-standing hypothesis is that the evolution of key differences in species’ niches or ecological requirements (a process known as niche differentiation) can minimize competition and promote coexistence.

Two processes are often invoked as contributing to niche differentiation: ecological sorting and character displacement. Traditionally, these processes have been considered in isolation, given that ecological sorting results from trait change in allopatry, while character displacement is produced by in situ evolution in sympatry.

In this issue, Kooyers et al. (2017) challenged this way of thinking by empirically demonstrating how both of these processes contributed to the co-occurrence of two *Mimulus* species (Fig. 1A and B). To determine whether the species’ niches were differentiated in sympatry, the authors analyzed climatic variables and measured soil depth in replicated sympatric and allopatric populations across an elevation gradient. They then conducted common garden and competition experiments using seeds from these populations to determine whether phenotypic differences were genetically based, and whether competition affected trait evolution. Results from the field study indicated that the species occupied patches with distinct soil types in sympatry, which suggested that niche differentiation initially resulted from ecological sorting (habitat partitioning).

Kooyers et al. (2017) also found evidence for character displacement, but not the commonly anticipated pattern of trait divergence between species in sympatry relative to allopatry. Rather, the authors referenced and contributed to an underappreciated body of literature that indicates that evolution in response to competition in sympatry can produce other patterns of trait change, including convergence (e.g., Fox and Vasseur 2008). When grown in a common garden and in competition experiments, the species displayed parallel or mutually convergent character change in a number of reproductive traits. These patterns varied along the elevation gradient, which suggested that the effects of competition-mediated selection are context dependent.

*Mimulus* has long been characterized as a model system for ecological and evolutionary functional genomics. The results of Kooyers et al. (2017) expand on the utility of the genus in general and *M. guttatus* in particular for addressing questions in ecology and evolutionary biology. This study marks the second reported instance of character displacement between *M. guttatus* and another *Mimulus* species. Grossenbacher and Stanton (2014) also found evidence of character displacement where *M. bicolor* co-occurs with *M. guttatus*. In sympatry, the bicolored (yellow and white) morph of *M. bicolor* (Fig. 1C) experienced less interspecific competition than the all-yellow morph that greatly resembles *M. guttatus* (Fig. 1D).
Figure 1. Both ecological sorting and character displacement have contributed to niche differentiation between *M. guttatus* (A) and *M. alsinooides* (B) (Kooyers et al. 2017). Character displacement has also occurred between *M. bicolor* and *M. guttatus* (Grossenbacher and Stanton 2014), as the bicolor morph of *M. bicolor* (C) experienced less competition in sympathy than the all-yellow morph (D) that greatly resembles *M. guttatus*. High levels of local species diversity in the genus make *Mimulus* conducive to future studies of ecological sorting and character displacement; in California alone, over half of the counties contain more than 20 species (E).

Although evidence for character displacement in plants has increased in recent years (Grossenbacher and Stanton 2014; Norton et al. 2015; Koski and Ashman 2016; Kooyers et al. 2017), reports of multiple instances of character displacement within a plant genus remain rare. *Mimulus* now joins three other plant genera in which signatures of character displacement have been detected in more than one pair of species: *Burmeistera* (e.g., Muchhala and Potts 2007), *Dalechampia* (e.g., Armbruster 1985), and *Stylidium* (e.g., Armbruster et al. 1994). Similar to these taxa, *Mimulus* contains many more interacting species than the three species included in these two studies, with over 23 species on average in each county of California alone (Fig. 1E).

Future studies can utilize the distribution and diversity of *Mimulus* species to build on the insights presented by Kooyers et al. (2017); the genus provides an ideal system for determining how ecological sorting and character displacement affect niche differentiation at a larger phylogenetic scale.
DATA ARCHIVING
Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.58fh6.

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