

# Digest: The role of postzygotic isolation in *Mimulus* speciation\*

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Recently diverged species often show incomplete reproductive isolation and subsequently experience hybridization and introgression. The plant genus *Mimulus* includes many such examples of closely related taxa that prove useful for studying incipient speciation. However, Sandstedt et al. show that in contrast to other *Mimulus* species, species of the *M. tilingii* complex are characterized by strong postzygotic isolation mediated by multiple barriers. This finding highlights the diverse speciation histories of related plant groups.

The study of speciation may focus on any stage of the speciation continuum, from the initial divergence of populations to the evolution of reproductively isolated taxa (Hendry et al. 2009). The conceptual framework of the speciation continuum provides a valuable context for investigating the accumulation of incompatibilities throughout divergence. However, many questions remain about the tempo and mode of evolution of reproductive barriers along this continuum, in particular: at what stage of divergence do different reproductive barriers arise? Are they necessary for speciation to go to completion, or are they simply the byproduct of divergence? Are related plant groups likely to experience the same progression along the speciation continuum?

Multiple barriers can mediate reproductive isolation in plants. These include pre-mating barriers that limit interspecific pollen transfer, post-mating prezygotic barriers resulting from pollen-pistil incompatibilities or pollen competition, and postzygotic barriers affecting hybrid viability or fertility. It has been

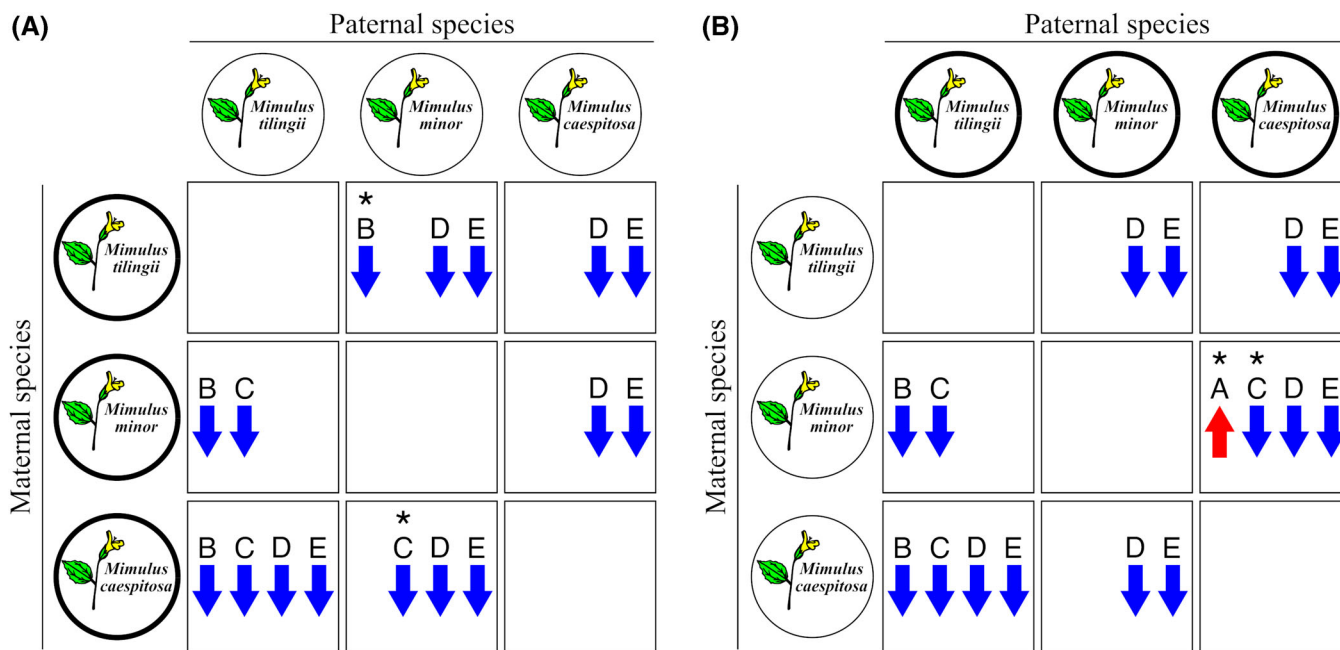
argued that prezygotic barriers play a more important role than postzygotic barriers in plant speciation; however, this may vary throughout the speciation process (Coughlan and Matute 2020).

The plant genus *Mimulus* is a well-established model system for investigating the genomic basis of adaptation and speciation (Twyford et al. 2015). Its success as a model is due partly to the dramatic variation of environments that *Mimulus* species inhabit and to the intercrossability of species, which facilitate genetic analyses. In this issue, Sandstedt et al. (2020) investigate a relatively understudied group of *Mimulus* species, the *M. tilingii* complex, comprising *M. tilingii*, *M. caespitosa*, and *M. minor*. This group is perhaps most notable for having adapted to high-elevation alpine environments. The authors explore the genetic and morphological diversity in this complex as well as the barriers maintaining reproductive isolation among these three species.

A linear discriminant analysis with floral and vegetative traits measured in a common garden and a principal component analysis with whole genome sequence data showed clear morphological and genetic differentiation among species. However, the most striking results came from experimental crosses and the general observation that interspecific crosses always resulted in

<sup>†</sup>These authors contributed equally to this manuscript.

\*This article corresponds to Sandstedt, G. D., C. A. Wu, and A. L. Schweigart. 2020. Evolution of multiple postzygotic barriers between species in the *Mimulus tilingii* species complex. *Evolution*. <https://doi.org/10.1111/evo.141105>



**Figure 1.** Direction of change in reproductive traits in interspecific crosses relative to intraspecific crosses. Upwards arrows indicate a significant increase and downwards arrows a significant decrease in reproductive trait values relative to (A) the maternal species (thick circles) self-crosses or (B) the paternal species (thick circles) self-crosses. Traits: A = seed set per fruit; B = proportion of fully round seeds per fruit; C = proportion of germinating seeds per fruit; D = proportion of viable pollen per flower in F1 individuals; E = seed set per fruit in F1 individuals. Asterisks (\*) indicate that the results change when the reference parental species changes, that is, differences between (A) and (B).

a reduction of fitness, as measured by reproductive trait values (Fig. 1).

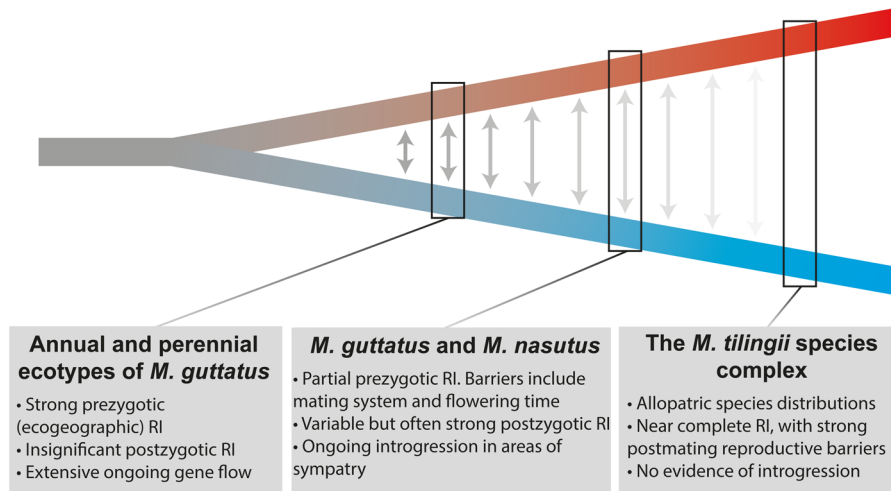
While the authors found no evidence of pollen-pistil incompatibilities, they observed an asymmetric, early-acting postzygotic barrier between *M. tilingii* and its two congeners, with a dramatic decline in seed viability when *M. tilingii* was used as a pollen donor. A difference in mating systems could be one factor promoting the evolution of such a barrier. In line with this hypothesis, a decrease in anther-stigma distance, corolla size, and nucleotide diversity was observed for *M. caespitosa* and *M. minor*, consistent with a transition toward a more highly selfing mating system.

Most interspecific crosses produced viable hybrids, with the notable exception of some involving *M. tilingii* and *M. caespitosa*, which showed evidence of hybrid necrosis. However, not all maternal families were affected, suggesting that the genes underpinning this barrier are polymorphic within the *M. tilingii* complex, as found in other plant groups (Scopece et al. 2010). Interestingly, crosses between paternal *M. caespitosa* and maternal *M. minor* plants resulted in higher seed production than *M. caespitosa* self-crosses (Fig. 1b, red arrow). However, F1 hybrids showed a strong reduction in both male and female fertility, indicating that selection against hybrids acts at a later stage in this case. Such a reduction was observed for all interspecific crosses,

but whether this late-acting postzygotic barrier is due to chromosomal rearrangements or genic interactions remains to be discovered.

Comparative analyses with other *Mimulus* species may show that speciation in the *M. tilingii* complex mirrors that found in the *M. guttatus* species group, where recurrent edaphic specialization and a transition to selfing underlies the formation of local endemic species, such as *M. laciniatus* and *M. filicifolius* (Ferris et al. 2014). We may also expect the signature of northwards postglacial range expansion evident in *M. guttatus* (Twyford et al. 2020) to be present in the *M. tilingii* complex, with the northern endemic *M. caespitosa* likely to show low genomic diversity consistent with a recent origin potentially combined with genetic bottlenecks. While there might be parallels, there may also be idiosyncratic features underlying some aspects of speciation in the *M. tilingii* complex, especially if divergence has occurred in isolated high elevation “islands” rather than in the face of gene flow like in many other *Mimulus* species.

This research adds to our growing knowledge of the diversification of *Mimulus*, with different groups representing different stages of the speciation continuum (Fig. 2). Unlike many other *Mimulus* taxa, species of the *M. tilingii* complex show strong postzygotic reproductive isolation preventing ongoing gene flow, making them a promising model for investigating the genetic



**Figure 2.** Stages of the speciation continuum and the extent of reproductive isolation (RI) between representative *Mimulus* taxa. Divergence from an ancestral population (grey) leads to the evolution of two lineages (blue and red) with decreasing gene flow (light grey arrows).

underpinning of such barriers, the evolutionary drivers promoting their establishment, and their relative contribution to speciation.

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