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1 **Digest: The role of postzygotic isolation in *Mimulus* speciation**

2

3 **Abstract**

4 Recently diverged species often show incomplete reproductive isolation and subsequently
5 experience hybridization and introgression. The plant genus *Mimulus* includes many such examples
6 of closely related taxa that prove useful for studying incipient speciation. However, Sandstedt et al.
7 (2020) show that in contrast to other *Mimulus* species, species of the *M. tilingii* complex are
8 characterized by strong postzygotic isolation mediated by multiple barriers. This finding highlights
9 the diverse speciation histories of related plant groups.

10 **Main text**

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

19 Multiple barriers can mediate reproductive isolation in plants. These include premating barriers that
20 limit interspecific pollen transfer, postmating prezygotic barriers resulting from pollen-pistil
21 incompatibilities or pollen competition, and postzygotic barriers affecting hybrid viability or fertility.
22 It has been argued that prezygotic barriers play a more important role than postzygotic barriers in
23 plant speciation; however, this may vary throughout the speciation process (Coughlan & Matute
24 2020).

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

33 A linear discriminant analysis with floral and vegetative traits measured in a common garden and a
34 principal component analysis with whole genome sequence data showed clear morphological and
35 genetic differentiation among species. However, the most striking results came from experimental
36 crosses and the general observation that interspecific crosses always resulted in a reduction of
37 fitness, as measured by reproductive trait values (**Fig. 1**).

38 While the authors found no evidence of pollen-pistil incompatibilities, they observed an asymmetric,
39 early-acting postzygotic barrier between *M. tilingii* and its two congeners, with a dramatic decline in
40 seed viability when *M. tilingii* was used as a pollen donor. A difference in mating systems could be

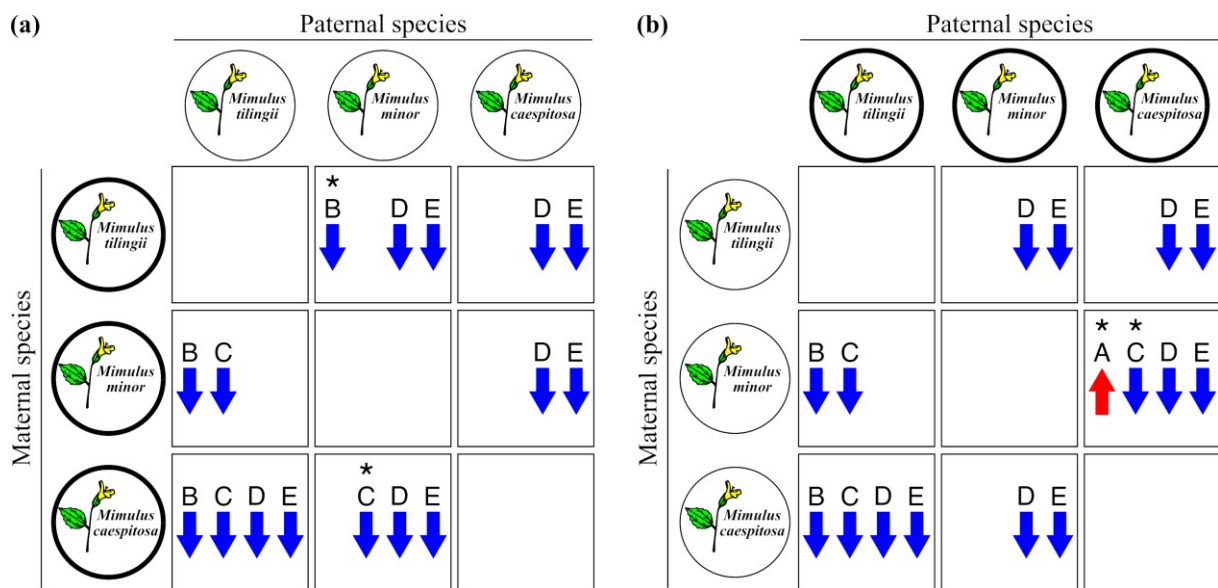
41 one factor promoting the evolution of such a barrier. In line with this hypothesis, a decrease in
42 anther-stigma distance, corolla size, and nucleotide diversity was observed for *M. caespitosa* and *M.*
43 *minor*, consistent with a transition towards a more highly selfing mating system.

44 Most interspecific crosses produced viable hybrids, with the notable exception of some involving *M.*
45 *tilingii* and *M. caespitosa*, which showed evidence of hybrid necrosis. However, not all maternal
46 families were affected, suggesting that the genes underpinning this barrier are polymorphic within
47 the *M. tilingii* complex, as found in other plant groups (Scopece et al. 2010). Interestingly, crosses
48 between paternal *M. caespitosa* and maternal *M. minor* plants resulted in higher seed production
49 than *M. caespitosa* self-crosses (**Fig. 1b, red arrow**). However, F1 hybrids showed a strong reduction
50 in both male and female fertility, indicating that selection against hybrids acts at a later stage in this
51 case. Such a reduction was observed for all interspecific crosses, but whether this late-acting
52 postzygotic barrier is due to chromosomal rearrangements or genic interactions remains to be
53 discovered.

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

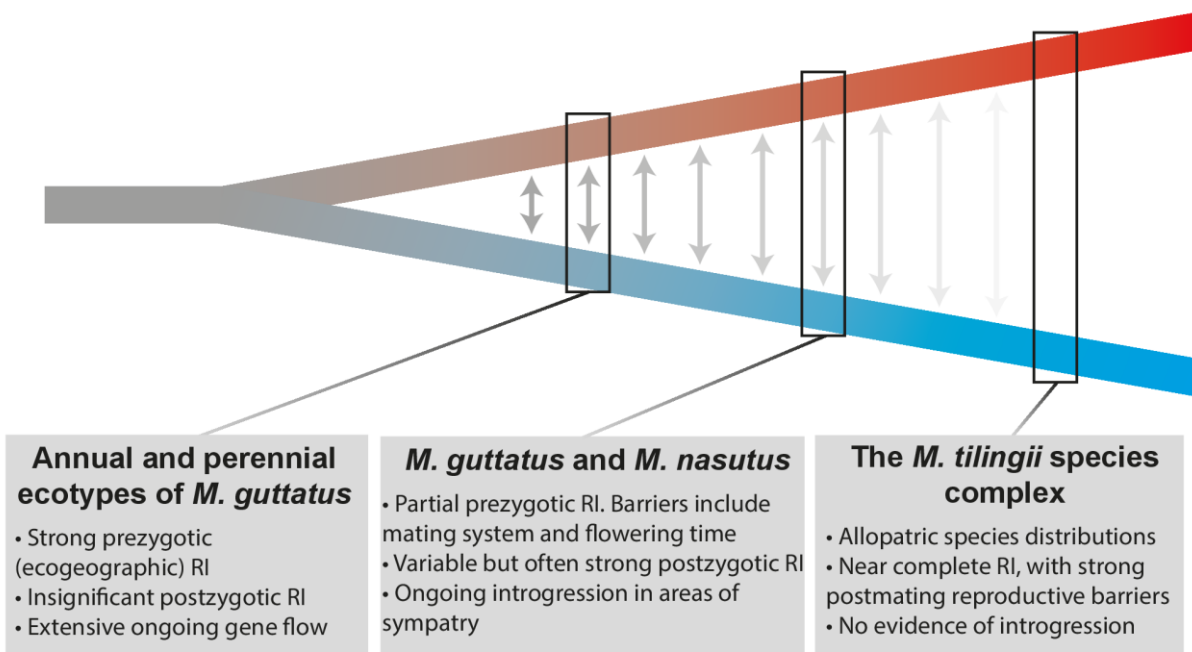
64 This research adds to our growing knowledge of the diversification of *Mimulus*, with different groups
65 representing different stages of the speciation continuum (**Fig. 2**). Unlike many other *Mimulus* taxa,
66 species of the *M. tilingii* complex show strong postzygotic reproductive isolation preventing ongoing
67 gene flow, making them a promising model for investigating the genetic underpinning of such
68 barriers, the evolutionary drivers promoting their establishment, and their relative contribution to
69 speciation.

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



79

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

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