

exclusively in plant systems (Levin 2010). Frequent cleistogamy (i.e., nonopening, self-pollinating flowers), for example, has been found to significantly reduce hybridization between sympatric *Mimulus* species (Martin and Willis 2007). The reduction in outcrossing accompanying selfing can protect reproductive investment by preventing the formation of hybrid progeny with maladaptive genetic combinations (Antonovics 1968; Allard 1975).

Selfing is considered to be an unusual isolating barrier, however. Because it usually isolates intra- and interspecific individuals equivalently, it has been argued that selfing cannot be regarded as directly promoting speciation (Coyne and Orr 2004, p. 212). Nonetheless, selfing commonly facilitates speciation indirectly by generating other isolating barriers; for example, the reduction in gene flow from maladapted populations promotes local adaptation, thereby accelerating genetic divergence (Coyne and Orr 2004, p. 212).

Here, we propose a novel mechanism by which selfing functions as a genuine isolating barrier that limits the success of interspecific hybrids to a greater extent than the progeny of intraspecific crosses. When reproduction is associated with early, intense competition between numerous sibling progeny for a limited resource, hybrids will always compete with selfed nonhybrids for establishment. If hybrids suffer any degree of fitness reduction, they will be unable to develop when the available resources restrict establishment to only a subset of the competing progeny. Interspecific gene flow is thus directly reduced by the combination of selfing and competition. We will henceforth refer to this mechanism as the “sibling competition arena.” The use of the term “arena” reflects the requirement for systematic and intense local competition for successful establishment prior to further development of the zygote. It thus resembles Stearns’ selection arena (1987), which proposes early selection of high fitness progeny by maternal choice and resource limitation among abundant offspring. However, several key assumptions are unique to our proposed model, as detailed in Table 1 and below.

Under this model, the systematic presence of numerous nonhybrid progeny promotes intense competition, magnifying the initial fitness handicap of hybrids. This strong selective sieve reduces the rate of hybrid production in the population well below that predicted solely by the selfing rate and the intrinsic, noncompetitive fitness reduction of hybrids relative to nonhybrids. Selfing and the production of numerous progeny strongly promote this process and may in fact be essential (Table 1, 2.1 and 3.1). First, these factors generate intense competitive pressure. Second, they ensure that the production of hybrid progeny is always coupled with the production of nonhybrid (selfed) progeny, even when the density of conspecifics is locally reduced. We emphasize that some degree of divergence between hybridizing genotypes is required, such that hybrid progeny face reduced competitive ability

relative to nonhybrid progeny (Table 1, 1.4). These factors in combination may then function as a true isolating barrier, with gene flow reduced in association with interspecific hybridization but not intraspecific outcrossing, provided that outcrossed progeny do not suffer reduced viability relative to selfed progeny.

The reproductive traits of many taxa, most notably plant and fungal taxa, suggest that the sibling competition arena may constitute an isolating barrier across many systems. Importantly, such a barrier does not absolutely require sibling competition: competition between any hybrid and nonhybrid individuals could suffice. However, mixed broods of hybrid and nonhybrid siblings automatically yield an early competitive arena, and this early competition is predicted to be a more powerful isolating mechanism in those systems in which the production of hybrids is inherently coupled to the production of nonhybrids. Thus, siblings are the most relevant competitors in many systems, including this study’s focal species (Table 1, 3.1). Moreover, the mechanism of isolation need not be adaptive (Table 1, 4.1), a key distinction between our model and Stearns’ selection arena (1987). In fact, sibling competition and any resulting reproductive isolation may merely be byproducts of the mating system. For example, fungal pathogens commonly produce large quantities of spores and predominantly perform haploid or diploid selfing (Giraud et al. 2008a). Both of these strategies facilitate reproduction and dispersal to new hosts. We hypothesize that, in the context of selfing and the sibling competition arena, these isolating mechanisms may additionally help explain, in an adaptive or nonadaptive manner, the abundance of cryptic, host-specific species within fungal pathogen taxa. The same hypothesis might be applied to plant taxa in which selfing and the overproduction of seeds are common strategies (Vogler and Kalisz 2001).

We tested this model using *Microbotryum violaceum sensu lato*, a complex of basidiomycete fungi causing anther-smut disease on plants of the Caryophyllaceae family (Le Gac et al. 2007a). Species of *Microbotryum* are highly host specific and apparently evolve without significant gene flow between closely related taxa (Le Gac et al. 2007b; Gladieux et al. 2011). Yet, the barriers to hybridization that have been described for this system thus far are insufficient to account for such extensive reproductive isolation. Host and pathogen ranges overlap significantly, with frequent sympatry of diseased hosts (Van Putten et al. 2005; Le Gac et al. 2007b; Refrégier et al. 2010). These fungi are spread by pollinators showing only a partial host specificity that fails to explain the observed species integrity in sympatry (Goulson and Jerrim 1997; Minder et al. 2007; Van Putten et al. 2007; Karrenberg and Favre 2008; Refrégier et al. 2010; Gladieux et al. 2011). Moreover, mating occurs prior to plant infection, so host specialization alone cannot act as a barrier to gene flow, as is suggested for ascomycete fungi (Le Gac and Giraud 2008; Giraud et al. 2010). In addition, there is no evidence for assortative mating in the