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Mating System Plasticity Promotes Persistence and Adaptation of Colonizing Populations of Hermaphroditic Angiosperms

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ABSTRACT: Persistence and adaptation in novel environments are limited by small population size, strong selection, and maladaptive gene flow. Mating system plasticity is common in angiosperms and may provide both demographic and genetic benefits that promote niche evolution, including reproductive assurance and isolation from maladaptive gene flow. Yet increased self-fertilization may also cause inbreeding depression, accumulation of deleterious mutations, and reduced adaptive potential. Here we use individual-based simulations to examine the consequences of mating system plasticity for persistence and adaptation in a novel environment that imposes selection on a quantitative trait. We examine the joint evolution of local adaptation, inbreeding depression, and genetic load. We find that a plastic shift to a mixed mating system generally promotes niche evolution by decreasing the risk of extinction, providing isolation from maladaptive gene flow, and temporarily increasing genetic variance in the trait under selection, whereas obligate self-fertilization reduces adaptive potential. These effects are most pronounced under conditions of mate limitation, strong selection, or maladaptive gene flow. Our results highlight the diverse demographic and genetic consequences of self-fertilization and support the potential role for plastic shifts in mating system to promote niche evolution in flowering plants.

Keywords: phenotypic plasticity, mating system, self-fertilization, niche evolution, Baker's law, pollen limitation.

Introduction

Demographic and genetic processes may limit or promote adaptation to novel environmental conditions. Such processes are fundamental to determining when and why adaptation to novel environments may fail, as at species range limits (Bridle and Vines 2007; Sexton et al. 2009), or when successful adaptation promotes the invasion of nonnative species (Gilchrist and Lee 2007) or the evolution of reproductive barriers (Rundle et al. 2000; Lowry et al. 2008). Properties that influence the evolvability of species have

been central to theory regarding the maintenance of sexual reproduction (Misevic et al. 2010) and outcrossing (Busch et al. 2004; Morran et al. 2011), as well as recent interest in predicting species' responses to global environmental change (Lavergne et al. 2010).

Historically, models of adaptation to novel environments focused on the genetic consequences of selection, gene flow, and genetic drift (e.g., Kirkpatrick and Barton 1997; Lenormand 2002) and on demographic processes such as immigration (Gomulkiewicz et al. 1999; Kawecki and Holt 2002; Holt et al. 2003; Kawecki 2003, reviewed in Kawecki 2008). However, recent work suggests that phenotypic plasticity may commonly play an important role in allowing population persistence in novel environments (Yeh and Price 2004; Chevin and Lande 2011; Reed et al. 2011). Unlike adaptive evolution, phenotypic plasticity can immediately increase local fitness following colonization of a new environment (Ghalambor et al. 2007; Lande 2009). Phenotypic plasticity may be particularly likely in harsh or stressful environments due to developmental instability or the expression of cryptic genetic variation (Badyaev 2005; Ledón-Rettig et al. 2010) and can shift a population to within the realm of attraction of a new fitness peak (Price et al. 2003). Phenotypic plasticity can evolve as an adaptive response to the range of environments typically encountered by an organism over space and time or can be a passive response to stress; in either case, it can be adaptive or maladaptive in a novel selective environment (Ghalambor et al. 2007).

Levin (2010) suggested that plasticity in traits affecting the mating system may have particularly important consequences for niche evolution in plants because the mating system has direct impacts on both the demographic and genetic properties of a population. Specifically, Levin (2010) suggested that niche evolution in plants may be facilitated if colonization of a novel environment is associated with increased self-fertilization via plasticity in floral traits or self-incompatibility systems. Diverse floral traits affect the self-fertilization rate in plants, including

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the spatial and temporal separation of stigma and anthers, the proportion of cleistogamous flowers, and the expression of self-incompatibility mechanisms (Darwin 1876, 1877). Plasticity in one or more of these traits resulting in increased self-fertilization has been widely documented in response to environmental stress, including herbivory (Steets and Ashman 2004; Ivey and Carr 2005; Schutzenhofer 2007; Penet et al. 2009), pollen limitation (Travers et al. 2004), drought (Kay and Picklum 2013), heat (reviewed in Good-Avila et al. 2008), salt (Fu Tingdong et al. 1992), and shade (Waller 1980). Conversely, several studies have found either no plasticity in mating system or increased outcrossing in response to environmental stress (Levri and Real 1998; Kay and Picklum 2013). Thus, the magnitude, underlying traits, and environmental drivers of mating system plasticity appear to vary greatly among taxa.

From a genetic perspective, increased self-fertilization may promote adaptation by acting as a partial reproductive barrier to maladaptive gene flow or by temporarily increasing genetic variation in traits under selection. Although self-fertilization is associated with reduced genetic variation over long timescales (Glémin 2006; Leffler et al. 2012), rapid increases in the self-fertilization rate are predicted to increase genetic variation temporarily by generating positive correlations between additive allelic effects within loci among offspring (Lande 1977). Such allelic correlations may increase the rate at which genetic variance recovers following a bottleneck (Lande 1977) and the response to selection in populations with mixed mating (Kelly 1999). Self-fertilization may further increase genetic variation in traits with more complex genetic architectures by converting epistatic or dominance variance to additive genetic variance (Carson 1990; Willis and Orr 1993; Cheverud and Routman 1996; Cheverud et al. 1999). Partial self-fertilization may also result in more rapid fixation of new, beneficial mutations (Charlesworth 1992; Glémin and Ronfort 2013) and essentially produces assortative mating for traits under selection (Lande 1977; Levin 2010).

From a demographic perspective, self-fertilization provides reproductive assurance by ensuring at least some reproduction when mates are limiting (Kalisz et al. 2004). Mate limitation may be severe in novel environments because of small population size and/or isolation. Plants with abiotic pollination mechanisms often exhibit density-dependent pollen limitation (Knight et al. 2005; Hesse and Pannell 2011). In animal-pollinated systems, scarce ancestral pollinators or ineffective novel pollinators may limit outcross pollen availability in new environments (Eckert et al. 2010; Rodger et al. 2013). The importance of reproductive assurance during colonization is supported by the observation that isolated or peripheral plant populations often exhibit increased self-fertilization (Baker 1967;

Busch 2005; Herlihy and Eckert 2005; Moeller 2006). Correspondingly, self-fertilization is associated with invasiveness in annual weeds (Petanidou et al. 2012) and larger range sizes in *Collinsia* (Randle et al. 2009).

Despite these potential benefits of mating system plasticity for the persistence and adaptation of colonizing populations, sudden increases in self-fertilization rate are commonly associated with reduced fitness due to the expression and fixation of deleterious alleles that accumulate in previously outcrossing populations (i.e., inbreeding depression; Charlesworth and Charlesworth 1999). If the segregating genetic load of an outcrossing population is high, a plastic increase in self-fertilization rate could decrease the efficiency of selection on quantitative traits and increase the probability of extinction following colonization (O'Grady et al. 2006). In addition, inbreeding depression is often environmentally dependent and may be most severe in stressful or novel environments (Heschel and Paige 1995; Armbruster and Reed 2005; but see Ronce et al. 2009). Alternatively, the process of colonization itself may result in the fixation or purging of deleterious alleles if the number of colonists is small (i.e., a bottleneck; Lopez et al. 2009; Pujol et al. 2009; but see Kirkpatrick and Jarne 2000). Population bottlenecks increase the frequency of rare deleterious alleles and may result in reduced fitness regardless of self-fertilization rate. Given the diverse potential effects of mating system plasticity on the demography and evolution of colonizing populations, its overall consequences for niche evolution remain unclear.

We used individual-based simulations to examine the evolutionary and ecological contexts in which mating system plasticity may promote or inhibit niche evolution. We tested the effect of a constant plastic increase in prior self-fertilization rate on population persistence and local adaptation by examining the evolution of a quantitative trait under stabilizing selection and the probability of extinction in a novel environment. Specifically, we focus on a region of genetic and demographic parameter space in which sink populations are in a race to become locally adapted prior to extinction. To distinguish reproductive assurance, increased genetic variation, and reproductive isolation as potential mechanisms, we tested the effects of pollen limitation, strength of selection, genetic architecture, and maladaptive gene flow on both extinction probability and local adaptation. We examined the evolution of inbreeding depression and genetic load in the colonizing population to test whether consideration of deleterious mutations alters the effects of mating system plasticity on niche evolution. Although this model includes several assumptions based on plant reproductive biology (e.g., pollen limitation and pollen dispersal), it could also be applied to hermaphro-

ditic animal systems with mate limitation and/or gamete dispersal (e.g., broadcast spawning).

Methods

We used stochastic simulations that track individual genotypes to model the evolution and demography of a colonizing sink population connected by gene flow with a source population. Our model is similar to that used by Holt et al. (2003), in which one-way migration occurs from a locally adapted source population to an initially maladapted sink population. However, we consider a plastic increase in self-fertilization rate following colonization of the sink habitat, the potential for pollen limitation, and the evolution of inbreeding depression and genetic load due to deleterious mutations.

Ecological Assumptions

The source and sink populations are composed of diploid and hermaphroditic individuals with discrete generations. Initially, the source population contains K individuals (see table 1 for parameter definitions and values) and the sink habitat is empty. The source population evolves for 1,000 generations to reach mutation-selection equilibrium before C individuals are randomly selected without replacement to colonize the sink habitat. Both populations evolve for 1,000 generations following colonization or until the sink population goes extinct. The order of life-history events within each generation is as follows: fertilization,

selection, density dependence, dispersal, reproduction, and death.

Prior to reproduction, individuals undergo selection. This selective period encompasses mortality at all life-history stages between fertilization and reproduction, including seed development, germination, and seedling growth. The fitness of an individual is determined by two forms of selection: optimizing selection on a quantitative trait and purifying selection on deleterious mutations. Optimizing selection can be either directional or stabilizing, depending on the similarity of the average phenotype to the optimum. The probability of survival of an individual in habitat i with phenotype z and genetic load m is given by $\max\{0, W_i(z, m)\}$, where

$$W_i(z, m) = \exp\left[-\frac{(z - \theta_i)^2}{w^2}\right] - m, \quad (1)$$

θ_i is the optimum phenotype in habitat i , and w^2 determines the strength of optimizing selection. Following Holt et al. (2003), the source optimum is kept constant at 0, so that the magnitude of the sink optimum reflects the severity of the sink habitat. Selection against deleterious mutations is the same in source and sink habitats and is always purifying (i.e., m is positive and determined solely by the genotype of an individual, not its habitat).

We assume that the source and sink habitats each support a finite population size K . If more than K individuals survive viability selection, then K individuals are randomly

Table 1: Description of parameters used in the model and ranges of values considered

Parameter	Description	Range of values
K	Carrying capacity of the source and sink	100
C	No. of colonists to the sink habitat	10
z	Phenotype of an individual	...
θ_{source}	Optimum phenotype in the source	0
θ_{sink}	Optimum phenotype in the sink	1.25–2.50
V_e	Environmental variance	.5
w^2	Strength of stabilizing selection	1.5
m	Genetic load of an individual	...
I	Proportion of outcross pollen pool drawn from the source population	.0–.5
B	No. of ovules produced by an individual	10
S	Proportion of ovules that receive self-pollen	0–1
P	Probability of an ovule receiving outcross pollen	.3–1.0
L	No. of loci underlying the quantitative trait	1–20
N	No. of loci underlying the genetic load	10–60
μ	Per-locus mutation rate	.001
s	Selection coefficient for deleterious mutations	.0–.1
H	Dominance of deleterious mutations	.0–.5
α^2	Mutational variance for the quantitative trait	.001–.050
W_{oc}	Mean fitness of outcrossed progeny	...
W_{sf}	Mean fitness of selfed progeny	...

sampled without replacement to become reproductive adults.

One-way pollen dispersal occurs each generation from the source population into the sink population. After colonization of the sink habitat, a proportion I of the outcross pollen pool in the sink population is randomly selected with replacement from individuals in the source population. Since we consider a one-time colonization event followed by pollen dispersal, extinction of the sink population is irreversible.

Each individual produces B ovules and contributes equally to the pool of available outcross pollen. In the source habitat, all individuals are obligately outcrossing and gametes are randomly paired between individuals in the population. In the sink habitat, all individuals self-fertilize a proportion S of unfertilized ovules. Proportion S is treated as a constant within simulations; thus, there is no genetic variation for plasticity in self-fertilization rate. We focus on prior self-fertilization, in which SB ovules are self-fertilized and the remaining $(1 - S)B$ ovules receive outcross pollen with probability P . Prior self-fertilization is an appropriate focus given plasticity in floral traits and results in a straightforward relationship between S and the realized self-fertilization rate (fig. A5; figs. A1–A5 available online). In addition, this mode of self-fertilization is considered more costly than delayed self-fertilization, because it occurs even if outcross pollen is abundant. However, we also consider a subset of simulations with delayed self-fertilization and find that the effects of the realized self-fertilization rate are similar (fig. A5).

Genetic Assumptions

We assume that the source and sink habitats exert divergent selection on a quantitative trait that is determined additively by L loci. The phenotype of an individual, z , is the sum of the allelic values at all L loci (i.e., the genotypic value) and an environmental value drawn from a normal distribution with mean zero and variance V_e . An additional N loci contribute to the genetic load via deleterious mutations. These loci are under purifying selection for the same wild-type allele in both the source and sink habitats, so that any mutation at these loci is equally deleterious in both habitats. We assume that there is no epistasis between loci and that all loci segregate independently.

Each generation, gametes receive a single mutation at a randomly selected locus with probability $(L + N)\mu$, where μ is the per-locus mutation rate. We set $\mu = 0.001$, which results in a per-gamete mutation rate of 0.011–0.080 (for $L + N = 11$ –80), within the range of empirical estimates (Charlesworth and Charlesworth 1999). For mutations at loci contributing to the quantitative trait, mutational values are drawn from a normal distribution with mean zero

and variance α^2 and added to the previous allelic value (Holt et al. 2003). Following empirical estimates, we consider values for α^2 between 1×10^{-3} and 50×10^{-3} (Lynch 1988) and values for L between 1 and 20. These values for L are in keeping with empirical evidence that many quantitative traits are largely determined by relatively few loci of major effect (Zeng 2005). To ensure that adaptation in sink populations is difficult, we consider parameter values that result in relatively low heritability for the quantitative trait. This allows the possibility of extinction in sink populations given the high fecundity of individuals ($B = 10$). The heritability of traits in stressful or novel environments is an open question (Hoffmann and Merilä 1999), but there is some evidence that heritability in wild populations may be reduced in unfavorable conditions, limiting the response to selection (Bennington and McGraw 1996; Charmantier and Garant 2005; Wilson et al. 2006). However, we also consider a subset of simulations with higher heritability (figs. A2, A3).

Mutations at loci contributing to the genetic load are always deleterious (i.e., there is no back mutation to the wild-type allele) and decrease fitness by a factor s when homozygous or sH when heterozygous, where s is the selection coefficient and H is the dominance of the deleterious mutation. We considered three mutation classes: $s = 0$, $H = 0$; $s = 0.10$, $H = 0$; and $s = 0.01$, $H = 0.5$. These models represent selectively neutral, strongly deleterious recessive mutations and weakly deleterious codominant mutations, respectively, and reflect empirical observations that highly deleterious mutations tend to be more recessive than mildly deleterious mutations (Charlesworth and Charlesworth 1999). The total decrease in survival due to deleterious mutations, or the genetic load of an individual m , is determined by the sum of the effects of the single-locus genotypes across all N loci. Thus, m is always positive, resulting in purifying selection (eq. [1]). We assume that deleterious mutations at separate loci contribute additively, rather than multiplicatively, to reductions in fitness to limit the total number of loci necessary to achieve high genetic load and/or inbreeding depression. Under an additive model, fitness declines more rapidly with increasing numbers of deleterious mutations, allowing a smaller total genome size per individual to improve computational efficiency. However, for the parameters we explore, these models are qualitatively similar.

We use the stochastic house-of-cards (SHC) approximation of the equilibrium genetic variance given by equation 14 in Burger and Lynch (1995; see also Burger et al. 1989) to determine the initial genotypes at the L quantitative trait loci for the source population. The K genotypes for the source population are drawn randomly from a set of five alleles per locus, generated from a normal distribution with mean zero and variance equal to the SHC

(Holt et al. 2003). The source population is initially fixed for the wild-type allele at all N genetic load loci.

Simulations

In each sink population, we monitored the number of individuals and the mean and variance of the quantitative trait and genetic load. Sink populations were censused following viability selection and prior to density-dependent mortality. We measured inbreeding depression by separately simulating the production of equal numbers of outcrossed and selfed progeny and then calculating inbreeding depression as

$$1 - \frac{W_{sf}}{W_{oc}}, \quad (2)$$

where W_{oc} is the mean fitness of outcrossed progeny and W_{sf} is the mean fitness of selfed progeny (where fitness is given by eq. [1]). These individuals were only used to measure the potential for inbreeding depression and did not contribute to the next generation.

For each combination of parameter values (see table 1), simulations were replicated 200–600 times and averaged to obtain general patterns (see the appendix, available online, for means and variances). We highlight patterns observed over many parameter combinations and select specific figures to illustrate these trends. All summary statistics are available in the appendix. Raw output and code files are deposited in the Dryad Digital Repository: <http://doi.org/10.5061/dryad.n5rd6> (Peterson and Kay 2014). The probability of extinction was calculated as the proportion of simulations that resulted in extinction of the sink population prior to 1,000 generations after colonization. All simulations were performed using R, version 2.13.0 (R Core Development Team 2011).

Results

Niche Evolution in Sink Populations

Immediately following colonization of the sink habitat, populations either begin to evolve toward the optimum phenotype and increase rapidly in size or decline toward extinction (fig. A1). Population size is strongly associated with the average genotypic value, and extinction occurs only in maladapted populations with sizes far below K (fig. A1). Thus, density dependence occurs only once sink populations have begun to adapt, and the value of K does not affect colonization success. Extinction mainly occurs within the first 10 generations following colonization, and no populations become extinct after 50 generations (fig. A1). Given that the key demographic and genetic dynamics determining colonization success operate within the first

50 generations, we focus our results on this period. However, we also examine longer-term outcomes after 500 or 1,000 generations to test whether these patterns change over time.

Genetic Variation and Adaptive Potential

Mating system plasticity has a profound and immediate effect on the genetic variance in colonizing sink populations (fig. 1A). In general, an increase in self-fertilization rate temporarily increases genetic variation relative to obligate outcrossing, but this effect decreases through time. Mixed mating ($0 < S < 1$) maintains higher genetic variation than obligate outcrossing for tens to hundreds of generations following colonization, whereas obligate self-fertilization results in an initial spike in genetic variation that declines rapidly to levels below obligate outcrossing populations (fig. 1A). This general pattern was observed across a range of parameter values, though the magnitude and duration of mating system effects on genetic variance depend on the genetic architecture of the quantitative trait (fig. A2).

The effects of mating system plasticity on genetic variance have consequences for niche evolution when adaptation is limited by low genetic variation or strong selection. Under these conditions, the sustained increase in genetic variance under mixed mating allows a greater response to selection following colonization. Mixed mating populations have higher fitness than outcrossing populations for tens to hundreds of generations following colonization, suggesting a consistent early advantage to mixed mating populations in responding to selection (fig. 1B). The magnitude of this fitness advantage for each generation is slight, but it has biologically important consequences for colonization success by decreasing the time to local adaptation (fig. 1C) and thus reducing the risk of extinction (fig. 1D) relative to obligate outcrossing. Alternatively, the rapid erosion of genetic variation in obligately self-fertilizing populations inhibits the response to selection (fig. 1B). When the sink habitat exerts strong selection, obligate self-fertilization results in a longer timescale for adaptation (fig. 1C) and faster extinction than mixed mating (fig. 1D). These general patterns are observed for a range of sink habitat severity (fig. 1C, 1D) and genetic architectures (fig. A3).

Inbreeding Depression and Genetic Load

In addition to effects on genetic variance, inbreeding due to mating system plasticity can increase the frequency or expression of deleterious alleles. The overall fitness effects of inbreeding may be best understood by examining inbreeding depression and genetic load together, since the

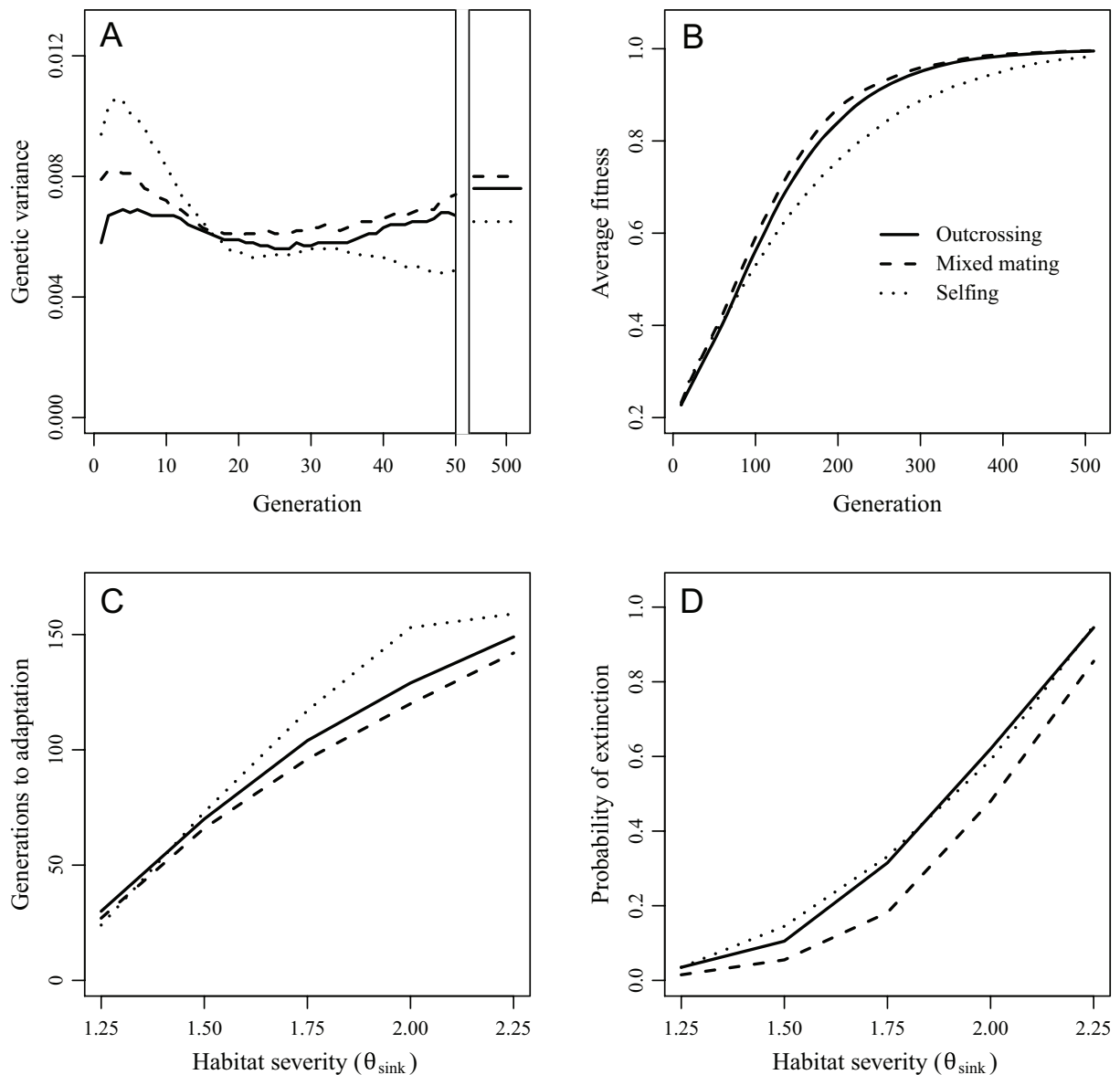


Figure 1: Effects of self-fertilization on niche evolution in sink populations. *A*, Evolution of genetic variance during the first 50 generations following colonization and final values after 500 generations. Data are the variance among genotypic values within a population. *B*, Average fitness within sink populations over 500 generations following colonization. *C*, Mean number of generations for the population mean fitness to reach 0.5. Data are averages for those simulations that reached this fitness threshold within 1,000 generations; no populations went extinct after reaching this point. *D*, Proportion of sink populations that went extinct within 1,000 generations. *A–D*, Data are averages for 200 replicate simulations for obligate outcrossing ($S = 0$, solid line), mixed mating ($S = 0.5$, dashed line), and obligate self-fertilization ($S = 1$, dotted line). For all simulations (unless otherwise stated), $\theta_{\text{sink}} = 1.5$, $I = 0$, $P = 1$, $C = 10$, $L = 10$, and $\alpha^2 = 2.5 \times 10^{-3}$.

former clarifies fitness differences between outcrossed and self-fertilized progeny within a population, whereas the latter encompasses the mean fitness effects of deleterious alleles for a population with a given breeding system. The consequences of mating system plasticity for inbreeding depression and genetic load depends on the mutation class considered.

Following colonization of the sink environment, individuals produced by self-fertilization exhibit both greater variance for the quantitative trait under selection (fig. 1A) and increased expression of segregating recessive deleterious alleles. Patterns of inbreeding depression reflect the balance of these two effects. In the absence of recessive deleterious mutations, inbreeding depression in sink pop-

ulations is initially negative following colonization, indicating that progeny produced by self-fertilization have, on average, higher fitness in the sink habitat than progeny produced by random outcrossing (fig. 2A, 2B). As populations become locally adapted, inbreeding depression slowly evolves toward slightly positive values for all self-fertilization rates. This pattern reflects the role of fitness variation under stabilizing selection: greater fitness variance in self-fertilized progeny is beneficial in maladapted populations but becomes costly as populations approach a fitness peak (Ronce et al. 2009). Weakly deleterious codominant alleles do not contribute to inbreeding depression, since their expression is not dependent on mating system and patterns reflect those observed in the absence of deleterious mutations (fig. 2B).

Incorporating recessive deleterious mutations alters the initial effects of self-fertilization and the final magnitude of inbreeding depression. Strongly deleterious recessive alleles drive a pulse of inbreeding depression following colonization that decreases with time and greater self-fertilization rates (fig. 2C). This pulse reflects the increased expression of segregating recessive alleles in self-fertilized individuals and decreases through time by purging. Purging occurs more rapidly with greater self-fertilization, as recessive alleles are exposed to selection.

Similarly, the evolution of genetic load also depends on the dominance and selection coefficients of deleterious mutations. Immediately following colonization, mating system plasticity has little effect on the genetic load due to codominant alleles (fig. 3A). In contrast, the colonization bottleneck causes a spike in the genetic load due

to recessive alleles that increases with greater self-fertilization (fig. 3B). Over time, alleles under weak purifying selection become fixed by drift, slowly increasing the genetic load, whereas strongly deleterious alleles are rapidly purged. Genetic load changes most long term under obligate self-fertilization, whereas mixed mating populations maintain a similar genetic load as obligate outcrossing populations. This effect is greatest for weakly deleterious alleles, which in turn contribute to a slight increase in the time to adaptation (fig. 3C) and an increased risk of extinction (fig. 3D) for all self-fertilization rates. These qualitative patterns are observed for a range of N (fig. A4). For high frequencies of strongly deleterious recessive mutations, the pulse of inbreeding depression and genetic load induced by mating system plasticity can outweigh the benefits of increased genetic variance, increasing the risk of extinction relative to obligate outcrossing (fig. A4).

Reproductive Isolation and Local Adaptation

Pollen dispersal from the source population inhibits niche evolution by increasing the time to adaptation and decreasing local adaptation in obligately outcrossing sink populations (fig. 4A, 4B). Self-fertilization reduces the opportunity for gene flow by decreasing the proportion of ovules that can be fertilized by immigrant gametes. For even limited pollen dispersal, mixed mating increases local adaptation and reduces the time to local adaptation relative to obligate outcrossing by acting as a partial reproductive barrier while maintaining high genetic variation and adaptive potential. When the potential for gene flow is high

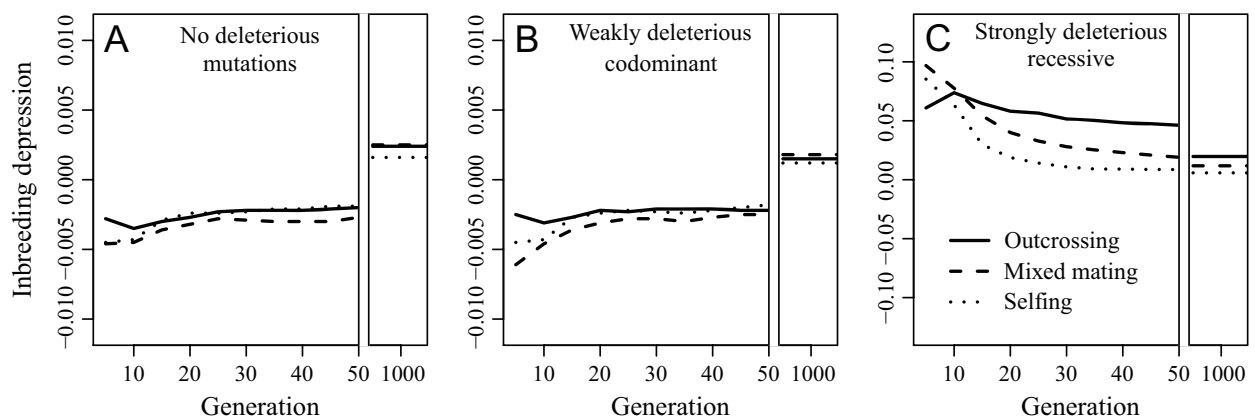


Figure 2: Evolution of inbreeding depression in sink populations for three mutation classes: no deleterious mutations (A), weakly deleterious codominant mutations ($s = 0.01$, $H = 0.5$; B), and strongly deleterious, recessive mutations ($s = 0.10$, $H = 0.0$; C). Data are inbreeding depression (eq. [2]) for separately simulated outcrossed and self-fertilized progeny. C, Note the different Y-axis scale and the break in the X-axis showing dynamics during the first 50 generations following colonization and final values after 1,000 generations. A–C, Data are averages for 200 replicate simulations for obligate outcrossing ($S = 0$, solid line), mixed mating ($S = 0.5$, dashed line), and obligate self-fertilization ($S = 1$, dotted line). For all simulations (unless otherwise stated), $\theta_{\text{sink}} = 1.75$, $I = 0$, $P = 1$, $C = 10$, $L = 10$, $N = 10$, and $\alpha^2 = 2.5 \times 10^{-3}$.

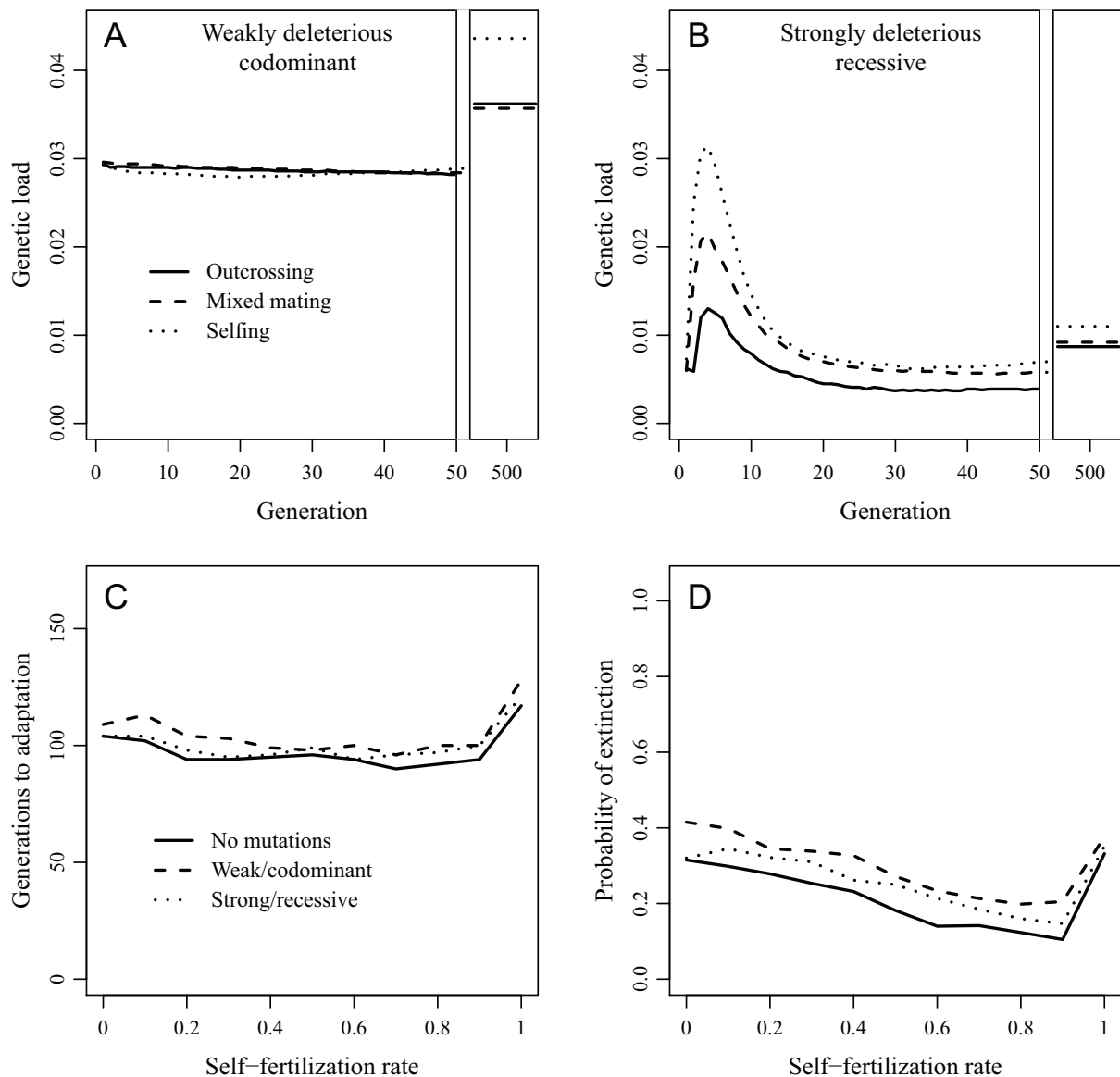


Figure 3: Consequences of deleterious mutations for niche evolution in sink populations. *A, B*, Evolution of genetic load in sink populations due to weakly deleterious codominant mutations ($s = 0.01$, $H = 0.5$; *A*) and strongly deleterious recessive mutations ($s = 0.10$, $H = 0.0$; *B*). Data are the mean genetic load (i.e., reduction in fitness due to deleterious mutations, or m) for obligate outcrossing (solid line), mixed mating (dashed line), and obligate self-fertilization (dotted line). Note the break in the X-axis showing dynamics during the first 50 generations following colonization and final values after 500 generations. *C, D*, Effects of no deleterious mutations (solid line), weakly deleterious codominant mutations ($s = 0.01$, $H = 0.5$, dashed line), and strongly deleterious recessive mutations ($s = 0.10$, $H = 0.0$, dotted line) as a function of the self-fertilization rate. *C*, Mean number of generations for the population mean fitness to reach 0.5. *D*, Proportion of sink populations that went extinct within 1,000 generations. *A–D*, Data are averages for 600 replicate simulations. For all simulations (unless otherwise stated), $\theta_{\text{sink}} = 1.75$, $I = 0$, $P = 1$, $C = 10$, $L = 10$, and $\alpha^2 = 2.5 \times 10^{-3}$.

(pollen dispersal > 10%), the benefits of obligate self-fertilization as a reproductive barrier outweigh its costs in terms of reduced adaptive potential, and any self-fertilization rate increases local adaptation relative to obligate outcrossing. Interestingly, pollen flow does not affect the

extinction rate (data not shown). This is because extinction is most likely within the first 10 generations following colonization (fig. A1), when populations are highly maladapted and pollen flow is just as likely to increase as decrease local fitness.

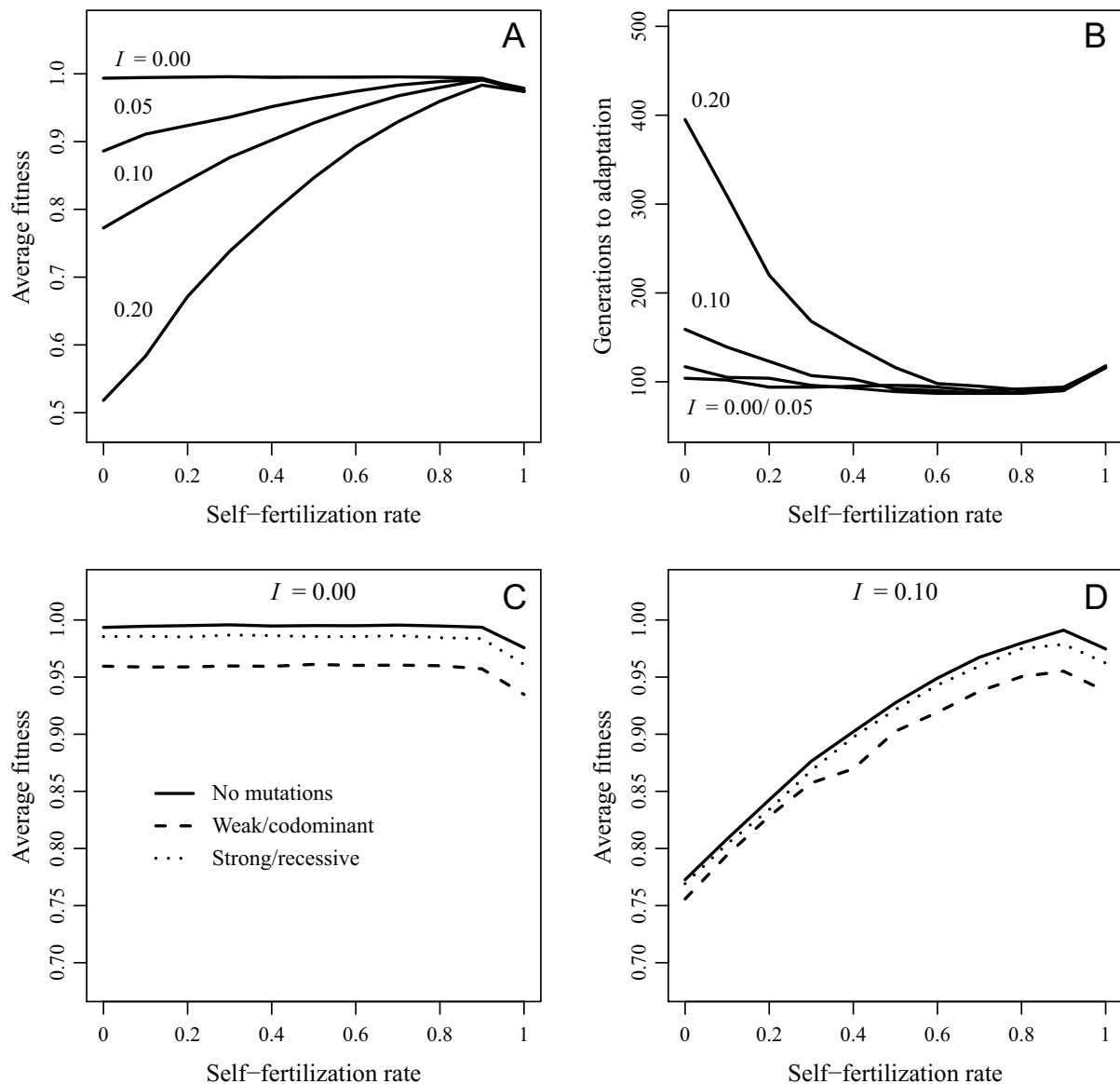


Figure 4: Effects of pollen flow on sink niche evolution as a function of the self-fertilization rate. *A*, Population mean fitness after 500 generations. *B*, Mean number of generations for the population mean fitness to reach 0.5. *C*, *D*, Population mean fitness after 500 generations with no pollen flow (*C*, $I = 0.00$) and moderate pollen flow (*D*, $I = 0.10$) for three mutation classes: no deleterious mutations (solid line), weakly deleterious codominant mutations ($s = 0.10$, $H = 0.5$, dashed line) and strongly deleterious recessive mutations ($s = 0.10$, $H = 0.0$, dotted line). *A–D*, Data are averages for 400 replicate simulations. For all simulations, $\theta_{\text{sink}} = 1.75$, $P = 1$, $C = 10$, $L = 10$, and $\alpha^2 = 2.5 \times 10^{-3}$.

The overall fitness of sink populations depends on the interaction between pollen dispersal, mutation class, and self-fertilization rate. In general, consideration of deleterious mutations decreases fitness in sink populations via genetic load relative to simulations in which fitness is determined solely by a quantitative trait. However, this fitness decrease is small relative to the effects of pollen dispersal from source populations (fig. 4*C*, 4*D*). In the absence of

pollen dispersal, obligately self-fertilizing populations exhibit lower fitness than populations with at least some outcrossing (fig. 4*C*). This pattern is driven by greater fixation of deleterious alleles (fig. 3) and decreased adaptive potential (fig. 1). When the potential for gene flow is high (pollen dispersal > 10%), the fitness benefit of reproductive isolation exceeds the costs of decreased selection efficiency in obligately self-fertilizing populations (fig.

4D). These general patterns are observed for all mutation classes.

Pollen Limitation and Reproductive Assurance

Niche evolution requires that colonizing populations persist in the sink environment. In general, extinction risk increases with ecological or genetic factors that act to reduce sink population fitness, including strong selection (θ_{sink} ; fig. 1D) and deleterious mutations (fig. 3D). Incorporating pollen limitation greatly increases the risk of extinction in obligately outcrossing sink populations (fig. 5A) but does not affect the timing or degree of local adaptation for populations that persist (data not shown). Thus, pollen limitation inhibits niche evolution demographically by preventing population persistence. Even moderate pollen limitation ($P < .7$) can result in high extinction risk when the sink habitat imposes strong selection ($\theta_{\text{sink}} > 2.00$; fig. 5B). In these cases, increased self-fertilization due to mating system plasticity decreases the risk of extinction by providing reproductive assurance. When pollen limitation and habitat severity are moderate ($.3 < P < .7$ and $1.50 < \theta_{\text{sink}} < 2.25$), even limited self-fertilization or obligate self-fertilization can greatly decrease the risk of extinction relative to obligately outcrossing populations (fig. 5). Similar patterns are observed when self-fertilization is delayed (fig. A5).

Discussion

A plastic shift to mixed mating promotes niche evolution under a broad range of ecological conditions. Mixed mating allows populations to respond more rapidly to selection, reduces the risk of extinction, and has little effect on the accumulation of genetic load. Alternatively, a shift to obligate self-fertilization may inhibit niche evolution by slowing the response to selection, increasing the risk of extinction, and allowing the fixation of deleterious alleles. However, even obligate self-fertilization provides important reproductive assurance and isolation benefits. The interactions between mating system plasticity and pollen limitation, selection, and gene flow determine its overall consequences for niche evolution and are discussed in greater detail below.

Extinction Risk and Reproductive Assurance

Even moderate pollen limitation can greatly increase the extinction risk of colonizing populations, particularly when coupled with strong selection in a novel environment. Pollen limitation is common among angiosperms, occurring in some form in 62%–63% of species examined (Burd 1994; Knight et al. 2005). Estimates of the magnitude of pollen limitation are subject to various methodological and publication biases (Harder and Aizen 2010), but several meta-analyses have found that fruit or seed set reductions may range from 15% to 75% on average (Burd 1994; Knight et al. 2005, 2006). Interestingly, pollen lim-

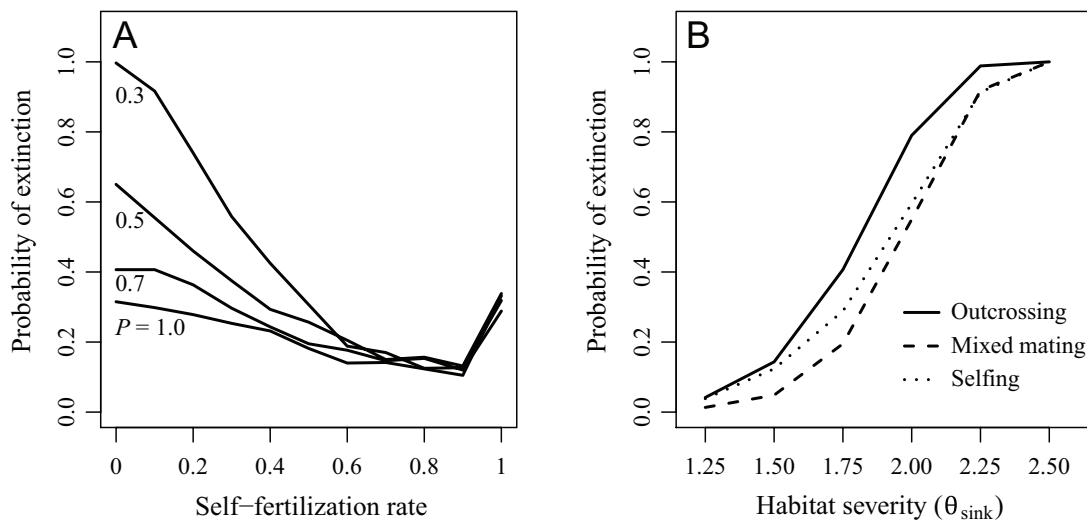


Figure 5: Effects of pollen limitation on the probability of extinction in sink populations. *A*, Effects of pollen limitation (P) as a function of the self-fertilization rate when $\theta_{\text{sink}} = 1.75$. *B*, Effects of habitat severity (θ_{sink}) when $P = .7$ for obligate outcrossing ($S = 0$, solid line), mixed mating ($S = 0.5$, dashed line), and obligate self-fertilization ($S = 1.0$, dotted line). Data are the proportions out of 400 replicate populations that became extinct within 1,000 generations following colonization. For all simulations, $I = 0$, $C = 10$, $L = 10$, and $\alpha^2 = 2.5 \times 10^{-3}$.

itation and strong selection interact during colonization to greatly increase the risk of extinction and the potential importance of reproductive assurance. Given this interaction, mixed mating can promote colonization of harsh environments even when the magnitude of pollen limitation is relatively low ($>10\%$). Previous work has emphasized the importance of immigration in allowing sink population persistence (Holt et al. 2003); here we demonstrate a similar demographic rescue effect caused by self-fertilization. The relative benefits of immigration versus self-fertilization for population persistence will depend on the fitness of immigrant genotypes and the strength of inbreeding depression. Although inbreeding depression decreases rapidly following colonization, selection against immigrant genotypes remains high. Thus, we find strong support for the hypothesis that self-fertilization, particularly mixed mating, will promote persistence in novel environments through reproductive assurance.

A general role for self-fertilization in range expansion is supported empirically. Baker's law emphasizes an association between self-compatibility and colonization success (Baker 1967) and is widely supported in native (Busch 2005; Randle et al. 2009) and invasive (Van Kleunen and Johnson 2007; Van Kleunen et al. 2008; Hao et al. 2011) floras, as well as in several island floras (McMullen 1987; Anderson et al. 2001; but see Miller et al. 2008). Further, pollen limitation and self-fertilization are associated with the colonization of human-disturbed environments (Eckert et al. 2010; Harder and Aizen 2010). Previous theoretical work has examined the role of reproductive assurance during colonization in a metapopulation framework, with mixed support for Baker's law (Pannell and Barrett 1998; Dornier et al. 2008). However, our model represents the first attempt to integrate pollen limitation and niche evolution during colonization of a novel selective environment. Our results suggest that at least partial self-fertilization may be critical for the persistence of colonizing populations under a broad set of ecological scenarios.

Gene Flow and Reproductive Isolation

Pollen dispersal from source populations decreases fitness in sink populations by introducing maladaptive alleles and reducing local adaptation. The potential for gene flow to swamp local adaptation is well supported empirically (reviewed in Lenormand 2002), and self-fertilization is an important reproductive barrier in a variety of systems (e.g., Fishman and Wyatt 1999; Martin and Willis 2007). Here we show that mixed mating increases fitness in colonizing populations when gamete dispersal is moderate ($>5\%$). Even obligate self-fertilization, which reduces fitness by limiting adaptive potential and accumulating deleterious mutations, increases fitness relative to outcrossing when

gamete dispersal is high ($>10\%$). Interestingly, these values may not be uncommon in systems with mobile gametes, such as plants or marine invertebrates. Estimates of pollen flow between plant populations are 8%–17% in *Raphanus sativus* (Ellstrand and Marshall 1985) and 8% in *Phlox drummondii* (Levin 1983). Sperm dispersal in marine invertebrates is highly variable, with estimates from 0% as close as 8 m (Yund 1990) to 20% as far as 100 m (Babcock et al. 1994). Sessile organisms may frequently experience distinct selective environments well within the spatial scale of gamete dispersal. In such cases, self-fertilization can provide an important reproductive barrier to allow local adaptation.

Self-Fertilization Rate and Adaptive Potential

In the absence of pollen limitation or gene flow, mating system plasticity can have immediate effects on the adaptive potential of colonizing sink populations. A shift from outcrossing to mixed mating confers a temporary increase in genetic variation that can accelerate adaptation and reduce the risk of extinction when adaptation is limited by low genetic variance. Although the effects of mixed mating on genetic variance and response to selection are small and transient, they occur during a critical stage in colonization and have biologically important consequences for the persistence of small populations. Obligate self-fertilization, however, limits adaptive potential by rapidly eroding genetic variation and increasing the timescale of adaptation. These effects occur in colonizing populations only if the response to selection is limited relative to the demographic risk of extinction, such as when heritability in the trait under selection is low. There is some evidence that heritability in wild populations is reduced under unfavorable conditions (Bennington and McGraw 1996; Charmantier and Garant 2005; Wilson et al. 2006; but see Husby et al. 2011), and adaptation to novel environments may be further limited by negative genetic correlations under multivariate selection (e.g., Etersson and Shaw 2001).

The effect of mating system on genetic variance and the response to selection is consistent with predictions from deterministic models. Lande (1977) found that inbreeding temporarily increases the rate of recovery of genetic variation after a bottleneck but that this is quickly eroded to levels below random mating when inbreeding is high ($>95\%$). Glémin and Ronfort (2013) found a similar pattern for the time to adaptation when selection favors a partially recessive allele at a single locus. Dominance or epistatic interactions may further increase the effect of self-fertilization on genetic variance (Carson 1990; Willis and Orr 1993; Cheverud et al. 1999), relative to our model, which considers selection only on an additive trait. In an

artificial selection experiment in *Mimulus*, Holeski and Kelly (2006) found that inbreeding increased the genetic variance of traits under selection. Further, when mating system had a significant positive effect on the response to selection, it was greatest for mixed mating and reduced for complete self-fertilization. Here we show that a plastic shift to mixed mating may enhance adaptive potential in maladapted populations when selection acts on an additive, polygenic trait.

The duration of a plastic mating system shift following colonization will depend on the biology of a specific organism, including the traits, timing (prior vs. delayed), environmental drivers, and genetic variation underlying the plastic response. Enhanced self-fertilization may also occur purely due to density-dependent effects on outcross pollen availability (i.e., mate or pollinator limitation) rather than plasticity in floral traits; in these cases, self-fertilization rates would decline rapidly as the colonizing population became more abundant. Although we focus on the immediate consequences of mating system plasticity within the first 50 generations, we also examine any longer-term consequences of a sustained increase in prior self-fertilization. Even under the extreme scenario that a shift from outcrossing to obligate self-fertilization is sustained over 1,000 generations, there is remarkably little long-term cost on adaptive potential. However, we consider adaptation to a single, constant environment; fluctuating environmental conditions, such as during coevolution, may further limit the adaptive potential of highly self-fertilizing populations (Busch et al. 2004; Glémin and Ronfort 2013). It is important to note that this model examines the immediate effects of mating system plasticity on the ability of populations to successfully colonize novel environments, not the evolution of mating systems themselves or the macroevolutionary consequences of self-fertilization. Over longer timescales, primarily self-fertilizing lineages may represent evolutionary dead ends (Stebbins 1957; Holsinger 2000; Escobar et al. 2010; Goldberg et al. 2010).

Inbreeding Depression, Genetic Load, and the Cost of Self-Fertilization

The accumulation of deleterious mutations is thought to limit the long-term fitness and adaptive potential of self-fertilizing populations (Heller and Smith 1978). However, comparative approaches testing for higher deleterious substitution rates in selfing lineages have yielded mixed results: no effect of mating system was found in *Triticeae* or *Arabidopsis* (Wright et al. 2002; Escobar et al. 2010), though signals of reduced selection efficiency were found across angiosperms and in *Eichhornia* (Glémin et al. 2006; Ness et al. 2012). By examining the evolution of deleterious alleles during colonization and niche evolution, we find

that obligate self-fertilization is associated with greater genetic load, reflecting decreased effective recombination (Muller's ratchet; Heller and Smith 1978; Charlesworth and Wright 2001). Interestingly, even limited outcrossing is sufficient to reduce the genetic load to outcrossing levels. This is consistent with previous theoretical work demonstrating that recombination rates are sufficient at intermediate self-fertilization rates to achieve levels of purging expected under random mating (Charlesworth et al. 1993). However, consideration of more strongly deleterious (e.g., lethal) mutations at more loci could alter the pattern of purging by generating identity disequilibrium or selective interference (Lande et al. 1994). Thus, sustained and/or stronger inbreeding depression could outweigh any demographic benefits for very high frequencies of strongly deleterious recessive alleles.

Mating System Plasticity versus Evolution

By focusing on the effects of mating system plasticity induced by a novel environment, this work differs from recent investigations of the adaptive potential of mating systems (Glémin and Ronfort 2013) or the evolution of self-fertilization (e.g., Morgan and Wilson 2005; Dornier et al. 2008). Adaptation to novel environmental conditions is limited by small population size, strong selection, and maladaptive gene flow. Thus, previous theoretical work has emphasized the importance of population persistence and isolation for niche evolution to occur (reviewed in Kawecki 2008). Increased self-fertilization in a historically outcrossing population will have unique genetic consequences, such as exposure of genetic variance and expression of recessive deleterious alleles, relative to a historically self-fertilizing population. Further, if a novel environment enhances the self-fertilization rate, then the benefits of reproductive assurance, isolation, and increased genetic variation will immediately act to reduce the risk of extinction and increase the response to selection following colonization.

However, it is not clear that these same benefits could be achieved through the evolution of increased self-fertilization for two reasons. First, the risk of extinction operated mainly within the first 10 generations following colonization, suggesting that the importance of reproductive assurance for niche evolution decreases rapidly with time since colonization, as populations either become extinct or begin to adapt. Second, the fate of any allele that acts to increase the self-fertilization rate will depend on the relative fitness of selfed and outcrossed progeny within a population (Lande and Schemske 1985). Colonization is associated with a spike in inbreeding depression due to the expression of recessive deleterious alleles, which may oppose the evolution of increased self-fertilization within

the first 10 generations, when extinction risk is greatest. Although these alleles are rapidly fixed or purged with self-fertilization, it remains unclear how the cost of inbreeding depression and the benefit of isolation and increased genetic variance would interact to drive the evolution of mating systems in novel environments.

Self-Fertilization Mechanisms and Levin's Model

In concordance with Levin's (2010) verbal model, we test the consequences of a plastic, constant shift to prior self-fertilization in a novel environment. This could represent plasticity in the degree of self-compatibility, the timing of male and female functions, the proportion of cleistogamous flowers, or any of the diverse floral traits that influence prior self-fertilization rates and respond to abiotic stress (reviewed in Levin 2010). However, novel environments may also enhance self-fertilization via density-dependent or delayed mechanisms, in which self-fertilization increases only when the population size is small and/or outcross pollen is limiting. These alternative mechanisms would operate early in the colonization process; self-fertilization would decline quickly as populations grew and outcross pollen became available. Density-dependent effects might also be greater (i.e., obligate self-fertilization in the absence of mates) relative to plasticity in floral traits. Empirical data on the relative frequency and strength of these contrasting mechanisms would clarify whether the duration and magnitude of environmental effects on self-fertilization rate are related and, perhaps, negatively correlated. Although we do not include density-dependent self-fertilization in this model, it is likely that the short duration of this mechanism would provide the benefits described here when extinction risk is greatest, while preventing any longer-term costs of self-fertilization or benefits of reproductive isolation. However, additional work is necessary to test these predictions.

We find that mating system plasticity via prior self-fertilization promotes persistence and local adaptation of colonizing populations under a broad range of ecological scenarios and self-fertilization rates. In combination with general empirical support for plasticity in mating system traits, pollen limitation, and gene flow across selective environments, these results provide strong theoretical support for Levin's (2010) verbal model of niche evolution via environment-enhanced self-fertilization.

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Clarkia concinna (Onagraceae) flower with synchronously receptive stigma and mature pollen under drought conditions. Photo credit: Devon A. Picklum.