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Plant Mating Systems in Small Populations

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Abstract

Habitat fragmentation and degradation are causing population declines in many species. In seed plants, mating patterns are expected to be influenced by both historical and contemporary population sizes and affect population viability. Historical population sizes influence overall genetic variation and accumulation of genetic load. Contemporary population size and density affect mating patterns as well as the degree of pollen limitation of seed production because of their effects on interactions with pollinators. Several ecological and genetic effects of small population size affect the fitness consequences of self-fertilization and favor reproductive assurance through autonomous self-pollination. Comparative and experimental studies demonstrate that selection on traits influencing the mating system can be strong under mate and pollen limitation and that evolutionary responses can be rapid given sufficient genetic variation. We highlight the prospects of using experimental evolution and artificial selection for understanding the interactions among population size, mating system, and population viability.

1. INTRODUCTION

Understanding the processes that influence mating patterns in natural populations is fundamental for understanding both population dynamics and evolutionary trajectories and is therefore also of considerable interest in applied areas such as conservation biology and plant breeding. The mating system can affect both fecundity and the quality of offspring produced and thereby whether plant populations will grow or decline. Moreover, the mating system will influence population genetic structure and the potential for adaptive evolution. It is therefore essential to consider the mating system when modeling population dynamics, and not the least when assessing ecological and evolutionary consequences of environmental change. In declining populations, mate limitation, pollen limitation, inbreeding depression, and drift load can reduce mean fitness and contribute to the "extinction vortex" (Frankham et al. 2017). However, the evolution of reproductive assurance through self-fertilization and the purging of inbreeding depression with increased inbreeding may provide "evolutionary rescue" in small populations. While variation in mating systems has been examined in relation to human disturbance and along geographic gradients (e.g., Eckert et al. 2010, Moeller et al. 2017, Karbstein et al. 2021), the ecological factors underlying variation among populations are still poorly known (Eckert et al. 2010, Barrett & Harder 2017, Whitehead et al. 2018). To develop informed management measures for rare and threatened plant species in response to current habitat fragmentation and degradation, researchers must consider how reductions in population size influence the mating system and its evolution as well as how the mating system influences the effects of population declines on population viability (e.g., Agrawal & Whitlock 2012, Cheptou 2019, Gavin-Smyth et al. 2021, Encinas-Viso et al. 2024). In this review, we examine the effect of population size on processes affecting the evolution of self-fertilization (selfing) but also discuss the opportunities for demographic rescue through the evolution of self-compatibility and autonomous self-pollination.

Use of the concept mating system and the related term breeding system varies in the literature. In many studies of plants, the "mating system" simply refers to the proportion of offspring produced through cross- versus self-fertilization (e.g., Grant & Kalisz 2020). However, the mating system can also include whether an individual reproduces sexually at all, whether plants are cosexual or whether some or all are unisexual (i.e., the sexual system), and whether cosexuals are self-compatible (Charlesworth 2006). In addition, plants also vary importantly in the extent to which individuals cross-fertilize with unrelated or closely related members of the population (biparental inbreeding), and in the diversity of outcross partners a plant has through male and female function (Barrett & Harder 2017, Christopher et al. 2021, Kulbaba & Shaw 2021). While some aspects of the mating system defined this way reflect inherent properties of the plant, realized mating patterns will clearly be a function of an interaction between plant phenotype and the environment. In this review, we use the terms mating system and mating patterns interchangeably to denote the outcome of this interaction.

Models of the evolution of self-fertilization identify the magnitude of inbreeding depression (the relative fitness of offspring produced after self-fertilization and outcrossing within a population), the degree to which seed production is limited by outcross pollen receipt, and levels of pollen discounting (reduced opportunity for pollen export due to self-pollination) and seed discounting (reduced opportunity for cross-fertilization of an ovule due to prior self-fertilization) as major determinants of whether a selfing variant would be favored by selection (Goodwillie et al. 2005, Winn et al. 2011). Population size has the potential to influence all these factors. Historical population size is expected to influence both the extent to which deleterious mutations have been fixed due to genetic drift (known as drift load) and the magnitude of inbreeding depression caused by segregation of deleterious mutations within populations (**Figure 1**). Contemporary plant population size and density are expected to affect mating patterns and selection on mating system

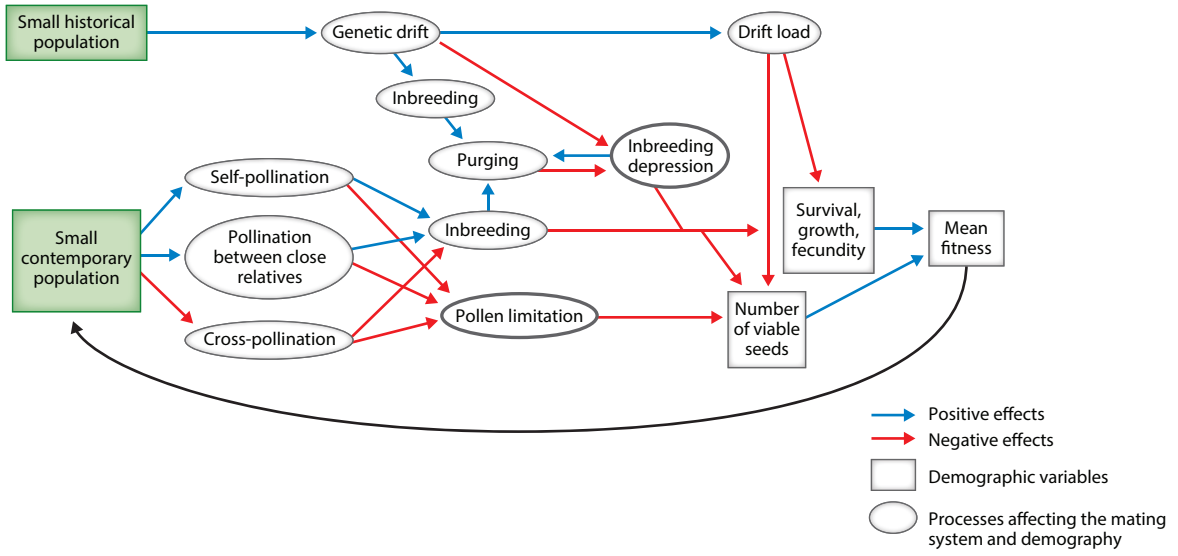

Figure 1

Outline of predicted effects of small population size on processes influencing plant fitness and selection on traits influencing the selfing rate (1− outcrossing rate). Positive effects are indicated with blue arrows, negative effects with red arrows. The effects of small contemporary and small historical population size have been separated to emphasize that current drift load and inbreeding depression are largely functions of historical population size and inbreeding. Mean plant fitness quantified as population growth rate will influence population size in the following generation as indicated by the black arrow. Small historical population size is expected to be associated with an increased influence of genetic drift and fixation of deleterious mutations (drift load), which will reduce population mean fitness. Fixation reduces the number of segregating deleterious mutations within populations and therefore reduces inbreeding depression quantified as the difference in fitness between offspring resulting from self- versus cross-fertilization. Small historical population size also increases the probability of matings between closely related individuals (biparental inbreeding), which, similar to selfing, negatively affects mean progeny fitness because of inbreeding depression but also increases the opportunity for selection to remove deleterious recessive mutations (purging). Purging will depend on the level of inbreeding, but also on the genetic basis and magnitude of inbreeding depression (indicated with arrows in two directions). Small contemporary population size is expected to be associated with reduced cross-pollination (pollen transfer among plants) because of a reduced number of pollinator visits per plant per unit time, but with increased geitonogamous self-pollination because of a higher number of flowers visited per plant, compared to the situation in large populations. In small contemporary populations with a capacity for autonomous self-pollination, a decrease in pollinator visitation may also increase autogamy. Finally, in small contemporary populations with a history of being small, pollination between close relatives is also more common than in historically large populations. Patterns of pollen transfer will affect "inbreeding," which includes both rates of self-fertilization and biparental inbreeding. The effect of inbreeding on fitness components depends on inbreeding depression, which is indicated by arrows that unite before reaching the "number of viable seeds" and "survival, growth, fecundity," respectively. In self-compatible species, self-pollination may reduce pollen limitation in the sense of number of unfertilized ovules but may, at the same time, reduce progeny fitness because of inbreeding depression. If self-fertilization reduces the opportunity for cross-fertilization, geitonogamy results in an opportunity cost (known as seed discounting), the size of which will depend on the magnitude of inbreeding depression. In addition to reducing female reproductive success, geitonogamous self-pollination also decreases male reproductive success by decreasing opportunities for siring seeds on other plants (known as pollen discounting). If the resulting mean fitness is associated with a population growth rate below 1, population size will decrease (indicated with the black arrow). This decrease would result in a negative feedback loop (known as the extinction vortex), which could be broken with the evolution of increased autonomous self-pollination provided that the fitness benefit of reduced pollen limitation is sufficiently large to result in positive population growth (evolutionary rescue).

traits mainly because of their effects on interactions with pollinators. More specifically, because of effects on pollinator visitation rates and behavior, population size and density influence the probability of pollen transfer among plants and the rate of geitonogamous self-pollination (pollen transfer between flowers on the same plant), and thereby the magnitudes of pollen limitation and pollen discounting. In self-compatible plants, population size and density may also affect the

selfing rate and thereby the influence of inbreeding depression on mean progeny fitness and seed discounting (**Figure 1**).

In this review, we outline how and why small historical and contemporary population sizes are expected to influence ecological and evolutionary processes governing mating patterns and mating system evolution. We also discuss the effects of mating patterns and the evolution of self-fertilization on population viability. We examine the extent to which theoretical predictions are upheld by empirical evidence and identify important gaps for future work. While population size is our main focus, we also include studies that examine the effects of plant density on mating patterns, as population size and density often covary in plant populations and most comparative studies cannot separate their effects. Most studies report only census population size, although it is the effective population size (N_e) that influences evolutionary processes (Charlesworth 2009). Below, we discuss, in turn, the effects of population size on (*a*) the magnitude of inbreeding depression and drift load, (*b*) outcross pollen limitation, (*c*) geitonogamous self-pollination and pollen and seed discounting, (*d*) the outcrossing rate of self-compatible plants, and (*e*) the evolution of selfing. Moreover, we consider (*f*) the demographic consequences of mating patterns and the evolution of selfing as a potential mechanism for demographic rescue of small populations. We note that several of the expected ecological and genetic effects of small population size favor reproductive assurance through autonomous self-pollination and affect the fitness consequences of self-fertilization, but also that limited genetic variation in small populations and slow purging of mildly deleterious mutations may constrain the evolution of increased selfing. Finally, we highlight the need to consider the genetic basis of inbreeding depression and the prospects of using experimental evolution and artificial selection for understanding the interactions among population size, mating system, and population viability.

2. EFFECTS OF POPULATION SIZE ON INBREEDING DEPRESSION AND FIXATION OF DELETERIOUS MUTATIONS

Inbreeding depression is a key factor in models of the evolution of self-fertilization and defines the relationship between degree of inbreeding and population fitness. In this section, we discuss why a small historical population size can be expected to be associated with increased fixation of deleterious mutations and reduced population mean fitness as well as reduced inbreeding depression. We then compare and discuss predicted and observed relationships among population size, inbreeding depression, and heterosis after crosses between populations.

Genetic drift in small populations is expected to increase fixation of mildly deleterious mutations (drift load; Ellstrand & Elam 1993) and increase the probability of mating between closely related plants (biparental inbreeding; Wagenius et al. 2010). Both of these effects are expected to reduce population mean fitness and therefore influence population extinction risk as well as the magnitude and evolution of inbreeding depression. Both inbreeding depression and drift load can be quantified by conducting controlled crosses. Inbreeding depression as defined in models of mating system evolution is the difference in fitness between progeny resulting from self-fertilization versus those from cross-fertilization ($\delta = 1 -$ fitness of progeny produced after self-fertilization/fitness of progeny produced after cross-fertilization) and is the result of genetic variation within a population at loci causing inbreeding depression. A minimum estimate of the drift load can be obtained by quantifying heterosis observed after between-population crosses (the difference in fitness between progeny resulting from within- versus between-population outcrossing). Heterosis will result from between-population differences in alleles fixed due to genetic drift (Keller & Waller 2002). There are two main hypotheses for the genetic basis of both inbreeding depression and heterosis: the dominance hypothesis, according to which deleterious alleles are recessive or partially recessive, and the overdominance hypothesis, according to which

the heterozygote has a fitness advantage (Charlesworth & Willis 2009). Most data are consistent with the former hypothesis, and both mutation–selection balance and balancing selection may contribute to the maintenance of recessive deleterious mutations in natural populations (Charlesworth & Charlesworth 1999, Ronce et al. 2009, Cheptou & Donohue 2011).

The genetic basis of inbreeding depression and the effect size of deleterious mutations will influence the evolution of inbreeding depression in response to increased inbreeding (Charlesworth & Charlesworth 1987) and the efficiency of selection in removing deleterious mutations in small populations (Wang et al. 1999, Glémin et al. 2001, Glémin 2003). Selection is expected to efficiently remove lethal and strongly deleterious mutations with increased inbreeding, whereas mildly deleterious mutations are less easily purged (Lande & Schemske 1985), especially in small populations (Wang et al. 1999, Glémin et al. 2001, Glémin 2003). Theory as well as empirical tests of purging suggest that mildly deleterious mutations contribute significantly to inbreeding depression in natural populations (Lande & Schemske 1985, Willis 1999, Charlesworth & Willis 2009, Baldwin & Schoen 2019). Moreover, because plants lack a separate germ line, mutations in somatic cells may be incorporated in gametes and transmitted to the next generation, and particularly high genomic mutation rates can therefore be expected in long-lived and clonal plants (Lande et al. 1994, Scofield & Schultz 2006). If the genomic mutation rate to (nearly) recessive lethal alleles and the associated inbreeding depression are very high, such that very few selfed offspring survive (δ close to 1), partial selfing may not be sufficient to efficiently purge specific deleterious mutations unless the selfing rate exceeds a threshold value that will depend on the mutation rate ("selective interference" among loci with recessive deleterious mutations; Lande et al. 1994). Such interference can explain why the magnitude of inbreeding depression is similar in outcrossing populations and in populations with a mixed mating system (Winn et al. 2011).

Inbreeding depression is expected to be lower, and heterosis higher after between-population crosses, in historically small compared with historically large populations. Fixation of deleterious mutations due to genetic drift will reduce the number of segregating deleterious mutations within small populations and therefore diminish fitness differences between progeny resulting from selfing versus those resulting from outcrossing (Byers & Waller 1999, Pujol et al. 2009, Pannell 2015, Charlesworth 2018, Toczydlowski & Waller 2023). Moreover, increased probability of mating between close relatives in small populations will increase opportunities for selection to remove segregating deleterious recessive mutations (purging). Both processes cause inbreeding depression to decrease with declining historical population size. The opposite is expected for heterosis after between-population crosses because small populations harbor higher drift load. Because mildly deleterious alleles are fixed at random by genetic drift, between-population crosses can restore heterozygosity and lead to heterosis (Crow 1948). Heterosis after between-population crosses can therefore be used as a minimum estimate of the magnitude of the drift load, and joint estimates of inbreeding depression and of heterosis in populations of different size can be used to compare the effects of population size on purging of large-effect deleterious mutations and on fixation of mildly deleterious mutations (Paland & Schmid 2003, Willi et al. 2013).

Across taxa, substantial evidence indicates that inbreeding depression is greater in large compared with in small populations (reviewed in Angeloni et al. 2011), consistent with purging of the genetic load or reduced genetic differences between selfed and outcrossed progeny in small populations. However, the results of comparing conspecific populations of different size and density are equivocal. In *Gentianella germanica*, inbreeding depression was detected only in large populations (Paland & Schmid 2003), and, in *Gymnadenia conopsea*, inbreeding depression increased with population density when controlling for population size (Söderquist et al. 2020). Several investigators have reported a weak relationship or no relationship between inbreeding depression and population size (e.g., van Treuren et al. 1993, Michaels et al. 2008, Oakley & Winn 2012, Thoen

et al. 2025), including a negative relationship between census size and inbreeding depression in *Sabatia angularis* (Spigler et al. 2017) (**Supplemental Table 1**). The latter group includes both studies documenting strong inbreeding depression (Michaels et al. 2008, Spigler et al. 2017) and studies reporting overall weak inbreeding depression (Oakley & Winn 2012, Thoen et al. 2025), suggesting that a lack of relationship cannot be explained by selective interference in all cases.

Heterosis is common after crosses between natural populations, and there is some evidence of stronger heterosis in crosses that involve small or low-density populations (Willi & Fischer 2005, Oakley & Winn 2012, Pickup et al. 2013, Söderquist et al. 2020). The empirical work includes studies that contrast a group of small versus large populations, that treat population size or density as a continuous variable, and that infer N_e on the basis of genetic diversity (**Supplemental Table 1**). Although the number of studies is limited, results indicate that small populations regularly harbor substantial drift load. Studies that combined estimates of inbreeding depression and heterosis also indicate a high drift load and some purging in small and sparse populations: Paland & Schmid (2003) found heterosis in crosses involving small populations and inbreeding depression in large populations of *Gentianella germanica*, and Söderquist et al. (2020) found increasing inbreeding depression and decreasing heterosis with population density of *Gymnadenia conopsea*. Similarly, Oakley & Winn (2012) documented low inbreeding depression in combination with high heterosis in small populations of *Hypericum cumulicola*. Others found no pattern (Thoen et al. 2025) or the expected relationship only with heterosis, despite substantial inbreeding depression (Willi et al. 2013, Spigler et al. 2017). The latter suggests the presence of drift load but no substantial purging. Overall, the support for a relationship between population size and the fixed drift load is stronger compared with that between population size and inbreeding depression observed after self-fertilization (**Supplemental Table 1**).

Relationships between population size and inbreeding depression may be inconsistent for several possible reasons, including a weak correlation between contemporary and historical population size, poor correspondence between census population size and N_e, temporal variation in outcrossing rate and inbreeding depression, and confounding effects of population size and density. The long lifespan of many perennial plants means that the flowering plants seen today could have been established at a very different population size, and if current small populations are a result of recent reductions in size, then we might not see any relationship yet. Census population size and N_e may be weakly correlated due to fluctuating population size, overlapping generations, or among-individual variation in reproductive output (Frankham 1995). For example, theoretical models have shown that for a given level of genetic diversity, populations experiencing stronger fluctuations in size express stronger heterosis and lower inbreeding depression, compared with more stable populations (Spigler et al. 2017). In addition, the magnitude and timing of inbreeding depression may depend on environmental context (Cheptou & Donohue 2011), potentially influencing the strength of relationships with population size. Finally, studies vary substantially both (*a*) in sample sizes and ranges in estimates of population sizes and what is considered a "small" and a "large" population and (*b*) in fitness components examined to quantify inbreeding depression and heterosis (**Supplemental Table 1**), which is likely to contribute to the variable results.

Genomic approaches are increasingly used to estimate the mutational load, but the relationship between sequence-derived estimates and fitness consequences under relevant field conditions is rarely tested (Bertorelle et al. 2022). In the self-incompatible *Arabidopsis lyrata*, the heterosis effect following between-population crosses was found to increase with the genomic estimate of load (Perrier et al. 2020). Populations with the strongest genomic signatures of load were located at the range edges and experienced strong reductions in population mean fitness.

To summarize, comparisons across species indicate that inbreeding depression is weaker in small compared with large populations, but results of studies of conspecific populations are less

consistent and several found weak relationships or no relationship. The results are consistent with a scenario where small populations often retain substantial inbreeding depression caused by recessive deleterious mutations that are difficult to purge. Heterosis observed after crosses between populations indicates that drift load reduces viability of small populations and increases the risk of population extinction. A major limitation of published studies of conspecific populations is that few include more than a handful of populations or contrast only a group of small versus large populations, where what is considered small is variable (**Supplemental Table 1**). This approach leaves little power to detect associations between population size and inbreeding depression or heterosis and prevents detection of potential nonlinear relationships.

Supplemental Material >

3. EFFECTS OF POPULATION SIZE ON POLLEN LIMITATION

In this section, we outline why plant population size can be expected to influence pollinator visitation rates and pollen transfer among plants, and we discuss comparative and experimental studies examining effects of population size on pollination intensity and outcross pollen limitation.

Pollination success depends on both the presence of compatible mates and the amount of pollen transfer among plants. In animal-pollinated plants, the latter depends on rates and patterns of pollinator visitation, whereas in wind-pollinated plants, it depends on both wind regimes and population density. Pollinator visitation has been predicted to be reduced both in small and sparse populations and in very large populations.

Small and sparse populations of reward-producing plant species offer a smaller resource for animal flower visitors and are therefore less attractive to pollinators compared with large populations with a high plant density (Sih & Baltus 1987, Ågren 1996, Kunin 1997). Moreover, they may not represent a sufficient resource to maintain a local pollinator population. As a result, pollinator visitation and pollen transfer among plants can be expected to be lower and pollen limitation of seed production stronger in small and sparse compared with large and dense populations, resulting in an Allee effect (Ashman et al. 2004, Knight et al. 2005, Duffy et al. 2013).

A positive relationship between population size and mean plant fecundity has been documented in many but not all species studied (reviewed by Leimu et al. 2006; see also, e.g., Brys et al. 2008, Klank et al. 2010, Phillips et al. 2014). Although a positive relationship may reflect an increase in pollen limitation of seed production in small populations (due to reduced quantity or quality of pollen received), it may also be driven by other factors, including associations between population size and availability of resources for plant growth and seed production or between population size and genetic load (Leimu et al. 2006). Correlations between population size and several indicators of pollination intensity (visitation rates to flowers, stigmatic pollen loads, and fruit initiation) have been used to assess whether differences in pollination intensity can explain an observed relationship between population size and plant fecundity (e.g., Waites & Ågren 2004, Ågren et al. 2008, Duffy et al. 2013, Patrick et al. 2018). However, to determine conclusively that variation in pollen limitation is the cause of among-population variation in fecundity requires that supplemental hand-pollinations are conducted in populations of different size and that the relationship between population size and degree of pollen limitation is evaluated. Experimental evidence that pollen limitation is greater in small populations has been obtained using this approach in the self-compatible annual herbs *Clarkia concinna* (Groom 1998) and *Clarkia xantiana* ssp. *xantiana* (Moeller 2004) and in the self-incompatible perennial herbs *Lythrum salicaria* (Ågren 1996), *Brunsvigia radulosa* (Ward & Johnson 2005), and *Phyteuma spicatum* (Kolb 2005). The results show that pollen limitation may increase with decreasing population size not only in self-incompatible plants, but also in self-compatible plants that lack the ability to self autonomously.

Increased outcross pollen limitation has been predicted also in very large populations. If populations become very large, they may satiate local pollinators, and pollinator visitation per plant may decrease and pollen limitation increase (Rathcke 1983). This effect could explain strong pollen limitation in several crop species grown in large monocultures (Reilly et al. 2020, Turo et al. 2024). The population size at which pollinator satiation occurs and the competition among plants for pollinators begin to increase depending on pollinator abundance. In the perennial geophyte *Lapeirousia oreogena*, which is pollinated almost exclusively by a long-proboscid fly species, supplemental hand-pollinations indicated that pollen limitation was stronger in large than in small patches (where large patches included several thousand plants; Johnson et al. 2012). Because reduced pollinator service is expected in both small and very large populations, a nonlinear relationship between population size and pollination success would be observed if a sufficiently wide range of population sizes is examined (Brys et al. 2008).

Nonrewarding, animal-pollinated plant species represent an interesting exception in that pollination success can be expected to be higher in small compared with in large plant populations because of the increased chance that flower visitors will learn to avoid the nonrewarding flowers in large populations (Alexandersson & Ågren 1996). A study of three nonrewarding food-deceptive orchid species in southern Sweden found a negative relationship between population size and pollen removal in all three species (*Anacamptis pyramidalis*, *Orchis palustris*, and *Orchis spitzelii*) but a negative relationship between population size and fruit set in only one (*Anacamptis pyramidalis*; Fritz & Nilsson 1994). Similarly, pollen removal, but not fruit set, was negatively related to population size in the boreal food-deceptive orchid *Calypso bulbosa* (Alexandersson & Ågren 1996), and the relationship between population size and proportion of flowers forming a fruit was either absent or weak in three sexually deceptive nonrewarding Australian orchids (Tremblay et al. 2005). Taken together, the results indicate that factors besides increased avoidance of nonrewarding flowers in large populations determine among-population variation in fruit set in these plants.

Finally, in wind-pollinated species, population size and density influence the pollen abundance in the air and therefore the probability of pollen receipt. Information on pollen limitation in wind-pollinated plants is limited (Friedman & Barrett 2009), but low population density has been associated with pollen limited seed production in a few species (Davis et al. 2004, Hesse & Pannell 2011). Unlike the situation in animal-pollinated species, we would not expect that a high density of pollen producers would reduce pollination success.

In situations where correlations between population size and other population attributes, such as density and isolation, are not too strong, the relative importance of population size for variation in pollen limitation and selection on mating system traits can be evaluated statistically. Multiple regression models indicated that outcross pollen limitation was related to population size but not to population density or isolation in *Phyteuma spicatum* (Kolb 2005). Similarly, in *Brunsvigia radulosa*, pollen limitation decreased with increasing population size but was not related to isolation or to habitat fragment area (Ward & Johnson 2005). Such statistical models can help identify the key factors for variation in plant fecundity and pollen limitation, but ideally population attributes should be manipulated experimentally. By manipulating both population size and isolation, Groom (1998) showed that the decrease in pollen limitation with increasing population size and with decreasing isolation observed in *Clarkia concinna* represented causal relationships. In systems for which such manipulations of relevant population attributes (size, density, isolation) are considered both ethical and logistically possible, they represent the preferred tool to establish causation.

A correlation between population size and pollen limitation is not expected in all species. In self-compatible species with capacity for autonomous self-pollination, reduced pollinator-mediated transfer of pollen between plants can be compensated by delayed selfing (Kalisz et al. 2004, Brys et al. 2011, Goodwillie & Weber 2018). In this case, the outcrossing rate and possibly

seed quality rather than seed production would be expected to be related to population size (see the following sections). Furthermore, reduced pollinator visitation to small populations of plant species lacking capacity for autonomous self-pollination does not necessarily result in a correlation between population size and pollen limitation. First, the lower visitation rate observed in small populations can be sufficient for full seed set (Phillips et al. 2014). Second, population size and density can positively affect not only pollination success and fruit initiation, but also the intensity of antagonistic biotic interactions, such as those with pathogenic fungi and seed predators. In this situation, the relative strength of these effects will determine the net outcome in terms of among-population variation in fecundity (Ågren et al. 2008, Klank et al. 2010).

Inconsistent correlations between pollinator visitation and plant population size, density, or isolation can be related to spatiotemporal variation in the composition of the pollinator community or in factors other than population size affecting pollinator visitation. In the perennial herb *Kniphofia linearifolia*, pollination by birds increased with increasing population size, whereas pollination by honey bees did not; in addition, plant fecundity increased with plant population size in a year when birds contributed substantially to pollination, but not in a year when honey bees dominated among flower visitors (Duffy et al. 2013). Finally, in species with generalized pollination systems (i.e., that are pollinated by a wide range of flower visitors), facilitation by or competition with other species with shared pollinators may interact with population size to determine the degree of pollen limitation (Moeller 2004) or may govern pollination success irrespective of population size (de Waal et al. 2015).

To conclude, increasing pollen limitation with decreasing population size has been documented in several species. However, studies that have used supplemental hand-pollinations to quantify pollen limitation of seed production in populations of varying size are still limited. Additional studies are required to determine whether effects of population size on outcross pollen limitation are more common in self-incompatible than in self-compatible species and in species requiring specialized pollinators compared to those pollinated by generalists.

4. EFFECTS OF POPULATION SIZE ON MATE AVAILABILITY, POLLEN, AND SEED DISCOUNTING

In this section, we outline why plant population size can be expected to influence the quality of pollen reaching stigmas. We discuss why population size affects (*a*) mate availability in self-incompatible species and (*b*) pollinator behavior, and thereby the proportion of self pollen deposited on stigmas, and pollen and seed discounting. In self-compatible plants, the relative value of self and cross pollen receipt will depend on the magnitude of inbreeding depression (see discussion above).

In self-incompatible plants, which constitute about half of all flowering plant species (Igic & Kohn 2001), a critical aspect of pollen quality is whether the pollen received is compatible. In these plants, effects of population size on pollination success have been predicted to be particularly strong because of stochastic loss of self-incompatibility alleles in small populations and the associated reduction in mate availability (Busch & Schoen 2008, Young & Pickup 2010). There are several examples showing that reduced mate availability in small populations of clonal as well as nonclonal, self-incompatible plants can lead to reduced fecundity (Glémin et al. 2008, Young & Pickup 2010, Cisternas-Fuentes et al. 2025 and references therein).

In both self-incompatible and self-compatible plants, geitonogamous self-pollination will reduce male reproductive success because it reduces the amount of pollen available for transfer to other plants (pollen discounting). In self-compatible plants, geitonogamy may, in addition, reduce the number of ovules available for outcrossing (seed discounting). The fitness consequences of

geitonogamous selfing and seed discounting will depend on the magnitude of inbreeding depression and possible trade-offs between seed production and other fitness components (Barrett & Harder 2017).

Based on foraging economics, pollinators are expected to visit more flowers per plant in small and sparse populations compared to large and dense ones (Charnov 1976, Pyke 1982), and, as a result, geitonogamous self-pollination would be higher. There is substantial support for the predicted effect on flower visitation by pollinators (e.g., Grindeland et al. 2005), and there is also empirical support for the predicted effect on level of self-pollination. Two studies of orchids using color-labeled pollen documented higher geitonogamous self-pollination in small or low-density populations and patches (Johnson et al. 2009, Söderquist et al. 2020). Moreover, Karron et al. (1995) showed experimentally that the increased proportion of pollinator flights between plants in high-density patches of *Mimulus ringens* was associated with increased outcrossing. Taken together, the results are consistent with the predicted effects of population size and density on both pollen and seed discounting.

Because population size and density affect patterns of pollinator visitation, they may also influence aspects of pollen quality beyond the distinction between self and cross pollen. High visitation rates combined with few flower visits per plant result in a higher diversity of conspecific pollen genotypes arriving on the stigma and therefore provide an increased opportunity for both pollen tube competition and female choice (Aizen & Harder 2007, Christopher et al. 2020). Finally, in species visited by generalist pollinators, the receipt of heterospecific pollen may increase in small and sparse populations, although whether more heterospecific pollen will interfere with the fertilization success of conspecific pollen varies among species (Arceo-Gómez 2021).

When considering the results of studies examining the effects of population size on estimates of plant fitness, pollinator visitation, and pollen transfer (see discussion in this section and the previous section), one should note that the delimitation of populations in ecological studies is often based on a pragmatic definition, such as the minimum distance to nearest patch with conspecifics or habitat differences. Thus, the difference between studies examining the effects of patch size and density within populations and those stated to examine the effects of population attributes is not always clear. This area of research needs studies that consider the possibility of processes simultaneously acting at several spatial scales.

To conclude, the available empirical evidence is consistent with an increase in geitonogamous self-pollination and pollen discounting in small populations, but there is clearly room for additional comparative and experimental work detailing pollen and seed discounting in populations of different size and density.

5. EFFECTS OF POPULATION SIZE ON MATING SYSTEM OF SELF-COMPATIBLE PLANTS

In this section, we examine the relationship between population size and selfing rate in self-compatible species. In self-compatible species, higher geitonogamous or autonomous self-pollination in small and sparse populations results in a higher primary selfing rate (selfing rate at the time of fertilization; Lande et al. 1994). A negative relationship between population size and selfing rate is also expected at the stage at which the selfing rate is typically measured (the seedling stage), unless inbreeding depression expressed during seed development and germination is very high. Consistent with this prediction, a substantial number of studies have documented higher selfing rates in small or low-density populations or patches of plants (e.g., Herlihy & Eckert 2004, Spigler et al. 2010, Christopher et al. 2021, Torres-Vanegas et al. 2021), including some wind-pollinated species (Robledo-Arnuncio et al. 2004, Chybicki & Dzialuk

2014). Similarly, habitat fragmentation (i.e., reduced stand density and increased disturbance) has been associated with increased selfing rates and decreased pollen diversity in animal-pollinated trees and shrubs (reviewed in Breed et al. 2015). In species lacking the capacity for autonomous self-pollination, higher selfing in small and sparse populations is due to pollinator-mediated selfing (e.g., Torres-Vanegas et al. 2021). In other species, flower emasculation has been used to separate the contributions from autogamy and geitonogamy. This approach has documented increased reliance on autogamy in small populations of *Aquilegia canadensis* (Herlihy & Eckert 2004), *Centaurium erythraea* (Brys et al. 2011), and *Sabatia angularis* (Spigler 2018). Finally, at least one study has documented interactive effects between population size and density. In the annual *Chamaecrista fasciculata*, outcrossing rate increased with density at high N_e but not at low N_e (Kulbaba & Shaw 2021). This finding suggests that complex interactions between population size and density may contribute to variable relationships between population size and mating patterns.

However, some empirical studies found no relationship between outcrossing rate and population size or density in self-compatible species (e.g., Kennington & James 1997, Neel et al. 2001, Tamaki et al. 2009). In some cases, early-acting inbreeding depression was invoked as an explanation (e.g., Kennington & James 1997). If inbreeding depression at the embryo stage is severe, estimates of outcrossing rate at the seedling stage may be uniformly high, as inbred seeds will be aborted early on. By contrast, in the invasive, self-compatible annual herb *Datura stramonium*, a very high selfing rate independent of population size was attributed to low rates of cross-pollination in the introduced range in South Africa (van Kleunen et al. 2007).

Several studies have found higher estimates of outcrossing rate than expected based on the proportion of self-pollen deposited (Husband & Schemske 1996). These higher estimates could be due to early-acting inbreeding depression, but also to postpollination processes that are difficult to distinguish from early-acting inbreeding depression such as pollen tube competition and selective abortion of ovules. Because such postpollination processes are expected to be more important when pollination intensity is high (Christopher et al. 2020), the strongest effect on mating systems is expected in large and dense populations, where pollen limitation is low. Both pollen pool diversity (e.g., Breed et al. 2012, Torres-Vanegas et al. 2021) and diversity of paternity (e.g., Tamaki et al. 2009) can increase with density and size of patches and populations, but to what extent this increase contributes to relationships between population size and outcrossing rate is unknown.

In small populations, the probability of biparental inbreeding, i.e., mating between related individuals, increases. Relatively few studies have examined if biparental inbreeding is higher in small and low-density populations. Herlihy & Eckert (2004) found increased levels of biparental inbreeding in small populations of *Aquilegia canadensis* and Torres-Vanegas et al. (2021) found biparental inbreeding in *Heliconia tortuosa* to decrease with forest patch size, whereas Spigler et al. (2010) found no relation between population size and biparental inbreeding in *Sabatia angularis*. In some cases, biparental inbreeding actually increased with plant density (Hodgins & Barrett 2006 and references therein), which was attributed to short interplant pollinator flight distances and restricted seed dispersal.

Does higher selfing over time result in more inbred and closely related plants in small and sparse populations? The empirical support for this notion is relatively weak. In line with predictions, Vekemans & Hardy (2004) found stronger fine-scale genetic structure at low compared to high density when comparing pairs of low- and high-density populations of five different species, but this comparison did not control for population size. Two reviews that included more species found no significant relationship between population size and the inbreeding coefficient (Leimu et al. 2006, Honnay & Jacquemyn 2007). Small populations of *Aquilegia canadensis* had higher selfing rates than did large ones, but parental plants in small populations were not more inbred

(Routley et al. 1999). The latter suggests that inbreeding depression expressed after the seedling stage maintains low relatedness among established plants. Likewise, several studies have documented higher inbreeding coefficients in progeny than in parents (e.g., Neel et al. 2001, Hodgins & Barrett 2006, Spigler et al. 2010); in addition, in at least one study, inbreeding coefficients at the seed stage decreased with population size, whereas those at the adult stage did not (Tamaki et al. 2009).

To conclude, the evidence suggests that patterns of pollen transfer are strongly affected by population size and density but that effects on outcrossing rate quantified at the seedling stage and relatedness of established plants are weaker and less consistent. Studies that explore the roles of postpollination processes and early-acting inbreeding depression would shed light on the variable relation between the primary selfing rate and mating system quantified at the seedling stage.

6. POPULATION SIZE AND THE EVOLUTION OF SELFING

As discussed above, small populations are expected to be characterized by reduced pollen transfer among plants, by reduced mate availability in self-incompatible species, and by reduced inbreeding depression. All these effects increase the probability that variants with capacity for autonomous selfing would be favored by selection in small populations. In this section, we discuss comparative and experimental support for the hypothesis that reduced population size influences mating system evolution and why population size may influence selection on traits affecting the capacity for autonomous self-pollination, including self-compatibility, and spatial and temporal separation of male and female function (herkogamy and dichogamy).

Selection favoring self-compatibility and capacity for autonomous self-pollination can be expected to be particularly strong in connection with population bottlenecks that reduce mate availability, such as those occurring during colonization events after long-distance dispersal from a large source population (Baker 1955, Barrett et al. 1989, Zell et al. 2025), in biological invasions (Elam et al. 2007, Rodger et al. 2013), in species subject to metapopulation dynamics (Pannell & Barrett 1998), or as a consequence of repeated colonization during range expansions (Pannell et al. 2015, Koski et al. 2019). Self-compatibility was strongly associated with island occurrence in a comparative study that also considered life history and floral traits as indicators of pollination system (Zell et al. 2025). This association likely reflects a higher probability of establishment after long-distance dispersal of self-compatible compared to self-incompatible species and genotypes. In small populations of several self-incompatible species, the stochastic loss of *S*-alleles and the concomitant reduced availability of compatible mates have been associated with reduced seed production (Busch & Schoen 2008, Young & Pickup 2010), which increases the probability that self-compatible or "pseudoself-compatible" (with a leaky self-incompatible system) variants become favored by selection (Busch & Schoen 2008). Consistent with this prediction, Cisternas-Fuentes et al. (2025) found leaky self-incompatibility to be higher in small than in large populations of the clonal herb *Argentina anserina*.

Allee effects due to insufficient pollen transfer favor the evolution of capacity for autonomous selfing, in particular, delayed autonomous self-pollination but potentially also prior self-pollination (Lloyd 1980, Morgan et al. 2005, Eckert et al. 2010). Capacity for delayed autonomous selfing may be a solution for spatiotemporal variation in pollen limitation in self-compatible species (Kalisz et al. 2004, Goodwillie et al. 2005, Hargreaves et al. 2015). Delayed selfing has the advantage that it is not associated with seed discounting unless it reduces the potential for developing seeds of higher quality from cross-fertilized flowers developing later in the season or in the following year (Morgan et al. 1997). However, in some genera, delayed selfing is associated with lower autofertility compared to other modes of autonomous selfing (Goodwillie &

Weber 2018). Spatiotemporal variation in pollen limitation may also contribute to the maintenance of mating system polymorphisms. In *Primula vulgaris*, differences in pollination intensity across years and populations were associated with variation in the relative fitness of the self-compatible homostylous morph and the self-incompatible heterostylous morphs (Piper et al. 1986).

If mate availability is high but pollinator visitation is low, alternative evolutionary responses could be the evolution of increased attractiveness to pollinators and increased flower longevity (Harder & Aizen 2010, Jacquemyn et al. 2012, Thomann et al. 2015). However, small populations are perhaps more likely to be characterized by both low mate availability and low pollinator visitation, in which case the evolution of reproductive assurance through nonsexual reproduction (apomixis or clonal propagation) is a more likely alternative to autonomous self-pollination (Eckert et al. 2010).

Field experiments have demonstrated that pollen limitation can result in selection for increased capacity for autonomous self-pollination. A factorial field experiment manipulating the presence of congeners and population size of the self-compatible annual herb *Clarkia xantiana* detected selection through female function for reduced herkogamy and protandry, i.e., in a direction that promotes autonomous self-pollination, but only in the pollen-limited small populations without congeners (Moeller & Geber 2005). In a field experiment conducted in a natural population of the self-compatible herb *Mimulus guttatus*, there was selection for reduced herkogamy through female function, but only when pollinators were experimentally excluded (Fishman & Willis 2008). In self-compatible populations of the short-lived perennial herb *Arabis alpina*, herkogamy and anther orientation affect efficiency of autonomous selfing (Toräng et al. 2017). When an F2 population segregating for these traits was planted at two native field sites, selection strongly favored a combination of introrse anthers and reduced anther–stigma distance at the site where pollinator activity was low, and supplemental hand-pollination demonstrated that this trait combination reduced pollen limitation (Toräng et al. 2017). The results of these studies are consistent with expected positive effects of reproductive assurance on female fitness when pollinator availability is low. However, a full assessment of selection on herkogamy and dichogamy in populations of different size should include quantitative estimates of the magnitude of inbreeding depression and possible seed discounting associated with increased autonomous selfing (Herlihy & Eckert 2004, Layman et al. 2017) as well as possible antagonistic selection through male and female function and pollen discounting (Briscoe Runquist et al. 2017).

To conclude, considerable comparative and experimental evidence demonstrates that self-compatibility and capacity for autonomous self-pollination provide an adaptive advantage in situations with low mate and pollinator availability. Comparative data indicate that these traits have evolved in association with range expansions in several species.

7. EVOLUTION OF SELF-FERTILIZATION AS AN EVOLUTIONARY RESCUE IN SMALL POPULATIONS

Reproductive assurance makes species less vulnerable to reductions in population size. In this section, we discuss whether the evolution of autonomous selfing can be a mechanism for evolutionary rescue of small populations in response to pollen limitation. We note that evolutionary rescue by this mechanism depends on available genetic variation in traits affecting capacity for autonomous selfing, the strength and genetic basis of inbreeding depression, and the effect of increased offspring production on population growth rate.

In the long term, selfing lineages have been suggested to go extinct because of limited adaptive potential and accumulation of deleterious mutations (Igic & Busch 2013). The direct evidence of

higher accumulation of harmful mutations in selfers compared to outcrossers is weak (Wright et al. 2013), but phylogenetic studies indicate that evolution of selfing leads to increased risk of lineage extinction (Goldberg et al. 2010), in line with the "evolutionary dead end" hypothesis (Takebayashi & Morrell 2001). Still, as discussed in the previous section, comparative data indicate that the evolution of capacity for autonomous selfing can provide at least short-term demographic rescue after population bottlenecks and/or loss of pollinators. Moreover, the evolution of autonomous reproduction has been associated with increased range sizes (Grossenbacher et al. 2015, Grant & Kalisz 2020), and the high frequency of self-fertilization among annuals inhabiting disturbed environments indicates that self-fertilizing populations are more resilient to habitat fragmentation and reductions in population size (Lloyd 1980).

Studies employing experimental evolution under greenhouse conditions have demonstrated that the mating system can evolve rapidly in response to selection. In *Mimulus guttatus*, experimental evolution without pollinators resulted in reduced anther–stigma separation and increased autogamous seed set (Bodbyl Roels & Kelly 2011, Busch et al. 2022), consistent with phenotypic selection on these traits in the source population when pollinators were excluded (Fishman & Willis 2008). In a rapid-cycling *Brassica rapa* population, capacity for autonomous selfing diverged between treatments subject to selection by either bumble bees or hover flies during nine generations of experimental evolution, which was attributed to differences in pollen limitation between treatments (Gervasi & Schiestl 2017). A resurrection experiment similarly found evidence of rapid evolution of the mating system across two decades in the annual *Viola tricolor* and related this rapid evolution to declining pollinator visitation (Acoca-Pidolle et al. 2024). Taken together, these studies show that mating system evolution can be rapid, given sufficient genetic variation. However, in historically small populations, standing genetic variation is likely to be low, and the lack of genetic variation in key traits may constrain their response to selection (Willi et al. 2006). Moreover, inbreeding depression can negate the positive effects of reproductive assurance on population growth rate and persistence (Cheptou 2019), and purging as a consequence of increased inbreeding can be inefficient if inbreeding depression is mainly due to mildly deleterious mutations (see above). Whether increased offspring production through selfing will have a sufficiently strong net-positive effect to result in a population growth rate greater than one depends on the strength of inbreeding depression, possible trade-offs between seed production and other fitness components, and the sensitivity of population growth to increased fecundity.

The potential for evolutionary rescue of declining populations through the evolution of increased selfing is higher in short-lived compared to long-lived species. Because pollen limitation affects primarily seed production, while inbreeding depression may reduce performance at several stages in the life cycle, the effect of selfing on population viability will depend on how sensitive the population growth rate is to reductions in different fitness components. The population growth rate of short-lived species is expected to be most sensitive to changes in fecundity (Franco & Silvertown 2004). In the annual *Clarkia concinna*, pollen limitation due to small population size caused increased patch extinction within 5–6 years (Groom 1998). In long-lived species, population growth is typically most sensitive to changes in adult performance, suggesting that the impact of late-acting inbreeding depression could be severe and that increased inbreeding in many situations may result in a reduced population growth rate. In addition, the genomic mutation rate per generation is greater in long-lived than in short-lived plant species (Lande et al. 1994). In the perennial herb *Geranium sylvaticum*, inbreeding depression expressed as reduced germination, juvenile survival, and flowering probability affected the population growth rate considerably more than did pollen limitation of seed production (Ramula et al. 2007), and models of introduced populations of the endangered shrub *Conradina glabra* showed that strong inbreeding depression expressed already at the seed germination stage would lead to declining populations if selfing rates substantially

increased (Bladow et al. 2017). Differences between short-lived and long-lived species with regard to how lifetime fitness is affected by pollen limitation and inbreeding depression after the seed stage contribute to the association between plant life history and the mating system (Munoz et al. 2016).

Finally, population history affects the conditions for evolutionary rescue of small declining populations through the evolution of selfing. Prospects are low if drift load has accumulated in a historically small population to the extent that it prevents population growth, and inbreeding depression is due mainly to mildly deleterious mutations that are difficult to purge. In this situation, increased inbreeding may further reduce population fitness and may push the population to extinction (Wang et al. 1999). By contrast, gene flow from other populations could restore heterozygosity and potentially result in population growth ("genetic rescue"; Frankham 2015). The opportunity for the evolution of selfing to provide evolutionary rescue is greater after a recent population bottleneck, after which the segregating load has decreased and before drift load has had the opportunity to accumulate (Pujol et al. 2009).

In summary, evolution of selfing may, under certain conditions, rescue small declining populations from extinction. However, additional empirical and theoretical work is required to determine how the effects of pollen limitation and inbreeding depression across the life cycle influence the relative fitness of a selfing variant, in particular in long-lived species.

8. FUTURE DIRECTIONS

As illustrated by this review, pollen limitation, drift load, and inbreeding depression may all combine to reduce the viability of small plant populations. However, there are several outstanding questions related to the evolution of selfing and its potential to provide evolutionary rescue in small, declining populations. Most importantly, to what extent does selection on mating system traits vary with population size and pollination regime? Is the evolution of selfing constrained by a lack of genetic variation, by a high drift load, or by inbreeding depression? Do these constraints vary with plant life history? These questions could profitably be addressed with a combination of comparative and experimental approaches.

First, artificial selection can be used to examine the extent to which evolution of traits affecting the mating system is constrained by a lack of genetic variation or genetic correlations with other traits that affect plant fitness.

Second, selection on traits affecting the selfing rate can be quantified in experiments where both population size and pollination intensity are manipulated. By quantifying selection not only through female but also through male function, and by considering possible effects of inbreeding depression, investigators can obtain a more complete understanding of selection on mating system traits. Such experiments would be particularly straightforward in species polymorphic for traits affecting their capacity for autonomous selfing. Studies could also be conducted using segregating populations derived from crosses among populations that differ in traits affecting the mating system. In either case, both the functional significance of floral traits in terms of pollinator visitation and pollen transfer and the adaptive significance in terms of effects on fitness can be examined.

Third, by allowing the experimental populations to evolve under relevant field conditions, the evolution of mating system traits and absolute fitness can be tracked in parallel with associated genetic changes. This work would provide information on the speed at which the mating system can evolve. It would also allow an evaluation of how positive effects of reproductive assurance on fecundity balance against possible trade-offs with other fitness components and against negative effects of inbreeding depression across the entire life cycle.

Fourth, the shapes of the relationships between population size and drift load and purging can be evaluated by jointly quantifying inbreeding depression and heterosis with controlled crosses

in multiple (>10) natural populations of varying size. Comparisons of systems with contrasting fragmentation history (having experienced rapid declines versus a long history of fragmentation) would be particularly interesting.

Fifth, the relationship between plant fitness and genomic estimates of drift load in populations of varying size should be examined in field experiments. This approach allows researchers to assess the genomic signatures of accumulation and purging of genetic load.

Sixth, theoretical models should explore the demographic effects of shifts in the mating system in declining populations. Such models should consider the effects of the genetic basis and environment dependence of inbreeding depression and plant life history as well as effects of increased inbreeding on genetic diversity and adaptive potential.

Taken together, these approaches would provide a more comprehensive understanding of the conditions for mating system evolution in small and declining populations. Of particular value would be to study plants with a perennial life history. Doing so poses practical and financial challenges for researchers. However, it is necessary for a full understanding of mating system evolution as well as of conservation implications of mating system variation, as many declining and threatened plants are long-lived perennials. Management efforts should consider the interplay among the mating system, life history, and population viability. Experimental studies of the demographic and genomic consequences of shifts in population size and mating system will provide new insight into the mechanisms underlying mating system evolution, but they will also facilitate predictions that can be used to inform management decisions.

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