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3

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5

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15

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1 ABSTRACT

2

3 A comprehensive understanding of plant mating system evolution requires detailed genetic
4 models for both the mating system and inbreeding depression, which are often intractable. A
5 simple approximation assuming that the mating system evolves by small infrequent
6 mutational steps has been proposed. We examine its accuracy by comparing the evolutionarily
7 stable selfing rates it predicts to those obtained from an explicit genetic model of the selfing
8 rate, when inbreeding depression is caused by partly recessive deleterious mutations at many
9 loci. Both models also include pollen limitation and pollen discounting. The approximation
10 produces reasonably accurate predictions with a low or moderate genomic mutation rate to
11 deleterious alleles, on the order of $U = 0.02$ to 0.2 . However, for high mutation rates, the
12 predictions of the full genetic model differ substantially from those of the approximation,
13 especially with nearly recessive lethal alleles. This occurs because when a modifier allele
14 affecting the selfing rate is rare, homozygous modifiers are produced mainly by selfing, which
15 enhances the opportunity for purging nearly recessive lethals and increases the marginal
16 fitness of the allele modifying the selfing rate. Our results confirm that explicit genetic models
17 of selfing rate and inbreeding depression are required to understand mating system evolution.

1 INTRODUCTION

2 Inbreeding depression, the relative decrease in fitness of inbred vs. outbred individuals, is a
3 critical force in the evolution of mating systems, with complex evolutionary dynamics.
4 Numerous theoretical approaches have explored these dynamics, and sometimes its joint
5 evolution with the mating system, when inbreeding depression is caused by overdominance
6 (Uyenoyama and Waller 1991b), or by deleterious recessive alleles at one (e.g. Uyenoyama
7 and Waller 1991a; Glemin 2003) or many loci with (Charlesworth et al. 1991) or without
8 (Lande and Schemske 1985; Charlesworth et al. 1990; Lande et al. 1994) epistatic interactions
9 or genetic linkage (Charlesworth et al. 1992). All these approaches stress the critical influence
10 of the genetic basis of inbreeding depression and its evolutionary dynamics on mating system
11 evolution (see e.g. Porcher et al. 2009 for an example of how the dynamics of inbreeding
12 depression substantially modify the predictions of an ecological model of mating system
13 evolution). Yet, most models that address the effect of ecological forces on mating system
14 evolution have overlooked the dynamics of inbreeding depression, which is often considered
15 fixed (Goodwillie et al. 2005). Simplified models of mating system evolution abound because
16 modeling the joint evolution of mating system and inbreeding depression requires detailed
17 genetic models for both characters, which are often intractable.

18 One approximation to modeling the joint evolution of inbreeding depression and mating
19 system was proposed by Lande and Schemske (1985) and later extended by Johnston (1998)
20 to incorporate ecological mechanisms (seed and pollen discounting) in the evolution of plant
21 mating systems. This approximation is used to find joint equilibria of the mating system and
22 inbreeding depression, by examining the indirect selection gradient on small changes in the
23 selfing rate, assuming the mating system evolves by infrequent small mutation steps. The
24 mating system is assumed to undergo no direct selection, but evolves because of its influence
25 on inbreeding depression. This approximation contains elements of Evolutionarily Stable

1 Strategies, as well as inclusive fitness by weighting selfed seed twice as much as outcrossed
2 seed to account for the automatic advantage of selfing described by Fisher (1941). It can
3 incorporate any genetic model of inbreeding depression, as well as ecological mechanisms
4 influencing the selfing rate (Johnston 1998; Johnston et al. 2009; Devaux et al. 2013).

5 This approximation ignores genotypic associations, due to both linkage (gametic)
6 disequilibrium and identity (zygotic) disequilibrium (Haldane 1949; Crow and Kimura 1970
7 eq. 3.9.3), between the mating system locus and viability loci controlling inbreeding
8 depression. Such genotypic associations have been observed in nature (Weber et al. 2012) and
9 theory predicts that in some cases they can greatly influence the dynamics of invasion of a
10 modifier of the selfing rate (Lande and Schemske 1985; Uyenoyama et al. 1993). Several
11 models have quantified the impact of genotypic associations on the spread of selfing
12 modifiers (Holsinger 1988; Charlesworth et al. 1990; Uyenoyama and Waller 1991a,b,c;
13 Schultz and Willis 1995), but intermediate selfing rates were never evolutionarily stable in
14 these models, unless they assumed inbreeding depression due to overdominance (Uyenoyama
15 and Waller 1991b), which has little support from experimental data (Charlesworth and Willis
16 2009). As a result, no study has quantified the influence of genotypic associations between
17 inbreeding depression and selfing modifiers on the evolutionarily stable selfing rates and the
18 accuracy of an approximation assuming no genetic association. Although it has previously
19 been thought that the approximation should be accurate for infrequent small mutations
20 affecting the selfing rate (Lande and Schemske 1985; Johnston et al. 2009), this was never
21 demonstrated.

22 Here we compare this approximation with a full genetic model for the joint evolution of
23 both the selfing rate and inbreeding depression. Both models also include pollen limitation
24 and pollen discounting, two ecological mechanisms that influence the evolution of plant

1 mating systems and create the conditions for the maintenance of intermediate selfing rates
 2 (Holsinger 1991; Knight et al. 2005; Porcher and Lande 2005).

3

4 THE MODELS

5 THE APPROXIMATION

6 We assume a large (effectively infinite) population with selfing rate \bar{r} in which an initially
 7 rare modifier with selfing rate r appears. The resident and modifier genotypes may differ (1)
 8 in their total seed set T , due to pollen limitation, and (2) in the amount of pollen exported for
 9 outcrossing, P , due to pollen discounting (the decrease in pollen export caused by self-
 10 fertilization, Harder and Wilson 1998). The fitness of the modifier genotype affecting the
 11 selfing rate incorporates the automatic advantage of selfing (Fisher 1941), by weighting selfed
 12 seed twice as much as outcrossed seed

13

$$14 \quad w = r\bar{w}_1 T(r) + (1-r)\frac{\bar{w}_0}{2} T(r) + (1-\bar{r})\frac{\bar{w}_0}{2} \frac{P(r)}{P(\bar{r})} T(\bar{r})$$

15

16 where \bar{w}_0 and \bar{w}_1 are the mean fitnesses of outcrossed and selfed progeny, respectively
 17 (Lande and Schemske 1985; Johnston 1998, eq. 2a). The intensity of selection on the modifier
 18 with a small effect on the selfing rate is approximately proportional to the selection gradient:

19

$$20 \quad \frac{1}{\bar{w}_0 T(\bar{r})} \left. \frac{\partial w}{\partial r} \right|_{r=\bar{r}} = \frac{1}{2} - \delta + \left[\frac{r(1-\delta)}{T(\bar{r})} \frac{\partial T(r)}{\partial r} + \frac{(1-r)}{2T(\bar{r})} \frac{\partial T(r)}{\partial r} + \frac{1-\bar{r}}{2P(\bar{r})} \frac{\partial P(r)}{\partial r} \right]_{r=\bar{r}}$$

21

22 where $\delta = 1 - \bar{w}_1 / \bar{w}_0$ is the inbreeding depression in the resident population assumed to be at
 23 mutation-selection equilibrium for the given selfing rate (Lande and Schemske 1985).

1 Evolutionary equilibrium selfing rates occur when the selection gradient is zero, which yields
 2 the level of inbreeding depression that exactly counterbalances all other constraints on the
 3 evolution of selfing, i.e. the automatic advantage, reproductive assurance in the presence of
 4 pollen limitation, and pollen discounting

5

$$6 \quad \delta(\bar{r}) = \frac{1}{2} \left[1 + \frac{\frac{\partial \ln T(r)}{\partial r} + (1 - \bar{r}) \frac{\partial \ln P(r)}{\partial r}}{1 + r \frac{\partial \ln T(r)}{\partial r}} \right]_{r=\bar{r}} . \quad (1)$$

7

8 The right-hand side of equation (1), hereafter referred to as the constraint function, can be
 9 compared to the inbreeding depression $\delta(\bar{r})$ expected at equilibrium in a population with
 10 selfing rate \bar{r} under any explicit genetic model for inbreeding depression. Equilibrium selfing
 11 rates occur at the intersections of the constraint function and $\delta(\bar{r})$ (Fig. 1).

12 To model inbreeding depression, we use the Kondrashov model (1985), which describes
 13 the evolution of the distribution of number of partly recessive deleterious alleles per mature
 14 plant in the population when mutations occur at an infinite number of unlinked loci in an
 15 infinite population (Lande et al. 1994; Porcher and Lande 2005). We considered separately
 16 two contrasting classes of deleterious mutations that are believed to cause inbreeding
 17 depression (Charlesworth and Willis 2009): nearly recessive lethal mutations vs. partially
 18 recessive, mildly deleterious mutations. We also analyzed a model incorporating a constant
 19 ‘background’ inbreeding depression into a Kondrashov model with nearly recessive lethals,
 20 because the equilibrium inbreeding depression due to stabilizing selection on quantitative
 21 characters, or to nearly additive, mildly deleterious mutations, undergoes relatively little
 22 purging in response to an increased selfing rate (Porcher and Lande 2005; and see Fig. S1 in
 23 Supporting Information).

1
 2 MAINTENANCE OF MIXED MATING WITH POLLEN DISCOUNTING AND POLLEN LIMITATION
 3 Pollen limitation and pollen discounting are described by the seed set $T(r)$ and pollen export
 4 $P(r)$ functions employing the mass-action model for pollination (Holsinger 1991; Porcher and
 5 Lande 2005). All genotypes are expected to produce the same number of flowers and the
 6 same amount of pollen P_T . A rare mating system modifier changes the selfing rate by altering
 7 the fraction α of pollen a genotype exports for outcrossing. Because the mating system
 8 modifier is rare, the amount of outcross pollen landing on the stigma of any plant is
 9 approximately $P_o = \bar{\alpha}\pi_o P_T$, where $\bar{\alpha}$ is the fraction of pollen exported by the resident
 10 genotype and π_o the probability that pollen exported for outcrossing actually lands on a
 11 stigma. The amount of self pollen landing on the stigmas of the resident and modifier
 12 genotypes are $\bar{P}_s = (1 - \bar{\alpha})\pi_s P_T$ and $P_s = (1 - \alpha)\pi_s P_T$, respectively, where π_s is the probability
 13 that pollen not exported actually lands on the stigma.

14 Under competing selfing, the primary selfing rate r of the modifier genotype, after
 15 fertilization, is the ratio of self-pollen to total pollen landing on the stigma $r = P_s/(P_s + P_o)$,
 16 which can also be written

17
 18
$$r(\alpha) = \frac{(1 - \alpha)\pi_s P_T}{(1 - \alpha)\pi_s P_T + \bar{\alpha}\pi_o P_T} = \frac{1 - \alpha}{1 - \alpha + \bar{\alpha}\pi} \quad (2)$$

19
 20 where $\pi = \pi_o/\pi_s$, the relative success of outcross vs. self pollen, quantifies the strength of
 21 pollen discounting (Porcher and Lande 2005).

22 The amount of pollen the modifier genotype exports for outcrossing is $P = \alpha\pi_o P_T$,
 23 which can be written as a function of the selfing rate using equation (2), $\alpha = 1 - r\bar{\alpha}\pi/(1 - r)$,
 24 so that

1

2

$$P(r) = \left(1 - \frac{r\bar{\alpha}\pi}{1-r}\right) \pi_o P_T. \quad (3)$$

3

4 Under pollen limitation, the total seed set T of the modifier genotype depends on the amounts
5 of self and outcross pollen landing on the stigma,

6

7

$$T = 1 - \exp[-P_o - P_s] = 1 - \exp[-\pi_o P_T (\bar{\alpha} + (1-\alpha)/\pi)]$$

8

9 which can also be written as a function of the selfing rate r using equation (2),

10

11

$$T(r) = 1 - \exp[-\pi_o P_T \bar{\alpha} / (1-r)]. \quad (4)$$

12

13 From equation (4), one can see that $\pi_o P_T$, the amount of pollen exported by a completely
14 outcrossing individual that reaches a stigma, can be used to quantify pollen limitation
15 independently of the population mating system.

16

Noting that $\bar{\alpha} = (1-\bar{r})/[1-\bar{r}(1-\pi)]$ and differentiating equations (3) and (4) we find

17

18

$$\left. \frac{\partial \ln P(r)}{\partial r} \right|_{r=\bar{r}} = -\frac{\pi}{(1-\bar{r})^2} \quad \text{and} \quad \left. \frac{\partial \ln T(r)}{\partial r} \right|_{r=\bar{r}} = \frac{[1-T(\bar{r})]\pi_o P_T}{T(\bar{r})(1-\bar{r})[1-\bar{r}(1-\pi)]}.$$

19

20 These are used to obtain the constraint function from equation (1). The intersection between
21 the constraint function and inbreeding depression $\delta(\bar{r})$ is then explored numerically to obtain
22 the equilibrium selfing rates expected under the approximation (Fig. 1A-C). The stability of
23 an equilibrium is found by comparing the values of the constraint function and $\delta(\bar{r})$ around

1 the equilibrium: equilibrium selfing rates are evolutionarily stable if an increase in \bar{r} results
2 in the inbreeding depression being larger than the constraint function (greater costs than
3 benefits of selfing) and vice versa.

4

5 THE FULL GENETIC MODEL

6 The equilibrium selfing rates predicted by the approximation are compared to those obtained
7 using the full genetic model of Porcher and Lande (2005) describing joint evolution of both
8 mating system and inbreeding depression in an infinite population. This uses the same
9 pollination model, where the selfing rate, seed set and pollen export are controlled by the
10 fraction α of pollen exported for outcrossing. The pollination model is coupled with the
11 Kondrashov (1985) model, in which inbreeding depression is caused either by nearly
12 recessive lethals (with or without an additional constant background inbreeding depression) or
13 by nearly additive, mildly deleterious mutations. To model the evolution of the selfing rate,
14 we added an unlinked locus modifying the mating system to the genetic model of inbreeding
15 depression, which accounts for associations between deleterious mutations and alleles
16 influencing the selfing rate. In a resident population at mutation-selection equilibrium, a
17 modifier allele with a pollen export fraction α slightly different from the resident is
18 introduced at a low frequency in linkage and identity equilibrium with deleterious mutations.
19 We examine the fate (invasion or not) of this initially rare modifier allele after 2,000
20 generations to find the evolutionarily stable selfing rates, i.e. resident selfing rates that cannot
21 be invaded.

22

23 PARAMETER VALUES

24 We varied genetic and ecological parameters to generate a wide range of intermediate stable
25 selfing rates that can be compared between the two theoretical approaches. The genomic

1 mutation rate to deleterious mutations was $U = 0.02, 0.2$ or 1 ; the dominance coefficient of
2 lethals was set to $h = 0.02$ (references in Lande and Schemske 1985; Lande et al. 1994);
3 mildly deleterious mutations were characterized by $s = 0.05$ and $h = 0.4$ (references in
4 Halligan and Keightley 2009). We also analyzed a model with such nearly recessive mutation
5 to lethals and a constant background inbreeding depression of $d = 0.25$ (Winn et al. 2011).
6 The relative success of self vs. outcross pollen π was varied between 10^{-4} (no pollen
7 discounting) and 0.9999 (strong pollen discounting). We also considered a wide range for the
8 strength of pollen limitation, from $\pi_o P_T = 0.5$ to $\pi_o P_T = 10^{10}$. These values correspond to seed
9 sets of 0.4 and 1 , respectively, for a completely outcrossing population. In the figures, we use
10 a value of $\pi_o P_T = 1.5$ for moderate pollen limitation, corresponding to a seed set of 0.78 in a
11 completely outcrossing population, which is representative of realistic values observed in
12 natural populations (Knight et al. 2005).

13 In the full genetic model, we examined the spread of a rare modifier allele that increased
14 or decreased the selfing rate compared to the resident population (see Porcher and Lande 2005
15 for details). Because we were interested in the accuracy of the approximation when the selfing
16 rate evolves by small steps, we considered a rare modifier that increased or decreased selfing
17 by 10^{-6} . The modifier allele was introduced at an initial frequency of 10^{-8} in a resident
18 population at mutation-selection equilibrium for lethals. The modifier genotypes were initially
19 at frequencies expected for a population with inbreeding coefficient $f = \bar{r}/(2 - \bar{r})$ (Wright
20 1921, 1969) and in linkage and identity equilibrium with lethal alleles. The recursion
21 equations were numerically iterated for 2,000 generations to detect successful invasion of the
22 modifier of the selfing rate. We verified that if the resident population is initially not at a
23 stable equilibrium selfing rate, a modifier allele causing a small change in the selfing rate
24 toward the equilibrium eventually becomes fixed.

25

1 RESULTS AND DISCUSSION

2 The approximation produces relatively accurate equilibrium selfing rates under low to
3 moderate genomic rates of mutation to lethals (Fig. 2A,D and, to a lesser extent, B,E) or with
4 nearly additive, mildly deleterious mutations (Fig. S2). We checked that with no inbreeding
5 depression, $U = 0$, both models predict identical equilibrium selfing rates. For example, with
6 no pollen limitation, $T(r) = 1$, equation (1) simplifies to $\delta_e(\bar{r}) = 1/2[1 - \pi(1 - \bar{r})]$ and the
7 evolutionarily stable selfing rate is $r^* = 1 - \pi$ (Holsinger 1991). With low inbreeding
8 depression, i.e. moderate genomic mutation rate to lethals ($U = 0.02$) or mildly deleterious
9 mutations, and no pollen limitation, the stable selfing rates are also close to $1 - \pi$ for both
10 models (Fig. 2A and Fig. S2A-C). As expected, higher pollen limitation generally favors
11 larger stable selfing rates but again the approximation is relatively accurate with moderate
12 mutation rates (Fig. 2D and Fig. S2D-E).

13 With higher genomic mutation rates to lethals, $U = 0.2$ and $U = 1$, the equilibria
14 predicted by the approximation can differ greatly from those of the full genetic model (Fig. 2)
15 and the discrepancy between the two models increases as U increases. For $U = 0.2$, the
16 predictions of the approximation agree reasonably well with those of the full model for
17 limited pollen discounting, especially with pollen limitation (Fig. 2B,E), but the discrepancy
18 between the models increases with more intermediate equilibrium selfing rates, which are
19 obtained in this case with increasing pollen discounting. For low pollen limitation and high
20 pollen discounting the full model predicts mixed mating when the approximation predicts
21 complete outcrossing (Fig. 2B,E). With a very high genomic mutation rate to lethals, $U = 1$,
22 the approximation becomes completely inaccurate (Fig. 2C,F), predicting that the only
23 evolutionarily stable mating system is complete outcrossing (and also complete selfing in the
24 case of no pollen discounting), because the genetic inbreeding depression usually exceeds the
25 constraint function (Fig. 1C). In contrast, the full genetic model predicts a number of

1 evolutionarily stable intermediate selfing rates, most of which are close to 1 and depend little
2 on pollen discounting and pollen limitation (see Porcher and Lande 2005).

3 A discrepancy between the full genetic model and the approximation is also observed,
4 although to a lesser extent, with high mutation rates to mildly deleterious mutations and
5 moderate pollen limitation ($U = 1$, Fig. S2F). Here, the full genetic model sometimes predict
6 complete selfing when the approximation predicts mixed mating systems with a large selfing
7 rate ($r > 0.6$). The combination of both types of mutations is therefore likely to exacerbate the
8 difference between both models. This was not tested here, because the Kondrashov model
9 with more than one mutation type is computationally demanding. Instead, we modeled the
10 combined effects of nearly recessive, highly deleterious mutations and nearly additive, mildly
11 deleterious mutations by adding a constant background inbreeding depression ($d = 0.25$) to
12 the Kondrashov model with lethals. The results remain qualitatively the same, with larger
13 discrepancies under higher mutation rates to lethals (Fig. 2G-L), but the inability of the
14 approximation to predict mixed mating appears at lower genomic mutation rates, as expected
15 (e.g. $U = 0.02$, Fig. 2J).

16 The discrepancy between the approximation and the full genetic model is caused by
17 genotypic associations between alleles at the modifier locus and the genetic basis of
18 inbreeding depression (Holsinger 1988; Charlesworth et al. 1990; Uyenoyama and Waller
19 1991a,c). In a partially selfing population, rare genotypes with a modified selfing rate may
20 differ from the resident population in their average history of inbreeding, which impacts their
21 associated genetic load (or mean number of recessive deleterious alleles), whereas the
22 approximation assumes identical genetic load regardless of the genotype at the modifier locus.
23 For example, when the modifier allele is rare, plants homozygous for the modifier are initially
24 produced mostly by selfing and therefore partially purged of recessive deleterious alleles (Fig.
25 1D-F). Extensive simulation showed that genetic associations between a modifier of selfing

1 and recessive lethal mutations build up over a few dozen generations. As a result, a modifier
2 allele that eventually invades and becomes fixed may initially decrease in frequency (Schultz
3 and Willis 1995). Thus the simulations were run for 2,000 generations to detect successful
4 invasion.

5 Differential purging of the load associated with modifier genotypes is transient; for a
6 modifier of small effect destined for fixation the homozygous modifier gains genetic load as it
7 becomes common (Schultz and Willis 1995). The initial differential purging for a rare
8 modifier depends little on the magnitude of the modifier effect, and also occurs for (neutral)
9 mutations with no impact on the selfing rate (Charlesworth 1991). However, it can strongly
10 influence the fate of mating system modifiers even with very small effect, and alter the
11 evolutionarily stable selfing rate and inbreeding depression by shifting the equilibrium selfing
12 rate, especially when inbreeding depression is caused by nearly recessive lethals. Overall, this
13 promotes enhancers of selfing under broader conditions than expected with the
14 approximation, as demonstrated in earlier studies (Lande and Schemske 1985; Charlesworth
15 et al. 1990; Uyenoyama and Waller 1991c; Schultz and Willis 1995). We have shown here
16 that the joint evolution of inbreeding depression and mating system, combined with common
17 mechanisms of pollination ecology, also favors mixed mating over complete outcrossing more
18 often than predicted by the approximation.

19

20 *Conclusion* – We show that the accuracy of the approximation depends primarily on the
21 genomic mutation rate to lethals, for which few estimates are available. The best estimates,
22 from *Drosophila*, indicate that $U = 0.01$ – 0.03 per genome per generation (Fry et al. 1999;
23 Charlesworth et al. 2004). Evidence suggests that annual plants may have comparable values
24 of U (e.g. Jürgens et al. 1991 in *Arabidopsis thaliana*). For such species, the approximation is
25 accurate. However, mutation rates to lethals may be an order of magnitude higher ($U = 0.2$) in

1 large perennial or partially asexual species due to mutation accumulation in somatic cell
2 divisions, as plants lack a separate germ line (Lande et al. 1994 and references therein;
3 Remington and O'Malley 2000). The approximation also tends to underestimate stable selfing
4 rates under high mutation rates to mildly deleterious, nearly additive alleles, although less so
5 than with lethals. High mutation rates to mildly deleterious alleles, sometimes greater than 1,
6 may also occur in multicellular organisms (Halligan and Keightley 2009). With high U the
7 approximation greatly underestimates the evolutionarily stable selfing rates, so that explicit
8 genetic models of both selfing rate and inbreeding depression are required for a
9 comprehensive understanding of mating system evolution.

10

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14

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- 13

1 FIGURE CAPTIONS

2 Figure 1. Inbreeding depression, constraint function and genetic load (mean number of
 3 deleterious alleles) when inbreeding depression is caused by nearly recessive lethals. The
 4 three variables are plotted as a function of the selfing rate for different values of U , the
 5 genomic mutation rate. A-C: Genetic inbreeding depression without (thick solid grey line) or
 6 with (thick dashed grey line) background inbreeding depression ($d = 0.25$) and constraint
 7 function (black lines) for different levels of pollen limitation and pollen discounting, with
 8 stable (squares) and unstable (circles) intermediate equilibria predicted at their intersections.
 9 Low and moderate pollen limitation (solid and dashed black lines respectively), $\pi_o P_T = 4$ and
 10 $\pi_o P_T = 1.5$, correspond to seed set of a completely outcrossing plant of 0.98 and 0.78. The
 11 upper pair of black solid and dashed lines correspond to low pollen discounting ($\pi = 0.1$), and
 12 the lower pair to high pollen discounting ($\pi = 0.9$). D-F: Genetic load in genotypes at a
 13 modifier increasing the selfing rate, when the modifier allele is rare, but after associations
 14 with lethals have built up (resident, solid line; heterozygote, dotted line; homozygous
 15 modifier, dashed line). Figures D-F do not include background inbreeding depression ($d = 0$).

16

17 Figure 2. Equilibrium selfing rates predicted by the approximation vs. the full genetic model,
 18 when inbreeding depression is caused by nearly recessive lethals, under different levels of
 19 pollen discounting, pollen limitation and background inbreeding depression. Stable or
 20 unstable equilibria are indicated by squares or circles. Only intermediate equilibria are shown.
 21 Points on the x -axis correspond to intermediate equilibria predicted by the full genetic model
 22 that do not exist under the approximation. Complete outcrossing and complete selfing are
 23 always equilibria; their stability depends on the existence of intermediate equilibria. When
 24 there is a single stable intermediate selfing rate, $r = 0$ and $r = 1$ are unstable; when the stable
 25 intermediate selfing rate coexists with a lower unstable intermediate selfing rate, $r = 0$ is

- 1 stable and $r = 1$ is unstable. Grey levels indicate pollen discounting values. Levels of pollen
- 2 limitation as in Figure 1.

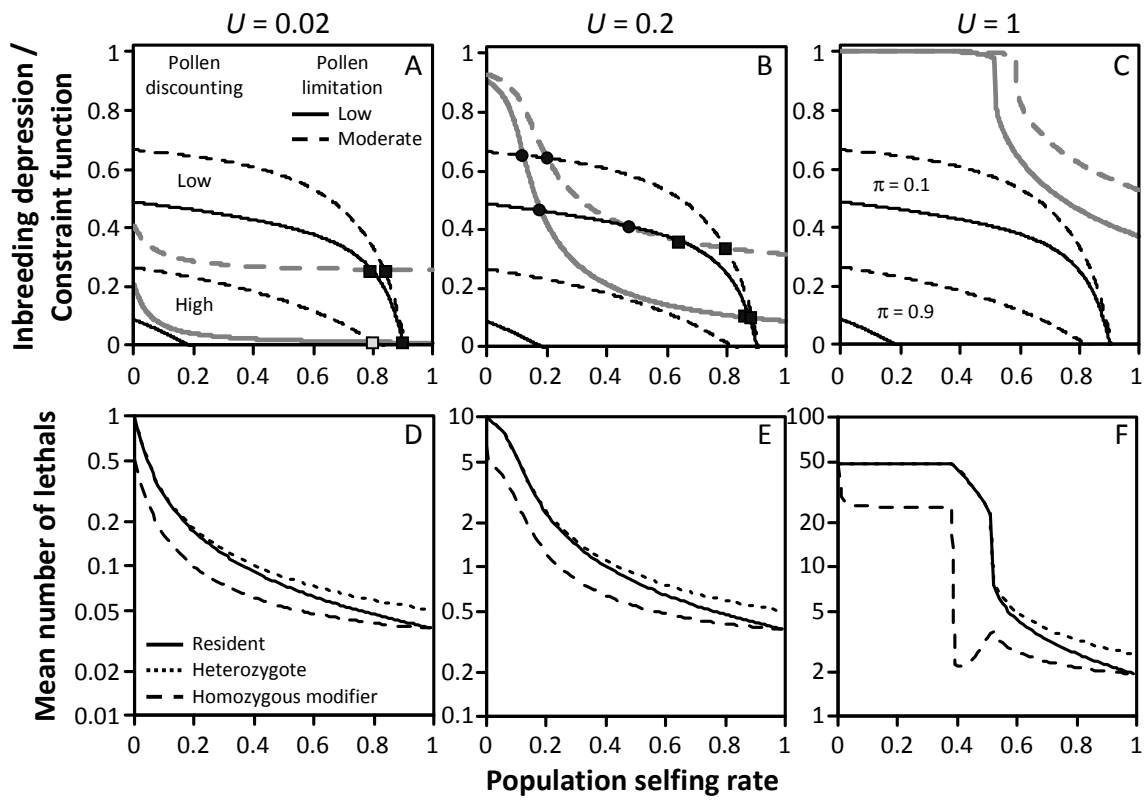


Figure 1

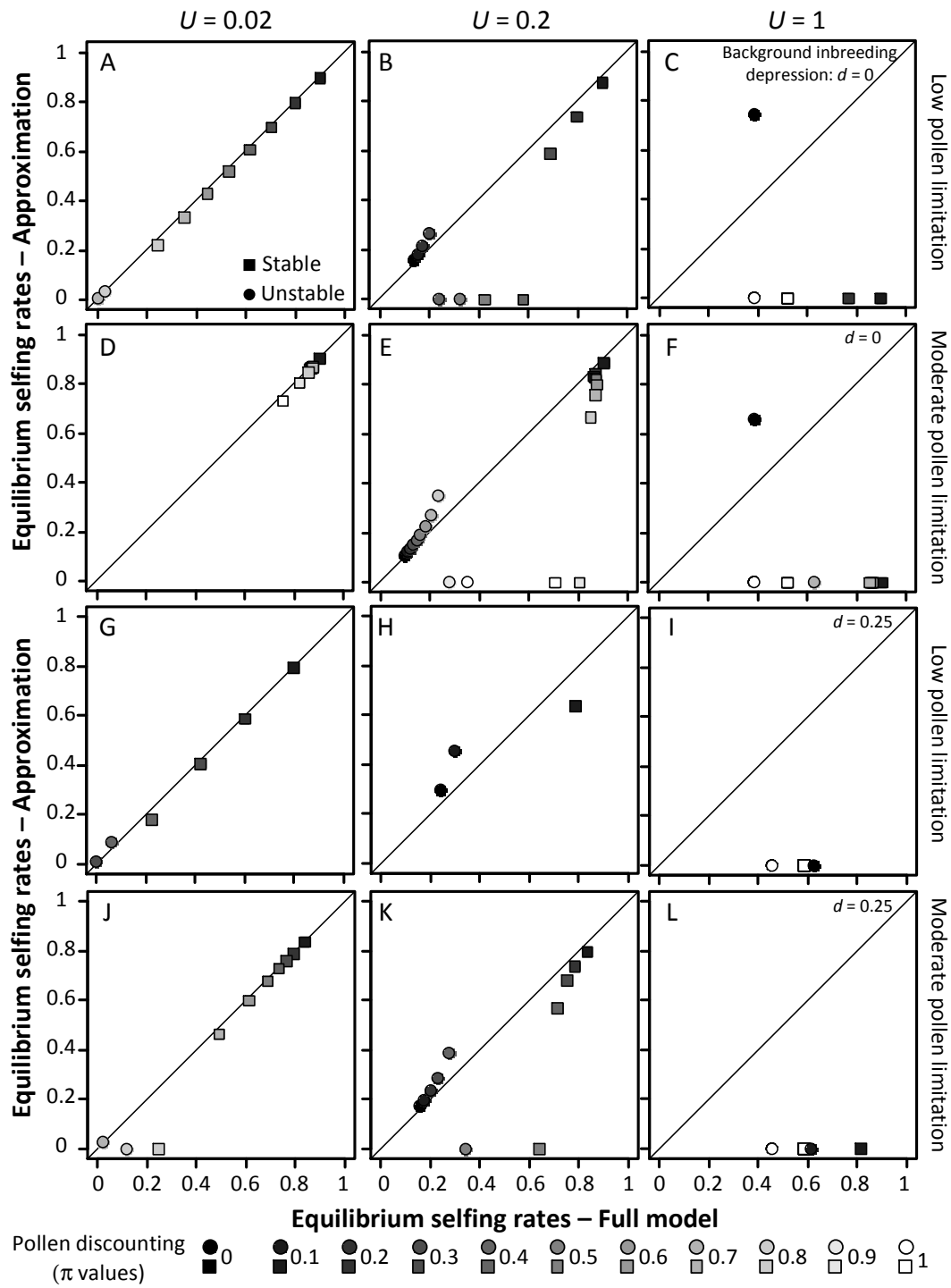


Figure 2