SELECTION FOR POLLEN COMPETITIVE ABILITY IN MIXED MATING SYSTEMS

ABSTRACT

Co-expression of genes in plant sporophytes and gametophytes allows correlated gametic and sporophytic selection. Theory predicts that, under outcrossing, an allele conferring greater pollen competitive ability should fix within a population unless antagonistic pleiotropy with the sporophyte stage is strong. However, under strong selfing, pollen competitiveness is immaterial as superior and inferior competitors are deposited on opposite stigmas, producing assortative competition. Because many plant species have mixed-mating systems, selfing should be critical in the spread and maintenance of pollen-expressed genes affecting competitiveness. We present two one-locus, two-allele population genetic models for the evolution of a locus controlling pleiotropic antagonism between pollen competitiveness and diploid fitness. Analytical solutions provide minimum and maximum selfing rates allowing invasion of alleles with greater diploid and haploid fitness respectively. Further, polymorphism is only maintained when diploid selection is recessive. Fixation of the allele conferring greater pollen competitiveness may be prevented, even with weak sporophytic counter-selection, with sufficiently high selfing. Finally, selfing expands and limits the range of haploid-diploid selection coefficients allowing polymorphism, depending on dominance and selfing mode.

Key Words: Assortative competition, gametic selection, sporophytic selection, population genetics, mixed mating, genetic correlation

INTRODUCTION

Over 7000 genes are expressed in male gametophytes—pollen grains and tubes and the sperm they transmit—as they compete in the pistil for ovules (Page and Grossniklaus 2002; Honys and Twell 2003; Rutley and Twell 2015). Upwards of 60% of known plant genes are expressed in both the gametophyte and sporophyte (Borges et al. 2009; Arunkumar et al. 2013). For example, over 100 cases of co-expression in pollen tubes and root hairs have been identified in tobacco (Hadif et al. 2012). This high degree of co-expression presents opportunity for pollen selection to affect sporophyte evolution, and *vice versa*. Haldane (1932) recognized this potential, writing "Clearly a higher plant species is at the mercy of its pollen grains. A gene which greatly accelerates pollen tube growth will spread through a species even if it causes moderately disadvantageous changes in the adult plant." Simply, genes conferring an advantage in the gametophyte should fix unless there is strong antagonistic pleiotropy with sporophyte fitness.

Selection should be strong on alleles with concordant impacts on both gametophyte and sporophyte stages. Deleterious recessive mutations, which are masked in heterozygous sporophytes, are fully exposed to selection in haploid gametophytes. This facilitates purging, diminishing inbreeding depression (Charlesworth and Charlesworth 1992). Some have suggested that alleles promoting pollen competition will increase offspring quality: large stigmatic pollen loads lead to intense competition in the style, favouring genetically superior gametophytes, which contribute their genes to the seed (Mulcahy and Mulcahy 1987; Winsor et al. 1987; Winsor et al. 2000; but see Baskin and Baskin 2015; Pélabon et al. 2016). Walsh and Charlesworth (1992) found that when fitness effects on the gametophyte and sporophyte are concordant, selection will quickly eliminate deleterious mutations and drive favourable ones to

46 fixation. But, as Haldane suggested, polymorphism may be maintained if increased pollen
47 competitive ability is counterbalanced by costs to the sporophyte.

48 Ploidally antagonistic selection has been considered previously (Ewing 1977). Immler,
49 Arnqvist and Otto (2012) explored the maintenance of genetic variation under discordant
50 selection between haploid and diploid phases, as well as under sex-specific selection.
51 Considering an autosomal gene, they demonstrated polymorphism is most easily maintained
52 under negative ploidy-by-sex interactions, under which sex-specific selection acts in opposite
53 directions in haploids and diploids. They conclude that polymorphism can be maintained, even in
54 the absence of sex differences in selection, when selection is opposing between sporophytic and
55 gametophytic stages.

56 High rates of self-pollination diminish the advantage of pollen competitiveness due to
57 assortative competition (Mazer et al. 2010). Imagine a one locus system, with allele C_g
58 conferring a competitive advantage to pollen (i.e., in the gametophytic phase) and the alternate
59 allele C_s advantages in the sporophytic phase. When a C_gC_g homozygote self-pollinates, the C_g
60 allele gets passed to the offspring by necessity. On the opposite homozygote, the C_s allele is
61 likewise successful by necessity, despite its competitive inferiority. The competitive advantage
62 of C_g- over C_s-bearing pollen is realized when heterozygotes self-pollinate, but because selfing
63 reduces heterozygote frequency, over time there are increasingly fewer opportunities for C_g to
64 exercise its superiority. Thus, with obligate selfing, the C_s allele gains refuge from competition
65 and quickly goes to fixation due to its higher sporophytic fitness. Consistent with these
66 predictions, Mazer et al. (2018) demonstrated faster pollen tube growth rates in the
67 predominantly outcrossing *Clarkia unguiculate* (Onagraceae) compared to the facultatively

68 selfing *C. exilis*. A similar result was found for selfing and outcrossing populations of *Clarkia*
69 *tembloriensis* (Smith-Huerta 1996).

70 About 40% of plant species have mixed-mating systems: individuals receive mixtures of
71 self and outcross pollen (Schemske and Lande 1985; Goodwillie et al. 2005). Of the 155 studies
72 of mixed-mating systems in plants reviewed by Barrett and Eckert (2012), two-thirds report
73 selfing rates in excess of 20%. In Whitehead et al. (2018), it was found that 63% of 105
74 surveyed species had at least one population with a mixed-mating system. How do intermediate
75 selfing rates influence the fate of a new mutation increasing pollen competitiveness at the
76 expense of the sporophyte?

77 An important paper by Jordan and Connallon (2014) considered the impact of self-
78 fertilization on sexual conflict in hermaphrodites. They found that selfing narrows invasion
79 conditions of new alleles conferring male-benefit in the haploid phase if they impose a cost on
80 diploid female function. Their model considered the case in which gamete quality is determined
81 by parental genotype. In this situation, a C_g-bearing gamete from a homozygous adult differs
82 from a C_g-bearing gamete produced by a heterozygote, weakening the gamete haplotype-
83 phenotype correspondence. Gene expression in animal sperm is limited (Parker and Begon
84 1993), and so it is reasonable to assume genetic paternal effects on sperm quality for these
85 species. In plants, adult diploid condition can affect pollen size and quality (Young and Stanton
86 1990; Mazer and Gorchov 1996; Galloway 2001; Smith-Huerta et al. 2007). Pollen size, which
87 could well be mediated by genetically influenced resource allocation in the sporophyte, readily
88 responds to artificial selection (Sarkissian and Harder 2001; McCallum and Chang 2016).

89 We explore a different situation, in which pollen competitiveness is affected by genes
90 expressed directly in the male gametophyte. Here one may expect stronger selection responses

91 due to stronger haplotype-phenotype correspondence. In our one-locus model, allele C_g increases
92 pollen competitive ability at the expense of sporophyte fitness. Analytical solutions show there
93 are maximum and minimum selfing rates allowing invasion of C_g and C_s alleles, respectively,
94 and that stable polymorphism is possible only when C_g is recessive. Further analyses show that
95 as selfing rate increases, C_g's competitive advantage is negated by increasingly smaller diploid
96 cost.

97 **METHODS**

98 ***The models***

99 Departures from Hardy-Weinberg equilibrium via selfing necessitate that selection be modelled
100 in terms of genotype frequencies (Crow and Kimura 1970). We refer to the frequencies of the
101 C_gC_g, C_gC_s and C_sC_s genotypes as X_0, X_1 and X_2, respectively, where subscripts denote the
102 number of C_s alleles. Allele frequencies are p and q for C_g and C_s, respectively.

103 Assume a pleiotropic effect by which the C_g allele increases pollen competitive ability
104 but decreases the number of pollen grains and ovules that the diploid plant contributes to the
105 gamete pool, either by reduced survival or lower flower production. The C_s allele is favoured
106 through both sex functions in the diploid stage, disfavoured in haploid pollen and has no effect
107 on ovules. Fitness of sporophyte C_sC_s is $W_2 = 1$, and that of C_gC_g is $W_0 = 1\text{-}s$, while the
108 heterozygote C_gC_s is $W_1 = 1\text{-}hs$, where h is the degree of dominance for fitness. As selection may
109 act either through survival or fertility, we assume a common dominance coefficient for male and
110 female function. (For a discussion of the effects of sex-specific dominance, see Appendix A).
111 The absolute competitive ability of pollen bearing the C_g allele is 1 and that of pollen bearing the
112 C_s allele is $1\text{-}t$. All individual plants are expected to have many flowers. Population size is
113 effectively infinite.

The level of self-pollination in the model depends on *r*, the proportion of pollen allocated to self-mating, which reflects the potential rate of self-fertilization. Absent selection, *r* equals the proportion of zygotes that are produced by self-pollination, *i.e.*, the realized selfing rate. As shown below, potential and realized selfing rates can differ when selection acts on the gametophyte. For sake of brevity, *r* is hereafter referred to as selfing rate. We assume all plants have the same *r* value. We model two selfing forms: fixed selfing and mass-action selfing, defined below. The models we present assume haploid genetic control over pollen competitive ability. As we present our results, we will for comparison also present results using models by Jordan and Connallon (2014; see Appendix B), which assume diploid control.

FIXED SELFING

The fixed selfing model echoes the biology of species such as *Impatiens* and *Viola*, where cleistogamous flowers are obligate selfers, and chastogamous flowers outcross (Schemske 1978, Winn and Moriuchi 2009). In this model, proportion *r* of flowers on each plant is dedicated to selfing while 1-*r* of flowers is allocated to outcrossing. Thus, a stigma receives either only self-pollen or only outcross-pollen. Selection for pollen competitiveness occurs on all outcrossing flowers, but among selfing flowers, occurs only on heterozygotes. Our recursion equations for genotype frequencies consider selection during the diploid and haploid stages in separate steps. After diploid selection, diploid genotype frequencies are:

$$x_0 = \frac{(1-s)X_0}{\bar{W}} \tag{1a}$$

$$x_1 = \frac{(1-hs)X_1}{\bar{W}} \tag{1b}$$

$$x_2 = \frac{X_2}{\bar{W}} \tag{1c}$$

where $\bar{W}$ is the mean diploid fitness:

$$\bar{W} = (1-s)X_0 + (1-hs)X_1 + X_2. \quad (2)$$

After mating and haploid selection, offspring genotype frequencies are

$$X_0' = r\left[x_0 + \tfrac{1}{2}x_1\left(\tfrac{1}{2-t}\right)\right] + (1-r)\left[\left(x_0 + \tfrac{1}{2}x_1\right)\alpha\right] \quad (3a)$$

$$X_1' = r\left[\tfrac{1}{2}x_1\right] + (1-r)\left[x_0(1-\alpha) + \tfrac{1}{2}x_1 + x_2\alpha\right] \quad (3b)$$

$$X_2' = r\left[x_2 + \tfrac{1}{2}x_1\left(\tfrac{1-t}{2-t}\right)\right] + (1-r)\left[\left(x_2 + \tfrac{1}{2}x_1\right)(1-\alpha)\right] \quad (3c)$$

where α reflects the relative competitiveness of C_g-bearing pollen as a function of the absolute competitiveness conferred by the C_g allele and the frequency of the C_g allele in the pollen pool as a result of genotype frequency following selection:

$$\alpha = \frac{x_0 + \frac{1}{2}x_1}{x_0 + \frac{1}{2}x_1(2-t) + x_2(1-t)}. \quad (4)$$

It follows that the relative competitiveness of C_s-bearing pollen is (1- α).

To understand Equations (3a-c), consider separately the offspring produced on selfing (*r)* and outcrossing (1-*r*) flowers. Under selfing, competition among pollen tubes carrying opposite alleles only occurs within heterozygote pistils. Assuming heterozygotes produce C_g and C_s pollen in equal numbers, ½ of their offspring will likewise be heterozygous, with the remaining offspring divided between C_gC_g and C_sC_s homozygotes in proportions of $\left(\frac{1}{2-t}\right)$ and $\left(\frac{1-t}{2-t}\right)$ (Appendix C). We assume each selfing flower produces enough pollen to fertilise its ovules, such that only female diploid fitness terms, and not α (*i.e.*, male diploid fitness terms), are included. Simply, the number of offspring produced via selfing is limited by seed production, not pollen production. Offspring produced through outcrossing will be a function of both female and

male diploid fitness, as well as allelic differences in pollen competitive ability, specified by α. For simplicity, we make no provision for inbreeding depression; increasing failure rate of selfed offspring has the same effect as reducing the basic selfing rate (see Jordan and Connallon 2014).

Mass-action selfing

Mass-action selfing (Holsinger 1991) echoes more general modes of mixed-mating. Here *r* still denotes the proportion of pollen individuals allocate to selfing, but in this case all stigmas receive a mix of self- and outcross-pollen, resulting in inter-allelic competition for all ovules. Under this scenario, the amount of self-pollen received by a stigma is a function of two factors, one being *r*, and the other being the quantity of pollen produced by the individual relative to that it receives through outcrossing. Thus, the true selfing rate is dependent on genotype frequency. We make no provisions for pollen discounting here but consider this elaboration in Appendix D.

Assuming diploid selection occurs according to Equations (1a-c), we arrive at the following genotype frequencies after mating and haploid selection:

$$X_0' = x_0\left[\frac{rW_0 + (1-r)\left(x_0 + \frac{1}{2}x_1\right)}{P_0}\right] + \frac{1}{2}x_1\left[\frac{r\frac{1}{2}W_1 + (1-r)\left(x_0 + \frac{1}{2}x_1\right)}{P_1}\right] \tag{5a}$$

$$X_1' = \frac{1}{2}x_1 + x_0\left[\frac{(1-r)\left(x_2 + \frac{1}{2}x_1\right)(1-t)}{P_0}\right] + x_2\left[\frac{(1-r)\left(x_0 + \frac{1}{2}x_1\right)}{P_2}\right] \tag{5b}$$

$$X_2' = x_2\left[\frac{rW_2(1-t) + (1-r)\left(x_2 + \frac{1}{2}x_1\right)(1-t)}{P_2}\right] + \frac{1}{2}x_1\left[\frac{r\frac{1}{2}W_1(1-t) + (1-r)\left(x_2 + \frac{1}{2}x_1\right)(1-t)}{P_1}\right] \tag{5c}$$

165 where P_0, P_1 and P_2 give the total pollen received by X_0, X_1 and X_2 individuals respectively and

166 are defined as:

$$P_0 = rW_0 + (1-r)\left(x_0 + \tfrac{1}{2}x_1(2-t) + x_2(1-t)\right) \tag{6a}$$

$$P_1 = r\frac{1}{2}W_1(2-t) + (1-r)\left(x_0 + \tfrac{1}{2}x_1(2-t) + x_2(1-t)\right) \tag{6b}$$

$$P_2 = rW_2(1-t) + (1-r)\left(x_0 + \tfrac{1}{2}x_1(2-t) + x_2(1-t)\right). \tag{6c}$$

167 In Eq. 5a, the two terms represent C_gC_g offspring seed produced by C_gC_g and C_gC_s plants with

168 post-diploid selection frequencies of x_0 and x_1. All ovules on the homozygote carry C_g, whereas

169 on heterozygotes only half do. The terms inside the square brackets are the probability that an

170 ovule receives C_g-bearing sperm, which depends on the amount of successful C_g pollen

171 (numerator) divided by the total amount of pollen arriving at the stigma (denominator). Eq. 5c

172 follows similar logic for C_sC_s offspring. Turning to Eq. 5b, the three terms represent C_gC_s

173 offspring produced by C_gC_s, C_gC_g and C_sC_s plants, respectively. Half of all seed produced by

174 C_gC_s individuals are also heterozygotes. The proportion of heterozygotes produced by C_gC_g

175 individuals are a function of the relative abundance and competitiveness of C_s pollen (numerator)

176 compared to the total pollen arriving on C_gC_g stigmas. This proportion is given by the term

177 inside the first square bracket. C_gC_s offspring from C_sC_s individuals follow identical logic but for

178 C_g pollen.

179 **Software and computation**

180 All analytical analyses were derived using Wolfram Mathematica 11.0.1.0. To find conditions

181 for stable polymorphism, we derived leading eigenvalues for Jacobian Matrices using genotype

182 recursions for gametophytic control (Eqs. 3a-c, 5a-c) and sporophytic control (Eqs. B9-B11,

183 Appendix B) of pollen competitiveness and determined the conditions that allowed invasion at a
184 boundary by solving for parameters producing a leading eigenvalue of absolute value greater
185 than 1. Invasion analyses were performed for two boundaries: the X_0 boundary, at which the C_s
186 allele appears in a population fixed for the C_g allele (i.e., $p = 1$), and the X_2 boundary, at which
187 the C_g allele appears in a population fixed for the C_s allele (i.e., $p = 0$). Code for analytical
188 analyses is provided in the online supplemental materials.

189 To find expressions for equilibrium allele frequencies, we generated power series
190 expansions (assuming weak selection for simplification) for expressions giving the single-
191 generation change in genotype frequencies. We then solved for the equilibrium by finding the p
192 value yielding zero change. Predicted equilibrium frequencies were verified numerically.
193 Numerical methods and results are presented in Appendix E.

194 **RESULTS**

195 **Analytical invasion conditions**

196 We explored the impact of selfing rate on invasion potential for both C_g and C_s when rare. For
197 fixed selfing, analytical conditions for invasion at the X_0 and X_2 boundaries are derived using
198 Equations (3a-c). Likewise, analytical conditions for mass-action selfing use Equations (5a-c).
199 For comparison with diploid control models (Jordan and Connallon 2014) and, in the case of
200 mass-action selfing, to produce tractable solutions, we assume weak selection (i.e., $0 < s, t << 1$),
201 though we do find good agreement between invasion conditions predicted under fixed selfing
202 both with and without weak selection (Appendix E).

203 **Fixed selfing**

204 Under fixed selfing, boundary selfing rates permitting invasion of the C_g and C_s alleles,
205 respectively, are as follows:

$$r < \frac{t+2hs}{s+t-2hs} \tag{7a}$$

$$r > \frac{t+2s(1-h)}{t+s(1+2h)} \tag{7b}$$

These analytical solutions are visualised in Figure (1a-c). Under random mating (i.e., $r = 0$), and when either fully dominant or recessive ($h = 0$ or 1), the C_g allele invades and goes to fixation if $s/t < 0.5$ (*i.e.*, when the haploid competitive benefit is more than twice the diploid fitness cost). When diploid fitness effects are additive ($h = 0.5$), fixation occurs even as s/t approaches 1.0. C_g wins under random mating as the C_s allele has no refuge from competition. Under complete selfing ($r = 1$), C_g never invades. Pollen competition occurs only on heterozygotes, and since selfing reduces heterozygote frequencies, opportunities for C_g-bearing pollen to outcompete C_s effectively vanish. As C_s confers higher sporophyte fitness in the homozygous state, it increases when rare.

The analytical solutions indicate that polymorphism can be maintained in mixed-mating systems ($0 < r < 1$) with fixed selfing only if the deleterious effect of the C_g allele in the diploid phase is recessive ($h < 0.5$) (Figures 1a-c, 2). When completely recessive ($h = 0$), there is a range of selfing rates in which both alleles can invade, implying protected polymorphism. The C_g allele invades because, when rare, it occurs exclusively in heterozygotes, where its negative effect on diploid fitness is masked from selection and moderate selfing allow opportunities to outcompete C_s-bearing pollen for ovules on heterozygotes. Within this range of selfing rates, the C_s allele also increases when rare because, 1) heterozygotes have higher relative fitness than C_gC_g homozygotes and 2) selfing reduces exposure of C_s pollen to competition with superior C_g pollen.

Additive fitness effects ($h = 0.5$) largely prohibit polymorphism (Figures 1b, 2). When $h = 0.5$, the critical r values for invasion (Eq. 7a-b) reduce to approximately $1 - \frac{s}{t}$ for both alleles.

227 As h increases, the relative fitness of heterozygotes decreases. It then follows that the initial
228 advantage enjoyed by both alleles when rare also diminishes. To invade, C_g requires low r values
229 to win enough contests to offset lower heterozygote fitness. C_s will require higher r values to
230 avoid competitive losses and produce enough high-fitness X_2 homozygotes to offset lower fitness
231 of heterozygotes.

232 When the diploid fitness disadvantage of the C_g allele is dominant (h = 1), there is a range
233 of selfing rates that prohibit either allele from invading (Figures 1c, 2). For a given value of s,
234 the maximum selfing rate allowing C_g invasion is lowered because its adverse effect on
235 sporophyte fitness is fully expressed by heterozygotes. Oppositely, the critical r for C_s invasion
236 increases. When rare, the positive diploid fitness effects of the C_s allele are concealed in
237 heterozygotes. Only very high selfing rates can produce C_s homozygotes quickly enough to
238 provide sufficient refuge from competition, allowing C_s to spread.

239 ***Mass-action selfing***

240 Considering mass-action selfing, the maximum and minimum r values allowing invasion of the
241 C_g and C_s alleles can be solved analytically. However, even under weak selection the expressions
242 are complex and difficult to interpret biologically; these are presented in Appendix F and are
243 visualised in Figure (1d-f).

244 While the expressions for critical r values are complex, similarly derived expressions for
245 critical diploid selection s values can be used to understand how selfing rate affects invasion
246 success. Expressions for maximum and minimum s values permitting invasion of C_g and C_s
247 alleles respectively are given below:

$$s < \frac{(-2+r+r^2)t}{(2h(r-1)-r)(r-2)(1+r)} \tag{8a}$$

$$s > \frac{(-2+r+r^2)t}{(2+2h(r-1)-r)(r-2)(1+r)}. \quad (8b)$$

Taking the partial derivative of Eqs. 8a and 8b with respect to *r* lends insight into how these critical *s* values change in response to selfing. (For a discussion of these partial derivative expressions, see Appendix G). These show an increase in selfing rate always decreases the maximum and minimum *s* values permitting invasion of *Cg* and *Cs* alleles respectively (Figure 1d-f). It then follows that increased selfing contracts the parameter space allowing invasion of an allele conferring a benefit to pollen competitiveness at the expense of diploid fitness.

Comparing invasion conditions for fixed and mass-action selfing

Invasion conditions for the two selfing modes were qualitatively similar, with modest quantitative differences. We compared sensitivity of the minimum and maximum *s* values permitting invasion of C_s and C_g alleles to increases in *r* for both systems. (Partial derivative expressions for fixed selfing are also provided in Appendix G). For a given set of *h, s* and *t* values, *r* values allowing C_g and C_s invasion are slightly lower under mass-action selfing relative to those of fixed-selfing (Figure 2), narrowing the permissible parameter space. Thus, under mass-action selfing, the C_g allele can persist at higher selfing rates. Additionally, the range of *r* values permitting polymorphism (when $h < 0.5$) or unstable equilibrium (when $h > 0.5$) contracts under mass-action selfing, which is consistent with narrowed parameter space regions for polymorphism and unstable equilibrium under mass-action selfing observed in Figure 2.

Under fixed selfing, male diploid fitness (pollen quantity) is moot since all flowers of each genotype are assumed to produce enough pollen to fertilise their ovules. Under mass-action selfing, the quantity of pollen produced by an individual affects its realized fertilisation success through self-pollen, as each stigma can receive a mixture of C_g- and C_s- bearing pollen, restricting the competition refuge for C_s. While each C_g-bearing grain has a greater chance of

success, this advantage is partially countered by lower pollen production in C_g homozygotes. The different impacts on male function shift the invasion boundary upward under mass-action selfing. For example, when $h = 0$, $s = 0.01$ and $t = 0.04$ (visualised as $s/t = 0.25$ on Figure 1), the maximum selfing rate allowing the C_g allele to invade increases from roughly $r = 0.8$ to $r = 0.84$. Likewise, the minimum selfing rate allowing C_s to invade increases from $r = 0.67$ to $r = 0.75$.

Fixation and protected polymorphism

Having established invasion conditions for the C_g and C_s alleles, this section explores their equilibrium frequencies. We first present analytical solutions to the recursion equations (Eqns. 3a-c, 5a-c) assuming weak selection ($0 < s, t << 1$). We then highlight the difference in outcomes when pollen competitiveness is under gametophyte genetic control, as Haldane speculated, versus sporophyte control (seen in Jordan and Connallon 2014). Under fixed selfing, the equilibrium value ($\hat{p}$) of the C_g allele is given as:

$$\hat{p} = \text{Min}\left[1, \text{Max}\left[0, \frac{1}{2} + \frac{t(1-r) - s}{(2\,(-1\,+\,2\,h)(-1\,+\,r)s)}\right]\right]. \tag{10}$$

When C_g is recessive ($h < 0.5$) and mating is mixed ($0 < r < 1$), the denominator of the far-right term is always positive. Whether $\hat{p}$ falls above or below 0.5 then depends on the sign of the numerator. If $r < 1 - s/t$, then $\hat{p}$ will fall above 0.5 but fall below if the inverse is true. Simply, the higher the selfing rate (r) the higher the diploid cost (s) needed to prevent C_g fixation, which is implied by a $\hat{p}$ value < 0.5. When C_g is dominant ($h > 0.5$), the above expression gives the repelling equilibrium frequency (above $\hat{p}$ the C_g allele goes to fixation and below is eliminated). When $h > 0.5$ and mating is mixed, the denominator of the far-right term is always negative. Thus, the repelling $\hat{p}$ value falls above 0.5 when the numerator is negative and below when positive. Looking at the effect of selfing rate on $\hat{p}$, the threshold $\hat{p}$ allowing C_g invasion decreases as r decreases, as the numerator will become increasingly positive. When $h = 0.5$, the

292 denominator of the far-right terms goes to zero, putting the whole term to infinity. Threshold
293 selfing rates permitting or preventing C_g invasion are thus given by the sign of infinity, which is
294 determined by if r is greater than or less than $1 - s/t$ respectively.

295 Under mass-action selfing, the equilibrium frequency of the C_g allele is:

$$\hat{p} = \text{Min}\left[1, \text{Max}\left[0, \frac{(2\,h\,(-1+r) - r)(-2+r)(1+r)s + (-1+r)(2+r)t}{2\,(-1+2\,h)\,(-2+r)\,(-1+r)\,(1+r)\,s}\right]\right]. \quad (11)$$

297 When $h < 0.5$, Eqs. 10 and 11 provide the equilibrium frequency of the C_g allele. When $h > 0.5$,
298 these expressions provide the 'repelling' allele frequency. Figure 3 plots the equilibrium
299 frequency of C_g as a function of selfing rate, r, under relatively weak selection. (For a
300 comparison of analytical results to numerically derived frequencies under strong selection, see
301 Appendix E).

302 When the negative diploid effect of C_g is dominant ($h = 1$), high selfing prevents C_g
303 invasion when rare, while low selfing prevents C_s invasion. Under intermediate selfing rates,
304 neither allele can increase when rare (Figure 3c, f). Following the appearance of the C_g allele in a
305 population by mutation, its initial frequency will almost inevitably fall below the repelling
306 frequencies predicted by Eqs. 10 or 11 and thus it will be eliminated.

307 Comparison of Eqs. 10 and 11 reveals that when $0 < h < 0.5$, the equilibrium frequency
308 $\hat{p}$ is higher under mass-action selfing relative to fixed selfing; however, when $h > 0.5$, the inverse
309 is true (for derivation, see online supplemental materials). As suggested by invasion conditions,
310 under mass-action selfing, minimum and maximum selfing rates allowing invasion of C_g and C_s
311 alleles respectively increase for given h, s and t values (Figure 3d-f). Additionally, parameter
312 space allowing both polymorphism (Figures 3d) and unstable equilibrium (Figures 3f) contracts
313 under mass-action selfing relative to fixed (Figures 3a, 3c).

As is visualised in Figures 1 and 3, invasion conditions and equilibrium allele frequencies under both selfing modes assuming haploid control of pollen competitiveness are qualitatively similar to those derived using models provided in Jordan and Connallon (2014), where competitiveness is under paternal genotype control (for derivation of analytical results, see online supplemental materials; for models and discussion of analytical solutions, see Appendix B). They also found selfing and dominance restrict potential for stable polymorphism and ultimately diminish selection through male function. Our results show, however, that gametophytic control substantially expands the conditions favouring an allele promoting pollen competitiveness. With gametophyte gene expression, pollen phenotype is more strongly correlated with haplotype. Heterozygotes always produce a 50:50 mix of phenotypically and genetically 'strong' and 'weak' pollen competitors. Under sporophytic control, heterozygotes can produce phenotypically all strong ($h = 0$), all weak ($h = 1$), or all intermediate ($h = 0.5$) competitors, despite always producing a 50:50 genetic mix. Further, under gametophytic control, variance in competitive ability between pollen carrying opposite alleles is constant. Under paternal control, variance in competitive ability changes with genotype frequency: increasing heterozygote frequency decreases the difference in mean competitiveness of the two pollen haplotypes. Consequentially, C_g invasion occupies a markedly smaller parameter space when under diploid genetic control (Figure 1). By extension, we see that the C_g allele reaches a lower equilibrium frequency, *i.e.*, invades with more difficulty, for a given selfing rate when it is expressed in the sporophyte rather than the gametophyte (Figure 3).

Returning to Haldane's conjecture that plants are at the mercy of their pollen grains, how strong must sporophyte selection against a pollen-competition allele be to prevent its fixation? The fate of the C_g allele depends on selection strength during the two life stages, which can be

337 considered as a ratio of diploid and haploid selection coefficients, *s/t*. At a given *s/t* ratio,
338 increasing the selfing rate will restrict opportunities for C_g pollen to exercise its superiority,
339 muting the selective advantage. Against this, at any given ratio, Mendelian dominance alters how
340 often the diploid cost is paid. If C_g is recessive ($h = 0$), heterozygotes pay no diploid cost. If
341 dominant ($h = 1$), it masks the C_s benefit and heterozygotes pay full cost; however, since selfing
342 decreases heterozygote frequency, the dominance issue becomes moot. These conditions produce
343 the general outcome that *s*/*t* ratios allowing C_g to invade, and to be maintained in polymorphism,
344 tend to decrease as both *r* and *s* increase (Figure 4).

345 **DISCUSSION**

346 Classical theory, which assumes random mating, predicts an allele conferring an advantage in
347 pollen competitiveness fixes unless a trade-off with sporophyte fitness sufficiently counters this
348 haploid advantage. Our models predict that even moderate selfing can prevent the spread of a
349 pollen-expressed allele that confers competitive superiority (Table 1). Increased selfing increases
350 assortative competition among pollen, restricting opportunity for a competitive allele to exercise
351 its superiority. When homozygotes self completely, they deposit only one pollen haplotype per
352 stigma, so by necessity that haplotype cannot be out-competed by another. Alternate haplotypes
353 compete only on heterozygotes. Further, selfing depresses heterozygote frequency such that the
354 proportion of the pollen pool engaged in competitive contests falls in proportion to the selfing
355 rate.

356 The dominance relationships between the competitive and non-competitive alleles in the
357 diploid stage also influence invasion. When the sporophyte fitness cost of the C_g allele is
358 recessive, it is shielded from negative selection during the diploid phase. Complete dominance

359 fully exposes it to negative selection. Thus, the conditions for invasion narrow with increases in
360 the dominance coefficient (Table 1, Figures 1-4).

361 Increased dominance also narrows the condition for stable polymorphism (Table 1,
362 Figures 1-4). When costs are recessive, heterozygotes gain success as fathers because 50% of
363 their pollen is competitively superior and they pay no cost. This can lead to overall heterozygote
364 superiority. Under random mating, this over-dominance in total fitness can maintain stable
365 polymorphism; however, selfing diminishes the impact of over-dominance by eroding
366 heterozygote frequency: heterozygosity lost to segregation is not replenished by matings between
367 opposite homozygotes, and so the competitive allele is eventually carried mostly by the
368 homozygote, who pay full cost. If the competitive allele is dominant, stable polymorphism is
369 precluded. In this case, the heterozygotes still get half the paternal benefit but pay full cost
370 (Table 1, Figures 1-4), making over-dominance for total fitness unachievable.

371 By comparing invasion conditions and equilibrium allele frequencies under haploid and
372 diploid control (as seen in Jordan and Connallon 2014) of pollen ability (Figures 1, 3), we
373 demonstrate that the form of genetic control overseeing competitive ability has important
374 implications for the fate of an allele conferring an advantage to pollen ability. The stronger
375 haplotype-phenotype correlation in our model is important during the early stages of invasion,
376 when pollen carrying the competitive allele is produced only by heterozygotes: it assures that the
377 pollen grains carrying the competitive allele are indeed competitive. This clear genetic signal
378 expands conditions for a costly allele to invade and spread; stronger selfing is required to counter
379 the advantage.

380 Our fixed and mass-action selfing models are caricatures representing two extremes in
381 pollination systems, but real systems can be intermediate. In *Impatiens palida*, cleistogamous

382 flowers always self whereas there is a small incidence of geitenogamous selfing in chastogamous
383 flowers (Schemske 1978). Gradations in selfing prior to bud opening or delayed self-pollination
384 when pollinator visitation is low (Loyd 1979) can generate variation in the proportion of self-
385 pollen involved with competitive contests with outcross. However, we have shown strong
386 qualitative agreement between the outcomes of the two extreme models, both leading to the
387 general prediction that selection favouring increased pollen competitive ability is weakened by
388 selfing.

389 Genomic analysis of exclusively pollen-expressed loci expressed, where diploid costs are
390 necessarily zero, bears out the prediction of relaxed selection under self-pollination. In the self-
391 incompatible *Capsella grandiflora*, evidence points to stronger purifying selection at sites
392 expressed solely in the pollen tubes than at sites expressed exclusively in the seedling (Arukumar
393 et al., 2011). In the highly selfing *Arabidopsis thaliana*, by contrast, purifying selection on
394 pollen-exclusive genes is weaker than on sporophyte-exclusive genes, as evidenced by a higher
395 frequency of premature stop codons in the former (Harrison et al. 2015). Greater scrutiny of loci
396 expressed during both stages are needed to clarify the general importance of negative pleiotropic
397 constraints on the evolution of gametophyte and sporophyte traits.

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Tables

TABLE 1. Summary of model outcomes for mutation to an allele that increases pollen (haploid gametophyte) competitive ability but reduces survivorship or fertility in the (diploid) sporophyte.

	MATING SYSTEM		
EXPRESSION OF C_g IN DIPLOID SPOROPHYTE	**Obligate Outcrossing ($r = 0$)** *Ample opportunities* to exercise pollen competitive superiority	**Mixed ($0 < r < 1$)** *Fewer opportunities* to exercise pollen competitive superiority	**Obligate selfing ($r = 1$)** *No opportunities* to exercise pollen competitive superiority
Recessive Fitness cost paid only by homozygote	C_g goes to fixation if sporophyte cost is less than ½ the pollen competitive benefit, otherwise reaches stable polymorphism– *conditions for stable polymorphism broad.*	C_g goes to fixation at increasingly lower sporophyte costs as selfing rate increases; upper limit for cost to permit polymorphism is increasingly reduced at higher selfing rates– *conditions for stable polymorphism narrowed.*	C_g unable to invade.
Dominant Fitness cost paid by *both* homozygote and heterozygote	C_g goes to fixation if sporophyte cost is less than ½ the pollen competitive benefit, but eliminated if costs are higher – *no stable polymorphism.*	C_g goes to fixation at increasingly lower sporophyte costs as selfing rate increases, but *eliminated* if costs are any higher – *no stable polymorphism.*	C_g unable to invade.

Figure captions

488 **Figure 1**

489 Conditions producing fixation, polymorphism and unstable equilibrium (i.e., fixation is
490 dependent on initial frequencies) of two alleles C_g and C_s at an autosomal gene under
491 antagonistic pleiotropy between pollen competitive ability and diploid fitness. Solid lines
492 delineate conditions under gametophytic genetic control and dashed lines under sporophytic
493 genetic control. (a-c) Analytical results for the fixed-selfing model assuming weak selection.
494 Potential for polymorphism diminishes as the dominance of the C_g allele increases, eventually
495 being replaced by unstable equilibrium when $h > 0.5$. As selfing rate (*i.e.*, proportion pollen
496 dedicated to selfing) increases, polymorphism requires greater diploid selection s against the C_g
497 allele to offset its greater pollen competitive ability t. (d-f) Analytical results assuming weak
498 selection for the mass-action model, where r is the proportion pollen dedicated to selfing and
499 stigmas receive a mixture of self- and outcross pollen. Conditions allowing invasion of the C_g
500 allele are notably greater than under fixed selfing, as individual stigmas never receive entirely
501 self-pollen except when $r = 1$, thus increasing opportunity for competition between C_g- and C_s-
502 bearing pollen. For both fixed and mass-action selfing, relative to haploid control, diploid control
503 expands conditions under which the C_s allele can be maintained while contracting those under
504 which the C_g allele can be maintained.

505 **Figure 2**

506 Conditions producing fixation, polymorphism and unstable equilibrium of C_g and C_s alleles
507 under variable diploid selection s and dominance h for both fixed and mass-action selfing.
508 Analytical solutions producing these conditions do not assume weak selection. Solid lines
509 indicate boundaries under fixed-selfing; dashed lines indicate those for mass-action selfing.
510 Potential for polymorphism diminishes as the dominance of the C_g allele increases, eventually

being replaced by unstable equilibrium when $h > 0.5$. As the diploid selection coefficient s increases relative to t, maintenance of the C_g allele requires either lower dominance h or less allocation of reproductive structures to selfing, given by r. Compared to fixed-selfing, mass-action selfing conditions permitting polymorphism versus unstable equilibrium are qualitatively similar but quantitatively more limited. The placement of mass-action lines to the right of those for fixed selfing are consistent with individual stigmas never receiving solely self-pollen except when $r = 1$, which increases the opportunity for C_g to exercise its competitive superiority.

Figure 3

Analytical results of equilibrium frequency of the C_g allele across selfing rates $0 < r < 1$ under gametophytic (haploid) and sporophytic (diploid) genetic control. Analytical solutions were derived assuming weak selection. Solid lines indicate equilibrium allele frequencies, while dashed lines indicated the analytical repelling frequency (i.e., the starting p frequency below which p will be lost and above which it will fix). (a-c) Under the fixed-selfing model, the window of selfing rates contracts as dominance increases. (d-f) Under the mass-action model, C_s pollen is never entirely protected from competition with C_g pollen as individual stigmas receive a mixture of both self and outcross pollen for intermediate selfing rates. Thus, maximum and minimum selfing rates allowing fixation or maintenance of C_g and C_s alleles respectively are right-shifted compared to under fixed selfing, reflecting the greater opportunity for the C_g allele to exercise its advantage in pollen competition with the C_s allele. Notably, for both selfing modes, the range of selfing rates at which the C_g allele can invade contracts under diploid genetic control relative to haploid control.

Figure 4

Analytical results for equilibrium frequency of the C_g allele across a range of *s/t*, i.e., ratios of diploid and haplod fitness values. Series specify selfing rates *r* ranging between 0 and 1. Under both (a-c) fixed and (d-f) mass-action selfing models, increases in dominance of the C_g allele sharply decrease the maintenance of polymorphism, particularly at lower selfing rates. Noticably, for a given combination of selfing rate *r* and dominance *h,* the C_g allele persists at higher ratios of *s* and *t* under mass-action selfing relative to fixed-selfing , reflecting the greater opportunity for C_g-bearing pollen to compete C_s-bearing pollen under mass-action selfing. For both selfing models, regardless of dominance, the C_g allele cannot invade under complete selfing, i.e., r = 1.

Appendices

Appendix A

Implications of sex-specific dominance

Given we assume diploid selection acts either through lower flower production or reduced survival, we also assume a common dominance coefficient *h* for female and male function (i.e., quantities of ovule and pollen produced). However, it is possible to consider the effects of different dominance coefficients for male and female function, given as h_m and h_f. In such a case, absolute fitness via female function for C_gC_s individuals is $W_{1f} = 1\text{-}h_f s$ and that via male function is $W_{1m} = 1\text{-}h_m s$. Absolute fitness terms for homozygote individuals remain unchanged from the main text. Using these sex-specific dominance coefficients, we can derive new expressions for equilibrium frequency of the C_g allele under weak selection for both fixed (Eq. A1) and mass-action (Eq. A2) selfing:

$$\hat{p} = \mathrm{Min}[1, \mathrm{Max}\left[0, \frac{-h_m\,(-1 + r)^2\,s + h_f\,(-1 + r^2)\,s + t - r\,(s + t)}{(2\,(-1 + r)\,(-1 + h_f + h_m + h_f\,r - h_m\,r)\,s)}\right]] \tag{A1}$$

$$\hat{p} = \mathrm{Min}[1, \mathrm{Max}\left[0, \frac{((1 + r)\,(2\,h_f\,(-1 + r) - 2\,h_m\,(-1 + r)^2 + (-2 + r)\,r)\,s - (-2 + r + r^2)\,t)}{(2\,(-2 + 2\,h_f - 2\,h_m\,(-1 + r) + r)\,(-1 + r\text{^}2)\,s)}\right]] \tag{A2}$$

To understand the relative impacts of changing h_f and h_m on $\hat{p}$, we can take the partial derivative of the above equations first with respect to h_f and then with respect to h_m. For fixed selfing, these partial derivatives are as follows:

$$\frac{\partial \hat{p}}{\partial h_f} = -\frac{(1 + r)\,(s + (-1 + r)\,t)}{2\,(1 - r)\left(-1 + h_f + h_m + h_f\,r - h_m\,r\right)^2 s} \tag{A3}$$

$$\frac{\partial \hat{p}}{\partial h_m} = -\frac{s + (-1 + r)\,t}{2\left(-1 + h_f + h_m + h_f\,r - h_m\,r\right)^2 s} \tag{A4}$$

With simple arranging, it can be shown that

$$\frac{\partial \hat{p}}{\partial h_f} = \frac{(1 + r)}{(1 - r)}\frac{\partial \hat{p}}{\partial h_m} \tag{A5}$$

In a mixed mating system where $0 < r < 1$, the far-left term of the right-hand side of Eq. A5 is always greater than 1 and increasing as selfing rate increases, meaning an increase in h_f always yields a greater change in $\hat{p}$ than a comparable increase in h_m. This is expected, as under fixed selfing, the cost to male diploid fitness is only paid through outcrossing, as we assume all plants produce enough pollen to self-fertilise. Conversely, diploid fitness effects on female function are recognised both in selfing and outcrossing. Thus, the effects of changing female and male dominance terms are only equivalent under complete outcrossing ($r = 0$) and Eq. A5 reduces to $\frac{\partial \hat{p}}{\partial h_f} = \frac{\partial \hat{p}}{\partial h_m}$.

We can also compare the effect of increasing h_f relative to a shared dominance coefficient h. Returning to Eq. A3, it is evident that the denominator is always positive, while the sign of the numerator changes from positive to negative when r switches from less than $\frac{-s+t}{t}$ to more than $\frac{-s+t}{t}$. This particular value, $\frac{-s+t}{t}$, gives the selfing rate r at which $\hat{p}$ is 0.5. Looking specifically at the effects of dominance, the magnitude of the slope of $\hat{p}$ in response to r can be controlled by

570 adjusting h_f in the denominator. Increasing the value of h_f increases the magnitude of the
571 denominator, thus yielding a more positive slope when $r < \frac{-s+t}{t}$ and a more negative slope when
572 $r > \frac{-s+t}{t}$. This effect is visualised in Figure A1. Compared to $h_f = h_m = 0$, increasing h_f to 0.25
573 allows p to remain fixed at higher selfing rates but also to be lost more quickly, thus contracting
574 the space for polymorphism. An identical effect, but for space allowing unstable equilibrium, is
575 observed when all dominance coefficients are above 0.5 (Fig. A2).

576 When h_f increases and the C_s allele is rare, the C_s allele confers a lesser advantage to
577 female diploid fitness as this advantage is increasingly masked by the C_g allele in heterozygotes
578 (in which it is predominantly found when rare). As an increase in h_f means the C_s allele enjoys
579 less of a diploid fitness benefit over the C_g allele when found in heterozygotes, the C_s allele
580 becomes increasingly dependent on the production of homozygotes to facilitate its invasion.
581 Thus, as h_f increases, C_g remains fixed up to higher values of r. A similar logic follows for
582 invasion of the C_g allele. When h_f increases, the C_g allele also suffers in the heterozygote. It thus
583 requires lower selfing rates so that it can exercise its pollen superiority competitive over the C_s
584 allele under outcrossing.

585 When h_m increases, qualitatively similar but quantitatively different effects occur.
586 Grouping h_f terms together in the denominators of Eqs. A3 and A4 produces $h_f(1+r)$, while
587 grouping h_m terms together produces $h_m(1-r)$. This means that an increase in h_m produces a
588 smaller change in the size of the denominator than an equivalent change in h_f. This is expected, as
589 diploid fitness effects through male function are only experienced under outcrossing, unlike
590 female fitness effects, which are experienced both under selfing and outcrossing. Otherwise, the
591 logic of how dominance affects invasion of both C_g and C_s alleles described above for h_f also
592 applies to h_m, but to a lesser magnitude. This difference is visualized in Figure A1, as the lines

depicting h_f= 0.25 and h_m = 0.25 both remain fixed for p up to higher selfing rates, but also drop (and thus lose p entirely) at lower selfing rates, when compared to $h_f = h_m = 0$.

Turning to mass-action selfing, the partial derivatives of Eq. A2 with respect to h_f (Eq. A6) and h_m (Eq. A7) are as follows:

$$\frac{\partial \hat{p}}{\partial h_f} = -\frac{(2 + r - r^2)\, s + (-2 + r + r^2)\, t}{\left(-2 + 2\, h_f - 2\, h_m(-1 + r) + r\right)^2 (-1 + r^2)\, s} \tag{A6}$$

$$\frac{\partial \hat{p}}{\partial h_m} = -\frac{2\, t + (1 + r)\,((-2 + r)\, s - r\, t)}{(1 + r)\left(-2 + 2\, h_f - 2\, h_m\,(-1 + r) + r\right)^2 s} \tag{A7}$$

Rearrangement of Eqs. A6 yields:

$$\frac{\partial \hat{p}}{\partial h_f} = \frac{1}{(1 - r)} \frac{\partial \hat{p}}{\partial h_m} \tag{A8}$$

As seen under fixed selfing, an increase to h_f will yield greater change to $\hat{p}$ than an equivalent change to h_m. Interestingly, the ratio of these changes is not the same between fixed and mass-action selfing. Relative to a change in h_m, an equivalent increase in h_f under mass-action selfing has a weaker effect on $\hat{p}$ than under fixed selfing, as evidenced by comparing the coefficients of Eqs. A5 and A8, $\frac{(1+r)}{(1-r)}$ and $\frac{1}{(1-r)}$ respectively (assuming $r > 0$). This can be understood by considering where diploid selection on male function acts in mass-action selfing. Unlike fixed selfing, costs to pollen production are paid both through both self-pollen and outcross-pollen, as both pollen types compete on the same stigma. Differences in pollen competitive ability offset costs through diploid male fitness, thus allowing an increase in h_m to still have less impact on $\hat{p}$ than an increase in h_f. The lesser effect of altering h_m on $\hat{p}$ can be seen in Figure A1. Compared to fixed selfing, increasing h_m produces less deviation from baseline series (*i.e.*, those with equivalent h_m and h_f values).

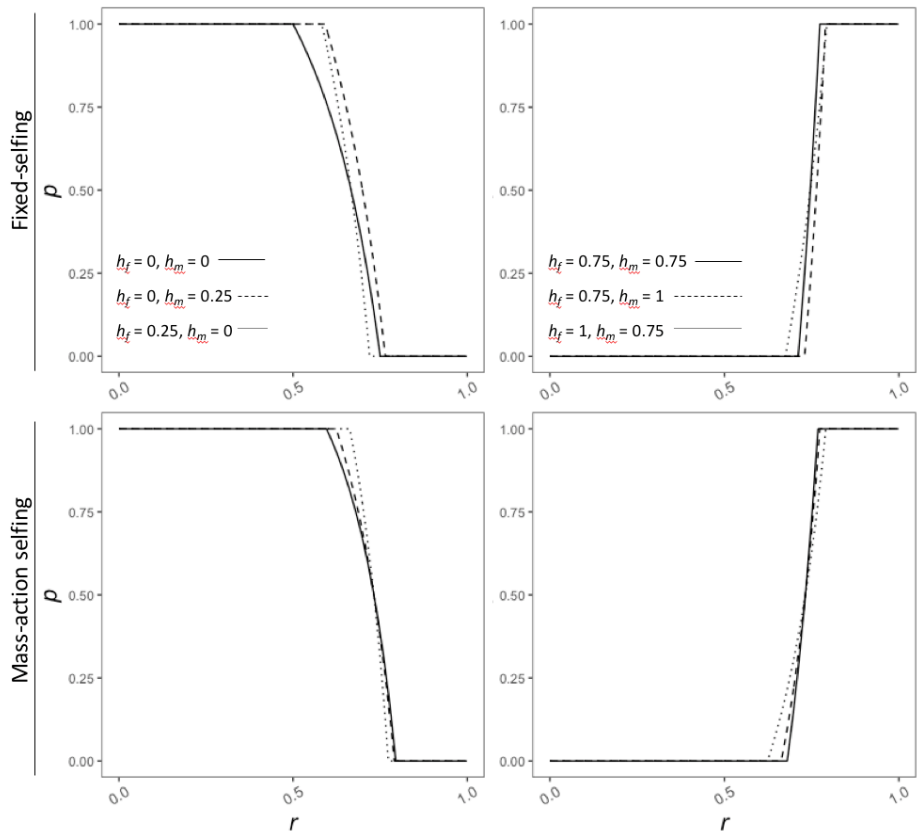


FIGURE A 1

Appendix B

Models for sporophytic control of pollen competitive ability (Jordan and Connallon 2014)

The relative frequencies of each genotype among the available ovules are given as:

$$x_{0f} = \frac{(1-s)X_0}{\overline{W_f}} \tag{B1}$$

$$x_{1f} = \frac{(1-hs)X_1}{\overline{W_f}} \tag{B2}$$

$$x_{2f} = \frac{X_2}{\overline{W_f}} \tag{B3}$$

Where s is the selection coefficient acting on female function, h is the dominance coefficient and $\overline{W_f}$ is defined as

$$\overline{W_f} = (1-s)X_0 + (1-hs)X_1 + X_2 \tag{B4}$$

The relative frequencies of each genotype among the pollen pool are given as:

$$x_{0m} = \frac{X_0}{\overline{W_m}} \tag{B5}$$

$$x_{1m} = \frac{(1-ht)X_1}{\overline{W_m}} \tag{B6}$$

$$x_{2m} = \frac{(1-t)X_2}{\overline{W_m}} \tag{B7}$$

Where *t* is the selection coefficient acting on male function, *h* is the dominance coefficient and $\overline{W_m}$ is defined as

$$\overline{W_m} = X_0 + (1-ht)X_1 + (1-t)X_2 \tag{B8}$$

Using these fitness expressions, the genotype recursion equations are:

$$X_0' = \rho\left[x_{0f} + \tfrac{1}{4}x_{1f}\right] + (1-\rho)\left[\left(x_{0f} + \tfrac{1}{2}x_{1f}\right)q_m\right] \tag{B9}$$

$$X_1' = \rho\left[\tfrac{1}{2}x_{1f}\right] + (1-\rho)\left[x_{0f}(1-q_m) + \tfrac{1}{2}x_{1f} + x_{2f}q_m\right] \tag{B10}$$

$$X_2' = \rho\left[x_{2f} + \tfrac{1}{4}x_{1f}\right] + (1-\rho)\left[\left(x_{2f} + \tfrac{1}{2}x_{1f}\right)(1-q_m)\right] \tag{B11}$$

where q_m is the frequency of the C_g allele in the pollen pool:

$$q_m = x_{0m} + \frac{1}{2}x_{1m} \tag{B12}$$

In the case of fixed selfing, selfing rate ρ is equivalent to *r (*i.e., proportion pollen allocated to selfing). Under mass-action selfing, ρ is frequency-dependent and genotype-specific:

$$\rho = \frac{rW_{im}}{rW_{im} + (1-r)\overline{W_m}} \tag{B13}$$

where $W_{0m} = 1, W_{1m} = (1-ht)$ and $W_{2m} = 1-t$ and *r* is the proportion of pollen dedicated to selfing.

Equilibrium allele frequencies for fixed and mass-action selfing assuming sporophytic control were derived using the same methods provided in the main text and are as follows:

$$\hat{p} = \mathrm{Min}[1, \mathrm{Max}\left[0, \frac{-r(1+r)s + (r-2)(r-1)t + 2h(r-1)(s+rs+t-rt)}{2(2h-1)(r-1)(s+rs+t-rt)}\right]] \quad \text{(B14)}$$

$$\hat{p} = \mathrm{Min}[1, \mathrm{Max}\left[0, \frac{rs - (r-2)(r-1)t - 2h(r-1)(s+t-rt)}{2(2h-1)(r-1)(s+t-rt)}\right]] \quad \text{(B15)}$$

We can understand the conditions under which the C_g allele will perform better under sporophytic control relative to haploid and *vice versa* by taking the difference between Eqs. 10 (main text) and B16 as well as Eqs. 11 (main text) and B15. Under fixed selfing:

$$\Delta\hat{p} = \frac{(1 - r)(s - t)t}{2\,(2h-1)\,s\,(s(1+r) + t(1-r)\,)} \quad \text{(B16)}$$

In Eq. B16, when $h < 0.5$, the denominator is always negative. The sign of the numerator is dependent on the size of s relative to t. When diploid selection s is larger than haploid selection t, the numerator is positive and thus $\Delta\hat{p}$ is negative, revealing the C_g allele is more successful under sporophytic than gametophytic genetic control. Inversely, when $s < t$ (as presented in the main text), $\Delta\hat{p}$ is positive and C_g reaches a higher frequency under gametophytic control.

Under mass-action selfing:

$$\Delta\hat{p} = \frac{t\,(\,(r^2 + r - 2)t - (\,2\,r^2 - r - 2)s\,)}{2\,(2h-1)\,(r-2\,)\,(1 + r)\,s\,(s + t - r\,t)} \quad \text{(B17)}$$

When $h < 0.5$ and $0 \leq r \leq 1$, the denominator of B17 is negative. Thus, the sign of $\Delta\hat{p}$ is dependent on the sign of the numerator. Given $0 \leq r \leq 1$, $(\,r^2 + r - 2)$ is always negative and $(\,2\,r^2 - r - 2)$ is always positive, meaning the numerator is always negative and $\Delta\hat{p}$ is always positive. In other words, when $h < 0.5$, the C_g allele will always do better under gametophytic control than under sporophytic control. Conversely, when $h > 0.5$, the denominator is positive

while the numerator remains unchanged. In such a case, $\Delta\hat{p}$ is always negative and the C_g allele reaches a higher equilibrium frequency under sporophytic control. These analytical results are visualised in Figure 3, in which, when $h = 0$, the equilibrium allele frequency $\hat{p}$ is higher for gametophytic (i.e., haploid) control relative to sporophytic and, when $h = 1$, the repelling allele frequency below which C_g cannot invade is higher under sporophytic control (meaning fixation requires a higher initial allele frequency). This result can be understood easily by considering the haplotype-phenotype correspondence under both gametophytic and sporophytic genetic control. Under gametophytic control, this correspondence is complete (i.e., phenotype reflects haplotype and the Cg allele always confers a benefit to pollen). Under sporophytic control, this correspondence is a function of the paternal genotype (homozygote or heterozygote) and the dominance coefficient h, and thus, the Cg allele will not always confer its maximum advantage to pollen ability, weakening its invasion ability.

Likewise, invasion conditions for fixed and mass-action selfing assuming sporophytic control were derived using the methods found in the main text. Under fixed selfing, maximum and minimum selfing rates permitting invasion of C_g and C_s alleles respectively are given as:

$$r < \frac{s + (3 - 4h)t - \sqrt{(1 - 4h)^2 s^2 + 2(7 - 12h)st + t^2}}{2(2h - 1)(s - t)} \tag{B18}$$

$$r > -\frac{-s + (1 - 4h)t + \sqrt{(3 - 4h)^2 s^2 + 2(12h - 5)st + t^2}}{2(2h - 1)(s - t)} \tag{B19}$$

The corresponding expressions for mass-action selfing are:

$$r < \frac{(2h - 1 + 2h)s + (4h - 3)t + \sqrt{(1 - 2h)^2 s^2 + 6(1 - 2h)st + t^2}}{2(2h - 1)t} \tag{B20}$$

$$r < \frac{-s + 2hs + (4h - 1)t - \sqrt{(1 - 2h)^2 s^2 + 6(1 - 2h)st + t^2}}{2(2h - 1)t} \tag{B21}$$

Appendix C

Production of heterozygote offspring via selfing with variable pollen competitiveness

With a simple Punnet square, it can be demonstrated that even with differential competitive ability between pollen haplotypes, selfing of heterozygotes produces ½ heterozygote offspring:

	C_g pollen $\frac{1}{2-t}$ *fertilisation success given 50% allele frequency*	**C_s pollen** $\frac{1-t}{2-t}$ *fertilisation success given 50% allele frequency*
C_g ovule *0.5 allele frequency*	$\frac{1}{2(2-t)}\ C_gC_g$	$\frac{1-t}{2(2-t)}\ C_gC_s$
C_s ovule *0.5 allele frequency*	$\frac{1}{2(2-t)}\ C_sC_g$	$\frac{1-t}{2(2-t)}\ C_sC_s$

TABLE C 1

Together, the frequency of heterozygote offspring produced via heterozygote selfing is $\frac{1}{2(2-t)} + \frac{1-t}{2(2-t)}$, which reduces to ½.

Appendix D

Analytical results for mass-action selfing with pollen discounting

Pollen discounting, i.e., loss of pollen for outcrossing during transport, can be incorporated by inclusion of an additional term, *d,* which gives the proportion of pollen lost and is identical to the pollen discounting term included in Jordan and Connallon (2014). Equations 5a-c are thus modified to be:

$$X_0' = x_0\left[\frac{rW_0 + (1-r)(1-d)\left(x_0 + \frac{1}{2}x_1\right)}{P_0}\right] + \frac{1}{2}x_1\left[\frac{r\frac{1}{2}W_1 + (1-r)(1-d)\left(x_0 + \frac{1}{2}x_1\right)}{P_1}\right] \tag{D1}$$

$$X_1' = \frac{1}{2}x_1 + x_0\left[\frac{(1-r)(1-d)\left(x_2 + \frac{1}{2}x_1\right)(1-t)}{P_0}\right] + x_2\left[\frac{(1-r)(1-d)\left(x_0 + \frac{1}{2}x_1\right)}{P_2}\right] \tag{D2}$$

$$X_2' = x_2\left[\frac{rW_2(1-t) + (1-r)(1-d)\left(x_2 + \frac{1}{2}x_1\right)(1-t)}{P_2}\right] + \frac{1}{2}x_1\left[\frac{r\frac{1}{2}W_1(1-t) + (1-r)(1-d)\left(x_2 + \frac{1}{2}x_1\right)(1-t)}{P_1}\right] \quad \text{(D3)}$$

Similarly, Eqs. 6a-c are also modified:

$$P_0 = rW_0 + (1-r)(1-d)\left(x_0 + \frac{1}{2}x_1(2-t) + x_2(1-t)\right) \quad \text{(D4)}$$

$$P_1 = r\frac{1}{2}W_1(2-t) + (1-r)(1-d)\left(x_0 + \frac{1}{2}x_1(2-t) + x_2(1-t)\right) \quad \text{(D5)}$$

$$P_2 = rW_2(1-t) + (1-r)(1-d)\left(x_0 + \frac{1}{2}x_1(2-t) + x_2(1-t)\right) \quad \text{(D6)}$$

Using Eqs. D1-6, and assuming weak selection, we can derive the equilibrium frequency of the C_g allele. For the full expression, see the corresponding online supplemental materials. To understand the effects of increasing d on $\hat{p}$, we take the partial derivative of the $\hat{p}$ expression with respect to d:

$$\frac{\partial \hat{p}}{\partial d} = -\frac{r(-2 + d^2(-2 + r)(-1 + r)^2 + r - 3r^2 - 2d(-1 + r)(2 + (-1 + r)r))t}{2(-1 + 2h)(-2 - 2d(-1 + r) + r)\text{^}2(1 + d(-1 + r) + r)\text{^}2s} \quad \text{(D7)}$$

To get a better handle on the above expression, we can isolate and rearrange the terms in which d appears to:

$$d(r - 1)((r - 2) * (2(r + 1) - d * (r - 1)) + 8) \quad \text{(D8)}$$

The term $d(r\text{-}1)$ is always negative (when $0 < r < 1$), so how d affects the equilibrium allele frequency is dependent on the sign of the following term:

$$((r - 2) * (2(r + 1) - d * (r - 1)) + 8) \tag{D9}$$

With further rearrangement, it can be shown that:

$$\frac{\partial \hat{p}}{\partial d} = \begin{cases} < 0, & d < 2 + \frac{8}{r-2} - \frac{4}{r-1} \\ > 0, & d > 2 + \frac{8}{r-2} - \frac{4}{r-1} \end{cases} \tag{D10}$$

As both d and r are constrained to between 0 and 1, $\frac{\partial \hat{p}}{\partial d}$ is always positive and thus an increase in d always lowers the equilibrium frequency of the C_g allele. This is not surprising as inclusion of a pollen discounting term $d > 0$ should decrease the relative proportion of outcross- versus self-pollen that a stigma receives, therefore decreasing the realised competitive advantage of C_g pollen, under the mass-action selfing model.

In other words, under mass-action selfing, intermediate r values indicate a stigma receives both self and outcross pollen. Successful invasion and fixation of either the C_g or C_s allele depends on the ratio of self to outcross pollen produced, with higher values of r favouring the C_s allele. Pollen discounting essentially alters this ratio, allowing the C_s allele to invade and fix at lower values of r, which thus implies limited invasion of the C_g allele.

Figure D1 displays this effect of pollen discounting on the success of the C_g allele using $t = 0.1$, $s = 0.05$ and d values of 0, 0.2 and 0.5. Indeed, as d is increased, the equilibrium frequency of the C_g allele becomes increasingly left-shifted, implying a decreased range of selfing rates at which it can successfully invade.

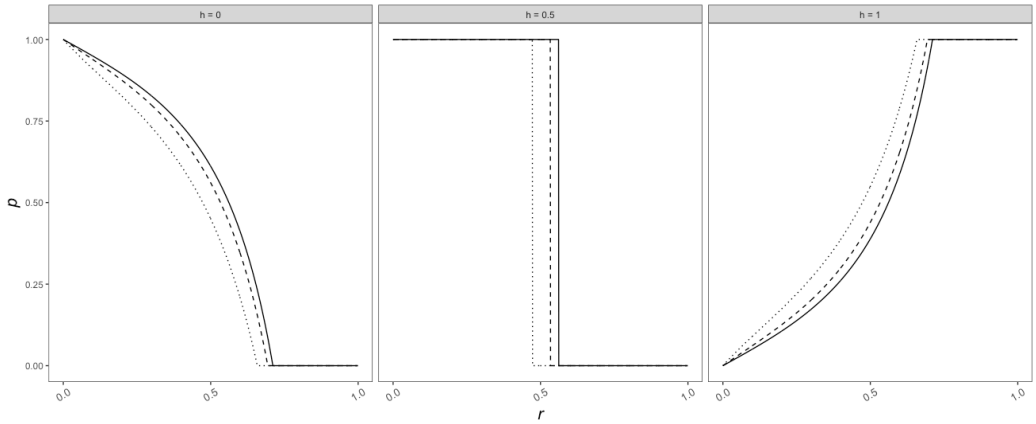


FIGURE D 1

Appendix E

Numerical validation and consideration of strong selection

Equilibrium and repelling allele frequencies presented in the main text are entirely analytical, i.e., derived using Equations 10 and 11. Confirmation of these analytically derived frequencies was done numerically. All numerical results were produced using RStudio Version 1.1.353, in which we generated and recorded genotype and allele frequencies over generations for different combinations of selfing, diploid fitness and pollen competitiveness. For invasion from X_0 and X_2 boundaries, initial frequency of the invading allele was always set to 0.0001, and initial genotype frequencies were at Hardy-Weinberg equilibrium. Equilibrium allele frequencies presented in Figures E1 were evaluated at selfing rates r ranging from 0 to 1 in increments of 0.01. Long-term allele frequencies were taken from the 50,000th generation and verified by a change in allele frequency, i.e., Δp, of less than 10^{-6}. We consider these long-term allele frequencies to be equilibrium frequencies, as we assume that, with such significantly small changes in allele frequencies, drift will dominate, and these long-term frequencies are good approximations of true equilibrium frequencies, where $\Delta p = 0$. As both models are deterministic, numerical results are the outcome of a single run.

As stated in the main text, analytical solutions assume weak (s, t << 1). However, we found that analytical results under relatively strong selection still provided a qualitatively good fit to their corresponding numerical results under both haploid and diploid control of pollen competitive ability (grey series, Figure E1), suggesting interpretations presented in the main text are broadly applicable across a wide range of selection strengths. In Figure E1, weak selection indicates s = 0.01 and t = 0.03 strong selection indicates s = 0.05 and t = 0.1.

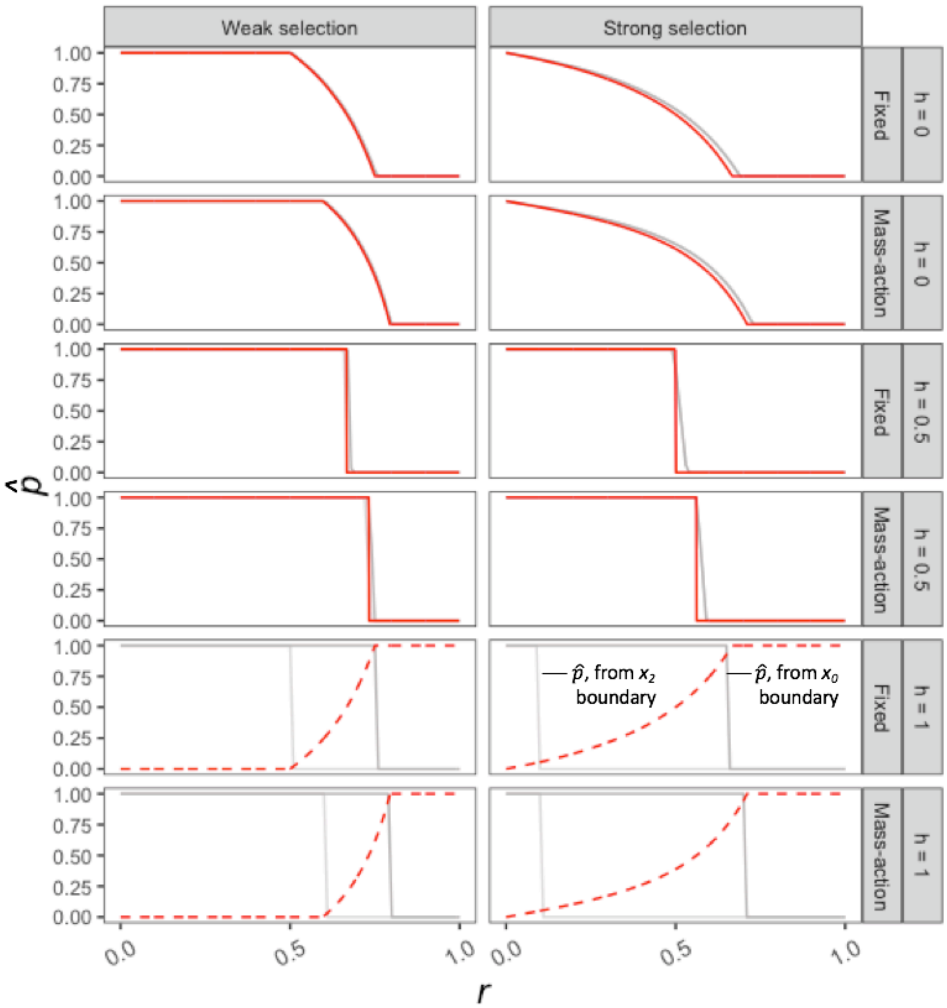


FIGURE E 1

Importantly, when h = 1.0, drops in equilibrium allele frequencies from 1 to 0 for all combinations of selection strength and selfing mode are immediate, i.e., there are no

intermediate equilibrium values (i.e., $0 < \hat{p} < 1$). Any slopes are the result of the increment chosen for the x axis ($0 \leq r \leq 1$ by 0.01).

In addition to a comparison with numerical results under strong selection, we can also compare invasion conditions under fixed selfing assuming weak selection to conditions derived without assuming weak selection. For example, Eqs. 7a and 7b in the main text give maximum and minimum selfing rates for C_g and C_s invasion respectively under weak selection. Without this assumption, these maximum and minimum r values are:

$$r < \frac{hs(-2+t)+t}{-(1+h(-2+s)s+(-1+s)(1-hs)t} \tag{E1}$$

$$r > \frac{(-1+s)(s(2+h(-2+t))-t)}{hs^2(-1+t)+t-s(1+h(-2+t)+t)} \tag{E2}$$

Comparison with expressions 7a and 7b in the main text can be easily considered visually (Figure E2), in which series were generated using $t = 0.1$.

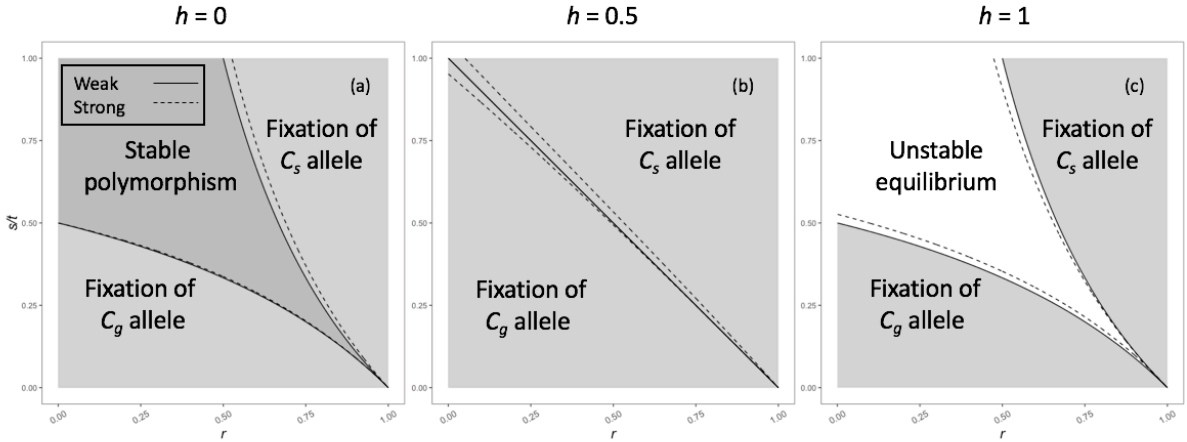


FIGURE E 2

Perhaps most notable in Figure E2 is the small space permitting polymorphism when $h = 0.5$ at low values of r. This result is consistent with Figure E1, in which under strong selection there are true numerically-derived intermediate equilibrium allele frequencies (i.e., $0 < \hat{p} < 1$) when $h = 0.5$, unlike under weak selection. Overall, we find strong qualitative agreement between invasion

conditions predicted both with and without weak selection, suggesting our results likely hold for a broader range of selection parameters than those presented in the main text.

Appendix F

Critical selfing rates under mass-action selfing

Using the methods described in the main text, the analytical solutions specifying the selfing rates required for invasion C_g and C_s alleles under mass-action selfing are as follows:

For C_g: $r <$

$$
\begin{aligned}
&-\frac{s-4hs+t}{3(-s+2hs)}- \\
&\Big(2^{1/3}\big(-(s-4hs+t)^2+3(-s+2hs)(2s-2hs+t)\big)\Big)\Big/\Big(3(-s+2hs)\Big(-20s^3+42hs^3+84h^2s^3-160h^3s^3+21s^2t-60hs^2t+12h^2s^2t- \\
&\quad 15st^2+42hst^2-2t^3+\sqrt{\Big(\big(-20s^3+42hs^3+84h^2s^3-160h^3s^3+21s^2t-60hs^2t+12h^2s^2t-15st^2+42hst^2-2t^3\big)^2+} \\
&\quad 4\big(-(s-4hs+t)^2+3(-s+2hs)(2s-2hs+t)\big)^3\Big)\Big)^{1/3}\Big)+ \\
&\frac{1}{3\times 2^{1/3}(-s+2hs)}\Big(-20s^3+42hs^3+84h^2s^3-160h^3s^3+21s^2t-60hs^2t+12h^2s^2t-15st^2+42hst^2-2t^3+ \\
&\quad\sqrt{\Big(\big(-20s^3+42hs^3+84h^2s^3-160h^3s^3+21s^2t-60hs^2t+12h^2s^2t-15st^2+42hst^2-2t^3\big)^2+} \\
&\quad 4\big(-(s-4hs+t)^2+3(-s+2hs)(2s-2hs+t)\big)^3\Big)\Big)^{1/3}
\end{aligned}
\tag{F1}
$$

For C_s: $r >$

$$
\begin{aligned}
&-\frac{-3s+4hs+t}{3s-6hs}+\Big(2^{1/3}\big((9-30h+28h^2)s^2+(-9+14h)st+t^2\big)\Big)\Big/ \\
&\Big(3(-1+2h)s\Big((54-270h+396h^2-160h^3)s^3-3(-9+12h+4h^2)s^2t+3(-9+14h)st^2+2t^3+3\sqrt{3}\sqrt{\big(-(s-2hs)^2\big(576h^4s^4-32h^3s^3} \\
&\quad (27s-37t)+12hst\big(135s^2-100st+17t^2\big)+4h^2s^2\big(81s^2-558st+205t^2\big)+t\big(-432s^3+441s^2t-134st^2+9t^3\big)\big)\big)\big)^{1/3}\Big)+ \\
&\frac{1}{3\times 2^{1/3}(-1+2h)s}\Big((54-270h+396h^2-160h^3)s^3-3(-9+12h+4h^2)s^2t+3(-9+14h)st^2+2t^3+ \\
&\quad 3\sqrt{3}\sqrt{\big(-(s-2hs)^2\big(576h^4s^4-32h^3s^3(27s-37t)+12hst\big(135s^2-100st+17t^2\big)+} \\
&\quad 4h^2s^2\big(81s^2-558st+205t^2\big)+t\big(-432s^3+441s^2t-134st^2+9t^3\big)\big)\big)\Big)^{1/3}
\end{aligned}
\tag{F2}
$$

Appendix G

Critical diploid selection coefficients under mass-action and fixed selfing

Taking the partial derivative of in-text Eqs. 8a and 8b with respect to r produces Eqs. G1 and G2 respectively, which in turn provide insights into the effect of increasing selfing rate on the conditions permitting invasion:

$$
\frac{\partial s}{\partial r}=\frac{\Big(-4+r\Big(4-2h(r-1)^2(4+r)-r\big(-5+r(2+r)\big)\Big)\Big)t}{(-2-2h(r-1)+r)^2(2+r-r^2)^2}
\tag{G1}
$$

$$\frac{\partial s}{\partial r} = \frac{\left(-4 + r\left(4 - 2h(r-1)^2(4+r) + r\left(-9 + r(2+r)\right)\right)\right)t}{(-2 - 2h(r-1) + r)^2(2 + r - r^2)^2} \tag{G2}$$

Assuming *h, s, t* and *r* all fall between 0 and 1, the above expressions are always negative, implying the critical value of *s* always decreases as *r* increases (Figure 1). When $h < 0.5$, the maximum value of *s* permitting C_g invasion decreases more slowly as *r* increases than the minimum *s* value permitting C_s invasion. This results in a range of *r* values in which *s* is below the maximum value for C_g invasion and above the minimum value for C_s value, producing the potential for polymorphism. Conversely, when $h > 0.5$, the minimum *s* for C_s invasion decreases more quickly in response to *r* than the maximum value for C_g invasion. This produces a range of *r* values in which neither allele can invade (i.e., unstable equilibrium). Focusing on the effect of selfing on the C_g allele, increasing *r* contracts the parameter space allowing invasion of an allele conferring a benefit to pollen competitiveness.

To compare effects of fixed versus mass-action selfing on invasion, we can compare how minimum and maximum *s* values permitting invasion of C_s and C_g alleles respond to increases in *r* in these two selfing systems. Below are expressions for how the maximum and minimum *s* values change in response to *r* under fixed selfing:

$$\frac{\partial s}{\partial r} = -\frac{t}{(-2\,h\,(-1\,+\,r)\,+\,r)^2} \tag{G3}$$

$$\frac{\partial s}{\partial r} = -\frac{t}{(-2\,-\,2\,h\,(-1\,+\,r)\,+\,r)^2} \tag{G4}$$

We can easily visualise differences between Eqs. G1,2 and G3,4, and thus how critical *s* values respond to *r* under mass-action versus fixed selfing, by considering the case in which $h = 0.25$ and $t = 0.03$ (Figure G1).

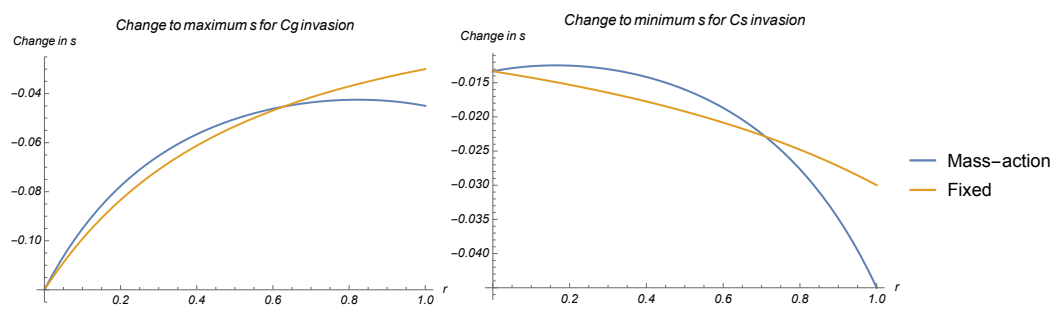


FIGURE G 1

For both maximum and minimum *s* values, it is clear that the critical *s* value decreases more rapidly for fixed selfing than mass-action as *r* increases from 0, as evidenced by the initially lower (*i.e.*, more negative) values for the fixed $\frac{\partial s}{\partial r}$ series than for mass-action series. This difference implies that for a given *s* value, the critical *r* value allowing C_g invasion will be lower than that of mass-action selfing. Indeed, we find this to be true.

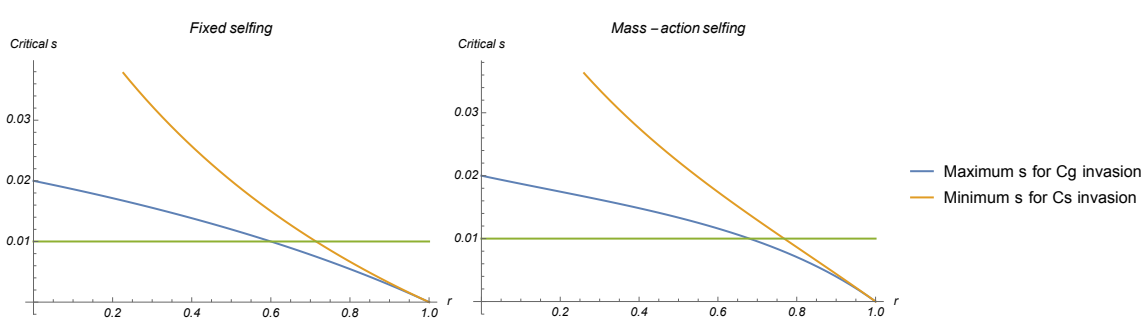


FIGURE G 2

For a given s value (in this case 0.01, as given by the green series in Figure G2), both maximum and minimum s values permitting invasion are right-shifted along the r axis. This indicates the C_g allele can be maintained at higher selfing rates under mass-action selfing than fixed selfing. Returning to Figure G1, the difference in $\frac{\partial s}{\partial r}$ between fixed and mass-action selfing for a given r value is greater when considering the maximum s permitting C_g invasion than the minimum s permitting C_s invasion. While the minimum s for C_s invasion is right-shifted under mass-action selfing compared to fixed selfing, the magnitude of this shift is less than that of the corresponding maximum s values. Put together, this results in a contracted range of r values permitting polymorphism, which can be seen in Figure G2 as the space in which the minimum s series falls above the s = 0.01 series and the maximum s series falls below ($0.69 < r < 0.77$ under mass-action selfing; $0.56 < r < 0.73$ under fixed selfing).

A similar analysis when $h > 0.5$ yields qualitatively the same results but with unstable equilibria, not protected polymorphism.

Figures

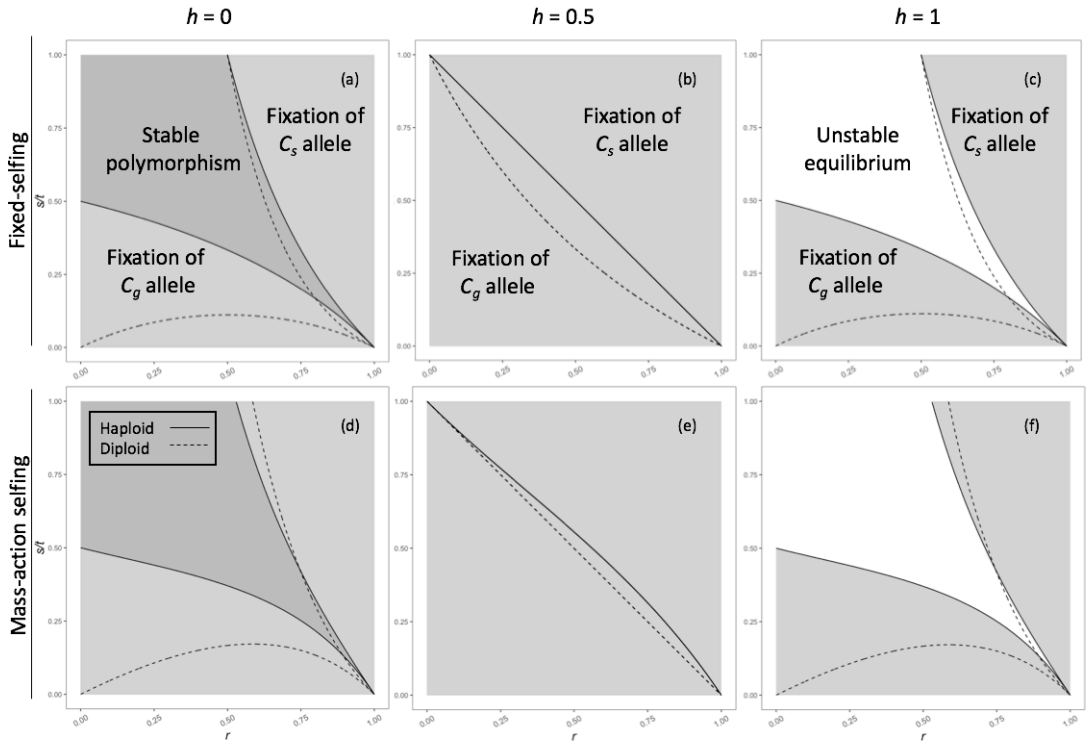
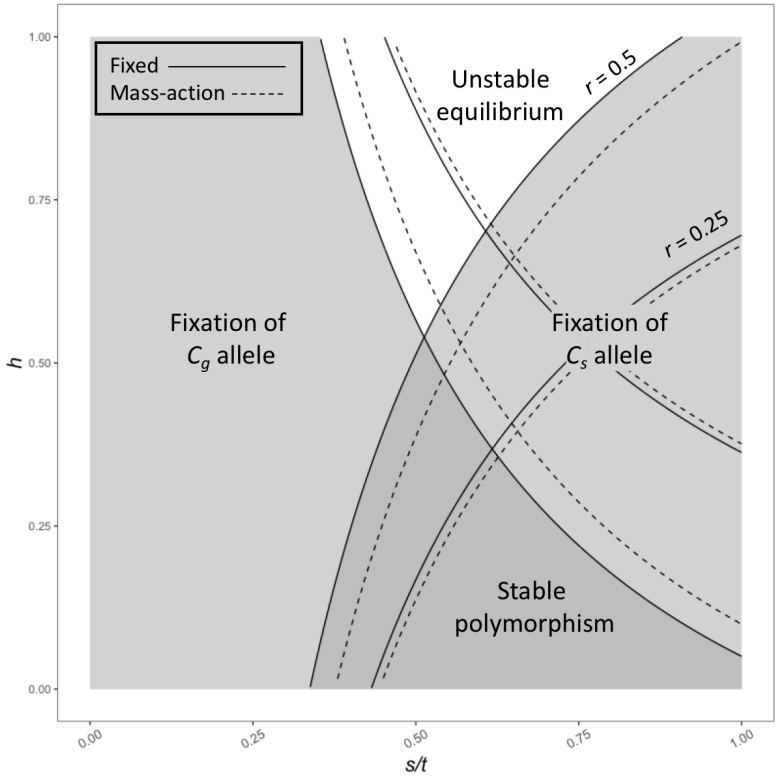

h = 0
h = 0.5
h = 1
Fixed-selfing
Mass-action selfing
(a)
(b)
(c)
(d)
(e)
(f)
Stable polymorphism
Fixation of C_s allele
Fixation of C_g allele
Unstable equilibrium
Haploid
Diploid
s/t
r

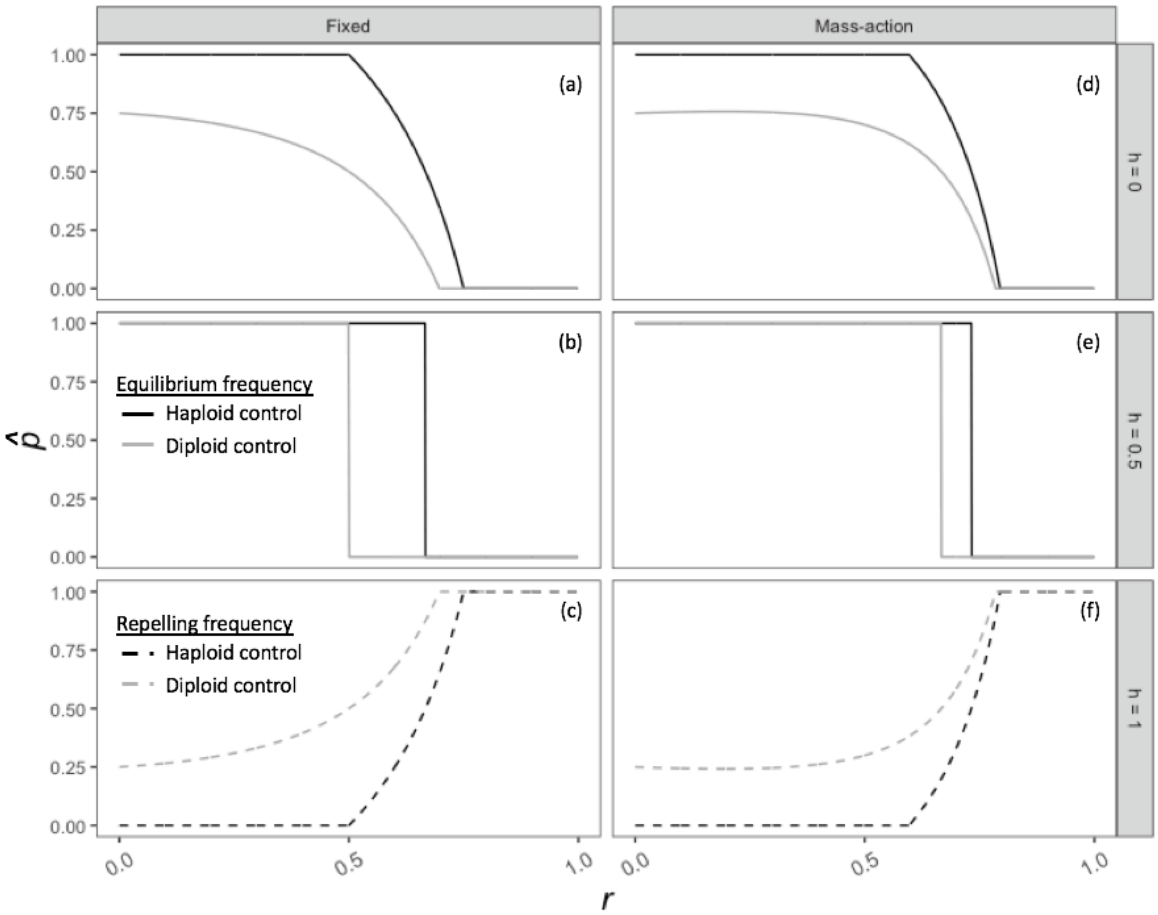
FIGURE 2



806

807 **FIGURE 3**

808



809

810 **FIGURE 4**

811

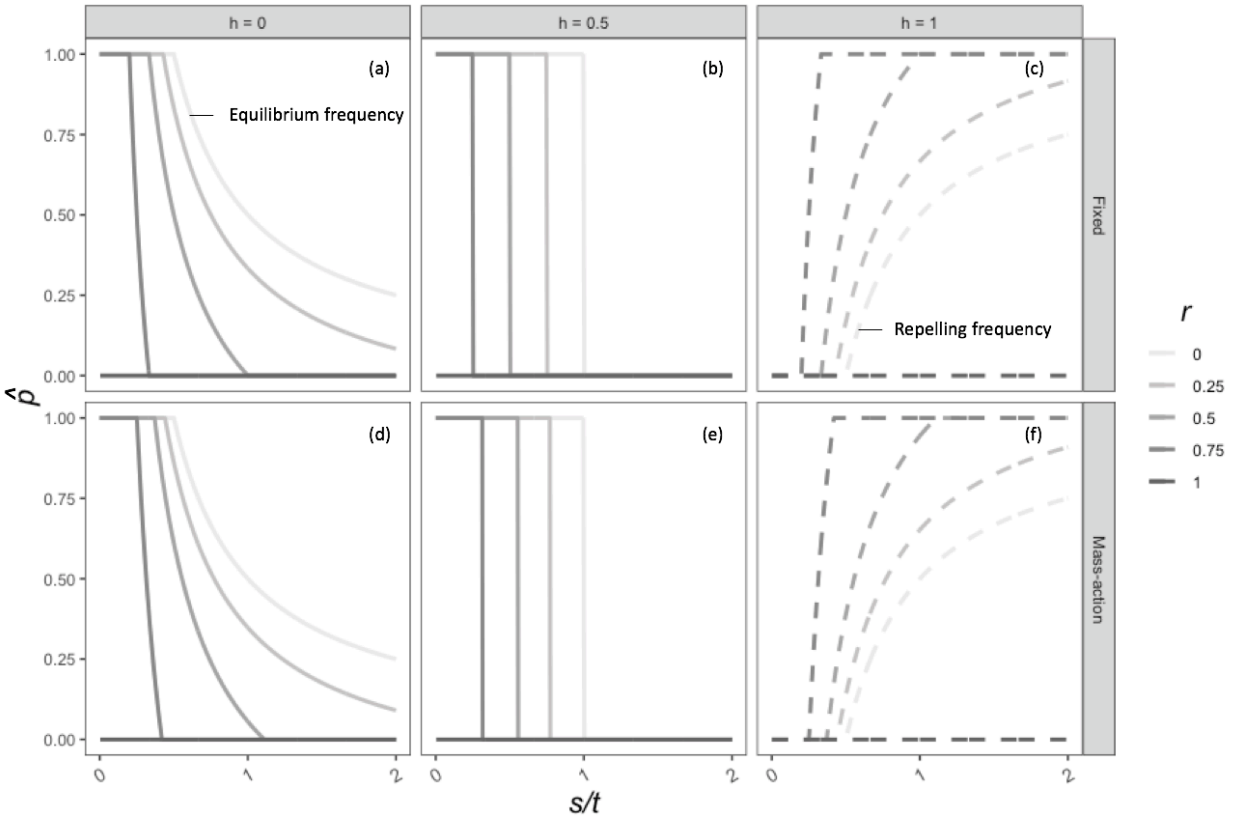

h = 0
h = 0.5
h = 1
(a)
(b)
(c)
(d)
(e)
(f)
Equilibrium frequency
Repelling frequency
Fixed
Mass-action
1.00
0.75
0.50
0.25
0.00
0
1
2
s/t
p̂
r
0
0.25
0.5
0.75
1

FIGURE 5