1   SELECTION FOR POLLEN COMPETITIVE ABILITY IN MIXED MATING SYSTEMS

2   ABSTRACT

3   Co-expression of genes in plant sporophytes and gametophytes allows correlated gametic and

4   sporophytic selection. Theory predicts that, under outcrossing, an allele conferring greater pollen

5   competitive ability should fix within a population unless antagonistic pleiotropy with the

6   sporophyte stage is strong. However, under strong selfing, pollen competitiveness is immaterial

7   as superior and inferior competitors are deposited on opposite stigmas, producing assortative

8   competition. Because many plant species have mixed-mating systems, selfing should be critical

9   in the spread and maintenance of pollen-expressed genes affecting competitiveness. We present

10   two one-locus, two-allele population genetic models for the evolution of a locus controlling

11   pleiotropic antagonism between pollen competitiveness and diploid fitness. Analytical solutions

12   provide minimum and maximum selfing rates allowing invasion of alleles with greater diploid

13   and haploid fitness respectively. Further, polymorphism is only maintained when diploid

14   selection is recessive. Fixation of the allele conferring greater pollen competitiveness may be

15   prevented, even with weak sporophytic counter-selection, with sufficiently high selfing. Finally,

16   selfing expands and limits the range of haploid-diploid selection coefficients allowing

17   polymorphism, depending on dominance and selfing mode.

18

19   *Key Words:* Assortative competition, gametic selection, sporophytic selection, population

20   genetics, mixed mating, genetic correlation

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INTRODUCTION

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25   Over 7000 genes are expressed in male gametophytes—pollen grains and tubes and the sperm

26   they transmit—as they compete in the pistil for ovules (Page and Grossniklaus 2002; Honys and

27   Twell 2003; Rutley and Twell 2015). Upwards of 60% of known plant genes are expressed in

28   both the gametophyte and sporophyte (Borges et al. 2009; Arunkumar et al. 2013). For example,

29   over 100 cases of co-expression in pollen tubes and root hairs have been identified in tobacco

30   (Hadif et al. 2012). This high degree of co-expression presents opportunity for pollen selection to

31   affect sporophyte evolution, and *vice versa*. Haldane (1932) recognized this potential, writing

32   "Clearly a higher plant species is at the mercy of its pollen grains. A gene which greatly

33   accelerates pollen tube growth will spread through a species even if it causes moderately

34   disadvantageous changes in the adult plant." Simply, genes conferring an advantage in the

35   gametophyte should fix unless there is strong antagonistic pleiotropy with sporophyte fitness.

36   Selection should be strong on alleles with concordant impacts on both gametophyte and

37   sporophyte stages. Deleterious recessive mutations, which are masked in heterozygous

38   sporophytes, are fully exposed to selection in haploid gametophytes. This facilitates purging,

39   diminishing inbreeding depression (Charlesworth and Charlesworth 1992). Some have suggested

40   that alleles promoting pollen competition will increase offspring quality: large stigmatic pollen

41   loads lead to intense competition in the style, favouring genetically superior gametophytes,

42   which contribute their genes to the seed (Mulcahy and Mulcahy 1987; Winsor et al. 1987;

43   Winsor et al. 2000; but see Baskin and Baskin 2015; Pélabon et al. 2016). Walsh and

44   Charlesworth (1992) found that when fitness effects on the gametophyte and sporophyte are

45   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.

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METHODS

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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 $W_0 = 1-s$, while the

108   heterozygote C_gC_s is $W_1 = 1-hs$, 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 $1-t$. All individual plants are expected to have many flowers. Population size is

113   effectively infinite.

114   The level of self-pollination in the model depends on r, the proportion of pollen allocated

115   to self-mating, which reflects the potential rate of self-fertilization. Absent selection, r equals the

116   proportion of zygotes that are produced by self-pollination, *i.e.*, the realized selfing rate. As

117   shown below, potential and realized selfing rates can differ when selection acts on the

118   gametophyte. For sake of brevity, r is hereafter referred to as selfing rate. We assume all plants

119   have the same r value. We model two selfing forms: fixed selfing and mass-action selfing,

120   defined below. The models we present assume haploid genetic control over pollen competitive

121   ability. As we present our results, we will for comparison also present results using models by

122   Jordan and Connallon (2014; see Appendix B), which assume diploid control.

123   **FIXED SELFING**

124   The fixed selfing model echoes the biology of species such as *Impatiens* and *Viola*, where

125   cleistogamous flowers are obligate selfers, and chastogamous flowers outcross (Schemske 1978,

126   Winn and Moriuchi 2009). In this model, proportion r of flowers on each plant is dedicated to

127   selfing while 1-r of flowers is allocated to outcrossing. Thus, a stigma receives either only self-

128   pollen or only outcross-pollen. Selection for pollen competitiveness occurs on all outcrossing

129   flowers, but among selfing flowers, occurs only on heterozygotes. Our recursion equations for

130   genotype frequencies consider selection during the diploid and haploid stages in separate steps.

131   After diploid selection, diploid genotype frequencies are:

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

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

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

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

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

133   After mating and haploid selection, offspring genotype frequencies are

134

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

136

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

137

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

139   where α reflects the relative competitiveness of C_g-bearing pollen as a function of the absolute

140   competitiveness conferred by the C_g allele and the frequency of the C_g allele in the pollen pool as

141   a result of genotype frequency following selection:

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

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

143   To understand Equations (3a-c), consider separately the offspring produced on selfing (*r*)

144   and outcrossing (1-*r*) flowers. Under selfing, competition among pollen tubes carrying opposite

145   alleles only occurs within heterozygote pistils. Assuming heterozygotes produce C_g and C_s pollen

146   in equal numbers, ½ of their offspring will likewise be heterozygous, with the remaining

147   offspring divided between C_gC_g and C_sC_s homozygotes in proportions of $\left(\dfrac{1}{2-t}\right)$ and $\left(\dfrac{1-t}{2-t}\right)$

148   (Appendix C). We assume each selfing flower produces enough pollen to fertilise its ovules,

149   such that only female diploid fitness terms, and not α (*i.e.*, male diploid fitness terms), are

150   included. Simply, the number of offspring produced via selfing is limited by seed production, not

151   pollen production. Offspring produced through outcrossing will be a function of both female and

152   male diploid fitness, as well as allelic differences in pollen competitive ability, specified by α.

153   For simplicity, we make no provision for inbreeding depression; increasing failure rate of selfed

154   offspring has the same effect as reducing the basic selfing rate (see Jordan and Connallon 2014).

155   **Mass-action selfing**

156   Mass-action selfing (Holsinger 1991) echoes more general modes of mixed-mating. Here r still

157   denotes the proportion of pollen individuals allocate to selfing, but in this case all stigmas

158   receive a mix of self- and outcross-pollen, resulting in inter-allelic competition for all ovules.

159   Under this scenario, the amount of self-pollen received by a stigma is a function of two factors,

160   one being r, and the other being the quantity of pollen produced by the individual relative to that

161   it receives through outcrossing. Thus, the true selfing rate is dependent on genotype frequency.

162   We make no provisions for pollen discounting here but consider this elaboration in Appendix D.

163   Assuming diploid selection occurs according to Equations (1a-c), we arrive at the

164   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.

RESULTS

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).

Fixed selfing

204   Under fixed selfing, boundary selfing rates permitting invasion of the C_g and C_s alleles,

205   respectively, are as follows:

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

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

206   These analytical solutions are visualised in Figure (1a-c). Under random mating (i.e., $r = 0$), and

207   when either fully dominant or recessive ($h = 0$ or 1), the C_g allele invades and goes to fixation if

208    $s/t < 0.5$ (*i.e.*, when the haploid competitive benefit is more than twice the diploid fitness cost).

209   When diploid fitness effects are additive ($h = 0.5$), fixation occurs even as s/t approaches 1.0. C_g

210   wins under random mating as the C_s allele has no refuge from competition. Under complete

211   selfing ($r = 1$), C_g never invades. Pollen competition occurs only on heterozygotes, and since

212   selfing reduces heterozygote frequencies, opportunities for C_g-bearing pollen to outcompete C_s

213   effectively vanish. As C_s confers higher sporophyte fitness in the homozygous state, it increases

214   when rare.

215   The analytical solutions indicate that polymorphism can be maintained in mixed-mating

216   systems ($0 < r < 1$) with fixed selfing only if the deleterious effect of the C_g allele in the diploid

217   phase is recessive ($h < 0.5$) (Figures 1a-c, 2). When completely recessive ($h = 0$), there is a range

218   of selfing rates in which both alleles can invade, implying protected polymorphism. The C_g allele

219   invades because, when rare, it occurs exclusively in heterozygotes, where its negative effect on

220   diploid fitness is masked from selection and moderate selfing allow opportunities to outcompete

221   C_s-bearing pollen for ovules on heterozygotes. Within this range of selfing rates, the C_s allele

222   also increases when rare because, 1) heterozygotes have higher relative fitness than C_gC_g

223   homozygotes and 2) selfing reduces exposure of C_s pollen to competition with superior C_g

224   pollen.

225   Additive fitness effects ($h = 0.5$) largely prohibit polymorphism (Figures 1b, 2). When h

226    $= 0.5$, 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:

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

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

248   Taking the partial derivative of Eqs. 8a and 8b with respect to r lends insight into how these

249   critical s values change in response to selfing. (For a discussion of these partial derivative

250   expressions, see Appendix G). These show an increase in selfing rate always decreases the

251   maximum and minimum s values permitting invasion of Cg and Cs alleles respectively (Figure

252   1d-f). It then follows that increased selfing contracts the parameter space allowing invasion of an

253   allele conferring a benefit to pollen competitiveness at the expense of diploid fitness.

254   **Comparing invasion conditions for fixed and mass-action selfing**

255   Invasion conditions for the two selfing modes were qualitatively similar, with modest

256   quantitative differences. We compared sensitivity of the minimum and maximum s values

257   permitting invasion of C_s and C_g alleles to increases in r for both systems. (Partial derivative

258   expressions for fixed selfing are also provided in Appendix G). For a given set of h, s and t

259   values, r values allowing C_g and C_s invasion are slightly lower under mass-action selfing relative

260   to those of fixed-selfing (Figure 2), narrowing the permissible parameter space. Thus, under

261   mass-action selfing, the C_g allele can persist at higher selfing rates. Additionally, the range of r

262   values permitting polymorphism (when $h < 0.5$) or unstable equilibrium (when $h > 0.5$) contracts

263   under mass-action selfing, which is consistent with narrowed parameter space regions for

264   polymorphism and unstable equilibrium under mass-action selfing observed in Figure 2.

265   Under fixed selfing, male diploid fitness (pollen quantity) is moot since all flowers of

266   each genotype are assumed to produce enough pollen to fertilise their ovules. Under mass-action

267   selfing, the quantity of pollen produced by an individual affects its realized fertilisation success

268   through self-pollen, as each stigma can receive a mixture of C_g- and C_s- bearing pollen,

269   restricting the competition refuge for C_s. While each C_g-bearing grain has a greater chance of

270 success, this advantage is partially countered by lower pollen production in C_g homozygotes. The

271 different impacts on male function shift the invasion boundary upward under mass-action

272 selfing. For example, when $h = 0$, $s = 0.01$ and $t = 0.04$ (visualised as $s/t = 0.25$ on Figure 1), the

273 maximum selfing rate allowing the C_g allele to invade increases from roughly $r = 0.8$ to $r = 0.84$.

274 Likewise, the minimum selfing rate allowing C_s to invade increases from $r = 0.67$ to $r = 0.75$.

275 **Fixation and protected polymorphism**

276 Having established invasion conditions for the C_g and C_s alleles, this section explores their

277 equilibrium frequencies. We first present analytical solutions to the recursion equations (Eqns.

278 3a-c, 5a-c) assuming weak selection ($0 < s,\ t << 1$). We then highlight the difference in outcomes

279 when pollen competitiveness is under gametophyte genetic control, as Haldane speculated,

280 versus sporophyte control (seen in Jordan and Connallon 2014). Under fixed selfing, the

281 equilibrium value ($\hat{p}$) of the C_g allele is given as:

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

282 When C_g is recessive ($h < 0.5$) and mating is mixed ($0 < r < 1$), the denominator of the far-right

283 term is always positive. Whether $\hat{p}$ falls above or below 0.5 then depends on the sign of the

284 numerator. If $r < 1 - s/t$, then $\hat{p}$ will fall above 0.5 but fall below if the inverse is true. Simply,

285 the higher the selfing rate (r) the higher the diploid cost (s) needed to prevent C_g fixation, which

286 is implied by a $\hat{p}$ value < 0.5. When C_g is dominant ($h > 0.5$), the above expression gives the

287 repelling equilibrium frequency (above $\hat{p}$ the C_g allele goes to fixation and below is eliminated).

288 When $h > 0.5$ and mating is mixed, the denominator of the far-right term is always negative.

289 Thus, the repelling $\hat{p}$ value falls above 0.5 when the numerator is negative and below when

290 positive. Looking at the effect of selfing rate on $\hat{p}$, the threshold $\hat{p}$ allowing C_g invasion

291 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:

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

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).

314   As is visualised in Figures 1 and 3, invasion conditions and equilibrium allele frequencies

315   under both selfing modes assuming haploid control of pollen competitiveness are qualitatively

316   similar to those derived using models provided in Jordan and Connallon (2014), where

317   competitiveness is under paternal genotype control (for derivation of analytical results, see

318   online supplemental materials; for models and discussion of analytical solutions, see Appendix

319   B). They also found selfing and dominance restrict potential for stable polymorphism and

320   ultimately diminish selection through male function. Our results show, however, that

321   gametophytic control substantially expands the conditions favouring an allele promoting pollen

322   competitiveness. With gametophyte gene expression, pollen phenotype is more strongly

323   correlated with haplotype. Heterozygotes always produce a 50:50 mix of phenotypically and

324   genetically 'strong' and 'weak' pollen competitors. Under sporophytic control, heterozygotes can

325   produce phenotypically all strong ($h = 0$), all weak ($h = 1$), or all intermediate ($h = 0.5$)

326   competitors, despite always producing a 50:50 genetic mix. Further, under gametophytic control,

327   variance in competitive ability between pollen carrying opposite alleles is constant. Under

328   paternal control, variance in competitive ability changes with genotype frequency: increasing

329   heterozygote frequency decreases the difference in mean competitiveness of the two pollen

330   haplotypes. Consequentially, C_g invasion occupies a markedly smaller parameter space when

331   under diploid genetic control (Figure 1). By extension, we see that the C_g allele reaches a lower

332   equilibrium frequency, *i.e.*, invades with more difficulty, for a given selfing rate when it is

333   expressed in the sporophyte rather than the gametophyte (Figure 3).

334   Returning to Haldane's conjecture that plants are at the mercy of their pollen grains, how

335   strong must sporophyte selection against a pollen-competition allele be to prevent its fixation?

336   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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483   **Tables**

484 TABLE 1.   Summary of model outcomes for mutation to an allele that increases pollen (haploid

485 gametophyte) competitive ability but reduces survivorship or fertility in the (diploid) sporophyte.

EXPRESSION OF C_g IN DIPLOID SPOROPHYTE	MATING SYSTEM		
	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.

486

487   **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

511   being replaced by unstable equilibrium when $h > 0.5$. As the diploid selection coefficient s

512   increases relative to t, maintenance of the C_g allele requires either lower dominance h or less

513   allocation of reproductive structures to selfing, given by r. Compared to fixed-selfing, mass-

514   action selfing conditions permitting polymorphism versus unstable equilibrium are qualitatively

515   similar but quantitatively more limited. The placement of mass-action lines to the right of those

516   for fixed selfing are consistent with individual stigmas never receiving solely self-pollen except

517   when $r = 1$, which increases the opportunity for C_g to exercise its competitive superiority.

518   **Figure 3**

519   Analytical results of equilibrium frequency of the C_g allele across selfing rates $0 < r < 1$ under

520   gametophytic (haploid) and sporophytic (diploid) genetic control. Analytical solutions were

521   derived assuming weak selection. Solid lines indicate equilibrium allele frequencies, while

522   dashed lines indicated the analytical repelling frequency (i.e., the starting p frequency below

523   which p will be lost and above which it will fix). (a-c) Under the fixed-selfing model, the

524   window of selfing rates contracts as dominance increases. (d-f) Under the mass-action model, C_s

525   pollen is never entirely protected from competition with C_g pollen as individual stigmas receive a

526   mixture of both self and outcross pollen for intermediate selfing rates. Thus, maximum and

527   minimum selfing rates allowing fixation or maintenance of C_g and C_s alleles respectively are

528   right-shifted compared to under fixed selfing, reflecting the greater opportunity for the C_g allele

529   to exercise its advantage in pollen competition with the C_s allele. Notably, for both selfing

530   modes, the range of selfing rates at which the C_g allele can invade contracts under diploid genetic

531   control relative to haploid control.

532   **Figure 4**

533   Analytical results for equilibrium frequency of the C_g allele across a range of s/t, i.e., ratios of

534   diploid and haplod fitness values. Series specify selfing rates r ranging between 0 and 1. Under

535   both (a-c) fixed and (d-f) mass-action selfing models, increases in dominance of the C_g allele

536   sharply decrease the maintenance of polymorphism, particularly at lower selfing rates. Noticably,

537   for a given combination of selfing rate r and dominance h, the C_g allele persists at higher ratios

538   of s and t under mass-action selfing relative to fixed-selfing , reflecting the greater opportunity

539   for C_g-bearing pollen to compete C_s-bearing pollen under mass-action selfing. For both selfing

540   models, regardless of dominance, the C_g allele cannot invade under complete selfing, i.e., $r = 1$.

<div align="center">**Appendices**</div>

542   **Appendix A**

543   *Implications of sex-specific dominance*

544   Given we assume diploid selection acts either through lower flower production or reduced

545   survival, we also assume a common dominance coefficient h for female and male function (i.e.,

546   quantities of ovule and pollen produced). However, it is possible to consider the effects of

547   different dominance coefficients for male and female function, given as h_m and h_f. In such a case,

548   absolute fitness via female function for C_gC_s individuals is $W_{1f} = 1-h_f s$ and that via male function

549   is $W_{1m} = 1-h_m s$. Absolute fitness terms for homozygote individuals remain unchanged from the

550   main text. Using these sex-specific dominance coefficients, we can derive new expressions for

551   equilibrium frequency of the C_g allele under weak selection for both fixed (Eq. A1) and mass-

552   action (Eq. A2) selfing:

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

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

553   To understand the relative impacts of changing h_f and h_m on $\hat{p}$, we can take the partial derivative

554   of the above equations first with respect to h_f and then with respect to h_m. For fixed selfing, these

555   partial derivatives are as follows:

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

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

556   With simple arranging, it can be shown that

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

557   In a mixed mating system where $0 < r < 1$, the far-left term of the right-hand side of Eq. A5 is

558   always greater than 1 and increasing as selfing rate increases, meaning an increase in h_f always

559   yields a greater change in $\hat{p}$ than a comparable increase in h_m. This is expected, as under fixed

560   selfing, the cost to male diploid fitness is only paid through outcrossing, as we assume all plants

561   produce enough pollen to self-fertilise. Conversely, diploid fitness effects on female function are

562   recognised both in selfing and outcrossing. Thus, the effects of changing female and male

563   dominance terms are only equivalent under complete outcrossing ($r = 0$) and Eq. A5 reduces to

564     $\frac{\partial \hat{p}}{\partial h_f} = \frac{\partial \hat{p}}{\partial h_m}.$

565   We can also compare the effect of increasing h_f relative to a shared dominance coefficient

566   h. Returning to Eq. A3, it is evident that the denominator is always positive, while the sign of the

567   numerator changes from positive to negative when r switches from less than $\frac{-s+t}{t}$ to more than

568     $\frac{-s+t}{t}$. This particular value, $\frac{-s+t}{t}$, gives the selfing rate r at which $\hat{p}$ is 0.5. Looking specifically

569   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

593   depicting $h_f = 0.25$ and $h_m = 0.25$ both remain fixed for p up to higher selfing rates, but also drop

594   (and thus lose p entirely) at lower selfing rates, when compared to $h_f = h_m = 0$.

595   Turning to mass-action selfing, the partial derivatives of Eq. A2 with respect to h_f (Eq.

596   A6) and h_m (Eq. A7) are as follows:

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

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

597   Rearrangement of Eqs. A6 yields:

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

598   As seen under fixed selfing, an increase to h_f will yield greater change to $\hat{p}$ than an equivalent

599   change to h_m. Interestingly, the ratio of these changes is not the same between fixed and mass-

600   action selfing. Relative to a change in h_m, an equivalent increase in h_f under mass-action selfing

601   has a weaker effect on $\hat{p}$ than under fixed selfing, as evidenced by comparing the coefficients of

602   Eqs. A5 and A8, $\frac{(1+r)}{(1-r)}$ and $\frac{1}{(1-r)}$ respectively (assuming $r > 0$). This can be understood by

603   considering where diploid selection on male function acts in mass-action selfing. Unlike fixed

604   selfing, costs to pollen production are paid both through both self-pollen and outcross-pollen, as

605   both pollen types compete on the same stigma. Differences in pollen competitive ability offset

606   costs through diploid male fitness, thus allowing an increase in h_m to still have less impact on $\hat{p}$

607   than an increase in h_f. The lesser effect of altering h_m on $\hat{p}$ can be seen in Figure A1. Compared

608   to fixed selfing, increasing h_m produces less deviation from baseline series (*i.e.*, those with

609   equivalent h_m and h_f values).

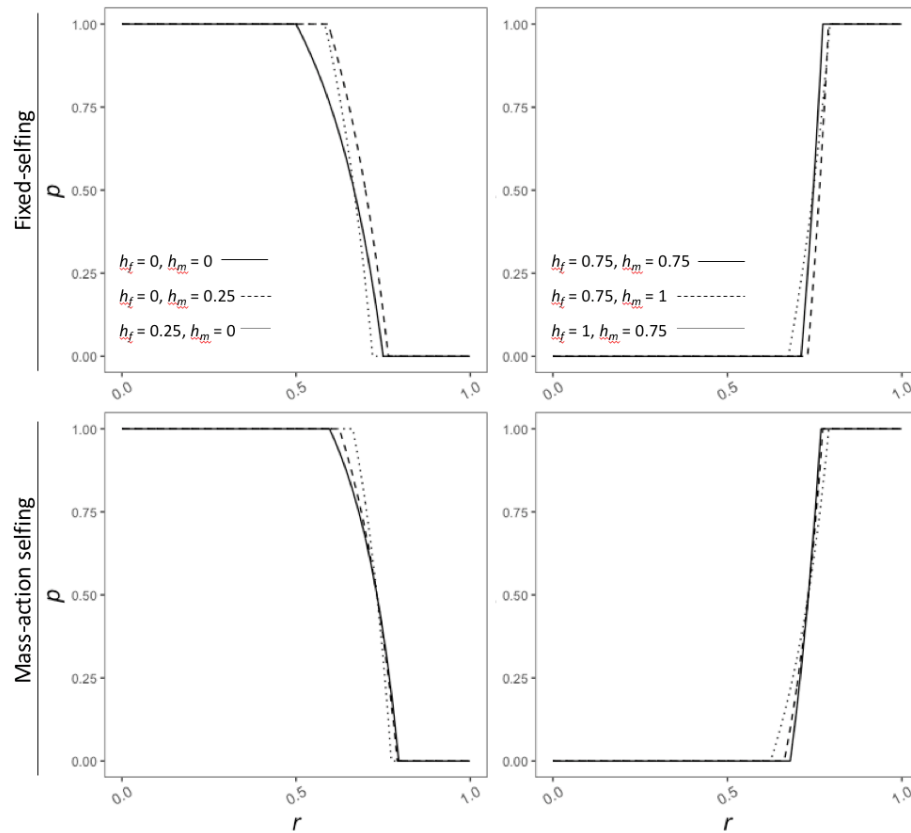611 <center>**FIGURE A 1**</center>

612 **Appendix B**

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

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

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

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

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

615 Where s is the selection coefficient acting on female function, h is the dominance coefficient and

616 $\overline{W_f}$ is defined as

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

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

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

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

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

618   Where t is the selection coefficient acting on male function, h is the dominance coefficient and

619    $\overline{W_m}$ is defined as

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

620   Using these fitness expressions, the genotype recursion equations are:

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

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

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

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

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

622   In the case of fixed selfing, selfing rate ρ is equivalent to r (i.e., proportion pollen allocated to

623   selfing). Under mass-action selfing, ρ is frequency-dependent and genotype-specific:

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

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

625   to selfing.

626   Equilibrium allele frequencies for fixed and mass-action selfing assuming sporophytic

627   control were derived using the same methods provided in the main text and are as follows:

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

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

628   We can understand the conditions under which the C_g allele will perform better under

629   sporophytic control relative to haploid and *vice versa* by taking the difference between Eqs. 10

630   (main text) and B16 as well as Eqs. 11 (main text) and B15. Under fixed selfing:

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

631   In Eq. B16, when $h < 0.5$, the denominator is always negative. The sign of the numerator is

632   dependent on the size of s relative to t. When diploid selection s is larger than haploid selection t,

633   the numerator is positive and thus $\Delta\hat{p}$ is negative, revealing the C_g allele is more successful under

634   sporophytic than gametophytic genetic control. Inversely, when $s < t$ (as presented in the main

635   text), $\Delta\hat{p}$ is positive and C_g reaches a higher frequency under gametophytic control.

636   Under mass-action selfing:

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

637   When $h < 0.5$ and $0 \le r \le 1$, the denominator of B17 is negative. Thus, the sign of $\Delta\hat{p}$ is

638   dependent on the sign of the numerator. Given $0 \le r \le 1$, (r^2+r-2) is always negative and

639    $(2r^2-r-2)$ is always positive, meaning the numerator is always negative and $\Delta\hat{p}$ is always

640   positive. In other words, when $h < 0.5$, the C_g allele will always do better under gametophytic

641   control than under sporophytic control. Conversely, when $h > 0.5$, the denominator is positive

642   while the numerator remains unchanged. In such a case, $\Delta\hat{p}$ is always negative and the C_g allele

643   reaches a higher equilibrium frequency under sporophytic control. These analytical results are

644   visualised in Figure 3, in which, when $h = 0$, the equilibrium allele frequency $\hat{p}$ is higher for

645   gametophytic (i.e., haploid) control relative to sporophytic and, when $h = 1$, the repelling allele

646   frequency below which C_g cannot invade is higher under sporophytic control (meaning fixation

647   requires a higher initial allele frequency). This result can be understood easily by considering the

648   haplotype-phenotype correspondence under both gametophytic and sporophytic genetic control.

649   Under gametophytic control, this correspondence is complete (i.e., phenotype reflects haplotype

650   and the Cg allele always confers a benefit to pollen). Under sporophytic control, this

651   correspondence is a function of the paternal genotype (homozygote or heterozygote) and the

652   dominance coefficient h, and thus, the Cg allele will not always confer its maximum advantage

653   to pollen ability, weakening its invasion ability.

654   Likewise, invasion conditions for fixed and mass-action selfing assuming sporophytic

655   control were derived using the methods found in the main text. Under fixed selfing, maximum

656   and minimum selfing rates permitting invasion of C_g and C_s alleles respectively are given as:

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

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

657   The corresponding expressions for mass-action selfing are:

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

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

658

659   **Appendix C**

660   *Production of heterozygote offspring via selfing with variable pollen competitiveness*

661   With a simple Punnet square, it can be demonstrated that even with differential competitive

662   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*	$\frac{1}{2(2-t)} C_g C_g$	$\frac{1-t}{2(2-t)} C_g C_s$
C_s **ovule** *0.5 allele frequency*	$\frac{1}{2(2-t)} C_s C_g$	$\frac{1-t}{2(2-t)} C_s C_s$

663   TABLE C 1

664   Together, the frequency of heterozygote offspring produced via heterozygote selfing is $\frac{1}{2(2-t)} +$

665     $\frac{1-t}{2(2-t)}$, which reduces to ½.

666   **Appendix D**

667   *Analytical results for mass-action selfing with pollen discounting*

668   Pollen discounting, i.e., loss of pollen for outcrossing during transport, can be incorporated by

669   inclusion of an additional term, *d,* which gives the proportion of pollen lost and is identical to the

670   pollen discounting term included in Jordan and Connallon (2014). Equations 5a-c are thus

671   modified to be:

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

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

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

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

$$+ \frac{1}{2}x_1 \left[\frac{r\frac{1}{2}W_1(1-t) + (1-r)(1-d)\left(x_2 + \frac{1}{2}x_1\right)(1-t)}{P_1} \right] \tag{D3}$$

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

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

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

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

673 Using Eqs. D1-6, and assuming weak selection, we can derive the equilibrium frequency of the

674 C_g allele. For the full expression, see the corresponding online supplemental materials. To

675 understand the effects of increasing d on $\hat{p}$, we take the partial derivative of the $\hat{p}$ expression

676 with respect to d:

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

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

678 appears to:

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

679 The term $d(r-1)$ is always negative (when $0 < r < 1$), so how d affects the equilibrium allele

680 frequency is dependent on the sign of the following term:

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

681   With further rearrangement, it can be shown that:

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

682   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

683   d always lowers the equilibrium frequency of the C_g allele. This is not surprising as inclusion of

684   a pollen discounting term $d > 0$ should decrease the relative proportion of outcross- versus self-

685   pollen that a stigma receives, therefore decreasing the realised competitive advantage of C_g

686   pollen, under the mass-action selfing model.

687   In other words, under mass-action selfing, intermediate r values indicate a stigma

688   receives both self and outcross pollen. Successful invasion and fixation of either the C_g or C_s

689   allele depends on the ratio of self to outcross pollen produced, with higher values of r favouring

690   the C_s allele. Pollen discounting essentially alters this ratio, allowing the C_s allele to invade and

691   fix at lower values of r, which thus implies limited invasion of the C_g allele.

692   Figure D1 displays this effect of pollen discounting on the success of the C_g allele using t

693     $= 0.1$, $s = 0.05$ and d values of 0, 0.2 and 0.5. Indeed, as d is increased, the equilibrium frequency

694   of the C_g allele becomes increasingly left-shifted, implying a decreased range of selfing rates at
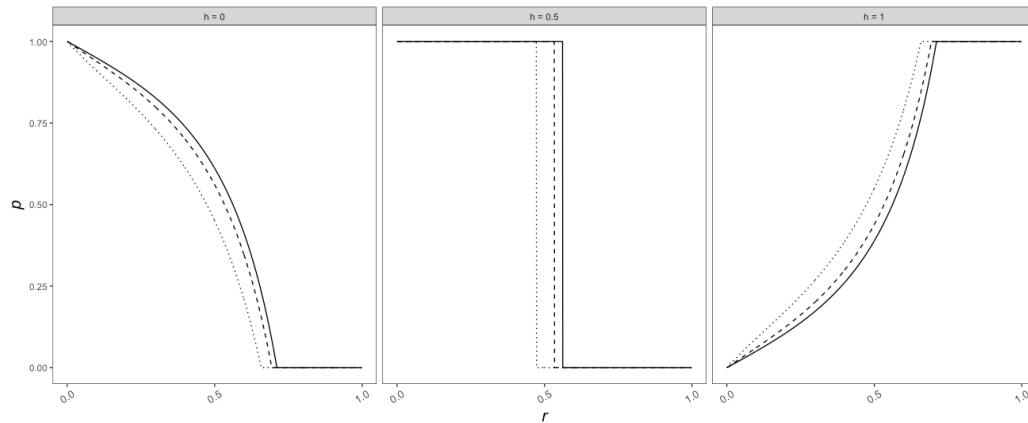
695   which it can successfully invade.

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 $50,000^{th}$ 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.

714   As stated in the main text, analytical solutions assume weak (s, $t \ll 1$). However, we

715   found that analytical results under relatively strong selection still provided a qualitatively good

716   fit to their corresponding numerical results under both haploid and diploid control of pollen

717   competitive ability (grey series, Figure E1), suggesting interpretations presented in the main text

718   are broadly applicable across a wide range of selection strengths. In Figure E1, weak selection

719   indicates $s = 0.01$ and $t = 0.03$ strong selection indicates $s = 0.05$ and $t = 0.1$.

720
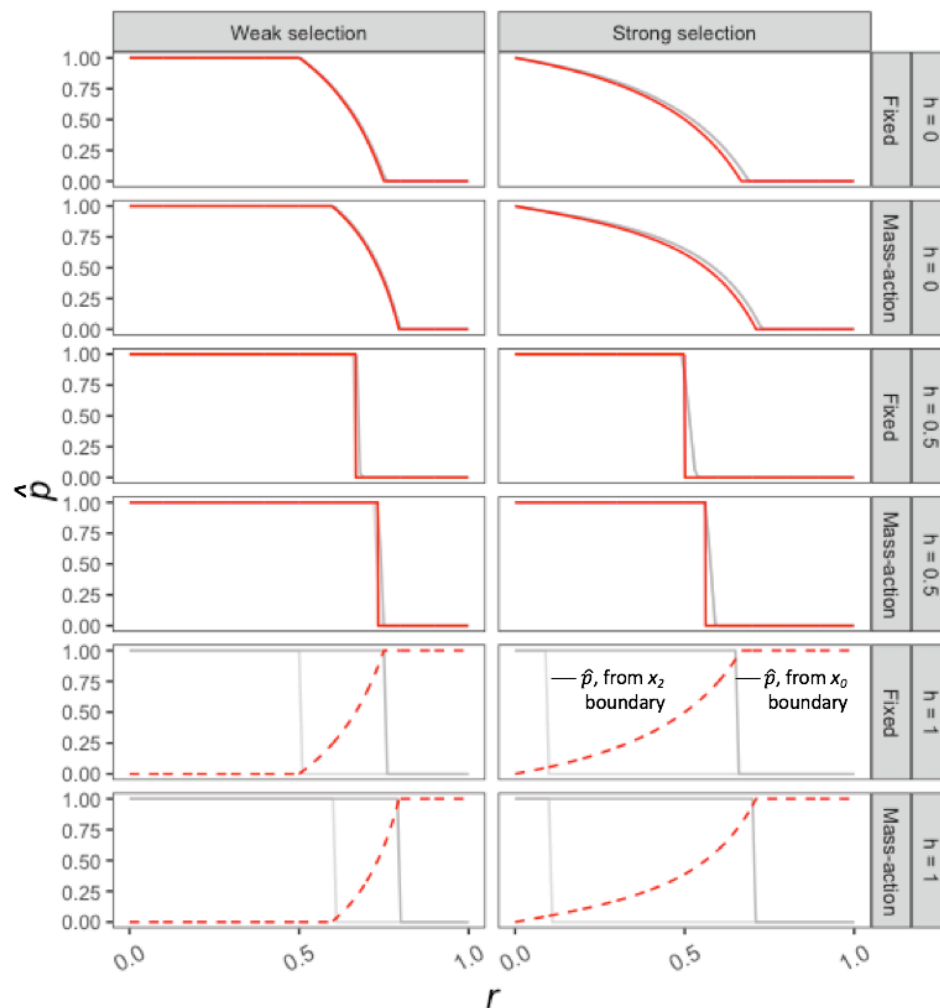
721   FIGURE E 1

722   Importantly, when $h = 1.0$, drops in equilibrium allele frequencies from 1 to 0 for all

723   combinations of selection strength and selfing mode are immediate, i.e., there are no

724   intermediate equilibrium values (i.e., $0 < \hat{p} < 1$). Any slopes are the result of the increment

725   chosen for the x axis ($0 \leq r \leq 1$ by 0.01).

726   In addition to a comparison with numerical results under strong selection, we can also

727   compare invasion conditions under fixed selfing assuming weak selection to conditions derived

728   without assuming weak selection. For example, Eqs. 7a and 7b in the main text give maximum

729   and minimum selfing rates for C_g and C_s invasion respectively under weak selection. Without

730   this assumption, these maximum and minimum r values are:

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

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

731   Comparison with expressions 7a and 7b in the main text can be easily considered visually

732   (Figure E2), in which series were generated using $t = 0.1$.

733
734   FIGURE E 2
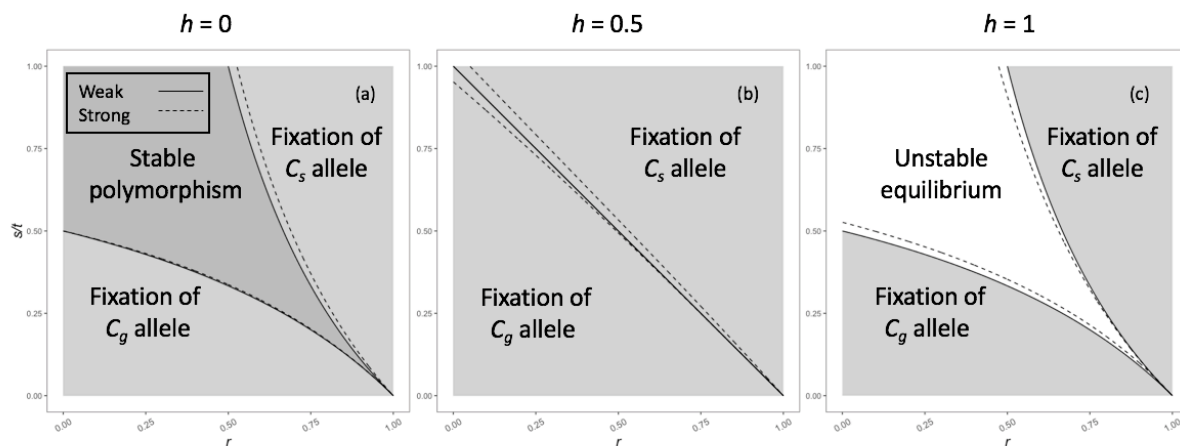
735   Perhaps most notable in Figure E2 is the small space permitting polymorphism when $h = 0.5$ at

736   low values of r. This result is consistent with Figure E1, in which under strong selection there are

737   true numerically-derived intermediate equilibrium allele frequencies (i.e., $0 < \hat{p} < 1$) when $h =$

738   0.5, unlike under weak selection. Overall, we find strong qualitative agreement between invasion

739 conditions predicted both with and without weak selection, suggesting our results likely hold for

740 a broader range of selection parameters than those presented in the main text.

741 **Appendix F**

742 *Critical selfing rates under mass-action selfing*

743 Using the methods described in the main text, the analytical solutions specifying the selfing rates

744 required for invasion C_g and C_s alleles under mass-action selfing are as follows:

745 For C_g: $r <$

$$
-\frac{s-4hs+t}{3\,(-s+2hs)} - \\
\left(2^{1/3}\left(-(s-4hs+t)^2+3\,(-s+2hs)\,(2s-2hs+t)\right)\right)\Big/\Big(3\,(-s+2hs)\,\big(-20\,s^3+42\,hs^3+84\,h^2s^3-160\,h^3s^3+21\,s^2t-60\,hs^2t+12\,h^2s^2t- \\
15\,st^2+42\,hst^2-2\,t^3+\sqrt{\big((-20\,s^3+42\,hs^3+84\,h^2s^3-160\,h^3s^3+21\,s^2t-60\,hs^2t+12\,h^2s^2t-15\,st^2+42\,hst^2-2\,t^3)^2+} \\
\overline{4\,\big(-(s-4hs+t)^2+3\,(-s+2hs)\,(2s-2hs+t)\big)^3\big)}\big)^{1/3}\Big)+ \\
\frac{1}{3\times2^{1/3}\,(-s+2hs)}\Big(-20\,s^3+42\,hs^3+84\,h^2s^3-160\,h^3s^3+21\,s^2t-60\,hs^2t+12\,h^2s^2t-15\,st^2+42\,hst^2-2\,t^3+ \\
\sqrt{\big((-20\,s^3+42\,hs^3+84\,h^2s^3-160\,h^3s^3+21\,s^2t-60\,hs^2t+12\,h^2s^2t-15\,st^2+42\,hst^2-2\,t^3)^2+} \\
\overline{4\,\big(-(s-4hs+t)^2+3\,(-s+2hs)\,(2s-2hs+t)\big)^3\big)}\Big)^{1/3}
$$

(F1)

746 For C_s: $r >$

$$
-\frac{-3s+4hs+t}{3s-6hs}+\left(2^{1/3}\left((9-30h+28h^2)\,s^2+(-9+14h)\,st+t^2\right)\right)\Big/ \\
\Big(3\,(-1+2h)\,s\,\big((54-270h+396h^2-160h^3)\,s^3-3\,(-9+12h+4h^2)\,s^2t+3\,(-9+14h)\,st^2+2\,t^3+3\sqrt{3}\sqrt{(-(s-2hs)^2\,(576\,h^4s^4-32\,h^3s^3}} \\
\overline{(27s-37t)+12\,hst\,(135\,s^2-100\,st+17\,t^2)+4\,h^2s^2\,(81\,s^2-558\,st+205\,t^2)+t\,(-432\,s^3+441\,s^2t-134\,st^2+9\,t^3))))}\big)^{1/3}\Big)+ \\
\frac{1}{3\times2^{1/3}\,(-1+2h)\,s}\Big((54-270h+396h^2-160h^3)\,s^3-3\,(-9+12h+4h^2)\,s^2t+3\,(-9+14h)\,st^2+2\,t^3+ \\
3\sqrt{3}\sqrt{(-(s-2hs)^2\,(576\,h^4s^4-32\,h^3s^3\,(27s-37t)+12\,hst\,(135\,s^2-100\,st+17\,t^2)+} \\
\overline{4\,h^2s^2\,(81\,s^2-558\,st+205\,t^2)+t\,(-432\,s^3+441\,s^2t-134\,st^2+9\,t^3))))}\Big)^{1/3}
$$

(F2)

747 **Appendix G**

748 *Critical diploid selection coefficients under mass-action and fixed selfing*

749 Taking the partial derivative of in-text Eqs. 8a and 8b with respect to r produces Eqs. G1 and G2

750 respectively, which in turn provide insights into the effect of increasing selfing rate on the

751 conditions permitting invasion:

$$
\frac{\partial s}{\partial r}=\frac{\left(-4+r\left(4-2h(r-1)^2(4+r)-r(-5+r(2+r))\right)\right)t}{(-2-2h(r-1)+r)^2(2+r-r^2)^2}
$$

(G1)

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

752   Assuming h, s, t and r all fall between 0 and 1, the above expressions are always negative,

753   implying the critical value of s always decreases as r increases (Figure 1). When $h < 0.5$, the

754   maximum value of s permitting C_g invasion decreases more slowly as r increases than the

755   minimum s value permitting C_s invasion. This results in a range of r values in which s is below

756   the maximum value for C_g invasion and above the minimum value for C_s value, producing the

757   potential for polymorphism. Conversely, when $h > 0.5$, the minimum s for C_s invasion decreases

758   more quickly in response to r than the maximum value for C_g invasion. This produces a range of

759   r values in which neither allele can invade (i.e., unstable equilibrium). Focusing on the effect of

760   selfing on the C_g allele, increasing r contracts the parameter space allowing invasion of an allele

761   conferring a benefit to pollen competitiveness.

762   To compare effects of fixed versus mass-action selfing on invasion, we can compare how

763   minimum and maximum s values permitting invasion of C_s and C_g alleles respond to increases in

764   r in these two selfing systems. Below are expressions for how the maximum and minimum s

765   values change in response to r under fixed selfing:

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

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

766   We can easily visualise differences between Eqs. G1,2 and G3,4, and thus how critical s values

767   respond to r under mass-action versus fixed selfing, by considering the case in which $h = 0.25$
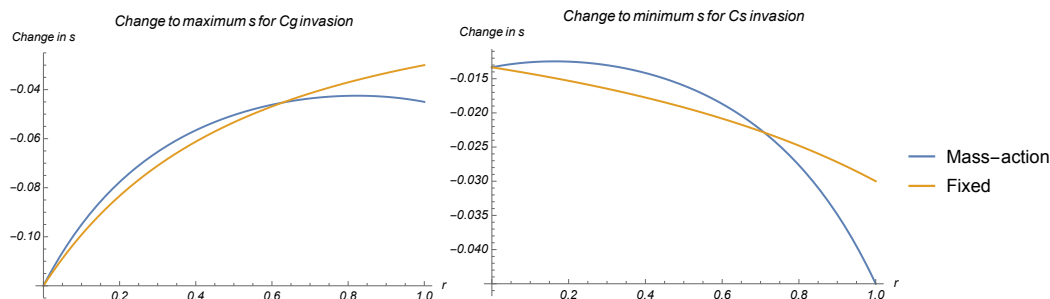
768   and $t = 0.03$ (Figure G1).

769

770   **FIGURE G 1**

771   For both maximum and minimum s values, it is clear that the critical s value decreases more

772   rapidly for fixed selfing than mass-action as r increases from 0, as evidenced by the initially

773   lower (*i.e.*, more negative) values for the fixed $\frac{\partial s}{\partial r}$ series than for mass-action series. This

774   difference implies that for a given s value, the critical r value allowing C_g invasion will be lower

775   than that of mass-action selfing. Indeed, we find this to be true.
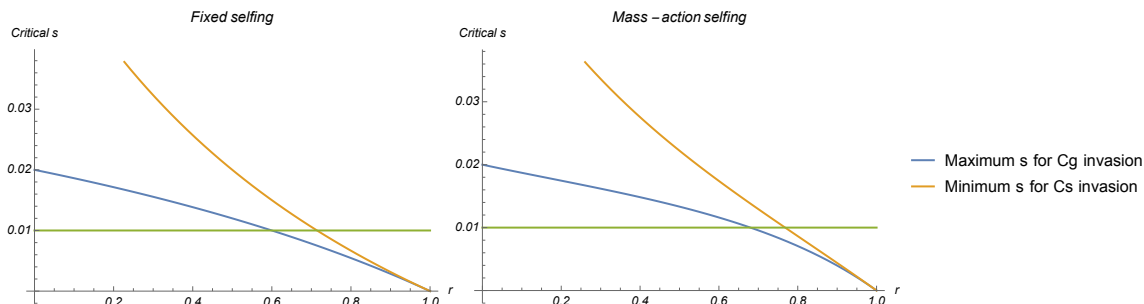
776

777   **FIGURE G 2**

778 For a given s value (in this case 0.01, as given by the green series in Figure G2), both maximum

779 and minimum s values permitting invasion are right-shifted along the r axis. This indicates the C_g

780 allele can be maintained at higher selfing rates under mass-action selfing than fixed selfing.

781 Returning to Figure G1, the difference in $\frac{\partial s}{\partial r}$ between fixed and mass-action selfing for a given r

782 value is greater when considering the maximum s permitting C_g invasion than the minimum s

783 permitting C_s invasion. While the minimum s for C_s invasion is right-shifted under mass-action

784 selfing compared to fixed selfing, the magnitude of this shift is less than that of the

785 corresponding maximum s values. Put together, this results in a contracted range of r values

786 permitting polymorphism, which can be seen in Figure G2 as the space in which the minimum s

787 series falls above the $s = 0.01$ series and the maximum s series falls below ($0.69 < r < 0.77$ under

788 mass-action selfing; $0.56 < r < 0.73$ under fixed selfing).

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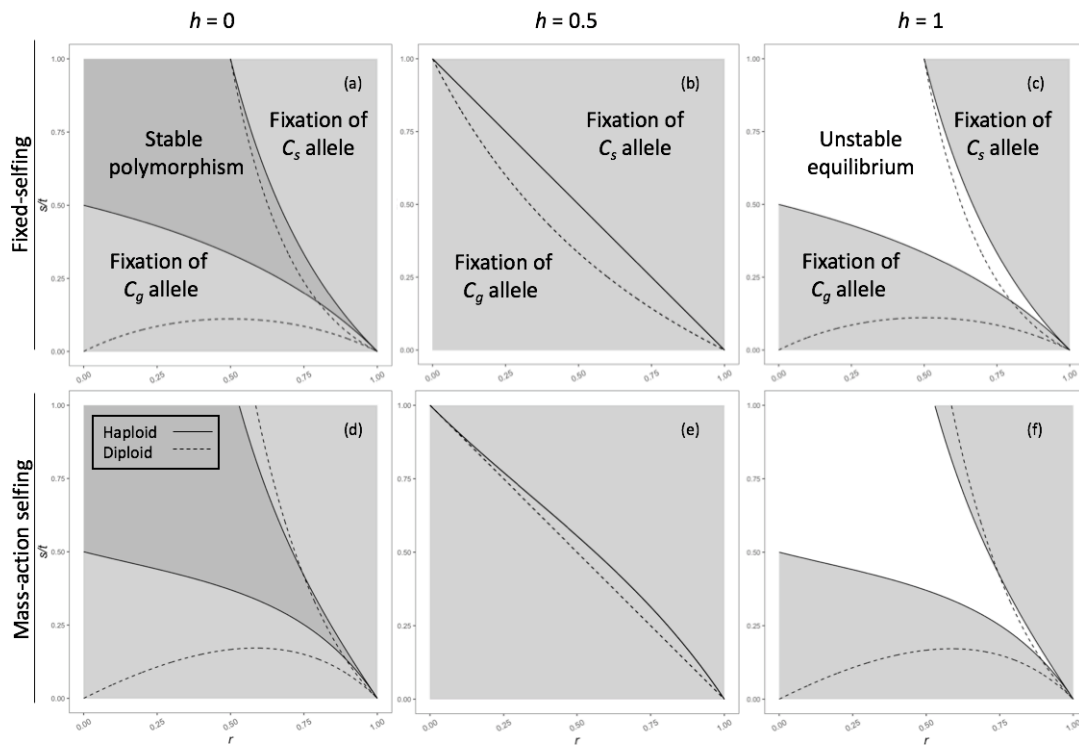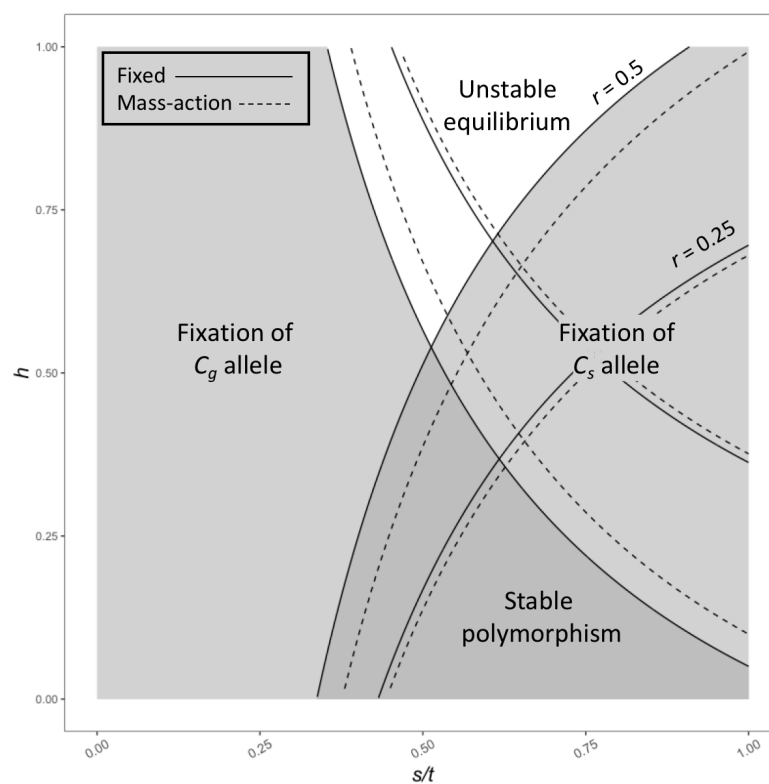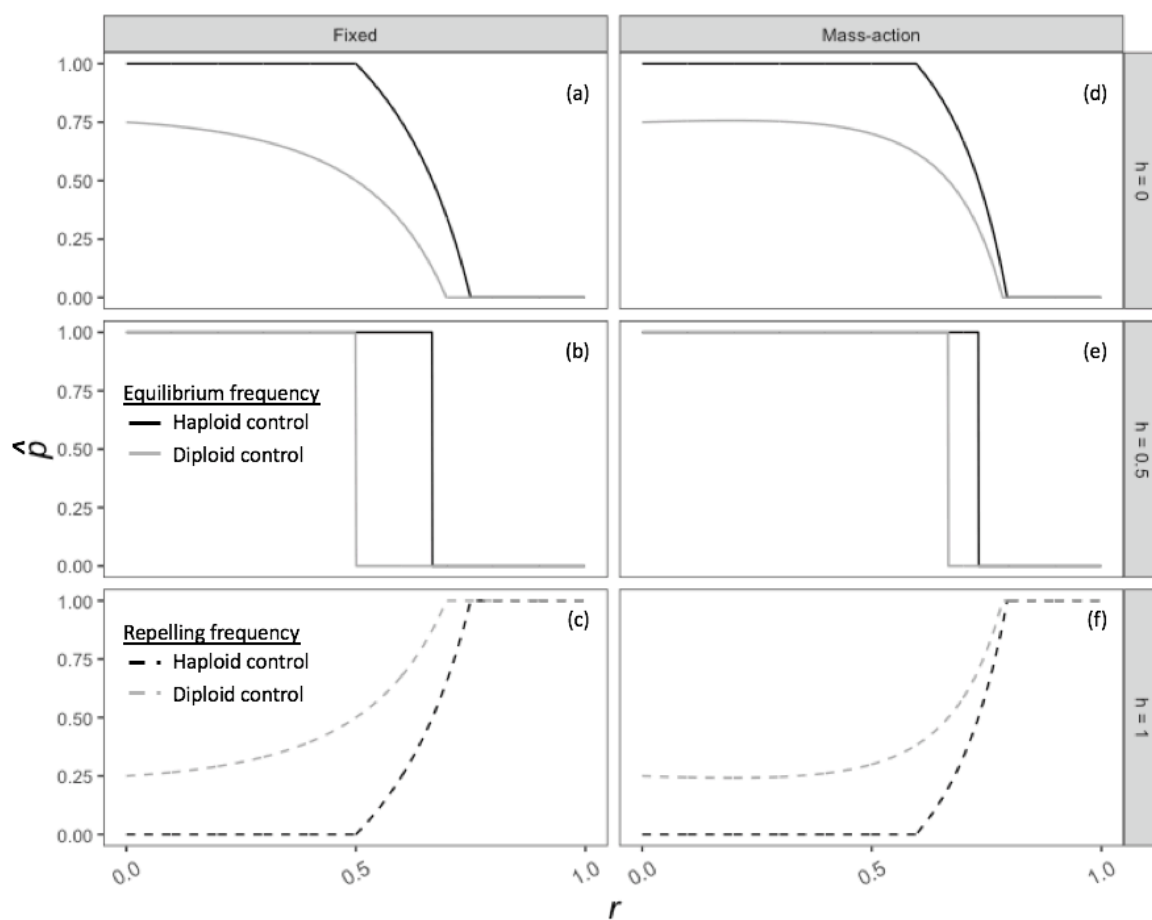
790 equilibria, not protected polymorphism.

803   **Figures**

FIGURE 2

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FIGURE 3

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810   **FIGURE 4**

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FIGURE 5