1   Too attractive to self: How pollinators can interfere with the evolution of selfing.

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8   **ABSTRACT**

9   Pollinators are widely invoked to explain the evolution of selfing despite genetic conditions

10   favoring outcrossing. But their role in maintaining outcrossing despite genetic conditions

11   favoring selfing remains unexplored. We use consumer-resource models to explicitly consider

12   the how the plant-pollinator mutualism can constrain the evolution of selfing. We model

13   outcrossing as a function of attractiveness and account for the cost of attractiveness as a

14   saturating, linear, or exponential function alongside the costs of selfing: inbreeding depression

15   and pollen discounting. We show specific, clear combinations of ecological and genetic

16   conditions where pure selfing can invade a resident population of partial selfers. Complete

17   selfing can evolve in the face of pollen discounting so long as there is a cost to pollinator

18   attraction and reward. However, we also predict conditions under which mixed mating is

19   maintained even when inbreeding depression is low. Our model highlights how under some

20   scenarios mixed mating represents the worst of both worlds, leaving plants to pay the costs of

21   both inbreeding depression and attraction and even leading to extinction. By linking pollinator

22   attraction to the selfing rate, our models provide a likely common mechanism to explain pollen

23   discounting and an alternative evolutionary pathway to the selfing syndrome.

24   **INTRODUCTION**

25   The evolutionary transition from outcrossing to selfing is considered among the most

26   common in Angiosperms (Stebbins, 1974). Classic models predicting this transition hinge on the

27   balance between two genetic factors: inbreeding depression and an automatic transmission

28   advantage (or cost of outcrossing) (Fisher, 1941; Nagylaki, 1976; Lloyd, 1979; Charlesworth,

29   1980; Lande and Schemske, 1985). Because complete outcrossers have only two pathways to

30   pass on their alleles (i.e. outcross seed, outcross siring) but partial selfers have three (i.e. outcross

31   seed, selfed seed, outcross siring), partial selfers should establish and spread within an

32   outcrossing population. That is, unless the reduction in fitness of selfed offspring relative to

33   outcrossed offspring through inbreeding depression is great enough to eliminate the 50%

34   automatic transmission advantage of selfing. Consequently, there should be disruptive selection

35   on the mating system. Despite early empirical data supporting this prediction (Schemske and

36   Lande, 1985), more recent analyses indicate that 63% of species have at least one population

37   with a mixture of selfing and outcrossing ('mixed mating'; Whitehead *et al.*, 2018) and 12% are

38   outcrossing despite low inbreeding depression (Winn *et al.*, 2011). Thus, the quest to understand

39   the drivers of mating system evolution endures.

40   While original models emphasize the role of genetic factors, mating in most flowering

41   plants is an ecological process involving interactions with pollinators. Not surprisingly,

42   consideration of pollination conditions, most notably pollen limitation, has solved part of the

43   problem of mixed mating (reviewed in Goodwillie, *et al.,* 2005; Knight *et al.*, 2005). Theoretical

44   and empirical work illustrates how partial selfing can be favored in the face of high inbreeding

45   depression if such selfing boosts seed production compared to outcrossed individuals when

46   mates or pollinators are limiting (Lande and Schemske, 1985; Lloyd, 1992; Jarne and

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47   Charlesworth, 1993; Kalisz, *et al.,* 2004; Eckert, *et al.,* 2006). Indeed, selection for reproductive

48   assurance in the face of pollen limitation is the most well accepted force favoring the evolution

49   of selfing more generally (Busch and Delph, 2012). However, reproductive assurance alone

50   cannot explain why outcrossing persists in spite of low inbreeding depression, underscoring that

51   we have not yet fully explored the conditions that favor or constrain the evolution of selfing.

52   Explicit consideration of pollination as a mutualism involving plant and pollinator as

53   equally interdependent actors can highlight how pollinators might constrain the evolution of

54   selfing (Devaux *et al*., 2014; Lepers, *et al.,* 2014; Spigler and Kalisz, 2017). Pollinators depend

55   critically on floral resources for their own metabolic demands and for provisioning their broods.

56   As long as this dependence exists and their local abundances are great enough, pollinators could

57   enforce outcrossing, even if plants are capable of autonomous selfing and even if genetic

58   conditions favor selfing (i.e., inbreeding depression is low) (Spigler and Kalisz, 2017). Near

59   exclusive focus on the role of pollen limitation on mating system evolution has neglected this

60   possibility, and it is worth noting that pollen limitation is often negligible and not necessarily

61   ubiquitous (Knight *et al.*, 2005; Rosenheim *et al.,*, 2014; Rosenheim *et al.*, 2016; but see Burd,

62   2016). Holsinger (1991) recognized the impact of pollinator abundance and plant density on the

63   evolution of selfing and rooted his single-locus model of the evolution of mixed mating on a

64   simple fact: the outcrossing rate is a function of how much outcross pollen is received. Also

65   explicit is the ecological trade-off of pollen discounting: pollen used for selfing cannot be used

66   for outcrossing and vice versa (Nagylaki, 1976b Charlesworth, 1980; Holsinger, *et al.,* 1984;

67   Holsinger, 1991). In considering the ecological dynamics of pollinators and pollen discounting,

68   Holsinger (1991) demonstrated theoretically not only that outcrossing could be favored in the

69   absence of inbreeding depression but also that complete selfing will never be stable unless there

70   is pollen limitation. We stress that this single-locus model does not account for the feedback

71   between plant and pollinator populations that is inherent to the mutualism. As an alternative,

72   consumer-resource models (e.g., Holland and DeAngelis, 2010) allow us to ask how pollinators

73   can influence the evolution of selfing by explicitly connecting plant and pollinator dynamics

74   (e.g., Lepers, *et al.,* 2014).

75   The economics of participating in the mutualism could also play a pivotal role in the

76   evolution of selfing. Specifically, plants pay a price for pollinator services through floral

77   attraction and rewards. Empirical studies of floral construction and maintenance costs of highly

78   outcrossing flowers indicate that they can be substantial (Schemske, 1978; Waller, 1979),

79   comprising a large fraction of a plant's carbon budget and exacting tolls via transpiration and

80   respiration (Nobel, 1977; Ashman and Baker, 1992; Ashman and Schoen, 1997; Ashman and

81   Schoen, 1994; Galen, 1999; Teixido and Valladares, 2014). Although floral investment costs are

82   not often considered in models of mating system evolution (but see Sakai, 1995 and Lepers, *et*

83   *al.,* 2014), the potential for links between investment in attractiveness and the mating system is

84   clear. Attraction should be positively correlated both with investment costs and outcrossing.

85   These associations tack on an additional cost of outcrossing and create a clear mechanism for

86   pollen discounting. Unattractive individuals may escape pollinators and thus achieve high selfing

87   even in the face of high pollinator abundance, but this comes at the expense of exporting pollen

88   and siring outcross offspring. Given these links, the question about the evolution of complete

89   selfing becomes one about whether reductions in investment costs could enable plants to not only

90   realize higher selfing rates but also to recoup some or all of the costs paid through inbreeding

91   depression and pollen discounting. Indeed, across angiosperms smaller flowers are associated

92   with higher rates of selfing ('selfing syndrome'; Sicard and Lenhard, 2011). Moreover, as the

93   population on average becomes less attractive and provides fewer rewards, pollinator densities

94   could decline, which in turn would further select for increased selfing rates via reproductive

95   assurance. We are aware of only one model that explicitly considered plant pollinator dynamics

96   in concert with floral costs (Lepers, *et al.,* 2014), but it does not address pollen discounting.

97   In this study, we present consumer-resource models that consider plant and pollinator

98   densities, selfing rate, inbreeding depression, plant attractiveness to pollinators, and the cost of

99   attraction (or unattractiveness) including pollen discounting to evaluate the conditions under

100   which higher rates of selfing can evolve. In contrast to most models that begin with a population

101   of outcrossers and evaluate invasion of partial selfers, we consider whether and how higher rates

102   of selfing can evolve within a population that is already partially selfing (mixed mating). First,

103   we ask under what general conditions can an unattractive, completely selfing mutant replace a

104   resident population of partial selfers whose selfing rate is a continuous function of attractiveness

105   (Model 1). Next, we explore conditions when a less attractive, potentially more highly selfing

106   mutant can invade a resident population of partial selfers at equilibrium with their pollinator

107   partner (Model 2). We highlight ecological conditions that may restrict the evolution of complete

108   selfing and uncover conditions where complete selfing may still be expected to evolve.

109

110   **METHODS**

111   Our two models explore the relationship between pollinator dynamics and the relative

112   success of an attractive resident vs. a less attractive invader with a higher effective selfing rate.

113   Each of these models is based on a system of three ordinary differential equations (ODE),

114   described below. All parameter definitions and default values are shown in Table 1. Explanations

115   for these values can be found in Appendix A.

116   *Model 1: Complete vs. partial selfers*

117   Model 1 explores the dynamics of our system where an attractive partial-selfer (P)

118   competes with an invader (S) that exclusively reproduces through selfing. In this system, the

119   animal pollinator (A) only interacts with the partial selfer, although it can maintain a positive

120   population size as a 'generalist' feeding on other flowers that are external to the two-species

121   system.

122   The growth rate of the resident partial selfer's population density, P, is given by equation

123   1. The resident produces r ovules per individual per unit time, representing its maximum intrinsic

124   growth rate. These ovules can either be fertilized through outcrossing or selfing, where

125   outcrossing occurs according to the rate of interactions between plants and pollinators.

126   Pollinators visit flowers according to their attractiveness, a_P, as a saturating function of plant and

127   animal densities with a half-saturation constant h_1. Any ovules that are not fertilized through

128   outcrossing are fertilized through delayed selfing (we assume no self-pollen limitation), with

129   survival discounted by inbreeding depression, δ. The resident plant experiences density

130   dependent mortality according to the density of P and S individuals combined, which are

131   assumed to be competing for common resources. The resident also experiences losses through

132   the cost it pays to produce attractive flowers and nectar for pollinators, where cost is a saturating

133   function of attractiveness, a_P, with a half saturation constant h_2, up to a maximum per capita cost

134   c. The cost of attraction as a single metric is supported by empirical evidence of positive

135   correlations between flower size and reward in some systems (e.g., Stanton and Young, 1994;

136   Campbell, 1996; Fenster *et al.*, 2006; Tavares, *et al.*, 2016).

137

138    $$\frac{dP}{dt} = rP\left(\frac{a_P PA}{h_1+PA} + (1-\delta)\left(1-\frac{a_P PA}{h_1+PA}\right)\right) - mP\left(1+\frac{P+S}{k}\right) - cP\left(\frac{a_P}{h_2+a_P}\right) \qquad (1)$$

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139

140   The invading complete selfer population density, S, also produces r ovules per individual,

141   and since all ovules are fertilized through selfing, successful fertilization is discounted by

142   inbreeding depression, δ. Because the selfer is completely unattractive to pollinators, there are no

143   mating events between the complete selfers and the resident partial selfers. The invader

144   experiences the same density-dependent mortality as the resident. Its growth rate is given as:

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146
$$\frac{dS}{dt} = rS(1 - \delta) - mS\left(1 + \frac{S+P}{k}\right) \tag{2}$$

147

148   The animal pollinator population density, A, grows based on its consumption of floral

149   resources, represented by an intrinsic growth rate ρ that is independent of the resident plant

150   density. The pollinator population can also benefit from feeding on the resident partial-selfer,

151   where β is the maximal per-capita benefit and the actual benefit is a saturating function of plant

152   density. The pollinator also experiences density-dependent mortality, with a maximum mortality

153   rate of μ scaled by a density-dependent factor K. Its growth rate is defined as:

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155
$$\frac{dA}{dt} = \rho A + \beta_P A\left(\frac{a_P P}{h_3 + P}\right) - \mu A\left(1 + \frac{A}{K}\right) \tag{3}$$

156

157   The model was run according to default parameter values shown in Table 1.

158

159   *Model 2: Invasion dynamics of a less attractive mutant*

160   Model 2 explores a case wherein a mutant genotype (M) arises in a resident population of

161   partial-selfing plants (P) fertilized by a generalist animal pollinator (A). The mutant genotype is

162   less attractive than the resident ($a_M<a_P$) but is otherwise biologically identical. Because the

163   mutant arises from the resident population, it is initially very rare (one individual) and arises in a

164   resident population that is initially at equilibrium with its animal pollinator. Consistent with

165   previously validated phenotypic models (Cheptou, 2004; Lepers, *et al.*, 2014), we assume that

166   when outcrossing occurs between resident and mutant genotypes, 50% of the offspring exhibit

167   the resident phenotype, while 50% exhibit the mutant phenotype.

168   This model consists of an ODE with three equations, one for the resident partial-selfer

169   (P), one for the less attractive mutant (M), and one for the animal pollinator (A).

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171
$$\frac{dP}{dt} = rP\left(\left(\frac{a_P PA}{h_1 + [P + (a_M/a_P)M]A} + \frac{1}{2}\frac{a_M MA}{h_1 + [P + (a_M/a_P)M]A}\right)\right.$$

172
$$+ (1-\delta)\left(1 - \left(\frac{a_P PA}{h_1 + [P + (a_M/a_P)M]A} + \frac{a_M MA}{h_1 + [P + (a_M/a_P)M]A}\right)\right)\right)$$

173
$$+ rM\left(\frac{1}{2}\frac{a_M PA}{h_1 + [P + (a_M/a_P)M]A}\right) - mP\left(1 + \frac{M+P}{k}\right) - cP\left(\frac{a_P}{h_2 + a_P}\right)$$

174   (4)

175

176
$$\frac{dM}{dt} = rM\left(\left(\frac{a_M MA}{h_1 + [P + (a_M/a_P)M]A} + \frac{1}{2}\frac{a_M PA}{h_1 + [P + (a_M/a_P)M]A}\right)\right.$$

177
$$+ (1-\delta)\left(1 - \left(\frac{a_M PA}{h_1 + [P + (a_M/a_P)M]A} + \frac{a_M MA}{h_1 + [P + (a_M/a_P)M]A}\right)\right)\right)$$

178
$$+ rP\left(\frac{1}{2}\frac{a_M MA}{h_1 + [P + (a_M/a_P)M]A}\right) - mM\left(1 + \frac{M+P}{k}\right) - cM\left(\frac{a_M}{h_2 + a_M}\right)$$

179   (5)

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180
$$\frac{dA}{dt} = \rho A + \beta_P A \left(\frac{a_P P}{h_3 + [P + (a_M/a_P)M]} \right) + \beta_M A \left(\frac{a_M M}{h_3 + [P + (a_M/a_P)M]} \right) - \mu A \left(1 + \frac{A}{K} \right)$$

181 $\hspace{38em}$ (6)

182

183   The resident partial selfer population density, P, grows according to the fraction of its total ovule

184   production (rP) devoted to outcrossing with other residents, outcrossing with mutants, and

185   selfing (Eqn 4). Within the parentheses following rP, the first term indicates the fraction of

186   ovules fertilized by the pollinator with pollen from other plants with the resident genotype.

187   Outcrossing is a saturating functional response (half saturation constant h_1) of plant and

188   pollinator densities, and depends upon the attractiveness, a_P, of the resident plant, with 100% of

189   these ovules result in an offspring with the resident phenotype. The second term indicates the

190   fraction of ovules fertilized by the pollinator with pollen from plants with the mutant genotype.

191   Again, outcrossing is a saturating functional response of plant and pollinator densities but

192   depends upon the attractiveness of the less-attractive mutant, a_M, such that when the mutant is

193   very unattractive, between-genotype outcrossing occurs at a low rate regardless of the

194   attractiveness of the resident, a_P. From these ovules, 50% of offspring exhibit the resident

195   phenotype, while 50% exhibit the mutant phenotype. The remaining term within the parentheses

196   following rP indicates the fraction of ovules produced by the resident that are not fertilized by

197   the pollinator, and therefore are fertilized through delayed selfing. Of these self-fertilized ovules,

198   a fraction $(1-\delta)$ survives, accounting for mortality due to inbreeding depression, δ. As with

199   Model 1, we assume no pollen limitation; all ovules not fertilized with outcrossed pollen are

200   fertilized with self-pollen. In the next model term, rM indicates total mutant ovule production,

201   and the term following rM indicates the fraction of these ovules fertilized through outcrossing

202   with resident plants that result in a resident phenotype. Finally, the resident plant experiences

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203   losses through density dependent mortality according to a maximum mortality rate m and a

204   density dependent term k. The resident also experiences a cost of pollination that is independent

205   of pollinator density but increases as a function of attractiveness following three alternative cost

206   functions (figure 1). In the first scenario the cost of pollination increases to a maximum cost c_P

207   at a saturating rate with attractiveness, a_P, based on a half-saturation constant h_2 (shown in text).

208   In the second, the cost of pollination increases linearly with attractiveness. In the third function,

209   the cost of pollination increases at an accelerating rate as the plant becomes more attractive.

210   The less attractive mutant population density, M, grows according to an identically

211   structured equation (Eqn 5), where the primary difference between species is that the mutant is

212   less attractive than the resident ($a_M < a_P$).

213   The animal pollinator population density, A, grows based on its consumption of the two

214   plant genotypes as well as through external floral resources (Eqn 6). When the pollinator is a

215   generalist, it feeds on external floral resources, represented by an intrinsic growth rate ρ that is

216   independent of the resident and mutant genotype densities. The pollinator population density can

217   also increase through feeding on the resident partial selfer and the mutant, where β_i is the

218   maximal per-capita benefit and the actual benefit is a saturating function of genotype densities

219   with a half-saturation constant h_3. The pollinator also experiences density-dependent mortality,

220   with a maximum mortality rate of μ scaled by a density-dependent factor K.

221   The model is written on the assumption that $a_M \leq a_P$, and therefore conditions where a

222   mutant that is more attractive than the resident partial selfer never exist. This assumption plays

223   into the model structure in the attractiveness terms, where the probability of outcrossing between

224   genotypes depends on the attractiveness of the mutant rather than the resident. This assumption

225   also influences the denominator of the pollination functional response, where pollinator satiation

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226   based on mutant abundance is weighted by the relative attractiveness of the mutant. We note that

227   where $a_M = 0$ (i.e., where the attractiveness differential $= 1$), the mutant is a complete selfer and

228   this model collapses to the case of Model 1.

229   *Model 2 Analysis*

230   We analyzed the model to determine under which conditions the mutant (M) would meet

231   the invasion criterion of exhibiting a positive population growth rate when rare when the resident

232   partial selfer (P) and the animal pollinator (A) were at equilibrium. The two-equation system for

233   the resident genotype and pollinator could not be solved analytically, so equilibrium densities

234   were calculated through numerical simulations. Under each set of parameter values, the model

235   was simulated for 5000-time steps in the software program *Mathematica*, using the 'NDSolve'

236   numerical integrator. This resulted in convergence on stable densities for both the resident

237   genotype, P, and its animal pollinator, A, under all conditions presented here. After equilibrium

238   densities were calculated for all relevant scenarios, initial mutant growth rate was calculated

239   based on Eqn 5.

240   We note that Model 2 is written to apply when the mutant is rare and that the simple

241   relationship between genotype and phenotype that we assumed here is unlikely to apply when the

242   mutant is common. As such, in contrast to Model 1, we cannot view Model 2 as an equilibrium

243   model. Instead, we analyze Model 2 based on the invasion criterion of the mutant exhibiting a

244   positive population growth rate when rare and cannot speak to the outcome of the mutant

245   invasion in the long-term.

246

247   **RESULTS**

248   *Model 1: Complete vs. partial selfer*

249   Model 1 examines the outcome when a partial selfer competes with a complete selfer.

250   Strikingly, we find a large parameter space over which the complete selfer wins (figure 2), even

251   in the face of complete pollen discounting. When the resident is highly attractive ($a_P = 0.8$), the

252   complete selfer can win at low inbreeding depression levels only ($\delta < 0.25$). At such levels, the

253   complete selfer fertilizes all ovules but pays neither the cost of making flowers nor a substantial

254   cost of inbreeding. Therefore, it replaces the partial selfer, who pays a high cost of attractiveness.

255   However, as inbreeding depression increases, the balance tips in favor of the partial selfer.

256   Although the partial selfer still pays the same cost of making flowers, its high rate of outcrossing

257   allows it to largely avoid the cost of inbreeding depression. The complete selfer, however, pays

258   the cost of inbreeding depression on all progeny. The partial selfer can persist even when

259   inbreeding depression is complete ($\delta=1$) because it maintains maximum levels of outcrossing

260   when it is highly attractive (figure B1), though equilibrium density of the partial selfer declines

261   with increasing inbreeding depression (figure 2 *A*).

262   As the attractiveness of the resident partial selfer decreases, the complete selfer wins at

263   increasingly higher levels of inbreeding depression while the range over which the partial selfer

264   can win becomes greatly restricted, instead going extinct. When the partial selfer is moderately

265   attractive (e.g., $a_P = 0.5$), the dynamics for the complete selfer do not change drastically from the

266   case of the highly attractive partial selfer (complete selfer now wins up to $\delta \sim 0.3$), but the partial

267   selfer only wins when inbreeding depression is between 0.3 and 0.6 and declines to extinction

268   when $\delta > 0.6$. The moderate reduction in attractiveness has two key consequences for the partial

269   selfer. First, under a saturating function this reduction in attractiveness barely reduces the cost of

270   attractiveness compared to the case of $a_P=0.8$ (figure 1). Second, the partial selfer now has a

271   higher selfing rate and so incurs a higher cost of inbreeding for a larger proportion of seeds. This

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272   combination represents the worst of both worlds associated with mixed mating, resulting in

273   greater net losses for the partial selfer. Consequently, the pure selfer wins at marginally greater

274   inbreeding depression values because it still pays no cost of attraction, and the partial selfer

275   occurs at a lower density even where it wins (figure 2 *A* vs 2 *B*). At even lower levels of

276   attractiveness (e.g., $a_P = 0.2$), the partial selfer fares even worse because it now self-fertilizes at a

277   rate nearly identically to the complete selfer yet continues to pay some cost of attractiveness.

278   This scenario tips the scale in favor of the complete selfer, such that the complete selfer wins up

279   to the boundary value of $\delta=0.5$. After that point, neither type of selfer persists (Fig 2 *C*).

280   *Model 2: Invasion dynamics of a less attractive mutant*

281   With Model 2, we fix the attractiveness level of a resident partial selfer and asked

282   whether a less attractive mutant can invade when rare. The attractiveness of the mutant is defined

283   relative to that of the resident in terms of an 'attractiveness differential'. When the resident is

284   highly attractive ($a_P=0.8$) and the maximum cost of pollination is set at $c=0.03$, a saturating cost

285   function means that initial decreases in the mutant's attractiveness relative to a highly attractive

286   resident—represented as low values of the attractiveness differential—do not appreciably

287   decrease floral investment costs (figure 1). Yet the selfing rate still increases linearly (figure 1).

288   This combination combined with inbreeding depression strongly restricts the ability of the

289   mutant to invade, even at $\delta<0.1$ (figure 3 *A*). Once the attractiveness differential reaches ~ 0.5 or

290   greater, however, the savings in investment costs for the mutant increases, and the benefits of

291   reduced flower/reward costs begin to offset the cost of greater selfing at even higher inbreeding

292   depression levels. This benefit is reflected in the rapidly growing region in which the mutant can

293   invade as attractiveness differential continues to increase (figure 3 *A*). Even still, the mutant

294   overall remains limited by inbreeding depression. Note that at an attractiveness differential of 1

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295   (a_P=0.8 and a_S=0), results are identical to our first model for a_P=0.8, since the mutant is a

296   complete selfer.

297   Compared to a saturating cost function, linear and exponential curves always result in a

298   lower cost for a given level of attractiveness (figure 1) and so create more favorable conditions

299   for a less attractive, more highly selfing mutant to invade when the resident is highly attractive

300   (figure 3). Now, the mutant can invade over a greater combination of attractiveness differentials

301   and inbreeding depression values than it can under a saturating curve. When the cost of attraction

302   is an increasing linear of attractiveness, it is inversely related to the selfing rate. Consequently,

303   any change in attractiveness (and thus cost of attraction) is balanced by a proportional change in

304   selfing rate (and thus proportion of individuals paying the cost of inbreeding depression). This

305   creates a critical threshold value of inbreeding depression; below this threshold the mutant can

306   invade at any attractiveness differential (figure 3). As long as inbreeding depression is below this

307   threshold, any losses the mutant pays from inbreeding depression will be outweighed by gains

308   from the reduction in attraction costs, and the initial growth rate of the mutant is positive.

309   When instead the cost function is exponential, the mutant is more successful at invading

310   at lower attractiveness differentials (figure 3). Under this cost function, small reductions in

311   attraction relative to a highly attractive resident (a_P=0.8) result in a dramatic decrease in costs

312   that is disproportionate to the linear increase in selfing rate. Hence, the savings from reduced

313   attractiveness offset the losses to inbreeding depression. With further decreases in attractiveness

314   under and exponential function, however, the reduction in cost diminishes. Functionally, this

315   leads to a slight retraction of the range of inbreeding depression values over which the mutant

316   can invade as the attractiveness differential increases.

317   We find that the impact of altering the attractiveness of the resident depends on the shape

318   of the cost function (figure 3 B vs. 3 A). When the resident is only moderately attractive (a_P=0.5),

319   the region over which the mutant can invade expands under a saturating cost curve, remains the

320   same under a linear cost curve, and contracts under an exponential curve. Under a saturating

321   curve, expansion arises when the resident starts out less attractive (a_P=0.5) because the mutant's

322   lower attractiveness finally begins to pay off in terms of cost savings (see figure 1). The reverse

323   occurs under an exponential cost function at a_P=0.5 because the reduction in attractiveness costs

324   with the reduction in attractiveness begins to slow down, and difference in floral costs paid by

325   the mutant at increasingly greater attractiveness differentials becomes minimal. In addition, a

326   less attractive resident exhibits negative growth rates and goes extinct over a range of inbreeding

327   depression values, with the threshold dictated by the cost curve (figure 3). As in Model 1, this

328   consequence arises because moderate attractiveness results in the worst of both worlds scenario

329   when inbreeding depression is high.

330   When we double the maximum cost of pollination to the resident (c=0.06), the shape of the

331   parameter space remains the same, but the size of the space in which the mutant can successfully

332   invade doubles (figure 3). Under this scenario, the equilibrium density of the resident is lower

333   compared to the case of c=0.03, making it easier for the mutant to have positive growth rates and

334   successfully invade at higher inbreeding depression levels. Another key difference when the

335   maximum pollination cost is greater is that the resident goes extinct over a larger range of

336   parameter values. For a highly attractive resident (a_P=0.8), we see this across all cost curves

337   (compare top and bottom panels of figure 3 A), though inbreeding depression threshold above

338   which the resident goes extinct varies across cost curves. When the resident is moderately

339   attractive (a_P=0.5), the level of inbreeding depression at which it goes extinct decreases slightly

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340 under an exponential cost function, remains the same under a linear cost function, and drastically

341 decreases under a saturating cost function such that extinction is predicted even when $\delta<0.5$.

342

343 **Discussion**

344   With our model we considered whether the role of pollinator availability can cut both

345 ways. That is, if a lack of pollinators can sustain mixed mating despite genetic conditions

346 selecting against selfing, can the presence of pollinators also sustain mixed mating despite

347 genetic conditions favoring greater selfing? If so, what are the conditions that define how and

348 when selfing can evolve when pollinators are abundant? Our consumer-resource modeling

349 approach reveals how the economics of floral investment, pollen discounting, and inbreeding

350 depression interact to maintain mixed mating in species capable of autonomous selfing and finds

351 limited circumstances under which greater selfing rates can evolve when pollinators are

352 abundant.

353 *Pay to Play*

354   Despite inclusion of pollination biology in theoretical models of mating system evolution

355 (reviewed in Goodwillie, Kalisz and Eckert, 2005), the cost of participating in the pollination

356 mutualism by generalist-pollinated plants has largely been ignored (but see Lepers, Dufay and

357 Billiard, 2014; Sakai, 1995). Most mutualisms, however, incur a cost (Bronstein, 2001),

358 including generalist pollination systems (Morris, Vázquez and Chacoff, 2010). Key to remaining

359 in the mutualism is whether the benefits provided outweigh such costs. For self-compatible plant

360 species, the alternative to investing in pollinator attraction is to fail to attract pollinators, self-

361 fertilize, and pay the potentially greater toll inflicted by inbreeding depression. Thus, to outcross,

362 plants must pay to play. When the cost of attraction enters the mating-system evolution equation,

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363   the situation becomes about whether reductions in investment costs enable plants to both realize

364   higher selfing rates and recoup the costs paid through inbreeding depression. Not surprisingly

365   then, we find that increasing maximum floral investment cost increases the parameter space over

366   which more highly selfing individuals can invade.

367   Consideration of the level of attractiveness of the resident partial selfer and its interaction

368   with the shape of the associated cost function leads to new and surprising results. In our first

369   model considering a pure selfer and a saturating cost curve, for example, we show that it is more

370   difficult for a complete selfer to win against a *more* attractive, partial selfer than a *less* attractive

371   partial selfer. This result is somewhat counterintuitive, since the greater the attraction, the greater

372   the floral costs paid by the partial selfer. But, attractive plants outcross and in doing so avoid

373   paying the cost of inbreeding depression. For a completely attractive plant in Model 1, paying

374   the cost of attraction alone is less expensive than the cost paid by a pure selfer in the currency of

375   inbreeding depression, until inbreeding depression is low enough such that the balance is tipped

376   in favor of the pure selfer (< 0.2 based on the parameter values modeled here). In contrast, less

377   attractive partial selfers begin paying the cost of inbreeding depression on top of floral costs,

378   paving the way for pure selfers to win at increasingly greater levels of inbreeding depression.

379   This result highlights the fact that mixed maters can get stuck paying double, and when the

380   combined costs of inbreeding depression and attraction become too great, go extinct.

381   Nevertheless, these dynamics create a parameter space over which mixed mating ($0.2<s<0.8$) and

382   even outcrossing ($s<0.2$) can win against a pure selfer when $ID<0.5$.

383   When we consider different cost functions and investigate conditions under which higher

384   selfing rates may evolve via the invasion of a less attractive mutant, we find that the shape of the

385   cost function can drive mating system evolution and the potential for the stability of mixed

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386 mating. In general, the evolution of selfing is more permissive under linear and exponential cost

387 functions than under a saturating one. However, we reveal an interaction between the resident's

388 attractiveness and the shape of the cost function: as the attractiveness of the resident increases,

389 the evolution of higher selfing rates becomes more permissive under an exponential cost function

390 but less permissive when the cost curve is saturating. Although there exist limited cost estimates

391 related to floral construction or maintenance (e.g., Oakley, Moriuchi and Winn, 2007; Ashman

392 and Schoen, 1994; Ashman and Schoen, 1997; Galen, 1999), the shape of the cost function is not

393 known for any species. Our model results suggest that variation among species in cost functions,

394 due to differences in factors such as reward type, flower size and floral longevity, could drive

395 variation in the conditions necessary for higher selfing rates to evolve.

396   Our approach complements and extends the work by Lepers et al. (2014). They too

397 emphasized the co-evolution of mating system and floral traits and showed how, in some cases,

398 pollinators may interfere with the evolution of selfing. However, there are important differences

399 between the studies. First, Lepers at al. (2014) considered a broader set of conditions including a

400 gradient of pollinator specialization. When the mutualism is highly specialized, plant and

401 pollinator densities are tightly coupled, which can feed back to create simultaneous mate and

402 pollinator limitation and favor selfing. In this way, Lepers at al. (2014) more fully take advantage

403 of consumer-resource dynamic feedbacks. However, we restricted our analysis to the case of the

404 more common generalized pollinator (Waser *et al.*, 1996; Ollerton, 1996; Thomson, 2003)

405 because our goal was to explore whether and how selfing could arise without pollinator

406 limitation. Second, and to that end, although both studies consider autonomous selfing, we

407 elected to model delayed selfing, while Lepers et al. (2014) modeled prior selfing (sensu Lloyd,

408 1979). Prior selfing could provide another avenue by which plants may be able to evolve selfing

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409   in the presence of pollinators (Brys, *et al.,* 2016; Randle, *et al.,* 2018; Spigler and Kalisz, 2017)

410   as could reduced herkogamy, but our emphasis on delayed selfing further allows for the

411   elimination of pollen limitation as plants compensate for reductions in outcross pollen receipt

412   (i.e. reproductive assurance). In addition, because the correlation between selfing rate and

413   attractiveness in our model arises from pollinator behavior and not underlying genetic

414   architecture, we create a scenario where pollinators enforce outcrossing, flipping the sign of the

415   interaction to negative for the plant when inbreeding depression is low. Delayed selfing with low

416   inbreeding depression might not be that uncommon (Goodwillie and Weber, 2018). Finally, the

417   model of Lepers et al. (2014) is free from pollen discounting, the reduction in pollen export with

418   increased self-pollination, a potentially critical parameter shaping mating system evolution

419   (Nagylaki, 1976; Charlesworth, 1980; Holsinger, Feldman and Christiansen, 1984; Johnston *et*

420   *al.*, 2009), whereas it an essential component in ours. Ultimately, while our model may represent

421   a more limited case, we are uniquely able to account for the presence of mixed-mating species

422   with low inbreeding depression (Winn *et al.*, 2011).

423   *Pollen discounting*

424   In our models, both the resident and less attractive mutant can experience pollen

425   discounting as a function of their attractiveness. Unattractive flowers self-pollinate more because

426   they receive fewer pollinator visits; yet because they do not receive as many visits they also

427   export less. In modeling this connection, we gain another novel outcome: even with pollen

428   discounting and abundant pollinators, the evolution of complete selfing is possible. This occurs

429   because less attractive, more highly selfing individuals are able to recoup or even overcome the

430   costs of inbreeding depression and pollen discounting through reduced floral expenses. Pollen

431   discounting in our model is independent of the cost of attractiveness, but an emergent property is

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432 that the severity of pollen discounting increases non-linearly with inbreeding depression (figure

433 B2). This is because as inbreeding depression increases, the *gains* to the mutant via selfing

434 decrease by a constant percentage while siring *gains* remain the same. This could also be

435 explained by density since resident density declines linearly with inbreeding depression (figure

436 B3). We see that selfing *rate* is impacted neither by inbreeding depression nor density of the

437 resident, but siring *rate* increases in proportion to density with higher rates of inbreeding

438 depression. We cannot say the degree to which pollen discounting and the change in its severity

439 with inbreeding depression (or density) influences our results relative the influence of the cost of

440 attractiveness. In particular, because the mutant is so rare, its highest siring rate is <1% of

441 resident ovules when resident density > 0. Nevertheless, these patterns highlight the importance

442 of considering the links between pollinator visitation, plant density, inbreeding depression, and

443 pollen discounting and suggests that selfers could pay an even higher cost of selfing when

444 inbreeding depression is high. Future modeling efforts will explicitly account for the role of

445 pollen discounting and its context dependency.

446 *Caveats*

447   Several features of our model and assumptions may limit its generality. Although

448 consumer-resource dynamic modeling can expand our understanding of the roles that

449 demography and ecological interactions have in mating system evolution, they are inherently

450 phenotypic, demographic models, not genetic models. Therefore, we can only count ovules

451 produced and cannot properly account for the transmission advantage, nor how it may change as

452 the frequency of selfing increases in the population (Holsinger, 1991). In addition, we note that

453 inbreeding depression stays constant within our model. Inbreeding depression may evolve

454 alongside the selfing rate and so influence the outcome of mating system evolution (Lande and

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455   Schemske, 1985; Charlesworth and Charlesworth, 1987; Charlesworth and Charlesworth, 1990;

456   Charlesworth, *et al.,* 1990; Husband and Schemske, 1996; but see Lande, *et al.,* 1994 and Winn

457   *et al.*, 2011). However, because our study is primarily concerned with initial invasion conditions

458   over relatively short ecological time periods, the assumption of equivalent inbreeding depression

459   levels between the mutant and resident is reasonable. Inclusion of additional parameters or

460   correlations such as those between flower size and ovule number or flower size and number (e.g.,

461   Worley and Barrett, 2000; Worley and Barrett, 2001; Caruso, 2004; Delph *et al.*, 2004; Spigler

462   and Woodard, 2019) would undoubtedly influence our outcomes. Further, pollinator-mediated

463   selfing is influenced by floral display size and flower size and can lead to pollen discounting

464   (Harder and Barrett, 1995) but is not consider here. Finally, we assumed that all genotypes are

465   equally capable of autonomous selfing, such that selfing ability, per se, and floral attraction (such

466   as flower size) vary independently. Future models can investigate variation in both attraction and

467   selfing ability to examine their joint evolution and outcomes for the evolution of selfing and the

468   selfing syndrome.

469   *Evolutionary implications*

470   Our model provides an alternative hypothesis for the origin of the selfing syndrome. We

471   consider: what if small flower size is what allows plants to achieve higher selfing rates to begin

472   with? That is, if pollinators are abundant and enforce outcrossing, then high rates of selfing can

473   only be achieved if flowers are unattractive. Our results illustrate how pure selfers only have an

474   advantage if their floral investment is sufficiently reduced. We recognize that because we are

475   modeling a case without pollen limitation, where individuals are already capable of autonomous

476   selfing, that this scenario may be applicable under a restrictive set of cases. Nevertheless, it

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477   provides an alternative pathway to the common association between flower size and mating

478   system in angiosperms (Sicard and Lenhard, 2011).

479   Our models also lead to predictions about the success of mutations with varying effect

480   sizes. Understanding the genetic basis of adaptation and the distribution of underlying effect

481   sizes represents active areas of theoretical and empirical research (Yeaman and Whitlock, 2011;

482   Savolainen, *et al.,* 2013; Dittmar *et al.*, 2016). Studies of floral and mating system traits have

483   found evidence for both alleles of large and small effects (Bradshaw *et al.*, 1995; Bernacchi and

484   Tanksley, 1997; Fishman, *et al.,* 2002; Goodwillie, *et al.,* 2006; Slotte *et al.*, 2012; Ferris *et al.*,

485   2017). Our models investigating the invasion of a more highly selfing mutant suggest that the

486   success of large vs. small effect alleles is highly context dependent, determined by the shape of

487   the cost function, maximum floral cost, attractiveness of the resident, and inbreeding depression.

488   Under a saturating cost function, a mutation of large effect, creating a large attractiveness

489   differential between the resident and mutant, will be successful at invading over a wider range of

490   inbreeding depression values and may allow for a more rapid evolutionary shift to higher selfing.

491   In contrast, invasion success of alleles of small effect is highly restricted to only the lowest

492   inbreeding depression levels. Lower maximum floral costs also translate into the need for a much

493   larger effect mutation for higher selfing to evolve for a given inbreeding depression level under a

494   saturating curve. For example, under conditions of $\delta = 0.25$ and $a_p=0.5$ (figure 3 *B*), we find that

495   a more highly selfing mutant can successfully invade when c=0.06 so long as the mutation(s)

496   results in >50% reduction in attraction relative to the resident. But, when *c*=0.03 only a mutation

497   resulting in a > 90% reduction—near complete selfing—would be successful. A similar effect

498   occurs when we hold the maximum floral cost and inbreeding depression constant for a

499   saturating curve but alter the attractiveness of the resident; the threshold for a small effect

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500   mutation to invade is much lower when the resident is less attractive. For a linear cost function,

501   alleles of all effect sizes are equally as likely to invade provided inbreeding depression is lower

502   than a threshold value. Finally, comparing across cost functions, small effect mutations, are more

503   successful at invading over a wider range of inbreeding depression values under an accelerating

504   or linear curve than under a saturating one.

505   In conclusion, our models illustrate how pollinators can interfere with mating system

506   evolution, even when the genetic conditions are expected to pave the way for the evolution of

507   complete selfing. By linking attractiveness to the selfing rate, we further provide a mechanism by

508   which pollen discounting can occur with autonomous selfing and consider attractiveness as a

509   cost of outcrossing. In this way, complete selfing can evolve in the face of pollen discounting so

510   long as there is a cost to attraction, but it is still restrictive. The economics of floral investment

511   are not traditionally viewed as a cost to outcrossing, creating a disconnect between models of

512   mating system evolution and floral evolution. Our model illustrates the importance of

513   understanding cost functions for attraction and reward to pollinators, and sets the stage for future

514   models melding ecological, genetic and resource costs to explore conditions that permit or

515   restrict the evolution of pure selfing.

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Literature Cited

Ashman, T.-L., & Baker, I. (1992). Variation in floral sex allocation with time of season and

currency. *Ecology, 73*(4), 1237-1243.

Ashman, T.-L., & Schoen, D. J. (1994). How long should flowers live? *Nature, 371*, 788-791.

Ashman, T.-L., & Schoen, D. J. (1997). The cost of floral longevity in *Clarkia tembloriensis*: An

experimental investigation. *Evolutionary Ecology, 11*(3), 289-300.

doi:10.1023/A:1018416403530

Bernacchi, D., & Tanksley, S. D. (1997). An interspecific backcross of *Lycopersicon esculentum*

× *L. hirsutum*: linkage analysis and a QTL study of sexual compatibility factors and floral

traits. *Genetics, 147*(2), 861-877.

Bradshaw, H. D., Wilbert, S. M., Otto, K. G., & Schemske, D. W. (1995). Genetic mapping of

floral traits associated with reproductive isolation in monkeyflowers (Mimulus). *Nature,*

376(6543), 762-765.

Bronstein, J. L. (2001). The costs of mutualism. *American Zoologist, 41*(4), 825-839.

Brys, R., van Cauwenberghe, J., & Jacquemyn, H. (2016). The importance of autonomous

selfing in preventing hybridization in three closely related plant species. *Journal of*

Ecology, 104(2), 601-610. doi:10.1111/1365-2745.12524

Burd, M. (2016). Pollen Limitation Is Common—Should It Be? (A Comment on Rosenheim et

al.,"Parental Optimism versus Parental Pessimism in Plants: How Common Should We

Expect Pollen Limitation to Be?"). *The American Naturalist, 187*(3), 388-396.

Busch, J. W., & Delph, L. F. (2012). The relative importance of reproductive assurance and

automatic selection as hypotheses for the evolution of self-fertilization. *Annals of botany,*

109(3), 553-562.

541   Campbell, D. R. (1996). Evolution of floral traits in a hermaphroditic plant: field measurements

542   of heritabilities and genetic correlations. *Evolution, 50*(4), 1442-1453.

543   Caruso, C. M. (2004). The quantitative genetics of floral trait variation in Lobelia: potential

544   constraints on adaptive evolution. *Evolution, 58*(4), 732-740.

545   Charlesworth, B. (1980). The cost of sex in relation to mating system. *Journal of Theoretical*

546   *Biology, 84*(4), 655-671. doi:10.1016/S0022-5193(80)80026-9

547   Charlesworth, D., & Charlesworth, B. (1987). Inbreeding depression and its evolutionary

548   consequences. *Annual Review of Ecology and Systematics*, *18*(1), 237-268.

549   Charlesworth, D., & Charlesworth, B. (1990). Inbreeding depression with heterozygote

550   advantage and its effect on selection for modifiers changing the outcrossing rate.

551   *Evolution, 44*(4), 870-888. doi:10.1111/j.1558-5646.1990.tb03811.x

552   Charlesworth, D., Morgan, M. T., & Charlesworth, B. (1990). Inbreeding depression, genetic

553   load, and the evolution of outcrossing rates in a multilocus system with no linkage.

554   *Evolution, 44*(6), 1469-1489. doi:10.1111/j.1558-5646.1990.tb03839.x

555   Cheptou, P. O. (2004). Allee effect and self-fertilizationin hermaphrodites: reproductive

556   assurance in demographically stable populations. *Evolution, 58*(12), 2613-2621.

557   doi:10.1111/j.1558-5646.2008.00464.x

558   Delph, L. F., Gehring, J. L., Frey, F. M., Arntz, A. M., & Levri, M. (2004). Genetic constraints

559   on floral evolution in a sexually dimorphic plant revealed by artificial selection.

560   *Evolution, 58*(9), 1936-1946. doi:10.1111/j.0014-3820.2004.tb00481.x

561   Devaux, C., Lepers, C., & Porcher, E. (2014). Constraints imposed by pollinator behaviour on

562   the ecology and evolution of plant mating systems. *Journal of Evolutionary Biology*,

563   27(7), 1413-1430.

564　Dittmar, E. L., Oakley, C. G., Conner, J. K., Gould, B. A., & Schemske, D. W. (2016). Factors

565　　　　influencing the effect size distribution of adaptive substitutions. *Proceedings of the Royal*

566　　　　*Society B: Biological Sciences, 283*(1828), 20153065-20153065.

567　　　　doi:10.1098/rspb.2015.3065

568　Eckert, C. G., Samis, K. E., & Dart, S. (2006). Reproductive assurance and the evolution of

569　　　　uniparental reproduction in flowering plants. In H. LD & B. SCH (Eds.), *Ecology and*

570　　　　*evolution of flowers* (pp. 183-203). Oxford: Oxford University Press Oxford.

571　Fenster, C. B., Cheely, G., Dudash, M. R., & Reynolds, R. J. (2006). Nectar reward and

572　　　　advertisement in hummingbird-pollinated *Silene virginica* (Caryophyllaceae). *American*

573　　　　*Journal of Botany, 93*(12), 1800-1807.

574　Ferris, K. G., Barnett, L. L., Blackman, B. K., & Willis, J. H. (2017). The genetic architecture of

575　　　　local adaptation and reproductive isolation in sympatry within the *Mimulus guttatus*

576　　　　species complex. *Molecular Ecology, 26*(1), 208-224.

577　Fisher, R. A. (1941). Average excess and average effect of a gene substitution. *Annals of*

578　　　　*Eugenics, 11*(1), 53-63. doi:10.1111/j.1469-1809.1941.tb02272.x

579　Fishman, L., Kelly, A. J., & Willis, J. H. (2002). Minor quantitative trait loci underlie floral traits

580　　　　associated with mating system divergence in mimulus. *Evolution, 56*(11), 2138-2155.

581　　　　doi:10.1111/j.0014-3820.2002.tb00139.x

582　Galen, C. (1999). Why do flowers vary? The functional ecology of variation in flower size and

583　　　　form within natural plant populations. *Bioscience, 49*(8), 631-640.

584　Goodwillie, C., Kalisz, S., & Eckert, C. G. (2005). The evolutionary enigma of mixed mating

585　　　　systems in plants: occurrence, theoretical explanations, and empirical evidence. *Annual*

586　　　　*Review of Ecology and Systematics*, *36*, 47-79.

587   Goodwillie, C., Ritland, C., & Ritland, K. (2006). The genetic basis of floral traits associated

588   with mating system evolution in Leptosiphon (polemoniaceae): an analysis of

589   quantitative trait loci. *Evolution, 60*(3), 491-504. doi:10.1111/j.0014-

590   3820.2006.tb01131.x

591   Goodwillie, C., & Weber, J. J. (2018). The best of both worlds? A review of delayed selfing in

592   flowering plants. *American Journal of Botany, 105*(4), 641-655. doi:10.1002/ajb2.1045

593   Harder, L. D., & Barrett, S. C. H. (1995). Mating cost of large floral displays in hermaphrodite

594   plants. *Nature, 373*(6514), 512-515.

595   Holland, J. N., & DeAngelis, D. L. (2010). A consumer–resource approach to the density-

596   dependent population dynamics of mutualism. *Ecology, 91*(5), 1286-1295.

597   Holsinger, K. E. (1991). Mass-action models of plant mating systems: the evolutionary stability

598   of mixed mating systems. *The American Naturalist*, *138*(3), 606-622.

599   Holsinger, K. E., Feldman, M. W., & Christiansen, F. B. (1984). The evolution of self-

600   fertilization in plants: a population genetic model. *The American Naturalist, 124*(3), 446-

601   453.

602   Husband, B. C., & Schemske, D. W. (1996). Evolution of the magnitude and timing of

603   inbreeding depression in plants. *Evolution, 50*(1), 54-70. doi:10.1111/j.1558-

604   5646.1996.tb04472.x

605   Jarne, P., & Charlesworth, D. (1993). The evolution of the selfing rate in functionally

606   hermaphrodite plants and animals. *Annual Review of Ecology and Systematics*, *24*(1),

607   441-466.

608   Johnston, M. O., Porcher, E., Cheptou, P. O., Eckert, C. G., Elle, E., Geber, M. A., Kalisz S.,

609   Kelly, J. K., Moeller, D. A., Vallejo-Marín, M., and Winn, A. A. (2009) Correlations among

610   fertility components can maintain mixed mating in plants. *American Naturalist, 173*(1),

611   1-11. doi:10.1086/593705

612   Kalisz, S., Vogler, D. W., & Hanley, K. M. (2004). Context-dependent autonomous self-

613   fertilization yields reproductive assurance and mixed mating. *Nature, 430*(7002), 884-

614   887.

615   Knight, T. M., Steets, J. A., Vamosi, J. C., Mazer, S. J., Burd, M., Campbell, D. R., ... &

616   Ashman, T. L. (2005). Pollen limitation of plant reproduction: pattern and process.

617   *Annual Review of Ecology, Evolution, & Systematics, 36*, 467-497.

618   Lande, R., & Schemske, D. W. (1985). The evolution of self-fertilization and inbreeding

619   depression in plants. I. Genetic models. *Evolution*, *39*(1), 24-40.

620   Lande, R., Schemske, D. W., & Schultz, S. T. (1994). High inbreeding depression, selective

621   interference among loci, and the threshold selfing rate for purging recessive lethal

622   mutations. *Evolution, 48*(4), 965-978. doi:10.1111/j.1558-5646.1994.tb05286.x

623   Lepers, C., Dufay, M., & Billiard, S. (2014). How does pollination mutualism affect the

624   evolution of prior self-fertilization? A model. *Evolution, 68*(12), 3581-3598.

625   Lloyd, D. G. (1979). Some reproductive factors affecting the selection of self-fertilization in

626   plants. *The American Naturalist, 113*(1), 67-79.

627   Lloyd, D. G. (1992). Self-and cross-fertilization in plants. II. The selection of self-fertilization.

628   *International journal of plant sciences, 153*(3, Part 1), 370-380.

629   Morris, W. F., Vázquez, D. P., & Chacoff, N. P. (2010). Benefit and cost curves for typical

630   pollination mutualisms. *Ecology, 91*(5), 1276-1285. doi:10.1890/08-2278.1

631   Nagylaki, T. (1976). A model for the evolution of self-fertilization and vegetative reproduction.

632   *Journal of Theoretical Biology, 58*(1), 55-58.

633   Nobel, P. S. (1977). Water relations of flowering of Agave deserti. *Botanical Gazette, 138*(1), 1-

634   6.

635   Oakley, C. G., Moriuchi, K. S., & Winn, A. A. (2007). The maintenance of outcrossing in

636   predominantly selfing species: ideas and evidence from cleistogamous species. *Annual*

637   *Review of Ecology, Evolution, and Systematics, 38*(1), 437-457.

638   doi:10.1146/annurev.ecolsys.38.091206.095654

639   Ollerton, J. (1996). Reconciling ecological processes with phylogenetic patterns: the apparent

640   paradox of plant--pollinator Systems. *Journal of Ecology, 84*(5), 767-769.

641   doi:10.2307/2261338

642   Randle, A. M., Spigler, R. B., & Kalisz, S. (2018). Shifts to earlier selfing in sympatry may

643   reduce costs of pollinator sharing. *Evolution, 72*(8), 1587-1599. doi:10.1111/evo.13522

644   Rosenheim, J. A., Williams, N. M., & Schreiber, S. J. (2014). Parental optimism versus parental

645   pessimism in plants: how common should we expect pollen limitation to be? *The*

646   *American Naturalist, 184*(1), 75-90.

647   Rosenheim, J. A., Williams, N. M., Schreiber, S. J., & Rapp, J. M. (2016). Modest pollen

648   limitation of lifetime seed production is in good agreement with modest uncertainty in

649   whole-plant pollen receipt:(A reply to Burd). *The American Naturalist, 187*(3), 397-404.

650   Sakai, S. (1995). Optimal resource allocation to vegetative and sexual reproduction of a plant

651   growing in a spatially varying environment. *Journal of Theoretical Biology, 175*(3), 271-

652   282.

653   Savolainen, O., Lascoux, M., & Merilä, J. (2013). Ecological genomics of local adaptation.

654   *Nature Reviews Genetics, 14*(11), 807-820. doi:10.1038/nrg3522

655   Schemske, D. W. (1978). Evolution of reproductive characteristics in Impatiens

656   (Balsaminaceae): the significance of cleistogamy and chasmogamy. *Ecology, 59*(3), 596-

657   613.

658   Schemske, D. W., & Lande, R. (1985). The evolution of self-fertilization and inbreeding

659   depression in plants. II. Empirical observations. *Evolution*, *39*(1), 41-52.

660   Sicard, A., & Lenhard, M. (2011). The selfing syndrome: a model for studying the genetic and

661   evolutionary basis of morphological adaptation in plants. *Annals of Botany, 107*(9), 1433-

662   1443.

663   Slotte, T., Hazzouri, K. M., Stern, D., Andolfatto, P., & Wright, S. I. (2012). Genetic architecture

664   and adaptive significance of the selfing syndrome in Capsella. *Evolution, 66*(5), 1360-

665   1374. doi:10.1111/j.1558-5646.2011.01540.x

666   Spigler, R. B., & Kalisz, S. (2017). Persistent pollinators and the evolution of complete selfing.

667   *American Journal of Botany, 104*(12), 1783-1786.

668   Spigler, R. B., & Woodard, A. J. (2019). Context-dependency of resource allocation trade-offs

669   highlights constraints to the evolution of floral longevity in a monocarpic herb. *New*

670   *Phytologist, 221*(4), 2298-2307. doi:10.1111/nph.15498

671   Stanton, M., & Young, H. J. (1994). Selecting for floral character associations in wild radish,

672   Raphanus sativus L. *Journal of Evolutionary Biology, 7*(3), 271-285. doi:10.1046/j.1420-

673   9101.1994.7030271.x

674   Stebbins, G. L. (1974). *Flowering plants: evolution above the species level*. Cambridge, MA:

675   Belknap Press.

676   Tavares, D. C., Freitas, L., & Gaglianone, M. C. (2016). Nectar volume is positively correlated

677   with flower size in hummingbird-visited flowers in the Brazilian Atlantic Forest. *Journal*

678   *of Tropical Ecology, 32*(4), 335-339.

679   Teixido, A. L., & Valladares, F. (2014). Disproportionate carbon and water maintenance costs of

680   large corollas in hot Mediterranean ecosystems. *Perspectives in Plant Ecology, Evolution*

681   *and Systematics, 16*(2), 83-92.

682   Thomson, J. (2003). When Is It Mutualism? (An American Society of Naturalists Presidential

683   Address). *The American Naturalist, 162*(S4), S1-S9.

684   Waller, D. M. (1979). The Relative Costs of Self- and Cross-Fertilized Seeds in Impatiens

685   capensis (Balsaminaceae). *American Journal of Botany, 66*(3), 313-320.

686   doi:10.2307/2442608

687   Waser, N. M., Chittka, L., Price, M. V., Williams, N. M., & Ollerton, J. (1996). Generalization in

688   pollination systems, and why it matters. *Ecology, 77*(4), 1043-1060.

689   Whitehead, M. R., Lanfear, R., Mitchell, R. J., & Karron, J. D. (2018). Plant mating systems

690   often vary widely among populations. *Frontiers in Ecology and Evolution*, *6*, 38.

691   Winn, A. A., Elle, E., Kalisz, S., Cheptou, P. O., Eckert, C. G., Goodwillie, C., . . . Vallejo-

692   Marín, M. (2011). Analysis of inbreeding depression in mixed-mating plants provides

693   evidence for selective interference and stable mixed mating. *Evolution, 65*(12), 3339-

694   3359. doi:10.1111/j.1558-5646.2011.01462.x

695   Worley, A. C., & Barrett, S. C. H. (2000). Evolution of floral display in Eichhornia paniculata

696   (Pontederiaceae): direct and correlated responses to selection on flower size and number.

697   *Evolution, 54*(5), 1533-1545.

698   Worley, A. C., & Barrett, S. C. H. (2001). Evolution of floral display in Eichhornia paniculata

699   (Pontederiaceae): genetic correlations between flower size and number. *Journal of*

700   *Evolutionary Biology, 14*(3), 469-481. doi:10.1046/j.1420-9101.2001.00296.x

701   Yeaman, S., & Whitlock, M. C. (2011). The genetic architecture of adaptation under migration–

702   selection balance. *Evolution, 65*(7), 1897-1911. doi:10.1111/j.1558-5646.2011.01269.x

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706   **Figure Legends**

707   **Figure 1.** Cost and selfing rate as a function of attractiveness. We consider three cost function

708   curves as shown (saturating, linear, accelerating) on the primary axis and indicated by the solid

709   lines. Maximum cost value, c, is shown here as $c = 0.03$. Selfing rate decreases as a linear

710   function of attractiveness, represented by the dotted line in reference to the secondary axis.

711

712   **Figure 2.** Evolutionary outcome for the evolution of complete selfing depending on inbreeding

713   depression (δ) and attractiveness of a resident partial selfer (a_p) that depends on a generalist

714   pollinator. The dark blue region indicates where the pure selfer dominates, and the yellow region

715   indicates dominance of the partial selfer; neither morph persists in the aqua region. To better

716   illustrate the underlying population dynamics, we show population sizes of the partial selfer,

717   pure selfer, and pollinator as a function of inbreeding depression when (a) $a_p = 0.8$, (b) $a_p = 0.5$,

718   and (c) $a_p = 0.2$. We also show how population sizes of the partial selfer, pure selfer, and

719   pollinator change over time when $a_p = 0.5$ and (i) $\delta = 0.2$, (ii) $\delta = 0.2$, and (iii) $\delta = 0.2$.

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721   **Figure 3.** Pairwise invisibility plots for three different cost functions (saturating, linear,

722   accelerating) and two maximum costs of attractiveness (c). A. Resident is highly attractive ($a_p =$

723   0.8). B. Resident is less attractive ($a_p = 0.5$). Four possible outcomes are represented according to

724   the figure legend: the mutant can successfully invade (increases when rare), the mutant cannot

725   invade (decreases when rare), density of the resident is 0 at demographic equilibrium, and

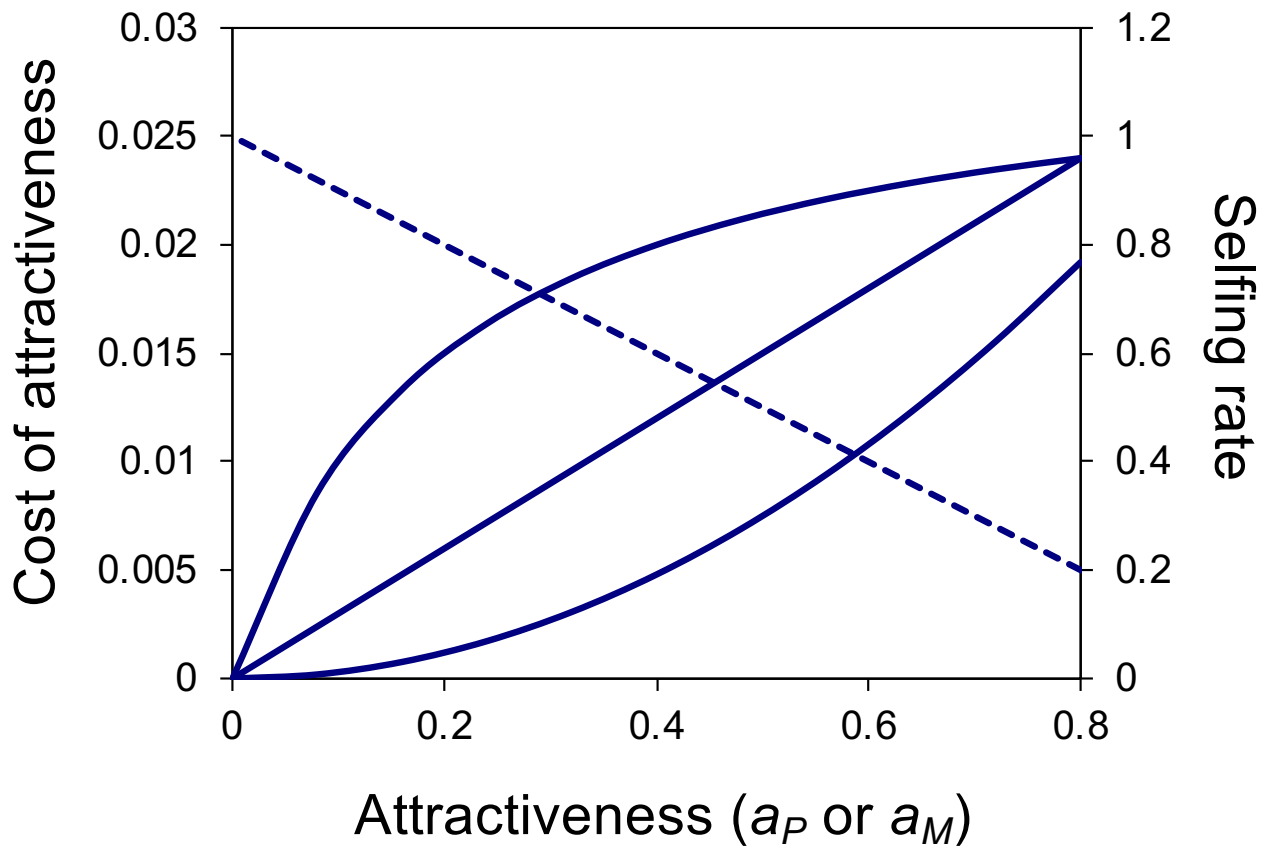726   density where the resident is 0 but the mutant can invade.

Figure 1. Cost and selfing rate as a function of attractiveness. We consider three cost function curves as shown (saturating, linear, accelerating) on the primary axis and indicated by the solid lines. Maximum cost value, c, is shown here as $c = 0.03$. Selfing rate decreases as a linear function of attractiveness, represented by the dotted line in reference to the secondary axis.
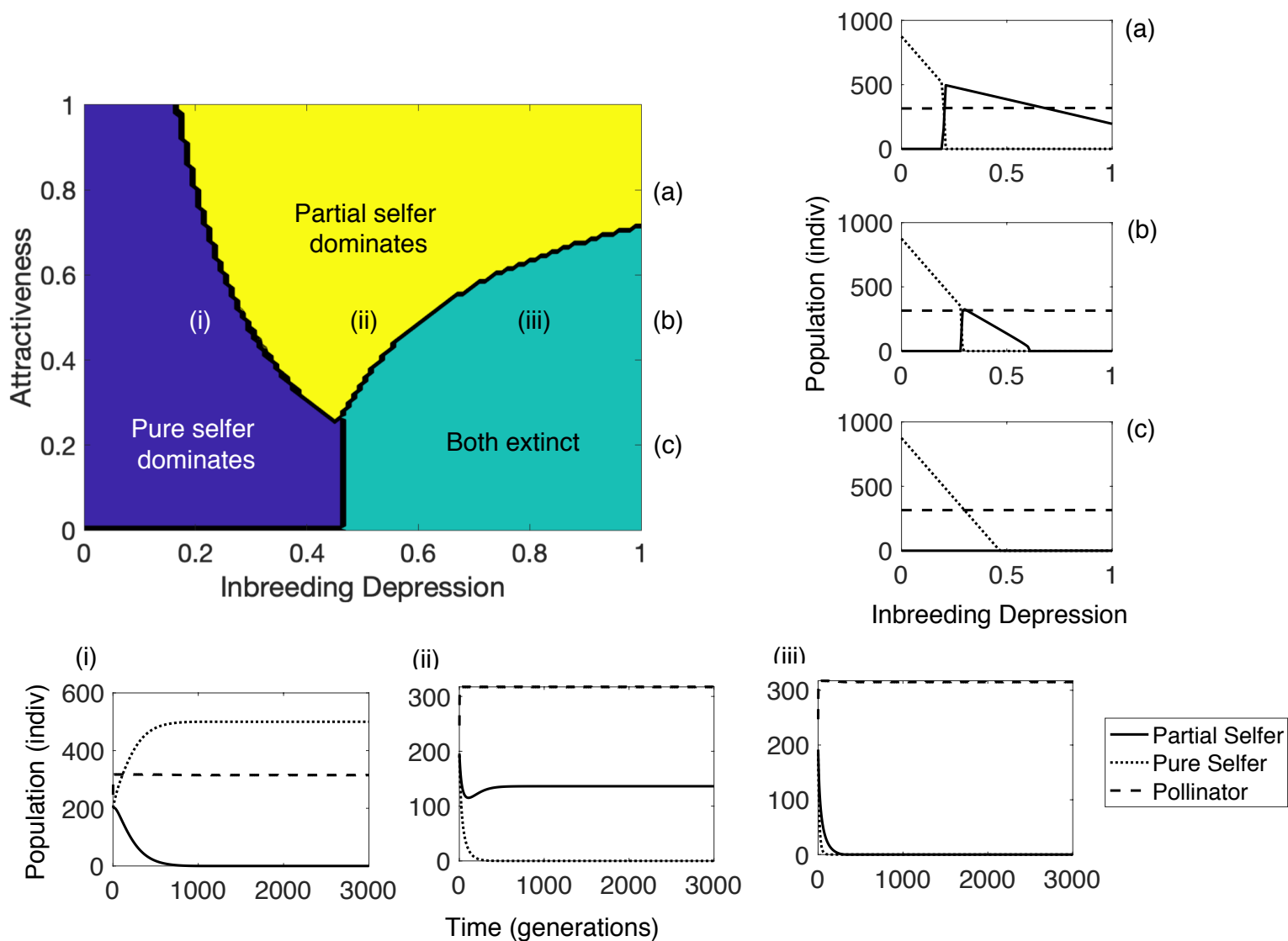
Figure 2. Evolutionary outcome for the evolution of complete selfing depending on inbreeding depression (δ) and attractiveness of a resident partial selfer (a_p) that depends on a generalist pollinator. The dark blue region indicates where the pure selfer dominates, and the yellow region indicates dominance of the partial selfer; neither morph persists in the aqua region. To better illustrate the underlying population dynamics, we show population sizes of the partial selfer, pure selfer, and pollinator as a function of inbreeding depression when (a) $a_p = 0.8$, (b) $a_p = 0.5$, and (c) $a_p = 0.2$. We also show how population sizes of the partial selfer, pure selfer, and pollinator change over time when $a_p = 0.5$ and (i) $\delta = 0.2$, (ii) $\delta = 0.2$, and (iii) $\delta = 0.2$.
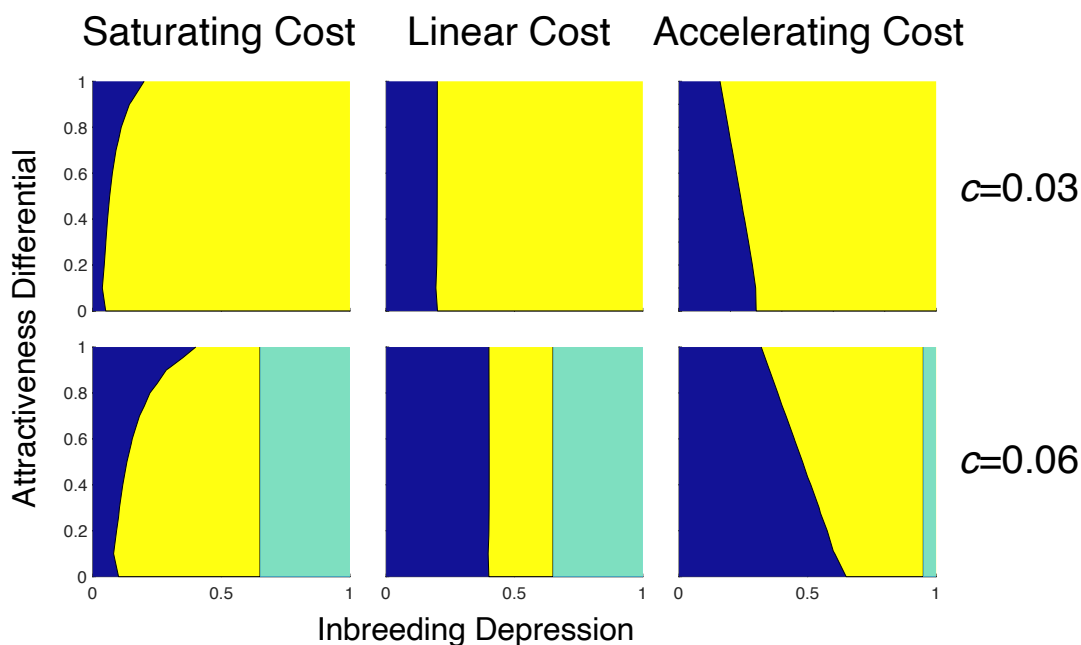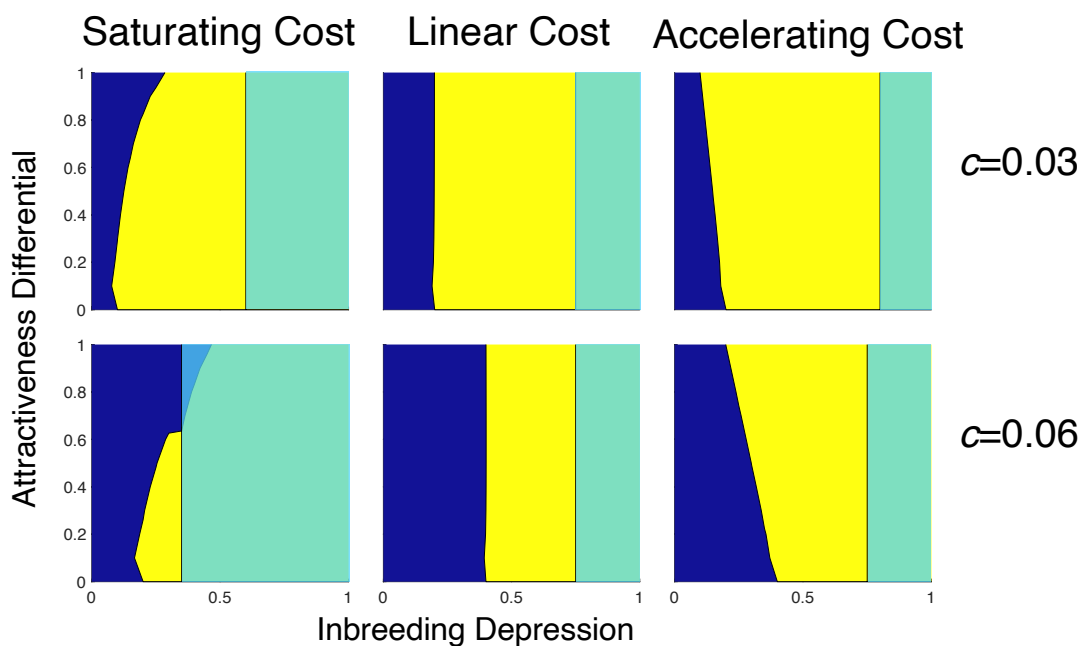
Figure 3. Pairwise invisibility plots for three different cost functions (saturating, linear, accelerating) and two maximum costs of attractiveness (c). A. Resident is highly attractive ($a_p = 0.8$). B. Resident is less attractive ($a_p = 0.5$). Four possible outcomes are represented according to the figure legend: the mutant can successfully invade (increases when rare), the mutant cannot invade (decreases when rare), density of the resident is 0 at demographic equilibrium, and density where the resident is 0 but the mutant can invade.