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# The eco-evolutionary dynamics of prior selfing rates promote coexistence without niche partitioning under conditions of reproductive interference

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7 Running head: coexistence promoted by the evolution of selfing

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**Abstract**

**1.** Pollinator-mediated reproductive interference can occur when two or more plant species share the same pollinators. Recent studies have suggested that prior autonomous selfing mitigates reproductive interference, potentially facilitating coexistence even in the absence of pollination niche partitioning (i.e. the pre-emptive selfing hypothesis). However, whether the evolution of prior selfing promotes coexistence, in the context of the eco-evolutionary dynamics of population size, selfing rates, and inbreeding depression, remains poorly understood.

**2.** We constructed an individual-based model to examine the conditions under which the evolution of prior selfing promotes coexistence in the context of mutual reproductive interference. In the model, two plant species compete by way of mutual reproductive interference, and both have the potential to evolve the capacity for prior autonomous selfing. We expected that purging of deleterious mutations might result in evolutionary rescue, assuming that the strength of inbreeding depression declines as the population selfing rate increases; this would enable inferior competitors to maintain population density through the evolution of prior selfing.

**3.** Our simulation demonstrated that evolution of prior selfing may promote coexistence, whereas reproductive interference in the absence of such evolution results in competitive exclusion. We found that lower pollinator availability is likely to favour rapid evolutionary shifts to higher prior selfing rates, thereby neutralising the negative effects of reproductive interference in both species. When the strength of inbreeding depression decreased with an increase in the population-level selfing rate, moderate pollinator availability resulted in long-term coexistence in which relative abundance-dependent selection on the prior selfing rate served to intermittently maintain the population density

49 of the inferior competitor.

50 **4.** *Synthesis.* We demonstrate that the evolution of prior selfing may increase population

51 growth rates of inferior competitors and may consequently promote long-term

52 coexistence via evolutionary rescue. This constitutes a novel mechanism explaining the

53 co-evolutionary coexistence of closely related plant species without niche partitioning,

54 and is consistent with recent studies reporting that closely related species with mixed

55 mating systems can co-occur sympatrically, even under conditions of mutual reproductive

56 interference.

57

58 **Key-words:** Co-evolution, evolutionary rescue, inbreeding depression, individual-based

59 model, mixed mating, pollinator-mediated competition, reproductive ecology, selfing

60 syndrome

61

62 **Introduction**

63 The condition under which competing species can coexist is a fundamental question in

64 ecology (May, 1974; Chesson, 2000). Numerous empirical and theoretical studies have

65 demonstrated that niche partitioning between competing species is important for

66 coexistence: i.e. intraspecific competition should be greater than interspecific

67 competition. Moreover, niche partitioning exerts a stabilising effect in modern

68 coexistence theory (Chesson, 2000; Silvertown, 2004; Barabás, 2018). Closely related

69 species that potentially share the same or very similar resource requirements and

70 reproductive traits are therefore expected to compete strongly, and are unlikely to coexist

71 (Gröning & Hochkirch, 2008; Burns & Straus, 2011; Whitton, Sears & Maddison; 2017).

72 Additionally, imperfect species recognition causes reproductive interference, further

73 increasing the vulnerability of species with lower relative abundance to extinction by

74 reducing fecundity (Gröning & Hochkirch, 2008; Schreiber et al., 2019; Iritani &

75 Noriyuki, 2021).

76 　　　　In flowering plants, when two or more plant species depend on the same

77 pollinators for reproduction, interspecific pollinator-mediated pollen transfer can cause

78 strong reproductive interference that results in either niche partitioning or competitive

79 exclusion of one species (Levin & Anderson, 1970; Takakura, Nishida, Matsumoto &

80 Nishida, 2008; Runquist & Stanton, 2013; Moreira-Hernández & Muchhala, 2019).

81 Reproductive interference via interspecific pollen transfer can occur via an increase in

82 heterospecific pollen deposition on the stigma, and/or conspecific pollen loss on

83 heterospecific flowers (Mitchell, Flanagan, Brown, Waser & Karron, 2009; Morales &

84 Traveset, 2008). Specifically, pollen deposition from closely related heterospecies

85 strongly decreases female reproductive success owing to pollen tube growth, competition

86    in the style, ovule discounting, and/or hybridisation (Harder, Cruzan & Thomson, 1993;

87    Nishida, Kanaoka, Hashimoto, Takakura & Nishida, 2014; Whitton et al. 2017). Thus,

88    reproductive interference via heterospecific pollen deposition may favour spatiotemporal

89    segregation in flowering or floral trait displacement, with the consequence that plants

90    interact with either different pollinator species or different parts of the same pollinator

91    (e.g. Runquist 2012; van der Niet & Johnson 2012; Huang & Shi, 2013).

92        Selfing has garnered much attention recently as an alternative mechanism for

93    mitigating reproductive interference by heterospecific pollen transfer from competing

94    relatives (Fishman & Wyatt, 1999; de Waal, Anderson & Ellis, 2015; Katsuhara &

95    Ushimaru, 2019). Recent studies have suggested that selfing constitutes a reproductive

96    barrier among related, sympatrically coexisting species (Fishman & Wyatt, 1999; Martin

97    & Willis, 2007; Goodwillie & Ness 2013; Brys, van Cauwenberghe & Jaquemyn, 2016).

98    Selfers with small and inconspicuous flowers (selfing syndrome), which receive fewer

99    pollinator visits, are thus likely to coexist with outcrossing relatives (Sicard & Lenhard,

100   2011; Kalisz et al. 2012). Reduced heterospecific pollen deposition, resulting from fewer

101   pollinator visits and/or reproductive assurance via self-pollination, might mitigate the

102   negative effects of reproductive interference in selfers, although this is difficult to

103   confirm (Fishman & Wyatt, 1999; Martin & Willis, 2007; de Waal et al. 2015; Brys et al.

104   2016).

105       Recent studies have further hypothesised that "prior" rather than "delayed"

106   autonomous selfing can mitigate the negative effects of reproductive interference via

107   interspecific pollen transfer, and may promote species coexistence independent of

108   pollinator visits (i.e. the pre-emptive selfing hypothesis; Randle, Spigler & Kalisz, 2018;

109   Katsuhara & Ushimaru, 2019). In this study, prior selfing is defined as the phenomenon

110    in which an ovule is self-fertilised before or in the absence of outcrossing opportunities,

111    such as bud pollination or cleistogamy, whereas delayed selfing is that which occurs after

112    an outcrossing opportunity (Lloyd, 1992). Theoretical and empirical studies have

113    suggested that prior selfing is unlikely to evolve under conditions of frequent pollinator

114    visits (Lloyd, 1992; Kalisz, Vogler & Hanley, 2004; Eckert et al. 2010); however, in the

115    presence of reproductive interference by an abundant competitor species, frequent

116    pollinator visits substantially reduce the outcrossing success of inferior competitor

117    species. In this scenario, the evolution of prior selfing may mitigate reproductive

118    interference, and may rescue the inferior competitor from competitive exclusion.

119        The pre-emptive selfing hypothesis should be tested in the context of the eco-

120    evolutionary dynamics of population size, selfing rates, and inbreeding depression.

121    Because the negative effects of reproductive interference (i.e. decreased outcrossing

122    success) become more pronounced as the relative abundance of competing species

123    increases (Levin & Anderson, 1970; Katsuhara & Ushimaru, 2019), the evolution of prior

124    autonomous selfing in any given species is likely driven by the population dynamics of

125    competing species. The evolution of prior selfing may facilitate population maintenance

126    by mitigating reproductive interference; however, conversely, it may promote self-

127    extinction when inbreeding depression has a strong negative effect on population growth

128    (Cheptou, 2019; Katsuhara & Ushimaru, 2019). Therefore, the dynamics of inbreeding

129    depression substantially influence the evolution of selfing: the strength of inbreeding

130    depression is often inversely related to a population's selfing rate due to the "purging" of

131    deleterious, recessive alleles (Schemske & Lande, 1985; Charlesworth, Charlesworth &

132    Morgan, 1990; Lloyd, 1992; Husband & Schemske, 1996; Crnokrak & Barrett, 2002;

133    Goodwillie, Kalisz & Eckert, 2005; Charlesworth & Willis, 2009). Thus, the dynamics of

134  population size, selfing rates, and the inbreeding depression of competing species should

135  be considered when investigating the adaptive significance of prior selfing under

136  conditions of reproductive interference. To the best of our knowledge, however, no

137  studies have examined the eco-evolutionary dynamics of these variables, and therefore

138  little is known about the possibility of coexistence under reproductive interference, and

139  how it relates to the evolution of prior selfing.

140      To investigate the pre-emptive selfing hypothesis, we constructed a model in

141  which two plant species, both sharing the same pollination niche and both capable of

142  evolving prior autonomous selfing, compete against one another in the form of mutual

143  reproductive interference (i.e. the eco-evolutionary dynamics model). We explored the

144  conditions and mechanisms of coexistence in the context of eco-evolutionary outcomes

145  for a wide range of parameter regions, mainly focusing on pollinator limitation

146  (outcrossing cost) and inbreeding depression (selfing cost) rather than using the

147  traditional "stability at an equilibrium point" or recent "mutual invasibility criterion"

148  analyses (Chesson, 2000, Hart et al., 2019). Our aim was not to explore general

149  mechanisms, but to focus on a specific plant species system with mutual reproductive

150  interference, as well as to analyse parameters and scenarios that can be easily applied to

151  empirical studies of plant mating systems. We addressed the following two questions:

152  first, can prior selfing evolve under mutual reproductive interference and promote

153  coexistence as an evolutionary rescue agent? Second, is inbreeding depression an

154  important determinant of the joint dynamics of population size and selfing rates? We then

155  discuss the conditions under which the evolution of prior selfing promotes the long-term

156  coexistence of closely related species sharing the same pollination niche.

157

158    **Model**

159    *Community structure, pollination, seed production, and germination processes*

160    We developed an individual-based model of two competing, annual flowering plant

161    species (species with discrete generations) at a site with a constant carrying capacity $K$,

162    wherein $K$ individuals of Species 1 (sp$_1$) and/or Species 2 (sp$_2$) occupied the site in each

163    generation. The default value of $K$ was 2,000. The relative abundance of sp$_i$ in the $t$-th

164    generation is denoted as $q_{i,t}$ , where $i$ is either 1 or 2, and $q_{1,t} + q_{2,t} = 1$ holds ($0 \leq q_{i,t}$

165    $\leq 1$). Thus, the number of individuals of sp$_i$ equals $K q_{i,t}$. We assumed complete overlap

166    in the ecological niches of both species, and no possibility of hybridisation.

167            We first described the pollination and fertilisation processes (Fig.1). Each

168    individual of both species produced $n$ ovules, which were fertilised by a combination of

169    prior autonomous selfing and pollinator-mediated outcrossing with $g$ pollen grains. The $j$-

170    th individual of sp$_i$ fertilised its ovules via prior autonomous selfing at a rate of $r_{i,j,t}$ in

171    the $t$-th generation ($1 \leq j \leq Kq_{i,t}$, $0 \leq r_{i,j,t} \leq 1$ for $i$ = 1 or 2). Thus, an integer number

172    of ovules, obtained by rounding $nr_{i,j,t}$, were fertilised via prior selfing, whereas the

173    remaining ovules were available for pollinator-mediated outcrossing (Fig.1). Here, we

174    assumed that an integer number of ovules, obtained by rounding the proportion $P$ ($0 \leq P$

175    $\leq 1$) of $n(1 - r_{i,j,t})$, were pollinated by pollinators with outcrossed conspecific and/or

176    heterospecific pollen grains. We introduced pollinator limitation using $P < 1$. We assumed

177    that pollinators visited flowers of both species indiscriminately and carried their pollen in

178    proportion to the relative abundance of flowers.

179            The pollen parent of each outcrossed ovule of individual $j$ was randomly

180    assigned to conspecifics with the probability of

181
$$\frac{\sum_{j=1}^{Kq_{i,t}} g(1-r_{i,j,t})}{\sum_{j=1}^{Kq_{i,t}} g(1-r_{i,j,t})+c_h \sum_{j=1}^{(1-q_{i,t})K} g(1-r_{h,j,t})},$$

182   where $c_h$ represents the strength of reproductive interference from heterospecific

183   individuals ($sp_h$), and $r_{i,j,t}$ and $r_{h,j,t}$ $(0 \leq c_h,\ r_{i,j,t}$ and $r_{h,j,t} \leq 1)$ represent rates of

184   prior selfing of the $j$-th individuals of $sp_i$ and $sp_h$, respectively. The parameter $c_h$ is

185   interpreted as the probability of ovule discounting by a heterospecific pollen grain during

186   the fertilisation of individual $j$. This expression is derived from the assumption that the

187   probabilities that pollen grains of individual $j$ will be assigned to conspecific or

188   heterospecific ovules are described as $\frac{g(1-r_{i,j,t})}{\sum_{j=1}^{Kq_{i,t}} g(1-r_{i,j,t})+c_h \sum_{j=1}^{(1-q_{i,t})K} g(1-r_{h,j,t})}$ and

189   $\frac{c_h g(1-r_{i,j,t})}{c_h \sum_{j=1}^{Kq_{i,t}} g(1-r_{i,j,t})+\sum_{j=1}^{(1-q_{i,t})K} g(1-r_{h,j,t})}$, respectively (cf. Holsinger, 1991). Here we assumed

190   that outcrossed pollen decreased proportionally with the prior selfing rate in both species;

191   this assumption mimics increased pollen discounting and/or anther-stigma interference

192   with increases in the prior selfing rate (Lloyd and Webb, 1986; Webb and Lloyd, 1986;

193   Karron, Jackson, Thumser & Schlicht, 1997; Fishman, 2000; Barrett 2002; Dai &

194   Galloway, 2011). Because we assumed random pollination, each ovule of the $j$-th

195   individual was fertilised by the pollen of the $j$-th individual (pollinator-mediated self-

196   pollination; geitonogamy) according to the aforementioned probability.

197        We then explored the seed production process. We assumed that only ovules

198   fertilised by self- and outcrossed-conspecific pollen could develop seeds, whereas those

199   assigned by heterospecific pollen did not produce seeds due to ovule discounting (Fig. 1).

200   Given the probability of outcrossing success for each ovule, the expected number of

201   outcrossed seeds in individual $j$ decreases with increases in relative abundance and a

202   lower population mean of the prior selfing rate of $sp_h$, indicating frequency-dependent

203    reproductive interference. The cost of selfing, relative to outcrossing, was also assumed

204    as follows: in sp$_i$, all outcrossed ovules were assumed to develop viable seeds, whereas

205    selfed ovules set seeds at a rate of $1 - I_{i,t}$, where $I_{i,t}$ $(0 \leq I_{i,t} \leq 1)$ is the strength of

206    inbreeding depression in generation $t$ in sp$_i$. $I_{i,t}$ can be interpreted as an evolutionary

207    variable owing to the balance between the accumulation and purging of deleterious

208    mutations (Schemske & Lande, 1985; Husband & Schemske, 1996; Crnokrak & Barrett,

209    2002). Here, $I_{i,t}$ is expressed as a function of the population selfing rate in the $(t-1)^{\text{th}}$

210    generation of sp$_i$, $S_{i,t-1}$:

211    $I_{i,t} = \beta e^{-\alpha S_{i,t-1}}.$

212    $S_{i,t-1}$ was calculated as the total number of viable selfed seeds divided by the total

213    number of viable seeds in sp$_i$ in the previous generation. This function is drawn as a

214    decreasing concave upward curve when the coefficient $\alpha$ is > 0; $\alpha$ expresses the

215    association of steep decreases in inbreeding depression with increases in population

216    selfing rates (Lande, Schemske & Schultz 1994; Porcher & Lande, 2016). The intercept $\beta$

217    $(0 \leq \beta \leq 1)$ indicates the level of inbreeding depression when complete outcrossing occurs

218    in the population. We simulated a variety of $\alpha$ and $\beta$ values to test different scenarios in

219    the eco-evolutionary dynamics of population size and selfing rates.

220           Finally, we randomly sampled *K* seedlings from all seeds of both species to form

221    the next generation $t+1$. We assumed no interspecific differences in competitive ability

222    in germination and establishment processes or other ecological or genetic features;

223    therefore, $c_h$, $\alpha$, and $\beta$ were identical for both species. In addition, our model had no

224    spatial structure. According to these assumptions, the expected value of the relative

225    abundance of sp$_i$ in the (*t* + *1*)-th generation is calculated as follows:

226 $$q_{i,t+1} = \frac{q_{i,t}\binom{\text{mean no. of seeds}}{\text{of sp}_i \text{ individual}}}{q_{i,t}\binom{\text{mean no. of seeds}}{\text{of sp}_i \text{ individual}}+(1-q_{i,t})\binom{\text{mean no. of seeds}}{\text{of sp}_h \text{ individual}}}$$ (also see Fig. S1).

227

228 *Inheritance and mutation of prior autonomous selfing*

229 To describe the evolutionary dynamics of prior autonomous selfing, our model assumed

230 that the prior selfing rate of individual $j$ in the next generation $r_{i,j,t+1}$ was equal to the

231 parental average. Thus, the prior selfing rate was assumed to be a quantitative, genetic

232 trait influenced by other traits (e.g. the degrees of herkogamy and/or dichogamy, and the

233 proportion of cleistogamous flowers; Culley & Klooster, 2007; Kalisz et al. 2012).

234 However, $r_{i,j,t+1}$ can be adjusted to represent deviations from the parental mean (i.e.

235 mutation) by adding a random value between $-\sigma$ and $+\sigma$ to the parental mean with a

236 probability $\mu$, where $\mu$ and $\sigma$ represent the rate and effect size of mutation, respectively.

237 We used default values of 0.05 for $\mu$ and 0.1 for $\sigma$. If a mutation-induced change results

238 in $r_{i,j,t+1}$ > 1 or < 0, we truncated the values to 1 and 0, respectively.

239

240 *Simulation settings and classification of eco-evolutionary outcomes*

241 To explore conditions for the coexistence of the two species, we examined the effects of

242 pollinator availability ($P$) and the relationship between inbreeding depression and selfing

243 rates ($\alpha$ and $\beta$) on the outcomes of evolution. We tested the following scenarios

244 describing the relationship between inbreeding depression and selfing rates: $I_{i,t}$ was

245 either fixed ($\alpha = 0$; $\beta = 0.1, 0.3, 0.5, 0.7$, or $0.9$) or variable in accordance with the

246 population selfing rate ($\alpha = 0, 0.5, 1, 2, 4$, or $8$; $\beta = 0.9$). The full parameter range was

247 $0 \leq P \leq 1$ (Table 1), and the initial number of individuals of both species was equal to

248 $K/2$ in each simulation run. Initial autonomous selfing rates for individuals were

249    randomly generated based on a normal distribution with a mean and standard deviation of

250    $r_{\text{intial}}$ (1/2) and $D_{\text{intial}}$ (1/6) for both species. Each run was terminated after 2,000

251    generations, or after one species went extinct.

252         After conducting 50 simulation runs for each parameter setting, we classified the

253    eco-evolutionary dynamics into four categories based on the ecological and evolutionary

254    status of the species. When the simulation ended with the extinction of either species, the

255    result was classified as either (1) competitive exclusion by the selfer in cases where the

256    population mean of prior autonomous selfing rate of survivors was > 0.5, or (2)

257    competitive exclusion by the outcrosser, when the prior selfing rate of survivors was ≤

258    0.5. Runs in which coexistence persisted until the 2,000$^{\text{th}}$ generation were also divided

259    into two categories, (3) coexistence with evolutionary rescue by prior selfing, and (4)

260    coexistence with neutral dynamics. Classification was based on the procedures described

261    below.

262         To detect evolutionary rescue, we calculated the population growth rate and

263    selection gradient for each generation of sp$_i$. Population growth rate ($W_{i,t}$) for the $t$-th

264    generation was calculated as $Kq_{i,t+1}/Kq_{i,t}$ $\left(= q_{i,t+1}/q_{i,t}\right)$. To clarify the selection

265    gradient on the prior selfing rate, we identified the seed and pollen parents of all seeds,

266    and assessed the correlation between the selfing rate $r_{i,j,t}$ and the seeding and siring

267    success of each individual; this comprised the selection gradient ($G_{i,t}$) at the $t$-th

268    generation. Positive or negative values of $G_{i,t}$ indicate that higher or lower rates,

269    respectively, were adaptive for sp$_i$ in the respective generation. Evolutionary rescue by

270    prior selfing was defined as a state requiring the following two conditions: a significant

271    negative correlation between $q_{i,t}$ and $G_{i,t}$ (i.e. population declines facilitate the

272    evolution of selfing), and a significant positive correlation between the population mean

273 prior selfing rate $\sum_{j=1}^{Kq_{i,t}} r_{i,j,t}/Kq_{i,t}$ and $W_{i,t}$ (i.e. the evolution of selfing increases

274 population growth). The significance of these two correlations in each run was examined

275 using permutation tests, as follows. Firstly, we calculated these two correlations for the

276 last 500 generations of a given run; next, we ran 10,000 permutations of the $W_{i,t}$ and

277 $G_{i,t}$ values among the generations, and repeatedly calculated the two correlations to

278 create a null distribution to obtain the 95% prediction interval for each. We deemed the

279 observed correlations significant when they deviated from the 95% prediction interval.

280 When both or either of the correlation coefficients were non-significant, the run was

281 classified as coexistence with neutral dynamics (Fig. 2). It should be noted that

282 coexistence with neutral dynamics indicates that both species persisted for 2,000

283 generations, whereas coexistence with evolutionary rescue indicates the presence of a

284 stabilising effect, arising from the evolution of selfing under reproductive interference by

285 a relatively abundant competitor.

286   We compared differences in the long-term stability of coexistence with neutral

287 dynamics and evolutionary rescue using a typical parameter set for each type of

288 coexistence: $P = 0.4$, $\alpha = 0.5$, and $\beta = 0.9$ for evolutionary rescue (ER set), and $P = 0.1$, $\alpha$

289 $= 4$, and $\beta = 0.9$ for coexistence with neutral dynamics (ND set). For each parameter set,

290 we conducted 200 simulations, which continued 10,000 generations unless either species

291 became extinct, and documented the number of generations during which both species

292 persisted for each simulation.

293   We also assessed how simulation results were affected by the strength of

294 reproductive interference and the mean selfing rate of the initial population. We ran

295 simulations in which $c_h$ ($= 0.0, 0.25, 0.5, 0.75,$ or $1.0$) and $r_{initial}$ ($= 0.0, 0.25, 0.5, 0.75,$ or

296  1.0) varied under the parameter settings described above (i.e. the ER and ND sets), using

297  50 simulations for each parameter set. To assess the population dynamics of the two

298  species under a scenario of fixed prior selfing rates, we conducted simulation runs in

299  which both species had either the same or different fixed prior selfing rates ($0 \leq r_{initial} \leq 1$),

300  again using the two parameter sets. Finally, we ran simulations, using both sets, that

301  assumed fixed abundances of each species, to examine the effects of fixed population size

302  on the evolution of prior selfing.

303       Many recent studies assessing stable coexistence have conducted invasion

304  analyses to test whether rare target species can increase in abundance (Chesson, 2000,

305  Barabás, 2018; Grainger et al., 2019; Ellner, 2019). In this study, we examined the extent

306  to which species with very low population density can invade the community under

307  conditions of coexistence with neutral dynamics and evolutionary rescue. As a first step,

308  we arbitrarily selected one simulation run from those in which both species coexisted for

309  2,000 generations, using the ER or ND parameter set (Supporting File 1). The species

310  with lower frequency in the 2,000$^{th}$ generation was treated as an invader species. The

311  simulation was then rerun to obtain invader species relative abundances of 0.1, 0.01, and

312  0.001 for ratios of invaders to resident species individuals of 200:1,800, 20:1,980, and

313  2:1,998, respectively. We performed 100 replications with different individuals. Each run

314  was terminated after 2,000 generations, or when either species became extinct.

315

316  **Results**

317  *Eco-evolutionary dynamics with fixed inbreeding depression*

318  We found that lower pollinator availability fostered the evolution of higher selfing rates

319  in both species and frequently promoted coexistence with neutral dynamics (Fig. 3a).

320   Coexistence with neutral dynamics was limited by higher inbreeding depression (Fig. 3a),

321   but invariably resulted when both species evolved a prior selfing rate close to 1.0, which

322   neutralised mutual reproductive interference (Fig. 2). During periods of coexistence, the

323   population dynamics of both species exhibited a random walk, indicating that coexistence

324   with neutral dynamics was unstable over the long term, and extinction of one species

325   occurred when simulations continued for more generations (see below, *Long-term*

326   *stability of coexistence*). When values of either or both of $I$ and $P$ were large, eco-

327   evolutionary dynamics frequently ended in competitive exclusion (Fig. 3a), whereas

328   when values for both variables were large, competitive exclusion by the outcrosser

329   invariably resulted (Fig. 3a). Coexistence with evolutionary rescue occurred only rarely

330   when inbreeding depression was both fixed and independent of population selfing rates

331   (Fig. 3a).

332

333   *Eco-evolutionary dynamics with variable inbreeding depression*

334   Conditions for both types of coexistence were more widened in scenarios with variable

335   inbreeding depression compared to scenarios assuming fixed inbreeding depression (Fig.

336   3). Of note, both types of coexistence were associated with intermediate levels of

337   pollinator availability and intermediate levels of the slope of the inbreeding depression

338   function (Fig. 3b).

339          Competitive exclusion by the selfer occurred under a wider range of conditions

340   when inbreeding depression decreased sharply with increases in population selfing rates

341   ($\alpha \geq 4.0$), as compared to scenarios with lower, fixed inbreeding depression rates ($\alpha = 0$

342   and $\beta = 0.1$ or $0.3$; Fig. 3). By contrast, when inbreeding depression decreased more

343   gradually with increases in the population selfing rate ($\alpha = 0.5$), competitive exclusion by

344     the outcrosser tended to occur in the presence of higher pollinator availability, similar to

345     cases in which both $I$ and $P$ were large in the fixed inbreeding depression scenario.

346

347     *Long-term stability of coexistence*

348     In the 96 out of 200 simulations with the ER set, both species persisted until the 10,000th

349     generation whereas either species went extinct before the 10,000th generation in all the

350     200 simulations with the ND set (Fig. 4). The extinctions of either species occurred

351     within a few hundreds of generations in the remaining 104 simulations with the ER set.

352     Meanwhile, the generation of the extinction varied largely among the simulations with

353     the ND set, although the extinction mostly occurred before the 4000th generation (Fig. 4).

354     These indicate that coexistence with evolutionary rescue could be maintained in the long

355     term in cases where fluctuations in relative abundance ($q_{i,t}$) and prior selfing rates ($r_{i,t}$)

356     initiated and that coexistence with neutral dynamics ended stochastically in the

357     simulations.

358

359     *Effects of $c_h$ and $r_{initial}$ on simulation outcomes*

360     In simulations using the ER set, we found that coexistence with evolutionary rescue

361     nearly always occurred in scenarios with a high initial population selfing rate ($r_{initial} \geq$

362     0.75) and the presence of mutual reproductive interference ($c_h > 0.0$). Neither type of

363     coexistence was common in either the ER or ND sets (Fig. 5) in cases where the initial

364     population selfing rate was low ($r_{initial} \leq 0.25$). Furthermore, competitive exclusion by the

365     outcrosser was not observed when the initial population selfing rate was high ($r_{intial} \geq$

366     0.75). The strength of reproductive interference ($c_h$) appeared to have little effect on

367     coexistence with neutral dynamics in the ND set; however, coexistence with evolutionary

368 rescue occurred in the ER set only in the presence of mutual reproductive interference ($c_h$

369 > 0.0).

370

*Simulation outcomes under fixed prior selfing rates and population size*

372 We found that both species very rarely persisted until 2,000 generations in either the ER

373 or ND sets when prior selfing rates were fixed in both species, except when both species

374 had identical, very high prior selfing rates (Fig. 6). In the ND set, the successful species

375 was always the one with a higher prior selfing rate. In the ER set, the successful species

376 was usually the one with lower and higher prior selfing rates in the areas below and

377 above the line representing $r_2 = -r_1 + 0.6$, respectively (Fig. 6). In simulations using the

378 ER set and assuming fixed abundances, an evolutionary shift to higher prior selfing rates

379 was favoured only when the relative abundance of the focal species was lower than 1/2

380 (Fig. 7). By contrast, a very high prior selfing rate was always favoured under the ND set,

381 irrespective of abundance (Fig. 7).

382

*Invasibility of species with low population density*

384 When the initial relative frequency of invader species was set at 0.1, the invader species

385 increased its abundance and persisted until 2,000 generations in 98% of runs with the ER

386 set, compared to 18% of runs with the ND set (Fig. 8). The proportion of runs with

387 successful invasion decreased as the initial frequency of invader species decreased (Fig.

388 8). Even when the frequency of invader species started at 0.001, coexistence of the

389 species in the 2,000[th] generation occurred in 10% of runs with the ER set, but never

390 occurred with the ND set (Fig. 8). With the ER set, invader species avoided stochastic

391 extinction in the first several generations regardless of the initial frequency, and stably

392 persisted with fluctuations within a relative abundance range of ca. 0.2 to 0.8 via

393 evolutionary rescue (Fig. 8).

394

395 **Discussion**

396 Our model demonstrated that the evolution of prior selfing could promote species

397 coexistence in the presence of mutual reproductive interference, whereas coexistence

398 rarely resulted without the evolution of prior selfing (Figs. 3 and 6). When controlling for

399 pollinator availability, both types of coexistence tended to occur more commonly in the

400 variable inbreeding depression scenario (in which inbreeding depression decreases with

401 an increase in the population selfing rate) than in the fixed inbreeding depression scenario

402 (Fig. 3). In particular, coexistence with evolutionary rescue occurred frequently and

403 remained stable in the long term under conditions of gradually diminishing inbreeding

404 depression strength and intermediate pollinator availability (Figs. 3, 4 and 8).

405 Coexistence with evolutionary rescue was achieved with both the strength of reproductive

406 interference from competing species and adaptive superiority of higher selfing rates being

407 dependent on relative abundance, and led to fluctuations in both population size and the

408 prior selfing rate in both species (Figs. 2, 5, 7 and 8).

409        Here, suitable conditions for coexistence with evolutionary rescue are discussed

410 using comparisons with empirical studies. Our simulations demonstrated that coexistence

411 with evolutionary rescue occurred under conditions of moderate pollinator limitation,

412 variable and moderate levels of inbreeding depression, relatively high initial prior selfing

413 rates, and the presence of reproductive interference. High pollinator availability always

414 favoured competitive exclusion by either outcrossers or selfers, depending on the level of

415 inbreeding depression. In other words, long-term coexistence in the context of

416    reproductive interference required pollinator-limited conditions, which are prevalent in

417    the wild (Larson & Barrett, 2000). Variable levels of inbreeding depression persisted as

418    the cost of selfing, even at very high population selfing rates. While inbreeding

419    depression resulting from deleterious recessive alleles is thought to be mitigated by

420    increases in population selfing rates, weak, mildly deleterious mutations and

421    heterozygous advantages resulting from overdominance cannot be purged even in

422    predominantly selfing species, leading to late-acting inbreeding depression (Charlesworth

423    et al. 1990; Husband & Schemske, 1996; Crnokrak & Barrett, 2002; Charlesworth &

424    Wills, 2009). In addition, we found that a higher initial prior selfing rate increased the

425    potential for coexistence with evolutionary rescue (Fig. 5), suggesting that stable

426    coexistence between a pair of predominantly selfing or mixed-mating species can occur

427    only under conditions of reproductive interference, which is consistent with recent studies

428    (Tokuda et al. 2015; Katsuhara & Ushimaru, 2019; Nishida et al. unpublished data). This

429    type of coexistence never occurred in our simulations in the absence of reproductive

430    interference, even when other parameter settings were suitable for coexistence (Fig. 5).

431    This result implies that mutual reproductive interference may be the cost of outcrossing

432    and may promote higher levels of selfing (Katsuhara & Ushimaru, 2019), likely resulting

433    in fluctuations in prior selfing rates across generations.

434         Coexistence with neutral dynamics was often found under conditions of lower

435    pollinator availability and weak, fixed or moderately varying inbreeding depression (Fig.

436    3). Higher prior selfing rates evolved very quickly under these conditions, reaching

437    nearly 1.0 in both species (Fig. 2), which should free the selfer from the negative effect of

438    reproductive interference. The population dynamics of both species exhibited neutral

439    random walks (Hubbell, 2001; Chave, 2004), indicating that stochastic events will end

440    coexistence with neutral dynamics at some point in time (Figs. 4 and 8). In our model,

441    coexistence with neutral dynamics was usually associated with the same parameter

442    conditions that promoted competitive exclusion by selfers, implying that these outcomes

443    are not qualitatively different (Figs. 3 and 5). The rate of evolutionary change in prior

444    selfing rates differed among categories, and coexistence occurred when high prior selfing

445    rates evolved more rapidly in both species (Fig. 2). Many predominately selfing weeds

446    coexist in human-disturbed habitats, in which pollinators are often limited (Baker, 1974);

447    this phenomenon is most likely attributable to coexistence with neutral dynamics.

448            Co-evolutionary shifts toward very high prior selfing rates (> 0.9) in both

449    species were necessary (Fig. 2) for both types of coexistence; however, many previous

450    empirical studies have reported coexistence of an extreme selfer and a related outcrosser

451    (Fishman & Wyatt, 1999; Brys et al. 2016; Randle et al. 2018). The difference between

452    field observations and our results may be attributable to two possible mechanisms that are

453    not accounted for in our model. First, ecological differences between species, such as

454    differences in competitive ability, germination, and strength of inbreeding depression,

455    may promote coexistence of species with different mating systems. Second, the selfers in

456    these studies exhibited reduced floral attractiveness, which minimised the negative effects

457    of reproductive interference (Fishman & Wyatt, 1999; Brys et al. 2016; Randle et al.

458    2018). Our model assumed that only the rate of prior selfing could evolve, as in the

459    previous model (Cheptou, 2019). Evolution of a selfing floral syndrome may enable

460    obligate selfers to coexist with outcrossing relatives. Recent studies have reported mutual

461    reproductive interference between two sympatrically growing, mixed-mating species with

462    showy flowers and traits promoting prior autonomous self-pollination, under conditions

463    of frequent pollinator visitation (i.e. cleistogamous flowers in *Impatiens noli-tangere* and

464    *I. textori*, Tokuda et al. 2015; bud pollination in *Commelina communis* and *C. communis*

465    f. *ciliata*, Katsuhara & Ushimaru, 2019). The coexistence documented in these study

466    systems may be explained by evolutionary rescue mediated by prior selfing, as predicted

467    in our model. Field monitoring of the eco-evolutionary dynamics of these species is

468    required to confirm this hypothesis. Although they may be time and resource intensive,

469    field investigations into the relationships between population selfing rates, inbreeding

470    depression, and relative abundance are an important first step towards improving our

471    understanding of co-evolutionary coexistence mechanisms in the absence of pollination

472    niche partitioning.

473           Empirical evidence for an effect of rapid evolution on plant coexistence remains

474    limited compared to theoretical studies (Grainger et al., 2019; Hart et al., 2019). Our

475    model, which incorporates the evolution of mating systems and plant–pollinator

476    interactions, is much more complex than those developed in recent studies to elucidate

477    the plant coexistence mechanism based on competitive experiments (Kraft et al., 2015;

478    Grainger et al., 2019; Hart et al., 2019; Siefert et al., 2021). Nevertheless, certain

479    advantages of our model support its application over empirical models. First, our model is

480    widely applicable because evolutionary transition from outcrossing to selfing occurred

481    repeatedly in various plant families, and even within species (Igic et al., 2015; Busch et

482    al., 2011). These events were traditionally interpreted as reproductive assurance to

483    overcome pollinator limitation (Cheptou, 2019); however, some events may be consistent

484    with our prediction that prior selfing evolved as an evolutionary rescue mechanism for

485    pollinator-mediated competition. Second, empirical studies have shown that evolutionary

486    shifts to higher prior selfing rates (often via reductions in herkogamy) can occur rapidly

487    under pollinator limitation (Roels & Kelly, 2011; Brys & Jacquemyn, 2012; Gravasi &

488 Schiestl, 2017; Cheptou, 2019). Experimental studies on the evolution of prior selfing at

489 ecological timescales are suitable to validate our results, and may provide a new

490 framework for determining how rapid evolution contributes to the maintenance of plant

491 diversity.

492 Our model successfully demonstrated that the evolution of prior selfing may

493 increase population growth rates of otherwise inferior competitors (Figs. 2 and 8), thus

494 enabling long-term coexistence via evolutionary rescue. We showed that evolutionarily

495 variable inbreeding depression, based on the balance between the accumulation and

496 purging of deleterious mutations (Lande et al., 1994; Porcher & Lande, 2016), both

497 increased the potential for coexistence and promoted coexistence over the long-term.

498 These results suggest that the genetic dynamics of inbreeding depression within a given

499 species may substantially influence dynamics in communities in which pollinator-

500 mediated competition occurs. Finally, we propose new mechanisms explaining the co-

501 evolutionary coexistence of closely related species under mutual reproductive

502 interference in the absence of niche differentiation and spatial structure. The applicability

503 and generality of these mechanisms should be confirmed via additional, empirical

504 investigations.

505

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515

516  **Conflict of Interest**

517  We have no potential sources of conflict of financial or nonfinancial interest in this

518  manuscript.

519

520  **Authors' Contributions**

521  KRK developed the model and conducted analyses. KRK wrote first draft together with

522  AU. KRK, YT, RI and AU discussed and wrote the manuscript.

523

524  **Data Availability**

525  Data available from the Dryad Digital Repository

526  https://doi.org/10.5061/dryad.2ngf1vhp1 (Katsuhara, Koki et al., 2021).

527

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713

714    **Supporting Information**

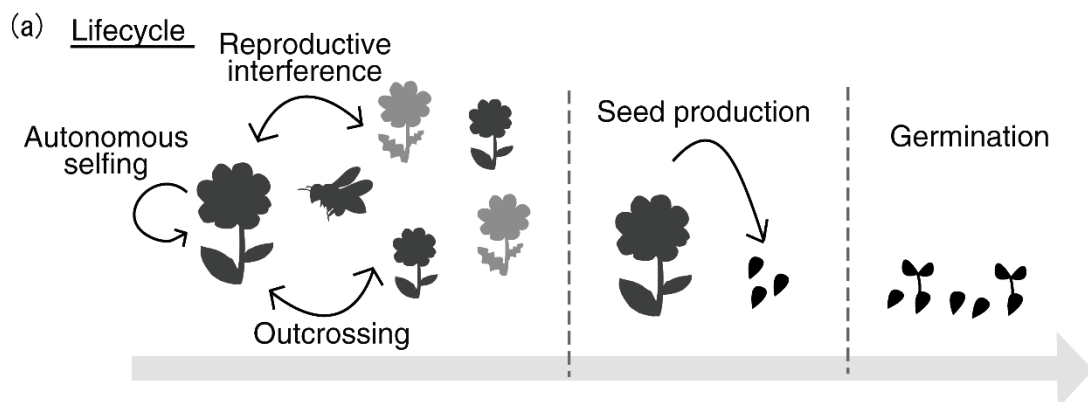715    Details of electronic Supporting Information are provided below.

716    Fig. S1. Frequency dependence of population growth rate in our model.

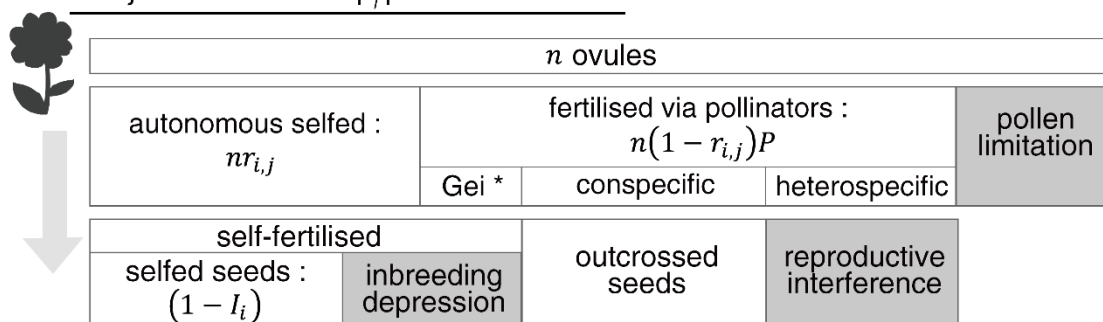717    Supporting file 1. The summary of data used in invasibility test.

718     **Table 1.** List of parameters included in the model.

| Parameter | Definition | Default value(s) |
|---|---|---|
| $r_{i,j,t}$ | Ratio of ovules fertilised via prior autonomous selfing in the $j$-th individual of sp$_i$ in the $t$-th generation | 0–1 |
| $q_{i,t}$ | Relative abundance of sp$_i$ in the $t$-th generation | 0–1 |
| $P$ | Pollinator availability | 0–1 |
| $c_h$ | Strength of reproductive interference | 1 |
| $\alpha$ | Slope of inbreeding depression function | 0, 0.5, 1, 2, 4, 8 |
| $\beta$ | Intercept of inbreeding depression function | 0.1, 0.3, 0.5, 0.7, 0.9 |
| $\mu$ | Mutation rate | 0.05 |
| $\sigma$ | Mutation effect size | 0.1 |
| $K$ | Carrying capacity (number of individuals) | 2,000 |
| $n$ | Number of ovules per individual plant | 200 |
| $r_{initial}$ | Mean initial prior autonomous selfing rate | 0.5 |
| $D_{intial}$ | Standard deviation of initial prior autonomous selfing rate | 1/6 |

719

(a) <u>Lifecycle</u> Reproductive interference

Autonomous selfing

Seed production

Germination

Outcrossing

(b) <u>The $j$-th individual of sp$_i$ produces $n$ ovules</u>

| $n$ ovules | | | | |
|---|---|---|---|---|
| autonomous selfed : $nr_{i,j}$ | fertilised via pollinators : $n(1 - r_{i,j})P$ | | | pollen limitation |
| | Gei * | conspecific | heterospecific | |
| self-fertilised | | outcrossed seeds | reproductive interference | |
| selfed seeds : $(1 - I_i)$ | inbreeding depression | | | |

Gei * : pollinator-mediated self-pollination (geitonogamy)

720

721 **Fig. 1.** Graphical overview of (a) the lifecycle, and (b) the pollination and fertilisation

722 processes of the species in the model. The model community comprised two annual

723 flowering plant species sharing the same pollination and ecological niches, and the model

724 parameterised pollination, seed production and germination (establishment) processes (a).

725 Ovules of an individual plant produced seeds fertilised via prior autonomous selfing or by

726 pollinator-mediated selfing and outcrossing (b). Some ovules remained unfertilised under

727 conditions of pollinator limitation ($P < 1$). Reproductive interference via heterospecific

728 pollination occurred according to the relative frequency of competing species (b).

729 Pollinators did not discriminate between species. In the seed production process, ovules

730 may be discounted by inbreeding depression ($I_i$; see Table 1), fertilisation by

731 heterospecific pollen, or pollen limitation. A certain number of seeds germinate and

732    establish based on the relative frequency of the species in the seed pool as the next
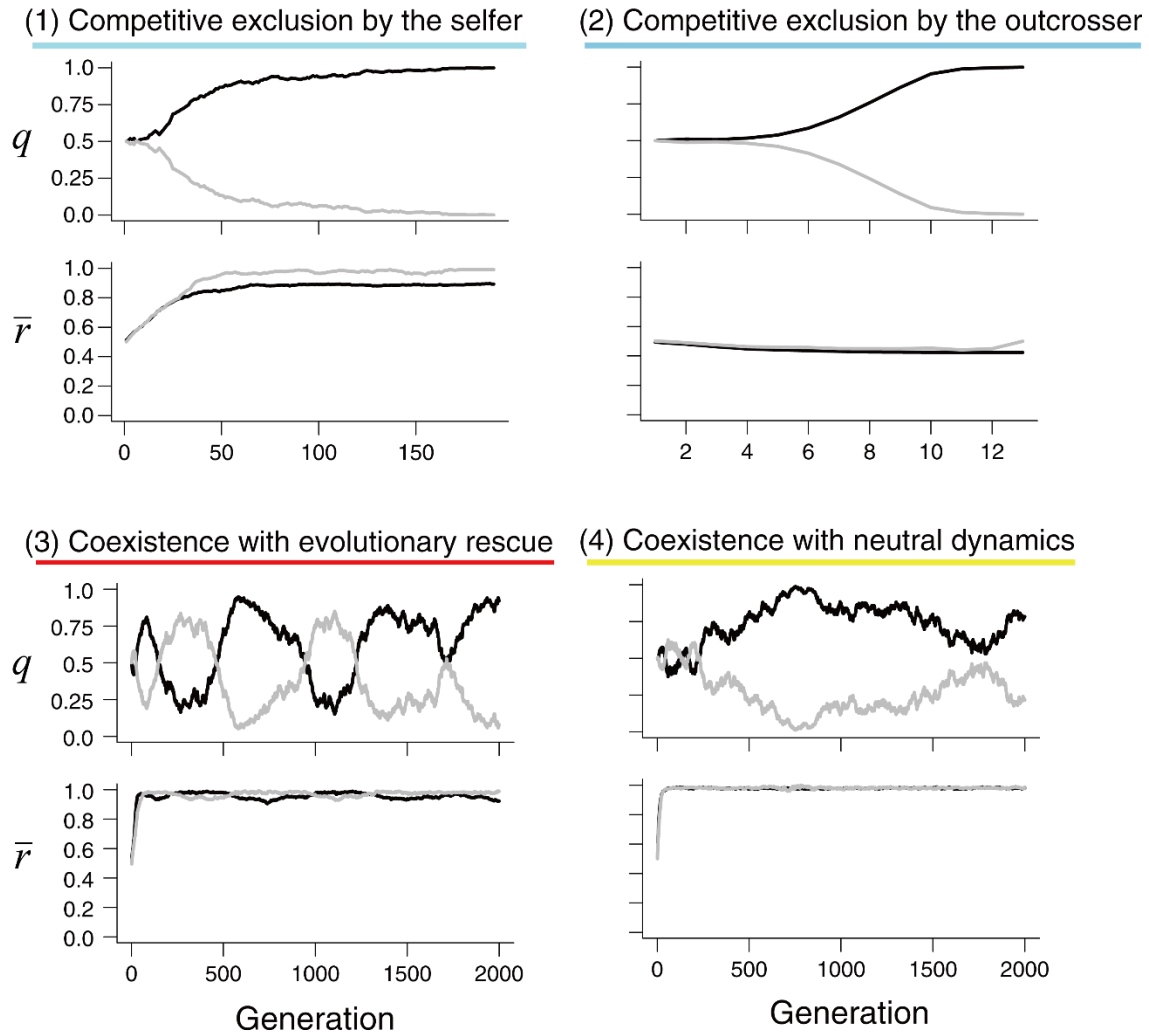
733    generation.

734

**(1) Competitive exclusion by the selfer**

**(2) Competitive exclusion by the outcrosser**

$q$

$\overline{r}$

**(3) Coexistence with evolutionary rescue**

**(4) Coexistence with neutral dynamics**

$q$

$\overline{r}$

Generation

Generation

**Fig. 2**. Examples of the four outcomes of eco-evolutionary dynamics in our simulations: (1) competitive exclusion by the selfer; (2) competitive exclusion by the outcrosser; (3) coexistence with evolutionary rescue; and (4) coexistence with neutral dynamics. The upper and lower panels of each category represent the relative abundance and mean population prior selfing rate dynamics, respectively, of $sp_1$ (black line) and $sp_2$ (grey).
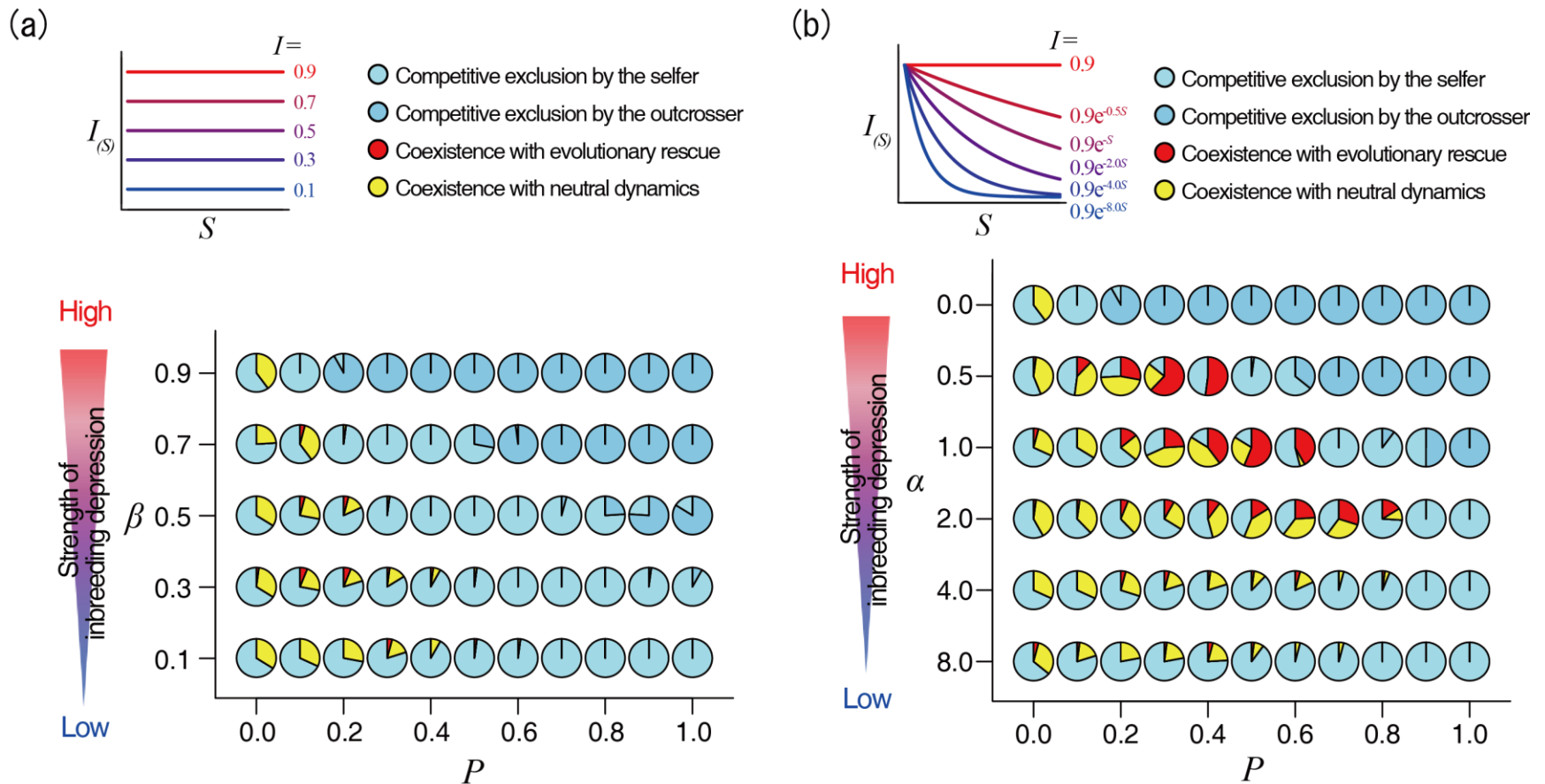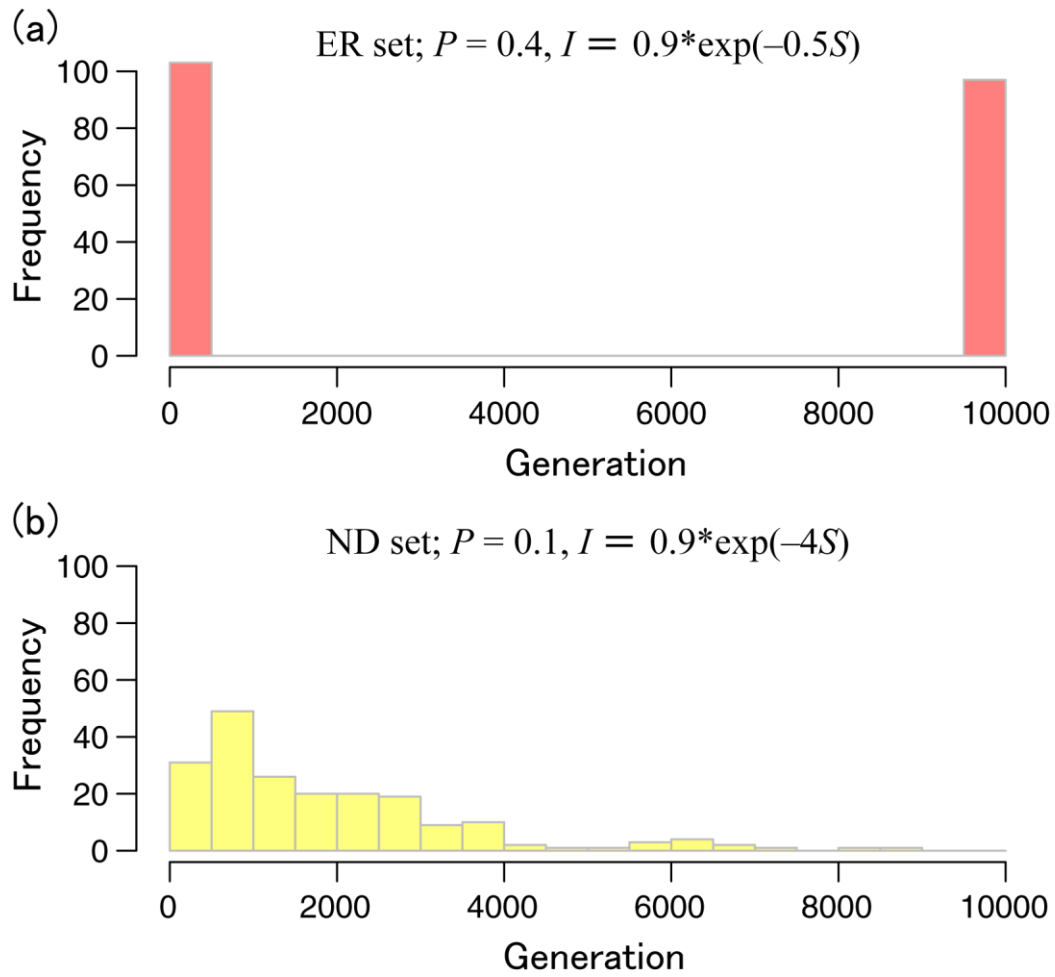
**Fig. 3**. Effects of pollinator availability and the strength of inbreeding depression on simulation outcomes in the fixed inbreeding depression scenario (a) and variable inbreeding depression scenario (b), respectively. Pie charts show the frequencies of the four eco-evolutionary outcomes after 50 simulation runs (Fig. 2).
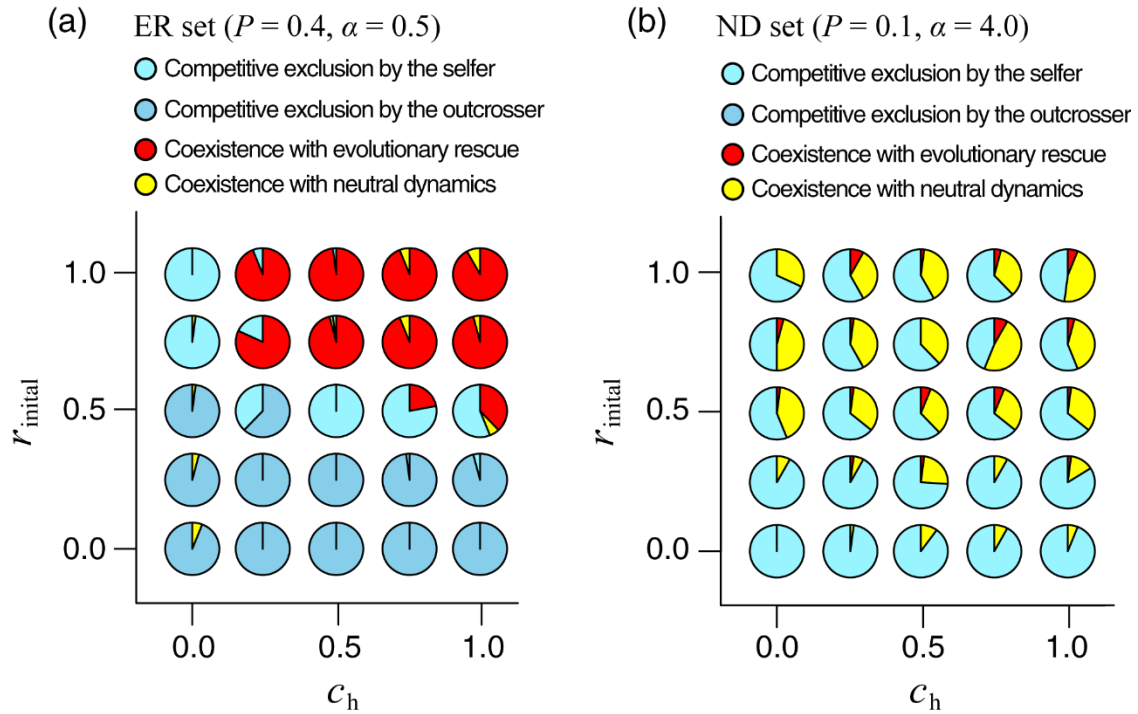
(a)

ER set; $P = 0.4, I = 0.9*\exp(-0.5S)$

(b)

ND set; $P = 0.1, I = 0.9*\exp(-4S)$

**Fig. 4**. Histograms for the number of simulations where either species went extinct for each generation interval in the ER set (a), and the ND set (b). Graphs represent the outcomes of 200 simulation runs.

**(a)** ER set ($P = 0.4$, $\alpha = 0.5$)

○ Competitive exclusion by the selfer
○ Competitive exclusion by the outcrosser
● Coexistence with evolutionary rescue
○ Coexistence with neutral dynamics

**(b)** ND set ($P = 0.1$, $\alpha = 4.0$)

○ Competitive exclusion by the selfer
○ Competitive exclusion by the outcrosser
● Coexistence with evolutionary rescue
○ Coexistence with neutral dynamics

**Fig. 5**. Effects of the strength of reproductive interference and initial population mean selfing rate in two typical parameter sets for coexistence with evolutionary rescue (a) and with neutral dynamics (b), respectively. Pie charts show the frequencies of the four eco-evolutionary outcomes after 50 simulation runs (Fig. 2).
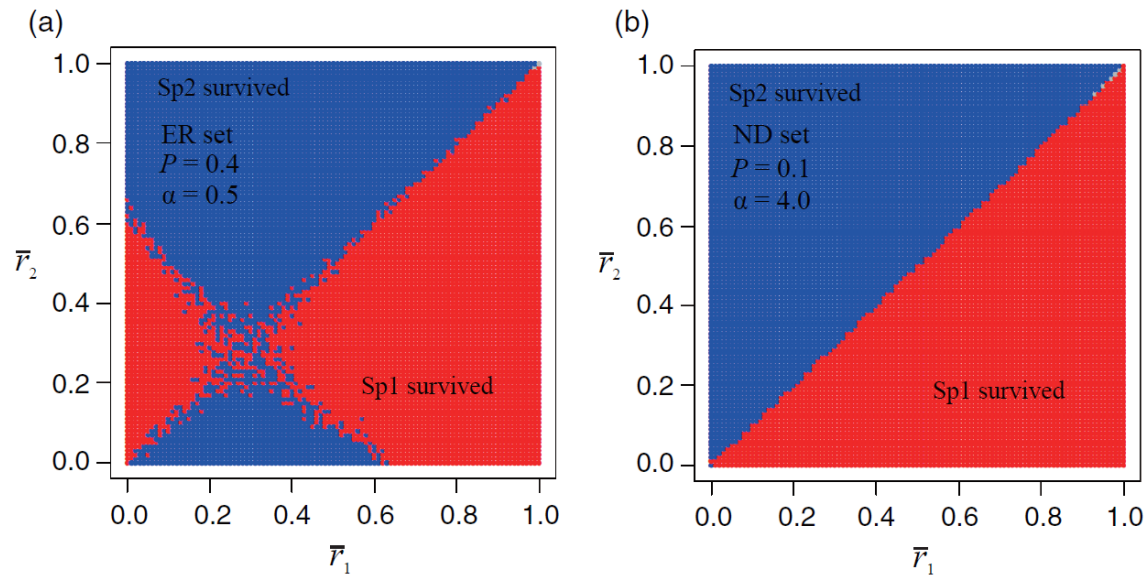
**Fig. 6**. Ecological consequences of fixed population prior selfing rates in the ER (a) and ND (b) sets. The x and y axes represent population mean prior selfing rates of $sp_1$ and $sp_2$, respectively. Red indicates survival of $sp_1$ whereas blue indicates survival of $sp_2$, and grey regions in the upper right corner of each panel indicate that coexistence persisted to the $2,000^{th}$ generation.
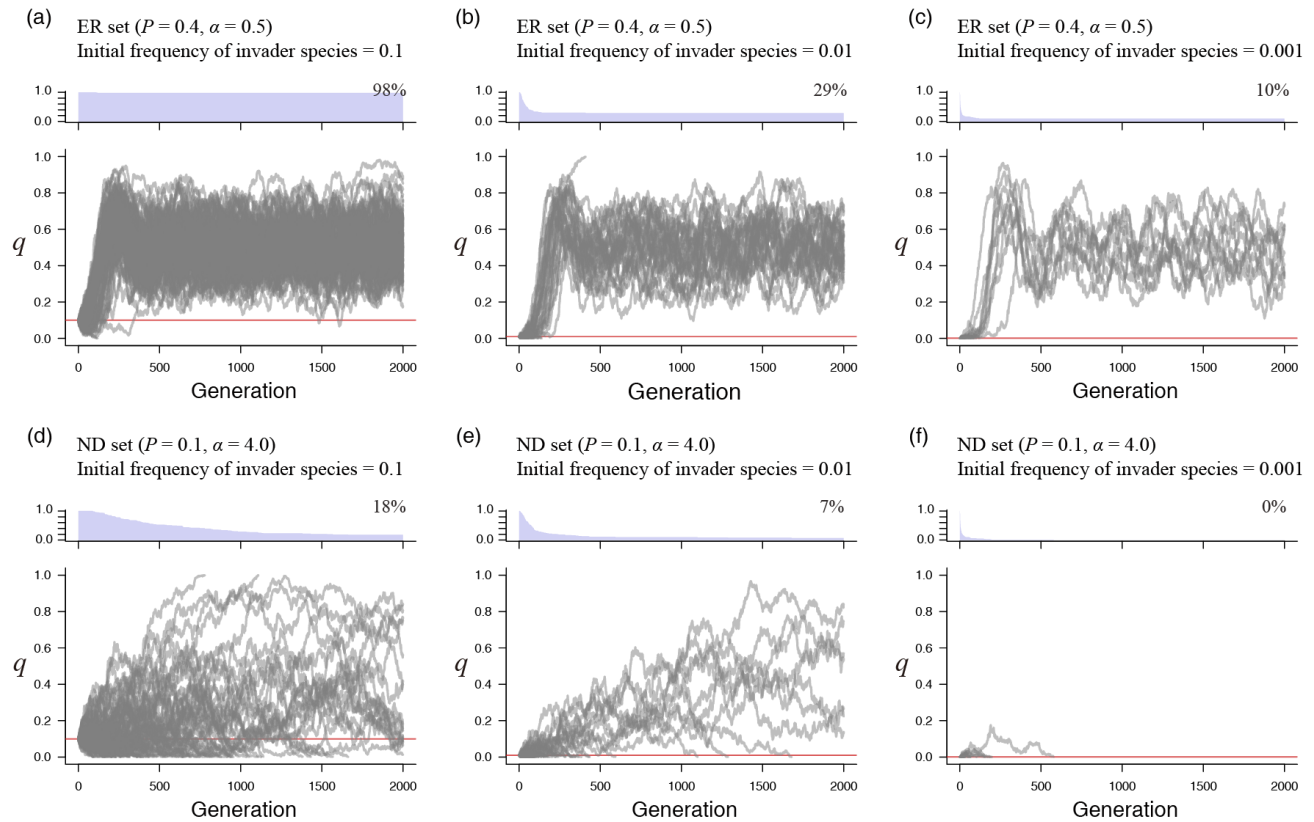
(a)

(b)



763
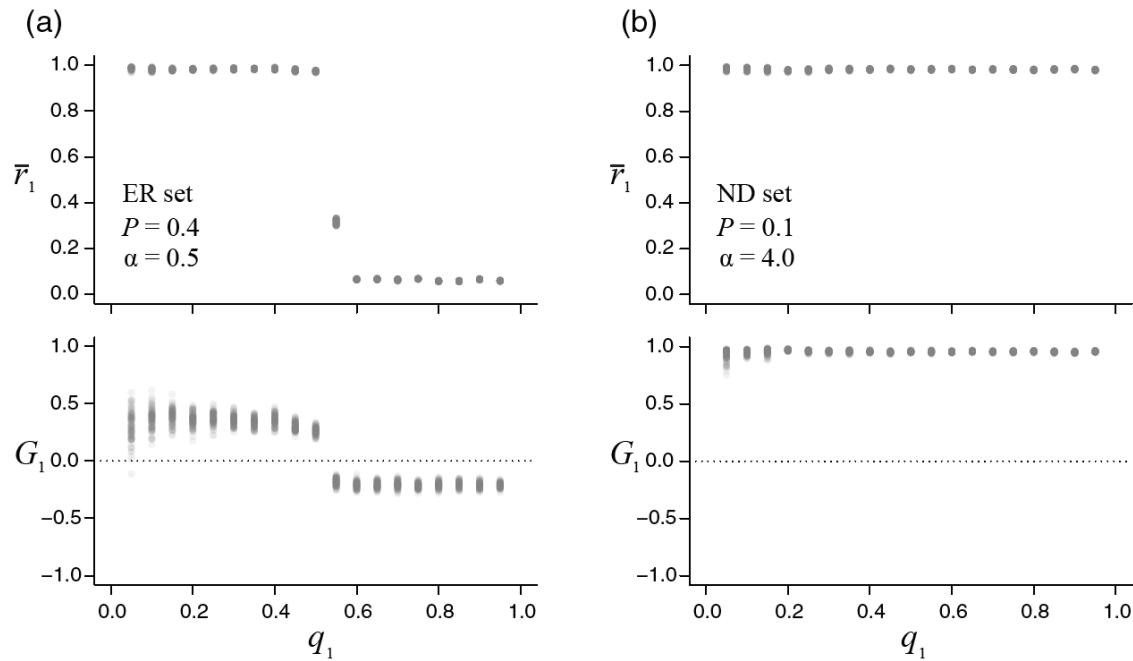
**Fig. 7**. Evolutionary outcomes of fixed relative abundance in the ER (a) and ND (b) sets.

Upper and lower graphs show correlations between population mean prior selfing rates and

the selection gradient, and relative abundance of the focal species in last 500 of 2,000

generations, respectively.

**Fig. 8.** Invasibility of species with low initial frequencies (left, 0.1; middle, 0.01; right, 0.001) under the (a–c) ER and (d–f) ND sets. (Upper panels) The proportion of simulations in which both species coexisted until the 2,000$^{th}$ generation. (Lower panels) Relative abundance of focal (invader) species. The red line in each panel indicates the level of the initial frequency of invader species.