

1 **Ecological success of sexual and asexual reproductive**
2 **strategies invading an environmentally unstable**
3 **habitat**

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Abstract

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Many aspects of sexual and asexual reproduction have been studied empirically and theoretically. The differences between sexual and asexual reproduction within a species often lead to a biased geographical distribution of individuals with different reproductive strategies. While sexuals are more abundant in the core habitat, asexuals are often found in marginal habitats along the edge of the species distribution. This pattern, called geographic parthenogenesis, has been observed in many species but the mechanisms responsible for generating it are poorly known. We used a quantitative approach using a metapopulation model to explore the ecological processes that can lead to geographic parthenogenesis and the invasion of new habitats by different reproductive strategies. We analyzed the Allee effect on sexual populations and the population sensitivity to environmental stress during the invasion of a marginal, unstable habitat to demonstrate that a complex interaction between the Allee effect, sensitivity to environmental stress and the environmental conditions can determine the relative success of competing reproductive strategies during the initial invasion and long-term establishment in the marginal habitat. We discuss our results in the light of previous empirical and theoretical studies.

30 **Author Summary**

31 Individuals can reproduce with or without sex. Very often, closely related species are dis-
32 tributed in a such a way that the sexually reproducing species is most frequently found in the
33 core habitat while the asexually reproducing species is found on the edge of the habitat range.
34 This biased distribution of reproductive strategies across a habitat range is called geographic
35 parthenogenesis and has been observed in several species. While many processes have been pro-
36 posed to explain such a pattern, a quantitative approach of the ecological processes was absent.
37 We investigated important differences between sexual and asexual reproduction and how these
38 differences affect the success of sexuals and asexuals invading a marginal, unstable environment.
39 We showed that the relative frequency of each reproductive strategy in the marginal habitat
40 depends on how much sexuals rely on population density to reproduce and how much asexu-
41 als are affected by environmental stress relative to sexuals. Our study presents a quantitative
42 ecological explanation for geographic parthenogenesis and provides the conditions under which
43 different distribution patterns can emerge.

44 Introduction

45 Niche and habitat range expansion are key ecological processes in both population dynamics
46 and interspecific competition. These processes are essentially dependent on the efficiency of
47 the reproductive strategies that are characteristic of each population in the new niches or habi-
48 tats. Therefore, understanding how different reproductive strategies can affect these processes
49 is fundamental for understanding population dynamics and interspecific competition during in-
50 vasion of previously uninhabited habitats [1]. Although many different reproductive strategies
51 exist, they can all be defined based on the occurrence of fusion of gametes provided by different
52 individuals (sexual) or absence of such process (asexual). These different strategies have differ-
53 ent benefits and disadvantages; for example, while asexual reproduction gives individuals the
54 independence to reproduce without the need to find compatible mating partners [2; 3], sexual
55 reproduction generates genetic diversity that may keep the population alive under adverse en-
56 vironmental conditions [4; 5; 6; 7]. Additionally, in many species, these reproductive strategies
57 are not mutually exclusive, with individuals frequently switching between sexual and asexual
58 reproduction [facultative modes of reproduction; 8; 9; 10; 11] or different populations having
59 different reproductive strategies.

60 Because of the differences between sexual and asexual reproduction within a species, the ge-
61 ographical distribution of individuals with different reproductive strategies often differs [12; 13].
62 While sexuals are more abundant in the core habitat, where the species might have existed for
63 a longer time, asexuals are often found in marginal habitats along the edge of the species distri-
64 bution [14; 15; 16; 17; 18]. This pattern can be observed along the south-north gradient in the
65 Northern Hemisphere, where glaciers have repeatedly wiped out northern populations and left
66 the landscape open for recolonization from the south [19; 20], and also along elevation gradients
67 in mountains, where climate becomes gradually harsher with altitude [21]. Similar patterns
68 have been observed in aquatic environments along the salinity and temperature gradients, for
69 example, in river-estuary complexes [22] and in the Baltic Sea [23; 24; 25; 26], where gradient
70 extremes may be physiologically stressful for certain reproductive strategies. The mechanisms
71 behind this spatial segregation (geographic parthenogenesis) are hotly debated and have been
72 attributed to both evolutionary [e.g., 18; 19] and neutral random processes [27].

73 Genetic distribution patterns of geographic parthenogenesis have been investigated with

74 empirical and theoretical approaches, both in plants [15; 28] and animals [14; 21; 29]. For
75 example, in the alpine plant species *Ranunculus kuepferi*, apomictic (asexual) populations ex-
76 hibit high genetic admixture near sexual populations but are highly uniform in remote areas,
77 with few well-supported genetic clusters [30], indicating the occurrence of multiple colonization
78 events by genetically different founders. However, in the genera *Taraxacum* (dandelion) and
79 *Chondrilla* (skeleton weed), apomictic populations exhibit high genetic diversity, which can be
80 explained by crosses between apomictics and sexuals (in regions where these reproductive strate-
81 gies are sympatric) followed by colonization of marginal regions, or crosses between facultative
82 apomictics in purely apomictic regions [31; 32]. In *Daphnia pulex* (water flea), asexual popu-
83 lations also exhibit elevated individual heterozygosities introduced by outcrosses [33], allowing
84 outcrossed asexuals to displace sexuals due to the competitive advantages conferred by their
85 admixed genotypes. Although these genetic differences between sexual and asexual *Daphnia*
86 can explain the differences in the geographic distribution of different reproductive strategies, it
87 is also possible that genetic differences can cause ecological differentiation between reproductive
88 strategies, allowing them to coexist in the same habitat, as has been suggested by experiments
89 [34]. In many cases, however, genetic diversity in parthenogenetic populations is generally low
90 [35; 36; 37; 38; 39], which may be explained by the invasion of marginal habitats by a small
91 number of asexual individuals.

92 Several theoretical aspects of geographic parthenogenesis have been studied [1]. The evo-
93 lution of spatial segregation between sexual and asexual populations was explored in annual
94 hermaphrodites with an individual-based model [20]. In the model, the metapopulation con-
95 sisted of patches arranged along a south-north axis, with reproductive rate gradually decreasing
96 in the north direction and each patching favoring a locally adapted phenotype. Population dy-
97 namics led to asexual individuals exhibiting higher frequencies than sexual individuals in the
98 north patches, which was explained by the gene flow from the south constraining sexual indi-
99 viduals to evolve local adaptations to the habitats in the north, while asexuals maintained their
100 locally advantageous genotype once it had appeared. It has been suggested that asexuals that
101 are well adapted to marginal habitats retain their adaptation while sexuals can suffer from gene
102 flow of suboptimal alleles from the core-habitat. Additionally, populations with metapopulation
103 dynamics tend to show geographic parthenogenesis because of the higher tolerance of asexuals

104 to population bottlenecks and drift, allowing them to invade marginal habitats in small numbers
105 [16]. On shorter time scales asexuals may also be better colonizers because they can reproduce
106 without mating, thus avoiding the Allee effect that sexuals are subject to [16; 18]. A different
107 model explored the effects of sexual conflict and mate limitation on the frequency of facultative
108 parthenogens [40]. The magnitude of these effects together with levels of environmental produc-
109 tivity were primary determinants of the spatial distribution of different reproductive strategies
110 (sexual or facultative parthenogenesis). Parthenogenesis was particularly favored when low
111 environmental productivity caused low population density at the edges of the habitat, making
112 mating either too difficult or too costly. Other models have also resulted in distribution patterns
113 of reproduction strategies that is typical of geographic parthenogenesis [e.g., 41].

114 However, many important aspects of geographic parthenogenesis remain, surprisingly, un-
115 explored. The existence of different types of asexual reproduction [42; 43] and the ability to
116 change between different reproductive strategies are important factors that need to be addressed.
117 The magnitude of the Allee effect, which can be particularly important in sexual populations
118 [44; 45; 46], may play an important role in leading to geographic parthenogenesis but has been
119 essentially ignored. And finally, population sensitivity to environmental variation in marginal
120 habitats may determine whether habitat range expansion is possible and which reproductive
121 strategies can be the most successful during range expansion, and yet these factors have been
122 overlooked in particular from the empirical perspective. Because of the necessity to address
123 these processes as leading causes of geographic parthenogenesis, we developed a metapopula-
124 tion model of competition between different reproductive strategies and assessed the ecological
125 success of each competing strategy during short-term invasions and long-term establishment
126 in unstable habitats, under different environmental conditions. Our model considers both the
127 Allee effect (weak and strong) that affects sexually reproducing populations and the population
128 sensitivity to stressful environmental conditions, which can be affected by genetic diversity. We
129 use the temporal mean population size during initial invasion and long-term establishment as
130 a measure of the ecological success of each competing strategy.

131 **Methods**

132 We model population dynamics in a metapopulation consisting of two qualitatively different
133 patches. One patch (South patch) is assumed to host the larger, ancestral population, while the
134 other patch (North patch or marginal habitat) is assumed to be a habitat that has been recently
135 made available to the species under focus. The availability of a patch to a certain species can
136 be affected by several factors (e.g., global warming may make northern ecosystems available
137 to species that are typical from temperate climates). In our model, the South and North
138 patches have different environmental properties, which are independent from the properties of
139 the populations that they host. The South patch is characterized by a high environmental
140 stability and hosts an ancestral population in equilibrium (Figure 1). Although, we use only
141 two patches in the current study, the equations can be adapted to any number of patches.

142 The ancestral population consists of individuals that reproduce according to one of the
143 following strategies, characterized by the properties of their growth rate:

144 (A) Obligate apomictic parthenogenesis (clonal reproduction): Individuals do not need to
145 find a mating partner in order to reproduce, which can be advantageous when population
146 density is low. However, parents and offspring are genetically identical (very limited
147 genetic variation), which makes the population very sensitive to changes in environmental
148 conditions.

149 (B) Obligate automictic parthenogenesis (non-clonal asexual reproduction): Individuals do
150 not need to find a mating partner in order to reproduce, but unlike strategy A, parents
151 and offspring are genetically different (to some extent) due to recombination during ga-
152 mate production (limited but existent genetic variation). Because of the higher genetic
153 variation, strategy B is assumed to be less sensitive to changes in environmental conditions
154 than strategy A.

155 (C) Obligate sexual reproduction: Individuals need to find a compatible partner to mate with
156 and parents and offspring are genetically different. Because of the difficulty in finding
157 compatible mating partners when the population density is low, strategy C is affected by
158 the Allee effect. With sexual reproduction, however, the population keeps a higher genetic
159 diversity that can be beneficial when environmental conditions change.

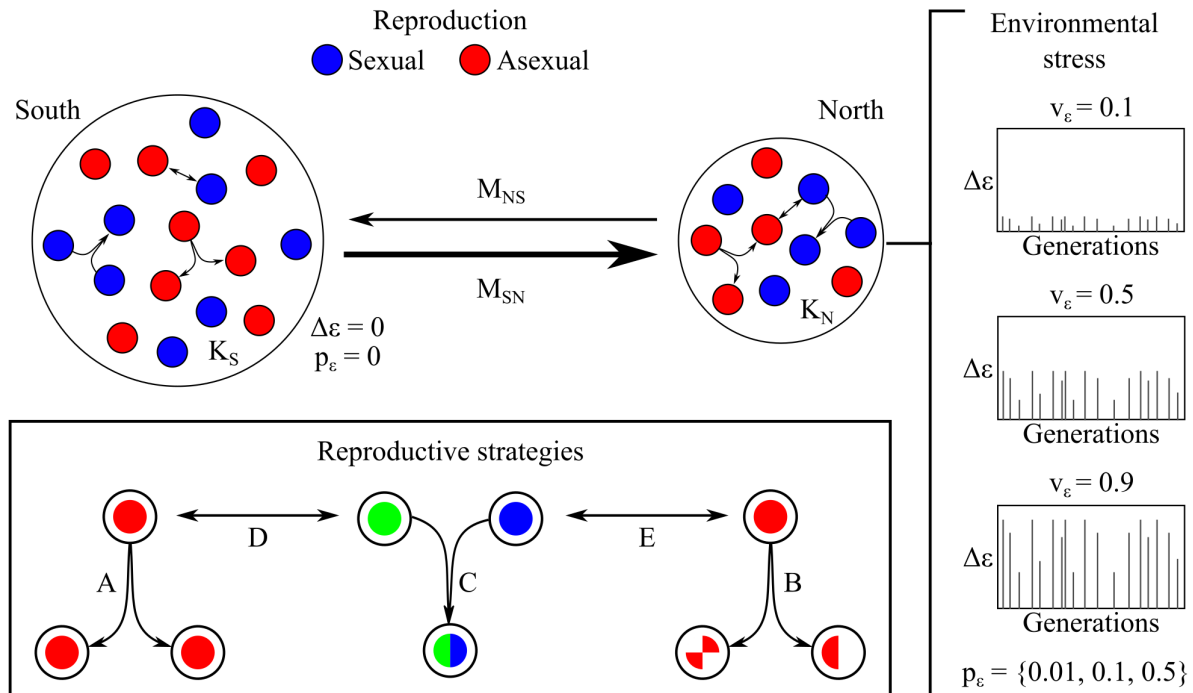


Figure 1: Graphical overview of the model design. Population dynamics include strategy-specific growth, transition and migration between an ancestral population (South patch) and a marginal habitat (North patch) where environmental conditions are unstable relative to the South patch. The panels to the right represent examples of three environmental regimes to which the North patch is exposed. Five different reproductive strategies were considered (bottom rectangle): obligate apomictic parthenogenesis or clonal reproduction (strategy A), obligate automictic parthenogenesis (strategy B), obligate sexual reproduction (strategy C), facultative apomictic parthenogenesis (strategy D) and facultative automictic parthenogenesis (strategy E). Complete description of the reproductive strategies in the main text. The subscripts/superscripts S and N indicate variables characterizing the South and North patches, respectively. The South patch differs from the North patch in its carrying capacity ($K_S > K_N$), probability of occurrence of stressful events ($p_\epsilon^S = 0$ and $p_\epsilon^N > 0$), maximum environmental stress level ($v_\epsilon^S = 0$ and $v_\epsilon^N > 0$) and effective stress level ($\Delta\epsilon^S = 0$ and $\Delta\epsilon^N \geq 0$). M represents migration between patches.

- 160 (D) Facultative apomictic parthenogenesis: Individuals can transition between strategies A
 161 and C after assessment of population density. Strategy D individuals are affected by the
 162 same factors that affect strategies A and C when individuals act like such strategies. Strat-
 163 egy D individuals reproducing asexually are designated D- and individuals reproducing
 164 sexually are designated D+.
- 165 (E) Facultative automictic parthenogenesis: Individuals can transition between strategies B
 166 and C after assessment of population density. Strategy E individuals are affected by
 167 the same factors that affect strategies B and C when individuals act like such strategies.
 168 Strategy E individuals reproducing asexually are designated E- and individuals reproduc-

169 ing sexually are designated E+.

170 It might be argued that strategy B (automictic parthenogenesis) is more sensitive to environ-
171 mental stress than strategy A (apomictic parthenogenesis) because of the loss of heterozygosity
172 in strategy B during reproduction. However, we consider the case where genomic diversity
173 produced by automictic parthenogenetic reproduction is more beneficial than genomic homo-
174 geneity under natural selection caused by environmental stress because homozygosity caused
175 by automictic parthenogenesis introduces new phenotypes into the population.

176 Different strategies can affect one another indirectly through their effects on the total popu-
177 lation density and transitions between reproductive strategies (sexual to asexual and vice-versa),
178 as explained below. For ease of reference, we define subpopulation as the fraction of the patch-
179 specific total population that is composed of individuals with a specific reproductive strategy.

180 Population dynamics

181 Population dynamics follow a logistic population growth model (Ricker model) with a variable
182 growth rate, which is affected by environmental quality (carrying capacity), the Allee effect on
183 strategies C-E, and environmental effects. Additionally, the total population density is affected
184 by migration from/to the South patch. Change in subpopulation size from generation t to
185 generation $t + 1$ due to growth is defined by the following difference equation:

$$N_{p_i,t+1}^s = N_{p_i,t}^s \cdot \exp \left[r_{p_i,t}^s \cdot \left(1 - \text{sgn}(r_{p_i,t}^s) \cdot \frac{N_{p_i,t}}{K_{p_i} \cdot (1 - E_{p_i,t}^s)} \right) \right] + T_{p_i,t}^s + M_{p_i,t}^s \quad (1)$$

186 where the exponential term determines the logistic population growth rate based on the Ricker
187 model and is equivalent to λ in exponential growth models, $M_{p_i,t}^s$ is the net change in population
188 size due to migration South-North or vice-versa and $T_{p_i,t}^s$ is the number of transitions from
189 sexual to asexual reproduction and vice-versa in strategies D-E. In strategies A-C, $T_{p_i,t}^s = 0$.
190 It is important to note that transitions follow growth and migration follows transitions, which
191 means that transitions are calculated based on the outcome of the logistic term and migration is
192 calculated after transitions happen. In the logistic growth term, $N_{p_i,t}^s$ is the subpopulation size of
193 the reproductive strategy indicated by the superscript s in the patch indicated by the subscript
194 p_i (p_S for patch in the South and p_N for patch in the North) at time t (given in generations),
195 $N_{p_i,t}$ is the patch-specific total population size, K_{p_i} is the patch-specific constant maximum

196 carrying capacity and $E_{p_i,t}^s$ is the effect of changes in environmental conditions (explained in
197 detail below). The variable $r_{p_i,t}^s$ is the effective growth rate for the species under analysis after
198 the reduction due to the Allee effect in strategies C-E. In strategies A and B, $r_{p_i,t}^s$ is simply
199 the intrinsic maximum growth rate (explained below). In order to account for possible negative
200 effects caused by both the Allee effect and reduction in environmental quality, it is necessary to
201 introduce $sgn(r_{p_i,t}^s)$ so that multiple negative effects do not cancel each other.

202 Growth rates

203 All reproductive strategies have an equal intrinsic maximum growth rate r_{max} , which leads to
204 exponential growth when the following conditions are met: unlimited resources or maximum
205 environmental quality ($K_{p_i} \rightarrow \infty$), no Allee effect ($r_{p_i,t}^s \rightarrow r_{max}$), no environmental effect
206 ($E_{p_i,t}^s \rightarrow 0$) and no migration ($M_{p_i,t}^s \rightarrow 0$). The maximum growth rate represents a biological
207 limit in reproduction in the species under focus. By setting $r_{max} = 1.1$, we limit reproduction
208 such that each individual can produce on average at most $\lambda = e^{1.1} \approx 3$ offspring per generation
209 (Figure S1).

210 Allee effect

211 The Allee effect is present in the sexually reproducing subpopulations (strategies C-E) and
212 accounts for the difficulty in finding compatible mating partners when the population size
213 is small. In strategies D-E, the Allee effect only affects sexuals (D+ and E+). In asexual
214 individuals (strategies A, B, D- and E-), $r_{p_i,t}^s = r_{max}$ because mating is not necessary in order
215 to reproduce.

216 The Allee-dependent growth rate ($A_{p_i,t}^s$) is lowest (r_{min}) when the number of sexuals $N_{p_i,t}^+ \rightarrow$
217 0 and increases as $N_{p_i,t}^+$ increases, until it reaches a biological limit (r_{max}). This dynamic growth
218 rate is defined by the following equation:

$$A_{p_i,t}^s = (r_{max} - r_{min}) \cdot \frac{\exp\left(\frac{N_{p_i,t}^+}{\alpha \cdot \beta \cdot K_{p_i}} - \frac{N_{p_i,t}^+}{\beta \cdot K_{p_i}}\right) - 1}{\exp\left(\frac{1}{\alpha} - 1\right) - 1} + r_{min} \quad (2)$$

219 where α is the curvature of the function and $\beta \cdot K_{p_i}$ is the population size (relative to the
220 carrying capacity K_{p_i}) at which $A_{p_i,t}^s = r_{max}$, that is, when growth rate reaches its biological
221 limit (Allee saturation point), such that $r_{p_i,t}^s = \min(A_{p_i,t}^s, r_{max})$ (Figure 2).

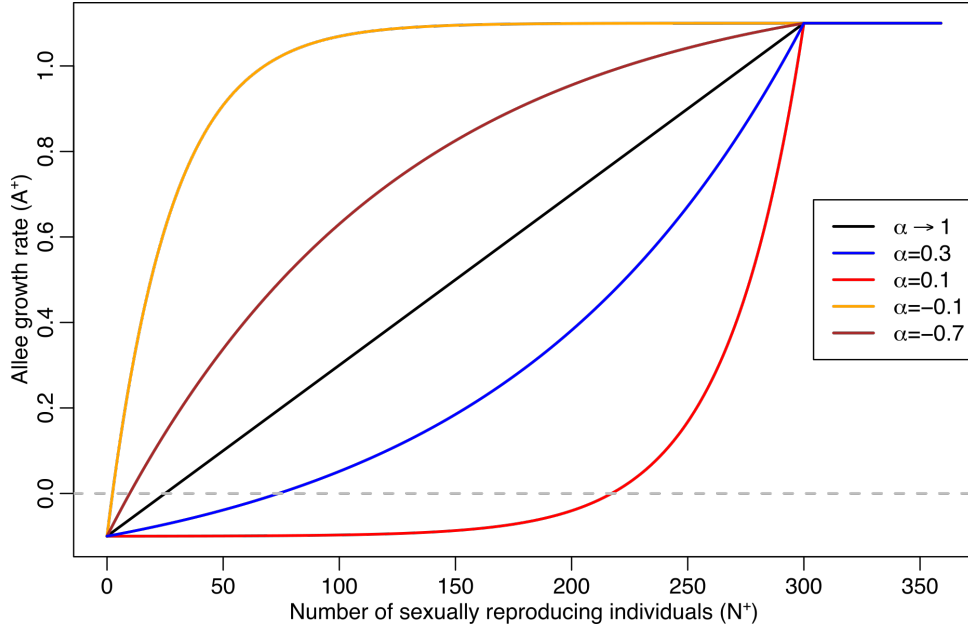


Figure 2: Allee function for different values of α . Parameter values used: $r_{min} = -0.1$, $r_{max} = 1.1$, $\beta = 0.3$, $K_{p_N} = 1000$.

222 Unlike previous models of the Allee effect, we assume that growth rate increases with pop-
 223 ulation density (with a monotonic relationship) and it is bound by an explicit upper biological
 224 limit. Difficulty in finding a compatible mating partner should always decrease with an increas-
 225 ing population density and Equation 2 allows us to explore this effect by changing the rate of
 226 change in growth rate (changes in α and β) as population density increases.

227 Our Allee model of growth rate has the following properties: (i) $r_{p_i,t}^s = r_{min}$ when $N_{p_i,t}^+ = 0$;
 228 (ii) $r_{p_i,t}^s = r_{max}$ when $N_{p_i,t}^+ = \beta \cdot K_{p_i}$; and (iii) $r_{p_i,t}^s = 0$ (no growth) when

$$N_{p_i,t}^+ = \frac{\alpha \cdot \beta \cdot K_{p_i} \cdot \text{Log} \left(\frac{e \cdot (r_{max} - r_{min})}{e \cdot r_{max} - e^{\frac{1}{\alpha}} \cdot r_{min}} \right)}{\alpha - 1} \quad (3)$$

229 We set $r_{min} = -0.1$ (such that $\lambda = e^{-0.1} \approx 0.9$) and assume that a very small subpopulation
 230 size (below the Allee threshold indicated by Equation 3) of sexuals results in many individuals
 231 dying before they have the chance to reproduce (negative net growth). Furthermore, we set
 232 $K_{p_S} = 5000$ and $K_{p_N} = 1000$ and explore values of $\beta \in \{0.1, 0.2, 0.3\}$, which means that the
 233 maximum growth rate of the sexually reproducing subpopulation in the North patch is achieved
 234 when the subpopulation size reaches $N_{p_N,t}^+ \geq \beta \cdot K_{p_N}$ (which corresponds to 100, 200 and 300
 235 individuals, respectively, as the population size at Allee saturation). The shape of the curve
 236 of the Allee effect was explored by setting $\alpha \in \{-0.7, 0.1, 0.3, \sim 1.0\}$ in different simulations.

237 When environmental conditions do not have an active effect on population dynamics ($E_{p_i,t}^s = 0$),
238 population growth is determined by the Allee effect and the carrying capacity of the patch,
239 reaching its maximum when $N_{p_i,t}^s = \beta \cdot K_{p_i}$. In weak Allee effect scenarios, we set $\alpha = 0.3$ and
240 $\beta = 0.1$; in strong Allee effect scenarios, we set $\alpha = 0.1$ and $\beta = 0.3$ (Figure S2).

241 Environmental conditions

242 Environmental stress can decrease the population growth rate because the population is not
243 adapted to the new environmental conditions (e.g., starvation, diseases, energetic stress, reduc-
244 tion in resource availability due to anthropogenic disturbances). In our model, environmental
245 stress reduces the effective carrying capacity of each reproductive strategy in the North patch,
246 which is defined by $K_{p_i} \cdot (1 - E_{p_i,t}^s)$ in Equation 1.

247 Because we are interested in how environmental stress affects population dynamics, we
248 directly modeled environmental stress levels ($\Delta\epsilon_t$) as scaled deviations from optimal environ-
249 mental conditions ($\Delta\epsilon_t^{p_i} = 0$) rather than the environmental variable itself. Our model assumes
250 that environmental stress levels ($\Delta\epsilon_t^{p_i}$) have the effect of reducing the patch-specific carrying
251 capacity and therefore has a range $0 \leq \Delta\epsilon \leq 1$, with $\Delta\epsilon = 0$ representing the complete absence
252 of stress (optimal conditions) and $\Delta\epsilon = 1$ representing maximum stress, with complete reduc-
253 tion of the effective carrying capacity. Environmental stress occurs according to the following
254 equation:

$$\Delta\epsilon_t^{p_i} = [U_t(0, 1) \leq p_\epsilon^{p_i}] \cdot U_t(0, v_\epsilon^{p_i}) \quad (4)$$

255 where $p_\epsilon^{p_i}$ is the patch-specific probability of deviation from optimal environmental condi-
256 tions and $v_\epsilon^{p_i}$ is the patch-specific maximum deviation (maximum stress level). The term
257 $[U_t(0, 1) \leq p_\epsilon^{p_i}]$ is a boolean indicator of presence (1) or absence (0) of change. Stressful en-
258 vironmental events across generations are stochastic and take a value drawn from a uniform
259 distribution $U(0, v_\epsilon^{p_i})$. We explored the effects of different probability values $p_\epsilon^{p_i} \in \{0.01, 0.1, 0.5\}$
260 and maximum stress levels $v_\epsilon^{p_i} \in \{0.1, 0.5, 0.9\}$ (Figure S3) on the initial invasion and long-term
261 establishment of different reproductive strategies in the marginal habitat (North patch).

262 Although environmental stress affects the effective carrying capacity of the patch, different
263 reproductive strategies are sensitive to these changes at different degrees due to their different

264 genetic/phenotypic variation. We thus define $0 \leq \phi^s \leq 1$ as the sensitivity to changes in the
 265 effective carrying capacity of a patch due to environmental stress. We explored how sensitivity
 266 can affect the ecological success of each strategy. Unless indicated otherwise, sensitivity to
 267 environmental stress was assumed to be high in strategy A (clonal reproduction; $\phi^A = 1.0$, used
 268 as a reference), intermediate in strategy B (non-clonal asexual reproduction; $\phi^B = 0.75$) and
 269 low in strategy C (sexual reproduction; $\phi^C = 0.5$) as a consequence of their genetic/phenotypic
 270 diversity. Note that strategy B differs from strategy A only in its sensitivity ($\phi^B < \phi^A$). This
 271 sensitivity effect is assumed to be a linear function of the environmental stress level, such that:

$$E_{p_i,t}^s = \phi^s \cdot \Delta \epsilon_t^{p_i} \quad (5)$$

272 Equation 5 indicates that environmental effects on population dynamics are absent when
 273 environmental conditions are optimal ($\Delta \epsilon_t^{p_i} = 0$) or the population is insensitive to changes in
 274 the environmental factors under focus ($\phi^s = 0$). As noted earlier, strategies D and E share the
 275 properties of strategies A/C and B/C, respectively.

276 Reproductive transitions

277 In facultative parthenogenetic strategies (D and E), transitions between sexual and asexual re-
 278 production (and vice-versa) happen at a maximum rate τ and are affected by population density.
 279 We assume that individuals cannot distinguish between those that are reproducing asexually
 280 and those that are potential mating partners (sexual reproduction), so population assessment is
 281 based on total population size. After assessment of population density, a proportion of strategy
 282 D individuals transition from D- (asexual) to D+ (sexual) and vice-versa. Similarly, a pro-
 283 portion of strategy E individuals transition from E- (asexual) to E+ (sexual) and vice-versa.
 284 The net number of transitions from asexual (D-/E-) to asexual (D+/E+) reproduction ($T_{p_i,t}^{s+}$)
 285 is calculated by the following equation:

$$T_{p_i,t}^{s+} = \tau \left[\left(\frac{\min(N_{p_i,t}, \beta \cdot K_{p_i})}{\beta \cdot K_{p_i}} \right) \cdot N_{p_i,t}^{s-} - \left(1 - \frac{\min(N_{p_i,t}, \beta \cdot K_{p_i})}{\beta \cdot K_{p_i}} \right) \cdot N_{p_i,t}^{s+} \right] \quad (6)$$

286 Equivalently, the net number of transitions from sexual (D+/E+) to asexual (D-/E-) repro-

287 duction ($T_{p_i,t}^{s-}$) is calculated by the following equation:

$$T_{p_i,t}^{s-} = \tau \left[\left(1 - \frac{\min(N_{p_i,t}, \beta \cdot K_{p_i})}{\beta \cdot K_{p_i}} \right) \cdot N_{p_i,t}^{s+} - \left(\frac{\min(N_{p_i,t}, \beta \cdot K_{p_i})}{\beta \cdot K_{p_i}} \right) \cdot N_{p_i,t}^{s-} \right] \quad (7)$$

288 where $N_{p_i,t}^{s-}$ is the patch-specific number of individuals in strategy D/E reproducing asexually (D-
289 /E-) and $N_{p_i,t}^{s+}$ is the patch-specific number of individuals in strategy D/E reproducing sexually
290 (D+/E+).

291 It is important to note that we assume no cost associated with the ability to transition in
292 strategy D/E and that these strategies are only reproducing sexually in the ancestral population
293 because population size is above the Allee saturation. We assumed $\tau = 0.2$ across all simulations.

294 Migration

295 Migration from/to the ancestral population in the South patch is density-dependent and is
296 assumed to be greater in the north direction to stress the importance of habitat expansion in
297 our model. Net migration ($M_{p_i,t}^s$, in number of individuals) is defined by the following equation:

$$M_{p_i,t}^s = \sum_{j \neq i} \left(\mu_{p_j \rightarrow i,t} \cdot \frac{\min(N_{p_j,t}, K_{p_j})}{K_{p_j}} \cdot N_{p_j,t}^s - \mu_{p_i \rightarrow j,t} \cdot \frac{\min(N_{p_i,t}, K_{p_i})}{K_{p_i}} \cdot N_{p_i,t}^s \right) \quad (8)$$

298 where $\mu_{p_j \rightarrow i,t}$ is the effective migration rate from patch p_j to patch p_i and $\mu_{p_i \rightarrow j,t}$ is the effective
299 migration rate from patch p_i to patch p_j .

300 We made migration stochastic by defining the effective migration rate according to the
301 following equation:

$$\mu_{p_i \rightarrow j,t} = \mu_{p_i \rightarrow j}^* \cdot [1 + \rho \cdot \mathcal{N}(0, 1)] \quad (9)$$

302 where $\mu_{p_i \rightarrow j}^*$ is the mean migration rate, ρ is the magnitude of the stochasticity and $\mathcal{N}(0, 1)$ is
303 a standard normal deviate. We assumed $\mu_{p_S \rightarrow N}^* = 0.01$, $\mu_{p_N \rightarrow S}^* = 0.001$ and $\rho = 0.1$ across all
304 simulations.

305 **Ecological success during pairwise competition between strategies**

306 Due to the stochastic environmental changes affecting population dynamics throughout time,
307 the population structure at the last time step cannot accurately describe the success of different
308 strategies in invading and establishing in the North patch. We therefore used the long-term
309 temporal mean population size of each reproductive strategy as a measurement of their ecological
310 success. Furthermore, we compared the long-term temporal mean with the initial short-term
311 temporal mean during the first one hundred generations (corresponding to the first 10% of the
312 total number of generations used in the simulations). This comparison between long-term and
313 initial temporal mean population sizes can indicate whether a particular reproductive strategy is
314 more successful at invading an unstable environment and/or outcompeting a competing strategy
315 in the long term.

316 In the competition simulations, we assumed that the South patch hosts a large ($K_{p_S} = 5000$)
317 ancestral population composed of individuals that reproduce using different strategies, while the
318 North patch is a smaller ($K_{p_N} = 1000$), empty marginal habitat that is open and available for
319 colonization. The North patch is partially connected to the South patch such that individuals
320 can migrate between patches at a specified rate. Environmental conditions in the South patch
321 are stable and do not change ($p_e^{p_S} = 0$ and $v_e^{p_S} = 0$), while the North patch experiences
322 environmental stress at different levels. For all initial ancestral populations tested, we explored
323 the effect of different environmental regimes in the North patch, in terms of probability of
324 occurrence of stressful environmental conditions ($p_e^{p_S} > 0$) and maximum level of stress ($v_e^{p_S} > 0$).

325 Different compositions of the ancestral population were used in order to explore the inter-
326 action effects of different strategies during habitat invasion and colonization. We analyzed the
327 pairwise dynamics of habitat colonization in the North patch by setting ancestral populations
328 composed of two different strategies for each possible combination of strategies, allowing us to
329 investigate the effect of each strategy on each other strategy when they compete for dominance
330 during invasion of the North patch. In the initial conditions, competing reproductive strategies
331 in the ancestral populations were equally represented in terms of initial number of individuals
332 ($N_{p_S,0}^s = 0.5 \cdot K_{p_S}$). Because the initial subpopulation size of each strategy in the ancestral
333 population is above the Allee threshold ($\beta \cdot K_{p_S}$), all strategies have the same initial growth
334 rate in the South patch. All simulations were performed on R version 3.5.2 [47].

335 Results

336 When the ancestral population in the South patch remains isolated (no migration between
337 patches) and environmental conditions are stable (no environmental stress), population struc-
338 ture (in terms of proportion of the population composed by each reproductive strategy) remains
339 constant and no particular reproductive strategy is ecologically more successful than any com-
340 peting strategy in terms of temporal mean population size. When the effect of density is
341 ignored, strategies that reproduce asexually (A, B, D- and E-) have their maximum growth rate
342 because environmental conditions are optimal and strategies that reproduce sexually (C, D+
343 and E+) have their maximum growth rate both because environmental conditions are optimal
344 and the subpopulation size is greater than the Allee saturation size. Therefore, sexual and asex-
345 ual reproduction are equally successful under the baseline conditions present in the ancestral
346 population.

347 In order to assess initial invasion and long-term ecological success of different reproductive
348 strategies in the North patch, we calculated the temporal mean population size of the com-
349 peting strategies during the first one hundred generations and in the long term (over the total
350 simulation time). We then systematically analyzed the success of different strategies in different
351 environments by changing the values of the parameters that control the Allee effect (α and β)
352 as well as environmental stress (p_e^{pN} and v_e^{pN}) and sensitivity to environmental stress (ϕ^B and
353 ϕ^C).

354 Population dynamics during invasion of a marginal, unstable habitat

355 When a marginal, unstable habitat (North patch) becomes available, migration from the ances-
356 tral population (South patch) to the North patch drives the initial invasion of the North patch
357 by both competing strategies proportionally to their frequencies in the ancestral population.
358 Nonetheless, because the Northern population faces environmental conditions that are different
359 from the conditions in the South patch, the population structure in the North patch diverges
360 considerably from that in the South patch (e.g., Figure S4). Despite fluctuations in population
361 size and composition due to environmental stress events, the population composition in the
362 North patch reaches a clear pattern in terms of frequency dominance of different reproductive
363 strategies for different environmental conditions. Note that, in many cases, strategies that per-

364 form better during the initial stages of invasion are not always the most successful in the long
365 term (explained in more detail below).

366 Furthermore, the population structure in the North patch can affect the population structure
367 in the South patch through migration. However, because the population size in the North patch
368 is much smaller than in the South patch ($K_{p_N} = 0.2K_{p_S}$) and migration from the North patch to
369 the South patch occurs at a lower rate than in the opposite direction, changes in the population
370 structure in the South patch occurs at a much lower rate (e.g., Figure S5). This lower rate of
371 change can be explained by the small effect of the number of incoming individuals to the South
372 patch relative to its population size.

373 **Allee effect and environmental stress**

374 In a general case, we simulated pairwise competitions between different strategies, focusing on
375 the Allee effect under two environmental scenarios where the probability of environmental stress
376 is $p_\epsilon^{p_N} = 0.1$ and stress levels can be either low ($v_\epsilon^{p_N} = 0.1$; Figures S6-S7) or high ($v_\epsilon^{p_N} = 0.9$;
377 Figures S8-S9). We then simulated pairwise competitions focusing on environmental variation
378 when sexuals are under weak ($\alpha = 0.3$ and $\beta = 0.1$; Figures S10-S11) or strong ($\alpha = 0.1$ and
379 $\beta = 0.3$; Figures S12-S13) Allee effects.

380 In our model, α and β determine the Allee effect curvature and saturation point, respectively,
381 and therefore can explain some of the differences in ecological success between parthenogens
382 (strategies A, B, D- and E-) and sexuals (strategies C, D+ and E+). According to our Allee
383 function, the Allee effect becomes stronger when $\alpha \rightarrow 0^+$ and $\beta \rightarrow \infty$; and weaker when
384 $\alpha \rightarrow 0^-$ and $\beta \rightarrow 0$. This can be observed in Figures S6-S9. The Allee effect is particularly
385 important during the initial invasion, when sexuals struggle to reproduce while parthenogens
386 thrive under low environmental stress. However, parthenogens are particularly sensitive to the
387 probability of encountering stressful conditions ($p_\epsilon^{p_N}$) and the level of stress experienced $v_\epsilon^{p_N}$,
388 often allowing sexuals to outcompete them under stressful conditions even when the Allee effect
389 is moderate (Figures S10-S13). In the long term, even when the Allee effect is strong, sexuals
390 can outcompete parthenogens, showing a greater temporal mean population size. Because
391 of the complex interactions between sensitivity to environmental stress and Allee effect, we
392 analyzed each pairwise competition separately focusing on the biological properties of each

393 strategy (below).

394 **Obligate apomictic vs. obligate automictic parthenogenesis**

395 Strategy A (obligate apomictic parthenogenesis) was assumed to have maximum sensitivity to
396 environmental stress ($\phi^A = 1.0$), while strategies B (obligate automictic parthenogenesis) and
397 C (obligate sexual reproduction) were assumed to have a lower sensitivity ($\phi^A > \phi^B > \phi^C$).
398 Since apomictic and automictic parthenogens differ only in the magnitude of their response to
399 environmental stress, competition between these strategies is expected to favor the dominance
400 of automictic parthenogens (strategy B), and lower sensitivity ($\phi^B \ll \phi^A$) leads to a greater
401 dominance of automictic parthenogens in the population (Figures [S14-S15](#)). This is a conse-
402 quence of the assumption that automictic parthenogenesis has no extra fitness cost relative
403 to apomictic parthenogenesis but generates phenotypic diversity which reduces the sensitivity
404 of the population to environmental stress. This difference in temporal mean subpopulation
405 size of apomictic and automictic parthenogens is particularly strong under highly stressful con-
406 ditions ($v_e^{pN} = 0.9$). However, although our model assumes there is a sensitivity difference
407 between apomictic and automictic parthenogenesis, empirical data quantifying the magnitude
408 of this difference is absent. Additionally, fitness costs of automictic parthenogenesis relative to
409 apomictic parthenogenesis remain unexplored.

410 **Obligate parthenogenesis vs. obligate sexual reproduction**

411 As mentioned above, growth rate of obligate sexuals is affected not only by their sensitivity to
412 environmental stress but also by the Allee effect caused by the difficulty in finding compatible
413 mating partners when the population size is small. If the Allee effect is weak ($\alpha = 0.3$ and
414 $\beta = 0.1$) during the initial invasion of the marginal habitat, parthenogenetic reproduction is
415 particularly favored when environmental stress is low ($v_e^{pN} = 0.1$), while sexual reproduction
416 is particularly favored under high environmental stress ($v_e^{pN} = 0.9$) as long as their sensitivity
417 is low enough to overcome the Allee effect (Figure [S16](#)). In the long term, sexuals outperform
418 parthenogens even when their sensitivity to environmental stress ($\phi^C = 0.9$) approaches that of
419 parthenogens, although in such cases the difference in ecological success is small (Figure [S17](#)). If
420 the Allee effect is strong ($\alpha = 0.1$ and $\beta = 0.3$), however, parthenogens ($\phi^A = 1.0$) are generally

421 more successful than sexuals during the initial invasion and in the long term, except when
 422 sexuals are considerably less sensitive than parthenogens under very stressful environmental
 423 conditions ($v_\epsilon^{pN} = 0.9$), significantly reducing the population growth rate of parthenogenetic
 424 invaders (Figure 3-4).

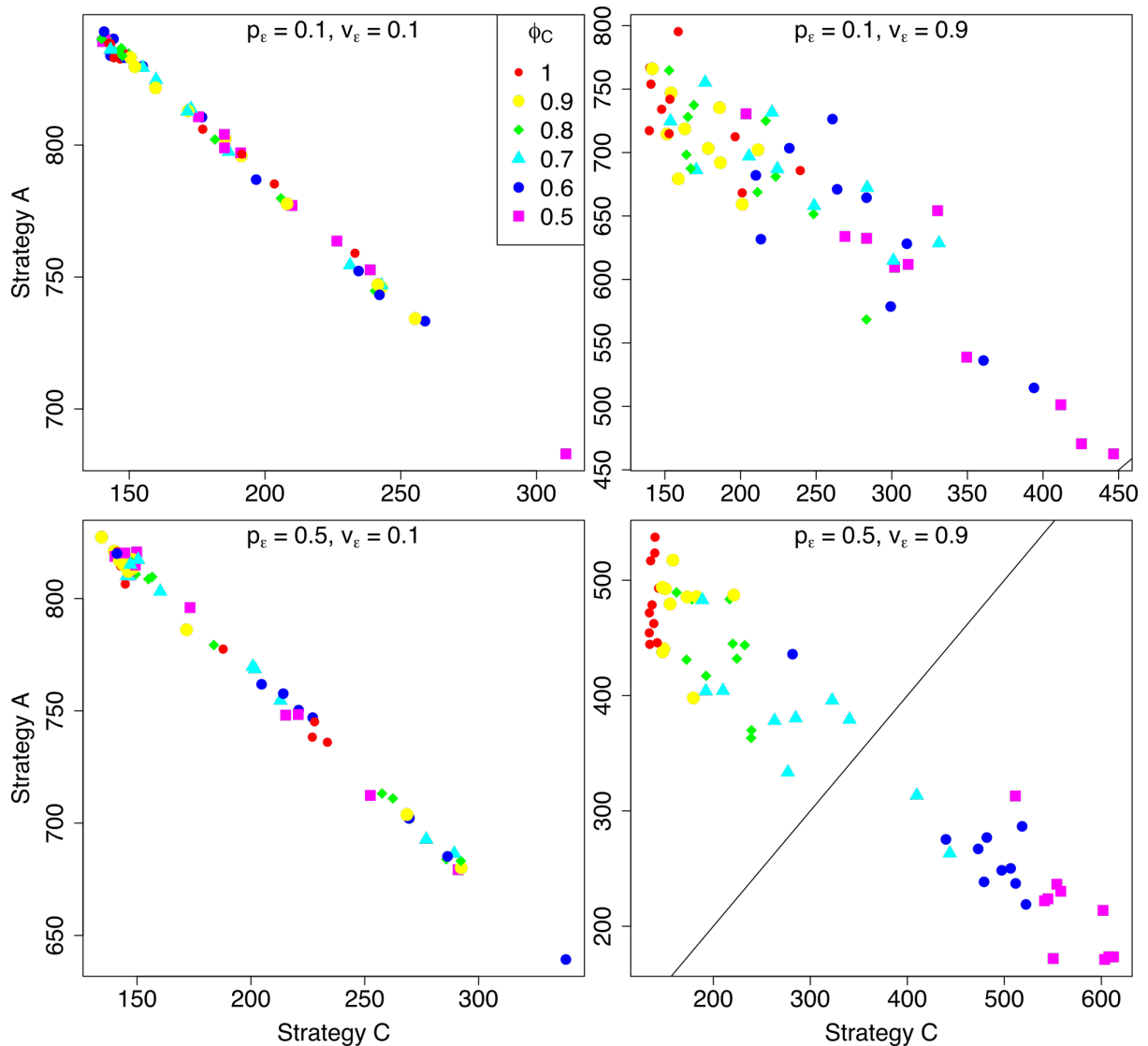


Figure 3: Obligate parthenogenesis (strategy A/B) vs. obligate sexual reproduction (strategy C). Axes represent the short-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a strong Allee effect ($\alpha = 0.1$ and $\beta = 0.3$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).

425 In a deterministic simulation, with a constant environmental stress level in the marginal
 426 habitat ($\Delta\epsilon \in \{0.1, 0.5, 0.9\}$) and constant migration rates ($\rho = 0$), increasing the magnitude
 427 of the Allee effect ($\alpha \rightarrow 0^+$; $\beta = 0.3$) and the environmental sensitivity of sexuals (ϕ^C) relative

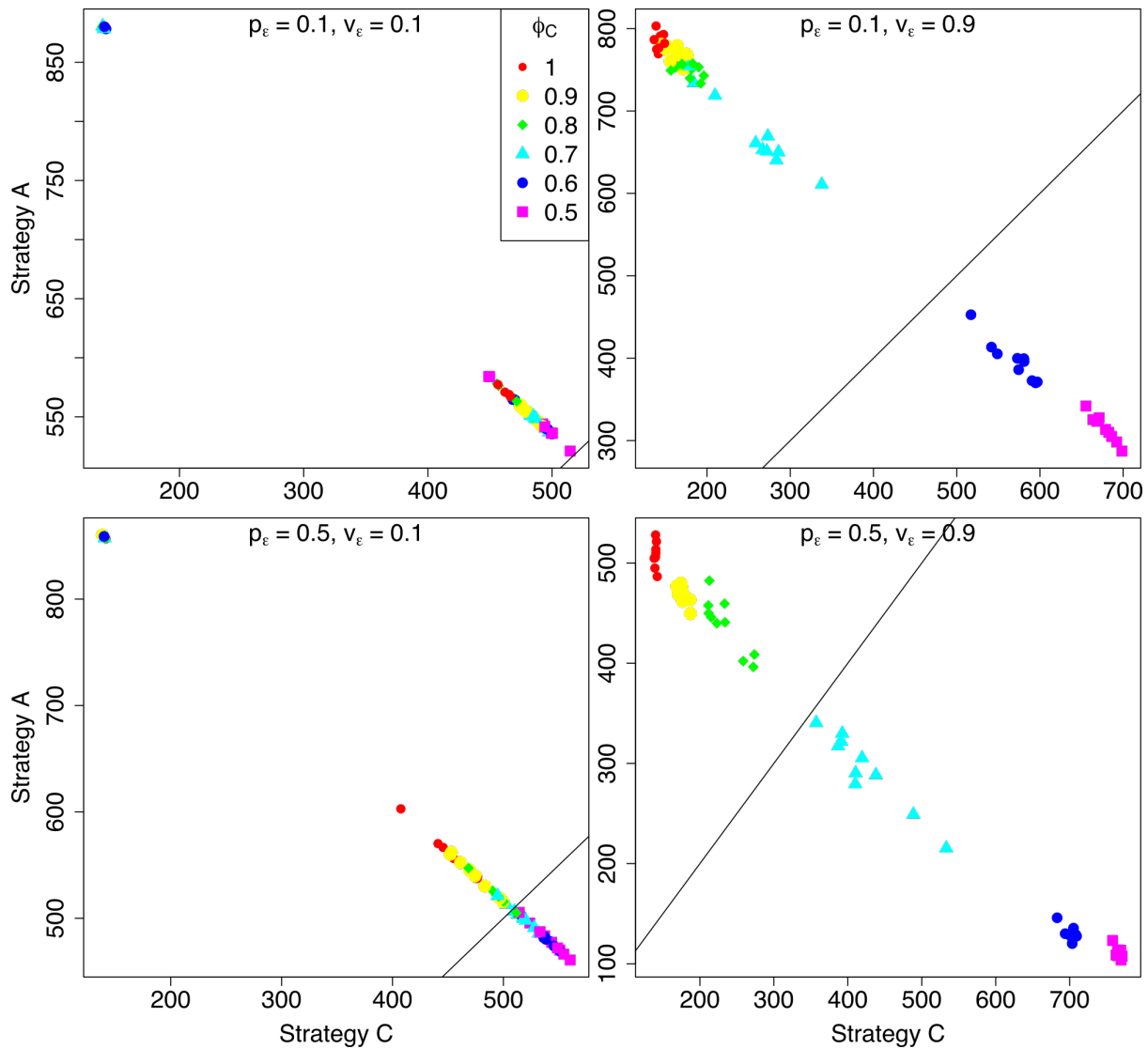


Figure 4: Obligate parthenogenesis (strategy A/B) vs. obligate sexual reproduction (strategy C). Axes represent the long-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a strong Allee effect ($\alpha = 0.1$ and $\beta = 0.3$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).

428 to parthenogens (ϕ^C approaches ϕ^A) increases the temporal dominance of parthenogens in the
 429 marginal habitat ($\overline{N}_A/\overline{N}_C > 1$; Figure 5). However, this effect is weaker in the long term.

430 In general, sexuals become less successful than parthenogens when β is large (e.g., $\beta = 0.3$),
 431 demanding a greater population size in order to reach Allee saturation ($\beta \cdot K_{p_N}$), and α is
 432 positive and close to zero ($\alpha = 0.1$, in our simulations), demanding a greater population size in
 433 order to reach the Allee threshold (Equation 3). If the Allee threshold and saturation point are
 434 large, sexuals will only be more successful than parthenogens under three conditions: over a very

435 large number of generations (assuming no extinction; > 1000 generations); when environmental
 436 stress levels are high such that parthenogens are affected more strongly than sexuals under a
 437 strong Allee effect; or when the *per capita* growth rate is high enough for the Allee threshold and
 438 saturation point to be reached in a relatively short period of time (not shown here). These results
 439 show that, for obligate sexuals (strategy C) to outcompete obligate parthenogens (strategies A
 440 and B), there must be a balance between their sensitivity to environmental stress and the Allee
 441 effect that they are subject to such that the net growth rate of obligate sexuals becomes greater
 442 than the net growth rate of obligate parthenogens.

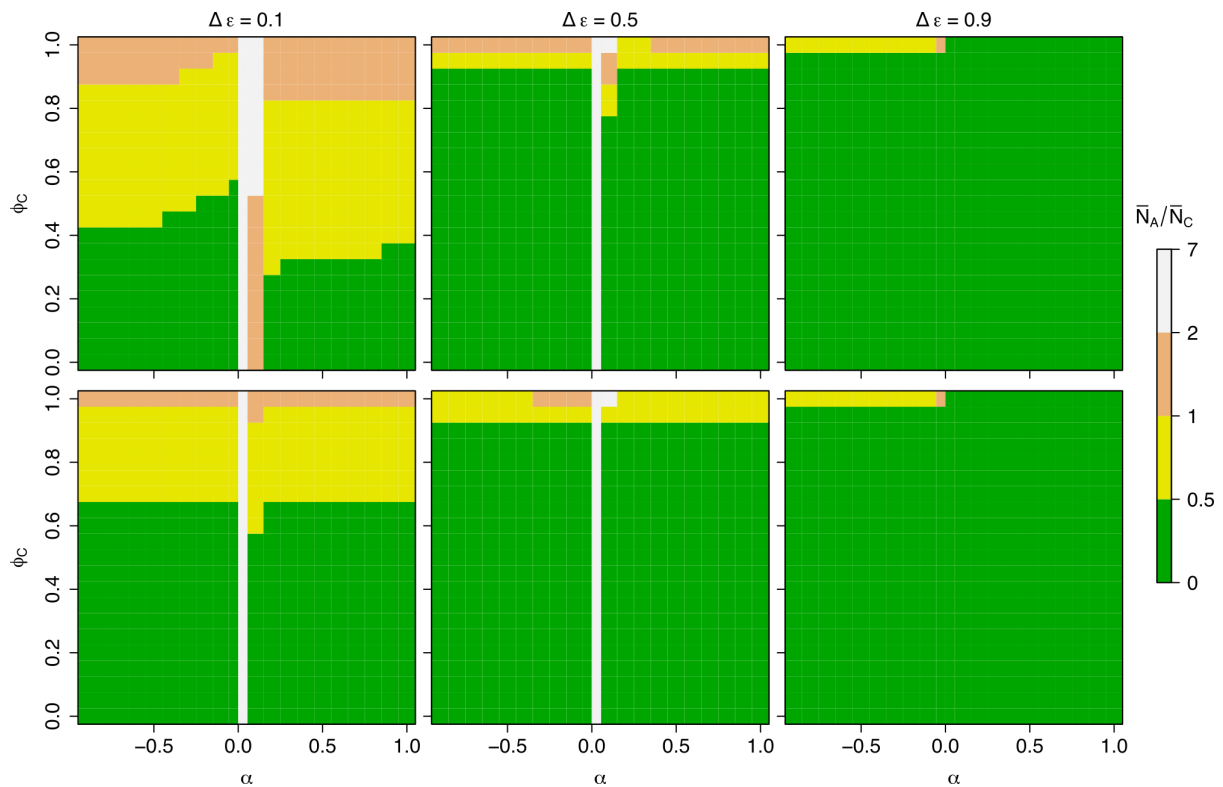


Figure 5: Obligate parthenogenesis (strategy A/B) vs. obligate sexual reproduction (strategy C). Deterministic ratio of short-term (top row) and long-term (bottom row) mean population sizes of obligate parthenogens to obligate sexuals (\bar{N}_A/\bar{N}_C) under constant environmental stress levels in the marginal habitat ($\Delta \epsilon \in \{0.1, 0.5, 0.9\}$), constant migration rates ($\rho = 0$), different values of α (Allee curve; $\beta = 0.3$) and different environmental sensitivity values of sexuals relative to parthenogens (variable ϕ^C , with constant $\phi^A = 1.0$).

443 Facultative parthenogenesis vs. obligate sexual reproduction

444 Among sexually reproducing strategies, facultative parthenogens (strategy D/E) can perform
 445 significantly better than obligate sexuals (strategy C) because of their ability to reproduce asexually
 446 when the population size is small, partially avoiding the Allee effect. Under a weak Allee

447 effect, both strategies are equally successful (Figures S18-S19). Differences are visibly signifi-
 448 cant when the Allee effect is strong (Figures 6-7) and transitions from sexual to parthenogenetic
 449 reproduction become particularly advantageous during the initial invasion. Furthermore, the
 450 difference in temporal mean population size between strategies increases as sexuals become
 451 more sensitive to environmental stress, reducing the advantage of sex even further especially
 452 under stressful conditions. A higher transition rate τ can also increase the success of faculta-
 453 tive parthenogens, but the increase is only visible under stressful environmental conditions and
 454 strong Allee effect on sexuals (Figures S20-S21).

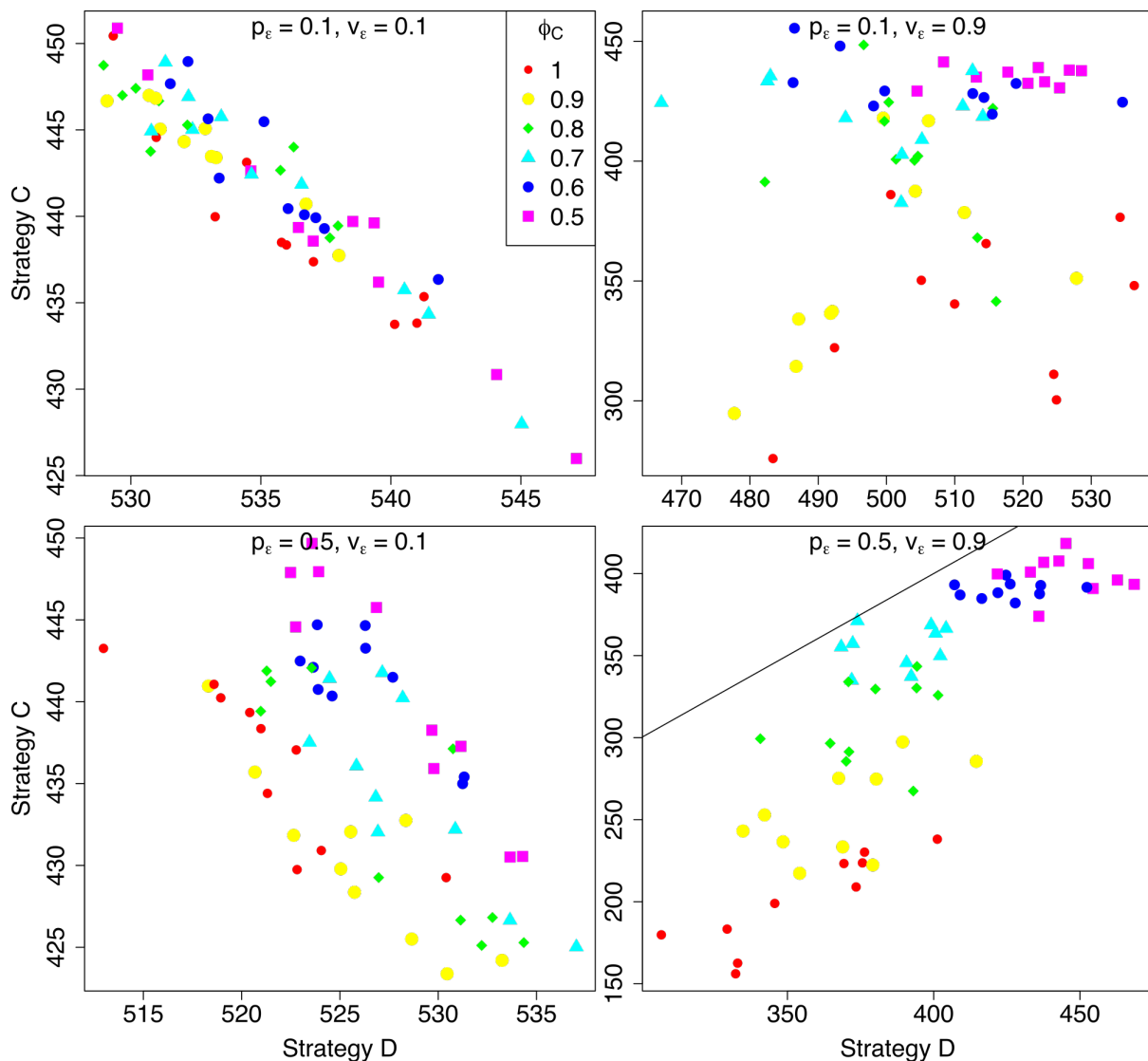


Figure 6: Obligate sexual reproduction (strategy C) vs. facultative parthenogenesis (strategy D/E). Axes represent the short-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a strong Allee effect ($\alpha = 0.1$ and $\beta = 0.3$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).

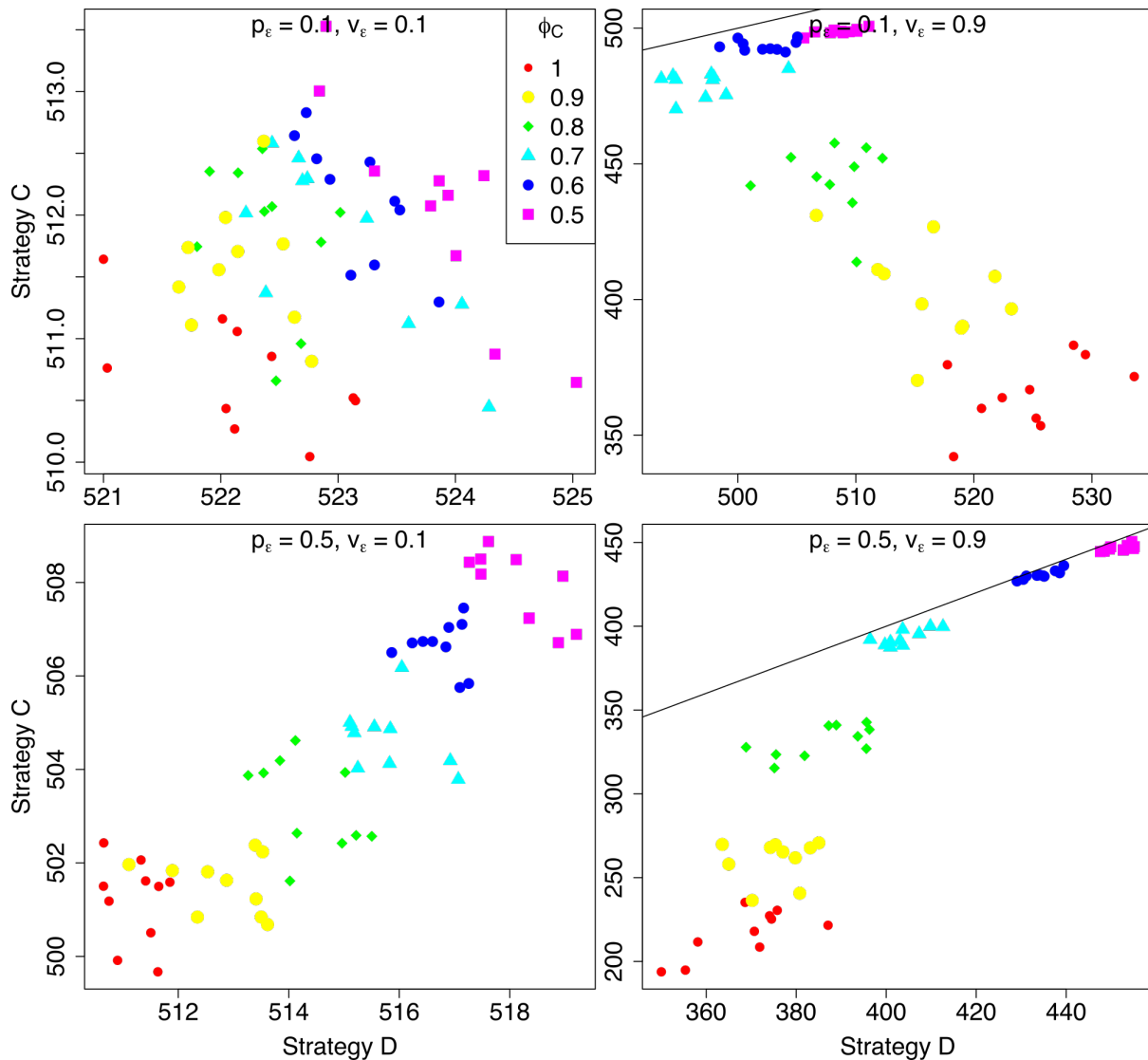


Figure 7: Obligate sexual reproduction (strategy C) vs. facultative parthenogenesis (strategy D/E). Axes represent the long-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a strong Allee effect ($\alpha = 0.1$ and $\beta = 0.3$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).

455 Obligate parthenogenesis vs. facultative parthenogenesis

456 As mentioned above, facultative parthenogens (strategy D/E) reproduce sexually in the ances-
 457 tral population because of the large population size and high environmental stability, so incom-
 458 ing migrants to the marginal habitat are subject to the Allee effect during the very first wave
 459 of migration, which can explain their lower ecological success relative to obligate parthenogens
 460 (strategy A/B) when sexuals and parthenogens have similar sensitivities to environmental stress

461 (Figures S22-S25). When sexuals are considerably less sensitive, the advantage of sex can com-
462 pensate for the Allee effect and lead to a higher ecological success of facultative parthenogens
463 even under a strong Allee effect. The balance between sensitivity to environmental stress and
464 the Allee effect that equalizes the success of sexuals (including facultative parthenogens) and
465 obligate parthenogens depends on the environmental conditions experiences. For example, un-
466 der highly stressful environmental conditions ($p_{\epsilon}^{pN} = 0.5$ and $v_{\epsilon}^{pN} = 0.9$), sexuals under a strong
467 Allee effect must be relatively less sensitive than sexuals under a weak Allee effect in order to
468 outcompete parthenogens.

469 Discussion

470 Our results show that the relative frequency of a reproductive strategy in a marginal habitat can
471 be determined by a complex interaction between the environmental conditions in that habitat,
472 the magnitude of the Allee effect and the relative sensitivity of competing strategies to environ-
473 mental stress. These factors may explain the empirically observed biased distribution of sexuals
474 and asexuals (parthenogens) along a habitat range, with asexuals being particularly abundant
475 in marginal habitats, a pattern that characterizes geographic parthenogenesis. In our model,
476 an equal maximum intrinsic growth rate was assumed for sexual and asexual reproduction and,
477 therefore, our results shed light on the importance of ecological (non-reproductive) processes as
478 explanatory causes of geographic parthenogenesis.

479 Geographic parthenogenesis and range expansion

480 Previous models explored different processes that can lead to geographic parthenogenesis. A
481 spatially explicit genetic model showed that asexuals may be favored by local adaptation to a
482 marginal habitat through clone selection and protection of optimal genotypes from gene flow
483 from the core habitat [20]. Geographic parthenogenesis can also result from selection for re-
484 sistance and high fecundity in a facultatively parthenogenetic metapopulation occupying an
485 environmental gradient, limiting mating at the edge of the habitat and forcing females to re-
486 produce asexually, generating a female bias [40]. However, the ecological success of asexual
487 reproduction certainly depends on the environmental conditions and the characteristics of the
488 competing reproductive strategy. A model exploring the frozen niche variation hypothesis [48]

489 indicated that, despite its two-fold advantage relative to sexual reproduction [2], asexual clonal
490 reproduction may have its invasion probability reduced due to a fast accumulation of deleterious
491 mutations in the initially small clonal population [49], decreasing its initial advantage of
492 local adaptation. Clonal invasion probability can be reduced even further when sexual popu-
493 lations have many niche phenotypes, requiring the occurrence of a beneficial mutation for niche
494 exploration within the asexual clonal population before individuals can invade a niche occupied
495 by sexuals [49]. Additionally, it has been proposed that metapopulation dynamics in marginal
496 habitats may be detrimental to sexuals because they may suffer more intensely from genetic
497 bottlenecks and inbreeding [16].

498 Although most studies focus on the coexistence or elimination of reproductive strategies as
499 a result of active selection leading to evolutionary change, it has been shown theoretically that
500 stochastic demographic processes may lead to geographic structure in the distribution of sexual
501 and asexual morphs in recently invaded areas without having to invoke adaptive differences.
502 However, these patterns (e.g. clone dominance) are transient and are eventually substituted by
503 sexual reproduction [27]. Other models explored the distribution of individuals within a habitat
504 and the factors that determine population range limits, although not in the context of geographic
505 parthenogenesis. However, because parthenogens are typically found in marginal habitats, the
506 study of range limits can be particularly useful for understanding the geography of reproductive
507 strategies. Range limits may have many causes, each leading to different evolutionary outcomes
508 [50], with range expansion being typically initiated through dispersal and subsequent niche
509 evolution in the new habitat. This process of dispersal leading to range expansion has been
510 explored in the context of a species invasion of a novel habitat, where niche evolution has
511 been found to be affected by several factors, including the initial maladaptation of the invading
512 population, mutation rate and degree of heterogeneity in the occupied range [51]. These factors,
513 as mentioned in the present study, can affect different reproductive strategies differently and
514 therefore lead to the observed biased geographic distribution at the population range limits
515 (e.g., [52]). The Allee effect on sexual populations, for example, can explain the difference in
516 the spatial distribution of sexuals and asexuals during range expansion.

517 **The Allee effect on population dynamics**

518 The Allee effect explored in our model reduces the growth rate of sexual populations when
519 the population size is small. This effect has been observed in many populations and has been
520 suggested to cause species extinctions [53; 54]. For example, experimental observations from
521 the annual herb *Clarkia concinna* suggest that small populations are more likely to go extinct
522 because of the Allee effect caused by the lack of effective pollination, leading to reproductive
523 failure [55]. In populations of the shrub *Banksia goodii*, there is a clear positive relationship
524 between population size, number of seeds per unit population size and fraction of fertile plants,
525 with very small populations producing a disproportionately small number of seeds, a pattern
526 that resembles the strong Allee effect ($\alpha = 0.1$ and $\beta = 0.3$) used in our model and that can
527 lead to local extinction [56]. In natural populations of the Glanville fritillary butterfly *Melitaea*
528 *cinxia*, the fraction of mated females decreases with decreasing local population density, resulting
529 in a reduced reproductive success in small populations [57]. This density-dependent growth rate
530 has also been detected in many populations of the Atlantic herring *Clupea harengus* [58] and
531 even in the bacterium *Vibrio fischeri* [59]. In the latter study, experiments using different
532 initial population sizes of *Vibrio fischeri* showed a non-linear positive relationship between
533 initial population density and the proportion of populations establishing in the media at the
534 time of measurement, indicating a reduction in population growth rate when population density
535 is low [59].

536 This positive density-dependent reproductive rate has also been explored from a theoretical
537 perspective. The Allee effect was used in a model to predict the rate of population spread in the
538 house finch *Carpodacus mexicanus* and density of birds near the center of the range [60], with a
539 weak Allee effect, measured in terms of the fraction of birds mated as a function of population
540 density, resembling the Allee curve with $\alpha = -0.1$ in our model. A different model explored the
541 Allee effect from the perspective of mate location dynamics, showing that very low population
542 densities decrease the recognition of potential conspecific mates and therefore the probability of
543 mating, driving the population to extinction [54]. The identification of conspecific mates is one
544 of the factors that affects the Allee effect and should be taken into consideration in the future
545 when calculating empirical values of α and β for the Allee curve given by Equation 2 in the
546 present model.

547 More general models showed that the Allee effect may reduce the rate at which an invader
548 moves to a new environment [61; 62] and the interaction between interspecific competition and
549 the Allee effect can result in stability patterns that differ from models that ignore Allee effects
550 [63; 64], which is also important for the competitive dynamics between different reproductive
551 strategies explored in the current study. In the context of metapopulations, it has been suggested
552 that the Allee effect may prevent small metapopulations from increasing even when resources
553 are abundant or make large metapopulations go extinct due to stochastic environmental stress
554 events when the number of occupied patches is small [65; 66]. Because of that, the effect of
555 stressful events on population growth can affect the invasion of marginal habitats and subsequent
556 range expansion.

557 **Environmental effects on population growth**

558 Our model also considered the sensitivity of the population to environmental stress, which may
559 depend on genetic and phenotypic diversity. Empirical studies in both animals and plants have
560 shown that the founder genotypic and heritable phenotypic diversity is key to successful inva-
561 sion, range expansion and establishment in new habitats where the population may find novel
562 (stressful) environmental conditions [67]. An experimental study in the flour beetle *Tribolium*
563 *castaneum* showed that the probability of a founding population going extinct and the mean
564 population size after several generations are, respectively, inversely proportional and directly
565 proportional to the founding level of genetic variation [68]. In the clonal plant *Ranunculus*
566 *reptans*, when introduced to previously unoccupied habitats and exposed to severe stressful
567 conditions (flood and drought), populations founded by different genetic sources increased in
568 abundance relative to populations founded by genetic monocultures [69]. Interestingly, studies
569 analyzing genetic diversity as a function of distance to the core habitat (central population)
570 show that central populations have significantly higher diversity than populations located at
571 marginal habitats [70], indicating that marginal populations may be more sensitive to environ-
572 mental stress and that genetic diversity may be restricted in such habitats.

573 It has been suggested that in populations where genetic diversity is very limited (e.g., clonal
574 populations) adaptation to stressful environmental conditions can be difficult when relying on
575 new mutations, leading populations to decline or go extinct [71]. This negative relationship be-

576 tween genetic diversity and risk of extinction affects parthenogenetic populations more strongly
577 than sexual populations but this risk can be reduced when the parthenogenetic population
578 is multiclonal instead of monoclonal [48]. In our model, parthenogenetic populations are more
579 sensitive to environmental stress and thus more likely to decline under stressful conditions. How-
580 ever, because of the constant migration from the ancestral population to the marginal habitat,
581 the dynamics in our model does not lead to local extinction. It is important to note that pop-
582 ulations declining due to sensitivity to stressful environmental conditions can resume growing
583 when new genetic variation is introduced from different sources, a process called evolutionary
584 rescue [72; 73], which may be achieved via, for example, sexual reproduction in clonal popula-
585 tions of facultative parthenogens. Because increased asexual reproduction is common towards
586 marginal habitats, those populations are also more likely to decline when challenged by changes
587 in environmental conditions, which can make facultative parthenogenesis particularly benefi-
588 cial. In the Baltic Sea, asexual recruitment seems to be very common in many macrophytic
589 populations, but sexual recruitment is not completely absent [74], supporting the idea that the
590 ability to transition between sexual and asexual reproduction is beneficial. Because of all these
591 processes related to the effect of environmental stress on population growth, it is important that
592 future studies provide empirical measurements of the correlation between genetic/phenotypic
593 diversity and population sensitivity to different types of environmental stress.

594 **Conclusion**

595 We used a quantitative approach to explore the ecological processes that can lead to geographic
596 parthenogenesis and the invasion of new habitats by different reproductive strategies. We an-
597 alyzed the Allee effect on sexual populations and the population sensitivity to environmental
598 stress during the invasion of a marginal, unstable habitat to demonstrate that a complex in-
599 teraction between the Allee effect, sensitivity to environmental stress and the environmental
600 conditions can determine the relative success of competing reproductive strategies during the
601 initial invasion and long-term establishment in the marginal habitat. In particular, sexuals need
602 to compensate for the reduction in growth rate due to the Allee effect through a reduced sensi-
603 tivity to environmental stress. However, the reduction in sensitivity is only strongly beneficial
604 under highly stressful environmental conditions. Unfortunately, despite the empirical evidence

605 for the Allee effect and differential sensitivity to environmental stress, empirical quantification
606 of such processes remain scarce. Controlled and accurate quantification of the Allee effect on
607 population growth in nature are difficult to obtain because many factors (both ecological and
608 genetic) may affect the magnitude of the effect. We suggest that the following processes may
609 play particularly important roles: (i) the distribution pattern of the immigrants (e.g., uniform
610 vs. aggregated distribution) in the marginal habitat; (ii) migration rate, which can affect the
611 speed at which the Allee threshold is reached; (iii) sexual selection (in particular, female choice,
612 which can limit mating); and (iv) sociality, which can create an Allee effect even in asexual
613 populations. Similarly, sensitivity to environmental stress is difficult to quantify because it is
614 highly dependent on the type of stress and the genetic diversity of the population. The follow-
615 ing factors may be particularly important for the quantification of sensitivity: (i) mutation rate
616 (particularly important for clonal populations); (ii) phenotypic diversity (e.g., apomictic vs. au-
617 tomictic parthenogenesis); and (iii) ability to respond (adaptively) to environmental conditions
618 (phenotypic plasticity). All these processes can potentially explain the distribution patterns
619 of different reproductive strategies and the present study suggests new patterns for empirical
620 investigation.

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630 **Competing interests**

631 The authors declare that they have no conflict of interest.

632 **Author contributions**

633 WTAFS conceived the initial numerical model, wrote the script and ran the simulations. All
634 authors contributed to the design and implementation of the research, the discussion of the
635 results and the writing of the manuscript.

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Supplementary Information

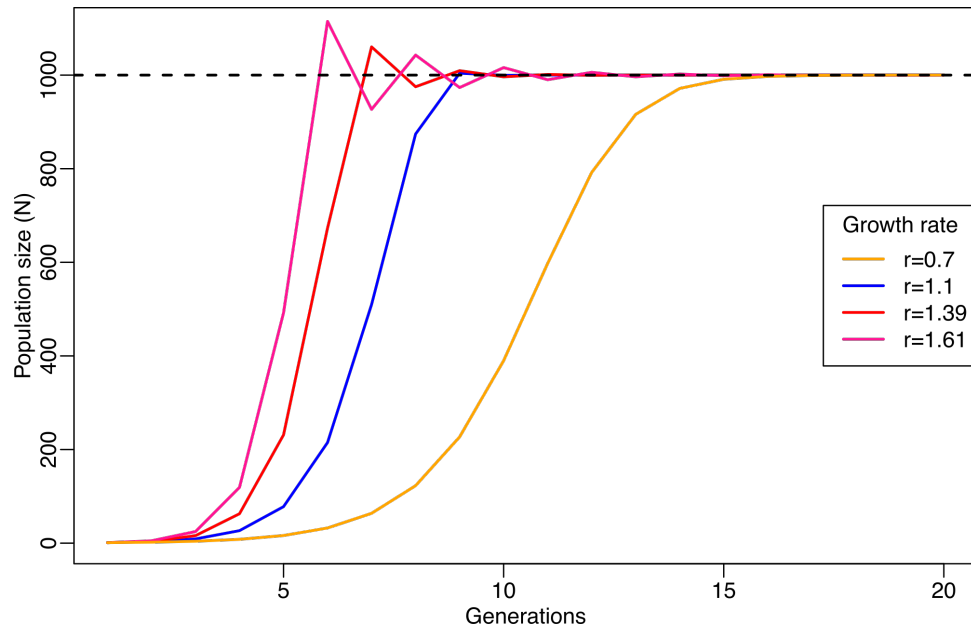


Figure S1: Logistic growth for different population growth rates. The maximum growth rate was set to $r_{max} = 1.1$ in all simulations.

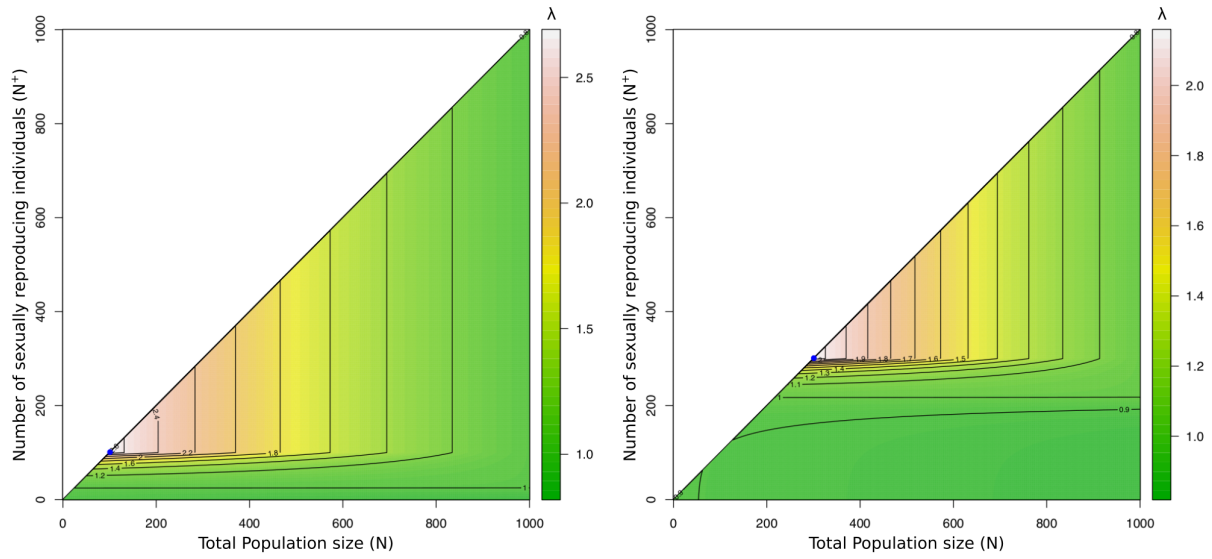


Figure S2: Density-dependent *per capita* growth rate (λ) of the sexually reproducing population under weak ($\alpha = 0.3$ and $\beta = 0.1$; left) and strong ($\alpha = 0.1$ and $\beta = 0.3$; right) Allee effects. Parameter values used across all simulations: $r_{min} = -0.1$, $r_{max} = 1.1$ and $K_{pN} = 1000$.

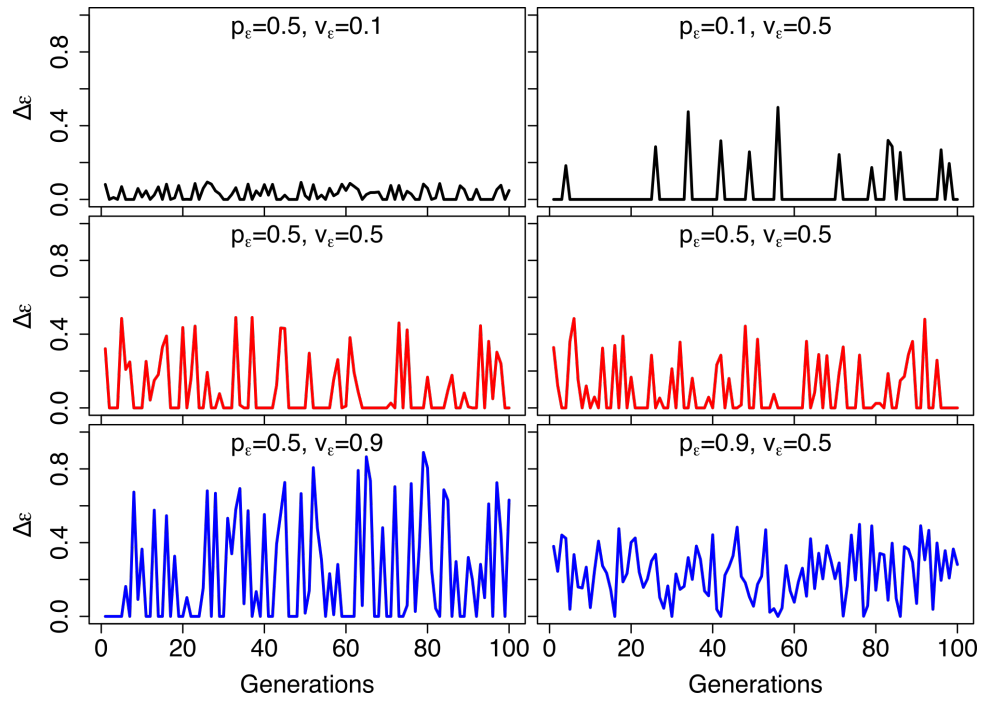


Figure S3: Examples of environmental dynamics showing environmental stress levels ($\Delta\epsilon$) for different probabilities of stress occurrence (p_ϵ) and maximum stress level (v_ϵ) throughout time.

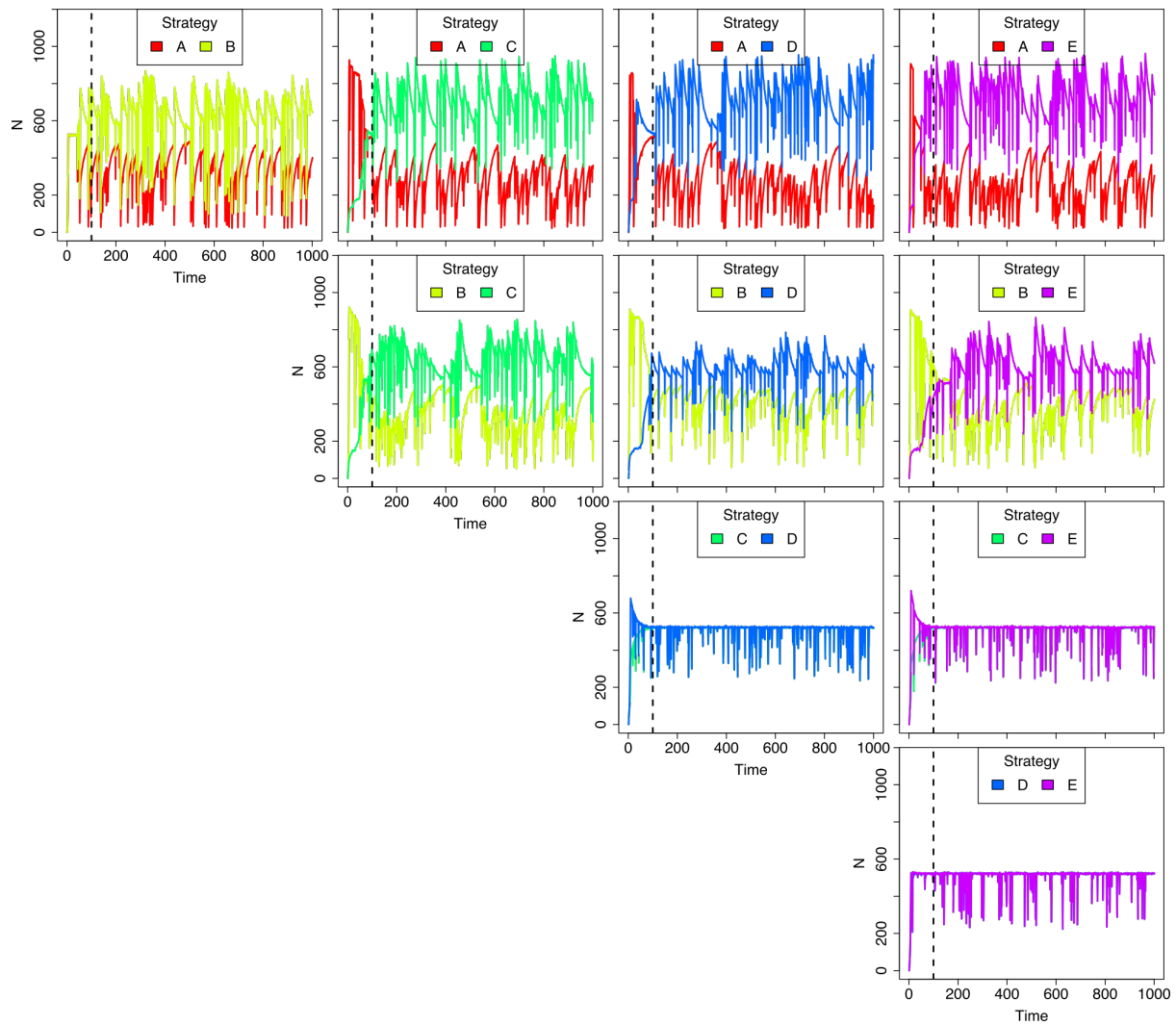


Figure S4: Pairwise competition between reproductive strategies and population dynamics during invasion of a marginal habitat (North patch) under high environmental stress ($p_{\epsilon}^{pN} = 0.1$ and $v_{\epsilon}^{pN} = 0.9$), with sexual strategies exposed to a relatively strong Allee effect ($\alpha = 0.1$ and $\beta = 0.3$). Dashed lines indicate generation 100. Sensitivity values: $\phi^A = 1.0$, $\phi^B = 0.75$, $\phi^C = 0.5$.

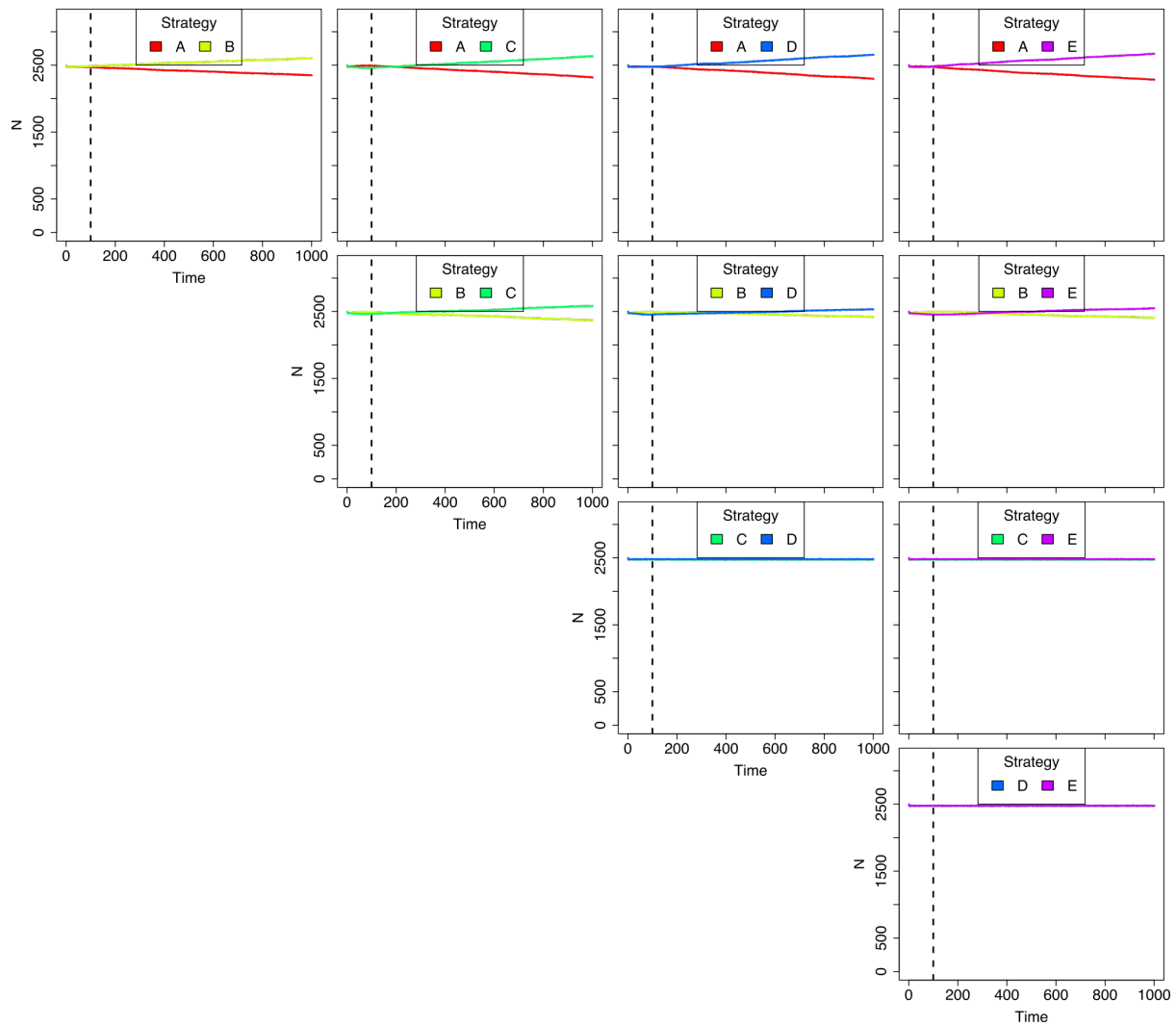


Figure S5: Pairwise competition between reproductive strategies and population dynamics in the ancestral population (South patch) during invasion of a marginal habitat (North patch) under high environmental stress ($p_{\epsilon}^{pN} = 0.1$ and $v_{\epsilon}^{pN} = 0.9$), with sexual strategies exposed to a relatively strong Allee effect ($\alpha = 0.1$ and $\beta = 0.3$). Dashed lines indicate generation 100. Sensitivity values: $\phi^A = 1.0$, $\phi^B = 0.75$, $\phi^C = 0.5$.

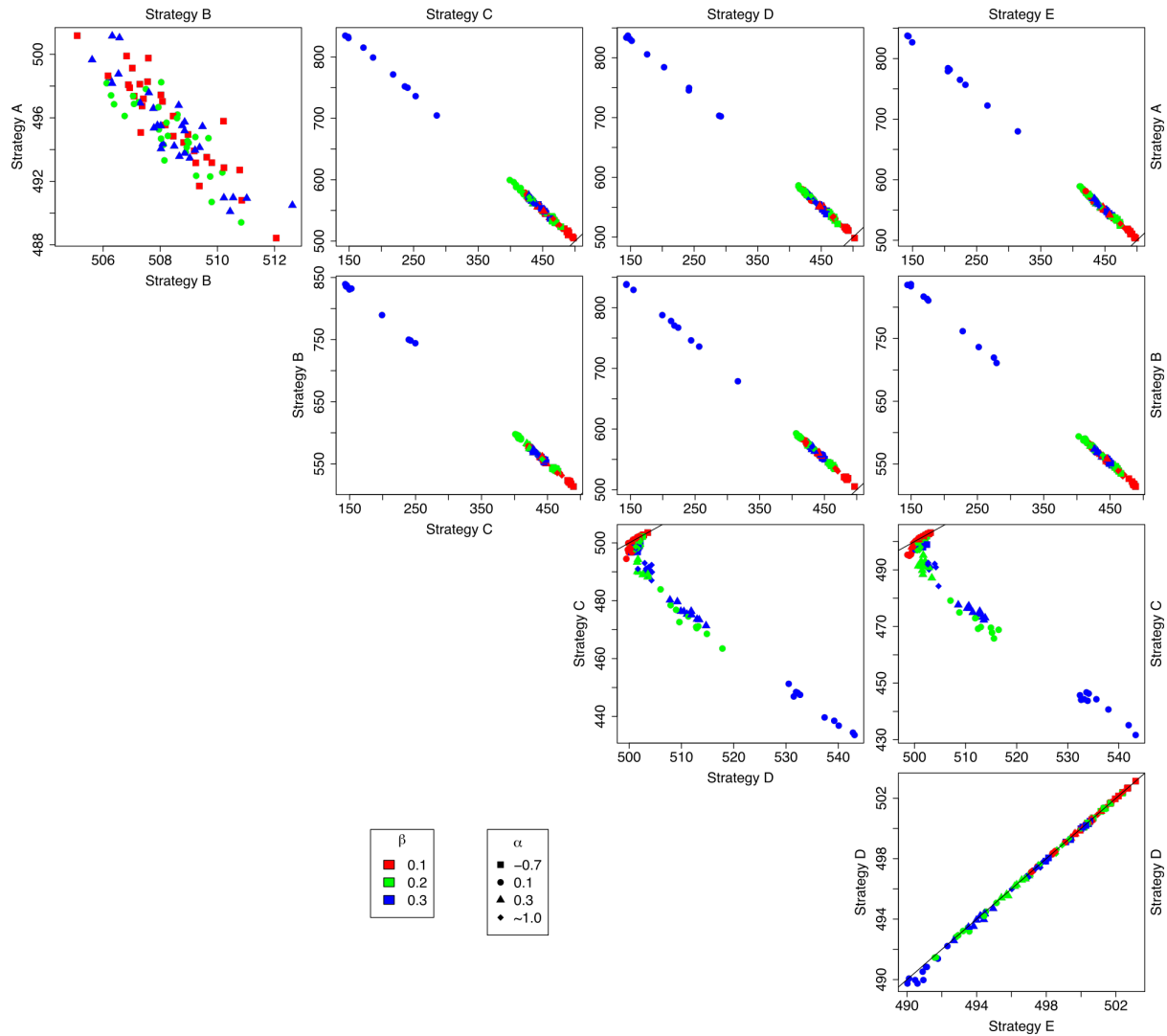


Figure S6: Pairwise competition between different reproductive strategies during invasion of a marginal habitat (North path) under low environmental stress ($p_e^{pN} = 0.1$ and $v_e^{pN} = 0.1$), with sexual strategies exposed to a variety of Allee effect magnitudes (α and β). Axes represent the short-term temporal mean population sizes of competing strategies. Diagonal lines indicate identical temporal mean population sizes of competing reproductive strategies and therefore equivalent ecological successes. Sensitivity values: $\phi^A = 1.0$, $\phi^B = 0.75$, $\phi^C = 0.5$.

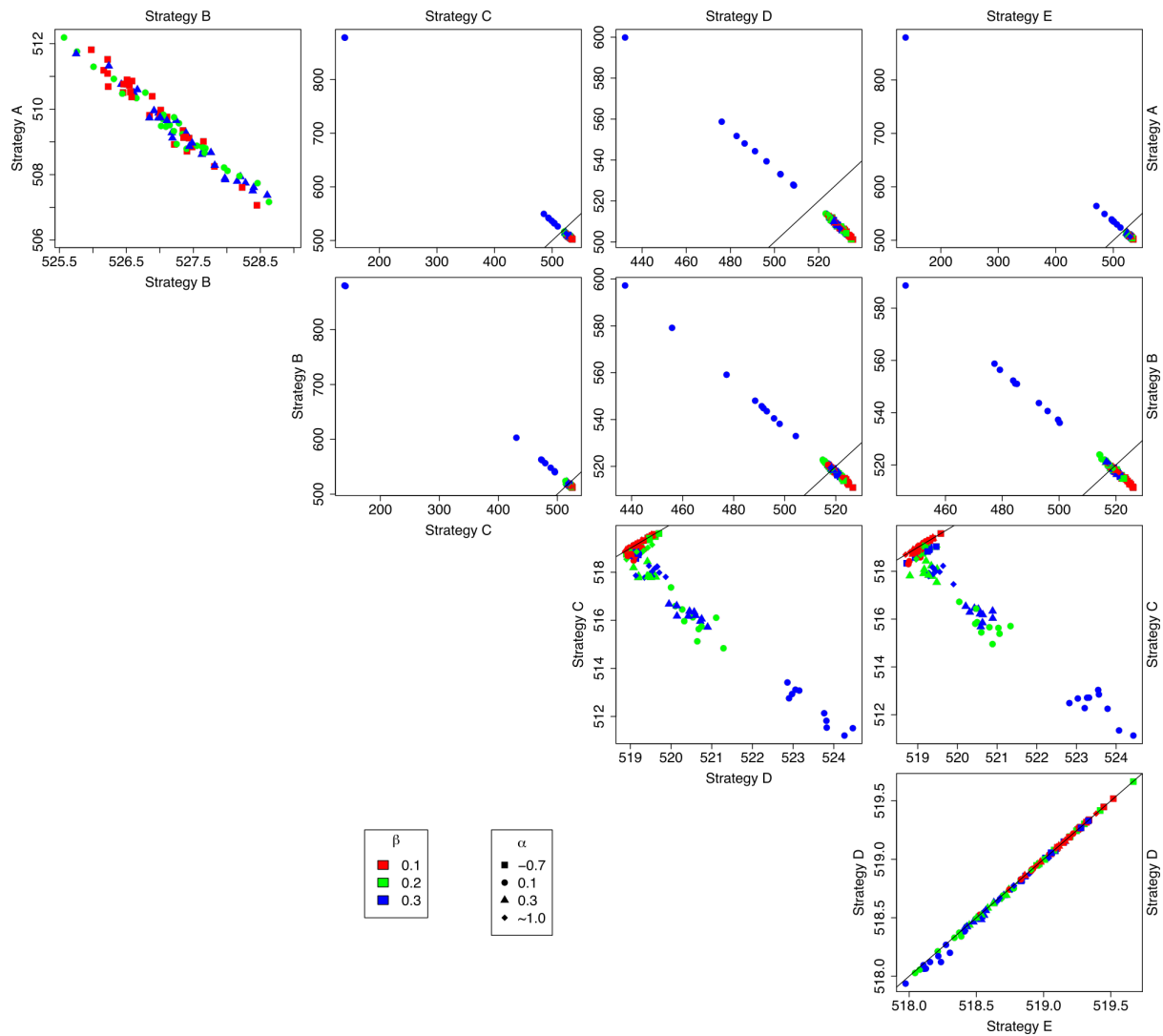


Figure S7: Pairwise competition between different reproductive strategies during invasion of a marginal habitat (North path) under low environmental stress ($p_{\epsilon}^{pN} = 0.1$ and $v_{\epsilon}^{pN} = 0.1$), with sexual strategies exposed to a variety of Allee effect magnitudes (α and β). Axes represent the long-term temporal mean population sizes of competing strategies. Diagonal lines indicate identical temporal mean population sizes of competing reproductive strategies and therefore equivalent ecological successes. Sensitivity values: $\phi^A = 1.0$, $\phi^B = 0.75$, $\phi^C = 0.5$.

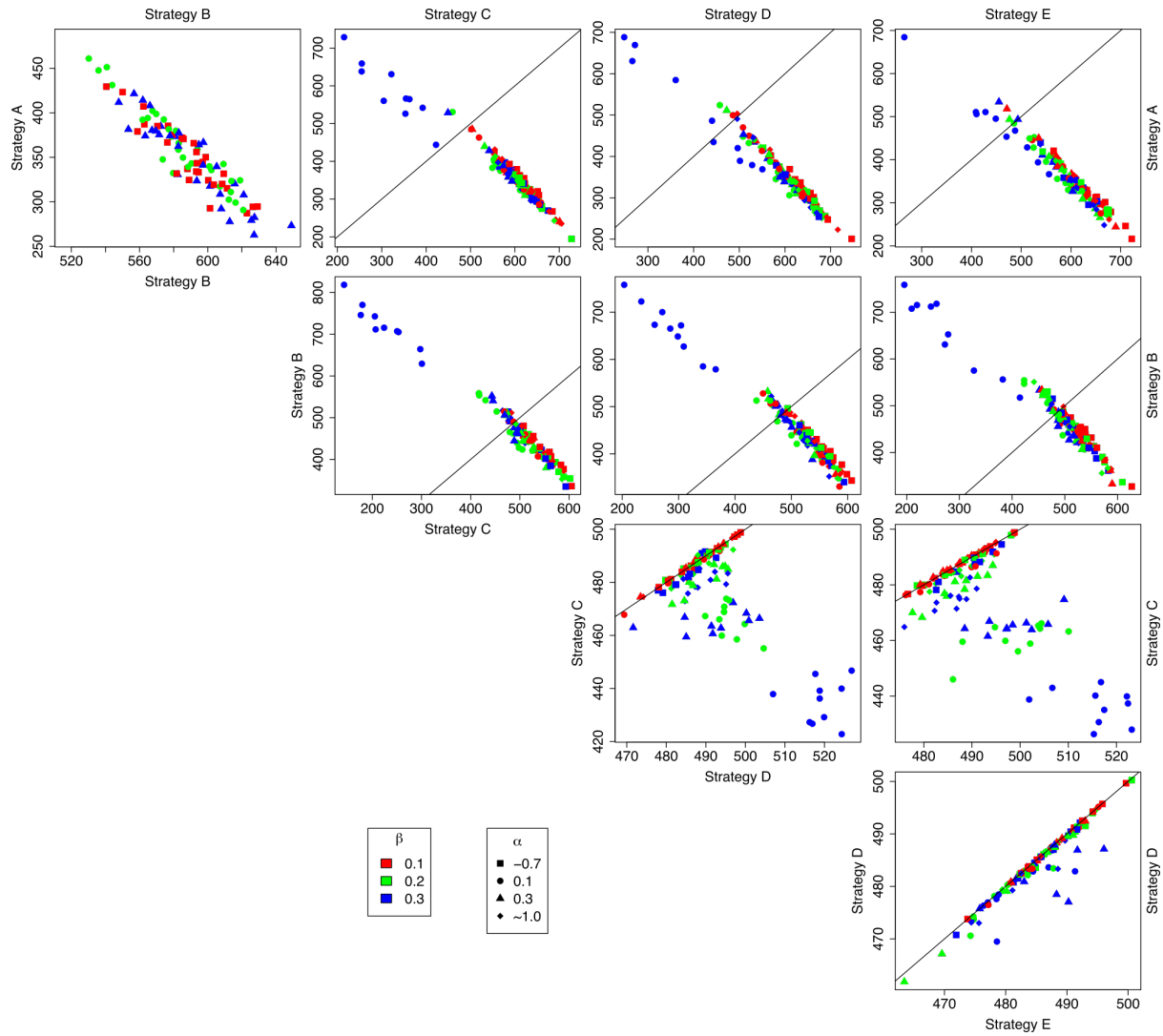


Figure S8: Pairwise competition between different reproductive strategies during invasion of a marginal habitat (North patch) under high environmental stress ($p_\epsilon^{p^N} = 0.1$ and $v_\epsilon^{p^N} = 0.9$), with sexual strategies exposed to a variety of Allee effect magnitudes (α and β). Axes represent the short-term temporal mean population sizes of competing strategies. Diagonal lines indicate identical temporal mean population sizes of competing reproductive strategies and therefore equivalent ecological successes. Sensitivity values: $\phi^A = 1.0$, $\phi^B = 0.75$, $\phi^C = 0.5$.

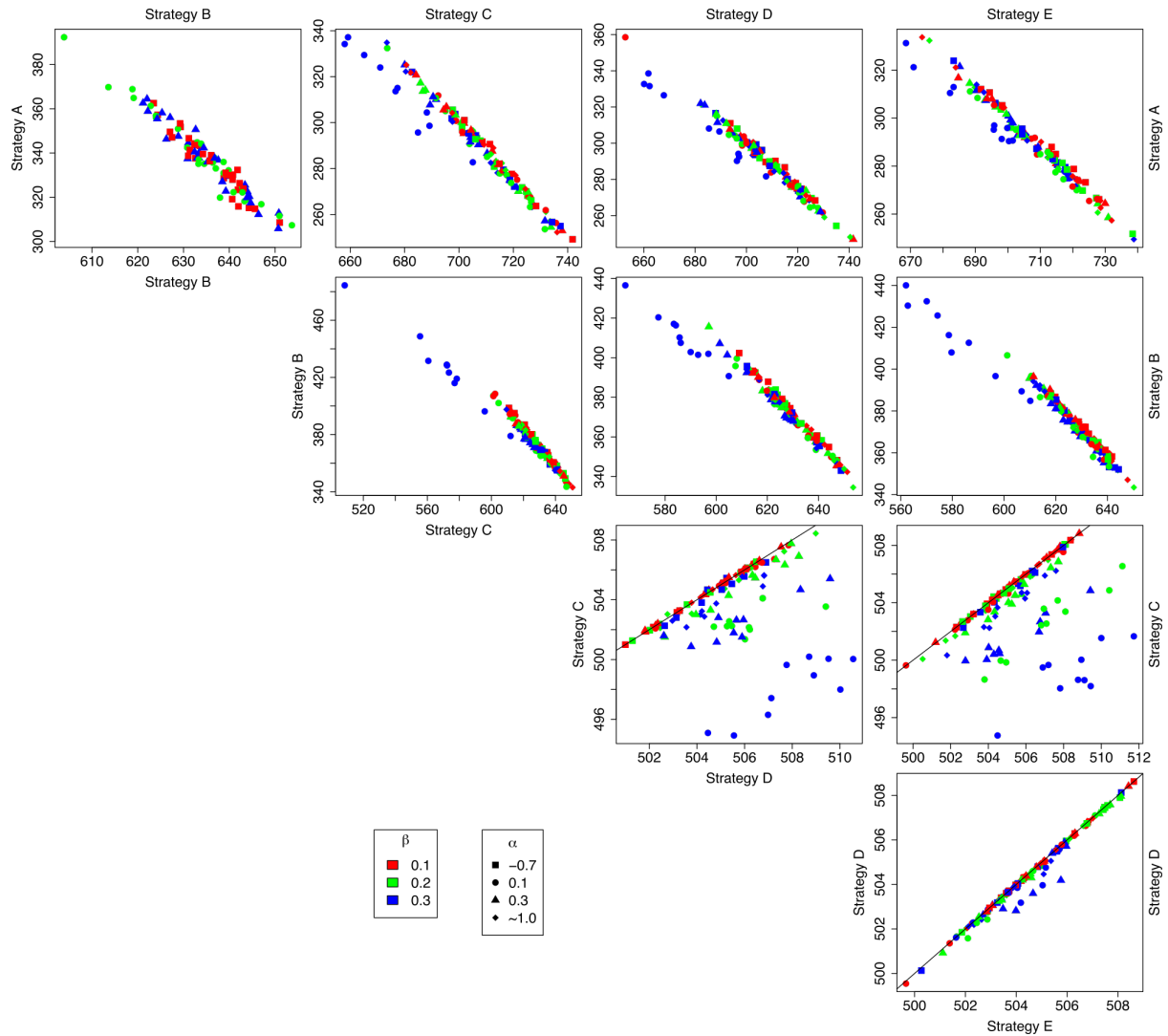


Figure S9: Pairwise competition between different reproductive strategies during invasion of a marginal habitat (North patch) under high environmental stress ($p_\epsilon^{pN} = 0.1$ and $v_\epsilon^{pN} = 0.9$), with sexual strategies exposed to a variety of Allee effect magnitudes (α and β). Axes represent the long-term temporal mean population sizes of competing strategies. Diagonal lines indicate identical temporal mean population sizes of competing reproductive strategies and therefore equivalent ecological successes. Sensitivity values: $\phi^A = 1.0$, $\phi^B = 0.75$, $\phi^C = 0.5$.

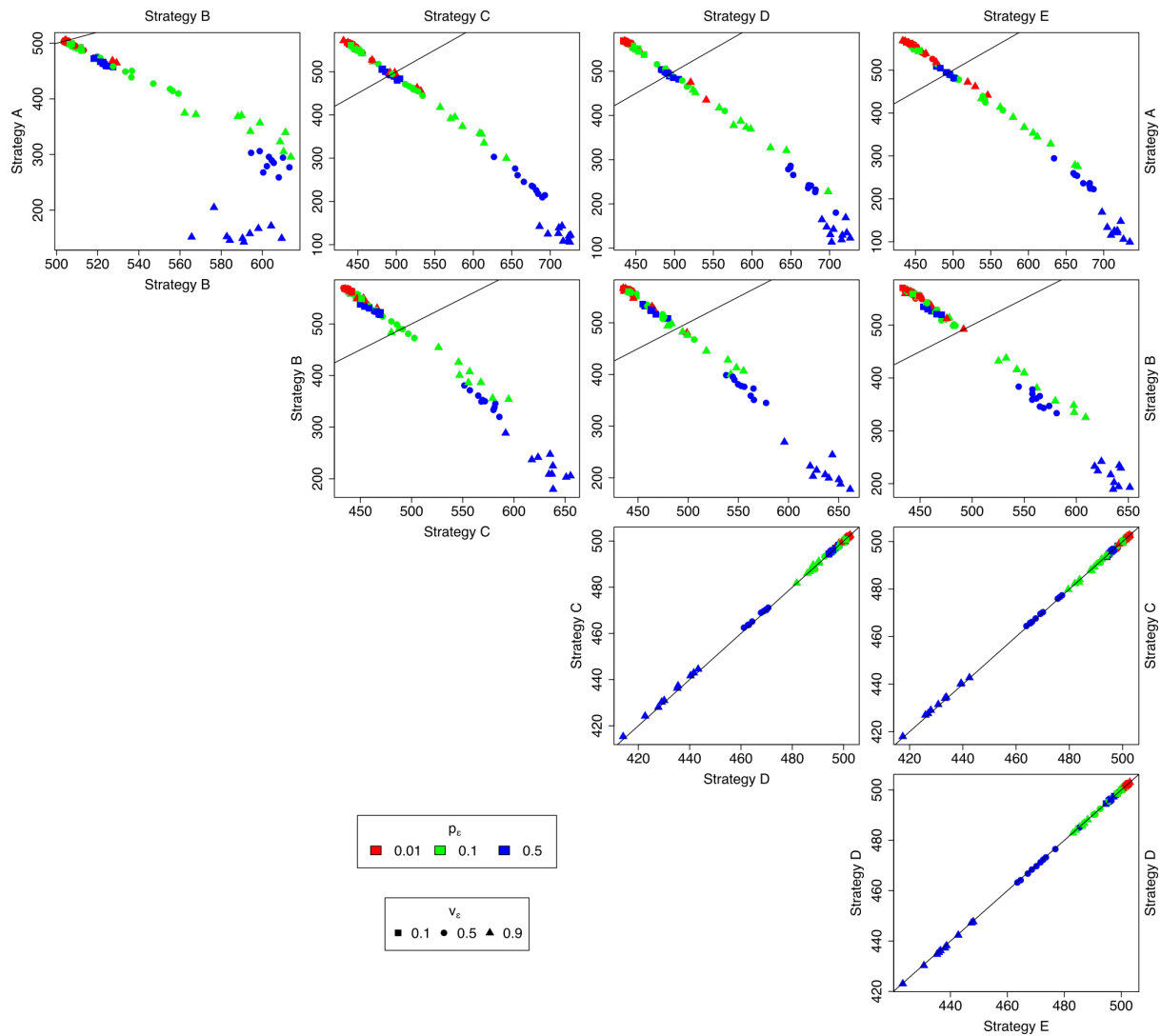


Figure S10: Pairwise competition between different reproductive strategies during invasion of a marginal habitat (North patch) under different probabilities of occurrence of stressful conditions (p_ϵ^{PN}) and maximum levels of stress (v_ϵ^{PN}), with sexual strategies exposed to a relatively weak Allee effect ($\alpha = 0.3$ and $\beta = 0.1$). Axes represent the short-term temporal mean population sizes of competing strategies. Diagonal lines indicate identical temporal mean population sizes of competing reproductive strategies and therefore equivalent ecological successes. Sensitivity values: $\phi^A = 1.0$, $\phi^B = 0.75$, $\phi^C = 0.5$.

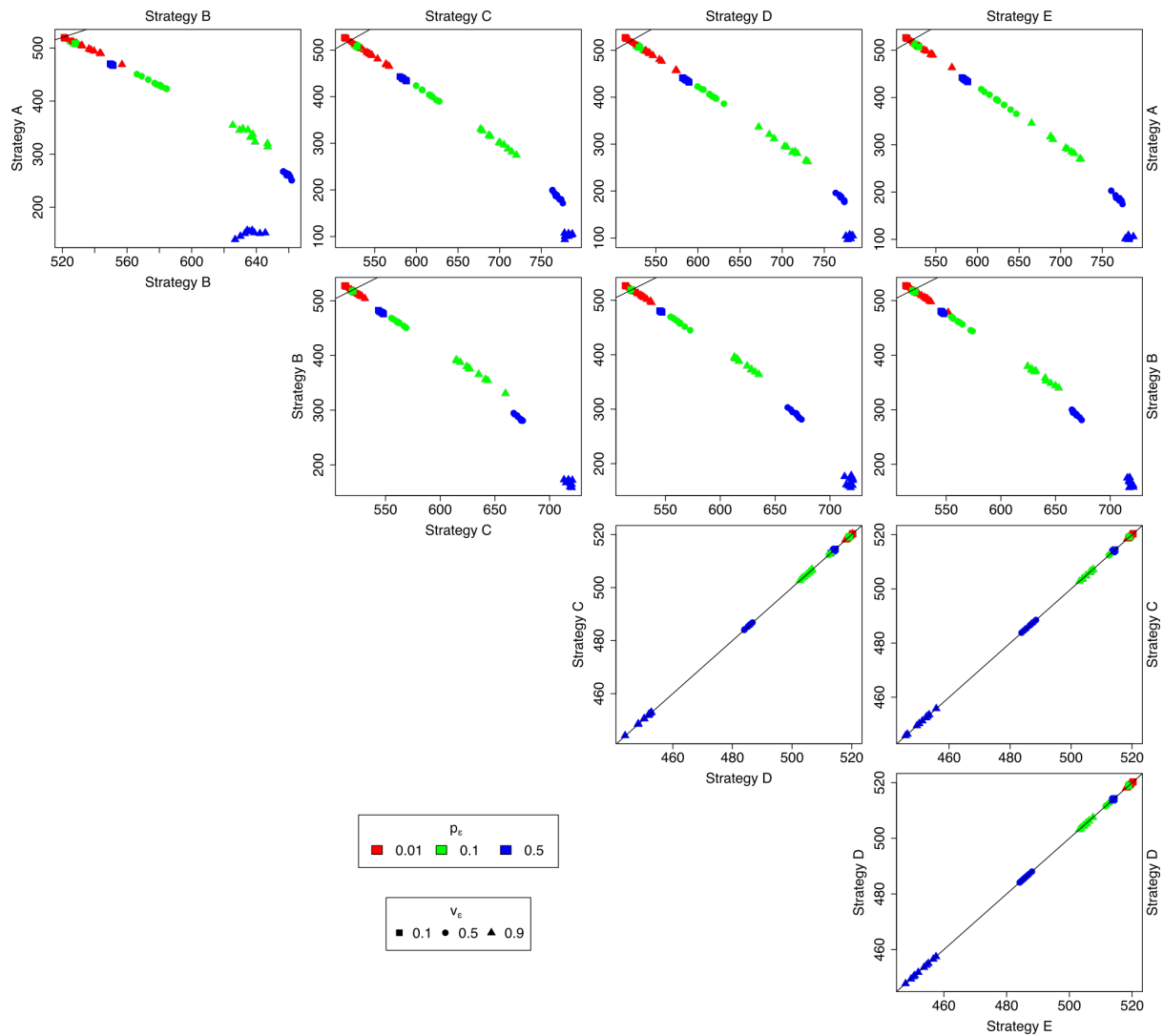


Figure S11: Pairwise competition between different reproductive strategies during invasion of a marginal habitat (North patch) under different probabilities of occurrence of stressful conditions (p_ϵ^{pN}) and maximum levels of stress (v_ϵ^{pN}), with sexual strategies exposed to a relatively weak Allee effect ($\alpha = 0.3$ and $\beta = 0.1$). Axes represent the long-term temporal mean population sizes of competing strategies. Diagonal lines indicate identical temporal mean population sizes of competing reproductive strategies and therefore equivalent ecological successes. Sensitivity values: $\phi^A = 1.0$, $\phi^B = 0.75$, $\phi^C = 0.5$.

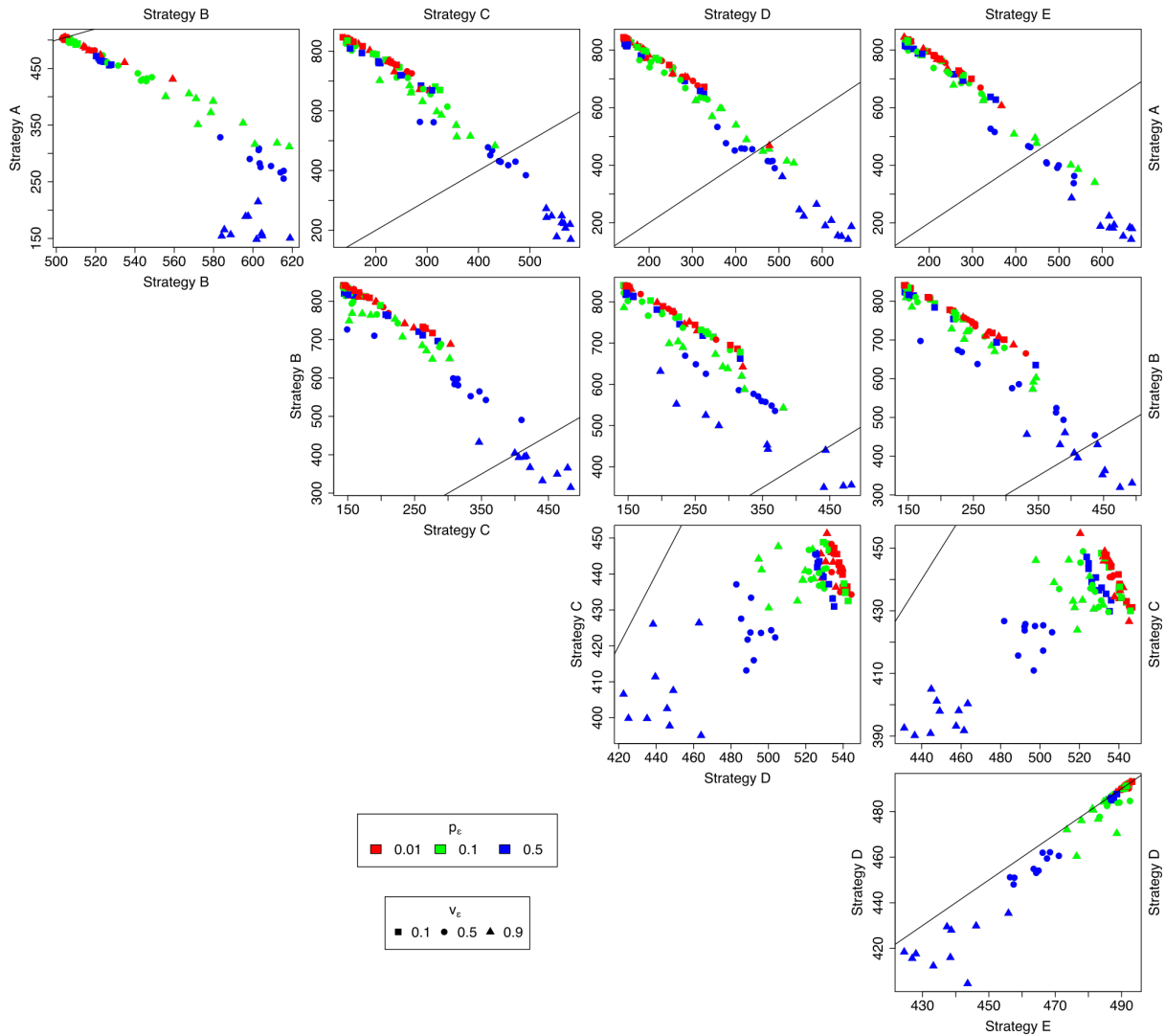


Figure S12: Pairwise competition between different reproductive strategies during invasion of a marginal habitat (North patch) under different probabilities of occurrence of stressful conditions (p_ϵ^{pN}) and maximum levels of stress (v_ϵ^{pN}), with sexual strategies exposed to a relatively strong Allee effect ($\alpha = 0.1$ and $\beta = 0.3$). Axes represent the short-term temporal mean population sizes of competing strategies. Diagonal lines indicate identical temporal mean population sizes of competing reproductive strategies and therefore equivalent ecological successes. Sensitivity values: $\phi^A = 1.0$, $\phi^B = 0.75$, $\phi^C = 0.5$.

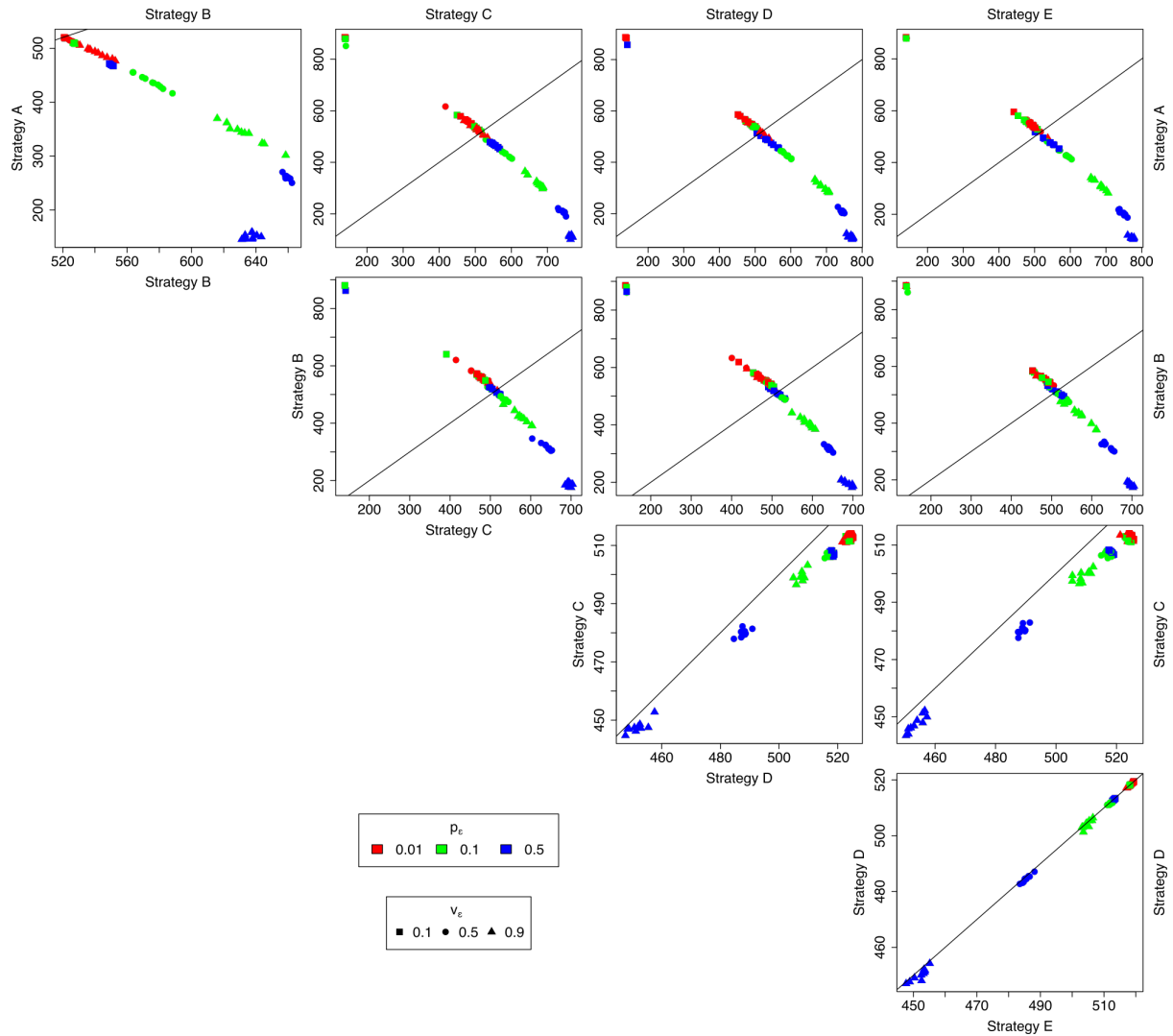


Figure S13: Pairwise competition between different reproductive strategies during invasion of a marginal habitat (North patch) under different probabilities of occurrence of stressful conditions (p_ϵ^{pN}) and maximum levels of stress (v_ϵ^{pN}), with sexual strategies exposed to a relatively strong Allee effect ($\alpha = 0.1$ and $\beta = 0.3$). Axes represent the long-term temporal mean population sizes of competing strategies. Diagonal lines indicate identical temporal mean population sizes of competing reproductive strategies and therefore equivalent ecological successes. Sensitivity values: $\phi^A = 1.0$, $\phi^B = 0.75$, $\phi^C = 0.5$.

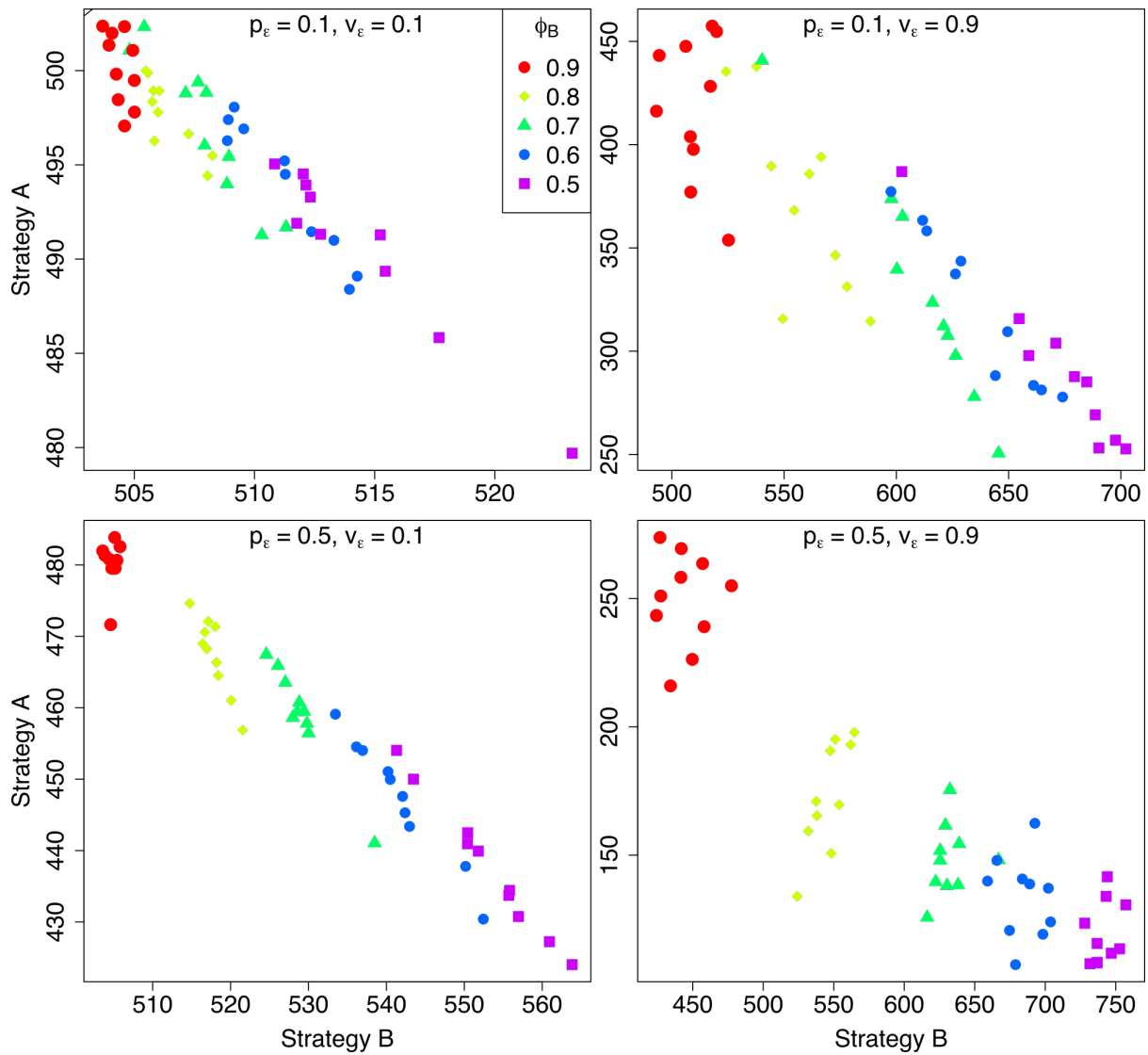


Figure S14: Obligate apomictic (strategy A) vs. obligate automictic parthenogenesis (strategy B). Axes represent the short-term temporal mean population sizes of competing strategies in the marginal habitat (North path). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).

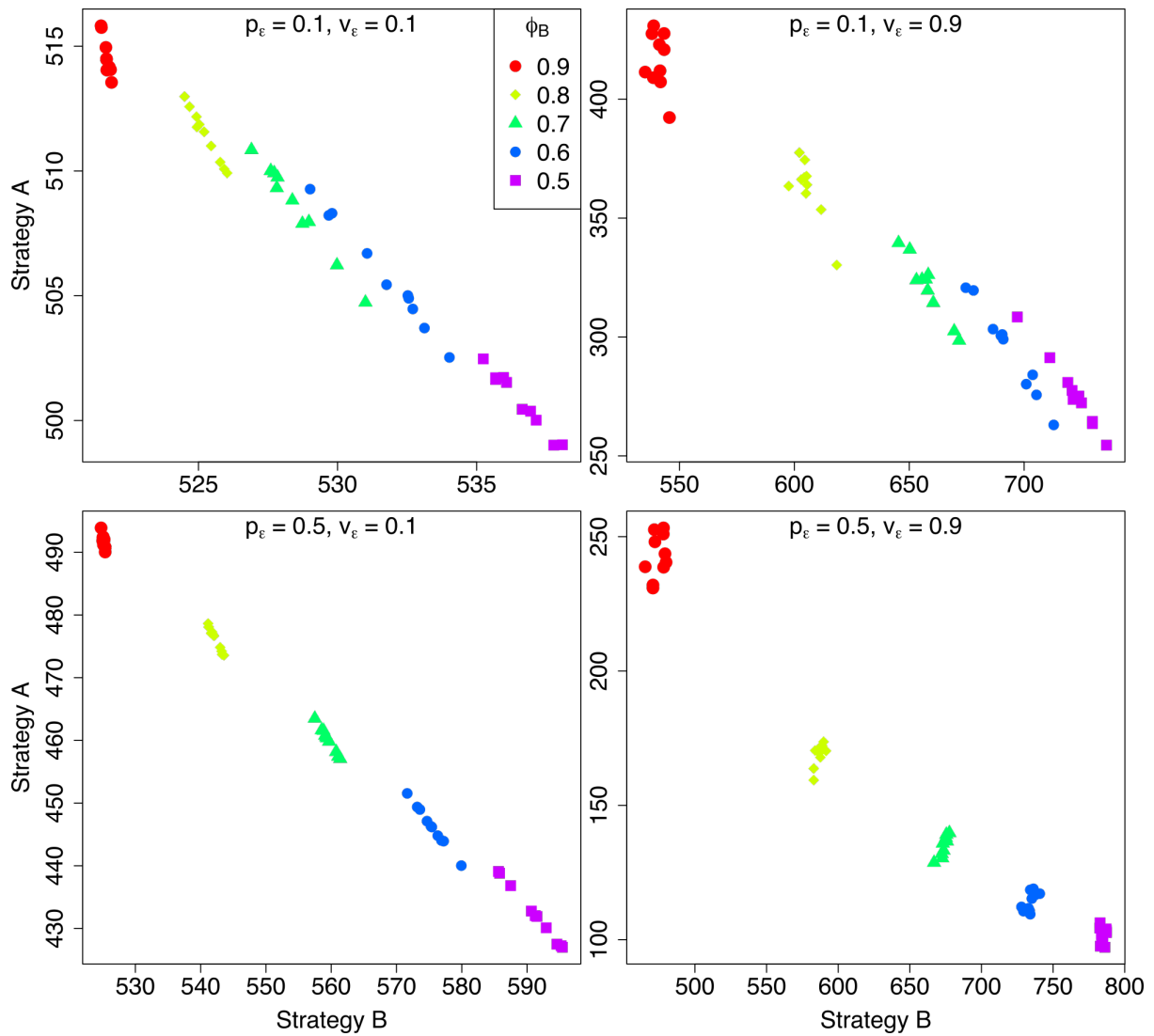


Figure S15: Obligate apomictic (strategy A) vs. obligate automictic parthenogenesis (strategy B). Axes represent the long-term temporal mean population sizes of competing strategies in the marginal habitat (North path). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).

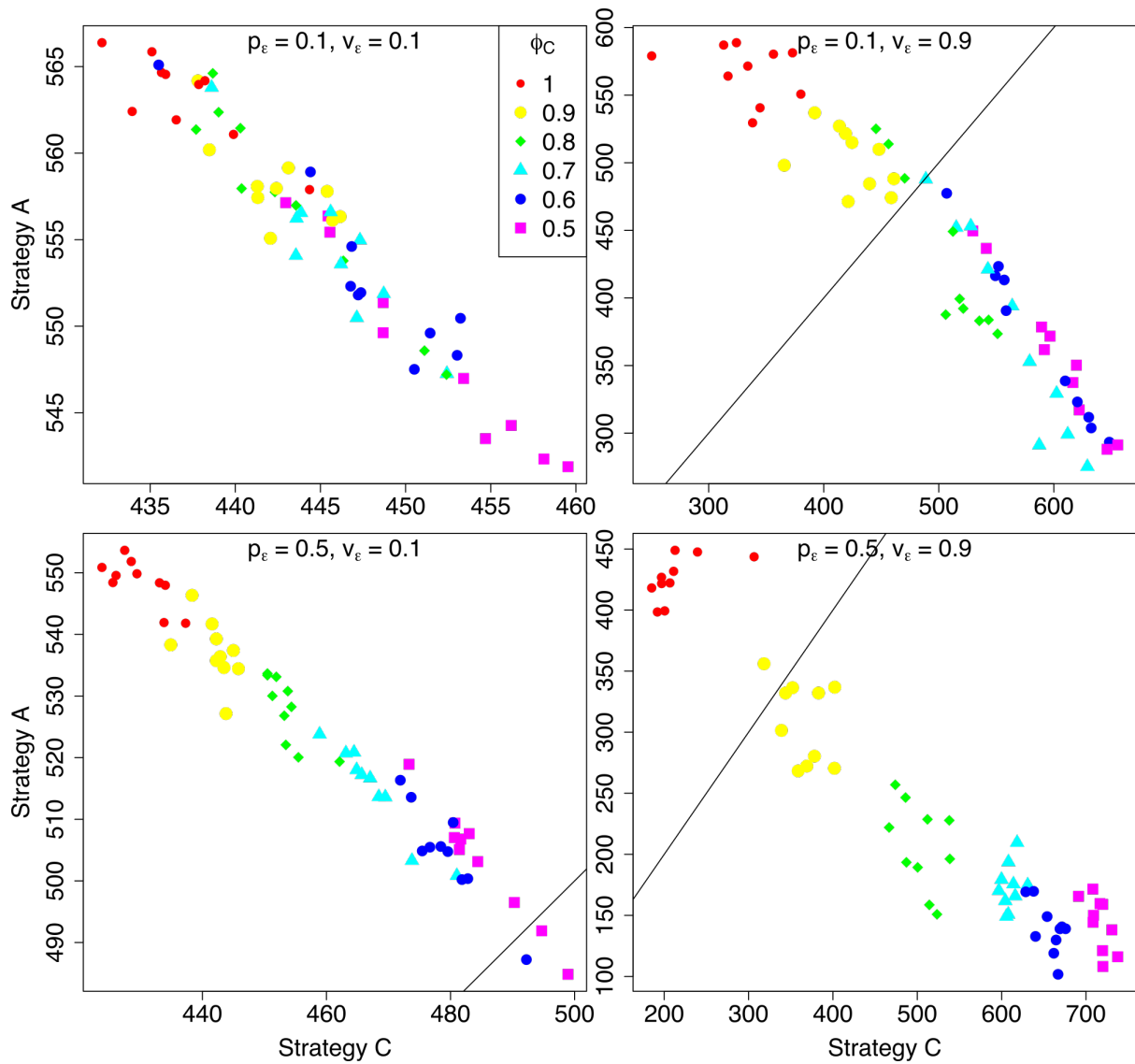


Figure S16: Obligate parthenogenesis (strategy A/B) vs. obligate sexual reproduction (strategy C). Axes represent the short-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a weak Allee effect ($\alpha = 0.3$ and $\beta = 0.1$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).

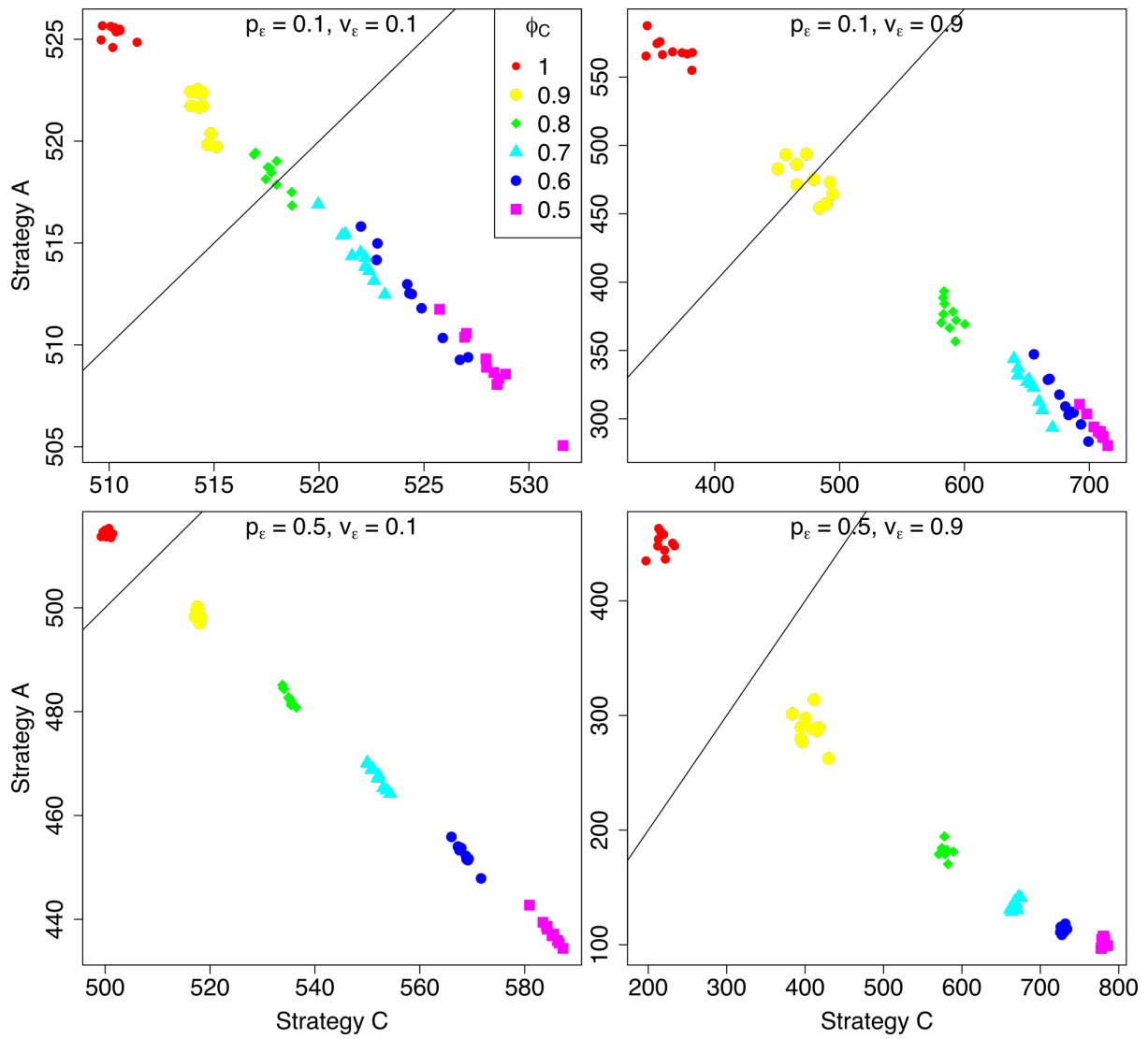


Figure S17: Obligate parthenogenesis (strategy A/B) vs. obligate sexual reproduction (strategy C). Axes represent the long-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a weak Allee effect ($\alpha = 0.3$ and $\beta = 0.1$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).

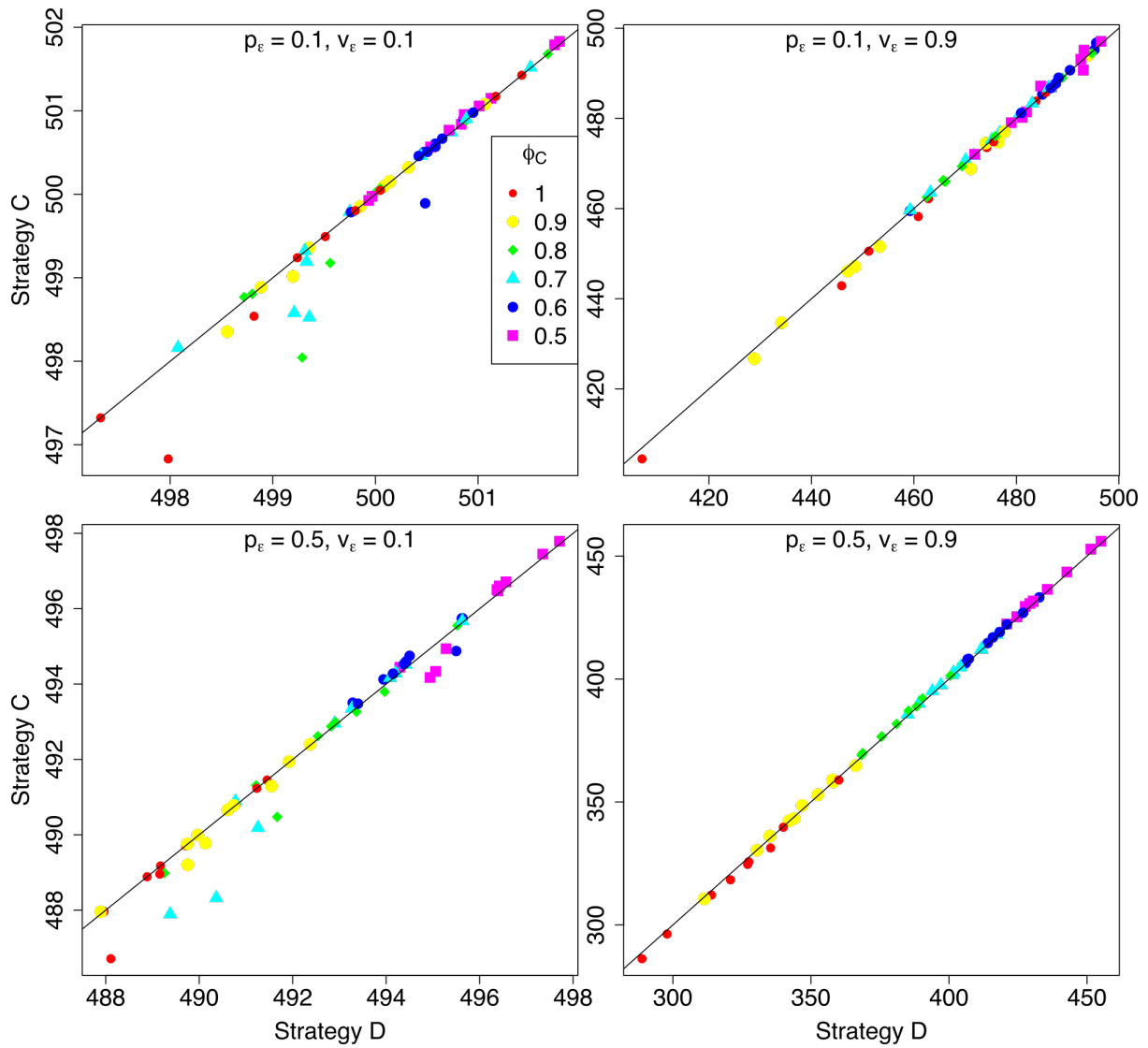


Figure S18: Obligate sexual reproduction (strategy C) vs. facultative parthenogenesis (strategy D/E). Axes represent the short-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a weak Allee effect ($\alpha = 0.3$ and $\beta = 0.1$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).

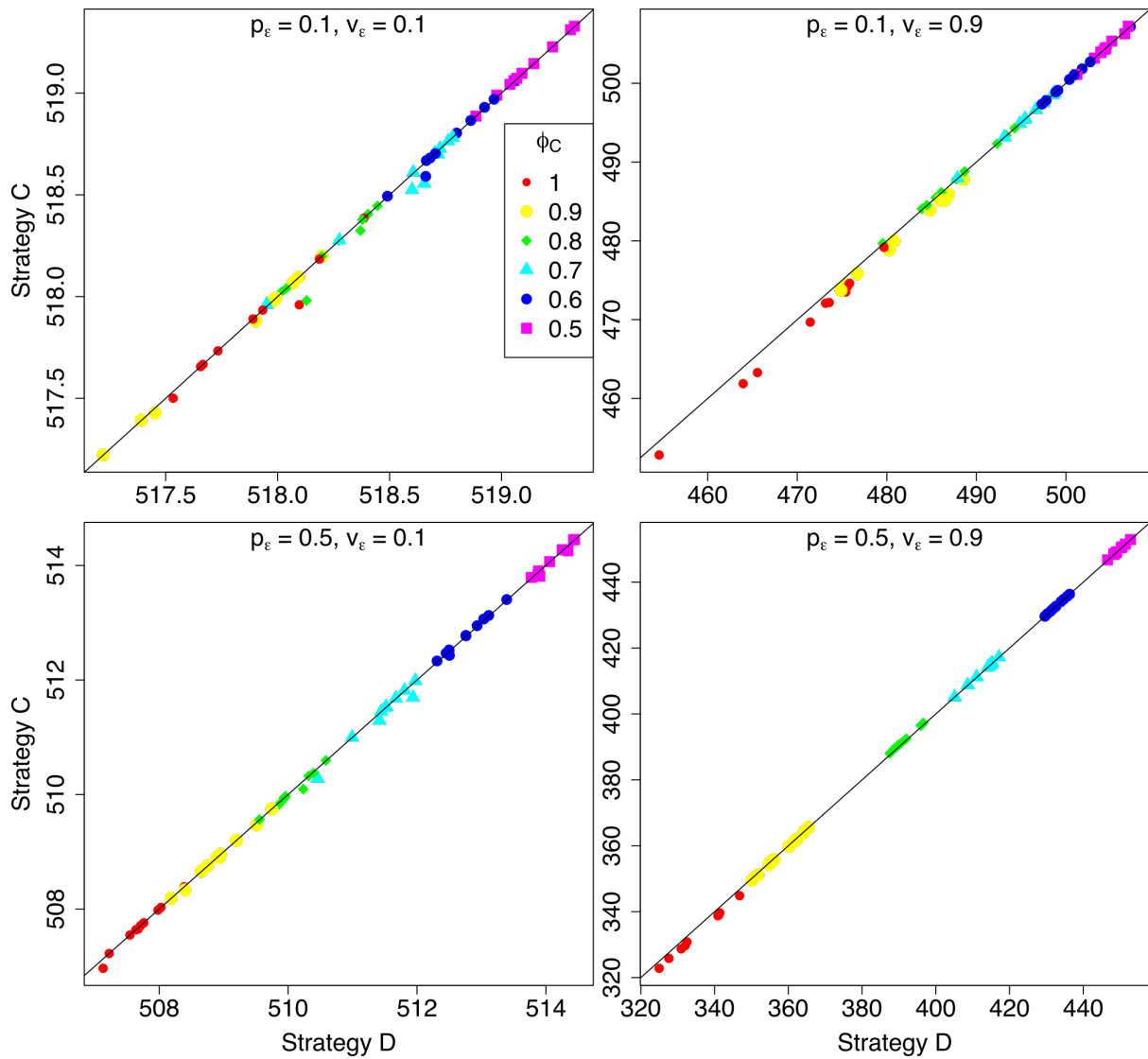


Figure S19: Obligate sexual reproduction (strategy C) vs. facultative parthenogenesis (strategy D/E). Axes represent the long-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a weak Allee effect ($\alpha = 0.3$ and $\beta = 0.1$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).

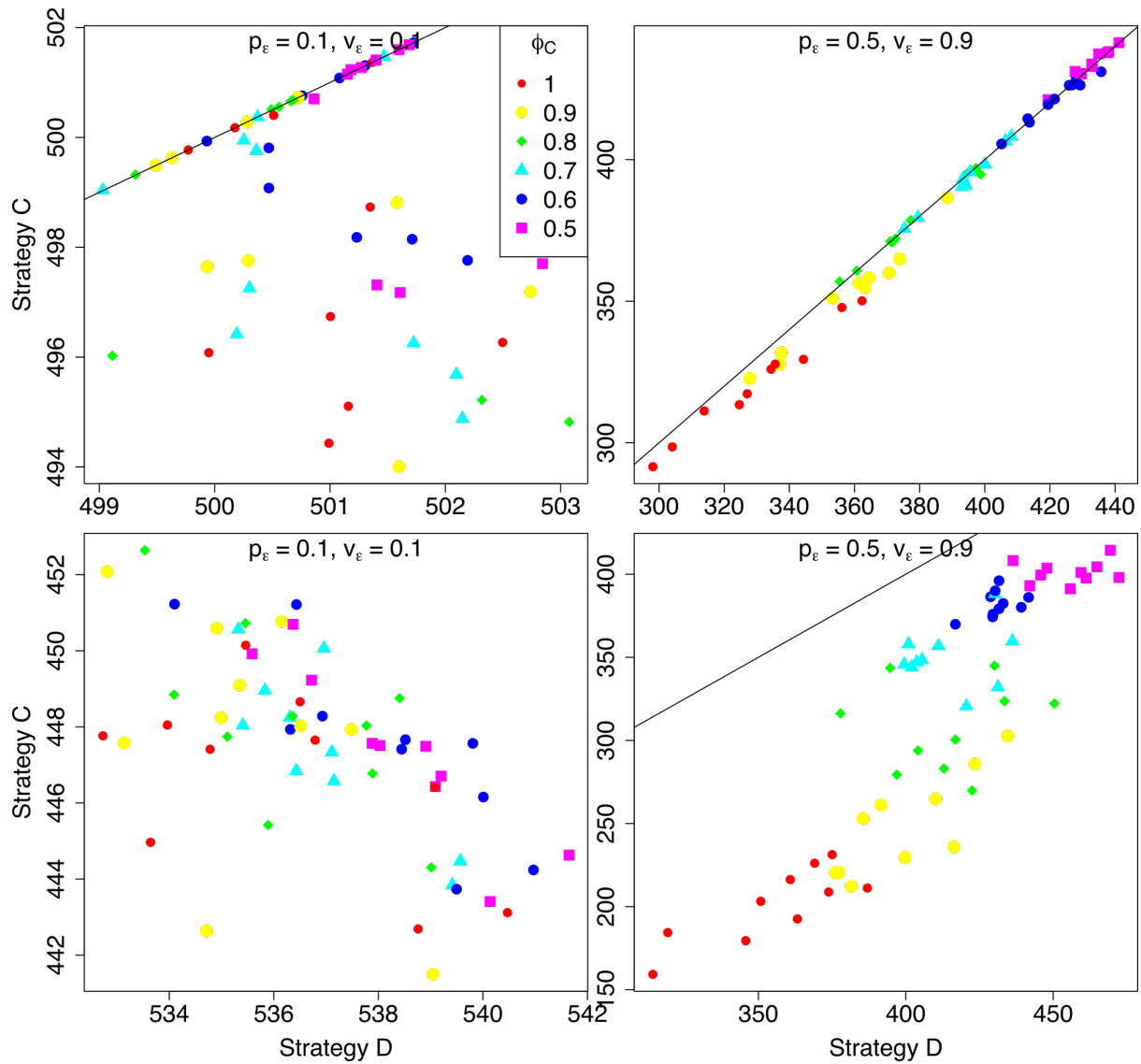


Figure S20: Obligate sexual reproduction (strategy C) vs. facultative parthenogenesis (strategy D/E). Axes represent the short-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a weak Allee effect (top row; $\alpha = 0.3$ and $\beta = 0.1$) and a strong Allee effect (bottom row; $\alpha = 0.1$ and $\beta = 0.3$), with a high transition rate ($\tau = 0.8$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C). high transition rate ($\tau = 0.8$).

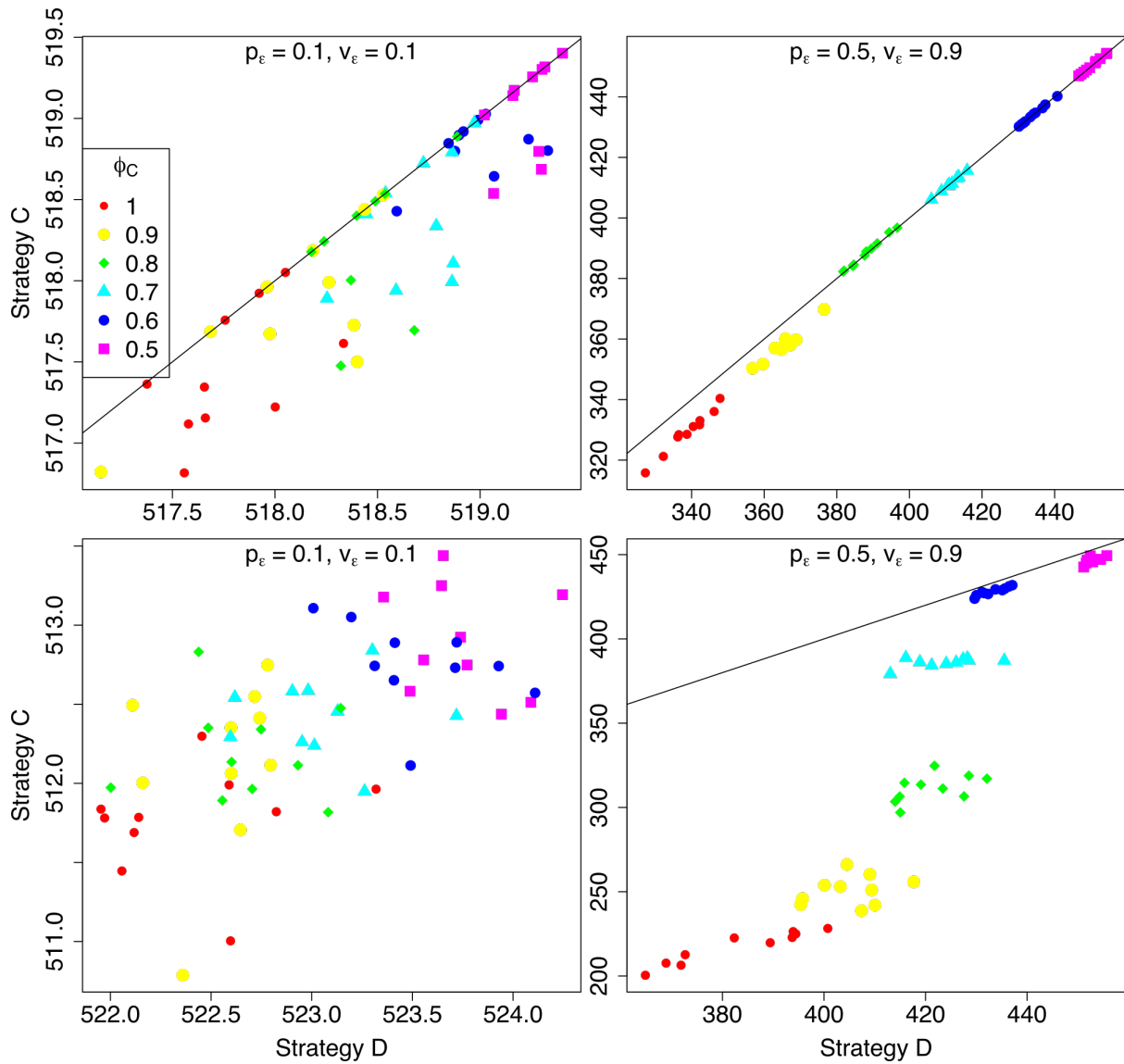


Figure S21: Obligate sexual reproduction (strategy C) vs. facultative parthenogenesis (strategy D/E). Axes represent the long-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a weak Allee effect (top row; $\alpha = 0.3$ and $\beta = 0.1$) and a strong Allee effect (bottom row; $\alpha = 0.1$ and $\beta = 0.3$), with a high transition rate ($\tau = 0.8$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C). high transition rate ($\tau = 0.8$).

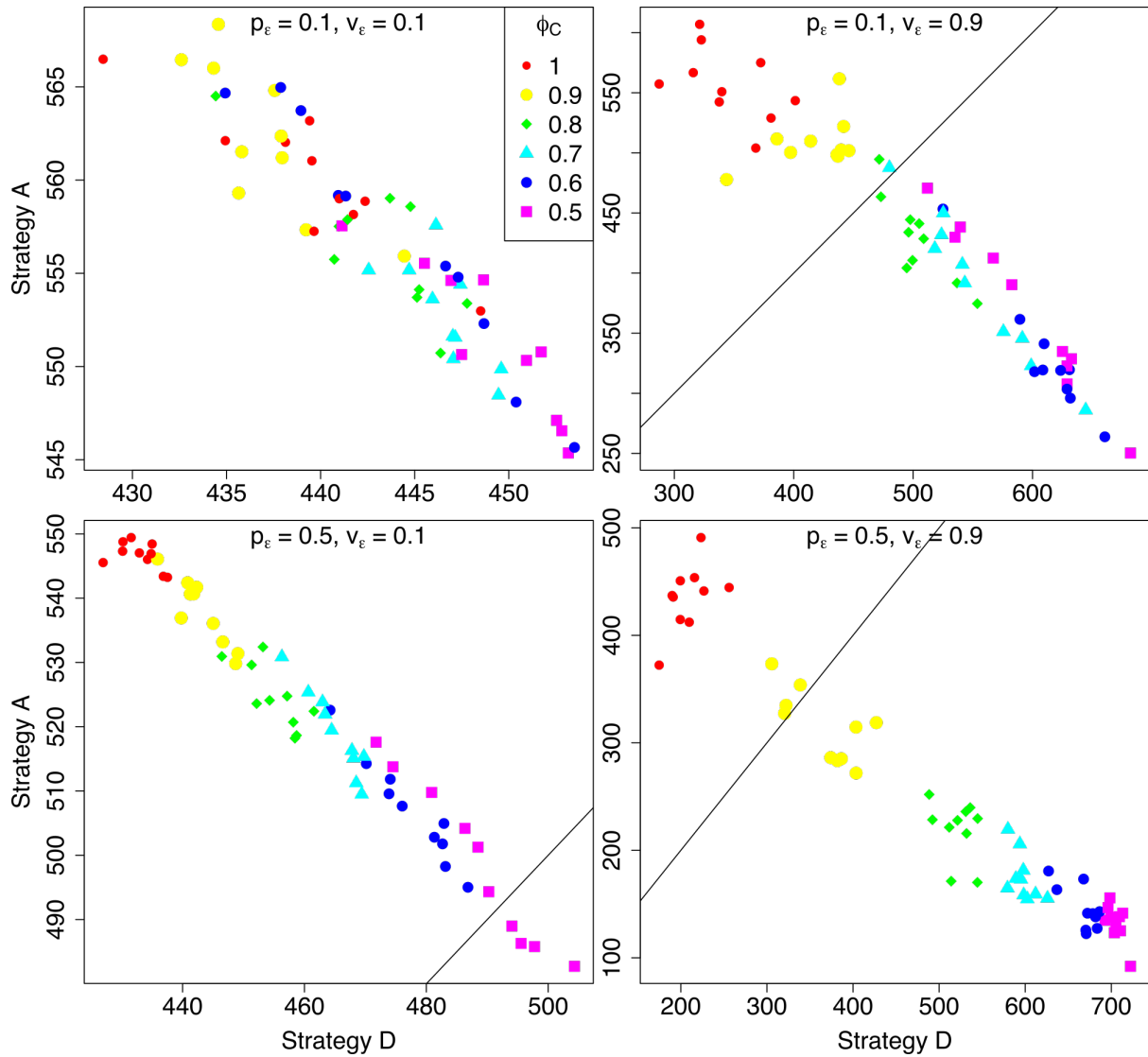


Figure S22: Obligate parthenogenesis (strategy A/B) vs. facultative parthenogenesis (strategy D/E). Axes represent the short-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a weak Allee effect ($\alpha = 0.3$ and $\beta = 0.1$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).

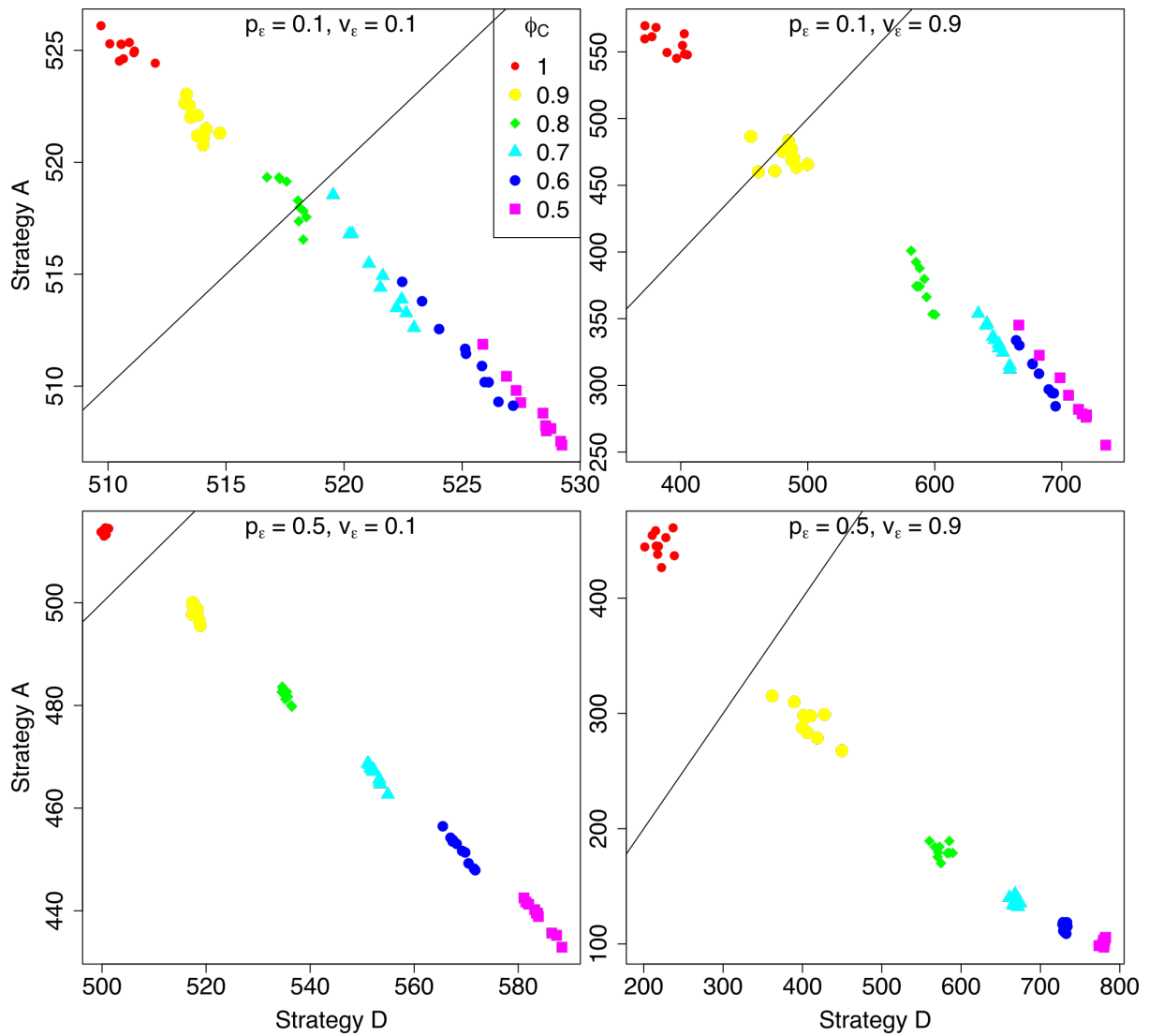


Figure S23: Obligate parthenogenesis (strategy A/B) vs. facultative parthenogenesis (strategy D/E). Axes represent the long-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a weak Allee effect ($\alpha = 0.3$ and $\beta = 0.1$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).

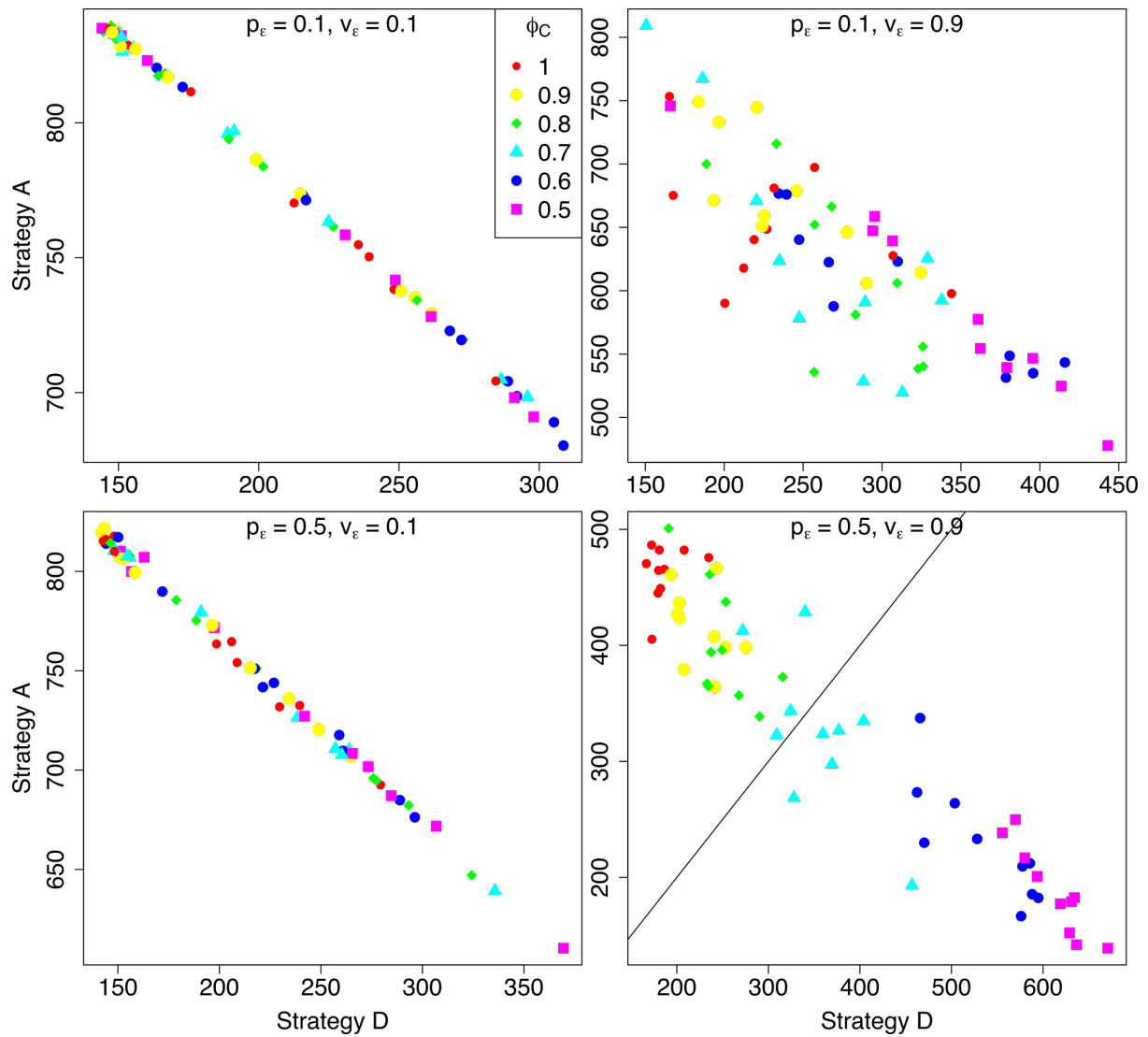


Figure S24: Obligate parthenogenesis (strategy A/B) vs. facultative parthenogenesis (strategy D/E). Axes represent the short-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a strong Allee effect ($\alpha = 0.1$ and $\beta = 0.3$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).

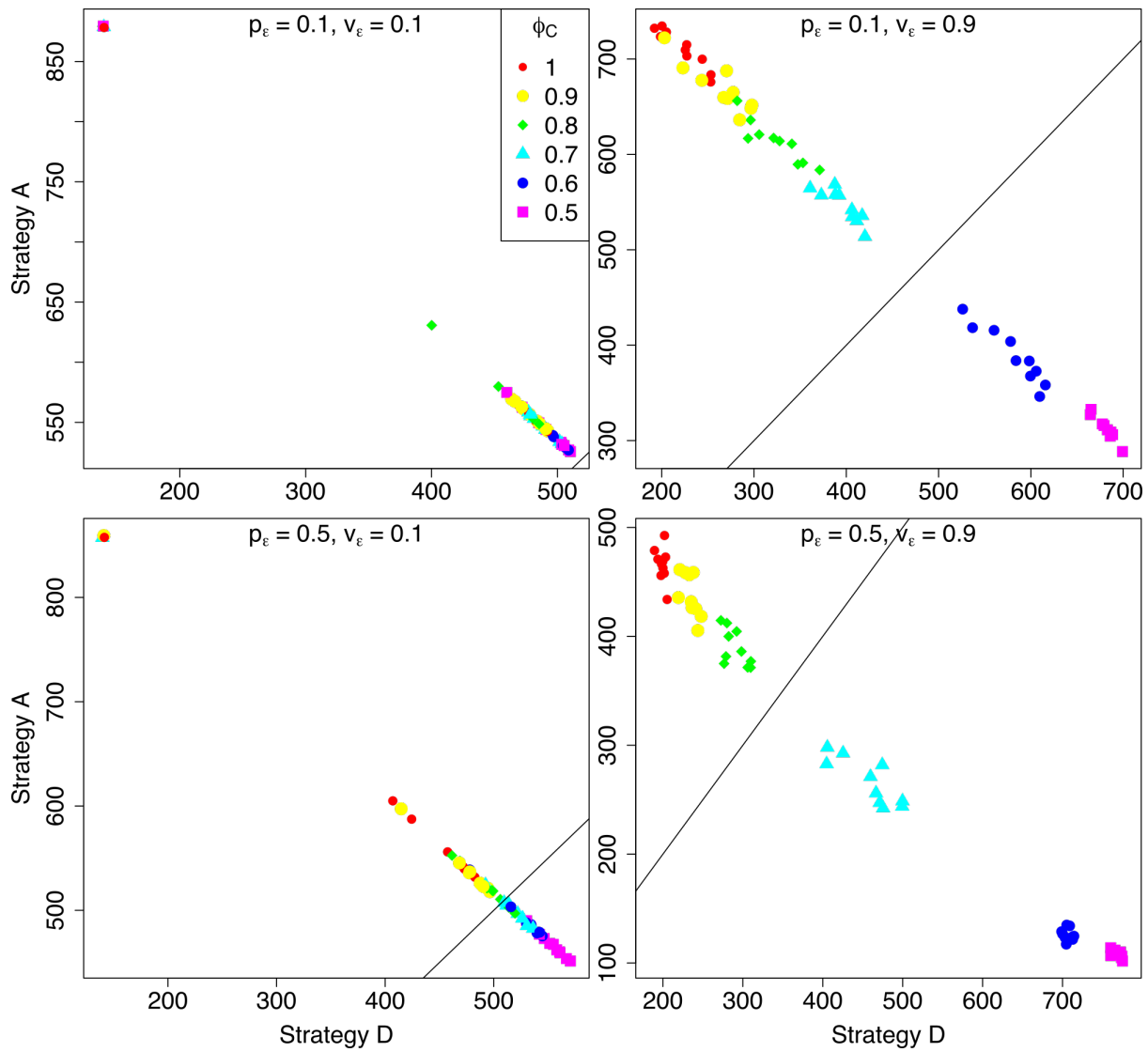


Figure S25: Obligate parthenogenesis (strategy A/B) vs. facultative parthenogenesis (strategy D/E). Axes represent the long-term temporal mean population sizes of competing strategies in the marginal habitat (North path) under a strong Allee effect ($\alpha = 0.1$ and $\beta = 0.3$). Note that ϕ represents the relative difference in sensitivity to environmental stress between apomictic (strategy A; $\phi^A = 1.0$) and automictic (strategy B; ϕ^B) parthenogenesis, or between parthenogenesis (strategy A; $\phi^A = 1.0$) and sexual reproduction (strategy C; ϕ^C).