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**Interim Report**

**IR-12-040**

**Spatial self-structuring accelerates adaptive speciation in sexual populations**

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**Approved by**

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# Spatial self-structuring accelerates adaptive speciation in sexual populations

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## Abstract

**Questions:** How does spatial self-structuring influence the waiting time until adaptive speciation in a population with sexual reproduction? Which mechanisms underlie this effect?

**Model:** Using a spatially explicit individual-based multi-locus model of adaptive speciation, we investigate the evolution of a sexually reproducing population, with different levels of spatial self-structuring induced by different distances of natal dispersal. We analyze how waiting times until speciation are affected by the mobility of individuals, the number of loci determining the phenotype under disruptive selection, and the mating costs for individuals preferring rare phenotypes.

**Conclusions:** Spatial self-structuring facilitates the evolution of assortative mating and accelerates adaptive speciation. We identify three mechanisms that are responsible for this effect: (i) spatial self-structuring promotes the evolution of assortativity by providing assortative mating “for free,” as individuals find phenotypically similar mates within their spatial clusters; (ii) it helps assortatively mating individuals with rare phenotypes to find mating partners even when the selected phenotype is determined by a large number of loci, so that strict assortativity is difficult; and (iii) it renders speciation less sensitive to costs of assortative mating, especially for individuals preferring rare phenotypes.

## 27 **Introduction**

28 Speciation without geographic isolation has long been surrounded by controversy in evolu-  
29 tionary-biology research. For speciation to occur in the presence of gene flow, two essential  
30 elements are necessary: ecological diversification and reproductive isolation between extreme  
31 phenotypes (e.g., Maynard Smith 1966). While a number of theoretical studies have shown  
32 that these elements can be established as a result of competitive interactions between individ-  
33 uals, and this scenario has received much attention in theoretical research (Rosenzweig 1978;  
34 Slatkin 1979; Felsenstein 1981; Seger 1985; Udovic 1980; Doebeli 1996; Dieckmann and  
35 Doebeli 1999; Bürger et al. 2006; Pennings et al. 2008; Ripa 2008), the exact conditions al-  
36 lowing for speciation without geographic isolation remain debated. Some of these conditions  
37 have been addressed in several recent studies, including the number of loci determining the  
38 trait under disruptive selection (e.g., Gourbiere 2004; Bolnick 2004; Bürger et al. 2006;  
39 Bürger and Schneider 2006; Rettelbach et al. 2011), the strength of assortative mating (e.g.,  
40 Kirkpatrick and Nuismer 2004; Doebeli et al. 2007; Otto et al. 2008), and the cost of choosi-  
41 ness (e.g., Matessi et al. 2002; Bürger and Schneider 2006; Schneider and Bürger 2006; Kopp  
42 and Hermisson 2008; Otto et al. 2008).

43 The number of loci determining phenotypic traits directly affects the phenotypic reso-  
44 lution at which these traits can be expressed: a larger number of loci results in a larger number  
45 of possible phenotypic classes. This interferes with the competition strength between individ-  
46 uals (Bürger et al. 2006) and affects the number of mates that fall within a given individual's  
47 range of acceptable phenotypes (Bolnick 2004). It has been shown that the likelihood of spe-  
48 ciation decreases when a large number of loci determine the traits under disruptive selection,  
49 with speciation then being possible only when the level of assortative mating is high  
50 (Gourbiere 2004; Bürger and Schneider 2006). Likewise, a large number of loci have been  
51 shown to increase the waiting time until sympatric speciation (Dieckmann and Doebeli 1999,  
52 2004; Bolnick 2004). However, also the opposite effect on the likelihood of speciation has  
53 been reported (Kondrashov and Kondrashov 1999; Bürger et al. 2006; Rettelbach et al. 2011).

54 Reproductive isolation in sympatry usually results from a form of assortative mating,  
55 which may be pre-established or may evolve simultaneously with divergence in the trait under  
56 disruptive selection. In the case of pre-established assortative mating, reproductive isolation is  
57 more likely to emerge under a moderate level of assortativity, while very strong assortative  
58 mating can in fact act against speciation, by reducing polymorphism and by generating stabi-  
59 lizing sexual selection (Kirkpatrick and Nuismer 2004; Bürger et al. 2006; Otto et al. 2008).  
60 On the other hand, assortative mating might evolve simultaneously with ecological diver-

61   gence under a complex interplay of natural and sexual selection. It has been established that  
62   the evolution of mating preference (from random to assortative) is generally favored when  
63   intermediate phenotypes are less fit (Dieckmann and Doebeli 1999; Otto et al. 2008; Pennings  
64   et al. 2008; Ripa 2008). It has been reported that if selection against intermediate phenotypes  
65   ceases once they are sufficiently rare, evolution of assortative mating might stop at an inter-  
66   mediate level, thus preventing speciation (Matessi et al. 2002; Pennings et al. 2008). On the  
67   other hand, in a model of secondary contact, an intermediate level of assortative mating has  
68   been found to promote maximal trait differentiation (Servedio 2011). And even though it is  
69   widely understood that recombination in sexual populations tends to obstruct adaptive specia-  
70   tion (Maynard Smith 1966; Felsenstein 1981), it has also been highlighted that under condi-  
71   tions of frequency-dependent selection recombination kernels of intermediate width can pro-  
72   mote ecological diversification and the evolution of assortative mating (Noest 1997; Doebeli  
73   et al. 2007).

74         Costs of choosiness restrict the number of mating trials per female and/or otherwise  
75   decrease the reproductive success of individuals preferring rare phenotypes. Recent findings  
76   confirm the intuitive expectation that when high costs are associated with assortative mating,  
77   this can prohibit the latter's evolution, thus reducing the range of conditions under which spe-  
78   ciation is possible (Matessi et al. 2002; Bürger and Schneider 2006; Schneider and Bürger  
79   2006; Kopp and Hermisson 2008; Otto et al. 2008). It has also been reported that when costs  
80   of choosiness are incorporated into models of adaptive speciation, waiting times until specia-  
81   tion are prolonged (Bolnick 2004).

82         The aforementioned studies considering conditions for non-allopatric speciation do  
83   not take into account spatial interactions among individuals, but instead assume that organ-  
84   isms compete and form reproductive pairs irrespective of the relative spatial location of other  
85   individuals. However, local interactions are important and inherent to most biological systems,  
86   and the spatial distribution of individuals within populations is therefore bound to influence  
87   the level of gene flow and the degree of intraspecific competition among the resident pheno-  
88   types. Local interactions between individuals are defined by spatial population structure,  
89   which broadly speaking can arise in two forms. First, spatial structuring can be induced by  
90   environmental heterogeneity. The evolutionary dynamics of populations with environmentally  
91   induced spatial structure have been investigated both in metapopulations comprising discrete  
92   spatially segregated patches (Gavrilets et al. 1998, 2000; Day 2001; Gavrilets and Vose 2005)  
93   and along continuous environmental gradients (Endler 1977; Day 2000; Doebeli and  
94   Dieckmann 2003, 2005; Mizera and Meszéna 2003; Heinz et al. 2009; Payne et al. 2011). Se-  
95   cond, if a spatial environment is homogeneous and uniform, the creation and maintenance of

96 spatial structure occurs only through self-structuring. Self-structuring emerges spontaneously  
97 as a result of intrinsic ecological dynamics (Lion and Baalen 2008), including those giving  
98 rise to reproductive pair correlations (Young et al. 2001). For populations with asexual repro-  
99 duction, it has recently been reported that the coexistence of species, as well as their emer-  
100 gence through evolutionary branching, occurs for more restrictive parameter combinations  
101 when modeled on a lattice than when modeled under well-mixed conditions (Mágori et al.  
102 2005).

103 Here we incorporate sexual reproduction into a model of adaptive speciation and in-  
104 vestigate the effect of spatial self-structuring on the waiting time until speciation. In this con-  
105 text, we also investigate the interactions of spatial self-structuring, first, with the effect of the  
106 number of loci determining the trait under disruptive selection, and second, with the conse-  
107 quences of mating costs for individuals preferring rare phenotypes.

## 108 **Methods**

### 109 **Model description**

110 **Overview.** Our individual-based model describes the genotypic and phenotypic evolu-  
111 tionary dynamics of sexual populations. The phenotypic traits of individuals are determined  
112 by several loci, which allows for a gradual evolution of resource specialization and mating  
113 behavior. The model is defined in continuous time and continuous space, with periodic  
114 boundary conditions in a uniform environment on the unit square. Algorithmically, the model  
115 is implemented according to the minimal-process method (Gillespie 1976).

116 **Individuals.** Each individual possesses two phenotypic traits, each of these being de-  
117 termined by two sets of diallelic diploid loci with equal additive effect. The first trait is an  
118 ecological character, which controls resource use and thus affects competition. The second  
119 trait is a mating preference, which regulates the degree of assortativeness when mating. Each  
120 trait is defined by the difference between the number of “+” and “-” alleles, divided by the  
121 total number of alleles, so that both traits can vary from  $-1$  to  $+1$ . The ecological trait  $u$  de-  
122 termines the type of resource or environment to which an individual is best adapted. Specifi-  
123 cally, the function  $K(u) = K_0 N_{\sigma_k}(u)$  describes how  $u$  determines an individual’s carrying-  
124 capacity density, where  $N_{\sigma}(z) = \exp(-\frac{1}{2} z^2 / \sigma^2)$  and  $K_0$  is the maximally attainable carrying-  
125 capacity density. The mating trait  $a$  determines the mating preference of individuals, based  
126 on similarity in the ecological trait. Mating preference can vary from disassortative ( $a < 0$ ) to  
127 assortative ( $a > 0$ ), with random mating occurring for  $a = 0$ . All individuals in the model are

128 characterized by the rates at which births, deaths, and dispersals occur, as well as by their spa-  
 129 tial location  $(x, y)$ , with  $0 \leq x, y \leq 1$ .

130 **Events.** All individuals  $i$  are assigned birth rates  $b_i$ , death rates  $d_i$ , and dispersal  
 131 rates  $m_i$ , for  $i = 1, \dots, N$ , where  $N$  is the current population size. These rates are updated after  
 132 each event. The time that elapses until the next event is based on the total rates  $B = \sum_{i=1}^N b_i$ ,  
 133  $D = \sum_{i=1}^N d_i$ ,  $M = \sum_{i=1}^N m_i$ , and  $E = B + D + M$ , being drawn from an exponential probability  
 134 density with mean  $1/E$ . The affected individual  $i$  for the next event (birth, death, or dispersal)  
 135 of the process is then chosen with probability  $(b_i + d_i + m_i)/E = e_i/E$ . The type of event is cho-  
 136 sen according to probabilities  $b_i/e_i$ ,  $d_i/e_i$ , and  $m_i/e_i$ , respectively. Accordingly, the affect-  
 137 ed individual will reproduce by giving birth to one offspring, will die, or will perform a dis-  
 138 persal step. Unless stated otherwise, the parameter values we use for model runs are shown in  
 139 Table 1.

140 **Reproduction.** The mating probability between individuals  $i$  and  $j$  is given by the  
 141 product of a phenotypic weight  $p_{ij}$  and a spatial weight  $q_{ij}$  (Doebeli and Dieckmann 2003).  
 142 For  $a < 0$ , the phenotypic weight is defined as  $p_{ij} = 1 - N_{\sigma_-}(\Delta u_{ij})$ , where  $\sigma_- = a^2$ , and  $\Delta u_{ij}$  is  
 143 the phenotypic difference between the potential mates  $i$  and  $j$ . For  $a > 0$ ,  $p_{ij} = N_{\sigma_+}(\Delta u_{ij})$ ,  
 144 where  $\sigma_+ = 1/(20a^2)$ . For  $a = 0$ ,  $p_{ij} = 1$ . The spatial weight  $q_{ij}$  decreases with the spatial  
 145 distance  $r_{ij} = \sqrt{\Delta x_{ij}^2 + \Delta y_{ij}^2}$  between potential mates  $i$  and  $j$  according to  
 146  $q_{ij} = N_{\sigma_p}(r_{ij})/(2\pi\sigma_p^2)$ . The offspring inherits alleles from both of its parents at each locus in-  
 147 dependently, implying free recombination. Random mutations that switch alleles from “+” to  
 148 “-”, and vice versa, occur with a small probability  $\mu$ . A cost for individuals preferring to ma-  
 149 te with locally rare phenotypes arises from a birth rate defined as  $b_i = bN_{p,i}/(c + N_{p,i})$ , where  
 150  $N_{p,i} = \sum_{j=1, j \neq i}^N p_{ij}q_{ij}$  is the number of suitable mating partners in the neighborhood of individu-  
 151 al  $i$ , and  $c$  is the strength of the cost.

152 **Death.** An individual’s death rate depends both on local logistic competition and its  
 153 carrying-capacity density. Specifically, the death rate of individual  $i$  with ecological trait  $u_i$   
 154 at location  $(x_i, y_i)$  is defined as  $d_i = [2\pi\sigma_s^2 K(u_i)]^{-1} \sum_{j=1, j \neq i}^N N_{\sigma_c}(\Delta u_{ij})N_{\sigma_s}(\Delta x_{ij})N_{\sigma_s}(\Delta y_{ij})$ , where  
 155 the competition function’s standard deviations are denoted by  $\sigma_c$  for phenotypic differences  
 156 and by  $\sigma_s$  for spatial distances.

157 **Dispersal.** There are two types of dispersal events. First, each newborn individual un-  
 158 dergoes natal dispersal from the location of its mother, i.e., of the parent that has chosen its  
 159 mate. Second, the subsequent dispersal of all individuals occurs at a constant rate  $m_i = m$ . In  
 160 either case, individuals are changing their locations by random displacements in the directions  
 161  $x$  and  $y$ , each drawn from a normal distribution with mean 0 and standard deviation  $\sigma_m$ .



## 162 Identification of speciation

163 To identify speciation, we apply the following criterion. We count the number of individuals  
164 for each of the phenotypic classes of the ecological trait (the number of these classes equals  
165 twice the number of loci determining the ecological trait plus 1). In the resulting histogram,  
166 we identify the two most prevalent phenotypic classes, denoting the corresponding number of  
167 individuals by  $h_1$  and  $h_2$ , while denoting the total number of individuals in all intermediate  
168 phenotypic classes by  $h_{\min}$ . We recognize speciation, if three conditions are met simultaneous-  
169 ly: (i) the two peaks are sufficiently separated, i.e., the phenotypes  $u_1$  and  $u_2$  that correspond  
170 to  $h_1$  and  $h_2$  differ by at least 0.5,  $|u_1 - u_2| \geq 0.5$ ; (ii) hybrids in between the two peaks are suf-  
171 ficiently rare, i.e., the total number  $h_{\min}$  of intermediate individuals is less than 5% of the av-  
172 erage of  $h_1$  and  $h_2$ ,  $h_{\min} < 0.05 (h_1 + h_2) / 2$ ; and (iii) the heights of the two peaks are suffi-  
173 ciently similar, i.e.,  $h_1$  and  $h_2$  differ by a factor of less than 2,  $0.5 < h_1 / h_2 < 2$ . Extensive  
174 numerical explorations confirm that this criterion ensures the stability of the phenotypic clus-  
175 ters resulting from speciation, across the full parameter range we investigate: if speciation is  
176 recognized, we never observe the subsequent collapse of those phenotypic clusters. We refer  
177 to the time at which this criterion is first met as the waiting time  $T$  until speciation. To ex-  
178 plore stochastic variation in this waiting time, we employ replicate model runs (using differ-  
179 ent random seeds). We perform these model runs across the parameter range that has previ-  
180 ously been identified as allowing for speciation (Dieckmann and Doebeli 1999, 2004). To en-  
181 sure that all model runs have enough time to result in speciation, we continued them until a  
182 sufficiently long maximal duration (5000 generations).

## 183 Identification of the average size of spatial clusters

184 In our model, spatial self-structuring implies the emergence of spatial clusters that are dynam-  
185 ic and have self-organized shapes and sizes. To measure the average size of these spatial clus-  
186 ters for different degrees of spatial self-structuring, we calculate the pairwise distances  $r$  be-  
187 tween all individuals of the population. For well-mixed populations in two-dimensional envi-  
188 ronments, the expected number  $C(r)$  of pairs of individuals with distances between  $r$  and  
189  $r + dr$  for small  $dr$  increases linearly with  $r$ , so we construct correlation histograms as  
190  $c(r) = C(r)/r$ . In well-mixed populations, there are no spatial aggregations of individuals, so  
191 the corresponding function  $c_m(r)$  is flat. Conversely, self-structuring results in the emergence  
192 of spatial clusters, so the function  $c_s(r)$  shows a peak at small values of  $r$ . With increasing  $r$ ,  
193  $c_s(r)$  decreases at a speed proportional to the level of self-structuring, first dropping below  
194 and then eventually converging to  $c_m(r)$ . The drop below  $c_m(r)$  corresponds to the empty  
195 areas around the spatial clusters. Thus, we identify the average cluster size as the distance at

196 which the function  $c_s(r)$  describing a self-structured population intersects with the function  
197  $c_m(r)$  for the corresponding well-mixed population (for the latter, we set  $\sigma_m = 0.2$ ). Since the  
198 mating radius  $\sigma_p$  also influences the size of spatial clusters, we consider 15 different values  
199 of  $\sigma_p$  for each of the 15 analyzed values of  $\sigma_m$  (Figure 2;  $0.01 \leq \sigma_m \leq 0.08$  and  
200  $0.01 \leq \sigma_p \leq 0.1775$ ). For each of these 225 combinations of  $\sigma_m$  and  $\sigma_p$ , we analyze 5,000  
201 snapshots of spatial structure. The average cluster size for each  $\sigma_m$  is averaged over the con-  
202 sidered 15 values of  $\sigma_p$ .

## 203 Results

### 204 Adaptive speciation is faster in self-structured than in well-mixed sexual 205 populations

206 Figure 1 shows typical results for the joint evolution of resource utilization and mating prefer-  
207 ence in spatially well-mixed populations and spatially self-structured populations, accompa-  
208 nied by snapshots of the corresponding initial and resulting spatial patterns. Initially, individ-  
209 uals are either randomly distributed in space (Figure 1a) or aggregated in spatial clusters (Fig-  
210 ure 1d). The evolution of resource utilization starts from monomorphic populations located at  
211 the resource optimum (Figures 1b and 1e, top panels). The mating preference first gradually  
212 changes from random to slightly assortative (Figures 1b and 1e, bottom panels); this reduces  
213 gene flow and allows for diversification of the ecological trait, with two phenotypic clusters  
214 emerging (Figures 1b and 1e, top panels). The degree of assortative mating eventually be-  
215 comes stronger, and this allows reproductive isolation to be established between those two  
216 phenotypic clusters.

217 In self-structured populations, assortatively mating individuals limit their partner  
218 search to spatial clusters, thus decreasing the probability of recombination between phenotyp-  
219 ic morphs occupying different clusters. As some phenotypes that prevail transiently become  
220 extinct only after more extreme phenotypes get locally established, the reduced supply of re-  
221 combinants means that the distribution of phenotypes across phenotypic clusters remains pol-  
222 ymorphic for longer periods.

223 After adaptive speciation, more individuals mate assortatively in self-structured popu-  
224 lations (Figure 1e, bottom panel) than in well-mixed populations (Figure 1b, bottom panel).  
225 Individuals of the two newly formed species are distributed across the whole habitat either  
226 randomly (Figure 1c) or in spatial clusters (Figure 1f). The resulting mosaic of spatial clusters  
227 is endogenously generated by intrinsic ecological dynamics, even though the considered habi-

228 tat is continuous and completely homogeneous. Spatial clusters dynamically arise as self-  
229 organized entities with characteristic average diameters (see below). The number of individu-  
230 als inside a cluster depends on the balance between the local birth and death processes  
231 (source-sink dynamics). The distance between clusters is defined by the spatial competition  
232 radius, and also arises endogenously.

233 It is noteworthy that inside the spatial clusters of self-structured populations,  
234 assortatively mating individuals are likely to encounter appropriate mating partners; this pro-  
235 vides conditions for assortative mating “for free,” which may in turn be responsible for the  
236 greater fraction of individuals mating assortatively, and thus for the earlier speciation in these  
237 populations. The next subsection confirms this interpretation.

### 238 **Optimal ratio of mating radius and dispersal radius promotes early speciation**

239 To understand in greater detail how spatial self-structuring provides conditions for assortative  
240 mating “for free,” and thus accelerates speciation, we compare waiting times until speciation  
241 for many different combinations of dispersal radius and mating radius. The degree of spatial  
242 self-structuring in sexually reproducing populations is determined by both of these parameters.  
243 While the dispersal radius directly affects the spatial population structure, the influence of the  
244 mating radius is indirect, by defining the spatial area across which mate search occurs: if this  
245 area is large, spatial population structure, even if present, has no impact on the availability of  
246 phenotypes that can be chosen as mates.

247 Figure 2 shows the dependence of the average waiting time until speciation on the dis-  
248 persal radius and the mating radius. Light and dark areas correspond to short and long waiting  
249 times until speciation, respectively. In populations with the highest considered level of self-  
250 structuring ( $\sigma_m = 0.01$ ), an increase in mating radius delays speciation. For intermediate levels  
251 of self-structuring ( $0.02 \leq \sigma_m \leq 0.05$ ), a very small or very large mating radius delays specia-  
252 tion. A further increase in dispersal radius (beyond  $\sigma_m = 0.05$ ) makes the spatial clusters in-  
253 distinguishable, so the waiting time until speciation is no longer affected.

254 The thick curve in Figure 2 shows the average size of spatial clusters for different dis-  
255 persal radii. Comparing the mating radii enabling the earliest speciation with these sizes of  
256 spatial clusters reveals that speciation times are shortest when the mating radius corresponds  
257 to one-fourth to one-third of the cluster size, as indicated by the two dashed curves in Figure 2.

### 258 **Spatial self-structuring weakens the effect of a large number of loci**

259 Figure 3 shows that increasing the number of loci determining the ecological trait delays spe-  
260 ciation. As we explain below, this delay is caused by the diminished level of strict assortative

261 mating when a large number of loci results in a higher resolution of the phenotypes that can  
262 be expressed for the ecological trait.

263 For a small number of loci, assortative mate choice easily becomes virtually restricted  
264 to partners with identical phenotypes (Figure 3b, panel for 5 loci), whereas for a large number  
265 of loci, the same degree of assortativity (as measured by the mating trait  $a$ ) leads to mating  
266 individuals accepting mates from a larger number of phenotypic classes (Figure 3b, panels for  
267 10 and 15 loci). This occurs because mating probabilities are a function of the absolute pheno-  
268 typic difference between potential partners. Therefore, if a large number of loci determine the  
269 ecological trait, the relative proportion of strictly assortative mating is smaller. This decreases  
270 the probability of alleles increasing assortativity spreading in the populations, and thereby de-  
271 lays speciation.

272 Importantly, we not only find that in self-structured populations the waiting time until  
273 speciation is shorter (Figures 1 and 2), but also that this effect of spatial self-structuring be-  
274 comes more noticeable with an increase in the number of loci determining the ecological trait.  
275 This suggests that in such populations the aforementioned effect of assortative mating “for  
276 free” is increasingly important for promoting the establishment of assortative mate choice and  
277 for accelerating speciation, by providing an alternative mechanism for enhancing the relative  
278 proportion of strictly assortative mating. This explains why for a small number of loci the ef-  
279 fect of spatial self-structuring is negligible, because strictly assortative mating is facilitated by  
280 the resultant low phenotypic resolution, so that speciation in this case occurs very fast.

### 281 **Spatial self-structuring renders mating costs less severe for rare phenotypes**

282 The influence of the mating cost on the average waiting time until speciation is shown in Fig-  
283 ure 4a. We find that in well-mixed populations ( $\sigma_m = 0.07$ ) an increase in the mating cost for  
284 individuals preferring rare phenotypes delays speciation. By contrast, in highly self-structured  
285 populations ( $\sigma_m = 0.01$ ), as well as in populations with an intermediate level of spatial self-  
286 structuring ( $\sigma_m = 0.035$ ), even a strong mating cost does not cause a significant delay in the  
287 average waiting time until speciation.

288 To find a mechanistic explanation for this observation, we track the evolution of a  
289 population’s average level of assortative mating. The mean values of mating traits among in-  
290 dividuals of populations for different degrees of spatial self-structuring and for different  
291 strengths of mating costs, are shown in the small panels of Figure 4b. Both for highly struc-  
292 tured populations ( $\sigma_m = 0.01$ ) and for intermediately structured populations ( $\sigma_m = 0.035$ ), the  
293 evolution of mate choice proceeds in a similar way, with the average mating trait gradually  
294 evolving toward assortative mating. By contrast, in well-mixed populations ( $\sigma_m = 0.07$ ), the

295 average level of assortative mating keeps fluctuating around random mating when the mating  
296 cost is strong ( $c = 10$ ). From these observations, we can thus conclude that the mating cost  
297 affects the waiting time until speciation by inhibiting the evolution of assortative mating and  
298 that this effect can be overcome by the spatial self-structuring of populations.

## 299 **Discussion**

300 In this study, we have investigated how the waiting time until adaptive speciation in a popula-  
301 tion with sexual reproduction is influenced by spatial self-structuring. We find that self-  
302 structuring generally facilitates the evolution of assortative mating and thus promotes earlier  
303 speciation. The main feature of a self-structured population is that individuals inside a spatial  
304 cluster tend to possess very similar phenotypes. This feature influences the evolutionary dy-  
305 namics in several ways. First, it allows for assortative mating “for free,” since individuals typ-  
306 ically find phenotypically similar mates inside their spatial clusters (Figure 2), jump-starting  
307 the evolution of assortative mating required for speciation. Second, it allows individuals pre-  
308 ferring rare phenotypes to find mating partners from the same phenotypic class, implying  
309 strict assortative mating, even when a large number of loci determine the ecological trait (Fig-  
310 ure 3). Third, spatial self-structuring enables fast speciation even when individuals preferring  
311 rare phenotypes experience additional fitness costs (Figure 4).

### 312 **Why an optimal ratio of mating radius and dispersal radius accelerates speciation**

313 We find that waiting times until speciation are shortest when there is a match between the  
314 mating radius and the (natal) dispersal radius of individuals (Figure 2). Our comparison of the  
315 mating radius with the average size of spatial clusters suggests that speciation is fastest when  
316 the spatial mating radius is 3-4 times smaller than the average size of spatial clusters. This ra-  
317 tio guarantees that even individuals preferring rare phenotypes find appropriate mates, and  
318 thus promotes the evolution of assortative mating. When the mating radius is very small ( $\sigma_p = 0.01$ ),  
319 early speciation is only possible in highly self-structured populations.

320 Our results extend previous findings by Kawata (2002), who studied a spatially explic-  
321 it model of sympatric speciation and found that the probability of speciation decreases with an  
322 increase in both mating area and dispersal radius. That study conjectured that an increase in  
323 both of these factors increases the dispersal of genes, which promotes recombination and thus  
324 homogenizes a population’s genetic structure. As a result, it can destroy any association be-  
325 tween alleles for ecological adaptation and alleles for assortative mating that might be created  
326 by natural selection (Felsenstein 1981). Our results suggest a different interpretation. While

327 Kawata (2002) investigated the influence of dispersal radius and of the size of the mating area  
328 independently from each other, here we have explored the joint effect of these factors on the  
329 evolutionary dynamics underlying speciation. We find that the interaction between these two  
330 factors is more complex, with our results suggesting that speciation is fastest for a certain ra-  
331 tio between the mating radius and dispersal radius.

### 332 **Why spatial self-structuring weakens the effect of a large number of loci**

333 Our results show that when the ecological trait is controlled by a large number of loci, the  
334 waiting time until speciation is longer (Figure 3). The mechanism underlying this effect can  
335 be described as follows: a large number of loci results in more phenotypic classes, and as mat-  
336 ing individuals accept a higher proportion of partners from different phenotypic classes, this  
337 hinders the establishment of assortative mating and delays speciation. Our results confirm and  
338 extend findings from previous studies in which a delay in speciation was observed resulting  
339 from of a large number of loci determining the ecological trait (Dieckmann and Doebeli 1999,  
340 2004; Bolnick 2004). Earlier, it was shown that (not surprisingly) increasing the phenotypic  
341 width of the mating function prolongs the waiting time until speciation (Bolnick 2004). We  
342 find that the this effect is weaker in self-structured populations, because appropriate mates are  
343 likely to be available in a mating individual's local neighborhood, which allows those mating  
344 individuals to find a large proportion of mates with identical phenotypes.

345 It has been reported that the likelihood of speciation depends in a “non-straightforward  
346 way” on the number of loci determining the ecological trait (Bürger et al. 2006). Specifically,  
347 Bürger and coauthors found that if disruptive selection is weak, the likelihood of speciation  
348 decreases with an increased number of loci. They suggest that, under these conditions, split-  
349 ting the phenotypic distribution of ecological traits requires the emerging phenotypic clusters  
350 in that trait to be located near the boundary of the corresponding phenotypic range, which  
351 could be easier to achieve for a smaller number of loci. This is because, under these condi-  
352 tions, the average phenotypic distance between all resident phenotypes is larger, so the aver-  
353 age mating probabilities across phenotypic classes are lower. For stronger disruptive selec-  
354 tion, speciation is possible only with strong assortative mating, and speciation occurs more  
355 readily with more loci, since the self-organized fine-tuning of the evolutionary dynamics  
356 helps to keep phenotypic clusters at the optimal distance for coexistence. In our model, in-  
357 creasing the number of loci invariably results in delayed speciation. This is because we mostly  
358 consider relatively weak disruptive selection, which results in phenotypic clusters always be-  
359 ing located at the boundary of the phenotypic range. When disruptive selection is strong, we  
360 also observe the emergence of more than two phenotypic clusters when ecological traits are

361 determined by more than 15 loci. In such cases, evolutionary dynamics are more complex  
362 than those underlying the emergence of two species, and will benefit from additional investi-  
363 gation.

### 364 **Why spatial self-structuring reduces mating costs for rare phenotypes**

365 Our results confirm that high mating costs increase the waiting time until speciation in well-  
366 mixed populations (Figure 4a), as mating individuals preferring rare phenotypes are less likely  
367 to find appropriate mates. In well-mixed populations, potential mates for individuals with rare  
368 phenotypes will usually be located at a significant spatial distance from those individuals  
369 seeking a partner, so the mating cost reduces their chance to reproduce. This delays the evolu-  
370 tion of assortative mating, which causes a longer waiting time until speciation (Figure 3b).  
371 Conversely, in self-structured populations, individuals possessing similar phenotypes form  
372 spatial clusters: as mating individuals are then more likely to find appropriate mates in their  
373 local neighborhood, the effect of mating cost is largely cancelled out.

374 Here we have modeled mating costs phenomenologically for individuals preferring  
375 (locally) rare phenotypes, similar to Doebeli and Dieckmann (2003) and Gurbieri (2004).  
376 Other studies have examined models of sympatric speciation in which costs for choosy indi-  
377 viduals are modeled more mechanistically, resulting from a restriction of their number of mat-  
378 ing trials (Drossel and McKane 2000; Doebeli and Dieckmann 2005; Bürger and Schneider  
379 2006; Bürger et al. 2006; Schneider and Bürger 2006; Kopp and Hermisson 2008). We expect  
380 the effect of spatial self-structuring on speciation readily to extend to those later models.

### 381 **Comparison with other speciation modes**

382 Throughout this study, we have referred to the examined diversification dynamics as adaptive  
383 speciation. This is because, in our model, the speciation process can be understood as an  
384 adaptive response that allows a population trapped at a fitness minimum through the action of  
385 frequency-dependent disruptive selection to escape from this trap (Dieckmann et al. 2004).

386 To further contextualize our findings, it might be worthwhile highlighting that the spe-  
387 ciation processes analyzed here also meet the specifications of competitive speciation (which  
388 occurs when “intermediate forms [are] fit if and only if some extreme forms are rare or ab-  
389 sent”; Rosenzweig 1978) and of ecological speciation (defined as the “evolution of reproduc-  
390 tive isolation between populations as a result of ecologically-based divergent natural selec-  
391 tion”; Schluter 2000; Schluter & Conte 2009).

392 In contrast to the aforementioned three process-based speciation modes of adaptive,  
393 competitive, and ecological speciation, traditional discussions of alternative speciation routes  
394 have instead focused on geographical patterns at the onset of species formation (e.g., Mayr

395 1942, 1963; Dobzhansky 1951). While the well-mixed populations we have analyzed here, by  
396 considering large radii for dispersal and mating, are essentially sympatric, smaller such radii  
397 result in ecological settings traditionally explored in the context of parapatric speciation sce-  
398 narios, with the role of isolation by distance (Wright 1943) increasing as those radii become  
399 smaller relative to the average distance between neighboring individuals and to the spatial  
400 scale of the considered habitat.

401 Last but not least, the speciation dynamics we have examined here are related to the  
402 notions of micro-allopatric speciation (Smith 1955, 1965) and mosaic sympatry (Mallet 2008;  
403 Mallet et al. 2009). Both terms are used to refer to spatial patterns in which species can be  
404 viewed as coexisting sympatrically when assessed at larger spatial scales, yet are recognized  
405 as being spatially segregated when assessed at smaller spatial scales. This description fully  
406 matches the spatial patterns resulting from self-structuring in our model, which could be taken  
407 to suggest that both terms apply to our study. It must be borne in mind, however, that micro-  
408 allopatry and mosaic sympatry are meant to arise from a heterogeneous external environment  
409 to which the coexisting species differentially latch on through habitat choice or habitat-  
410 dependent reproductive success, whereas the small-scale spatial segregation between the co-  
411 existing species observed in our model arises in a homogeneous external environment through  
412 limited dispersal and phenotype-dependent local competition. Consequently, the spatial pat-  
413 terns emerging in our model should not be misunderstood as examples of either micro-  
414 allopatry or mosaic sympatry.

### 415 **Comparison with related studies and extensions**

416 While our results show that spatial self-structuring accelerates speciation in sexual popula-  
417 tions, in populations with asexual reproduction the opposite effect has been found. Specifical-  
418 ly, a study by Day (2001) reported that limited dispersal in deme-structured metapopulations  
419 inhibits disruptive selection, because mutants rarely gain a fitness benefit when being sur-  
420 rounded by very similar phenotypes. Mágori et al. (2005) investigated the coexistence of spe-  
421 cies, and their emergence through evolutionary branching, on a lattice and found that both of  
422 these occur only for more restrictive parameter combinations than in well-mixed populations.  
423 Also this latter result was explained by the reduced fitness advantage of rare mutant pheno-  
424 types.

425 To analyze the effects of spatial self-structuring on evolutionary branching in asexual  
426 populations, we can readily eliminate sexual reproduction and assortative mate choice from  
427 our model. Our corresponding investigations confirm the aforementioned previous findings  
428 by Day (2001) and Mágori et al. (2005), as well as the mechanism conjectured by those stud-



429 ies to underlie the observed delay of adaptive speciation. Going beyond those previous stud-  
430 ies, we find that an additional mechanism contributes to the observed delay: in self-structured  
431 asexual populations, common phenotypes, being situated at the fitness minimum causing dis-  
432 ruptive selection, escape extinction for longer durations than in well-mixed populations, due  
433 to their local coexistence with different phenotypes in spatial clusters (Fazalova and  
434 Dieckmann, submitted).

435 In sexual populations, by contrast, the two aforementioned delaying effects of spatial  
436 self-structuring arising from natural selection are being overshadowed by the consequences of  
437 sexual selection: assortatively mating rare phenotypes gain an extra fitness benefit from co-  
438 occurring with similar phenotypes, while assortatively mating common phenotypes incur an  
439 extra fitness cost from co-occurring with other phenotypes.

440 In our study, spatial self-structuring arises from limited offspring dispersal. The result-  
441 ant spatio-phenotypic correlations facilitate the evolution of assortative mating, in turn pro-  
442 moting faster adaptive speciation. Analogous conditions favoring assortative mating may in-  
443 stead be generated through, or further enhanced by, other mechanisms, such as dispersal with  
444 philopatry, dispersal with natal homing, conditional dispersal triggered by phenotype-based  
445 quorum sensing, and/or dispersal concluding with habitat choice. All of these alternative or  
446 additional mechanisms – being widespread among animal species and occurring even for mi-  
447 croorganisms – result in the kind of spatio-phenotypic correlations emerging in our model an-  
448 alyzed here, and can thus be expected likewise to facilitate and accelerate adaptive speciation.

449 It also needs to be highlighted that spatial self-structuring, by increasing the mating  
450 frequency among relatives, can sometimes result in inbreeding depression. Hence, an interest-  
451 ing extension of our model would be to examine possible costs and benefits of inbreeding,  
452 and to ascertain their impacts on the waiting times until adaptive speciation.

453 While we have focused our analyses here on competition for a unimodal resource, we  
454 expect spatial self-structuring to promote adaptive speciation also in scenarios with bimodal  
455 or multimodal resource distributions (e.g., Doebeli 1996; Thibert-Plante and Hendry 2011).  
456 For non-unimodal resource distributions, the inhibiting effect of stabilizing selection on adap-  
457 tive diversification might be even weaker, and the resource distribution's intrinsic minima  
458 may further facilitate the evolution of assortative mating. In future studies, it would therefore  
459 be interesting to analyze interactions between the effects of non-unimodal resource distribu-  
460 tions and spatial self-structuring in models of adaptive speciation.

## 461 Conclusions

462 The role of spatial self-structuring for adaptive speciation is complex. On the one hand, it de-  
463 lays adaptive speciation in populations with asexual reproduction (Fazalova and Dieckmann,  
464 submitted). On the other hand, as demonstrated in this study, self-structuring facilitates and  
465 accelerates speciation in sexually reproducing populations: this occurs by allowing for  
466 assortative mating “for free,” by reducing the effect of a large number of loci on the probabilit-  
467 y of strict assortative mating, and by cancelling out costs for assortative mating. Our results  
468 suggest that no very high level of spatial self-structuring is necessary for fast speciation; in-  
469 termediate levels can suffice, and are sometimes even optimal for accelerating speciation in  
470 sexual populations.

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## 480 Figure captions

481 **Figure 1.** Comparison of initial spatial structure, evolutionary dynamics of ecological trait  
482 and mating trait, and resulting spatial structure in spatially well-mixed ( $\sigma_m = 0.08$ ; a,b,c) and  
483 spatially self-structured ( $\sigma_m = 0.01$ ; d,e,f) populations. In the snapshots of spatial structures,  
484 taken at times  $t = 50$  and  $t = 500$ , the horizontal and vertical axes measure the spatial position  
485 of individuals, while the color scale indicates the ecological trait  $u$ . In the panels showing  
486 evolutionary dynamics, the color scale indicates the number of individuals within the shown  
487 phenotypic classes.

488 **Figure 2.** Dependence of the average waiting time until speciation on the dispersal radius  $\sigma_m$   
489 and on the mating radius  $\sigma_p$ . Each cell shows an average over 100 replicate model runs. The  
490 thin gray contour lines are inferred from a polynomial approximation of the data. The thick  
491 black curve describes how the average size of spatial clusters varies with the dispersal radius

492  $\sigma_m$ . Dashed black curves correspond to one-third and one-fourth of this average cluster size.  
 493 The bottom row shows snapshots of spatial structures, for  $\sigma_p = 0.1$  and values of  $\sigma_m$  shown  
 494 along the main panel's horizontal axis.

495 **Figure 3.** (a) Dependence of the waiting time until speciation on the level of spatial self-  
 496 structuring for different numbers of loci determining the ecological trait. The shaded areas  
 497 extend between the 40% and 60% percentiles of the distribution of waiting times until specia-  
 498 tion for 100 replicate model runs, while the continuous curves show the corresponding medi-  
 499 ans. (b) Corresponding frequencies of mates, according to the difference between the pheno-  
 500 typic classes of mating partners. Other parameters:  $\sigma_p = 0.2$  and  $K_0 = 800$ .

501 **Figure 4.** (a) Dependence of the waiting time until speciation on the mating cost  $c$  for well-  
 502 mixed ( $\sigma_m = 0.07$ ), intermediately self-structured ( $\sigma_m = 0.035$ ), and highly self-structured  
 503 ( $\sigma_m = 0.01$ ) populations. The shaded areas extend between the 40% and 60% percentiles of the  
 504 distribution of waiting times until speciation for 100 replicate model runs, while the continu-  
 505 ous curves show the corresponding medians. (b) Corresponding evolution of the average mat-  
 506 ing trait  $a$ ; time series end when reaching the average waiting time until speciation. Other  
 507 parameters:  $l_e = 5$ .

## 508 Table

509 **Table 1.** Overview of model parameters.

Parameter	Description	Default value
$b$	Birth rate	1.0
$m$	Dispersal rate after birth	0.0
$\sigma_c$	Phenotypic competition width (= phenotypic standard deviation of competition function)	1.0
$\sigma_s$	Spatial competition radius (= spatial standard deviation of competition function)	0.2
$\sigma_k$	Phenotypic resource width (= phenotypic standard deviation of resource distribution)	2.0
$\sigma_m$	Dispersal radius (= spatial standard deviation of probability density for dispersal distance)	0.01
$\sigma_p$	Mating radius (= spatial standard deviation of probability density for mate choice)	0.1
$K_0$	Maximal carrying-capacity density	500

$\mu$	Mutation probability	0.002
$c$	Mating cost	0
$l_e$	Number of loci determining ecological trait	15
$l_m$	Number of loci determining mating trait	5

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Figure 1

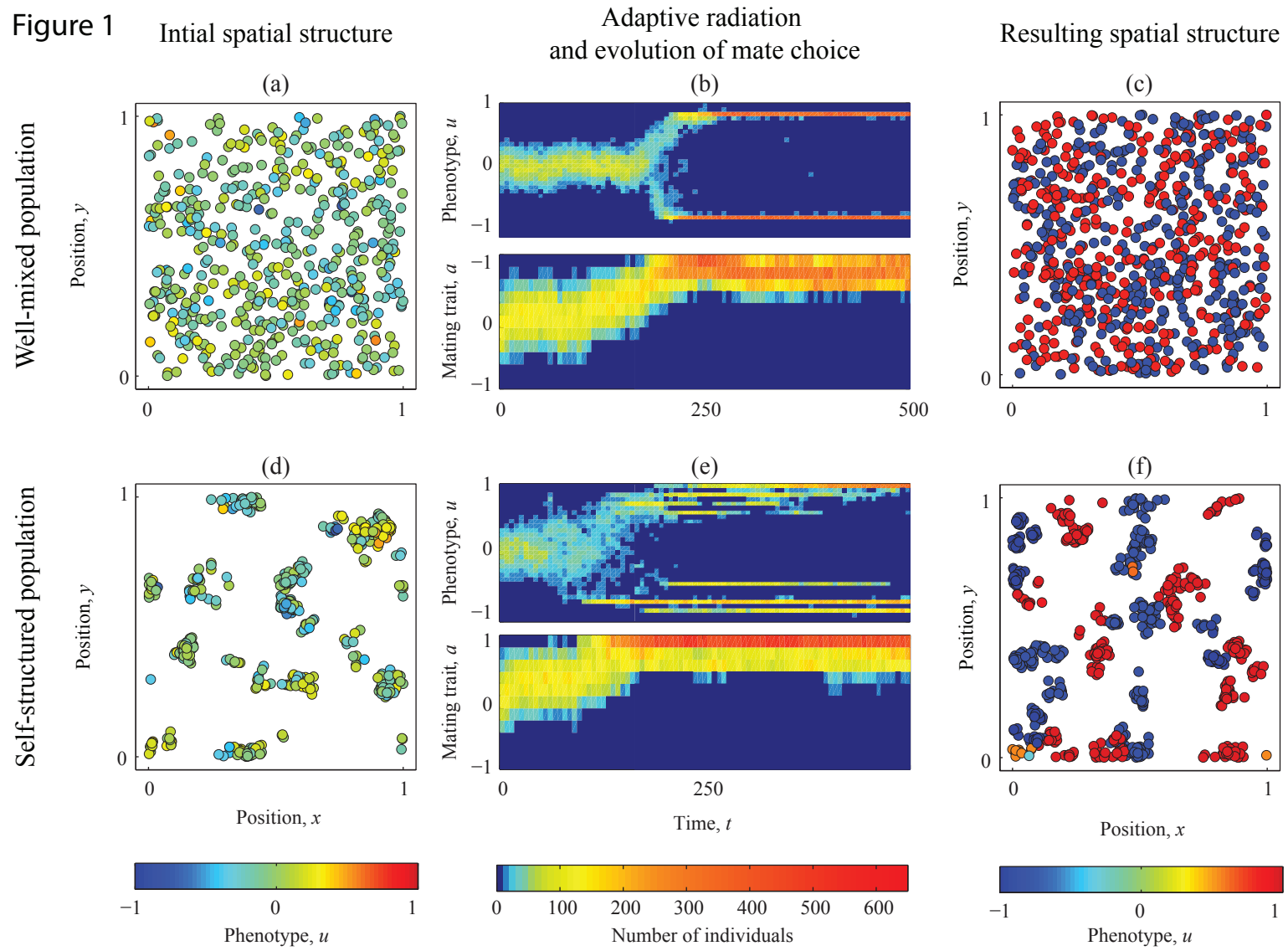




Figure 2

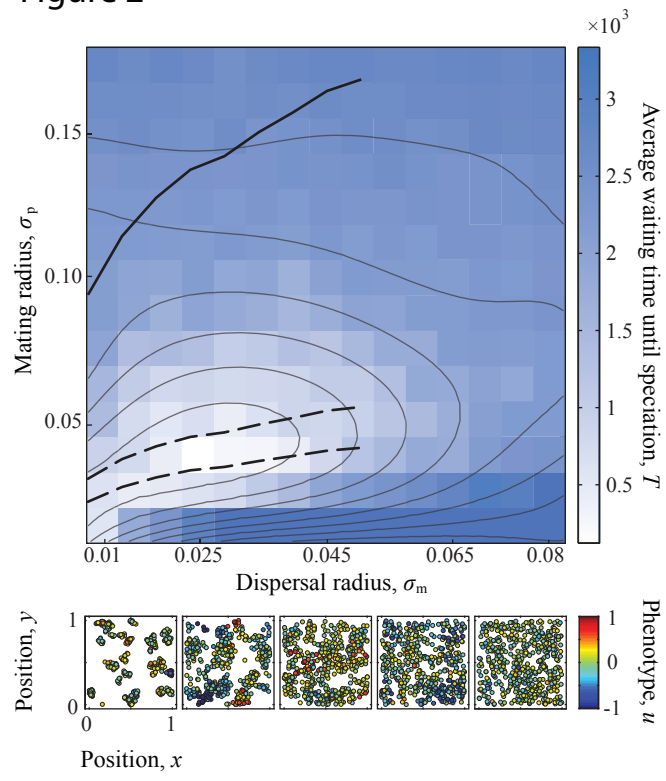


Figure 3

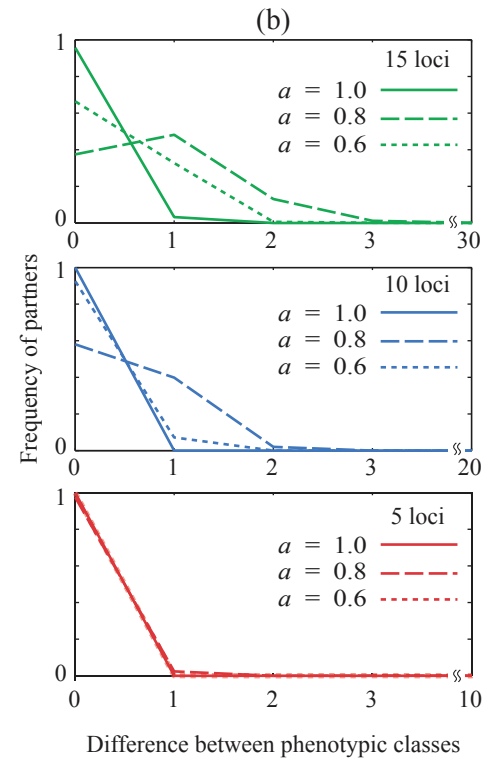
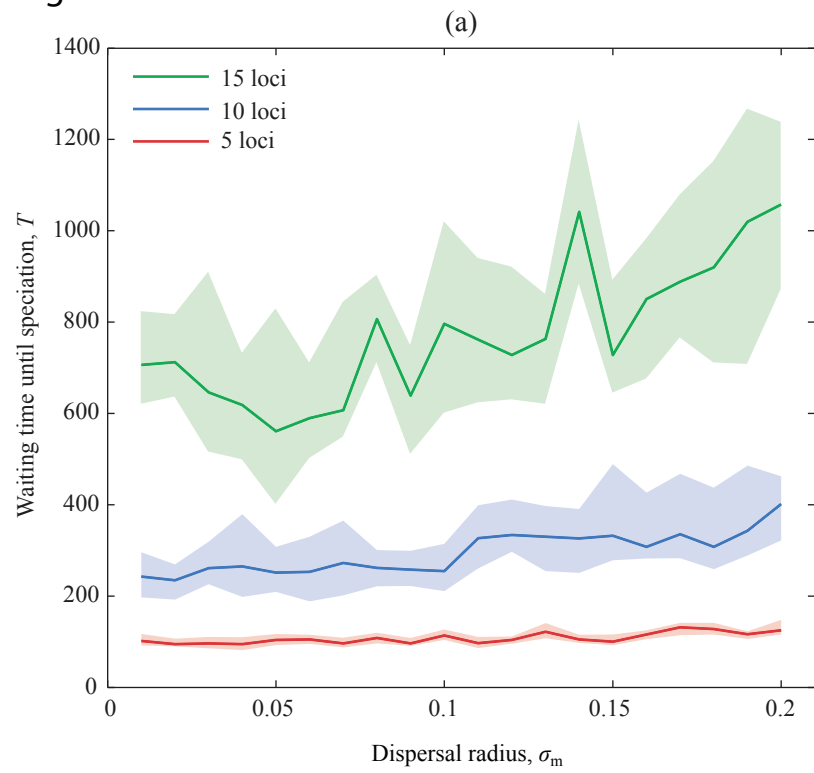


Figure 4

