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## Interim Report

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### **Speciation and the evolution of dispersal along environmental gradients**

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1                   **Speciation and the evolution of dispersal**  
2                   **along environmental gradients**

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9                   **Abstract**

10                  We analyze the joint evolution of an ecological character and of dispersal distance in asexual  
11                  and sexual populations inhabiting an environmental gradient. Several interesting  
12                  phenomena resulting from the evolutionary interplay of these characters are revealed. First,  
13                  asexual and sexual populations exhibit two analogous evolutionary regimes, in which either  
14                  speciation in the ecological character occurs in conjunction with evolution of short-range  
15                  dispersal, or dispersal distance remains high and speciation does not occur. Second, transi-  
16                  tions between these two regimes qualitatively differ between asexual and sexual  
17                  populations, with the former showing speciation with long-range dispersal and the latter  
18                  showing no speciation with short-range dispersal. Third, a phenotypic gradient following  
19                  the environmental gradient occurs only in the last case, i.e., for non-speciating sexual popu-  
20                  lations evolving towards short-range dispersal. Fourth, the transition between the  
21                  evolutionary regimes of long-range dispersal with no speciation and short-range dispersal  
22                  with speciation is typically abrupt, mediated by a positive feedback between incipient  
23                  speciation and the evolution of short-range dispersal. Fifth, even though the model of sex-  
24                  ual evolution analyzed here does not permit assortative mating preferences, speciation  
25                  occurs for a surprisingly wide range of conditions. This illustrates that dispersal evolution  
26                  is a powerful alternative to preference evolution in enabling spatially distributed sexual  
27                  populations to respond to frequency-dependent disruptive selection.

28                  **Introduction**

29                  The study of speciation is an active area of research in evolutionary biology and is stimulat-  
30                  ing wide-ranging discussions (see Turelli et al. 2001 for a review). Mounting empirical

evidence suggests that sympatric speciation can occur in nature (e.g., Schliewen et al. 1994; Bush and Smith 1998; Filchack et al. 2000; Wilson et al. 2000; Schliewen et al. 2001). This has spawned corresponding theoretical research striving to identify key mechanisms that may promote such speciation (e.g., Maynard Smith 1966; Turner and Burrows 1995; Kawecki 1997; Kondrashov and Kondrashov 1999; Higashi et al. 1999; Dieckmann and Doebeli 1999; Drossel and Kane 2000; Doebeli and Dieckmann 2003; see also the review by Via 2001). In particular, resource competition leading to frequency-dependent disruptive selection has received wide recognition as a potential ecological driver of sympatric speciation (MacArthur and Levins 1967; Rosenzweig 1978; Christiansen and Loeschke 1980; Slatkin 1980; Seger 1985; Taper and Case 1985; Maynard Smith and Brown 1986; Abrams et al. 1993; Vincent et al. 1993; Doebeli 1996a, 1996b; Metz et al. 1996; Law et al. 1997; Meszéna et al. 1997; Geritz et al. 1998; Dieckmann and Doebeli 1999; Geritz et al. 1999; Jansen and Mulder 1999; Kisdi 1999; Kondrashov and Kondrashov 1999; Day 2000; Doebeli and Dieckmann 2000; Drossel and McKane 2000; Kisdi 2001; Kisdi and Geritz 2001; Kisdi et al. 2001; Schreiber and Tobaison 2003; Egas et al. 2004, 2005; Doebeli et al. 2007; Ito and Dieckmann 2007).

Related research has shown that parapatric speciation driven by frequency-dependent competition can be promoted by environmental gradients (Doebeli and Dieckmann 2003; Mizera and Meszéna 2003; Leimar et al. 2008). This facilitation results from a gradient-induced type of frequency-dependent selection: local competition and local adaptation along an environmental gradient imply phenotype-dependent competition and thus frequency-dependent selection (Doebeli and Dieckmann 2003). Local adaptation is thus a prerequisite for gradient-induced frequency-dependent selection and, obviously, can be impeded by frequent or long-range dispersal. This means that the potential for parapatric speciation driven by gradient-induced frequency-dependent selection is bound to depend on the dispersal rates and distances of individuals: for relatively low mobility, speciation was found to occur readily, whereas increasing mobility first reduces and eventually extinguishes gradient-induced speciation (Doebeli and Dieckmann 2003).

It is important to realize that the mobilities for which speciation through gradient-induced frequency-dependent selection can occur are too large to imply isolation by distance (Doebeli and Dieckmann 2003). In general, speciation processes in sexual populations are hindered by the mixing of gene pools through segregation and recombination (e.g., Felsenstein 1981). In parapatric speciation, this obstacle may be overcome by assortative mating preferences (Doebeli and Dieckmann 2003) or by isolation by distance (Wright 1943). The traditional notion of isolation by distance, which is applicable when mobilities are very low compared to the spatial distances between subpopulations, thus

67 highlights a qualitatively different mechanism by which gradients may facilitate diversification  
68 gene pools of low-mobility ecotypes favored by local selection along environmental  
69 gradients (Turesson 1922) are genetically segregated from each other to an extent that al-  
70 lows processes of local adaptation, and potentially also of speciation, to run their course  
71 relatively unhindered (e.g., Slatkin 1973; Turelli et al. 2001).

72 Decreasing a population's mobility thus has a twofold effect on the potential for parapat-  
73 tric speciation: a decrease of mobility below a relatively high threshold enables speciation  
74 through gradient-induced frequency-dependent selection and the resultant evolution of as-  
75 sortative mating preferences, while a decrease to a much lower level enables speciation  
76 through isolation by distance. This realization puts a spotlight on the evolution of dispersal  
77 in parapatric speciation.

78 In more general contexts, many model-based analyses have investigated the evolution of  
79 dispersal rates (McPeek and Holt 1992; Holt and McPeek 1996; Olivieri et al. 1995;  
80 Doebeli and Ruxton 1997; Gandon 1999; Ronce et al. 2000, 2005; Mathias et al. 2001; Po-  
81 ethke and Hovestadt 2002; Cadet et al. 2003; Parvinen et al. 2003; Kisdi 2004), dispersal  
82 distances (Ezoe 1998; Savill and Hogeweg 1998; Hovestadt et al. 2001; Murrell et al.  
83 2002), and, more recently, directedness of dispersal (Armsworth and Roughgarden 2005;  
84 Heinz and Strand 2006). Selection has been shown to favor dispersal through mechanisms  
85 including inbreeding avoidance (Bengtsson 1978; Waser 1986; Motro 1991; Gandon 1999)  
86 and kin competition (Hamilton and May 1977; Frank 1986; Taylor 1988; Gandon and  
87 Michalakis 1999; Rousset and Gandon 2002).

88 Doebeli and Dieckmann (2003) investigated the implications of mobility for parapatric  
89 speciation through gradient-induced frequency-dependent selection by assuming different,  
90 but fixed, levels of mobility. This naturally begs the question how such mobility would  
91 adapt if it were subject to evolution. Classical trade-offs affecting dispersal evolution of  
92 course also apply to the model by Doebeli and Dieckmann (2003). On the one hand, com-  
93 petition in this model is higher between individuals with similar phenotypes than for  
94 dissimilar individuals, favoring offspring that move away from their parents. On the other  
95 hand, the change of environmental conditions along a sufficiently steep gradient is bound to  
96 favor low mobility. The balance between these two opposing forces of selection might thus  
97 be expected to cause the evolution of intermediate mobility. Such simple qualitative reason-  
98 ing, however, ignores the intricacies resulting from the dynamic interplay between  
99 speciation and dispersal evolution. As explained above, the potential for parapatric speci-  
100 ation is certainly influenced by dispersal, but also the converse applies: the evolution of  
101 dispersal is expected to be influenced by the distribution of phenotypes around and along an  
102 environmental gradient, and thus by speciation.

103 Here we analyze the joint evolution of an ecological character and population mobility  
104 in asexual and sexual populations inhabiting an environmental gradient. We thus extend the  
105 parapatric speciation model of Doebeli and Dieckmann (2003) by letting dispersal and mat-  
106 ing distances evolve, instead of using fixed values. Of the three dimensionless parameters  
107 of this model identified by Doebeli and Dieckmann (2003), two parameters (the scaled  
108 slope of the environmental gradient and the scaled width of the phenotypic competition  
109 function) were systematically varied, while the third parameter (the scaled dispersal dis-  
110 tance) was allowed to evolve. In this way, our results below offer an exhaustive overview  
111 of the interplay between the evolution of local adaptation and mobility in a simple model of  
112 parapatric speciation, by showing which dispersal and mating distances evolve under dif-  
113 ferent conditions and by examining the circumstances under which speciation can occur.

## 114 **Model Description**

115 The structure of the model description below is inspired by suggestions for describing indi-  
116 vidual- and agent-based models in a standardized manner (Grimm and Railsback 2005;  
117 Grimm et al. 2005, 2006).

### 118 **Purpose**

119 The purpose of the model is to understand the interplay between speciation and dispersal  
120 evolution along environmental gradients. The model extends the one by Doebeli and  
121 Dieckmann (2003) by incorporating the evolution of dispersal distances, and, in the case of  
122 sexual reproduction, of mating distances. We consider either asexual or sexual reproduc-  
123 tion, without, however, ever incorporating assortative mating preferences. The resultant  
124 model operates in continuous space and time and provides an individual-based, stochastic,  
125 and spatially explicit description of phenotypic evolution.

### 126 **Environment and state variables**

127 The environment considered in the model is two-dimensional and continuous, with spatial  
128 locations identified by coordinates  $0 \leq x, y \leq 1$ . An environmental gradient exists in the  $x$ -  
129 direction, while the  $y$ -direction is ecologically neutral. Individuals living in this environ-  
130 ment differ by location and phenotype. Phenotypes are denoted by  $u$  and  $v$ , where  $u$  is the  
131 ecological character affecting local adaptation along the environmental gradient and  $v$  is  
132 the dispersal character affecting distances of natal dispersal. In the sexual model, an addi-  
133 tional mating character  $w$  affects the distance of mate searching. At any moment in time,  
134 the state of the system is fully given by the state  $(x_i, y_i, u_i, v_i)$  or  $(x_i, y_i, u_i, v_i, w_i)$ , respec-  
135 tively, of all individuals  $i = 1, \dots, N$ , where  $N$  is the current number of individuals.

136    **Environmental gradient**

137    The carrying capacity density for the ecological phenotype  $u$  at spatial location  $(x, y)$  is  
138     $K(u, x, y) = K_0 \cdot N_{\sigma_K}(u - u_0(x))$ , where  $N_\sigma(z) = \exp(-\frac{1}{2}z^2/\sigma^2)$  denotes a normal, or Gaus-  
139    sian, function, and  $u_0(x) = g \cdot (x - \frac{1}{2}) + \frac{1}{2}$  describes which ecological phenotype maximizes  
140     $K$  at location  $x$ . This implies an environmental gradient with slope  $g$ . Along this gradi-  
141    ent, the phenotypic range around  $u_0(x)$  that offers high carrying capacity has a width of  
142     $\sigma_K$ .

143    **Boundary conditions**

144    Boundaries in the ecologically neutral  $y$ -direction are chosen to be periodic. Owing to the  
145    environmental gradient, environmental conditions differ at locations  $x=0$  and  $x=1$ , so  
146    that periodic boundary conditions in the  $x$ -direction are not biologically meaningful. We  
147    thus investigate two other kinds of boundary conditions in the  $x$ -direction: impermeable  
148    and cline-periodic. Impermeable boundaries imply that values  $x < 0$  (or  $x > 1$ ) are replaced  
149    with values 0 (or 1, respectively). Cline-periodic boundary conditions (Leimar et al. 2008)  
150    imply that values  $x < 0$  (or  $x > 1$ ) are replaced with values  $x+1$  (or  $x-1$ , respectively),  
151    while at the same time ecological phenotypes are replaced with values  $u+g$  (or  $u-g$ , re-  
152    spectively). The latter ensures that the carrying capacity density experienced by individuals  
153    is unaffected by the imposed relocation. Cline-periodic boundary conditions are thus simi-  
154    lar to spatially periodic boundary conditions, except for the additional correction of the  
155    ecological phenotype  $u$ .

156    **Phenotype ranges and initialization**

157    Initially, individuals are distributed randomly across the two-dimensional environment,  
158    with uniform probability density. For impermeable boundary conditions, the ecological  
159    characters of all individuals are initially set to  $u_i = 0.5$  and the dispersal characters are set  
160    to  $v_i = 0.5$ ; the mating characters, where applicable, are set to  $w_i = 0.2$ . All characters are  
161    then kept in the range  $0 \leq u, v, w \leq 1$ . For cline-periodic boundary conditions, the initial eco-  
162    logical characters  $u_i$  are randomly drawn from the range  $0 \leq u \leq 1$  with uniform probability  
163    density, and are subsequently left unbounded.

164    **Process overview and scheduling**

165    Individuals undergo a continuous-time birth-death process, so that generations are overlap-  
166    ping. The current system state determines the birth and death rates,  $b_i$  and  $d_i$ , of all  
167    individuals. On this basis, the population-level birth, death, and event rates are obtained as  
168     $B = \sum_{i=1}^N b_i$ ,  $D = \sum_{i=1}^N d_i$ , and  $E = B + D$ , respectively. The time lapse until the next event

169 is drawn from an exponential distribution with mean  $1/E$ . After the type of event is chosen  
170 according to probabilities  $B/E$  and  $D/E$ , the affected individual is chosen according to  
171 probabilities  $b_i/B$  or  $d_i/D$ . According to the chosen event type, the chosen individual ei-  
172 ther reproduces or dies.

### 173 **Interactions**

174 Individuals interact through local resource competition affecting their death rates. Individu-  
175 als that are far apart either in space or in ecological phenotype interact less strongly than  
176 individuals that are spatially close or ecologically similar. When reproduction is sexual, in-  
177 dividuals also interact by locally choosing a mating partner for producing offspring.  
178 Through these interactions, the fitness  $b_i - d_i$  of individual  $i$  is locally frequency-  
179 dependent, as it varies with the distribution of phenotypes in the vicinity of individual  $i$ . In  
180 the case of periodic ( $y$ -direction) and cline-periodic ( $x$ -direction) boundary conditions,  
181 interactions stretch across boundaries.

### 182 **Stochasticity**

183 The model comprises several types of stochasticity: demographic stochasticity, affecting  
184 time lapses between events, as well as the sequence of events; dispersal stochasticity, af-  
185 fecting the direction and distance of natal dispersal; and mutation stochasticity, affecting  
186 the direction and distance of phenotypic changes resulting from mutation. When reproduc-  
187 tion is sexual, these are complemented by two further types of stochasticity: mating  
188 stochasticity, affecting the choice of mating partner in an individual's vicinity; and segrega-  
189 tion-recombination stochasticity, affecting the phenotypes of offspring depending on those  
190 of their parents.

### 191 **Death events**

192 The death rate of individual  $i$  is  $d_i = n_{\text{eff}}(u_i, x_i, y_i)/K(u_i, x_i, y_i)$ , where  $n_{\text{eff}}(u_i, x_i, y_i)$  is the  
193 effective number of individuals with which individual  $i$  is competing,

$$194 n_{\text{eff}}(u_i, x_i, y_i) = (2\pi\sigma_s^2)^{-1} \sum_{j=1, j \neq i}^N N_{\sigma_c}(u_j - u_i) N_{\sigma_s}(x_j - x_i) N_{\sigma_s}(y_j - y_i).$$

195 This means that individuals compete the less strongly the more their spatial coordinates and  
196 ecological phenotypes differ, with the attenuation of competition strength being described  
197 by normal functions with standard deviations  $\sigma_c$  (the width of the phenotypic competition  
198 function scaling the effect of  $u$ ) and  $\sigma_s$  (the width of the spatial competition function scal-  
199 ing the effects of  $x$  and  $y$ ). The normalization factor  $(2\pi\sigma_s^2)^{-1}$  ensures that  $n_{\text{eff}}$  is

200 independent of  $\sigma_s$  in a spatially uniform population. Upon its death, the individual is re-  
201 moved from the population.

202 **Birth events and dispersal**

203 The birth rates of individuals are constant,  $b_i = b$ . Upon its birth, the new individual is in-  
204 serted into the population. Its spatial coordinates  $x$  and  $y$  are drawn from normal  
205 distributions with means equal to values  $x_i$  and  $y_i$  of the focal parent, and with standard  
206 deviations  $v_i$  reflecting the effect of natal dispersal.

207 When reproduction is sexual, the focal parent  $i$  randomly chooses a mating partner  $j$ ,  
208 with mating weights given by  $N_{w_i}(x_j - x_i)N_{w_i}(y_j - y_i)$ , where  $w_i$  is the mating distance of  
209 individual  $i$ . The choice of partner thus depends on spatial distance alone, so that mating  
210 preferences are never assortative with regard to phenotype. There is no direct cost associ-  
211 ated with having a high mating distance  $w_i$  and there is also no direct cost of dispersal. The  
212 offspring's phenotypes  $u$ ,  $v$ , and  $w$  are drawn from normal probability distributions with  
213 means equal to mid-parental values  $\frac{1}{2}(u_i + u_j)$ ,  $\frac{1}{2}(v_i + v_j)$ ,  $\frac{1}{2}(w_i + w_j)$  and with standard  
214 deviations  $\frac{1}{2}|u_i - u_j|$ ,  $\frac{1}{2}|v_i - v_j|$ ,  $\frac{1}{2}|w_i - w_j|$ , reflecting the effects of segregation and re-  
215 combination. The expressions used for the standard deviations ensure that normal  
216 distributions of parental phenotypes are invariant under segregation and recombination.  
217 (Some other studies used population-level averages to specify these standard deviations,  
218 usually setting them equal to a quarter of the population-level standard deviation in the  
219 character considered: such an approach, however, is nonsensical when populations, as is the  
220 case here, are not panmictic.)

221 When reproduction is asexual, the phenotypes  $u = u_i$  and  $v = v_i$  are faithfully inherited  
222 from parent to offspring (up to mutation, see next paragraph).

223 Finally, the offspring's phenotypes  $u$ ,  $v$ , and  $w$  may be displaced with probability  $\mu_m$   
224 by random increments drawn from a normal distribution with mean 0 and standard devia-  
225 tion  $\sigma_m$ , reflecting the effect of mutation.

226 **Observables**

227 For model testing, it is helpful to observe the spatio-phenotypic distribution of individuals.  
228 For model analysis, the marginal phenotypic distributions of ecological character, dispersal  
229 character, and mating character are recorded.

230 Speciation is identified as follows. For asexual populations, we require the initially uni-  
231 modal phenotype distribution to branch into a visibly bi- or multimodal distribution (Fig.  
232 5a,b). For sexual populations, we additionally require that not more than a very few hybrids

233 be present between candidate branches, implying sharp modes of the bi- or multimodal  
234 phenotype distribution (Fig. 5d).

## 235 **Parameters**

236 A list of default parameter values is provided in Table 1. Doebeli and Dieckmann (2003)  
237 showed that the asexual model defined above has no more than three essential parameters:  
238 the scaled width of the phenotypic competition function,  $c = \sigma_c / \sigma_K$ , the scaled slope of the  
239 environmental gradient,  $s = g\sigma_s / \sigma_K$ , and the scaled dispersal distance,  $v / \sigma_s$ . In our  
240 analyses below, we systematically vary the two dimensionless parameters  $c$  and  $s$ , while  
241 allowing the dispersal distances  $v$ , and in the sexual model, the mating distances  $w$ , to  
242 evolve.

## 243 **Results**

244 Results below are first presented for asexual populations, thus offering a helpful baseline  
245 for the subsequent investigation of evolution in sexual populations.

### 246 **Asexual populations**

247 When reproduction is asexual, the joint evolution of the ecological phenotype and the dis-  
248 persal phenotype results in three qualitatively different evolutionary outcomes: (i) spe-  
249 ciation with short-range dispersal (Fig. 5a), (ii) speciation with long-range dispersal  
250 (Fig. 5b), and (iii) no speciation with long-range dispersal (Fig. 5c).

251 These outcomes occur in three sharply delineated regions of the model's parameter  
252 space, spanned by the scaled slope  $s$  of the environmental gradient and by the scaled width  
253  $c$  of the phenotypic competition function (Fig. 1, for impermeable boundary conditions in  
254 the  $x$ -direction; see Table 2 for an overview). First is a large parameter region on the right-  
255 hand side of Fig. 1a, in which speciation occurs in conjunction with the evolution of short-  
256 range dispersal. The existence of this region is in line with results by Doebeli and Dieck-  
257 mann (2003) showing that for  $c \geq 1$  speciation occurs for a larger range of mobilities when  
258 gradients are steep (as long as  $s \leq 1$ ). Second is a parameter region in the upper left corner  
259 of Fig. 1a, in which dispersal distance remains high without speciation. This is of course  
260 facilitated by shallow environmental gradients. That speciation does not occur here is in  
261 line with results by Dieckmann and Doebeli (2003) showing that speciation is not expected  
262 for  $c \geq 1$  unless facilitated by a sufficiently steep environmental gradient and accompanied  
263 by sufficiently low mobility. Third is a parameter region in the lower left corner of Fig. 1a,  
264 in which speciation occurs in conjunction with the evolution of long-range dispersal. Again,  
265 the latter evolution is promoted by the shallowness of the environmental gradient in this

region, and speciation is expected since  $c < 1$ . Very similar results are obtained when cline-periodic boundary conditions are used for the  $x$ -direction (Fig. 2). Here, the shift of ecological phenotypes by  $g$  when individuals traverse the  $x$ -boundaries appears to facilitate the evolution of short-range dispersal.

Of the three identified regions, the upper part of the first region is perhaps most remarkable ( $c \geq 1$ , and  $s \leq 1$  but large). In this part, speciation cannot occur in the absence of a gradient ( $s = 0$ ), so that all speciation encountered here is strictly gradient-induced. Doebeli and Dieckmann (2003) showed that under such conditions speciation can only occur if mobility is sufficiently low. Dispersal evolution takes care of this, so that the latter proviso disappears.

### Abrupt transition between long-range and short-range dispersal

What is surprising is the abrupt nature of the transition between evolutionary outcomes with long-range and short-range dispersal. Plotting the evolved dispersal distance as a function of the environmental gradient's slope (Fig. 1b) shows that a gradually decreasing slope  $s$  triggers an abrupt increase in the evolved dispersal distance  $v$ , especially for higher values of  $c$ .

The mere fact that dispersal distance increases when  $s$  is decreased is easily understood. The cost of dispersal – resulting from the likelihood of reaching a location to which the dispersing individual is less adapted – decreases with  $s$ . This means that the benefit of dispersal – resulting from the likelihood of reaching a location that is less crowded and at which competition is thus diminished – prevails when  $s$  is low.

But how can the observed threshold effect be explained? Speciation through gradient-induced frequency-dependent selection has been shown to occur more easily when mobility is low (Doebeli and Dieckmann 2003). Short-range dispersal thus facilitates speciation. Interestingly, also the converse is true: speciation may facilitate the evolution of short-range dispersal. Once a unimodal distribution of phenotypes has split into several phenotypic clusters along the environmental gradient, dispersal becomes less favorable, as it likely implies moving to locations where the dispersing individual has to compete with other, better-adapted phenotypes. Therefore, short-range dispersal not only facilitates speciation, but the onset of speciation also facilitates the evolution of short-range dispersal. This positive feedback between dispersal evolution and speciation causes a threshold effect in the evolution of dispersal distances. When this feedback loop is disrupted – because there is no incipient speciation, or because selection does not favor short-range dispersal – evolved dispersal distances suddenly increase. This explains why the transition between short-range and long-range dispersal is so sharp for  $c \geq 1$ , since here speciation is contingent on low

301 mobility. For  $c < 1$ , speciation can occur independent of mobility, so that the mutual de-  
302 pendence between speciation and dispersal evolution becomes one-sided instead, resulting  
303 in a more gradual transition. This effect also explains the shift of the regime boundary in  
304 the cline-periodic case (Fig. 2).

305 **Sexual populations**

306 Also when reproduction is sexual, evolution results in three qualitatively different evolu-  
307 tionary outcomes (Figs. 3, 4, 5d,e,f; see Table 2 for an overview): (i) speciation with short-  
308 range dispersal (upper right corner of Figs. 3a, 4a; Fig. 5d), (ii) no speciation with short-  
309 range dispersal (lower right corner of Figs. 3a, 4a; Fig. 5e), and (iii) no speciation with  
310 long-range dispersal (left-hand side of Figs. 3a, 4a; Fig. 5f). While cases (i) and (iii) both  
311 occur under asexual as well as under sexual evolution, case (ii) for sexual evolution (no  
312 speciation, short-range dispersal) and case (ii) for asexual evolution (speciation, long-range  
313 dispersal) characterize diametrically opposite evolutionary outcomes.

314 For sexual evolution, speciation occurs when  $c$  and  $s \leq 1$  are both sufficiently large,  
315 while short-range dispersal evolves when  $s \leq 1$  is sufficiently large. It is interesting to high-  
316 light that speciation in this model thus requires sufficiently *large* values of  $c$ . By contrast,  
317 speciation in non-spatial models of sexual evolution, based on the evolution of assortative  
318 mating, is facilitated by *small* values of  $c < 1$  (Dieckmann and Doebeli 1999). Figs. 3 and 4  
319 also show that, as expected, speciation under sexual evolution cannot occur in conjunction  
320 with long-range dispersal: in the absence of potential for the evolution of assortative mating  
321 preferences, sexual parapatric speciation is contingent on sufficiently low mobility.

322 A more detailed comparison with the outcomes of asexual evolution yields the following  
323 observations. First, the parameter region corresponding to case (i) under sexual evolution is  
324 a bit smaller, and shifted towards higher values for  $c$  and  $s$ , as compared to asexual evolu-  
325 tion. Second, the parameter region corresponding to case (iii) is larger and extends towards  
326 all lower values of  $c$ . And third, as was already emphasized above, the transition between  
327 cases (i) and (iii) is mediated by an entirely different class of cases (ii). It is worth empha-  
328 sizing that under sexual evolution it is only case (ii) that implies a phenotypic gradient  
329 following the environmental gradient.

330 As in the asexual model, we found a threshold effect for how evolved dispersal distances  
331 depend on the gradient's slope (Figs. 3b, 4b). This threshold effect is again explained by the  
332 interplay between speciation and dispersal evolution. In contrast to the asexual case, how-  
333 ever, speciation of sexual populations requires short-range dispersal even for  $c < 1$ . The  
334 mutual dependence between speciation and dispersal evolution thus extends across all val-

335    ues of  $c$ . Accordingly, the transition of evolved dispersal distances remains relatively sharp  
336    along the entire boundary of the parameter region enabling speciation.

337    The evolution of mating distances with increasing slope of the environmental gradient at  
338    first follows the evolution of the dispersal distance. It is only after the onset of speciation  
339    that mating distances no longer seem to be driven to particularly small values. To explain  
340    this, we have to appreciate that the evolution of short-range dispersal in conjunction with  
341    speciation amounts to the formation of spatially segregated phenotypic clusters. While such  
342    clusters can only form if the mating distance is sufficiently small, merely searching for a  
343    mate outside an individual's own cluster will not lead to any significant production of hy-  
344    brids when distances between adjacent clusters are so large that actual matings across  
345    cluster boundaries are very rare. This understanding is corroborated by our finding that  
346    small mating distances are selected for much more strongly when competition widths, and  
347    hence distances between adjacent clusters, are small (Fig. 3b, 4b; bottom panels).

348    In summary, the propensity for speciation in this model of sexual parapatric speciation is  
349    shaped by two key mechanisms: first, frequency-dependent selection is induced by the joint  
350    effect of local competition and local adaptation along the environmental gradient (Doebeli  
351    and Dieckmann 2003), and second, a positive feedback exists between incipient speciation  
352    and the evolution of short-range dispersal (as explained above).

## 353    **Discussion**

354    In this study we investigated the joint evolution of an ecological character and of dispersal  
355    distance in asexual and sexual populations inhabiting an environmental gradient. We identi-  
356    fied several interesting phenomena resulting from the evolutionary interplay of these  
357    characters.

358    Using a dimensionless representation of the model's two essential parameters, the scaled  
359    slope  $s$  of the environmental gradient and the scaled width  $c$  of the phenotypic competi-  
360    tion function, we showed that most parameter combinations lead to speciation in  
361    conjunction with the evolution of short-range dispersal. For shallow gradients, dispersal  
362    distance can remain large, precluding speciation. These two types of evolutionary outcome  
363    occur in asexual as well as in sexual populations. The third type of evolutionary outcome,  
364    occurring at the transition between the two former regimes, qualitatively differs between  
365    asexual and sexual populations. In the corresponding parameter regions, asexual popula-  
366    tions speciate while evolving long-range dispersal, whereas sexual populations do not  
367    speciate while evolving short-range dispersal. A phenotypic gradient following the envi-

368 ronmental gradient only arises in the last case, i.e., for non-speciating sexual populations  
369 evolving towards short-range dispersal.

370     Transitions between the three identified evolutionary regimes are typically sharp. This  
371 finding is explained by the existence of a positive feedback loop between incipient speci-  
372 ation and evolution of short-range dispersal: short-range dispersal facilitates speciation and  
373 speciation promotes short-range dispersal. This feedback not only accounts for the abrupt-  
374 ness of transitions between regimes but also for the prevalence of short-range dispersal over  
375 a wide range of conditions. When gradients are sufficiently steep, ecological diversification  
376 is a better means of expanding an organism's home range than long-range dispersal.

377     In populations with sexual reproduction, the parameter range over which speciation oc-  
378 curs is smaller than for asexual populations, but still surprisingly large. This illustrates that  
379 dispersal evolution can be a powerful alternative means to preference evolution of allowing  
380 sexual populations to respond to the frequency-dependent disruptive selection pressures  
381 resulting from ecological interactions. The positive feedback between speciation and dis-  
382 persal evolution contributes to the pertinence of this mechanism.

383     It has been proposed that clustering along an environmental gradient with impermeable  
384 boundaries (Doebeli and Dieckmann 2003) “is driven by edge effects, rather than by fre-  
385 quency-dependent competition” (Polechová and Barton 2005). In agreement with a related  
386 investigation of parapatric clustering (Leimar et al. 2008), our analysis here shows that  
387 clustering occurs both for impermeable and for cline-periodic boundary conditions. So  
388 while impermeable boundaries may affect the details of evolutionary outcomes along envi-  
389 ronmental gradients – in ways that are worth learning about, since spatial boundaries in  
390 nature are real and cannot be conveniently assumed away by theorists – we can conclude  
391 that phenotypic clustering in our model occurs independently of boundary effects.

392     In order not to overload our study with too many parameters, we focused attention on  
393 the evolution of natal dispersal distance, as measured by the standard deviation  $v$ . Several  
394 extensions could be worthwhile. For example, one might want to consider the evolution of  
395 adult dispersal rates  $m$ . However, to the extent that dispersal is diffusive, only the com-  
396 pound parameter  $\frac{1}{2}(b+m)v^2$  matters (Doebeli and Dieckmann 2003), so that the  
397 consequences of evolution in  $m$  are equivalent to those of evolution in  $v$ . An analogous  
398 compound parameter,  $\frac{1}{2}bv^2 + \frac{1}{2}m\tilde{v}^2$ , applies when the standard deviation  $v$  of natal disper-  
399 sal distances differs from that of adult dispersal distances,  $\tilde{v}$ .

400     Other extensions are expected to be more consequential. In particular, it could be inter-  
401 esting to study costs of dispersal, or spatiotemporal variation in local environmental  
402 conditions. These factors can have opposite effects on the evolution of dispersal, and their  
403 interaction can lead to complex dynamics. Spatiotemporal variation has been shown to im-

pact dispersal rates (Van Valen 1971; Travis and Dytham 1998; Travis 2001) as well as dispersal distances (Murrell et al. 2002). Such variation can also lead to dispersal dimorphism, resulting in the coexistence of dispersal morphs with high and low mobility (McPeek and Holt 1992; Johst et al. 1999; Mathias et al. 2001; Parvinen 2002; Heinz and Strand 2006). Travis (2001) found that the evolution of dispersal rates depends not only on whether or not there is temporal or spatial variability in the environment, but also on the form of such variability. Demographic stochasticity (which our model includes) creates spatiotemporal variation in local environmental conditions and has been shown to favor dispersal (Holt and Mc Peek 1996; Cadet et al. 2003; Parvinen et al. 2003), but also to impact the costs of dispersal (Cadet et al. 2003). Increasing costs of dispersal, in the form of dispersal mortality and/or diminished fecundity, naturally favor lower dispersal rates (Pothke and Hovestadt 2002) and shorter dispersal distances (Murell et al. 2002). Yet, when considering kin competition (which our model also includes), the relationship between dispersal mortality and evolved dispersal rate was found to be non-monotonic (Gandon and Michalakis 1999; Gandon 1999; Kisdi 2004). Another interesting extension would be to include the evolution of dispersal directedness. Recent empirical work showed that there is an important link between the directedness of dispersal and the evolution of species: non-random dispersal can produce genetic differentiation (Postma and van Noordwijk 2005; Garant et al. 2005) and thereby trigger speciation. The evolution of dispersal directedness in turn has been shown to be dependent on spatial variability (Heinz and Strand 2006) and temporal variability (Armsworth and Roughgarden 2005). One could also consider the population genetics of the phenotypes studied here: for example, Billiard and Lenormand (2005) investigated how linkage between two loci for dispersal and local adaptation affects the evolution of dispersal rates. Finally, it could be interesting to vary the shape of the kernels for competition, dispersal, and mating. In this context, it must be borne in mind – as this sometimes gets overlooked (Polechová and Barton 2005) – that the structural instability of simple deterministic models with normal competition kernels (May and MacArthur 1972; Roughgarden 1974; Sasaki and Ellner 1995; Sasaki 1997; Gyllenberg and Meszéna 2005; Doebeli et al. 2007; Pigolotti et al. 2007) does not apply to the stochastic individual-based models studied here.

Dispersal is subject to evolution and also drives evolutionary dynamics by being an important determinant of the mixing and isolation of populations. It is therefore essential to understand the interaction between dispersal as an evolving character on the one hand and dispersal as an evolutionary factor on the other. Our finding of a positive feedback leading to the combination of short-range dispersal and speciation under a wide range of conditions shows how intricate this interaction can be. We thus hope that this study serves as a first

440 step towards understanding the complex interplay between dispersal evolution and speci-  
441 ation.

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**Table 1.** Overview of parameters and their default values.

Maximal carrying capacity density, scaling the number of individuals in the system	$K_0$	300
Standard deviation of carrying capacity density, scaling the reduction of carrying capacity density with increased phenotypic distance in the ecological character from the locally optimal phenotype	$\sigma_K$	0.3
Standard deviation of phenotypic competition function, scaling the reduction of competition strength with increased phenotypic distance in the ecological character between individuals	$\sigma_c$	variable
Standard deviation of spatial competition function, scaling the reduction of competition strength with increased spatial distance between individuals	$\sigma_s$	0.2
Slope of environmental gradient	$g$	variable
Per capita birth rate, scaling time	$b$	1
Mutation probability	$\mu_m$	0.02
Standard deviation of distribution of mutation effects	$\sigma_m$	0.01
Scaled standard deviation of phenotypic competition function	$c$	$\sigma_c / \sigma_K$
Scaled slope of environmental gradient	$s$	$g\sigma_s / \sigma_K$

**Table 2.** Overview of evolutionary outcomes.

Asexual populations		Sexual populations	
Steep slope	Speciation, short-range dispersal	Steep slope, wide competition	Speciation, short-range dispersal
Shallower slope, narrow competition	Speciation, long-range dispersal	Steep slope, narrow competition	No speciation, short-range dispersal
Shallower slope, wide competition	No speciation, long-range dispersal	Shallower slope	No speciation, long-range dispersal

651   **Figure 1.** Outcomes of asexual evolution when boundaries in the  $x$ -direction are impermeable.  
652   (a) Dependence of outcomes on the model's two dimensionless parameters  $s$  (scaled  
653   slope of environmental gradient) and  $c$  (scaled width of phenotypic competition function).  
654   Three types of outcomes can occur, resulting in three sharply delineated regions in parame-  
655   ter space: (i) speciation and short-range dispersal (right-hand side), (ii) speciation and long-  
656   range dispersal (lower left corner), and (iii) no speciation and long-range dispersal (upper  
657   left corner). (b) Dependence of scaled dispersal distances on  $s$ , for three different values of  
658    $c$ . The standard deviation of evolved distances is indicated by the gray areas. Decreasing  
659   the slope results in the sharp rise of scaled dispersal distance for  $c = 2$  and  $c = 1$ , while this  
660   transition is less abrupt for  $c = 0.5$ . Other parameters as shown in Table 1.

661   **Figure 2.** Outcomes of asexual evolution when boundaries in the  $x$ -direction are cline-  
662   periodic. (a) Dependence of outcomes on the model's two dimensionless parameters  $s$  (scaled  
663   slope of environmental gradient) and  $c$  (scaled width of phenotypic competition function). (b)  
664   Dependence of scaled dispersal distances on  $s$ , for three different values of  $c$ . Other details as in Fig. 1.

666   **Figure 3.** Outcomes of sexual evolution when boundaries in the  $x$ -direction are imperme-  
667   able. (a) Dependence of outcomes on the model's two dimensionless parameters  $s$  (scaled  
668   slope of environmental gradient) and  $c$  (scaled width of phenotypic competition function).  
669   Three types of outcomes can occur, resulting in three sharply delineated regions in parame-  
670   ter space: (i) speciation and short-range dispersal (upper right corner), (ii) no speciation and  
671   short-range dispersal (lower right corner), and (iii) no speciation and long-range dispersal  
672   (left-hand side). (b) Dependence of scaled dispersal and mating distances on  $s$ , for three  
673   different values of  $c$ . The standard deviations of evolved distances are indicated by the  
674   gray areas and thin continuous curves, respectively. Decreasing the slope results in the  
675   sharp rise of scaled dispersal distance for  $c = 2$ ,  $c = 1$ , and  $c = 0.5$ . Other parameters as  
676   shown in Table 1.

677   **Figure 4.** Outcomes of sexual evolution when boundaries in the  $x$ -direction are cline-  
678   periodic. (a) Dependence of outcomes on the model's two dimensionless parameters  $s$   
679   (scaled slope of environmental gradient) and  $c$  (scaled width of phenotypic competition  
680   function). (b) Dependence of scaled dispersal and mating distances on  $s$ , for three different  
681   values of  $c$ . Other details as in Fig. 3.

682   **Figure 5.** Evolution of phenotypic and spatial distributions when boundaries in the  $x$ -  
683   direction are impermeable. Three examples each are shown for asexual populations (left

684 column) and sexual populations (right column). The left panel of each example shows the  
685 evolution of the distribution of the ecological character in the range  $0 \leq u \leq 1$  from time 0  
686 (bottom) to time 15,000 (top). The corresponding right panel shows the final spatial distri-  
687 bution of individuals at time 15,000 with different grayscales depicting different values of  
688 the ecological character. Asexual populations: (a) speciation with short-range dispersal  
689 ( $s = 0.66$ ,  $c = 1.33$ ), (b) speciation with long-range dispersal ( $s = 0.16$ ,  $c = 0.47$ ), and (c)  
690 speciation with short-range dispersal ( $s = 0.10$ ,  $c = 1.53$ ). Sexual populations: (d) speci-  
691 ation with short-range dispersal ( $s = 0.83$ ,  $c = 1.66$ ), (e) no speciation with short-range  
692 dispersal ( $s = 0.80$ ,  $c = 0.33$ ), and (f) no speciation with long-range dispersal ( $s = 0.13$ ,  
693  $c = 0.80$ ). The examples illustrate that short-range dispersal induces spatial structure and  
694 facilitates speciation.

Figure 1

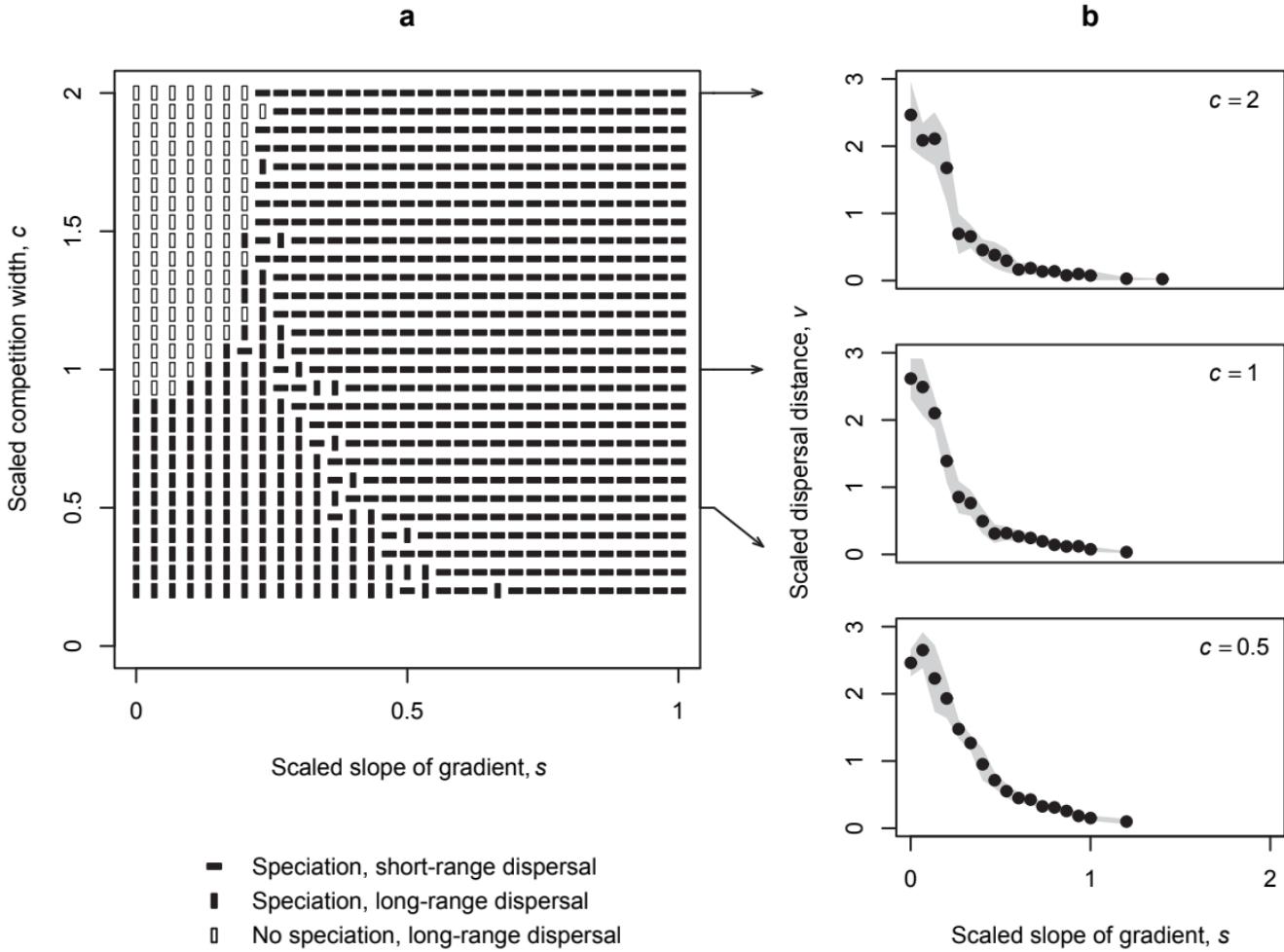


Figure 2

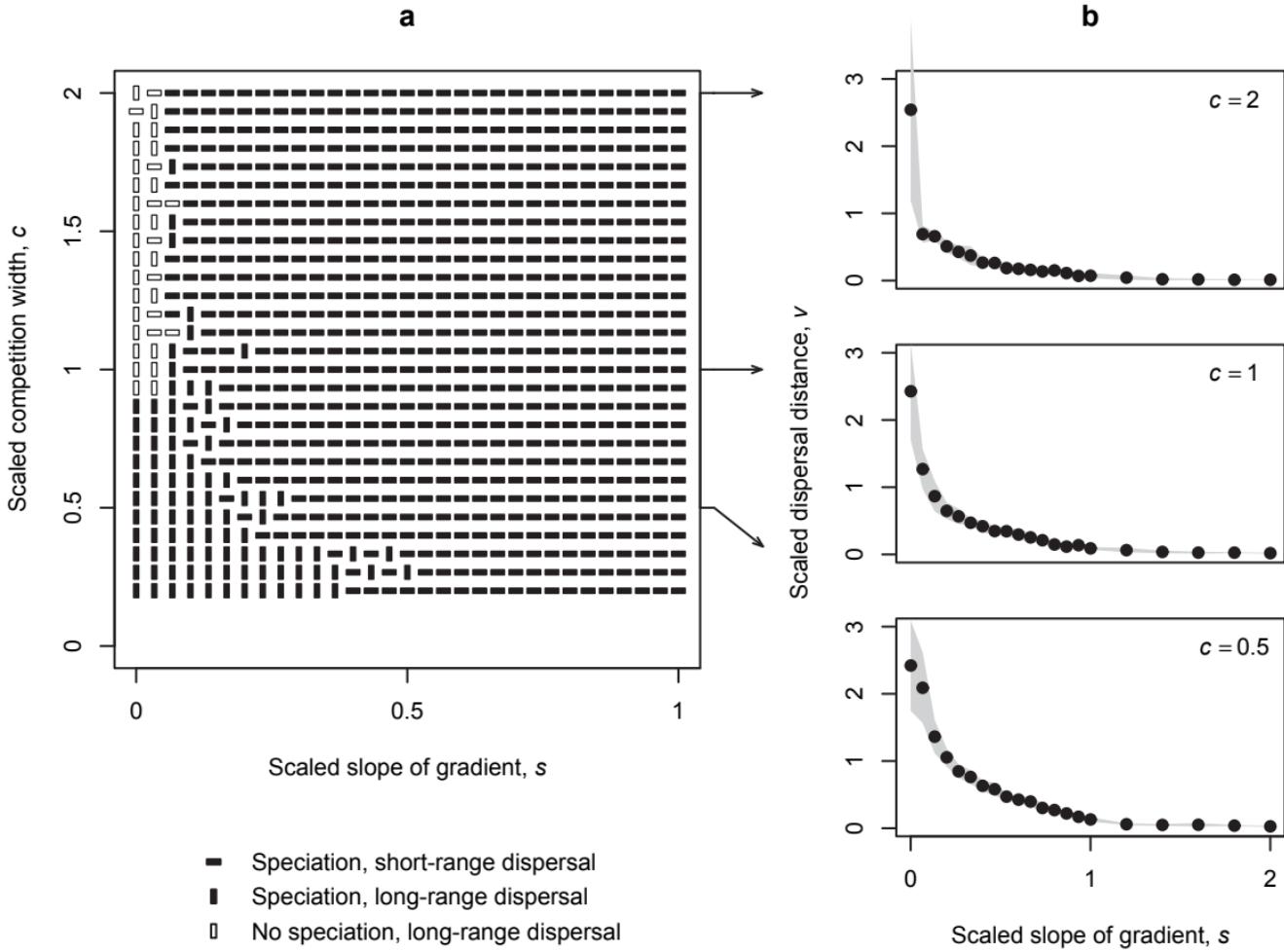


Figure 3

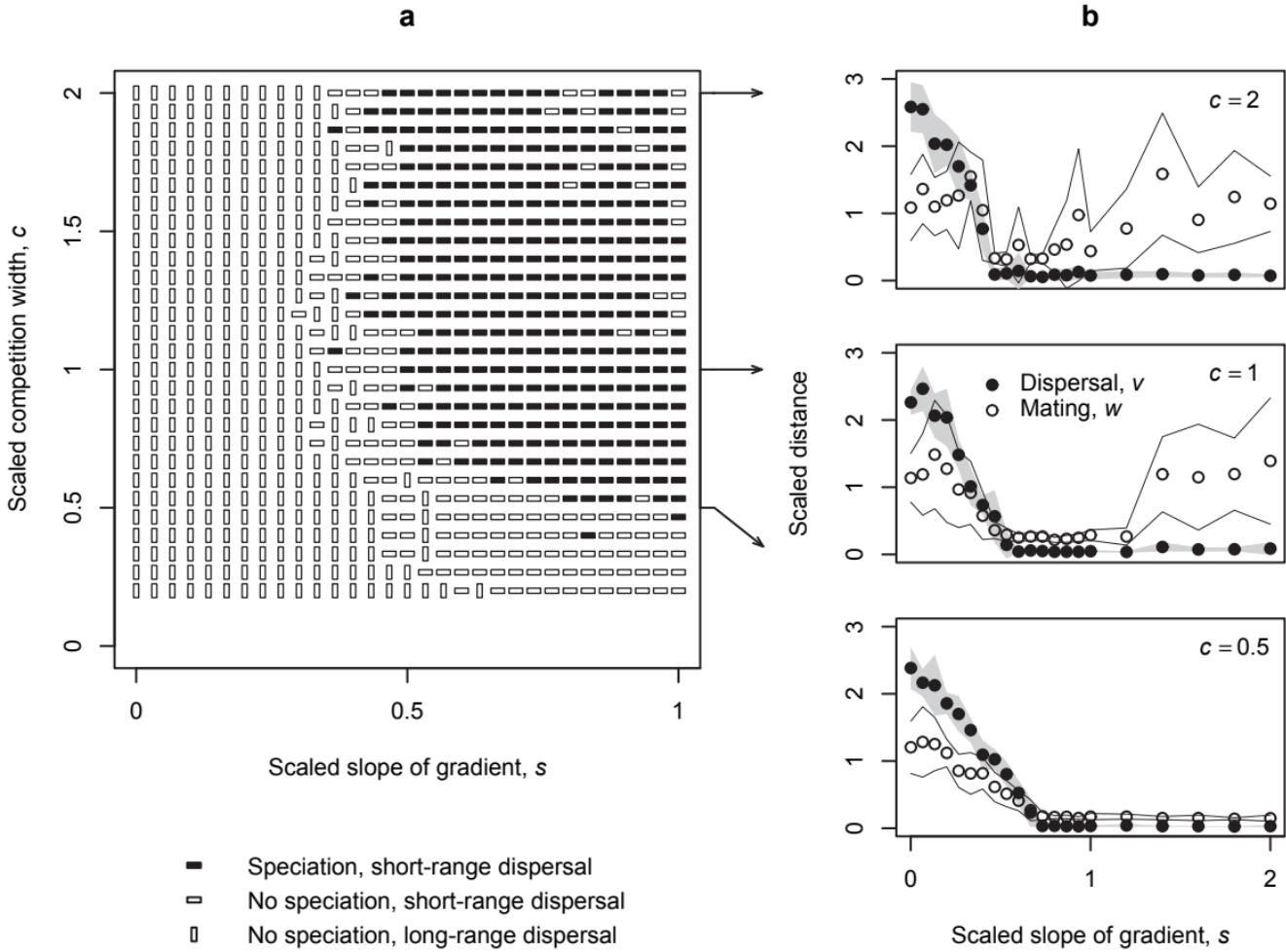


Figure 4

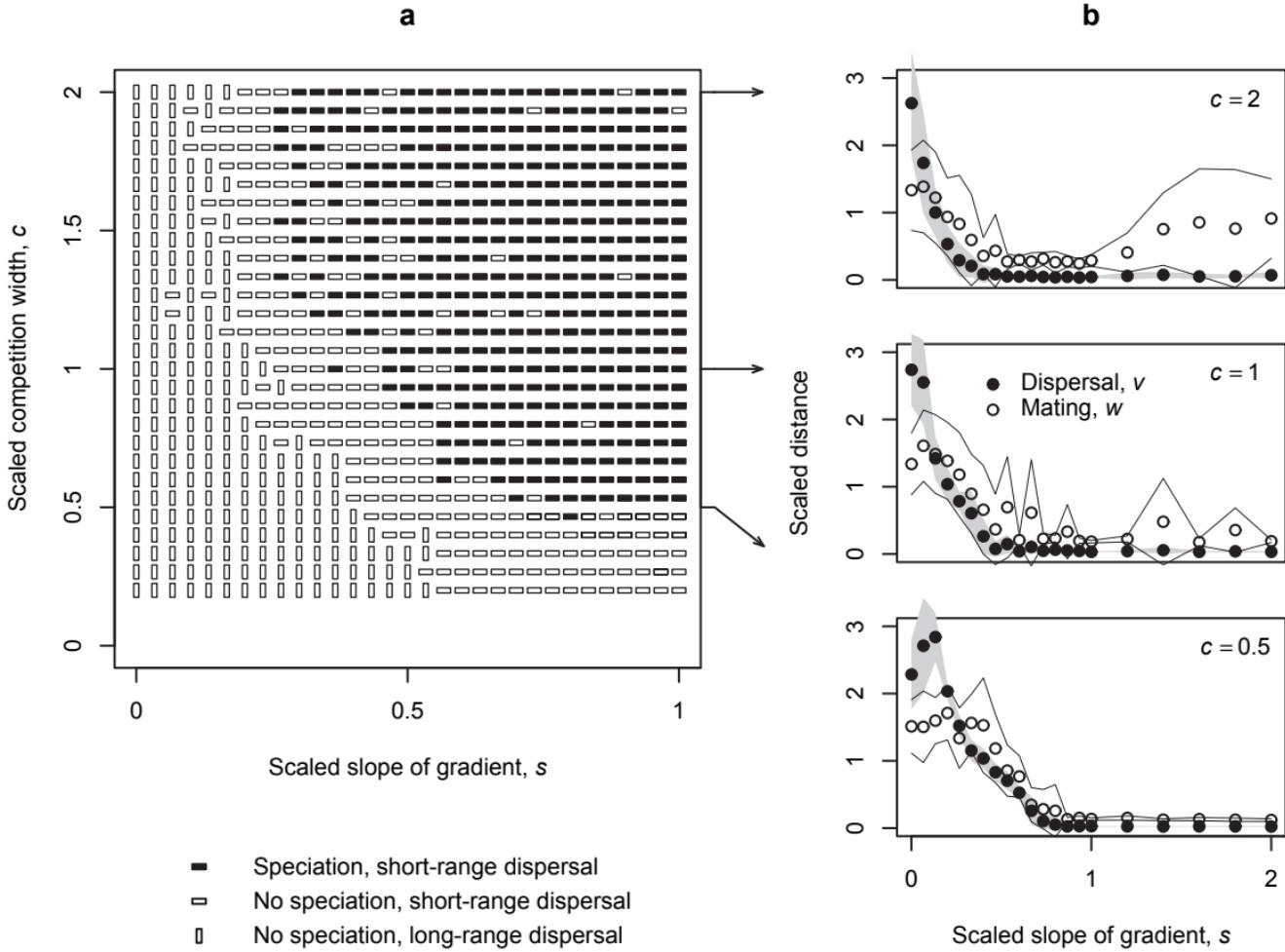
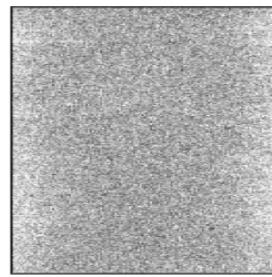
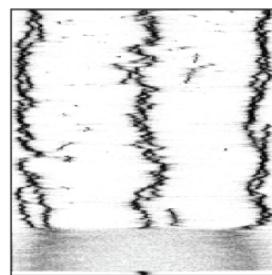
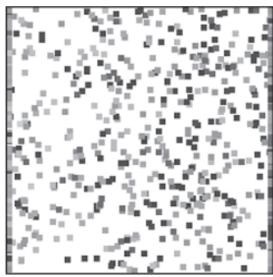
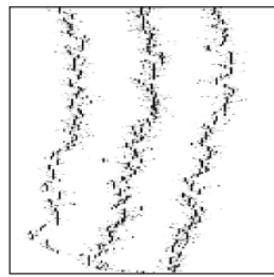
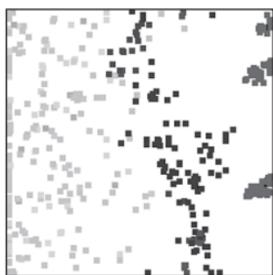
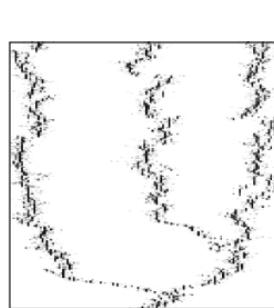


Figure 5

## Asexual populations



## Sexual populations