



International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

Interim Report

IR-09-063

Speciation and the evolution of dispersal along environmental gradients

Simone K. Heinz (simone.heinz@fa.uib.no)
Rupert Mazzucco (mazzucco@iiasa.ac.at)
Ulf Dieckmann (dieckmann@iiasa.ac.at)

Approved by

Detlof Von Winterfeldt
Director

July 2011

Interim Reports on work of the International Institute for Applied Systems Analysis receive only limited review. Views or opinions expressed herein do not necessarily represent those of the Institute, its National Member Organizations, or other organizations supporting the work.

Speciation and the evolution of dispersal along environmental gradients

Simone K. Heinz¹, Rupert Mazzucco² & Ulf Dieckmann^{2,3}

¹ Department of Biology, University of Bergen, P.O. Box 7800, 5020 Bergen, Norway

² Evolution and Ecology Program, International Institute for Applied Systems Analysis,
Schlossplatz 1, 2361 Laxenburg, Austria

³ Section Theoretical Biology, Institute of Biology, Leiden University, Kaiserstraat 63,
2311 GP Leiden, The Netherlands

Abstract

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

Introduction

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

31 evidence suggests that sympatric speciation can occur in nature (e.g., Schlieven et al. 1994;
32 Bush and Smith 1998; Filchack et al. 2000; Wilson et al. 2000; Schlieven et al. 2001). This
33 has spawned corresponding theoretical research striving to identify key mechanisms that
34 may promote such speciation (e.g., Maynard Smith 1966; Turner and Burrows 1995;
35 Kawecki 1997; Kondrashov and Kondrashov 1999; Higashi et al. 1999; Dieckmann and
36 Doebeli 1999; Drossel and Kane 2000; Doebeli and Dieckmann 2003; see also the review
37 by Via 2001). In particular, resource competition leading to frequency-dependent disruptive
38 selection has received wide recognition as a potential ecological driver of sympatric speci-
39 ation (MacArthur and Levins 1967; Rosenzweig 1978; Christiansen and Loeschcke 1980;
40 Slatkin 1980; Seger 1985; Taper and Case 1985; Maynard Smith and Brown 1986; Abrams
41 et al. 1993; Vincent et al. 1993; Doebeli 1996a, 1996b; Metz et al. 1996; Law et al. 1997;
42 Meszéna et al. 1997; Geritz et al. 1998; Dieckmann and Doebeli 1999; Geritz et al. 1999;
43 Jansen and Mulder 1999; Kisdi 1999; Kondrashov and Kondrashov 1999; Day 2000;
44 Doebeli and Dieckmann 2000; Drossel and McKane 2000; Kisdi 2001; Kisdi and Geritz
45 2001; Kisdi et al. 2001; Schreiber and Tobiason 2003; Egas et al. 2004, 2005; Doebeli et al.
46 2007; Ito and Dieckmann 2007).

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

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

67 highlights a qualitatively different mechanism by which gradients may facilitate diversifica-
68 tion: 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 parapa-
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 (McPeck and Holt 1992; Holt and McPeck 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 σ_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,

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

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 σ_c (the width of the phenotypic competition
 198 function scaling the effect of u) and σ_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_{eff} is

200 independent of σ_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 μ_m
224 by random increments drawn from a normal distribution with mean 0 and standard devia-
225 tion σ_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 / σ_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)
249 speciation 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

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

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

276 **Abrupt transition between long-range and short-range dispersal**

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

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

287 But how can the observed threshold effect be explained? Speciation through gradient-
288 induced frequency-dependent selection has been shown to occur more easily when mobility
289 is low (Doebeli and Dieckmann 2003). Short-range dispersal thus facilitates speciation. In-
290 terestingly, also the converse is true: speciation may facilitate the evolution of short-range
291 dispersal. Once a unimodal distribution of phenotypes has split into several phenotypic
292 clusters along the environmental gradient, dispersal becomes less favorable, as it likely im-
293 plies moving to locations where the dispersing individual has to compete with other, better-
294 adapted phenotypes. Therefore, short-range dispersal not only facilitates speciation, but the
295 onset of speciation also facilitates the evolution of short-range dispersal. This positive
296 feedback between dispersal evolution and speciation causes a threshold effect in the evolu-
297 tion of dispersal distances. When this feedback loop is disrupted – because there is no
298 incipient speciation, or because selection does not favor short-range dispersal – evolved
299 dispersal distances suddenly increase. This explains why the transition between short-range
300 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-
344brids 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-

404 pact dispersal rates (Van Valen 1971; Travis and Dytham 1998; Travis 2001) as well as
405 dispersal distances (Murrell et al. 2002). Such variation can also lead to dispersal dimor-
406 phism, resulting in the coexistence of dispersal morphs with high and low mobility
407 (McPeck and Holt 1992; Johst et al. 1999; Mathias et al. 2001; Parvinen 2002; Heinz and
408 Strand 2006). Travis (2001) found that the evolution of dispersal rates depends not only on
409 whether or not there is temporal or spatial variability in the environment, but also on the
410 form of such variability. Demographic stochasticity (which our model includes) creates
411 spatiotemporal variation in local environmental conditions and has been shown to favor
412 dispersal (Holt and Mc Peek 1996; Cadet et al. 2003; Parvinen et al. 2003), but also to im-
413 pact the costs of dispersal (Cadet et al. 2003). Increasing costs of dispersal, in the form of
414 dispersal mortality and/or diminished fecundity, naturally favor lower dispersal rates (Po-
415 ethke and Hovestadt 2002) and shorter dispersal distances (Murell et al. 2002). Yet, when
416 considering kin competition (which our model also includes), the relationship between dis-
417 persal mortality and evolved dispersal rate was found to be non-monotonic (Gandon and
418 Michalakis 1999; Gandon 1999; Kisdi 2004). Another interesting extension would be to
419 include the evolution of dispersal directedness. Recent empirical work showed that there is
420 an important link between the directedness of dispersal and the evolution of species: non-
421 random dispersal can produce genetic differentiation (Postma and van Noordwijk 2005;
422 Garant et al. 2005) and thereby trigger speciation. The evolution of dispersal directedness
423 in turn has been shown to be dependent on spatial variability (Heinz and Strand 2006) and
424 temporal variability (Armsworth and Roughgarden 2005). One could also consider the
425 population genetics of the phenotypes studied here: for example, Billiard and Lenormand
426 (2005) investigated how linkage between two loci for dispersal and local adaptation affects
427 the evolution of dispersal rates. Finally, it could be interesting to vary the shape of the ker-
428 nels for competition, dispersal, and mating. In this context, it must be borne in mind – as
429 this sometimes gets overlooked (Polechová and Barton 2005) – that the structural instabil-
430 ity of simple deterministic models with normal competition kernels (May and MacArthur
431 1972; Roughgarden 1974; Sasaki and Ellner 1995; Sasaki 1997; Gyllenberg and Meszéna
432 2005; Doebeli et al. 2007; Pigolotti et al. 2007) does not apply to the stochastic individual-
433 based models studied here.

434 Dispersal is subject to evolution and also drives evolutionary dynamics by being an im-
435 portant determinant of the mixing and isolation of populations. It is therefore essential to
436 understand the interaction between dispersal as an evolving character on the one hand and
437 dispersal as an evolutionary factor on the other. Our finding of a positive feedback leading
438 to the combination of short-range dispersal and speciation under a wide range of conditions
439 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.

442 **Acknowledgements**

443 We thank Øyvind Fiksen and all members of the modeling group of the Department of Bi-
444 ology at the University of Bergen for fruitful discussions. S.H. gratefully acknowledges
445 financial support by the EU project ETHOFISH (QLRT-2001-00799). R.M. and U.D.
446 gratefully acknowledge financial support by the Vienna Science and Technology Fund
447 (WWTF).

References

- 448
449
450
451
452
453
454
455
456
457
458
459
460
461
462
463
464
465
466
467
468
469
470
471
472
473
474
475
476
477
478
479
- Abrams PA, Matsuda H, Harada Y (1993) Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evolutionary Ecology* 7:465-487
- Armsworth PR, Roughgarden JE (2005) Disturbance induces the contrasting evolution of reinforcement and dispersiveness in directed and random movers. *Evolution* 59:2083-2096
- Bengtsson BO (1978) Avoiding inbreeding: At what cost? *Journal of Theoretical Biology* 73:439-444
- Billiard S, Lenormand T (2005) Evolution of migration under kin selection and local adaptation. *Evolution* 59:13-23
- Bush GL, Smith JJ (1998) The genetics and ecology of sympatric speciation: A case study. *Researches on Population Ecology* 40:175-187
- Cadet C, Ferrière R, Metz JAJ, van Baalen M (2003) The evolution of dispersal under demographic stochasticity. *American Naturalist* 162:427-441
- Christiansen FB, Loeschcke V (1980) Evolution and intraspecific exploitative competition. I. One locus theory for small additive gene effects. *Theoretical Population Biology* 18:297-313
- Day T (2000) Competition and the effect of spatial resource heterogeneity on evolutionary diversification. *American Naturalist* 155:790-803
- Dieckmann U, Doebeli M (1999) On the origin of species by sympatric speciation. *Nature* 400:354-357
- Doebeli M (1996a) A quantitative genetic competition model for sympatric speciation. *Journal of Evolutionary Biology* 9:893-909
- Doebeli M (1996b) An explicit genetic model for ecological character displacement. *Ecology* 77:510-520
- Doebeli M, Blok HJ, Leimar O, Dieckmann U (2007) Multimodal pattern formation in phenotype distributions of sexual populations. *Proceedings of the Royal Society London Series B* 274:347-357
- Doebeli M, Dieckmann U (2000) Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *American Naturalist* 156:S77-S101
- Doebeli M, Dieckmann U (2003) Speciation along environmental gradients. *Nature* 421:259-263

- 480 Doebeli M, Ruxton GD (1997) Evolution of dispersal rates in metapopulation models:
481 Branching and cyclic dynamics in phenotype space. *Evolution* 51:1730-1741
- 482 Drossel B, McKane A (2000) Competitive speciation in quantitative genetic models. *Journal of Theoretical Biology* 204:467-478
- 484 Egas M, Dieckmann U, Sabelis MW (2004) Evolution restricts the coexistence of special-
485 ists and generalists: The role of trade-off structure. *American Naturalist* 163:518-531
- 486 Egas M, Sabelis MW, Dieckmann U (2005) Evolution of specialization and ecological
487 character displacement of herbivores along a gradient of plant quality. *Evolution* 59:507-
488 520
- 489 Ezoe H (1998) Optimal dispersal range and seed size in a stable environment. *Journal of*
490 *Theoretical Biology* 190:287-293
- 491 Felsenstein J (1981) Skepticism towards Santa Rosalia, or why are there so few kinds of
492 animals? *Evolution* 35:124-238
- 493 Filchack KE, Roethele JB, Feder JL (2000) Natural selection and sympatric divergence in
494 the apple maggot *Rhagoletis pomonella*. *Nature* 407:739-742
- 495 Frank SA (1986) Dispersal polymorphisms in subdivided populations. *Journal of Theoreti-*
496 *cal Biology* 122:303-309
- 497 Gandon S (1999) Kin competition, the cost of inbreeding and the evolution of dispersal.
498 *Journal of Theoretical Biology* 200:245-364
- 499 Gandon S, Michalakis Y (1999) Evolutionarily stable dispersal rate in a metapopulation
500 with extinctions and kin competition. *Journal of Theoretical Biology* 199:275-290
- 501 Garant D, Kruuk LEB, Wilkin TA, McCleery RH, Sheldon BC (2005) Evolution driven by
502 differential dispersal within a wild bird population. *Nature* 433:60-65
- 503 Geritz SAH, Kisdi É, Meszéna G, Metz JAJ (1998) Evolutionarily singular strategies and
504 the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology Re-*
505 *search* 12:35-57
- 506 Geritz SAH, Van der Meijden E, Metz JAJ (1999) Evolutionary dynamics of seed size and
507 seedling competitive ability. *Theoretical Population Biology* 55:324-343
- 508 Grimm V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J, Goss-Custard J, Grand T,
509 Heinz S, Huse G, Huth A, Jepsen JU, Jørgensen C, Mooij WM, Müller B, Pe'er G, Piou
510 C, Railsback SF, Robbins AM, Robbins MM, Rossmanith E, Rüger N, Strand E, Souissi
511 S, Stillman RA, Vabø R, Visser U, DeAngelis DL (2006) A standard protocol for de-
512 scribing individual-based and agent-based models. *Ecological Modelling* 198:115-126

513 Grimm V, Railsback SF (2005) *Individual-based Modeling and Ecology*. Princeton Univer-
514 sity Press

515 Grimm V, Revilla E, Berger U, Jeltsch F, Mooij WM, Railsback SF, Thulke HH, Weiner J,
516 Wiegand T, DeAngelis DL (2005) Pattern-oriented modeling of agent-based complex
517 systems: Lessons from ecology. *Science* 310:987-991

518 Gyllenberg M, Meszéna G (2005) On the impossibility of coexistence of infinitely many
519 strategies. *Journal of Mathematical Biology* 50:133-160

520 Hamilton WD, May RM (1977) Dispersal in stable habitats. *Nature* 269:578-581

521 Heinz SK, Strand E (2006) Adaptive patch searching strategies in fragmented landscapes.
522 *Evolutionary Ecology* 20:113-130

523 Higashi M, Takimoto G, Yamamura N (1999) Sympatric speciation by sexual selection.
524 *Nature* 402:523-526

525 Holt RD, McPeck MA (1996) Chaotic population dynamics favors the evolution of disper-
526 sal. *American Naturalist* 148:709-718

527 Hovestadt T, Messner S, Poethke HJ (2001) Evolution of reduced dispersal mortality and
528 ‘fat-tailed’ dispersal kernels in autocorrelated landscapes. *Proceedings of the Royal So-*
529 *ciety of London Series B* 268:385-391

530 Ito HC, Dieckmann U (2007) A new mechanism for recurrent adaptive radiations. *Ameri-*
531 *can Naturalist* 170:E96-E111

532 Jansen VAA, Mulder GSEE (1999) Evolving biodiversity. *Ecology Letters* 2:379-386

533 Johst K, Doebeli M, Brandl R (1999) Evolution of complex dynamics in spatially struc-
534 tured populations. *Proceedings of the Royal Society of London B* 266:1147-1154

535 Kawecki TJ (1997) Sympatric speciation via habitat specialization driven by deleterious
536 mutations. *Evolution* 51:1751-1763

537 Kisdi É (1999) Evolutionary branching under asymmetric competition. *Journal of Theoretic-*
538 *al Biology* 197:149-162

539 Kisdi É (2001) Long-term adaptive diversity in Levene-type models. *Evolutionary Ecology*
540 *Research* 3:721-727

541 Kisdi É (2004) Conditional dispersal under kin competition: Extension of the Hamilton-
542 May model to brood size-dependent dispersal. *Theoretical Population Biology* 66:369-
543 380

544 Kisdi É, Geritz SAH (2001) Evolutionary disarmament in interspecific competition. *Pro-*
545 *ceedings of the Royal Society of London B* 268:2589-2594

- 546 Kisdi É, Jacobs FJA, Geritz SAH (2001) Red Queen evolution by cycles of evolutionary
547 branching and extinction. *Selection* 2:161-176
- 548 Kondrashov AS, Kondrashov F (1999) Interactions among quantitative traits in the course
549 of sympatric speciation. *Nature* 400:351-354
- 550 Law R, Mallow P, Dieckmann U (1997) On evolution under asymmetric competition. *Evo-*
551 *lutionary Ecology* 11:485-501
- 552 Leimar O, Doebeli M, Dieckmann U (2008) Evolution of phenotypic clusters through com-
553 petition and local adaptation along an environmental gradient. *Evolution*, in press
- 554 MacArthur RH, Levins R (1967) The limiting similarity, convergence, and divergence of
555 coexisting species. *American Naturalist* 101:377-385
- 556 Mathias A, Kisdi É, Olivieri I (2001) Divergent evolution of dispersal in a heterogeneous
557 landscape. *Evolution* 55:246-259
- 558 May RM, MacArthur RH (1972) Niche overlap as a function of environmental variability.
559 *Proceedings of the National Academy of Science of the USA* 19:1109-1113
- 560 Maynard Smith J (1966) Sympatric speciation. *American Naturalist* 100:637-650
- 561 Maynard Smith J, Brown RL (1986) Competition and body size. *Theoretical Population*
562 *Biology* 30:166-179
- 563 McPeck MA, Holt RD (1992) The evolution of dispersal in spatially and temporally vary-
564 ing environments. *American Naturalist* 140:1010-1027
- 565 Meszéna G, Czibula I, Geritz SAH (1997) Adaptive dynamics in a 2-patch environment: A
566 toy model for allopatric and parapatric speciation. *Journal of Biological Systems* 5:265-
567 284
- 568 Metz JAJ, Geritz SAH, Meszéna G, Jacobs FJA, van Heerwaarden JS (1996) Adaptive dy-
569 namics: A geometrical study of the consequences of nearly faithful reproduction. In
570 *Stochastic and Spatial Structures of Dynamical Systems*, Proceedings of the Royal
571 Dutch Academy of Science (KNAW Verhandelingen), eds. van Strien SJ, Verduyn Lu-
572 nel SM, pp. 183-231. Dordrecht, Netherlands:North Holland
- 573 Mizera F, Meszéna G (2003) Spatial niche packing, character displacement and adaptive
574 speciation along an environmental gradient. *Evolutionary Ecology Research* 5:363-382
- 575 Motro U (1991) Avoiding inbreeding and sibling competition: The evolution of sexual di-
576 morphism for dispersal. *American Naturalist* 137:108-115
- 577 Murrell DJ, Dytham C, Travis JMJ (2002) The evolution of dispersal distance: Conse-
578 quences for population dynamics. *Oikos* 97:229-236

579 Olivieri I, Michalakis Y, Gouyon PH (1995) Metapopulation genetics and the evolution of
580 dispersal. *American Naturalist* 146:202-228

581 Parvinen K (2002) Evolutionary branching of dispersal strategies in structured metapopula-
582 tions. *Journal of Mathematical Biology* 45:106-124

583 Parvinen K, Dieckmann U, Gyllenberg M, Metz JAJ (2003) Evolution of dispersal in meta-
584 populations with local density dependence and demographic stochasticity. *Journal of*
585 *Evolutionary Biology* 16:143-153

586 Pigolotti S, López C, Hernández-García E (2007) Species clustering in competitive Lotka-
587 Volterra models. *Physical Review Letters* 98:258101

588 Poethke HJ, Hovestadt T (2002) Evolution of density and patch-size dependent dispersal
589 rates. *Proceedings of the Royal Society of London Series B* 269:637-645

590 Polechová J, Barton NH (2005) Speciation through competition: A critical review. *Evolu-*
591 *tion* 59:1194-1210

592 Postma E, van Noordwijk AJ (2005) Gene flow maintains a large genetic difference in
593 clutch size at a small spatial scale. *Nature* 433:65-68

594 Ronce O, Brachet B, Olivieri I, Gouyon PH, Clobert J (2005) Plastic changes in seed dis-
595 persal along ecological succession: Theoretical predictions from an evolutionary model.
596 *Journal of Ecology* 93:431-440

597 Ronce O, Perret F, Olivieri I (2000) Evolutionary stable dispersal rates do not always in-
598 crease with local extinction rates. *American Naturalist* 155:485-496

599 Rosenzweig ML (1978) Competitive speciation. *Biological Journal of the Linnean Society*
600 10:275-289

601 Roughgarden J (1974) Species packing and the competition function with illustrations from
602 coral reef fish. *Theoretical Population Biology* 5:163-186

603 Rousset F, Gandon S (2002) Evolution of the distribution of dispersal distance under dis-
604 tance-dependent cost of dispersal. *Journal of Evolutionary Biology* 15:515-523

605 Sasaki A (1997) Clumped distribution by neighborhood competition. *Journal of Theoretical*
606 *Biology* 186:415-430

607 Sasaki A, Ellner S (1995) The evolutionarily stable phenotype distribution in a random en-
608 vironment. *Evolution* 40:337-350

609 Savill NJ, Hogeweg P (1998) Spatially induced speciation prevents extinction: The evolu-
610 tion of dispersal distance in oscillatory predator-prey systems. *Proceedings of the Royal*
611 *Society of London Series B* 265:25-32

- 612 Schliewen U, Rassmann K, Markmann M, Markert J, Kocher T, Tautz D (2001) Genetic
613 and ecological divergence of a monophyletic cichlid species pair under fully sympatric
614 conditions in Lake Ejagham, Cameroon. *Molecular Ecology* 10:1471-1488
- 615 Schliewen UK, Tautz D, Pääbo S (1994) Sympatric speciation suggested by monophyly of
616 crater lake cichlids. *Nature* 368:629-632
- 617 Schreiber SJ, Tobiason GA (2003) The evolution of resource use. *Journal of Mathematical*
618 *Biology* 47:56-78
- 619 Seger J (1985) Intraspecific resource competition as a cause of sympatric speciation. In
620 *Evolution: Essays in Honour of John Maynard Smith*, eds. Greenwood PJ, Harvey PH,
621 Slatkin M, pp. 43-53. Cambridge, UK: Cambridge University Press
- 622 Slatkin M (1973) Gene flow and selection in a cline. *Genetics* 75:733-756
- 623 Slatkin M (1980) Ecological character displacement. *Ecology* 61:163-177
- 624 Taper ML, Case TJ (1985) Quantitative genetic models for the coevolution of character dis-
625 placement. *Ecology* 66:355-371
- 626 Taylor PD (1988) An inclusive fitness model for dispersal of offspring,. *Journal of Theo-*
627 *retical Biology* 130:363-378
- 628 Travis JMJ (2001) The color of noise and the evolution of dispersal. *Ecological Research*
629 16:157-163
- 630 Travis JMJ, Dytham C (1998) The evolution of dispersal in a metapopulation: A spatially
631 explicit, individual-based model. *Proceedings of the Royal Society London B* 265:17-23
- 632 Turelli M, Barton NH, Coyne JA (2001) Theory and speciation. *Trends in Ecology and*
633 *Evolution* 16:330-343
- 634 Turesson G (1922) The genotypical response of the plant species to the habitat. *Hereditas*
635 3:211-350
- 636 Turner GF, Burrows MT (1995) A model of sympatric speciation by sexual selection. *Pro-*
637 *ceedings of the Royal Society of London B* 260:287-292
- 638 Van Valen L (1971) Group selection and the evolution of dispersal. *Evolution* 25:591-598
- 639 Via S (2001) Sympatric speciation in animals: The ugly duckling grows up. *Trends in Ecol-*
640 *ogy and Evolution* 16:381-390
- 641 Vincent TL, Cohen Y, Brown JS (1993) Evolution via strategy dynamics. *Theoretical*
642 *Population Biology* 44:149-176
- 643 Waser NM (1986) Flower constancy: Definition, cause, and measurement. *American Natu-*
644 *ralist* 127:593-603

- 645 Wilson AB, Noack K, Meyer A (2000) Incipient speciation in sympatric Nicaraguan crater
646 lake cichlid fishes: Sexual selection vs. ecological diversification. Proceedings of the
647 Royal Society of London Series B 267:2133-2141
- 648 Wright S (1943) Isolation by distance. Genetics 28:114-138

649 **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	σ_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	σ_c	variable
Standard deviation of spatial competition function, scaling the reduction of competition strength with increased spatial distance between individuals	σ_s	0.2
Slope of environmental gradient	g	variable
Per capita birth rate, scaling time	b	1
Mutation probability	μ_m	0.02
Standard deviation of distribution of mutation effects	σ_m	0.01
Scaled standard deviation of phenotypic competition function	c	σ_c / σ_K
Scaled slope of environmental gradient	s	$g\sigma_s / \sigma_K$

650 **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 imperme-
652 able. (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
663 (scaled slope of environmental gradient) and c (scaled width of phenotypic competition
664 function). (b) Dependence of scaled dispersal distances on s , for three different values of
665 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

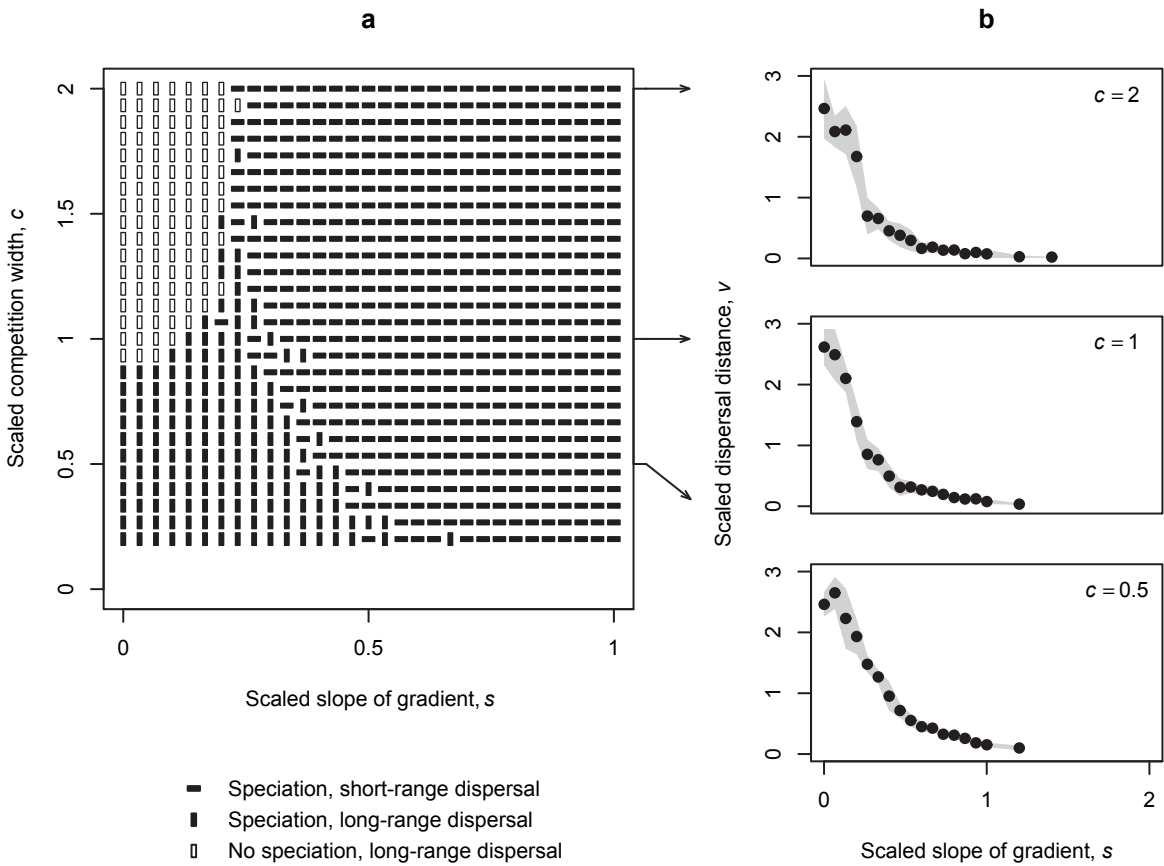


Figure 2

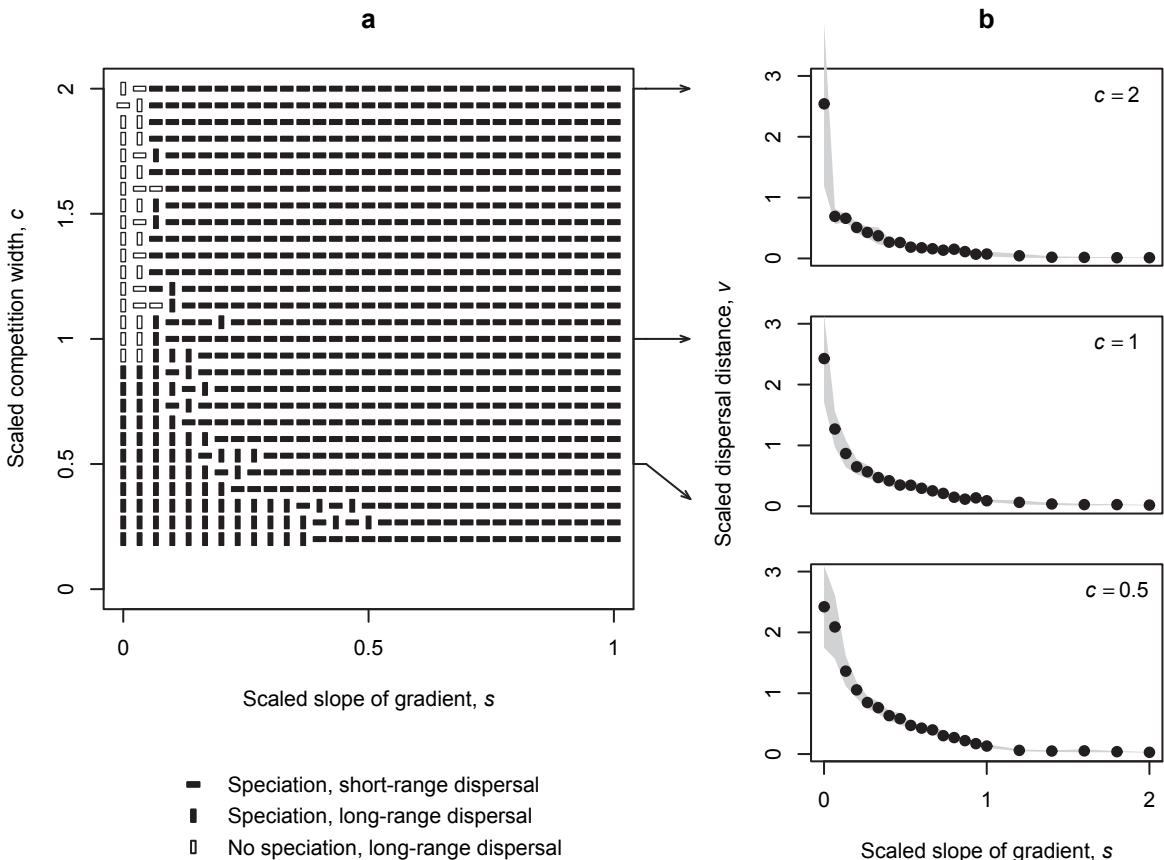


Figure 3

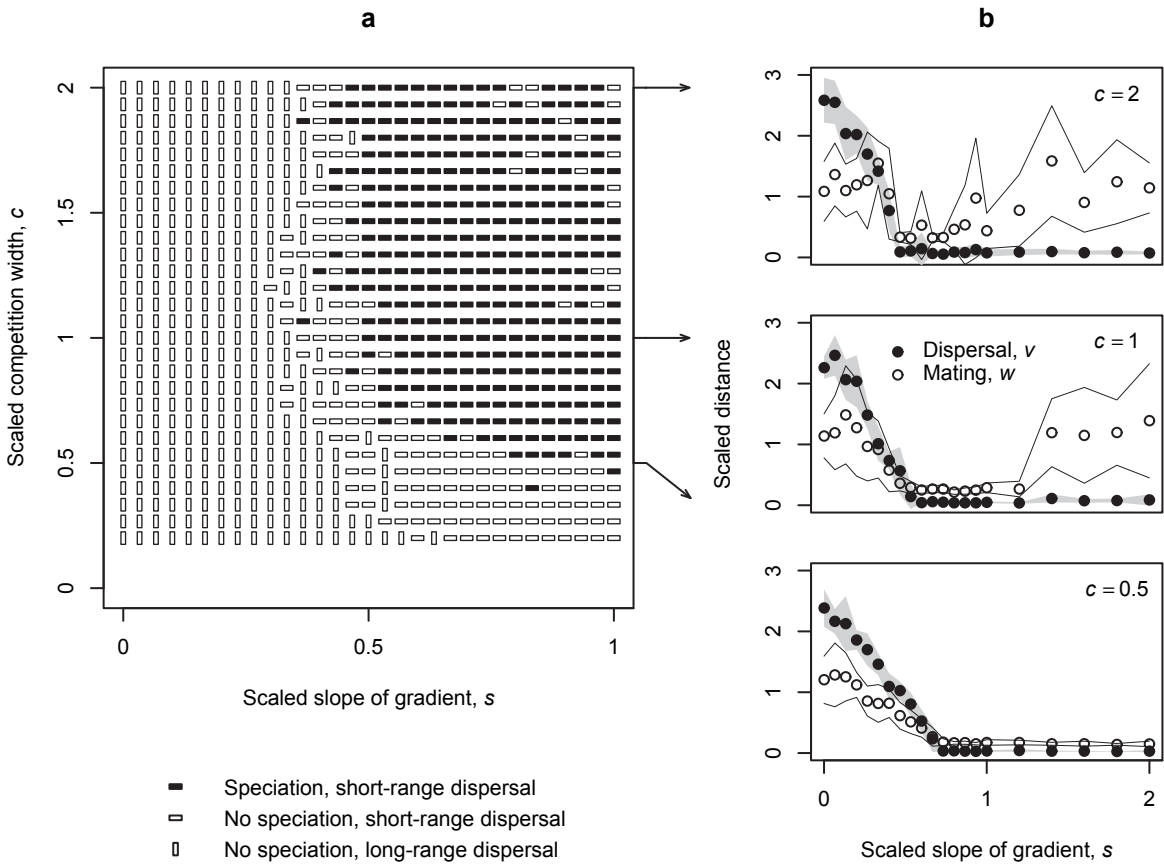


Figure 4

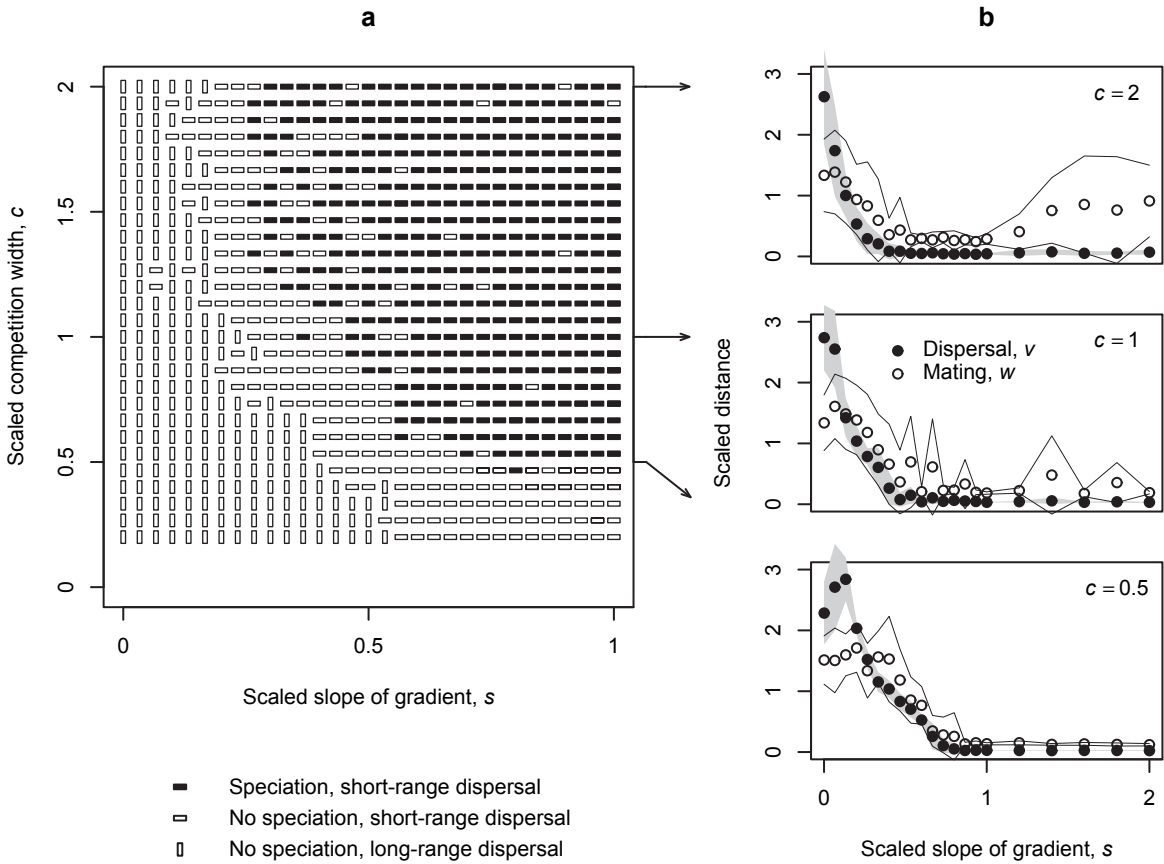
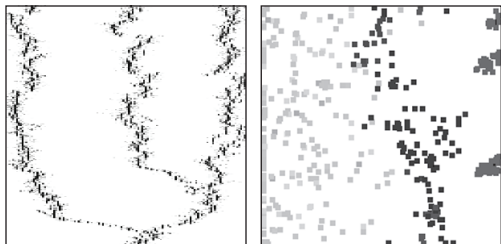


Figure 5

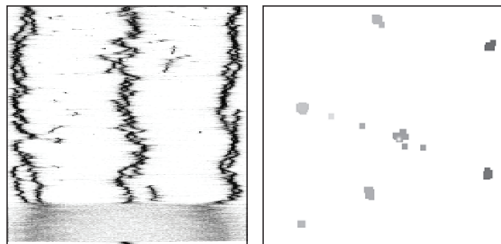
Asexual populations

Sexual populations

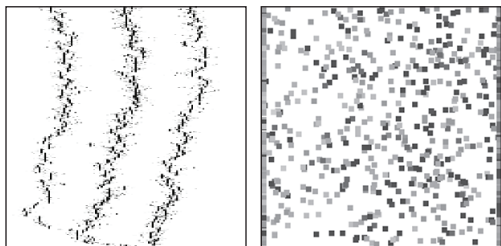
a



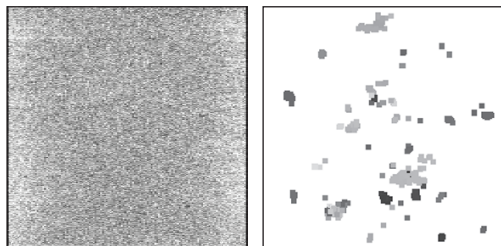
d



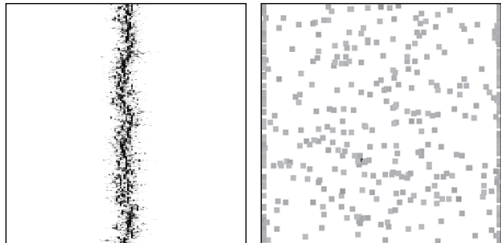
b



e



c



f

