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## Interim Report

IR-12-050

### **Sexual selection enables long-term coexistence despite ecological equivalence**

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#### **Approved by**

Pavel Kabat  
Director General and Chief Executive Officer

February 2015

**Running head:** SEXUAL SELECTION AND COEXISTENCE

# Sexual selection enables long-term coexistence despite ecological equivalence

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4        **Empirical data indicate that sexual preferences are critical for maintaining species**  
5 **boundaries<sup>1-4</sup>, yet theoretical work has suggested they can play only a minimal role**  
6 **in maintaining biodiversity on their own<sup>5-9</sup>. This is because long-term coexistence**  
7 **within overlapping ranges is thought to be unlikely in the absence of ecological**  
8 **differentiation<sup>9</sup>. Here we challenge this widely held view by generalizing a standard**  
9 **model of sexual selection to include two ubiquitous features of populations with**  
10 **sexual selection: spatial variation in local carrying capacity and mate-search costs in**  
11 **females. We show that, when these two features are combined, sexual preferences can**  
12 **single-handedly maintain coexistence, even when spatial variation in local carrying**  
13 **capacity is so slight that it might go unnoticed empirically. This is the first theoretical**  
14 **study to demonstrate that sexual selection alone can promote the long-term**  
15 **coexistence of ecologically equivalent species with overlapping ranges, and it thus**  
16 **provides a novel explanation for the maintenance of species diversity.**

17        A central objective of evolutionary ecology is to understand the mechanisms that  
18 allow species coexistence. One such mechanism is ecological differentiation. By  
19 occupying different niches, species in overlapping ranges are able to reduce direct  
20 competition among one another<sup>10</sup>. While there are numerous examples of closely related  
21 species occupying different ecological niches, many recently diverged and coexisting  
22 taxa are known to differ most dramatically in their secondary sexual characters,  
23 exhibiting few, if any, ecological differences<sup>1-4</sup>. It seems, therefore, that sexual selection  
24 is an important mechanism for maintaining coexistence. Indeed, models of sexual  
25 selection have shown that populations of choosy females and their preferred males can  
26 arise and, under various conditions, form reproductively isolated mating groups<sup>11-15</sup>.  
27 However, because sexual selection does not lead to ecological differentiation, species  
28 differing only in their mating preferences compete for the same ecological niche. This  
29 has traditionally led to the conclusion that, if their ranges overlap, one of these species

30 will eventually displace the other<sup>5-9</sup>.

31 Coexistence is facilitated by mechanisms that reduce range overlap among species.  
32 Sexual selection provides one such mechanism. Any process that creates spatial variation  
33 in female preferences indirectly also creates selection on male display traits, locally  
34 favouring those males that are most preferred by the local females. As a consequence,  
35 spatially segregated mating domains, characterized by the co-occurrence of matching  
36 display and preference traits, can emerge from populations with an initially random  
37 spatial distribution. Once segregated, interactions between different mating types are  
38 limited to individuals at the peripheries of these domains. In finite populations,  
39 however, the mating domains may shrink or grow, and the interface between them may  
40 drift randomly in space. Such fluctuations eventually lead to one mating domain  
41 replacing all others (Fig. 1a, c). In a pioneering study, Payne and Krakauer<sup>16</sup> argued that  
42 lower dispersal in males with better mating prospects facilitates spatial segregation and  
43 maintains coexistence. In finite populations, however, such mating-dependent dispersal  
44 fails to stabilize long-term coexistence (Fig. S3). Given these difficulties associated with  
45 sexual selection, a recent review concluded that sexually divergent, but ecologically  
46 equivalent, species cannot coexist for significant lengths of time<sup>9</sup>.

47 Here we report model results that suggest the contrary and demonstrate that sexual  
48 selection can promote long-term coexistence, even without any ecological  
49 differentiation. Building on a standard model of sexual selection<sup>14</sup>, we develop an  
50 individual-based model to examine the long-term fate of species differing only in their  
51 secondary sexual characters in an ecologically neutral context with finite population  
52 sizes (details in Supplementary Information, SI). We assume a simple genetic structure  
53 with two unlinked haploid loci: the first locus (with alleles  $Q$  and  $q$ ) governs a display  
54 trait that is expressed only in males, while the second (with alleles  $P$  and  $p$ ) governs a

55 preference trait that is expressed only in females (more than two alleles and quantitative  
56 mating traits are considered in the SI and Fig. 4c–d). Because we are interested in  
57 coexistence, and not speciation, we assume that the genetic variation at both loci is  
58 already present, for example, due to recent migration from allopatric ranges. All else  
59 being equal, females bearing a  $P$  ( $p$ ) allele prefer<sup>14–16</sup> to mate with males carrying a  $Q$  ( $q$ )  
60 allele by a factor  $\alpha$ , and a female's preference for a given male attenuates with increasing  
61 distance between them. Likewise, competition decreases as the distance between  
62 individuals increases. Competition is assumed to reduce an individual's probability of  
63 surviving until reproductive maturity (similar results are obtained if competition  
64 reduces fecundity, Fig. S4). Importantly, hybrids suffer no intrinsic fitness costs, other  
65 than potentially carrying mismatched preference and trait alleles.

66 Mating domains can be lost either through movement of the interface between  
67 them, or when individuals of one mating type colonize the domain of another mating  
68 type. In particular, because selection at the preference locus disappears when there is no  
69 variation at the display locus, foreign preference alleles may drift into regions with low  
70 variation in male display alleles, eventually causing displacement. Loss of mating  
71 domains can, however, be prevented by including two features ubiquitous in  
72 populations experiencing sexual selection: spatial variation in local carrying capacity  
73 and mate-search costs in females. Spatial variation in carrying capacity is present in  
74 most, if not all, biological systems (see Figs. 1 and 4 and the SI for model details).  
75 Mate-search costs occur if a female spends time and energy looking for a suitable mate  
76 and rejecting non-preferred males, thereby reducing her ability to invest in offspring. To  
77 account for such costs we assume that the fecundity of a particular female increases from  
78 0 to a maximum level with the local density of available males, weighted according to  
79 her preference (SI).

80 Our model confirms the longstanding view that sexual selection in homogeneous  
81 spatial models, without mate-search costs, does not facilitate coexistence and can, in fact,  
82 hasten the loss of diversity (compare Fig. 2a to 2b). Spatial variation in local carrying  
83 capacity, on its own, also has little, if any, effect in stabilizing populations (compare  
84 Fig. 2b to 2c). Sexual selection with mate-search costs slightly prolongs coexistence in a  
85 spatially homogeneous environment by helping to prevent mixing of the mating  
86 domains, but this effect is weak (Fig. 2d). However, in an environment with spatial  
87 variation in local carrying capacity, sexual selection with mate-search costs dramatically  
88 increases coexistence times (compare Fig. 2e to Fig. 2b and also Fig. 1a, c to Fig. 1b, d). In  
89 this case, mate-search costs curb the neutral drift of preference alleles, thus preventing  
90 the dilution of mating domains, while areas of high local carrying capacity provide  
91 spatial “anchors”, stabilizing the location and size of these domains (Fig. 1b, d).

92 While neither spatial variation in local carrying capacity nor mate-search costs  
93 suffice on their own to stabilize populations, surprisingly little of both can be enough to  
94 ensure the long-term persistence of divergent mating types (Fig. 3). When mate-search  
95 costs in females are high, long-term coexistence can be maintained with less than 20%  
96 spatial variation in local carrying capacity. When mate-search costs are low, 50% spatial  
97 variation in local carrying capacity is sufficient to stabilize mating domains. Throughout,  
98 we have kept population sizes relatively small, so as to exacerbate the challenge of  
99 coexistence in finite populations. When population sizes are larger, we find that as little  
100 as 10% variation in local carrying capacity suffices to stabilize mating domains  
101 (Fig. S5d). Levels of variation in this range may be difficult to detect in nature, especially  
102 if they are to be inferred from observing the stochastic spatial distribution of individuals.

103 The stabilizing effect of spatial variation in local carrying capacity and mate-search  
104 costs readily extends to more realistic and natural landscapes (Fig. 4) and also to multiple



105 genotypes (Fig. 4c–d) . As long as spatial variation in local carrying capacity does not  
106 become so insignificant that it hardly affects the landscape, or so asymmetric that a  
107 single local population dominates, different mating domains are maintained in mosaic  
108 sympatry<sup>17,18</sup> (Fig. S7). Our findings are also robust to changes in female-preference  
109 strength, mate-search distance, movement distance, and competition distance (Figs. S5a,  
110 S6), to changes in the relative importance of ecological competition versus sexual  
111 selection (Fig. S5b–c), to changes in the genetic architecture of the display and preference  
112 traits (Fig. S8), and to including selective differences between male display traits  
113 (Fig. S9). Generally, long-term coexistence occurs if female preferences are sufficiently  
114 strong to prevent extensive interbreeding, and if individuals move and interact on a  
115 spatial scale such that they are affected by spatial variation in local carrying capacity.  
116 This phenomenon can be interpreted more generally: whenever positive frequency  
117 dependence creates multiple stable states, global coexistence of these states becomes  
118 possible in a spatially structured environment if this structure allows the domains in  
119 which those states are realized to become anchored in space. In this vein, our results in  
120 Fig. 4 extend a previous finding from theoretical work on hybrid zones, predicting that  
121 the spatial interface between species moves in space until settling in a region of low  
122 population density<sup>19,20</sup>. Similarly, earlier theoretical work<sup>21</sup> using habitat boundaries for  
123 anchoring mating-domains, has shown that ecologically equivalent types can coexist  
124 when fecundity drops, or mortality or mobility rise, in the company of heterospecifics.

125 Because both spatial variation in local carrying capacity and costs associated with  
126 mate search are ubiquitous in nature, our model may provide an explanation for the  
127 coexistence of many species whose reproductive barriers primarily involve mating  
128 preferences. For example, local habitat availability and quality vary around the shoreline  
129 of Lake Victoria<sup>22</sup>. The mechanism reported here could help explain how ecologically  
130 similar cichlid species can coexist in such vast diversity. That sexual differences have

131 been a primary force maintaining cichlid species' boundaries is supported by the  
132 increasing frequency of hybridization that is occurring as a consequence of high  
133 turbidity levels, which reduce a female's ability to discern male phenotypes<sup>22</sup>. Similar  
134 explanations could plausibly be applied to other species that seem to be largely  
135 maintained by sexual selection (e.g., species of fruit flies<sup>23</sup>, weakly electric fish<sup>24</sup>,  
136 frogs<sup>25</sup>, crickets<sup>3</sup>, and grasshoppers<sup>26</sup>, among others). To test this hypothesis, one could  
137 analyse spatial associations between mating domains and local carrying capacity: Fig. 4  
138 suggests that boundaries of mating domains often align with troughs of low local  
139 carrying capacity.

140 Our work demonstrates that, with variation in local carrying capacity over space  
141 and costs to females that encounter few preferred mates, sexual selection can maintain  
142 species that are not ecologically differentiated. This is in stark contrast to the widespread  
143 opinion that sexual selection, on its own, is unable to maintain ecologically equivalent  
144 species that overlap in space. Throughout, we have deliberately avoided making any  
145 claims about the emergence of diversity and speciation, choosing instead to focus on the  
146 coexistence of mating types. Further theoretical work is, therefore, needed to determine  
147 which conditions are most conducive to the initial appearance of multiple mating types,  
148 and further empirical work is needed to show how the mechanism presented here helps  
149 explain natural patterns of coexistence and diversity.

## 150 **Methods Summary**

151 We develop an individual-based model of sexual selection<sup>14</sup> in a spatially explicit  
152 ecological framework. Individuals are distributed across a continuous habitat in one or  
153 two dimensions with wrap-around boundaries. All individuals compete for resources,

154 whose density at any location is given by a local carrying capacity. Except where noted,  
155 the local carrying capacity exhibits two peaks, each of the same Gaussian shape.  
156 Competition reduces an individual's resource share, and thereby its survival probability,  
157 with the competitive impact of other individuals decreasing with distance according to a  
158 Gaussian function. Surviving females encounter surviving males with a probability  
159 decreasing with distance according to a Gaussian function, and females choose mates  
160 based on their preferences for the male's displays. After mating, females produce  
161 offspring in proportion to their fecundities, which are lower for females who  
162 experienced higher mate-search costs. After producing offspring, the parents die and the  
163 offspring move a distance drawn from a Gaussian function in a direction chosen at  
164 random. While the female preference trait and the male display trait are genetically  
165 based (each being determined by a diallelic locus, except where noted), there are no  
166 genetic differences in ecological function or competitive ability among individuals,  
167 which are, therefore, all ecologically equivalent. See SI for complete model details and  
168 for information about alternative models explored to examine the robustness of our  
169 results.

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## 181 **Author Contributions**

182 U.D. and L.K.M. conceived this project. L.K.M., R.M., S.P.O., and U.D. discussed and  
183 designed the model. L.K.M. implemented the model with input from R.M., analysed the  
184 results together with R.M., S.P.O., and U.D. and prepared the manuscript. L.K.M., R.M.,  
185 S.P.O., and U.D. jointly edited the manuscript.

## 186 **Author Information**

187 Simulation code is available at [www.zoology.ubc.ca/prog/coexist](http://www.zoology.ubc.ca/prog/coexist). Correspondence and  
188 requests for materials should be addressed to L.K.M. ([mgonigle@zoology.ubc.ca](mailto:mgonigle@zoology.ubc.ca)).

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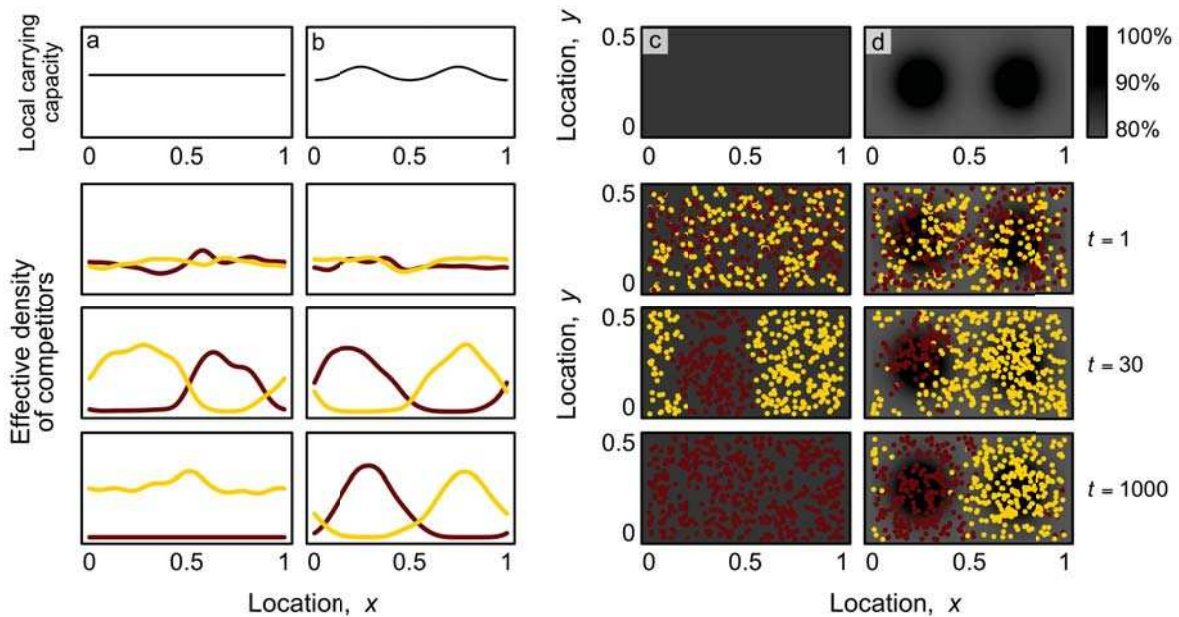


Figure 1: Sexual selection enables long-term coexistence of ecologically equivalent species. We consider a population distributed across a continuous habitat in one dimension (columns **a**, **b**) or two dimensions (columns **c**, **d**) with a local carrying capacity that is either spatially uniform (**a**, **c**: top panels) or that exhibits two peaks (**b**, **d**: top panels). Each peak is of Gaussian shape with standard deviation  $\sigma_k$ . The level  $v$  of spatial variation may be altered by changing the height of these peaks relative to the troughs between them. A value of  $v = 0.25$ , as in **b** and **d**, means that local carrying capacity at the peaks is elevated by 25%. The three lower rows show model runs through time. Each generation, individuals survive after a round of local competition and reproduce after a round of local mating, followed by offspring movement and the death of all parents. Competition between individuals decreases with their distance according to a Gaussian function with standard deviation  $\sigma_s$ . Coloured curves in **a** and **b** show the effective local density of competitors of each type (weighted by their competitive effect, SI, Eq. 4), while dots in **c** and **d** show surviving adults. Individuals are coloured according to their display locus genotype (similar patterns are observed at the preference locus; Fig. S2). Females are  $\alpha$  times more likely to mate with a preferred male, when encountered. Males are encountered with a probability that decreases with the distance between them and the female according to a Gaussian function with standard deviation  $\sigma_f$ . Female fecundity declines with the strength of mate-search costs  $m$ . Movement distances are drawn from a Gaussian function with standard deviation  $\sigma_m$ , centered at 0, with wrap-around boundaries. The total carrying capacity is  $K = 500$ , supporting the survival of approximately half of the  $N = 1000$  offspring produced each generation; other parameters:  $\sigma_k = 0.1$ ,  $\sigma_s = 0.05$ ,  $\alpha = 5$ ,  $\sigma_f = 0.05$ ,  $\sigma_m = 0.05$ , and  $m/K = 1$  (roughly halving fecundity, Fig. S1).



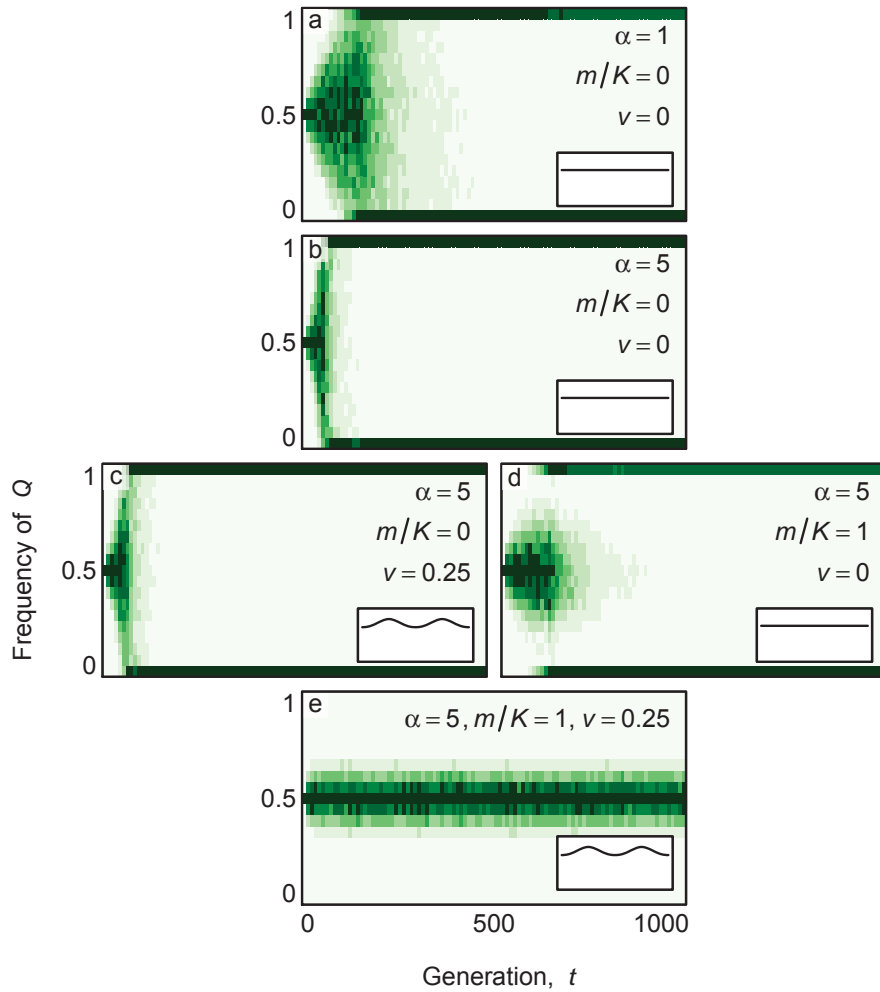


Figure 2: Conditions for long-term coexistence. Panels show distributions of allele frequencies at the display locus through time across 1000 model runs in a two-dimensional landscape; coexistence occurs only while these frequencies remain intermediate. Inset panels depict the spatial variation in local carrying capacity as viewed along transects at  $y = 0.25$ . **a** Homogeneous environment with no sexual selection ( $\alpha = 1$ ). **b** Same as a, except that females are choosy ( $\alpha = 5$ ). **c** Same as b, except with variation in local carrying capacity ( $v = 0.25$ ). **d** Same as b, except with mate-search costs in females ( $m/K = 1$ ). **e** Same as b, except with spatial variation in local carrying capacity ( $v = 0.25$ ) and mate-search costs in females ( $m/K = 1$ ); only when both features are combined is long-term coexistence observed. To focus on the maintenance of coexistence, we begin with two equally sized and spatially segregated populations of  $PQ$  and  $pq$  genotypes (all individuals on the left half of the arena initially have the  $PQ$  genotype, while all individuals on the right initially have the  $pq$  genotype). This mimics a scenario in which types that previously arose in allopatry come back into contact, revealing the conditions under which they can persist in sympatry. All other parameters are as in Fig. 1.

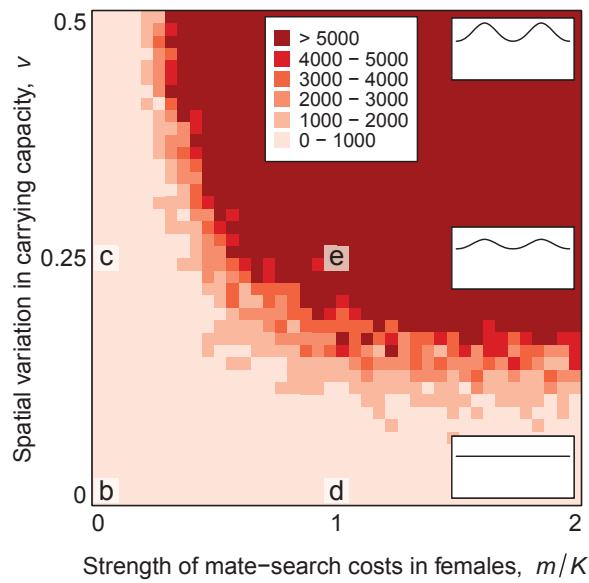


Figure 3: Conditions for long-term coexistence. Shading indicates the number of generations that polymorphism at the display locus persists when females are choosy ( $\alpha = 5$ ) in a two-dimensional landscape (darker = longer). Each cell represents the mean time to loss of polymorphism for 10 replicate model runs. Letters indicate parameter combinations used to generate the lower four panels in Fig. 2. Inset panels illustrate the extent of spatial variation in local carrying capacity for the three parameter values shown along the vertical axis. Model runs are initialized as in Fig. 2. All other parameters are as in Fig. 1.

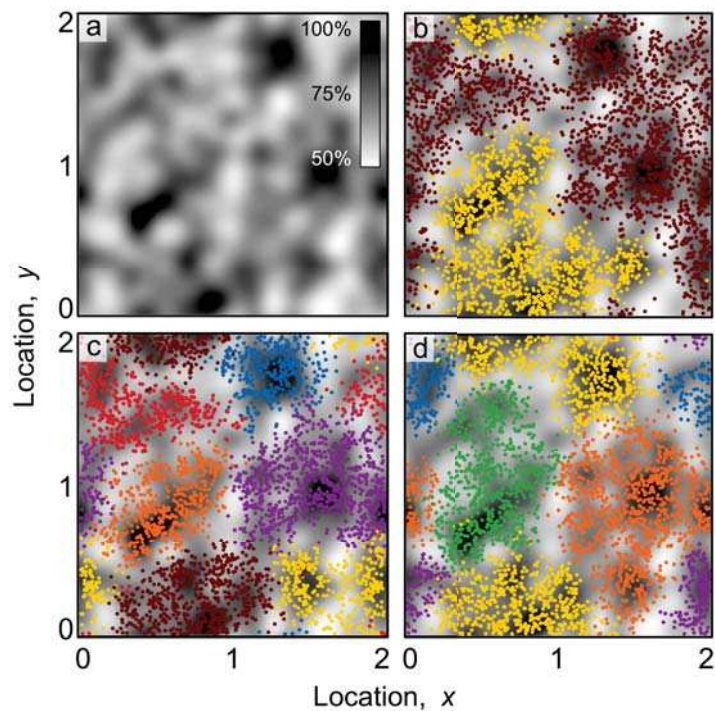


Figure 4: Mosaic sympatry. Four representative model runs in a patchy two-dimensional landscape with random variation in local carrying capacity. Panel **a** depicts the underlying spatial variation in local carrying capacity, while panels **b–d** show results from independent model runs after 10,000 generations overlaid on the local carrying capacity. Panel **b** is initialized with two types, whereas panels **c** and **d** are initialized with ten display alleles and ten corresponding preference alleles, all at equal frequencies and distributed randomly across the arena (SI, Section S2.2). Some of these alleles are then lost during the colonization phase. As in Fig. 1, individuals are coloured according to their genotype at the display locus. The spatial arena is eight times larger than in Fig. 1 and the total carrying capacity is  $K = 4000$ , supporting the survival of approximately half of the  $N = 8000$  offspring produced each generation. All other parameters are as in Fig. 1 (except for  $v$ , which is defined specifically for bimodal landscapes); for comparison, the coefficient of variation in local carrying capacity is 0.125 here, compared with 0.066 in Fig. 1d.

# Supplementary Information

247

## S1 Model description

248

249 We consider an individual-based model with discrete non-overlapping generations in  
250 one- or two-dimensional continuous space with wrap-around boundaries. Below, we  
251 describe the two-dimensional model, from which the corresponding one-dimensional  
252 model is readily generated by removing the spatial  $y$ -dimension. Each individual has a  
253 spatial location and is characterized by a display trait (expressed only in males) and a  
254 preference trait (expressed only in females). In our main set of model runs, these traits  
255 are assumed to be governed by separate unlinked haploid loci, each with two alleles  
256 (display alleles are denoted by  $Q/q$  and preference alleles by  $P/p$ ). Each generation,  $N$   
257 individuals are produced and compete for resources, with those experiencing stronger  
258 competition being more likely to die before reaching reproductive maturity. Resources in  
259 our model may be interpreted in the broadest possible sense, describing the biotic and  
260 abiotic factors that are subject to local ecological competition. Among the individuals  
261 surviving ecological competition, females choose mates, with the probability of a specific  
262 male being chosen depending on her mating preference and the spatial distance  
263 separating them. Females produce offspring in proportion to their fecundities. Offspring  
264 then disperse from their natal location and the parents die. Below we detail these steps  
265 in the order in which they occur. The names and descriptions of all parameters and  
266 variables are listed in Table S1.

## 267 **S1.1 Competition for resources**

268 The habitat at each location  $(x, y)$  is characterized by the local density  $k(x, y)$  of available  
269 resources. The total amount of resources over the spatial arena is given by  
270  $K = \iint k(x, y) dx dy$ . The function relating resource gain to survival is chosen such that  
271 if every individual received an equal share of these resources, the expected number of  
272 survivors would be  $K$ . Consequently, we refer to  $k(x, y)$  as the local carrying capacity  
273 and to  $K$  as the total carrying capacity. Except for Figs. 4 and S7, we investigate a local  
274 carrying capacity that is symmetrically bimodal, with two peaks located at  
275  $(x, y) = (0.25, 0.25)$  and  $(x, y) = (0.75, 0.25)$ . If we considered only these two focal  
276 Gaussians, the resource availability would not be symmetric about the peaks. To avoid  
277 such an asymmetry, we constructed a periodic landscape given by

$$k(x, y) = \left( b + \sum_{i,j} \exp\left(-\frac{(x - (0.25 + i/2))^2 + (y - (0.25 + j/2))^2}{2\sigma_k^2}\right) \right) k_0, \quad (1)$$

278 for  $x$  in  $[0, 1]$  and  $y$  in  $[0, 0.5]$ , where the sum is taken over all pairs of integers, and where  
279  $\sigma_k$  denotes the widths of the Gaussian peaks. The parameters  $b$  and  $k_0$  allow us to adjust  
280 the average height and degree of variation in  $k(x, y)$ . Specifically, the height is adjusted  
281 such that the total carrying capacity equals  $K$ , and the degree of variation is adjusted to  
282 give the desired relation between peaks and troughs. For the local carrying capacity in  
283 Eq. (1), it is natural, for easy comparison between the one-dimensional and the  
284 two-dimensional model, to measure the degree of spatial variation along the transect  
285 spanning both peaks as

$$v = \frac{\max k(x, y) - \min k(x, y)}{\min k(x, y)}. \quad (2)$$

286 A value of  $v = 0.25$  therefore means that the local carrying capacity is 25% higher at the  
287 peaks than at the troughs between them. For Fig. S7, landscapes are generated in a

288 similar way, except that the heights and widths of the two peaks differ. For Fig. 4, the  
 289 landscape is generated by adding white noise to the baseline level, filtered to have a  
 290 reasonable amount of spatial autocorrelation, with the highest peak set to twice the  
 291 height of the lowest trough.

292 Through competition, each individual obtains a share of the local carrying capacity,  
 293 which we refer to as its resource share,

$$\rho_i = \frac{k(x_i, y_i)}{\sum_j n_{ij}}, \quad (3)$$

294 where  $n_{ij}$  is the contribution of individual  $j$  to the effective density of competitors at the  
 295 location of individual  $i$ , and the sum extends over all  $N$  individuals. The competitive  
 296 impact of individual  $j$  on individual  $i$  decreases with the distance  $d_{ij}$  separating them,  
 297 according to a Gaussian function with standard deviation  $\sigma_s$ ,

$$n_{ij} = \exp(-d_{ij}^2 / (2\sigma_s^2)) / (2\pi\sigma_s^2); \quad (4)$$

298 in the one-dimensional model, the divisor is  $\sqrt{2\pi}\sigma_s$ . Note that the effect  $n_{ii}$  of an  
 299 individual  $i$  on itself declines as  $\sigma_s$  increases, because the individual then competes for  
 300 resources over larger distances and thus has less of a negative impact on its available  
 301 resources.

302 As defined, the resource share of an individual  $i$  is approximately  $K/N$ . This can be  
 303 seen by assuming that the  $N$  individuals in the population are distributed over the arena  
 304 according to the local carrying capacity, so that their expected density is  $Nk(x, y)/K$ .

305 Replacing the sum over individuals in Eq. 3 with an integral over space, we obtain

$$\begin{aligned}\rho_i &= \frac{k(x_i, y_i)}{\iint \frac{N k(x, y)}{K} \frac{\exp(-((x_i - x)^2 + (y_i - y)^2) / (2\sigma_s^2))}{2\pi\sigma_s^2} dx dy} \\ &= K/N + O(v),\end{aligned}\tag{5}$$

306 where the second line assumes that spatial variation in the local carrying capacity is low.  
307 In our individual-based model runs, departures from the above occur due to clumping,  
308 fecundity variation over space (Section S1.4), as well as discrepancies due to replacing  
309 the sum in Eq. 3 with the integral in Eq. 5 (especially when  $\sigma_s$  is very small or large  
310 relative to the arena). That said, the mean resource share is typically close to  $K/N$  in our  
311 model runs.

312 In Fig. S1 we show the effect of spatial variation in local carrying capacity  $k(x_i, y_i)$   
313 on various components of fitness, including the resource share  $\rho_i$ . Interestingly,  
314 ecological competition is weaker ( $\rho_i$  is higher) in regions of low carrying capacity  
315 (Fig. S1a), increasing the survival probability  $s_i$  of individuals in these regions  
316 (Section S1.2 and Fig. S1b). This occurs because females are less likely to encounter  
317 preferred males wherever the carrying capacity is low, causing their fecundity to be  
318 lower due to increased mate-search costs  $c_i$  (Section S1.4 and Fig. S1c). Consequently,  
319 fewer offspring are produced than expected based on the low local carrying capacity,  
320 resulting in weaker competition among those offspring. The net result of lower  
321 ecological competition and higher mate-search costs in regions with low local carrying  
322 capacity is that females have roughly equal fitness across space.

## 323 S1.2 Survival

324 We assume that individuals that gain more resources are more likely to survive to  
325 reproductive maturity. The probability  $s_i$  of such survival is assumed to be zero when an  
326 individual fails to gain any resources, to rise approximately linearly with its resource  
327 share  $\rho_i$  when that share is small, and to taper off at a maximal survival probability of  
328  $s_{\max}$  (ranging between 0 and 1). Specifically, we use a hyperbolic (or Holling type-2)  
329 function<sup>1</sup> to relate resource share to the probability of survival,

$$s_i = \frac{s_{\max}}{1 + r/\rho_i}, \quad (6)$$

330 where  $r$  is the resource share that must be obtained for an individual to survive with a  
331 probability equal to half the maximal survival probability. Unless stated otherwise, we  
332 assume that the maximum probability  $s_{\max}$  of surviving to reproductive maturity equals  
333 1.

334 The value of  $r$  is chosen to ensure that, on average,  $K$  individuals survive to  
335 reproduce if all individuals obtain an equal share of resources ( $\rho_i = K/N$ ). By setting the  
336 expected survival probability  $s_i$  to  $K/N$  in Eq. 6 and substituting  $\rho_i = K/N$ , we obtain  
337  $r = s_{\max} - K/N$ . With this choice of  $r$ , approximately  $K$  individuals survive each  
338 generation (with a variance that is typically small). For example, in Fig. S1, the average  
339 survival probability is 0.484, close to the expected value of  $K/N = 0.5$ . While  
340 competition for resources causes substantial mortality, survival probabilities across the  
341 arena differ only slightly (Fig. S1b). Importantly, the survival of an individual does not  
342 depend on whether or not it is a hybrid.



### 343 **S1.3 Mating**

344 Of the individuals that survive to mate, the probability that female  $i$  chooses male  $j$  as a  
345 mate depends on whether his display trait matches her preference trait and on the  
346 spatial distance separating them. Females bearing a  $P$  ( $p$ ) allele prefer males bearing a  $Q$   
347 ( $q$ ) allele by a factor  $\alpha$ . We assume that females encounter males in the vicinity of their  
348 home location. Specifically, each female spends a proportion of time at distance  $d_{ij}$  from  
349 her home that is described by a Gaussian distribution with standard deviation  $\sigma_f$ , so that  
350 her encounter probability  $e_{ij}$  with a male at distance  $d_{ij}$  is proportional to

$$e_{ij} = \exp(-d_{ij}^2 / (2\sigma_f^2)) / (2\pi\sigma_f^2); \quad (7)$$

351 in the one-dimensional model, the divisor is  $\sqrt{2\pi}\sigma_f$ . In our main model, we assume that  
352 females encounter resources and males over the same spatial scales (i.e.,  $\sigma_f = \sigma_s$ ); we  
353 relax this assumption in Fig. S6. The probability that female  $i$  chooses male  $j$  as a mate is  
354 proportional to

$$p_{ij} = \alpha^{\delta_{ij}-1} e_{ij}, \quad (8)$$

355 where  $\delta_{ij}$  equals 1 when the display trait of male  $j$  matches the preference trait of female  
356  $i$ , and 0 otherwise. Once a female chooses a mate, we assume that all her offspring are  
357 sired by that male (monogamy).

### 358 **S1.4 Reproduction**

359 The fecundity of a female  $i$  is given by:

$$f_i = f_{\max}(1 - c_i), \quad (9)$$

360 where  $f_{\max}$  is the maximum fecundity and  $c_i$  (ranging from 0 to 1) measures the cost  
 361 associated with finding a preferred mate for female  $i$ . The factor  $1 - c_i$  is assumed to be  
 362 zero when there are no preferred males locally, to rise approximately linearly with the  
 363 local density of preferred males,

$$\mu_i = \sum_{\text{males } j} p_{ij}, \quad (10)$$

364 and to taper off at 1 when preferred mates are readily encountered, resulting in maximal  
 365 fecundity. Specifically, we use a hyperbolic (or Holling type-2) function<sup>2</sup>,

$$1 - c_i = \frac{1}{1 + m/\mu_i}, \quad (11)$$

366 where  $m$  is the value of  $\mu_i$  at which a female's fecundity is halved by mate-search costs.  
 367 Because  $\mu_i$  is obtained by summing over the entire male population, its value can be  
 368 large, on the order of the number of surviving males, so values of  $m$  on the order of the  
 369 surviving population's size  $K$  are needed for costs to be appreciable. This is why we  
 370 express  $m$  relative to  $K$ , specifying the ratio  $m/K$  in the figures. We refer to  $c_i$  as the  
 371 mate-search cost of female  $i$  and to  $m$  as the strength of mate-search costs.

372 Unless noted otherwise, we use  $m = 500$ . In our main set of model runs (with  
 373  $m/K = 1$ ), mate-search costs reduce female fecundity by about 50%, on average, from  
 374 the maximum fecundity (Fig. S1c), with relatively minor differences in fecundity among  
 375 females over space. Other values of  $m$  are explored in Fig. 3. For  $m = 0$ , all females have  
 376 equal and maximal fecundity. As  $m$  is raised, fecundity declines and becomes more  
 377 variable, with females in low-density regions or surrounded by non-preferred males  
 378 having lower fecundity (Fig. S2).

379 After mating, offspring are produced. Inheritance at both loci is Mendelian, and we  
 380 assume no linkage between the display and preference loci, except where noted (Section

381 S2.8). To allow us to explore various parameters relating to competition and mate-search  
382 costs independently, we hold the total number of offspring constant at  $N$ . For each  
383 offspring, a mother is chosen in proportion to the females' fecundities. Consequently, the  
384 maximum fecundity  $f_{\max}$  only matters insofar as it is high enough to result in at least  $N$   
385 offspring being produced across the population. Similar patterns are observed when  
386  $f_{\max}$  is fixed and offspring numbers are given by a Poisson distribution with a mean of  $f_i$   
387 for each female (data not shown). We consider  $N$  to be the total number of offspring  
388 surviving the phase during which resources are largely provided by the parents, after  
389 which the offspring move and begin the next phase of competition for resources.

## 390 **S1.5 Movement**

391 Each offspring moves from its mother's location according to a distance drawn from a  
392 Gaussian function with mean 0 and standard deviation  $\sigma_m$ . Movements occur in all  
393 directions with equal probability.

## 394 **S2 Model extensions**

395 To assess the robustness of our results, we consider several extensions and/or  
396 modifications to our main model described above.

### 397 **S2.1 Allowing mating to impact dispersal**

398 To compare our results with those of Payne and Krakauer<sup>3</sup>, we consider  
399 mating-dependent dispersal. In their model, male movement distances are lower for  
400 males with better mating prospects, and we thus assume that the movement distance of

401 male  $j$  is drawn from a Gaussian function with mean 0 and standard deviation

$$\sigma_{m,j} = \sigma_m \exp\left(-l \frac{\sum_i p_{ij}}{\sum_{ik} p_{ik}}\right), \quad (12)$$

402 where  $l$  determines how quickly movement distances decrease with increasing mating  
403 prospects and  $p_{ij}$  is given by Eq. 8 in Section S1.3. For  $l = 0$ , the above reduces to our  
404 main model. We find that the addition of mating-dependent dispersal in males extends  
405 coexistence times only marginally, if at all (compare Fig. S3a to S3b). We also examine  
406 the related case in which males with low mating prospects move farther, but again,  
407 coexistence times are not appreciably prolonged in our individual-based model.

## 408 **S2.2 Introducing multiple allelic types**

409 To examine whether long-term coexistence of more than two types is possible, we extend  
410 our main model so that one of  $n$  alleles  $p_1, \dots, p_n$  can occur at the preference locus and  
411 one of  $n$  alleles  $q_1, \dots, q_n$  can occur at the display locus. Specifically, in Fig. 4, we  
412 consider  $n = 10$  preference and display types. A female with preference allele  $p_i$  prefers  
413 males with display allele  $q_i$  to all other males by the factor  $\alpha$ . All other components of  
414 mate choice remain the same as for our main model with  $n = 2$  mating types.

## 415 **S2.3 Allowing competition to impact fecundity**

416 In our main model, competitive interactions reduce the survival probability of an  
417 individual. Alternatively, individuals that gain fewer resources might survive, but have  
418 lower fecundity. To explore this possibility, we allow all  $N$  offspring to survive, while  
419 reducing their reproductive success according to the impact of competition, as measured  
420 by  $s_i$ . Specifically, for males, the probability of being chosen as a mate is set to

421  $p_{ij} = \alpha^{\delta_{ij}-1} e_{ij} s_i$ . Likewise for females, fecundity is set to  $f_i = f_{\max}(1 - c_i) s_i$ . Such  
422 competition-dependent fecundity generates less demographic stochasticity, because all  
423 individuals reach reproductive maturity and can mate, albeit with reduced probability  
424 when their resource share  $\rho_i$  is low. Indeed, all else being equal, incorporating  
425 competitive effects on fecundity, rather than survival, enables long-term coexistence  
426 over a wider range of parameters (compare Fig. S4 to Fig. 3).

## 427 **S2.4 Altering the strength of density-dependent competition**

428 We define the strength of density-dependent competition as

$$\lambda = r/(1 - K/N), \quad (13)$$

429 with  $r = s_{\max} - K/N$  (Section S1.2). In our main model, the maximum survival rate  $s_{\max}$   
430 is set to 1 so that  $\lambda = 1$ , indicating that survival is strongly density-dependent. At the  
431 other extreme, if  $s_{\max}$  is set to  $K/N$ , all individuals survive with probability  $s_{\max} = K/N$ ,  
432 regardless of their resource share, so there is no density-dependent effect on survival  
433 ( $\lambda = 0$ ). As shown in Fig. S5b, coexistence does not occur in the absence of density  
434 dependence ( $\lambda = 0$ ); spatial variation in local carrying capacity then becomes irrelevant  
435 and cannot stabilize mating domains in space. As the importance of competition  
436 increases (larger  $\lambda$ , or equivalently, larger  $s_{\max}$ ), long-term coexistence can occur over a  
437 wider range of parameters. Once about half of the mortality is due to density-dependent  
438 competition ( $\lambda > 0.5$ ), results become similar to those for  $\lambda = 1$ .

## 439 **S2.5 Altering the impact of ecological competition**

440 We explore the impact of ecological competition by varying the expected survival  
441 probability  $\bar{s} = K/N$  of offspring, while the total carrying capacity  $K$  and the strength  $\lambda$   
442 of density-dependent competition are held constant (Fig. S5c). When the impact of  
443 ecological competition is small ( $\bar{s}$  near 1), long-term coexistence requires much higher  
444 levels of spatial variation in local carrying capacity. Once ecological competition is  
445 sufficiently strong (removing at least 40% of offspring;  $\bar{s} < 0.6$ ), results become less  
446 sensitive to  $\bar{s}$ .

## 447 **S2.6 Altering the degree of demographic stochasticity**

448 If each of  $N$  offspring survives with probability  $\bar{s}$ , the number of mating individuals  
449 follows a binomial distribution with mean  $N\bar{s}$  and variance  $N\bar{s}(1 - \bar{s})$ . The resultant  
450 coefficient of variation thus equals  $\sqrt{1/\bar{s} - 1}/\sqrt{N}$ , which grows as  $\bar{s}$  shrinks. The  
451 associated rise in demographic stochasticity with smaller  $\bar{s}$  may contribute to the slight  
452 rise in spatial variation in local carrying capacity required for maintaining long-term  
453 coexistence below  $\bar{s} = 0.5$  in Fig. S5c.

454 The effects of demographic stochasticity can also be seen in Fig. S5d, where the total  
455 carrying capacity  $K$  is varied (together with the time point at which coexistence is  
456 evaluated, at generation  $10K$ ), while the strength  $\lambda$  of density-dependent competition  
457 and the expected survival probability  $\bar{s} = K/N$  are held constant. Because we are  
458 interested in the effects of population size per se, we also keep constant the relative  
459 strength of mate-search costs ( $m/K = 1$ ), so the ease with which females encounter  
460 preferred mates remains unaffected by variation in  $K$ . All else being equal, larger  
461 population sizes facilitate the long-term maintenance of coexisting types, as expected

462 given the associated reduction in demographic stochasticity (the aforementioned  
463 coefficient of variation falls in proportion to  $1/\sqrt{N}$ ).

## 464 **S2.7 Altering the spatial scales of competition, mate search, and** 465 **movement**

466 In our main model, we equate the spatial scales of three processes: competition  
467 ( $\sigma_s = 0.05$ ), mate search ( $\sigma_f = 0.05$ ), and movement ( $\sigma_m = 0.05$ ). Fig. S6 shows what  
468 happens when those three spatial scales are varied independently. Coexistence is easier  
469 to maintain if female mate search and movement are more localized (smaller  $\sigma_f$  and  
470 smaller  $\sigma_m$ ), because mating types predominating in different spatial regions then  
471 undergo less mixing. By contrast, coexistence is easier to maintain if competition occurs  
472 across a wider spatial range (larger  $\sigma_s$ ), because individuals near the resource peaks then  
473 compete more strongly for resources in the troughs, reducing population density there  
474 and thus promoting isolation of the mating types predominating near each peak.

## 475 **S2.8 Incorporating alternative genetic architectures**

476 Our main model assumes free recombination between the trait and preference loci.  
477 Fig. S8 explores the effect of linkage, finding no substantial differences between  
478 complete linkage and free recombination between the preference and display loci.

479 To test whether our findings are robust to changes in the number of loci, we  
480 consider a quantitative genetic model in which an individual's preference and display  
481 traits are determined by two quantitative characters. This model can be interpreted as  
482 assuming that a large (infinite) number of additive loci code for each of the two traits.  
483 Complementing our main model, which features a finite number of alleles, this

484 extension allows for arbitrarily many mating types. In this quantitative genetic model,  
485 the probability that female  $i$  mates with male  $j$  is proportional to

$$p_{ij} = \exp(-(p_i - q_j)^2 / (2\sigma_p^2))e_{ij}, \quad (14)$$

486 where  $p_i - q_j$  is the difference between the preference trait of female  $i$  and the display  
487 trait of male  $j$ ,  $\sigma_p$  denotes the strength of female preference (smaller  $\sigma_p$  means females  
488 are choosier), and  $e_{ij}$  is proportional to the encounter probability between female  $i$  and  
489 male  $j$ , as defined in Eq. 7. Offspring trait values are drawn from a Gaussian function  
490 centred at the mean of the parental phenotypes for each trait, with a standard deviation  
491  $\sigma_o$  that measures the variation among offspring due to segregation, recombination, and  
492 mutation. All other details of the quantitative genetic model are the same as for our  
493 main model.

494 Despite the different genetic assumptions, the behaviour of the quantitative genetic  
495 model closely resembles that of the allelic model (Fig. S8). Long-term coexistence of  
496 mating domains is again possible over a wide range of parameters, provided female  
497 preferences are sufficiently strong (small  $\sigma_p$ ). As in the allelic model, loss of mating  
498 domains in the quantitative genetic model, when it happens, tends to occur through the  
499 replacement of one type by the other. Compared with the allelic model, the quantitative  
500 genetic model exhibits two additional mechanisms through which mating domains may  
501 be lost. First, when female preference is weak (large  $\sigma_p$ ), interbreeding between adjacent  
502 mating domains may become so common that the resultant offspring form their own  
503 mating domains, facilitating the merging of the original domains. Second, the random  
504 drift of matched trait and preference values in one mating domain may cause them to  
505 coincide by chance with the values in an adjacent mating domain, so the two originally  
506 separate domains may merge due only to the random genetic drift of quantitative



507 mating traits that results from segregation, recombination, and mutation in finite  
508 populations.

## 509 **S2.9 Incorporating asymmetric display costs**

510 Display traits can incur fitness costs in males. Our main model assumes that such costs,  
511 if present, affect all individuals equally. It may often be the case, however, that display  
512 traits differ in their effects on fitness. We therefore examine what happens when the  $Q$   
513 allele causes males to have a reduced survival probability relative to those carrying the  $q$   
514 allele (i.e., for  $Q$ -bearing individuals, the survival probability  $s_i$  is reduced by a factor  
515  $1 - a$ , with  $a$  ranging between 0 and 1). Provided that the resultant cost is not so strong  
516 that the stabilizing effect of spatial variation in local carrying capacity is overwhelmed  
517 by selection against  $Q$ -bearing males, our main findings remain largely unchanged  
518 (Fig. S9).

## 519 **References**

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Symbol	Eq.	Description
Model parameters		
$a$		Strength of selection against $Q$ -bearing males (only S2.9)
$k(x, y)$	1	Local carrying capacity at location $(x, y)$
$l$	12	Strength of mating-dependence in male dispersal (only S2.1)
$m$	11	Strength of mate-search costs
$s_{\max}$	6	Maximum survival probability
$v$	2	Spatial variation in local carrying capacity
$K$		Total carrying capacity
$N$		Number of offspring
$\alpha$	8	Strength of female preference
$f_{\max}$	9	Maximum female fecundity
$\lambda$	13	Strength of density-dependent competition
$\sigma_f$	8	Width of female-preference distribution
$\sigma_k$	1	Width of peaks in local carrying capacity
$\sigma_m$		Width of movement distribution
$\sigma_o$		Width of offspring distribution (only S2.8)
$\sigma_p$	14	Width of female preference (only S2.8)
$\sigma_s$	4	Width of competition distribution
Model variables		
$c_i$	11	Mate-search costs of female $i$
$d_{ij}$	4	Spatial distance between individuals $i$ and $j$
$e_{ij}$	7	Propensity for female $i$ to encounter male $j$
$f_i$	9	Fecundity of female $i$
$n_{ij}$	4	Competitive effect of individual $j$ on individual $i$
$p_{ij}$	8	Propensity for female $i$ to choose male $j$ as a mate
$s_i$	6	Survival probability of individual $i$
$\mu_i$	10	Local density of preferred males as seen by female $i$
$\rho_i$	3	Resource share of individual $i$

Table S1: Model parameters and model variables.

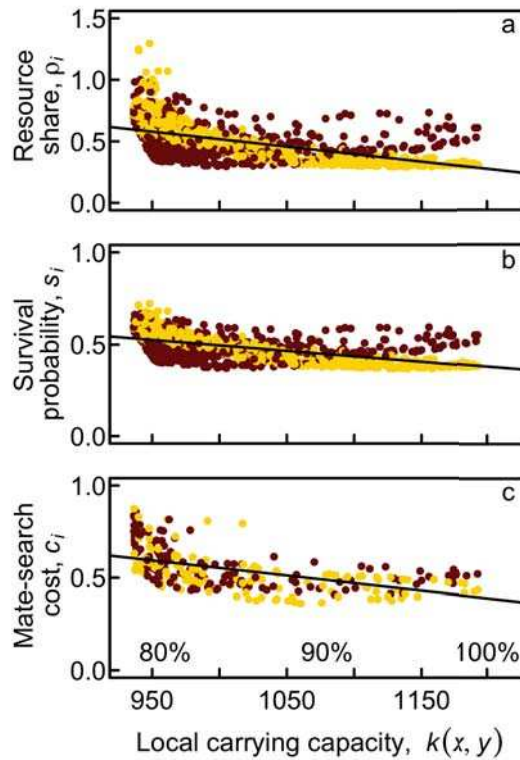


Figure S1: Variation in three components of fitness as a function of the local carrying capacity experienced by each individual at  $t = 1000$  for the model run in Fig. 1d. Individuals are coloured according to their genotype at the display locus. **a** Resource share  $\rho_i$  in males and females. **b** Survival probability  $s_i$  of males and females. **c** Mate-search costs  $c_i$  of females. Lines show least-squares regression lines.

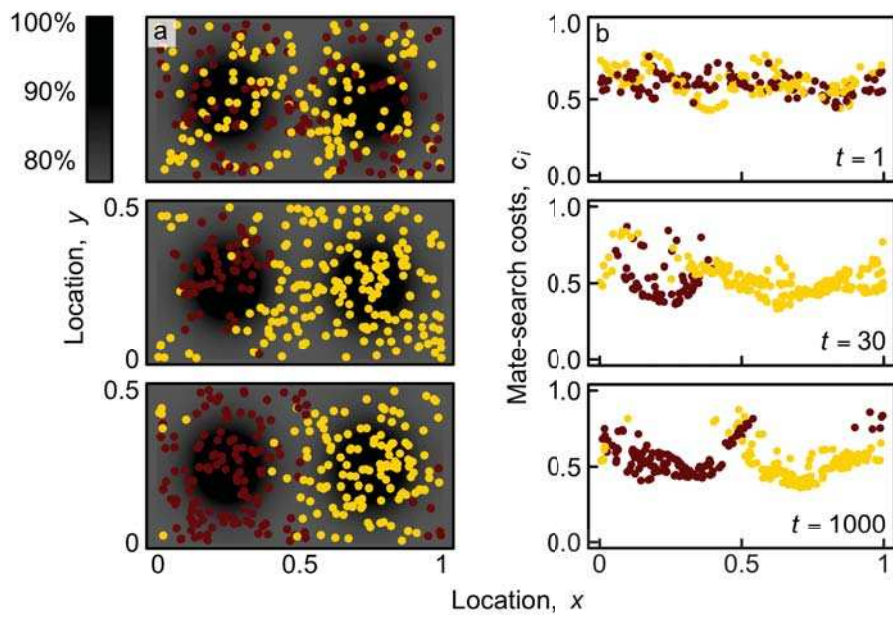


Figure S2: Mate-search costs for the model run in Fig. 1d. Panels in column **a** are identical to those in Fig. 1d, except that only females are shown and they are coloured according to their preference allele. Panels in column **b** show the costs associated with searching for a mate and rejecting non-preferred males for each female (Eq. 9), as a function of her location  $y$ . For  $m/K = 1$ , female fecundity is typically only halved by mate-search costs.

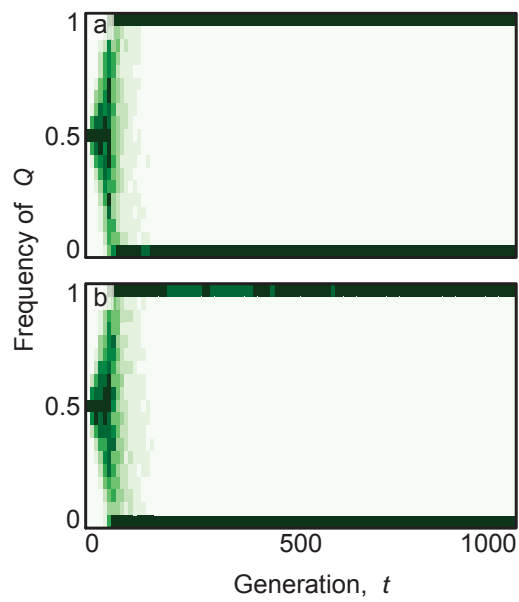


Figure S3: Effects of mating-dependent dispersal in males. Panels show distributions of allele frequencies at the display locus through time across 1000 replicate model runs in a two-dimensional homogeneous landscape; coexistence occurs only while these frequencies remain intermediate. Darker shading indicates a higher probability of observing a given frequency of the  $Q$  allele. Panel **a** is identical to Fig. 2b. Panel **b** is the same as **a**, except with mating-dependent dispersal in males ( $l = 100$ ). Results for other values of  $l$  are qualitatively identical. Model runs are initialized as in Fig. 2. All other parameters are as in Fig. 1b.

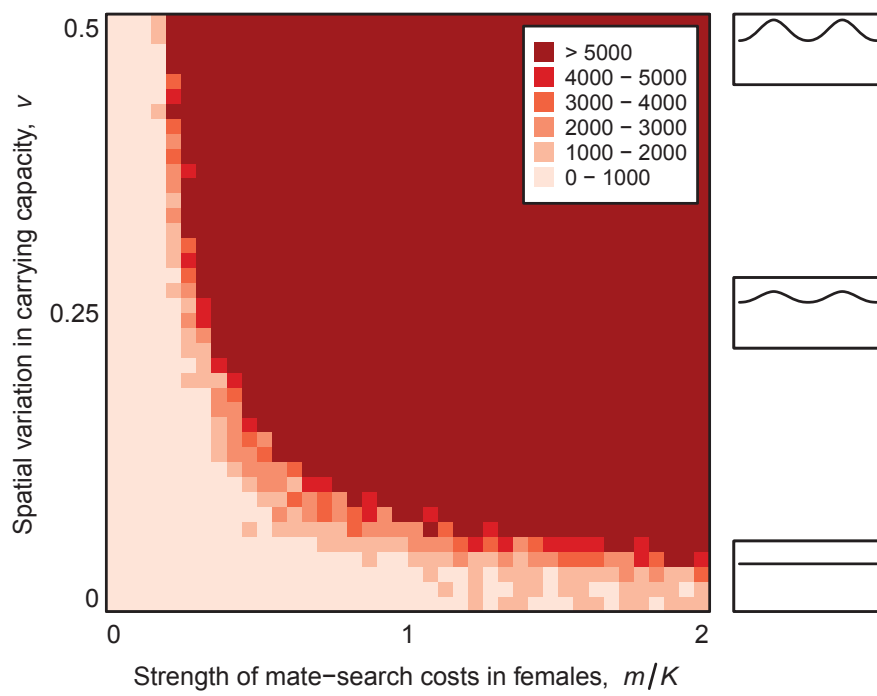


Figure S4: Conditions for long-term coexistence with competition-dependent fecundity (Section S2.3) in a two-dimensional bimodal landscape. All parameters are as in Fig. 3.

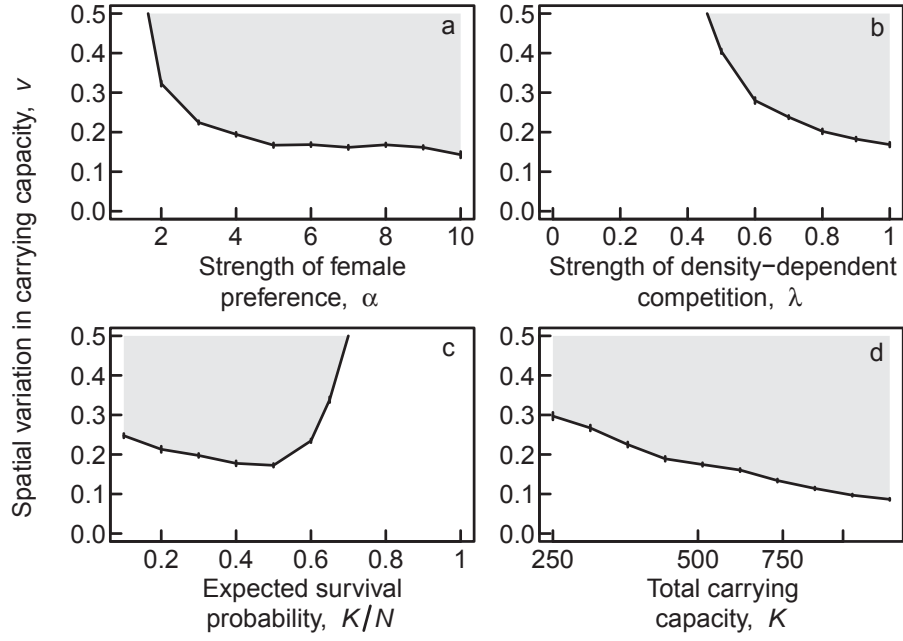


Figure S5: Minimum level of spatial variation  $v$  in local carrying capacity needed to ensure long-term coexistence (grey regions) in a two-dimensional bimodal landscape. The spatial variation  $v$  is increased until the average persistence time of 20 replicate runs exceeded  $10K$  generations (vertical lines indicate standard errors). **a** Effect of the strength  $\alpha$  of female preference. Coexistence becomes more likely as female preferences become stronger (larger  $\alpha$ ), although once preference exceeds  $\alpha \approx 5$ , its impact is small. **b**. Effect of the strength  $\lambda$  of density-dependent competition (varying  $s_{\max}$  while holding  $K = 500$  and  $N = 1000$  constant). The limit  $\lambda = 0$  corresponds to completely density-independent survival, while the limit  $\lambda = 1$  corresponds to completely density-dependent survival. **c**. Effect of the expected survival probability  $K/N$  (varying  $N$  while holding  $K = 500$  and  $\lambda = 1$  constant). Values near  $K/N = 0$  correspond to very strong ecological competition, while the limit  $K/N = 1$  corresponds to no ecological competition. **d**. Effect of the total carrying capacity  $K$  (varying  $K$  while holding  $K/N = 0.5$ ,  $\lambda = 1$ , and  $m/K = 1$  constant). All other parameters are as in Fig. 1d.

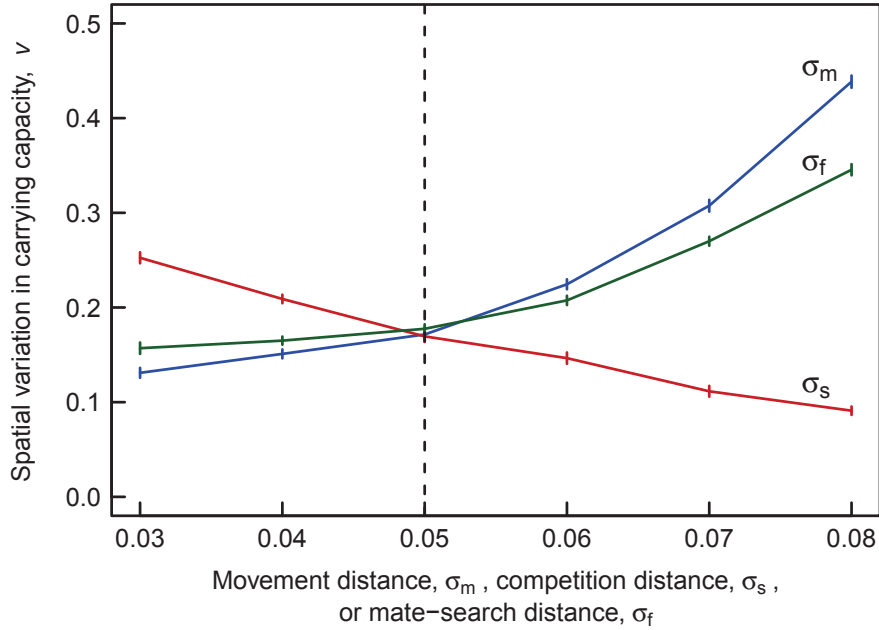


Figure S6: Minimum level of spatial variation  $v$  in local carrying capacity needed to ensure long-term coexistence in a two-dimensional bimodal landscape. The spatial variation  $v$  is increased until the average persistence time of mating types in 20 replicate runs exceeded 10K generations (vertical lines indicate standard errors). The three curves show the effects of the width  $\sigma_s$  of the competition distribution (red), the width  $\sigma_f$  of the mate-search distribution (green), and the width  $\sigma_m$  of the movement distribution (blue), while holding all other parameters constant at their values in Fig. 1d. In the other figures, the following values (indicated by the vertical dashed line) are used:  $\sigma_s = 0.05$ ,  $\sigma_f = 0.05$ ,  $\sigma_m = 0.05$ .



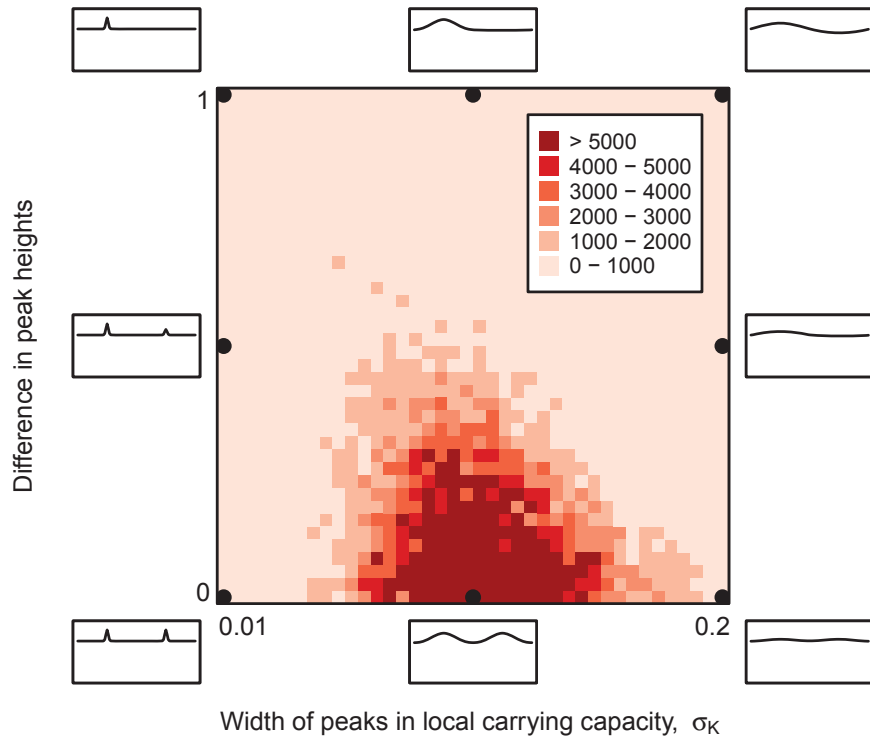


Figure S7: Effects of altering the shape of the local carrying capacity (Eq. 1) in a two-dimensional bimodal landscape. Shading indicates how long polymorphism persists at the display locus (darker = longer). Each cell represents the mean time to loss of polymorphism for 10 replicate model runs. Side panels indicate the extent of spatial variation in local carrying capacity along transects at  $y = 0.25$  for nine parameter combinations indicated by the closest black circle. The inset at the bottom center corresponds to the parameter combination used in Fig. 3. Spatial variation in local carrying capacity is relatively weak throughout this figure, with  $v$  ranging from 0.28 for  $\sigma_k = 0.01$  (far left) to 0.049 for  $\sigma_k = 0.2$  (far right). All other parameters are as in Fig. 1d.

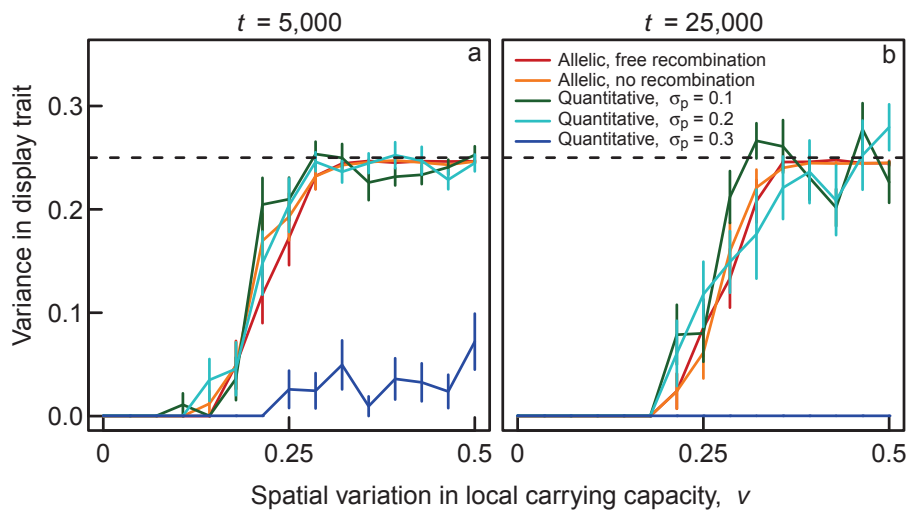


Figure S8: Effects of changes in genetic architecture in a two-dimensional bimodal landscape. Variance in display trait after 5,000 (a) and 25,000 (b) generations for a variety of genetic architectures, averaged over 20 replicate model runs (vertical lines indicate standard errors). The dashed line indicates the maximum possible variance in the allelic model (0.25). For determining variances in the allelic model, alleles  $Q$  and  $q$  are assigned trait values 0 and 1, respectively. In the quantitative genetic model, the initial preference/display trait values are set to 0/0 or 1/1 (corresponding to  $P/Q$  or  $p/q$  in the allelic model) with equal probability, yielding an initial variance of 0.25. Over time, the variance of 0.25 can be exceeded due to random genetic drift. For comparison, the red curve shows results of our main model. Model runs are initialized as in Fig. 2. All other parameters are as in Fig. 1; in the quantitative genetic model,  $\sigma_o = 0.01$ .

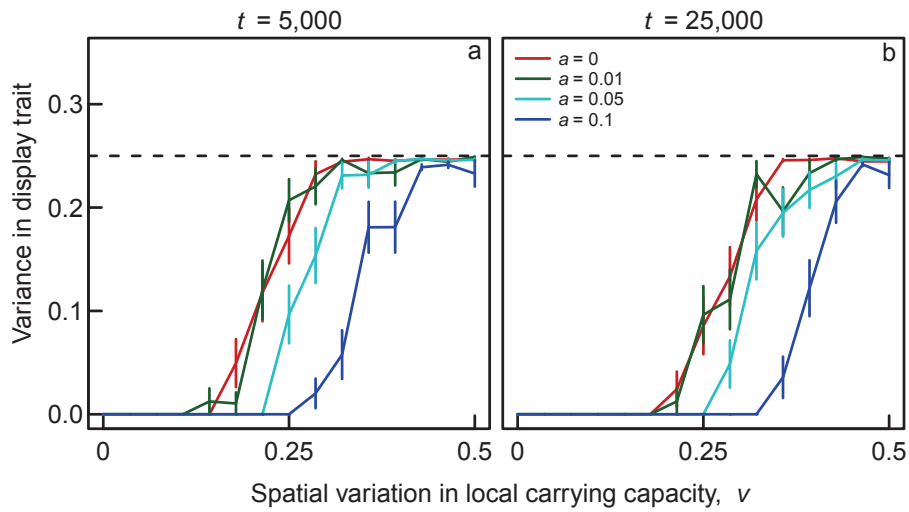


Figure S9: Effects of asymmetric fitness costs of display traits in the allelic model in a two-dimensional bimodal landscape. Variance in display trait after 5,000 (**a**) and 25,000 (**b**) generations when males bearing the  $Q$  allele have their survival lowered by a factor  $1 - a$  relative to males bearing the  $q$  allele, averaged over 20 replicate model runs (vertical lines indicate standard errors). The dashed line indicates the maximum possible variance in this allelic model (0.25). For comparison, the red curve (identical to that in Fig. S8) shows results of our main model, corresponding to the limit  $a = 0$ . Model runs are initialized as in Fig. 2. All other parameters are as in Fig. 1.