

1 Competitive speciation and costs of choosiness

2 Michael Kopp^{1,2} and Joachim Hermisson^{1,2}

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4 Running title: Costs of choosiness in speciation models

5 ¹Section of Evolutionary Biology, Department of Biology II, Ludwig-Maximilian University
6 Munich, Großhaderner Straße 2, D-82152 Planegg-Martinsried, Germany.

7 ²Mathematics and Biosciences Group, Max F. Perutz Laboratories, University of Vienna,
8 Dr. Bohr-Gasse 3, A-1030 Vienna, Austria

9 Author for correspondence: Michael Kopp, Dr. Bohrgasse 3, A-1030 Vienna, Austria. Phone:
10 ++43-1-79044-4583, Fax: ++43-1-4277-9240, Email: michael.kopp@univie.ac.at

Abstract

We investigate how costs of choosiness affect the evolution of assortative mating in a simple model of competitive speciation. The model allows for a comprehensive analysis by analytical and numerical techniques. We obtain results for two types of costs: Mating costs, which restrict the number of males a choosy female can evaluate, and viability costs, which decrease a choosy female's survival. Mating costs significantly reduce the range of parameters for which speciation is possible, but only if the number of males a female can evaluate is small (less than 10). This type of costs can be eliminated if females are allowed to mate randomly at the end of the mating period. Although, in this case, it is not possible to achieve complete reproductive isolation, our results show partial isolation with strong phenotypic clustering. Viability costs counteract selection for assortative mating. As this selection is typically weak, speciation is only possible if viability costs, too, are weak. The above restrictions are less severe if extreme phenotypes have an intrinsically higher carrying capacity.

Keywords: assortative mating, competition, costs of choosiness, disruptive selection, frequency-dependent selection, invasion fitness, female choice, population-genetic model, sexual selection, sympatric speciation

1 Introduction

2 In the last decade, the study of sympatric speciation has gained much momentum (Coyne
3 & Orr, 2004; Gavrillets, 2004; Dieckmann et al., 2004; Bolnick & Fitzpatrick, 2007). This
4 has been in part due to empirical research (Schliewen et al., 1994; Gíslason et al., 1999;
5 Savolainen et al., 2006a; Barluega et al., 2006b) and in part due to advances in theoretical
6 modeling (e.g. Dieckmann & Doebeli, 1999; Kondrashov & Kondrashov, 1999; Kirkpatrick &
7 Ravigné, 2002; Gavrillets, 2004). It is now widely accepted that sympatric speciation can –
8 and does – occur (Bolnick & Fitzpatrick, 2007). However, it is still very much debated how
9 common it is in nature. This controversy applies to both empirical data (Barluega et al.,
10 2006a; Schliewen et al., 2006; Savolainen et al., 2006b; Stuessy, 2006) and models (Doebeli &
11 Dieckmann, 2005; Doebeli et al., 2005; Gavrillets, 2005; Polechová & Barton, 2005; Waxman
12 & Gavrillets, 2005a,b; Doebeli et al., 2007).

13 On the theoretical side, part of the debate has focused on costs of choosiness. One possible
14 path to sympatric speciation is the evolution of non-random mating in populations sub-
15 ject to frequency-dependent disruptive selection. For example, in populations experiencing
16 intraspecific competition, fitness may be reduced for individuals with an intermediate phe-
17 notype. Females can prevent the production of low-fitness offspring by choosing males whose
18 phenotype is close to their own. In other words, there is selection for positive assortative mat-
19 ing (Rosenzweig, 1978; Doebeli, 1996; Dieckmann & Doebeli, 1999; Doebeli & Dieckmann,
20 2000; Matessi et al., 2001; Bolnick, 2004; Doebeli, 2005; Bolnick, 2006; Pennings et al., 2008;
21 de Cara et al., 2008; Otto et al., 2008; Ripa, 2008), in a process similar to reinforcement
22 (Servedio & Noor, 2003). If assortative mating gets strong enough, the population can split
23 into two reproductively isolated clusters (Gourbiere, 2004; Bürger & Schneider, 2006; Bürger
24 et al., 2006; Schneider & Bürger, 2006; Doebeli et al., 2007). However, speciation may fail if
25 choosy females experience fitness costs.

26 Whether or not costs of choosiness represent a serious obstacle for sympatric speciation
27 has been a matter of much recent debate (Matessi et al., 2001; Bolnick, 2004; Gourbiere,
28 2004; Kirkpatrick & Nuismer, 2004; Doebeli, 2005; Doebeli & Dieckmann, 2005; Waxman
29 & Gavrillets, 2005a,b; Gourbiere & Mallet, 2005; Bürger & Schneider, 2006; Bürger et al.,

1 2006; Schneider & Bürger, 2006; de Cara et al., 2008; Otto et al., 2008). For example,
2 Gavrilets repeatedly claims that “costs of being choosy ... can easily prevent speciation”
3 (Gavrilets, 2004, p. 398) or even that “absence of costs” is among the “conditions for sym-
4 patric speciation” (Gavrilets, 2005). Others have rejected this conclusion and maintain that
5 “the evolution of assortative mating remains possible even when such costs are substantial”
6 (Doebeli & Dieckmann, 2005, see also Doebeli, 2005; Doebeli et al., 2007).

7 There are several reasons for this disagreement. To some degree, what constitutes “substan-
8 tial” costs or “possible” speciation is a matter of personal interpretation. Different authors
9 have used different criteria for successful speciation (e.g., evolution of strong assortative
10 mating versus formation of phenotypic clusters), and have focused on different aspects of
11 the speciation process (strength of selection for assortative mating, time to speciation, main-
12 tenance of polymorphism, cluster formation). Matters are further complicated by the fact
13 that results are usually derived from individual-based simulations, which cover only a lim-
14 ited range of parameters and make generalizations difficult. Only very recently, analytical
15 approaches have been suggested by three groups of authors (Pennings et al., 2008; de Cara
16 et al., 2008; Otto et al., 2008; building on preliminary work by Matessi et al., 2001), which
17 allow for a comprehensive understanding of the evolutionary dynamics under simple but
18 non-trivial conditions.

19 Here, we use the model by Pennings et al. (2008) to analyze costs of choosiness. The key
20 simplification of this model relative to previous studies (e.g., Dieckmann & Doebeli, 1999;
21 Bolnick, 2004) is that the genetic basis of the ecological trait (which underlies competition)
22 is reduced to a single biallelic locus. The benefit is that the model can be analyzed in great
23 detail and in the full parameter space by using a combination of analytical and numerical
24 techniques. In Pennings et al. (2008), choosiness was costs-free. Here, we introduce two types
25 of costs, which we refer to as mating costs and viability costs. Mating costs arise if choosy
26 females run the risk of not finding an acceptable male before the end of the mating period
27 (Gavrilets & Boake, 1998; Arnegard & Kondrashov, 2004; Bolnick, 2004; Schneider & Bürger,
28 2006; Bürger & Schneider, 2006; Bürger et al., 2006). Viability costs directly decrease the
29 survival of choosy females (Doebeli et al., 2007; Otto et al., 2008), for example, due to an
30 increased predation risk. Our main interest is in how costs of choosiness alter the strength

1 and direction of selection on assortative mating, and, in particular, whether costs prevent
2 the evolution of phenotypic isolation.

3 **Model description**

4 Below, we give a short, but self-contained description of the model; for additional details, the
5 reader is referred to Pennings et al. (2008). We assume that natural selection acts on a single,
6 diploid locus (termed the ecological locus) with two alleles, ‘+’ and ‘-’. The three ecological
7 genotypes (+/+), (+/-), and (-/-) may be viewed as coding for a quantitative trait (e.g.
8 with value x , 0, and $-x$), but we will not need to make explicit reference to the phenotype
9 in most of the following. The total population size is $N = N_{\text{hom}}^+ + N_{\text{het}} + N_{\text{hom}}^-$, where
10 N_{hom}^+ , N_{het} , and N_{hom}^- denote the number of individuals in the three genotype classes, and
11 ‘hom’ and ‘het’ stand for homozygotes and heterozygotes. In symmetric cases, we will write
12 $N_{\text{hom}}^+ = N_{\text{hom}}^- = N_{\text{hom}}$. The relative genotype frequencies will be denoted by $P_{\text{hom}}^\pm = N_{\text{hom}}^\pm/N$
13 and $P_{\text{het}} = N_{\text{het}}/N$. Unless otherwise stated, the terms ‘homozygotes’ and ‘heterozygotes’ will
14 always refer to the ecological genotype. Time is continuous, and generations are overlapping.
15 Individuals are assumed to be either simultaneous hermaphrodites (no selfing) or males and
16 females with a sex ratio of 1 : 1.

17 **Viability selection**

18 Viability selection is modeled using a Lotka-Volterra approach (Roughgarden, 1972). The car-
19 rying capacity for heterozygotes is K_{het} , whereas the carrying capacity for both homozygotes
20 is $K_{\text{hom}} = K_{\text{het}}(1 - k)$, with $k \leq 1$. For $k > 0$, $K_{\text{het}} > K_{\text{hom}}$, that is, the carrying capacity
21 function (K as a function of phenotype) is unimodal, whereas for $k < 0$, $K_{\text{het}} < K_{\text{hom}}$ and
22 the carrying capacity function is bimodal. The strength of competition is 1 between identical
23 genotypes, $1 - c$ between heterozygotes and either of the homozygotes, and $1 - c'$ between the
24 two different homozygotes ($c' \geq c$). Typically, we will assume $c' = 1 - (1 - c)^4$, which corre-
25 sponds to a Gaussian relationship at the phenotypic level. The total amount of competition
26 experienced by the various genotypes is

$$C_{\text{hom}}^{\pm} = N_{\text{hom}}^{\pm} + (1 - c)N_{\text{het}} + (1 - c')N_{\text{hom}}^{\mp}, \quad (1a)$$

$$C_{\text{het}} = (1 - c)N_{\text{hom}}^{+} + N_{\text{het}} + (1 - c)N_{\text{hom}}^{-}. \quad (1b)$$

1 These can be viewed as “ecologically effective population sizes”, with $1 - c$ and $1 - c'$ acting
 2 as competition coefficients. In the absence of viability costs (see below), the genotype-specific
 3 death rates are given by

$$d_{\text{hom}}^{\pm} = \frac{C_{\text{hom}}^{\pm}}{K_{\text{hom}}}, \quad d_{\text{het}} = \frac{C_{\text{het}}}{K_{\text{het}}}. \quad (2)$$

4 An extension of the model to cases with an asymmetric carrying capacity or competition
 5 function is possible (see Pennings et al., 2008) but did not lead to qualitative changes in the
 6 results. We therefore limit our analysis to the symmetric case here and only briefly comment
 7 on the asymmetric case in the Results section.

8 Assortative mating

9 Assortative mating is modeled as female choice and is based on similarity with respect to
 10 the ecological locus. Females are characterized by evolvable mating traits m and m' , which
 11 indicate their readiness to reject males of a different genotype. When a female encounters
 12 a male of her own genotype mating occurs with probability 1. When a heterozygous female
 13 encounters a homozygous male (or vice-versa) mating occurs with probability $1 - m$. Similarly,
 14 when a $(+ / +)$ female meets a $(- / -)$ male (or vice versa) they will mate with probability
 15 $1 - m'$. In the following, we will always assume that m and m' are determined by the same
 16 set of genes and that m' is an increasing function of m . For numerical calculations (e.g., in
 17 the Figures), we choose $m' = 1 - (1 - m)^4$, making mating probability a Gaussian function
 18 of phenotypic distance. We consider two types of costs: *mating costs* and *viability costs*.

19 Mating costs

20 Mating costs arise if a choosy female runs the risk of not finding a suitable mate by the end of
 21 the mating period. Here, we follow an approach introduced by Gavrillets & Boake (1998) and

1 subsequently used by a number of authors (Matessi et al., 2001; Arnegard & Kondrashov,
 2 2004; Bolnick, 2004; Doebeli, 2005; Waxman & Gavrillets, 2005b; Schneider & Bürger, 2006;
 3 Bürger & Schneider, 2006; Bürger et al., 2006). Denote the probability that an encounter of
 4 a female with a random male leads to mating by

$$\pi_{\text{hom}}^{\pm} = [P_{\text{hom}}^{\pm} + (1 - m)P_{\text{het}} + (1 - m')P_{\text{hom}}^{\mp}], \quad (3a)$$

$$\pi_{\text{het}} = [(1 - m)P_{\text{hom}}^{+} + P_{\text{het}} + (1 - m)P_{\text{hom}}^{-}]. \quad (3b)$$

5 Furthermore, assume that there is a fixed maximum number M of encounters or mating trials
 6 before the mating period ends. Then, the mating rates of homozygous and heterozygous
 7 females are

$$\phi_{\text{female, hom}}^{\pm} = 1 - (1 - \pi_{\text{hom}}^{\pm})^M, \quad (4a)$$

$$\phi_{\text{female, het}} = 1 - (1 - \pi_{\text{het}})^M, \quad (4b)$$

8 which depend on m and m' . For $M \rightarrow \infty$, mating costs are absent and we recover model 2
 9 of Pennings et al. (2008). In the terminology of Kirkpatrick & Nuismer (2004), this is the
 10 “animal model”, whereas the opposite case $M = 1$ is the “plant model”.

11 The rates of matings between females of type i and males of type j , $Q_{i,j}$, are given by

$$Q_{\text{hom}^{\pm}, \text{hom}^{\pm}} = \phi_{\text{female, hom}}^{\pm} \frac{P_{\text{hom}}^{\pm}}{\pi_{\text{hom}}^{\pm}}, \quad (5a)$$

$$Q_{\text{hom}^{\pm}, \text{het}} = \phi_{\text{female, hom}}^{\pm} \frac{P_{\text{het}}(1 - m)}{\pi_{\text{hom}}^{\pm}}, \quad (5b)$$

$$Q_{\text{hom}^{\pm}, \text{hom}^{\mp}} = \phi_{\text{female, hom}}^{\pm} \frac{P_{\text{hom}}^{\mp}(1 - m')}{\pi_{\text{hom}}^{\pm}}, \quad (5c)$$

$$Q_{\text{het}, \text{hom}^{\pm}} = \phi_{\text{female, het}} \frac{P_{\text{hom}}^{\pm}(1 - m)}{\pi_{\text{het}}}, \quad (5d)$$

$$Q_{\text{het}, \text{het}} = \phi_{\text{female, het}} \frac{P_{\text{het}}}{\pi_{\text{het}}}. \quad (5e)$$

12 To understand these equations, note that ϕ_{female} gives the probability that a female mates
 13 at all, whereas the fractional term gives the probability that she mates with a male of a
 14 particular genotype.

1 Flexible mating strategy

2 Females can avoid costs of choosiness by accepting a random male at the end of the mating
 3 period (Doebeli & Dieckmann, 2005). Therefore, we also consider a variant of the above
 4 model, in which females that have been unsuccessful in M trials at assortative mating go
 5 on to mate randomly at their next encounter. In this case, $\phi_{\text{female, hom}}^{\pm}$ and $\phi_{\text{female, het}}$ are the
 6 rates of *assortative* mating only, and the total pairwise mating rates $Q_{i,j}$ become

$$Q_{\text{hom}^{\pm}, \text{hom}^{\pm}} = P_{\text{hom}}^{\pm} \left(\frac{\phi_{\text{female, hom}}^{\pm}}{\pi_{\text{hom}}^{\pm}} + 1 - \phi_{\text{female, hom}}^{\pm} \right), \quad (6a)$$

$$Q_{\text{hom}^{\pm}, \text{het}} = P_{\text{het}} \left(\frac{\phi_{\text{female, hom}}^{\pm}(1-m)}{\pi_{\text{hom}}^{\pm}} + 1 - \phi_{\text{female, hom}}^{\pm} \right), \quad (6b)$$

$$Q_{\text{hom}^{\pm}, \text{hom}^{\mp}} = P_{\text{hom}}^{\mp} \left(\frac{\phi_{\text{female, hom}}^{\pm}(1-m')}{\pi_{\text{hom}}^{\pm}} + 1 - \phi_{\text{female, hom}}^{\pm} \right), \quad (6c)$$

$$Q_{\text{het}, \text{hom}^{\pm}} = P_{\text{hom}}^{\pm} \left(\frac{\phi_{\text{female, het}}(1-m)}{\pi_{\text{het}}} + 1 - \phi_{\text{female, het}} \right), \quad (6d)$$

$$Q_{\text{het}, \text{het}} = P_{\text{het}} \left(\frac{\phi_{\text{female, het}}}{\pi_{\text{het}}} + 1 - \phi_{\text{female, het}} \right). \quad (6e)$$

7 Viability costs

8 Alternatively, or in addition to effects on female mating rate, costs of choosiness could also
 9 affect viability (see Doebeli, 2005; Doebeli & Dieckmann, 2005; Doebeli et al., 2007; Otto
 10 et al., 2008). There can be a number of reasons for this, such as direct costs of the choosiness
 11 mechanism, increased predation risk due to mate choice, or a disadvantage in competition
 12 for the best feeding or nesting sites.

13 We consider two subtypes of viability costs: *absolute* and *relative* ones (using the terminology
 14 of Otto et al., 2008). Absolute viability costs depend directly on the parameters m and m' ,
 15 independent of the availability of mating partners. For example, absolute costs could arise
 16 if the choosiness mechanism itself is costly. For mathematical reasons, we assume a soft
 17 selection scheme, where costs depend on the difference between a female's own choosiness
 18 and the mean choosiness in the population:

$$d. = \frac{C.}{K.} + f_{\delta}(m - \bar{m}, m' - \bar{m}'), \quad (7)$$

1 with a cost function f_{δ} that is non-decreasing in both of its arguments. An example is the
 2 simple linear cost function

$$f_{\delta}(m - \bar{m}, m' - \bar{m}') = \delta(m - \bar{m}) + \delta'(m' - \bar{m}'), \quad (8)$$

3 where $\delta, \delta' \geq 0$ measure costs linked to m and m' , respectively. Because of soft selection,
 4 these costs do not affect the dynamics of a population that is monomorphic with respect
 5 to choosiness. Absolute viability costs can be introduced in various alternative ways, but
 6 models seem to behave very similar as long as costs are not too strong. For example, we also
 7 numerically analyzed a hard selection model with a multiplicative cost term, $d. = (C./K.)(1 +$
 8 $\delta m + \delta' m')$, and obtained results comparable to the ones discussed below (not shown).

9 In contrast to absolute costs, relative costs depend on the number of males a female rejects
 10 before mating. Mating costs, as introduced above, are necessarily relative. However, also
 11 viability costs can easily be relative, for example if predation risk is proportional to the
 12 number of unsuccessful mating trials. In particular, we assume

$$d. = \frac{C.}{K.} + \sum_{k=1}^{\infty} \gamma_k (1 - \pi.)^k. \quad (9)$$

13 The coefficient γ_k measures the cost for the k th unsuccessful mating trial. If costs are equal
 14 for each trial, $\gamma_k \equiv \gamma$, equation (9) simplifies to

$$d. = \frac{C.}{K.} + \gamma \left(\frac{1}{\pi.} - 1 \right), \quad (10)$$

15 where $(1/\pi. - 1)$ is the average number of rejected males per female of a given ecological
 16 type.

17 We only consider viability costs that act equally on males and females. For hermaphrodites,
 18 this assumption holds automatically. For separate sexes it is a necessary condition to maintain
 19 an 1:1 sex ratio.

1 Although, in principle, different types of costs can act simultaneously, in this paper, we
 2 will only analyze them separately. Thus, a population subject to mating costs will not also
 3 experience viability costs, and vice versa.

4 **Population dynamics**

5 Using the above definitions and the laws of Mendelian inheritance, the birth rates of the
 6 various ecological genotypes are given by

$$B_{\text{hom}}^{\pm} = N_{\text{hom}}^{\pm} \left(Q_{\text{hom}^{\pm}, \text{hom}^{\pm}} + \frac{1}{2} Q_{\text{hom}^{\pm}, \text{het}} \right) + N_{\text{het}} \left(\frac{1}{2} Q_{\text{het}, \text{hom}^{\pm}} + \frac{1}{4} Q_{\text{het}, \text{het}} \right), \quad (11a)$$

$$B_{\text{het}} = N_{\text{hom}}^{+} \left(\frac{1}{2} Q_{\text{hom}^{+}, \text{het}} + Q_{\text{hom}^{+}, \text{hom}^{-}} \right) + \frac{1}{2} N_{\text{het}} \left(Q_{\text{het}, \text{hom}^{+}} + Q_{\text{het}, \text{het}} + Q_{\text{het}, \text{hom}^{-}} \right) \\ + N_{\text{hom}}^{-} \left(\frac{1}{2} Q_{\text{hom}^{-}, \text{het}} + Q_{\text{hom}^{-}, \text{hom}^{+}} \right). \quad (11b)$$

7 Finally, the population dynamics are given by

$$\dot{N}_{\text{hom}}^{\pm} = B_{\text{hom}}^{\pm} - N_{\text{hom}}^{\pm} d_{\text{hom}}^{\pm}, \quad (12a)$$

$$\dot{N}_{\text{het}} = B_{\text{het}} - N_{\text{het}} d_{\text{het}}. \quad (12b)$$

8 Equations (11) and (12) assume that all females in the population follow the same mating
 9 strategy (i.e., their m and m' values are identical). In the next section and in the Appendix,
 10 we show how the model can be extended to incorporate mutant mating strategies.

11 **Invasion analysis**

12 Our main aim is to understand the evolution of the choosiness parameters m and m' , which
 13 we will summarize in the vector $\mathbf{m} = (m, m')$. For this purpose, we assume a population that
 14 is monomorphic with respect to \mathbf{m} , and we ask under what conditions a rare mutant with
 15 a slightly different value $\tilde{\mathbf{m}} = (\tilde{m}, \tilde{m}')$ can invade. (Recall that m' is an increasing function

1 of m , so a single mutation will increase or decrease both parameters.) Without costs of
2 choosiness, considerable analytical progress is possible. In particular, it can be shown that
3 mutants with increased choosiness can invade if and only if the total fitness of homozygotes
4 is greater than that of heterozygotes (where fitness is determined by both natural and sexual
5 selection, see below and Pennings et al., 2008). The reason is that choosy females tend to
6 have more homozygous offspring. With costs of choosiness, no such simple criterion exists,
7 because females now face a trade-off between their own fitness and that of their offspring.
8 Choosiness can increase only if the benefit of having more homozygous offspring more than
9 offsets the disadvantage of having a reduced mating rate or viability. In other words, invasion
10 depends not only on the sign (and magnitude) of the fitness difference between homozygotes
11 and heterozygotes, but also on how many more homozygote offspring an average invading
12 mutant will produce. To determine the strength and direction of selection on m , it is therefore
13 necessary to calculate the invasion fitness gradient (Geritz et al., 1998).

14 We assume that the population dynamics are fast relative to the evolutionary dynamics
15 (Hammerstein, 1996). This means that invasion of new modifier alleles for choosiness always
16 occurs at the population dynamical equilibrium of a “resident population” with a monomor-
17 phic mating strategy. For speciation to be possible, the resident population must be polymor-
18 phic at the ecological locus. Due to the symmetries of the model, a symmetric equilibrium
19 with $N_{\text{hom}}^+ = N_{\text{hom}}^- = N_{\text{hom}}$ always exists. For viability costs with soft selection, the ratio
20 $n = N_{\text{het}}/N_{\text{hom}}$ at this equilibrium can be derived following Pennings et al. (2008). In all other
21 cases, it needs to be calculated numerically for $0 < m < 1$. The stability of the symmetric
22 equilibrium is not guaranteed under non-random mating (Matessi et al., 2001; Kirkpatrick
23 & Nuismer, 2004; Bürger & Schneider, 2006; Bürger et al., 2006; Pennings et al., 2008). It
24 can be determined by numerically calculating the leading eigenvalue of system (12).

25 Let ν_{het} be the number of heterozygote individuals (with genotype $(+/-)$ at the ecological
26 locus) that carry the mutant choosiness allele. Similarly, ν_{hom} is the total number of mutant
27 homozygotes (i.e., the sum of the number of mutants with ecological genotypes $(+/+)$ and
28 $(-/-)$). The dynamics of the mutant subpopulation is described by

$$\begin{pmatrix} \dot{\nu}_{\text{het}} \\ \dot{\nu}_{\text{hom}} \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} \nu_{\text{het}} \\ \nu_{\text{hom}} \end{pmatrix} \quad (13)$$

1 with the elements of the matrix $\mathbf{A}_{\mathbf{m}, \tilde{\mathbf{m}}}$ being

$$a_{11} = \frac{\tilde{Q}_{\text{het}, \text{hom}^\pm}}{2} + \frac{\tilde{Q}_{\text{het}, \text{het}}}{4} + \frac{Q_{\text{hom}^\pm, \text{het}}}{2} + \frac{Q_{\text{het}, \text{het}}}{4} - d_{\text{het}}, \quad (14a)$$

$$a_{21} = \frac{\tilde{Q}_{\text{het}, \text{hom}^\pm}}{2} + \frac{\tilde{Q}_{\text{het}, \text{het}}}{4} + \frac{Q_{\text{hom}^\pm, \text{het}}}{2} + \frac{Q_{\text{het}, \text{het}}}{4}, \quad (14b)$$

$$a_{12} = \frac{\tilde{Q}_{\text{hom}^\pm, \text{hom}^\mp}}{2} + \frac{\tilde{Q}_{\text{hom}^\pm, \text{het}}}{4} + \frac{Q_{\text{hom}^\pm, \text{hom}^\mp}}{2} + \frac{Q_{\text{het}, \text{hom}^\pm}}{4}, \quad (14c)$$

$$a_{22} = \frac{\tilde{Q}_{\text{hom}^\pm, \text{hom}^\pm}}{2} + \frac{\tilde{Q}_{\text{hom}^\pm, \text{het}}}{4} + \frac{Q_{\text{hom}^\pm, \text{hom}^\pm}}{2} + \frac{Q_{\text{het}, \text{hom}^\pm}}{4} - d_{\text{hom}}, \quad (14d)$$

2 where terms marked with a tilde refer to the mutants. The leading eigenvalue $\lambda(\mathbf{m}, \tilde{\mathbf{m}})$
3 of $\mathbf{A}_{\mathbf{m}, \tilde{\mathbf{m}}}$ is the invasion fitness (Metz et al., 1992) for the \tilde{m} mutant. It can be visualized
4 using pairwise invasibility plots (Geritz et al., 1998; see Appendix 1 for some examples and
5 discussion of peculiarities). The direction of selection for choosiness is determined by the
6 invasion fitness gradient (Geritz et al., 1998)

$$D_\lambda(m) = \left. \frac{\partial \lambda(\mathbf{m}, \tilde{\mathbf{m}})}{\partial \tilde{\mathbf{m}}} \right|_{\tilde{\mathbf{m}}=\mathbf{m}}. \quad (15)$$

7 D_λ describes how, in the vicinity of the resident mating strategy, a rare mutant's strategy
8 influences its (invasion) fitness. Choosiness (m) increases if D_λ is positive and decreases
9 if D_λ is negative. A convergence-stable intermediate equilibrium is achieved if $D_\lambda = 0$ and
10 $\partial D_\lambda / \partial m < 0$. In most cases, a convergence-stable equilibrium for m also is an ESS. However,
11 in Appendix 1, we also present an example where it is a branching point, which might give
12 rise to a polymorphic mating strategy in the population (Fig. A1f).

13 In Appendix 2, we derive the invasion fitness gradient for mating costs as well as absolute
14 and relative viability costs. We also determine the sign of the invasion fitness gradient at
15 random mating ($m = m' = 0$) and at complete isolation ($m = m' = 1$), which determines
16 whether these two states can be evolutionary endpoints. For intermediate m , we must resort
17 to numerical analysis of equation (15). The model with a flexible mating strategy is analyzed

1 in Appendix 3. We show that, in this model, invasion again depends only on the sign of the
2 fitness difference between homozygotes and heterozygotes.

3 **Results**

4 **Basic model without costs**

5 The basic model without mating or viability costs (with $M \rightarrow \infty$ and $f_\delta = 0$) has been
6 analyzed in Pennings et al. (2008). Here, we briefly summarize its results. In the model,
7 all females are assured to mate, but rare males are less likely to be chosen by a female.
8 Thus, female choosiness induces sexual selection against rare males (Kirkpatrick & Nuismer,
9 2004). (This effect has been termed a “cost to rarity” by Doebeli & Dieckmann (2003), but
10 it is not a cost that is paid by the choosy females themselves.) Because females do not pay
11 for being choosy, choosiness increases if and only if homozygotes have higher fitness than
12 heterozygotes. Depending on the ecological parameters k and c , there are five regimes for the
13 evolution of female choosiness (Fig. 1a). Three regimes are monostable and lead to a unique
14 outcome: random mating ($m = 0$, R), partial isolation ($0 < m < 1$, P), or complete isolation
15 ($m = 1$, C). In addition, there are two bistable regimes, in which the outcome depends
16 on initial conditions: random mating or complete isolation (R/C), and partial isolation or
17 complete isolation (P/C). Furthermore, for low values of c , the polymorphic equilibrium
18 at the ecological locus (which is a prerequisite for speciation) is unstable for at least some
19 (intermediate) values of m (see Bürger & Schneider, 2006; Bürger et al., 2006), which prevents
20 the evolution of complete isolation in small steps.

21 The pattern of the invasion fitness gradient in each regime is shown in Figure 2, along
22 with the fitness difference between homozygotes and heterozygotes (Δ_W). Note that, while
23 both functions have the same roots, they have different shapes. In particular, in the C,
24 P/C and R/C regimes, D_λ tends to zero for $m \rightarrow 1$, because, in this parameter region,
25 heterozygotes are almost absent and a change in m has little influence on the offspring
26 phenotype distribution. This effect is not reflected in the fitness difference Δ_W . Therefore,
27 it is always the invasion fitness gradient that determines not only the direction but also the

1 speed of evolution (according to the ‘canonical equation’ of adaptive dynamics; Dieckmann
2 & Law, 1996).

3 In Pennings et al. (2008), we explain the above results by the interplay of natural and
4 sexual selection. Briefly, natural selection (due to the carrying capacity and competition
5 functions) is negatively frequency-dependent and reflects the structure of ecological niches.
6 It favors a specific proportion of heterozygotes (which may be zero). Sexual selection (due
7 to female choosiness) is positively frequency-dependent and favors common genotypes. It is
8 sexual selection that creates the bistability in the R/C and P/C regimes and the potential
9 instability of the ecological polymorphism. Both natural and sexual selection can prevent
10 the evolution of full assortative mating and, instead, lead to a stable intermediate value of
11 choosiness.

12 We note two differences in Figure 1a as compared to the analogous Figure 1c in Pennings
13 et al. (2008): First, the present figure extends to negative k values, showing (not surprisingly)
14 that speciation is easiest if the carrying capacity function is bimodal (provided competition
15 creates enough negative frequency-dependence to maintain the ecological polymorphism).
16 Second, we demand that the domain of attraction of complete isolation in the P/C and
17 R/C regimes must not be too small. In Figure 1, parameter combinations are included into
18 these regimes only if complete isolation evolves from a starting population with $m' \leq 0.999$
19 (meaning that the probability of a (+/+) female to accept a (-/-) male, and vice versa,
20 is ≥ 0.001). The original boundary for stability of complete isolation is included as dotted
21 line in Figure 1a, which shows that there is a large area in parameter space where complete
22 isolation is mathematically stable but has a vanishingly small domain of attraction.

23 **Mating costs**

24 Mating costs do not change the basic structure with five evolutionary regimes. However,
25 mating costs induce sexual selection against rare and choosy females (in addition to sexual
26 selection against rare males). Therefore, for given values of k and c , mating costs decrease the
27 likelihood that complete isolation can evolve from random mating in small steps. This results
28 in a shift of the complete isolation regime towards lower (and negative) k values (Fig. 1b-f).

1 Yet, marked deviations from the no-costs case appear only for $M \lesssim 10$. A special case is
2 given for $M = 1$, where no amount of choosiness can evolve at all. This is easy to understand,
3 since a female that has only a single mating opportunity should never reject it. The following
4 discussion refers only to the case $M \geq 2$.

5 Figure 3a illustrates how mating costs affect the invasion fitness gradient $D_\lambda(m)$. Costs
6 decrease D_λ for intermediate values of choosiness, but not for very small or very large m .
7 In the limit $m \rightarrow 0$, D_λ remains unchanged. This means that local stability of the random
8 mating regime is unaffected by mating costs (Appendix 2). The reason is that any benefit of
9 being choosy scales linearly with m for $m \rightarrow 0$, while the costs scale like m^M (the probability
10 to reject a mating partner is proportional to m , and females go unmated if they reject M
11 mating partners). Consequently, the line separating the C, P and P/C regimes from the R
12 and R/C regimes is identical in all subplots of Figure 1 with $M \geq 2$.

13 For $m \rightarrow 1$, mating costs induce strong sexual selection against heterozygotes (both males
14 and females), as long as these are very rare. As a consequence, complete isolation is always
15 locally stable, at least in the mathematically strict sense (Appendix 2). This means that
16 mating costs actually increase the invasion fitness gradient in the P and R regimes, where
17 complete isolation is unstable without costs (note that Fig. 3a only shows the C regime).
18 However, this effect is limited to values of m very close to 1 and is thus of no real biological
19 significance. Indeed, the domain of attraction of the $m = 1$ equilibrium is exceedingly small
20 for parameter values outside those marked as the C, P/C and R/C regimes in Figure 1 (see
21 above). Once we require a minimal domain of attraction for complete isolation (see above),
22 mating costs lead to a slight reduction of these regimes. Where complete isolation is stable
23 in the absence of costs, the effect of mating costs on the invasion fitness gradient vanishes
24 for $m \rightarrow 1$.

25 Furthermore, strong mating costs increase the area where the polymorphic equilibrium at the
26 ecological locus becomes unstable (for some values of m in $[0, 1]$). The reason is that mating
27 costs reduce the fitness of rare phenotypes (due to increased sexual selection). This may lead
28 to a failure of speciation, which requires a polymorphic population. Unlike in the no-costs
29 case (Pennings et al., 2008), the monomorphic equilibria at the ecological locus are always
30 locally stable for sufficiently large m (Appendix 2), but this should be of little significance

1 as long as the polymorphic equilibrium is locally stable, too.

2 Finally, we also performed some limited numerical analysis of an asymmetric model with
3 $K_{\text{hom}}^+ = K_0(1 - \frac{2}{3}k)$ and $K_{\text{hom}}^- = K_0(1 - \frac{4}{3}k)$ (results not shown; see Appendix E and Fig. E1
4 in Pennings et al., 2008 for the evolutionary regimes of the asymmetric model without costs).
5 We find that consequences of mating costs are similar to the symmetric case. In particular
6 there is no significant effect for $M = 10$.

7 **Flexible mating strategy**

8 One way to avoid costs of choosiness is for females to become less choosy towards the end
9 of the mating period. In the simplest case, we might assume that a female behaves choosily
10 during the first M encounters with males, but mates randomly afterwards. In this model,
11 reproductive isolation can never be complete, because some females will always reach the
12 random mating step. For the sake of continuity, we nevertheless retain nomenclature such as
13 “C regime” for the evolution of $m = 1$, even though this no longer refers to complete isolation
14 in the strict sense. As each female is guaranteed to mate, costs of choosiness are absent in
15 this model. We therefore recover the invasion criterion from the model with $M \rightarrow \infty$, namely
16 that choosiness increases (the invasion fitness gradient is positive) if and only if homozygotes
17 have higher fitness than heterozygotes (Appendix 3).

18 Figure 4 shows the distribution of evolutionary regimes in the k versus c plane for the model
19 with a flexible mating strategy, together with the maximal possible degree of reproductive
20 isolation (measured as the equilibrium proportion of heterozygotes for $m = 1$). For small
21 values of M , the domain of the C regime increases in size, whereas the domains of the P
22 regime and of the bistable regimes decrease. These results can be explained as follows: The
23 P regime tends to be replaced by the C regime because, for small M , even the C regime
24 leads only to partial isolation (see above). The bistable regimes become less prominent
25 because a small M (high readiness of females to mate randomly) reduces sexual selection on
26 males, which is the driving force behind bistability due to its positive frequency dependence.
27 Unlike in the previous model (Fig. 1), the case $M = 1$ is not qualitatively different from
28 the other cases. Obviously, the maximal possible degree of reproductive isolation (i.e., the

1 proportion of heterozygotes at $m = 1$) decreases with decreasing M . We observe “almost
2 complete” isolation (less than 1% heterozygotes) if and only if the effects of mating costs
3 in the corresponding non-flexible model are weak ($M \sim 10$). For stronger mating costs, a
4 flexible strategy leads to only partial isolation even in parameter regions where complete
5 isolation evolves in the absence of flexibility. In these cases, we find a large parameter region
6 where evolution of assortative mating leads to pronounced phenotypic clustering (for $M \geq 2$,
7 the phenotype distribution at a stable equilibrium with $m = 1$ is always at least bimodal).

8 **Viability costs**

9 **Absolute viability costs** The effect of absolute viability costs with soft selection on the
10 invasion fitness gradient $D_\lambda(m)$ can be calculated analytically (Appendix 2). For a given
11 cost function f_δ , $D_\lambda(m)$ is decreased by the derivative

$$df_\delta = \frac{\partial f_\delta}{\partial m} + \frac{\partial f_\delta}{\partial m'} \frac{\partial m'}{\partial m} \quad (16)$$

12 (see eq. A3). For the linear cost function (eq. 8) it follows that $D_\lambda(m)$ is reduced by a
13 constant, δ , if costs are directly linked to m (Fig. 3b). In contrast, the effect of costs linked
14 to m' is proportional to $(1 - m)^3$, meaning that it is strongest for low m and vanishes for
15 $m \rightarrow 1$ (Fig. 3c). (Note that costs linked to m' reduce the invasion fitness gradient by a
16 constant if the gradient is derived with respect to m' instead of m . In general, one should use
17 a scale, proportional to m or m' or any combination thereof, where choosiness modifiers have
18 a constant average effect, independent of the resident choosiness.) Because of soft selection,
19 there is no change in the stability of the ecological polymorphism in the resident population.

20 It is easy to see that arbitrary shapes of the cost function f_δ can lead to an arbitrary number
21 of additional evolutionary regimes (other than those described in Fig. 1), because they may
22 create additional (stable or unstable) equilibria. For example, in Figure 3b, for $\delta = 0.02$,
23 there is a regime with two stable intermediate equilibria for m . More generally, if costs are
24 proportional to m , complete isolation ($m = 1$) can never be stable, since the invasion fitness
25 gradient tends to 0 for $m \rightarrow 1$ even in the absence of costs. This is because m' is already
26 close to 1 for large m (under the assumption of the Gaussian shape $m' = 1 - (1 - m)^4$) and

1 selection in homozygotes against mating with heterozygotes vanishes once the heterozygotes
2 are nearly extinct. Note that there is no such effect if costs are linked to m' rather than m .
3 Instead of focusing on isolation in the strict sense, it may be more relevant biologically to
4 discuss whether assortative mating can evolve to a point where two clear clusters emerge in
5 phenotype space. A minimal condition for cluster formation is the evolution of a bimodal
6 phenotype distribution ($N_{\text{het}} \leq 1/3N$), where heterozygotes are less frequent than either type
7 of homozygotes. More stringently, one might demand that heterozygotes should be almost
8 absent from the population (e.g., $N_{\text{het}} = 0.01N$). The values of m corresponding to both of
9 these criteria are highlighted in Figure 3 (crosses and dots, respectively). Whether or not a
10 given degree of clustering can evolve depends on the shape of the invasion fitness gradient
11 (in the absence of costs), on the shape of the costs function, and on the mutational step-size
12 at the choosiness locus (i.e., on the intermediate values of m that are actually realized).
13 Viability costs will always impede cluster formation if the minimum in the derivative of the
14 cost function df_{δ} exceeds the maximum in the invasion fitness gradient $D_{\lambda}(m)$ (without costs)
15 for sufficiently small m . In contrast, cluster formation is always possible if the maximum in
16 df_{δ} is smaller than the minimum in $D_{\lambda}(m)$. The minimal and maximal values of D_{λ} acting in
17 the population before either bimodality or strong clustering is reached are shown in Fig. 5.
18 For the range of parameters analyzed, D_{λ} is on the order of 10^{-1} to 10^{-2} . We note that if
19 sexual selection on males is absent (as in model 1 of Pennings et al., 2008) D_{λ} is higher, but
20 still within the same order of magnitude (results not shown).

21 **Relative viability costs** The effect of relative viability costs is intermediate between those
22 of absolute viability costs and of (relative) mating costs (Fig. 3d). Like for mating costs, the
23 effect of relative viability costs is maximal for intermediate m (although this maximum is
24 much less pronounced for costs that are proportional to the number of rejected males, eq. 10)
25 and vanishes for $m \rightarrow 1$. Complete isolation is always locally stable (although the domain
26 of attraction may be vanishingly small, see above) as long as costs are not extremely high
27 ($\gamma < 1/4$; see Appendix 2). Relative viability costs also decrease the stability of the ecological
28 polymorphism, in a pattern similar to that shown in Figure 1. In contrast to mating costs,
29 however, relative viability costs are linear in m for $m \rightarrow 0$. This is because part of the costs
30 is already paid after the first potential partner is rejected (given that $\gamma_1 > 0$ in eq. 9). Close

1 to random mating, therefore, relative viability costs have an effect similar to that of absolute
2 costs with a linear cost function.

3 **Discussion**

4 We have investigated how costs of choosiness affect the evolution of assortative mating in a
5 simple model of competitive speciation. Our analysis focuses on two types of costs: Mating
6 costs, which restrict the number of mating trials per female, and viability costs, which reduce
7 survival. We show that mating costs have a significant effect only if the number of mating
8 trials per female is less than about ten. Viability costs must be weak for assortative mating
9 to evolve, because selection for assortative mating is weak itself.

10 **The strength of selection for assortative mating**

11 Sufficiently strong costs can inhibit the evolution of any trait. But how strong is too strong
12 for the evolution of assortative mating driven by resource competition? Clearly, assortative
13 mating can evolve only if positive selection due to competition (and, potentially, sexual
14 selection) is stronger than negative selection resulting from costs of choosiness. Therefore,
15 the first question to be asked is how strong positive selection for assortative mating can be.

16 As shown in Fig. 5, the strength of selection for assortative mating depends strongly on
17 the shape of the carrying capacity function (which is determined by the parameter k). For
18 positive k , that is for unimodal carrying capacity functions, the invasion fitness gradient in
19 the absence of costs is typically on the order of 10^{-2} . Therefore, the selection coefficient s
20 for a new mutation that increases choosiness by 10% is on the order of 10^{-3} . This is weak,
21 but not very weak selection and well within the range of selection coefficients inferred from
22 molecular data (e.g., Andolfatto, 2007). It is worth noting that selection on mating modifiers
23 is stronger by at least two orders of magnitude than selection on dominance modifiers in the
24 classical Fisher theory for the evolution of dominance at mutation-selection balance (Mayo
25 & Bürger, 1997; note, however, that this is not true under frequency-dependent disruptive
26 selection, where the strength of selection on dominance is comparable to that on assortative

1 mating in our model, e.g., Peischl & Bürger, 2008). Thus, speciation should still be possible
2 in the presence of weak costs, but it is likely to be prevented if costs are moderate or high.
3 Furthermore, the fate of mutations with a given selection coefficient depends strongly on
4 the effective population size N_e . In particular, selection dominates genetic drift if $N_e s \gg 1$.
5 Irrespective of costs, this suggests that competitive speciation is more likely in species with
6 large effective population sizes.

7 Selection for assortative mating is significantly stronger if the carrying capacity function
8 is bimodal ($k < 0$). For example, for $k = -0.5$, the invasion fitness gradient for m can
9 exceed 0.1. This is hardly surprising, as a bimodal carrying capacity directly favors extreme
10 phenotypes (i.e., homozygotes). Under these conditions, speciation should be possible even
11 in the presence of moderate costs. Indeed, the prime obstacle to speciation in this case
12 seems to be the potential instability of the ecological polymorphism for low and intermediate
13 values of c (as opposed to the existence of stable low or intermediate evolutionary equilibria
14 for m). A bimodal carrying capacity function can result, for example, if the population
15 uses two discrete resource. Given the large effort invested in models with unimodal resource
16 distributions (following Dieckmann & Doebeli, 1999), we suggest that more attention should
17 be paid to models with bimodal or discrete resource distributions (e.g., Doebeli, 1996; Kisdi &
18 Geritz, 1999; Ito & Shimada, 2007; Ripa, 2008). It seems possible that competitive speciation
19 then appears more likely than inferred from previous models.

20 **The strength of costs**

21 The next question is how strong costs of choosiness are likely to be relative to the strength
22 of selection for assortative mating. This is an empirical question, but unfortunately, too few
23 data exist for a general answer (Kokko et al., 2006; Bolnick & Fitzpatrick, 2007). Absolute
24 viability costs, which are independent of a female's actual search effort, are particularly hard
25 to measure, although it has been suggested that costs for female preferences (which may be
26 comparable to absolute costs of choosiness) might be very low (Kokko et al., 2006). Some
27 studies show that relative viability costs (such as search costs) can be quite high (e.g., Byers
28 et al., 2005). This conclusion is corroborated by indirect evidence from studies showing
29 that females behave less choosily under conditions of resource limitation (Byers et al., 2006),

1 predation risk (Godin & Briggs, 1996) or increased energy expenditure (Milinski & Bakker,
2 1992). In other species, however, viability costs seem to be very low (Gibson & Bachman,
3 1992).

4 With regard to mating costs, Bolnick & Fitzpatrick (2007) recently reviewed data about the
5 number of males females visit before mating. These estimates should be viewed as a lower
6 bound for the parameter M in our model (the maximal number of males a female can evaluate
7 during the mating period), because it is not clear whether females in the study populations
8 accepted a male because the benefit of further search was low (i.e., the chosen male satisfied
9 the female's preferences) or because the costs (risk of remaining unmated) were high. In
10 some cases, females evaluate up to 100 males before mating, but often, they mate after looking
11 at fewer than 10. Since, in our model, we find a significant effect for $M \lesssim 10$, this suggests
12 that mating costs can indeed be an important factor opposing competitive speciation.

13 Furthermore, there is some evidence that mating costs might play a larger role if the ecological
14 trait has a more complex genetic architecture. Although our estimate that mating costs are
15 relevant for $M \lesssim 10$ is in accordance with results by Schneider & Bürger (2006) and Bürger
16 et al. (2006), it is in slight contrast to Bolnick (2004) and Waxman & Gavrillets (2005b),
17 who find a significant effect already for $M \lesssim 30$. These differences can be explained by
18 differences in the effective number of ecological phenotypes. The more different types there
19 are, the less likely it is that a choosy female finds a male of exactly her own type. Bolnick
20 (2004) and Waxman & Gavrillets (2005b) study the time to speciation in models with 4 to
21 10 ecological loci. As pointed out by Bolnick (2004), this time is largely determined by the
22 time it takes to sort genetic variation in an initially highly polymorphic population that is
23 close to random mating. Assuming, for simplicity, that all phenotypes are equally frequent,
24 the probability of a female encountering a male of the same phenotype within $M = 10$ trials
25 is 0.983 for one locus (as in our model), 0.692 for 4 loci, and 0.386 for 10 loci. After 30 trials,
26 these probabilities increase to 0.971 and 0.769 for 4 and 10 loci, respectively. Schneider &
27 Bürger (2006) and Bürger et al. (2006) also allow for more ecological phenotypes than we do,
28 but their focus is on the number of phenotypic clusters formed at the ecological equilibrium
29 for a given level of choosiness, and this number is typically quite low. Nevertheless, both
30 Bolnick (2004) and Bürger et al. (2006) find evidence that costs become more important as
31 the number of ecological loci increases.

1 Several authors have focused on the extreme case $M = 1$, mostly because it is analytically
2 tractable (Drossel & McKane, 2000; Gourbiere, 2004; Kirkpatrick & Nuismer, 2004; de Cara
3 et al., 2008). Not surprisingly, these studies find that speciation is impossible in the presence
4 of costs (cf Fig. 1f). Indeed, this is obvious even without formal analysis, since a female
5 should never reject the only male she can expect to meet. However, the case $M = 1$ is clearly
6 not representative for the general model, as even for $M = 2$, the results are qualitatively very
7 different. Therefore, claims regarding the general importance of costs should not be based
8 on this extreme case.

9 An argument by Bolnick & Fitzpatrick (2007) suggests an interesting difference between the
10 expected strength of mating costs and viability costs. Mating costs should be most severe
11 in low-density populations, where encounters between potential mates are rare. However,
12 this is not likely to be the case in populations experiencing strong intraspecific competition,
13 such as the ones considered in our model. An opposite argument can be put forward for
14 viability costs: These are indeed most likely to be strong in resource-limited, high-competition
15 environments, and this might create a ‘catch 22’ for speciation (Bolnick & Fitzpatrick, 2007).

16 **The pattern of effects**

17 Different types of costs not only differ in their strength but also in the precise pattern of
18 change they inflict on the invasion fitness gradient (Fig. 3). This, in turn, determines their
19 exact biological consequences. Consider a situation where speciation is possible in the absence
20 of costs (C regime). In principal, costs that have a strong effect at low degrees of choosiness
21 (low m) tend to prevent the onset of speciation, whereas costs that are strong at high degrees
22 of choosiness tend to prevent the completion of speciation. Viewed differently, costs whose
23 effect is weak at low m but gets stronger with increasing m tend to halt speciation at partial
24 isolation, whereas costs whose effect decreases near complete isolation (i.e., for $m \rightarrow 1$) favor
25 bistability. They can prevent speciation from random mating, but not the completion of
26 speciation, for example after secondary contact. Thus, there is a potential difference in the
27 effect of costs on sympatric speciation versus reinforcement (i.e., completion of speciation
28 after secondary contact).

1 It is worth pointing out that both types of relative costs (mating costs and relative viability
2 costs) belong to this latter class (Fig. 3a, d). Relative costs have no effect at or near complete
3 isolation, because the only way for a mutant (homozygote) female to increase her mating rate
4 is to mate with a male from the opposite homozygote class. However, the (heterozygote)
5 offspring resulting from this mating will have a very low mating rate themselves, due to the
6 strong sexual selection against rare heterozygotes. Both mating costs and relative viability
7 costs have their largest effect at intermediate m . However, the effect of mating costs vanishes
8 also towards random mating (Fig. 3a), whereas relative viability costs have a strong effect
9 already at low degrees of choosiness (Fig. 3d). In consequence, mating costs favor bistability
10 between partial isolation and complete isolation (P/C regime; see Fig. 1), whereas relative
11 viability costs favor bistability between random mating and complete isolation (R/C regime;
12 not shown).

13 Absolute viability costs can exhibit any number of patterns. For example, linear costs linked
14 to m have a constant effect on the invasion fitness gradient (Fig. 3b), whereas linear costs
15 linked to m' have their maximal effect in populations close to random mating (Fig. 3c). It
16 is also conceivable that costs are low for low m but increase for large m (not shown). Such
17 costs would most likely lead to partial isolation.

18 All costs that do not tend to zero for $m \rightarrow 1$ will prevent the evolution of strictly complete
19 isolation (Fig. 3b). However, even in this case, we often find that isolation can still become
20 ‘almost complete’, and that the resulting population shows a strongly bimodal distribution
21 with almost no intermediate phenotypes present (see also Doebeli et al., 2007). If gene flow is
22 severely restricted, the two incipient species might conceivably evolve complete reproductive
23 isolation by additional mechanisms (e.g., divergent evolution along other trait axis, temporal
24 and/or spatial isolation, gradual build-up of incompatibilities).

25 **Avoidance of costs**

26 In many situations, females should be able to avoid costs of choosiness by flexibly adjusting
27 their mate choice behavior. In this paper, we have investigated a model in which females
28 avoid mating costs by abandoning choosiness after M unsuccessful trials at assortative mating

1 (Fig. 4). More generally, such a strategy is always possible if the cost of rejecting a male
2 increases over time. In the examples used in the figures above, this is true for mating costs
3 (where all costs are paid only after the M th unsuccessful mating trial), but not for viability
4 costs: Absolute viability costs are paid before the first male is encountered and, thus, can
5 never be avoided. Relative viability costs with a linear cost function (eq. 10) are identical in
6 every round, so that the cost/benefit ratio is the same for each new trial.

7 As female mating behavior is generally highly plastic (Bolnick & Fitzpatrick, 2007), cost-
8 saving mechanisms should be common in nature. This is particularly true for mechanisms
9 avoiding mating costs, because these entail sexual selection against females that is effectively
10 created by the females' own behavior. In other words, refusing to mate if the likelihood of
11 future encounters with males is low does not seem to be a viable adaptive strategy. We stress
12 that a flexible mating strategy is favored for any level of choosiness in the population, even at
13 $m = 1$. It is, therefore, always the flexible strategy that is the evolutionary stable endpoint,
14 and models for costs of choosiness should account for this fact.

15 A flexible strategy will never allow the evolution of complete reproductive isolation. Our
16 results show that 'almost complete' isolation results whenever costs are weak in the non-
17 flexible case. Otherwise ($M \lesssim 10$ in our model), cost avoidance leads to partial isolation as
18 the evolutionary outcome in a large parameter region. In this case, we find strong phenotypic
19 clustering (about 10% heterozygotes), but gene-flow between the clusters is still considerable,
20 and there is no obvious mechanism leading to complete isolation.

21 **Conclusions**

22 Previous authors have voiced largely different opinions about costs of choosiness and their
23 importance for competitive speciation (see Introduction). For our model, as may often be
24 the case, the truth is found in the middle. In the light of our results, occasional claims that
25 "absence of costs" is a prerequisite for speciation (e.g., Gavrillets, 2005) are exaggerated:
26 Evolution of assortative mating is not structurally unstable and does not break down imme-
27 diately once biologically meaningful costs are allowed for. On the other hand, even moderate
28 costs clearly will inhibit speciation in many biological scenarios. Therefore, any model of
29 competitive speciation is incomplete if it does not account for this point.

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1 Appendix

2 Appendix 1: Pairwise invasibility plots for female choosiness

3 Figure A1 shows pairwise invasibility plots (Geritz et al., 1998) for female choosiness m in
4 the models with mating costs and with absolute viability costs. In the absence of costs, the
5 non-diagonal boundary lines are vertical (Fig. A1a; see Pennings et al., 2008). This is also
6 true in the flexible model, which is cost-free, too (not shown). As a consequence of vertical
7 boundary lines, modifiers with small effect can invade if and only if modifiers with large effect
8 can invade (see also Otto et al., 2008).

9 Pairwise invasibility plots with vertical boundary lines represent a non-generic case in the
10 classification of Geritz et al. (1998), and it has been argued that they arise if the model
11 assumptions are overly simplistic (Dieckmann & Metz, 2006). As seen in Figure A1b to e,
12 the boundary lines are no longer vertical if choosiness is costly. From the point of view of
13 Dieckmann & Metz (2006), therefore, costs of choosiness contribute to the added ecological
14 realism that is needed to break up the degeneracy of the simple model.

15 With mating costs (Fig. A1b, c), the non-diagonal boundary line for the singular strategy
16 corresponding to the stable intermediate equilibrium of m is always decreasing. This equi-
17 librium is therefore always an ESS (i.e., uninvadable), and in the neighborhood of such an
18 equilibrium, only modifiers with small effect can invade. With absolute viability costs that
19 are proportional to m , the boundary line at this singular point is decreasing for small δ , but
20 can be increasing for high δ . In the latter case, the singular point is a so-called evolutionary
21 branching point (Geritz et al., 1998), that is, invasion will lead to a protected polymorphism
22 of coexisting mating strategies.

23 Appendix 2: Invasion analysis with costs: analytical results

24 In this Appendix, we derive the invasion fitness gradient for the model with mating costs and
25 for the models with absolute and relative viability costs. In addition, we derive the conditions
26 for stability of random mating and complete isolation in each of these models. In particular,

1 we show that stability of random mating is unaffected by mating costs (for $M \geq 2$), and that
 2 complete isolation is always (locally) stable in the presence of mating costs, but never stable
 3 in the presence of absolute viability costs directly linked to m . We also study the stability
 4 of the monomorphic equilibria in the model with mating costs. We start with the model
 5 with absolute viability costs, where the assumption of soft selection makes a full analytical
 6 treatment possible.

7 **Absolute viability costs and soft selection**

8 **The invasion fitness gradient** Since absolute viability costs with soft selection do not
 9 affect the population dynamics, we can calculate the invasion fitness gradient analytically.
 10 Denote the matrix of the mutant invader dynamics in the model without costs by $\mathbf{A}^{(0)}$. The
 11 full invasion matrix with costs (see eq. 13) is then given by

$$\mathbf{A}^{(\delta)} = \mathbf{A}^{(0)} - \begin{pmatrix} f_\delta(\tilde{m} - m, \tilde{m}' - m') & 0 \\ 0 & f_\delta(\tilde{m} - m, \tilde{m}' - m') \end{pmatrix} \quad (\text{A1})$$

12 Since the contribution of costs is proportional to the identity matrix, the leading eigenvalue
 13 in the model with costs relates to the eigenvalue without costs as

$$\lambda_\delta(\mathbf{m}, \tilde{\mathbf{m}}) = \lambda_0(\mathbf{m}, \tilde{\mathbf{m}}) - f_\delta(\tilde{m} - m, \tilde{m}' - m'), \quad (\text{A2})$$

14 and the invasion fitness gradient is

$$D_\lambda(m) = \left. \frac{\partial \lambda_\delta(\mathbf{m}, \tilde{\mathbf{m}})}{\partial \tilde{m}} \right|_{\tilde{\mathbf{m}}=\mathbf{m}} = \frac{w_2(v_1 - v_2)}{4\mathbf{v}\mathbf{w}} \left. \frac{\partial \Delta Q}{\partial \tilde{m}} \right|_{\tilde{\mathbf{m}}=\mathbf{m}} - \frac{\partial f_\delta}{\partial m} - \frac{\partial f_\delta}{\partial m'} \frac{\partial m'}{\partial m}. \quad (\text{A3})$$

15 Since the entries of \mathbf{w} are proportional to the equilibrium distribution of the residents, we
 16 have $w_1/w_2 = n/2$, and hence $w_2/(\mathbf{v}\mathbf{w}) = 1/(v_2 + v_1 n/2)$. From (A30) in the limit $M \rightarrow \infty$,
 17 we obtain $\Delta Q = Q(\tilde{\mathbf{m}}) - Q(\mathbf{m})$ with

$$\Delta Q(\tilde{\mathbf{m}}) = \frac{-\tilde{m}'}{2 - \tilde{m}' + (1 - \tilde{m})n} \quad (\text{A4})$$

18 and thus

$$D_\lambda(m) = \frac{1 - v_1/v_2}{1 + (n/2)v_1/v_2} \frac{m'n + 4(1 - m)^3(2 + (1 - m)n)}{4(2 - m' + (1 - m)n)^2} - \frac{\partial f_\delta}{\partial m} - \frac{\partial f_\delta}{\partial m'} \frac{\partial m'}{\partial m}. \quad (\text{A5})$$

1 The ratio $n = N_{\text{het}}/N_{\text{hom}}$ depends only on the resident population with monomorphic mating
 2 type. Due to soft selection, it keeps the same value as in the model without costs and can be
 3 derived from an fourth-order equation (see Pennings et al., 2008). The value of v_1/v_2 follows
 4 from the eigenvalue equation. For a linear cost function (eq. 8) and a Gaussian mating
 5 function, we further have

$$\frac{\partial f_\delta}{\partial m} - \frac{\partial f_\delta}{\partial m'} \frac{\partial m'}{\partial m} = \delta + \delta' 4(1 - m)^3. \quad (\text{A6})$$

6 **Stability of random mating** In particular, for random mating ($m = m' = 0$), we find
 7 $v_1/v_2 = n/2$ and

$$D_\lambda(m = 0) = \frac{1 - n/2}{(1 + n^2/4)(2 + n)} - \delta - 4\delta'. \quad (\text{A7})$$

8 and from Eq. (12),

$$n = \frac{B_{\text{het}}d_{\text{hom}}}{B_{\text{hom}}d_{\text{het}}} = \frac{2}{1 - k} \frac{2 - c' + (1 - c)n}{2 - 2c + n} \Rightarrow k = \frac{n^2 - 2(2 - c')}{n^2 + 2n(1 - c)}. \quad (\text{A8})$$

9 From the condition $D_\lambda(m = 0) = 0$ we get n as the solution of a cubic equation. Using this
 10 solution in (A8), we then obtain k as a function of c and c' , defining the boundary of the
 11 area where random mating is stable.

12 **Stability of complete isolation** At complete isolation ($m, m' \rightarrow 1$ and $N_{\text{het}} \rightarrow 0$), we
 13 find $v_1/v_2 \rightarrow |3 + 4(d_{\text{het}} - d_{\text{hom}})|^{-1}$ and $d_{\text{hom}} \rightarrow 1$, and thus

$$D_\lambda(m, m' \rightarrow 1) \rightarrow \left(\frac{1}{2} - \frac{1}{|8d_{\text{het}} - 2|} - \delta' \right) \frac{\partial m'}{\partial m} \Big|_{m, m' \rightarrow 1} - \delta. \quad (\text{A9a})$$

14 Since $\partial m'/\partial m \rightarrow 0$ for $m, m' \rightarrow 1$, we always have $D_\lambda(m = m' = 1) < 0$ if $\delta > 0$, i.e. complete
 15 isolation is unstable. For $\delta = 0$, the stability condition for complete isolation ($D_\lambda > 0$) is

$$d_{\text{het}} > \frac{1}{2} \frac{1 - \delta'}{1 - 2\delta'}. \quad (\text{A9b})$$

1 Relative viability costs and hard selection

2 Any hard selection scheme, as used for the relative viability costs (as well as for the mating
3 costs, see below), will affect the population dynamics. We thus cannot use the results from
4 the cost-free model for $n = N_{\text{het}}/N_{\text{hom}}$, and generally need to rely on numerical methods.
5 However, for invasion at random mating or at complete isolation a full analytical treatment
6 is still possible.

7 **The invasion fitness gradient** With relative viability costs, the invasion matrix (eq. 10)
8 is given by

$$\mathbf{A}_{\mathbf{m}, \tilde{\mathbf{m}}}^{(\gamma)} = \mathbf{A}_{\mathbf{m}, \tilde{\mathbf{m}}}^{(0)} - \begin{pmatrix} \sum_{k=1}^{\infty} \gamma_k \left(\frac{2\tilde{m}}{2+n}\right)^k & 0 \\ 0 & \sum_{k=1}^{\infty} \left(\frac{\tilde{m}n + \tilde{m}'}{2+n}\right)^k \end{pmatrix}, \quad (\text{A10})$$

9 and the invasion fitness gradient by

$$D_{\lambda}^{(\gamma)}(m) = \frac{\mathbf{v} \frac{\partial}{\partial \tilde{m}} \mathbf{A}_{\mathbf{m}, \tilde{\mathbf{m}}}^{(\gamma)} \Big|_{\tilde{\mathbf{m}}=\mathbf{m}} \mathbf{w}}{\mathbf{v} \mathbf{w}} \quad (\text{A11})$$

10 where \mathbf{v} and \mathbf{w} are the left and right leading eigenvectors of $\mathbf{A}_{\mathbf{m}, \mathbf{m}}^{(\gamma)}$. The above equation can
11 be evaluated to

$$D_{\lambda}^{(\gamma)}(m) = \frac{1}{1 + (n/2)(v_1/v_2)} \left[\frac{\frac{1}{4}(1 - v_1/v_2)(m'n + \frac{\partial m'}{\partial m}(2 + (1 - m)n))}{(2 - m' + (1 - m)n)^2} - \frac{n(v_1/v_2)}{2 + n} \sum_{k=1}^{\infty} k \gamma_k \left(\frac{2m}{2+n}\right)^{k-1} - \frac{n + \frac{\partial m'}{\partial m}}{2 + n} \sum_{k=1}^{\infty} k \gamma_k \left(\frac{nm + m'}{2+n}\right)^{k-1} \right] \quad (\text{A12})$$

1 **Stability of random mating** For random mating ($m = m' = 0$), where $v_1/v_2 = n/2$, and
 2 with a Gaussian mating function, the invasion gradient reduces to

$$D_\lambda^{(\gamma)}(0) = \frac{1 - (n/2) - \gamma_1(4 + n + n^2/2)}{(1 + n^2/4)(n + 2)}. \quad (\text{A13})$$

3 The condition $D_\lambda(0) = 0$ leads to $n = (\sqrt{1 + 12\gamma - 28\gamma^2} - 2\gamma - 1)/(2\gamma)$ and we obtain the
 4 boundary lines of the random mating regimes from (A8), as for the absolute viability costs
 5 (results not shown).

6 **Stability of complete isolation** At complete isolation,

$$D_\lambda^{(\gamma)}(1) = \frac{1}{2} \left(1 - \frac{v_1}{v_2} - \sum_{k=1}^{\infty} \frac{k\gamma_k}{2^{k-1}} \right) \frac{\partial m'}{\partial m} \Big|_{m, m' \rightarrow 1}. \quad (\text{A14})$$

7 As in the case of absolute viability costs, we have $v_1/v_2 = |3 + 4(d_{\text{het}} - d_{\text{hom}})|^{-1}$ with $d_{\text{hom}} = 1$.
 8 Since $d_{\text{het}}(\tilde{m} \rightarrow 1) \rightarrow \frac{C_{\text{het}}}{K_{\text{het}}} + \sum_k \gamma_k$ for $n = 0$, the heterozygous death rate diverges if
 9 $\sum_k \gamma_k = \infty$. We then have $v_1/v_2 \rightarrow 0$ and conclude that complete isolation is always stable
 10 as long as $\sum_k (k\gamma_k/2^{k-1}) < 1$ (i.e. $\gamma < 1/4$ for $\gamma_k \equiv \gamma$).

11 Mating costs and hard selection

12 **The invasion fitness gradient** For mating costs, the invasion matrix reads

$$\mathbf{A}_{m, \tilde{m}}^{(M)} = \mathbf{A}_{m, \tilde{m}}^{(0)} - \frac{1}{4} \begin{pmatrix} \phi_{\text{female, het}}(\tilde{\mathbf{m}}) - 1 & \phi_{\text{female, hom}}(\tilde{\mathbf{m}}) - 1 \\ \phi_{\text{female, het}}(\tilde{\mathbf{m}}) - 1 & \phi_{\text{female, hom}}(\tilde{\mathbf{m}}) - 1 \end{pmatrix}. \quad (\text{A15})$$

13 where $\mathbf{A}_{m, \tilde{m}}^{(0)}$ is again the invasion matrix without costs.

14 We then obtain the invasion fitness gradient as

$$D_\lambda^{(M)}(m) = \frac{\mathbf{v} \frac{\partial}{\partial \tilde{m}} \mathbf{A}_{m, \tilde{m}}^{(M)} \Big|_{\tilde{m}=m} \mathbf{w}}{\mathbf{v} \mathbf{w}} \quad (\text{A16})$$

15 with \mathbf{v} and \mathbf{w} again denoting the left and right leading eigenvectors of $\mathbf{A}_{m, m}^{(M)}$. The above
 16 equation can be evaluated to

$$D_\lambda^{(M)}(m) = D_\lambda^{(0)}(m) + \partial_m \bar{\phi}_{\text{female}} \cdot \frac{1}{4} \frac{(1 - n/2)(1 + v_1/v_2)}{(n/2)(v_1/v_2) + 1} \quad (\text{A17})$$

1 where $D_\lambda^{(0)}(m)$ is the gradient without costs and

$$\partial_m \bar{\phi}_{\text{female}} = 2P_{\text{hom}} \partial_m \phi_{\text{female, hom}} + P_{\text{het}} \partial_m \phi_{\text{female, het}} \quad (\text{A18})$$

$$= -\frac{2M}{(2+n)^{M+1}} ((mn + m')^{M-1} (n + \partial m' / \partial m) + n(2m)^{M-1}) \quad (\text{A19})$$

2 is the derivative of the average female mating rate with respect to choosiness.

3 **Stability of random mating** Since $\partial_m \bar{\phi}_{\text{female}} \propto m^{M-1}$ we see that mating costs do not
 4 affect the invasion fitness gradient at random mating ($m = m' = 0$) for $M \geq 2$ (which is
 5 given by eq. (13) of Pennings et al., 2008).

6 **Stability of complete isolation** For a resident population at complete isolation ($N_{\text{het}} = 0$
 7 and $m = m' = 1$), the invasion matrix reads as follows:

$$\mathbf{A}_{1, \tilde{m}}^{(M)} = \frac{1}{4} \begin{pmatrix} 1 - \tilde{m}^M - 4d_{\text{het}} & \frac{1 - (\tilde{m}'/2)^M}{1 - \tilde{m}'/2} (1 - \tilde{m}') \\ 1 - \tilde{m}^M & \frac{1 - (\tilde{m}'/2)^M}{1 - \tilde{m}'/2} + 2(1 - (1/2)^M) - 4d_{\text{hom}} \end{pmatrix} \quad (\text{A20})$$

8 From the equilibrium condition for the dynamics of the resident population (Eq. 12) we find
 9 $d_{\text{hom}} = 1 - (1/2)^M$. Using this and Eq. (2) gives $d_{\text{het}} = 2(1 - c)(1 - k)(1 - (1/2)^M)/(2 - c')$.
 10 We then see, in particular, that the matrix element a_{22} is 0 for $M = 1$ and always negative for
 11 $M \geq 2$ and $\tilde{m}' < 1$. For \tilde{m}, \tilde{m}' sufficiently close to 1, we further see (by considering leading
 12 order terms) that the trace of $\mathbf{A}_{\tilde{m}, \tilde{m}}$ is always negative, while the determinant is negative for
 13 $M = 1$, but positive for $M \geq 2$. This corresponds to a positive leading eigenvalue for $M = 1$,
 14 but a negative leading eigenvalue for $M \geq 2$. We conclude that mutants of a very small
 15 effect for weaker choosiness can invade for $M = 1$, but never for $M \geq 2$. Strict complete
 16 isolation is therefore always locally stable for $M \geq 2$. Note, however that this result is of
 17 limited relevance since it is often possible for mutants with a slightly larger effect to invade
 18 (depending on the parameter values for k, c , and c').

1 **Stability of monomorphic equilibria** Local stability of the monomorphic equilibrium
2 (say with the + allele) is given if rare mutants with the – allele cannot invade. Since all
3 these mutants will appear as heterozygotes, we can focus on the heterozygote fitness. The
4 monomorphic equilibrium is stable if $W_{\text{het}} = (\phi_{\text{female, het}} + \phi_{\text{male, het}})/2 - d_{\text{het}} < 0$. Here,
5 $\phi_{\text{male, het}}$ is the mating rate of heterozygous males. From Eq. (12) we get $d_{\text{hom}} = 1$ and
6 from Eq. (2) follows $d_{\text{het}} = (1 - k)(1 - c)$. The mating rate of a female heterozygote is
7 $\phi_{\text{female, het}} = 1 - m^M$. A heterozygote male must be chosen by a homozygote female in her
8 first try since otherwise she will certainly choose a male of her own type. Each of N females
9 will meet the rare heterozygote male first with probability $1/N$ and take him with probability
10 $1 - m$. We thus have $\phi_{\text{male, het}} = 1 - m$ and

$$W_{\text{het}} = 1 - \frac{m}{2} - \frac{m^M}{2} - (1 - k)(1 - c). \quad (\text{A21})$$

11 For $c < 1$ and $k < 1$ this is always negative for sufficiently large $m \rightarrow 1$.

12 **Appendix 3: Invasion criterion for the model with flexible mating** 13 **strategy**

14 In this appendix, we prove the invasion criterion for the model where costs of choosiness are
15 avoided due to a flexible female mating strategy, as defined in Eq. 6. The criterion claims that
16 invasion of mutants for increased choosiness is possible if and only if the fitness of homozygotes
17 W_{hom} is larger than the fitness of heterozygotes W_{het} in the population dynamical equilibrium
18 of the residents.

19 Note first that the total female mating rates are all equal to 1 for this model since every
20 female is guaranteed to mate. Explicitly, using (6),

$$Q_{\text{hom}^\pm, \text{hom}^\pm} + Q_{\text{hom}^\pm, \text{het}} + Q_{\text{hom}^\pm, \text{hom}^\mp} = 1, \quad (\text{A22})$$

$$Q_{\text{het, het}} + Q_{\text{het, hom}^+} + Q_{\text{het, hom}^-} = 1. \quad (\text{A23})$$

21 We can thus write the elements of the invasion matrix for rare mutants $\mathbf{A}_{\mathbf{m}, \tilde{\mathbf{m}}}$ (Eq. 13) as
22 follows,

$$a_{11} = \frac{1}{4} (1 + 2Q_{\text{hom}^\pm, \text{het}} + Q_{\text{het}, \text{het}}) - d_{\text{het}}, \quad (\text{A24})$$

$$a_{21} = \frac{1}{4} (1 + 2Q_{\text{hom}^\pm, \text{het}} + Q_{\text{het}, \text{het}}), \quad (\text{A25})$$

$$a_{12} = \frac{1}{4} \left(1 + \tilde{Q}_{\text{hom}^\pm, \text{hom}^\mp} - \tilde{Q}_{\text{hom}^\pm, \text{hom}^\pm} + 2Q_{\text{hom}^\pm, \text{hom}^\mp} + Q_{\text{het}, \text{hom}^\pm} \right), \quad (\text{A26})$$

$$a_{22} = \frac{1}{4} \left(1 - \tilde{Q}_{\text{hom}^\pm, \text{hom}^\mp} + \tilde{Q}_{\text{hom}^\pm, \text{hom}^\pm} + 2Q_{\text{hom}^\pm, \text{hom}^\pm} + Q_{\text{het}, \text{hom}^\pm} \right) - d_{\text{hom}}. \quad (\text{A27})$$

- 1 Define the so-called resident matrix $\mathbf{A}_{\mathbf{m}, \tilde{\mathbf{m}}}$ where the mutant variables \tilde{m} and \tilde{m}' are set equal
 2 to the resident values m and m' . Since this matrix reproduces the population dynamics of the
 3 resident population, it must have leading eigenvalue 0 in the population dynamic equilibrium.
 4 Consider now the difference of the mutant and the resident matrix,

$$\Delta \mathbf{A} := \mathbf{A}_{\mathbf{m}, \tilde{\mathbf{m}}} - \mathbf{A}_{\mathbf{m}, \mathbf{m}} = \frac{1}{4} \begin{pmatrix} 0 & \Delta Q \\ 0 & -\Delta Q \end{pmatrix} \quad (\text{A28})$$

5 where

$$\Delta Q = \underbrace{\tilde{Q}_{\text{hom}^\pm, \text{hom}^\mp} - \tilde{Q}_{\text{hom}^\pm, \text{hom}^\pm}}_{:=Q(\tilde{\mathbf{m}})} - \underbrace{(Q_{\text{hom}^\pm, \text{hom}^\mp} - Q_{\text{hom}^\pm, \text{hom}^\pm})}_{:=Q(\mathbf{m})}. \quad (\text{A29})$$

6 and

$$Q(\mathbf{m}) = -m' P_{\text{hom}} \left(\frac{1 - (1 - \pi_{\text{hom}})^{M+1}}{\pi_{\text{hom}}} \right) \quad (\text{A30})$$

7 We can prove that

$$\frac{\partial}{\partial m} Q(\mathbf{m}) < 0 \quad ; \quad \frac{\partial}{\partial m'} Q(\mathbf{m}) < 0 \quad (\text{A31})$$

8 and thus $\Delta Q \geq 0$ for $m \geq \tilde{m}$. To see this, note that

$$\frac{\partial}{\partial m} Q(\mathbf{m}) = -m' P_{\text{hom}} \frac{\partial \pi_{\text{hom}}}{\partial m} \frac{\partial}{\partial \pi_{\text{hom}}} \left(\frac{1 - (1 - \pi_{\text{hom}})^{M+1}}{\pi_{\text{hom}}} \right) \quad (\text{A32})$$

9 and $\partial \pi_{\text{hom}} / \partial m = -N_{\text{het}} / N < 0$ and

$$\frac{\partial}{\partial \pi_{\text{hom}}} \left(\frac{1 - (1 - \pi_{\text{hom}})^{M+1}}{\pi_{\text{hom}}} \right) = \frac{\pi_{\text{hom}}(M+1)(1 - \pi_{\text{hom}})^M - 1 + (1 - \pi_{\text{hom}})^{M+1}}{\pi_{\text{hom}}^2} < 0 \quad (\text{A33})$$

1 since $1 = (1 - \pi_{\text{hom}} + \pi_{\text{hom}})^{M+1} > (1 - \pi_{\text{hom}})^{M+1} + (M+1)\pi_{\text{hom}}(1 - \pi_{\text{hom}})^M$. The derivation
 2 for m' is analogous.

3 Next, we denote \mathbf{w} the right leading eigenvector of the mutant matrix $\mathbf{A}_{\mathbf{m}, \tilde{\mathbf{m}}}$ and \mathbf{v} the left
 4 leading eigenvector of the resident matrix $\mathbf{A}_{\mathbf{m}, \mathbf{m}}$ (with corresponding eigenvalue 0). We can
 5 then express the leading eigenvalue $\lambda(\mathbf{m}, \tilde{\mathbf{m}})$ of $\mathbf{A}_{\mathbf{m}, \tilde{\mathbf{m}}}$ as

$$\lambda(\mathbf{m}, \tilde{\mathbf{m}}) = \frac{\mathbf{v} \Delta \mathbf{A} \mathbf{w}}{\mathbf{v} \mathbf{w}} = \frac{w_2(v_1 - v_2) \Delta Q}{4\mathbf{v} \mathbf{w}}. \quad (\text{A34})$$

6 Because of the Perron-Frobenius theorem, all elements of the vectors \mathbf{v} and \mathbf{w} must be
 7 positive. We conclude that $\lambda(\mathbf{m}, \tilde{\mathbf{m}}) > 0$ for $\mathbf{m} < \tilde{\mathbf{m}}$, and hence mutants for stronger
 8 choosiness can invade, if and only if $v_2 > v_1$. For the last step note that the column sums of
 9 the resident matrix reproduce the fitness values,

$$a_{11} + a_{21} = W_{\text{het}}, \quad (\text{A35})$$

$$a_{12} + a_{22} = W_{\text{hom}}. \quad (\text{A36})$$

10 Because of the equilibrium condition, we have

$$N_{\text{het}} W_{\text{het}} + 2N_{\text{hom}} W_{\text{hom}} = 0 \quad (\text{A37})$$

11 and thus W_{het} and W_{hom} have opposite sign. From $v_1 a_{11} + v_2 a_{21} = 0$ we get

$$v_1 = -\frac{a_{21}}{a_{11}} v_2 = \frac{a_{21}}{a_{21} - W_{\text{het}}} v_2 \quad (\text{A38})$$

12 and thus $v_2 > v_1$ if and only if $W_{\text{het}} < 0 < W_{\text{hom}}$.

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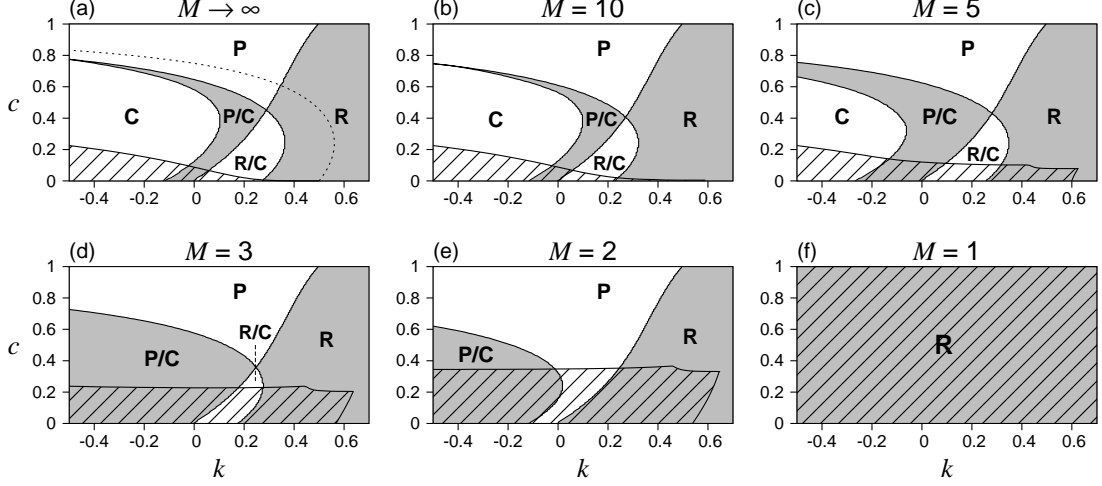


Figure 1: Evolutionary regimes for female choosiness m in the model with mating costs, as a function of the ecological parameters k and c . k is the strength of stabilizing (positive values) or disruptive (negative values) selection arising from phenotype-specific carrying capacities. c is the strength of frequency-dependent selection induced by competition. Mating costs are quantified by the number of mating trials per female, M . $M \rightarrow \infty$ corresponds to the model without costs (model 2 of Pennings et al., 2008). The five regimes are named according to the outcome of evolution in small steps; R: random mating ($m = 0$); P: partial isolation ($0 < m < 1$); C: complete isolation ($m = 1$); R/C: random mating or complete isolation; P/C: partial or complete isolation. In the R/C and P/C regimes, low initial values of m lead to random mating or partial isolation, respectively, whereas high initial values of m lead to complete isolation. Only points where complete isolation can be reached from an initial value of $m' \leq 0.999$ ($m \leq 0.823$) are assigned to these bistable regimes (see main text). In (a), the dotted line shows the boundary of the bistable regimes if the domain of attraction of the complete isolation equilibrium can be arbitrarily small (critical $m' \rightarrow 1$). In (b) to (f) (i.e., for $M < \infty$), the complete isolation equilibrium is always locally stable, but often with a vanishingly small domain of attraction. In the hatched area, the polymorphic equilibrium at the ecological locus is unstable for at least some values of m . In (d) and (e), the C regime is present for values of k smaller than those shown in the plots. In (f), only the R regime exists and the polymorphic equilibrium is always unstable.

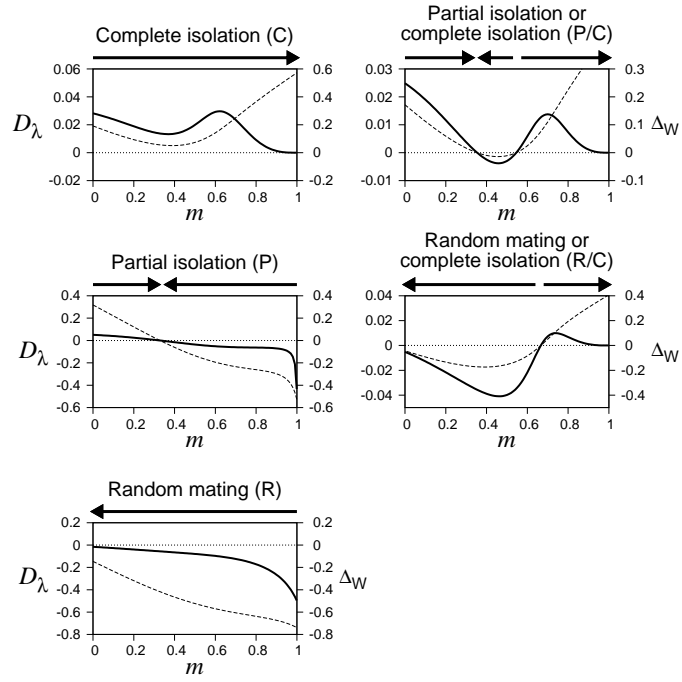


Figure 2: The invasion fitness gradient D_λ (solid line, left axis) and the fitness difference between homozygotes and heterozygotes Δ_W (dashed line, right axis) as a function of female choosiness m , in the absence of costs and for each of the five evolutionary regimes (cf. Fig. 1a). Choosiness increases whenever D_λ and Δ_W are positive and decreases when they are negative. Parameters: (C) $k = 0.05$, $c = 0.3$, (P) $k = 0.05$, $c = 0.8$, (R) $k = 0.6$, $c = 0.95$, (PC) $k = 0.12$, $c = 0.4$, (RC) $k = 0.2$, $c = 0.2$.

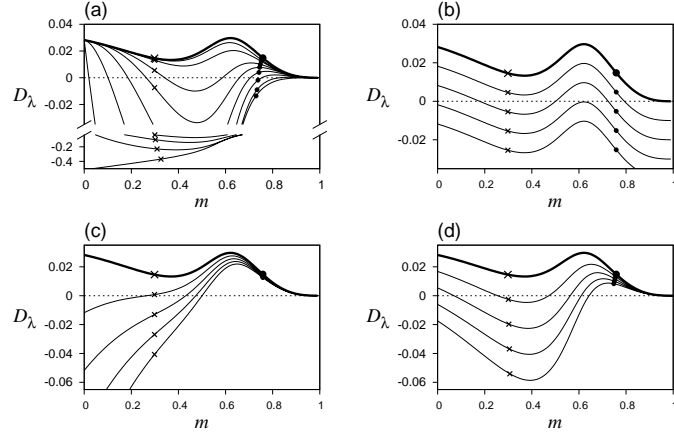


Figure 3: The invasion fitness gradient $D_\lambda(m)$ for female choosiness m in the presence of costs of choosiness. For values of m to the right of the crosses, the proportion of heterozygotes is less than $1/3$ (bimodal phenotype distribution). To the right of the dots, the proportion of heterozygotes is less than 0.01 (strong phenotypic clustering). The ecological parameters are $k = 0.05$, $c = 0.3$ (cf. Fig. 2, first panel). **(a)** Mating costs with a limited number of mating trials, M , per female. From top to bottom $M = \infty$ (thick line), 10, 8, 6, 5, 4, 3, 2, 1. Decreasing M leads to a switch from the C regime ($M = 10, 8, 6$ to the P/C regime ($M = 5, 4, 3$) and further on to the P regime ($M = 2$) and R regime ($M = 1$), cf. Fig 1. Note the break in the y-axis and the different scales in its lower and upper parts. **(b)** Absolute viability costs linked directly to m (i.e., eq. 8 with $\delta' = 0$), with (from top to bottom) $\delta = 0, 0.01, 0.02, 0.03, 0.04$. **(c)** Absolute viability costs linked directly to m' (i.e., $\delta = 0$), with (from top to bottom) $\delta' = 0, 0.01, 0.02, 0.03, 0.04$. **(d)** Relative viability costs linked to the average number of males rejected by a female before mating (according to eq. 10), with (from top to bottom), $\gamma_k \equiv \gamma = 0, 0.01, 0.02, 0.03, 0.04$.

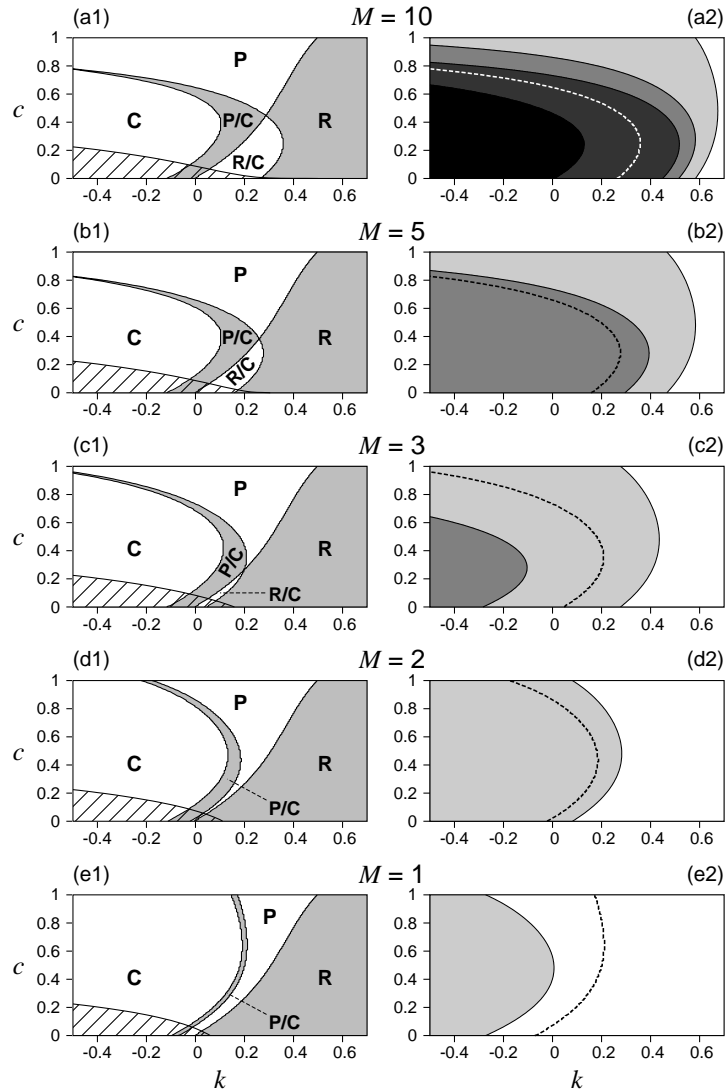


Figure 4: Evolutionary regimes for female choosiness m in the alternative model with a flexible mating strategy. Females are choosy in their first M encounters with males but mate randomly afterwards. Plots in the left-hand column are analogous to those in Fig. 1 (see there for further details). Plots in the right-hand column show the proportion of heterozygotes at the maximal choosiness value $m = 1$; black: Proportion of heterozygotes less than 0.001, dark grey: ≤ 0.01 , intermediate grey: ≤ 0.1 , light grey $\leq (1/3)$ (bimodal), white: $> 1/3$. The dotted line is identical to the line separating the C, P/C and R/C regimes from the P and R regimes in the left-hand plots, with $m = 1$ being locally evolutionarily stable to the left of this line.

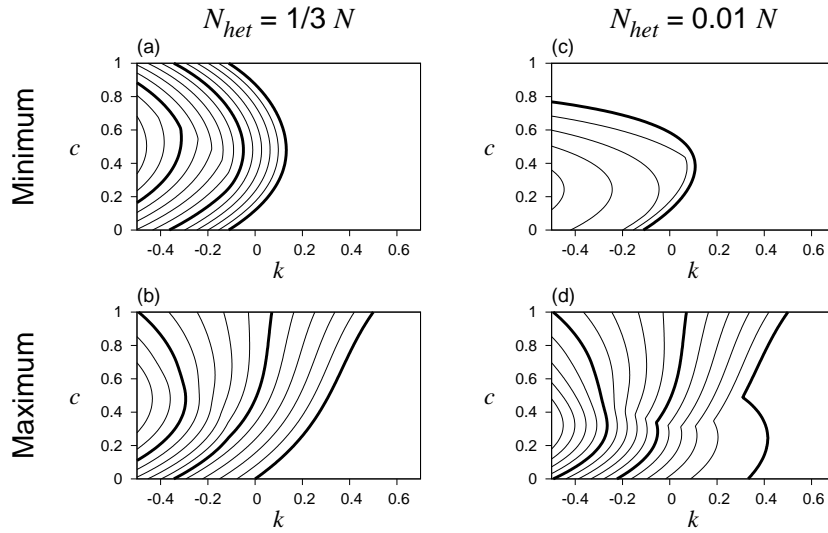


Figure 5: The invasion fitness gradient $D_\lambda(m)$ in the absence of costs of choosiness. The graphs are contour plots in the c versus k plane (see Fig. 1) for the minimal (**a, c**) and maximal (**b, d**) value of D_λ before the population reaches either a bimodal phenotype distribution (**a, b**) or strong phenotypic clustering with 1% heterozygotes (**c, d**). The values shown correspond to the minimum and maximum of the top-most functions in Fig. 3 to the left of the crosses or dots, respectively. From right to left, the thick lines are isoclines for $D_\lambda = 0, 0.05,$ and 0.1 . The thin lines are isoclines in steps of 0.01 . Only isoclines for positive values of D_λ are shown.

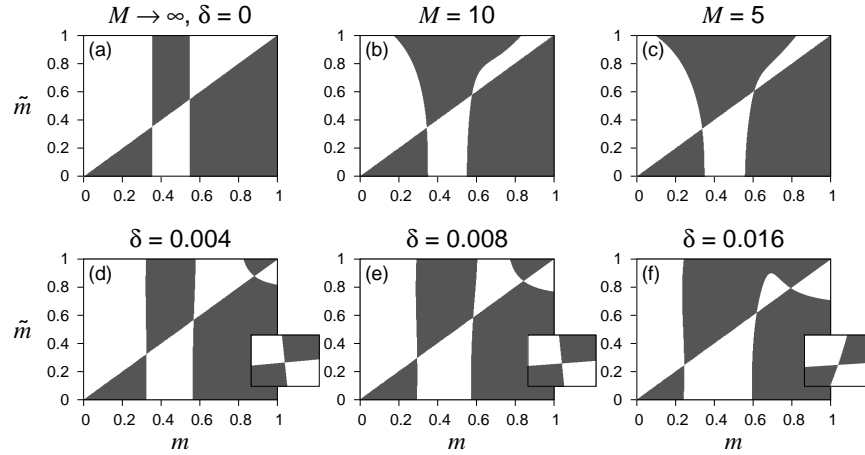


Figure A1: Pairwise invasibility plots for female choosiness m in the presence of costs of choosiness. M is the maximal number of mating trials per female in the model with mating costs. δ determines the magnitude of absolute viability costs linked directly to m . For each resident choosiness value m , it is shown whether a mutant with choosiness \tilde{m} can (white) or cannot (grey) invade the resident population. Intersections of boundary lines mark evolutionarily singular points (Geritz et al., 1998). **(a)** No costs. For the chosen ecological parameters ($k = 0.12$, $c = 0.4$), there are two such points, with the lower one being an evolutionary attractor and the higher one an evolutionary repeller (corresponding to the P/C regime). **(b, c)** Mating costs ($\delta = \delta' = 0$). The evolutionary attractor is uninvadable, that is, it is an evolutionarily stable strategy (ESS). **(d-f)** Absolute viability costs linked to m ($M = \delta' = 0$). The insets show close-ups of the neighborhood of the evolutionary attractor (the left-most singular point). In (d) and (e), the attractor is an ESS. In (f), the attractor is invadable and, hence, an evolutionary branching point.