

Adaptive speciation when assortative mating is based on female preference for male marker traits

M. DOEBELI

Departments of Zoology and Mathematics, University of British Columbia, University Boulevard, Vancouver, BC, Canada

Keywords:

adaptive speciation;
assortative mating;
disruptive selection;
female preference;
marker trait;
sympatric speciation.

Abstract

Adaptive speciation occurs when frequency-dependent ecological interactions generate conditions of disruptive selection to which lineage splitting is an adaptive response. Under such selective conditions, evolution of assortative mating mechanisms enables the break-up of the ancestral lineage into diverging and reproductively isolated descendent species. Extending previous studies, I investigate models of adaptive speciation due to the evolution of indirect assortative mating that is based on three different mating traits: the degree of assortativity, a female preference trait and a male marker trait. For speciation to occur, linkage disequilibria between different mating traits, e.g. between female preference and male marker traits, as well as between mating traits and the ecological trait, must evolve. This can lead to novel speciation scenarios, e.g. when reproductive isolation is generated by a splitting in the degree of assortativeness, with one of the emerging lineages mating assortatively, and the other one disassortatively. I investigate the effects of variation in various model parameters on the likelihood of speciation, as well as robustness of speciation to introducing costs of assortative mating. Even though in the models presented speciation requires the genetic potential for strong assortment as well as rather restrictive ecological conditions, the results show that adaptive speciation due to the evolution of assortative mating when mate choice is based on separate female preference and male marker traits is a theoretically plausible evolutionary scenario.

Introduction

In recent years, it has become clear that speciation under conditions of ecological contact between the emerging lineages is a theoretically plausible evolutionary scenario (Doebeli, 1996; Dieckmann & Doebeli, 1999; Higashi *et al.*, 1999; Kondrashov & Kondrashov, 1999; Doebeli & Dieckmann, 2000; Drossel & McKane, 2000; Dieckmann *et al.*, 2004). In fact, what has emerged is that, in theory, there is whole class of speciation processes that require ecological contact. These speciation processes are subsumed under the term adaptive speciation (Dieckmann *et al.*, 2004). Generally speaking, adaptive speciation occurs in two phases. First, frequency-dependent interactions within the ancestral population generate conditions of disruptive selection to which lineage splitting is

an adaptive response. Second, assortative mating mechanisms that are either already in place or evolve as a consequence of selection for lineage splitting enable the break-up of the ancestral population into diverging and reproductively isolated descendent species.

The theory of adaptive dynamics (Dieckmann & Law, 1996; Metz *et al.*, 1996; Geritz *et al.*, 1998) provides a powerful mathematical framework for studying the first phase of adaptive speciation. In particular, the concept of evolutionary branching points captures the important phenomenon of evolutionary convergence to regimes of disruptive selection (Christiansen, 1991; Abrams *et al.*, 1993; Geritz *et al.*, 1998; Doebeli & Dieckmann, 2000). Models of evolutionary branching in asexual populations have yielded two important insights.

First, regimes of disruptive selection are not, in general, unstable or unattainable, as one would perhaps expect on intuitive grounds if one adheres to a static view of unchanging fitness landscapes, according to which disruptive selection is a knife's edge situation that would very rarely materialize in the real world. Instead, evolutionary

Correspondence: Michael Doebeli, Departments of Zoology and Mathematics, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada.
Tel.: +1 604 822 3326; fax: +1 604 822 2416;
e-mail: doebeli@zoology.ubc.ca

branching points are attractors for the evolutionary dynamics in phenotype space, attractors, however, at which the selection regime becomes disruptive. Thus, populations converge evolutionarily to locations in phenotype space at which there is selection for lineage splitting (Metz *et al.*, 1996; Geritz *et al.*, 1998).

Second, the study of models of evolutionary branching has shown that such evolutionary convergence onto disruptive selection regimes is a generic outcome of all types of ecological interactions generating negative frequency dependence, as well as of frequency-dependent sexual selection (a long list of relevant publications can e.g. be found at <http://www.helsinki.fi/~mgyllenb/addyn.htm>). Thus, in theory the first phase of adaptive speciation, in which lineage splitting becomes an adaptive response to frequency-dependent biological interactions, is a common evolutionary occurrence.

In asexual lineages, the emergence of diverging lineages is an immediate consequence of convergence to an evolutionary branching point, i.e. the second phase of adaptive speciation does not require assortative mating. In sexual populations, however, random mating continuously creates intermediate phenotypes and thus prevents the establishment of distinct and diverging phenotypic clusters. Therefore, in sexual populations adaptive speciation requires some form of nonrandom, assortative mating with respect to the trait that is under disruptive selection. Such assortativeness can come about in various ways. For example, it could be a pleiotropic consequence of the trait under disruptive selection, e.g. if this trait is habitat choice, and if habitat choice in turn determines mate choice. Alternatively, assortative mating with respect to the trait under disruptive selection could arise evolutionarily. For example, it is likely that in many species there is genetic variation for assortative mating that is directly based on ecologically important traits such as body size (e.g. Schluter & Nagel 1995). But the most adverse scenario for adaptive speciation occurs when assortative mating is based on selectively neutral marker traits. In this case, for assortative mating to latch on to the ecological trait that is under disruptive selection, linkage disequilibrium between the marker trait and the ecological trait needs to develop, a process that is continually undermined by recombination. In fact, it is in part because of this difficulty that adaptive speciation was long considered a theoretically unlikely scenario (Felsenstein, 1981).

However, some recent models have shown that this need not be the case in the context of multilocus models, and that in fact earlier reservations about the evolution of assortative mating and subsequent splitting into reproductively isolated lineages may have been unfounded. Specifically, Kondrashov & Kondrashov (1999) have shown that reproductive isolation between diverging lineages is a generic outcome in two variants of a multilocus model. In the first variant, the marker trait was the same in males and females, and assortative mating was

based on similarity in this marker trait. The second variant had two different traits, a preference trait in females and a marker trait in males, and assortative mating was based on a match between female preference and male marker. This makes the evolution of reproductive isolation even more difficult, as recombination now not only breaks up linkage disequilibrium between mating and ecological traits, but also between female preference and male marker traits. Kondrashov & Kondrashov (1999) showed that, nevertheless, reproductive isolation evolved if the degree of assortative mating, that is, the degree with which a female with a given preference trait prefers a male with matching marker trait, was fixed at a high enough value. They did not, however, study the evolution of this degree of assortativeness.

Evolution of the degree of assortativeness was indeed considered in the models of Dieckmann & Doebeli (1999), who showed that the degree of assortativeness evolved to levels that are high enough to lead to reproductive isolation even if assortative mating is based on marker traits. However, Dieckmann & Doebeli (1999) only studied the case in which the marker trait is the same in males and females, i.e. they did not consider the case of separate preference and marker traits in females and males.

In this paper, I extend these results by considering models in which the degree of assortativeness can evolve, and in which assortative mating is determined by a female preference trait that acts on male marker traits. Thus, the paper fills two gaps left by the models of Kondrashov & Kondrashov (1999) and Dieckmann & Doebeli (1999), gaps that need to be filled in order to progress towards understanding processes of adaptive speciation in sexual populations.

Model

The model I used to investigate adaptive speciation mediated through the evolution of assortative mating based on female preference is an extension of the stochastic-individual-based model used in Bolnick & Doebeli (2003), which was in turn based on the model of Dieckmann & Doebeli (1999). In the present model, each individual is assigned four phenotypic traits:

- an ecological trait, x , that determines the strength of competitive interaction between individuals; this trait is determined by N_{ecol} loci;
- an assortative mating trait, a , that determines the strength of assortativeness in females (see below); this trait is determined by N_{asso} loci;
- a female preference trait, p , that determines the 'reference point' for assortative mating (see below); this trait is determined by N_{pref} loci;
- a male marker trait, m , that determines the 'target' for assortative mating (see below); this trait is determined by N_{mark} loci.

Each trait is determined by a set of diploid loci with additive effects. Each locus has two alleles, with phenotypic value 0 or 1. A trait value is determined as the number of 1-alleles present at the corresponding set of loci, divided by twice the number of loci in this set. This ensures that all phenotypic values lie between 0 and 1, independent of the number of loci that determine a particular phenotype. All individuals possess all four sets of loci, but females only express the first three phenotypes above, i.e. the ecological trait, the assortativity trait, and the preference trait, whereas males only express the first and the last, i.e. only the ecological and the marker trait.

The individual-based model is set in discrete time with non-overlapping generations, and in each generation ecological viability selection is followed by mating and the production of the offspring comprising the population at the start of the next generation. Ecological selection does not distinguish between males and females and is based on the Beverton–Holt equation, which is the discrete-time analogue of the logistic equation and in its basic form is given by

$$N(t+1) = \frac{rN(t)}{1 + \frac{r-1}{K}N(t)}. \quad (1)$$

This equation describes the dynamics of a population in which r is the maximal number offspring per individual and K is the carrying capacity. The model always exhibits equilibrium dynamics. In this model, a single time step from time t to time $t+1$ can be broken down into two steps occurring within a single generation: first each individual survives with probability

$$\frac{1}{1 + \frac{r-1}{K}N(t)},$$

then the survivors produce r offspring on average (and then die). For the present purposes, I assume that the parameter r is independent of an individual's phenotype, but that the carrying capacity $K(x)$ is a function of the ecological trait x with an intermediate optimum:

$$K(x) = K_0 \exp\left(-\frac{(x-1/2)^2}{2\sigma_K^2}\right). \quad (2)$$

Here K_0 scales the overall population abundance, and σ_K measures how fast the carrying capacity declines with phenotypic distance from the optimal trait values, which is assumed to be 1/2. The function $K(x)$ thus imposes stabilizing selection on the trait x . Frequency-dependent selection is incorporated by assuming that the strength of competition between individuals with phenotypes x and x' decreases with phenotypic distance according to

$$c(x, x') = \exp\left(-\frac{(x-x')^2}{2\sigma_c^2}\right). \quad (3)$$

Here σ_c measures how fast competitive impacts decrease with an increase in the distance between the

ecological phenotype of interacting individuals. Using the competition function $c(z, z')$, the effective population size that an individual with phenotype x experiences is calculated as

$$n_{\text{eff},x}(t) = \sum_{x' \neq x} c(x, x'), \quad (4)$$

where the sum runs over all individuals (males and females) in the population (except the focal individual x). This effective population size replaces the total density $N(t)$ in the Beverton–Holt equation to yield the probability of survival to the reproductive period of an individual with ecological phenotype x as:

$$\frac{1}{1 + \frac{r-1}{K(x)}n_{\text{eff},x}(t)}. \quad (5)$$

Note that the effective population size for a given phenotype x depends on the distribution of phenotypes. Therefore, viability selection is frequency-dependent. If reproduction is asexual, each surviving individual produces r offspring (on average) whose phenotype is the same as that of the single parent except for (small) mutations. In this case, the evolutionary dynamics of the system are such that the population always first converges to the intermediate phenotype $x^* = 1/2$ that maximizes the carrying capacity. This phenotype is an evolutionary branching point if

$$\sigma_c < \sigma_K, \quad (6)$$

in which case the asexual population splits into two diverging phenotypic clusters (Dieckmann & Doebeli, 1999).

If reproduction is sexual, mating behaviour is determined by the remaining three phenotypes. The author assumes that the female assortativity trait a determines the degree of choosiness of the female, and that mate choice is based on the phenotypic distance between the female preference trait p and the male marker trait m . More precisely, if a female with trait values (x, a, p, m) encounters a male with trait values (x', a', p', m') , where the notation refers to the four traits introduced above, then the probability that mating occurs, and hence offspring production, is proportional to the function:

$$P(a, p, m') = \begin{cases} \exp\left[-\frac{1}{2}\left(\frac{2a-1}{s}\right)^2 |p-m'|^2\right] & \text{for } a > 1/2 \\ 1 & \text{for } a = 1/2 \\ \exp\left[-\frac{1}{2}\left(\frac{2a-1}{s}\right)^2 (1-|p-m'|)^2\right] & \text{for } a < 1/2 \end{cases} \quad (7)$$

This functional form for mating probabilities implies the following. For assortative mating traits a that are larger than 1/2, females mate assortatively, that is, they prefer males with marker traits m that are similar to the females' preference trait p (if $a > 1/2$, $P(a, p, m')$ increases with decreasing distance $|p-m'|$). In contrast, for assortative mating traits a that are smaller than 1/2, females

mate disassortatively, that is, they prefer males with marker traits m that are dissimilar to the females' preference trait p (if $a < 1/2$, $P(a, p, m')$ decreases with decreasing distance $|p - m'|$). Females with assortative mating trait $a = 1/2$ mate randomly.

The parameter s that appears in eqn (7) determines how the degree of assortativeness changes with changes in the mating trait a . Lower values of s induce faster change in assortativity and more pronounced assortativity and disassortativity for extreme values of a (i.e. for values of a near the boundary values 0 and 1). The mating function P is shown in Fig. 1 for two choices of the parameter s . We will see that the magnitude of this parameter is an important determinant of the likelihood with which speciation occurs in the present model, which has also been noted by Bolnick & Doebeli (2003) and by Bolnick (2004).

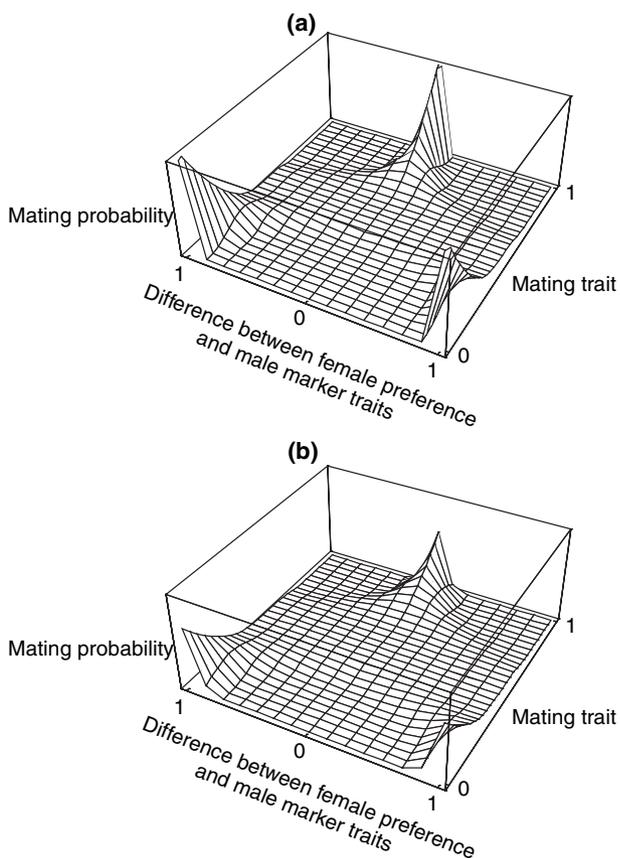


Fig. 1 Mating probabilities are given by, eqn (7) and depend on the difference between the female preference trait and the male marker trait, as well as on the female's degree of assortative mating, a . The parameter s in eqn (7) determines the shape of the mate choice function. (a) Lower values of s steepen the surface and correspond to a higher genetic potential for assortative mating; (b) higher values of s flatten the surface and correspond to a lower genetic potential for assortative mating.

To produce the next generation, each surviving female chooses a mating partner with relative probabilities determined by the function $P(a, p, m')$. More precisely, the probability that a male with marker trait m' is chosen by a female with assortative mating trait a and preference p is equal to $P(a, p, m') / \sum_{m''} P(a, p, m'')$, where the sum runs over all males in the population. This implies that there is no cost to choosiness, but I will later relax this assumption. Once a mating pair has been formed, it produces a number of offspring that is drawn from a Poisson distribution with mean $2r$ [as the total number of matings is equal to the number of females, i.e. on average, equal to half the total number of individuals in the population, each mating must yield $2r$ offspring to conform to the basic model given by eqn (1)]. The genotype of each offspring is determined by Mendelian segregation and under the assumption of free recombination between all loci. All alleles in an offspring genome undergo mutation to the other allelic type with probability μ . Finally, offspring are assigned to either sex with probability $1/2$.

The evolutionary dynamics of this system can now be obtained by iterating the numerical procedures described above after specifying the following: the numerical values for the parameters r , K_0 , σ_K , σ_c , s , and μ ; the number of loci determining each of the four traits; and the initial number of males and females, together with their genetic make-up.

The parameters r and K_0 do not have a qualitative effect on the results reported below, essentially because the basic ecological model given by eqn (1) always exhibits equilibrium dynamics, independent of the values of r and K_0 (of course, we need $r > 1$ for a viable population). These parameters do affect the equilibrium population size of the system, and hence the amount of demographic stochasticity and genetic drift, but my numerical simulations indicate that these effects generally appear to be small. Therefore, I have fixed these parameters at $r = 5$ and $K_0 = 1200$ throughout the paper.

Similarly, the parameter μ was fixed at 0.001 for most results. For the numbers of loci considered here, this value ensures reasonable per trait mutation rates. For example, if the ecological trait is determined by five loci in the above model, then in each generation, fewer than one in a hundred offspring have a mutation in this trait. This appears to be a rather small number for ecologically important traits, such as body size. A per locus mutation rate of 0.001 might seem unrealistic, but only if the term 'locus' is understood in its molecular genetic sense. However, the loci in the model above should not really be envisaged in this way, but rather as independent stretches of DNA of variable length that have approximately additive effects on the trait under consideration and that recombine freely with other such stretches of DNA. For example, if the ecological trait is determined by five loci in the model, this corresponds to the, admittedly

still very idealistic, assumption that there are five freely recombining regions in the genome that each have two alternative states affecting the ecological trait additively. These DNA regions might be much longer than a single locus, hence the mutation rate per such region might be quite high.

The initial populations used to obtain the results described in the next section were always generated by assigning 200 males and 200 females genotypes that were formed randomly under the assumption that the frequency of the 1-allele was 1/2 at each locus. For the ecological trait, the assumption of allele frequencies at 1/2 simply reflects the outcome of the initial phase of the evolutionary dynamics, during which the phenotype distribution evolves to a mean of 1/2, corresponding to the maximal carrying capacity. If selection is disruptive at this stage, which is the scenario of interest, the genetic variance will increase, and allele frequencies will equilibrate at 1/2. For the mating loci, the assumption of allele frequencies at 1/2 is simply the most parsimonious assumption and guarantees that initially, the population is, on average, mating randomly. Although changes in the assumptions about the initial conditions can lead to variations in the time it takes for a particular population to reach evolutionary equilibrium, my numerical simulations indicate that the results reported below are robust to such changes (see below).

The next section describes the propensity for adaptive speciation in this model as a function of the remaining parameters σ_K , σ_c , s , and the number of loci determining each of the four traits.

Results

If speciation occurs in the model described in the previous section, it is because of a positive feedback between the buildup of linkage disequilibria and selection on assortative mating. Initially, small amounts of linkage disequilibrium between the ecological trait and the various mating traits allow for assortative mating to latch on to the ecological trait. Disruptive selection on the ecological trait then selects for higher degrees of assortativity (or disassortativity, depending on the signs of the linkage disequilibria), which in turn increases the linkage disequilibria. This feedback loop eventually results in speciation.

The basic result of this paper is simply that adaptive speciation does indeed happen in the model described in the previous section under suitable conditions. In fact, there are three qualitatively different ways in which the evolution of assortative mating can lead to reproductive isolation between diverging phenotypic clusters. These are illustrated in Fig. 2. In all three scenarios, the frequency distribution of the ecological trait is bimodal, and the two modes represent incipient species that are reproductively isolated due to prezygotic isolation, i.e. due to assortative mating. However, the way in which

prezygotic isolation is mediated by the five loci determining mate choice differs between the three scenarios. The first scenario (Fig. 2a) is the one that one might expect by default: all females mate strongly assortatively, and the female preference trait and the male marker trait are split into two matching clusters. Each of those matching clusters is in linkage disequilibrium with one of the ecological clusters (not shown), so that assortative mating effectively latches onto the ecological trait and leads to reproductive isolation between the two ecological clusters.

The second scenario (Fig. 2b) is the analogue of the first when mating is disassortative: in this case, all females mate strongly disassortatively, and again both the female preference trait and the male marker trait are split into two clusters, but the male and female clusters that are compatible with each other are now at opposite ends of their respective character interval (because mating is disassortative). Again, the two corresponding clusters of female preference and male marker are each associated with one of the ecological clusters (not shown) and effectively represent different species.

In the third scenario (Fig. 2c), the female preference does not split into two different clusters. Instead, the distribution of the assortative mating trait becomes bimodal, so that one cluster of females mates assortatively, and the other female cluster mates disassortatively. At the same time, the male marker trait is split into two clusters, one of which is preferred by the females that mate assortatively, whereas the other is preferred by the females that mate disassortatively. Again, the resulting two mating clusters are in linkage disequilibrium with the two modes of the distribution of the ecological trait (not shown), which therefore represent incipient ecological species.

The three panels in Fig. 2 represent snapshots of the evolving populations after they have speciated. The three corresponding simulation runs were all obtained for the same combination of model parameters, and the runs only differed in their random initialization. Thus, when speciation occurs in this model, the actual form of assortative mating that evolves, i.e. whether after speciation mating is assortative, disassortative, or a mixture of both, generally depends on the initial conditions.

The remaining figures illustrate the likelihood of speciation in dependence of various model parameters. For these figures, I did not distinguish between the three types of assortative mating shown in Fig. 2. What is common to all three scenarios is that the distribution of the ecological phenotype becomes bimodal, which was taken as the basis for deciding whether speciation had occurred in a particular run. Bimodal distributions of the ecological trait only occurred once assortative mating had evolved, and hence represent at least incipient speciation.

Figure 3 shows the average time to speciation as a function of the two ecological parameters σ_K and σ_c for different choices of the mating parameter s . For a given

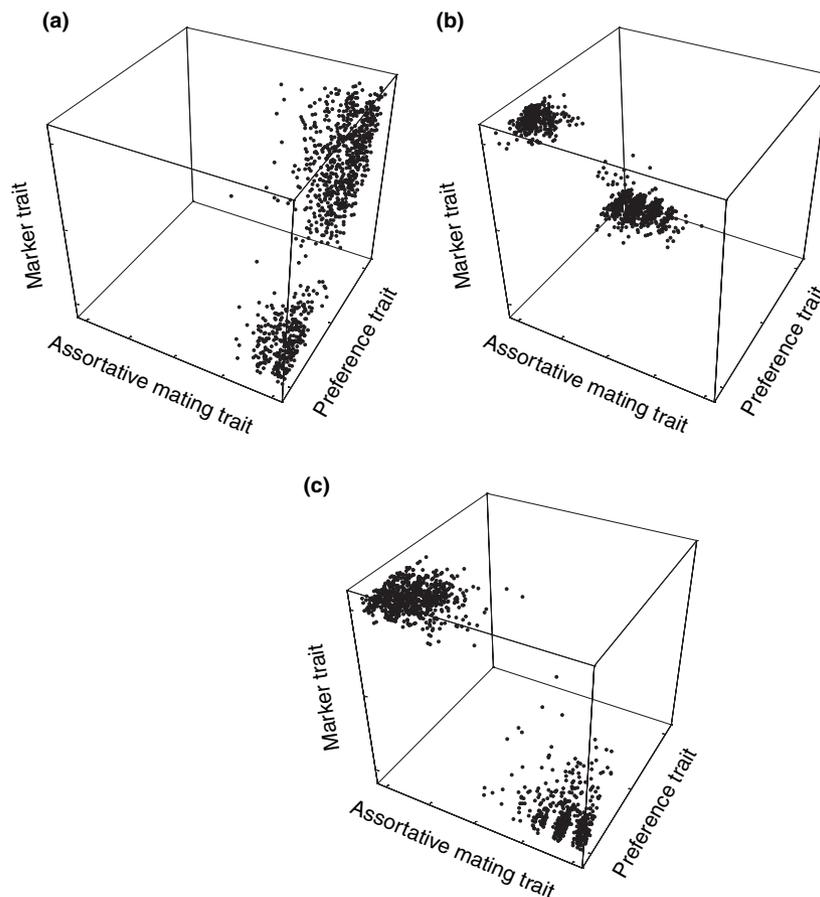


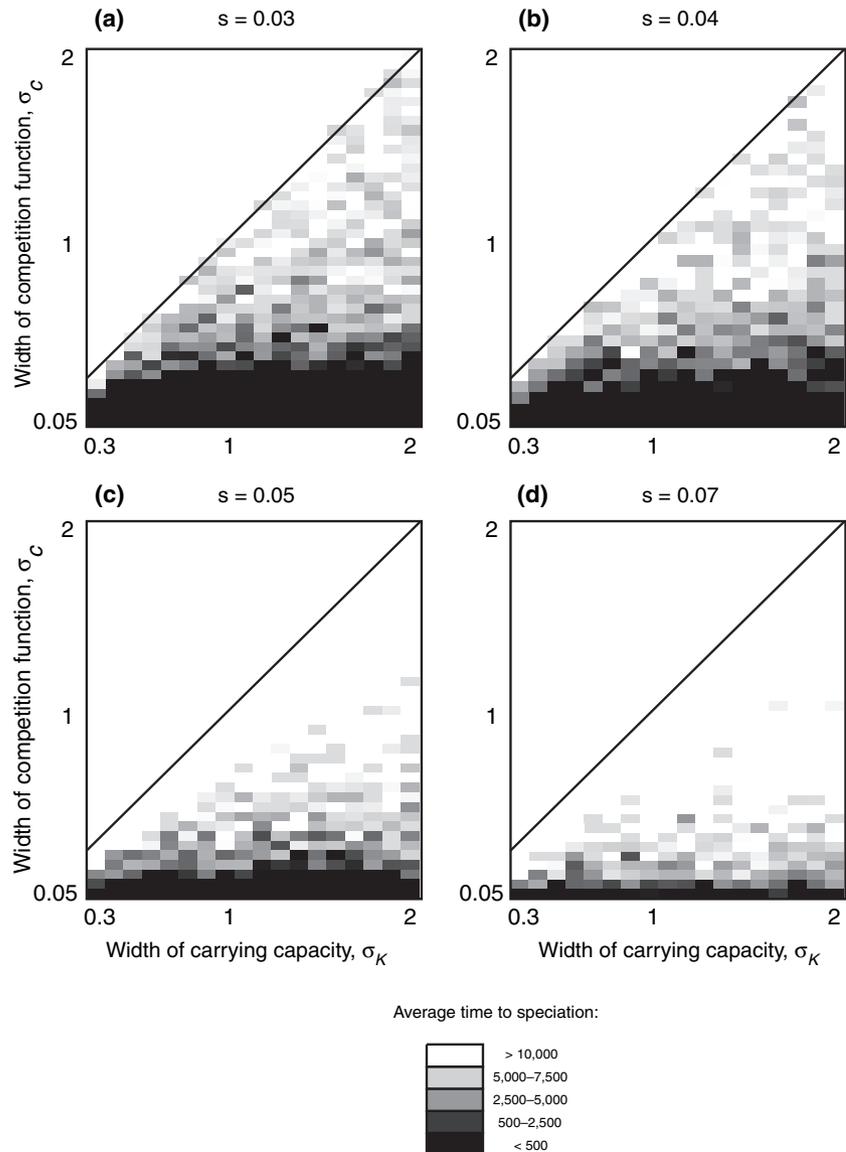
Fig. 2 Different speciation scenarios occurring in the individual-based model. All panels show populations at a point in time after speciation has occurred; trait values are used as coordinates to depict individuals as points in phenotype space. (a) Speciation after evolution of strong assortative mating and bimodality in the female preference trait and the male marker trait, with a strong linkage between loci coding for corresponding clusters in the preference and marker traits. (b) Speciation after evolution of strong disassortative mating and bimodality in the female preference trait and the male marker trait, with a strong linkage between loci coding for corresponding clusters in the preference and marker traits (note that because mating is disassortative, corresponding clusters are now opposites of each other, i.e. females with small preference trait values prefer males with large marker trait values and vice versa). (c) Speciation after the evolution of bimodality in the assortative mating trait. The loci determining the two modes of this trait are in linkage disequilibrium with the loci determining the two modes of the male marker trait distribution, whereas the female preference distribution remains unimodal, hence the preference loci are not in linkage disequilibrium with the other loci. In the two emerging species, females thus have the same preference traits, but they are split into assortative and disassortative clusters, each preferring the corresponding male marker cluster. In all scenarios the various mating trait clusters shown are in linkage disequilibrium with two corresponding clusters in the ecological trait, which are not shown. The three different speciation scenarios are obtained with different initial conditions for the same set of parameters: $r = 5$, $K_0 = 1200$, $\sigma_K = 1$, $\sigma_c = 0.25$, $s = 0.04$, and each of the four traits was determined by five diploid loci. To facilitate presentation of the population in the scatter plots, a small random number was added to each of the coordinates of all individuals (otherwise many individuals would have the same coordinates in phenotype space due to the discrete nature of the genetic determination of trait values).

combination (σ_K , σ_c), five simulations with different random initializations were run, which kept track of a moving average over 50 generations of the distribution of the ecological trait. If this average distribution exhibited two distinct maxima, speciation had occurred, and the run was stopped and the time to speciation recorded. If speciation did not occur within 10 000 generations, the run was also stopped. For each pair (σ_K , σ_c), the average time to speciation over the

five runs is displayed in the panels of Fig. 3 in shades of grey.

For Fig. 3, I assumed that each of the four traits was determined by five diploid loci. In asexual models, evolutionary branching is predicted if $\sigma_K < \sigma_c$ (Dieckmann & Doebeli, 1999), i.e. for all pairs (σ_K , σ_c) that lie below the diagonal line in each panel. As expected, parameter ranges for speciation because of preference mating are more restricted, and increasingly so for higher values of

Fig. 3 Time to speciation as a function of the ecological parameters σ_K (width of the carrying capacity function) and σ_c (width of the competition function) for various values of the mating function parameter s (see eqn 7). σ_K was varied between 0.3 and 2 in steps of 0.1, and σ_c was varied between 0.05 and 2 in steps of 0.05. For each combination of σ_K and σ_c , the model was run five times with different random initial conditions for 10 000 generations, and the average time to speciation was recorded (with an average of 10 000 corresponding to no speciation in all five runs). Shades of grey indicate the time to speciation, ranging from black (rapid speciation; average time to speciation <500 generations over five runs) to white (average time to speciation >10 000 generations, i.e. no speciation after 10 000 generations in each of the five runs), as indicated at the bottom of the figure. In each panel, the continuous diagonal line indicates the line $\sigma_c = \sigma_K$, i.e. the boundary for evolutionary branching to occur in the underlying adaptive dynamics model (speciation occurs in asexual models for $\sigma_c < \sigma_K$). (a) mating function parameter $s = 0.03$; (b) mating function parameter $s = 0.04$; (c) mating function parameter $s = 0.05$; (d) mating function parameter $s = 0.07$. Note that the mating functions corresponding to $s = 0.04$ (panel b) and $s = 0.07$ (panel d) are shown in Fig. 1. Other parameter values: $r = 5$, $K_0 = 1200$, and each of the four traits was determined by five diploid loci.



the mating parameter s . Thus, this parameter, which determines how fast mating becomes strongly assortative or disassortative when the mating trait deviates from intermediate values, is an important determinant for whether speciation occurs in this model. This is in accordance with results obtained by Bolnick & Doebeli (2003) and by Bolnick (2004).

Regarding the range of parameter values for σ_K and σ_c tested, it is of some importance to note that even though in the corresponding analytical adaptive dynamics model for asexual populations, only the ratio σ_K/σ_c matters for whether evolutionary branching occurs, in the explicit multilocus model considered here the absolute values of these parameters are also important. This is because in the sexual model, the total range of phenotypes was

always scaled to the interval $[0,1]$, which implies that the range of fitness variation due to stabilizing selection on the ecological trait interval varies with σ_K . In particular, if σ_K becomes too small, i.e. if the stabilizing selection component is too strong, then the phenotypic resolution provided by the finite number of loci may be too small, so that even if there is disruptive selection at the phenotype $1/2$, the population cannot become bimodal, because the fitness of individuals that differ by only one 1-allele from the intermediate phenotype is already too low. In the five-locus model used for Fig. 3, this essentially prevents speciation for $\sigma_K < 0.3$, independent of the value of σ_c . On the contrary, the stabilizing fitness profile becomes essentially flat over the phenotypic range $[0,1]$ for values of σ_K near 2.

Figure 4 follows the same general scheme as Fig. 3 and illustrates the effects of varying the number of loci for the various traits. In this figure, the value of the mating parameter was fixed at $s = 0.04$, which was the value used before in Fig. 3b (for comparison, panel 3b is shown again at the bottom of Fig. 4). Also as in Fig. 3b the number of loci was 5, except for the trait under consideration, for which it was 10. In Fig. 4a, the

ecological trait was determined by 10 loci, and comparison with Fig. 3b shows that speciation is somewhat less likely to occur. This is in agreement with the results obtained by Dieckmann & Doebeli (1999) for the case where preference and marker trait are identical. The effect appears to be due to the fact that the trait fluctuations because of genetic drift are smaller with more loci, which makes it harder to establish the linkage

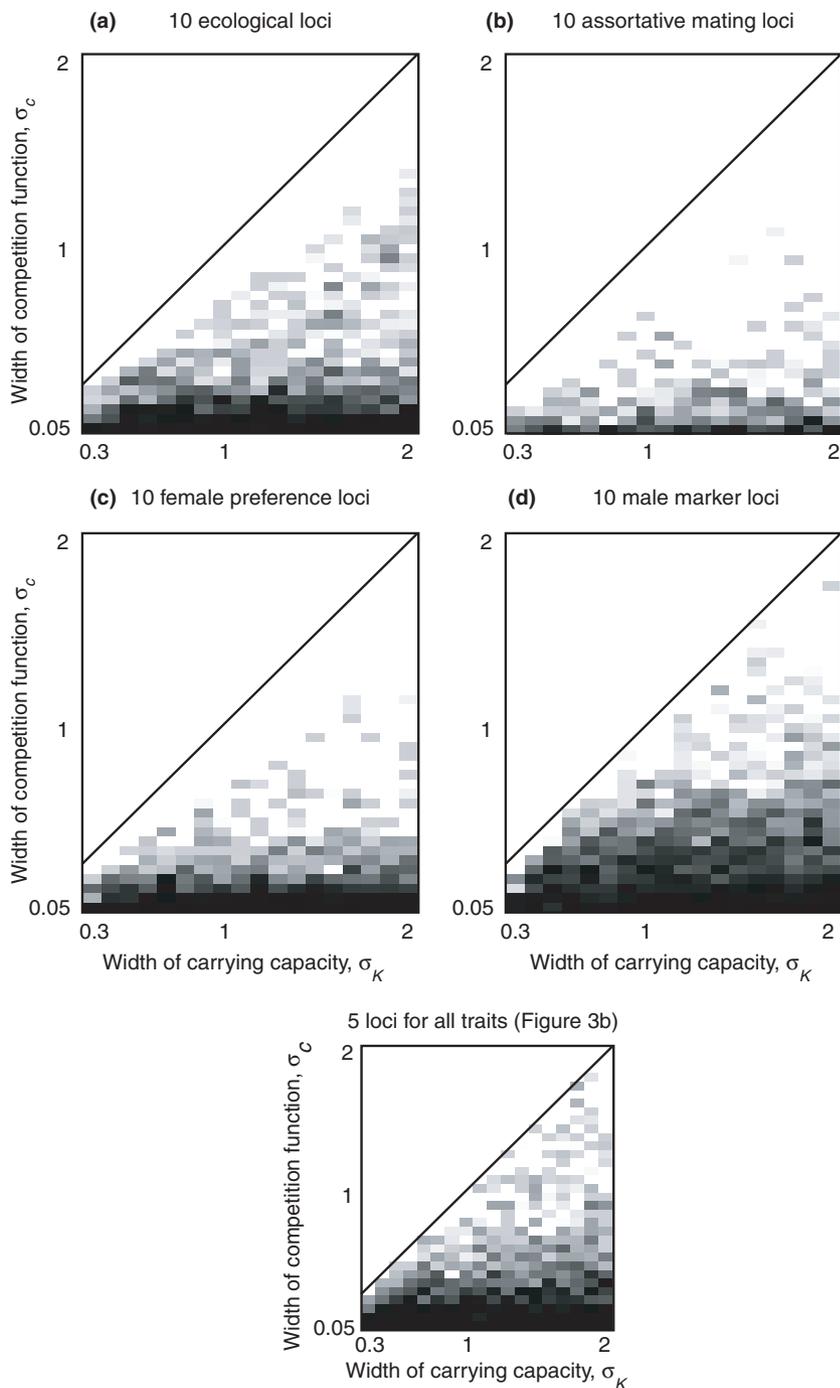


Fig. 4 Effects of varying the number of loci on the likelihood of speciation. Everything is the same as in Fig. 3b, except that for each panel, the number of loci was increased from five to ten for one of the four traits involved. (a) 10 ecological loci; (b) 10 assortative mating loci; (c) 10 female preference loci; (d) 10 male marker loci. For comparison, panel 3b is shown again at the bottom figure.

disequilibria between preference and marker trait and between mating traits and ecological trait that are needed for speciation.

Increasing the number of loci for the assortative mating trait has a more drastic negative effect on the likelihood of speciation (Fig. 4b). More loci imply decreased allelic effects, which means that the increase in assortativity (or disassortativity) per allele substitution becomes smaller. Therefore, selection on these alleles, which is in any case only mediated through already existing linkage disequilibria, becomes weaker. As a consequence, the positive feedback leading to the further buildup of linkage disequilibria is weakened, and hence speciation becomes less likely. The negative effect of increasing the number of assortative mating loci mirrors the decline of the propensity to speciation with increasing the mating parameter s , because higher s , and hence flatter mating functions (Fig. 1), also induce a smaller increase in assortativity per allele substitution.

Increasing the number of loci for the female preference trait (Fig. 4c) has a similar effect as increasing the number of ecological loci (Fig. 4a). Interestingly, however, increasing the number of loci determining the male marker trait does not decrease the likelihood of adaptive speciation (Fig. 4d). In fact, my numerical simulations indicate that with 10 loci for the male marker trait, speciation due to reproductive isolation between different mating trait clusters occurs even without a bimodal split in the ecological trait. In particular, speciation occurs even for parameter values $\sigma_K < \sigma_c$, for which evolutionary branching would not even occur in the corresponding asexual models. This means that speciation can occur even if the total ecological selection due to frequency-dependent competition and variation in resource abundance is stabilizing. In these cases, speciation must therefore be due to sexual selection alone. Because the distribution of the ecological character does not become bimodal in these scenarios, speciation by sexual selection has not been included in the results reported here. However, such scenarios have recently been studied by Arnegard & Kondrashov (2004), who showed that even though speciation through sexual selection alone may not be very common, it can occur under the right set of circumstances. My simulations indicate that speciation through sexual selection may actually be more common if there is an asymmetry in the number of loci determining female preference and male marker traits, i.e. with a larger number of loci determining the male trait.

I conclude this section by addressing some robustness properties of the model. Figure 5a shows results for the same scenario as in Fig. 3b, but with different initial conditions for the individual runs (for comparison, panel 3b is shown again at the bottom right of Fig. 5). For Fig. 5a, all traits were initially monomorphic, except the assortative mating trait, which was almost monomorphic. In addition, the initial female preference traits and the

male marker traits were asymmetric, with the female preference lying close to one end of the character interval, and the male marker lying close to the other end. Although the waiting times to speciation may be longer with such monomorphic and asymmetric initial conditions, the figure clearly illustrates that speciation is not an artefact of assuming allele frequencies of 0.5 at all loci for the initial conditions.

Figure 5b shows results for identical scenarios as in Fig. 3b, except that the per locus mutation rate was an order of magnitude lower, i.e. $\mu = 10^{-4}$. This slows down the evolutionary process considerably, and the simulations for Fig. 5b were therefore run to 20 000 generations. Although speciation is still possible for suitable parameter combinations, it is less likely to occur than for higher mutation rates. Note, however, that because of the stochastic nature of the speciation process, speciation would become more likely if even longer time horizons were considered. Note also that for the population sizes used in the present simulations, which typically range from *c.* 500–2000, a mutation rate of $\mu = 10^{-4}$ implies that on the order of one mutation per generation would occur in a trait that is determined by five loci. This seems to be an unrealistically low number for the quantitative traits assumed to underlie the speciation scenarios modelled here. In fact, increasing the population size accordingly, e.g. by a factor of 10, is likely to counteract the effects of lower mutation rates. Unfortunately, the corresponding simulations are still too time-consuming at present.

So far, I have made the assumption that there is no explicit cost to choosiness in females. While this assumption serves as a useful baseline case and may be approximately true in some natural populations, it may also quite often be violated. I therefore consider three different ways of incorporating costs of assortativeness into the model. First, costs can be introduced by assuming that the probability of mating for the choosiest female in the population is a certain percentage of a (potentially hypothetical) randomly mating female. The lower this percentage, the higher is the cost of choosiness. Specifically, in each generation, using the mating function P introduced in section 2, the sum $Q(a, p) = \sum_{m'} P(a, p, m')$ was calculated for each female, where a and p are the female mating and preference traits, and where the sum runs over all males in the population. Note that if a female mates randomly, i.e. if $a = 1/2$, then this sum is equal to the number of males in the population [because $P(1/2, p, m) = 1$ for all p and m]. Next, the female with the lowest sum $Q(a, p)$ was assumed to have a probability of mating equal to $1 - c$, where c is a parameter that measures the cost of choosiness. The probabilities of mating for all the other females were proportionally ordered between $1 - c$ and 1 according to their 'choosiness sums' $Q(a, p)$, so that females that were similarly choosy as the most choosy female had a probability of mating close to $1 - c$, whereas

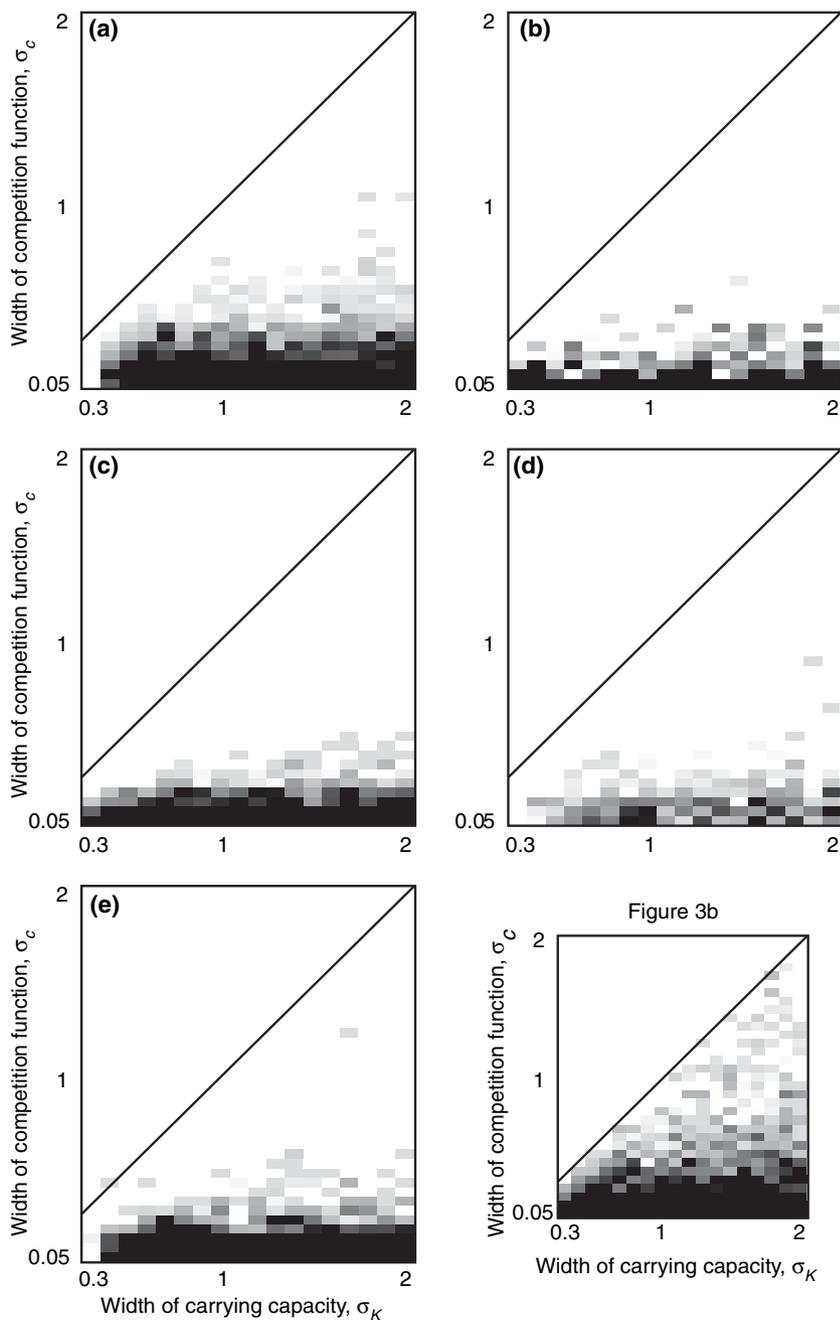


Fig. 5 Robustness to various model assumptions. In each of the panels, everything is the same as in Fig. 3b, except for the change indicated. For comparison, panel 3b is shown again at the bottom right of the figure. (a) Different initial conditions: instead of using allele frequencies of 1/2 at all loci, these runs were all initialized as follows: all alleles at the ecological loci were set to 0, except at one locus, where they were all set to 1; alleles at the assortative mating loci were set to 0 at two loci, to 1 at two loci, and at frequency 1/2 at the fifth locus, so that the assumption of initial random mating was satisfied; all alleles at the female preference loci were set equal to 0, except at one locus where they were all set to 1; all alleles at the male marker loci were set equal to 1, except at one locus where they were all set to 0. (b) Decreased mutation rate of 10^{-4} per locus. In this case, simulations were run for 20 000 generations, and shades of grey indicate average times to speciation over five runs ranging from <500 (black) to 20000 (white). (c) Relative costs of assortative mating; in each generation, the choosiest female has a chance of $1 - c$ of reproducing, compared to a randomly mating female that has a chance of 1; $c = 0.15$. (d) Costs of assortative mating based on mate choice trials; in each generation, females have 200 mate choice trials; if a female has not accepted a mate after 200 trials, she forgoes reproduction. Note that each mate choice trial may only take a short period of time, so that 200 trials may actually be a rather conservative number. (e) Direct cost to assortative mating; in each generation, a female with mating trait a ($0 < a < 1$) has a chance of $1 - d|2a - 1|$ of reproducing; $d = 0.2$.

those that were less choosy had higher mating probabilities, and randomly mating females had a mating probability of 1. Whether a female mated or not was then determined randomly based on these probabilities of mating, and in case a female mated, the procedure for selecting a male was the same as the one described in the Model section. Figure 5c shows results for this cost scenario with $c = 0.15$, i.e. for a case where in each generation, the probability of mating of the choosiest female is 85% that of a randomly mating female.

Alternatively, costs of assortativeness can be incorporated by assuming that in each generation, females are allowed a finite number N of 'mate choice trials'. In each trial, a potential mate is randomly selected and accepted or rejected on the basis of the mating probability as determined by the female's choosiness and preference. This is the same as the sequential mode model in Arnegard & Kondrashov (2004; see also Matessi *et al.*, 2001; Bolnick, 2004). In contrast to the first scenario, which has an explicit cost parameter c , it is not

straightforward to determine the actual magnitude of the costs in the sequential mode model for a given number of mate choice trials N . Generally speaking, as the number of mate-choice trials N decreases, the probability that females with a given degree of assortativity reject all N males, and hence the cost of assortativeness, increases. Figure 5d shows results for the second cost scenario with the number of mate choice trials $N = 200$. Other parameters were as in Fig. 3b.

Finally, I introduced costs of choosiness by assuming that there is a direct cost to the assortative mating trait, so that a female with assortative mating trait a ($0 \leq a \leq 1$) has a probability of reproducing equal to $1 - d \cdot |2a - 1|$ (this again implies that randomly mating females, i.e. females with $a = 1/2$, have a probability of reproducing equal to 1). Figure 5e shows results for this cost scenario with $d = 0.2$. Again, everything else was the same as in Fig. 3b, to which Fig. 5c–e should be compared. Overall, conditions for speciation are more restrictive with costs to assortativeness, as expected. However, despite the costs speciation still occurs for a sizable region in parameter space in all three cost scenarios considered.

Conclusions

In this paper, I argue that adaptive speciation, that is, the evolution of reproductive isolation between lineages diverging under disruptive selection from an evolutionary branching point, is theoretically possible even if it requires the evolution of assortative mating based on ecologically neutral female preference and male marker traits. Previous models have studied adaptive speciation scenarios when the degree of assortative mating was fixed (Kondrashov & Kondrashov, 1999), or when the male marker trait was identical to the female preference trait (Dieckmann & Doebeli, 1999). In contrast, here I considered models in which the degree of assortative mating can evolve, and in which female preference and male marker are separate traits. The basic driving force for speciation is the disruptive selection on the ecological trait that is generated by frequency-dependent competitive interactions, but speciation can only occur if linkage disequilibria between the ecological trait and the various mating traits evolve. This can happen when a high degree of assortative mating evolves together with two corresponding clusters in the female preference trait and the male marker trait that are in linkage disequilibrium with each other as well as with the two emerging ecological trait clusters (Fig. 2a). However, speciation can also occur when a high degree of disassortative mating evolves (Fig. 2b), and when the assortative mating trait itself splits into a highly assortative and a highly disassortative cluster (Fig. 2c). The latter two scenarios appear to be new in the theoretical literature.

The propensity for speciation depends on various model parameters. In particular, the ecological conditions

for adaptive speciation are determined by the parameters σ_K , the width of the resource distribution, and σ_c , the width of the competition function: for a given σ_K , frequency-dependent competition induces disruptive selection if σ_c is small enough, and smaller σ_c induce greater disruptiveness, and hence greater propensity to speciation [see Ackermann & Doebeli (2004) for an article addressing the evolutionary dynamics of σ_c]. On the contrary, the evolution of assortative mating hinges on the parameter s , which determines how the degree of assortativeness changes with changes in the mating trait. Lower values of s induce faster change in assortativity and more pronounced assortativity and disassortativity for extreme values of the mating trait. Consequently, lower values of s facilitate the evolution of assortative mating, and hence speciation (Fig. 3). This point has also been made by Bolnick (2004), who strikes a cautionary note about the biological feasibility of the s -values needed for speciation. While I agree that in the models considered here speciation requires the genetic potential for strong assortment (i.e. low values of s), Bolnick's (2004) estimates of the rather high male–female mating correlation that are needed for speciation may be at least partially misleading, because they only refer to the correlation induced by the maximal value of the assortative mating trait a , i.e. for $a = 1$. However, much lower values of a can already induce speciation, for which the male–female correlation is correspondingly lower. In addition, it is worth noting that there are many natural systems, particularly in insects, in which the male–female correlation with respect to mating traits, e.g. genital morphology, is very high (Eberhard, 1985). Of course, I agree with Bolnick (2004) that this issue requires further empirical investigation.

The mating function employed in this paper (Fig. 1) reflects a situation in which females exhibit relative preference for males: the preferred male marker trait depends on the female preference trait. In contrast, in models with absolute preference females simply prefer the most extreme male marker traits. In the context of the models presented here, this could be described by assuming that the mating function $P(a, p, m')$, eqn (7), is replaced by

$$P(a, p, m') = \exp[(d \cdot (2a - 1)) \cdot p \cdot m], \quad (8)$$

where, as before, a is the value of the trait determining the degree of assortative mating in females, p is the female preference trait and m is the male marker trait. The parameter d scales the degree of assortativity induced by a given value of the mating trait a ; in particular, d determines the maximal assortativity reached for $a = 0$ and $a = 1$. Equation (8) was used for example in Higashi *et al.* (1999) and in Arnegard & Kondrashov (2004) to model absolute preference in models of speciation through sexual selection. Based on such models, it is generally believed that absolute female preference is more conducive to speciation than relative preference

(Wu, 1985; Higashi *et al.*, 1999), and this should also hold in models of adaptive speciation that incorporate disruptive selection on ecological traits. Indeed, eqn (8) can easily be incorporated into the individual-based simulations used in this article, and speciation can readily be observed with absolute female preference (Fig. 6). While it is not straightforward to compare the propensity for speciation under the two preference modes (e.g. because it not clear how to gauge the parameter s , determining relative preference, against the parameter d , determining absolute preference), it appears that using relative female preference as in this paper represents the more conservative approach.

Another quantity that can have substantial effects on the likelihood of adaptive speciation in the models considered here is the number of loci determining the various traits. In general, increasing the number of loci has an adverse effect on speciation, either because it decreases the likelihood of reaching the necessary amounts of linkage disequilibrium between mating traits and the ecological trait, or because it decreases the strength of selection per allele at the assortative mating loci. This is in general agreement with previous findings for related models (Kondrashov & Kondrashov, 1999; Dieckmann & Doebeli, 1999). The one exception occurs when increasing the number of loci determining the marker trait in males (Fig. 4d), which appears to be in contrast to conclusions from previous studies (Kondra-

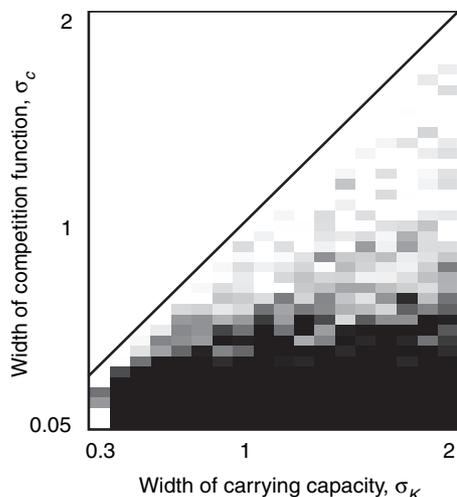


Fig. 6 Likelihood of speciation with absolute female preference. Everything is the same as in Fig. 3, except that the relative mating function, eqn (7) (see Fig. 2), was replaced by the absolute mating function, eqn (8). The parameter $d = 25$ was chosen so that females with extreme mating traits $a = 0$ and $a = 1$ have roughly the same strength of preference as used in Arnegard & Kondrashov (2004) ($\alpha = 30$ in their Fig. 1) and in Higashi *et al.* (1999) ($\alpha = 0.2$ in their Fig. 1, which corresponds to $d = 20$ in the present model when the preference and marker traits in Higashi *et al.* (1999) are normalized to the interval $[0,1]$).

shov & Kondrashov, 1999; Arnegard & Kondrashov, 2004), although I am not aware of any studies that explicitly addressed the effect of an asymmetry in the number of loci determining female preference and male marker traits. Arnegard & Kondrashov (2004) discuss the question of how many loci are likely to determine mating traits in natural systems, but in that discussion they do not explicitly talk about male marker loci. They argue that the number of loci determining female preference can range from small to large, and it seems that a similar conclusion would hold for male marker traits. The authors' results suggest that it might be important to determine whether there exists an asymmetry in the genetic architecture of female preference and male marker traits.

The models of Dieckmann & Doebeli (1999) have been criticized by Waxman & Gavrilets (2005), and their criticism would, in principle, also apply to the models in the present paper. In particular, Waxman & Gavrilets (2005) suggest that some of the assumptions in these models are biologically unjustified. For example, they claim that different initial conditions would fundamentally change the outcome of the simulations. Even though the initial conditions used here appear to be reasonable, my simulations also show that different initial conditions lead to qualitatively similar results with regard to the likelihood of speciation, as illustrated in Fig. 5a (note that initial conditions may be very important in determining the type of speciation that occurs, as illustrated in Fig. 2). In the models of Arnegard & Kondrashov (2004), the initial conditions, and in particular initial symmetry of female preference and male marker trait distributions, are crucial for determining whether speciation occurs. However, because these models are for sexual selection alone, they lack the organizing force of evolutionary branching points, i.e. the disruptive selection regime on the ecological trait, which serves as a continual source of selection for a split in the mating traits, leading to reproductive isolation between diverging ecological lineages. It is intuitively clear that in the presence of this ecological organizing force, the initial conditions for the mating traits should become much less important. To appreciate the role of disruptive ecological selection further, it is important to note that the split in the mating traits can occur in any one of a potentially large number of dimensions in the space of potential female preference and corresponding male marker traits. Because the population is trapped at an evolutionary branching point, i.e. at an ecological fitness minimum, it can, in principle, wait until the right set of mating characters shows the right kind of genetic variation, thus allowing for adaptive speciation to occur.

Waxman & Gavrilets (2005) also assert that the mutation rates in our models are unrealistic. As described in the Model section, this claim is based on a narrow perspective on the genetic architecture of quantitative traits: the 'loci' in the type of models considered here should really be viewed as freely recombining

chromosomal blocks, whose per block mutation rate can be quite high. In fact, with the population sizes of roughly 10^3 individuals used in the authors' models, and with five diploid loci with the standard per locus mutation rate of 10^{-6} that Waxman and Gavrillets would perhaps accept as realistic, there would be, for each quantitative trait, one small additive mutation in the population roughly every 100 generations. This is in stark contrast to empirical data, which suggests on the order of 5–10 small mutations per generation, which, for the population sizes used, translates quite closely to mutation rates of 10^{-3} as used here. It should also be noted that natural populations often seem to harbour genetic variation necessary for rapid adaptive change, including diversification (e.g. Hendry *et al.*, 2000; Koskinen *et al.*, 2002), and hence the occurrence of new mutations may not be a limiting factor for processes of adaptive speciation in real systems. Nevertheless, in the models presented here speciation still occurs when the mutation rate is decreased by an order of magnitude (Fig. 5b), although rates of speciation are lower, an effect that can, in principle, be counteracted by an increase in population size.

Finally, Waxman & Gavrillets (2005) note that costs would likely impede the speciation process. This is a valid, albeit obvious point: one expects that costs of assortative mating restrict the range of ecological and mating parameters for which speciation occurs, but that speciation is still possible as long as costs are not too high. This has been shown to be true in the models of Bolnick (2004) and of Kirkpatrick & Nuismer (2004), and my simulations confirm this expectation (Fig. 5c–e). Thus, the question is not so much whether or not speciation occurs when costs of assortativeness are introduced in the types of models studied here, but whether or not it occurs for relevant parameter regions in natural systems, a point that was strongly advocated by Bolnick (2004). What is clear is that Waxman & Gavrillets (2005) insinuation that speciation breaks down in these models as soon as any costs of assortativeness are present is unwarranted. As this is true for the four-trait models studied here, in which recombination between different mating traits as well as between mating traits and ecological traits opposes speciation, it is a fortiori true in the simpler two- and three-trait models of Dieckmann & Doebeli (1999). This is in line with results from Bolnick (2004) and Doebeli & Dieckmann (2005).

Overall, the results presented here show that the evolution of assortative mating mechanisms can, in theory, lead to adaptive speciation even if assortative mating is based on ecologically neutral female preference and male marker traits. This is arguably the most adverse mating scenario for adaptive speciation, because not only are the mating loci freely recombining with the ecological loci, but there is also free recombination between the preference and the marker loci. In reality, it seems likely that mating traits are often much more tightly linked to

ecologically important traits, such as various aspects of body size (e.g. Schluter & Nagel, 1995), and hence that conditions prevail that make adaptive speciation a more robust expectation (Dieckmann & Doebeli, 1999). It should also be kept in mind that for the most part, the simulations presented here were only run up to a time horizon of 10 000 generations, and that because of the stochastic nature of build-up of the necessary linkage disequilibria, speciation may well occur after that time horizon. If the ecological conditions conducive to adaptive speciation do not change substantially over prolonged periods of time, the populations will remain trapped at the fitness minimum generated by the frequency-dependent ecological interactions, and hence poised for adaptive speciation.

As the second phase of adaptive speciation, i.e. the evolution of assortative mating mechanisms enabling a splitting of populations experiencing disruptive selection, emerges as a theoretically feasible process, the first phase of adaptive speciation, i.e. the adaptive convergence to an evolutionary branching point and hence to a fitness minimum, thus comes to the fore as an issue of central importance. On the theoretical side, the framework of adaptive dynamics has led to the insight that regimes of disruptive selection due to frequency-dependent interactions are not a rare or ephemeral evolutionary occurrence. In fact, evolutionary branching points are a common feature of adaptive dynamics models for many different types of ecological scenarios (Kisdi & Gyllenberg, 2005), and populations that are attracted by evolutionary branching points remain there until rescued by mechanisms, such as assortative mating, that allow for an escape from the underlying fitness minima. Whether ecological conditions conducive to adaptive speciation are common in natural systems, and hence whether adaptive speciation is indeed more common in nature than was previously believed, must await further empirical studies investigating the ecology of speciation.

Acknowledgments

I thank Ulf Dieckmann for discussions, and Jabus Tyerman for technical help. Financial support from the James S. McDonnell Foundation (USA) and from the Natural Sciences and Engineering Council (Canada) is gratefully acknowledged.

References

- Abrams, P.A., Matsuda, H. & Harada, Y. 1993. Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evol. Ecol.* **7**: 465–487.
- Ackermann, M. & Doebeli, M. 2004. Evolution of niche width and adaptive diversification. *Evolution* **58**: 2599–2612.
- Arnegard, M.E. & Kondrashov, A.S. 2004. Sympatric speciation by sexual selection alone is unlikely. *Evolution* **58**: 222–237.

- Bolnick, D.I. 2004. Waiting for sympatric speciation. *Evolution* **58**: 895–899.
- Bolnick, D.I. & Doebeli, M. 2003. Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. *Evolution* **57**: 2433–2449.
- Christiansen, F.B. 1991. On conditions for evolutionary stability for a continuously varying trait. *Theor. Popul. Biol.* **7**: 13–38.
- Dieckmann, U. & Doebeli, M. 1999. On the origin of species by sympatric speciation. *Nature* **400**: 354–357.
- Dieckmann, U. & Law, R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.* **43**: 1308–1311.
- Dieckmann, U., Doebeli, M., Metz, J.A.J. & Tautz, D. (eds) 2004. *Adaptive Speciation*. Cambridge University Press, Cambridge, UK.
- Doebeli, M. 1996. A quantitative genetic competition model for sympatric speciation. *J. Evol. Biol.* **9**: 893–909.
- Doebeli, M. & Dieckmann, U. 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *Am. Nat.* **156**: S77–S101.
- Doebeli, M. & Dieckmann, U. 2003. Speciation along environmental gradients. *Nature* **421**: 259–264.
- Doebeli, M. & Dieckmann, U. 2005. Adaptive dynamics as a mathematical tool for studying the ecology of speciation processes. *J. Evol. Biol.* **18**: 1194–1200.
- Drossel, B. & McKane, A. 2000. Competitive speciation in quantitative genetic models. *J. Theor. Biol.* **204**: 467–478.
- Eberhard, W.G. 1985. *Sexual Selection and Animal Genitalia*. Harvard University Press, Cambridge, MA, USA.
- Felsenstein, J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* **35**: 124–238.
- Geritz, S.A.H., Kisdi, É., Meszéna, G. & Metz, J.A.J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol. Res.* **12**: 35–57.
- Hendry, A.P., Wenburg, J.K., Bentzen, E., Volk, E.C. & Quinn, T.P. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* **290**: 516–518.
- Higashi, M., Takimoto, G. & Yamamura, N. 1999. Sympatric speciation by sexual selection. *Nature* **402**: 523–526.
- Kirkpatrick, M. & Nuismer, S.L. 2004. Sexual selection can constrain sympatric speciation. *Proc. Roy. Soc. B* **271**: 687–693.
- Kisdi, E. & Gyllenberg, M. 2005. Adaptive dynamics and the paradigm of diversity. *J. Evol. Biol.* **18**: 1170–1173.
- Kondrashov, A.S. & Kondrashov, F.A. 1999. Interactions among quantitative traits in the course of sympatric speciation. *Nature* **400**: 351–354.
- Koskinen, M.T., Haugen, T.O. & Primmer, C.R. 2002. Contemporary fisherian life-history evolution in small salmonid populations. *Nature* **419**, 826–830.
- Matessi, C., Gimelfarb, A. & Gavrilets, S. 2001. Long-term buildup of reproductive isolation promoted by disruptive selection: how far does it go? *Selection* **2**: 41–64.
- Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A. & van Heerwaarden, J.S. 1996. Adaptive dynamics: a geometrical study of the consequences of nearly faithful reproduction. In: *Stochastic and Spatial Structures of Dynamical Systems, Proceedings of the Royal Dutch Academy of Science (KNAW Verhandelingen)* (S. J. van Strien & S. M. Verduyn Lunel, eds), pp. 183–231. North Holland, Dordrecht, Netherlands.
- Schluter, D. & Nagel, L.M. 1995. Parallel speciation by natural selection. *American Naturalist* **146**: 292–301.
- Waxman, D. & Gavrilets, S. 2005. 20 questions on adaptive dynamics. *J. Evol. Biol.* **18**: 1139–1154.
- Wu, C.-I. 1985. A stochastic simulation study on speciation by sexual selection. *Evolution* **39**: 66–82.

Received 16 September 2004; revised 16 December 2004; accepted 6 January 2005