Adaptive dynamics in diploid, sexual populations and the evolution of reproductive isolation

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Evolutionary branching is the process whereby an initially monomorphic population evolves to a point where it undergoes disruptive selection and splits up into two phenotypically diverging lineages. We studied evolutionary branching in three models that are ecologically identical but that have different genetic systems. The first model is clonal, the second is sexual diploid with additive genetics on a single locus and the third is like the second but with an additional locus for mate choice. Evolutionary branching occurred under exactly the same ecological circumstances in all three models. After branching the evolutionary dynamics may be qualitatively different. In particular, in the diploid, sexual models there can be multiple evolutionary outcomes whereas in the corresponding clonal model there is only one. We showed that evolutionary branching favours the evolution of (partial) assortative mating and that this in turn effectively restores the results from the clonal model by rendering the alternative outcomes unreachable except for the one that also occurs in the clonal model. The evolution of assortative mating during evolutionary branching can be interpreted as the initial phase of sympatric speciation with phenotypic divergence and partial reproductive isolation.

Keywords: adaptive dynamics; evolutionary branching; reproductive isolation; evolution of assortative mating; sympatric speciation

1. INTRODUCTION

The theory of adaptive dynamics (Metz *et al.* 1992, 1996; Dieckmann & Law 1996; Geritz *et al.* 1997, 1998, 1999) provides a general framework for modelling non-equilibrium phenomena in adaptive evolution such as evolutionary branching, evolutionary cycles and the extinction of evolutionary branches. Concrete models in which these phenomena have been studied mostly assume clonal reproduction (see Dieckmann *et al.* 1995; Doebeli & Ruxton 1997; Law *et al.* 1997; Meszéna *et al.* 1997; Boots & Haraguchi 1999; Geritz *et al.* 1999; Jansen & Mulder 1999; Kisdi 1999; Mosquera & Adler 1999; Parvinen 1999). To what extent can conclusions from clonal models of adaptive dynamics be applied to populations of sexual organisms? In this paper we focus on evolutionary branching, that is the process whereby frequency-dependent selection drives an ecologically relevant trait to a point where selection becomes disruptive so that a split occurs in which the single prevailing trait value is replaced by two prevailing trait values separated by a gradually widening gap (Metz *et al.* 1996; Geritz *et al.* 1997, 1998). The emergence of two diverging lineages is reminiscent of speciation, but the origin of biological species can only be investigated in a genetic context.

Kisdi & Geritz (1999) and Van Dooren (2001) showed that the adaptive dynamics of a continuous trait with additive genetics on a single locus (or, equivalently, a group of tightly linked loci) in monomorphic populations of diploid, sexual organisms with random mating are the same as in populations of clonal organisms. In particular, evolutionary stability (i.e. the property of being uninvadable by new mutants) (Maynard Smith 1982) and

convergence stability (i.e. the property of being an evolutionary attractor) (Eshel 1983; Christiansen 1991) are preserved when we go from a clonal model to a model with sexual reproduction. However, in polymorphic populations the adaptive dynamics may be quite different due to the occurrence of phenotypically intermediate heterozygotes resulting from crosses between different homozygote branches (Kisdi & Geritz 1999). Without tight linkages in multilocus systems, evolutionary branching into distinct genotypes may be prevented altogether because of recombination (Abrams *et al.* 1993; Dieckmann & Doebeli 1999), but an increase in phenotypic variance can be observed (Taylor & Day 1997). Thus, conclusions from clonal models do not simply generalize to polymorphic populations of diploid, sexual organisms.

The discrepancy between the adaptive dynamics in polymorphic populations of clonal and diploid, sexual organisms can be cured by blithely assuming that individuals from different homozygote branches do not interbreed (Doebeli 1996). Indeed, various authors (Brown & Pavlovic 1992; Brown & Vincent 1992; Geritz *et al.* 1997, 1998) have argued that branching is likely to favour the evolution of reproductive isolation because, during branching, phenotypically intermediate offspring from parents from different homozygote branches have low fitness, so that mating between different homozygote branches is disadvantageous and will be selected against (cf. Dobzhansky 1951). Specific simulation models for the evolution of assortative mating and reproductive isolation support this view (Dieckmann & Doebeli 1999; Doebeli & Dieckmann 2001).

In this paper, we study the evolution of partial reproductive isolation and its evolutionary consequences in polymorphic populations of diploid, sexually reproducing organisms. First, we compare two related studies on

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adaptive dynamics in, respectively, clonal populations (Geritz *et al.* 1998) and sexual populations with random mating (Kisdi & Geritz 1999) under otherwise the same ecological circumstances. Next, we extend the model of Kisdi & Geritz (1999) by the imposition of an additional locus for assortative mating and investigate under what conditions and how evolutionary branching leads to the evolution of non-random mating and how this in turn affects the evolution of polymorphic populations. Unlike various simulation studies of adaptive dynamics in multilocus systems (e.g. Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999), the present study takes a more analytical approach (i.e. numerical equation solving and stability analysis) and, therefore, provides a more direct insight into the evolution of assortative mating and speciation.

2. ADAPTIVE DYNAMICS IN A CLONAL MODEL

Geritz *et al.* (1998) used a clonal version of Levene's (1953) 'soft selection' model in order to study the adaptive dynamics of a single continuous trait of an annual organism in an environment consisting of a finite number of discrete habitats. During dispersal all offspring are distributed evenly into the various habitats. There is first a period of viability selection within each habitat such that the survival probability ($f_i(x)$) of an individual with trait value x in the i th habitat is given by

$$f_i(x) = \alpha_i \exp \left(-\frac{(x - \mu_i)^2}{2\sigma^2} \right), \quad (1)$$

where α_i is the maximum survival probability in the i th habitat and σ^2 is the rate of decline in survival probability for deviations of x from the locally optimal trait value μ_i . Following the selective phase there is a phase of non-selective contest competition so that, in each habitat, a fixed number of individuals become established. The fecundity is the same for all, irrespective of habitat or trait value. In a population dynamic equilibrium, the number of types present at positive densities is always less than or equal to the number of different habitats (Strobeck 1979).

The exponential growth rate or 'fitness' (Metz *et al.* 1992) of an initially rare mutant phenotype y in a resident population of n different phenotypes ($x_1, \dots, x_n$) in population dynamic equilibrium in a system of m different habitats is

$$s_{x_1, \dots, x_n}(y) = \log \left(\sum_{i=1}^m c_i f_i(y) \right) / \left(\sum_{j=1}^n q_j f_j(x_j) \right), \quad (2)$$

where c_i is the relative 'size' (or carrying capacity) of the i th habitat measured as the fraction of the total number of established individuals in all habitats together and q_j is the relative frequency of phenotype x_j during dispersal. Since at a population dynamic equilibrium all resident types have zero growth rate, the resident frequencies q_j follow from the equations $s_{x_1, \dots, x_n}(x_i) = 0$ for $i = 1, \dots, n$. The mutant phenotype y can invade only if it has a positive fitness.

Assuming that single mutations have only a small phenotypic effect each and that, by the time a new mutant comes along, the resident population has reached its

Figure 1. Evolution in the clonal model with $c_1 = c_2 = 0.5$ and $\sigma_\mu^2 = 2.25\sigma^2$. (a) Shaded regions indicate pairs of x_1 and x_2 that can coexist as a protected dimorphism ($s_{x_1}(x_2) > 0$ and $s_{x_2}(x_1) > 0$). Arrows indicate the direction of evolution in x_1 or x_2 . Lines separating regions with a different direction for one of the residents can be evolutionarily stable with respect to changes in the corresponding direction (continuous lines) or may lack evolutionary stability (dotted lines). A dimorphic population will evolve to the single evolutionarily stable dimorphism marked by a dot. (The plot is symmetrical in the 45° line because labelling the two coexisting types is arbitrary; both dots therefore represent the same dimorphic population. Symmetry in the -45° line is a consequence of both habitats being of the same size, i.e. $c_1 = c_2 = 0.5$.) (b) Simulated evolutionary tree. An initially monomorphic population first evolves to x^* , where it undergoes evolutionary branching. At the evolutionarily stable dimorphism, the population consists of two habitat specialists. (For details of the simulation procedure, see Appendix A of Kisdi & Geritz (1999).)

equilibrium, then an initially monomorphic population first undergoes directional selection towards the intermediate trait value:

$$x^* = \sum_{i=1}^m c_i \mu_i, \quad (3)$$

which is the weighted average of the locally optimal trait values. With only two habitats, x^* represents a generalist strategy that exploits both habitats at the same time. If the variance of μ_i across different habitats is small, that is if

$$\sigma_\mu^2 = \sum_{i=1}^m c_i (\mu_i - x^*)^2 \leq \sigma^2, \quad (4)$$

then x^* is evolutionarily stable, in which case the population undergoes stabilizing selection and stays near x^* for ever. However, if $\sigma_\mu^2 > \sigma^2$, then x^* is a so-called branching point, in which case the population is subject to disruptive selection and undergoes evolutionary branching as soon as it has come sufficiently close to x^* (Geritz *et al.* 1998). Subsequent branching events are possible depending on the number of habitats and the magnitude of the differences between the μ_i s. However, with only two habitats the population converges to an evolutionarily stable dimorphism consisting of two specialists, each adapted to its own habitat (figure 1).

3. ADAPTIVE DYNAMICS WITH DIPLOID, MENDELIAN GENETICS ON A SINGLE LOCUS

Kisdi & Geritz (1999) used a diploid version of the previous model in order to study the adaptive dynamics of a continuous trait with additive genetics on a single locus in populations of diploid, sexual organisms with random mating across the entire population, in a system that is ecologically identical to the clonal model. The fitness of an initially rare allele y in a resident population with alleles $x_1, \dots, x_n$ at a population genetic equilibrium in a system of m different habitats is

$$s_{x_1, \dots, x_n}(y) = \log \sum_{i=1}^m c_i \sum_{j=1}^n q_j f_i(\varphi(x_j, y)) \bigg/ \sum_{j=1}^n \sum_{k=1}^n q_j q_k f_i(\varphi(x_j, x_k)), \quad (5)$$

where q_j denotes the frequency of allele x_j during dispersal and $\varphi(x, y) = (x + y)/2$ is the phenotype corresponding to the (x, y) genotype. Notice that alleles are identified with the phenotype of the corresponding homozygote genotype, that is by definition $x = \varphi(x, x)$. Moreover, evolution is described in allele space (i.e. the set of all potential allele types) instead of phenotype space as in the clonal model. The resident allele frequencies q_j at a population dynamic equilibrium follow from the equations $s_{x_1, \dots, x_n}(x_i) = 0$ for $i = 1, \dots, n$. The mutant y can invade only if $s_{x_1, \dots, x_n}(y) > 0$.

Analogous to the clonal model, an initially monomorphic population always evolves first towards the average allele type x^* given by equation (3). If $\sigma_\mu^2 \leq \sigma^2$ (cf. equation (4)), then x^* is evolutionarily stable, but otherwise x^* is a branching point. While in the latter case the allele pool splits up into two gradually diverging allele types, we observe branching, in genotype space as well as in phenotype space, into three different types corresponding to the two homozygotes and the heterozygote, respectively.

In contrast to the clonal model where, after branching in a system consisting of two habitats of equal size (i.e.

$c_1 = c_2 = 0.5$) there is only a single possible evolutionary outcome (figure 1), the adaptive dynamics in the sexual model can in essence follow three possible patterns.

- (i) If $\sigma^2 < \sigma_\mu^2 < 1.45\sigma^2$, then there is a single convergence-stable, as well as evolutionarily stable, genetic polymorphism of two alleles (figure 2a). Both homozygote phenotypes are habitat specialists, while the intermediate heterozygote phenotype is a generalist and has the lowest fitness.
- (ii) If $1.45\sigma^2 < \sigma_\mu^2 < 4.06\sigma^2$, then there are two convergence-stable, as well as evolutionarily stable, genetic polymorphisms separated by an evolutionary saddle (figure 2b). At the stable polymorphisms the heterozygote and one of the homozygotes are habitat specialists, while the remaining homozygote is not well adapted to any habitat and has the lowest fitness.
- (iii) If $4.06\sigma^2 < \sigma_\mu^2$, then there are three convergence-stable, as well as evolutionarily stable, genetic polymorphisms separated by two saddles (figure 2c). The stable polymorphism in the middle is similar to the one in pattern (i) and the other two stable polymorphisms are similar to those in pattern (ii). If the rate of evolution is the same for both allele types, the population is most likely to evolve to the stable polymorphism in the middle.

4. EVOLUTION OF ASSORTATIVE MATING IN A TWO-LOCUS MODEL

During evolutionary branching a population undergoes disruptive selection such that intermediate phenotypes are selected against. In a diploid population with additive genetics, phenotypically intermediate heterozygotes are thus at a selective disadvantage. The strength of selection against heterozygotes in a resident population with allele types x_1 and x_2 and corresponding frequencies q_1 and q_2 can be measured by the deficiency of heterozygotes after selection $F_A = (H_E - H_A)/H_E$, where $H_E = 2q_1q_2$ is the expected frequency of heterozygotes at Hardy-Weinberg equilibrium under random mating and H_A is the actual frequency of heterozygotes observed after selection. In the present model we have

$$F_A = 1 - \sum_{i=1}^2 c_i f_i \left(\frac{x_1 + x_2}{2} \right) \bigg/ \left(q_1^2 f_i(x_1) + 2q_1q_2 f_i \left(\frac{x_1 + x_2}{2} \right) + q_2^2 f_i(x_2) \right). \quad (6)$$

Positive values of F_A correspond to heterozygote inferiority. Notice that protected polymorphisms are possible despite heterozygote inferiority because of frequency-dependent selection (figure 2a–c, lower panels) (Pimm 1979; Udovic 1980).

Immediately after branching the population inevitably evolves through a region of heterozygote inferiority. In the cases of figure 2a,c, the population always stays inside this region and, moreover, at the polymorphism to which the population evolves, selection against heterozygotes is maximal (i.e. F_A attains its maximum). However, in the case of figure 2b the population eventually leaves the area of heterozygote inferiority, but the evolutionary

Figure 2. Evolution in the single-locus, sexual model with $c_1 = c_2 = 0.5$. The upper panels show the direction of evolutionary change in x_1 and x_2 in polymorphic populations (notations as in figure 1). (a) With $\sigma_\mu^2 = 1.27\sigma^2$, the population evolves to the single, evolutionarily stable polymorphism indicated by the dot. (b) With $\sigma_\mu^2 = 2.25\sigma^2$, there are two convergence-stable and evolutionarily stable polymorphisms (dots) separated by a saddle (open circle). (c) With $\sigma_\mu^2 = 6.25\sigma^2$, three convergence-stable and evolutionarily stable polymorphisms (dots) are separated by two saddles (open circles). The lower panels show for which pairs of x_1 and x_2 heterozygotes are at a disadvantage (shaded regions), with contour lines given for (a) $F_A = 0.0, 0.005, 0.01$ and 0.015 , (b) $F_A = 0.0, 0.05, 0.1, 0.15$ and 0.2 , and (c) $F_A = 0.0, 0.2, 0.4, 0.6$ and 0.8 . The thick lines are simulated evolutionary trajectories starting near the branching point (x^*, x^*) . In (a) and (c) these trajectories lead to where F_A is maximal, whereas in (b) the trajectory passes through the region where F_A is maximal.

trajectories still first pass through the part of the region where heterozygotes are at a maximum disadvantage, that is near the saddle point. Although theoretically heterozygote inferiority could lead to the evolution of assortative mating (e.g. Udovic 1980), it still remains to be seen whether selection against heterozygotes is not too weak (Felsenstein 1981) and whether, in the case of figure 2b, assortative mating can evolve fast enough before the population leaves the region of heterozygote disadvantage.

In order to investigate the evolution of assortative mating, we incorporated an additional locus with two alleles B and b into the model, such that individuals with BB or Bb alleles and individuals with bb alleles belong to two different mating groups. Otherwise the locus does not affect fitness. One possible interpretation is that the B and b alleles affect the time or place of mating. Individuals mate within their own group with probability p , whereas with probability $1 - p$ mating is random across the entire population (in other words, p can be considered as the penetrance of assortativeness). The recombination rate between the locus for the ecological trait and the locus for mate choice is denoted by r . At linkage equilibrium (LE) mating is random with respect to the ecological trait and, consequently, the locus for mate choice

is selectively neutral and does not affect evolution on the ecological locus. However, at linkage disequilibrium (LD) the allele frequencies on the two loci are correlated, so that mating will be assortative with respect to the ecological trait whenever $p > 0$. Because of this, the locus for mate choice will no longer be selectively neutral and will also affect evolution on the ecological locus. We consider the evolution of LD for fixed values of p and r .

The population genetic stability of LE and LD depends on the strength of selection against heterozygotes as measured by the heterozygote deficiency F_A for given values of p and r . Elaborating on the example given in figure 2b, we show which combinations of x_1 and x_2 can coexist as a protected polymorphism at LE with $p = 0.9$ and $r = 0.5$ in figure 3a. Since at LE the locus for mate choice is selectively neutral, the figure is identical to figure 2b except for the ‘hole’ in the middle where selection against heterozygotes is too strong for LE to be stable. The stability of LE is lost through a subcritical (or catastrophic) pitch-fork bifurcation.

Figure 3b shows the combinations of x_1 and x_2 where LD is stable. Outside this region, selection against heterozygotes is too weak to maintain LD. At the edge, LD is lost through a fold (or tangent) bifurcation. The LD region covers a wider area than the hole in the LE region

Figure 3. Evolution in the two-locus, sexual model with assortative mating and $c_1 = c_2 = 0.5$, $\sigma_\mu^2 = 2.25\sigma^2$, $p = 0.9$ and $r = 0.5$ (notations as in figure 1). LE is stable only for pairs of x_1 and x_2 inside the shaded region in (a). The edge of the hole in the LE region coincides with $F_A = 0.11$ (contour line in figure 2b). LD is stable only for pairs of x_1 and x_2 inside the shaded region in (b). The edge of the LD region coincides with $F_A = 0.07$ (contour line in figure 2b). With LD there is a single, evolutionarily stable polymorphism (dot) at which both homozygotes are habitat specialists.

in figure 3a. Although there are two possible forms of LD (where x_1 and B are either positively or negatively correlated), their domains in allele space are identical. At LD, evolution is essentially different from that at LE, because at LD there is only a single possible evolutionary outcome, such that at the evolutionary equilibrium the two homozygotes are habitat specialists (figure 3b).

Immediately after branching the population will be at LE (except during the short bursts of transient dynamics when a mutant comes along and before population genetic equilibrium at LE is restored). As the population evolves through the LE region (figure 3a), selection against heterozygotes increases to a point where LE becomes unstable and the population switches to LD. From that point on mating is assortative with respect to the ecological trait. Depending on the allele frequencies on the locus for mate choice, this may already happen before the 'hole' in the LE region has actually been reached. The reason for this is that, as selection against

heterozygotes becomes stronger, the stability of LE requires a progressively lower frequency of the recessive b allele. If the frequency of b is close to zero, stability can be maintained almost all the way to the edge of the hole. However, if the frequency of b is close to unity, then stability is lost almost immediately after the edge of the LD region is crossed. Although at LE the locus for mate choice is selectively neutral, the frequencies of B and b may change due to genetic 'hitchhiking' during the transient phase of invasion by a new successful mutant on the ecological locus, particularly when the recombination rate is low. Once at LD, the population converges to the evolutionary equilibrium at the centre of the LD region (figure 3b). Notice that, if mutations were consistently more frequent in one direction than in the other, then the evolving population could stay sufficiently far away from the hole in the LE region and eventually escape from the region of heterozygote inferiority, but this possibility has only a low probability and, moreover, has never been observed in the simulations (cf. the simulated trajectories in figure 2b).

The degree of assortative mating at LD can be measured by the heterozygote deficiency before selection $F_B = (H_E - H_B)/H_E$, where H_E is the expected frequency of (x_1, x_2) heterozygotes at Hardy-Weinberg equilibrium under random mating and H_B is the actual frequency observed before selection (Udovic 1980). If $F_B = 0$, mating is random with respect to the x_1 and x_2 alleles. Mating is perfectly assortative if $F_B = 1$. After branching of the ecological trait, F_B initially stays zero while F_A gradually increases until LE becomes unstable (figure 4a). Once the population has switched to LD, F_B increases rapidly and levels off as the population reaches the evolutionary equilibrium. Compare this with the one-locus model of the previous section. After branching of the ecological trait, F_A first increases but then decreases again (figure 4b) as the population evolves out of the region of heterozygote inferiority. At the evolutionary equilibrium, F_A attains a negative value indicating heterozygote superiority, reflecting the fact that the heterozygote is now a habitat specialist. Since in the one-locus model mating is random, F_B remains zero.

The positions of the F_A contour lines in allele space are independent of r and p because they are a property of the population at LE not LD. The critical value of F_A at which LE loses its stability depends only on p : as p decreases, stronger selection against heterozygotes is required for destabilization of LE, which amounts to a smaller hole in the LE region of figure 3a corresponding to a contour line at a higher value of F_A . The lowest value of F_A at which LD still can exist depends on both r and p : as r increases or p decreases, the existence of LD requires stronger selection against heterozygotes, which amounts to a smaller LD region in figure 3b. For combinations of r and p inside the black region in figure 5, the minimum value of F_A necessary for LD cannot be achieved for any combination of x_1 and x_2 so that LD is not possible and LE is stable everywhere in the allele space (no hole in the LE region). Inside the grey region LD is possible, but LE is still stable everywhere. LD can be reached if the frequency of the b allele is sufficiently high. Inside the white region, LE is no longer stable everywhere (a hole has appeared in the LE region) so that a switch to

Figure 4. The left panels show simulated evolutionary trees with $c_1 = c_2 = 0.5$ and $\sigma_\mu^2 = 2.25\sigma^2$ for (a) the two-locus, sexual model with $p = 0.9$ and $r = 0.5$, and (b) the one-locus, sexual model. The right panels show the evolution of the deficiency of heterozygotes compared to Hardy–Weinberg equilibrium before selection (F_B , thick line) and after selection (F_A , thin line).

LD is inevitable, independent of the frequency of b . The relative sizes of the three regions in figure 5 depend on σ_μ^2 such that the black and grey regions become larger at the cost of the white region as σ_μ^2 decreases. For sufficiently small values of r and sufficiently large values of p , LD is possible (and, hence, assortative mating can evolve) whenever there is branching in the ecological trait. The F_B contour lines in figure 5 indicate the degree of reproductive isolation between the homozygote phenotypes at the evolutionary equilibrium at LD for any given values of r and p .

So far, we have focused on the case of habitats of equal size (i.e. $c_1 = c_2 = 0.5$) but the conclusions generalize to habitats of unequal size as well. In the clonal model, the position of the evolutionarily stable dimorphism (figure 1b) remains unaffected, although the relative frequency of the two specialists at the evolutionary equilibrium will vary with the relative size of the habitats. In the one-locus sexual model, the number of evolutionary equilibria as well as their attainability may vary depending on the relative habitat sizes (Kisdi & Geritz 1999). However, the evolutionary trajectories tend to pass through the part of the region of heterozygote inferiority where the disadvantage of heterozygotes is maximal. In the two-locus model this readily leads to LD and assortative mating with

respect to the ecological trait. At LD, there is always a single evolutionary equilibrium at which the homozygotes are the habitat specialists. Evolutionary branching occurs whenever $\sigma_\mu^2 > \sigma^2$ but for given μ_1 and μ_2 this condition will no longer be met if the habitats have very different sizes.

5. DISCUSSION

The adaptive dynamics in a polymorphic population of diploid, sexual organisms can be qualitatively different from that in the corresponding clonal system. First, after evolutionary branching an additional third phenotypic branch of intermediate heterozygotes appears. Second, there can be multiple alternative evolutionary outcomes whereas in the clonal model there is only one (cf. figures 1 and 2a–c). We have shown that evolutionary branching favours the evolution of (partial) assortative mating (i.e. with respect to the ecological trait) leading to various degrees of reproductive isolation of the homozygotic phenotypic branches under a wide range of parameter values (figure 5). This restores the basic characteristics of the clonal model. First, even at high levels of recombination and moderate penetrance, the frequency of heterozygotes before selection is drastically reduced (figure 5). For example, at the evolutionary equilibrium in figure 4a, there are 63% less heterozygotes produced than with random mating. Second, whenever assortative mating evolves, irrespective of its actual strength, there remains only a single evolutionary outcome. As in the clonal model, the homozygote phenotypes at this outcome are the habitat specialists (cf. figures 1 and 3b).

The evolution of assortative mating does not require very strong selection against heterozygotes. For example, in figure 3 a heterozygote deficiency (F_A) of 7–11% after selection suffices. Within this range, both LE and LD between the loci for the ecological trait and for mate choice are stable in the population genetic sense. Inside the basin of attraction of LD, the frequency of the recessive b allele on the locus for mate choice cannot be very low, because otherwise almost all individuals would belong to the same mating group of BB and Bb individuals where any association between alleles on different loci is immediately destroyed. Thus, a high initial frequency of the recessive b allele favours LD for a wider range of parameter values (figure 5) and at a lower level of heterozygote inferiority (as measured by F_A). Consequently, assortative mating occurs most easily if the genetic variation on the locus for mate choice is due to a new, initially rare mutant that is dominant rather than recessive. Bistability in the population genetics (i.e. both LE and LD stable at the same time) accounts for the abrupt change in heterozygote deficiency (F_B) before selection when the population switches from LE to LD (figure 4a, right panel).

Since recombination only occurs in double heterozygotes, the reduced frequency of heterozygotes at LD will greatly facilitate LD with additional assortative mating loci, which in turn will further improve the degree of reproductive isolation. The first step towards partial reproductive isolation is therefore probably the most critical one. We used the classic model of different mating groups (e.g. Maynard Smith 1966; Udovic 1980)

Figure 5. Bifurcation analysis of the two-locus, sexual model with respect to the penetrance (p) and recombination rate (r) for $c_1 = c_2 = 0.5$ and $\sigma_\mu^2 = 2.25\sigma^2$. For combinations of p and r inside the black region no polymorphism with LD exists. Inside the grey region LD is possible for certain polymorphisms, but LE is also stable. Inside the white region there are polymorphisms where LD is stable while LE is not. The contour lines inside the grey and white regions indicate the strength of assortative mating at the evolutionarily stable polymorphism at LD as measured by the heterozygote deficiency before selection (F_B).

as a 'worst case' where the evolution of assortative mating depends on the establishment of an LD between two (at least partially) independent loci (Felsenstein 1981). As an alternative and more direct mechanism, mate choice could be based on differences in the ecological trait (Dieckmann & Doebeli 1999) or reproductive isolation could be a direct by-product of differences in the ecological trait (Rice & Hostert 1993). In addition, in multiple-habitat environments low migration rates (Balkau & Feldman 1973), habitat choice (Diehl & Bush 1989) and mating before dispersal automatically give rise to some degree of assortative mating and are selectively advantageous. These mechanisms are not mutually exclusive, but can act in concert (Johnson *et al.* 1996).

Instead of combining different assortative mating mechanisms, reproductive isolation could also be further improved by selection for higher penetrance (p), that is provided LD has already been established (Udovic 1980; Felsenstein 1981). If penetrance is very low, LD may not exist for the given rate of recombination and LE is globally stable (figure 5). If this is the case, then, in small populations, penetrance may increase in response to chance correlations due to genetic drift (Dieckmann & Doebeli 1999) up to a level where LD becomes stable.

As an alternative to the evolution of assortative mating, Van Dooren (1999) showed that selection against heterozygotes during and after evolutionary branching may also favour the evolution of dominance among the alleles on the locus for the ecological trait. Dominance and assortative mating can be seen as alternative mechanisms for eliminating inferior heterozygotes. With full dominance, the diploid adaptive dynamics are identical to that in the corresponding clonal system. The two alternatives are antagonistic in the sense that, once dominance has evolved, there is no longer selection for assortative mating and, once assortative mating has evolved, there is no selection for dominance.

Empirical evidence for sympatric speciation is growing rapidly (e.g. Tauber & Tauber 1989; Schlieven *et al.* 1994; Johannesson *et al.* 1995; Feder 1998; Taylor & McPhail 1999). Evolutionary branching produces variation in an ecological trait and creates an environment that selectively favours assortative mating. The theory of adaptive dynamics provides a powerful tool for studying the ecological possibility of the evolution of assortative mating and its ultimate consequence, sympatric speciation.

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