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Evolutionary branching of a magic trait

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Abstract We study the adaptive dynamics of a so-called magic trait, which is under natural selection and which also serves as a cue for assortative mating. We derive general results on the monomorphic evolutionary singularities. Next, we study the long-term evolution of single-locus genetic polymorphisms under various strengths of assortativity in a version of Levene's soft-selection model, where natural selection favours different values of a continuous trait within two habitats. If adaptive dynamics leads to a polymorphism with sufficiently different alleles, then the corresponding homozygotes cease to interbreed so that sympatric speciation occurs.

Mathematics Subject Classification (2000) 92D15, Problems related to evolution

1 Introduction

The origin of species is a cardinal question of biology. For speciation to occur in sexually reproducing organisms, two essential processes need to take place (Coyne and Orr 2004): First, genetic polymorphism must arise and be maintained in the population; and second, reproductive isolation must evolve such that genetically different lineages cease to interbreed. Most traditional models of sympatric speciation (e.g. Maynard Smith 1966; Dickinson and Antonovics 1973; Caisse and Antonovics 1978; Udovic 1980; see Gavrilets 2004 for review) assumed that ecological selection maintains polymorphism in one locus, whereas a second locus controls reproductive isolation via mate choice (for example it may control flowering time in plants, where early and late flowering individuals are reproductively isolated from one another). In such models,

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ecologically different lineages become reproductively isolated if linkage disequilibrium arises between the two loci such that the ecological trait and mate choice become genetically correlated. Recombination between the ecological locus and the mating locus, however, efficiently destroys any linkage disequilibrium, rendering speciation impossible unless ecological selection is strong (Felsenstein 1981).

Reproductive isolation might arise easier if mate choice is based on the ecological trait itself, with like individuals mating preferentially with each other. For example, different habitats or different pollinators may exert ecological selection for early vs late flowering in plants (as it happens between edaphic plants and their normal varieties, cf. Macnair and Gardner 1998). In this case, mate choice itself is under ecological selection; or in other words, reproductive isolation evolves as a natural byproduct of ecological divergence. After Gavrilets (2004), traits which are under ecological selection and also influence mate choice are called *magic traits*. Magic traits are free of the problem of recombination because the mating cue and the ecological trait are one and the same.

Empirical evidence shows that magic traits are common. Body size, a common target of ecological selection, is also a common cue for mating. Body size is a magic trait in sticklebacks (Nagel and Schluter 1998; Hatfield and Schluter 1999; Rundle 2002), in sea horses (Jones et al. 2003), intertidal snails (Cruz et al. 2004), in amphipods (Wellborn 1994; McPeek and Wellborn 1998), and in Drosophila (Hegde and Krishna 1997). Colour patterns serve as mating cues but are also under disruptive ecological selection in butterflies (Jiggins et al. 2001, 2004) and in coral reef fishes (Puebla et al. 2007). The shape and colour of animal-pollinated flowers are obvious candidates for magic traits, although the empirical evidence is less clear in this case (Waser and Campbell 2004; Gegear and Burns 2007). The call frequency of bats determines both the prey and the mates they can locate (Kingston and Rossiter 2004). The flowering time of some plants (Macnair and Gardner 1998) and the time of eclosion and mating in the apple maggot fly (Felsenstein 1981) are also magic traits. Beak morphology and song are determined partly by the same genes in Darwin's finches (Podos 2001; Huber et al. 2007), such that there is a common magic trait on the genetic level that correlates with both phenotypic traits, one influencing resource use and the other used for mate choice. Many of the examples mentioned above are putative cases of incipient sympatric speciation. Conversely, in most cases where ongoing sympatric speciation is suspected and the mechanisms of ecological divergence and reproductive isolation are known, reproductive isolation emerges as a byproduct via ecological selection on a magic trait (Bolnick and Fitzpatrick 2007).

In this paper, we analyze the adaptive dynamics of a magic trait. Adaptive dynamics (Geritz et al. 1997, 1998) is a leading mathematical framework to investigate how continuous traits evolve under ecological selection and small mutational steps, and, in particular, how diversity evolves via evolutionary branching. Since evolutionary branching of a magic trait can lead to reproductive isolation as a byproduct, the adaptive dynamics of magic traits offer an analytically tractable model of speciation.

Whether speciation occurs via the evolution of a magic trait depends on whether reproductive isolation becomes sufficiently strong. Reproductive isolation, in turn, depends on how big a difference the diverging lineages evolve in their magic traits, and how strongly mate choice is discriminative (the latter referred to as mating assortativity or "choosiness"). Several models have investigated the evolution of choosiness while they kept magic trait values unchanged (Matessi et al. 2001; Pennings et al. 2008; Kopp and Hermisson 2008; Otto et al. 2008). Here we make the complementary assumption that the magic trait evolves and the level of choosiness remains fixed. Our results however also enable conclusions to be drawn on the joint evolution of the magic trait and of choosiness, provided that the latter evolves sufficiently slowly (see Sect.4).

In the first part of the paper, we analyze the evolution of magic traits in monomorphic populations and address in particular the question whether evolutionary branching occurs in a diploid sexual population under the most popular mating model (introduced by Doebeli 1996, Gavrilets and Boake 1998 and Matessi et al. 2001, and used e.g. by Kirkpatrick and Nuismer 2004; Schneider 2005; Schneider and Bürger 2006; Pennings et al. 2008; Kopp and Hermisson 2008; Ripa 2009). In this part, we accommodate arbitrary ecological selection and thereby provide general results for the stability properties of monomorphic evolutionary singularities under sexual reproduction and assortative mating. Stability properties of a monomorphic singularity were also analyzed by Schneider (2005) in a special case of the mating model considered here, but with haploid genetics and in only one specific ecological model.

The second part of this paper investigates the evolution of the magic trait after evolutionary branching has taken place, and in particular asks whether the evolutionary divergence of the magic trait continues far enough to provide reproductive isolation of the strength seen inbetween biological species. Whereas evolutionary branching depends only on the local properties of the fitness function and therefore can be analyzed without making particular assumptions about the ecological system, evolution after branching is determined by global properties that depend on the concrete ecological model at hand. In this second part, we use the so-called Levene's soft-selection model, a simple ecological model with selection in two contrasting habitats. The population genetics of this model is extremely well known (Levene 1953; see e.g. Roughgarden 1979; Hartl and Clark 1989, Nagylaki and Lou 2001, 2006; Nagylaki 2009; Bürger 2010), and it served as a classic framework of speciation models (e.g. Maynard Smith 1966; Felsenstein 1981). Furthermore, it was used to explore how adaptive dynamics can be applied to evolving alleles in diploid sexual populations under random mating (Kisdi and Geritz 1999; Van Dooren 1999, Geritz and Kisdi 2000). Here we add assortative mating to the Levene model to study speciation after evolutionary branching of a magic trait.

2 General model: monomorphic singularities and evolutionary branching

We consider a population of sexually reproducing diploid individuals with discrete generations. The population is assumed to be sufficiently large to ignore random genetic drift. A continuous trait $\phi \in X \subseteq \mathbb{R}$ is determined by a single autosomal locus which evolves by mutation and natural selection. We assume that the map between homozygote genotypes and phenotypes is a bijection, and denote the alleles of the locus by the phenotype of the corresponding homozygote individual such that $\phi_{xx} = x$ (when appropriate, we shall also use single-letter designations such as g for a diploid genotype). The genotype-phenotype map ϕ_{xy} is assumed to be at least twice continuously differentiable with respect to the allelic values x and y and to be strictly monotonic such that $\frac{\partial \phi_{xy}}{\partial x} \neq 0$ [see Van Dooren (2000) for the consequences of violating this assumption]. We assume no difference between maternally and paternally derived alleles so that $\phi_{xy} = \phi_{yx}$. With these assumptions, the allelic effects are locally additive (i.e., $\phi_{xy} \to \frac{1}{2}(\phi_{xx} + \phi_{yy})$ as $|y - x| \to 0$) and $\frac{\partial \phi_{xy}}{\partial y}\big|_{y=x} = \frac{1}{2}$.

Let $P_g^{(t)}$ denote the frequency of diploid genotype g among the newborn offspring in generation t. An offspring with genotype g survives to adulthood with probability $v_{E(t)}(\phi_g)$, where the selective environment $E(t)$ is determined by which phenotypes are present and what is their population density in generation t. In this section, we do not have to specify the concrete form of ecological selection encapsulated in v; later we shall investigate an example based on Levene (1953) multiple habitat model. For convenience, let $w_E(\phi_g) = Bv_E(\phi_g)$ denote the absolute genotypic fitness in ecological selection, where B is the average number of offspring produced by a mated female. We shall assume that $w_E(\phi_g)$ is positive for all admissible values of its arguments, twice differentiable with respect to ϕ_g and E, and E depends sufficiently smoothly on the phenotypes and their population densities. After ecological selection, the frequency of genotype g among the adults is

$$\tilde{P}_g^{(t)} = \frac{w_{E(t)}(\phi_g)}{\bar{w}_{E(t)}} P_g^{(t)}, \tag{1}$$

where $\bar{w}_{E(t)} = \sum_g P_g^{(t)} w_{E(t)}(\phi_g)$.

Adult females choose mates nonrandomly such that a female of genotype g mates (and produces offspring) with a male of genotype h with probability $Q_{g,h}\tilde{P}_h^{(t)}$. The quantity $Q_{g,h}$ measures the affinity of g females towards h males and depends on their phenotypic resemblance as described below by Eq. (7). Note that in general $Q_{g,h} \neq Q_{h,g}$. $\sum_h Q_{g,h}\tilde{P}_h^{(t)}$ may be less than 1, in which case the female remains unmated with a positive probability.

The genotypic frequencies at the beginning of the new generation are

$$P_r^{(t+1)} = \frac{1}{\bar{Q}} \sum_{g,h} \tilde{P}_g^{(t)} \tilde{P}_h^{(t)} Q_{g,h} R_{g,h\to r}, \tag{2}$$

where $\bar{Q} = \sum_{g,h} \tilde{P}_g^{(t)} \tilde{P}_h^{(t)} Q_{g,h}$ is the mean mating success and $R_{g,h\to r}$ denotes the probability that parents with genotypes g and h produce an offspring with genotype r according to the Mendelian rules. Total population size changes according to

$$N^{(t+1)} = \bar{Q}\bar{w}_{E(t)} N^{(t)}. \tag{3}$$

2.1 Assortative mating

Mate choice is based on phenotypic similarity of the ecological trait ϕ between the mating partners. The assumption that the same trait ϕ determines fitness in ecological selection and controls mate choice makes ϕ a “magic” trait as called by Gavrilets (2004). To formulate the probability of mating, we follow the assumptions Doebeli

1996, Gavrilets and Boake (1998) and Matessi et al. (2001). These assumptions are widely used (see e.g. Kirkpatrick and Nuismer 2004; Schneider 2005; Schneider and Bürger 2006; Pennings et al. 2008; Kopp and Hermisson 2008; Ripa 2009).

Assume that females encounter males at random. If a female with phenotype ϕ_g encounters a male with phenotype ϕ_h, she accepts the male for mating with probability

$$\mu(\phi_g, \phi_h) = \mu_{max}\pi(\phi_h - \phi_g), \tag{4}$$

where $0 < \mu_{max} \leq 1$ is the maximum mating probability and π is a twice continuously differentiable function that attains its maximum at 0 with $\pi(0) = 1$ and is bounded away from zero for all admissible values of $\phi_h - \phi_g$. If the female does not accept the male, she may try again until the total number of encounters has reached a maximum number M. Females mate at most once but males can participate in several matings. The probability that an encounter between a female of type ϕ_g and a random male results in mating is

$$\bar{\mu}(\phi_g) = \sum_h \mu(\phi_g, \phi_h)\tilde{P}_h \tag{5}$$

and the probability that she eventually mates with a male of type ϕ_h is

$$\sum_{i=0}^{M-1} [1 - \bar{\mu}(\phi_g)]^i \mu(\phi_g, \phi_h)\tilde{P}_h \tag{6}$$

such that we have

$$Q_{g,h} = \mu(\phi_g, \phi_h)\frac{1 - (1 - \bar{\mu}(\phi_g))^M}{\bar{\mu}(\phi_g)} \tag{7}$$

to be inserted into Eq. (2). Matessi et al. (2001) observed that with $M = 1$, the model can be seen as a model of fertility selection (Bodmer 1965; Hadeler and Liberman 1975) or as a model of parental selection (Gavrilets 1998); Schneider (2005) studied the evolution of a magic trait in a haploid model with $M = 1$, $\mu_{max} = 1$.

With $M < \infty$, females may remain unmated. This results in sexual selection favoring common females: Females whose phenotype is rare prefer to mate with rare male phenotypes and therefore run a higher risk of remaining unmated. With $M \to \infty$, females experience no sexual selection. Males, however, may remain unmated also in this case, and the average number they mate depends on their phenotype and on the phenotypic distribution of females. Males therefore always experience frequency-dependent sexual selection next to natural selection on the ecological trait.

In a population monomorphic for allele x, females are eventually mated with probability

$$Q_{xx,xx} \equiv Q = 1 - (1 - \mu_{max})^M. \tag{8}$$

This probability is independent of the resident phenotype but is less than 1, unless $\mu_{max} = 1$ so that females accept the first male for mating or $M \to \infty$ so that females can keep trying until they mate. The mating process therefore affects the dynamics of the population [see Eq. (3)] even if every male and female is equally likely to mate.

2.2 Invasion fitness

We assume that alleles undergo mutations with small phenotypic effect, mutant alleles have initially low frequency, and mutations occur infrequently such that the resident population has reached its population genetic attractor by the time a new mutant comes along. Under these assumptions, we can use adaptive dynamics (Geritz et al. 1998) to study long-term evolution in the space of alleles (Kisdi and Geritz 1999). For simplicity, we also assume that the resident population dynamics attains a unique point attractor such that the environment E is constant and uniquely determined by the resident allele(s) (see Geritz et al. 2002 for extension to multiple attractors). We shall write $w_{\hat{E}(\phi_{xx})}(\phi_g)$ to denote ecological fitness of genotype g in the environment set by a monomorphic resident population with phenotype ϕ_{xx}.

In Appendix 1, we derive invasion fitness (the marginal fitness of a rare allele) as shown in Eq. (11) below; here we shall arrive at the same result in a more heuristic way. Consider a mutant allele y in a population otherwise monomorphic for the resident allele x. If the mutant allele is sufficiently rare, then the probability of forming a mutant homozygote offspring is negligible. This is obvious in the case of random mating, but remains true also in our assortative mating model given that $w_{\hat{E}(\phi_{xx})}(\phi_{xy}) > 0$ and $\pi(\phi_{xx} - \phi_{xy}) > 0$ (see Appendix 1). The dynamics of the mutant allele are then governed by the dynamics of heterozygotes,

$$P_{xy}^{(t+1)} = \frac{1}{2} \frac{Q_{xy,xx} + Q_{xx,xy}}{Q} \tilde{P}_{xx}^{(t)} \tilde{P}_{xy}^{(t)} + \mathscr{O}((\tilde{P}_{xy}^{(t)})^2) \tag{9}$$

(cf. Eqs. (2), (8)). In the first term of this equation, $Q_{xy,xx}\tilde{P}_{xx}^{(t)}$ is the probability for a heterozygote female to eventually mate with a resident homozygote male; in the second term, $Q_{xx,xy}\tilde{P}_{xy}^{(t)}$ is the probability for a resident homozygote female to eventually mate with a heterozygote male; both types of mating produce heterozygote offspring with probability 1/2. With the resident population in equilibrium, $Qw_{\hat{E}(\phi_{xx})}(\phi_{xx}) = 1$ [cf. Eq. (3)] and hence from Eq. (1), we obtain $\tilde{P}_{xy}^{(t)} = Qw_{\hat{E}(\phi_{xx})}(\phi_{xy})P_{xy}^{(t)}$. Substituting this and noting that $\tilde{P}_{xx}^{(t)} = 1 + \mathscr{O}(\tilde{P}_{xy}^{(t)})$ in Eq. (9), we arrive at

$$P_{xy}^{(t+1)} = \frac{1}{2} \left(Q_{xy,xx} + Q_{xx,xy}\right) w_{\hat{E}(\phi_{xx})}(\phi_{xy}) P_{xy}^{(t)} + \mathscr{O}((P_{xy}^{(t)})^2) \tag{10}$$

from which the marginal fitness of the rare allele, i.e., the invasion fitness of allele y in the resident population of x is

$$W_x(y) = \frac{1}{2} \left(Q_{xy,xx} + Q_{xx,xy}\right) w_{\hat{E}(\phi_{xx})}(\phi_{xy}). \tag{11}$$

Simplifying from Eq. (7),

$$Q_{xy,xx} = 1 - \left[1 - \mu_{max}\pi(\phi_{xx} - \phi_{xy})\right]^M \tag{12}$$

describes sexual selection on heterozygote females in Eq. (11) and

$$Q_{xx,xy} = \left[1 - (1 - \mu_{max})^M\right]\pi(\phi_{xy} - \phi_{xx}) \tag{13}$$

gives sexual selection on males.

If mating is random, i.e., $\pi \equiv 1$ and a female accepts any male with probability μ_{max}, then Eq. (11) simplifies to

$$W_x(y) = Qw_{\hat{E}(\phi_{xx})}(\phi_{xy}). \tag{14}$$

We thus recover the marginal fitness of the rare allele $W_x(y)$ as the fitness of heterozygotes in ecological selection. Recall, however, that the mating process affects the dynamics of the population and therefore affects the resident environment $\hat{E}(\phi_{xx})$ even with random mating. When we compare results obtained for assortative mating with those under random mating, we always assume that the mating process is as described above (with $\pi \equiv 1$ for random mating), and therefore only a fraction Q of the resident females is mated, regardless of whether mating is assortative or random. Simply removing the mating process from the model, and assuming instead that each female mates with the first male she encounters, would introduce a change in the ecological environment unless $Q = 1$, i.e., unless $\mu_{max} = 1$ or $M \to \infty$.

To obtain invasion fitness in a polymorphic resident population, note that a rare mutant allele y in a resident population with alleles x_1 and x_2 is almost exclusively in heterozygotes and therefore the initial invasion dynamics can be written as

$$\mathbf{P}_{het}^{(t+1)} = \mathbf{M}\mathbf{P}_{het}^{(t)}, \tag{15}$$

where $\mathbf{P}_{het} = (P_{x_1y}, P_{x_2y})^T$ and $\mathbf{M}$ is a 2×2 matrix that depends on the allelic values y and x_1, x_2 (see Appendix 1 for details). The invasion fitness of the mutant, $W_{x_1,x_2}(y)$, is the dominant eigenvalue of $\mathbf{M}$. For small mutations (i.e., if either $|y - x_1|$ or $|y - x_2|$ is sufficiently small), this is equivalent to

$$\tilde{W}_{x_1,x_2}(y) = \mathrm{Tr}\mathbf{M} - \mathrm{Det}\mathbf{M} > 1 \tag{16}$$

(see Appendix 1). $\tilde{W}_{x_1,x_2}(y)$ is a proxy for invasion fitness: Because $\log \tilde{W}$ is sign-equivalent to $\log W$ and has the same smoothness properties, we can find the diallelic singularities and their stability properties using $\tilde{W}_{x_1,x_2}(y)$ (which is easier to calculate) in place of the dominant eigenvalue $W_{x_1,x_2}(y)$ [see Metz and Leimar (2010) for a related approach].

2.3 Monomorphic singularities and evolutionary branching

The mutant allele y, when it appears in a single copy in a large resident population fixed for allele x, has a positive probability of invasion if $W_x(y) > 1$; otherwise the mutant goes extinct with probability 1 (Jagers 1975). By repeated mutations and allele substitutions, the magic trait evolves in the direction of the selection gradient $\partial W_x(y)/\partial y\big|_{y=x}$ until it reaches either an endpoint of the trait space X or an evolutionary singular trait value x^* at which

$$\left.\frac{\partial W_x(y)}{\partial y}\right|_{y=x=x^*} = \frac{1}{2} Q \left.\frac{\partial w_{\hat{E}(\phi_{xx})}(\phi_{xy})}{\partial \phi_{xy}}\right|_{y=x=x^*} = 0 \tag{17}$$

(Geritz et al. 1998; Geritz 2005). Notice that the selection gradient does not depend on function π because $\pi'(0) = 0$, and therefore, the existence, number, and position of evolutionary singularities are independent of assortativity of mating. The singularity is convergence stable (i.e., approached by gradual evolution via small mutation steps) if

$$\left[\frac{\partial^2 W_x(y)}{\partial x \partial y} + \frac{\partial^2 W_x(y)}{\partial y^2}\right]_{y=x=x^*} = \frac{1}{2} Q \left[\frac{\partial^2 w}{\partial \phi_{xx} \partial \phi_{xy}} + \frac{\partial^2 w}{\partial \phi_{xy}^2}\right]_{y=x=x^*} < 0 \tag{18}$$

(Eshel 1983; Christiansen 1991), where we wrote $w = w_{\hat{E}(\phi_{xx})}(\phi_{xy})$ for short. This condition is again independent of mating assortativity, as expected, because convergence stability follows directly from the selection gradient.

The singularity is evolutionarily stable (sensu Maynard Smith 1982) if

$$\left[\frac{\partial^2 W_x(y)}{\partial y^2}\right]_{y=x=x^*} = \frac{1}{4}\left(Q\left[\frac{\partial^2 w}{\partial \phi_{xy}^2}\right]_{y=x=x^*} + q\pi''(0)\right) < 0, \tag{19}$$

where

$$q = \frac{1}{2}\left[1 + \frac{M\mu_{max}(1-\mu_{max})^{M-1}}{1-(1-\mu_{max})^M}\right]. \tag{20}$$

In (19), sexual selection from assortative mating contributes a negative term via $\pi''(0) < 0$. Assortative mating stabilizes x^* against the invasion of mutants because rare phenotypes are at a disadvantage during mating.

The strength of the stabilizing effect of assortative mating depends on parameters μ_{max} and M via quantity q. To interpret the relative weight of ecological and sexual selection in (19), note that Q, the coefficient in front of the term corresponding to ecological selection, simply corrects w for the population dynamical effect of the mating process, i.e., the product Qw is the invasion fitness under random mating [cf. Eq. (14)]. If $M = 1$, then (20) simplifies to $q = 1$ and we recover a result of Schneider (2005): the curvatures of fitness in ecological and in sexual selection contribute equally and additively to the condition of evolutionary stability. If $M > 1$

and $\mu_{max} \to 1$, then $q = \frac{1}{2}$ so that only male sexual selection contributes to (19). This is because the probability that a heterozygote female remains unmated $[(1 - \mu_{max}\pi(\phi_{xx} - \phi_{xy}))^M]$ is in this case a "flat" function of the phenotypic difference with vanishing second derivative at zero, so that for small mutations, female sexual selection is negligible compared to sexual selection on males and to ecological selection. Finally if $M \to \infty$ with arbitrary μ_{max}, then again $q = \frac{1}{2}$; in this case all females are eventually mated and hence there is no sexual selection on females, who are half the parents of the next generation (see also Kirkpatrick and Nuismer 2004; Schneider and Bürger 2006 on evolutionary stability in face of stabilizing sexual selection).

Evolutionary branching occurs in initially monomorphic populations at a singularity that is convergence stable but not evolutionarily stable (Geritz et al. 1998). Assortative mating does not change convergence stability but hinders evolutionary branching via stabilizing sexual selection: increasing assortativity, which corresponds to increasing $\pi''(0)$ in absolute value, can turn an evolutionary branching point [where (19) is violated] into an ESS [where (19) is satisfied].

2.4 Polymorphism near singularities

An important property of a singularity is whether there are pairs of alleles in its neighbourhood such that each of the two alleles can invade the other's monomorphic resident population (*mutual invasibility*) or, to the contrary, there are pairs such that neither can invade the other and therefore the rare allele goes extinct regardless of which of the two alleles is rare (*mutual exclusion*). In the vicinity of x^*, there exist pairs of alleles that exhibit mutual invasibility and hence form a protected polymorphism if

$$\left[\frac{\partial^2 W_x(y)}{\partial x \partial y}\right]_{y=x=x^*} = \frac{1}{4}\left(Q\left[2\frac{\partial^2 w}{\partial \phi_{xx}\partial \phi_{xy}} + \frac{\partial^2 w}{\partial \phi_{xy}^2}\right]_{y=x=x^*} - q\pi''(0)\right)$$
$$= -\frac{1}{4}\left(Q\left[\frac{\partial^2 w}{\partial \phi_{xx}^2}\right]_{y=x=x^*} + q\pi''(0)\right) < 0, \tag{21}$$

where in the last step we used that $w_{\hat{E}(\phi_{xx})}(\phi_{xx}) = 1/Q$ is constant for all x and hence $[\frac{\partial^2 w}{\partial \phi_{xx}^2} + 2\frac{\partial^2 w}{\partial \phi_{xx}\partial \phi_{xy}} + \frac{\partial^2 w}{\partial \phi_{xy}^2}]_{y=x} = 0$; the opposite of (21) implies the existence of allele pairs with mutual exclusion near x^* (Geritz et al. 1998).

There are two aspects of condition (21) to interpret. Concerning ecological selection, recall that in a clonal model of adaptive dynamics, there are strategy pairs with phenotypes ϕ_{xx} and ϕ_{xy} near $\phi_{x^*x^*}$ that mutually invade each other if $[\frac{\partial^2 w}{\partial \phi_{xx}\partial \phi_{xy}}]_{x^*} < 0$. The ecological selection part (derivatives of w in the brackets) in (21) is at variance with this clonal condition. This is because of diploid inheritance: Alleles x and y mutually invade each other if the heterozygote phenotype ϕ_{xy} invades both ϕ_{xx} and ϕ_{yy} (whereas the clonal condition requires that ϕ_{xy} and ϕ_{xx} invade each other). Assume that the singular phenotype $\phi_{x^*x^*}$ can invade all other phenotypes in its vicinity. Then at least alleles placed symmetrically around x^* (such as $x = x^* - \epsilon$ and $y = x^* + \epsilon$)

can invade each other, because due to locally additive allelic effects, they produce the heterozygote phenotype $\phi_{xy} = \phi_{x^*x^*}$, which invades any phenotype in the vicinity, including ϕ_{xx} and ϕ_{yy}. In the opposite case if $\phi_{x^*x^*}$ cannot invade other phenotypes in its vicinity, then alleles near x^* cannot invade each other even if they are symmetrically placed (as easily seen e.g. from pairwise invasibility plots, this is the most favourable configuration for mutual invasibility). Hence the diploid condition of mutual invasibility of alleles coincides with the clonal condition of the singular phenotype being able to invade other similar phenotypes. The latter is given by $[\frac{\partial^2 w}{\partial \phi_{xx}^2}]_{x^*} > 0$ (Geritz et al. 1998), which directly corresponds to the ecological part of (21).

Concerning sexual selection, $\pi''(0) < 0$ makes it more difficult to satisfy (21), i.e., assortative mating hinders mutual invasibility. The weight of sexual selection (q) is the same as in the ESS-condition (19) above. Because rare alleles are at a disadvantage in sexual selection, mutual invasibility can turn into mutual exclusion near the singularity if the assortativity of mating is increased. The remainder of this section explores the consequences of the bifurcation between mutual invasibility and mutual exclusion.

Mutual invasibility yields (protected) polymorphism, but a locally stable polymorphism may occur also without mutual invasibility when the population genetic equations [our Eqs. (1) and (2)] have multiple attractors. We shall refer to a locally asymptotically stable polymorphic equilibrium of two alleles as *unprotected polymorphism* when one or both boundary equilibria (fixation of an allele) are also locally stable. The alleles can coexist indefinitely in an unprotected polymorphism, provided that the population is never subject to large perturbations that would bring the system into the basin of attraction of a boundary equilibrium.

Because sexual selection disfavours rare alleles, it stabilizes the boundary equilibria and for a given pair of alleles, this can lead to loss of mutual invasibility or to mutual exclusion. Sexual selection however weakens when the alleles have more comparable frequencies, i.e., sexual selection does not necessarily destabilize an internal (polymorphic) equilibrium when it does stabilize a boundary equilibrium. One can therefore readily expect that unprotected polymorphisms occur under assortative mating. Below, Fig. 1 illustrates using the Levene model as an example that this is indeed the case. Actually, it is proved in a separate paper (Priklopil in prep.) that unprotected polymorphism generically occurs when mutual invasibility near a singularity turns into mutual exclusion (or vice versa). Therefore, if in the present model ecological selection promotes mutual invasibility near the singularity such that (21) is satisfied for random mating, then strengthening the assortativity of mating [increasing $\pi''(0)$ in absolute value] will cause a bifurcation into mutual exclusion, and unprotected polymorphism necessarily occurs near x^* for some values of $\pi''(0)$. Note however that starting with a monomorphic population, unprotected polymorphism could be reached only if a new allele appears with sufficiently high frequency (e.g. due to secondary contact with a formerly isolated population).

3 Levene model: adaptive dynamics and speciation in polymorphic populations

In the second part of the paper, we aim at investigating the adaptive dynamics of a magic trait when the resident population is already polymorphic. This analysis will show whether the alleles evolve sufficiently far apart such that homozygotes become

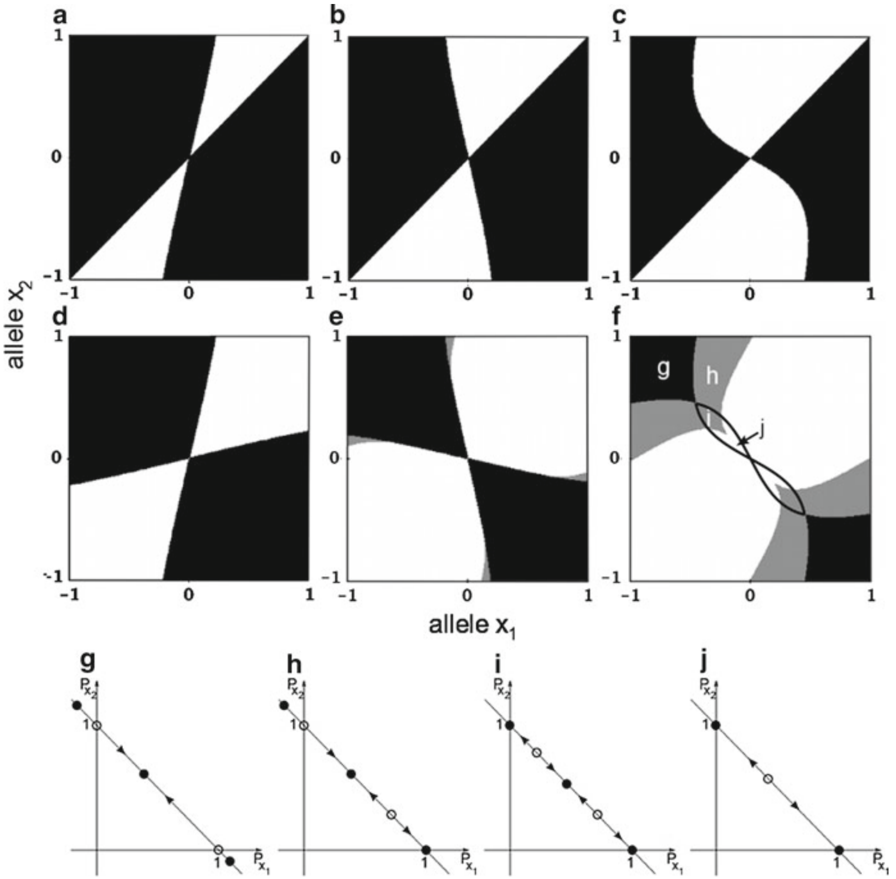


Fig. 1 *Top row* pairwise invasibility plots (*black color* denotes the area where allele x_2 can invade the resident allele x_1 and *white color* where it can not) for $c_1 = c_2 = 0.5, d = 3, \sigma_s = 1$, and **a** $\sigma_m = \infty$ (random mating), **b** $\sigma_m = 0.50$ (moderate assortativness) and **c** $\sigma_m = 0.36$ (strong assortativeness). *Middle row* areas of mutual invasibility (protected polymorphism, *black*) and unprotected polymorphism (*grey*); mutual exclusion occurs in **f** in the area adjacent to the singularity in between the invasion boundaries (*bold lines*). Parameters for **d**–**f** as in **a**–**c**. *Bottom row* dynamics of allele frequencies with **g** protected polymorphism; **h** unprotected polymorphism; **i** unprotected polymorphism with mutual exclusion; and **j** mutual exclusion. The *filled circles* and *empty circles* indicate stable and unstable equilibria, respectively. **g**–**j** represent the dynamics which occurs in the corresponding regions of **f**

reproductively isolated by assortative mating. Because this analysis depends on the global properties of the fitness function, we need to make specific assumptions about the ecological setting underlying $w_{E(t)}(\phi_g)$. We shall thus use a version of Levene's soft-selection model (Levene 1953).

3.1 Assumptions

For the ecological model, we consider a population in which the offspring of each discrete generation are distributed randomly over two habitats (Levene 1953). Within each habitat, there is first a period of viability selection, which an individual with phenotype ϕ_g survives with probability

$$f_1(\phi_g) = \alpha_1 \exp\left(-\frac{(\phi_g - m_1)^2}{2\sigma_s^2}\right) \tag{22a}$$

in habitat 1 and

$$f_2(\phi_g) = \alpha_2 \exp\left(-\frac{(\phi_g - m_2)^2}{2\sigma_s^2}\right) \tag{22b}$$

in habitat 2, respectively, where α_1 and α_2 are the maximum survival probabilities, m_1 and m_2 are the optimal phenotypes in the two habitats, and $\sigma_s > 0$ controls the strength of stabilizing selection within a habitat. Without loss of generality, we set $m_1 = -d/2$ and $m_2 = d/2$, where d is the distance between the two habitat-specific optima.

Viability selection is followed by non-selective "contest" competition, where a fixed number K_i of individuals survive to adulthood within habitat i ($i = 1, 2$; we assume that fecundity is sufficiently large such that the number of offspring after viability selection exceeds K_i in both habitats and for all phenotypes considered). As a result, a fraction $c_1 = K_1/(K_1 + K_2)$ of the adult population is recruited from habitat 1 and the remaining fraction $c_2 = 1 - c_1$ comes from habitat 2. All adults form a single population where mating is assortative with respect to phenotype but not with respect to habitat.

As we derive in Appendix 2, fitness in ecological selection under these assumptions is given by

$$w_{E(t)}(\phi_g) = c_1 \frac{f_1(\phi_g)}{\sum_h P_h(t) f_1(\phi_h)} + c_2 \frac{f_2(\phi_g)}{\sum_h P_h(t) f_2(\phi_h)}. \tag{23}$$

Note that the selective environment

$$E(t) = \left(\sum_h P_h(t) f_1(\phi_h), \sum_h P_h(t) f_2(\phi_h)\right) \tag{24}$$

depends on the frequencies and phenotypes of all genotypes present and changes in time until the genotypic frequencies arrive at an equilibrium, but can always be given by only two variables that are the habitat-specific mean probabilities of survival during viability selection. Contrary to clonal models, in a diploid sexual population the number of environmental feedback variables does not give an upper bound on the number of alleles that can form a polymorphism, except if the alleles act additively on the within-habitat viabilities (Nagylaki and Lou 2001) or there is partial dominance that is constant across habitats in the Levene model (Nagylaki 2009). In our model, allelic effects determine the phenotype ϕ additively but (24) implies nonadditive effects on the viabilities with variable dominance and possible overdominance; as a consequence, more than two alleles can be present at equilibrium (Kisdi and Geritz 1999; Nagylaki 2009).

For the mating process, in this example we shall assume $M \to \infty$ such that all females are eventually mated. This immediately implies $\bar{Q} = Q = 1$. Eqs. (12) and (13) simplify to $Q_{xy,xx} = 1$ and $Q_{xx,xy} = \pi(\phi_{xy} - \phi_{xx})$, respectively, and in the invasion fitness

$$W_x(y) = \frac{1}{2}(1 + \pi(\phi_{xy} - \phi_{xx}))w_{\hat{E}(\phi_{xx})}(\phi_{xy}), \tag{25}$$

purely ecological selection on females is combined with ecological and sexual selection on males. We adopt the mating function

$$\pi(\phi_h - \phi_g) = \exp\left(-\frac{(\phi_h - \phi_g)^2}{2\sigma_m^2}\right) \tag{26}$$

for the probability that a ϕ_g female accepts a ϕ_h male when they encounter each other (the same has been used e.g. by Doebeli 1996, Matessi et al. 2001; Pennings et al. 2008; Ripa 2009). In (26), decreasing σ_m^2 corresponds to decreasing $\pi''(0) = -1/\sigma_m^2$ and stronger assortativity.

Finally, we assume that the alleles act additively on the phenotype, i.e.,

$$\phi_{x_i x_j} = \frac{x_i + x_j}{2} \tag{27}$$

holds also for large differences between x_i and x_j (local additivity follows already from the smoothness assumptions made in the general model).

By scaling the allelic values, one can set $\sigma_s = 1$ without loss of generality. Hence the adaptive dynamics of alleles depend on three parameters only: the relative size of habitats, c_1 (with $c_2 = 1 - c_1$); the (scaled) difference between the habitat-specific optima, d/σ_s; and the (scaled) strength of assortative mating, σ_m/σ_s. With random mating ($\sigma_m/\sigma_s \to \infty$), this model is identical to the one investigated by Kisdi and Geritz (1999).

3.2 Monomorphic singularities of the Levene model

Before turning to speciation in polymorphic populations, we briefly illustrate our general results on monomorphic singularities in the Levene model. Substituting the ecological model (23) and genotype-phenotype map (27) into Eq. (25), we arrive at

$$W_x(y) = \frac{1}{2}\left(1 + \pi\left(\frac{y - x}{2}\right)\right)\left(c_1 \frac{f_1\left(\frac{x+y}{2}\right)}{f_1(x)} + c_2 \frac{f_2\left(\frac{x+y}{2}\right)}{f_2(x)}\right) \tag{28}$$

for the the invasion fitness with π and f_i given as in Eqs. (26) and (22), respectively. Using (17), we obtain a unique evolutionary singularity at

$$x^* = (c_2 - c_1)d/2 \tag{29}$$

and this singularity is always convergence stable [condition (18) simplifies to $-1/\sigma_s^2 < 0$]. The ESS condition (19) is not satisfied so that the singularity x^* is an evolutionary branching point if

$$c_1 c_2 (d/\sigma_s)^2 > 1 \quad \text{and} \quad (\sigma_m/\sigma_s)^2 > \frac{1}{2(c_1 c_2 (d/\sigma_s)^2 - 1)}. \tag{30}$$

The first of these inequalities is the condition for evolutionary branching under random mating (cf. Kisdi and Geritz 1999). Assortative mating hinders evolutionary branching so that branching occurs only if it does under random mating, and, in addition, mating is not too assortative so that σ_m is sufficiently large to satisfy the second inequality in (30). In the vicinity of x^*, there are pairs of alleles that mutually invade each other and hence form a protected polymorphism [see (21)] if

$$(\sigma_m/\sigma_s)^2 > \frac{1}{2(c_1 c_2 (d/\sigma_s)^2 + 1)} \tag{31}$$

whereas there are allele pairs with mutual exclusion if the opposite inequality holds. Notice that under random mating ($\sigma_m \to \infty$), the condition for mutual invasibility is always satisfied, but it can be violated if mating is sufficiently assortative.

The resulting bifurcation patterns are illustrated in Fig. 1. The top row contains pairwise invasibility plots [i.e., sign plots of $\log W_x(y)$] for increasing assortativeness, taking parameter values such that evolutionary branching occurs under random mating. The middle row shows the areas of mutual invasibility ($W_x(y) > 1$ and $W_y(x) > 1$) as derived from the pairwise invasibility plots, and areas of unprotected polymorphism as found by numerical continuation of equilibria. As σ_m decreases, x^* first bifurcates from an evolutionary branching point (Fig. 1a) into an ESS with mutual invasibility in its neighbourhood (Fig. 1b); next, mutual invasibility (Fig. 1d, e) bifurcates into mutual exclusion near x^* (Fig. 1f). When mating is sufficiently assortative, unprotected polymorphism appears (Fig. 1e, f). When mutual invasibility has bifurcated into mutual exclusion such that the invasion boundary lines [where $W_x(y) = 1$ and $W_y(x) = 1$, respectively] intersect away from the main diagonal $y = x$, unprotected polymorphism is always found in the neighbourhood of the intersection (Fig. 1f; see Priklopil in prep. for proof). The bottom row of Fig. 1 (where p_{x_i} denotes the frequency of allele x_i) illustrates the dynamics of allelic frequencies in protected and unprotected polymorphisms, and mutual exclusion with no polymorphism.

Figure 2 shows all bifurcations of monomorphic evolutionary singularities for equal habitat sizes ($c_1 = c_2 = \frac{1}{2}$) from (30) and (31). When disruptive selection generated by the contrasting habitats is weak ($d/\sigma_s < 2$), the monomorphic singularity is always an ESS. When the ecological conditions generate stronger disruptive selection ($d/\sigma_s > 2$)

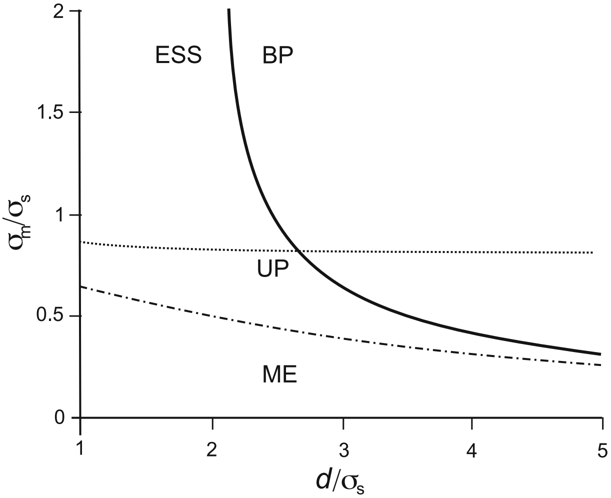


Fig. 2 Bifurcation plot for monomorphic singularities assuming equal habitat size ($c_1 = c_2 = 0.5$). On the *continuous line*, x^* bifurcates between an ESS and an evolutionary branching point BP [equality in the second condition of (30)]; on the *dash-dotted line*, x^* bifurcates between having mutual invasibility and mutual exclusion ME attached to it [equality in condition (31)]. Below the *dotted line*, unprotected polymorphism UP exists for some allelic values (x_1, x_2) (this region is found numerically)

and assortativness is weak (σ_m is sufficiently high), then the singularity is a branching point, but branching is lost if stabilizing sexual selection is too strong (σ_m is small). Strong sexual selection can always generate mutual exclusion near the singularity.

3.3 Adaptive dynamics in polymorphic resident populations and speciation by magic traits

In this section, we investigate the dynamics of evolution after evolutionary branching of a magic trait, with particular attention to whether speciation occurs and whether the existing species are stable in face of changes in the environment. We adhere to the biological species concept, i.e., define species by substantial (although not necessarily complete) reproductive isolation between them (see e.g. Coyne and Orr 2004). The evolution of a magic trait leads to reproductive isolation, and thus to speciation if the phenotypes become sufficiently different relative to the width of the mating function σ_m in Eq. (26), so that separate phenotypes cease to interbreed and heterozygotes ("hybrids" between the homozygote species) become rare. σ_m may depend on environmental factors. A famous example is found in the cichlid fish of Lake Victoria (Seehausen et al. 1997): Mate choice is determined by colour in normal clear water, but since recent eutrophication of the lake has increased water turbidity and made colours difficult to recognize, mating has become less assortative and formerly isolated species started to fuse. Below, we shall also investigate the consequences of environmental changes affecting σ_m.

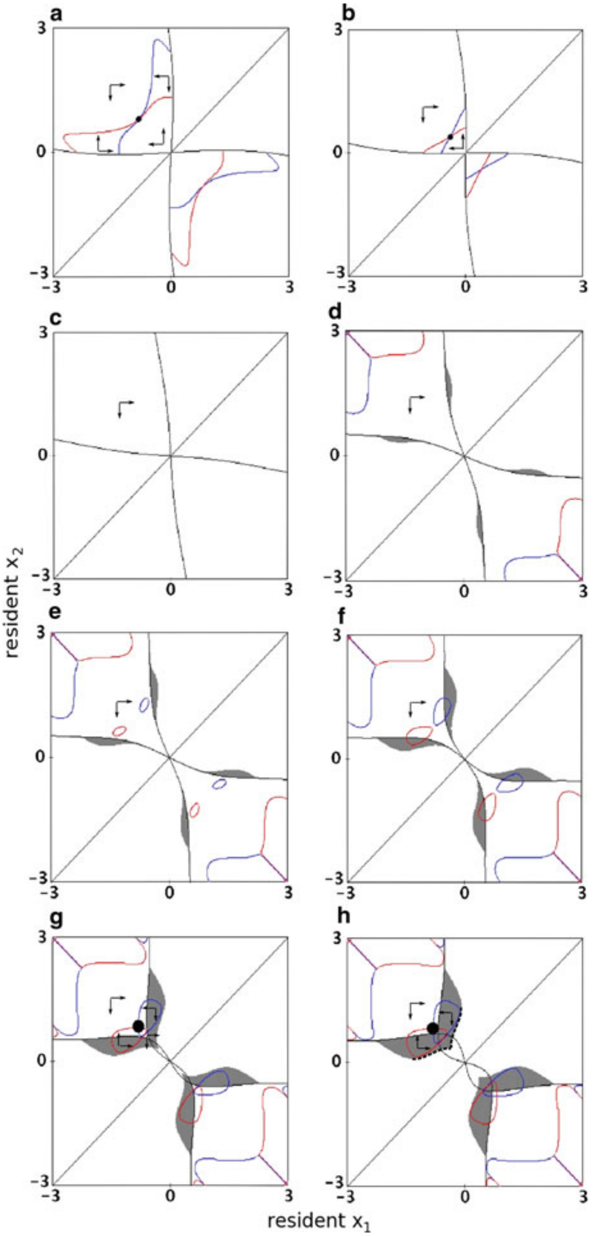


Fig. 3 Trait evolution plots for $d = 2.25$ and **a** $\sigma_m = \infty$, **b** $\sigma_m = 1.6$, **c** $\sigma_m = 1.0$, **d** $\sigma_m = 0.6$, **e** $\sigma_m = 0.57$, **f** $\sigma_m = 0.5$, **g** $\sigma_m = 0.43$ and **h** $\sigma_m = 0.38$. *Arrows* indicate the direction of the selection gradient in allele x_1 (*horizontal*) and allele x_2 (*vertical*); isoclines are the null clines of the selection gradients and diallelic singularities are at the intersection of isoclines. *Dots* indicate convergence stable diallelic singularities (these are also evolutionarily stable). The *size of the dot* indicates the strength of reproductive isolation at the singularity; *smallest dot* denotes $F < 0.9$ (**a**, **b**), *middle sized dot* denotes $0.9 < F < 0.99$ (not in this figure), *biggest dot* denotes $0.99 < F$ (**g**, **h**). *Grey areas* denote unprotected polymorphisms. In **h**, we marked the boundaries across which evolutionary suicide can occur, but analogous boundaries are found in every panel with unprotected polymorphism. The monomorphic singularity at $(x^*, x^*) = (0, 0)$ is an evolutionary branching point for $\sigma_m > 1.37$ (**a**, **b**) and an ESS below this threshold (**c**–**h**); there is mutual invasibility in the neighbourhood of (x^*, x^*) for $\sigma_m > 0.47$ (**a**–**f**) and there is mutual exclusion below this threshold (**g**, **h**)

To analyze the dynamics of evolution after evolutionary branching, we construct so called trait evolution plots, i.e., combined sign plots of the selection gradients $[\partial W_{x_1,x_2}(y)/\partial y]_{y=x_1}$ and $[\partial W_{x_1,x_2}(y)/\partial y]_{y=x_2}$ (Geritz et al. 1998), where the fitness proxy $\tilde{W}$ defined in (16) can be used in place of W. In Figs. 3, 4, 5, arrows

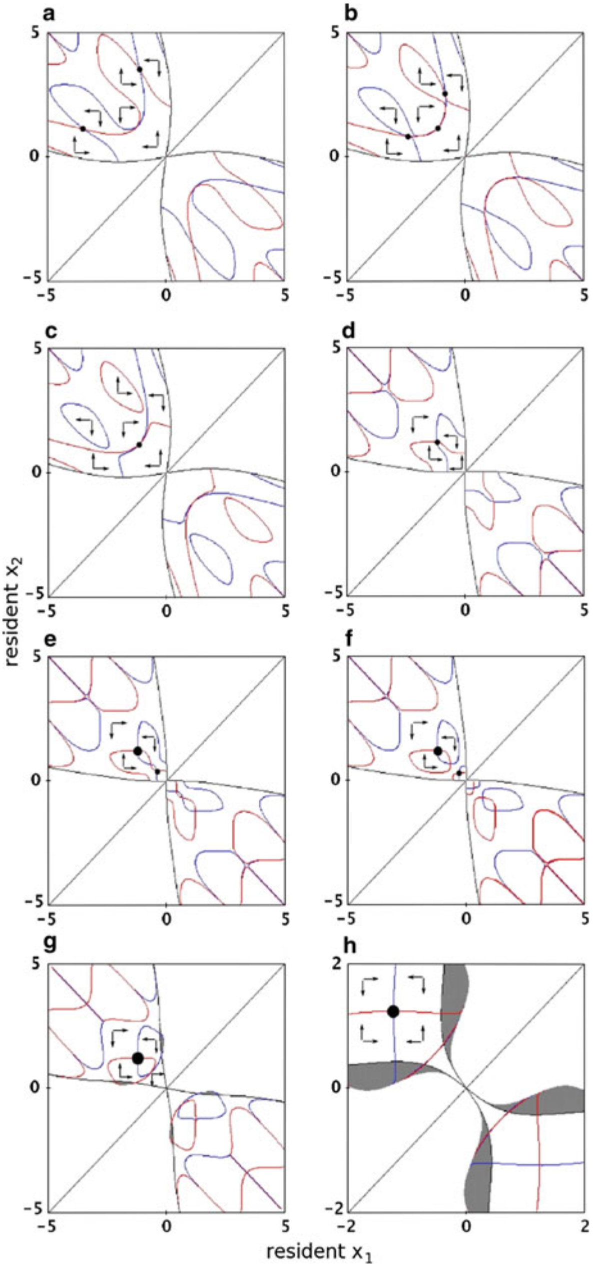
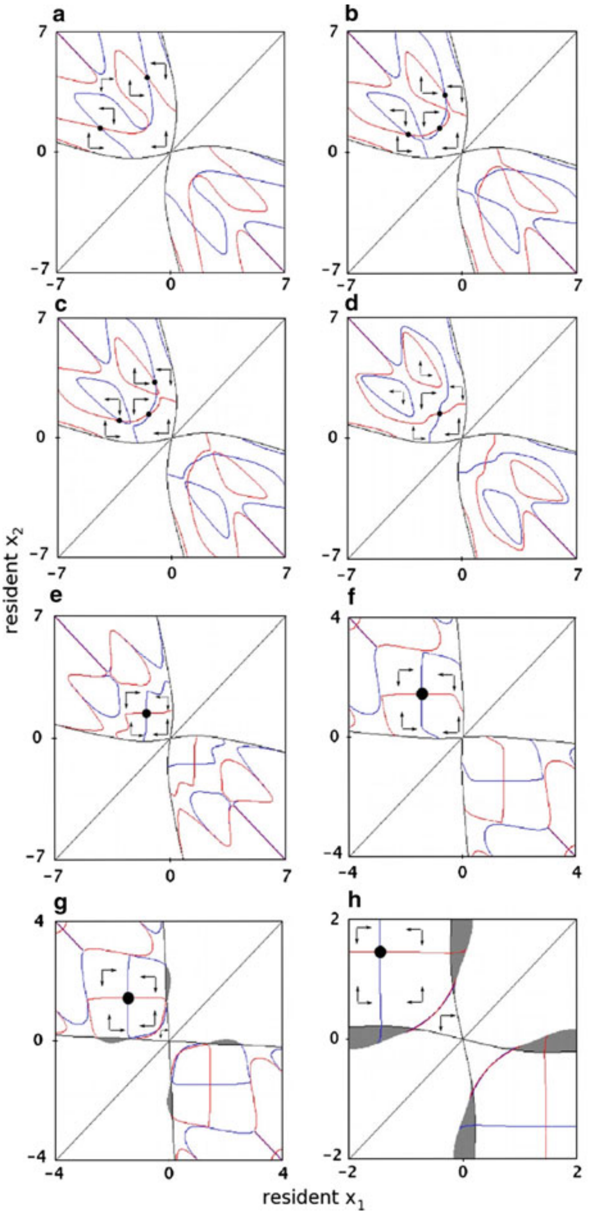


Fig. 4 Trait evolution plots for $d = 2.66$ and **a** $\sigma_m = \infty$, **b** $\sigma_m = 2.9$, **c** $\sigma_m = 2.6$, **d** $\sigma_m = 0.9$, **e** $\sigma_m = 0.83$, **f** $\sigma_m = 0.82$, **g** $\sigma_m = 0.61$ and **h** $\sigma_m = 0.45$. Notations as in Fig. 3. Note that in the *upper left* and *lower right* of each plot, the x_1- and x_2-isoclines are very near to each other especially for small values of σ_m, but there is no isolated singularity in these regions [the outermost symmetric singularity is around $(x_1, x_2) = (-1.2, 1.2)$ in every panel]. Note also the change of scale in **h**. The monomorphic singularity at $(x^*, x^*) = (0, 0)$ is an evolutionary branching point for $\sigma_m > 0.81$ (**a**–**f**) and an ESS below this threshold (**g**–**h**); there is mutual invasibility in the neighbourhood of (x^*, x^*) for $\sigma_m > 0.42$ (in all panels shown here)

show the direction of selection gradients inside the area of coexistence; the boundary lines where the corresponding selection gradient changes sign are referred to as x_1- and x_2-isoclines. Note that the isoclines extend smoothly into the areas of unprotected polymorphism (grey areas). The intersections of isoclines correspond to diallelic

Fig. 5 Trait evolution plots for $d = 3$ and **a** $\sigma_m = \infty$, **b** $\sigma_m = 2.0$, **c** $\sigma_m = 1.95$, **d** $\sigma_m = 1.5$, **e** $\sigma_m = 1.0$, **f** $\sigma_m = 0.7$, **g** $\sigma_m = 0.6$ and **h** $\sigma_m = 0.5$. Notations as in Fig. 3. Note that in the *upper left* and *lower right*, the x_1- and x_2-isoclines are very near to each other but there is no isolated singularity in these regions [the outermost symmetric singularity is around $(x_1, x_2) = (-1.4, 1.4)$ in every panel]. Note also the changes of scale. The monomorphic singularity at $(x^*, x^*) = (0, 0)$ is an evolutionary branching point for $\sigma_m > 0.63$ (**a**–**f**) and an ESS below this threshold (**g**, **h**); there is mutual invasibility in the neighbourhood of (x^*, x^*) for $\sigma_m > 0.39$ (in all panels shown here)



evolutionary singularities [cf. Eq. (39)], and the singularities which are evolutionarily as well as convergence stable (see Appendix 3) are marked with filled circles. Trait evolution plots are symmetric with respect to the main diagonal $x_2 = x_1$ because labelling of the resident alleles is arbitrary. In addition, the trait evolution plots in Figs. 3, 4, 5 are also symmetric with respect to the secondary diagonal $x_2 = -x_1$ because we assume equal habitat size, $c_1 = c_2 = 0.5$ (see Appendix 3 for relaxing this symmetry). In case of random mating ($\sigma_m = \infty$), we recover the trait evolution plots of Kisdi and Geritz (1999).

To assess the degree of reproductive isolation at the evolutionary singularities, we calculate the deficiency of heterozygotes among newborns (before ecological selection) at the population genetic equilibrium of the two resident alleles of the diallelic singularity, as compared to Hardy-Weinberg equilibrium: $F = 1 - P_{x_1 x_2}/(2p_{x_1} p_{x_2})$, where p_{x_i} denotes the frequency of allele x_i ($p_{x_1} = p_{x_2} = \frac{1}{2}$ by symmetry on the secondary diagonal $x_2 = -x_1$). $F = 0$ corresponds to random mating and $F = 1$ implies that the two homozygotes are fully isolated and hence behave as separately evolving species. In Figs. 3, 4, 5 we indicate three different regimes of reproductive isolation with three different sized circles; the smallest circle (as in Fig. 3a) denotes $F < 0.9$, the middle sized circle (as in Fig. 4e) denotes $0.9 < F < 0.99$ and the biggest circle (as in Fig. 4g) denotes $0.99 < F$.

It will be necessary to distinguish between strong discrimination against males even with small phenotypic differences to the female phenotype (small σ_m in Eq. (26)) and strong reproductive isolation due to large phenotypic differences ($|x_1 - x_2|$). Henceforth we shall refer to small σ_m as "strongly assortative", and use "strongly isolated" when the probability of interbreeding between different phenotypes is small and therefore F is close to 1.

Moderate difference between habitat optima. In Fig. 3, there is only a moderate difference between the within-habitat optima ($d/\sigma_s = 2.25$), and therefore disruptive ecological selection is weak. In absence of assortative mating (Fig. 3a), evolutionary branching at $x^* = 0$ is followed by evolution to a unique convergence and evolutionarily stable diallelic singularity, where two alleles segregate in a randomly mating population ($F = 0$). With weak assortativity (Fig. 3b), the qualitative outcome is the same, and mating is nearly random at the singularity ($F = 0.017$). Increasing assortativity by decreasing σ_m leads to the loss of evolutionary branching as the diallelic singularity converges to (x^*, x^*) (Fig. 3c).

At stronger assortativity, an area of unprotected polymorphism appears (grey areas in Fig. 3d–h). At the outer edge of the area of unprotected polymorphism, the diallelic population genetic attractor disappears via a fold bifurcation. This is a "catastrophic" bifurcation where the frequency of an allele drops to zero discontinuously, which makes evolutionary suicide possible (Gyllenberg and Parvinen 2001). In Fig. 3h, we have marked those parts of the boundary of unprotected polymorphism where evolutionary suicide can happen. Above the main diagonal of the figure ($x_2 > x_1$), the selection gradient in x_1 is positive whereas the selective gradient in x_2 is negative along the outer edge of unprotected polymorphism. At the marked boundary above the secondary diagonal ($x_2 > -x_1$), an evolutionary step downwards leads to the loss of polymorphism and fixation of the x_1 allele: Hence an invading mutant of x_2 causes the extinction of the same allele. Below the secondary diagonal, x_1 may be lost via evolutionary suicide in a similar manner; and below the main diagonal, the roles are reversed. Evolutionary suicide events can happen also for other parameter values, whenever unprotected polymorphism is present.

When assortativity is strong, new diallelic singularities are created via a fold bifurcation (Fig. 3g, h). At the convergence stable (outer) singularity, the two homozygotes are strongly isolated and heterozygotes are nearly absent ($F > 0.99$). The convergence stable singularity thus corresponds to two biological species. Because two isolated species evolve independently and analogously to two clonal strategies, the position of the diallelic singularity is close to the dimorphic singularity of the corresponding clonal model whenever reproductive isolation is strong (cf. Geritz and Kisdi 2000). Note however that in contrast to the clonal model, the convergence stable diallelic singularity in Fig. 3g, h is not attainable via evolutionary branching from an initially monomorphic population: This is because stabilizing sexual selection in the vicinity of the monomorphic singularity $(x^*, x^*) = (0, 0)$ prevents evolutionary branching when mating is strongly assortative. Even though separate species are stable, for these parameters speciation cannot happen by evolving the magic trait from monomorphic populations.

Suppose now that two isolated species exist at the diallelic convergence stable singularity in Fig. 3g, h, but mating assortativity decreases (σ_m increases) due to a change in the environment. If this change is not too large, then the diallelic singularity is lost (cf. Fig. 3c–f): The two species hybridize to some extent, and the hybrid species complex eventually loses genetic polymorphism by evolving to a monomorphic ESS. Note that there may be significant variations in the transient dynamics: If σ_m increases to just above the fold bifurcation point of the diallelic singularity, then the species initially remain reproductively well isolated but start evolving their magic trait towards the common ESS, and reproductive isolation slowly dissolves as the species evolve towards each other. If σ_m increases more dramatically, then reproductive isolation breaks down instantly and the species fuse on the short population genetic timescale, before evolutionary changes occur in the magic trait. Eventually, however, the two species will in both cases be replaced with a single monomorphic species at the ESS, and the system will stay there also if the original small value of σ_m is restored. If the environment changes such that σ_m jumps to a very high value, then the system settles at a diallelic singularity (Fig. 3a, b) where genetic polymorphism is preserved, although the two separate species are fused into a single, nearly randomly mating population. Restoring the small value of σ_m will, interestingly, restore the original two species only if the disturbed value of σ_m was sufficiently large. If, during the environmental disturbance, the alleles evolve according to Fig. 3a, then they remain in the basin of attraction of the convergence stable diallelic singularity of Fig. 3g, h so that if σ_m assumes its original value after the disturbance, the two species become isolated again. If however the disturbed population evolves as in Fig. 3b, then the alleles evolve out of the basin of attraction in Fig. 3g, h such that restoring the original σ_m will not restore the two species; instead, upon reducing σ_m, one species will eventually go extinct and the other will evolve to the monomorphic ESS.

Increasing the difference between habitat optima. With somewhat larger difference between the habitats ($d/\sigma_s = 2.66$, Fig. 4), the symmetric diallelic singularity is a saddle point under random mating (Fig. 4a), but it undergoes a pitchfork bifurcation and becomes convergence stable under weak assortativity (Fig. 4b). In contrast to the previous scenario, this symmetric convergence stable singularity is not lost as σ_m decreases, and there is substantial reproductive isolation maintaining two separate species at this singularity when mating is fairly assortative ($F > 0.9$ at the outermost singularity in Fig. 4e, f and $F > 0.99$ in Fig. 4g, h). However, as mating becomes more assortative, this singularity becomes isolated from the evolutionary branching point by a new pair of singularities (Fig. 4e, f). There we see an interesting evolutionary bistability: On the one hand, two reproductively almost isolated species exist at the outer singularity, with few heterozygotes present at mating and therefore with stabilizing sexual selection around the two homozygote phenotypes. This singularity is close to the singular coalition of strategies in the clonal model. On the other hand, however, there is an almost randomly mating population at the inner singularity, where heterozygote females are common and exert stabilizing selection on males, thereby preventing the further divergence of alleles. Evolutionary branching thus does not lead to speciation, because the evolution of the magic trait stops at the innermost singularity, where reproductive isolation is very weak ($F < 0.1$ in Fig. 4e, f). Increasing the strength of assortativity further (Fig. 4g, h) leads to the loss of evolutionary branching, although a pair of well isolated species continues to be convergence and evolutionarily stable.

Environmental changes inducing changes in σ_m can destroy species, but here, they will not destroy genetic polymorphism. When mating assortativity drops, then separate species fuse into a single polymorphic population (e.g. in Fig. 4c, $F < 0.1$ at the diallelic singularity); reproductively isolated species appear instantly if the environment is restored such that σ_m assumes a low value again. If mating becomes almost random (σ_m becomes very large), then the magic trait evolves away from the symmetric diallelic singularity (Fig. 4a), but still remains polymorphic. This change is reversible but with a hysteresis effect: σ_m needs to get below the simultaneous fold bifurcation that destroys the asymmetric singularities in order to allow the magic trait to evolve back to the symmetric diallelic singularity.

With fairly large difference between habitats ($d/\sigma_s = 3$, Fig. 5), the evolution of a magic trait leads to speciation provided that assortativity is sufficiently strong, such that it provides sufficient reproductive isolation at the diallelic singularity, but not too strong, such that it does not prevent evolutionary branching. These conditions hold e.g. in Fig. 5f: Evolutionary branching leads to the evolution of two alleles with $F = 0.999$, i.e., to the evolution of two reproductively isolated homozygote species. For stronger assortativity of mating, the monomorphic singularity $x^* = 0$ becomes an ESS and a saddle point bifurcates from x^* that isolates the diallelic convergence stable singularity. Otherwise, similar conclusions hold as for $d/\sigma_s = 2.66$.

In summary, two species can coexist in an evolutionarily stable manner if the habitats are substantially different (d/σ_s is large) and mating assortativity is sufficiently strong (σ_m/σ_s is not too large). Very strong assortativity however prevents evolutionary branching, so that even though there is an evolutionarily stable pair of species, these species cannot evolve from an initially monomorphic population. Speciation by the evolution of a magic trait occurs for intermediate levels of assortativity. We summarize these results in Fig. 6, which shows where the symmetric diallelic singularities correspond to speciation and whether these can be reached via evolutionary branching from an initially monomorphic population. Appendix 3 contains a full bifurcation analysis of the diallelic singularities, which provides a comprehensive overview of the patterns seen in Figs. 3, 4, 5, and discusses how the bifurcation structures unfold when the habitats are not precisely of the same size.

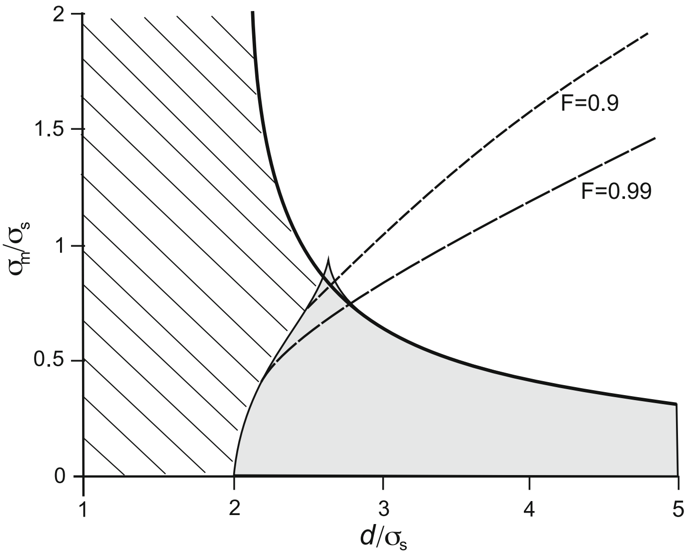


Fig. 6 Strength of reproductive isolation at the symmetric convergence stable diallelic singularity. Such a singularity exists in *white* and *grey areas*. If there is more than one symmetric singularity then F values refer to the outer singularity (see Appendix 3). F increases with decreasing σ_m/σ_s such that $F < 0.9$ above the *upper dashed line*, $0.9 < F < 0.99$ in between the *dashed lines* and $F > 0.99$ below the *lower dashed line*. In the *grey area*, the singularity cannot be reached by evolutionary branching from a monomorphic population. In the *striped area* there are no diallelic singularities

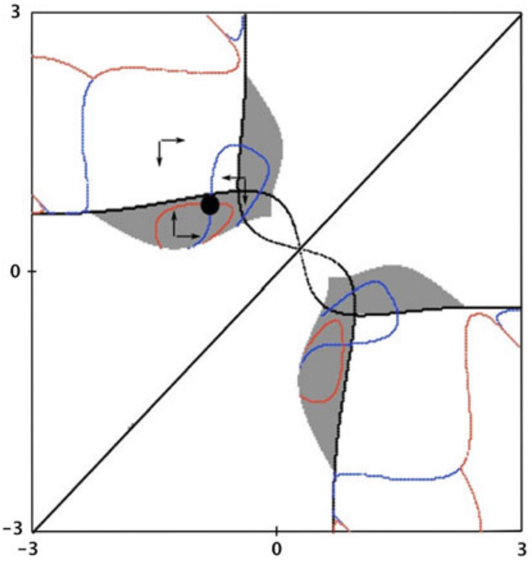
3.4 Species in unequally sized habitats

Analyzing the adaptive dynamics of polymorphic populations with arbitrary habitat sizes (c_1, c_2) is beyond the scope of this paper. However, in Fig. 7 we show one example where the habitats differ substantially in their size $(c_1 = 0.38, c_2 = 0.62)$. In this example, the convergence stable diallelic singularity lies in the area of unprotected polymorphism. Reproductive isolation is strong at this singularity $(F > 0.99)$, i.e., the singularity corresponds to two biological species that coexist at a locally stable equilibrium of their joint population dynamics. This coexistence is however not protected, i.e., not globally stable: If the species harboring allele x_1 becomes rare or goes extinct due to some ecological disturbance, then it is no longer able to invade and recover from low initial population densities. The species loss is therefore permanent, and the remaining species will subsequently evolve to the monomorphic ESS. This is in contrast to the diallelic singularities of Figs. 3, 4, 5, which all occur in the area of protected polymorphism such that any of the two alleles (or species) can invade if rare, provided that it is re-introduced shortly on the evolutionary time scale before the remaining population could evolve away.

4 Discussion

In the first part of this paper, we investigated the evolution of a magic trait under the most commonly used model of assortative mating (originally due to Doebeli 1996;

Fig. 7 The convergence stable diallelic singularity lies in the area of unprotected polymorhism when the difference between the habitat sizes is sufficiently large. The parameter values are $d = 2.25$, $\sigma_m = 0.38$ and $c_1 = 0.38$ (the singularity moves to the area of unprotected polymorhism when $c_1 \approx 0.43$)



Gavrilets and Boake 1998; Matessi et al. 2001) and under arbitrary ecological selection. Assortative mating occurs via female preference for males with similar phenotypes to the female herself. Because assortative mating exerts no directional selection, the position and convergence stability of monomorphic evolutionary singularities are not affected by assortativity and coincide with those under random mating (Eqs. (17), (18)); which, in turn, coincide with the monomorphic singularities of the corresponding clonal model of adaptive dynamics (Geritz and Kisdi 2000; Van Dooren in press). Thus as far as the number, position, and convergence stability of monomorphic singularities are concerned, sexual reproduction and assortative mating makes no difference.

In polymorphic populations, however, the abundance of resident genotypes depends on the assortativity of mating, and this affects the selection gradient experienced by rare mutants through both ecological and sexual selection. As ecological and sexual selection interact, the adaptive dynamics of diallelic populations (as shown by the example of the Levene model in Figs. 3, 4, 5) are much richer than adaptive dynamics under random mating (no sexual selection; Kisdi and Geritz 1999) or the adaptive dynamics of clonal phenotypes in the same ecological model (Geritz et al. 1998; Geritz and Kisdi 2000). For the existence and convergence stability of polymorphic singularities, we can draw a general (model-independent) conclusion only for the limiting case where female reproduction is not affected by mating ($M \to \infty$) and assortativity is very strong ($\sigma_m \to 0$), so that heterozygotes are absent and the model reduces to its clonal counterpart.

It is important to recall that if some females remain unmated due to assortative mating ($M < \infty$), then mating also affects ecological fitness via changing the densities of resident genotypes. When relaxing assortativeness ($\sigma_m \to \infty$), the model converges to the corresponding sexual model without mate choice only if all females reproduce ($\mu_{max} = 1$). Likewise, under full reproductive isolation ($\sigma_m \to 0$) but with $M < \infty$

and $\mu_{max} < 1$, females reproduce less on average than in the corresponding clonal model and because this alters the population densities of the residents, ecological selection will be different.

Sexual selection from assortative mating has no directional component but it is stabilizing around the common phenotypes (Kirkpatrick and Nuismer 2004; Schneider 2005; Pennings et al. 2008). At a monomorphic singularity, stabilizing sexual selection counteracts disruptive ecological selection, and therefore may prevent evolutionary branching. Schneider (2005) obtained a similar result in a more specific model, assuming a particular ecological scenario (trait-dependent competition in a Lotka-Volterra model), haploid sexual genetics, and a single opportunity for mating ($M = 1$; $\mu_{max} = 1$); the numerical analysis of two models by Ripa (2009) showed the same. Here, we give the general analytic condition for evolutionary branching to occur in a diploid population in face of assortative mating (Eq. 19).

Stabilizing sexual selection can prevent not only the evolution of polymorphism via evolutionary branching, but also the maintenance of polymorphism of given (fixed) alleles (Matessi et al. 2001; Schneider 2005; Schneider and Bürger 2006; Pennings et al. 2008). We found that under strong assortativity, mutual invasibility near an evolutionary singularity is replaced by mutual exclusion, a situation such that a monomorphic population of either allele resists invasion by the other allele [Eq. (21); see examples in Figs. 1, 2]. Although sexual selection can prevent protected polymorphisms, it can result in an unprotected polymorphism, where there is a stable internal (polymorphic) equilibrium even though both fixation equilibria are also stable (cf. Schneider and Bürger 2006). This is again because assortativity favours the common phenotypes: An allele may be unable to invade when rare but may reach a stable equilibrium when sufficiently common. A set of unprotected polymorphisms appears when mutual invasibility at an evolutionary singularity bifurcates into mutual exclusion (Priklopil in prep.).

To retain analytical tractability (and similarly to previous analytical models of sympatric speciation such as Udovic 1980; Matessi et al. 2001; Schneider 2005; Pennings et al. 2008; Kopp and Hermisson 2008; Otto et al. 2008; Ripa 2009), we assumed throughout that the magic trait is determined by a single gene. While this is a simplification, it may even be close to reality in some cases: The number of genes underlying adaptations and species differences vary and may be as low as one or few (Orr 2001; Woodruff and Thompson 2002). Interestingly, the adaptive dynamics of two loci under random mating in the Levene model leads to loss of genetic variability in one locus, so that eventually the ecological trait is determined by the alleles of a single locus as assumed here (Kisdi and Geritz 1999; Van Doorn and Dieckmann 2006).

4.1 Speciation

In our model, speciation occurs by the evolution of sufficiently large differences between the allelic values of the magic trait, which implies that the homozygotes become reproductively isolated by assortative mating. We studied the evolution of polymorphic populations and in particular speciation in the Levene model as an example. First of all, this model was used as the basis of many classic studies of speciation assuming non-evolving allelic values (e.g. Maynard Smith 1966; Felsenstein 1981; see Kirkpatrick and Ravigne 2002 and Gavrilets 2004 for reviews); secondly, the adaptive dynamics of allelic values are well understood in this model under random mating (Kisdi and Geritz 1999) and also under linkage disequilibrium with a separate mating locus (Geritz and Kisdi 2000; Kisdi and Geritz in press). In this paper, we explored the evolution of a magic trait rather than separate ecological and mating traits. As recent empirical data demonstrate, this is probably a more common route to sympatric speciation than linkage disequilibrium between separate traits (see Sect. 1).

In the Levene (1953) model, viability selection occurs in two contrasting habitats. The model assumes that adults emerging from both habitats form a single mating population so that mating is independent of habitat origin; in other words, all mating assortativity is due to mate choice by the magic trait and speciation is fully sympatric. This assumption is met if the environment is “fine grained”, i.e., if the habitats exist in many randomly placed patches so that distances across different habitats are short relative to the mobility of the organism. A weakness of Levene’s soft selection model is that it assumes fully saturated habitats; when the population is maladapted to a habitat, this implies that fecundity must be large. Under random mating and with Gaussian functions as assumed in (22a,b), the monomorphic singularity of the Levene model is always convergence stable, but this does not hold for other choices of functions (Kisdi 2001) and also not in models where the habitats are not always saturated (e.g. Meszéna et al. 1997, Day 2000, Kisdi 2002, Ravigne et al. 2009). If convergence stability of the monomorphic singularity is lost when the habitats differ strongly, then this further limits the possibility of speciation via the evolutionary branching of a magic trait in heterogeneous habitats.

Several models have considered the evolution of mating assortativity, i.e., the evolution of σ_m, with fixed allelic values (x_1, x_2) of the magic trait (Matessi et al. 2001; Pennings et al. 2008; Kopp and Hermisson 2008; Otto et al. 2008; Ripa 2009). These models concluded that for speciation, disruptive ecological selection on the magic trait needs to be strong. As assortativity gradually increases by the evolution of σ_m, stabilizing sexual selection strengthens, and may fully balance disruptive ecological selection: If this happens, then the selection gradient on σ_m vanishes before the prospective species become reproductively isolated, so that the process of speciation stalls (Matessi et al. 2001; Pennings et al. 2008).

In this paper, we made the complementary assumption that only the magic trait x evolves whereas σ_m is fixed (see also Schneider 2005). Our model uncovers other difficulties of speciation by magic traits. Unless ecological selection is strong even for moderately different alleles (i.e., unless d/σ_s is large in the Levene model), an initially monomorphic population cannot evolve into two isolated species because when assortativity is sufficiently strong to provide reproductive isolation at a polymorphic singularity, then evolutionary branching either does not occur (as in Figs. 3g, h, 4g, h) or evolution after branching stops before the alleles become sufficiently different to achieve reproductive isolation (Fig. 4e, f). Ripa (2009) investigated speciation by a magic trait in two other ecological models, where again if assortativity is sufficiently strong for reproductive isolation at the diallelic singularity, then it is likely to prevent evolutionary branching of the monomorphic population. Although the numerical analysis of Ripa (2009) was less complete, it seems that the bifurcation structures of his models are simpler, and alternative diallelic attractors do not prevent speciation as seen in our Fig. 4e, f.

The above-mentioned problems are particularly relevant for the evolution of species diversity after an extinction event. If initially two species are isolated by assortative mating but one goes extinct due to some environmental disturbance, then mating can remain strongly assortative in the remaining species. The remaining species will evolve to the monomorphic singularity, where assortative mating can prevent evolutionary branching (or prevent the evolution of sufficiently different alleles for obtaining reproductively isolated species after branching) so that the initial species diversity will not be restored. This problem is not particular to the example of the Levene model: If assortativity is sufficiently strong for the given ecological parameters, then the monomorphic singularity is always an ESS [Eq. (19)], and evolutionary branching cannot restore an extinct species. In principle, assortativity could evolve arbitrarily strong between two species, but in practice the selection gradient on assortativity will become weak once the species are well isolated. How strong assortativity does evolve relative to ecological selection determines whether evolutionary branching remains possible after an extinction event or not.

Distinction needs to be made between the questions whether evolutionary branching is possible, whether there is a locally stable polymorphic evolutionary singularity where homozygotes are reproductively isolated, and whether such a singularity can be reached from an evolutionary branching point. Evolutionary branching is possible if assortativity is not too strong relative to disruptive ecological selection [Eq. 19]. A singularity with two separate species exists if assortativity is strong enough and ecological selection is able to maintain two clonal phenotypes in an evolutionarily stable coalition. Note that assortativity needs to be both sufficiently weak so as not to exert too strong stabilising selection on similar alleles near the monomorphic singularity, and also sufficiently strong so as to provide reproductive isolation between distinct homozygotes: Given the Gaussian mating function in Eq. (26), this is possible if disruptive ecological selection is sufficiently strong at the branching point and the homozygotes of the diallelic singularity are sufficiently far apart. In the Levene model, both these requirements hold if d/σ_s is large. But evolutionary branching and the existence of a diallelic singularity with strong reproductive isolation does not yet guarantee speciation (cf. Fig. 4e, f): An initially monomorphic population can evolve into two separate species only if disruptive ecological selection is sufficiently strong to overcome sexual selection for *all* allelic values from the monomorphic singularity to a polymorphic singularity with reproductive isolation. Such a case is shown in Fig. 5f.

In reality, the assortativity of mating (σ_m) can co-evolve with the magic trait (x). We did not investigate the joint evolution of the magic trait and of mating assortativity directly (see Ripa 2009), but we can infer the selection gradient on σ_m using a result of Pennings et al. (2008; see also Otto et al. 2008): Assuming that all females are mated ($M \to \infty$), the heterozygote phenotype is exactly inbetween the homozygotes [as in Eq. (27)], and the mating function is Gaussian [as in Eq. (26); but also under some other mating functions], a mutant gene increasing the assortativity of mating (decreasing σ_m) can invade if and only if both homozygote genotypes of the magic trait have higher fitness than the heterozygote. This condition holds at every symmetric diallelic singularity in Figs. 3, 4, 5, therefore assortativity increases as long as the magic trait is at or near such a singularity. Assume that σ_m evolves much slower than the magic trait (x), so that the magic trait attains quasi-equilibria at its convergence stable singularities. Under such a separation of evolutionary time scales, speciation occurs by gradual evolution of σ_m in an initially randomly mating population if a symmetric diallelic singularity exists for every σ_m from random mating to full isolation. For moderate values of d/σ_s this is not the case, because the diallelic singularity is lost at intermediate values of σ_m as shown in Fig. 3. Note however that a modifier with large effect on σ_m could cause instant speciation by bringing the population directly from the diallelic attractor of Fig. 3a to that of Fig. 3g, h. A modifier decreasing σ_m can invade a (nearly) randomly mating population independently of the size of its effect (Pennings et al. 2008), although it remains to see if a modifier with large effect goes to fixation. Earlier studies also found that assortment is more likely to evolve in large steps, but for a different reason: If there is an interval of σ_m where assortativeness is not selected for, a large mutation can “jump” over this (e.g. Matessi et al. 2001, Schneider and Peischl, in prep.). At the symmetric diallelic singularities of our model, assortative mating is always selected for, but a large mutation in σ_m could help to jump an interval where a diallelic singularity does not exist.

For larger values of d/σ_s, speciation is prevented by the evolution of the magic trait while the population is nearly randomly mating. In Fig. 4a, the symmetric diallelic singularity is a saddle point and the magic trait evolves to an asymmetric singularity, where the heterozygotes have higher fitness than homozygotes and therefore assortativity is not selected for (cf. Geritz and Kisdi 2000). If however some assortativity exists already in the initial population, then this can stabilize the symmetric singularity [as in Fig. 4b]; from this point, the evolution of assortativity preserves the symmetric singularity of the magic trait and leads to speciation (cf. Figs. 4b–h, 5b–h; Ripa 2009). The symmetric singularity can also be stabilized if migration between the two habitats is somewhat restricted (Kisdi and Geritz in press). Since in a spatially heterogeneous environment a moderate isolation between habitats can easily occur, such a weak initial reproductive isolation by distance can help initializing the process of speciation, which then continues by the evolution of mate choice while the magic trait is at a symmetric singularity. Finally for $d/\sigma_s > 4.03$, the symmetric diallelic singularity is convergence stable in a randomly mating population (Kisdi and Geritz 1999) as well as for any value of σ_m (Appendix 3). This implies that speciation can occur via slow evolution of mating assortativity in an initially randomly mating population. Note however that this requires very strong ecological selection; and for large d/σ_s the assumption of fully saturated habitats breaks down unless fecundity is large.

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Appendix 1

In this Appendix, we derive the invasion fitness of a rare allele y in a resident population harbouring alleles $x_1, \ldots, x_k$. Invasion fitness in a monomorphic population, Eq. (11), follows directly. We also derive the fitness proxy in Eq. (16), which we use in diallelic resident populations.

Let vector **P** be the frequency vector of genotypes containing allele y, $\mathbf{P}^{(t)} = (P_{x_1 y}^{(t)}, \ldots, P_{x_k y}^{(t)}, P_{yy}^{(t)})^T$. From (1) and (2), the full dynamics of allele y is given by

$$
\begin{aligned}
P_{x_l y}^{(t+1)} = \frac{1}{\bar{Q}\bar{w}_{E(t)}^2} \Bigg[& \frac{1}{4}\sum_{i=1}^{k}\sum_{j=1}^{k} P_{x_i y}^{(t)} P_{x_j x_l}^{(t)} w_{x_i y} w_{x_j x_l} (Q_{x_i y, x_j x_l} + Q_{x_j x_l, x_i y}) \\
& + \frac{1}{4}\sum_{i=1}^{k} P_{x_i y}^{(t)} P_{x_l x_l}^{(t)} w_{x_i y} w_{x_l x_l} (Q_{x_i y, x_l x_l} + Q_{x_l x_l, x_i y}) \\
& + \frac{1}{4}\sum_{i=1}^{k} P_{x_i y}^{(t)} P_{x_l y}^{(t)} w_{x_i y} w_{x_l y} (Q_{x_i y, x_l y} + Q_{x_l y, x_i y}) \\
& + \frac{1}{2}\sum_{i=1}^{k} P_{yy}^{(t)} P_{x_i x_l}^{(t)} w_{yy} w_{x_i x_l} (Q_{yy, x_i x_l} + Q_{x_i x_l, yy}) \\
& + \frac{1}{2} P_{yy}^{(t)} P_{x_l x_l}^{(t)} w_{yy} w_{x_l x_l} (Q_{yy, x_l x_l} + Q_{x_l x_l, yy}) \\
& + \frac{1}{2} P_{yy}^{(t)} P_{x_l y}^{(t)} w_{yy} w_{x_l y} (Q_{yy, x_l y} + Q_{x_l y, yy}) \Bigg]
\end{aligned} \tag{32}
$$

$$
\begin{aligned}
P_{yy}^{(t+1)} = \frac{1}{\bar{Q}\bar{w}_{E(t)}^2} \Bigg[& \frac{1}{4}\sum_{i=1}^{k}\sum_{\substack{j=1 \\ j \neq i}}^{k} P_{x_i y}^{(t)} P_{x_j y}^{(t)} w_{x_i y} w_{x_j y} (Q_{x_i y, x_j y} + Q_{x_j y, x_i y}) \\
& + \frac{1}{4}\sum_{i=1}^{k} (P_{x_i y}^{(t)})^2 w_{x_i y}^2 Q_{x_i y, x_i y} + \frac{1}{2}\sum_{i=1}^{k} P_{yy}^{(t)} P_{x_i y}^{(t)} w_{yy} w_{x_i y} (Q_{yy, x_i y} + Q_{x_i y, yy}) \\
& + (P_{yy}^{(t)})^2 w_{yy}^2 Q_{yy,yy} \Bigg]
\end{aligned}
$$

where we used the shorthand notation $w_{x_i x_j}$ for $w_{E(t)}(\phi_{x_i x_j})$. To see whether y can invade when rare, we need to investigate the linearized dynamics

$$
\mathbf{P}^{(t+1)} = \mathbf{A}\mathbf{P}^{(t)} \tag{33}
$$

where **A** is the $(k+1) \times (k+1)$ Jacobian derived from (32) and evaluated at the trivial equilibrium $\mathbf{P} = \mathbf{0}$.

It is easily seen from (32) that each element in the last row of **A** is zero, but all other elements of **A** are strictly positive provided that $w_g > 0$ and $Q_{g,h} > 0$ for all genotypes g, h. With the Gaussian functions (26) and (22) used in our example, these conditions are satisfied if the allelic values are bounded and respectively $\sigma_s > 0$ and

$\sigma_m > 0$. Let **M** be the $k \times k$ matrix obtained from **A** by deleting its last row and last column. Since

$$\mathrm{Det}(\mathbf{A} - \lambda\mathbf{I}) = -\lambda\mathrm{Det}(\mathbf{M} - \lambda\mathbf{I}), \tag{34}$$

the eigenvalues of **A** are the eigenvalues of **M** and zero. Because **M** is strictly positive, the Perron-Frobenius theorem guarantees that the dominant eigenvalue of **M** is simple and strictly positive. The dominant eigenvalue of **A**, which is the invasion fitness of the rare allele y, is therefore also simple and positive. If the dominant eigenvalue exceeds 1, y can invade.

Notice further that because the last row of **A** is zero, the last element of $\mathbf{P}^{(t+1)}$ in Eq. (33) is zero for all $t \geq 0$ irrespectively of the initial frequency vector $\mathbf{P}^{(0)}$. In contrast, the first k elements of **P** converge to the strictly positive eigenvector of **M** corresponding to its dominant eigenvalue. During the invasion process, therefore, the frequency of mutant homozygotes, which is the last element of **P**, is negligible compared to the frequency of mutant heterozygotes in the first k elements of **P**. In the main text, we denote the vector of the first k elements of **P** with $\mathbf{P}_{het}$.

Invasion fitness for monomorphic resident populations. When $k = 1$, the resident population consists entirely of homozygotes xx and, using that $Q_{xx,xx}w_{xx} = 1$ in resident equilibrium, (32) simplifies to

$$\begin{aligned}
P_{xy}^{(t+1)} &= \frac{1}{w_{xx}} \left[\frac{1}{2} P_{xy}^{(t)} P_{xx}^{(t)} w_{xy} w_{xx} (Q_{xy,xx} + Q_{xx,xy}) \right. \\
&\quad + \frac{1}{2} (P_{xy}^{(t)})^2 w_{xy}^2 Q_{xy,xy} \\
&\quad + P_{yy}^{(t)} P_{xx}^{(t)} w_{yy} w_{xx} (Q_{yy,xx} + Q_{xx,yy}) \\
&\quad \left. + \frac{1}{2} P_{yy}^{(t)} P_{xy}^{(t)} w_{yy} w_{xy} (Q_{yy,xy} + Q_{xy,yy}) \right] \\
P_{yy}^{(t+1)} &= \frac{1}{w_{xx}} \left[\frac{1}{4} (P_{xy}^{(t)})^2 w_{xy}^2 Q_{xy,xy} \right. \\
&\quad + \frac{1}{2} P_{yy}^{(t)} P_{xy}^{(t)} w_{yy} w_{xy} (Q_{yy,xy} + Q_{xy,yy}) \\
&\quad \left. + (P_{yy}^{(t)})^2 w_{yy}^2 Q_{yy,yy} \right]
\end{aligned} \tag{35}$$

The Jacobian matrix is thus

$$\mathbf{A} = \begin{pmatrix} \frac{1}{2} w_{xy} (Q_{xy,xx} + Q_{xx,xy}) & w_{yy} (Q_{yy,xx} + Q_{xx,yy}) \\ 0 & 0 \end{pmatrix}. \tag{36}$$

M in this case is the upper left element of **A**, which is also the dominant eigenvalue of **A** and equals the invasion fitness given in Eq. (11).

Invasion fitness for diallelic resident populations. When **M** is a 2×2 matrix, we can simplify our calculations using the Routh–Hurwitz criterion. Using also that **M** has positive elements, its eigenvalues λ_1 and λ_2 are both less than 1 in absolute value if

$$\mathrm{Det}\mathbf{M} < 1 \quad \text{and} \quad \mathrm{Tr}\mathbf{M} - \mathrm{Det}\mathbf{M} < 1. \tag{37}$$

$\mathbf{M}$ depends continuously on the allelic values (x_1, x_2) and on y. If y equals either x_1 or x_2 such that the mutant allele is neutral, then the dominant eigenvalue of $\mathbf{M}$ equals 1, and hence $\mathrm{Det}\mathbf{M} = \lambda_1\lambda_2 < 1$. By continuity, the first inequality of the Routh–Hurwitz criterion holds also when y is sufficiently close to either resident allele. With small mutations, therefore, it is the second inequality that determines whether a mutant can invade, and we can use $\mathrm{Tr}\mathbf{M} - \mathrm{Det}\mathbf{M}$ as a fitness proxy to see which mutants can invade a diallelic resident population [cf. Eq. (16)].

Appendix 2

Here we derive fitness during ecological selection in the Levene model [Eq. (23)]. The mating population consists of $K = K_1 + K_2$ individuals, who produce a total of $K\bar{Q}B$ offspring, where $\bar{Q}$ is the probability that a female is mated and B is the per capita fecundity (the number of offspring per mated female times the relative frequency of females in the population). Each offspring has probability γ_i to land in habitat i $(i = 1, 2)$. An offspring with phenotype ϕ_g survives viability selection with probability $f_i(\phi_g)$ in habitat i, and then becomes one of the K_i individuals who survive till adulthood in habitat i with probability $K_i/[\gamma_i K\bar{Q}B\sum_h P_h f_i(\phi_h)]$ (where the denominator is the total number of offspring surviving viability selection and thus competing for the K_i places of adults). The product of the probability that a newborn survives till reproduction and the per capita fecundity is thus

$$w_{E(t)}(\phi_g) = \sum_i \gamma_i f_i(\phi_g) \frac{K_i}{\gamma_i K\bar{Q}B\sum_h P_h f_i(\phi_h)} B, \tag{38}$$

which, with $\bar{Q} = 1$, simplifies to Eq. (23) of the main text. Note that B is assumed to be large enough such that $K_i/[\gamma_i K\bar{Q}B\sum_h P_h f_i(\phi_h)]$ is always less than one to be a probability; such B can be found if the admissible allelic values are bounded, $\sigma_s > 0, \sigma_m > 0$, and $\gamma_i > 0$ for all i. Moreover, γ_i and B cancel in $w_{E(t)}(\phi_g)$ due to "contest" competition (i.e., a fixed number K_i of survivors) within each habitat.

Appendix 3

This Appendix reports the full numerical bifurcation analysis of diallelic singularities in the Levene model with equal habitat size $(c_1 = c_2 = 0.5)$, and also shows how the degenerate bifurcations unfold when this symmetry assumption is relaxed.

Analogously to the monomorphic case, a diallelic evolutionary singularity (x_1^*, x_2^*) is determined by

$$\left.\frac{\partial W_{x_1,x_2}(y)}{\partial y}\right|_{\substack{y=x_i \\ x_1=x_1^*, x_2=x_2^*}} = 0 \quad \text{for } i = 1, 2 \tag{39}$$

and it is evolutionarily stable if

$$\left.\frac{\partial W^2_{x_1,x_2}(y)}{\partial y^2}\right|_{\substack{y=x_i\\ x_1=x_1^*,x_2=x_2^*}} < 0 \quad \text{for } i = 1, 2. \tag{40}$$

Convergence stability in more than one dimension may depend on the frequency and size of mutations (e.g. if allele x_1 mutates more frequently or with somewhat larger mutation steps than allele x_2). In this paper, we adopt the concept of "absolute convergence stability" (Leimar 2001, 2009) and rely on the conditions derived by Matessi and Di Pasquale (1996; see also Kisdi 2006). To formulate the criteria for convergence stability of a diallelic singularity, we introduce the notation

$$E_i = \left.\frac{\partial W^2_{x_1,x_2}(y)}{\partial y^2}\right|_{\substack{y=x_i\\ x_1=x_1^*,x_2=x_2^*}} \tag{41}$$

$$M_i = \left.\frac{\partial W^2_{x_1,x_2}(y)}{\partial x_i \partial y}\right|_{\substack{y=x_i\\ x_1=x_1^*,x_2=x_2^*}} \tag{42}$$

$$A_i = \left.\frac{\partial W^2_{x_1,x_2}(y)}{\partial x_j \partial y}\right|_{\substack{y=x_i\\ x_1=x_1^*,x_2=x_2^*}} \qquad \text{with } j \neq i \tag{43}$$

for $i = 1, 2$. Matessi and Di Pasquale (1996) classified all generic singularities of a population with two co-evolving resident strategies or alleles into three groups:

(i) All possible allele substitution sequences starting in the neighbourhood of (x_1^*, x_2^*) converge to the singularity if

$$(E_1 + M_1)(E_2 + M_2) > |A_1 A_2| \quad \text{and} \quad E_1 + M_1 < 0, E_2 + M_2 < 0. \tag{44}$$

(ii) There exist both converging and diverging allele substitution sequences from every initial point in the neighbourhood of (x_1^*, x_2^*) if

$$|(E_1 + M_1)(E_2 + M_2)| < |A_1 A_2| \quad \text{and} \quad A_1 A_2 < 0. \tag{45}$$

(iii) In all other cases, every possible allele substitution sequence diverges from a non-zero measure set of initial points.

The above conditions are valid for all possible allele substitution sequences, including those that occur with vanishing probabilities. All singularities we found in the diallelic Levene model are either in (i) or in (iii), i.e., we have evolutionary attractors with absolute convergence stability and evolutionary repellers. We adopt the shorthand names "convergence stable" for singularities with absolute convergence stability and "saddle" for the repellers. The fitness proxy $\tilde{W}$ of Eq. (16) can be used in place of W in all of the conditions given above. We obtained the diallelic singularities of the Levene model by solving Eq. (39) numerically and evaluated the conditions of evolutionary and convergence stability as outlined above.

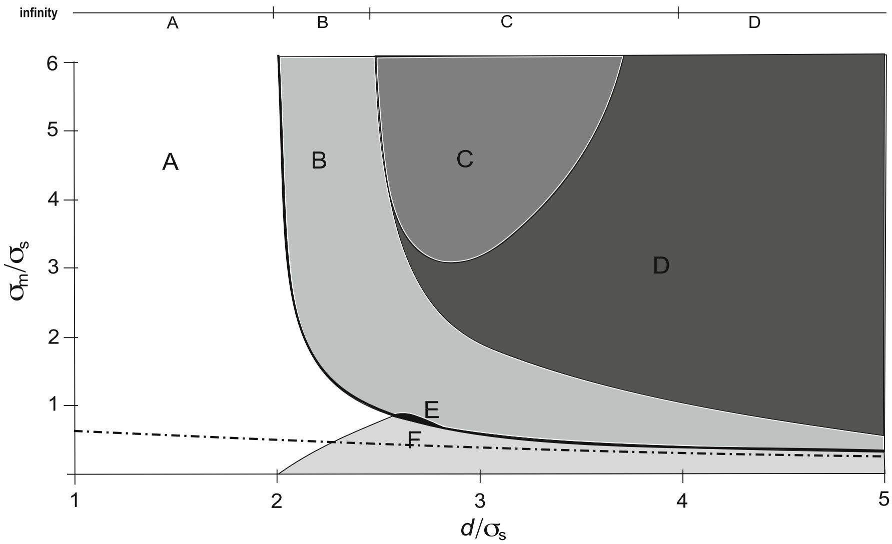

Fig. 8 Bifurcation plot of diallelic singularities for equal habitat size ($c_1 = c_2 = 0.5$). *Region A* no diallelic singularity, *B* one convergence stable singularity, *C* a pair of asymmetric convergence stable singularities separated by a symmetric saddle point, *D* three convergence stable singularities (one in symmetric position and a pair of asymmetric singularities) separated by a pair of asymmetric saddles, *E* two symmetric convergence stable singularities separated by a symmetric saddle, *F* one symmetric convergence stable singularity and one symmetric saddle. *Regions A–D* extend to σ_m/σ_s at infinity as indicated. All convergence stable singularities of this plot are also evolutionarily stable. The *thick line* coincides with the bifurcation line of the monomorphic singularity: $x^* = 0$ is evolutionarily stable in *A* and *F* whereas it is an evolutionary branching point elsewhere. The *dash-dotted line* is same as in Fig. 2

Figure 8 shows the bifurcations of diallelic singularities for equal habitat size ($c_1 = c_2 = 0.5$). There can be up to five diallelic singularities (three convergence stable singularities separated by two saddle points). All convergence stable diallelic singularities found in this bifurcation plot are also evolutionarily stable, hence further branching (leading to tri-allelic polymorphisms) does not occur. (Note however that with substantially unequal habitat sizes, further branching does occur, as found in a narrow range of parameters under random mating by Kisdi and Geritz 1999.)

In region A, there is no diallelic singularity, and two resident alleles are always subject to convergent coevolution (see Fig. 3c for an example). When crossing the bifurcation line to region B, the monomorphic singularity $x^* = 0$ becomes an evolutionary branching point and, simultaneously, a diallelic convergence stable singularity is born with $(x_1^*, x_2^*) = (x^*, x^*)$ at the bifurcation. Within region B, evolutionary branching yields two distinct alleles and these evolve to the unique convergence stable diallelic singularity with symmetric allelic values $x_1^* = -x_2^*$ (as in Fig. 3a, b).

Between regions B and C, a pitchfork bifurcation occurs such that the symmetric convergence stable diallelic singularity of region B becomes a saddle in region C, and two new convergence stable singularities arise, which occupy asymmetric positions but are mirror images of each other such that $x_1^{*(1)} = -x_2^{*(2)}$ and $x_1^{*(2)} = -x_2^{*(1)}$ (compare Figs. 3a, 4a for an example). When crossing from region C to region D, the symmetric singularity undergoes another pitchfork bifurcation such that it becomes convergence stable again, and two saddles arise that separate the basin of attraction of the symmetric singularity from the two asymmetric convergence stable singularities (compare panels a and b in Fig. 5). The bifurcations described so far occur also with random mating ($\sigma_m/\sigma_s \to \infty$) and are therefore identical to those discussed by Kisdi and Geritz (1999).

At moderate values of σ_m/σ_s, region B (with a single symmetric diallelic singularity) and region D (with three convergence stable singularities and two saddles) have adjacent parts, which are separated by a line of two simultaneous fold bifurcations. Each fold bifurcation involves an asymmetric convergence stable singularity and a saddle point, leaving the symmetric convergence stable singularity unchanged (compare Fig. 5c,d for an example).

There is another fold bifurcation that is independent of all the above, and separates regions A from F and B from E. The convergence stable singularity and the saddle born on this bifurcation line are both in symmetric position. In region F, there are no other singularities but this pair (as in Fig. 3g), whereas in region E, the pair coexists with the symmetric convergence stable singularity also present in region B (as in Fig. 4e). When crossing from E to F, a convergence stable singularity collides with the monomorphic singularity, and simultaneously the latter becomes an ESS (compare Fig. 4f, g), whereas between B and F, a diallelic saddle interacts with the monomorphic singularity (compare Fig. 5f, g).

In the limit of very strong mating assortativity ($\sigma_m \to 0$), the homozygotes are fully isolated and heterozygotes are absent at any diallelic singularity isolated from $(x^*, x^*) = (0, 0)$. Hence the resident population contains two phenotypes just as a dimorphic clonal population; and since assortativity with $M \to \infty$ implies $\bar{Q} = 1$ in Eq. (3), the population densities of the two phenotypes are also the same. Because $\pi'(0) = 0$, the selection gradient is not affected by sexual selection [cf. Eq. (17)]. The two homozygote subpopulations therefore evolve exactly as two clonal phenotypes evolve in absence of sexual reproduction, and the diallelic singularities coincide with the clonal dimorphic singularities. In particular, the clonal version of the Levene model with equal habitat size has a dimorphic singularity for $d/\sigma_s > 2$ (Geritz and Kisdi 2000). Accordingly, in our model, the diallelic singularity in region F disappears at $d/\sigma_s = 2$ when $\sigma_m \to 0$. Note that $d/\sigma_s > 2$ is also the condition for evolutionary branching under random mating ($\sigma_m \to \infty$), which is always the same as the condition for branching in the corresponding clonal model (Van Dooren in press). However, the condition for clonal evolutionary branching coincides with the condition for having a dimorphic singularity only because of equal habitat size (Kisdi and Geritz 1999; see below).

Unequal habitat size. The pitchfork bifurcations found above are degeneracies due to equal habitat size, and they unfold into fold bifurcations producing a convergence stable singularity and a saddle independently of an existing singularity. The simultaneous fold bifurcations between regions B and D separate into two simple fold bifurcations when habitat sizes are not precisely equal. This is shown in Fig. 9: The lines of pitchfork bifurcations (between B and C and between C and D, respectively) and the line of simultaneous fold bifurcation (between B and D) are all replaced by

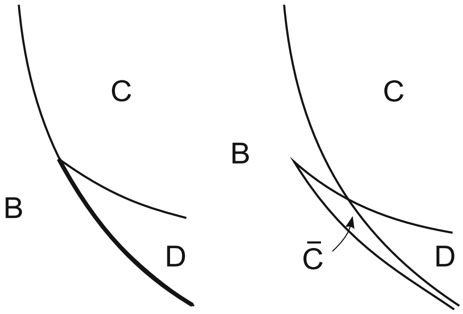

Fig. 9 Detail of the bifurcation plot for equal habitat size in Fig. 8 (*left*) and the same for c_1 close but not equal to 0.5 (*right*). With equal habitat size, pitchfork bifurcations separate *B* from *C* and *C* from *D* (*thin lines*), and two simultaneous fold bifurcations occur between *B* and *D* (*thick line*). With unequal habitat size, the simultaneous fold bifurcations separate and the pitchfork bifurcations are replaced by fold bifurcations. In the new region $\bar{C}$ that opens up between *B* and *D*, there are two convergence stable singularities separated by a saddle. A cusp bifurcation occurs at the peak of $\bar{C}$

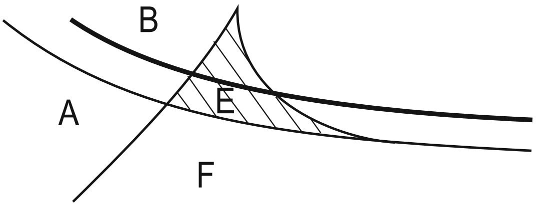

Fig. 10 Detail of the bifurcation plot with slightly unequal habitat sizes. The *thick line* is the bifurcation line of the monomorphic singularity such that $x^* = 0$ is an ESS below and an evolutionary branching point above the line. A convergence stable diallelic singularity appears across the *thin line* and coexists with the monomorphic ESS in the *band-shaped region* below the *thick line*; the ESS-branching point bifurcation of the monomorphic singularity no longer coincides with the boundary between *A* and *B* (see Fig. 8). Another pair of a convergence stable singularity and a saddle are born across the fold bifurcation line on the boundary of regions *E* and *F*

lines of fold bifurcations, and a new region, with two convergence stable singularities and a saddle, emerges between regions B and D.

Another type of degeneracy emerges because equal habitat size implies symmetry about the point $x^* = 0$, such that any diallelic singularities must exist either in symmetric pairs (such as $x_1^{*(1)} = -x_2^{*(2)}$ and $x_1^{*(2)} = -x_2^{*(1)}$) or in a symmetric position (with $x_1^* = -x_2^*$). Singularities which are forced to retain their symmetric position collide with the monomorphic singularity ($(x_1^*, x_2^*) \to (x^*, x^*)$), and therefore changes in the evolutionary stability of the monomorphic singularity x^* are linked to the appearance of a diallelic singularity. As a result, the bifurcation line in Fig. 8 on which the monomorphic singularity changes between an ESS and an evolutionary branching point (thick line) coincides with the boundary between regions A and B, between E and F, and between B and F. The unfolding of this degeneracy is shown in Fig. 10: When habitat size is perturbed, a diallelic singularity exists in a band of the parameter space outside the region where the monomorphic singularity is a branching point (and instead of colliding with the monomorphic singularity, it appears from across the extinction boundary delineating the set of possible diallelic polymorphisms). This pattern corresponds to what is expected in generic models of adaptive dynamics (see the Appendix of Geritz et al. 1999), and implies an evolutionary hysteresis effect (Kisdi and Geritz 1999): Suppose a polymorphic population exists at the diallelic singularity within the band where x^* is an ESS. If this population loses an allele due to a temporary change in its environment, then polymorphism cannot be regained without a greater change in the environment that not only restores the existence of a diallelic singularity but also makes x^* an evolutionary branching point.

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