IIASA

INTERIM REPORT   IR-97-001 / January

Adaptive dynamics in a 2-patch environment: a simple model for allopatric and parapatric speciation

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IIASA Studies in Adaptive Dynamics   No. 15

ADN

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The pivotal role of evolutionary theory in life sciences derives from its capability to provide causal explanations for phenomena that are highly improbable in the physicochemical sense. Yet, until recently, many facts in biology could not be accounted for in the light of evolution. Just as physicists for a long time ignored the presence of chaos, these phenomena were basically not perceived by biologists.

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Adaptive dynamics in a 2-patch environment: a simple model for allopatric and parapatric speciation

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Abstract

Adaptation to an environment consisting of two patches (each with different optimal strategy) is investigated. The patches have independent density regulation ('soft selection'). If the patches are similar enough and migration between them is strong, then evolution ends up with a generalist ESS. If either the difference between the patches increases or migration weakens, then the generalist strategy represents a branching singularity: The initially monomorphic population first evolves towards the generalist strategy, there it undergoes branching, and finally two specialist strategies form an evolutionarily stable coalition. Further increasing the between-patch difference or decreasing migration causes the generalist to lose its convergence stability as well, and an initially monomorphic population evolves towards one of the specialists optimally adapted to one of the two patches. Bifurcation pattern of the singularities is presented as a function of patch difference and migration rate.

Connection to speciation theory is discussed. The transition from the generalist ESS to the coexisting pair of specialist strategies is regarded as a clonal prototype of parapatric (if the between-patch difference increases) or allopatric (if the migration decreases) speciation. We conclude that the geographic and the competitive speciation modes are not distinct classes.

1

1 Introduction

The usual theoretical framework of thinking on biological evolution and, especially, on speciation is population genetics. However, species are supposed to occupy different niches according to MacArthur & Levins (1967). The niche structure of the environment implies frequency-dependent selection: The fitness of a strategy depends on the presence of other strategies occupying some niches while leaving open others. So a complete theory of speciation cannot be formulated in the context of frequency-independent population genetics.

Unfortunately, frequency-dependent population genetics is hard and not well understood. To explore the ecological conditions of speciation we neglect the complications of the sexual reproduction. Competition between clonal strategies will be investigated. This approach is usual in evolutionary ecology and game theory. It is highly unprobable, that only a heterozygote can produce the optimal behaviour, as Maynard-Smith (1982) argued. [See Hammerstein (1996) for mathematical elaboration of the same reasoning.]

The concept of evolutionarily stable strategy (ESS) introduced by Maynard-Smith & Price (1973), Maynard-Smith (1982) served as a starting point to explore the realm of frequency-dependent selection. It was introduced in a game-theoretical context, but has a more general meaning. Strategy x is an ESS, if it cannot be invaded by any other strategy when established. Under frequency-dependent selection one cannot rely on fitness maximisation and the concept of ESS is supposed to apply, instead. ESS was thought to be the fixed point of evolution: it stops as soon as an ESS becomes established.

A serious problem was discovered concerning the stability of the "Evolutionarily Stable Strategy", however. It is -by definition- stable against the invasion of a new mutant of itself, but it is not necessarily an evolutionary attractor! Let the strategy x_0 be an ESS, and suppose that a nearby strategy x_1, which is not an ESS, has become established. If x_0 was a stable fixed point in the sense of dynamical systems, one would expect the population with strategy x_1 to evolve to the strategy x_0 provided that x_1 is near enough to x_0. But this is far from sure. Actually, it turns out, that these two kinds of stability properties are independent of each other. This inequivalence was noted by Eshel (1983), Taylor (1989), Brown & Vincent (1987), Vincent et al. (1993), Abrams et al. (1993) and Eshel (1996).

A general theory of the dynamics of adaptation was developed by Metz et al. (1996), Geritz et al. (1997ab). [See also: Ferrière, R. & G.A. Fox (1995) and Diekmann (to appear).] If an arbitrary strategy x is established, the population experiences directional selection and evolves in the direction of the local fitness gradient. The exceptions are the so called singular strategies, or the singular points of the strategy space, where the directional selection force vanishes. One can classify the singular points according to the different stability criteria including the evolutionary and the convergence stability. The most interesting type of singular point is the branching point. It is an attractor of the evolution of an initially monomorphic population, but not an ESS as it was defined by Maynard-Smith. Once evolution has reached this strategy, the population splits, then the two (or more) daughter

populations evolve away from each other. This process is the speciation, at least in an asexual population. The simplest source of this disruptive selection between the daughter populations (species) is the selection for niche segregation: it is advantageous to consume something else or to live in a different habitat than the rest of the population. [Competitive speciation, Rosenzweig (1987).]

In the simplest ecological situation populations are living on, and limited by, a finite number of resources. The number of coexisting populations cannot be higher than the number of resources as it was pointed out by MacArthur & Levins (1964) and Tilman (1982). (Relation between adaptive dynamics and partitioning of a continuous resource distribution is beyond our topics.)

If only a single resource is present, the principle of competitive exclusion applies: The single species which is best at exploiting this resource will survive. This is the situation, when the classical "optimisation" approach is applicable (Metz et al., 1995). The single-resource situation is usually described as "density-dependent selection" (Michod, 1979, Pásztor, 1986, Meszéna & Pásztor, 1990, Pásztor et al., 1995,1996, Leon, 1995, Mylius & Diekmann, 1995).

Many authors emphasise the importance of spatial structure for speciation. Allopatric speciation is initiated by a geographic change separating two habitats from each other. In this paper the role of spatial structure and migration will be investigated in the simplest case when the environment consists of two patches. Independent density regulation in the patches [soft selection, Christiansen (1975)] corresponds to one limiting resource per patch. This two-resource situation limits the number of coexisting populations to 2. It is clear that eventually two things can happen in this model: either a single generalist occupies both of the patches, or two specialist strategies occupy each a single patch. However, the bifurcation pattern of the evolutionary dynamics is surprisingly complex in this simple model. Our model is very similar to the one which was investigated by Brown & Pavlovic (1992).

General concepts of adaptive dynamics will be summarised in the next session, while Section 3 deals with the model itself. Relevance of our toy-model for speciation theory will be discussed in the last section.

2 General concepts of adaptive dynamics

As it is known since Malthus, populations tend to grow exponentially, just because the number of birth and death events tend to be proportional to the number of individuals present. More formally:

$$\frac{d}{dt}\mathbf{N} = \mathbf{M}(\mathbf{E}) \cdot \mathbf{N} \tag{1}$$

where $\mathbf{N}$ is the state vector of the population (number of individuals in different age groups, etc., each element is non-negative). The projection matrix $\mathbf{M}(\mathbf{E})$ (e.g. the Leslie matrix for simple age structured populations) contains the demographic parameters (Caswell 1989, Metz et al., 1992) which depend on the state $\mathbf{E}$ of the environment.

Irreducibility of the matrix $\mathbf{M}$ is supposed. (For reducible problems one has to deal with the component problems separately.) All of the non-diagonal elements are transition rates, so they are non-negative. For such a matrix the leading eigenvalue (the eigenvalue with the largest real part) is real, and the corresponding eigenvector is positive, as one can demonstrate easily by the Frobenius theorem. The population grows/decreases exponentially with the leading eigenvalue $\varrho(\mathbf{E})$ of the matrix $\mathbf{M}$.

Obviously, exponential growth cannot be sustained forever. Every population has to be regulated. If $\varrho(\mathbf{E}) > 0$, the growing population deteriorates the environment until the leading eigenvalue becomes zero, and the population becomes stable - at least in the simple case we consider in the following. [See Metz et al. (1996) for a more general treatment, which includes chaotic dynamics as well as fluctuating environment.]

Let us investigate the selection process within this framework. Let $\varrho = \varrho(x, \mathbf{E})$ denote the growth rate of a strategy x in an environment $\mathbf{E}$. (We will restrict ourselves to the case where the strategy x is taken from a continuous, one dimensional quantity.) If strategies x_1, x_2,...,x_n are living together in the same environment, demographic equilibrium requires

$$\varrho(x_i, \mathbf{E}) = 0 \qquad \text{for} \quad i = 1, 2, ..., n \tag{2}$$

These are n equations for the environmental variables. They can be satisfied generically only if $n \leq K = \dim\mathbf{E}$. The number of coexisting strategies cannot be larger than the number of environmental variables involved in the population regulation feedback. Concentrations of different resources are the most typical environmental variables of such. Resource diversity is considered to be the main factor behind species diversity (MacArthur & Levins, 1964). Other variables as predator densities may have a similar role according to Tilman (1982). Environmental parameters, like temperature, humidity, etc., which are not involved in population regulation because populations cannot "deteriorate" them, must not be counted in K. The bound K will be referred to as the dimension of the population regulation. The situation is complicated further by spatial heterogeneity of the environment if the local populations are regulated separately (Tilman, 1982).

Let $\mathbf{E}_{x_1, x_2, ..., x_n}$ stand for the environment when populations with strategies x_i ($i = 1, 2, ..., n$) are living in equilibrium, that is, for the solution of Eq. 2. If we are interested in the fate of a new and rare mutant with strategy y, then the growth rate of the mutant $\varrho(y, \mathbf{E}_{x_1, x_2,...x_n})$ is the relevant quantity. It corresponds to the 'fitness generating function' of Brown & Vincent (1987) and Vincent et al. (1993). If it is positive, the mutant can grow, otherwise it can't. If it can, the mutant invades and the system will reach a new equilibrium. We suppose that the new equilibrium is reached before the arrival of the next mutant.

Let us first consider the situation where a single strategy x is established, that is the case of a monomorphic population. The local fitness gradient

$$F(x) = \left[\frac{\partial \varrho(y, \mathbf{E}_x)}{\partial y}\right]_{y=x} \tag{3}$$

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drives the evolution of the strategy x. If $F(x) > 0$, a strategy x_1 slightly higher than x has a positive growth rate in the environment $\mathbf{E}_x$. So, a new mutant with strategy $x_1 > x$ will grow until deterioration of the environment stops it. If x_1 is near enough to x, one can safely suppose that the change in $\mathbf{E}$ will be small and, consequently, the local fitness gradient does not change signs. This means that when x_1 stops growing, the original strategy x must experience a negative growth rate and therefore dies out soon. That is, the strategy x will be substituted by a slightly higher mutant strategy x_1, if $F(x) > 0$. Similarly, if $F(x) < 0$, x will be substituted by some strategy $x_1 < x$. Evolution proceeds in the direction of the local fitness gradient, while the population remains homogeneous. Dieckmann & Law (1996) discusses the theory of this "trait substitution process" in detail, especially the condition of approximating it by a deterministic dynamics of directional evolution.

If $F(x_0) = 0$, x_0 is a fixed point of the *directional* evolution. Such a strategy will be referred to as a singular strategy or singular point of the strategy space. A singular strategy is an attractor of the trait substitution process if, and only if the local fitness gradient points towards to the singular point from both directions, that is

$$\left[\frac{dF(y)}{dy}\right]_{y=x_0} = \left[\frac{\partial^2 \varrho(y, \mathbf{E}_{x_0})}{\partial y^2}\right]_{y=x_0} + \left[\frac{\partial \mathbf{E}_x}{\partial x}\right]_{x=x_0} \cdot \left[\frac{\partial^2 \varrho(y, \mathbf{E})}{\partial y \partial \mathbf{E}}\right]_{y=x_0,\ \mathbf{E}=\mathbf{E}_{x_0}} < 0. \quad (4)$$

(See Fig. 1.) This property of the singular point will be referred as "convergence stability". A singular point which is convergence unstable cannot be approached by small evolutionary steps. Such a strategy will be referred to as a repellor.
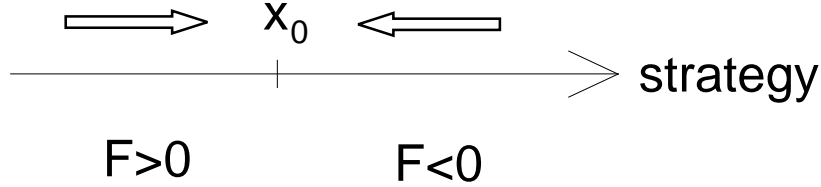

Figure 1: *Convergence stable singular strategy. Arrows show the local fitness gradient.*

A singular strategy is a (local) ESS, that is, it cannot be invaded by a new, rare mutant similar to itself, if it is a local optimum of the fitness:

$$\left[\frac{\partial^2 \varrho(y, \mathbf{E}_{x_0})}{\partial y^2}\right]_{y=x_0} < 0 \quad (5)$$

Conditions (4) and (5) would be equivalent, if the environment was independent of the population living in it.

Singular strategies that are convergence as well as evolutionarily stable are the real traps of the evolutionary process. [Such fixed points were called 'continuously stable' by Eshel (1983). Note, that Brown & Vincent (1987) and Vincent et al. (1993) used the term 'ESS' in a sense even stronger than the continuous stability.] Directional evolution of a homogenous population approaches such a strategy, but after reaching it, further mutations are doomed to fail. If a convergence stable singular point happens to be evolutionarily unstable, something more interesting happens. To understand this, we have to study first the situation in which two similar strategies coexist.
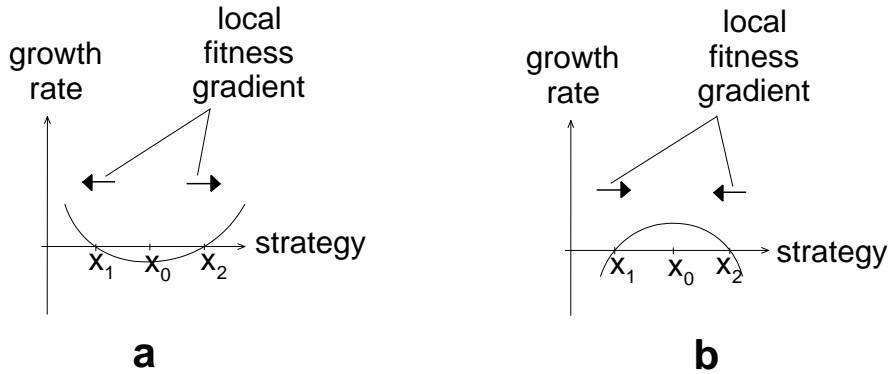

Figure 2: *Coexistence of two similar strategies. Arrows show the local fitness gradient felt by the coexisting strategies. a: diverging evolution near to a local minimum; b: converging evolution near to a local maximum.*

If two (similar enough) strategies x_1 and x_2 coexist in the environment $\mathbf{E}_{x_1,x_2}$, the requirement $\varrho(x_1, \mathbf{E}_{x_1,x_2}) = \varrho(x_2, \mathbf{E}_{x_1,x_2}) = 0$ implies that x_1 and x_2 must lie on the opposite sides of a local minimum or maximum of the function $\varrho(x, \mathbf{E}_{x_1,x_2})$ except in the non-generic case in which $\varrho(x)$ is constant. As it is clear from Fig. 2, the local fitness gradient will drive the strategies x_1 and x_2 away from each other in the first case (Fig. 2a), and towards each other in the second case (Fig. 2b). However, a local fitness maximum is equivalent to the ESS property. Two coexisting populations near to an ESS will converge and, eventually, form a homogenous population. [According to Metz et al. (1996), one of them will die out, before the other reach the ESS, if the stochastic nature of the process is taken into account.] Two coexisting populations near to an evolutionarily unstable singular strategy experience disruptive selection and evolve away from each other. This argumentation relies on the assumption that $\frac{\partial^2 \varrho}{\partial y^2}$ has the same sign when the singular strategy x_0 is established as when the strategy pair $\{x_1, x_2\}$ is established. This assumption is justified when x_1 and x_2 are similar enough to x_0, because in this case $\mathbf{E}_{x_0} \approx \mathbf{E}_{x_1,x_2}$.

So, what will happen once an initially monomorphic population has reached a small neighbourhood of an evolutionarily unstable singular strategy? The population cannot evolve away from this strategy while remaining monomorphic and must

Figure 3: *Evolutionary branching in the two-patch model defined in Section 3.1. Parameter values: $d = 1.5$, $\mu = 0.275$. Evolution converges to the central (generalist) strategy first. After branching coexistence of two generalist strategies is established.*

become polymorphic. But as soon as two coexisting populations have replaced the homogenous one, they begin to evolve away from each other! For this reason we call the convergence stable but evolutionarily unstable singular points, branching points (Fig. 3). [The term 'evolutionarily stable fitness minimum' was introduced for such a point by Abrams et al. (1993) without realising the branching nature of it.]

After branching, each population evolves in the direction of its respective local fitness gradient. Further branching can happen. The whole process is a dynamical system in a space with a variable number of dimensions: each subpopulation present is represented by a strategy parameter. The process stops if all of the populations arrive to a convergence and evolutionarily stable (that is, a continuously stable) singular point. Obviously, for each population the fitness gradient as well as the properties of the singular points are affected by the presence of the other populations. It is outside the scope of this paper to discuss polymorphic evolution in more detail.

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[See Metz et al. (1996), Vincent et al. (1993).]

Having more than one definition of stability complicates bifurcation picture. Changing external parameters (parameters of the abiotic environment, for instance) may change the evolutionary and/or convergence stability of a singular point. Change of convergence stability is related to the bifurcation of the fixed points just like in the fixed dimensional dynamics. Something similar happens in the variable dimensional space if a singular point loses evolutionary stability. [See Geritz et al. (1997b) for details.] We will refer to such transitions as ESS and convergence bifurcations, respectively. The bifurcation structure of a specific model will be explored in Section 3. The evolutionary significance of the bifurcation diagrams will be the subject of the Discussion.

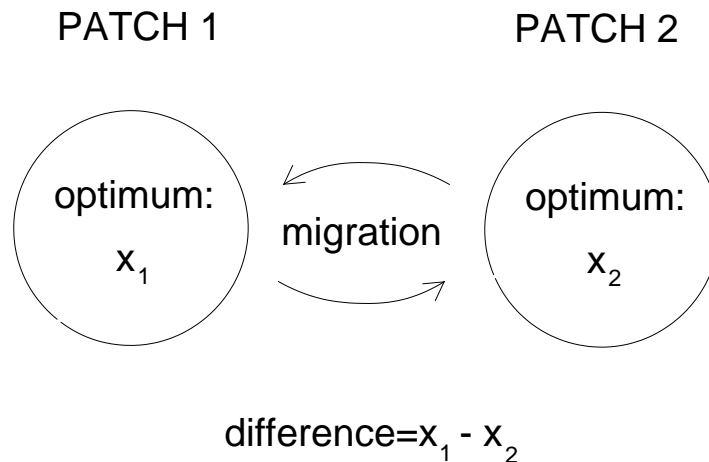# 3 The model

3.1 Definition of the model

Figure 4: *The model: two (different) patches with migration between them.*

Competition between clonal strategies is investigated. The set of possible strategies is a 1-dimensional continuum. There are two habitats (patches) (Fig. 4). The local growth rate of a strategy in one of the patches is a given function of the strategy and the patch density. Optimising selection and logistic, nonselective, density regulation are supposed. The optimal strategies are different in the two patches. Individuals migrate between the patches with a rate independent of the strategy. Time is continuous, no population structure other than the patches is assumed.

The population abundance of the strategy x is characterised by the population vector

$$\mathbf{N}(x) = \begin{pmatrix} N_1(x) \\ N_2(x) \end{pmatrix} \tag{6}$$

where $N_i(x)$ is the number of individuals of strategy x in patch i. The local growth rate of the strategy x in the ith patch is

$$r_i(x) = \frac{1}{\sqrt{2\pi}} e^{-(x-x_i)^2/2} - \alpha N_i^{tot} \tag{7}$$

where x_i is the optimal strategy in the patch i while N_i^{tot} is the total number of individuals in this patch. Let d denote the difference between the two optima. Without losing generality we may assume that $x_1 = d/2$, $x_2 = -d/2$. Denoting the migration rate by μ, the dynamics are described by Eq. 1 with the matrix $\mathbf{M}$ given by:

$$\mathbf{M}(x, \mathbf{E}) = \begin{pmatrix} r_1(x) - \mu & \mu \\ \mu & r_2(x) - \mu \end{pmatrix}. \tag{8}$$

In this model the environment determining the growth rate of the populations is characterised by the total densities in the patches: $\mathbf{E} = (N_1^{tot}, N_2^{tot})$. The population state is described by the number of individuals of the different strategies in the patches $(N_i(x))$, but the growth rates are affected through the total number of individuals in the patches only. So, in our model the population regulation is two-dimensional and one can be sure that at most 2 strategies can coexist. Intuitively, there are two possibilities: a single species (the "generalist") exploits both patches, or two coexisting strategies specialise on a single patch each.

Note the symmetry property of the model: it is invariant under the transformation $x \to -x$. The central strategy $x_0 = (x_1 + x_2)/2 = 0$ is obviously a singular strategy where the local fitness gradient vanishes. It represents the compromise between the requirements of the two patches, so this strategy is the prime candidate for being the generalist one.

We suppose, that the population dynamics converge to a unique stable fixed point.

3.2 How can we analyse this model?

From (7) and (8) it is very easy to calculate the overall growth rate of a strategy in a given environment, that is, when the patch densities N_1^{tot} and N_2^{tot} are known. (See Section 3.3.) The result is intuitively very transparent. Determining the equilibrium patch densities is much harder, however. For a single established population one must solve the pair of quadratic equations (leading to a single cubic one) coming from the equilibrium condition

$$\mathbf{M}(\mathbf{N}) \cdot \mathbf{N} = 0 \tag{9}$$

It can be done analytically, but not easily. We used the computer algebra package $Mathematica^{TM}$ to solve this system of equations and to derive an analytic formula for $\varrho(y, \mathbf{E}_x)$. It is quite long, so we will not write it down here, but still useful, as will be shown in Section 3.5. In this sense, the model can be fully analysed analytically.

Fortunately, because of the symmetry $x \to -x$ of the model, some central features can be derived without computer algebra. If the established strategies are

located symmetrically with respect to the central strategy $x_0 = 0$, the total densities of the two patches must be equal: $N_1^{tot} = N_2^{tot}$. (This is a consequence of the assumption that the population dynamics has a unique, stable fixed point.) In this case densities are trivial additive constants in (7) and (8) so they need not be calculated.

Two different symmetric situations are possible. In one of them the central strategy is the unique established strategy. Stability properties of the central strategy will be discussed in Section 3.4 on this basis. The other symmetric situation in which two strategies coexist, will be explored in Section 3.5.

3.3 The fitness of a rare strategy

The overall growth rate of the strategy y is the larger root of the eigenvalue-equation

$$\det(\mathbf{M} - \varrho\mathbf{1}) = 0. \tag{10}$$

that is:

$$\varrho\left(y, (N_1^{tot}, N_2^{tot})\right) = \lambda_+ = \frac{r_1(y) + r_2(y)}{2} + \sqrt{\left(\frac{r_1(y) - r_2(y)}{2}\right)^2 + \mu^2} - \mu. \tag{11}$$

To get a feeling, it is worthwhile to calculate the two extremes of Eq. 11:

$$\varrho(y, \mathbf{E}) = \begin{cases} \max\left[r_1(y),\ r_2(y)\right] - \mu, & \text{if } \mu \ll |r_1(y) - r_2(y)|/2 \\ [r_1(y) + r_2(y)]/2, & \text{if } \mu \gg |r_1(y) - r_2(y)|/2 \end{cases} \tag{12}$$

The matrix $\mathbf{M}$ becomes reducible at $\mu = 0$ when the patches become separated. In this case the growth rate of a strategy becomes equal to the local growth rate of the patch in which the strategy happens to live. At very low, but nonzero migration rate the strategy can manage to live in the patch better for it, so the maximum of the local growth rates becomes the overall growth rate. At the other extreme, at high migration rate, the difference between the patches is averaged out.

3.4 Behaviour of the central strategy

One can easily calculate the second partial derivative that determines the evolutionary stability of the central strategy:

$$\frac{\partial^2 \varrho(y, \mathbf{E}_{x_0})}{\partial y^2}\Big|_{y=x_0} = (d^2 - 4)\frac{e^{-d^2/8}}{4\sqrt{2\pi}} + \frac{1}{\mu}\frac{d^2}{8\pi}e^{-\frac{d^2}{4}}. \tag{13}$$

For high values of μ the second term is small so that the derivative is negative (that is, x_0 is an ESS) if, and only if, $d < 2$. A lower value of μ tends to make the derivative positive even for low values of d. As it can be seen in Fig. 5, [low d, high μ] is the only combination leading to evolutionary stability of the central/generalist strategy.

If the migration rate is very high (top row of Fig. 5), $\varrho(y)$ is nearly equal to $[r_1(y) + r_2(y)]/2$ (cf. Eq. 12), that is, the two patches are indistinguishable and the

strategy feels an average environment. It does not imply, however, that the central/generalist strategy is the superior one. The growth rate has a single maximum at $y = 0$ if $d < 2$, and a double peak (with minimum at $y = 0$) if $d > 2$. In other words, if the two patches are similar enough, the generalist strategy is evolutionarily stable. However, by increasing the difference between the patches we make it evolutionarily unstable, and a stable polymorphism of specialists emerges instead.
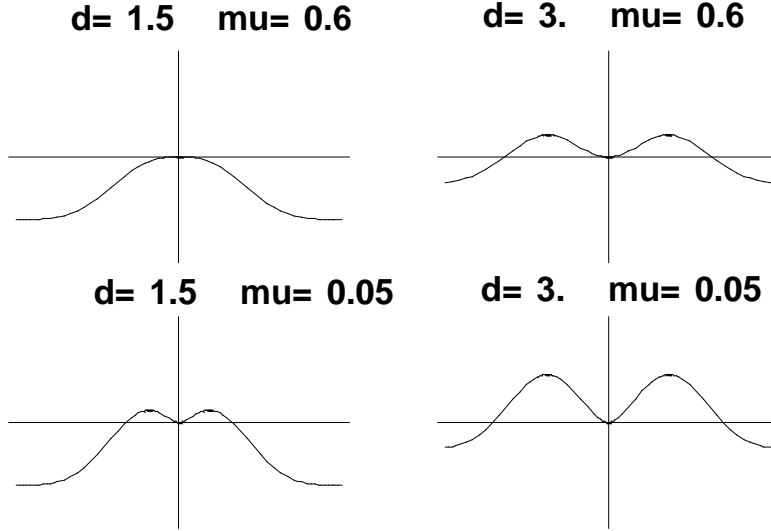

Figure 5: *Fitness function when the central strategy is established at four combinations of the parameters d and μ. Central strategy is an ESS, that is the fitness has a local maximum at this point, if d is low enough and μ is high enough. In any other cases the central strategy is a local minimum between two local maxima representing specialist strategies.*

Low migration rate leads to a different situation (bottom row of Fig. 5). $\varrho(y)$ is nearly equal to $\max(r_1(y), r_2(y)) - \mu$ rather than $[r_1(y) + r_2(y)]/2$ except in the vicinity of $y = 0$, where the curves $r_1(y)$ and $r_2(y)$ cross (cf. Eq. 12). Consequently, $\varrho(y)$ is double-peaked with a minimum at $y = 0$ even for low d. The strategy y tends to live in the patch better for it. (Migration from the better patch is a net loss.)

It is more difficult to find the conditions for convergence stability, because the term $\frac{\partial^2 \varrho}{\partial y \partial \mathbf{E}} \cdot \frac{\partial \mathbf{E}_x}{\partial x}$, making the difference between the two kinds of stability, involves environmental (total density) parameters. A relatively long derivation (see Appendix) leads to the result

$$\left[\frac{\partial^2 \varrho}{\partial y \partial \mathbf{E}} \right]_{y=0} \cdot \left[\frac{\partial \mathbf{E}_x}{\partial x} \right]_{x=0} = \sum_i \frac{\partial^2 \varrho}{\partial y \partial N_i^{tot}} \cdot \frac{\partial N_i^{tot}}{\partial x} =$$

$$= -\frac{d^2}{8\,\mu\,\sqrt{2\,\pi^3}} \cdot \frac{e^{-3\,d^2/8}}{2\,\mu + \frac{1}{\sqrt{2\,\pi}} \cdot e^{-d^2/8}} < 0. \tag{14}$$

The negative sign of this term ensures that condition (5) implies condition (4), that

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is, evolutionary stability is a stronger property than convergence stability *in this specific model.*

Fig. 6 shows the parameter regions where the central strategy is stable in both senses. The inverse migration rate $\frac{1}{\mu}$ was used instead of μ to stress the behaviour at low migration rate.
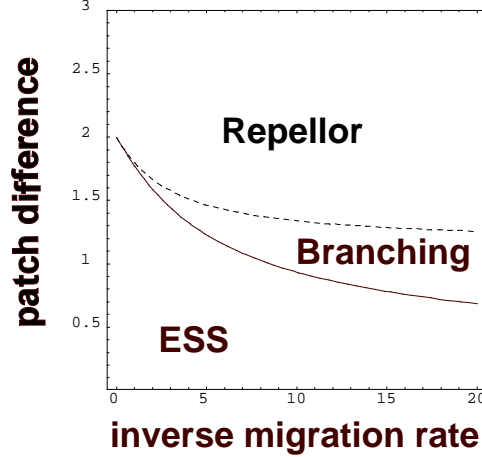

Figure 6: *Stability properties of the central strategy as a function of the parameters. It loses the evolutionary stability and becomes a branching strategy if either the migration rate decreases or the difference between the patches increases. Further change in this direction causes loss of convergence stability making the central strategy an evolutionary repellor. At very high migration rates the environment can be regarded as homogeneous, so the evolutionary and the convergence stability conditions coincide at very high μ.*

3.5 Full behaviour of the model

What is happening when the central strategy is unstable, that is, if $\varrho(x, \mathbf{E}_0)$ has a local minimum at the central strategy 0? The homogenous population with this strategy branches and the daughter populations evolve away from each other. If the two populations reach the two (symmetrical) maxima x_1^{max} and x_2^{max} of $\varrho(x, \mathbf{E}_0)$, evolution stops, because both populations sit in their respective fitness maxima. (Note, that $\varrho(x, \mathbf{E}_{x_1^{max}, x_2^{max}}) = \varrho(x, \mathbf{E}_0) + const.$ if x_1^{max} and x_2^{max} are symmetrical.)

Fig. 7a shows the behaviour of the model as a function of the inverse migration rate $\frac{1}{\mu}$. (The parameter d was fixed at $d = 1.5$.) The central strategy $x = 0$ is an ESS at high migration rate, a branching strategy at medium μ, and a repellor at low μ, as it was discussed above. The three regimes are separated by two bifurcation points: an ESS one at $\frac{1}{\mu} = 2.582$ and a convergence one at $\frac{1}{\mu} = 4.226$. The thick dimorphic branches emerging at the ESS bifurcation point represent the evolutionarily stable state of the dimorphic population as calculated from the local maxima of $\varrho(x, \mathbf{E}_0)$.
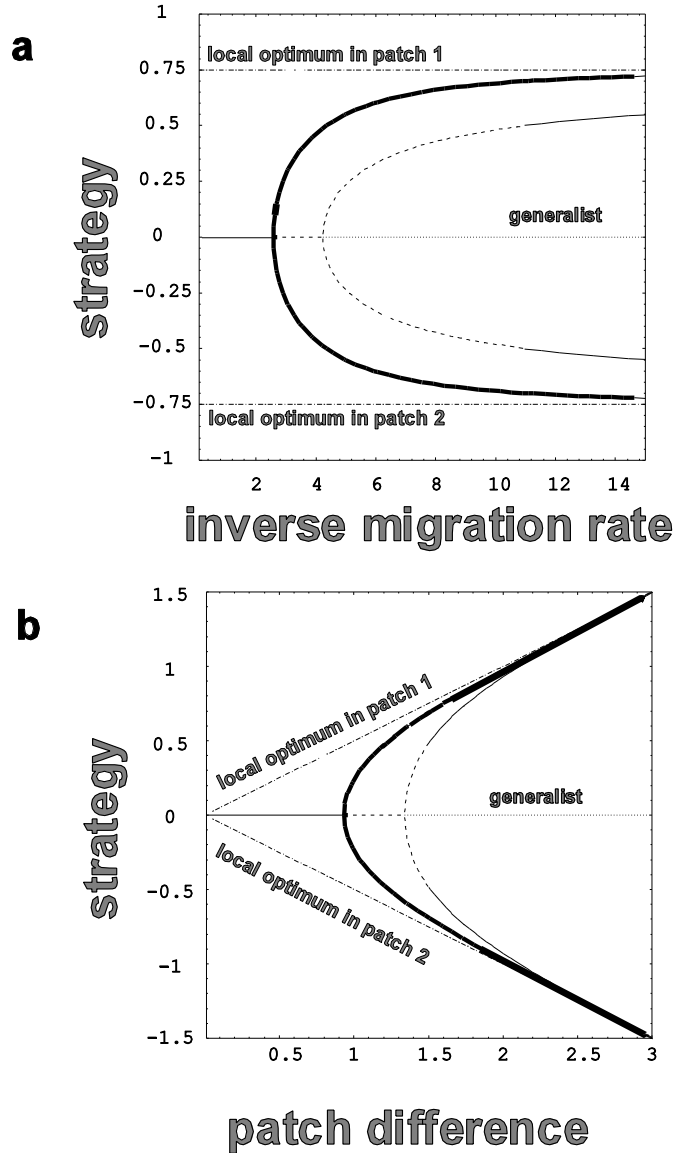
Figure 7: *Behaviour of the model. a: as a function of the inverse migration rate $\frac{1}{\mu}$ (d = 1.5); b: as a function of patch difference d ($\mu = 0.1$). Vertical axis: strategy. Dotted-dashed lines at $x = \pm\frac{d}{2}$ represent the local optima in the patches. All other lines represent singular strategies. Thin lines: monomorphic singular strategy; thick line: dimorphic singular strategy; continuous lines: ESS; dashed: branching strategy; dotted: repellor.*

(Note that the two branches correspond to the two coexisting strategies, rather than to two alternative states of the population!) The thin lines emerging at the convergence bifurcation points are singular strategies (other than the central one) of the monomorphic strategies.

The convergence bifurcation point separating the convergence stable (branching) and unstable (repellor) strategies is a pitchfork bifurcation of the monomorphic adaptive dynamics. When the central strategy loses convergence stability, two new,

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convergence stable branches of fixed points (singular strategies) emerge. The population evolves to one of them from the vicinity of the repelling central strategy. (All of the singular points in the vicinity of this bifurcation are evolutionarily unstable.) The stable branches were calculated by computer algebra using condition (2). They cross the central strategy line at the convergence bifurcation point calculated in the previous paragraph without using computer algebra. This nontrivial coincidence is a useful check of the calculations.

The ESS bifurcation point separates the evolutionarily stable and unstable ($\frac{1}{\mu} > 2.582$ for $d = 1.5$) regimes. The central strategy is an attractor of the monomorphic dynamics on both sides of this bifurcation point. This type of bifurcation is a special phenomenon of adaptive dynamics: the number of dimensions of the state space changes here. There is an apparent similarity between the ESS bifurcation and the pitchfork bifurcation: two new stable branches (thick lines) emerge at the ESS bifurcation point, as well. However, the two points on the two branches at a given $\frac{1}{\mu}$ value *together* represent the stable fixed point of the dimorphic population emerging from the branching.

There are two other ESS bifurcation points in the figure. The convergence stable branches emerging at the convergence bifurcation point become evolutionarily stable at very low migration rate ($\frac{1}{\mu} > 10.97$, extreme right side of the figure). No new dimorphic branches emerge here, because the dimorphic branches emerging at the ESS bifurcation point of the central strategy still exist at this very low migration rate. So, what is happening at different migration rates? We have four regimes:

Case 1. At very high migration rate the situation is very simple. The highly migrating population is not affected by the difference between the patches. A monomorphic population evolves to the central strategy and evolution stops here. An originally dimorphic population becomes monomorphic and follows the central strategy, too.

Case 2. At a slightly lower migration rate a monomorphic population evolves to the central strategy and branches there (Fig. 3). Daughter populations evolve to an evolutionarily stable coalition.

Case 3. At even lower migration rate the central strategy is no longer an attractor of the monomorphic evolution. Monomorphic evolution converges to one of the off-central convergence stable singular strategies and branches there. Then the daughter populations evolve to an evolutionarily stable coalition.

Case 4. At very low migration rate this off-central convergence stable strategy becomes evolutionarily stable. Consequently, a monomorphic population evolves to one of the off-central ESS points, and evolution stops there. A dimorphic equilibrium is still possible, but unreachable from a monomorphic population by continuous evolution except if it starts off exactly from the central strategy.

Note that some of the cases above are missing when $d > 2$, as it can be seen on the phase plot Fig. 6.

The same story can be seen in Fig. 7b as a function of d at fixed migration rate $\mu = 0.1$.

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4 Discussion

The dynamics of monomorphic evolution is governed by the convergence stability (instability) of the singular (fixed) points just like the stability properties of the fixed points govern the dynamics of a constant-dimension system. A convergence stable singular point is a stable fixed point of the monomorphic evolution, but not necessarily of the whole evolutionary process. If it is evolutionarily unstable, evolution proceeds further in the polymorphic portion of the evolutionary state space. The number of coexisting strategies was limited to 2 by the mode of population regulation, so further branching was not seen in this model.

It is very important to stress that the fact that evolutionary stability is a stronger property than convergence stability is a peculiarity of this specific model. In other models, ESS points which are convergence unstable can be found [see Kisdi & Meszéna (1993, 1994), Abrams (1993) for instance]. Such an ESS point is unreachable by small mutation steps. Even if it were reached, it would not be stable, because the population would evolve away from this strategy following a small perturbation in the environment.

Symmetry of the model was very important to keep the basic derivations simple. Unfortunately, this symmetry made our toy-model less realistic. In an asymmetric model one can expect that one of the daughter populations is more similar to the ancestor than the other one. This behaviour would be more similar to the real life where *one* new species is born and the old species does not necessarily die out. (Of course, identity of species remains vague until introducing diploid genetics.) Preliminary studies show that the bifurcation pattern reported here is altered considerably by introducing asymmetry.

Brown & Pavlovic (1992) considered a very similar, although asymmetric, model. They stressed already the role of migration rate on patch specialisation. Their local growth rate function is different from (7). In their model, the generalist strategy depends on the migration rate as a consequence of the asymmetry. In one of the model versions of Brown & Pavlovic, the specialist strategies are constant because of the specific form of the fitness function chosen. Unfortunately, they did not consider the different kind of stabilities separately, so their results are not completely comparable to ours.

Speciation is called *sympatric* if the new species coexists with its ancestor in the same habitat. It is called *allopatric* if the new species occupies a separate habitat and *parapatric* if the two species are living in different, but adjacent, habitats without any migration barrier between them.

The allopatric mode of speciation is the most commonly accepted one. In this case a geographic change (a new river or mountain range, for instance) divides the population into two subpopulations, then the subpopulations evolve to their respective evolutionary optima. A theoretical advantage of this speciation mode is that it can be discussed without referring to frequency-dependent selection. If the two habitats separated by the new barrier are different, optimising selection will lead to different strategies in the two places. Emergence of reproductive isolation is supposed to be a side-effect: if members of the two populations meet each other

later, they will be too different already to breed successfully.

Sympatric speciation is regarded to be more problematic. It starts as genetic polymorphism within a single diploid population. Reproductive isolation has to emerge by selection. There are conflicting requirements here, at least within the framework of frequency-independent population genetics. Genetic polymorphism is maintained if the heterozygotes are superior, but selection for reproductive isolation requires heterozygotes to be inferior.

However, there are definite examples of sympatric speciation. The species flocks of the *Cichlid* fishes are obvious ones: a large number of species of monophyletic origin are living together in different lakes in East Africa. The phenomenon was explained along the lines of the allopatric theory by hypothesising that level-changes divide the shallow Lake Victoria into smaller ones regularly [see, for instance, Skelton (1993)]. However, a similar *Cichlid* flock can be found in the Lake Barombi Mbo in Cameroon, which is a deep crater lake remaining connected even at large level-changes (Schilewen, 1994)!

Population genetics tends to regard frequency-dependent selection as a complicated, but, hopefully, rare special case. However, it is the normal situation in an environment consisting of more than one resource, that is, with more than one niche. The selection force depends on the availability of the different resources (niches), which, in turn, depends on the presence or absence of other species. There is no theoretical problem with sympatric speciation in such an environment. (We do not expect speciation in an environment consisting of a single niche, anyway.) A population experiences disruptive selection in a branching point. Disruptive selection can maintain genetic polymorphism (Christiansen & Loeschcke, 1980, 1987) and selects for reproductive isolation (Seger, 1985) at the same time.

So, spatial separation is not a necessary ingredient of speciation. There is ample evidence of its role in evolution, however. [It is enough to mention the *Drosophila*s in Hawaii (Skelton, 1993).] Explanation of allopatric speciation by frequency-independent selection is far from satisfactory. It supposes the extreme situation in which the geographic separation of the subpopulations is complete. We demonstrated that complete isolation is not a requirement for separation-induced speciation. If, by decreasing the migration rate, we cross the ESS bifurcation point, the population, which was monomorphic so far, loses evolutionary stability and branches. We regard this process as a clonal prototype of allopatric speciation. No speciation occurs if the migration rate jumps from region 1 to region 4 immediately. (Note that our approach is not applicable to the complete separation case because of the loss of irreducibility.)

Losing evolutionary stability in the model, when d increases, is a clonal prototype of parapatric speciation. No new migration barrier emerges in this case, but the difference between the adjacent habitats becomes large enough to allow two different species to exploit them. As in the former case, no speciation occurs if the change of the environment is too large and too fast. The population then remains homogenous and readapts to one of the habitats instead. Fig. 8 summarises the speciation modes as represented in our model.

Working with clonal populations we could not incorporate emergence of repro-
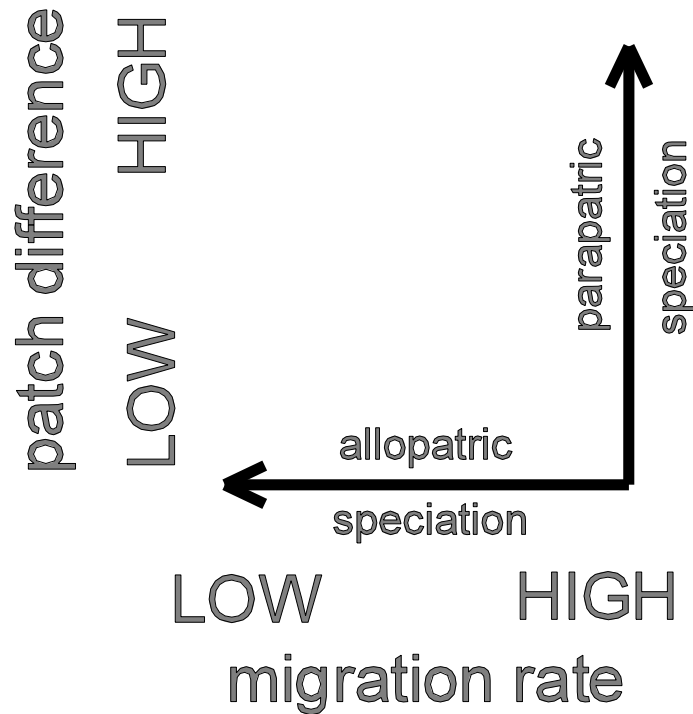
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Figure 8: *Speciation scenarios in the model.*

ductive isolation into our model. We think that it can be done by the mechanism introduced by Seger (1985). Our intention was to explore the ecological situation making the speciation possible here and to proceed with detailed genetics later. Note, that two of the three primary kingdoms of life (Woese, 1987) are clonal: of the *Bacteria*, the *Archebacteria* and the *Eucariotes*, only the last group reproduces sexually.

Rosenzweig (1978, 1995) introduced the term 'competitive speciation', emphasising the role of the ecology-generated disruptive selection in sympatric speciation. It was contrasted with geographic (allopatric) speciation and polyploidy, when factors other than disruptive selection drives speciation. The model presented here demonstrates, however, that geographic (allopatric and parapatric) speciation can be competitive as well, because spatial structure can be a source of disruptive selection.

Note that the overall growth rate (11) is a strictly decreasing function of the

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migration rate μ. If the migration rate was an evolving parameter, this model would end up with non-migrating specialists for each value of the parameter d. For an evolutionary explanation of migration, one has to consider more complicated models including environmental fluctuation.

Acknowledgements

5 Appendix

The equilibrium conditions for a single strategy reads:

$$[R_1(x) - \alpha N_1]N_1 + \mu[N_2 - N_1] = 0$$
$$[R_2(x) - \alpha N_2]N_2 + \mu[N_1 - N_2] = 0. \tag{15}$$

where $R_i(x) = \frac{1}{\sqrt{2\pi}}e^{-(x-x_i)^2/2}$. For the central strategy 0 the equilibrium densities are

$$N_1(0) = N_2(0) = N = \frac{R_1(0)}{\alpha}. \tag{16}$$

($R_1(0) = R_2(0)$ was used.) Using this result implicit function theorem leads to

$$\left[\frac{dN_1}{dx}\right]_{x=0} = \frac{R_1(0)d/2\alpha}{R_1(0) + 2\mu}$$

$$\left[\frac{dN_2}{dx}\right]_{x=0} = -\left[\frac{dN_1}{dx}\right]_{x=0} \tag{17}$$

From here, it is straightforward to derive (14).

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