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Spatial niche packing, character displacement and adaptive speciation along an environmental gradient

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ABSTRACT

In this study, we examine the ecology and adaptive dynamics of an asexually reproducing population, migrating along an environmental gradient. The living conditions are optimal at the central location and deteriorate outwards. The different strategies are optimized to the ecological conditions of different locations. The control parameters are the migration and the tolerance of the strategies towards the environmental condition (location). Locally, population growth is logistic and selection is frequency-independent, corresponding to the case of a single limiting resource. The behaviour of the population is modelled by numerically integrated reaction-diffusion equations as well as by individual-based simulations. Limiting similarity, spatial niche segregation and character displacement are demonstrated, analogous to resource-heterogeneity based niche partitioning. Pairwise invasibility analysis reveals a convergent stable singular strategy optimized to the central, optimal location. It is evolutionarily stable if the migration rate and the tolerance are large. Decreasing migration or decreasing tolerance bifurcates the singular strategy to an evolutionary branching point. Individual-based simulation of evolution confirms that, in the case of branching singularity, evolution converges to this singular strategy and branches there. Depending on the environmental tolerance, further branching may occur. The branching evolution in the asexual model is interpreted as a sign that the ecology of an environmental gradient is prone to adaptive geographic speciation.

Keywords: adaptive dynamics, adaptive speciation, character displacement, environmental gradient, spatial niche packing.

INTRODUCTION

Environmental gradients are common in nature and are considered to have a major effect on biogeographical patterns. Examples include temperature and rainfall gradients. The spatial scale of the gradients varies from the very local, such as a hill-slope, to the continental, such as a latitude gradient. The aims of this study are to examine the evolutionary ecology of gradients and to establish the connection between ecology and speciation for a particular environment.

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The relationship between ecology and genetics is the focal point of the ongoing debate on speciation. The theory of competitive/ecological adaptive speciation (Rosenzweig, 1978, 1995; Dieckmann and Doebeli 1999; Doebeli and Dieckmann, 2000; Schluter, 2001; Dieckmann *et al.*, in press; Geritz *et al.*, in press) considers this interaction in a way analogous to other evolutionary processes: reproductive isolation is an adaptive response to the selective regime determined by the ecological circumstances. Specifically, it is supposedly driven by disruptive selection generated by competition. In contrast, the traditional 'allopatric' (Mayr, 1947) theory of speciation considers emergence of reproductive isolation as a 'by-product' (Turelli *et al.*, 2001) of diverging evolution in allopatry and may be 'reinforced' later by selection.

Competitive/adaptive speciation was coined to explain sympatric speciation. Empirical support for sympatric speciation (Schliewen *et al.*, 1994; see summaries in Berlocher, 1998; Doebeli and Dieckmann, 2000; Geritz and Kisdi, 2000; Via, 2001) can be considered indirect support for adaptive speciation, especially if adaptation to different feeding niches is also documented (for an example, see Galis and Metz, 1998). Theoretical advances (Seger, 1985; Dieckmann and Doebeli, 1999; Geritz and Kisdi, 2000) show that adaptive emergence of reproductive isolation may be a natural consequence of the ecological situation of resource partitioning. On the other hand, there is a large body of data to support geographic (allopatric and parapatric) speciation modes (Mayr, 1947; Grant, 1986; Rosenzweig, 1995). With this background, it is natural to consider the possibility of adaptive geographic speciation. The main aim of this study is to demonstrate that an environmental gradient is prone to selection-induced parapatric speciation due to niche segregation along the gradient.

The theory of adaptive dynamics (Dieckmann and Law, 1996; Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998), which will be our main tool, is important for understanding sympatric adaptive speciation (Doebeli and Dieckmann, 2000). Based on the concept of 'invasion fitness', it is a mathematical framework for the study of arbitrary ecology-induced frequency-dependent selection in asexually reproducing populations. The main conclusions of the theory are summarized by the following two statements:

1. Evolution proceeds in the direction of a local fitness gradient until a 'singular' strategy is reached where this gradient vanishes.
2. At a singular point, fitness has either a minimum or a maximum. The first case corresponds to an evolutionarily stable strategy (ESS). In the second case, disruptive selection leads to 'evolutionary branching'; that is, to diverging evolution of two sub-populations.

One of the key points of (asexual) evolutionary branching is the possibility that directional evolution of a monomorphic population results in a local minimum instead of a local maximum of the fitness function (Eshel, 1983; Taylor, 1989; Christiansen, 1991; Brown and Pavlovič, 1992). Partitioning of a continuous resource scale is the most intuitive example of this surprising phenomenon (Metz *et al.*, 1996; Doebeli and Dieckmann, 2000). Like asexual evolutionary branching, sympatric speciation of sexual organisms is also unimaginable in the frequency-independent context: disruptive selection, which would favour diverging evolution and reproductive isolation, makes polymorphism unstable (Maynard Smith, 1966). The only way to explain speciation without involving frequency dependence is to suppose that sub-populations are well separated to allow independent evolution and postulate that reproductive isolation appears as a by-product of the divergent evolution

(allopatric theory: Mayr, 1947). Adaptive sympatric speciation works surprisingly well, however, when considered in the appropriate ecological framework, as suggested by asexual adaptive dynamics. Resource partitioning provides just the proper combination of disruptive selection and stable co-existence (Christiansen and Loeschcke, 1980, 1987; Loeschcke and Christiansen, 1984; Christiansen, 1988) that leads to evolutionary branching in the asexual model (Metz *et al.*, 1996) and to adaptive reproductive isolation in the sexual one (Dieckmann and Doebeli, 1999). The conclusion is that adaptive speciation is a natural phenomenon. The ecological conditions allowing co-existence of different species often produce that kind of disruptive selection, which makes the situation prone to speciation.

The adaptive dynamics of geographic speciation has been studied in a two-patch model, in which the optimal strategy was different in the two patches (Meszéna *et al.*, 1997; Day, 2000). When the difference between the patches is small and the migration rate is high, the 'compromise' strategy is the resting point of the evolutionary process. Decreasing the migration rate or increasing the patch difference changes the compromise strategy from fitness maximum to 'branching'-type fitness minimum. These transitions were considered to be the asexual prototypes of allopatric (when the migration rate decreases) and parapatric (when the patch difference increases) adaptive speciation. A further increase of the patch difference, or a further decrease of the migration rate, leads to a variety of other evolutionary patterns.

Here we continue this analysis by considering, instead of the two patches, an environmental gradient. Using pairwise invasibility analysis, we investigate ecological and evolutionary issues in the same model. In particular, within this framework we consider niche packing, character displacement and evolutionary branching as stepping stones from ecology to speciation. The final step, the modelling of emergence of reproductive isolation in a sexual population, will be examined by Dieckmann and Doebeli (in press) in a similar model.

MODEL DEFINITION

Competition between asexual populations utilizing the same resource is considered along an environmental gradient in one-dimensional space. The competing populations with different strategies are best adapted to different environmental conditions – that is, to different locations along the gradient. The strategy s_i of the ith population shows that the population is best adapted to the conditions of location $x = s_i$.

Individuals reproduce, change position and die at given rates irrespective of their age. The rate of reproduction r and the rate of movement μ are constant and strategy-independent. A newborn individual has the same position as its parent. The strategy is inherited either faithfully or with a small probability of mutation. In the latter case, mutations represent a small change in strategy. During a movement, the individual changes its position by $+\Delta x$ or $-\Delta x$, with probability 0.5.

Death rate v is strategy-dependent and affected by local logistic competition. Let L be the number of strategies present and $n_i(x, t)$ ($i = 1, \ldots, L$) the concentration of individuals of the ith strategy at location x at time t. The death rate of strategy i at location x is calculated as

$$v_i(x) = r \cdot \frac{\sum_{j=1}^{L} n_j(x, t)}{K_i(x)} \tag{1}$$

where $K_i(x)$ ($i = 1, \ldots, L$) is the carrying capacity for the ith strategy at location x. Note that we prescribed locally complete competition between the strategies, according to the biological assumption of a single, shared resource.

The carrying capacity of a strategy is specified in the following way:

$$K_i(x) = K_{\mathrm{E}}(x)T(x - s_i) \tag{2}$$

The function $T(x - s_i)$ describes the spatial tolerance of the strategy around the optimal location $x = s_i$. [We assume that $T(x - s_i) \leq 1$. The equality holds only for $x = s_i$.] The Gaussian shape

$$K_{\mathrm{E}} = K_0\, \mathrm{e}^{-\frac{x^2}{2w^2}} \qquad T(x - s_i) = \mathrm{e}^{-\frac{(x - s_i)^2}{2\sigma^2}} \tag{3}$$

is used in the simulations if not indicated otherwise.

SIMULATION METHODS

We will use two different mathematical realizations of the model:

- numerical integration of a reaction-diffusion equation;
- individual-based simulation.

Computation time is proportional to the number of strategies considered in the first realization, whereas it is proportional to the number of individuals in the second one. Accordingly, after demonstrating their equivalence, we use the first realization for ecological simulations and the second one for evolutionary simulations.

Reaction-diffusion equations

If the step size Δx is small and the population sizes are large, the behaviour of the population can be approximated by the non-linear reaction-diffusion equation

$$\frac{\partial n_i(x, t)}{\partial t} = r\left(1 - \frac{\sum_j n_j(x, t)}{K_i(x)}\right) n_i(x, t) + D\frac{\partial^2}{\partial x^2} n_i(x, t) \tag{4}$$

(see Czárán, 1998, for the derivation of such equations). Here, the diffusion coefficient D, which will be considered as the measure of mobility, is connected to the individual-level parameters as:

$$D = \frac{1}{2}\mu\Delta x^2 \tag{5}$$

Analytical solution of these equations is not known, even for a single strategy. Therefore, we investigated the system using numerical integration.

During the ecological simulations, we proceeded until reaching the stationary spatial distribution for all of the strategies. The pairwise invasibility plots were produced in the following way. First, we determined the equilibrium distribution of the resident strategy, when alone. Then, this distribution was fixed and the behaviour of the mutant was

simulated with this fixed background such that its own density was neglected in the density dependence. We observed whether the mutant population grows, or declines, after reaching its stationary spatial distribution. This procedure was repeated for each resident–mutant strategy pair.

Individual-based simulations

This realization of the model is a literal translation of the model definition (see pp. 365–366) into computer code. Individuals, described by their strategy and position, are stored in the computer's memory. The reproduction, movement and death of individuals are carried out by an 'event loop'. The type of the next event and the individual affected by the event is chosen randomly in accordance with the specified rates. Death rates are re-calculated after each event.

The number of individuals, and thus the speed of the simulation, is controlled by the scaling factor K_0 of the carrying capacity.

ANALYSIS OF THE MODEL BEHAVIOUR

Ecological aspects

The ecological simulations were performed with a fixed set of strategies, without mutation. We found that the spatial distributions of the strategies always converged to equilibrium distributions, which were independent of the initial distributions. The two model realizations behaved identically even for moderate population sizes (Fig. 1). Knowing this, we performed most of the ecological simulations with the reaction-diffusion approach, which is faster for a small number of strategies.

Figure 2 shows equilibrium spatial distributions of a single strategy for different mobility values. The distributions are similar, but not identical, to a Gaussian distribution. As expected, increased mobility broadens the distribution. Nevertheless, the possibility of broadening is limited, as a population cannot live outside the region that is appropriate for it.

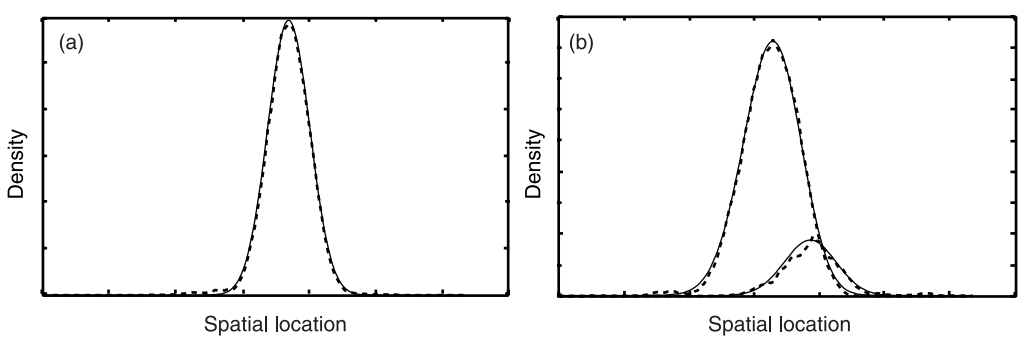

Fig. 1. Equilibrium spatial distribution: comparison of the two model realizations. Continuous curve = reaction-diffusion equation, dashed curve = individual-based simulations smoothed by time averaging. (a) A single strategy, $s = 0.1$; (b) two co-existing strategies, $s = 0.05$ and $s = 0.1$. Other parameter values: $r = 1$, $w = 0.25$, $\sigma = 0.2$, $D = 1 \times 10^{-6}$. Space scales from −1 to 1 along the horizontal axis.

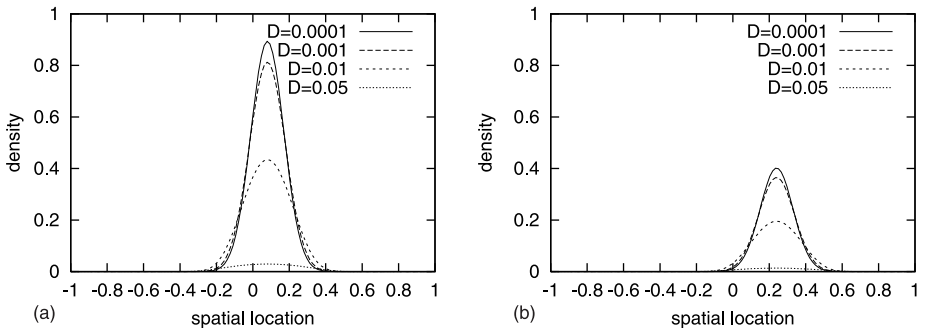

Fig. 2. Equilibrium spatial distribution of a strategy at different values of the diffusion constant. (a) $s = 0.1$, (b) $s = 0.25$. Other parameter values: $r = 1$, $w = 0.3$, $\sigma = 0.2$.

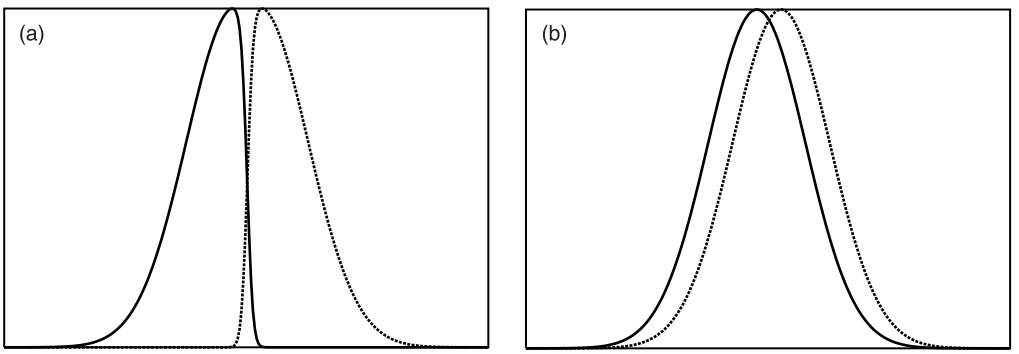

Fig. 3. (a) Spatial density distributions of two competing strategies, $s = \pm 0.05$. Space scales from –1 to 1 along the horizontal axis. (b) Spatial distributions of the same strategies, when alone. Note the narrowing of the distributions by competition. Other parameter values: $w = 10$, $r = 0.01$, $\sigma = 0.2$, $D = 1 \times 10^{-7}$.

Figure 3 demonstrates the effect of competition between two different strategies. The distributions of the two strategies, when alone, overlap significantly. However, if both strategies are present, competition between them distorts their distributions and reduces the overlap. The higher the mobility, the wider the residual overlap and the smaller the distortion in the shape of the distribution curves.

When the simulation was initiated with a large number of strategies, only a few of them survived typically. This behaviour is demonstrated in Fig. 4. To avoid degeneracies (see Discussion), a parabolic carrying capacity curve was used for this investigation:

$$K_{\mathrm{E}}(x) = 1 - \frac{x^2}{2w^2} \qquad T(x - s_i) = \left(1 - \frac{(x - s_i)^2}{2\sigma^2}\right) \tag{6}$$

The ultimate distribution of the surviving strategies was roughly consistent with the picture of 'niche packing'. Only the strategies with limited spatial overlap survived. It is a notable exception that two symmetrically located strategies can co-exist even with high overlap.

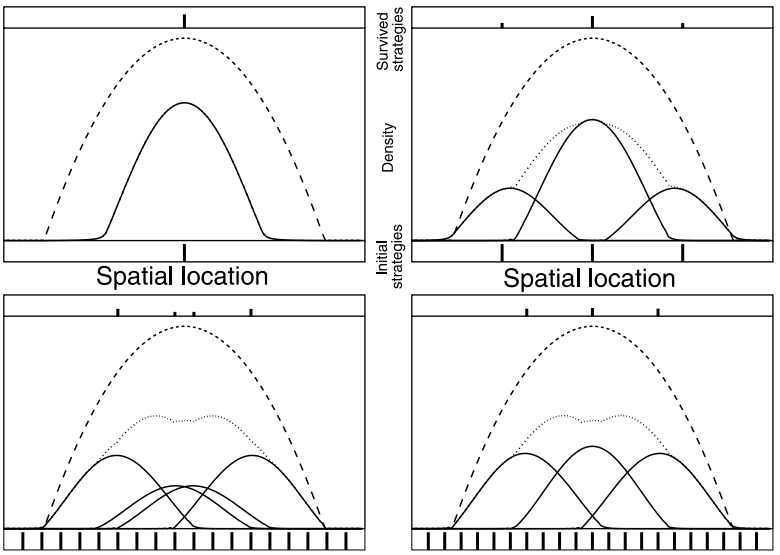

Fig. 4. Niche packing. Equilibrium density distributions of the surviving strategies are shown (continuous curves). The four simulations differ in the initial number (1, 3, 18 and 21) of competing strategies. Bars at the bottom of the figures represent optimal location of the strategies present initially. Bars at the top represent optimal locations of the surviving strategies; height of the top bars is proportional to the peak density. Dashed line = carrying capacity of environment, dotted line = total density. Other parameter values: $w = 0.55$, $\sigma = 0.3$, $D = 0.000244$, $r = 0.01$.

Adaptive dynamics of the model

The main tool of adaptive dynamics in bridging the gap between ecology and evolution is pairwise invasibility analysis. Unequivocal definition of invasibility requires two assumptions:

- The resident population had reached its equilibrium size and distribution when the invader population was introduced.
- The invaders were introduced in very low numbers such that their presence, initially, did not affect the resident population.

Introducing the invader in low numbers implies that invasion takes long enough for the invader to reach its equilibrium spatial distribution while still rare. Consequently, as far as these assumptions are valid, invasion success does not depend on the initial conditions.

In the upper row of Fig. 5, two typical pairwise invasibility plots are shown. The '+' and the '–' regions represent the strategy combinations in which the invader strategy can successfully invade the resident strategy. If the strategy of the invader coincides with that of the resident, then the invader population neither grows nor declines. That is, generically, the main diagonal of a pairwise invasibility plot is a border line between a '+' and a '–' region, independently of the specific model.

Observing whether the '+' region is immediately above or immediately below the main diagonal is instructive about directional evolution. The small arrows on the figures represent

evolution via consecutive, small and rare mutation steps. It is obvious from the figures that directional evolution ceases at the 'singular' strategies, which are represented by the crossing points between the main diagonal and another boundary between the ' + ' and ' – ' regions.

With the usual choice of the function $K_E(x)$, with a unimodal maximum at the centre, we found a single singular strategy at this maximum. This strategy is 'convergence stable' – that is, the direction of evolution of a monomorphic population points towards the singular strategy from both sides.

The attractor strategy may or may not be evolutionarily stable. The two upper plots in Fig. 5 show the two possibilities. In Fig. 5b, no strategy can invade the singular strategy. This is a convergence and evolutionarily stable strategy (or, continuously stable; see Eshel, 1983), which is a final resting point of the evolutionary process. On the other hand, the (still convergent stable) singular point is not an ESS in Fig. 5a, because there are strategies able to invade it. As shown by Geritz *et al.* (1997, 1998), the latter type of singular strategy mandates evolutionary branching in asexual models. The phenomenon will be demonstrated for our model in the next section.

Pairwise invasibility plots are also useful for predicting which strategy pairs can co-exist. It is a sufficient condition for the co-existence of two strategies if they can mutually invade each other. Graphically, the intersection of the '+' region of the pairwise invasibility plot and its mirror image across the main diagonal represents these strategy combinations (lower

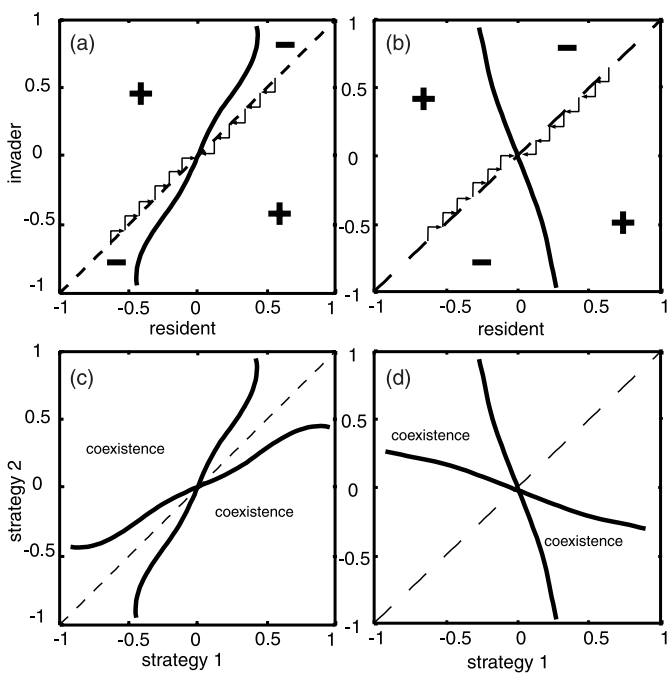

Fig. 5. (a,b) Pairwise invasibility plots. Areas denoted by '+' and '–' represent the resident–invader strategy combinations for which the invasion is successful. The strategy $s = 0$ is an ESS in (b) ($r = 0.01$, $w = 0.25$, $\sigma = 0.2$, $D = 0.0001$) and a branching point in (a) ($r = 0.01$, $w = 0.25$, $\sigma = 0.6$, $D = 0.0001$). In both cases, the central strategy is convergence stable. (c,d) Regions of co-existence of two strategies based on the criterion of mutual invasibility for the same parameter combinations. Figures (c) and (d) can be generated from the pairwise invasibility plots by mirror-imaging across the main diagonal.

plots in Fig. 5). It is clear from Fig. 5 that co-existence of very similar strategies is restricted to the vicinity of the singular strategy. Away from the singularity, the difference between the strategies should be large enough for co-existence. This is in accordance with the findings in the previous section.

Parameter dependence of the adaptive dynamics of the model is presented in Figs 6 and 7. Because of the possibility of rescaling in time and in spatial direction, one can fix two parameters, r and w, without losing generality. The remaining two parameters, the mobility D and the spatial tolerance σ, affect the pairwise invasibility plot in a similar way. As shown in Fig. 6, the tilt of the boundary line changes monotonically when D or σ is increased. The singular strategy remains convergence stable for any parameter values. However, it bifurcates from being a branching point to being an ESS during an increase in either the mobility or the tolerance.

The phase diagram in Fig. 7 demonstrates the combined effect of the two parameters on the evolutionary stability of the singular strategy. It is an ESS if both mobility and tolerance assume a high value. Decreasing either of them bifurcates the singular point into a branching type singularity.

Mirror imaging of the pairwise invasibility plots in Fig. 6 (not shown) also reveals that the region of co-existence of two strategies shrinks when either the mobility or the tolerance is increased. At high parameter values, the conditions for co-existence are strict. To co-exist, the two strategies must assume values that are almost symmetrical with respect to the singular strategy. Smaller D and/or σ relaxes this condition and allows co-existence of a wider range of strategies. In the case of extremely small mobility or spatial tolerance, almost any strategy is able to co-exist with almost any other. The only exception remains that very similar strategies, away from the singular one, cannot co-exist.

Simulation of evolution

Figure 8 demonstrates a typical process of evolution starting from a single strategy that is different from the singular one. In the case of small mutation steps, directional evolution

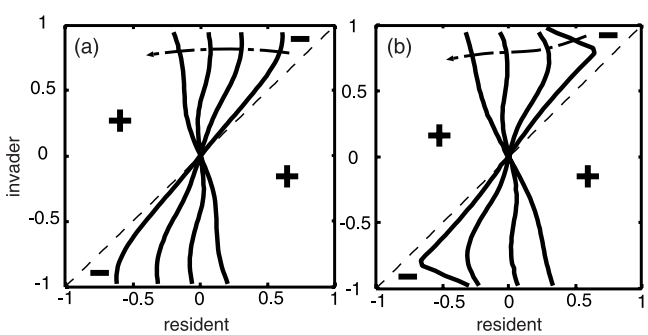

Fig. 6. Dependence of the pairwise invasibility plot on mobility (a) and on spatial tolerance (b). Fixed parameters: $r = 0.01$, $w = 0.25$. In (a) spatial tolerance is kept constant ($\sigma = 0.4$) while mobility assumes the values $D = 1 \times 10^{-5}$, 6×10^{-5}, 2×10^{-4} and 8×10^{-4}. In (b) mobility is kept constant ($D = 6 \times 10^{-4}$) while spatial tolerance assumes the values $\sigma = 0.12$, 0.2, 0.35 and 0.5. The arrows represent the changing tilt of the boundary line with increasing mobility (spatial tolerance). Both kinds of parameter change transforms the singular strategy from a branching point to an ESS. Moreover, the area of co-existence decreases in both cases. The latter can be judged from mirror imaging of the figures across the main diagonal (see Fig. 5).

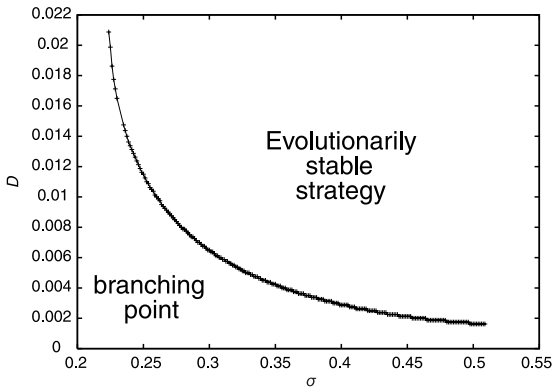

Fig. 7. The phase diagram of the model. The singular point is an ESS for high mobility and spatial tolerance. Otherwise, it is a branching point. Parameter values: $w = 0.2$, $r = 1.0$.

proceeds towards the singular point at first. If the singular strategy is an ESS, evolution stops here. In the case of a branching type singularity, evolutionary branching occurs, the population becomes dimorphic and the two emerging strategies evolve away from each other. Consecutive branching may happen several times depending on the parameter values.

Larger mutation steps often result in branching away from the singular point, as such a mutation allows jumping over the non-allowed range of strategies. This dependence on the mutation step is demonstrated in Fig. 9 for the case of an asymmetric environmental carrying capacity:

$$K_{\mathrm{E}}(x) = \begin{cases} \mathrm{e}^{-\frac{(x-s_z)^2}{2w_1^2}} & \text{if } x < s_z \\ \mathrm{e}^{-\frac{(x-s_z)^2}{2w_2^2}} & \text{if } x \geq s_z \end{cases} \tag{7}$$

Finally, evolution in a bimodal environment described by

$$K_{\mathrm{E}}(x) = A_1 \mathrm{e}^{-\frac{(x-s_1)^2}{2w^2}} + A_2 \mathrm{e}^{-\frac{(x-s_2)^2}{2w^2}} \tag{8}$$

is demonstrated in Fig. 10. A monomorphic population living in one of the peaks is able to split into two strategies. Then the new strategy moves towards the other peak and occupies it. If the spatial tolerance σ of a strategy is small enough, more strategies can co-exist in both of the peaks.

Diverging evolution after branching can be investigated separately by starting the simulation with two strategies, instead of one, at the vicinity of the branching point (Fig. 11). This is a representation of the phenomenon of character displacement.

DISCUSSION

Spatial niche segregation

In a stable environment, resource partitioning and spatial separation are the two basic means of niche segregation (Hutchinson, 1978). The first, based on resource heterogeneity, is the most common framework for model investigations in community ecology (beginning

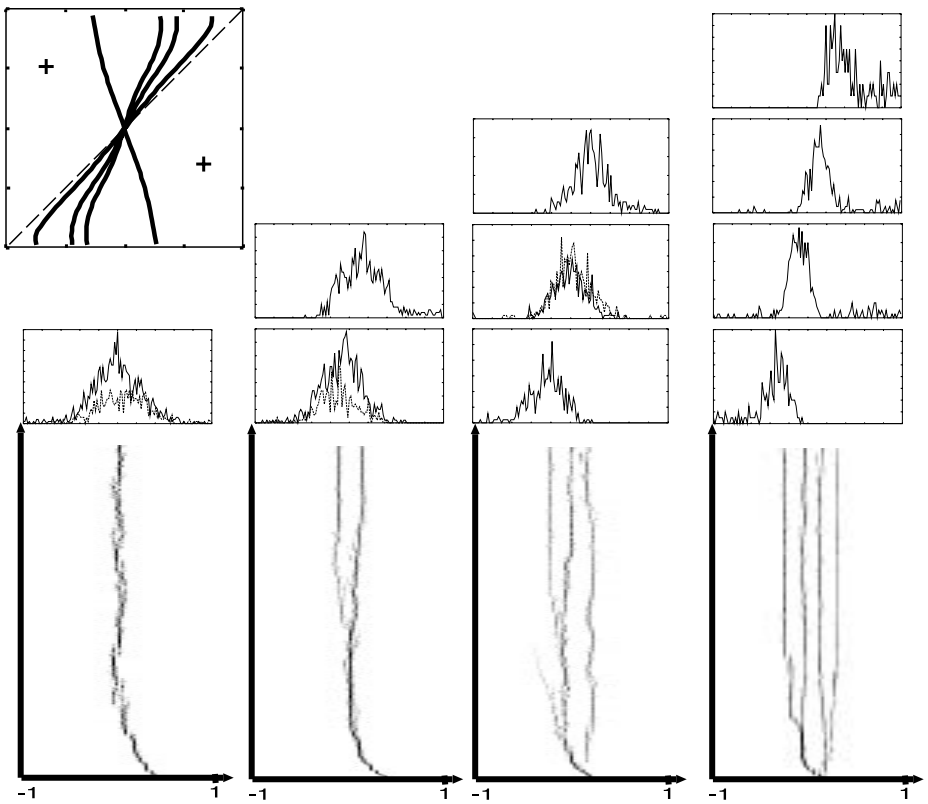

Fig. 8. The bottom row of figures represent evolution of strategies in time, started from a single strategy (horizontal axis = strategy; vertical axis = time; darker shades of grey represent higher density). The small insets at the top of the time diagrams show the spatial distribution of the strategies (without time-averaging) in the different branches present at the end of the simulation. (Each inset contains more than one curve when the corresponding branch contains more than one strategy.) The pairwise invasibility plots corresponding to the simulation are present in the top left-hand corner. The four simulations differ in their spatial tolerance parameter. The simulation with $\sigma = 0.9$ on the left exhibits the behaviour when the singular strategy is an ESS. At $\sigma = 0.4$ (second from left), a single branching occurs with two final strategies. Decreasing σ further in the third and fourth simulations ($\sigma = 0.3$ and $\sigma = 0.1$) increases the number of branchings and the number of emerging strategies. Other parameter values: $r = 0.01$, $w = 0.25$, $D = 6 \times 10^{-5}$; resolution of the strategy space = 64, mutation rate = 0.001.

with MacArthur and Levins, 1964) and studies of ecological/adaptive/sympatric speciation (see, for example, Dieckmann and Doebeli, 1999). The second, based on spatial heterogeneity, has two extreme types: a patchy environment with different conditions in the patches and an environmental gradient. The evolutionary consequences of patchiness have been investigated by Meszéna *et al.* (1997), Day (2000), Ronce and Kirkpatrick (2001) and Kisdi (2002). The present study looked at the case of the environmental gradient. We found validity for the concepts of limiting similarity, niche segregation, character displacement and evolutionary branching in this context. In doing so, we established that the environmental gradient is prone to adaptive parapatric speciation.

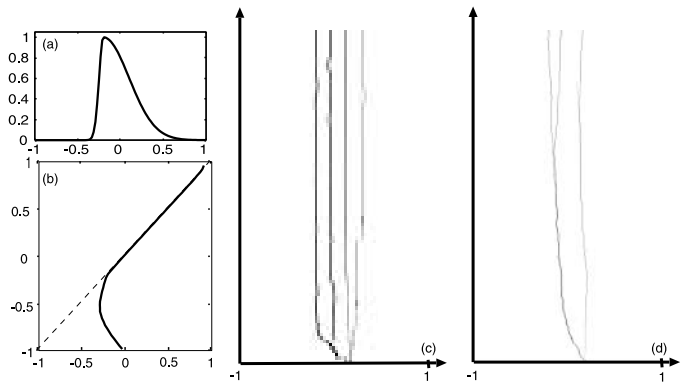

Fig. 9. Evolution in an asymmetric environment with finite mutation steps. (a) The carrying capacity curve. (b) The pairwise invasibility plot; the non-invasion region is extremely narrow for resident strategy values higher than that of the singular one. (c) Evolution with mutation steps large enough to step across the non-invasion region and form a new branch without reaching the branching point. (d) The mutation steps are smaller, so that only one branching happens before reaching the singular strategy. Parameter values: $s_z = -0.2$, $w_1 = 0.05$, $w_2 = 0.3$, $r = 0.01$, $\sigma = 0.2$, $D = 6.1 \times 10^{-7}$; mutation rate = 0.0001, resolution of the strategy space = 64 in (c) and 256 in (d).

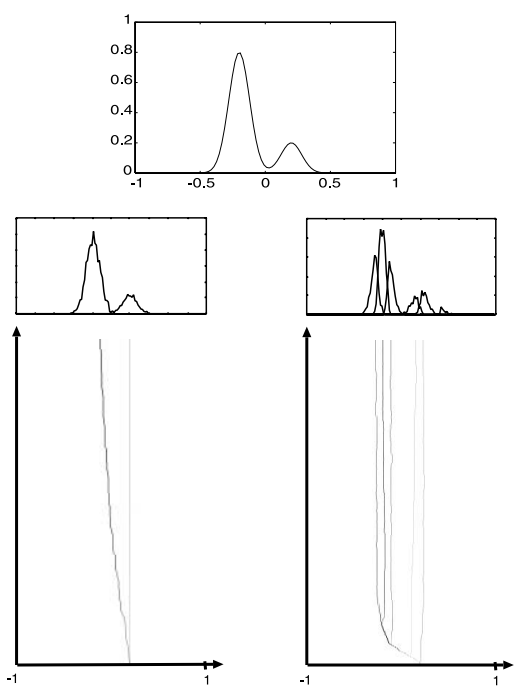

Fig. 10. Evolution and the final spatial distributions in a bimodal environment. The carrying capacity defined in (8) is shown at the top. $\sigma = 0.25$ on the left and $\sigma = 0.14$ on the right. Parameter values: $A_1 = 0.8$, $s_1 = -0.2$, $A_2 = 0.2$, $s_2 = 0.2$, $w = 0.08$, $r = 0.01$, $D = 6.1 \times 10^{-8}$.

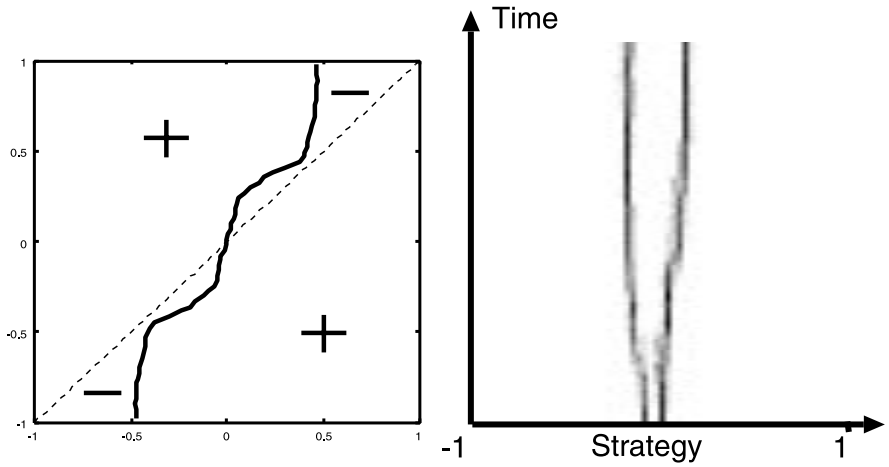

Fig. 11. Character displacement. Evolution starts with two strategies with strategy values −0.06 and 0.06. Because of disruptive selection, they evolve apart from each other to share the available resources in different niches. The carrying capacity curves of species are of a parabolic shape described in (6) with parameters $w = 0.4$, $\sigma = 0.4$, $D = 0.000122$, $r = 0.01$.

To investigate a clear ecological situation, no explicit or implicit resource heterogeneity was supposed. Accordingly, we assumed locally complete competition. The sole source of reduced competition between the different strategies, a necessity for stable co-existence, was the spatial segregation along the gradient.

The distinction between patchiness and gradient is analogous to the difference between discrete resources (as in MacArthur and Levins, 1964, Tilman, 1982) and a continuous scale of resources (for which MacArthur and Levins, 1967, is the classical study). For discrete resources, the well-known argument ensures that the number of resources bounds the number of co-existing populations (Levin, 1970). The same reasoning applies to patchy environments and constrains species diversity by the number of patches, provided that no resource heterogeneity is present. Limiting similarity is the analogous concept for a continuous scale of resource quality (MacArthur and Levins, 1967). Our simulation results support the expectation that limiting similarity and niche packing apply to the environmental gradient as well.

Limiting similarity is not a trivial issue even for resource competition. The principle was challenged by Roughgarden (1979), who showed that a continuous set of species can co-exist in a Lotka-Voltera competition model with a Gaussian carrying-capacity curve. However, Sasaki and Ellner (1995) showed that the choice of the Gaussian carrying capacity is structurally unstable. That is, an arbitrarily small change of this curve destroys the continuous co-existence. Similarly, asymmetric competition can maintain continuous co-existence, but only in non-generic situations (Geritz, 1995; Geritz *et al.*, 1999; see Buttel *et al.*, 2002, for the case of metapopulations). Meszéna and Szathmáry (2001) demonstrated the same situation in a model of prebiotic replicators. M. Gyllenberg and G. Meszéna (submitted) and Meszéna *et al.* (in prep.) have shown the non-genericity of continuous co-existence in a model-independent manner.

We know of no analytic way to establish which is the exceptional choice of the carrying-capacity curve, allowing continuous co-existence, in an environmental gradient.

Our experiences are consistent with the assumption that it is the Gaussian one, again (results not shown). Following Metz *et al.* (1996), we chose a quadratic carrying capacity curve for the niche-packing simulations to ensure that we studied the generic case. This subject requires further investigation.

Conditions of co-existence and branching

We assumed optimal conditions at the middle of the spatial range. As an immediate consequence, evolution of a lone type converges to the strategy optimized for the central location. This strategy is evolutionarily stable, and represents a resting point of the evolutionary process, if both mobility and spatial tolerance are large. The spatial distribution of the ESS spreads over the whole area and does not allow any other strategy to enter. On the other hand, if either the mobility or the spatial tolerance is small, evolutionary branching takes place and the population becomes polymorphic. In a similar vein, the conditions of co-existence for two fixed strategies become more relaxed when either parameter is decreased.

We conclude that both restricted mobility and restricted tolerance increase the possibility of the presence of multiple types. Accordingly, there are two ecologically distinct sets of circumstances in which multiple types can be observed:

- At one extreme, individual tolerance is very narrow but mobility is quite large. The species may almost be perfectly mixed, but for each species only a very narrow fraction of the sites can serve as a suitable habitat. Mobile species, such as marine invertebrate benthos with planktonic larvae, may exhibit such behaviour.
- At the opposite extreme, a zonation is formed by the low migration ability of the species. Even if the differences in the survivorship are minute, the presence of other species can restrict the spread of any species for a narrow range. The zonation of trees along the altitudinal gradient is a possible example, as most trees have a rather short range of seed dispersal (Y. Iwasa, personal communication).

One can interpret this result in the context of the analogy between resource-based and spatial-niche segregation. The spatial distribution of a species in the spatial case corresponds to the resource utilization function of the species in the resource competition case. Decreasing mobility allows the population to concentrate in its optimal location when it is outcompeted in the sub-optimal locations. That is, spatial distribution is determined jointly by the tolerance for conditions and by the mobility. Consequently, these two parameters of the spatial case, in combination, correspond to the resource tolerance (niche-width) parameter of the resource competition case.

Our conditions for evolutionary branching are in line with the results of Meszéna *et al.* (1997) for a two-patch environment. In the two-patch model, a strategy that represents a compromise between the requirements of the patches is an ESS when the migration rate is high and the difference between the patches is small. The compromise strategy becomes a branching strategy when either migration is decreased or the patch difference is increased. When comparing the two models, note that a steeper gradient, which is the analogue of the larger patch difference, is represented here by a smaller spatial tolerance σ.

The main difference between the two-patch case and the environmental gradient examined here is that the latter may allow further branching. Although the number of

co-existing types is limited to two for two patches (to k for k number of patches), the maximal number of species in a gradient is determined by tolerance and mobility. Extremely small tolerance and/or mobility leads to very narrow spatial niches, allowing a large number of species to co-exist.

Robustness of the model behaviour

Reaction-diffusion equation (4) is the multi-species generalization of the Fisher equation (Fisher, 1937). The Fisher equation, and its descendants, have been used to analytically study spreading in homogeneous as well as in heterogeneous environments (Shigesada and Kawasaki, 1997; Diekmann and Heesterbeek, 2000). In these studies, an infinite world was assumed and, consequently, the population was never equilibrated with the environment. Like Case and Taper (2000), we have concentrated on the stationary solution, which exists if the area of the possible distributions is limited. As no analytic solution was known, we used numerical techniques to determine this stationary state.

In the individual-based realization of the model, we assumed local reproduction and movement of individuals. These assumptions are more appropriate for animals of limited mobility than for plants. However, a plant-type model, with localized individuals and reproduction to the neighbourhood, would lead to the very same differential equation. This is clear from the way the Fisher equation is derived (see, for instance, Czárán, 1998; this topic will be investigated further elsewhere).

There are two important conditions for the derivation of Fisher-type equations. The first is that the population should propagate in small steps, either during the individual's life or during reproduction. One can make the frequency of these steps arbitrarily high for modelling high mobility. In contrast, propagation via rare but large steps cannot be described by a reaction-diffusion equation. The behaviour of such a model would depend significantly on the details of the rules for propagation.

The other condition is that the interaction range of the individuals should be small compared with the ecologically relevant scales. In our model, these interactions determine the death rate of an individual. When the interaction range is sufficiently small, the death rate can be expressed by the local density of the individuals. In the general case, this expression may involve a 'moment closure' (see, for instance, Bolker *et al.*, 2000). However, this problem is irrelevant for a model like ours in which the event rate is linear in density.

We obeyed these restrictions and, moreover, verified the coincidence in behaviour of the two realizations of the model. In doing so, we are confident that our results are insensitive to the detailed rules for propagation and for interactions. We believe the model can be applied equally well to plant- and animal-type propagation.

Comparison with sexual models

Evolutionary problems always have two aspects: an ecological one (behavioural, etc.) determining selection pressures and a population genetic one determining evolutionary responses to these pressures. As sexual models are complicated and depend on specific assumptions about the details of the genetic make-up, it is useful to investigate the ecological/behavioural aspect using asexual models (Maynard Smith, 1982).

Apart from the phenomenon of evolutionary branching, the behaviour of an asexual model can be interpreted such that the strategies represent separate species. This inter-

pretation neglects genetic variance within a species. In real life, genetic variance may widen the range of a species via local adaptation. In a cline, a single population adapts to an environmental gradient with a wide, and shifting, genotype distribution (Endler, 1977; Barton, 1999). On the other hand, gene flow tends to destroy local adaptation (Kirkpatrick and Barton, 1997). Our model represents the limiting case when gene flow prevails over local adaptation. Accordingly, our clonal model is unable to reproduce the continuous change of phenotype along the cline.

Doebeli (1996b), Taper and Case (1985, 1992) and Drossel and McKane (1999) modelled character displacement with explicit representation of genetic variance in the context of non-spatial niche segregation. Their results are consistent with the expectation that within-species variance does not alter the process qualitatively, provided that the variance of a single species occupies only a sufficiently small fraction of the niche space. Case and Taper (2000) investigated the problem in the presence of an environmental gradient. However, this model mixed the resource-based and the spatial segregation models by assuming decreased local competition between the different species.

Note that the genetic variance is modelled differently in the different models. For instance, Taper and Case (1985, 1992; Case and Taper, 2000) assumed the variances to be constant. This can be a good approximation in the limit of infinite loci. Doebeli (1996a,b,c) applied the 'hypergeometric' model to describe a multi-locus character with diallelic loci, the applicability of which is not entirely clear. Drossel and McKane (1999) assumed linkage equilibrium and a Gaussian allelic distribution on each locus. This approach allows unlimited growth of the genetic variance. These differences in the genetic assumptions, especially whether variance is fixed or not, should affect the model behaviour whenever population variance matters.

While our clonal approach neglects important effects, it saves us from depending on genetic assumptions and allows us to investigate a wider range of phenomena within the framework of a single model. Nevertheless, one of them, the evolutionary branching, goes beyond the interpretation of strategies as separate species and leads us to the field of speciation.

CONCLUSIONS FOR SPECIATION THEORY

The theory of adaptive speciation of Dieckmann and Doebeli (1999) revealed that reproductive isolation may develop by selection due to the disruptive selection operating at the branching point. Observing evolutionary branching in an asexual model can be indicative of an ecological situation promoting speciation of sexual organisms. We propose to extend this understanding to various types of geographic speciation. The appearance of a branching singularity in the two-patch model (Meszéna *et al.*, 1997), or in the current model of an environmental gradient, suggests the possibility of an adaptive route to allopatric or parapatric speciation. Dieckmann and Doebeli (in press) reached a similar conclusion by extending their earlier model with the introduction of an environmental gradient.

Spatial separation during geographic speciation is expected to have two, conflicting, effects on the development of genetic segregation:

- spatial separation helps to decrease the gene flow between two populations; and
- decreased gene flow decreases selection for assortative mating.

A detailed analysis of these phenomana is beyond the scope of the current paper. Note, however, that even if the populations live sympatrically, mating within separate habitats

causes the same type of early isolation as spatial segregation. Previously, such ecology-related genetic segregation was considered essential for sympatric speciation (Bush, 1994; Rosenzweig, 1995). Since the work of Dieckmann and Doebeli (1999), it is clear that mating in different habitats is not a requirement. A detailed comparison of the habitat/host-based and resource-based forms of sympatric speciation has yet to be made. Nevertheless, from the point of view of genetic isolation, habitat/host-based sympatric speciation is more similar to geographic adaptive speciation than to resource-based sympatric speciation.

Unfortunately, the different models for the genetics of speciation are not comparable. Dieckmann and Doebeli (1999) investigated selection for reproductive isolation using resource competition ecology and multi-locus genetics. In contrast, Kisdi and Geritz (1999; Geritz and Kisdi, 2000) studied the problem in a two-habitat system with a single-locus ecological character. Kawecki (1996, 1997) studied basically the same two-habitat ecology but did not address the emergence of assortative mating. Kondrashov and Kondrashov (1999) used a fixed assortment rule and imposed a fixed level of disruptive selection. It is clear that we are not at the stage when we can draw conclusions about the conditions of adaptive emergence of reproductive isolation.

Note that disruptive sexual selection is also a possible evolutionary force behind sympatric speciation. See, for example, Turner and Burrows (1995) and Higashi *et al.* (1999) for supporting models and Turelli *et al.* (2001) for objections. Seehausen and van Alphen (1999) suggested sexual selection as an explanation for the sympatric component of the fast cichlid radiation in Lake Victoria beyond the ecological limits. It remains to be seen whether sexual selection can play a role in adaptive geographic speciation as well.

The models of evolutionary branching along an environmental gradient and in the two-patch environment (Meszéna *et al.*, 1997) behave analogously to the branching models without spatial structure. Evolution to a minimum of the frequency-dependent fitness function and the emergence of disruptive selection at this point are the crucial features of this process. Although the genetic aspects are far from clear, there is no reason to identfy adaptive speciation with the sympatric mode. Therefore, we propose that the issue of adaptive versus 'by-product' (Schluter, 2001) emergence of reproductive isolation is orthogonal to the issue of sympatric, parapatric or allopatric speciation. Recent advances in speciation research suggest a pluralistic approach to speciation modes in terms of ecological/spatial structure and the genetic details of isolation mechanisms. At a deeper level, however, the concept of adaptive speciation via frequency-dependent disruptive selection is a possible candidate for the common cause of most types of speciation.

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REFERENCES

Barton, N.H. 1999. Clines in polygenic traits. *Genet. Res.*, **74**: 223–236.

Berlocher, S.H. 1998. Can sympatric speciation via host or habitat shift be proven from phylogenetic and biogeographic evidence? In *Endless Forms: Species and Speciation* (D.J. Howard and S.H. Berlocher, eds), pp. 99–113. Oxford: Oxford University Press.

Bolker, B.M., Pacala, S.W. and Levin, S. 2000. Moment methods for ecological processes in continuous space. In *The Geometry of Ecological Interactions: Simplifying Spatial Complexity* (U. Dieckmann, R. Law and J.A.J. Metz, eds), pp. 388–411. Cambridge: Cambridge University Press.

Brown, J.S. and Pavlovič, N.B. 1992. Evolution in heterogeneous environments: effects of migration on habitat specialization. *Evol. Ecol.*, **6**: 360–382.

Bush, G. 1994. Sympatric speciation in animals – new wine in old bottles. *Trends Ecol. Evol.*, **9**: 285–288.

Buttel, L.A., Durrett, R. and Levin, S.A. 2002. Competition and species packing in patchy environments. *Theor. Pop. Biol.*, **61**: 265–276.

Case, T.J. and Taper, M.L. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *Am. Nat.*, **155**: 583–605.

Christiansen, F.B. 1988. Frequency dependence and competition. *Phil. Trans. R. Soc. Lond. B*, **319**: 587–600.

Christiansen, F.B. 1991. On conditions for evolutionary stability for a continuously varying character. *Am. Nat.*, **138**: 37–50.

Christiansen, F.B. and Loeschcke, V. 1980. Evolution and intraspecific exploitative competition I. One-locus theory for small additive gene effects. *Theor. Pop. Biol.*, **18**: 297–313.

Christiansen, F.B. and Loeschcke, V. 1987. Evolution and intraspecific competition. III. One-locus theory for small additive gene effects and multidimensional resource qualities. *Theor. Pop. Biol.*, **31**: 33–46.

Czárán, T. 1998. *Spatiotemporal Models of Population and Community Dynamics*. London: Chapman & Hall.

Day, T. 2000. Competition and the effect of spatial resource heterogeneity on evolutionary diversification. *Am. Nat.*, **155**: 790–803.

Dieckmann, U. and Doebeli, M. 1999. On the origin of species by sympatric speciation. *Nature*, **400**: 354–357.

Dieckmann, U. and Doebeli, M. in press. Speciation along an environmental gradient. *Nature*.

Dieckmann, U. and Doebeli, M. in press. Adaptive speciation along an environmental gradient. In *Adaptive Speciation* (U. Dieckmann, J.A.J. Metz, M. Doebeli and D. Tautz, eds). Cambridge: Cambridge University Press.

Dieckmann, U. and Law, R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.*, **34**: 579–612.

Dieckmann, U., Metz, J.A.J., Doebeli, M. and Tautz, D., eds. in press. *Adaptive Speciation*. Cambridge: Cambridge University Press.

Diekmann, O. and Heesterbeek, J.A.P. 2000. *Mathematical Epidemiology of Infectious Diseases*. New York: Wiley.

Doebeli, M. 1996a. Quantitative genetics and population dynamics. *Evolution*, **50**: 532–546.

Doebeli, M. 1996b. An explicit genetic model for ecological character displacement. *Ecology*, **77**: 510–520.

Doebeli, M. 1996c. A quantitative genetic competition model for sympatric speciation. *J. Evol. Biol.*, **9**: 893–909.

Doebeli, M. and Dieckmann, U. 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *Am. Nat.*, **156**: S77–S101.

Drossel, B. and McKane, A. 1999. Ecological character displacement in quantitative genetic models. *J. Theor. Biol.*, **196**: 363–376.

Endler, J.A. 1977. *Geographic Variation, Speciation, and Clines*. Princeton, NJ: Princeton University Press.

Eshel, I. 1983. Evolutionary and continuous stability. *J. Theor. Biol.*, **103**: 99–111.

Fisher, R.A. 1937. The wave of advance of advantageous genes. *Ann. Eugenics*, **7**: 353–369.

Galis, F. and Metz, J.A.J. 1998. Why are there so many cichlid species? *Trends Ecol. Evol.*, **13**: 1–2.

Geritz, S.A.H. 1995. Evolutionary stable seed polymorphism and small scale spatial variation in seedling density. *Am. Nat.*, **146**: 685–707.

Geritz, S.A.H. and Kisdi, É. 2000. Adaptive dynamics in diploid, sexual populations and the evolution of reproductive isolation. *Proc. R. Soc. Lond. B*, **267**: 1671–1678.

Geritz, S.A.H., Metz, J.A.J., Kisdi, É. and Meszéna, G. 1997. The dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.*, **78**: 2024–2027.

Geritz, S.A.H., Kisdi, É., Meszéna, G. and Metz, J.A.J. 1998. Evolutionary singular strategies and the adaptive growth and branching of evolutionary trees. *Evol. Ecol.*, **12**: 35–57.

Geritz, S.A.H., van der Meijden, E. and Metz, J.A.J. 1999. Evolutionary dynamics of seed size and seedling competitive ability. *Theor. Pop. Biol.*, **55**: 324–343.

Geritz, S.A.H., Kisdi, É., Meszéna, G. and Metz, J.A.J. in press. Adaptive dynamics of speciation. In *Adaptive Speciation* (U. Dieckmann, J.A.J. Metz, M. Doebeli and D. Tautz, eds). Cambridge: Cambridge University Press.

Grant, P.R. 1986. *Ecology and Evolution of Darwin's Finches*. Princeton, NJ: Princeton University Press.

Higashi, M., Takimoto, G. and Yamamura, N. 1999. Sympatric speciation by sexual selection. *Nature*, **402**: 523–526.

Hutchinson, G.E. 1978. *An Introduction to Population Ecology*. New Haven, CT: Yale University Press.

Kawecki, T.J. 1996. Sympatric speciation driven by beneficial mutations. *Proc. R. Soc. Lond. B*, **263**: 1515–1520.

Kawecki, T.J. 1997. Sympatric speciation driven by deleterious mutations with habitat-specific effects. *Evolution*, **51**: 1751–1763.

Kirkpatrick, M. and Barton, N.H. 1997. Evolution of a species' range. *Am. Nat.*, **150**: 1–23.

Kisdi, É. 2002. Dispersal: risk spreading versus local adaptation. *Am. Nat.*, **159**: 579–596.

Kisdi, É. and Geritz, S.A.H. 1999. Adaptive dynamics in allele space: evolution of genetic polymorphism by small mutations in a heterogeneous environment. *Evolution*, **53**: 993–1008.

Kondrashov, A.S. and Kondrashov, F.A. 1999. Interactions among quantitative traits in the course of sympatric speciation. *Nature*, **400**: 351–354.

Levin, S.M. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *Am. Nat.*, **104**: 413–423.

Loeschcke, V. and Christiansen, F.B. 1984. Evolution and intraspecific competition. II. A two-locus model for additive gene effects. *Theor. Pop. Biol.*, **26**: 228–264.

MacArthur, R. and Levins, R. 1964. Competition, habitat selection and character displacement in a patchy environment. *Proc. Natl. Acad. Sci. USA*, **51**: 1207–1210.

MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.*, **101**: 377–385.

Maynard Smith, J. 1966. Sympatric speciation. *Am. Nat.*, **100**: 637–650.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.

Mayr, E. 1947. *Evolution and the Diversity of Life: Selected Essays*. Cambridge, MA: Belknap Press.

Meszéna, G. and Szathmáry, E. 2001. Adaptive dynamics of parabolic replicators. *Selection*, **2**: 147–159.

Meszéna, G., Czibula, I. and Geritz, S.A.H. 1997. Adaptive dynamics in a 2-patch environment: a toy model for allopatric and parapatric speciation. *J. Biol. Syst.*, **5**: 265–284.

Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A. and van Heerwaarden, J.S. 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In *Stochastic and Spatial Structures of Dynamical Systems* (S.J. van Strien and S.M. Verduyn Runel, eds), pp. 183–231. Amsterdam: North-Holland.

Ronce, O. and Kirkpatrick, M. 2001. When sources become sinks: migrational meltdown in heterogeneous habitats. *Evolution*, **55**: 1520–1531.

Rosenzweig, M.L. 1978. Competitive speciation. *Biol. J. Linn. Soc.*, **10**: 275–289.

Rosenzweig, M.L. 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.

Roughgarden, J.A. 1979. *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. New York: Macmillan.

Sasaki, A. and Ellner, S. 1995. The evolutionary stable phenotype distribution in a random environment. *Evolution*, **49**: 337–350.

Schliewen, U.K., Tautz, D. and Pääbo, S. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature*, **368**: 623–629.

Schluter, D. 2001. Ecology and the origin of species. *Trends Ecol. Evol.*, **16**: 372–380.

Seehausen, O. and van Alphen, J.J.M. 1999. Can sympatric speciation by disruptive sexual selection explain rapid evolution of cichlid diversity in Lake Victoria? *Ecol. Lett.*, **2**: 262–271.

Seger, J. 1985. Intraspecific resource competition as a cause of sympatric speciation. In *Evolution: Essays in Honour of John Maynard-Smith* (P.J. Greenwood, P.M. Harvey and M. Slatkin, eds), p. 43. Cambridge: Cambridge University Press.

Shigesada, N. and Kawasaki, K. 1997. *Biological Invasion: Theory and Practice*. Oxford: Oxford University Press.

Taper, M.L. and Case, T.J. 1985. Quantitative genetic models for the coevolution of character displacement. *Ecology*, **66**: 355–371.

Taper, M.L. and Case, T.J. 1992. Models of character displacement and the theoretical robustness of taxon cycles. *Evolution*, **46**: 317–333.

Taylor, P. 1989. Evolutionary stability in one-parameter models under weak selection. *Theor. Pop. Biol.*, **36**: 125–143.

Tilman, D. 1982. *Resource Equilibrium and Community Structure*. Princeton, NJ: Princeton University Press.

Turelli, M., Barton, N.H. and Coyne, J.A. 2001. Theory and speciation. *Trends Ecol. Evol.*, **16**: 330–343.

Turner, G.F. and Burrows, M.T. 1995. A model of sympatric speciation by sexual selection. *Proc. R. Soc. Lond. B*, **260**: 287–292.

Via, S. 2001. Sympatric speciation in animals: the ugly duckling grows up. *Trends Ecol. Evol.*, **16**: 381–390.