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Diversification along environmental gradients in spatially structured populations

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ABSTRACT

Questions: Does frequency-dependent and spatially localized competition in geographically structured populations generate phenotypic diversification in the form of multimodal phenotype distributions? Is such pattern formation an artifact of the boundary conditions assumed for numerical simulations? Do environmental gradients facilitate phenotypic diversification, and how does the slope of the environmental gradient influence this facilitation?

Mathematical methods: We solve numerically partial differential equations models for the dynamics of density distributions of phenotypically varying populations that occupy a continuous geographical area.

Key assumptions: We assume a linear spatial gradient in the optimal phenotype for the stabilizing component of selection (carrying capacity). To address the role of boundary conditions, we use two types of models. First, we use models in which the carrying capacity declines to 0 in both the phenotypic and the spatial dimensions as the corresponding coordinates become either large or small enough. Second, we use models with periodic boundary conditions in both the phenotypic and the geographical dimensions. For sexual populations, we assume assortative mating without Allee effects.

Conclusions: Multimodal pattern formation in phenotype space – that is, phenotypic diversification and speciation – is a robust outcome of models incorporating frequency-dependent and spatially localized competition in geographically structured populations. Also, spatial gradients in the optimal phenotype lead to a facilitation of diversification. Confirming earlier results from individual-based models, this facilitation appears to be most pronounced for gradients of intermediate slopes. The pattern formation observed in our models is not an artifact of boundary conditions.

Keywords: adaptive speciation, diversification, environmental gradients,
partial differential equations, spatially structured populations.

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INTRODUCTION

The role of spatial structure for evolutionary diversification and speciation is a classic topic in evolutionary biology (Endler, 1977). Recent studies of the evolution of quantitative traits along an environmental gradient revealed that frequency-dependent competition in trait space and local competition in geographical space can lead to clustering in phenotype space in the form of multimodal trait distributions (Doebeli and Dieckmann, 2003; Mizera and Meszéna, 2003). The formation of multimodal trait distribution due to frequency-dependent selection is called 'adaptive diversification' or, in sexual populations with assortative mating, 'adaptive speciation' (Dieckmann *et al.*, 2004). It has also been shown that environmental gradients in spatially structured populations can facilitate adaptive diversification, in that speciation occurs over a significantly wider range of parameters determining the strength of frequency-dependent phenotypic competition than in unstructured populations (Doebeli and Dieckmann, 2003). However, it has been argued by Polechová and Barton (2005) that the phenotypic clustering observed in these models is an artifact of the boundary conditions chosen for the numerical implementation of the models, and that, for example, in infinite systems, in which boundaries are absent, a gradual environmental cline will lead to gradual, rather than clustered, variation in trait space. The results and conclusions in Polechová and Barton (2005) were obtained from partial differential equations (PDE) models for asexual populations with commonly used Gaussian functions describing frequency-dependent competition in trait space and localized competition in geographical space. For such competition kernels, the corresponding PDE models for asexual and spatially unstructured populations also do not yield multimodal phenotype distributions (Gyllenberg and Meszéna, 2005; Polechová and Barton, 2005; Doebeli *et al.*, 2007). Later, Leimar *et al.* (2008) presented numerical results as well as analytic approximations for spatial PDE models of asexual populations to show that, similar to the non-spatial case, Gaussian competition kernels do indeed not lead to phenotypic clustering, but that PDE models with platykurtic competition kernels, which are more 'box-like' than the Gaussian models, do indeed produce phenotypic clustering even in infinite systems.

Here we contribute further to resolving the controversy regarding whether cluster formation is an intrinsic property of spatially structured populations experiencing an environmental gradient or an artifact of boundary conditions. To achieve this goal, we use PDE models for both asexual and sexual spatially structured populations and for the following two scenarios:

- There is a carrying capacity with finite range in both trait and geographical space. This makes the population density decrease towards 0 within a finite range, and hence renders the actual form of the boundary conditions irrelevant, provided that the system size is significantly larger than the range of the carrying capacity.
- Periodic boundary conditions are implemented in both trait and geographical space. When the system size is significantly larger than the range of competition, these boundary conditions effectively mimic an infinite system.

We observed that:

- In asexual populations, cluster formation in trait space does not occur in either the system with finite-range carrying capacity or the system with periodic boundary conditions if the competition kernels are Gaussian. However, cluster formation does occur in both systems if the competition kernels are platykurtic enough [for infinite systems, this confirms the results of Leimar *et al.* (2008)].

- In sexual populations with assortative mating, cluster formation in trait space can occur even for Gaussian competition kernels in both the system with finite-range carrying capacity and the system with periodic boundary conditions. This extends the findings of Doebeli *et al.* (2007) to spatially structured sexual populations. Using our PDE models, we also confirm the findings of Doebeli and Dieckmann (2003), obtained using stochastic individual-based models, that environmental gradients can greatly facilitate diversification in spatially structured populations, and that this facilitation is most pronounced for intermediate slopes of the environmental gradient.

Overall, these results shows that multimodal cluster formation in phenotype space is a robust outcome in spatially structured populations with an environmental gradient, and that the existence of such clustering is not an artifact of boundary conditions.

MODEL DEFINITION

We consider a deterministic model describing the dynamics of the density distribution of an infinite population. This population is characterized by a one-dimensional quantitative trait x and lives along an environmental gradient with one-dimensional coordinate z denoting the spatial position. The local density of individuals with trait x and spatial position z at time t is denoted by $n\ (x, z, t)$ and changes according to the following deterministic partial differential equation:

$$\begin{aligned}\frac{\partial n(x, z, t)}{\partial t} &= \int \phi_a(x' - x) b(x', z, t) dx' \\ &- \frac{n(x, z, t)}{K(x, z)} \iint \phi_x(x' - x)\, \phi_z(z' - z) n(x', z', t) dx'\, dz' \\ &+ m\left[\int \phi_m(z' - z) n(x, z', t) dz' - n(x, z, t)\right]. \qquad (1)\end{aligned}$$

The first term on the right-hand side of this equation describes birth events, which occur with the standardized rate of 1 per capita (which defines the time unit), and $b(x, z, t) = n(x, z, t)$ for an asexual population (see below for sexual populations). The offspring produced during birth events are offset from the ancestor trait x' by a mutation of size $x - x'$ that is distributed with probability density $\phi_a(x' - x)$. The second term on the right-hand side denotes the rate of death of the individuals at (x, z) from the competition between them and the rest of the population. The strength of competition between an individual at x, z and another individual with a different trait and spatial location x', z' is quantified by the product of two competition kernels, $\phi_x(x' - x)\ \phi_z(z' - z)$, where $\phi_x(x' - x)$ describes frequency-dependent competition in phenotype space, and $\phi_z(z' - z)$ describes local competition in geographical space. The death rate is also inversely proportional to the carrying capacity K, which is given by a product of Gaussian functions, $K(x, z) = K_0 \exp[-(x - \alpha z)^2/2\sigma_K^2] \exp[-z^2/2\sigma_{KZ}^2]$. The first Gaussian in K describes the decrease of the carrying capacity with increasing phenotypic distance from the optimal phenotype, which varies linearly with spatial location z. Thus, at each spatial location the optimal phenotype is given by αz, and this variation constitutes the linear environmental gradient (Doebeli and Dieckmann, 2003, 2004; Leimar *et al.*, 2008). The second Gaussian in K describes the finite range of the carrying capacity in geographical space. Infinite geographical range of the carrying capacity, as used in Doebeli and Dieckmann (2003), Polechová and Barton (2005), and Leimar *et al.* (2008), corresponds to the limit $\sigma_{KZ} \to \infty$. Finally, the third term on the right-hand side of equation (1) describes the migration of individuals in geographical space (i.e. along the z-axis), which is given by the migration rate m and by the assumption that the migration distance $z - z'$ is distributed with probability density $\phi_m(z)$.

The main difference between our model and the evolutionary systems considered in Doebeli and Dieckmann (2004), Polechová and Barton (2005), and Leimar *et al.* (2008) is in the form of the boundary conditions. We considered two scenarios. In the first, the boundary conditions were made irrelevant by using finite σ_{KZ} and a sufficiently large system for the numerical simulations of the partial differential equations (usually $z_{\max} > 4 \times \sigma_{KZ}$). Alternatively, we used periodic boundary conditions, in which case following Polechová and Barton (2005) we chose large values of x_0 and z_0 such that all integrations in equation (1) were carried out within the limits $\int_{x-x_0}^{x+x_0} \ldots dx'$ and $\int_{z-z_0}^{z+z_0} \ldots dz'$ and it was postulated that for $x > x_0$ and $z > z_0$, $n(x, z) \equiv n(x - 2x_0, z - 2z_0)$, and similarly for $x < -x_0$ and $z < -z_0$, $n(x, z) \equiv n(x + 2x_0, z + 2z_0)$.

Even though there are minor differences concerning the mutation and migration terms, equation (1) is essentially the same as the PDE models studied by Doebeli and Dieckmann (2004), Polechová and Barton (2005), and Leimar *et al.* (2008). To study the dynamics of the density distribution $n(x, z, t)$, we solved rate equation (1) numerically. A simple Euler time update scheme has been used together with the trapezoidal integral evaluations method. Discretization in x and z spaces was always kept finer, by at least a factor of two, than the width of the narrowest kernels in equation (1).

ASEXUAL POPULATIONS

We observed that after a fairly short transitory period, the population density usually converged to a steady state that was independent of the initial conditions. We classified these steady states as *unimodal* when they consisted of either a central 'peaked' ridge along the environmental gradient in systems with a finite spatial range of carrying capacities, or of 'cline-like' infinite ridges along the environmental gradient (Leimar *et al.*, 2008) in systems with periodic boundary conditions. Alternatively, an equilibrium state was called *multimodal* if it consisted of two or more peaks in phenotype space (i.e. along the phenotypic axis).

We explored the nature of the equilibrium density distribution for several-fold variation of parameters of equation (1) and for different functional forms of the competition kernels $\phi_x(x)$ and $\phi_z(z)$ (i.e. for different ε, see below). For asexual populations, the general trends that, according to our observations, exist for a wide range of parameters can be summarized as follows. First, for Gaussian competition kernels, i.e. $\phi_x(x) = 1/(\sqrt{2\pi}\sigma_x)\ \exp(-x^2/2\sigma_x^2)$ and $\phi_z(z) = 1/(\sqrt{2\pi}\sigma_z)\ \exp(-z^2/2\sigma_z^2)$, the population distribution converged to a unimodal form for both the finite-range carrying capacity and periodic boundary conditions, as illustrated in Fig. 1. This is also true for the competition kernels that are 'close' to the Gaussian form, having the form $\propto \exp[-|x/\sigma_x|^{2+\varepsilon}/2]$ with $\varepsilon \ll 1$, and similarly for $\phi_z(z)$.

Second, for distinctly non-Gaussian, platykurtic competition kernels, i.e. when $\phi_x(x) \propto \exp[-|x/\sigma_x|^{2+\varepsilon}/2]$ and $\varepsilon > 1$ (and similarly for the spatial competition kernel $\phi_z(z)$), the population density converges to a multimodal form even for rather narrow carrying

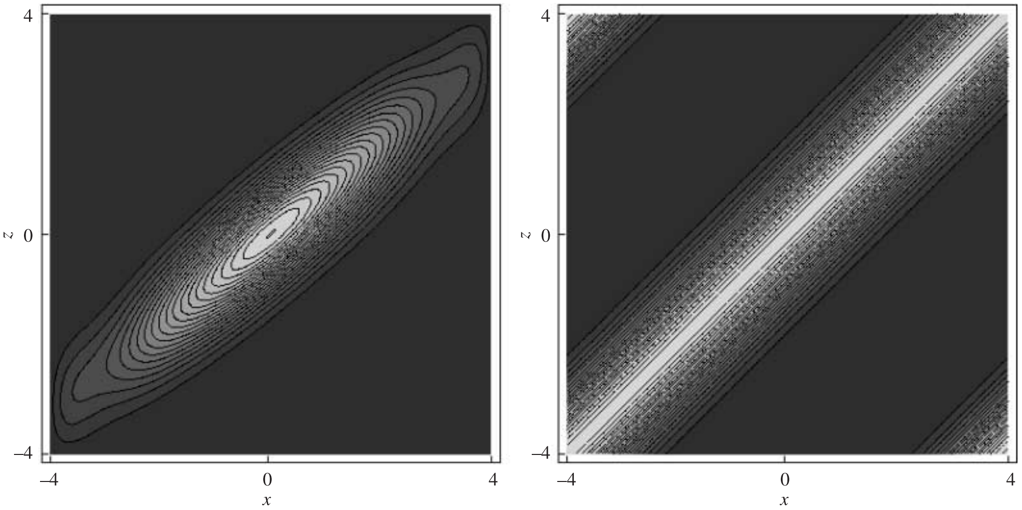

Fig. 1. Unimodal population density for the Gaussian competition kernel and $\sigma_{KZ} = 0.8$ (left) and periodic boundary conditions (right). Other parameter values were $m = 5$, $K_0 = 1$, the mutation and migration kernels $\phi_a(x)$ and $\phi_m(x)$ were Gaussian, $1/(\sqrt{2\pi}\sigma)\exp(-x^2/2\sigma^2)$ with the widths $\sigma_a = 0.05$ and $\sigma_m = 0.2$, competition kernels $\phi_x(x' - x)$ and $\phi_z(z' - z)$ were Gaussian with widths $\sigma_x = \sigma_z = 1$, and the slope of the environmental gradient was $\alpha = 1$.

capacity widths, as illustrated in Fig. 2. Again, this holds for both the systems with finite spatial carrying capacity and periodic boundary conditions.

SEXUAL POPULATIONS

Here we investigate an extension of the model (1) to sexual populations. We consider a spatial extension of the the sexual birth term used in Doebeli *et al.* (2007):

$$b(x, z, t) = \iiiint \delta[x - (x_1 + x_2)/2]\delta[z - (z_1 + z_2)/2]$$
$$\times \frac{n(x_1, z_1, t)n(x_2, z_2, t)\,\phi_{AX}(x_1 - x_2)\phi_{AZ}(z_1 - z_2)}{\iint n(x_3, z_3, t)\,\phi_{AX}(x_1 - x_3)\,\phi_{AZ}(z_1 - z_3)dx_3dz_3}\,dx_1dz_1dx_2dz_2. \qquad (2)$$

This term incorporates birth of an offspring with trait value x and spatial location z from two parents with trait values x_1 and x_2 and coming from spatial locations z_1 and z_2. Before convolution with the segregation kernel (which is described by the first line in equation 1), the offspring has a trait value equal to the mean of the parental traits. The spatial position of the offspring is equal to the average of the parental spatial positions. This is expressed by two delta-functions in the first row of equation (2). The product of the phenotypic and spatial assortative mating kernels, $\phi_{AX}(x)$ and $\phi_{AZ}(z)$, describes the probability of mating between parents that are separated by a trait distance x and geographical distance z. The denominator in equation (2) accounts for the normalization that makes the reproduction rate the same for all parent individuals (and equal to one per capita as in the asexual case). This ensures that there is no cost to assortment in the form of Allee effects and will be assumed throughout. We assumed that the assortative mating kernels $\phi_{AX}(x)$ and $\phi_{AZ}(z)$ are

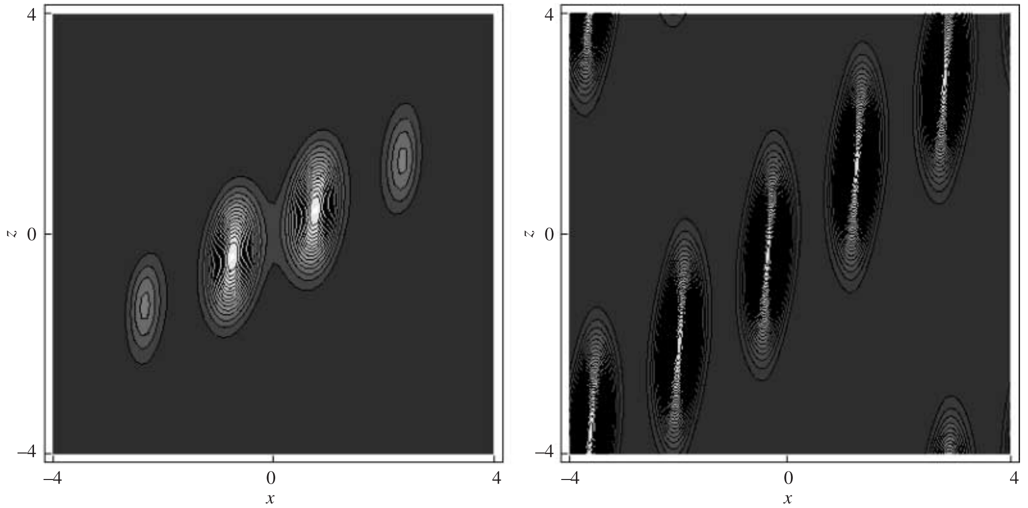

Fig. 2. Multimodal population density for non-Gaussian competition kernel of the form $C/\sigma \exp[-|x/\sigma|^{2+\varepsilon}/2]$ with $\varepsilon = 1$ and $\sigma_{KZ} = 1$ (left) and $\varepsilon = 2$ with periodic boundary conditions (right). Other parameter values as for Fig. 1.

Gaussian. When the assortative widths σ_{AX} and σ_{AZ} become negligible, the model is reduced to the asexual case considered above. In the sexual model, the expression for $b(x, z, t)$ given by equation (2) has to be inserted into equation (1) as the birth term, which is then convoluted with the segregation kernel, which replaces the mutation kernel in the asexual model. Thus, in the sexual model the segregation kernel describes the phenotype distribution of offspring born to parents with different trait values (Doebeli *et al.*, 2007). Our model assumes constant widths of the segregation kernels, which corresponds to assuming constant additive genetic variance. This is at best an approximation, as it is known that genetic variances can change in the course of evolution. If one had an underlying mechanistic model for the genetic architecture generating offspring distributions (such as multi-locus additive genetics), it would be possible to incorporate changing segregation variances into the model. However, if the interval of genetically possible trait values is much larger than the interval of ecologically feasible trait values, and if negative frequency-dependent selection on these traits – and hence variation on the underlying loci – is maintained, a constant segregation variance seems a permissible simplifying assumption.

It was observed by Doebeli *et al.* (2007) that non-spatial models for frequency-dependent competition in sexual populations exhibit trait clustering even with Gaussian competition kernels when the assortative width of the sexual birth term is increased from 0 (i.e. away from the asexual model, in which clustering does not occur with Gaussian competition kernels). The same effect is observed in the two-dimensional trait–geographic models considered here: when the assortative widths in both trait and geographical dimensions become comparable or larger than the corresponding segregation and migration widths, the unimodal equilibrium distributions become unstable and the system instead converges to multimodal equilibrium distributions, as illustrated in Figs. 3 and 4. (*A fortiori*, similar multimodal equilibrium distributions can be observed for platykurtic competition kernels.)

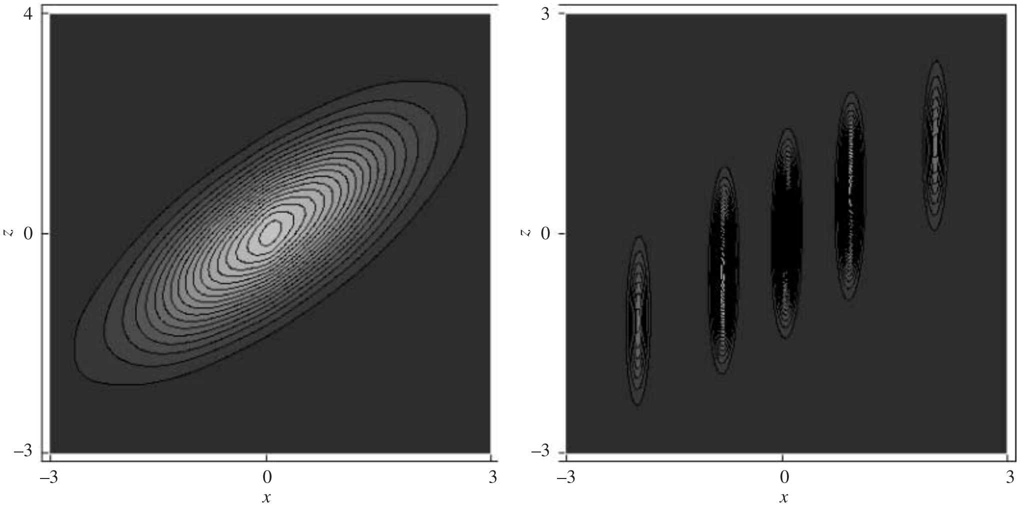

Fig. 3. Equilibrium density distribution in systems with sexual reproduction for finite-range carrying capacity and for assortative widths $\sigma_{AX} = \sigma_{AZ} = 0.05$ (left) and $\sigma_{AX} = \sigma_{AZ} = 0.15$ (right). The model has a finite spatial range of carrying capacity, $\sigma_{KZ} = 1$, and the competition kernels are Gaussian. Other parameter values as in Fig 1.

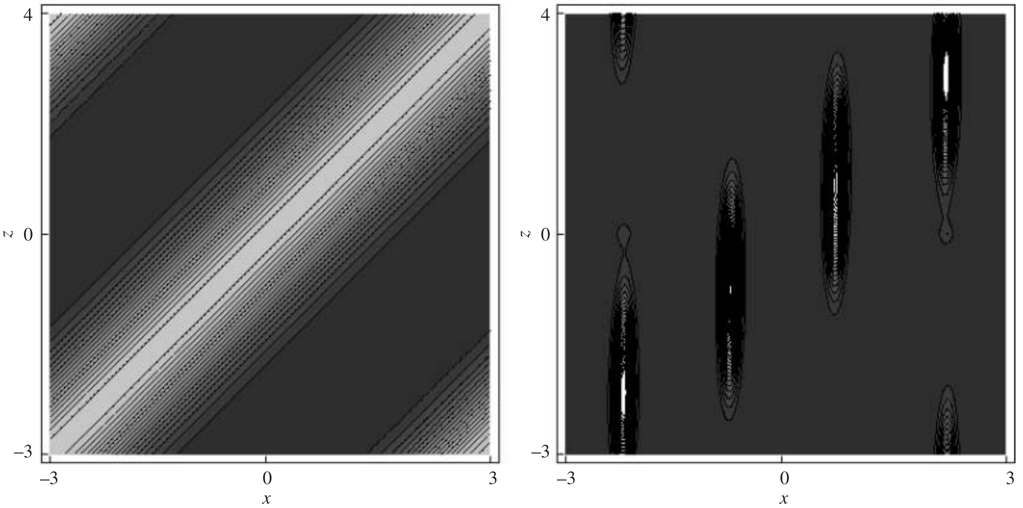

Fig. 4. Equilibrium density distribution in systems with sexual reproduction for periodic boundaries and for assortative widths $\sigma_{AX} = \sigma_{AZ} = 0.01$ (left) and $\sigma_{AX} = \sigma_{AZ} = 0.25$ (right). The competition kernels are Gaussian. Other parameter values as in Fig 1.

ENVIRONMENTAL GRADIENTS FACILITATE SPECIATION

Doebeli and Dieckmann (2003) have argued that environmental gradients in spatially structured populations with local competition facilitate phenotypic diversification, in that phenotypic clustering occurs for a wider range of phenotypic competition parameters in spatial models than in the corresponding non-spatial competition models. In some sense, it is easy to understand why this should be the case. Just as frequency-dependent competition in phenotype space can lead to phenotypic cluster formation, spatially localized competition in geographical space can lead to spatial cluster formation (in fact, the two forms of competition are mathematically equivalent in the models presented here). Thus, even if frequency-dependent competition on phenotypes is weak, sufficiently localized competition (i.e. sufficiently small values of the parameter σ_z) can generate spatial clusters of population density. In the presence of an environmental gradient, these spatial clusters will come to lie along the gradient, and hence the different spatial clusters will correspond to separate phenotypic clusters. In other words, the environmental gradient separates the clusters emerging due to spatially localized competition along the phenotypic axis and hence generates phenotypic diversification even if frequency-dependence is weak in the phenotypic component of competition.

Doebeli and Dieckmann (2003) showed that facilitation of diversification occurs in spatially structured asexual populations, and we investigated whether this phenomenon can also be observed in our PDE models for sexual populations by comparing them with the non-spatial sexual population model of Doebeli *et al.* (2007). Typical findings are illustrated in Tables 1 and 2, for which we first took a given set of parameters for the non-spatial model and determined the threshold value of the phenotypic competition width, σ_x^*, for which the onset of multimodality occurs in non-spatial populations. We then considered corresponding spatial models with finite-range carrying capacity and with different values of the spatial competition parameters σ_z, and again determined the threshold value of the phenotypic competition width, σ_x^*, for which the onset of phenotypic multimodality occurs. (In our spatial models, a phenotypic distribution is considered multimodal if its projection on the phenotypic (x-) axis has at least one minimum.) This was done for different values α for the slope of the environmental gradient in Tables 1 and 2. We note that in both the non-spatial and the spatial models, all kernels were Gaussian. As Tables 1 and 2 illustrate, facilitation of diversification occurs in these spatial models. In fact, if spatial competition is localized enough, for a certain range of slopes of the environmental gradient, phenotypic diversification occurs even in the absence of phenotypic frequency-dependence (i.e. even for very large σ_x), as is apparent from the first columns of Tables 1 and 2.

It is intuitively clear that when spatial competition is localized enough, increasing the slope of the environmental gradient leads to increasing facilitation of phenotypic diversification: if the slope is too close to 0, phenotypic diversification through separation of the spatial clusters along the phenotypic axis does not occur, whereas steeper slopes make it easier to separate the spatial clusters along the phenotypic axis. Note that the model with zero slope is equivalent to the non-spatial case. What is less clear is why facilitation of phenotypic diversification should decrease again when the environmental gradient becomes very steep, i.e. why facilitation is greatest for some intermediate slope of the environmental gradient, as reported by Doebeli and Dieckmann (2003). In fact, this phenomenon is also confirmed by the results from our PDE models for sexual populations, as is shown in Tables 1 and 2. In Table 1, for which the slope of the gradient was $\alpha = 1$, facilitation is more pronounced than in Table 2, for which $\alpha = 2$. We even observe that for very wide spatial competition widths and very steep slopes, the phenotypic diversification is inhibited (right column of Table 2).

We think that the reason for this is an interaction between the environmental gradient and the spatial cluster formation. Specifically, as the gradient gets steeper, the spatial extension of each individual spatial cluster shrinks, because the margins of a given spatial

Table 1. Threshold value of trait competition width σ_x^*, below which phenotypic clusters emerge in the spatial PDE models for sexual populations, as a function of spatial competition width σ_z for the gradient coefficient $\alpha = 1$

σ_z	0.5	1	2
σ_x^*	∞	2	1.1

Note: Other parameter values were $\sigma_{AX} = 0.15$, $\beta = 1$, $m = 1$, $K_0 = 1$, $\sigma_a = 0.05$, $\sigma_{AZ} = 0.15$, $\sigma_m = 0.2$, $m = 5$, and $\sigma_{KZ} = 1$. In the corresponding non-spatial sexual models, multimodal equilibrium distributions occur for the competition width below the threshold of $\sigma_x^* \approx 1$.

Table 2. Threshold value of trait competition width σ_x^*, below which phenotypic clusters emerge in the spatial PDE models for sexual populations, as a function of spatial competition width σ_z for the gradient coefficient $\alpha = 2$

σ_z	0.5	1	2
σ_x^*	∞	1.25	0.75

Note: Other parameter values as for Table 1.

cluster become increasingly maladapted due to the steep gradient. Thus, the gradient may have an effect on the size of the spatial clusters, which may in turn influence the spatial cluster formation itself, because narrower spatial clusters leave room for the emergence of new clusters that lie between two clusters that already exist. This may eventually destroy the spatial pattern, and hence also the phenotypic pattern.

CONCLUSIONS

In this paper, we have used partial differential equations models to investigate the dynamics of density distributions of phenotypically variable populations that occupy a continuous geographical area with a linear environmental gradient. We have considered both asexual populations and sexual populations with assortative mating. Our main focus was on the question of phenotypic diversification, i.e. on multimodal pattern formation in phenotype space. It has previously been claimed that such models would not lead to pattern formation in phenotype space, and that pattern formation observed in related models was an artifact due to boundary conditions. We find that these claims are invalid in general.

We used two types of models in which boundary conditions do not play a role: either the models had a finite spatial range of carrying capacities, in which case a finite system size can be chosen large enough so that population densities are essentially 0 at the system boundaries, or the models had periodic boundaries, and hence represented an essentially infinite system. In both types of models, we find that pattern formation does not occur in asexual populations in which competition kernels are Gaussian. However, pattern formation does occur in sexual populations with Gaussian competition kernels and with intermediate degrees of assortative mating, and in asexual populations with sufficiently platykurtic competition kernels. Thus, phenotypic diversification is a robust feature in these models that is not an artifact of boundary conditions. All our results are in basic agreement with previous findings for both spatial and non-spatial models (Doebeli and Dieckmann, 2003, 2004; Polechová and Barton, 2005; Doebeli *et al.*, 2007; Leimar *et al.*, 2008). However, this paper represents the first investigation of PDE models for spatially structured sexual populations with assortative mating. For such models, we confirm earlier results for asexual models showing that the interaction of environmental gradients and spatially localized competition can facilitate phenotypic diversification, and that this phenomenon is most pronounced for intermediate slopes of the environmental gradient. Overall, our results show that multimodal pattern formation in phenotype space, i.e. phenotypic diversification and speciation, is a robust outcome of models incorporating frequency-dependent and spatially localized competition in geographically structured populations, and that spatial gradients in the optimal phenotype lead to a facilitation of such diversification, which appears to be most pronounced for gradients of intermediate slopes. By the construction of our models, the results are not artifacts of boundary conditions.

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