Robustness of Spontaneous Pattern Formation in Spatially Distributed Genetic Populations

M.A.M. de Aguiar[1,2], M. Baranger[2,3], Y. Bar-Yam[2,4], and H. Sayama[5]

[1] *Instituto de Física Gleb Wataghin, Universidade Estadual de Campinas, 13083-970 Campinas, São Paulo, SP, Brazil*

[2] *New England Complex Systems Institute, Cambridge, Massachusetts 02138, USA*

[3] *Physics Department, University of Arizona, Tucson, Arizona 85721, USA*

[4] *Department of Molecular and Cellular Biology, Harvard University, Cambridge, MA 02138, USA*

[5] *Department of Human Communication, University of Electro-Communications, Chofu, Tokyo 182-8585, Japan*

Spatially distributed genetic populations that compete locally for resources and mate only with sufficiently close neighbors, may give rise to spontaneous pattern formation. Depending on the population parameters, like death rate per generation and size of the competition and mating neighborhoods, isolated groups of individuals, or demes, may appear. The existence of such groups in a population has consequences for genetic diversity and for speciation. In this paper we discuss the robustness of demes formation with respect to two important characteristics of the population: the way individuals recognize the demarcation of the local neighborhoods and the way competition for resources affects the birth rate in an overcrowed situation. Our results indicate that demes are expected to form only for sufficiently sharp demarcations and for sufficiently intense competition.

I Introduction

Animals don't live completely free in the wild because their living space is confined by natural boundaries. The size of the area used is determined often by individual and species needs and environmental limitation. Within the geographic distribution of the species, the *range*, only areas of suitable habitat are occupied.

The living area normally inhabited by an animal is its *Home Range*. It may belong to a single individual, a mated pair, or a social unit. Within the home range there is often a defended area which is identified as a *territory*. Typical behavior is usually associated with establishing and defending or protecting the animal's territory. This behavior and the reproductive behavior associated with the territory is unique for each species, and allows several different animal species to live in the same space without rivalry, using different niches within the habitat. Territories are marked so that other members of the species can recognize it. Optical, acoustic, or olfactory cues, or a combination of these are often used. Olfactory demarcation is very common among mammals with a well-developed sense of smell. Urine, feces and products of special scent glands are used alone or in conjunction to mark out the territory.

Theoretical biologists have become increasingly aware of the importance of space in ecology, evolution and epidemiology. Home ranges and territories have become important parameters in mathematical models of population dynamics [1, 2]. It has also become apparent that inhomogeneities in spatially distributed populations can fundamentally change the dynamics of these systems [3-10]. The spatial variations so common to species in the wild, for instance, is usually attributed to variations in selective forces, i.e., differences in the environment. However, it has been shown that spatially distributed systems can develop inhomogeneity through symmetry breaking and spontaneous pattern formation, independently of environmental inhomogeneity [11, 12]. Understanding the mechanisms that may lead to spatial inhomogeneities, and the eventual isolation of groups, is of fundamental importance for the study of genetic diversity and speciation [14-18].

In a previous paper [12] we studied the process of pattern formation in spatially distributed evolutionary processes using a model involving population density variations and genetic variations. The main ingredient of the model is the assumption that individuals mate and compete for resources only locally. The competing neighborhood can be associated with the territory. The mating neighborhood is a different range, where the individual looks for a mate. The size of these neighborhoods play a crucial role in the spatial equilibrium configuration attained by the system. In this paper we show that, in fact, it is not only the size of these neighborhoods that matters, and we explore the way neighborhoods are identified by the individuals as a key element in the formation of isolated groups.

We also analyze the effects of crowding in pattern formation. As the local population grows above the average site capacity, individuals start to die by lack of food. We model the effects of crowding by decreasing the birth rate at large population densities. The specific way this happens, however, may differ from species to species. Here

we consider three different types of what we call *crowding functions* and study their influence in the process of pattern formation. We are interested in studying the robustness of these patters with respect to variations in the crowding functions and the sharpness of the boundaries. What we mean by robustness with respect to a parameter or function is that the patterns continue to appear if the parameter or function is modified slightly.

Our main conclusion is that isolated groups, or demes, form only if competition for resources is sufficiently intense, in the sense that lack of resources implies a drastic reduction of the birth rate, and if territories are marked sufficiently sharply. If territory boundaries are too fuzzy, the overlap between demes leads to a single homogeneous group. In order to focus on the population density, we shall simplify the genetic variations enormously, taking only four interbreeding genomes with equally fit genotypes.

The paper is organized as follows: in section II we describe our model, in section III we discuss the spatially homogeneous solutions, and in section IV we study their stability as function of the several parameters describing the population behavior. Demes arise when these homogeneous solutions become unstable. We check our analytical findings with numerical simulations of the spatial model. In section V we summarize our conclusions.

II Model

We consider a population distributed over a large two-dimensional region. For the sake of computational convenience, space will be considered discrete, and the population located in a square lattice with periodic boundary conditions. We use the notation $\vec{r}$ or $\vec{r}_{ij} = (x_i, y_j)$ for a point on the 2-D lattice. The local population densities on each site of the grid consists of non-negative real numbers with no predefined upper bound.

For most living organisms the genome contains thousands of genes. Here we shall focus on only two genes, each of which is assumed to have only two alleles. The individuals reproduce sexually, so that one copy of each gene is inherited from each of the parents. Representing the alleles by the symbols $+$ and $-$, we have four possible genotypes: $[+, +]$, $[+, -]$, $[-, +]$ and $[-, -]$. The genotypes can represent either a two-locus haploid genetics where gene recombination is enforced in every mating, or one-locus diploid genetics if $[+, -]$ and $[-, +]$ are identified with each other. For simplicity we assume that any pair of individuals can mate to produce offspring, i.e., we make no distinction between males and females. We use the notation $n_{\alpha\beta}(\vec{r})$ or $n_{\alpha\beta}^t(\vec{r})$ to denote the population of genotype $[\alpha, \beta]$ at site $\vec{r}$ and time t. $n(\vec{r})$ or $n^t(\vec{r})$ is used for the total population.

The population at each site is updated at discrete time intervals. At each time step (breeding season), offspring are born and part of the previous population dies. Sexual reproduction between individuals introduces genetic mixing. We assume that individuals mate preferentially with nearby members of the population, i.e., mating takes place within local *mating neighborhoods* that range over several sites. Genetic mixing, therefore, occurs only locally. The total number of offspring born per site per breeding season is bounded by the introduction of an intrinsic carrying capacity, modeling a limitation of resources for reproduction.

Finally, competition for finite resources also takes place locally, within *competition neighborhoods*, ranging again over several sites, but whose size may be different from that of the mating neighborhoods.

The general form of the iterative equation for the local population on each site is

$$
\begin{aligned}
n'_{\alpha\beta}(\mathbf{r}) &= \sigma_{\alpha\beta}\, n_{\alpha\beta}(\mathbf{r}) + \lambda_{\alpha\beta}\, \langle n(\mathbf{r})\rangle_M \frac{\langle n_{\alpha*}(\mathbf{r})\rangle_M}{\langle n(\mathbf{r})\rangle_M} \frac{\langle n_{*\beta}(\mathbf{r})\rangle_M}{\langle n(\mathbf{r})\rangle_M} f(\langle n(\mathbf{r})\rangle_C) \\
&= \sigma_{\alpha\beta}\, n_{\alpha\beta}(\mathbf{r}) + \frac{\lambda_{\alpha\beta}\, \langle n_{\alpha*}(\mathbf{r})\rangle_M\, \langle n_{*\beta}(\mathbf{r})\rangle_M}{\langle n(\mathbf{r})\rangle_M} f(\langle n(\mathbf{r})\rangle_C)
\end{aligned}
\tag{1}
$$

where $\sigma_{\alpha\beta}$ is the survival rate of the parents, $\lambda_{\alpha\beta}$ is the reproductive rate, M is the mating neighborhood, C is the competition neighborhood, $n_{\alpha*} = n_{\alpha+} + n_{\alpha-}$, $n_{*\beta} = n_{+\beta} + n_{-\beta}$. The prime on the left-hand-side indicates the population at time $t + 1$ and the angular brackets denote average over the indicated neighborhood. The function f on the right-hand-side is the crowding function. Its role is to limit the average population over the competition neighborhood C. We shall discuss the crowding function and the neighborhood types shortly. The genetic composition of the newborns is determined by the product of two allelic probabilities averaged within the mating neighborhood.

In this model, the concept of 'site capacity' is replaced by that of average site capacity, in such a way that when the average population around a certain site becomes closer to a critical value, individuals start to die by lack of food. In our previous work [12] we modeled the crowding function by a logistic type of function, namely $f(\langle x \rangle) = 1 - \langle x \rangle / K$, where K is the site capacity parameter. This function multiplies the birth rate. When the average population around a site, $\langle x \rangle$, is much smaller than K, f is very close to 1 and has essentially no effect. As $\langle x \rangle$ gets close to K, f decreases to near zero, cutting off drastically the birth rate. The actual form of the crowding function is an important characteristic

of the population being considered. Here we shall only consider simple functions to model competition, but that will be enough to highlight the importance of f in the process of pattern formation. To simplify the notation we shall measure populations in units of the site capacity, which amounts to make $K = 1$ in all equations.

The average value $\langle x \rangle$ can be defined in a number of ways. In our original work [12] this average was computed using the so called characteristic function of the neighborhood, which is 1 for points inside a certain radius around the site and 0 for points outside. However, sharp boundaries are not likely to occur in practice, and the definition of territorial boundaries might vary from organism to organism. We have shown, in particular, that Gaussian averages never lead to the formation of demes for a logistic type of crowding function. We shall show in this paper that the sharpness of boundaries turns out to be a crucial parameter for pattern formation.

As a last remark we emphasize the role of the model parameters to the issue of territoriality. The size and shape of the competition neighborhood C defines the individual's territory. The mating neighborhood M defines the area around the home range where the individual looks for a mate (in the case of birds this is also termed the *breeding dispersal* range, and it usually larger than the territory [18]). We shall describe neighborhoods by a two-parameter family of functions, containing information about the size of the range *and* sharpness of the range boundaries. We shall focus on the neighborhood sharpness, keeping the sizes fixed. Finally, the crowding function controls the *effectiveness* of competition, i.e., how the birth rate decreases when the population grows close to the site capacity. As examples, we shall consider three types of crowding functions.

II.1 The Flat Fitness Case

Our main goal here is to investigate the role of competition in the process of demes formation. In order to focus on this issue we shall restrict ourselves to the *flat fitness* case, where all types have identical death and birth rates. In this case the only relevant parameter is the total population $n = n_{++} + n_{--} + n_{+-} + n_{-+}$ and the dynamical equation for n simplifies to

$$n'(\vec{r}) = \sigma n(\vec{r}) + \lambda \langle n(\vec{r}) \rangle_{R_M} f(\langle n(\vec{r}) \rangle_{R_C}) . \quad (2)$$

II.2 The Crowding Function

In our model, competition acts through two separate mechanisms: the crowding function f, which controls how the birth rate decreases when the population increases beyond the average site capacity, and the competition neighborhood itself. The crowding function has to satisfy $f(0) = 1$ and $f(x) < 1$ for $x > 0$. We shall consider three types of

functions here:

$$f(x) = \begin{cases} 1 - x & if & x < 1 \\ 0 & if & x > 1 \end{cases} \quad \text{(Logistic)}$$

$$f(x) = e^{-x} \quad \text{(Exponential)}$$

$$f(x) = e^{-x^2} \quad \text{(Gaussian)} \quad (3)$$

II.3 Neighborhoods

The average of $n(\vec{r})$ depends on the definition of the neighborhoods. Since space is homogeneous and isotropic, we restrict ourselves to circular neighborhoods. We write

$$\langle n(\vec{r}) \rangle_R = \int_0^\infty n(\vec{r'}) \rho_R(r - r') 2\pi r' dr' \quad (4)$$

with

$$2\pi \int_0^\infty \rho_R(r) r dr = 1 . \quad (5)$$

ρ is the averaging, or smoothing, function. It tells how sharply the territorial boundaries are identified by the individuals. Sharp boundaries correspond to taking ρ as the characteristic function of the neighborhood R:

$$\rho_R(r) = \frac{1}{\pi R^2} \begin{cases} 1 & if & r \le R \\ 0 & if & r > R . \end{cases} \quad (6)$$

In order to generalize the way the averages are performed, and therefore the way territories are marked, we define the two-parameter family of smoothing functions

$$\rho_{R,\alpha}(r) = N \frac{1}{1 + e^{(r-R)/\alpha}} \quad (7)$$

with normalization

$$N^{-1} = 2\pi \int_0^\infty \frac{r dr}{1 + e^{(r-R)/\alpha}} = -2\pi\alpha^2 PolyLog[2, -e^{\alpha/R}] \quad (8)$$

where

$$PolyLog[2, z] = \sum_{k=1}^\infty \frac{z^k}{2^k} . \quad (9)$$

α is the smoothing parameter. It is zero for the sharp average, Eq.(6). As α grows from zero the neighborhood's boundary becomes more and more diffuse.

III   Homogeneous Solutions

Homogeneous (space independent) solutions satisfy the dynamical equation

$$n' = \sigma n + \lambda n f(n) . \quad (10)$$

There are two stationary solutions, where $n' = n$:

$$n_0 = 0 \quad \text{(extinction)} \quad (11)$$

and

$$f(n_0) = \frac{1 - \sigma}{\lambda} \quad \text{(thriving)} . \quad (12)$$

The stability of these homogeneous stationary solutions are determined by the behavior of small perturbations. For extinction we write $n = 0 + \delta n$ and obtain, to first order in δn,

$$\begin{aligned} \delta n' &= \sigma \delta n + \lambda \delta n f(0) \\ &= (\sigma + \lambda)\delta n \, . \end{aligned} \quad (13)$$

Therefore extinction is stable if $\sigma + \lambda < 1$ and unstable if $\sigma + \lambda > 1$.

For the second solution we first note that the equation for n_0 can be written $f(n_0) = 1 + (1 - \sigma - \lambda)/\lambda$. Since we assume $f(n_0) < 1$ for $n_0 > 0$, we must have $1 - \sigma - \lambda < 0$. Therefore thriving is possible only if $\sigma + \lambda > 1$. Expanding Eq.(10) around n_0 we obtain

$$\delta n' = \left(1 + \lambda n_0 \frac{\partial f}{\partial n}(n_0)\right) \delta n \, . \quad (14)$$

Since $\partial f/\partial n < 0$, the thriving solution starts stable as $\sigma + \lambda$ grows from 1. The stability range, however, depends of the particular crowding function one uses. For the three functions listed in Eq.(3) we get the following explicit solutions and stability conditions:
(a) Logistic

$$n_0 = (\sigma + \lambda - 1)/\lambda \, , \quad (15)$$

stable if $1 < \sigma + \lambda < 3$.

(b) Exponential

$$n_0 = \log\left[\lambda/(1 - \sigma)\right] \, , \quad (16)$$

stable if $0 < (1 - \sigma) \log\left[\lambda/(1 - \sigma)\right] < 2$.

(c) Gaussian

$$n_0 = \sqrt{\log\left[\lambda/(1 - \sigma)\right]} \, , \quad (17)$$

stable if $0 < (1 - \sigma) \log\left[\lambda/(1 - \sigma)\right] < 1$.

IV   The Dynamics of Demes Formation

Spatial patterns arise when the homogeneous solutions become unstable under small *spatial* perturbations. Let us look for solutions of eq.(2) in the linear approximation, assuming them to be of the form

$$n(\vec{r}) = n_0 + \xi \mu^t s(\vec{r}) \quad (18)$$

where
$$s(\vec{r}) = \sin(vx + \phi) \sin(wy + \psi) \quad (19)$$

represents a spatial perturbation of specific wavelength, μ^t is an exponential time-dependence, possibly complex, and ξ is a small coefficient. We shall insert (18) into (2) and study the change of μ^t over one time-step, to find out under what circumstances n_0 becomes unstable. To do that we need to

calculate the average of the perturbation over the mating and competing territories, $\langle s(\vec{r})\rangle_R$. We find

$$\langle s(\vec{r})\rangle_R = s(\vec{r}) \, A_{R,\alpha}(k) \quad (20)$$

where

$$A_{R,\alpha}(k) = 2\pi \int_0^\infty r J_0(kr)\rho_{R,\alpha}(r)dr \, , \quad (21)$$

with $k = \sqrt{v^2 + w^2}$. The effect of the averaging is to *renormalize* the amplitude of the perturbation. We shall call $A_{R,\alpha}(k)$ the *Amplitude Factor* and we note that it depends on the wavelength of the perturbation.

Inserting Eq.(7) into Eq.(21) we find

$$A_{R,\alpha}(k) = -\frac{1}{\omega^2} \frac{I(r,\omega)}{PolyLog\left(2, -e^{r/\omega}\right)} \quad (22)$$

where

$$I(r,\omega) = \int_0^\infty \frac{u J_0(u)}{1 + e^{(u-r)/\omega}} du \, , \quad (23)$$

$r = Rk$, J_0 is the Bessel function of order zero and $\omega = \alpha k$.

Finally, inserting (18) into (2) and expanding to first order in ξ we obtain an equation for μ after one time-step:

$$\mu = \sigma + (1-\sigma)A_{R_M,\alpha}(k) + \lambda n_0 \frac{\partial f}{\partial n}(n_0) A_{R_C,\alpha}(k) \, . \quad (24)$$

The homogeneous solution n_0 is unstable under spatial perturbations if $\mu > 1$. For the three crowding functions listed in section II we obtain the following conditions for instability:
(a) Logistic

$$\sigma + (1 - \sigma)A_{R_M,\alpha} - (\lambda + \sigma - 1) A_{R_C,\alpha} > 1 \quad (25)$$

or

$$h \equiv 1 - A_{R_M,\alpha} + \frac{\lambda + \sigma - 1}{1 - \sigma} A_{R_C,\alpha} < 0 \, . \quad (26)$$

(b) Exponential

$$\sigma + (1-\sigma)A_{R_M,\alpha} - (1-\sigma)\log\left(\frac{\lambda}{1 - \sigma}\right)A_{R_C,\alpha} > 1 \quad (27)$$

or

$$h \equiv 1 - A_{R_M,\alpha} + \log\left(\frac{\lambda}{1 - \sigma}\right)A_{R_C,\alpha} < 0 \, . \quad (28)$$

(c) Gaussian

$$\sigma + (1 - \sigma)A_{R_M,\alpha} - 2(1 - \sigma)\log\left(\frac{\lambda}{1 - \sigma}\right) A_{R_C,\alpha} > 1 \quad (29)$$

or

$$h \equiv 1 - A_{R_M,\alpha} + 2\log\left(\frac{\lambda}{1 - \sigma}\right)A_{R_C,\alpha} < 0 \, . \quad (30)$$

In the limit of a sharply defined neighborhood, $\alpha \to 0$ (or $\omega \to 0$) we get

$$I(r,0) = \int_0^r u J_0(u)du = r J_1(r) \, , \quad (31)$$

$$\lim_{\omega \to 0}[PolyLog(2, -e^{r/\omega})] = -\frac{1}{2}[\log{(1 + e^{r/\omega})}]^2 = -\frac{r^2}{2\omega^2} \tag{32}$$

and

$$A_{R,0}(k) = \frac{2J_1(r)}{r} \ . \tag{33}$$

Figure 1 shows plots of h as a function of $r = R_m k$ for different values of $\omega = \alpha k$. In all cases $R_M = 5$, $R_C = 10$, $\lambda = 2.0$ and $\sigma = 0.9$. The regions where

$h < 0$ indicate instabilities of the homogeneous distribution. The value of r where the negative minimum occurs, r_0, contains information about the size of the spatial structures that should form as a result of the perturbation. For fixed R_M we find $k_0 \equiv r_0/R_M$ and $\lambda_0 \equiv 2\pi/k_0$ as the critical perturbation wavelength under which the homogeneous solutions become unstable. This is the approximate size of the demes that are formed. From the figures we find $r_0 \approx 2.5$, which gives $\lambda_0 \approx 15$.
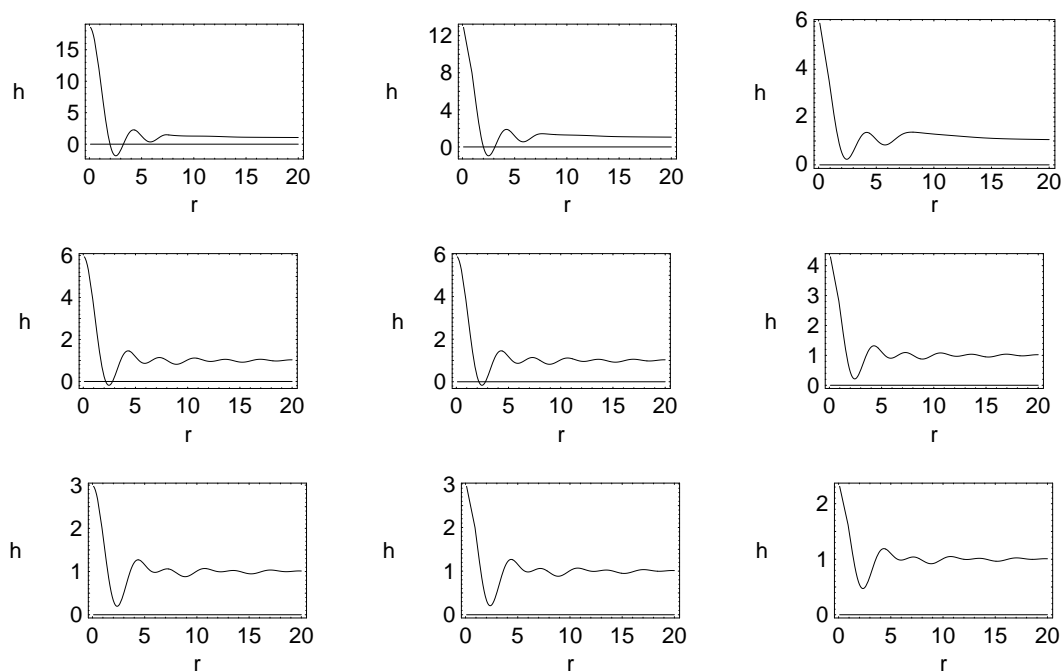

Figure 1. Stability function $h(r)$ for the three crowding functions. Top: logistic function for $\omega = 0.1$, 0.5 and 1.0; Middle: Gaussian function for $\omega = 0.05$, 0.1 and 0.5; Bottom: exponential function for $\omega = 0.05$, 0.1 and 0.5. In all cases $R_M = 5$, $R_C = 10$, $\lambda = 2.0$ and $\sigma = 0.9$.

For the logistic type of competition function (first three plots), the homogeneous solution is stable against perturbations of any wavelength if $\omega \gtrsim 0.8$. Fixing $k_0 = r_0/R_m = 0.5$ we find a critical smoothing parameter $\alpha_0 = \omega/k_0 \approx 1.6$. For the Gaussian competition function the homogeneous solution is stable if $\omega \gtrsim 0.25$, which gives $\alpha_0 \approx 0.5$. Finally, for the exponential function the homogeneous solution is expected to be always stable, completely preventing the appearance of demes.

In order to confirm these predictions we show in Figs. 2 and 3 the results of numerical simulations with our spatial model. We have used a grid of 128 by 128 points with periodic boundary conditions. The initial configuration for the time evolution is the uniform homogeneous solution plus a small random spatial perturbation. All simulations with the exponential crowding function resulted indeed in spatially homogeneous populations and we do not show them here. Fig. 2 corresponds to the logistic crowding function and Fig. 3 to the Gaussian crowding function. In both cases

demes form for α sufficiently small, according to our analytical predictions. The simulations also show that the logistic type of competition leads to faster deme formation than the Gaussian type.

V   Conclusion

The main reason for the existence of territories is competition for finite resources. In the case of animals, competition is usually for food; in the case of plants it may be light. For substrate organisms it may be space [19]. In our previous paper we showed that spatially isolated groups may form spontaneously for populations that mate and compete for resources locally, assuming a logistic type of crowding function and sharp demarcation of territories.

In this paper we have studied the robustness of these isolated groups against changes in the competition functions and sharpness of the local neighborhoods, the home ranges,
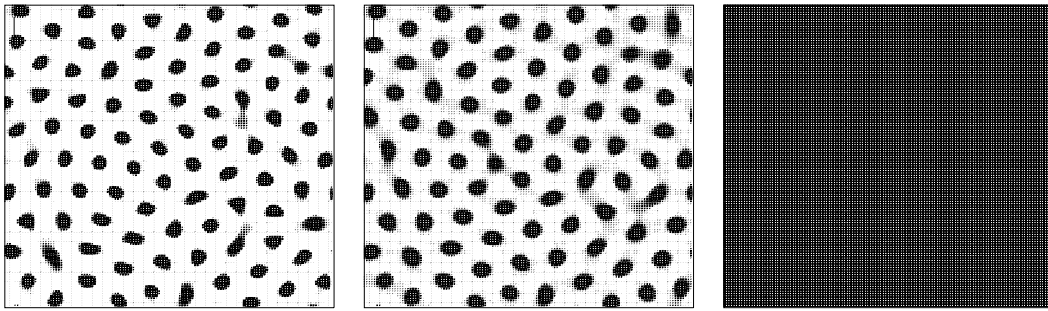
Figure 2. Spatial distribution of the population for the case of a logistic crowding function. From left to right $\alpha = 0.5$, 1.0 and 2.0. Demes are seen in the first two cases, but not the third. The dynamical equations were integrated for T=128 time steps. Space consists of a discrete grid with 128 by 128 points and periodic boundary conditions. The population parameters are the same as in Fig.1.
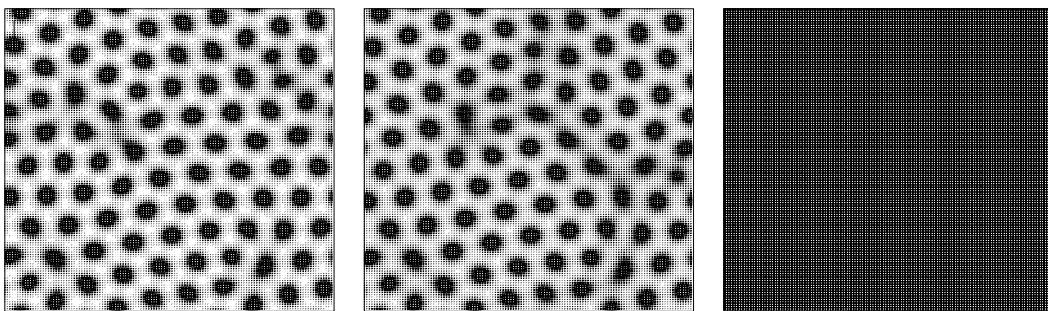

Figure 3. Spatial distribution of the population for the case of a Gaussian crowding function. From left to right $\alpha = 0.1$, 0.5 and 1.0. Demes are seen in the first two cases, but not the third. The dynamical equations were integrated for $T = 512$ for $\alpha = 0.1$ and for $T = 1024$ for $\alpha = 0.5$ and 1.0. Space consists of a discrete grid with 128 by 128 points and periodic boundary conditions. The population parameters are the same as in Fig.1.

as seen by individuals. We have shown that both of these factors can be decisive in defining the population density profile over the species range. If competition is sufficiently intense, the population divides spontaneously into isolated groups. The territory (deme) boundaries are dictated by (average) individual characteristics, such as death and birth rate per generation, and group factors, such as the size, shape and sharpness of local mating and competition neighborhoods. Among the crowding functions considered, the logistic leads to faster formation of demes and is the most robust against changes in the smoothness of the boundaries. But even a logistic type of crowding cannot garantee the formation of demes if the demarcation of territories is too fuzzy.

Once isolated demes are established, genetic mixing between demes is largely reduced, although some mixing might still occur via inter-demes migration [13, 14, 9]. As we have shown in [12], this spatial isolation contributes to the maintenance of genetic diversity in the presence of disruptive selection. In this case, when, for instance, heterozigous individuals $[+, -]$ are less fit than homozigous individuals, $[+, +]$ or $[-, -]$, homogeneous populations tend to be either all $[+, +]$ or all $[-, -]$. When demes form, the population in each deme is still either all $[+, +]$ or all $[-, -]$, but different demes may be inhabited by different types. In the long run, genetic isolation might also lead to genetic divergence, since random mutations are not shared among demes.

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