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Dynamics and spatial organization in two-species competition

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Abstract. We investigate the time evolution of a prototypical population biology reaction which involves reproduction, self-regulation and competitive annihilation of two distinct species. In one dimension, we use a quasistatic analysis to argue that for a system with equal initial densities of two strongly competing species, an alternating pattern of domains forms whose lengths grow logarithmically with time. A scaling analysis of the underlying master equation, as well as numerical integration of the reaction–diffusion equations support this result. For unequal initial densities, the concentration of the minority species undergoes a power-law decay with a non-universal exponent. We generalize the model by allowing for a nonlinear self-regulation term in the rate equations. As a function of the exponent of this nonlinearity, the typical domain size may grow either as a power law with time or saturate at a finite value. Our general approach also suggests that a coarsening domain mosaic occurs in arbitrary spatial dimensions. In two dimensions, numerical integration of the reaction–diffusion equations indicates that the average domain area grows approximately as $t^{0.84}$.

1. Introduction

Spatial heterogeneities play an important role in determining the temporal behaviour of the diffusion-controlled two-species annihilation process $A + B \rightarrow \text{inert}$ [1–4]. For equal initial densities of the two species, a random distribution of reactants evolves into a continuously-coarsening mosaic of A-rich and B-rich domains whose linear dimension grows with time as $t^{1/2}$, when the spatial dimension d is less than 4. This segregation implies that reaction takes place only on domain boundaries, leading to the density decaying with time as $t^{-d/4}$, compared to the mean-field prediction of t^{-1}. There is also a non-trivial spatial variation of the density across a domain, a feature which implies the existence of new characteristic length scales to fully describe the spatial organization of reactants [5].

These results motivate our investigation into the effects of spatial heterogeneities on the temporal evolution and the spatial organization in a generic reaction process which may have relevance for competitive population biology dynamics [6]. The model we investigate involves two species which separately undergo logistic growth (i.e. reproduction and self-regulation), and which annihilate whenever opposite species meet [7]. This system has been previously investigated by Burlatsky and Pronin [8] and we have independently re-derived some of their results. According to the rate equations, if the annihilation is relatively weak, the system eventually reaches a spatially homogeneous co-existing state [7]. On the other hand, if the annihilation

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is sufficiently strong, only one of the two species survives, as long as the initial density difference is not exactly equal to zero. This extinction lends credence to the general principle that only the stronger of the species survives when there is strong competition for limited resources.

Our primary result is that an initially homogeneous distribution of reactants in one dimension evolves into a mosaic of single-species domains which coarsens at a logarithmic rate, in the limit of strong competition and for a diffusion-limited reaction. This conclusion is based on a quasistatic analysis to determine the density profile of a large domain. When a mosaic of domains forms, competition takes place only on the domain boundaries, leading to an extinction time for the smaller domain which is an exponential function of its length. Additionally, we find that the time development of the domains can be tuned between power-law growth and asymptotic saturation by varying the functional form of the self-regulation term in the rate equations. In two dimensions also, the quasistatic analysis suggests that a homogeneous system evolves into a mosaic of domains, but with the average domain size growing as a power law with time. This prediction is corroborated by numerical integration of the reaction–diffusion equations.

In section 2, we define the model and recall some basic results that emerge from the rate equations. We then analyse the one-dimensional reaction–diffusion equation in the steady-state, from which we can infer basic facts about the time evolution of large single-species domains. A generalized model, with a variable nonlinearity in the self-regulation term, is also introduced, and the behaviour of the average domain size is investigated. We then analyse the master equation for the evolution of the complete domain-size distribution in section 3. A scaling approach to the master equation supports our general conclusions based on the analysis of a single domain. The master equation approach is also extended to the case of unequal initial densities of the two species. In section 4, we outline some of the basic features of the reaction in higher spatial dimensions. Numerical results, which are based on the integration of the reaction–diffusion equations, are presented in section 5. We end with conclusions and some open questions in section 6.

2. The two-species competition model

Consider two reactive species, A and B which evolve both by reproduction and bimolecular self-regulation, as well as through bimolecular annihilation of opposite species whenever they meet. If the reactants move by diffusion, then the time evolution of the system may be described by the reaction–diffusion equations

$$\begin{aligned} \frac{\partial A(\boldsymbol{r},t)}{\partial t} &= \nabla^2 A(\boldsymbol{r},t) + A(\boldsymbol{r},t)(1 - A(\boldsymbol{r},t) - kB(\boldsymbol{r},t)) \\ \frac{\partial B(\boldsymbol{r},t)}{\partial t} &= \nabla^2 B(\boldsymbol{r},t) + B(\boldsymbol{r},t)(1 - B(\boldsymbol{r},t) - kA(\boldsymbol{r},t)). \end{aligned} \tag{1}$$

Here $A(\boldsymbol{r},t)$ and $B(\boldsymbol{r},t)$ denote the densities of each species at position $\boldsymbol{r}$ at time t, the time and unit of length have been rescaled so that the diffusion coefficient and the growth rate of each species is unity. The constant k measures the strength of competition between the two species.

In the mean-field limit, the reactant densities are spatially homogeneous, so that all dependences on $\boldsymbol{r}$ can be ignored. This implies that the diffusion terms are absent.

The resulting coupled rate equations have 4 fixed points at $(A,B) = (0,0)$, $(1,0)$, $(0,1)$, and $(1,1)$. There are two distinct behaviours depending on whether k is less than or greater than unity. In the former case, the stable fixed point is at $(1,1)$. The competition is sufficiently weak that it only serves to renormalize the quadratic self-regulation term for each species, yielding two-species co-existence. In the opposite case, the fixed point $(1,1)$ is unstable with respect to $(1,0)$ and $(0,1)$. For any initial condition, except for exactly equal initial densities, the system quickly flows to one of the two stable fixed points, corresponding to survival of a single species.

Since we are primarily interested in the case of strong competition in one dimension, we will employ an approximate analysis for the reaction–diffusion equations, equation (1), which is suited to treat a heterogeneous system. We assume that the competition is sufficiently strong that there is no co-existence of As and Bs in the rate equation approximation. Thus we are led to examine the properties of a single-species (A) domain of length $2L$, in a quasistatic approximation, in which the enclosing B domains act as absorbing boundaries at $x = \pm L$. This density profile is governed by

$$A''(x) = -A(x)(1 - A(x)) \tag{2}$$

with $A(\pm L) = 0$, and where the prime denotes differentiation with respect to x. To find the solution to equation (2), we first multiply by $A'(x)$, and integrate from $-L$ (the left edge of the domain) to an arbitrary point x. This gives

$$A'^2(x) - A'^2(-L) = \tfrac{2}{3}A^3(x) - A^2(x). \tag{3}$$

Evaluating this at $x = 0$ yields

$$A'^2(-L) \equiv \phi_L^2 = A_{\max}^2 - \tfrac{2}{3}A_{\max}^3 \tag{4}$$

which relates the slope at the edge of the domain, i.e. the flux ϕ_L of particles leaving the domain, to the maximum value of the reactant concentration in the domain, $A_{\max} = A(0)$. As $L \to \infty$, this flux approaches a limiting value $\phi_\infty = 1/\sqrt{3}$. Substituting equation (4) into equation (3) and integrating once again yields

$$L = \int_0^{A_{\max}} \frac{\mathrm{d}A}{\sqrt{\frac{2}{3}(A^3 - A_{\max}^3) - (A^2 - A_{\max}^2)}} \tag{5}$$

which implicitly relates the length of a domain to the maximum value of the concentration. While this relation can be written in terms of an elliptic function, it is more instructive to estimate the integral directly. Since the primary contribution to the integral arises when A is close to $A_{\max}$, we substitute $A = A_{\max} - \delta$ and $A_{\max} = 1 - \epsilon$ into the integrand to yield

$$L \cong \int_0^{A_{\max}} \frac{\mathrm{d}\delta}{\sqrt{2A_{\max}\epsilon\delta + \delta^2}} \to -\ln \epsilon. \tag{6}$$

For $\epsilon \to 0$ the domain has a nearly static core where the density is close to unity, and a interface region whose extent is of order unity where the slope is close to ϕ_∞. We call such domains 'fully developed'. On the other hand, for small values of $A_{\max}$, the nonlinear term in equation (2) is negligible. For this system, which is described by

the linearized reaction–diffusion equation, the density profile is closely approximated by a half-sinusoid. The growth in density is roughly proportional to the length of the domain, while the efflux is roughly a constant. Consequently, there is a minimum domain length of π below which all solutions yield a density which decays to zero.

From equations (4) and (6), we now infer that the flux leaving one edge of a large domain of length L is

$$\phi_L \cong \frac{1}{\sqrt{3}} - \text{constant} \times e^{-2L}. \tag{7}$$

Since the net flux between two large domains of lengths L_1 and L_2 is $\phi_{L_1} - \phi_{L_2}$, this leads, in the quasistatic approximation, to a rate of change in the length of an L-domain, surrounded by an L_1-domain and an L_2-domain, which is

$$\frac{dL}{dt} \propto e^{-L_1} + e^{-L_2} - 2e^{-L} \equiv \lambda(L_1, L_2, L). \tag{8}$$

This result implies that a domain of the typical size or larger, which is surrounded by typical-size domains, grows as $\ln t$. This extremely slow growth is a direct consequence of an exponentially small net flux across two large domains.

The logarithmic dependence of the domain length on time suggests that the two-species competition model is, in some sense, marginal. This leads us to consider a generalized process with a tunable self-regulation term to control the time dependences of the average domain length. The reaction–diffusion equations for our generalized model are

$$\begin{aligned} \frac{\partial A(\boldsymbol{r},t)}{\partial t} &= \nabla^2 A(\boldsymbol{r},t) + A(\boldsymbol{r},t)(1-A(\boldsymbol{r},t))^{\beta}\,\mathrm{sgn}(1-A(\boldsymbol{r},t)) - R(\boldsymbol{r},t) \\ \frac{\partial B(\boldsymbol{r},t)}{\partial t} &= \nabla^2 B(\boldsymbol{r},t) + B(\boldsymbol{r},t)(1-B(\boldsymbol{r},t))^{\beta}\,\mathrm{sgn}(1-B(\boldsymbol{r},t)) - R(\boldsymbol{r},t). \end{aligned} \tag{9}$$

Here the mutual reaction term $R(\boldsymbol{r},t)$ can be arbitrary, as long as it it sufficiently strong to rule out the co-existence of As and Bs in stable equilibrium. For this generalized model, we again investigate the steady state of a single domain with absorbing boundary conditions, using the same analysis as that employed in equations (3)–(7). We thereby find the following relation between the length of the domain and the maximum value of the density

$$L = \int_0^{A_{\max}} dA \left\{ \frac{(1-A)^{\beta+1} - (1-A_{\max})^{\beta+1}}{\beta+1} - \frac{(1-A)^{\beta+2} - (1-A_{\max})^{\beta+2}}{\beta+2} \right\}^{-1/2} \tag{10}$$

As in the case of equation (7), the primary contribution to the integral for $\beta > 1$ comes from values of A close to $A_{\max}$. Thus, to find the asymptotic behaviour of the integral, we again substitute $A = A_{\max} - \delta$, $A_{\max} = 1 - \epsilon$, and retain only the lowest order terms in these small parameters. By this approach we find, after some calculation

$$\phi_\infty - \phi_L \sim L^{-\gamma} \tag{11}$$

with $\gamma = 2(\beta + 1)/(\beta - 1)$. The time evolution of a domain of length L, with neighbours of lengths L_1 and L_2, is now governed by

$$\frac{dL}{dt} \propto L_1^{-\gamma} + L_2^{-\gamma} - 2L^{-\gamma}. \tag{12}$$

For a relatively large domain surrounding by typical size domains, this immediately leads to $L(t) \sim t^{1/(1+\gamma)}$. For $\beta < 1$, on the other hand, the integral in equation (10) converges as $A_{max} \to 1$ and the domain size is finite in this limit. This, in turn, implies that the flux difference, $\phi_\infty - \phi_L$, tends to zero at a finite value of L. Thus when neighbouring domains reach this limiting size, there is no additional flux of reactants across the interface and large domains 'freeze'. We will consider only $\beta > 1$ in what follows.

3. Master equation and scaling analysis

To gain further insight into the spatial organization of reactants, we examine the master equation for size distribution of the domains. Consider a system of total length C, with equal initial concentrations of the two species. We define $n(L,t)$ to be the number density of domains of length L at time t, i.e. the number of domains in the system with length between L and $L + dL$ is $n(L,t)dL$. The total number of domains in the system is

$$N(t) = \int_0^\infty n(L,t)\,dL. \tag{13}$$

Here we have assumed that C is much larger than the typical domain size so that the upper limit of integration can be extended to infinity. The corresponding probability density for domains of size L is $p(L,t) = n(L,t)/N(t)$. Since the total length of the domains must be equal to the length of the system and independent of time, the following normalization condition must hold

$$C = \int_0^\infty L\,n(L,t)\,dL. \tag{14}$$

Consider now the change in $n(L,t)$ as a function of time. There are two mechanisms by which the number of domains of a given size can change. Firstly, domains grow or shrink at a rate which depends on the sizes of their neighbours (equation (8) or (12)). Secondly, domains can disappear by shrinking to zero length, thus allowing their neighbours to coalesce and create a larger domain. The results of these two processes are described by the following master equation

$$\frac{\partial n(L,t)}{\partial t} = -\frac{\partial}{\partial L}(\lambda(L,t)n(L,t)) - 2|\lambda_0|\,p_0\,n(L,t) + |\lambda_0|\,p_0 \int_0^L dL'\,n(L',t)\,n(L-L',t) \tag{15}$$

where

$$\lambda(L,t) = \int_0^\infty \mathrm{d}L_1\,\mathrm{d}L_2\,p(L_1,t)\,p(L_2,t)\,\lambda(L_1,L_2,L) \tag{16}$$

and where the subscript 0 stands for the argument L being zero. The first (convection) term in equation (15) accounts for the change in $n(L,t)$ due to the growth or shrinkage of a domain as its boundaries move. The second term accounts for the loss of a domain of length L due to its coalescence with a neighbour, as an intervening small domain shrinks to zero. The third term represents the gain in the density of L-domains due to the (length conserving) coalescence of two smaller domains. The mean-field assumption is implicit in equation (15), as we have approximated the exact growth rate of a domain, which depends on its size and that of its two nearest-neighbours, by an average growth rate. This average is performed over the size distribution of the two neighbours under the additional assumption that there are no spatial correlations between domains. In the same spirit, we also replace the three-domain distribution function by a product of three one-domain distribution functions.

One can now in a straightforward manner derive the change in the total number of domains as a function of time by integrating equation (15) with respect to L. We find

$$\frac{\mathrm{d}N}{\mathrm{d}t} = -2|\lambda_0|n_0. \tag{17}$$

This result simply reflects the fact that the number of domains changes only when a domain shrinks to zero. The rate of occurrence of such an event is $|\lambda_0|n_0$. For every domain collapse, two domains are lost, one by the collapse itself and another by the coalescence of the two neighbouring domains.

Let us now attempt a scaling solution of equation (15) by rescaling all lengths in terms of the typical domain length, $s(t)$. This approach has proved to be a useful tool in a variety of aggregation phenomena [9]. We therefore make the scaling ansatz

$$n(L,t) = s(t)^{-2}\,\phi(u) \qquad \text{with } u \equiv \frac{L}{s(t)}. \tag{18}$$

Here the normalization factor of $s(t)^{-2}$ ensures the invariance of the total length, equation (14). Under the assumption that nearly all domains are in the order of the typical size, the total number of domains is simply

$$N(t) = \frac{C}{s(t)} \tag{19}$$

and the probability density of domain sizes is given by

$$p(L,t) = \frac{n(L,t)}{N} = \frac{\phi(u)}{C\,s(t)}. \tag{20}$$

To analyse the master equation, we need to write the growth rate $\lambda(L,t)$ in a scaling form. If we assume that the two enclosing neighbours of a given domain are of the typical size, then

$$\lambda(L,t) \to \begin{cases} 2(s^{-\gamma} - L^{-\gamma}) & \beta > 1 \\ 2(\mathrm{e}^{-s} - \mathrm{e}^{-L}) & \beta = 1. \end{cases} \tag{21}$$

For $\beta > 1$, $\lambda(L,t)$ is already in a scaling form, while a scaling form cannot hold when $\beta = 1$. Nevertheless, to see where the scaling assumption will lead, we postulate the following scaling forms for $\lambda(L,t)$

$$\lambda(L,t) \propto \begin{cases} s^{-\gamma}(1-u^{-\gamma}) \equiv s^{-\gamma} f(u) & \beta > 1 \\ e^{-s} f(u) & \beta = 1. \end{cases} \tag{22}$$

In addition to the approximations already made, it should be remembered that $\lambda(L,t)$ depends on the domain size distribution itself. Thus the above ansatz can only be regarded as a plausible guess for $\lambda(L,t)$.

Substituting the scaling forms for $\lambda(L,t)$ into the master equation, the dependence on $s(t)$ and u separates. We thus obtain for the time dependence of $s(t)$

$$s(t) \propto \begin{cases} t^{1/\gamma+1} & \beta > 1 \\ \ln t & \beta = 1 \end{cases} \tag{23}$$

and for the shape of the scaling function

$$2\phi + u\phi' = -\frac{\mathrm{d}}{\mathrm{d}u}(f\phi) - 2\frac{\phi_0|f_0|}{\mathcal{C}}\phi + \frac{\phi_0|f_0|}{\mathcal{C}^2}\int_0^u \phi(u_1)\phi(u-u_1)\,\mathrm{d}u_1 \tag{24}$$

where f_0 denotes $f(u=0)$. Thus the probability distribution obeys scaling, subject to the aforementioned caveats about the form of $\lambda(L,t)$. The above two consequences of scaling are borne out by our numerical studies.

Consider now the long-time behaviour of the system in the case when the initial concentrations of the two species are unequal. For simplicity and concreteness, we treat the case where the concentrations of the two species are very different ($c_B \ll c_A$). This implies that most of the B domains are smaller than the size of a typical A domain in the initial state. Consequently, almost all B domains will decrease in length as a function of time. From equation (21), it immediately follows that a B domain of initial length L_0 will shrink to a length

$$L(t) = \begin{cases} \ln(\exp(L_0) - t) & \beta = 1 \\ (L_0^{\gamma+1} - t)^{\frac{1}{\gamma+1}} & \beta > 1 \end{cases} \tag{25}$$

in time t. This decrease is independent of the typical length of the A domains, provided that they are initially larger than the B domains. Since there are two length scales in the problem, the average A- and B-domain lengths, one-parameter scaling should no longer hold. This is confirmed numerically.

To determine the time dependence of the minority species concentration, we follow the time evolution of the length distribution of minority domains. Denoting this distribution at $t = 0$ by $n_0(L_0)$, then at time t this distribution evolves to

$$n(L(t),t) = n(L_0,0)\frac{\mathrm{d}L(0)}{\mathrm{d}L(t)} \qquad L(t) > 0 \tag{26}$$

and the minority concentration at time t can be written as

$$c_B(t) \approx \int_0^\infty n(L(t),t)\,L(t)\,\mathrm{d}L(t). \tag{27}$$

To evaluate this integral, we shall assume a Poissonian initial distribution of minority species domain lengths, $n_0(L_0) = c_B(0)C\rho^2 \exp(-\rho L_0)$, where ρ is related to p_B, the probability of occupation of a lattice site by a particle of the minority species, by $\rho = -\ln(p_B)/a = \ln(ac_B)/a$, with a the lattice constant. In a biological context a would be the smallest territory required by a single member of the species. Using the steepest descent method, we estimate the time dependence of the minority species concentration to be

$$c_B(t) \sim \begin{cases} t^{-\rho} & \beta = 1 \\ \exp -(\text{constant} \times \rho t^{1/\gamma+1}) & \beta > 1. \end{cases} \tag{28}$$

The behaviour is non-universal, since the exponent depends on the initial concentration of the minority species. This feature was predicted earlier by Burlatsky and Pronin for $\beta = 1$ [8]. However, the detailed nature of our respective results are somewhat different, due to the assumption that $\rho \approx c_B$ for small c_B in [8]. A more complete understanding of the time dependence of the minority species concentration would be useful in understanding the time scale of the extinction of minority species in biological problems.

4. Higher dimensions

To describe the behaviour of biological organisms, it is necessary to consider the reaction in at least a two-dimensional space. For organisms not strictly confined to the surface of the earth, e.g. birds and fish, it may be sufficient to consider motion in two space dimensions, since the range in the third dimension is much smaller than in the plane. In contrast to the one-dimensional case, each domain possesses only a single neighbour, i.e. a domain is completely surrounded by its neighbour. If there are more than two competing species, then domain topologies akin to a map colouring problem can occur.

As in one dimension, we attempt to gain some insight about the dynamics of competing domains by considering first the simpler problem of a single species in a spherical box of radius R with absorbing boundary conditions. The equation for the (spherically symmetric) density profile in d dimensions becomes

$$A''(r) + \frac{(d-1)}{r} A'(r) + A(r)(1 - A(r)) = 0 \tag{29}$$

with the boundary condition $A(R) = 0$. Unfortunately, the first derivative term prevents a solution in quadratures by the analysis of section 2. However, by qualitative arguments and by numerical integration of equation (29), the following basic features are found. First, the domain radius R and the maximum value of A, $A_{\max} = 1 - \epsilon$, continue to be related by $R \sim -\ln \epsilon$. However, the dependence of the flux on the domain radius is different than that in one dimension. To see this, multiply equation (29) by $A'(r)$ and integrate from 0 to R, to yield

$$A'(R)^2 + 2(d-1) \int_0^R \frac{dr}{r} A'(r)^2 = A_{\max}^2 - \tfrac{2}{3} A_{\max}^3. \tag{30}$$

Although we cannot explicitly compute the second term, we can estimate it by observing that the slope is very small for most of the interval, $0 \leqslant r \leqslant R$, but becomes appreciable (of order unity) near the domain edge. Therefore, the integral must have the following behaviour in the limit of large R

$$\int_0^R \mathrm{d}r \frac{A'(r)^2}{r} \propto \frac{1}{R} \tag{31}$$

Since $R \sim \ln \epsilon$, where $\epsilon = 1 - A_{\max}$, we therefore deduce that

$$A'(\infty) - A'(R) = \frac{\text{constant}}{R} \tag{32}$$

where $A'(\infty) = 1/\sqrt{3}$.

Thus the two-dimensional system behaves in a manner similar to our generalized one-dimensional model, but with $\gamma = 1$ (equation (11)), corresponding to an unphysical negative value of the one-dimensional β. Nevertheless, using $\gamma = 1$ in equation (23) leads to the prediction that the average domain size grows as $s(t) \propto \sqrt{t}$. The area of the domain should therefore grow linearly with time. The feature of a power-law behaviour for the efflux of a spherical domain is the mechanism which leads to power-law domain growth. Modifying the exponent of the self-regulation term will not affect the growth rate of domains in dimensions higher than 1, since the $1/R$ term in equation (32) will always dominate the $1/R^\gamma$; $\gamma > 1$ coming from the modified self-regulation term (equation (12)).

5. Numerical results

To test our predictions, we performed a straightforward numerical integration of the reaction–diffusion equations (equation (1)). For a typical simulation in one dimension, we discretized the system into a periodic ring of 16384 grid points with the distance between successive points, $\delta x = 0.2$ and the time step $\delta t = 0.016$, close to, but slightly less than, the stability limit of the integration scheme [10]. Initially, each lattice site is assigned the value $A = 0.3$ with probability p_A, or $B = 0.3$ with probability $p_B = 1 - p_A$. Qualitatively similar behaviour was found for other types of random initial conditions. Our results are based on averaging 500–1000 different initial conditions. In the long-time limit, this system evolves into an alternating array of large domains, with the domain shape very close to that predicted by our quasistatic approach (see figure 1).

Figure 2 shows the increase in the average domain size as a function of time for the case $\beta = 1$ and for equal initial densities of the two species. There is an initial transient of fast domain growth that lasts until approximately 10 time units. We attribute this feature to the rapid smoothing out of the initial density discontinuities. At later times, however, the average domain length appears to grow logarithmically with time. Figure 3 shows corresponding results for the average domain size for the case $\beta = 3$, where the average domain length now appears to grow as a power law with time. The data does exhibit some downward curvature, when plotted on a double logarithmic scale, but the last few datum points are nearly linear with a limiting slope

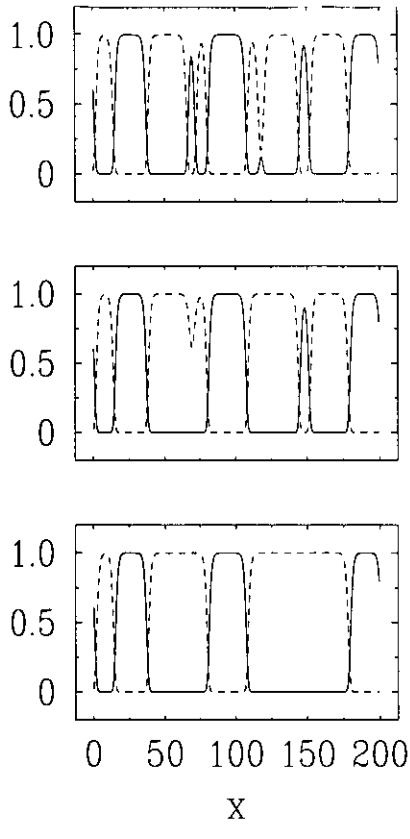

Figure 1. The dependence of the densities $A(x)$ and $B(x)$ on position x for a one-dimensional periodic system of length $C = 200$ at $t \cong 16$, $t \cong 56$, and $t \cong 193$ (top to bottom).

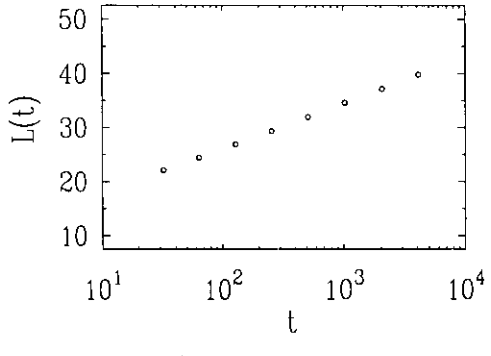

Figure 2. The time dependence of the average domain length in one dimension for the case $\beta = 1$.

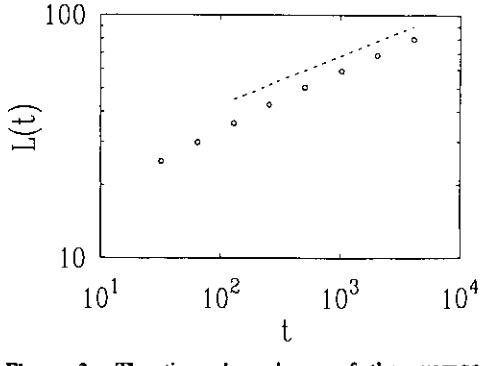

Figure 3. The time dependence of the average domain length in one dimension for the case $\beta = 3$. The dashed line of slope $1/5$ is meant as a guide to the eye.

that is approximately equal to 0.22. This compares favourably with our theoretical prediction of $1/5$, from equation (23).

To test scaling for the domain length distribution, we plot the probability of finding a domain length L, multiplied by $s(t)$, i.e. $p(L,t)s(t)$, versus $L/s(t)$, on a semi-logarithmic scale (figure 4). The domain length distribution for equal initial densities at three different representative times collapses onto a single universal curve. The

behaviour of this scaling distribution at large lengths appears to be a pure exponential decay. Figure 5 shows the decay of the minority species for the case of unequal initial densities. This decay is evidently a power law, but with the exponent dependent on the initial density. The dependence of the exponent on the initial condition is, however, relatively weak however. Thus the numerical data is not sufficient to provide an unambiguous test of our theoretical prediction, equation (28), which is most accurate when $c_B(0) \ll c_A(0)$. Additionally, an astronomically large system is required to ensure that the Bs have not all quickly disappeared when $c_B(0) \ll c_A(0)$.

In two dimensions, the structure of the domains is qualitatively similar to that encountered in spinodal decomposition [11] (figure 6). The reaction process gives

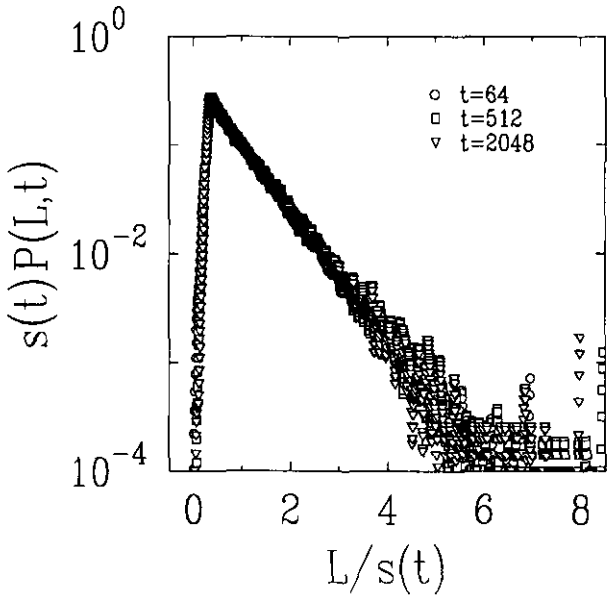

Figure 4. The scaled domain size distribution in one dimension for equal initial densities. Here $s(t)$ is the typical domain size at time t for $\beta = 1$. Data for $t = 64$ (o), $t = 512$ (□) and $t = 2048$ (▽) are displayed.

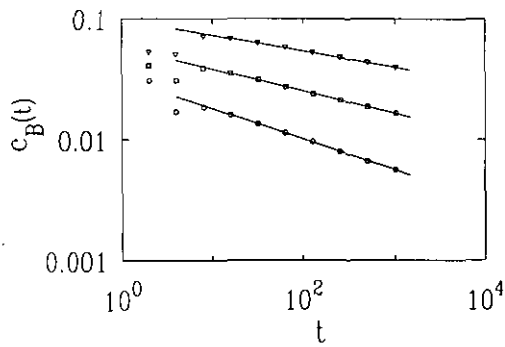

Figure 5. Time dependence of the the average concentration of the minority species for a one-dimensional system with $\beta = 1$. Shown are data for $c_B = 0.38$ (o), $c_B = 0.40$ (□), and $c_B = 0.42$ (▽). The lines are the least-squares fit to the data for $t \geqslant 10$, whose respective slopes are 0.25, 0.18 and 0.13, up to 2-digit accuracy.

rise to an effective surface tension which attempts to smooth out domain boundaries, as is observed in the numerical integration. Over the relatively short temporal range for which we were able to obtain data, the average domain area appears to grow as a power law with time, with the corresponding exponent equal to 0.84 (figure 7). If the domains are relatively compact, this would correspond to an average domain radius which grows approximately as $t^{0.42}$, compared to our heuristic estimate of $t^{1/2}$.

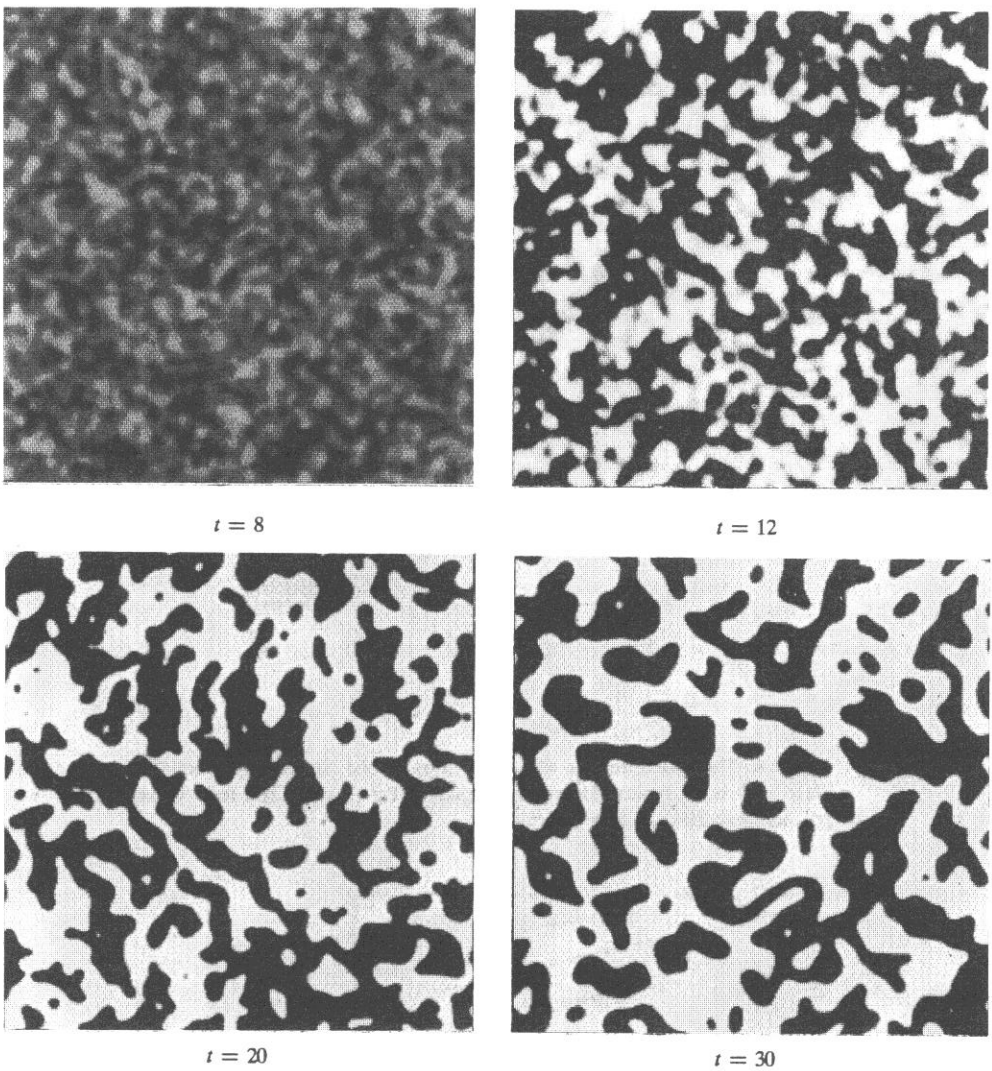

Figure 6. Snapshot of the densities for a two-dimensional system with equal initial densities at times $t = 8$, 12, 20, and 30.

6. Conclusions

In this paper we have addressed the dynamics of competitive two-species logistic growth, focusing on the spatially inhomogeneous patterns that develop. Our principal

theoretical tool in investigating the evolution of domains is the quasistatic approximation, where we assume that the flux of population leaving a growing domain of length L is the same as the flux from a static domain enclosed in a box of length L with absorbing boundary conditions. In order for this approximation to be valid the domains must be fully developed and slowly growing. Here, a fully developed domain is characterized by a 'dead' interior region where the concentration is essentially unity and a boundary region which is much smaller than the interior. As the dimension of space increases, the radius at which a domain becomes fully developed increases. Thus, the crossover time, defined as the time it takes for most of the domains to become fully developed, increases as the spatial dimension increases. Our results hold only after the crossover time. Furthermore, the domains must be slowly growing, in the sense that the boundary must move much more slowly than a Fisher wave [12].

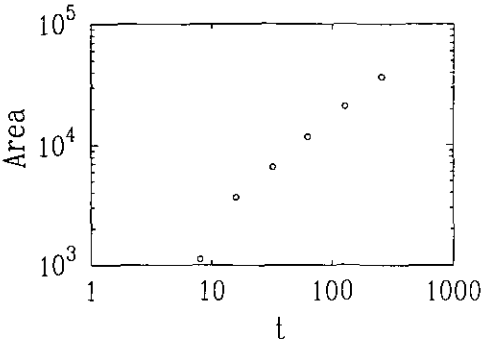

Figure 7. The time dependence of the average domain area in two dimensions. The last five data points are well-fit by a straight line of slope 0.84.

With these caveats in mind, our theoretical analysis predicts that, for equal initial densities of the two species, the average domain size grows logarithmically with time in one dimension, whereas in any higher dimension it grows as $\sqrt{t}$. If the self-regulation of each species has a nonlinear form, the growth rate of a domain becomes a power law in one dimension, while the two-dimensional result is unchanged. It is encouraging that as the domains get larger, they grow more slowly, thus self-consistently satisfying the criterion of slow growth, implicit in the quasistatic approximation. Numerical computations seem to bear out our predictions to a large extent, despite the fact that we have ignored correlations between neighbouring domains and variations in domain shape. In particular, in two dimensions, the shape of the typical domain is not even close to circular, as can be seen in figure 6. For unequal initial densities, the situation is more complex, and in one dimension, the minority species becomes extinct in a non-universal way which depends on the initial conditions.

One can also ask whether this model has an upper critical dimension beyond which the concentrations behave according to the mean field, uniform density predictions. To appreciate the relevant issues, consider first two-species annihilation ($A+B \rightarrow$ inert) [1–4], for which there is an upper critical dimension of $d_c = 4$. In this model, diffusion tends to smooth out initial density fluctuations and this competes with the annihilation of reactants at domain boundaries. In large spatial dimension, however, there is an increasing tendency for particles of one species to substantially penetrate domains of the opposite species as time increases. This mechanism homogenizes the densities and leads to mean field behaviour. In the two-species competition model,

the logistic growth of each species in isolation leads to fully developed domains of relatively high density. Consequently, there is negligible penetration of one species into an opposite species domain. These considerations suggest that the two-species competition model will not have an upper critical dimension.

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