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Stochastic spatial models: a user's guide to ecological applications

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SUMMARY

Spatial pattern, how it arises and how it is maintained, are central foci for ecological theory. In recent years, some attention has shifted from continuum models to spatially discrete analogues, which allow easy treatment of local stochastic effects and of non-local spatial influences. Many of these fall within the area of mathematics known as 'interacting particle systems', which provides a body of results that facilitate the interpretation of the suite of simulation models that have been considered, and point towards future analyses. In this paper we review the basic mathematical literature. Three influential examples from the ecological literature are considered and placed within the general framework, which is shown to be a powerful one for the study of spatial ecological interactions.

1. INTRODUCTION

Spatial pattern and the processes that generate and maintain pattern have been major objects of scientific attention for decades. (See for example, reviews in Levin & Segel (1985) and Haken (1983).) Most work has focused on continuum descriptions; however, in the past few years there has been a rapid increase in the use of discretized models, in which space is represented by a grid of 'cells' or 'sites' that can be in one of a finite number of states (see Durrett 1988*a*,*b*,*c*, 1992; Czaran & Bartha 1992). Biology, in particular, has been a rich area of application for such models, especially in the study of pattern formation in ecological systems; however, in most cases in the biological literature, the analysis of these models has been carried out without reference to the broad range of investigations in the field of interacting particle systems, spatial stochastic processes that include as deterministic special cases cellular automata (see, for example Fisch *et al.* (1991) or Hassell *et al.* (1991)). The aim of this article is to bridge this gap by describing some of the mathematical results that are useful for applications, and applying these results to some systems that have been considered in the literature.

We begin by describing the general set-up of our models. In each system there is a collection of spatial locations called sites, which in all our examples will be the d-dimensional integer lattice, $\mathbf{Z}^d$; that is, the points in d-dimensional space with all integer co-ordinates. In most cases of interest in biology we will have $d=2$, or occasionally $d=3$; but it will also be interesting to consider the behaviour in $d=1$ and $d>3$. Our models are generally formulated on the infinite lattice as this simplifies the mathematical theory. However, we will also discuss the behaviour of these systems on finite lattices with various boundary conditions, since this is what one encounters in applications or computer simulations.

Our systems can evolve in discrete time ($t=0,1,2,\ldots$) or continuous time (t is any non-negative number). Because discrete time models are used almost universally in the biological literature and are simpler to formulate, we will begin with that case. The models are slightly more difficult to formulate in continuous time, as one must deal with transition rates instead of probabilities; but as we will explain in § 6, continuous time models are simpler to analyse than discrete time models and they do not need 'collision rules' to decide what happens when several events occur at one site in one time step.

At each time $t=0,1,2,\ldots$, each site can be in one of a finite number of possible states; the set of all possible states being denoted by F. The state of the site x at time t is denoted by $\xi_t(x)$, and hence the state of the process at time t is given by a function ξ_t that assigns to each site in $\mathbf{Z}^d$ a state in F. We will say that the function $\xi_t:\mathbf{Z}^d\rightarrow F$ describes the configuration of the system at time t. In this paper, we will typically allow a site to be either vacant or to be occupied by a single individual and we will interpret 0 as vacant, and a value of i with $1\leqslant i\leqslant \kappa-1$ as indicating that the site is occupied by one individual of type i.

The temporal evolution of these models is determined by specifying, for each i and x, the conditional probability that site x will be in state i at time t given that the whole process was in configuration ξ at time $t-1$. This transition probability is denoted by $p_i(x,\xi)$. We will always suppose that p_i depends on the state at x and on the states of a finite number of neighbours: $x+y_1,\ldots,x+y_n$, and that it does not depend on time.

Phil. Trans. R. Soc. Lond. B (1994) **343**, 329–350
Printed in Great Britain

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That is,

$$p_i(x,\xi) = f_i(\xi(x), \xi(x+y_1), \ldots, \xi(x+y_n)). \tag{1}$$

Of course, because the p_is are probabilities for fixed x and ξ we will have

$$p_i(x,\xi) \geqslant 0 \quad \text{and} \quad \sum_i p_i(x,\xi) = 1.$$

Our formulation of the transition probabilities makes the system rules spatially homogeneous. In the jargon our transition probabilities are 'translation invariant'. That is, if we shift (or translate) the initial configuration then the temporal evolution is only translated in space. The assumption of translation invariance is needed for most of the mathematical results; however, it can be dropped if one is content to study the model by simulation. Indeed, one of the attractions of interacting particle system models is that they can be used to study spatially inhomogeneous systems.

The first step in formulating a concrete model is to decide on the neighbourhood set $N = \{y_1, \ldots, y_n\}$ to be used. In many cases in two dimensions we will take

$$N = \left\{ \begin{array}{ccc} & (0,1) & \\ (-1,0) & & (1,0) \\ & (0,-1) & \end{array} \right\}.$$

These points are often called the 'nearest neighbours' of 0, as these are the lattice points that are the closest to 0. N is sometimes called the 'von Neumann neighbourhood'. A second common choice is the 'Moore neighbourhood',

$$N = \left\{ \begin{array}{ccc} (-1,1) & (0,1) & (1,1) \\ (-1,0) & & (1,0) \\ (-1,-1) & (0,-1) & (1,-1) \end{array} \right\}.$$

These neighbourhoods are named for two mathematicians who were early contributors to the theory of cellular automata. To help keep the definitions straight via a pun, notice that the Moore neighbourhood has more points.

In some situations we will want to look at larger neighbourhoods. Let $\|z\|$ be any distance function (two that are well suited to the d-dimensional integer lattice are $\|z\|_1 = |z_i| + \ldots + |z_d|$, or $\|z\|_\infty = \max\{|z_1|, \ldots, |z_d|\}$) and let $\mathcal{N} = \{z : 0 < \|z\| \leqslant r\}$, the set of points within distance r of the origin. Here r gives the range of the interaction. Using our new notations, we can express the von Neumann and Moore neighbourhoods as $\{z : \|z\|_1 = 1\}$ or $\{z : \|z\|_\infty = 1\}$, respectively. The next two figures show the distances from 0 for $\| \, \|_1$ and $\| \, \|_\infty$. The corresponding neighbourhoods are diamonds and squares respectively.

$$\begin{array}{ccccccccc}
 & & & & 4 & & & & \\
 & & & 4 & 3 & 4 & & & \\
 & & 4 & 3 & 2 & 3 & 4 & & \\
 & 4 & 3 & 2 & 1 & 2 & 3 & 4 & \\
4 & 3 & 2 & 1 & 0 & 1 & 2 & 3 & 4 \\
 & 4 & 3 & 2 & 1 & 2 & 3 & 4 & \\
 & & 4 & 3 & 2 & 3 & 4 & & \\
 & & & 4 & 3 & 4 & & & \\
 & & & & 4 & & & &
\end{array}$$

$\|x\|_1$

$$\begin{array}{ccccccccc}
4 & 4 & 4 & 4 & 4 & 4 & 4 & 4 & 4 \\
4 & 3 & 3 & 3 & 3 & 3 & 3 & 3 & 4 \\
4 & 3 & 2 & 2 & 2 & 2 & 2 & 3 & 4 \\
4 & 3 & 2 & 1 & 1 & 1 & 2 & 3 & 4 \\
4 & 3 & 2 & 1 & 0 & 1 & 2 & 3 & 4 \\
4 & 3 & 2 & 1 & 1 & 1 & 2 & 3 & 4 \\
4 & 3 & 2 & 2 & 2 & 2 & 2 & 3 & 4 \\
4 & 3 & 3 & 3 & 3 & 3 & 3 & 3 & 4 \\
4 & 4 & 4 & 4 & 4 & 4 & 4 & 4 & 4
\end{array}$$

$\|x\|_\infty$

Variants on these two choices are possible modifying their shape or extent. For example, one can define the usual Euclidean norm $\|x\|_2 = (x_1^2 + \ldots + x_d^2)^{1/2}$ and let $N = \{x : 0 < \|x\|_2 \leqslant r\}$. However, one should not worry too much about what neighbourhood to choose. In most cases the qualitative behaviour of the model does not depend on the neighbourhood used.

The purpose of this brief introduction has been simply to spell out in a general way the rules of the games that we will study in more detail below. The reasons for interest in these models and the range of possible applications will become clearer as we study specific examples. Our approach will be to discuss the theory and its applications in alternation. In the lengthy § 2 we will discuss contact processes and introduce some general results. In § 3, we will apply these results to the daffodil model of Barkham and Hance (1982). In § 4 we will discuss the behaviour of a version of the contact process in which dispersal occurs over long distances, as a prelude to analysing Crawley and May's (1987) model of competition of annuals and perennials in § 5. The message of these two sections is that if dispersal occurs over large distances, then the particle system behaves much like a system in which all sites interact equally. In § 6 we discuss continuous time versions of the discrete time systems studied in §§ 4 and 5 and show that in this case it is possible to get more detailed information. This state of affairs is analogous to (and related to) the distinction between iteration of functions and ordinary differential equations. In §§ 4–6 we are concerned with competition of plants that fall in a successional sequence. In § 7 we turn our attention to models appropriate for the competition of different genets of the same species or different species of the same type of plant. These results are then applied in § 8 to Inghe's (1989) model of the competition of different genets of a fixed perennial.

One of the features that makes the study of interacting particle systems interesting for mathematicians is that many of the results in the theory are simple to state but difficult to prove. We have not tried to explain any of the more complicated aspects of the theory here, but have included proofs of some of the simpler results to make the theory a little less mysterious, and because some of the ideas are useful in simulations. Proofs appear in the text with their beginnings marked by *Proof* and their end by □. The material between these marks can be skipped without loss.

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2. CONTACT PROCESSES

We begin by discussing the simplest interesting model. As we go along we will add a number of features to enhance realism. Each site can be in state 0 = vacant or 1 = occupied by a 'particle', which the reader should think of as being a single plant. From the viewpoint of the particles, the system evolves as follows:

1. Particles die with probability γ and survive with probability $1-\gamma$. That is, in each time step the probability of death is γ for any plant.
2. If the particle at x survives, then with probability $\beta(x,y)$ it gives birth to a new particle (propagule) that is sent to y. The birth events for different values of y or from different values of x are independent. That is, independent of what other births may have taken place in a given time step, there is probability $\beta(x,y)$ that a plant at x sends a propagule to site y.
3. If one or more propagules is sent to y, or if there is a particle at y that survives, y is occupied at the next time step; otherwise y is vacant.

In order for the transition probability to have the form given in equation (1), we must assume that $\beta(x,y)=g(y-x)$ and that $g(z)\neq 0$ for only finitely many values of z. An important special case, called the basic contact process, has $g(z)=\lambda$ when z is one of the nearest neighbours of the origin, and 0 otherwise. We will concentrate on the basic contact process because it is concrete and simple, and because, as the reader will see, a large class of more complicated models have the same qualitative behaviour.

Rule 3 says that there can be at most one particle per site. This is a reasonable constraint for a model of the spread of a plant species, but this realism makes the model very difficult to analyse.

Let ξ_t^A be the state at time t when initially the sites in A are occupied (that is, $\xi_0^A(x)=1$ if and only if $x\in A$). Let $\tau^A=\min\{t:\xi_t^A(x)=0$ for all $x\}$ be the first time that there are no particles. If there are no particles then none can be born, so at all times $t\geqslant\tau^A$ we will have $\xi_t^A\equiv 0$, that is, $\xi_t^A(x)=0$ for all x. In words, the 'all 0' state is an absorbing state: once the process enters this state it cannot leave. For obvious reasons, we say the system dies out at time τ^A.

The first question to be addressed is 'When does the system have positive probability of not dying out starting from a single occupied site?' or in symbols 'When is $P(\tau^{\{0\}}=\infty)>0$?' Here, without loss of generality, we have chosen the initial occupied site to be the origin, i.e. the point in $\boldsymbol{Z}^d$ with all co-ordinates 0. Note that there is probability γ that the initial particle will die before it has a chance to give birth, so if $\gamma>0$ then $P(\tau^{\{0\}}=\infty)<1$. When $P(\tau^{\{0\}}=\infty)>0$, we say the process survives, otherwise we say that the process dies out. Suppose for the moment that we hold λ fixed and vary γ. Because increasing γ makes it harder for the process to survive, there will be a critical value $\gamma_c(\lambda)$ (possibly 0 or 1) so that

$$P(\tau^{\{0\}}=\infty)\begin{cases}=0 & \text{if}\quad \gamma>\gamma_c(\lambda)\\ >0 & \text{if}\quad \gamma<\gamma_c(\lambda)\end{cases}.$$

That is, when $\gamma>\xi_c$, the species will almost certainly die out; whereas for $\gamma<\gamma_c$, there is positive probability that the species will avoid extinction.

Our next goal is to give bounds on γ_c and to show that $0<\gamma_c(\lambda)<1$. The first thing we will do is to show that if γ is too large then the system dies out. To do this we note that if, for comparison, we change rule 3 so that each propagule results in a new particle (that is, local competitive exclusion is ignored), then the number of particles alive at time t is a branching process in which each particle dies with probability γ and with probability $(1-\gamma)$ gives birth to an average of $2d\lambda$ new particles. The expected number of offspring (counting the particle if it survives) is $\mu=(1-\gamma)(2d\lambda+1)$. Iterating we see that the expected number of offspring in generation t is μ^t. Now the probability of having at least one survivor is smaller than the expected value, so if $\mu<1$ the probability of surviving until time t goes to 0 exponentially fast. By comparison, in the contact process some of the birth rate will be wasted on occupied sites, so the probability of surviving also tends to 0 if $\mu<1$ and we have proved the easy half of the following result. The second conclusion can be proved using the methods in Durrett (1992).

If

$$\gamma>2d\lambda/(2d\lambda+1)$$

then the basic contact process dies out.

If

$$\gamma<1-\{0.82+2(1-\lambda)^{dn}\}^{1/(2n-1)}$$

for some integer $n\geqslant 1$ then the basic contact process survives. (2.1)

These results give only very crude bounds on $\gamma_c(\lambda)$:

$$\frac{2d\lambda}{2d\lambda+1}\geqslant\gamma_c(\lambda)\geqslant\min_{n\geqslant 1}\,(1-\{0.82+2(1-\lambda)^{dn}\}^{1/(2n-1)})$$

For example, when $d=1$ and $\lambda=1$, the upper bound is 2/3 and taking $n=1$ the lower bound is $\gamma<2\lambda-1.82=0.18$ while numerical results suggest that $\gamma_c(1)\approx 0.47$. The lower bound in (2.1) is ugly to look at, but it does have the nice feature that it can be made positive for any $\lambda>0$. (Just take n large enough so that $(1-\lambda)^{dn}<0.09$.) Figure 1 shows a picture of the crude bounds given above in the special case $d=1$ and a numerical estimate (the middle curve) of $\{(\lambda,\gamma_c(\lambda)):0\leqslant\lambda\leqslant 1\}$, the boundary between the two behaviours. We will have more to say later in this section about how this boundary was estimated. For the moment, we will concentrate on the special case in which $\lambda=1$.

The first step in estimating $\gamma_c(1)$ is to see what happens for various parameter values. Figure 2 shows a simulation of the process with $\gamma=0.49$ starting with an interval of 160 occupied sites. In this simulation, space goes across, time runs down the page, and the process died out well before we reached the end of the simulation, which represents time 480. Figure 4 shows a simulation of the process with $\gamma=0.45$, again

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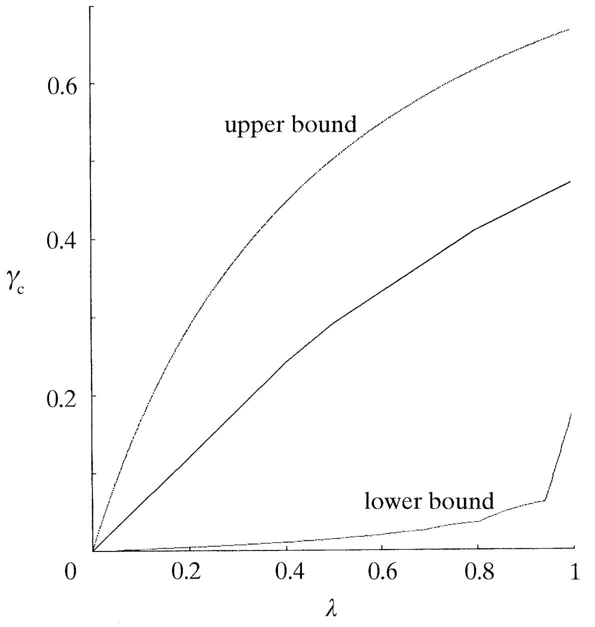

Figure 1. Upper and lower bounds on the critical values $\gamma_c(\lambda)$ for the discrete time basic contact process.

starting from an interval of occupied sites. In this case the interval grows linearly in time; and, in between the two endpoints, more than half of the sites are occupied. Finally, figure 3 shows a simulation of the system with $\gamma = 0.47 \approx \gamma_c$. Figure 3 and 4 are consistent with the fact that the critical value can be characterized by the asymptotic behaviour of $r_t = \max\{x : \xi_t^{(-\infty,0)}(x) = 1\}$, the position of the right-most particle when we start with all the nonpositive integers occupied. Durrett (1980) has shown that for any γ, $r_t/t \rightarrow \alpha(\gamma)$ as $t \rightarrow \infty$ and recent work of Bezuidenhout & Grimmett (1991) implies that the critical value $\gamma_c = \max\{\gamma : \alpha(\gamma) > 0\}$. In words, when a half line of 1s can spread into empty space at a positive rate, the system survives; otherwise, it will die out. Knowing this characterization of γ_c and looking at figures 3 and 4 one can convince oneself that the drift in the edge is close to 0 in the first case and positive in the second.

Now that we know that the contact process does not always die out, the next question to answer is 'What does the process look like when it survives?' To answer this question, we begin by introducing some simple general results. The transition probabilities for the contact process have the property that if $\xi(x) \leqslant \xi'(x)$ for all x then $p_1(x,\xi) \leqslant p_1(x,\xi')$. In words, if a configuration ξ' has more 1s than another one ξ then the probability of having a 1 at a site x on the next time step will be larger in ξ'. (Here, and throughout the paper, larger means $\geqslant$.) When this monotonicity property holds we say that the system is attractive, a somewhat strange sounding term that came to the subject from the study of the Ising model in statistical mechanics. A more colloquial way of expressing attractiveness is that 'more is better'. That is, if we increase the set of occupied sites then we increase the probability of having occupied sites at the next time step.

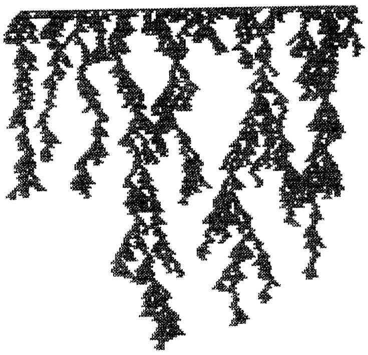

Figure 2. Discrete time basic contact process in one dimension with $\beta = 1.0$ and $\gamma = 0.49$.

Figure 3. Discrete time basic contact process in one dimension with $\beta = 1.0$ and $\gamma = 0.47$.

The most important consequence of the attractiveness property is that there is a limiting probability distribution as $t \rightarrow \infty$.

If we start from an initial configuration with all sites occupied ($\xi_0^1(x) = 1$ for all x) then as $t \rightarrow \infty$ the state at time t converges in distribution to a limit ξ_∞^1, which is a stationary distribution for the process. (2.2)

Here the superscript 1 indicates that we are starting from all 1s. The next things we have to explain are the

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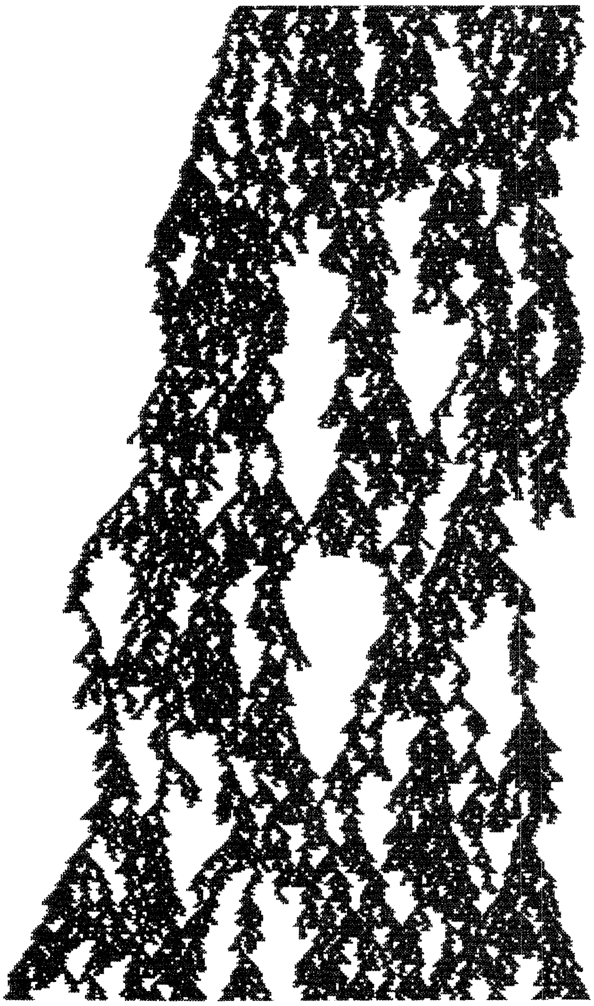

Figure 4. Discrete time basic contact process in one dimension with $\beta = 1.0$ and $\gamma = 0.45$.

two phrases in italics. To do this we need another definition. We say that ξ_t^1 converges in distribution to ξ_∞^1 and write $\xi_t^1 \Rightarrow \xi_\infty^1$ if for any choice of $x_1, \ldots, x_k \in \boldsymbol{Z}^d$ and $i_1, \ldots, i_k \in \{0,1\}$, the probabilities

$$P(\xi_t^1(x_1) = i_1, \ldots, \xi_t^1(x_k) = i_k)$$
$$\rightarrow P(\xi_\infty^1(x_1) = i_1, \ldots \xi_\infty^1(x_k) = i_k).$$

That is, if we focus our attention on any finite set of points $x_1, \ldots, x_k$ the joint distribution of $\xi_t^1(x_1), \ldots \xi_t^1(x_k)$ converges. To say that ξ_∞^1 is a stationary distribution means that if we start from an initial configuration ξ_0 with this distribution then the state at time t will have this distribution for any $t \geqslant 1$. In other words, ξ_∞^1 represents a possible equilibrium distribution for our Markov chain.

We will not prove (2.2) but only try to convince the reader this is reasonable. The basic idea is that we are starting with the largest possible initial state and our system is attractive so ξ_t^1 should be decreasing and hence have a limit. (To turn the last idea into a proof one shows that $P(\xi_t^1(x) = 1$ for some $x \in A)$ is a decreasing sequence for any choice of A and that this implies that all the finite dimensional distributions converge. See Liggett (1985) or Durrett (1988*b*) for details.) Because limit ξ_∞^1 is the limit starting from the largest possible initial state, it should not be surprising that it is the largest stationary distribution. That is, if $\zeta(x)$ is another stationary distribution then we can construct ζ and ξ_∞^1 on the same probability space in such a way that $\zeta(x) \leqslant \xi_\infty^1(x)$ for all x. At the other extreme, the distribution that assigns probability one to the 'all 0' state, denoted δ_0, is a trivial stationary distribution. Of course, it can happen that $\xi_\infty^1 = \delta_0$, and indeed this will happen if λ is too small or γ is too large. An inspired reader might guess, correctly, that

$\xi_\infty^1 \neq \delta_0$ if and only if $P(\tau^{\{0\}} = \infty) > 0$. (2.3)

In a fair amount of generality, the survival of a process starting from a large enough finite set implies the existence of a non-trivial stationary distribution (see Bezuidenhout & Gray 1991) but the converse is not true. A counterexample is provided by a process that mathematicians call the 'sexual reproduction model': $p_1(x,\xi) = 1 - \gamma$ if $\xi(x) = 1$; $p_1(x,\xi) = \beta$ if $\xi(x) = 0$; and $\xi(x + (1,0)) = \xi(x + (0,1)) = 1$; and $p_1(x,\xi) = 0$ otherwise.

In words, a site x will be occupied at time $t+1$ if (i) it was occupied at time t and the particle survived or if (ii) it was vacant at time t, and its northern and eastern neighbours combined to produce a new particle. The birth rule can be liberalized to allow any diagonally adjacent pair of particles to make a new one. Here we will be content to explore the curious theoretical properties of the mathematically simplest version of the model. The next two results hold both for the simple and for the liberal versions of the model.

If $\gamma > 0$ then $P(\tau^A < \infty) = 1$ for any finite set A. (2.4)

That is, as long as there is positive probability of death, the process beginning from any finite set almost certainly will become extinct in finite time.

Proof. If all the 1s in the initial state are inside a rectangle B, then there will never be 1s in B^c, the complement of B, as any point in B^c has at most one neighbour in B. Once we know that the process cannot grow outside of B, it must die out as eventually there will be a time at which bad luck produces a death at every point in B. □

Somewhat surprisingly this process, which dies out starting from any finite set, can have a non-trivial stationary distribution.

If γ is small enough and β is close enough to 1 then the sexual reproduction model has a non-trivial stationary distribution. (2.5)

It is clear how one should go about producing such a stationary distribution. The system is attractive so we start from all 1s and let the system run. The hard part is to show that if we do this the process does not converge to the 0s state. The intuitive explanation for this is that if γ is small and β is close to 1 then the process is very good at filling in holes that develop in the initial all 1s configuration, and this allows it to avoid extinction starting from all sites occupied. The conclusion of (2.5) is a special case of Toom's Eroder

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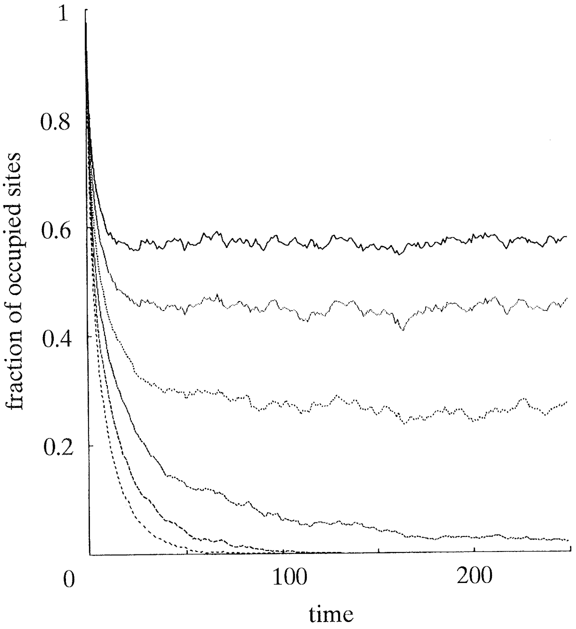

Figure 5. Fraction of occupied sites versus time for the two-dimensional discrete time basic contact process with $\lambda = 0.25$ and $\gamma = 0.32$, 0.35, 0.38, 0.41, 0.44, 0.47.

Figure 6. Two-dimensional discrete time basic contact process equilibrium state when $\lambda = 0.25$ and $\gamma = 0.35$.

Theorem (see Toom 1980). For a more recent proof see Bramson & Gray (1992) and for more on this model see Durrett & Gray (1986) and Chen (1992).

We now return to the basic contact process. Before delving further into the theory we pause to look at some simulations. Figure 5 gives a graph of the fraction of occupied sites versus time for a two-dimensional basic contact processes on a 100 × 100 lattice $\{0,1,\ldots,99\}^2$ starting from all sites occupied. To avoid boundary effects we have used periodic boundary conditions. That is, for $0 \leqslant k \leqslant 99$ we consider $(99,k)$ to be a neighbour of $(0,k)$, and consider $(k,99)$ to be a neighbour of $(k,0)$. We have fixed $\lambda = 0.25$ and looked at six values of γ: 0.32, 0.35, 0.38, 0.41, 0.44, 0.47. In the first three cases the process survives and theory tells us (see Bezuidenhout & Grimmett 1990) that the process will converge to equilibrium exponentially rapidly. This is clearly visible in the top three graphs, although there are fluctuations in the density coming from the fact that we are only looking at 10000 sites, and in the third case convergence to equilibrium is not complete by the right edge of the graph, which represents time 250. This observation is consistent with the theoretical result which says that the rate of convergence to equilibrium is small when we are close to the region where the process dies out. Figure 6 gives a picture of the process with $\lambda = 0.25$ and $\gamma = 0.35$ at time 250, which should be a reasonable approximation to ξ^1_∞. Theory tells us that the states of adjacent sites are not independent but the correlations between the states of sites decay exponentially fast in the distance between them. We will have more to say about these correlations in § 6.

The bottom two graphs have hit 0 before time 250 indicating that the system died out. In the third case we expect that this will occur before time 1000. Theory tells us (see Bezuidenhout & Grimmett 1991) that, except for points on the boundary between surviving and dying out, the density of occupied sites converges to 0 exponentially fast but the rate of convergence approaches 0 as we approach the boundary. Some readers may be worried, as was Caswell (1978, p. 135), that all of these systems will eventually die out as they are Markov chains on a finite state space and the $\equiv 0$ state is an absorbing state. However, this will take a very very long time. Theory tells us (see Durrett & Liu 1988; Durrett & Schonmann 1988; Durrett *et al.* 1989; Mountford 1992) that the expected time for an $N \times N$ system to die out is of the order of $\exp(cN^2)$. Again $c \to 0$ as we approach the boundary of the survival region but $\exp(cN^2)$ is a huge number even when $\lambda = 0.25$ and $\gamma = 0.38$. For these parameter values one can run the system on a 100 × 100 lattice for several billion units of time without the process dying out.

Figure 7 shows estimates of the equilibrium densities for the one-dimensional basic contact process when λ is a multiple of 0.1 and γ is a multiple of 0.01. Note that, as expected, equilibrium density increases with birth rate and decreases with death rate, with a sharp increase in the density near the critical value. To obtain our estimates for $\lambda \geqslant 0.3$ we ran the process on $\{0,1,\ldots,9999\}$ with periodic boundary conditions (i.e. 9999 is a neighbour of 0) until time 8000, recorded the number of occupied sites every 10 units of time starting at time 3000, and then averaged the counts to get our estimate of the equilibrium density. The same procedure was used for $\lambda = 0.1$ and 0.2 but as these systems evolve more slowly we took data from time 15000 to time 20000. In these simulations we waited a 'long' time to allow the process to converge to equilibrium or to die out. Our estimates of the

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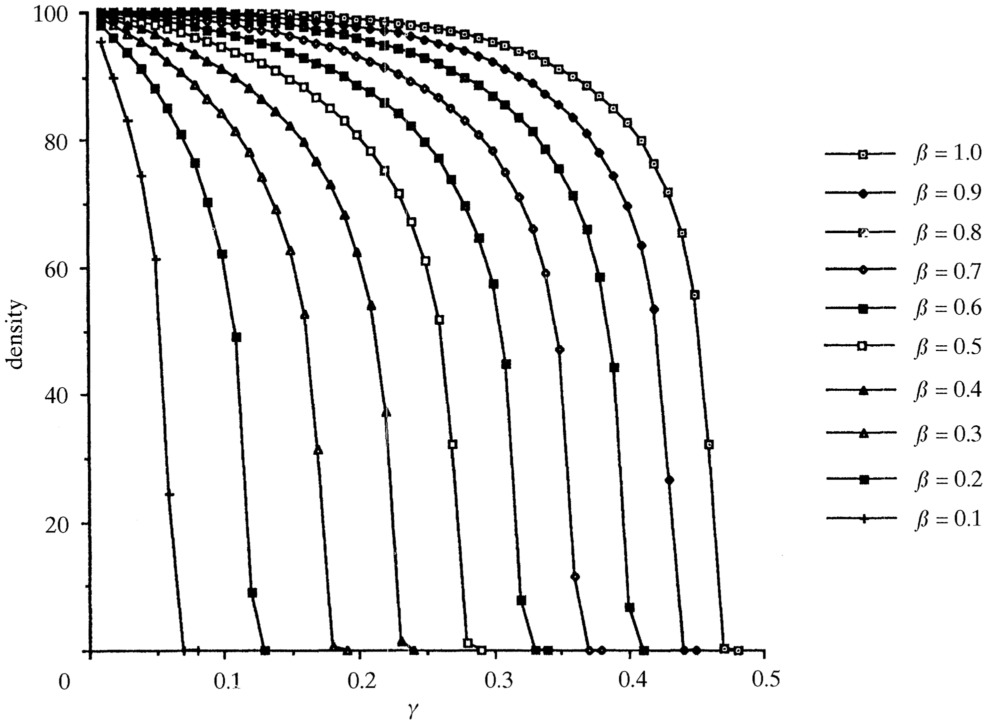

Figure 7. Estimates for the equilibrium density of the one-dimensional discrete time basic contact process as a function of γ for $\beta = 1.0, 0.9, \ldots 0.1$.

critical value given in figure 1 are the largest values of γ for which the system had not died out by the end of our taking data. There are much more accurate ways of estimating γ_c described in Buttel *et al.* (1992). That paper also explains the trick (which will be used again in § 5) that allows us to treat the 100 values of γ for a fixed value of β in one simulation run.

At this point we have considered only the limiting behaviour starting from all sites occupied. The next result, called the complete convergence theorem, describes the limiting behavior starting from an arbitrary initial configuration. The last result took fifteen years to evolve to its current form. Harris (1974), Griffeath (1978), Durrett (1980), Durrett & Griffeath (1982) and Durrett & Schonmann (1987) proved increasingly more general results before Bezuidenhout & Grimmett (1990) completed the solution. (For an exposition of their proof that contains most of the results cited in this section, see Durrett (1991).) In words, the next result says that if the process survives to time t and t is large then it looks like the system starting from all sites occupied. An immediate consequence of this result is that any stationary distribution is a convex combination of δ_0, the point mass on the all 0 state and ξ^1_∞, the limit starting from all 1s.

Theorem. Let $(\xi^A_t | \tau^A > t)$ denote the distribution of ξ^A_t conditioned on the event of being alive at time t. As $t \to \infty$, $(\xi^A_t | \tau^A > t) \Rightarrow \xi^1_\infty$. (2.6)

The results in this section remain valid for a variety of generalizations of the contact process that have 'asexual reproduction'. They hold in particular for the class of models we are about to describe, a class that has been chosen to cover the biological applications we will discuss.

1. The first generalization is to allow disturbances to affect more than one site at once. For any point x and set D, with probability γ_D all the points y with $y - x \in D$ are made vacant. The death events for different x and D are independent, but $\gamma_D \neq 0$ for only a finite number of finite sets D.

2. The second generalization is to introduce dependence between the destinations of the propagules. If the particle at x survives then it gives birth to k new particles (propagules) with probability p_k. When k propagules are produced they are sent to locations $x + Y_1, \ldots, x + Y_k$ where $(Y_1, \ldots, Y_k)$ have a joint distribution F_k on $(Z^d)^k$ that is concentrated on points y_i within a distance R of 0.

3. The third rule stays the same. If one or more propagules is sent to y, or if there is a particle at y that survives, y is occupied at the next time step; otherwise y is vacant.

Section summary. In this section we have introduced the contact process, a simple but widely applicable interacting particle system, and a larger class of models with more realistic dispersal and disturbance distributions. For all of these models the following results hold. If the birth rates are too small or the death rates are too large then the process dies out with probability one when we start with a finite set of occupied sets. When survival for all time starting from a single occupied site has positive probability there is a nontrivial stationary distribution ξ^1_∞ which is defined as the limit as $t \to \infty$ starting from all sites occupied. The

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last and most important result for these processes is that (2.6) holds. That is, when the process does not die out it looks like ξ^1_∞ at large times.

3. BARKHAM & HANCE'S DAFFODIL MODEL

Barkham & Hance (1982) have used a contact process to model the spread of wild daffodils (*Narcissus pseudonarcissus*). We will begin this section by describing the model in their words (which have been edited somewhat to shorten the description). We imagine a 1 m^2 area divided into 10000 units of 1 cm^2. Within this area 100 adult individuals of *Narcissus* are randomly distributed. Each is capable of reproduction and is of a different genet. The unit of time is considered to be one year. Each year, each individual may function in one of eight ways; it may continue to exist without reproducing, it may reproduce vegetatively, it may reproduce by seed, it may reproduce vegetatively and by seed, it may reproduce in either or both ways and die, or it may die without reproducing.

There are three variables in the model: the probability of an adult dying in a year (pm), the probability of an adult producing an adult vegetative offspring per year (pv), and the probability of an adult producing offspring from seed per year (ps). The following constraints were applied to the model.

1. The area occupied by each plant is a constant 1 cm^2.
2. The vegetative daughter must occupy randomly any one of the eight 1 cm^2 locations adjacent to the parent individual.
3. An offspring produced by seed must occupy randomly a 1 cm^2 location 15 cm distant from the parent. This distance is an approximate mean of the length of the scape which, under normal circumstances, bends over at senescence and releases seeds.
4. When the location to which a potential offspring is randomly assigned is already occupied, the offspring is not produced (density-dependent fertility).
5. When a vegetative and a seed offspring compete for the same square, the vegetative offspring always wins.
6. Any offspring allocated a position outside the boundary of the 1 m^2 plot is lost from the analysis.

Based on field studies, Barkham & Hance assigned the following values: shaded sites, $pm = 0.056$, $pv = 0.059$, $ps = 0.001$; open sites, $pm = 0.038$, $pv = 0.167$, $ps = 0.005$. In the notation of the last section this means $\gamma = pm$. We interpret distance to mean the Euclidean distance $\|z\|_2 = (z_1^2 + z_2^2)^{1/2}$ and that offspring produced by seed will be displaced by an amount that lies on the discrete approximation to the circle of radius 15 given by (15,0), (15,1), (15,2), (15,3), (15,4), (14,5), (14,6), (13,7), (13,8), (12,9), (11,10), (10,11), ... This model fits into the general framework introduced at the end of the last section, although it is not pleasant to write down the model in that form. Here the probability of two offspring $p_2 = pv \cdot ps$ with Y_1 (the random variable representing the displacement of the vegetative offspring from the parent) uniform on the eight Moore neighbours and Y_2 (the random variable for the offspring produced by seed) an independent variable uniform on our circle of radius 15. The probability of one offspring $p_1 = pv(1 - ps) + (1 - pv)ps$ with Y_1 in this case being a combination of the uniform distribution on the eight neighbours and the uniform distribution on our circle of radius 15. Finally, the probability of no offspring $p_0 = (1 - pv)(1 - ps)$.

Barkham & Hance simulated the system with the open sites parameters and found to their chagrin that 'the population rises rapidly to over 7000 m^{-2} before stabilizing at this unrealistically high level'. Readers who have looked at figure 7 should not be surprised at this. Equilibrium densities are high except for birth probabilities close to the critical value. When Barkham & Hance simulated the system with the shaded sites parameters, they found that the population became extinct rapidly. At first sight these results may be distressing. However, they simply are a warning that one cannot hope to make quantitative predictions about equilibrium densities from the models. Taking a lesson from how these models are used in statistical physics, we can say that the precise location of the boundary between the survival and extinction regions depends on the details of the model but the qualitative properties of the system (e.g. exponentially rapid convergence to an equilibrium state in the survival region) do not. In other words, because these systems do not model the local interactions accurately, we do not expect the quantitative information they provide to be reliable and we should look only at their qualitative properties.

After throwing out the field values, Barkham & Hance attempted to stabilize the population at several hundred plants by keeping pm and ps constant at the field values and varying pv. However, as they found, this can occur only for parameter values very close to the boundary between survival and extinction (Barkham & Hance 1982, p. 329, figure 3). Barkham & Hance next experimented with changing pm and ps by an order of magnitude. They found that values ten times less (figure 4(f)) stabilize the density at a similar level but oscillations are damped very markedly.

There is a simple explanation for the last observation. Suppose we set $pm = a\varepsilon$, $pv = b\varepsilon$, and $ps = c\varepsilon$ where ε is a small number, and then change the timescale so that one cycle of the simulation corresponds to ε units of time. If we then let $\varepsilon \to 0$ then our process will converge to a limiting continuous time contact process, which will be discussed in § 6. Reducing the probabilities by a factor of 10 in essence slows the rate at which we are moving through time by a factor of 10 so understandably the oscillations are reduced.

The ideas of the last paragraph can also be applied to the basic contact process to elucidate the behaviour of the critical curve near the point $\beta = 0$, $\gamma = 0$. If we let $\gamma = \varepsilon$, $\lambda = \theta\varepsilon$, change the timescale so that one cycle of the simulation corresponds to ε units of time and then let $\varepsilon \to 0$, the discrete time basic contact process will converge to the continuous time basic contact process. The latter model has only one parameter, so it is natural to talk about θ_c = the smallest value of θ for which survival occurs. Numeri-

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cal work suggests that $\theta_c \approx 3.3$ (see Brower *et al.* 1978), so the critical curve will have slope approximately 1/3.3 as it nears (0,0).

Much of the rest of Barkham & Hance's paper is devoted to the study of a simulated 10 year coppice cycle with alternating 5 year periods of open and shade values. This is one type of investigation for which particle system models are ideally suited: answering questions about how the equilibrium densities change as various attributes of the environment are manipulated. Barkham & Hance also investigate how the genets are distributed in the plot. We will return to that question in § 8, in which we consider Inghe's work.

Section summary. In this section we have, following Barkham & Hance (1982), used the contact process to model the spread of wild daffodils. One important lesson here is that since interacting particle systems do not model the local interactions accurately, we do not expect the quantitative information they provide to be reliable but only look at the qualitative properties.

4. LONG RANGE CONTACT PROCESS

To prepare for our analysis of the competition model of Crawley & May (1987) in § 5, we will now discuss the behaviour of the contact process in which the birth/dispersal function is constant on a square of side $2r + 1$ centered at the point, i.e. $\beta(x,y) = \lambda$ for $0 < \|x - y\|_\infty \leqslant r$ and 0 otherwise. The reader should think of r as being large and will see in a moment the reason that we want to assume that propagules are dispersed over large distances. The square shape of the neighbourhood is for mathematical convenience only. The main result, (4.4) below, can be extended to more reasonable dispersal distributions. For instance, we could set $\beta(x,y) = \beta q((x-y)/r)/r^d$ where q is a fixed function with $\int q(z)\mathrm{d}z = 1$. We divide by r^d so that $\Sigma_y \beta(x,y) \rightarrow \beta$ as $r \rightarrow \infty$.

If we pretend that at all times the states of the sites in our grid are independent then we can write the following equation for the density v_t of vacant sites at time t.

$$v_{t+1} = (v_t + \gamma(1 - v_t))\ (1 - (1 - v_t)(1 - \gamma)\lambda)^R. \qquad (4.1)$$

Here $R = |\{y{:}0 < \|y\|_\infty \leqslant r\}| = (2r+1)^d - 1$ is the number of neighbours. To explain equation (4.1), we notice that in order for a site to be vacant at time $t + 1$ then (i) either the site is vacant at time t or occupied and the plant there dies and (ii) none of its neighbours sends a propagule. The first factor gives the probability of (i), and the second gives the probability of (ii).

Physicists call the reasoning in (4.1) 'mean field theory' because each site feels only the average value of the states of the other sites. As in most contexts where 'mean field' methods are used by physicists, equation (4.1) is only an approximation for the contact process as the states of various sites are not independent, but are positively correlated. (This follows from a result of Harris (1960), see Durrett (1988*b*, p. 129).) However, as we are about to see, analysing (4.1) provides useful information that becomes exact in the limit as $r \rightarrow \infty$. Let

$$\phi(x) = \{x(1 - \gamma) + \gamma\}(1 - (1 - x)(1 - \gamma)\lambda)^R,$$

so that (4.1) becomes $v_{t+1} = \phi(v_t)$.

The next result describes the behaviour of the sequence defined by $v_0 = 0$ and $v_{t+1} = \phi(v_t)$ for $t \geqslant 0$. The reason for interest in the limiting behaviour of v_t is that starting with $v_0 = 0$ (all sites occupied) and iterating is like starting the particle system with all sites occupied and letting time run. So the limit of the v_t is the mean field value of the density of vacant sites in equilibrium. Figure 8 shows a graph of ϕ when $\lambda = 0.25$, $\gamma = 0.35$, and $R = 4$. There the iteration is shown geometrically by drawing lines from (0,0) to $(0,\phi(0))$ to $(\phi(0),\phi(0))$ to $(\phi(0),\phi(\phi(0)))$, etc. As that picture shows and the next result proves, the limit of the v_t is the smallest fixed point of ϕ in [0,1].

Let $v_0 = 0$ and let $v_{t+1} = \phi(v_t)$ for $t \geqslant 0$. As $t \rightarrow \infty$, $v_t \rightarrow w$ the smallest solution of $\phi(w) = w$ in (0,1]. (4.2)

Hence the iteration in (4.1) tends to a limit, possibly at the boundary 1.

Proof. ϕ is the product of increasing functions and hence increasing. Now $v_1 = \phi(0) > 0 = v_0$, so $v_2 = \phi(v_1) > \phi(v_0) = v_1$, and continuing we see that $v_t > v_{t-1}$ for $t \geqslant 1$. Because v_t is increasing and $\leqslant 1$, lim v_t exists. If we call the limit v_∞ then letting $t \rightarrow \infty$ in the relationship $v_t = \phi(v_{t-1})$ shows that $v_\infty = \phi(v_\infty)$. To see that $v_\infty = w$, we note that $v_0 \leqslant w$, so $v_1 = \phi(v_0) \leqslant \phi(w) = w$, and continuing we have $v_t \leqslant w$. Letting $t \rightarrow \infty$, it follows that $v_\infty \leqslant w$; but v_∞ is a solution of $\phi(x) = x$ so we must have $v_\infty = w$. ☐

The next result tells us when there is a solution < 1.

There is a solution of $\phi(x) = x$ with $0 < x < 1$ if and only if $\phi'(1) > 1$. That is, if and only if $\lambda > \gamma/R(1 - \gamma)$. (4.3)

Proof. To see this note that $u(x) = \phi(x) - x$ is such that $u(0) > 0$, $u(1) = 0$, and $u''(x) > 0$ (as $R > 1$). Since the tangent line to the graph of a strictly convex function lies strictly below the graph, it is easy to see that there is a root of u in (0,1) if and only if $u'(1) > 0$. ☐

Remark. In treating concrete examples it is useful to note that the fact that ϕ is convex implies that there is at most one solution of $\phi(x) = x$ in (0,1).

The function (4.3) tells us that, from the viewpoint of mean field theory, there is a non-trivial stationary distribution if and only if $\lambda > \gamma/R(1 - \gamma)$. Rewriting the condition as $(1 - \gamma)R\lambda > \gamma$, we see that it says something quite reasonable biologically: the mean number of offspring must be larger than the probability we lose a plant due to death, exactly as in threshold theorems in epidemiology. As we mentioned before, the argument leading to this conclusion is not valid for the contact process, but the conclusion is half right. A simple generalization of the first result in (2.1) implies that if $\lambda < \gamma/R(1 - \gamma)$, then the contact process dies out.

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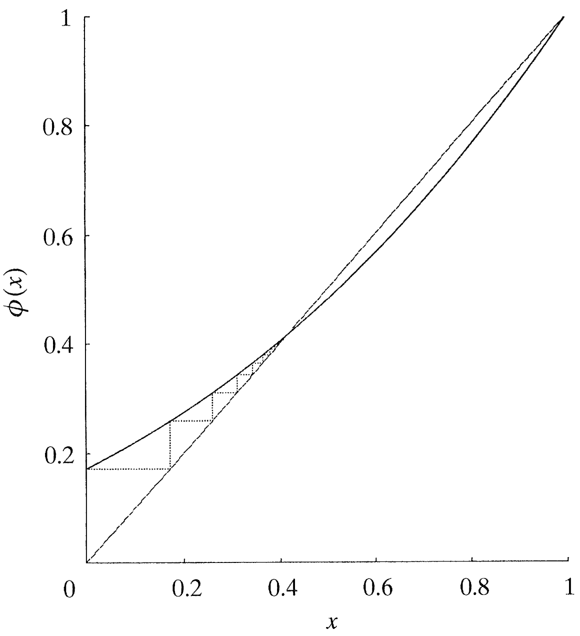

Figure 8. Iteration of equation (4.2) when $\lambda = 0.25$, $\gamma = 0.35$.

If we let $\beta = R\lambda$ and let $R \to \infty$ then $\phi(x)$ converges to

$$\psi(x) = (\gamma + (1-\gamma)x)e^{-\beta(1-\gamma)(1-x)}.$$

Writing $\alpha = \beta(1-\gamma)$ and differentiating twice gives

$$\psi'(x) = e^{-\alpha(1-x)}((1-\gamma) + \{(\gamma + (1-\gamma)x)\alpha\}),$$

$$\psi''(x) = \alpha\psi'(x) + e^{-\alpha(1-x)}(1-\gamma)\alpha,$$

so $\psi'(x) > 0$ and $\psi''(x) > 0$ for $0 \leqslant x \leqslant 1$. The proofs of (4.2) and (4.3) generalize immediately from ϕ to ψ. From the formula for the derivative it is clear that $\psi'(1) > 1$ (and hence there is a non-trivial solution of $\psi(x) = x$) if and only if $\alpha + 1 - \gamma > 1$; that is, $\beta(1-\gamma) > \gamma$. Again, the last condition is quite reasonable as it says that the expected number of propagules per plant is larger than the probability of the loss of a particle due to death. The next result justifies our remark that the mean field calculation is almost exact for large r. For this result we will suppose that $\beta(x,y) = \beta q((x-y)/r)/r^d$ where q is a fixed function with $\int q(z)dz = 1$.

Theorem. Suppose that $\beta(1-\gamma) > \gamma$ and let v be the solution of $\psi(x) = x$ in $(0,1)$. If r is large then the long range contact process has a nontrivial stationary distribution in which the density of vacant sites is approximately v. (4.4)

This result is the discrete time analogue of the main result of Bramson *et al.* (1989) and can be proved in the same way. (For a considerably simpler proof, see Durrett (1989).) The key to the proof is establishing that if t is fixed and the range is large then the sites at all times $s \leqslant t$ are almost independent and hence the density of occupied sites at time t is almost the density predicted by mean field theory. It is a consequence of the proof of (4.4) that in the nontrivial stationary distribution (which we know to be unique by results cited in § 2) the states of different sites are almost independent.

Section summary. 'Mean field theory' refers to the practice of assuming adjacent sites are independent (which they are not in the particle system) and then writing equations for the evolution of the density of occupied sites. The lesson to be learned from (4.4) and the remarks after that result is that if propagules are dispersed over distances that are large when compared to the size of the cells that correspond to the sites in the model, then the mean field calculation of the equilibrium density (and hence of the survival region) is almost correct since the states of different sites are almost independent.

5. CRAWLEY & MAY'S MODEL

In this section we will discuss a model of competition between annuals and perennials, which was introduced by Crawley & May (1987). In their words, the model may be described as follows.

1. There are two plant species: (i) an annual invading only by seed; and (ii) a perennial, invading only by lateral spread (through the production of 'ramets').
2. The plants exist in a spatially uniform environment in which habitable sites (cells) are distributed in a hexagonal pattern. This is the simplest tesselation of the plane, and is selected for convenience rather than as a quantitatively accurate description of the spatial spread of real plants.
3. The size of a cell is such that it can accommodate a single individual of the annual species or a single ramet of the perennial species.
4. The time unit of the model is taken to represent one generation of the annual plant.
5. In any one generation, the perennial is capable of occupying only those cells that are immediately adjacent to it; it may, however, occupy any or all of its six first-order neighbouring cells in one generation.
6. In competition, perennial ramets always exclude the annual.
7. The annual has no effect on the demography of the perennial.
8. In any generation, the order of events is as follows: (i) death of the perennial ramets; (ii) birth of the perennial ramets (occupation of empty cells); and (iii) recruitment of annuals from seed.
9. Recruitment of annuals by seed can only occur in empty cells (i.e. into cells not containing a surviving or newly born perennial ramet).
10. The probability of recruitment by annuals in any given empty cell is a function of the number of seeds produced in the previous generation. Specifically, we assume for each cell that recruitment occurs with probability 1 − exp(− mean number of seeds per cell), and that the entire crop of annual seeds is mixed and distributed at random over all cells whether empty or not.
11. Death of perennial ramets occurs in each generation with probability d, independent of the age of the ramet.
12. For each empty cell, the probability of being

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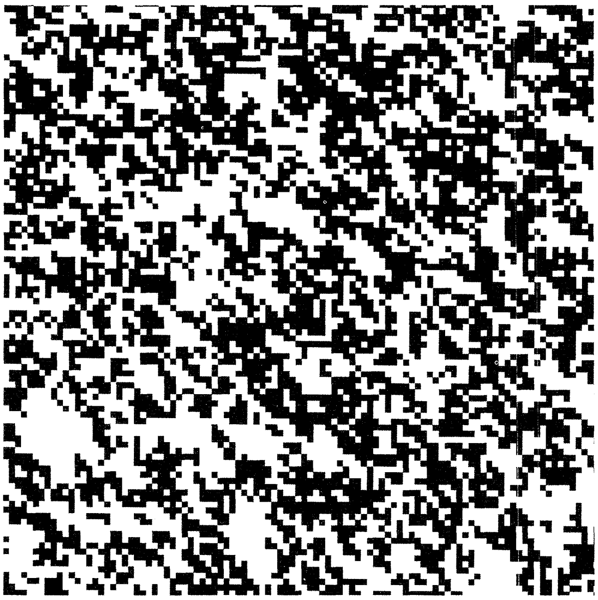

Figure 9. Equilibrium distribution for the two-dimensional discrete time basic contact process on the hexagonal lattice when $\lambda = 0.25$ and $\gamma = 0.35$.

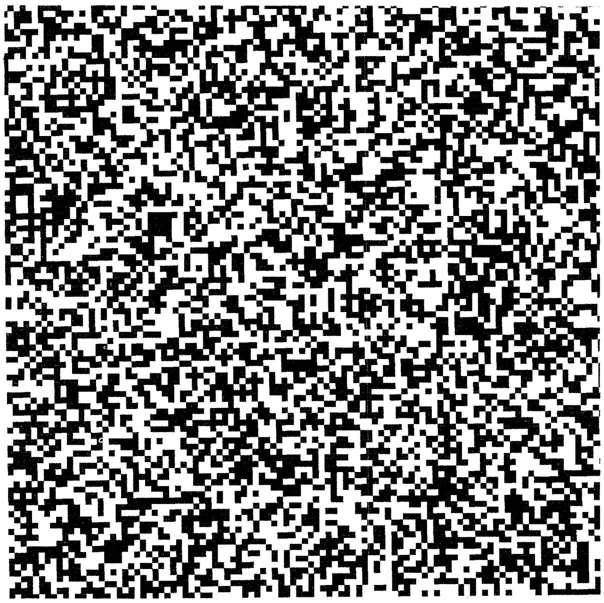

Figure 10. Sites independently occupied with probability 0.49.

invaded by a perennial ramet from a given neighbouring cell containing a surviving ramet is b, and if k out of the six first-order neighbours contain surviving ramets, the probability that a cell is invaded is given by $1 - (1 - b)^k$.

13. To minimize edge effects, the universe has wrap-around margins, so that the upper neighbouring row of the top row is the bottom row (and vice versa), and the left-hand neighbouring column of the leftmost column is the rightmost column (and vice versa).

The hexagonal lattice is ideal because it is the geometry that allows us to pack in the largest number of circles per unit area. However, from a theoretical point of view there is very little difference between the contact process on the hexagonal and on the square lattice. The survival region is larger for the hexagonal lattice as a site has six neighbours instead of four, but the qualitative properties of the model described in § 2 are the same. Given this, and the fact that the square lattice is easier to implement in a computer, we would have formulated the model on a square lattice for simplicity but we will stick with Crawley & May's choice here.

To begin to analyse this model, observe that the reproduction of perennials (2s) is not hindered by the presence of annuals (1s), so the set of sites occupied by 2s is a contact process in which occupied cells remain occupied with probability $1 - d$, and if they remain occupied give birth onto each neighbour independently with probability b. Crawley & May begin their analysis by deriving a difference equation (see page 477 of their paper) for the density of sites not occupied by 2s at time t, E_t:

$$E_{t+1} = [E_t(1 - d) + d][1 - b(1 - d)(1 - E_t)]^6, \quad (5.1)$$

and then observing that there is a globally stable equilibrium point with $E^* < 1$ if and only if

$$b > d/6(1 - d). \quad (5.2)$$

Readers should recognize (5.1) as (4.1) with $v_t = E_t$, $\gamma = d$, $\lambda = b$, $R = 6$, and the first factor rewritten in the form in (4.2). As we remarked in the last section, equation (5.1) is based on the mean-field assumption that the states of various sites are always independent and hence, as Crawley & May (1987) realized, equation (5.2) gives only an approximation to the true condition for the survival of the perennials. The easiest way to see that there is a significant amount of dependence among sites is to look at a simulation. Figure 9 gives a picture of the system with $b = 0.25$ and $d = 0.45$ on a 100×100 lattice at time 100, which in this case should be close to equilibrium. There are 4901 particles present in the simulation. The picture may look random but comparison with figure 10, which shows sites that are independently occupied with probability 0.49, shows that the particles in figure 9 tend to occur in clumps.

The correlations between the states of adjacent sites are almost impossible to calculate analytically in the contact process, so to estimate the values for which coexistence occurs we have to resort to simulation. Following part (b) of figure 1 on p. 478 of Crawley & May, we set $b = 0.25$ and look at the density in equilibrium as a function of the ramet death rate d. Figure 11 gives the estimates that we obtained by running the system with parameters $b = 0.01, 0.02, \ldots 0.60$ until time 3000, recording the fraction of occupied sites every 10 units of time starting at time 2000, and then averaging these observations. This may sound like a lot of work; but by taking advantage of a trick of Buttel *et al.* (1992) mentioned in § 2, we were able to treat the 60 values of b in one simulation run, which only took a few hours on a personal computer. The lower curve in the graph gives our estimate of the density of perennials in equilibrium, while the upper curve gives the mean field value for the equilibrium density. The two curves are quite close when $d < 0.3$,

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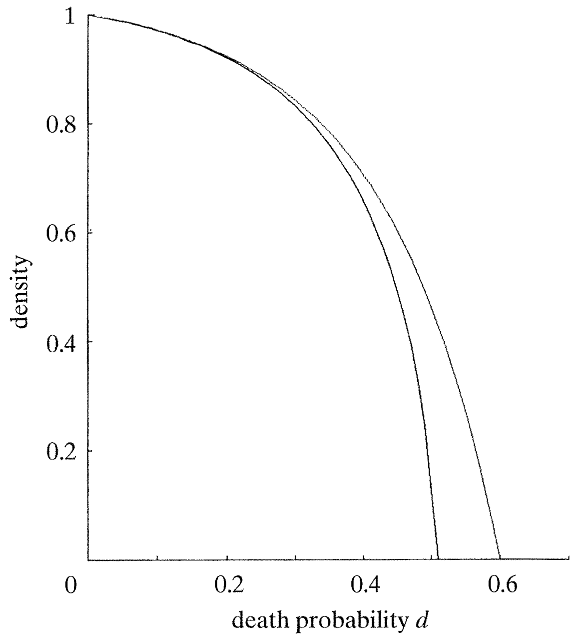

Figure 11. Actual equilibrium density for the two-dimensional discrete time contact process with $b = 0.25$ as a function of death probability d compared with upper bound from mean field theory.

but diverge for larger values; the lower curve hits 0 somewhere between 0.51 and 0.52.

Although equation (5.2) is only an approximate condition for the survival of perennials, it becomes correct in the limit of large range if one replaces E^* by the density of sites not occupied in the perennial equilibrium. Results quoted in § 2 above imply that when the perennial species persists, it converges exponentially rapidly to an equilibrium state that has exponentially decaying correlations, so if we consider an $L \times L$ grid with L large, the fraction of sites not occupied by perennials will be almost constant in time. However, the density of vacant sites will not be the fixed point E^* but instead the equilibrium density of vacant sites for the contact process of perennials. If one pretends that the density of sites not occupied by perennials is F independent of t then for large L the fraction of these gaps occupied by annuals will (almost) satisfy

$$p_{t+1} = 1 - \exp(-cp_tF), \qquad (5.3)$$

where c is the mean number of seeds produced by each plant. To explain (5.3), we note that at time t there are L^2p_tF annuals each of which will send a seed to a given open site with probability $\approx c/L^2$, so if L is large the number of seeds that land on a given open site has approximately a Poisson distribution with mean cp_tF, and hence will be positive with probability $1 - \exp(-cp_tF)$.

Equation (5.3) is essentially (6) on p. 479 of Crawley & May (1987). Let $\psi(x) = 1 - \exp(-cxF)$. The absence of annuals is a stable situation ($\psi(0) = 0$) but we would like to know if they can persist at a positive level, i.e. is there a solution of $\psi(x) = x$ with $x > 0$? Differentiating we see that $\psi'(x) = cF \exp(-cxF)$ and $\psi''(x) = -(cF)^2 \exp(-cF)$ so ψ is increasing and concave. Imitating the proof of (4.3), it is easy to see that there is a non-trivial solution if and only if $\psi'(0) > 1$, that is, $c > 1/F$, which is the conclusion on p. 479 of Crawley & May with the fixed point E^* replaced by the density of vacant sites F in the perennial contact process equilibrium.

The analysis above is based on the assumption that annuals can disperse their seeds uniformly across the entire system under study. By using ideas from the last section, one can obtain the same conclusions under the more palatable assumption that dispersal occurs over a large distance. That is, instead of model feature 10 described on p. 338 we can assume:

10′. Each annual plant independently produces k seeds with probability p_k and if the annual is at x these seeds are sent to sites chosen at random according to a distribution of the form $c_rq((x-y)/r)/r^d$, where c_r is constant chosen to make the sum of the probabilities equal to 1.

Theorem. Let $c = \Sigma kp_k$ be the mean number of seeds produced by an annual plant and F the fraction of vacant sites in the perennial equilibrium. If $c > 1/F$ and r is sufficiently large then coexistence occurs. That is, there is a non-trivial translation invariant stationary distribution in which both types are present. Conversely, if $c < 1/F$ and r is sufficiently large then the annuals die out. That is, if we start from an initial state with infinitely many annuals and perennials, the probability of having an annual at x goes to 0 as $t \to \infty$. (5.4)

For a proof of this result, see Durrett & Schinazi (1992).

Section summary. In this section, we have presented an analysis of the competition of annuals and perennials due to Crawley & May (1987). They assumed that annual seeds were dispersed uniformly across the entire system and used mean field reasoning. Using interacting particle systems we have shown that the same conclusions hold for non-uniform dispersal functions that are sufficiently spread out.

6. CONTINUOUS TIME MODELS

The results in the last two sections, and indeed much of the theory of interacting particle systems, become simpler if time is continuous rather than discrete (i.e. time is indexed by the non-negative real numbers rather than by the non-negative integers). We will devote this section to a discussion of continuous time models. Suppose first that we are simulating a system on $\{0,1,\ldots,L-1\}^d$ with some boundary conditions. In discrete time we go from time t to time $t+1$ by setting $\xi_{t+1}(x) = i$ with probability $p_i(x,\xi_t)$, with the choices being made independently for each x. In continuous time, we change one site at a time: if the current state is ξ, we pick a site x at random, and change its state to i with probability $p_i(x,\xi)$, and repeat the process, with cL^d changes corresponding to one unit of time, where c is a constant that describes

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the overall rate at which transitions are occuring. The main difference then is that we update one site at a time rather than all sites at once. In the terminology of the theory of cellular automata we use asynchronous rather than synchronous updating. Asynchronous updating makes it easier to prove theorems since the state of the system changes gradually rather than abruptly. From a modelling point of view asynchronous updating is simpler as we do not need 'collision rules' to decide what should happen when several events try to influence a site at once.

We begin our explanation of continuous time processes by formulating the basic contact process in continuous time. This model was mentioned in our discussion of Barkham & Hance's work in § 3: (i) particles die at rate γ, give birth at rate β; (ii) a particle born at x is sent to a y chosen at random from the $2d$ nearest neighbours; (iii) if y is occupied the birth is suppressed. Here, we say something happens at rate r if the probability of an occurrence between times t and $t+h$ is $\sim rh$, that is, the probability when divided by rh converges to 1 as $h \rightarrow 0$. When the rate is a constant r, as the death rates and birth rates are in the basic contact process, the times t_i between successive occurrences of the event are independent and have an exponential distribution with parameter r, that is $P(t_i > t) = e^{-rt}$.

To simulate the continuous time process when $\beta \geqslant \gamma$ (the only interesting case since the system dies out when $\beta < \gamma$) we use the general recipe above with $c = \beta$, and transition probabilities $p_0(x,\xi) = \gamma/\beta$, when $\xi(x) = 1$; and $p_1(x,\xi) = n(x,\xi)/2d$ when $\xi(x) = 0$ and $n(x,\xi)$ neighbours of x are occupied in ξ. This recipe is based on the idea that each site is independently trying to change at rate β, so to make deaths happen at rate γ, we kill the particle with probability γ/β and leave it alive otherwise. Likewise, only vacant sites with all neighbours occupied experience births at rate β, so to get the right rate we have to do nothing with a probability equal to the fraction of vacant sites. This is easily implemented in a computer simulation by picking a neighbour at random and making the site occupied if the neighbour chosen is.

The competition model of the last section can be generalized to include long-range dispersal and formulated in continuous time. The state at time t is ξ_t: $\boldsymbol{Z}^d \rightarrow \{0,1,2\}$ and the system evolves as follows: (i) particles of type i die at rate γ_i and give birth at rate β_i; (ii) a particle of type i born at x is sent to a y with a probability proportional to $q_i((x-y)/r)/r^d$ where q_i is a fixed function and c_r is a proportionality constant chosen to make the sum of the probabilities equal to 1; (iii) if $\xi_t(y) \geqslant \xi_t(x)$ then the birth is suppressed.

To analyse this system we begin by observing that the 2s do not feel the presence of the 1s and are themselves a long range contact process. As in § 5, we will begin by considering the system in which 1s are absent, so we will drop the subscript 2s and refer to the process as the long range contact process. If we pretend that adjacent sites are independent then the fraction of sites occupied by 2s at time t, u_t will satisfy

$$u_t' = -\gamma u_t + \beta(1-u_t)u_t. \qquad (6.1)$$

The first term comes from particles dying at rate γ. To see the second, think about the computer formulation of the process. When we pick a vacant site, we pick one of its neighbours at random and a birth occurs if it is occupied. Events occur at rate β and a birth occurs if the site is vacant and the chosen neighbour is occupied, an event of probability $(1-u_t)u_t$.

Now, $u_t \equiv \rho$ (i.e. constant in space and time) is a solution of equation (6.1) if and only if $-\gamma\rho + \beta\rho(1-\rho) = 0$, so there are two solutions: $\rho = 0$ and $\rho = (\beta-\gamma)/\beta$, with the latter being positive only when $\beta > \gamma$. In order for the process not to die out, it is trivially necessary that the particles give birth at a faster rate than they die. The next result due to Bramson *et al.* (1989) shows that this condition is asymptotically sharp as $r \rightarrow \infty$.

Theorem. Suppose $\beta > \gamma$. If r is large then the long-range contact process has a stationary distribution in which the density of occupied sites is close to $(\beta-\gamma)/\beta$. (6.2)

Comparing the last result with (4.4) shows one immediate advantage: we now have an explicit expression for the equilibrium density. This will pay off in an explicit condition for the coexistence region for the competition model.

Theorem. Suppose that $\beta_2 > \gamma_2$ and $\gamma_1 + \beta_2 - \gamma_2 < \beta_1\gamma_2/\beta_2$. If r is large then the competition model has a non-trivial stationary distribution in which 2s have density close to $(\beta_2-\gamma_2)\beta_2$ and 1s have density close to

$$\left(\frac{\beta_1\gamma_2}{\beta_2} - \gamma_1 - (\beta_2-\gamma_2)\right)\Big/\beta_1 \qquad (6.3)$$

To explain the formula for the equilibrium density of 1s, we note that if v_t is the density of sites occupied by 1s at time t then reasoning as we did for (6.1)

$$v_t' = -\gamma_1 v_t - \beta_2 v_t u_t + \beta_1 v_t(1-u_t-v_t). \qquad (6.4)$$

The first term comes from deaths at rate γ_1, the second from 2s giving birth onto sites occupied by 1s, and the third from 1s giving birth onto sites not occupied by 1s or 2s. If we suppose that the 2s are in equilibrium, that is, $u_t = (\beta_2-\gamma_2)/\beta_2$, and ask when $v_t \equiv \sigma$ is a solution, we find the trivial root $\sigma = 0$ and a second root with

$$-\gamma_1 - (\beta_2-\gamma_2) + \beta_1\left(\frac{\gamma_2}{\beta_2} - \sigma\right) = 0.$$

Solving we find the formula given in (5.3), which is positive if and only if $\gamma_1 + \beta_2 - \gamma_2 < \beta_1\gamma_2/\beta_2$.

The conditions for coexistence are hardly intuitive but it is easy to see that they have the right monotonicity properties in the parameters. That is, increasing β_1 or γ_2 or decreasing γ_1 or β_2 makes it easier for the 1s to survive. Although the answer in (6.3) is somewhat messy, it is much simpler than the analogous answer in discrete time. We leave it as a challenge for the reader to derive the discrete time analogue of (6.4) and find the conditions for coexis-

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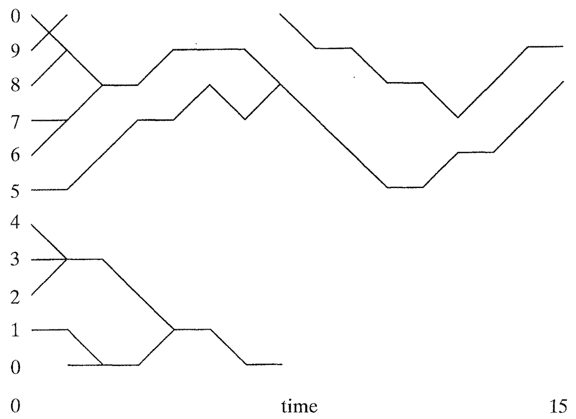

Figure 12. Voter model duality.

tence that come from the equation. If you can solve this problem, let us know. The function (5.3) is from Durrett & Swindle (1991). A complete convergence theorem (i.e. a result analogous to (2.6)) was proved for this model in Durrett & Møller (1991).

Section summary. In this section we introduced interacting particle systems in 'continuous time'. In this formulation, only one site changes at a time, and we do not need the collision rules that discrete time models need to decide what happens when several effects try to influence a site simultaneously. An additional bonus is that when we reformulate the long-range limit results of the § 5 in continuous time we get explicit formulas for the limiting coexisting region.

7. SYMMETRIC COMPETITION PROCESSES

In this section we will consider a model that is appropriate for the competition of different genets of the same species of plant or several species of the same type of plant. We begin by describing a much simpler system called the voter model introduced by Holley & Liggett (1975) that is a spatial version of the Wright–Fisher model from genetics. (For information on the Wright–Fisher model, see Kingman (1980, 1982), Donnelly (1984), Tavaré (1984) and Feldman (1989).) In the voter model, the state at time t is $\xi_t\colon \boldsymbol{Z}^d \rightarrow \{1,2,\ldots,\kappa\}$. The name voter model refers to the fact that one can think of $1,2,\ldots,\kappa$ as indicating the preference of the voter at x among the κ candidates in an election. With this interpretation in mind, the evolution can be formulated as follows: the state of x at time $t+1$ is equal to the state of x at time t with probability $1-\gamma$ and with probability γ is equal to that state (at time $t-1$) of a randomly chosen neighbour. Here the neighbourhood can be any finite irreducible set $\mathscr{N}$. That is, any point x in $\boldsymbol{Z}^d$ can be reached from 0 by a path $x_0 = 0, x_1, \ldots, x_n = y$ so that for $1 \leqslant m \leqslant n$, $x_m - x_{m-1} \in \mathscr{N}$. This means that it is possible for any voter to influence any other through some chain of events.

In the genetics literature, the Wright-Fisher model is usually considered on a finite set $\{1,\ldots,N\}$ with no spatial structure. Time t is thought of as generation t and each individual at time $t+1$ chooses a parent at random from the previous generation. The voter model is then a version of the Wright–Fisher model in which the spatial distribution plays a role in determining the possible genetic lines. The spatial version of the Wright–Fisher model is usually called the stepping stone model. See Kimura (1953), Kimura & Weiss (1964), Rohlf & Schnell (1971), Felsenstein (1975), Sawyer (1976, 1977, 1979), and Cox & Griffeath (1986, 1987, 1990).

Because the transitions in the voter model make sites equal, it is natural to ask if the system will approach consensus as $t\rightarrow\infty$. That is, will we have $P(\xi_t(x) = \xi_t(y)) \rightarrow 1$ as $t\rightarrow\infty$ for all x and y? The answer to the last question is 'yes' in $d = 1,2$ and 'no' in $d \geqslant 3$. To explain the reason for this answer we will introduce dual processes $X_s^{x,t}$ that trace the origin of the opinion at x at time t. We start with $X_0^{x,t} = x$ and work backwards in time. If $X_s^{x,t} = y$ and the individual at y at time $t-s$ chose to imitate z from generation $t-s-1$ then we set $X_{s+1}^{x,t} = z$. (Here $z = y$ with probability $1-\gamma$ and is a randomly chosen neighbor with probability γ.) This definition guarantees that the genetic type of the individual at x at time t is the same as that of $X_s^{x,t}$ at time $t-s$. Figure 12 shows a picture of the dual process for $\{0,1,\ldots,9\}$. The left edge of the picture represents time 15, the right edge time 0. To avoid edge effects we have used periodic boundary conditions. That is, the top and bottom sites in the figure both represent 0, so when a jump to the left of 0 occurs the particle reappears at the top of the picture (see time 8) or when a jump to the right from 9 occurs the particle reappears at the bottom (see time 15). Notice that the voters at 5, 6, 7, 8 and 0 trace their opinion back to that of 8 at time 0, whereas the other voters trace their opinions back to 9.

The process $X_s^{x,t}$, $0 \leqslant s \leqslant t$ is what is called a random walk as the step taken at time s, $X_{s+1}^{x,t} - X_s^{x,t}$, is independent of the first s steps. If one thinks about the evolution of two of these processes, $X_s^{x,t}$ and $X_s^{y,t}$ then it is easy to see that they move independently until they hit (i.e. occupy the same site) and then stay together after that. Because of this, the collection $\{X_s^{x,t}\colon 0 \leqslant s \leqslant t\}$ is called a coalescing random walk. When two particles hit they coalesce to one. Well known results about random walk imply that two independent random walkers will hit with probability one in $d = 1,2$ but can avoid each other for all time with positive probability in $d \geqslant 3$. To see how this implies the result given we notice that

$$P(\xi_t(x) \neq \xi_t(y)) \leqslant P(X_t^{x,t} \neq X_t^{y,t}) \rightarrow 0 \quad \text{as} \quad t\rightarrow\infty \quad \text{in} \quad d = 1,2. \tag{7.1}$$

To show that consensus need not be approached in $d \geqslant 3$, we take $\kappa = 2$ and start with an initial configuration ξ_0^θ in which sites are independently 1 or 2 with probabilities θ and $1-\theta$. Now two sites x and y will have different opinions at time t if and only if they trace their opinions back to different sites at time 0 and find different opinions there so

$$P(\xi_t^\theta(x) \neq \xi_t^\theta(y)) = 2\theta(1-\theta)P(X_t^{x,t} \neq X_t^{y,t}) \not\rightarrow 0 \quad \text{as} \quad t\rightarrow\infty \quad \text{in} \quad d \geqslant 3. \tag{7.2}$$

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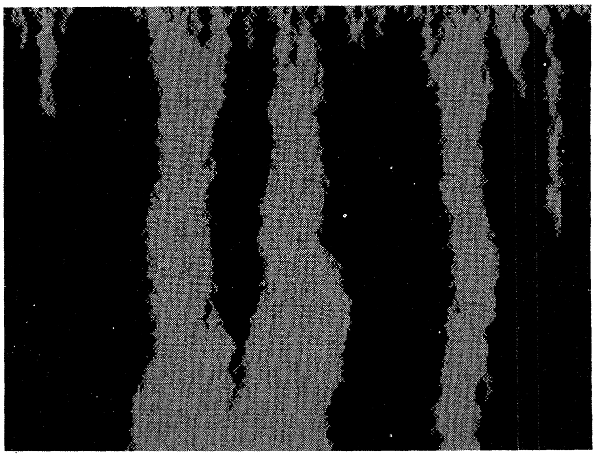

Figure 13. One-dimensional voter model, times 0–239.

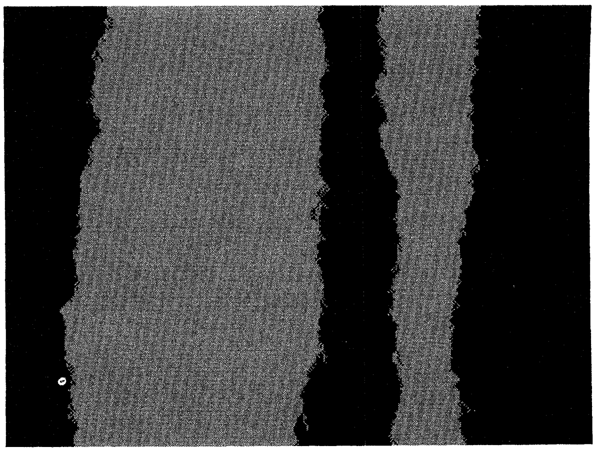

Figure 14. One-dimensional voter model, times 1200–1439.

The density of sites with opinion 1,

$$P(\xi_t^\theta(x) = 1) = P(\xi_0^\theta(X_t^{x,t}) = 1) = \theta, \tag{7.3}$$

for all t. The last equation generalizes easily to

$$P(\xi_t^\theta(x) = 1 \quad \text{for all} \quad x \in A) = E(\theta^{N_t^A}), \tag{7.4}$$

where N_t^A is the number of particles at time t in the coalescing random walk starting with one particle on each site in A at time 0. Because the number of points in a coalescing random walk only decreases, the right-hand side of the last equation increases to a limit as $t \to \infty$. Because all finite dimensional distributions can be written in terms of the ones in (7.4) it follows that ξ_t^θ converges to a limiting stationary distribution ν_θ in which 1s have density θ. Holley & Liggett (1975) have shown that the ν_θ are the only interesting stationary distributions. That is, all the stationary distributions are convex linear combinations of the ν_θ. The reader should note that while the contact process has only one non-trivial stationary distribution, the voter model has a one parameter family of stationary distributions. This occurs because in the voter model the average density of sites in state 1 is preserved by the time evolution.

To help explain the theoretical results we have just stated, we turn to computer simulations. In all the cases we will examine, $\mathcal{N}$ is the set of nearest neighbours of 0. Our next two figures give a space-time picture of the voter model with $\kappa = 2$ starting from an initial state in which sites are independently 0 or 1 with probability 1/2. Here we are looking at an interval $\{0,1,\ldots,319\}$ with periodic boundary conditions. That is, 319 is a neighbour of 0. Figure 13 shows the system from time 0 to time 239. It should be clear from the picture that the intervals on which opinions are constant are getting longer. Figure 14 shows the system from time 1200 to time 1439. At this time there are four large intervals of sites with the same opinion, and the 'boundaries' between these intervals (which are not precisely defined) move like random walks. Because random walks move about $\sqrt{t}$ in time t, it should not surprise you to learn that if we let τ_N be the first time that all the voters in $\{0,1,\ldots, N-1\}$ have the same opinion, then

$$E\tau_N \sim (C_1/\gamma)N^2, \tag{7.5}$$

as $N \to \infty$ where $a_N \sim b_N$ means that the ratio $a_N/b_N \to 1$. The time required is inversely proportional to γ as our voters keep their opinion for an average of $1/\gamma$ steps before they look at a neighbour. Cox (1988) has proved (7.5) and calculated that if we start from all sites having different opinions then the constant $C_1 = 1/6$. In our simulation, $\gamma = 2/3$ (the particle at x picks an opinion from $x-1$, x and $x+1$ at random), and $N = 320$ so $E\tau_N = 17\,066$. The reason for Cox's choice of the initial condition in which all sites are different is that in this case the time to reach consensus is the same as the time it takes a coalescing random walk starting with all sites occupied to reduce to one particle. The coalescing random walk problem is much easier to study. In particular, by considering the time it takes the particles at 0 and $N/2$ to hit, we see that about N^2 units of time will be required or to be precise $E\tau_N \geqslant (1/8\gamma)N^2$.

Figures 15 and 16 give a look at the two-dimensional voter model at times 250 and 2000 starting from an initial state in which each site was randomly assigned a symbol from a list of 50 possibilities. The message in these pictures is that in two dimensions the clustering occurs very slowly. Cox & Griffeath (1986)

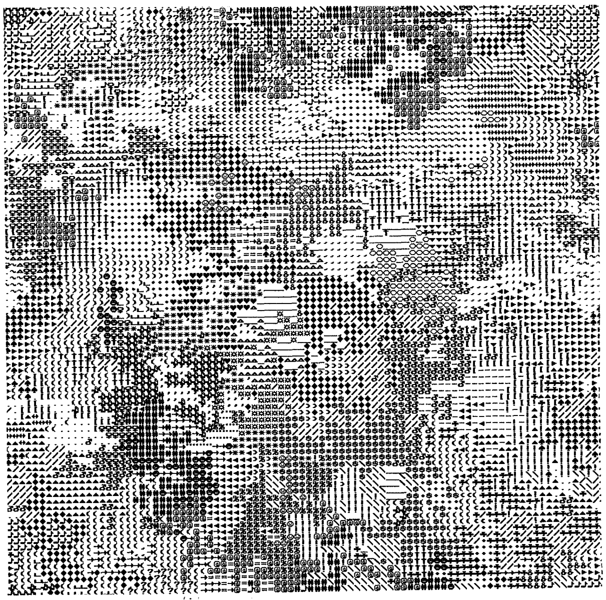

Figure 15. Two-dimensional voter model at time 250.

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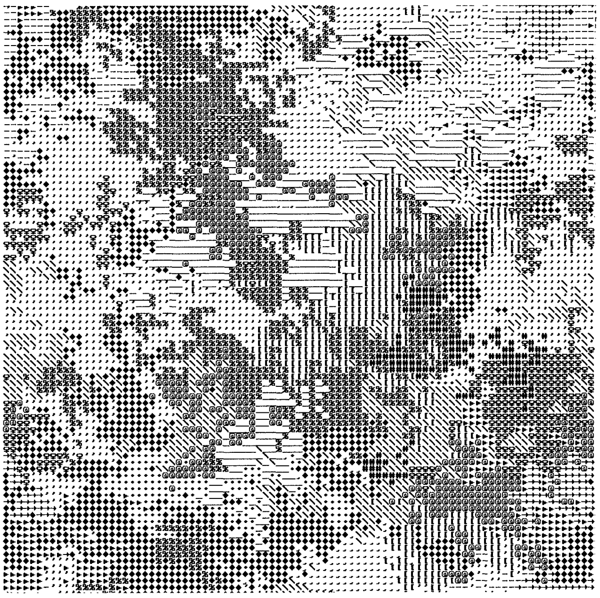

Figure 16. Two-dimensional voter model at time 2000.

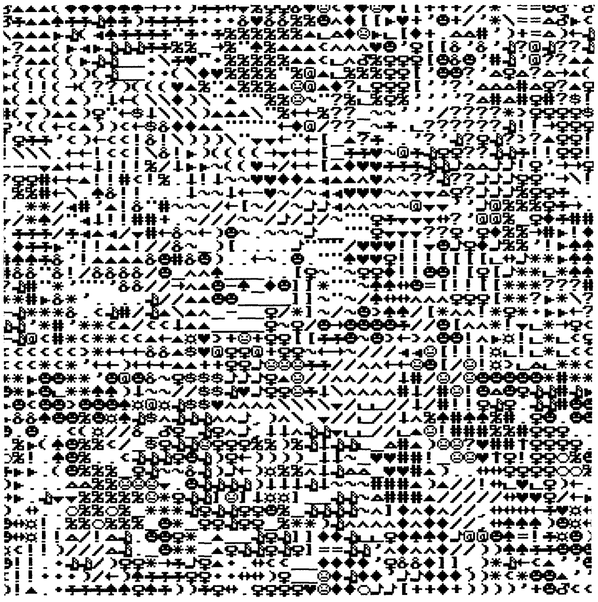

Figure 17. One plane from the three-dimensional voter model at time 250.

and Bramson *et al.* (1988) have proved some very interesting mathematical results about how the clustering occurs in two dimensions. Again, Cox (1988) has studied the time to reach consensus, τ_N, for the voter model on $\{0,1,\ldots,N-1\}^2$ with periodic boundary conditions starting from all sites different and shown that in $d=2$

$$E\tau_N \sim (2/\pi\gamma)N^2 \log N. \tag{7.6}$$

In our simulation, $\gamma = 1/2$ and $N = 90$ so $E\tau_N = 46\,407$. To explain why the answer is proportional to $N^2 \log N$, we note that the difference of two random walks starting at (0,0) and $(N/2,N/2)$ is a random walk that will take about N^2 steps to get close to (0,0). The extra $\log N$ comes from the fact each site that the random walk has hit before time N^2 has been visited about $\log N$ times, so the total number of sites visited by time N^2 is only of order $N^2/\log N$ and we have to wait until time $N^2 \log N$ so that the random walk has visited a positive fraction of the sites and hence has a positive probability of having hit (0,0).

Our final picture in figure 17 shows a two-dimensional slice through a three-dimensional voter model on $\{0,1,\ldots,44\}^3$ with periodic boundary conditions at time 250. This should be a fairly good approximation of the limiting equilibrium state. Note that in contrast to the picture of the two-dimensional voter model at time 250, here the typical cluster of sites with the same opinion consists of fewer than 10 sites. Again, Cox (1988) has studied the asymptotic behaviour of the consensus time τ_N starting from all sites different and found that in $d \geqslant 3$

$$E\tau_N \sim (C_d/\gamma)N^d, \tag{7.7}$$

where C_d in an explicitly computable constant that only depends on the dimension. The reason for the N^d is that a random walk in three dimensions only visits each site that it has hit some constant number of times by time N^d, so by that time one walk will have visited a positive fraction of the sites in the space and hence two independent random walks will have a positive probability to have hit.

Our symmetric competition model is a hybrid of the voter model and the contact process. The state at time t is $\xi_t : \boldsymbol{Z}^d \to \{0,1,\ldots,\kappa\}$ and we think of 0 as vacant and $1,\ldots,\kappa$ as indicating different genets of the same species, or different species of the same type of plant. With these interpretations in mind the dynamics are formulated as follows:

1. Each particle dies with probability γ and survives with probability $1-\gamma$.
2. If the particle at x survives and y is one of the neighbours of x, then with probability λ, a new particle of the same type as x is sent to y. The birth events for different ys and from different xs are independent.
3. If the particle at y survives it retains control of the site. If there is no particle at y or the particle at y dies, then the new state is chosen at random from the propagules sent to y. If there is no survivor at y and no propagules are sent to y then y is vacant.

If we ignore the different types and look only at whether the site is occupied or not then we get a contact process, so clearly nothing interesting will happen unless that contact process survives. We will suppose this for (6,8) and (6.9), which for simplicity will be stated only for the case $\kappa = 2$. By generalizing the proofs in Neuhauser's (1990) thesis one can show

Theorem. In dimensions d $\leqslant 2$, for any initial configuration, we have

$$P(\xi_t(x) = 1, \xi_t(y) = 2) \to 0 \qquad \text{for all} \qquad x,y \in \boldsymbol{Z}^d$$

so all stationary distributions are trivial. (7.8)

Theorem. In dimensions d $\geqslant 3$, there is a one-parameter family of stationary distributions ν_θ, $\theta \in [0,1]$,

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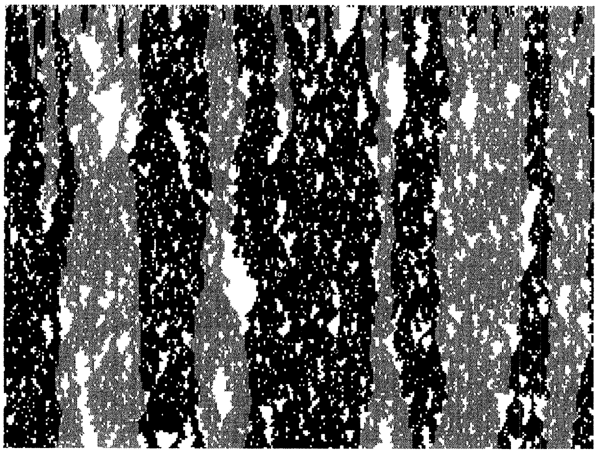

Figure 18. Symmetric competition model in one dimension, times 0–239.

and all translation-invariant stationary distributions are convex combinations of the ν_θ. (7.9)

As in the voter model, the dichotomy between the behaviour in $d \leqslant 2$ and $d \geqslant 3$ comes from the fact that two independent random walks will hit with probability 1 in the first case and but may avoid each other for all time in the second. The stationary distributions are constructed by starting the system from an initial configuration in which the $\xi_0(x)$ are independent with $P(\xi_0(x) = 1) = \theta$ and $P\ (\xi_0(x) = 2) = 1 - \theta$. The proofs of (7.8) and (7.9) are based on the same strategy used for the voter model – we compute the state of x at time t by working backwards in time, but the resulting 'dual process' is very complicated.

Figures 18 and 19 show a simulation of the competition model in one dimension with $\lambda = 0.6$ and $\gamma = 0.25$. Except for the vacant sites, the pictures look much like the pictures of the voter model in figures 13 and 14. Figures 20 and 21 show the competition model in two dimensions in which each site is initially assigned a randomly chosen character from a list of 50 possibilities. Again these pictures look much like those of the two-dimensional voter model in figures 15 and 16.

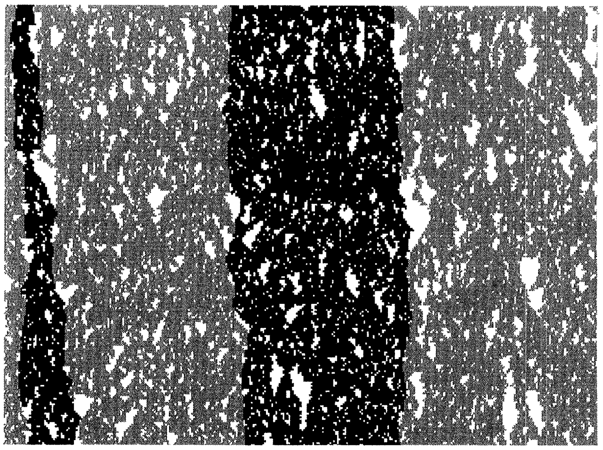

Figure 19. Symmetric competition model in one dimension, times 1200–1439.

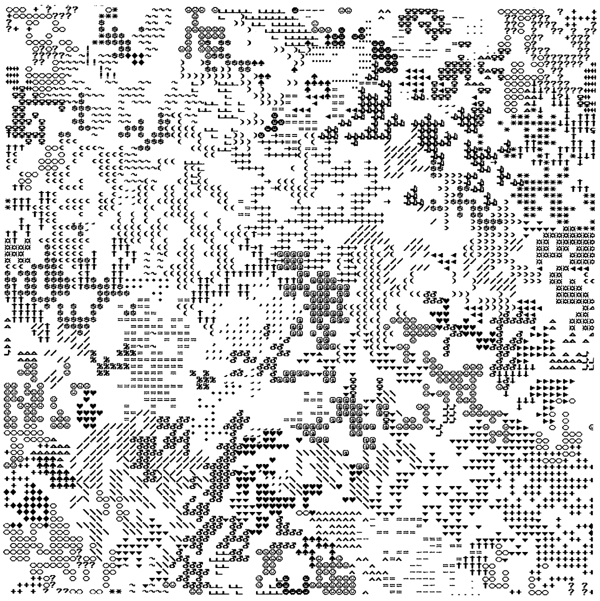

Figure 20. Two-dimensional symmetric competition model at time 250.

Section summary. In this section we introduced the voter model (which is useful in genetics) and a related class of symmetric competition models. In both cases clustering occurs in dimensions $d \leqslant 2$, i.e., the probability of seeing one type at x and a different type at y goes to 0 for any x and y, while coexistence is possible in dimensions $d \geqslant 3$, that is, there is a non-trivial stationary distribution in which both types are present.

8. INGHE'S COMPETITION MODEL

In this section we will discuss a model of the competition of different genets of a fixed perennial due to Inghe (1989). We begin by describing the model in Inghe's own words. We have removed Inghe's justifications of the model to shorten its description and we

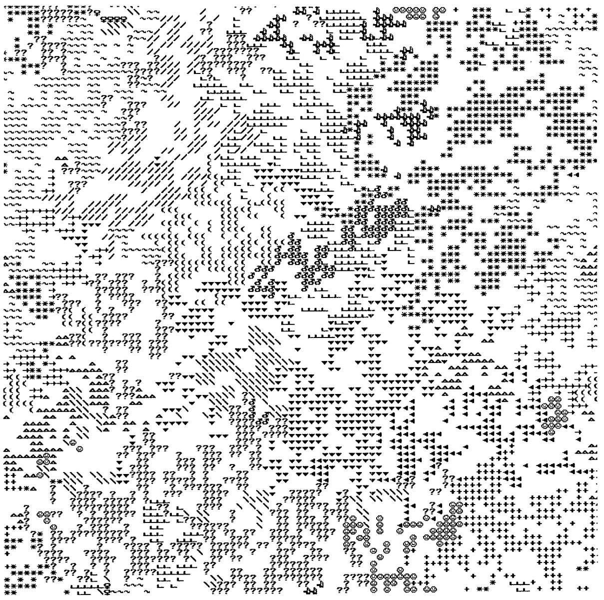

Figure 21. Two-dimensional symmetric competition model at time 2000.

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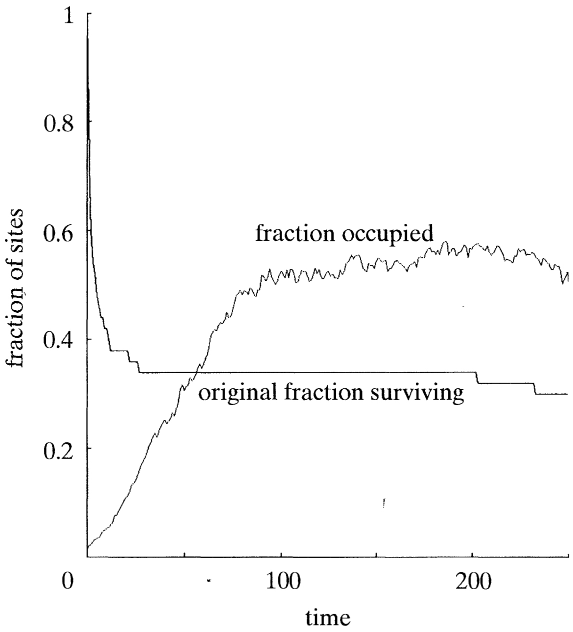

Figure 22. Fraction of the initial 60 genets surviving to time t and fraction of sites occupied at time t for Inghe's competition model with $\lambda = 0.25$ and single site deaths with probability $\gamma = 0.325$.

have rewritten some of the rules to more clearly specify the dynamics.

1. Simulations are carried out in a universe of 3600 sites (cells), arranged in a square of 60 rows and 60 columns. Each site can be empty or occupied by exactly one ramet. We think of each cell as being $2 \times 2\ \text{cm}^2$ so the universe is $1.2 \times 1.2\ \text{m}^2$.
2. Sites are assumed to be placed in a square lattice.
3. To avoid edge effects, the universe has wrap-around margins, so that the upper row and the bottom row are neighbours of each other, and the rightmost column and the leftmost column are neighbours of each other.
4. Each site has a neighbourhood of 12 sites (to be precise, $\mathcal{N} = \{y : \|y\|_1 \leqslant 2\}$, see the table of probabilities below). For each site i in the neighbourhood, there is a certain probability P_i for a propagule to be sent there, and providing it is the only propagule sent there, to colonize the site. If more than one propagule competes for colonizing an empty site, the actual probability for a ramet in position I to colonize the empty place, P_I' is given by

$$P_I' = \frac{P_I}{\sum_{i=1}^{12} P_i}\left(1 - \prod_{i=1}^{12}(1 - P_i)\right),$$

where P_i, $i = 1,2,3, \ldots, 12$ are values from the 12 neighbouring positions if the position is occupied and 0 otherwise. The expression in parentheses is the probability that some ramet in the neighbourhood colonizes the empty site. The expression in front of it is the proportion of the probability assigned to the ramet in position I. The probabilities P_i are given by the following table

$$\begin{array}{ccccc} & & 0.1 & & \\ & 0.25 & 0.4 & 0.25 & \\ 0.1 & 0.4 & x & 0.4 & 0.1, \\ & 0.25 & 0.4 & 0.25 & \\ & & 0.1 & & \end{array}$$

which are intended to represent a clonal herb growing in 'phalanx mode', i.e. with most of the daughter ramets placed very near the original ramet.

5. Death of ramets is caused by randomly choosing squares of areas A in a grid of non-overlapping squares covering the universe and killing all ramets present within them. Edge effects are averted by letting the position of the grid vary randomly in both spatial dimensions between generations. The size of squares (measured as side length in cell units A), and total number of cells affected in each generation (L) are the two parameters varied between simulation runs.
6. A simulation starts by 'sowing' 50 genets, each consisting of one ramet, at random over the universe, which is then exposed to death events according to (5). This is called generation 0. The following generations each consist of an episode of clonal growth (4) followed by an episode of death (5).

Inghe investigated this model for a variety of combinations of values of A and L (see table on p. 261 to Inghe's paper) and made three runs of 250 generations for each combination of parameter values. Based on these simulations Inghe estimated the number of ramets in equilibrium (see figure 4 on page 263). As one should expect the number of ramets in equilibrium decreases when L increases, and becomes 0 when L is too large. That is, there is a critical value of L at which the process goes extinct. The figure also shows the less intuitive fact that the critical value of L (the total area disturbed) decreases as the size of the disturbances increases.

Inghe also investigated the number of ramets and genets versus time for several parameter values. To understand the graphs in figure 5 on p. 264 of his paper, we have performed analogous simulations for the competition model described in the last section. This is a version of Inghe's model in which births occur from x to each of its nearest neighbours with probability λ, and individual sites are made vacant with probability γ. On an $N \times N$ lattice this corresponds to taking $A = 1$ and $L = N^2\gamma$ in Inghe's model, with two differences: (i) we have modified the birth probabilities to be uniform over the nearest neighbours, and (ii) in our case we flip a coin for each cell to see if it is disturbed rather than disturbing a fixed number of cells L. We have modified Inghe's model primarily to make it simple to simulate, but also to make the point that the qualitative properties of the system do not depend on the details of the birth and death mechanisms.

Figure 22 gives a graph of the number of ramets and genets versus time for the model with $\lambda = 0.25$, $\gamma = 0.325$, and $N = 60$, which corresponds roughly to $A = 1$ and $L = 1170$ in Inghe's scheme. The non-increasing curve gives the fraction of the 60 original genets that remain at time t. The wiggly curve gives the fraction of sites that are occupied by a ramet of

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some type. The graph we obtain is similar to the first two in figure 5 on p. 264 of Inghe (1989) and performs as we would expect from theory. Since we start with only 50 plants in a grid of 3600 sites, it takes a while for the plants to expand throughout the space, but soon after they do, we see only small fluctuations in the number of ramets away from the equilibrium level. The number of genets decreases quickly from 50 to 17. The next table gives the number of genets versus time. At intermediate times, the number of genets is constant. For example at times 13 to 21 there are 19 genets.

time	0	1	2	3	4	5	6	7
genets	50	36	30	27	26	24	23	22
time	9	11	12	22	27			
genets	21	20	19	18	17			

The initial rapid decrease corresponds to the fact that some of the original plants start family lines that die out. In the long flat region in the graph the clusters of the various genetic types are not in equilibrium but are growing and fighting for territory. As time goes on we start to lose types due to competition. The next table describes how the number of types drops from 17 to 1:

time	203	233	270	393	499	510	640
genets	16	15	14	13	12	11	10
time	1649	2283	2345	3385	3408		
genets	9	8	7	6	5		
time	7068	7578	13898	16875			
genets	4	3	2	1			

By analogy with results of Sawyer (1979) and Bramson & Griffeath (1980), we expect that (for the two-dimensional system under consideration) the number of genets at time t will decay to 0 like $C(\log t)/t$ where C is a constant that depends on the number of particles that escape dying out in the first phase.

One of the most interesting ideas in Inghe's paper is to investigate how the behaviour of the process changes when disturbances affect more then one site at once, so we have looked at a variation of our competition model in which deaths can affect more than one site at once. One can, and Inghe did, investigate disturbances that are 2 × 2, 3 × 3, 4 × 4 and so on. Some of the most interesting behaviour occurs when the disturbances are large, so we have looked at a model in which there are three disturbances at each time step that are 15 × 15 squares and then births occur from each site to its nearest neighbours with probability $\lambda = 0.55$. In Inghe's scheme this corresponds to $A = 15$ and $L = 675$, but we have chosen our three squares at random from all possible 15 × 15 squares rather than from a randomly translated sublattice of nonoverlapping squares. Figure 23 shows a graph of the number of ramets and genets versus time for our model on a 60 × 60 lattice. Again, the non-increasing curve gives the fraction of the 60 original genets that remain at time t and the wiggly curve gives the fraction of sites that are occupied by a ramet of some type. The oscillatory behaviour in the number of ramets versus time that occurs is comparable to that in the last graph in figure 5 on p. 264 of Inghe's paper. These oscillations are a 'finite size effect'. That is, the disturbance squares have a length that is 1/4 the system size so occasionally the placement of squares at successive times will be very effective in decimating the population. Figure 24 shows a simulation of the system on a 120 × 120 and displays much less oscillation. If we were to simulate the system on a 240 × 240 grid then the oscillations

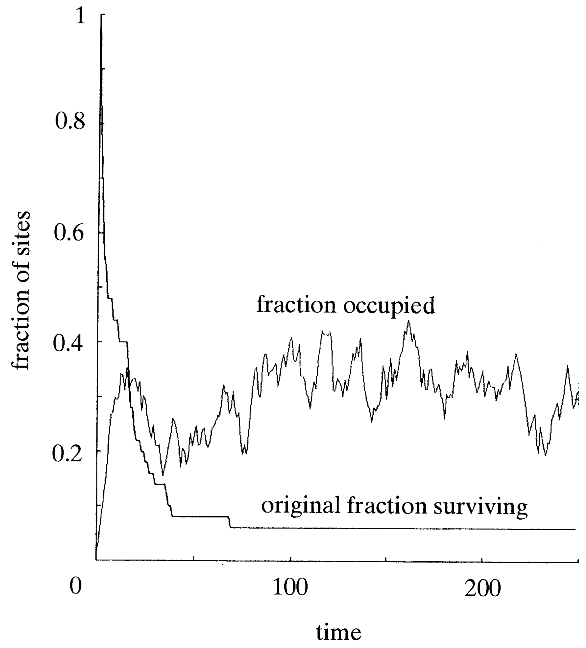

Figure 23. Fraction of the initial 60 genets surviving to time t and fraction of sites occupied at time t for Inghe's competition model with $\lambda = 0.55$ and three 15 × 15 death events on a 60 × 60 lattice.

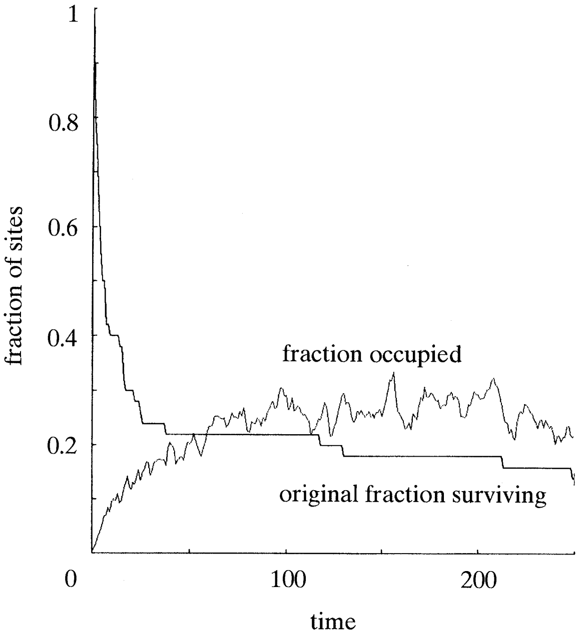

Figure 24. Fraction of the initial 60 genets surviving to time t and fraction of sites occupied at time t for Inghe's competition model with $\lambda = 0.55$ and three 15 × 15 death events on a 120 × 120 lattice.

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would be reduced even further and the graph would look much like figure 22.

Section summary. In this section we described a model due to Inghe (1989) which describes the competition of genets of a given species. This model is a discrete time analogue of the symmetric competition model in the previous section and like those models has behaviour closely related to that of the voter model.

9. SUMMARY

The analysis of pattern formation has long been one of the unifying themes in mathematical biology. In ecology, the importance of such analysis has stimulated much recent activity because of the need to relate phenomena across scales, and to interpret patterns on one scale in terms of processes on other scales.

Traditionally, most models of pattern formation have been continuous in space and time, reliant on diffusion-reaction systems. Such models have shaped our understanding of how pattern forms, but are inadequate for investigating phenomena that have localized stochastic events, or treat spatial influences that are non-local. Extensions (see Levin & Segel 1985) can address some of these problems; but a fundamentally distinct approach, through interacting particle systems, is ideally suited for investigating many phenomena. These are the focus of attention in this paper.

The models we have described have the following general features. Space is represented by a grid of 'sites', which in most cases is the d-dimensional integer lattice. Each site can be in a finite set of states: 0 (vacant) or $i=1, \ldots, \kappa-1$ indicating the presence of one plant of type i. When $\kappa=2$ (i.e. we are dealing with the spread of a single species) the models can encompass a wide variety of death and asexual birth mechanisms, but all the systems have the following general features. If the birth probabilities are not large enough the system always dies out, but if the birth probabilities are large enough there is a non-trivial equilibrium state, which is typically unique and is the limiting state whenever the system avoids extinction. The parameter values at which the transition from 'dying out' to 'surviving' occurs are almost impossible to compute theoretically but can easily be estimated from computer simulations.

When $\kappa \geqslant 3$, attention focuses on conditions for the $\kappa-1$ species to coexist in equilibrium. Again, analytical results are hard to obtain, but become possible if one is willing to make the assumption that offspring are displaced a large distance, measured on the lattice, from their parents. Calculations were carried out for two or more species that are (i) part of a successional sequence, or (ii) compete on an equal footing, but these computations generalize easily to a variety of other systems (e.g. the model in Caswell's (1978) paper on predator-mediated coexistence). In the analysis of these systems we saw that continuous time processes, while taking some sophistication to formulate, were actually easier to analyse and did not require collision rules that discrete time systems need to determine what happens when several events try to influence a site simultaneously.

One of the attractions of interacting particle system models is that they can easily take into account spatial and temporal inhomogenities. However, as these models only try to capture the 'essential' features of the interactions and do not try to accurately model the microscopic dynamics, one cannot expect to obtain quantitative predictions but only seek to understand how properties of the system change in response to changes in the model, and to infer from this what aspects of a system are responsible for its observed qualitative behaviour.

Both authors were partly supported by a Small Grant for Exploratory Research from the National Science Foundation and by the Army Research Office through the Mathematical Sciences Institute at Cornell University. S.L. is pleased to acknowledge the support of the Department of Energy and the National Aeronautics and Space Administration through grants to Princeton University, and the Office of Naval Research through the URIP award to Woods Hole Oceanographic Institution.

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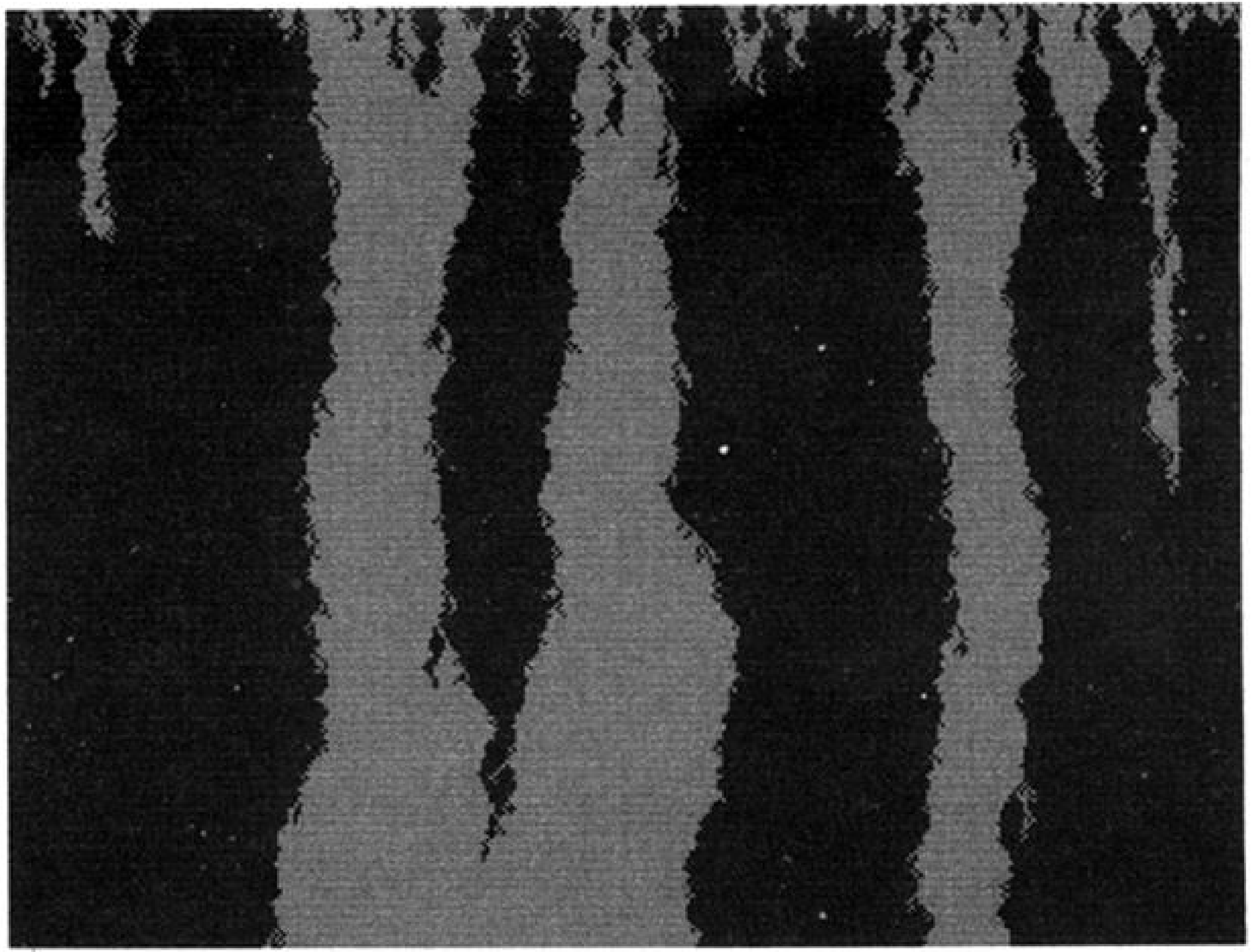

Figure 13. One-dimensional voter model, times 0–239.

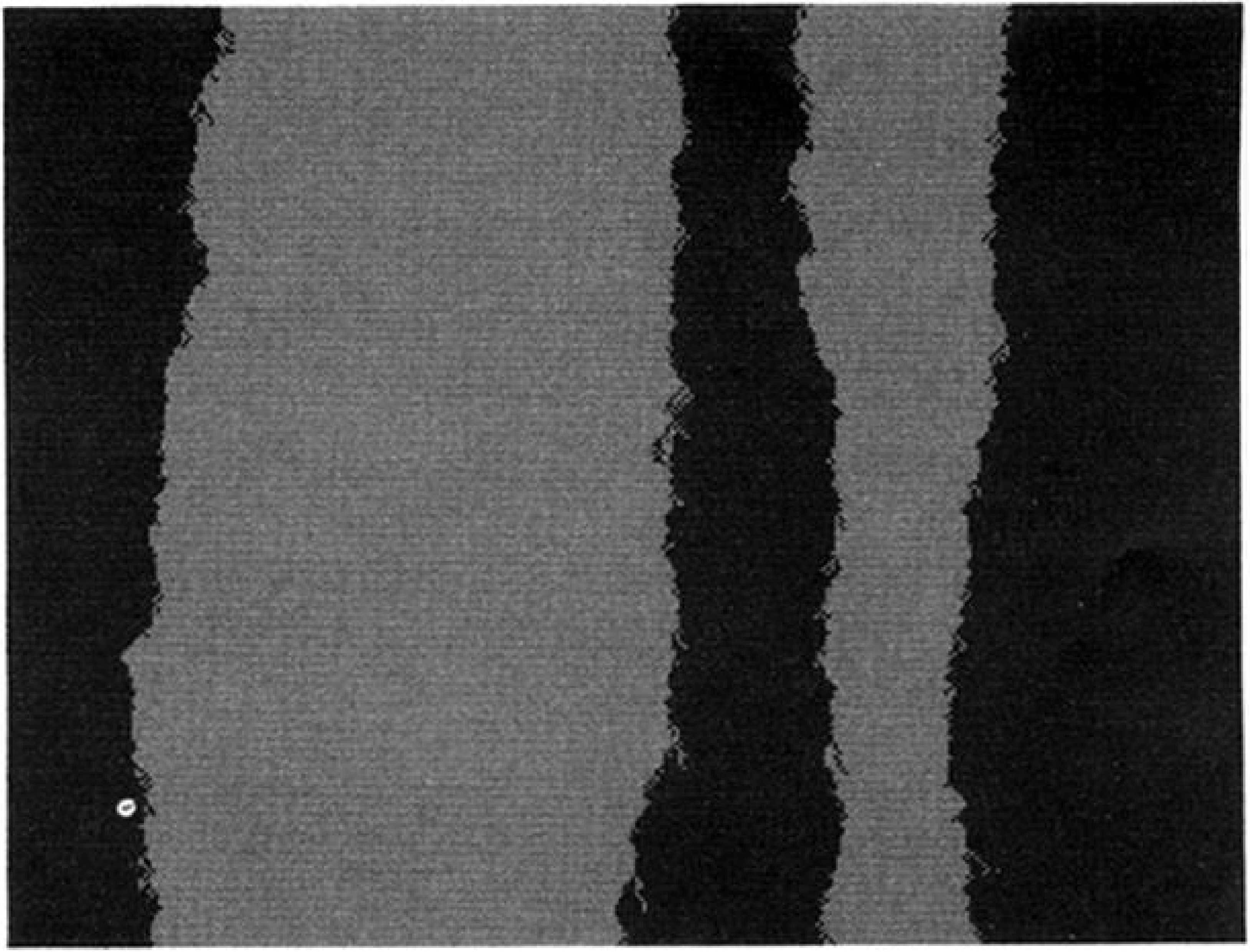

Figure 14. One-dimensional voter model, times 1200–1439.

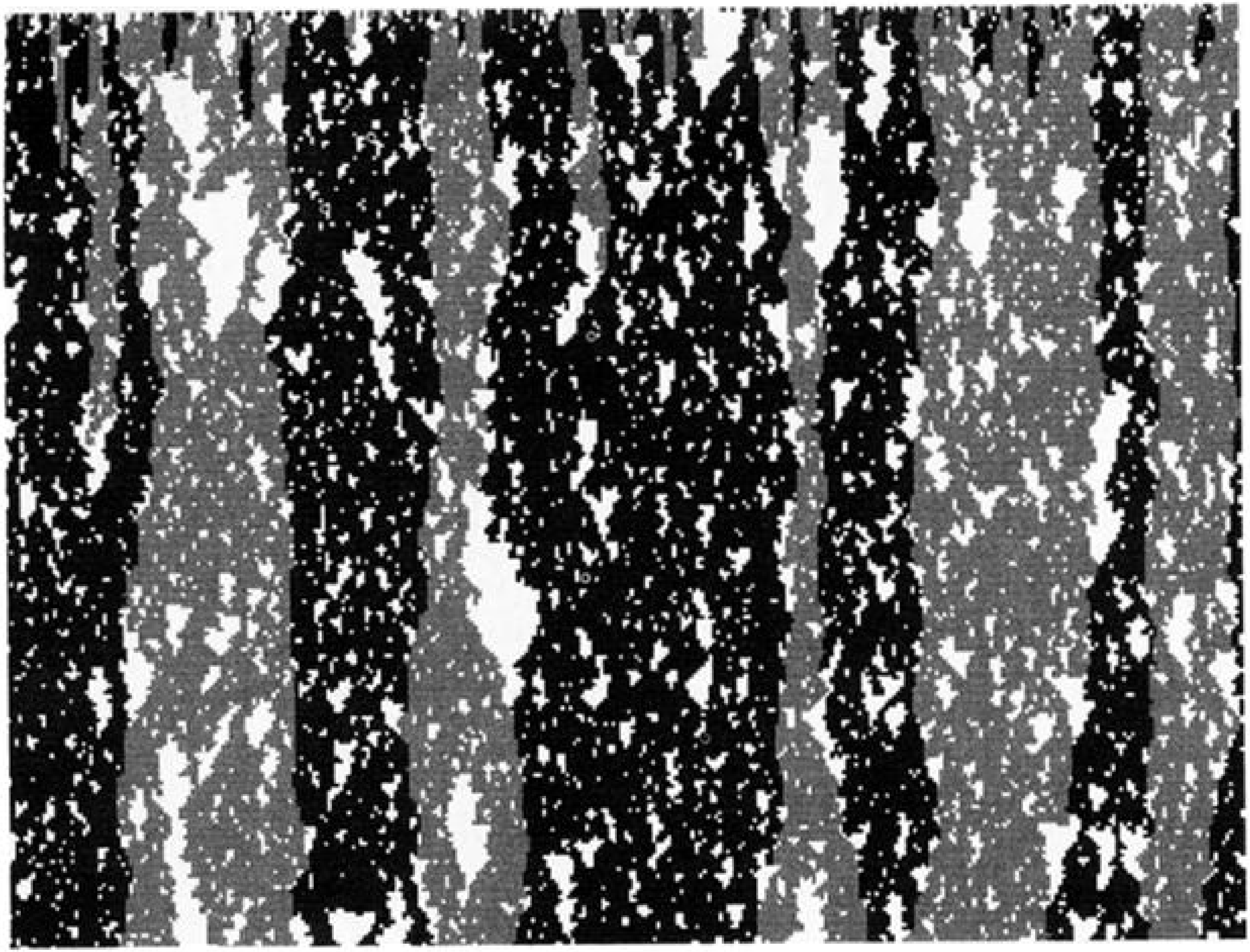

Figure 18. Symmetric competition model in one dimension, times 0–239.

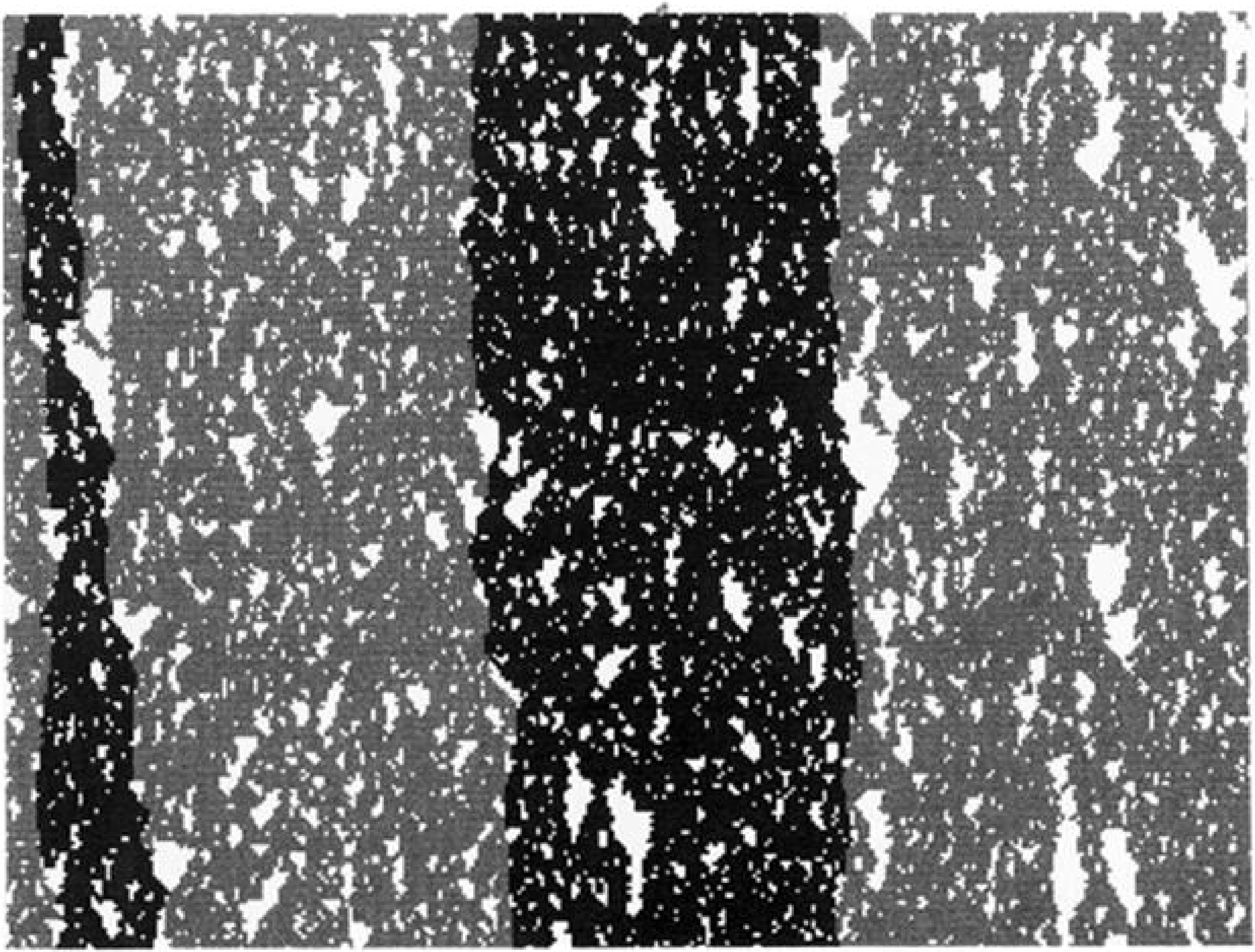

Figure 19. Symmetric competition model in one dimension, times 1200–1439.