

Stochastic Spatial Models*

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Abstract. In the models we will consider, space is represented by a grid of sites that can be in one of a finite number of states and that change at rates that depend on the states of a finite number of sites. Our main aim here is to explain an idea of Durrett and Levin (1994): the behavior of these models can be predicted from the properties of the mean field ODE, i.e., the equations for the densities of the various types that result from pretending that all sites are always independent. We will illustrate this picture through a discussion of eight families of examples from statistical mechanics, genetics, population biology, epidemiology, and ecology. Some of our findings are only conjectures based on simulation, but in a number of cases we are able to prove results for systems with “fast stirring” by exploiting connections between the spatial model and an associated reaction diffusion equation.

Key words. interacting particle system, contact process, stepping stone model, epidemics, predator-prey system, evolutionary games, reaction-diffusion equations

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In the beginning of the theory of ecology, it was natural to consider interactions as happening in a group of N individuals with no spatial structure in order to reduce the system (in the $N \rightarrow \infty$ limit) to an ordinary differential equation (ODE). This approach, which we will call a mean field analysis, is adequate for many problems, but in some situations the answers that it gives are different from those that come from models with a collection of individuals that are distributed in space and interact only with nearby neighbors. The notion that explicit spatial locations for individuals may change the answers to some questions in biology led a number of individuals to consider spatially explicit models of many different types.

With modern computers it is possible to simulate very complicated models that keep track of an individual’s exact location in (continuous) space as well as a large amount of information about that individual. One example of this approach is Pacala’s forest model SORTIE; see Pacala, Canham, and Silander (1993) and Pacala et al. (1996). In contrast, the models we discuss will follow a minimalist approach. First, we will abandon continuous space for a grid, the d -dimensional integer lattice \mathbf{Z}^d . Second, we declare that each site x can be in one of a small finite set of states S , and that it changes its state at a rate that depends upon the states of a finite number of neighboring sites. In symbols, the state of the system at time t is described by giving the state of each site $\xi_t(x)$, so the state of the system is a function $\xi_t : \mathbf{Z}^d \rightarrow S$ and the rate at which the state at x changes to j at time t is $c_j(x, \xi_t)$.

The models we will discuss are too simple to be used for making quantitative predictions but have proved useful for answering the qualitative questions in a variety of

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different settings. To illustrate the breadth of possible applications, we will introduce eight examples from statistical mechanics, genetics, population biology, epidemiology, and ecology. Our first example has the longest and most distinguished history.

Example 1. Ising model. In this model, we think of the sites in the three-dimensional lattice as atoms in a piece of iron. To avoid the headaches of considering a two-dimensional space of possible spin directions, we declare that each site is in states $+1$ (spin up) or -1 (spin down). To prepare for our treatment of later models, we will begin not with the Ising model but with the earlier “mean molecular field theory” Weiss put forward in 1907 to explain ferromagnetism. In what would now be called a metapopulation model (see, e.g., Hanski and Gilpin (1996) and Hanski (1998)), Weiss had n sites without any spatial structure. Each spin interacted with the average of the other spins resulting in the following equilibrium probability distribution:

$$(1) \quad \exp \left(\beta \sum_{i=1}^n \xi(i) \cdot \frac{1}{n} \sum_{j=1}^n \xi(j) \right) \cdot \frac{1}{Z(\beta, n)},$$

where $Z(\beta, n)$ is a constant chosen to make the sum over configurations equal to 1. If we let N_+ be the number of $+$ spins and $N_- = n - N_+$ be the number of $-$ spins, the above is equal to

$$(2) \quad \exp \left(\frac{\beta}{n} (N_+ N_+ + N_- N_- - 2N_+ N_-) \right) \cdot \frac{1}{Z(\beta, n)}.$$

Calculations with the binomial distribution and Stirling’s formula show that if $\beta \leq \beta_c = 1/2$ the exponential factor has very little effect, and in the limit the spins are independent $\{-1, +1\}$ -valued random variables with mean 0, a measure we will denote by ν_0 . On the other hand, if $\beta > \beta_c$ the limiting spin distribution is a mixture $(1/2)\nu_\rho + (1/2)\nu_{-\rho}$, where the “mean magnetization” $\rho(\beta)$ is the solution of

$$(3) \quad \rho = \tanh(2\beta\rho).$$

For more on this, see section IV.4 of Ellis (1985). A little calculus shows that as $\beta \downarrow \beta_c$, $\rho(\beta) \sim C(\beta - \beta_c)^{1/2}$, so the mean rises sharply from 0 at β_c . It is unfortunate, however, that real magnets have even steeper behavior in their magnetization near their critical values.

The last observation and the desire to have a nontrivial joint distribution for the spins are important motivations for the problem that Lenz gave to Ising as a thesis project: consider the probability distribution on configurations of spins in $\Lambda = [-L, L]^d$ defined by

$$(4) \quad \exp \left(\beta \sum_{x \in \Lambda, |y-x| \leq 1} \xi(x)\xi(y) \right) \cdot \frac{1}{Z(\beta, \Lambda)}.$$

Here β is a constant times inverse temperature and $Z(\beta, \Lambda)$ is the normalizing constant to make this a probability distribution.

Our first task is to let $L \rightarrow \infty$ to get a process defined on the infinite lattice. If we let $\partial\Lambda = \{y : |y - x| \leq 1 \text{ for some } x \in \Lambda\}$ and let η be ξ restricted to $\partial\Lambda$, we see that the definition in (4) depends also on the boundary conditions η . The set of all limits that can be obtained by letting $L_k \rightarrow \infty$ and choosing a sequence of boundary conditions η_k is the set of *Gibbs states*, i.e., the possible equilibrium distributions of the system.

Ising (1925) worked out the one-dimensional case of this model and proved that there was a unique Gibbs state. Today this is a straightforward exercise in Markov chain theory. If Ising had been right when he conjectured that the same result held true in any dimension, his name would not be as famous as it is today. Peierls (1936) was the first to demonstrate that at sufficiently low temperature (i.e., sufficiently large β) the Ising model in two or more dimensions exhibits ferromagnetism. To be precise, if we let $L \rightarrow \infty$ and use the all +1 boundary conditions we get a limit μ_+ in which the average value of the spins is positive. Of course, using -1 boundary conditions will lead to a limit μ_- with negative mean, so there are two Gibbs states corresponding to the possibility of magnetization in the up and down states.

Peierls' "contour argument" has become a basic tool in proving the existence of phase transitions. However, in the case of the Ising model (and in most of its other applications), it gives only a very crude upper bound on the critical value β_c . The first step toward the exact computation of the critical value for the two-dimensional Ising model was the discovery by Kramers and Wannier (1941) of a high-temperature/low-temperature duality that related the Ising models with parameters β and β^* , where

$$(5) \quad \sinh(2\beta) \sinh(2\beta^*) = 1.$$

This suggested that the critical value β_c was the fixed point $\sinh(2\beta_c) = 1$ or $\beta_c = 0.4407$, a fact that was later confirmed by Onsager's (1944) solution. Later, Yang (1952) computed the *spontaneous magnetization*, i.e., the expected value of $\xi(x)$ under the distribution μ_+ :

$$(6) \quad \rho(\beta) = \begin{cases} [1 - (\sinh(2\beta))^{-4}]^{1/8}, & \beta > \beta_c, \\ 0, & \beta \leq \beta_c. \end{cases}$$

Climbing our soapbox for the first time to proclaim "spatial models are better," we note that this quantity has $\rho(\beta) \sim C(\beta - \beta_c)^{1/8}$, which is in closer agreement with the properties of real magnets.

In the late 1960s, there was a resurgence of interest in the Ising model, sparked by a program to prove rigorous results in statistical mechanics; see Dobrushin (1968) and Ruelle (1969). At this point, several people followed up on earlier work of Glauber (1963) and constructed stochastic spin flip models that had Gibbs states as stationary distributions and proved more general existence results for infinite particle systems. See Dobrushin (1971), Holley (1972), and Liggett (1972). There are many possible choices for the rate at which a spin flips to the opposite value (see Liggett (1985), section IV.2). A simple and commonly used one is $\exp(-2\beta n_x)$, where n_x is the number of neighboring spins that agree with the one at x . Note that in this formulation flips occur at rate 1 for sites that disagree with all of their neighbors but at rate $\exp(-12\beta)$ for those that agree with all of their neighbors.

The Ising model is a special example, not only because of its connection with physics but also because it has the property of *reversibility*. In words, a movie of the system in equilibrium looks the same (in distribution) when seen forward or backward. Mathematically, if we let $\xi^{x,i}$ be the configuration ξ modified so that the value at x is i , then reversibility for a distribution π is equivalent to the *detailed balance condition*

$$(7) \quad \pi(\xi^{x,i})c_j(x, \xi^{x,i}) = \pi(\xi^{x,j})c_i(x, \xi^{x,j}).$$

In words, the rate of flow of probability mass from $\xi^{x,i}$ to $\xi^{x,j}$ is exactly balanced by the flow from $\xi^{x,j}$ to $\xi^{x,i}$. Using the identity $\sum_y \xi(x)\xi(y) = 2n_x - d$ it is easy to check that Gibbs states in (4) are reversible measures for our rates. The converse question,

whether there are any non-Gibbsian stationary distributions, has been answered only in dimensions $d \leq 2$, where Holley and Stroock (1977) showed there were no others. Their failure to prove the result in $d \geq 3$ may be related to the fact that in those dimensions there are a number of nontranslation invariant stationary distribution with magnetization in each plane but different orientations in different groups of planes. See Dobrushin (1972, 1973).

At this point much is known about the stochastic Ising model. See Chapter IV of Liggett (1985) and references therein. Part of the reason for this rich theory is the existence of a stochastic Lyapunov function called the *free energy*; see Holley (1971). However, the most important key to the success of studying the Ising model is property (7), which makes it easy to compute the stationary distribution by setting $\pi(\xi^*) = 1$ for some configuration ξ^* and then computing all the other values from (7). A second system with this useful property is given in the following example.

Example 2. Simple exclusion process. The simple exclusion process is the special case of a “lattice gas” of statistical mechanics when there is a hard-core potential between the particles. For easy visualization, consider the process on a two-dimensional lattice. The states are 0 = vacant and 1 = occupied by a particle. Following Frank Spitzer (1970), we view the system as one of independent random walks subject to the exclusion rule of at most one particle per site. To be precise, a particle at x attempts to jump at rate 1, and when it does so, tries to go to one of the four nearest neighbors chosen at random. If the chosen neighbor is vacant, then the particle goes there; otherwise no jump occurs.

It is somewhat surprising (to me at least) that even though the particles interfere with each other, the random state in which adjacent sites are independent and occupied with probability p is a stationary distribution. Though this may be surprising, it is trivial to check this using the detailed balance condition (2). The reader should note that in the simple exclusion process there is a one-parameter family of stationary distributions, one for each $0 \leq p \leq 1$. This is due to the fact that particles are conserved and hence the density of occupied sites stays constant in time. There has been a great deal of study by probabilists of the properties of the simple exclusion process showing that (for the case we consider) convex combinations of the one-parameter family above give all of the stationary distributions and proving associated convergence theorems. See Liggett (1985, Chapter VII), and Liggett (1999). Here, we will be interested primarily in the simple exclusion process as a mechanism for moving particles around in more complicated models.

Our first two models were special since they were time reversible, as the physics of the situation demands. Biological systems, in which birth does not look like death going backward, do not have this property, so the study of these systems leads to the more challenging class of irreversible models. Our first example with this property is from genetics.

Example 3. Stepping stone model. As Sewall Wright (1943) was the first to observe, if the size of a whole area is large compared with the migration distance of an individual, then the species may not behave as a single panmictic unit, an effect he called “isolation by distance.” In natural populations, individuals often are distributed more or less discontinuously to form numerous colonies, and individuals will migrate only between adjacent or nearby colonies. To analyze such a situation, Kimura (1953) proposed a model he called the stepping stone model of population structure. For simplicity, we will suppose that there is only one individual per site, who has one genetic locus of interest with k alleles $1, 2, \dots, k$, which give the state of

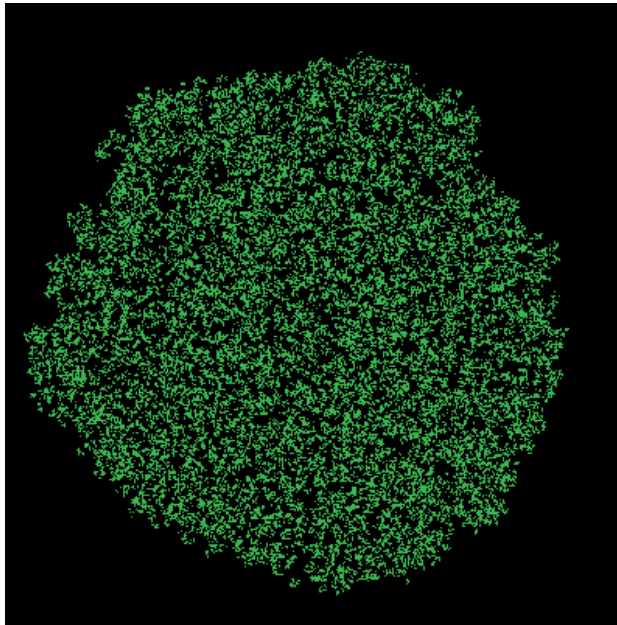


Fig. 1

the site. Thinking of overlapping generations, we declare that an individual at x dies at rate 1 and then is replaced by the state at y with probability $p(y - x)$.

The first significant mathematical analysis of this model was carried out by Kimura and Weiss (1964), who studied the decay of genetic correlations among sites as the distances between the sites increase in the model in which $p(y - x) = 1/2d$ when x and y are nearest neighbors. Much theoretical work on the model and computer simulation soon followed in the genetics literature; see Weiss and Kimura (1965); Rohlf and Schnell (1971); Maruyama (1972a), (1972b); Malecotti (1975); and Felsenstein (1975). The main message of this work is that genetic characteristics of continuous populations depend on the size of the local breeding units or neighborhoods. In particular, smaller neighborhoods result in high levels of inbreeding, homozygosity, and patchiness in the spatial distribution of genotypes. For more on this, see Turner, Stephens, and Anderson (1982), where a system of flowers with nearest-neighbor pollination was simulated.

In the early 1970s, the Kimura–Weiss model was reinvented in the probability literature by Clifford and Sudbury (1973) and Holley and Liggett (1975). The latter pair of authors thought in terms of opinions or political parties rather than genotypes, so they named their system the “voter model.” They concentrated on the model on the infinite lattice and showed that the model converges to complete consensus in $d \leq 2$ but not in $d > 2$. Sawyer (1976), (1977a), (1977b) and Bramson and Griffeath (1980a) studied the growth of clusters of sites with the same opinion in $d \leq 2$. Cox and Griffeath (1986) followed up on that work and developed a detailed understanding of the structure of the typical configuration of the two-dimensional voter model at time t . Instead of writing a thousand words about these results, we will instead give a picture (see Figure 1) of the two-dimensional voter model starting with each site randomly colored one of 16 colors and let you guess what you can from that.

Most of the results in the previous paragraph were inspired by probabilists' fascination with random walks and proved for their intrinsic interest. However, this rich body of theoretical results makes the voter model useful for biological applications. Durrett and Levin (1996) and Bramson, Cox, and Durrett (1996), (1998) have considered a voter model with mutation and have used it to understand species-area curves and the abundance of species. Durrett, Buttel, and Harrison (1999) have used biased voter models with spatially varying selection to model hybrid zones.

The first three models have been included primarily for historical reasons and to give a broader view of the possible applications. Most of this paper will concentrate on examples like the next five.

Example 4. Contact processes. Here we are thinking of the spread of a plant species, so 1 = occupied and 0 = vacant. The dynamics are the simplest possible: individuals die at rate δ and give birth at rate β , with a birth from x going to y with probability $p(y-x)$. If y is vacant, it becomes occupied. If y is occupied, then nothing happens. By scaling time we can take $\delta = 1$. If we do this, then there is a critical value β_c , which will depend on the displacement kernel p , so that if $\beta < \beta_c$ then the system dies out (i.e., goes to the all-0s absorbing state), while if $\beta > \beta_c$ the system survives (i.e., has a nontrivial stationary distribution).

This model was introduced by Harris (1974) and soon studied intensively in the probability literature. See Harris (1976), Griffeath (1978), Durrett (1980), Griffeath (1981), Durrett and Griffeath (1982), (1983), Durrett (1984), and other references given in Chapter V of Liggett (1985). Later, this system was rediscovered in the biology literature by Crawley and May (1987). The parallel evolution here is due undoubtedly to the fact that the contact process is the simplest nontrivial spatial growth model. Deaths occur at a constant rate, while births occur at a linear rate, proportional to the number of occupied neighbors.

If we pretend that adjacent sites are independent, then the density of occupied sites in the contact process will satisfy

$$(8) \quad \frac{du}{dt} = -u + \beta u(1-u) = \beta u \left(\frac{\beta-1}{\beta} - u \right).$$

If we consider n sites and have births from x to y with probability $1/n$, then in the limit as $n \rightarrow \infty$ the density of occupied sites will satisfy the same equation (see Example 1.1 below). So by analogy with Weiss's study of magnetism, we will call (8) the *mean field equation*. As the second equality shows, this is just a logistic growth model in which the per particle growth rate is β and the carrying capacity is $\rho = (\beta-1)/\beta$. The contact process is, in a sense, a stochastic version of the partial differential equation (PDE)

$$(9) \quad \frac{\partial u}{\partial t} = \frac{\sigma^2}{2} \Delta u + \beta u(\rho - u),$$

where $\Delta u = \partial^2 u / \partial x_1^2 + \cdots + \partial^2 u / \partial x_d^2$. The stochasticity comes from the fact that the model has discrete individuals rather than the infinite local populations implicit in the PDE.

Based on this analogy and a knowledge of the properties of the PDE in (9) (see, e.g., Fife and McLeod (1977) and Aronson and Weinberger (1978)), one can correctly guess the two most important results for the supercritical contact process, $\beta > \beta_c$:

(i) if the process survives starting from a finite initial state, then it grows linearly and has an asymptotic shape;

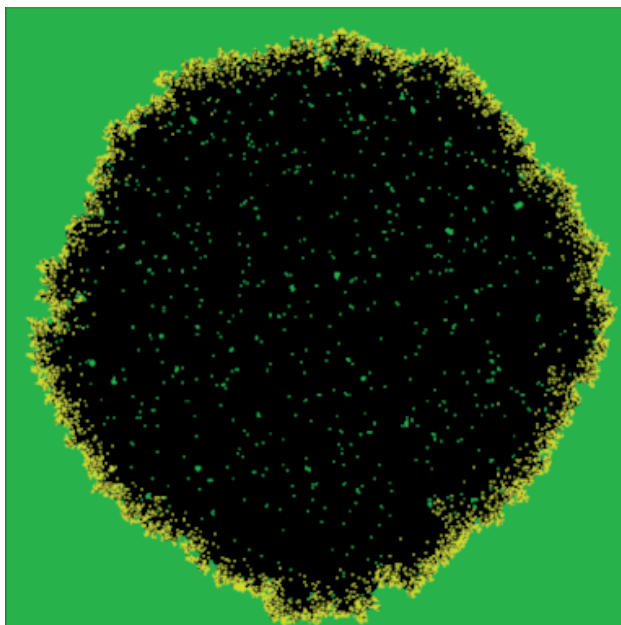


Fig. 2

(ii) there is a unique nontrivial stationary distribution which describes the distribution away from the edge of the growing ball and that is the limit as $t \rightarrow \infty$ whenever the process does not die out.

See Figure 2 for a picture of the result in (i). These results were proved in $d = 1$ by Durrett (1980). The proof in $d > 1$ was considerably trickier and required a decade of work by a variety of people: Durrett and Griffeath (1982), (1983), Durrett and Schonmann (1987), Bezuidenhout and Grimmett (1990), (1991). For an explanation of these and many of the other known results about the contact process, see Durrett (1992) or Liggett (1999). The contact process is a very simple model of the growth of one species and will be our basic ingredient for constructing the following example.

Example 5. Multispecies competition models. Most questions of interest in ecology today involve the interaction of two or more species, so we will generalize from the previous model to have states $0 = \text{vacant}$ and $i = 1, 2, \dots, k$ to indicate that the site is occupied by type i . In the first three models we consider

(i) Individuals of type i die at rate δ_i and give birth at rate β_i , a birth from x going to y with probability $p_i(y - x)$;

(ii) If y is vacant then y becomes occupied with type i .

There are, however, various things we can decide to do when y is occupied. The simplest and most symmetric is that if y is occupied then the birth is suppressed. This system, though natural, turns out to be disappointing: we can never have coexistence. Biologists will recognize this as a consequence of Gause's principle (see, e.g., Levin (1970)). Since all the species are competing for the same resource, there can be only one winner. Neuhauser (1992) has been able to show that this occurs in the stochastic spatial model with two species and $\delta_1 = \delta_2$. Proving this in the general case $\delta_1 \neq \delta_2$ seems like a difficult problem.

Though the simplest symmetric rule is boring, the strict hierarchical version in which individuals of type i can give birth onto sites of type $j < i$ turns out to be quite

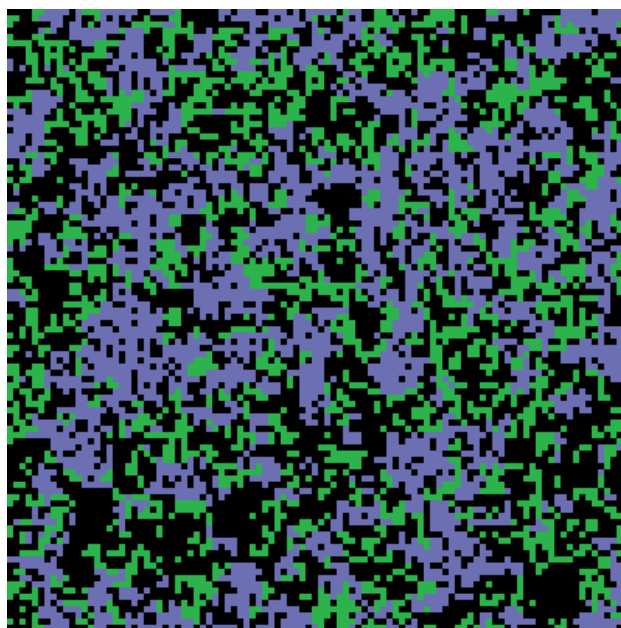


Fig. 3

interesting. Crawley and May (1987) considered a version of the model in which 2 = perennial plants and 1 = annuals. In Durrett and Swindle (1991), 0 = grass, 1 = bushes, 2 = trees, while in the related model studied by Tilman (1994), the states are different classes in a competitive hierarchy. In each of these three situations, there is an open set of parameters in which all species coexist. The spatial patterns of the equilibrium states are pretty boring, however. See Figure 3 for a simulation of the model of Durrett and Swindle (1991) with $\beta_1 = \beta_2 = 1$, $\delta_1 = 0.2$, and $\delta_2 = 0.575$. We will discuss this model further in Example 1.2.

The competition models in the last two paragraphs are special cases of one introduced by Silvertown et al. (1992). In that system the general set-up is the same, but when i tries to invade j there is success (i.e., the site changes to i) with probability $p_{i,j}$. As will be explained in Example 4.1, the two-species system is boring (showing competitive exclusion), but a three-species version with a paper-scissors-stone intransitive competition relationship leads to interesting pattern formation in the spatial model.

A second type of modification that we can make to the basic two-species contact process set-up is to preserve the exclusion rule (no births onto occupied sites) but modify the death rates to be a linear function of the number of neighbors of the two types. In symbols, we give the death rate for type i as $\delta_i + \sum_j \gamma_{ij} f_j$, where f_j is the fraction of neighbors in state j . The colicin model in Durrett and Levin (1997a) is one of the simplest cases of this: $\gamma_{21} = \gamma > 0$, but all the other $\gamma_{ij} = 0$. In words, the first type is an *E. coli* that produces colicin, while the second is sensitive to that chemical and suffers an increased death rate due to the presence of nearby 1's. We will discuss this model further in Example 3.2.

Example 6. Epidemics. There is a large body of work that studies epidemics by assuming that populations are homogeneously mixing and using differential equations. Due to long-distance connections between people in a community, such models are

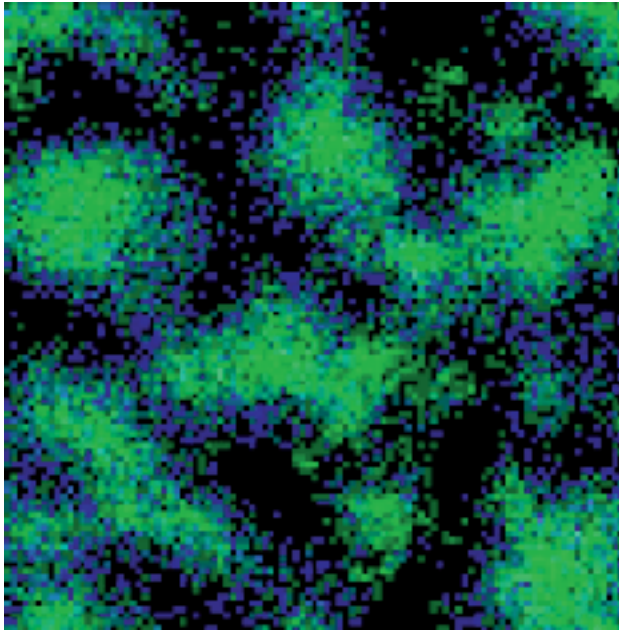


Fig. 4

fine for representing the spread of the latest variety of flu through a town. However, in some situations, such as rabies in animals, the infection process is local and the epidemics travel through the countryside as fronts that move a predictable number of miles per year. To treat such situations where the spatial distribution of infectives is important, we formulate a model with three states, 0 = susceptible, 1 = infected, and 2 = removed. The word “removed” will mean dead in the case of a fatal disease like rabies. However, we prefer to think about measles, where the term means that the individual has had the disease once and is immune to having it again. The dynamics are again a simple combination of constant and linear rates. Susceptible individuals become infected at a rate proportional to the fraction of neighbors infected, βf_1 . Infected individuals become removed at a constant rate δ , which we set equal to 1. Finally, removed individuals become susceptible at rate α . In formulating the last transition we are thinking of removed individuals dying (or moving out of town) and being replaced by new susceptible individuals.

In order to understand this model it is natural to begin with the case $\alpha = 0$, which occurs, for example, in modeling a flu epidemic where there is no perceptible regrowth of susceptibles on the time scale of the epidemic. The first observation to be made is that if the infection rate β is too small then the epidemic dies out, while if $\beta > \beta_c$ there is a positive probability that the infection persists for all time. After one gives up on the hopeless problem of computing the threshold β_c , it is natural to ask: what happens if we start the process with $\alpha = 0$ with one infected individual in a sea of susceptibles? The answer, after a lot of work by a number of people (see Mollison (1975), Mollison and Kuulasmaa (1985), Cox and Durrett (1988), and Zhang (1990)), is that if the epidemic were supercritical, i.e., $\beta > \beta_c$, then the radius of the set of removed individuals would grow linearly and have an asymptotic shape. See Figure 4 for a picture of this result. Later work of Durrett and Neuhauser (1991) showed that if

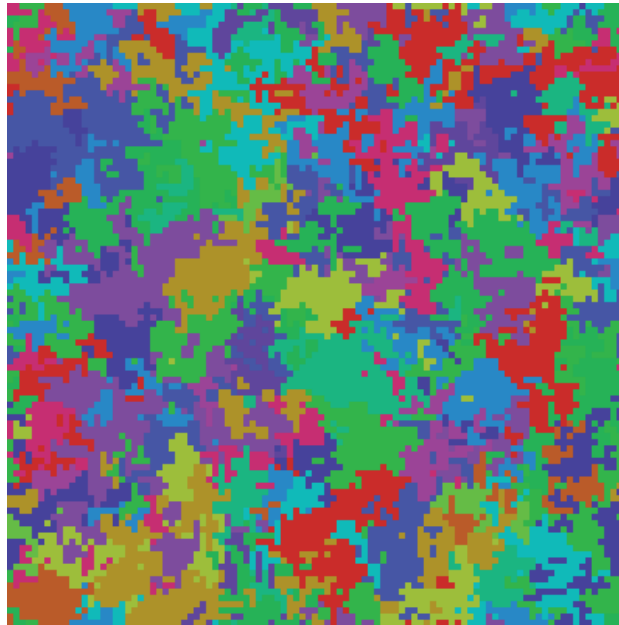


Fig. 5

$\beta > \beta_c$, then the system with any positive amount of regrowth $\alpha > 0$ has a nontrivial stationary distribution. For more on spatial epidemic models, see Bak, Chen, and Tang (1990), Drossel and Schwabl (1992), Henley (1993), Durrett (1995c), or the conference proceedings edited by Mollison (1995) and by Grenfell and Dobson (1995).

Example 7. Predator-prey systems. Huffaker (1958) was the first to construct a spatial model of a predator-prey system. He investigated a system of two mites and a predator on a network of oranges connected with wooden rods. He found that while persistence was impossible in a homogeneously mixing system, it was greatly prolonged on the spatial grid. Pimentel et al. (1963) complemented Huffaker's classic work, again demonstrating how space can lead to the persistence of predator-prey systems. Hilborn (1975) provided the first theoretical examination of Huffaker's experimental system, formulating a model in which there are N sites with no spatial structure. Nachman (1987a), (1987b) seems to have been the first to simulate Huffaker's system as a truly spatial model.

This pioneering work inspired others to study the impact of the spatial distribution of competitors on the behavior of predator-prey systems. See Hassell, Comins, and May (1991), DeRoos, McCauley, and Wilson (1991), McCauley, Wilson, and DeRoos (1993), Wilson, DeRoos, and McCauley (1993), Satulovsky and Tome (1994), Rand, Keeling, and Wilson (1995), Neubert, Kot, and Lewis (1995), Wilson (1996), Comins and Hassell (1996), Satulovsky (1996), and Pascual and Caswell (1997). Here, we will keep to what we know best and discuss our own results. The simplest situation occurs in Durrett (1993), when all the rates are linear. See Example 2.1. More recently, Durrett and Levin (1999) have considered a nonlinear model in which predators search q adjacent sites looking for food. As q is increased, the homogeneously mixing version of the system develops periodic orbits, leading to interesting structures in the spatial model. See Figure 5 for a simulation and Example 4.5 below for more details.

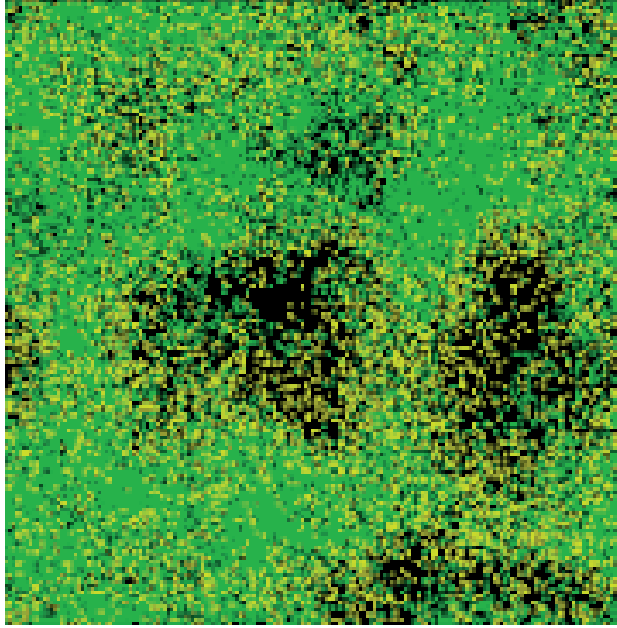


Fig. 6

Example 8. Evolutionary games. Our final class of models is a spatial version of a system introduced by Maynard Smith (1982), which we formulate following Brown and Hansell (1987). At each site there can be any nonnegative number of each of two types, $i = 1, 2$. At a site with m_i individuals of type i and n_i individuals of type i in its neighborhood (which we take to include the site itself), each individual of type i gives births to new individuals of type i located at that site at rate

$$(10) \quad \beta_i + a_{i1} \frac{n_1}{n_1 + n_2} + a_{i2} \frac{n_2}{n_1 + n_2}$$

and experiences deaths at rate $\delta_i + \gamma_{i1}m_1 + \gamma_{i2}m_2$.

The bounded per particle birth rates versus the linearly growing per particle death rates implies that the number of particles at each site does not grow without bound. In some cases both species will die out. However, if the birth rates are large enough in comparison to the death rates, then there will be a nontrivial stationary distribution in which one or both types are present. Durrett and Levin (1994b) studied this model and identified three cases based on the structure of the matrix a_{ij} . Those results were the beginning of the classification scheme to be presented here. As we will see, the “Prisoner’s Dilemma” case in which strategy 1 dominates strategy 2 (i.e., $a_{1i} > a_{2i}$ for $i = 1, 2$ but $a_{11} < 0 < a_{12}$) is the most interesting. See Figure 6 for a simulation of this situation. For another approach to this problem that makes prettier pictures, see Nowak and May (1992), (1993), Nowak, Bonhoeffer, and May (1994), or the surveys by May (1994), (1995), which give a number of other references

The examples described above only begin to illustrate the breadth of applications of stochastic spatial models. Given that it took 15 years to come to grips with the contact process, it is clear that the only way theory can keep up with the growing number of applications is to formulate general principles to allow for the solution

of large classes of problems at once. Durrett and Levin (1994b) proposed that the behavior of stochastic spatial models could be determined from the properties of the mean field ODE, i.e., the equations for the densities of the species which result from pretending that adjacent sites are always independent. In their scheme there are three cases depending upon the properties of the ODE:

Case 1. One attracting fixed point with all components positive. The prediction in this case is that there will be *coexistence* in the stochastic spatial model; i.e., there is a stationary distribution in which each state has positive density.

Case 2. Two locally attracting fixed points. In the ODE, the limiting behavior depends on the initial densities. However, in the stochastic spatial model, there is one stronger equilibrium that is the winner starting from any positive initial density. To determine the stronger equilibrium, we can start with one half-plane in each equilibrium and watch the direction of movement of the front.

Case 3. Periodic orbits in the ODE. In the spatial model, densities fluctuate wildly on small scales, oscillate smoothly on moderate scales, and after an initial transient are almost constant on large scales. That is, there is an equilibrium state with an interesting spatial structure.

This classification scheme is a heuristic, designed to predict the behavior of the many interacting particle systems that arise in biological applications. However, there is a growing list of examples where the conclusions have been proved mathematically or demonstrated by simulation. In this paper, we will explain some of the results that have been obtained in support of this picture and list a number of the open questions that remain.

As one can probably guess, many of the mathematical questions lie in probability theory or in the study of ODEs. However, there are also a number of problems concerning PDEs, specifically the asymptotic behavior of reaction-diffusion equations, since those results are used to make the rigorous connection between properties of the ODE and of the stochastic spatial model. In what follows we will concentrate on mathematical results and problems. By following the references given above and in the text, the reader can find many papers in the biology literature. For surveys of the use of spatial models in ecology, see the books edited by Levin, Powell, and Steele (1993) and Tilman and Kareiva (1997), or the articles of Czaran and Bartha (1992) and Durrett and Levin (1994a).

I. Case I. Attracting Fixed Point. To illustrate this case, we begin with a simple but fundamentally important special case, which has already appeared in the introduction as Example 4.

Example 1.1. Contact process. As described earlier, each site can be in state 0 = vacant or 1 = occupied. The system evolves according to the following rules:

- i. An occupied site becomes vacant at a rate δ .
- ii. An occupied site gives birth at rate β . A particle born at x is sent to y with probability $p(y - x)$.
- iii. If y is vacant, it becomes occupied. If y is occupied, nothing happens.

The contact process as formulated above has two parameters, but only needs one. By scaling time we can, in contrast to the choice made in the introduction, suppose that $\beta = 1$. In this case, particles die at rate δ and give birth at rate at most 1, since births onto occupied sites are lost. From this it is easy to see that if we start with a finite number of occupied sites and $\delta > 1$, then the contact process will *die out*, i.e., reach the all-0 configuration with probability 1. We define the critical value δ_f , for

survival from finite sets, to be the supremum of all of the values of δ so that dying out has a probability < 1 for some finite initial state.

There is a second, slightly more sophisticated notion of “survival” for the contact and other processes: the existence of a stationary distribution for the Markov chain that does not concentrate on the absorbing state in which all sites are vacant. To see when such a stationary distribution will exist, we start with the observation that the contact process is *attractive*: i.e., increasing the number of 1s increases the birth rate and decreases the death rate. Then we give the following lemma.

LEMMA 1.1. *Let ξ_t^1 denote the process starting from all 1s. If the process ξ_t is attractive, then as $t \rightarrow \infty$, $\xi_t^1 \Rightarrow \xi_\infty^1$, a stationary distribution.*

Here \Rightarrow is short for *converges in distribution*, which means that for any sites x_1, \dots, x_n and possible states i_1, \dots, i_n we have convergence of the *finite-dimensional distributions*

$$P(\xi_t^1(x_1) = i_1, \dots, \xi_t^1(x_n) = i_n) \rightarrow P(\xi_\infty^1(x_1) = i_1, \dots, \xi_\infty^1(x_n) = i_n).$$

This result and all the others we cite for the contact process can be found in Liggett (1985), Griffeath (1979), Durrett (1988), (1995b).

Of course the limit in Lemma 1.1 could assign probability 1 to the all-0 configuration, and it will if δ is too large, for example, $\delta > 1$. Let δ_e be the supremum of the values of δ for which the limit is not all 0s. For the quadratic contact process, Example 3.1, we will have

$$0 = \delta_f < \delta_e < \infty.$$

However, for the contact process, these two critical values coincide. To explain why this is true, we note that by using a variety of methods, one can show the following duality relationship.

LEMMA 1.2. *Let $p_t(A, B)$ be the probability that some site in B is occupied at time t when we start with 1s on A (and 0s elsewhere) at time 0. Then*

$$p_t(A, B) = p_t(B, A).$$

Taking A = all sites and B = a single point, we see that the density of occupied sites at time t is the same as the probability of surviving until time t starting from a single occupied site. Thus $\delta_e = \delta_f$ and we denote their common value by δ_c , where the c stands for *critical value*.

Mean field theory. If we consider the contact process on a grid with n sites and modify the rules so that all sites are neighbors, then the number of occupied sites at time t is a Markov chain $N(t) \in \{0, 1, \dots, n\}$ with transition rates

$$\begin{aligned} N(t) &\rightarrow N(t) - 1 \text{ at rate } \delta N(t), \\ N(t) &\rightarrow N(t) + 1 \text{ at rate } \beta N(t) \left(1 - \frac{N(t)}{n}\right). \end{aligned}$$

If we let $u_n(t) = N(t)/n$ be the fraction of occupied sites and let $n \rightarrow \infty$, then by computing the variance, it is not hard to show that the u_n converge to the solution of the “mean field” ODE

$$(1.1) \quad \frac{du}{dt} = -\delta u + \beta u(1 - u) = \beta u \left\{ \frac{\beta - \delta}{\beta} - u \right\}.$$

The term in quotes refers to the fact that each site only feels the average value of all the other sites, i.e., the density of occupied sites. The mean field equation can also be obtained from the spatial model by letting $u(t)$ be the fraction of sites occupied at time t and assuming that adjacent sites are independent. Since the second recipe is simpler, we will use it for our later computations.

The mean field ODE for the contact process predicts that the critical value δ_c is 1, and for $\delta < \delta_c$ the equilibrium density of occupied sites is $1 - \delta$. In the nearest neighbor contact process there is a significant positive correlation between the states of neighboring sites (see Harris (1977)) so $\delta_c < 1$. Numerical results tell us that for the two-dimensional nearest neighbor contact process, $\delta_c \approx 0.607$. See Brower, Furman, and Moshe (1978) and Grassberger and de la Torre (1979). For rigorous bounds on the critical value for the contact process, see Holley and Liggett (1978) and Liggett (1995a), (1995b).

Although the nearest neighbor case has been the most studied, it turns out that the contact process gets much simpler when we consider long-range limits. Bramson, Durrett, and Swindle (1989) have shown the following.

THEOREM 1.1. *Let $\mathcal{N} = \{z : \|z\|_\infty \leq r\}$. As $r \rightarrow \infty$, $\delta_c(r) \rightarrow 1$ and*

$$P(\xi_\infty^1(x) = 1) \rightarrow 1 - \delta.$$

In words, as $r \rightarrow \infty$ the critical value and equilibrium densities converge to those predicted by mean field theory.

A simple proof of Theorem 1.1 can be found in the expository article, Durrett (1992). Bramson, Durrett, and Swindle (1989) went further by identifying the rate of convergence. Let $N = (2r + 1)^d$ be the number of points in $|\mathcal{N}|$. If r is large then

$$(1.2) \quad \beta_c(r) - 1 \approx \begin{cases} C/N^{2/3} & \text{in } d = 1, \\ C(\log N)/N & \text{in } d = 2, \\ C/N & \text{in } d \geq 3, \end{cases}$$

where \approx means that inserting a large enough value of C results in an upper bound $\beta_c(r) - 1$ and a small enough positive value of c gives a lower bound. Recently, Durrett and Perkins (1999) have sharpened this conclusion to

$$(1.3) \quad \beta_c(r) - 1 \sim \begin{cases} C_2(\log N)/N & \text{in } d = 2, \\ C_d/N & \text{in } d \geq 3, \end{cases}$$

where $C_2 = 6/\pi$, and in $d \geq 3$,

$$C_d = \sum_{n=1}^{\infty} P(U_n \in [-1, 1]^d),$$

with U_n the discrete-time random walk that takes steps uniformly on $[-1, 1]^d$. The key to the proof of (1.3) is showing that a rescaled version of the long-range contact process converges to super-Brownian motion plus drift. This conclusion is false in one dimension, where Mueller and Tribe (1995) have shown that the limit is the stochastic PDE (SPDE)

$$(1.4) \quad du = \left(\frac{u''}{6} + \theta u - u^2 \right) dt + \sqrt{2u} dW.$$

It is natural to conjecture as follows.

CONJECTURE 1.1. *The sharp constant in (1.3) for one dimension is $C_1 = \theta_c$, the critical value for the SPDE in (1.4).*

See Mueller and Tribe (1994) for the definition and existence of the critical value for the SPDE.

Example 1.2. Grass, bushes, trees. In our second model, the possible states are 0 = grass, 1 = bushes, 2 = trees. Zeros are thought of as vacant sites. Types 1 and 2 behave like contact processes subject to the rule that 2s can give birth onto sites occupied by 1s but not vice versa. In formulating the dynamics, we are thinking of the various types as species that are part of a successional sequence. With Tilman's (1994) work in mind, we define the model for an arbitrary number of species.

- i. If $i > 0$, type i individuals die at a constant rate δ_i and give birth at rate β_i .
- ii. A particle of type i born at x is sent to y with probability $p_i(y - x)$.
- iii. If the number of the invading type is larger than that of the resident type, the invader takes over the site. Otherwise no change occurs.

Starting our analysis with the case of two types, we note that 2s don't feel the presence of 1s, so they are a contact process and will survive if $\delta_2/\beta_2 < \delta_c$. The main question then is: when can the 1s survive in the space that is left to them?

To investigate this question Durrett and Swindle (1991) considered what happens when long-range limits are taken. As in the case of the long-range contact process, the motivation is that in this case the densities will behave like solutions to the mean field ODE, which is derived by pretending that adjacent sites are always independent:

$$(1.5) \quad \begin{aligned} du_1/dt &= u_1 \{ \beta_1(1 - u_1 - u_2) - \delta_1 - \beta_2 u_2 \}, \\ du_2/dt &= u_2 \{ \beta_2(1 - u_2) - \delta_2 \}. \end{aligned}$$

For example, in the du_1/dt equation the first term represents births of 1s onto sites in state 0 (vacant), the second term represents constant deaths, and the third, births of 2s onto sites occupied by 1s.

From the second equation in (1.5) the equilibrium density of 2s will be

$$\bar{u}_2 = \frac{\beta_2 - \delta_2}{\beta_2}.$$

Inserting this into the first equation and solving, one finds that there is an equilibrium with $\bar{u}_1 > 0$ if

$$(1.6) \quad \beta_1 \cdot \frac{\delta_2}{\beta_2} - \delta_1 - \{\beta_2 - \delta_2\} > 0.$$

As written, this condition can be derived by asking the question: "Can the 1s invade the 2s when they are in equilibrium?" That is, will u_1 increase when it is small enough?

The next two results say that when the range r is large enough the spatial model behaves like the ODE. First we need to define the behaviors that we will observe. We say that *coexistence* occurs if there is a stationary distribution that concentrates on configurations with infinitely many sites in each of the possible states. We say that 1s *die out* if whenever there are infinitely many 2s in the initial configuration, $P(\xi_t(x) = 1) \rightarrow 0$ as $t \rightarrow \infty$.

THEOREM 1.2. *If (1.6) holds then coexistence occurs for large range.*

THEOREM 1.3. *If we have $<$ in (1.6) then the 1s die out for large range.*

Theorem 1.2 is from Durrett and Swindle (1991) and Theorem 1.3 from Durrett and Schinazi (1993). These results also apply to the Crawley and May (1987) model

of the competition between annuals and perennials. In this case the perennials are a nearest neighbor contact process, but annuals have a long dispersal distance. For other models that have been analyzed using long-range limits, see Neuhauser (1994), Durrett and Neuhauser (1997), and Bramson and Neuhauser (1997).

2. Rapid Stirring Limits. In the previous section we saw that stochastic spatial models simplify considerably when the range is large. Our next goal is to explain that this also occurs when the particles are subject to fast stirring. Formally, a stirring event involving x and y will change the state of the process from ξ to $\xi^{x,y}$, where

$$\xi^{x,y}(y) = \xi(x), \quad \xi^{x,y}(x) = \xi(y), \quad \xi^{x,y}(z) = \xi(z), \quad z \neq x, y.$$

In words, we would say that stirring exchanges the values found at x and y .

The stirring mechanism has product measures as its stationary distributions. See Griffeath (1979, section II.10). So when it acts at a rapid rate we expect that nearby sites will be almost independent. To keep the particles from flying out of our field of vision as the stirring rate is increased, we scale space by multiplying by $\epsilon = \nu^{-1/2}$. Since this is the usual diffusion scaling, it should not be surprising that the particle system converges to the solution of a reaction-diffusion equation.

To state a general result, we consider processes $\xi_t^\epsilon : \epsilon \mathbf{Z}^d \rightarrow \{0, 1, \dots, \kappa\}$ that have

i. *translation invariant finite-range flip rates*; i.e., the rate at which site x flips to state i when the configuration of the system is ξ has the form

$$c_i(x, \xi) = h_i(\xi(x), \xi(x + \epsilon y_1), \dots, \xi(x + \epsilon y_N))$$

for some neighbor set $\mathcal{N} = \{y_1, \dots, y_N\}$;

ii. *rapid stirring*: for each $x, y \in \epsilon \mathbf{Z}^d$ with $|x - y| = \epsilon$, we exchange the values at x and y at rate ϵ^{-2} .

With these assumptions we get the following *mean field limit theorem* of De Masi, Ferrari, and Lebowitz (1986). For the version given here, see Durrett and Neuhauser (1994).

THEOREM 2.1. *Suppose $\xi_0^\epsilon(x)$ are independent and let $u_i^\epsilon(t, x) = P(\xi_t^\epsilon(x) = i)$. If $u_i^\epsilon(0, x) = g_i(x)$ is continuous, then as $\epsilon \rightarrow 0$, $u_i^\epsilon(t, x) \rightarrow u_i(t, x)$, the bounded solution of*

$$(2.1) \quad \partial u_i / \partial t = \Delta u_i + f_i(u), \quad u_i(0, x) = g_i(x),$$

where

$$(2.2) \quad f_i(u) = \langle c_i(0, \xi) 1_{(\xi(0) \neq i)} \rangle_u - \sum_{j \neq i} \langle c_j(0, \xi) 1_{(\xi(0) = i)} \rangle_u$$

and $\langle \varphi(\xi) \rangle_u$ denotes the expected value of $\varphi(\xi)$ under the product measure in which state j has density u_j , i.e., when $\xi(x)$ are independently and identically distributed (i.i.d.) with $P(\xi(x) = j) = u_j$.

To explain the form of the reaction term, we note that when ϵ is small, stirring operates at a fast rate and keeps the system close to a product measure. The rate of change of the densities can then be computed assuming that adjacent sites are independent. The reader should recognize

$$du_i/dt = f_i(u)$$

as the mean field ODE.

Theorem 2.1 only concerns expected values, but once it is established one can easily demonstrate the next result, which says that in the limit of fast stirring the particle system on the rescaled lattice becomes deterministic and looks like solutions of the PDE.

THEOREM 2.2. *If $h(t, x)$ is a continuous function with compact support in $[0, \infty) \times \mathbf{R}^d$, then as $\epsilon \rightarrow 0$*

$$\epsilon^d \sum_{x \in \epsilon \mathbf{Z}^d} \int_0^\infty h(t, x) 1_{(\xi_t^\epsilon(x)=i)} dt \rightarrow \iint_0^\infty h(t, x) u_i(t, x) dt dx \quad \text{in probability.}$$

Our main interest in the PDE limit described in Theorems 2.1 and 2.2 is to obtain information about the particle system with fast (but finite) stirring rate. To do this we need one more result. The main assumption may look strange. Its form is dictated by the “block construction” technique (see, e.g., Durrett (1995b)) that we use to prove things. In words, the condition says that the PDE will make one pile of particles three times as large and improve the bounds on the density.

(\star) *There are constants $A_i < a_i < b_i < B_i$, L , and T so that if $u_i(0, x) \in (A_i, B_i)$ when $x \in [-L, L]^d$, then $u_i(T, x) \in (a_i, b_i)$ when $x \in [-3L, 3L]^d$.*

Durrett and Neuhauser (1994) have shown the following.

THEOREM 2.3. *If (\star) holds for the PDE, then there is coexistence for the particle system with fast stirring.*

At this point we have reduced the task of proving theorems for particle systems to proving a specific type of result (\star) for the associated PDE. Leaving the reader to meditate on whether or not this is progress, we turn to the first of several concrete examples that can be treated by this method.

Example 2.1. Predator-prey systems. Each site in $\epsilon \mathbf{Z}^d$ can be in state 0 = vacant, 1 = fish, or 2 = shark. If we let f_i be the fraction of the nearest neighbors of x (i.e., y with $\|y - x\|_1 = \epsilon$) that are in state i , then we can write the flip rates as follows:

$$\begin{array}{lll} 0 \rightarrow 1 & \beta_1 f_1, & 1 \rightarrow 2 \quad \beta_2 f_2, \\ 1 \rightarrow 0 & \delta_1, & 2 \rightarrow 0 \quad \delta_2 + \gamma f_2. \end{array}$$

Here we have shifted our perspective from occupied sites giving birth to vacant sites receiving particles from their neighbors. After this translation is made, the two rates on the left say that in the absence of sharks, the fish are a contact process.

The third rate says that sharks can reproduce by giving birth onto sites occupied by fish, an event that kills the fish. This transition is more than a little strange from a biological point of view, but it has the desirable properties that (i) the density of sharks will decrease when the density of fish is too small, and (ii) the mean field ODE is a traditional predator-prey equation; see (2.4) below. The final rate in the table says that sharks die at rate δ_2 when they are isolated, and the rate increases linearly with crowding.

To be able to use our results about rapid stirring limits we also have to suppose that the sharks and fish swim around. That is, for each pair of nearest neighbors x and y , stirring occurs at rate ϵ^{-2} . Applying Theorem 2.1 we see that if $\xi_0^\epsilon(x)$, $x \in \epsilon \mathbf{Z}^d$, are independent and $u_i^\epsilon(t, x) = P(\xi_t^\epsilon(x) = i)$ for $i = 1, 2$, then as $\epsilon \rightarrow 0$, $u_i^\epsilon(t, x) \rightarrow u_i(t, x)$ as $\epsilon \rightarrow 0$, the bounded solution of

$$(2.3) \quad \begin{aligned} \frac{\partial u_1}{\partial t} &= \Delta u_1 + \beta_1 u_1(1 - u_1 - u_2) - \beta_2 u_1 u_2 - \delta_1 u_1, \\ \frac{\partial u_2}{\partial t} &= \Delta u_2 + \beta_2 u_1 u_2 - u_2(\delta_2 + \gamma u_2) \end{aligned}$$

with $u_i(0, x) = f_i(x)$. To check the right-hand side, we note that if x is vacant and neighbor y is occupied by a fish—an event of probability $(1 - u_1 - u_2)u_1$ when sites are independent—births from y to x occur at rate $\beta_1/2d$ and there are $2d$ such pairs. The $-\beta_2 u_1 u_2$ in the first equation and the $\beta_2 u_1 u_2$ in the second come from sharks giving birth onto fish. The last term in each equation comes from the death events.

When the initial functions $f_i(x)$ do not depend on x , we have $u_i(t, x) = v_i(t)$, where the v_i 's satisfy the ODE

$$(2.4) \quad \begin{aligned} \frac{dv_1}{dt} &= v_1\{(\beta_1 - \delta_1) - \beta_1 v_1 - (\beta_1 + \beta_2)v_2\}, \\ \frac{dv_2}{dt} &= v_2\{-\delta_2 + \beta_2 v_1 - \gamma v_2\}. \end{aligned}$$

Here we have rearranged the right-hand side to show that the system is an example of the standard predator-prey equations for species with limited growth. See, e.g., p. 263 of Hirsch and Smale (1974).

The first step in understanding (2.3) is to look at (2.4) and ask, “What are the fixed points, i.e., solutions of the form $v_i(t) \equiv \rho_i$?” It is easy to solve for the ρ_i . There is always the trivial solution $\rho_1 = \rho_2 = 0$. In the absence of sharks the fish are a contact process, so if $\beta_1 > \delta_1$ there is a solution $\rho_1 = (\beta_1 - \delta_1)/\beta_1$, $\rho_2 = 0$. Finally, if we assume that the $\rho_1, \rho_2 \neq 0$, we can solve two equations in two unknowns to get

$$(2.5) \quad \rho_1 = \frac{(\beta_1 - \delta_1)\gamma + \delta_2(\beta_1 + \beta_2)}{\beta_1\gamma + \beta_2(\beta_1 + \beta_2)}, \quad \rho_2 = \frac{(\beta_1 - \delta_1)\beta_2 - \delta_2\beta_1}{\beta_1\gamma + (\beta_1 + \beta_2)\beta_2},$$

which has $\rho_2 > 0$ if

$$(2.6) \quad (\beta_1 - \delta_1)/\beta_1 > \delta_2/\beta_2.$$

To understand this condition we note that if the fish are in equilibrium and the sharks have small density, then neglecting the $-\gamma v_2$ term and inserting the equilibrium value for v_1 , the second equation in (2.4) becomes

$$(2.7) \quad \frac{dv_2}{dt} = v_2 \left\{ -\delta_2 + \beta_2 \cdot \frac{\beta_1 - \delta_1}{\beta_1} \right\}.$$

The condition (2.6) says that the quantity in braces is positive, i.e., that the density of sharks will increase when it is small.

Having found conditions that guarantee the existence of an interior fixed point, the next step is to check that it is attracting. Figure 7 shows an example of the ODE, which confirms this in the special case considered there. However, one does not need to use a computer to see that this will occur. To prove that the fixed point is attracting, one begins with the easy-to-check fact that if ρ_i are the equilibrium densities given in (2.5),

$$H(v_1, v_2) = \beta_2(v_1 - \rho_1 \log v_1) + (\beta_1 + \beta_2)(v_2 - \rho_2 \log v_2)$$

is a Lyapunov function for the ODE; i.e., it is decreasing along solutions of (2.4). A simple argument by contradiction then shows that all orbits starting at points with each density $v_i > 0$ converge to (ρ_1, ρ_2) . The presence of a globally attracting fixed point leads us to guess the following theorem.

THEOREM 2.4. *Suppose that $(\beta_1 - \delta_1)/\beta_1 > \delta_2/\beta_2$. If ϵ is small there is a nontrivial translation-invariant stationary distribution in which the density of sites of type i is close to ρ_i .*

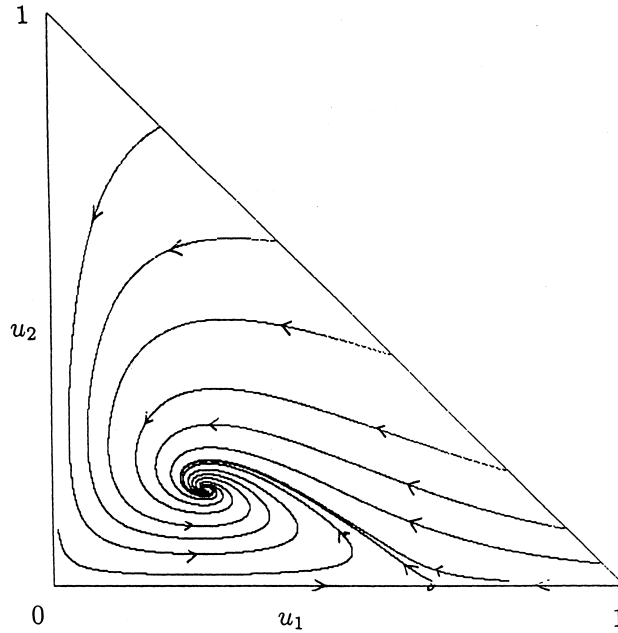


Fig. 7

In view of Theorem 2.3 it suffices to prove (\star) . For details see Durrett (1993). The proof involves Brownian motion in a minor role, but is otherwise an analytic proof built on results of Redheffer, Redlinger, and Walter (1988), who considered the problem in a bounded domain with Neumann boundary conditions. Durrett (1993) did not consider the problem of the converse to Theorem 2.4. Using ideas from Durrett and Neuhauser (1994), (1997) one should be able to conjecture as follows.

CONJECTURE 2.1. *Suppose that $(\beta_1 - \delta_1)/\beta_1 < \delta_2/\beta_2$. If ϵ is small then the 2s die out.*

Example 2.2. Predator-mediated coexistence. Here the possible states of a site are $0 =$ vacant, $1, 2 =$ two-prey species, $3 =$ predator. Types $i = 1, 2$ behave like a contact process, dying at a constant rate δ_i and being born at vacant sites at rate β_i times the fraction of neighbors in state i . 3s die at a constant rate δ_3 , are born at sites occupied by 1s at rate β_3 times the fraction of neighbors in state 3, and are born at sites occupied by 2s at rate β_4 times the fraction of neighbors in state 3. Finally, of course, there is stirring at rate ν : for each pair of nearest neighbors x and y we exchange the values at x and at y at rate ν .

In the absence of predators, this system reduces to the following example.

Example 2.3. Multitype contact process. In this system 1s and 2s are two competing species, but births are only allowed onto vacant sites:



Neuhauser (1992) has shown the following theorem.

THEOREM 2.5. *If $\delta_1 = \delta_2$ and $\beta_1 > \beta_2$ then the 2s die out.*

It is natural to conjecture as follows.

CONJECTURE 2.2. *If $\beta_1/\delta_1 > \beta_2/\delta_2$ then the 2s die out.*

However, if we restrict our attention to the case in which the death rates are equal, Neuhauser's result implies that when $\beta_1 \neq \beta_2$ there is no coexistence in the competing contact process. Predator-mediated coexistence is the phenomenon that if the predator's feeding rate on the stronger species is larger, its presence may stabilize the competition between the two species. One way of seeing that this should be possible is to consider the mean field ODE:

$$(2.8) \quad \begin{aligned} dv_1/dt &= v_1 \{ \beta_1(1 - v_1 - v_2 - v_3) - \delta_1 - \beta_3 v_3 \}, \\ dv_2/dt &= v_2 \{ \beta_2(1 - v_1 - v_2 - v_3) - \delta_2 - \beta_4 v_3 \}, \\ dv_3/dt &= v_3 \{ \beta_3 v_1 + \beta_4 v_2 - \delta_3 \}. \end{aligned}$$

Here, one can solve three equations in three unknowns to find conditions for an interior fixed point, but a more fruitful approach is to derive conditions from an *invadability analysis*. Half of this may be described as follows. By results for predator-prey systems in (2.6), 2s and 3s can coexist if

$$\frac{\beta_2 - \delta_2}{\beta_2} > \frac{\delta_3}{\beta_4},$$

and when this holds their equilibrium densities given in (2.5) are given by (recall $\gamma = 0$ here) $v_2 = \delta_3/\beta_4$ and

$$v_3 = \frac{(\beta_2 - \delta_2)\beta_4 - \delta_3\beta_2}{(\beta_2 + \beta_4)\beta_4}.$$

Examining the behavior of the ODE near $(0, v_2, v_3)$, we see that 1s can invade the (2,3) equilibrium if

$$(2.9) \quad \beta_1 - \delta_1 - \beta_1 v_2 - (\beta_1 + \beta_3) v_3 > 0.$$

In a similar way, one can derive conditions for the 1s and 3s to coexist and for the 2s to be able to invade their equilibrium. When both sets of conditions hold, we say there is *mutual invadability*. It is easy to prove that in this case the ODE has an interior fixed point. By considerably extending the methods of Durrett (1993), Nikhil Shah (1997) has shown the following theorem.

THEOREM 2.6. *If mutual invadability holds for the ODE, then coexistence occurs for the stochastic spatial model with fast stirring.*

To get a feel for the resulting phase diagram, set $\beta_3 = 4$, $\beta_4 = 3/2$, all the $\delta_i = 1$, and vary β_1 and β_2 . The formulas above imply that 1 and 3 coexist if $\beta_1 > 4/3$, 2 and 3 coexist if $\beta_2 > 3$, and finally, all three species can coexist inside the region bounded by the equations

$$\beta_1 > \beta_2, \quad \beta_2 < \frac{17}{32}\beta_1 + \frac{5}{8}, \quad \beta_2 > \frac{9}{14}\beta_1 + \frac{15}{14}.$$

The last few lines are summarized in Figure 8. Note that there is a region where all three species can coexist but 2s and 3s cannot. Though we have not considered this possibility in stating Theorem 2.6, it is covered by Nikhil Shah's (1997) result. Upon reflection, the existence of this possibility is not paradoxical. It simply says that the 2s are not a sufficiently good food source to sustain the predator by themselves.

3. Case 2. Two Locally Attracting Fixed Points. As in our consideration of Case 1, we will begin with an example that has two states, 0 = vacant and 1 = occupied. The rules are like the contact process, but now it takes two particles to

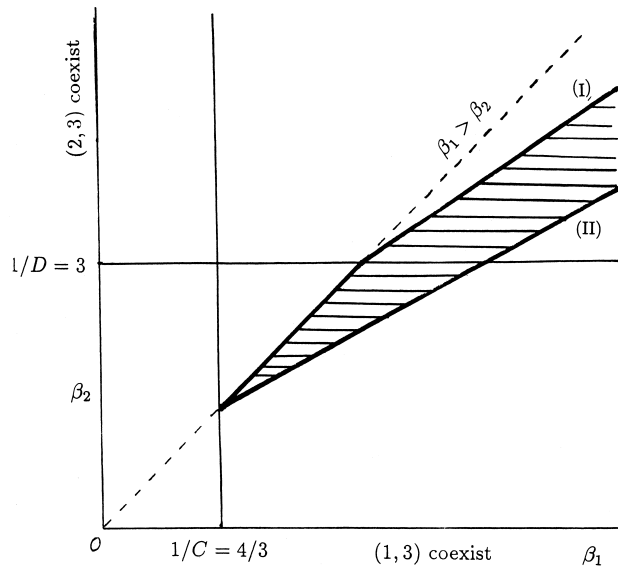


Fig. 8

make a new one. For this reason many of the early papers refer to this model as the “sexual reproduction process.” However, to emphasize that here the birth rate is simply quadratic instead of linear we will use the more modest name.

Example 3.1. Quadratic contact process. This system is also sometimes called Schlögl’s second model. See Schlögl (1972) and Grassberger (1982).

i. An occupied site becomes vacant at a rate δ .

ii. A vacant site becomes occupied at a rate equal to $k/4$, where k is number of diagonally adjacent pairs of occupied neighbors.

Note that, as in the contact process, we have scaled time to make the maximum possible birth rate = 1.

The critical value for survival of this process starting from a finite set

$$(3.1) \quad \delta_f = 0.$$

To see this, note that if the initial configuration starts inside a rectangle it can never give birth outside the rectangle and hence is doomed to die out whenever δ is positive. Somewhat surprisingly, the critical value for the existence of a stationary distribution

$$(3.2) \quad \delta_e > 0.$$

Bramson and Gray (1991) have shown the following theorem.

THEOREM 3.1. *There is a $\delta_0 > 0$ so that if $\delta \leq \delta_0$ then the limit starting from all 1s is a nontrivial stationary distribution.*

The numerical value of δ_0 produced in the proof of Theorem 3.1 is very small. To obtain quantitative results we can turn to simulation to conclude that $\delta_e \approx 0.1$. Here we will instead use Theorems 2.1 and 2.2 to conclude that with rapid stirring the system behaves like the following PDE:

$$(3.3) \quad \frac{du}{dt} = \Delta u - \delta u + (1 - u)u^2.$$

As in the study of the predator-prey model, we begin with the mean field ODE

$$(3.4) \quad \frac{dv}{dt} = -\delta v + (1-v)v^2.$$

When $\delta > 1/4$, $-\delta + v(1-v) < 0$ for all $v \in (0, 1)$, so 0 is a globally attracting fixed point. When $\delta \in (0, 1/4)$ the quadratic equation $\delta = v(1-v)$ has two roots

$$0 < \rho_1 = \frac{1 - \sqrt{1 - 4\delta}}{2} < \rho_2 = \frac{1 + \sqrt{1 - 4\delta}}{2} < 1.$$

This might suggest that as stirring becomes more rapid the critical value for a nontrivial equilibrium δ_e approaches $1/4$. However, results of Noble (1992) and Durrett and Neuhauser (1994) have shown the following theorem.

THEOREM 3.2. *As $\epsilon \rightarrow 0$, the critical value $\delta_e(\epsilon) \rightarrow 2/9$. Furthermore, if $\delta < 2/9$ then the equilibrium density $P(\xi_\infty^1(x) = 1) \rightarrow \rho_2$.*

To explain the value $2/9$, we recall that in one dimension the limiting reaction-diffusion equation has *traveling wave solutions*

$$(3.5) \quad u(x, t) = w(x - ct)$$

that keep their shape but move at velocity c . This and the other PDE results we will quote for this example can be found in Fife and McLeod (1977).

Setting $f(u) = -\delta u + (1-u)u^2$, since it will be clearer to do things for a general reaction term, it is easy to check that the recipe in (3.5) will lead to a solution of (3.3) if and only if

$$(3.6) \quad -cw'(y) = w''(y) + f(w(y)).$$

Suppose that to fix an orientation of the wave, w tends to ρ_2 as $y \rightarrow -\infty$ and $w \rightarrow 0$ as $y \rightarrow \infty$. Multiplying by $w'(y)$ and integrating, we have

$$(3.7) \quad \begin{aligned} -c \int w'(y)^2 dy &= \int w''(y)w'(y) dy + \int f(w(y))w'(y) dy \\ &= 0 - \int_0^{\rho_2} f(z) dz. \end{aligned}$$

Here, to get the 0, we observed that the antiderivative of $w''w'$ is $(w')^2/2$, which vanishes at infinity, and in the second integral we have changed variables $z = w(y)$ and reversed the order of the limits.

Equation (3.7) does not allow us to compute the value of c , but since $\int w'(y)^2 dy > 0$ it does tell us that the sign of c is the same as that of $\int_0^{\rho_2} f(z) dz$. A little calculus now confirms that the speed is positive for $\delta < 2/9$ and negative for $\delta > 2/9$. To check this easily, note that when $\delta = 2/9$ the three roots of the cubic are 0, $1/3$, and $2/3$, so symmetry dictates that the positive and negative areas must cancel and that the speed must be 0.

Sketch of the proof of Theorem 3.2. To prove that if $\delta < 2/9$ coexistence occurs for rapid stirring, it suffices to check (\star) in section 2 and apply Theorem 2.3. This can be done easily with the help of results in Fife and McLeod (1977), and was the main result in Noble's (1992) Ph.D. thesis.

The other direction is a little more tricky since one must show that if $\delta > 2/9$ and stirring is rapid, the 1s die out, not just that their density in equilibrium is close to 0. Durrett and Neuhauser (1994) do this by using the PDE result to drive the density

of 1s to a low level and then use auxiliary arguments to check that the 1s will then die out. \square

Up to this point we have concentrated only on the critical value for a nontrivial equilibrium. From the proof of Theorem 3.2 one easily gets the following theorem.

THEOREM 3.3. *As $\epsilon \rightarrow 0$, the critical value for survival from a finite set $\delta_f(\epsilon) \rightarrow 2/9$.*

It is known in a fair amount of generality that $\delta_f \geq \delta_e$. See Bezuidenhout and Gray (1994). Once there is stirring at a positive rate, $\delta_f > 0$. In fact, we conjecture as follows.

CONJECTURE 3.1. *If the stirring rate $\nu > 0$ then $\delta_f = \delta_e$.*

Remark. The techniques described above have been used by Durrett and Swindle (1994) to prove results for a model of a catalytic surface. Keeping to biological models, we will continue with the following example.

Example 3.2. Colicin. The inspiration for this model came from work of Chao (1979) and Chao and Levin (1981). Bacteria may produce toxic substances, known collectively as bacteriocins, that kill or inhibit the growth of competing bacteria of different genotypes. In general, bacteria that are capable of producing such chemicals are immune to their action.

The colicins, the most extensively studied class of bacteriocins, are produced by the bacterium *Escherichia coli* and other members of the family Enterobacteriaceae. For more about the biology, and an alternative approach based on differential equations, see Frank (1994).

To model the competition we will use a system with three states: 0 = vacant, 1 = occupied by a colicin producer, 2 = occupied by a colicin-sensitive bacterium. If we let f_i be the fraction of the four nearest neighbors in state i , we can formulate the transition rates as follows:

birth	rate	death	rate
$0 \rightarrow 1$	$\beta_1 f_1$,	$1 \rightarrow 0$	δ_1 ,
$0 \rightarrow 2$	$\beta_2 f_2$,	$2 \rightarrow 0$	$\delta_2 + \gamma f_1$.

In words, each type is born at empty sites at a rate proportional to the fraction of neighbors of that type. The colicin-producing strain dies at a constant rate δ_1 , while the colicin-sensitive strain experiences deaths at rate δ_2 plus γ times the fraction of colicin-producing neighbors.

To see what behavior to expect from the spatial model, we begin by writing down the mean field ODE. Let u_1 be the density of colicin-producing bacteria and let u_2 be the density of the ordinary, colicin-sensitive bacteria. Assuming that all sites are independent we have

$$(3.8) \quad \begin{aligned} \frac{du_1}{dt} &= \beta_1 u_1 (1 - u_1 - u_2) - \delta_1 u_1, \\ \frac{du_2}{dt} &= \beta_2 u_2 (1 - u_1 - u_2) - \delta_2 u_2 - \gamma u_1 u_2. \end{aligned}$$

The system (3.8) has locally stable boundary equilibria at

$$(1 - \delta_1/\beta_1, 0) \quad \text{and} \quad (0, 1 - \delta_2/\beta_2),$$

provided

$$(3.9) \quad \delta_i < \beta_i, \quad \frac{\delta_2}{\beta_2} < \frac{\delta_1}{\beta_1} < \frac{\delta_2 + \gamma}{\beta_2 + \gamma}.$$

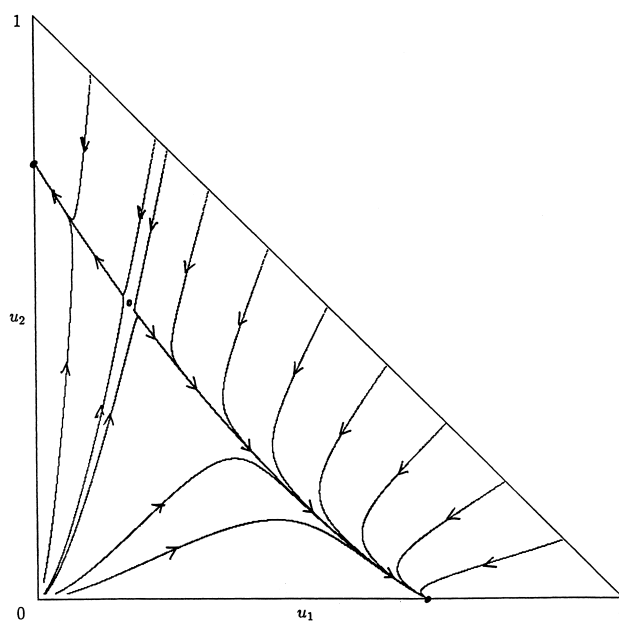


Fig. 9

There is, moreover, an interior saddle point (\bar{u}_1, \bar{u}_2) in this case. See Figure 9 for a picture of what happens when $\delta_1 = \delta_2 = 1$, $\beta_1 = 3$, $\beta_2 = 4$, and $\gamma = 3$. The interpretation of the inequalities in order from left to right is:

- i. the birth rate exceeds the death rate so either type can maintain a population in isolation from the other;
- ii. there is a cost to colicin production, metabolic or otherwise, reflected in a lower carrying capacity in isolation;
- iii. the competitive benefit of colicin production is sufficiently large so that an established colicin-producing community can repel invasion by the wild type.

The implication of this analysis is that each of the strategies, “don’t produce colicin” and “produce colicin,” are *evolutionarily stable strategies*. In other words, if the density of the colicin-sensitive bacteria is near its equilibrium value, then the colicin-producing bacteria cannot invade. Reversing roles, we also have that if the density of the colicin-producing bacteria is near its equilibrium value, then the colicin-sensitive bacteria cannot invade. Using the terminology of genetics, we can say that selection will only favor genotypes when they are common, rare species cannot invade, and genetic diversity will not be maintained. This situation is “disruptive frequency-dependent selection” (see Levin (1988), Thoday (1959–1964)).

The last paragraph identifies the colicin system as belonging to Case 2, so we expect that there is one stronger type that is the winner starting from configurations in which there are infinitely many sites in each of the possible states. To be precise, we conjecture as follows.

CONJECTURE 3.2. Fix δ_1 , δ_2 , and β_2 . For each fixed value of β_1 there is a critical value $\gamma_c(\beta_1)$ so that 1s die out when $\gamma > \gamma_c(\beta_1)$ while 2s die out when $\gamma < \gamma_c(\beta_1)$.

For simulation results in support of this, see Durrett and Levin (1997a).

In attacking this problem, the reader should feel free to introduce rapid stirring or even long-range limits, even though neither of these is a natural assumption for

colicin. In the case of long-range limits, it suffices to check (*). Some help with the PDE can be found in section 3 of Durrett and Swindle (1994). The major obstacle is to prove the existence of a traveling wave connecting the two boundary equilibria. The reader should note that even if this can be done, the integration-by-parts trick in (3.7) fails for the system. So, as in Durrett and Swindle (1994), we will not emerge with a formula for $\gamma_c(\beta_1)$.

Example 3.3. A three-species colicin system. In the two examples above, the ODE and the spatial model sometimes disagreed on who would win the competition, but both approaches agreed that one type would always competitively exclude the other. We will now describe a system in which three species coexist in the spatial model, but in the ODE, there is always only one winner.

To describe the system in words, we assume that 1s and 2s both produce colicin, to which they are immune, and to which 3 is sensitive. The rates for this system are:

birth	rate	death	rate
$0 \rightarrow 1$	$\beta_1 f_1$,	$1 \rightarrow 0$	δ_1 ,
$0 \rightarrow 2$	$\beta_2 f_2$,	$2 \rightarrow 0$	δ_2 ,
$0 \rightarrow 3$	$\beta_3 f_3$,	$3 \rightarrow 0$	$\delta_3 + \gamma_1 f_1 + \gamma_2 f_2$.

Here, f_i is the fraction of the four nearest neighbors in state i . In our concrete example we will set all the $\delta_i = 1$ and

$$\beta_1 = 3, \quad \beta_2 = 3.2, \quad \beta_3 = 4, \quad \gamma_1 = 3, \quad \gamma_2 = 0.5.$$

Here we imagine that species 1 produces more colicin than 2 does but has the lowest birth rate. The parameters are chosen so that 1s win against 3s while 3s win against 2s. When only 1s and 2s are present the system reduces to the multitype contact process, Example 2.3. Since $\beta_2 > \beta_1$, the 2s win against the 1s in this case.

If we write u_i for the fraction of sites in state i , then the mean field ODE is

$$(3.10) \quad \begin{aligned} \frac{du_1}{dt} &= \beta_1 u_1 u_0 - \delta_1 u_1, \\ \frac{du_2}{dt} &= \beta_2 u_2 u_0 - \delta_2 u_2, \\ \frac{du_3}{dt} &= \beta_3 u_3 u_0 - u_3(\delta_3 + \gamma_1 u_1 + \gamma_2 u_2). \end{aligned}$$

If we insert the values for the concrete example then the picture in Figure 10 results. In the $u_1 u_3$ and $u_2 u_3$ planes, we see the colicin picture from Figure 9. In the $u_1 u_2$ plane all trajectories starting with u_1 and u_2 positive are attracted to $(0, \hat{u}_2, 0)$, where $\hat{u}_i = (\beta_i - \delta_i)/\beta_i$. In the three-dimensional ODE, there is a surface that connects the two separatrices in the $u_1 u_3$ and $u_2 u_3$ planes, so that above-the-surface trajectories converge to $(0, 0, \hat{u}_3)$ while those below converge to $(0, \hat{u}_2, 0)$. These conclusions are true whenever $\beta_1 < \beta_2$ and equilibria exist in the interior of the $u_1 u_3$ and $u_2 u_3$ planes. (Conditions for this can be derived from (3.9).)

In contrast to the behavior of the ODE, the spatial model shows coexistence, at least for a long time. See Figure 11 for a simulation of the process on a 200×200 grid with periodic boundary conditions. Here we started in an initial product measure in which the states $i = 1, 2, 3$ each have density $1/3$ and plotted the observed density of the three species every one thousand units of time out to time 50,000. The densities fluctuate but none of them seems in danger of hitting 0 so we make the following conjecture.

CONJECTURE 3.3. *For suitably chosen values of the parameters β_i and δ_i , there is coexistence in the three-species colicin model.*

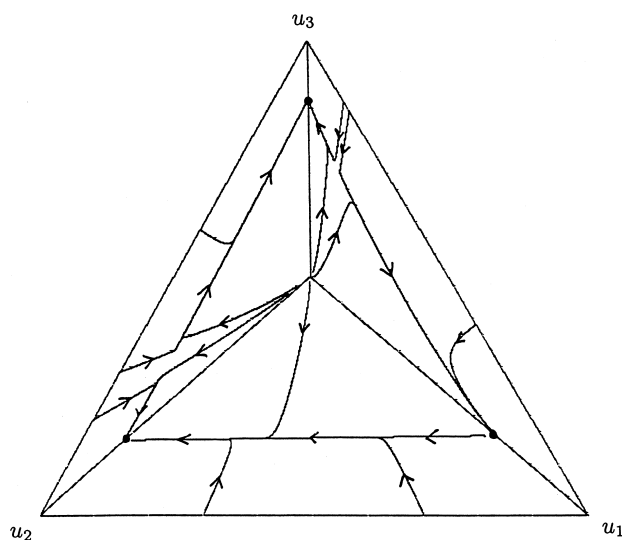


Fig. 10

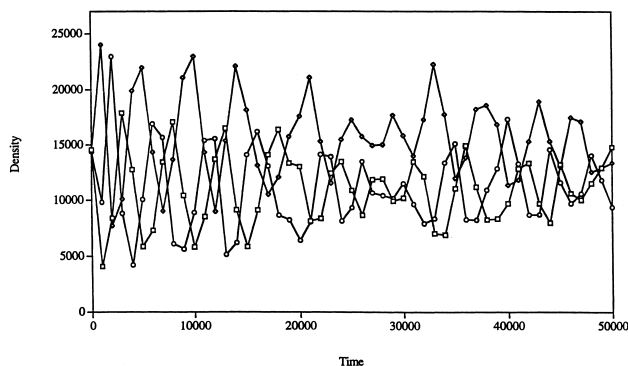


Fig. 11

4. Case 3. Periodic Orbits. Our first example was introduced by Silvertown et al. (1992) to investigate the competitive interaction of five grass species. We have given it a new name to place it in context in the theory of interacting particle systems.

Example 4.1. The multitype biased voter model. Each site will always be occupied by exactly one of the species $1, 2, \dots, K$. The process is described by declaring that:

- i. An individual of species i produces new offspring of its type at rate β_i .
- ii. An offspring of type i produced at x is sent to y with probability $p_i(|y - x|)$, where $|y - x|$ is the distance from x to y . To avoid unnecessary complications, we will suppose that $p_i(1) > 0$ and that there is an $R < \infty$ so that $\varphi_i(r) = 0$ when the distance $r > R$. In other words, there is a finite dispersal range, but nearest neighbors are always accessible.
- iii. If site y is occupied by type j , and type i disperses to that site, a successful invasion occurs (i.e., the state of y changes from j to i) with probability p_{ij} ; if invasion does not occur, the site y is unchanged.

To explain the name we note that if there are only two types, then the model reduces to the biased voter model introduced by Williams and Bjerknes (1972) and studied by Griffeath (1979) and Bramson and Griffeath (1980b), (1981). For a summary of their results, see Chapter 3 of Durrett (1988).

If we were to ignore space and assume that the states of the sites in the grid are always independent, then the fraction of sites occupied by species i , u_i , would satisfy

$$(4.1) \quad \frac{du_i}{dt} = \sum_j u_i u_j \{\beta_i p_{ij} - \beta_j p_{ji}\}.$$

In the stochastic spatial model (and of course also in the mean field ODE) only the value of $\lambda_{ij} = \beta_i p_{ij}$ is important, so we can describe the concrete example investigated by Silvertown et al. (1992) by giving the matrix λ_{ij} :

i	$j \rightarrow$	1	2	3	4	5
1	<i>Agrostis</i>	0	0.09	0.32	0.23	0.37
2	<i>Holcus</i>	0.08	0	0.16	0.06	0.09
3	<i>Poa</i>	0.06	0.06	0	0.44	0.11
4	<i>Lolium</i>	0.02	0.06	0.05	0	0.03
5	<i>Cynosurus</i>	0.02	0.03	0.05	0.03	0

Simulations of this process from a randomly chosen initial state are not very interesting to watch. As Silvertown et al. (1992) observed, “Three of the five species went extinct very rapidly. The two survivors *Agrostis* and *Holcus* were the same as the species that survived the longest in the aggregated models.” To explain why this occurs, we say that species i *dominates* species j and we write $i \geq j$ if $a_{ij} = \lambda_{ij} - \lambda_{ji} \geq 0$. When the difference is > 0 , we say that i *strictly dominates* j and write $i > j$. In the concrete case given above, *Agrostis* strictly dominates all other species but beats *Holcus* by 0.09 to 0.08, so it should not be surprising that *Agrostis* takes over the system, with *Holcus* offering the most resistance. Indeed, Durrett and Levin (1997b) have shown the following theorem.

THEOREM 4.1. *Assume that the dispersal distribution φ_i does not depend on i and that type 1 is strictly dominant over type i for $2 \leq i \leq K$. If we let A_t^1 denote the event that type 1 is still alive at time t , then $P(A_t^1, \xi_t(x) \neq 1) \rightarrow 0$ as $t \rightarrow \infty$.*

This result says simply that if all species disperse equally, a competitive dominant type will almost certainly drive the others to extinction. To explain the mathematical statement, note that if we only start with finitely many 1s, then bad luck in the early stages can wipe out all the 1s. Our result says that if this does not happen then the 1s will take over the system.

The outcome in Theorem 4.1 is the one we should expect. However, the reader should note that the assumption that all the dispersal distributions are equal is crucial for the result. Suppose for simplicity that there are only two species with $p_{1,2} = p_{2,1} = 1$. In this case we can have situations where $\beta_1 < \beta_2$, but the long-range disperser 1 outcompetes the nearest neighbor disperser 2. See Durrett and Levin (1997b) for details.

Example 4.2. Cyclic biased voter model. In view of the discussion just completed, the simplest system that can have interesting behavior is a three-species system with a competitive loop: $1 < 2 < 3 < 1$. Bramson and Griffeath (1989) have considered this system with $n \geq 3$ competitors in one dimension. Griffeath alone (1988) and with his coworkers Fisch and Gravner (1991a), (1991b) has studied related cellular automata. Tainaka (1993), (1994), (1995) has considered a variation on the model in which 1s mutate into 3s with the paradoxical result that this enhances the density of 1s.

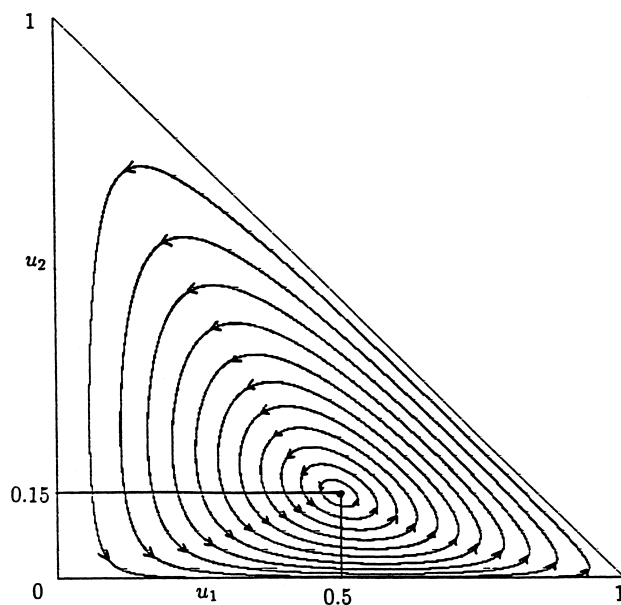


Fig. 12

In our situation, if we suppose $1 < 2 < 3 < 1$ and let

$$\beta_1 = \lambda_{13}, \quad \beta_2 = \lambda_{21}, \quad \beta_3 = \lambda_{32},$$

then the system (4.1) can be written as

$$(4.2) \quad \begin{aligned} \frac{du_1}{dt} &= u_1(\beta_1 u_3 - \beta_2 u_2), \\ \frac{du_2}{dt} &= u_2(\beta_2 u_1 - \beta_3 u_3), \\ \frac{du_3}{dt} &= u_3(\beta_3 u_2 - \beta_1 u_1). \end{aligned}$$

If, for example, we take $\beta_1 = 0.3$, $\beta_2 = 0.7$, and $\beta_3 = 1.0$, then the ODE behaves as indicated in Figure 12. There is a family of periodic orbits around the fixed point $(0.5, 0.15, 0.35)$.

To show that in general we get pictures similar to the concrete example, we begin by dividing each equation by the product of the betas that appear in it to conclude that any fixed point ρ has

$$\frac{\rho_3}{\beta_2} = \frac{\rho_2}{\beta_1} = \frac{\rho_1}{\beta_3}.$$

Recalling that the equilibrium densities must sum to 1, we conclude that

$$\rho_1 = \frac{\beta_3}{\beta_1 + \beta_2 + \beta_3}, \quad \rho_2 = \frac{\beta_1}{\beta_1 + \beta_2 + \beta_3}, \quad \rho_3 = \frac{\beta_2}{\beta_1 + \beta_2 + \beta_3}.$$

To see that there is a family of periodic orbits surrounding the fixed point we write

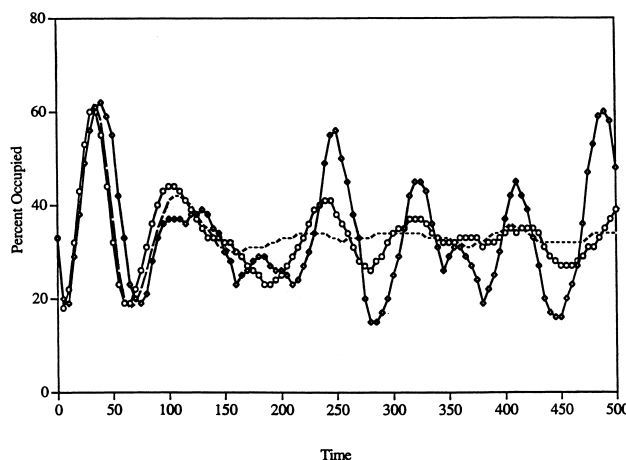


Fig. 13

$H(u) = \sum_i \rho_i \log u_i$ and note that

$$\begin{aligned} \frac{\partial H}{\partial t} &= \sum_i \frac{\rho_i}{u_i} \frac{du_i}{dt} \\ &= c \left(\frac{u_3}{\beta_2} - \frac{u_2}{\beta_1} \right) + c \left(\frac{u_1}{\beta_3} - \frac{u_3}{\beta_2} \right) + c \left(\frac{u_2}{\beta_1} - \frac{u_1}{\beta_3} \right) = 0, \end{aligned}$$

where $c = \beta_1 \beta_2 \beta_3 / (\beta_1 + \beta_2 + \beta_3)$. Thus H is constant along solutions of the ODE.

The situation described above is similar to that of May and Leonard (1975) and Gilpin (1975), who considered a system in which there were invariant sets of the form $\sum_i \log u_i = K$. Gilpin (1975) observed that the “system is neutrally stable on the plane $u_1 + u_2 + u_3 = 1$, therefore stochastic effects (environmental noise) will cause it to decay to a single species system.” This conclusion does not apply to the stochastic spatial model. Well-separated regions oscillate out of phase, and the result is a stable equilibrium in which each of the three types is present at a positive density.

Figure 13 gives the percentage of sites occupied by species 1 for the first 500 units of time when we look at the system in windows of size 30×30 or 120×120 , or average over the whole 480×480 system (which again has periodic boundary conditions). In this case the densities oscillate on small length scales, but after an initial transient are constant on large length scales. This leads to the following conjecture.

CONJECTURE 4.1. *For any $\beta_i > 0$ there is coexistence in the cyclic biased voter model.*

Rand and Wilson (1995) and Keeling et al. (1996) have considered the problem of finding the “most interesting” scale on which to view the densities. This length scale is what physicists would call the *correlation length*, so it should be surprising that its rigorous definition is in terms of the variances of the empirical densities observed in boxes of various sizes. To be precise, in two dimensions we would let $u_i(L)$ be the number of sites in an $L \times L$ box in state i , and let $v_i(L)$ be the variance of $u_i(L)$. As $L \rightarrow \infty$, $v_i(L)/L^2$ converges to a limit σ_i^2 . If one picks a constant $\delta > 0$, for example, $1/5$, then the correlation length can be defined as the last time $v_i(L)/L^2$ differs from its limit by more than $\delta \sigma_i^2$.

Example 4.3. Hawks and doves. Our next model is a spatial version of Maynard Smith's (1982) evolutionary games, called Hawks and Doves, whose interaction is described by a game matrix. The three examples we will be interested in are given by:

#1	<i>H</i>	<i>D</i>	#2	<i>H</i>	<i>D</i>	#3	<i>H</i>	<i>D</i>
<i>H</i>	.4	.8	<i>H</i>	.7	.4	<i>H</i>	-.6	.9
<i>D</i>	.6	.3	<i>D</i>	.4	.8	<i>D</i>	-.9	.7.

Finally we list the general case, which serves to define notation we will use:

	<i>H</i>	<i>D</i>
<i>H</i>	<i>a</i>	<i>b</i>
<i>D</i>	<i>c</i>	<i>d</i> .

To explain the general game matrix we note that b is, for example, the payoff to a hawk when interacting with a dove, while c is the payoff to a dove when interacting with a hawk. When the population consists of a fraction p of hawks and $1 - p$ of doves, then the payoff for hawks is $ap + b(1 - p)$. We interpret $ap + b(1 - p)$, which may be positive or negative (see, e.g., game #3), as the net birth rate of hawks in this situation.

Once we have decided on a game matrix, then following Brown and Hansell (1987), the dynamics can be formulated as follows:

i. *Migration.* Each individual changes its spatial location at rate ν , and when it moves, it moves to a randomly chosen nearest neighbor of x ; i.e., it picks with equal probability one of the four points $x + (1, 0)$, $x - (1, 0)$, $x + (0, 1)$, $x - (0, 1)$ that differ from x by 1 in one of the coordinates.

ii. *Deaths due to crowding.* Each individual at x at time t dies at rate $\kappa(\eta_t(x) + \zeta_t(x))$.

iii. *Game step.* Let $\mathcal{N} = \{z \in \mathbf{Z}^2 : |z_1|, |z_2| \leq 2\}$ be a 5×5 square centered at $(0, 0)$. Let

$$\hat{\eta}_t(x) = \sum_{z \in \mathcal{N}} \eta_t(x + z), \quad \hat{\zeta}_t(x) = \sum_{z \in \mathcal{N}} \zeta_t(x + z)$$

be the number of hawks and doves in the interaction neighborhood of x at time t , and let

$$p_t(x) = \hat{\eta}_t(x) / (\hat{\eta}_t(x) + \hat{\zeta}_t(x))$$

be the fraction of hawks. Each hawk experiences a birth (or death) rate of $ap_t(x) + b(1 - p_t(x))$, while each dove experiences a birth (or death) rate of $cp_t(x) + d(1 - p_t(x))$.

If we assume that all sites remain independent, then we arrive at the following mean field ODE for the densities of hawks (u) and doves (v):

$$(4.3) \quad \begin{aligned} \frac{du}{dt} &= u \left\{ a \frac{u}{u+v} + b \frac{v}{u+v} - \kappa(u+v) \right\}, \\ \frac{dv}{dt} &= v \left\{ c \frac{u}{u+v} + d \frac{v}{u+v} - \kappa(u+v) \right\}. \end{aligned}$$

Note that a species-specific linear term in the net birth (death) rate, r , is easily accommodated within this framework as part of a and b or c and d since $u/(u+v) + v/(u+v) = 1$.

The hawks and doves model quite naturally divides itself into three cases, which was the motivation for formulating the scheme announced at the beginning of this paper. To motivate the division into cases, we change variables $p = u/(u + v)$, $s = u + v$ in the dynamical system to get

$$(4.4) \quad \begin{aligned} \frac{dp}{dt} &= (a - b - c + d)p(1 - p)(p - p_0), \\ \frac{ds}{dt} &= s \{ \alpha p^2 + \beta p + \gamma \} - \kappa s^2, \end{aligned}$$

where

$$p_0 = \frac{b - d}{b - d + c - a}, \quad \alpha = a - b - c + d, \quad \beta = b + c - 2d, \quad \gamma = d - \kappa s.$$

The equation for dp/dt is identical to the usual equation from population genetics for weak selection with selection coefficient $a - b - c + d$. If the hawk strategy is never worse than the dove strategy, i.e., if $a \geq c$ and $b \geq d$, then $p_0 \geq 1$ or $p_0 \leq 0$ (ignoring the trivial case $a = c$, $b = d$). The same conclusion holds if the dove strategy dominates the hawk strategy; but if neither strategy dominates the other, p_0 represents a mixed strategy equilibrium. That is, if a fraction p_0 of the players play the hawk strategy and a fraction $1 - p_0$ play the dove strategy, both strategies have the same payoff. To check this note that

$$p_0 a + (1 - p_0)b = p_0 c + (1 - p_0)d \quad \text{if and only if} \quad p_0 = \frac{b - d}{b - d + c - a}.$$

When $p_0 \in (0, 1)$, it may be an attracting (Case 1) or a repelling (Case 2) fixed point. Matrices #1 and #2 above are examples of Case 1 and Case 2, respectively. Since we have discussed these situations at length, we turn now to the case in which $p_0 = 1$, i.e., when the hawk strategy always dominates the dove strategy. If $a > 0$ the system is boring since the hawks will take over the system. However, if $a < 0$ and $d > 0$, as in matrix #3, things are quite interesting. In this case, the hawks always do better than the doves, but a population consisting purely of hawks dies out, so when hawks are rare, the doves will regenerate.

This case is often called the prisoner's dilemma after the two-person nonzero sum game in which two individuals have a choice to cooperate (C) or defect (D). The payoffs to the first and second players for their actions are given as follows:

	C	D
C	(R, R)	(S, T)
D	(T, S)	(P, P)

Here $T > R > P > S$, so the defector strategy dominates cooperation, but double defection leads to less happiness than the cooperation of each player. See Luce and Raiffa (1957) or Owen (1968).

It is easy to see that in Case 3, both species die out in the ODE. Figure 14 gives a picture of the ODE for matrix #3. From the picture it should be clear that the fraction of individuals that are hawks increases in time. This observation leads easily to the following theorem.

THEOREM 4.2. *If the initial condition for the dynamical system has $u(0) > 0$, then $(u(t), v(t)) \rightarrow (0, 0)$.*

Proof. From (4.4) it follows that $p(t) = u(t)/(u(t) + v(t))$ converges to 1 as $t \rightarrow \infty$. Once $p(t)$ gets close enough to 1, both growth rates are negative and the populations decay to 0 exponentially fast. \square

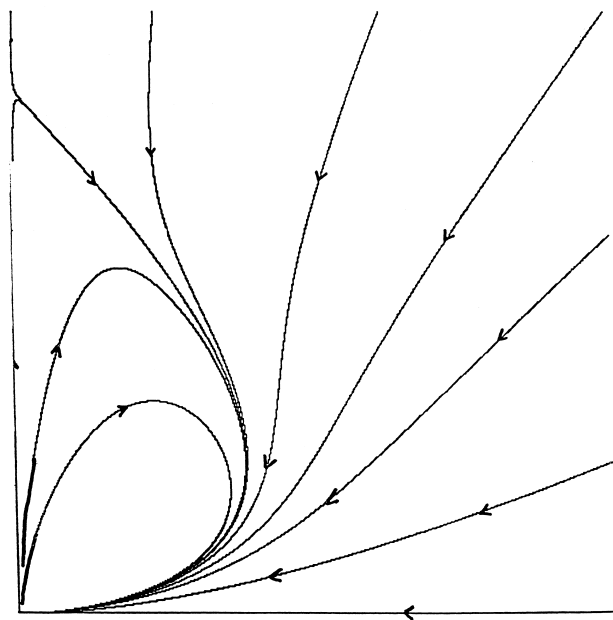


Fig. 14

In contrast, we have the following conjecture.

CONJECTURE 4.2. *In Case 3, hawks and doves coexist in our stochastic spatial model, at least for fast migration.*

A typical simulation of the interacting particle system in Case 3 begins with a period in which the hawk population grows faster than the dove population until the fraction of hawks is too large and both species start to die out. When the density gets low we have a few doves who are completely isolated and give birth at rate $d = 0.7$. These doves start colonies that grow and would fill up the space to the doves' preferred equilibrium density, except for the fact that along the way they encounter a few hawks that managed to escape extinction. These hawks then reproduce faster than the doves, the fraction of hawks grows, and the cycle begins again.

Figure 15 gives a graph of the density of hawks and doves vs. time for a simulation on a 50×50 grid, while Figure 16 shows the same statistics for a 150×150 grid. As the system size increases, the oscillations decrease. The explanation for this is simple: if we look at a 150×150 grid, then the cycle of growth of the hawks fraction, decrease of the population, and regrowth from isolated doves in any 50×50 subsquare is much like that of the simulation on the 50×50 grid. However, the 150×150 system consists of nine 50×50 subsquares which do not oscillate in a synchronized fashion, so the cycles cancel each other out to some extent.

Example 4.4. Epidemics with regrowth of susceptibles. In this model the states are 0 = susceptible, 1 = infected, and 2 = removed. Writing f_i for the fraction of the four nearest neighbors in state i , we can write the rates as

$$0 \rightarrow 1 \quad \beta_1 f_1, \quad 1 \rightarrow 2 \quad \delta, \quad 2 \rightarrow 0 \quad \alpha.$$

Durrett and Neuhauser (1991) have shown the following theorem.

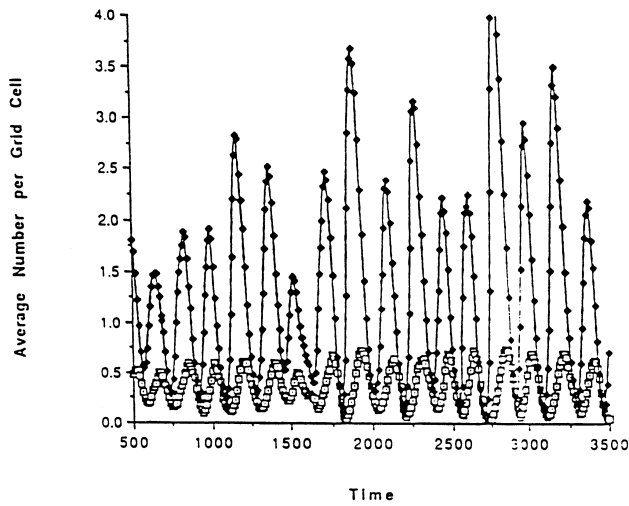


Fig. 15

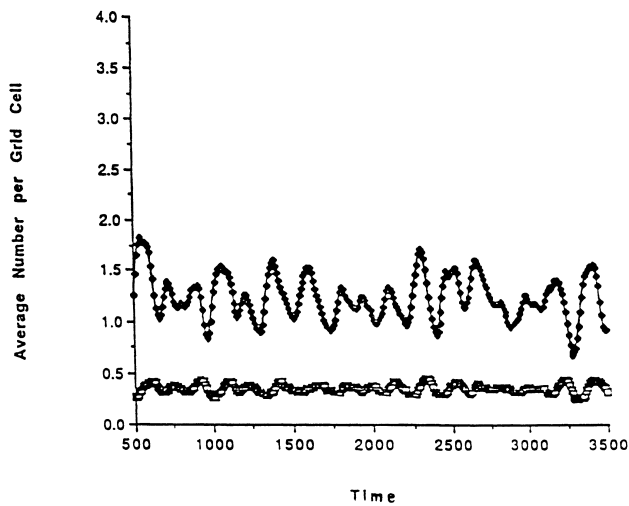


Fig. 16

THEOREM 4.3. *If the epidemic without regrowth (i.e., when $\alpha = 0$) does not die out, then coexistence occurs whenever $\alpha > 0$.*

If α is small and we make the correspondence: infecteds = hawks, susceptibles = doves, and removed = vacant, then the behavior of the model (when viewed in windows of size $1/\alpha$) is much like the hawks-doves system.

- i. Epidemics sweep through the system, wiping out most susceptibles.
- ii. When susceptibles are scarce, the epidemic becomes subcritical and the density of infecteds then drops to a low level.
- iii. When infecteds are scarce, susceptibles increase. When the density of susceptibles is large enough, one of the few surviving infecteds starts another epidemic.

For simulation results on this phenomenon, see Durrett (1995c). The conference proceedings, Mollison (1995), in which that paper appears is an excellent source for information on all sorts of epidemic models.

Example 4.5. WATOR. The name and the inspiration for the model comes from A. K. Dewdney's "Computer Recreations" column in *Scientific American* in December 1984. Each site can be in state 0 = vacant, 1 = occupied by a prey (fish), or 2 = occupied by a predator (shark). The original model was defined in discrete time, but we reformulate it in continuous time as follows:

- i. Fish are born at vacant sites at rate β_1 times the fraction of neighbors occupied by fish.
- ii. Each shark at rate 1 inspects q neighboring sites, chosen without replacement from the neighbor set. It moves to the first fish it finds and eats it. A shark that has just eaten gives birth with probability β_2 . A shark that finds no fish dies with probability δ .
- iii. There is *stirring* (also called *swimming*) at rate ν : for each pair of nearest neighbor sites x and y we exchange the values at x and at y at rate ν .

The stirring mechanism automatically preserves the restriction of at most one individual per site and has the mathematical advantage that the trajectory of any single particle is just a continuous-time random walk. Of course, if one watches the movements of two particles there is a (very small) correlation between their locations due to the occasional stirring steps that affect both particles at the same time.

Letting $u_i(t)$ be the fraction of sites in state i at time t , and computing the rate of change by supposing that adjacent sites are always independent,

$$(4.5) \quad \begin{aligned} du_1/dt &= \beta_1 u_1 (1 - u_1 - u_2) - u_2 \{1 - (1 - u_1)^q\}, \\ du_2/dt &= \beta_2 u_2 \{1 - (1 - u_1)^q\} - \delta u_2 (1 - u_1)^q. \end{aligned}$$

Here, the first term on the right represents the birth of fish onto vacant sites. To explain the second and third terms, we note that $u_2 \{1 - (1 - u_1)^q\}$ gives the fraction of sites occupied by sharks times the probability a given shark will find at least one fish when it inspects q neighbors, so β_2 times this gives the rate at which new sharks are produced. For similar reasons the fourth term represents the sharks who find no fish to eat, got a bad coin flip, and were told to die.

To begin to understand the ODE we note that in the absence of fish, sharks can't breed and their density drops to 0. Conversely, in the absence of sharks, fish don't die and will fill up the space. The last two results give the direction of motion of the ODE on two sides of the right triangle that we use for the possible states of the system: $\Gamma = \{(u_1, u_2) : u_1, u_2 \geq 0, u_1 + u_2 \leq 1\}$.

Since fish do not die in the absence of sharks, there is a boundary equilibrium at $(1, 0)$. Considering the second equation in (4.4) and setting $u_1 = 1 - \epsilon_1$ and $u_2 = \epsilon_2$, where the ϵ_i are small, shows that $(1, 0)$ is always a saddle point. This behavior suggests the presence of a fixed point (\bar{u}_1, \bar{u}_2) with both components positive, a fact which can easily be confirmed by algebraic manipulation. To do this neatly, and to pave the way for later calculations, we will first rewrite the system in (4.5) as

$$(4.6) \quad \begin{aligned} du_1/dt &= A(u_1) - u_2 B(u_1), \\ du_2/dt &= u_2 C(u_1), \end{aligned}$$

where $A(u_1) = \beta_1 u_1 (1 - u_1)$,

$$B(u_1) = \beta_1 u_1 + \{1 - (1 - u_1)^q\},$$

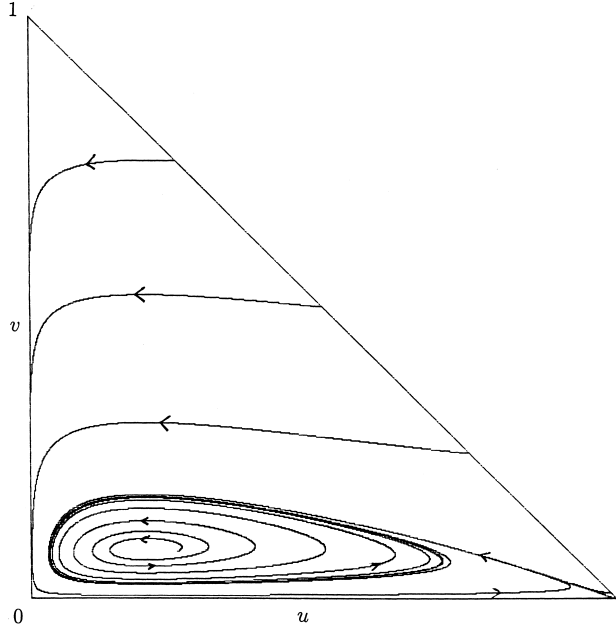


Fig. 17

and $C(u_1) = \beta_2 - (\beta_2 + \delta)(1 - u_1)^q$. In order for $du_2/dt = 0$ we must have

$$(4.7) \quad C(\bar{u}_1) = 0 \quad \text{or} \quad \bar{u}_1 = 1 - \left(\frac{\beta_2}{\beta_2 + \delta} \right)^{1/q}.$$

Having found \bar{u}_1 we can now set $du_1/dt = 0$ in (4.5) to find that

$$(4.8) \quad \bar{u}_2 = A(\bar{u}_1)/B(\bar{u}_1).$$

To investigate the nature of the fixed point at (\bar{u}_1, \bar{u}_2) we let $v_i = u_i - \bar{u}_i$ be the displacement from it in the i th component. Assuming the v_i are small and using (4.7) and (4.8) we arrive at the linearized equation

$$(4.9) \quad \begin{aligned} dv_1/dt &= Fv_1 + Gv_2, \\ dv_2/dt &= Hv_1, \end{aligned}$$

where $F = A'(\bar{u}_1) - \bar{u}_2 B'(\bar{u}_1)$, $G = -B(\bar{u}_1)$, and $H = u_2 C'(\bar{u}_1)$. This ODE is analyzed in Durrett and Levin (1999) with the following result.

THEOREM 4.4. *The interior fixed point is always locally attracting when $q \leq 3$. Conversely, if $q > 3$ and the values of β_2 and δ are held constant, decreasing β_1 leads to a Hopf bifurcation that produces a limit cycle.*

Figure 17 gives a picture of a case of the ODE with a limit cycle: $\beta_1 = 1/3$, $\beta_2 = 0.1$, $\delta = 1$, and $q = 4$.

To make connections between our model and reaction-diffusion equations, we use Theorems 2.1 and 2.2 to conclude that if we let the stirring rate $\nu \rightarrow \infty$ and consider our process on a scaled version of the square lattice in which the spacing between sites

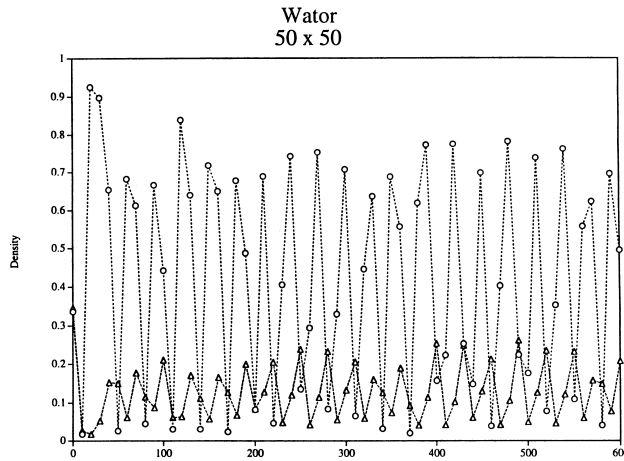


Fig. 18

is reduced to $\nu^{-1/2}$, then the densities of fish and sharks converge to the solution of the PDE:

$$(4.10) \quad \begin{aligned} \partial u_1 / \partial t &= \Delta u_1 + g_1(u_1, u_2), \\ \partial u_2 / \partial t &= \Delta u_2 + g_2(u_1, u_2), \end{aligned}$$

where the g_i are the right-hand sides of the equations in (4.5).

The next result, also proved in Durrett and Levin (1999), says that sharks and fish coexist in the reaction-diffusion equation.

THEOREM 4.5. *Suppose that the initial conditions $u_i(x, 0) \geq 0$ are continuous and satisfy $u_1 + u_2 \leq 1$, and that each u_i is not identically 0. Then there are positive constants ρ , ϵ_1 , and ϵ_2 so that for large t , $u_i(x, t) \geq \epsilon_i$ whenever $|x| \leq \rho t$.*

In other words, the densities stay bounded away from zero on a linearly growing set. Using (★) from section 2 then gives the following theorem.

THEOREM 4.6. *When the stirring rate is large there is coexistence.*

The last result proves the existence of the stationary distribution but does not yield much information about its spatial structure. To understand that, we turn to simulation. Immediately, however, we run into the difficulty that while fast stirring is convenient for making connections with reaction-diffusion equations, it is painful to implement on the computer, since most of the computational effort is spent moving the particles around.

To find a variant of the WATOR model that we can more easily simulate, we note that at any moment, when a fish or shark at x inspects its neighbors, it sees a set of sites that have been subject to stirring at rate ν since the previous time site x decided to try to change. Since the flip rates stay constant as the stirring rate $\nu \rightarrow \infty$, this time is of order 1, and the neighbors will move a distance of order $\nu^{1/2}$. With this in mind, we will replace stirring by choosing our neighbors at random (with replacement) from a square of radius $r = \nu^{1/2}$ centered at the point of interest.

Figures 18 and 19 show results of computer simulations when $r = 5$, i.e., when neighbors are chosen at random from an 11×11 square centered at the point. Note that densities oscillate when measured in a 50×50 window but are much smoother in time in a 200×200 window. Again, this corresponds to our picture of Case 3

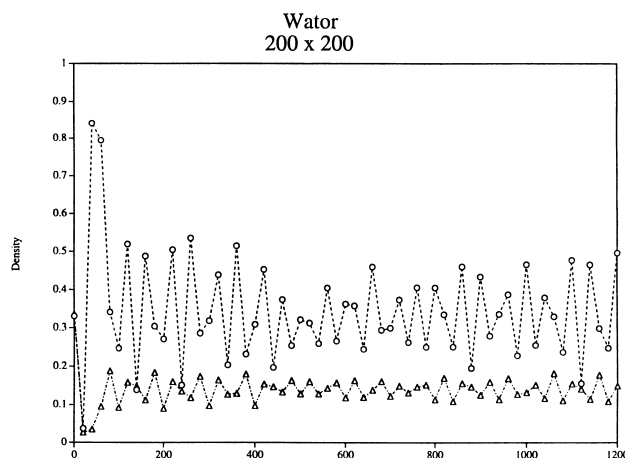


Fig. 19

announced at the end of the introduction. Having mentioned long-range limits in the simulation we should also close by stating the following conjecture.

CONJECTURE 4.3. *When the range of interaction is large there is coexistence.*

The problem here is stated for WATOR but also can be posed for predator-mediated coexistence (Example 2.2).

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