COEXISTENCE IN STOCHASTIC SPATIAL MODELS*

By Rick Durrett [†]

Cornell University

In this paper I will review twenty years of work on the question: When is there coexistence in stochastic spatial models? The answer, announced in Durrett and Levin (1994), and that we explain in detail in this paper is that this can be determined by examining the mean-field ODE. There are a number of rigorous results in support of this picture, but we will state eight challenging and important open problems.

Introduction. There is an incredible diversity of species that coexist in the world. At the Botanic Garden in Singapore one can see 1000 species of orchids. These are cultivated, of course, but if one examines the food web in a small lake one finds dozens of species coexisting. An important problem in ecology is to identify mechanisms that permit the coexistence of species. In this paper we will examine that question in the context of stochastic spatial models. In these interacting particle systems, space is represented by the d-dimensional integer lattice $\mathbb{Z}^d$. With ecological problems in mind, we will usually take $d = 2$.

Historically the first multi-species system to be considered was

Example 1. Competing contact processes

- Each site in $\mathbb{Z}^2$ can be in state $0 =$ vacant, or in state $i = 1, 2$ to indicate that it is occupied by one individual of type i
- Individuals of type i die at rate δ_i, give birth at rate β_i. Here, at rate λ means that these events happen at times of a rate λ Poisson process.
- A type i born at x goes to $x + y$ with probability $p_i(y)$. If the site is vacant it changes to state i, otherwise nothing happens.

When there is only one type this reduces to the system introduced by Harris (1974). After several decades of work this model is very well understood. See Liggett (1999) for a survey.

If we assume that the states of adjacent sites are independent then the fraction of sites u_i in state $i = 1, 2$ satisfies

(1)
$$\frac{du_1}{dt} = \beta_1 u_1 (1 - u_1 - u_2) - \delta_1 u_1$$
$$\frac{du_2}{dt} = \beta_2 u_2 (1 - u_1 - u_2) - \delta_2 u_2$$

This is called the *mean-field ODE*, because if we consider the system on N sites with a uniform dispersal distribution then in the limit as $N \to \infty$ the densities converge to this limit. In the spatial model adjacent sites are not independent. However, writing and analyzing the mean-field ODE is a good first step in guessing what the system will do.

In (1) $du_i/dt = 0$ when $(1 - u_1 - u_2) = \delta_i/\beta_i$. These lines are parallel, so they either do not intersect or coincide. Figure 1 shows the mean-field ODE when $\beta_1 = 4$, $\beta_2 = 2$, and $\delta_1 = \delta_2 = 1$.
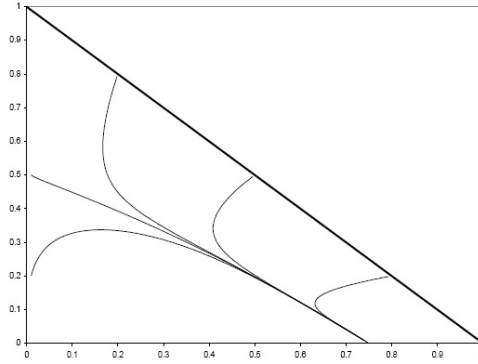

FIG 1. *Competing contact process ODE*

In (1992) Neuhauser proved the following result:

THEOREM 1. *If the dispersal distributions $p_1 = p_2 = p$, $\delta_1 = \delta_2$, and $\beta_1 > \beta_2$ then species 1 out competes species 2. That is, if the initial condition is translation invariant and has $P(\xi_0(x) = 1) > 0$ then $P(\xi_t(x) = 2) \to 0$.*

Sketch of proof. We construct the process from a "graphical representation." For each site x there is a rate 1 Poisson process D_n^x, $n \geq 1$ that kills the particle at x (if there is one). For each x and y, there are Poisson processes $B_n^{x,y}$, $n \geq 1$ and $A_n^{x,y}$, $n \geq 1$ with rates $\beta_1 p(y)$ and $(\beta_2 - \beta_1)p(y)$. The first

causes births from x to $x+y$ if x is occupied and $x+y$ is vacant. The second causes births x to $x+y$ if x is occupied by a 1 and $x+y$ is vacant. To see if 0 is occupied at time t we work backwards in time to define a dual process $\tilde{\xi}_s^t$ which has the property that

$$\xi_t(0) = 1 \text{ if and only if } \xi_{t-s}(x) = 1 \text{ for some } x \in \tilde{\xi}_s^t$$

If $\tilde{\xi}_s^t = \emptyset$ for some $s < t$ then 0 is vacant. If $\tilde{\xi}_t^t \neq \emptyset$ then there is a natural ordering on $\tilde{\xi}_t^t$ so that the first occupied site at time 0 dictates the type at 0 at time t. One then argues that due to the fact that the 1's have their own special arrows, the site will be a 1 with high probability. We refer the reader to Neuhauser (1992) for more details. □

The behavior in Theorem 1 is what biologists expect based on the *Competitive Exclusion Principle*. A version of this can be found in work of Levin (1970). Consider an ODE of the form:

$$\frac{du_i}{dt} = u_i f_i(z_1, \ldots z_m) \quad 1 \leq i \leq n$$

Here the z_i are resources. In previous model there is one resource: $z_1 = 1 - u_1 - u_2$ free space.

THEOREM 2. *If $n > m$ then no stable equilibrium in which all n species are present is possible.*

In words, the number of coexisting species is smaller than the number of resources.

PROOF. Linearize around the fixed point. $n > m$ implies there is a zero eigenvalue, so the fixed point cannot be locally attracting. □

In the mean-field ODE, only the ratios β_i/δ_i matters, so it is natural to guess.

Problem 1. *Show that the conclusion holds if the dispersal distributions are the same and $\beta_1/\delta_1 > \beta_2/\delta_2$.*

To try to build some excitement about Problem 1, we note that Chan and Durrett (2006) proved that a "fugitive species" that disperses long distances (with a truncated power law distribution) and at a fast rate, can coexist with a superior competitor with a nearest neighbor dispersal distribution. This does not contradict the competitive exclusion principle, because in addition
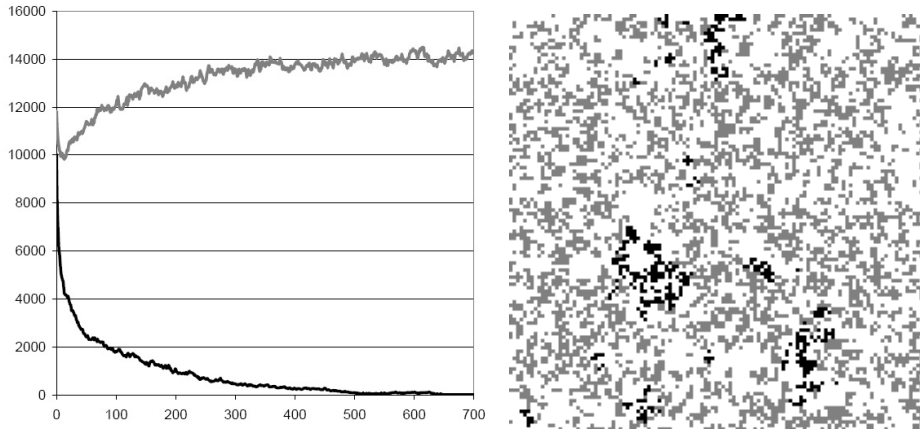
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FIG 2. *Simulation of competing contact process. $\beta_1 = 3.9$, $\delta_1 = 2$ (black) versus $\beta_2 = 2$, $\delta_1 = 1$ (gray). The picture is a snapshot of part of the grid at time 300.*

to single site deaths their model has forest fires, which destroy large squares of occupied sites at a small rate. Thus the model has a second type of space, "recently disturbed space," and is entitled to have two coexisting species.

As announced in the abstract, one goal of this paper is to explain the idea of Durrett and Levin (1994) that one can determine whether coexistence happens in the stochastic spatial model by examining properties of the mean-field ODE. The discussion is divided into three cases according to the properties of the ODE.

Case 1. Attracting Fixed Point

When the mean-field ODE has an attracting fixed point, we expect coexistence in the spatial model, i.e., there is a stationary distribution which concentrates on configurations that have infinitely many sites occupied by each species.

Example 1.1. Durrett and Swindle (1991). Grass Bushes Trees

In this variant of the contact process there is a hierarchy of types. In hind sight this is a very natural model. However, it owes its invention to talking to Simon Levin about successional sequences in a forest.

- Each site in $\mathbb{Z}^2$ can be in state 0 = grass, 1 = bush, 2 = tree.
- Individuals of type i die at rate δ_i, give birth at rate β_i.
- A type i born at x goes to $x + y$ with probability $p_i(y)$. If the site is in state $j < i$ it changes to state i, otherwise nothing happens.

The mean field ODE is

$$
(2) \qquad
\begin{aligned}
\frac{du_1}{dt} &= \beta_1 u_1(1 - u_1 - u_2) - \delta_1 u_1 - \beta_2 u_2 u_1 \\
\frac{du_2}{dt} &= \beta_2 u_2(1 - u_1) - \delta_2 u_2
\end{aligned}
$$

If $\beta_2 > \delta_2$, $u_2^* = (\beta_2 - \delta_2)/\beta_2$. Given this, one can solve for u_1^* and see when it is positive. However, it is better to approach the question by examining when the 1's can invade 2's in equilibrium, i.e., if the 2's are in equilibrium and the 1's are at a small density then the density of 1's will increase. Ignoring the possibility that a 1 will see another 1 nearby, the condition is:

$$
(3) \qquad \beta_1 \cdot \frac{\delta_2}{\beta_2} > \delta_1 + \beta_2 \cdot \frac{\beta_2 - \delta_2}{\beta_2}
$$

The left hand-side gives the rate at which 1's give birth onto vacant sites, while on the right, the first term is the death rate of 1's and the second is the rate at which they eliminated by births of 2's.

When $\delta_1 = \delta_2 = 1$, (3) becomes $\beta_1 > \beta_2^2 > 1$. For simplicity, we will consider only this case.

THEOREM 3.   *Durrett and Swindle (1992). If $\beta_1 > \beta_2^2 > 1$ then when p_i is uniform on $\{x : 0 < \|x\| \le L\}$ and L is large, there is a stationary distribution μ_{12} that concentrates on configurations with infinitely many 1's and 2's.*

SKETCH OF PROOF. The survival of the 2's is not a problem because they are a contact process and don't feel the presence of the 1's. To prove that the 1's can persist in the space that remains, we use a "block construction," which consists of comparing the particle system with a mildly dependent oriented percolation in which sites are open with probability close to 1.

For an account of this method and a number of examples, see my St. Flour lecture notes, Durrett (1995). Suppose, for simplicity, that $d = 1$. At an intuitive level, what one shows is that "one pile can make two piles with high probability." That is, L and T can be chosen so that if $[-L, L]$ is good at time 0, i.e., there are not too many 2's in $[-L, L]$ and there are enough 1's, then $[-3L, -L]$ and $[L, 3L]$ will be good at time T even if we kill all of the 1's that wander outside $[-10L, 10L]$. The last condition is needed so that there is a finite range of dependence between the events in the construction.

The block construction gives a lower bound on the density of sites occupied by 1's. Taking the Cesaro average of the distribution from time 0 to

time t, and finding a convergent subsequence produces the desired stationary distribution. For more details on this point, see Liggett (1985). □

The block construction technology has improved quite a bit since 1992, so at this point it should be fairly routine to do the following:

Exercise. Show that if $\delta_1 = \delta_2 = 1$, $\beta_2 > 1$ and $\beta_1 < \beta_2^2$ then the 1's die out when the range is large.

In the setting of Theorem 3, in addition to existence of a stationary distribution, we have a uniqueness result.

THEOREM 4. *Durrett and Moller (1991). Suppose $\delta_1 = \delta_2 = 1$, $\beta_1 > \beta_2^2 > 1$. If the range is large then whenever the 1's and the 2's do not die out then the process converges to μ_{12}.*

There are stationary distributions μ_1 and μ_2 with only 1's and 2's respectively. By results for the one-type contact process, these are unique if one specifies that there is no mass on the all 0's state. In addition there is the trivial stationary distribution μ_0 that assigns mass 1 to all 0's. The convergence result in Theorem 4 when combined with results for the one-type contact process implies that all stationary distributions are convex combinations of μ_0, μ_1, μ_2 and μ_{12}. There are many situations in which we can prove the existence of stationary distributions, but convergence results like Theorem 4 are rare.

There are, at this point, a number of coexistence results for particle systems with long range interactions: Durrett (1992), Durrett and Schinazi (1993), Durrett and Neuhauser (1997), Durrett and Lanchier (2008), etc. However, the proofs of these results are done on a case by case basis. Things are simpler if, instead of long range, we assume that there is "fast stirring:" suppose that for each pair of nearest neighbors x and y, at rate ϵ^{-2} exchange the values $\xi_t(x)$ and $\xi_t(y)$. In this case there is a general result.

THEOREM 5. *Suppose there is a repelling function ϕ that (i) decreases along solutions of the mean-field ODE, and (ii) $\phi(u) \to \infty$ when $\min_i u_i \to 0$. Then there is coexistence in the model with fast stirring when $\epsilon < \epsilon_0$.*

Durrett (2002) applies this result to a wide variety of systems: epidemics, predator-prey models, predator mediated coexistence, etc.

SKETCH OF PROOF The existence of a repelling function and a few lines of calculus implies that for solutions of the PDE

$$\frac{du}{dt} = \Delta u + f(u)$$

$\min_i u_i(t, x) \geq \epsilon$ for $t \geq T$, $|x| \leq ct$. As $\epsilon \to 0$ the particle system on $\epsilon \mathbb{Z}^d$ converges to the solution of the PDE. Using this with the result for the PDE, we have shown that "one pile makes two piles" with high probability and the result follows from the block construction. □

Question. Is there a similar general result for systems with long-range interactions?

Example 1.2. Host-pathogen models

In Durrett (2002) it was shown that predation can cause two competing species to coexistence. Durrett and Lanchier (2008) have shown that coexistence can occur if there is a pathogen in one species. In the next model 1 and 3 are the two species, while 2 is species 1 in the presence of a pathogen. Letting f_i be the fraction of neighbors in state i, the rates are

$$
\begin{aligned}
1 &\to 2 & \alpha f_2 \\
2 &\to 1 & \gamma_2 (f_1 + f_2) \\
3 &\to 1 & \gamma_3 (f_1 + f_2) \\
1 &\to 3 & \gamma_1 f_3 \\
2 &\to 3 & \gamma_2 f_3
\end{aligned}
$$

The first condition says that if we think of 1=vacant and 2=occupied then the 1's and 2's are a contact process. To explain the other four rates: at rate γ_i individuals of type i are replaced by the offspring of a randomly chosen neighbor. If the neighbor is in state $j = 1$ or 3 then the offspring has the same type as the parent. However if the neighbor is of type 2, the offspring is of type 1 because the pathogen is not passed into the seeds.

It is straightforward to write down the mean-field ODE, so we content ourselves to draw a picture. Here the 1's and 2's are a contact process so on the boundary $u_3 = 0$, $u_1 = \gamma_2/\alpha$ is an attracting fixed point.

THEOREM 6. *Suppose $\gamma_1 < \gamma_3 < \gamma_2 < \alpha$ and*

(4) $$\gamma_1 \frac{\gamma_2}{\alpha} + \gamma_2 \left(1 - \frac{\gamma_2}{\alpha}\right) > \gamma_3$$
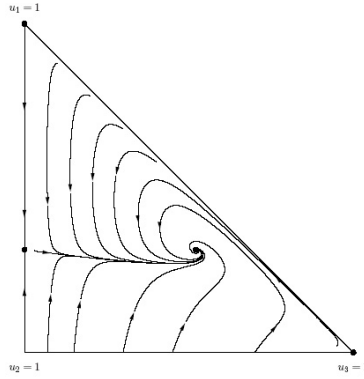
Fig 3. *Host pathogen mean-field ODE.*
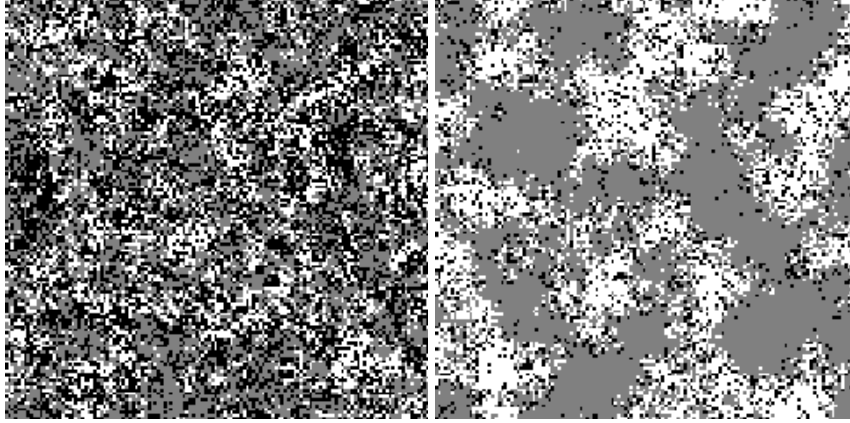
Fig 4. *Host-pathogen examples with coexistence and no coexistence.*

then there is coexistence for large range.

The displayed condition says that the 3's can invade the 1's and 2's in equilibrium. The key to the proof is using an understanding of the ODE to show that if the density of some type becomes small then a sequence of events will occur that results in all of the densities being bigger than some ϵ. Figure 4 gives two simulations. $1 = $ black, $2 = $ white, $3 = $ gray.

Problem 2. *Coexistence is not possible if $\gamma_2 < \gamma_3 < \gamma_1$, (mutualist).*

Why should this be true? If we start with the 1's and 2's in equilibrium and a small density of 3's then once the invasion of the 3's starts the fraction of

2's gets smaller, and the 3's have an even bigger advantage over the 1's and 2's. It is not hard to check in this case that there is no interior fixed point. For more results and problems about host-pathogen models see Lanchier and Neuhauser (2006).

Case 2. Two locally attracting fixed points

In this case, the limiting behavior of the ODE depends on the initial density. However, this is not the expected behavior for the particle system, and in this case the outcome of competition is dictated by the behavior of the PDE. The reason is that even if the initial distribution is translation invariant and hence has a well-defined density, there will be regions of space where the density of 1's is close to 1 and others where it is close to 0. To explain this, we consider an example:

Example 2.1. Sexual reproduction. Durrett-Neuhauser (1994).

The flip rates are as follows:

- $1 \to 0$ at rate 1
- $0 \to 1$ at rate $\beta k(k-1)/n(n-1)$ if k of the n neighboring sites are occupied.

In words, at rate β, a vacant site picks two of its neighbors at random and become occupied if they both are.

The mean-field equation is:

$$(5) \qquad \frac{du}{dt} = -u + \beta u^2(1-u) = u(-1 + \beta u(1-u))$$

Remembering that $u(1-u)$ is maximized at $1/2$, where the value is $1/4$, we see that there are nontrivial fixed points $\rho_1 < \rho_2$ if and only if $\beta > 4$, while if $\beta = 4$, $1/2$ is a double root.

At this point one might think that in the presence of fast stirring, $\beta_c \approx 4$ but that is not correct. To determine the asymptotics of the critical value you have to consider the mean-field PDE:

$$\frac{\partial u}{\partial t} = \Delta u + g(u)$$

where $g(u) = u(-1 + \beta u(1-u))$.

A solution of the form $u(t,x) = w(x-ct)$ with $w(-\infty) = \rho_2$ and $w(+\infty) = 0$ is called a traveling wave. In order to be a solution w must satisfy

$$-cw' = w'' + g(w)$$

Multiplying by w' and integrating from $-\infty$ to ∞

$$-c \int (w')^2 dx = \int w'' w' dx + \int g(w) w' dx$$

The first antiderivative on the right is $(w')^2/2$ which vanishes at $-\infty$ and ∞. Changing variables $y = w(x)$ in the second we have

$$c \int (w')^2 dx = \int_0^{\rho_2} g(y)\, dy$$

Thus the sign of $c =$ the sign of $\int_0^{\rho_2} g(u)\, du$. When $\beta = 4.5$, the cubic has roots at $2/3$, $1/3$, and 0 and symmetry dictates that $\int_0^{\rho_2} g(y)\, dy = 0$. Thus $c > 0$ if and only if $\beta > 4.5$.

THEOREM 7. *If we introduce fast stirring at rate ϵ^{-2} then in the sexual reproduction model, $\beta_c \to 4.5$ as $\epsilon \to 0$.*

SKETCH OF PROOF. The key is the PDE fact that if the initial condition is $u(0, x) \geq \rho_1 + \epsilon$ for $|x| \leq L$ and L is large enough then $u(t, x) \approx \rho_2$ for $|x| \leq (c - \delta)t$. Combining this with the convergence of the particle system with fast stirring to the PDE, we have the "one pile makes two piles with high probability" needed for the block construction. □

Example 2.2. Catalyst

Moving away from ecology, our next system is a model for the catalytic converter in a car's exhaust system. States are $0 =$ vacant, $1 = CO$ (carbon monoxide attached to the surface), $2 = O$ (single oxygen atom attached to the surface). The rates are as follows:

- $0 \to 1$ at rate p.
- A pair of neighboring 0's $\to 22$ at rate $q/4$.
- Adjacent $12 \to 00$ at rate $r/4$ (reaction to form CO_2).

In this model all 1's and all 2's are absorbing states corresponding to poisoning of the catalyst surface. In order for the catalytic converter to work and turn CO into CO_2 there must be coexistence in the spatial model. Ziff, Gulari and Barshad (1986) considered the case in which $r = \infty$ and $q/2 = 1 - p$ (the latter condition can be imposed by scaling time). Their simulations shows coexistence for $0.389 \leq p \leq 0.525$.

Since 1's land at rate p and two 2's land at rate $\leq q = 2(1 - p)$, it seems clear that the system converges to all 1's when $p \geq q$. There is a simple argument, see Theorem 1 in Durrett and Swindle (1992), which shows that

if $p \geq q$ then $P(\xi_t(x) = 0) \to 0$ and if x and y are neighbors, $P(\xi_t(x) = 1, \xi_t(y) = 2) \to 0$, so

$$P(\xi_t(x) \equiv 1 \text{ on } [-K, K]^2) + P(\xi_t(x) \equiv 2 \text{ on } [-K, K]^2) \to 1$$

but we do not know how to prove that if we start from the $\equiv 0$ configuration, the system converges to all 1's. It is not hard to show, see Theorem 2 in Durrett and Swindle (1992), that the system converges to all 2's for small p. However, it is much more interesting to

Problem 3. Prove coexistence for $p \in (p_1, p_2)$.
Simulations suggest that the density of O atoms in equilibrium drops to 0 discontinuously at the upper critical value.

Bramson and Neuhauser (1992) have proved coexistence when the O_2's are replaced by an $N \times N$ polymer. Durrett and Swindle (1994) proved coexistence in the original model by introducing fast stirring. The mean-field PDE is:

$$(6) \qquad \begin{aligned} \frac{\partial u_1}{\partial t} &= \Delta u_1 + p(1 - u_1 - u_2) - r u_1 u_2 \\ \frac{\partial u_2}{\partial t} &= \Delta u_2 + q(1 - u_1 - u_2)^2 - r u_1 u_2 \end{aligned}$$

If $p < q$, ODE has four fixed points: two stable $(1, 0)$ and (α, β) and two unstable: $(0, 1)$ and (β, α), where

$$\alpha < \beta = \frac{(q - p) \pm \sqrt{(q - p)^2 - 4qp^2/r}}{2q}$$

The PDE results which were routine for the sexual reproduction model are now difficult. To prove the existence of a traveling wave with $u(-\infty) = (\alpha, \beta)$ and $u(\infty) = (1, 0)$ one goes to the four dimensional phase plane: (u_1, u_1', u_2, u_2'), and looks for a curve connecting $(\alpha, 0, \beta, 0)$ and $(1, 0, 0, 0)$ which will exist only for one value of the speed c. Fortunately this was done previously by Volpert and Volpert (1988). With the existence of a traveling wave established the next step is to prove a convergence theorem for PDE, which can be done with comparison techniques because of monotonicity property of system $(u_1, -u_2)$. Once the PDE result is established the rest is a routine application of the block construction.

Example 2.3. Colicin

Durrett and Levin (1997) considered a competition between two types of *E. coli*, one of which produces colicin (a chemical that kills other E. coli):
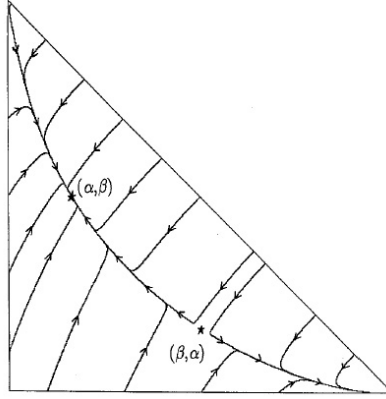
FIG 5. *Mean-field ODE for the catalyst*

| birth	rate	death	rate
$0 \to 1$	$\beta_1 f_1$	$1 \to 0$	δ_1
$0 \to 2$	$\beta_2 f_2$	$2 \to 0$	$\delta_2 + \gamma f_1$

Here the rates are like the two-species contact process, except for the γf_1 in the death rate $2 \to 0$, which comes from 1's killing 2's with colicin. For simplicity we suppose that the basic death rates are equal $\delta_1 = \delta_2 = 1$. Having done this it is natural to suppose that $\beta_1 < \beta_2$, for otherwise it is clear that the 1's will out compete the 2's.

A little algebra shows that when

$$\delta_i < \beta_i \quad \frac{\delta_2}{\beta_2} < \frac{\delta_1}{\beta_1} < \frac{\delta_2 + \gamma}{\beta_2 + \gamma}$$

the mean-field ODE has an interior fixed point but it is unstable. Figure 6 shows the situation when $\beta_1 = 3$, $\gamma_1 = 2.5$ and $\beta_2 = 4$.

Figure 7 gives the density versus time in the system on a 200×200 grid. To emphasize that the behavior is different from the ODE, we start the gray colicin producer (1's) at a small density. By time 1000 it has eliminated the black colicin sensitive strain (2's). The other panel shows the state at time 600. Note that the two types have segregated. A movie would show that the interface moves in a direction that favors the 1's. It would be interesting to show that if one started the model in one dimension with 1's on one half line and 2's on the other then a well-defined interface existed and had a speed which predicts who wins the competition.
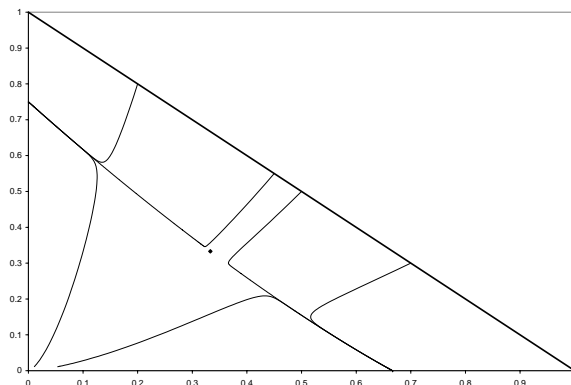
FIG 6. *Colicin mean field ODE*
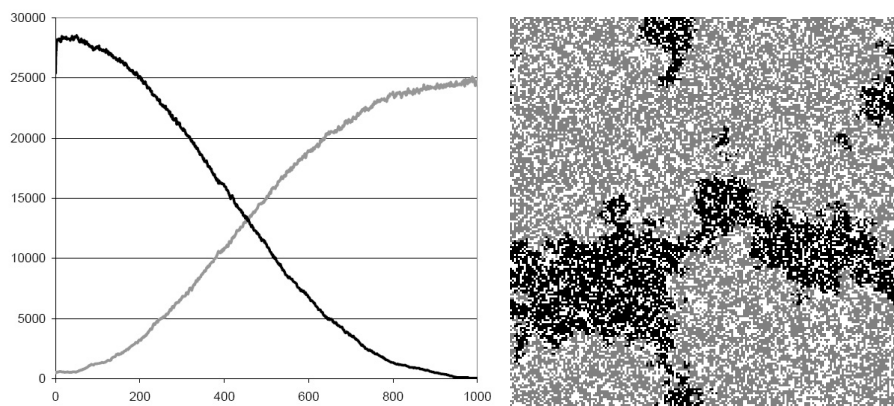
FIG 7. *Simulation of colicin model*

Problem 4. Show that coexistence is not possible in the colicin model when $\beta_1 < \beta_2$ and $\delta_1 = \delta_2 = 1$.

Case 3. Cyclic systems, Periodic orbits

In this case, we see coexistence with significant spatial structure. The pictures are pretty but the problems are hard.

Example 3.1. Multitype biased voter model.

Each site can be in state 1, 2, ... k, and $j \to i$ at rate $f_i \lambda_{ij}$. In words, i's

eat j's at rate λ_{ij}. The mean field ODE is

$$\frac{du_i}{dt} = u_i \sum_j (\lambda_{ij} - \lambda_{ji}) u_j$$

Silvertown et al. (1992) who were interested in the competition of grass species, studied the five species case in which

$$\lambda_{ij} = \begin{pmatrix} 0 & 0.09 & 0.32 & 0.23 & 0.37 \\ 0.08 & 0 & 0.16 & 0.06 & 0.09 \\ 0.06 & 0.06 & 0 & 0.44 & 0.11 \\ 0.02 & 0.06 & 0.05 & 0 & 0.03 \\ 0.02 & 0.03 & 0.05 & 0.03 & 0 \end{pmatrix}$$

This example is not very interesting because $\lambda_{1j} > \lambda_{j1}$ for $2 \le j \le 5$, so using ideas of Grannan and Swindle (1991) and their improvement by Mountford and Sudbury (1992) one can show that if A_t^1 is the event 1's are alive at time t then

$$P(A_t^1, \xi_t(x) \ne 1) \to 0$$

so if the 1's don't die out they take over the system. The key to the proof is that if θ is small

$$Z_t = \sum_{z:\xi_t(x)=1} e^{-\theta|z|} \quad \text{is a submartingale.}$$
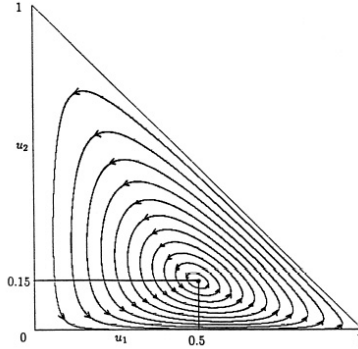

FIG 8. *Cyclic particle system with $\beta_1 = 0.3$, $\beta_2 = 0.7$, $\beta_3 = 1.0$*

Durrett and Levin (1998) studied the cyclic case in which $\lambda_{13} = \beta_3$, $\lambda_{21} = \beta_2$, $\lambda_{32} = \beta_3$, and the other $\lambda_{ij} = 0$. This system with $\beta_i = 1$ and the corresponding discrete time deterministic cellular automata had

been studied earlier by Bramson and Griffeath (1989), Fisch, Gravner, and Griffeath (1991), and Durrett and Griffeath (1993). The mean-field ODE has equilibrium:

$$\rho_i = \beta_{i-1}/(\beta_1 + \beta_2 + \beta_3)$$

where $i - 1$ is computed modulo 3 with the result in $\{1, 2, 3\}$. Around this fixed point are concentric periodic orbits. To prove mathematically that this occurs, write $H(u) = \sum_i \rho_i \log u_1$ and check that $H(u)$ is constant along solutions of the ODE.

Problem 5. Show that coexistence occurs in the cyclic case of Silvertown's model.
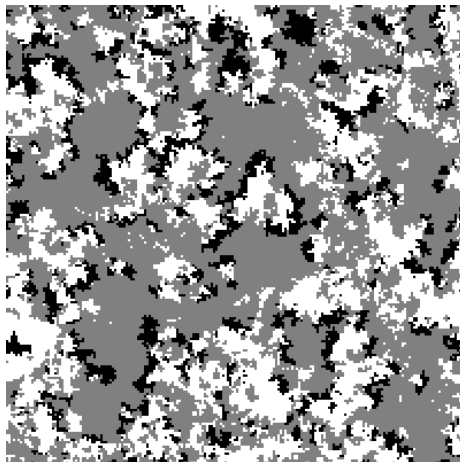
Figure 9 gives a proof by simulation.

FIG 9. *Simulation of cyclic particle system with $\beta_1 = 0.3$, $\beta_2 = 0.7$, $\beta_3 = 1.0$*

May and Leonard (1975) studied a related model. Let $\alpha < 1$ and $\alpha + \beta > 1$. If we let $u = u_1 + u_2 + u_3$ the ODE is

$$\frac{du_1}{dt} = u_1(1 - u) - (\alpha - 1)u_1 u_2 - (\beta - 1)u_1 u_3$$

$$\frac{du_2}{dt} = u_2(1 - u) - (\alpha - 1)u_2 u_3 - (\beta - 1)u_2 u_1$$

$$\frac{du_3}{dt} = u_3(1 - u) - (\alpha - 1)u_3 u_1 - (\beta - 1)u_3 u_2$$

The solutions to the ODE spiral out toward the boundary, and the system cycles from being composed almost wholly of population 1, to almost wholly 2, to almost wholly 3, and then back to 1.

To define the corresponding particle system we say write $1 < 2 < 3 < 1$ and read $1 < 2$ as 2 outcompetes 1.

- Vacant sites become occupied by type i at rate f_i
- An occupied site x at rate $\beta - 1$ attacks a randomly chosen neighboring site y.
- If y is occupied by the type that x can outcompete the individual at y is killed, and a new individual of the type at x is born with probability $(1 - \alpha)/(\beta - 1)$

Example 3.2. Three species colicin.

Durrett and Levin (1997) considered an E. coli competition model with rates

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

Here, 1's and 2's are colicin producers, while 3 is colicin sensitive. In the two species system (we conjecture) there is no coexistence, but as we will see coexistence is possible with three species.

Consider for concreteness, the situation when $\delta_i = 1$, $\beta_1 = 3$, $\beta_2 = 3.2$, $\beta_3 = 4.0$, $\gamma_1 = 3$, and $\gamma_2 = 0.5$. In this case the 2's beat the ones since they have a larger birth rate, the 3's beat the 2's since the colicin they make is not nasty enough, while the 1's beat the 3's.

Thus again the three competitors have the same relationship as in the child's game paper-rock-scissors. Such systems exist in nature. In the side-blotched lizard (*Uta stansburiana*), males have one of three throat colors, each one declaring a particular strategy. Dominant, orange-throated males establish large territories within which live several females. But these territories are vulnerable to infiltration by males with yellow-striped throats – known as sneakers – who mimic the markings and behavior of receptive females. The orange males can't successfully defend all their females against these disguised interlopers, who cluster on the fringes of the territories held by the orange lizards.

However, a large population of sneakers, which have no territory of their own to defend, can be quickly overrun by blue-throated males, who defend territories large enough to hold just one female. Sneakers have no chance against a vigilant, blue-throated guard. But once the sneakers become rare, powerful orange males flourish, grabbing territory and females from the blue

lizards. Now, the blue males lose out. See Sinervo and Lively (1996) for more on this example.

Figure 10 gives a picture of the mean-field ODE for the three-species colicin model as we look down into the tetrahedron $u_i \geq 0$, $u_1 + u_2 + u_3 \leq 1$. On the $(u_1, 0, u_3)$ and $(0, u_2, u_3)$ faces we see the colicin ODE, while on the $(u_1, u_2, 0)$ face we have the competing contact process.
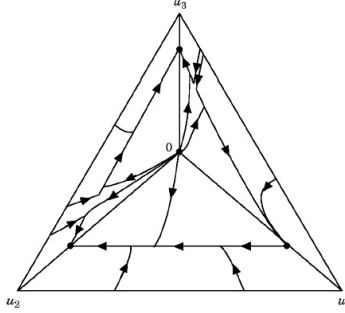

FIG 10. *Three species colicin mean-field ODE*

Figure 11 gives a simulation. The graph gives the densities on a 200×200 grid, while the picture gives a snapshot of part of the system at the final time. Coexistence has been verified experimentally by Kirkup and Riley (2004). They began with a sensitive strain (S) of E. coli, introduced colicin plasmids to make a colicin-producing strain (C), and exposed the sensitive strain to the colicin-producer to obtain a resistant strain (R). A number of unlucky mice were then chosen to have the competition drama play out in their colons. After reading the paper, I think I will stick to computer simulations. In four cases, the experiment had to be discontinued because the mice were fighting or several mice died.

Problem 6. Prove mathematically that coexistence can occur.

Example 3.3. Spatial Prisoner's Dilemma: Durrett-Levin (1994).

This time we allow multiple hawks $\eta_t(x)$ and doves $\zeta_t(x)$ at each site.

- *Migration.* Each individual at rate ν migrates to a nearest neighbor.
- *Death due to crowding.* Each individual at x dies at rate $\kappa(\eta_t(x) + \zeta_t(x))$.
- *Game step.* Let $p_t(x)$ be the fraction of hawks in the 5×5 square centered at x. Hawks give birth (or death) at rate $ap_t(x) + b(1 - p_t(x))$, doves at rate $cp_t(x) + d(1 - p_t(x))$.
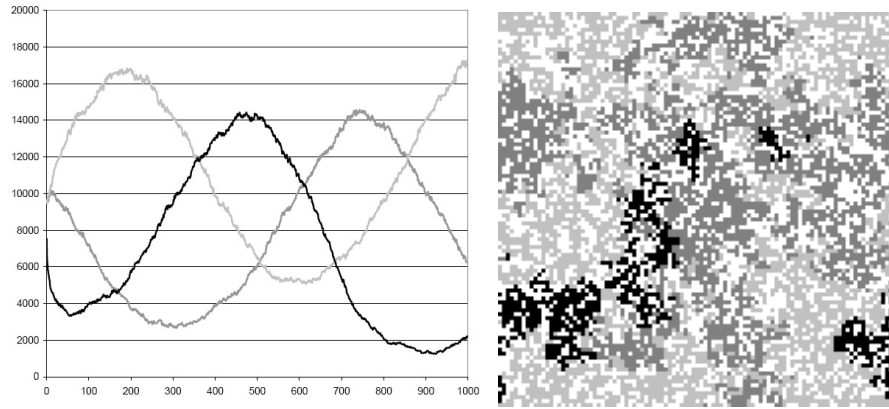
Fig 11. *Three species colicin simulation*

An interesting choice for the game matrix is a Prisoner's Dilemma

$$
\begin{array}{ccc}
 & H & D \\
H & a = -0.6 & b = 0.9 \\
D & c = -0.9 & d = 0.7
\end{array}
$$

The H strategy dominates D, so it is the better choice, but the payoff for (D, D) is better than that for (H, H). This is the Prisoner's Dilemma "paradox." If everyone played D then the world would be a nice place, but this leads to the temptation to play H and increase your payoff.
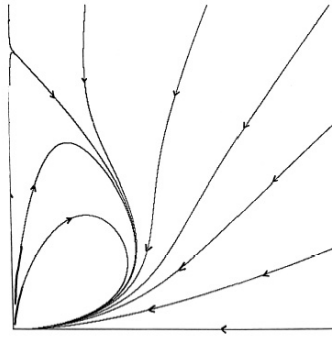
Fig 12. *Hawks-Doves ODE*

In a homogeneously mixing population the densities of Hawks and Doves

would evolve according to

$$(7) \qquad \begin{aligned} \frac{du}{dt} &= u\left\{a\frac{u}{u+v} + b\frac{v}{u+v} - \kappa(u+v)\right\} \\ \frac{dv}{dt} &= u\left\{a\frac{u}{u+v} + b\frac{v}{u+v} - \kappa(u+v)\right\} \end{aligned}$$

In the concrete example under consideration, we have the following behavior. On the vertical axis one can see that in the absence of Hawks, Doves reach an equilibrium. However, when both are present, the ratio of Hawks to Doves increases until the population crashes to 0.

Simulations suggest that in the spatial model Hawks and Doves can coexist. Intuitively this occurs because the dynamics of the ODE happen locally, but when the Hawk population crashes to 0 then there are some Doves left behind to recolonize space, but when the Doves grow to a significant density then the remaining Hawks again take over.

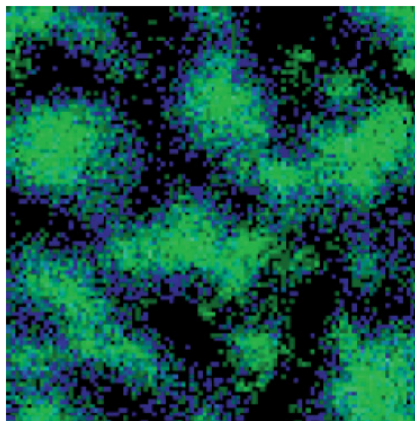**Problem 7.** Prove that the hawks and doves can coexist.

FIG 13. *Hawks-Doves simulation*

Example 3.4. Deterministic spatial games.

The Hawks-Doves model is complicated because each site is in a state (m, n) where m is the number of Hawks and n is the number of Doves. Nowak and May (1992) introduced a much simpler discrete time model in which each site is occupied by a cooperator or a defector. The payoff's to the first player

in the game are

$$
\begin{array}{ccc}
 & C & D \\
C & a & c \\
D & b & d
\end{array}
$$

To evolve the spatial model in discrete time, we calculate for each site the total payoff when the game is played with its eight neighbors. The cell is taken over by the type in the 3×3 square that has the highest payoff. The discrete time model is said to have synchronous updating because all sites are changed at once. One can also consider the continuous time case or asynchronous updating, where repeatedly a site is chosen at random and the rule is applied.

Nowak and May (1992) mostly consider the case $d = 1$, $c > 1$, $a = b = 0$. Since the possible values for a cooperator are $1 \leq j \leq 8$ and for a defector are jb where $1 \leq j \leq 8$, then for $b < 2$ the behavior changes at

$$8/7,\ 7/6,\ 6/5,\ 5/4,\ 8/6,\ 7/5,\ 3/2,\ 8/5,\ 5/3,\ 7/4,\ 9/5.$$

The most interesting pictures occur when $1.75 < b < 1.8$.

Problem 8. Prove coexistence results for the deterministic version in discrete or continuous time (asynchronous updating).

For more on this model see Nowak, Bonhoeffer, and May (1994) and references therein.

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523 Malott Hall, Ithaca , NY 14853 E-mail: rtd1@cornell.edu