Wald Lecture 3
Coexistence in Stochastic Spatial Models

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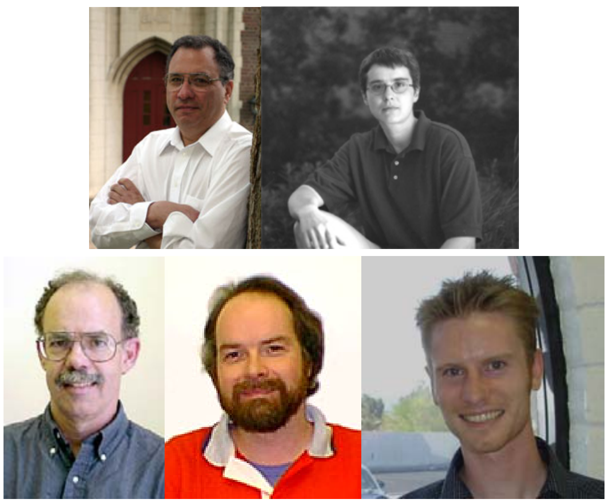
The plan

In this talk I will review 20 years of work on

Q. When is there coexistence in stochastic spatial models?

The answer, announced in Durrett and Levin (1994), is that this can be determined by the properties of the mean-field ODE. (We will explain this later.)

There are a number of rigorous results in support of this picture, but we will state 8 open problems. Solve one before the next WCPS and win a trip to Ithaca and a $1000 honorarium.



Two type contact process

- 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.
- 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.

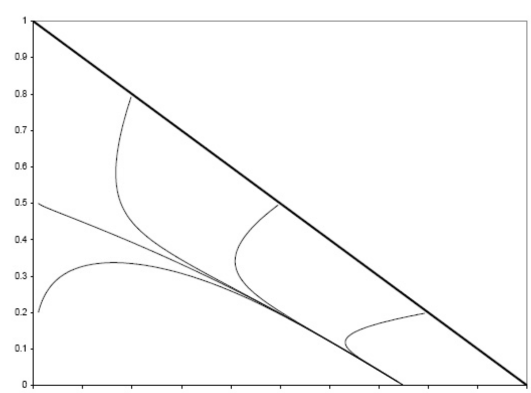
Mean field ODE

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

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

$du_i/dt = 0$ when $(1 - u_1 - u_2) = \delta_i/\beta_i$, so null clines are parallel.

$\beta_1 = 4,\ \delta_1 = 1.\ \beta_2 = 2,\ \delta_2 = 1$

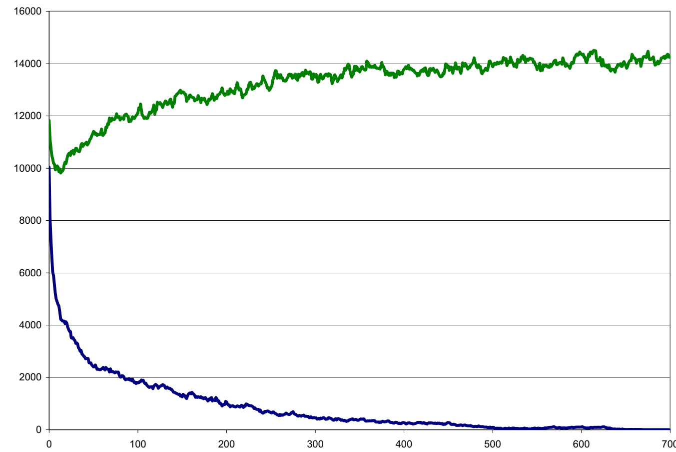


Neuhauser (1992)

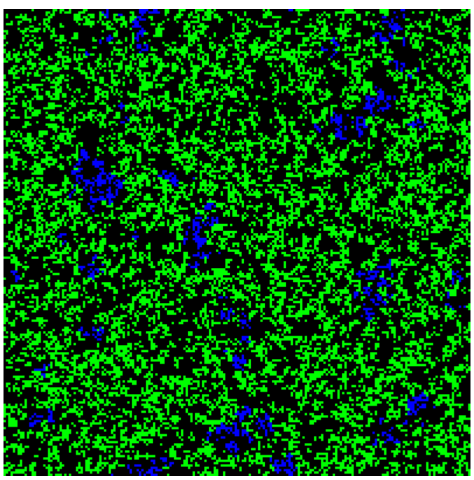
Theorem. *If the dispersal distributions are the same for the two species, $\delta_1 = \delta_2$, and $\beta_1 > \beta_2$ then species 1 out competes species 2. That is, if the initial condition is translation invariant and has $P(\xi_0(x) = 1) > 0$ then $P(\xi_t(x) = 2) \to 0$.*

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

Blue: $\beta_1 = 3.9$, $\delta_1 = 2$. Green: $\beta_2 = 2.0$, $\delta_1 = 1.0$



State at time 300



Competitive Exclusion Principle, Levin (1970)

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

z_i are resources. In previous model $z_1 = 1 - u_1 - u_2$ free space.

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

Proof. Linearize around the fixed point. $n > m$ implies there is a zero eigenvalue.

In words, coexisting species $\le$ resources.

Case 1: Attracting Fixed Point

Coexistence in the spatial model,
i.e., there is a nontrivial stationary distribution

Boring pictures, easy theorems

Durrett and Swindle (1991): Grass Bushes Trees

- Each site in $\mathbb{Z}^2$ can be in state $0 =$ grass, $1 =$ bush, $2 =$ tree. Biologists call this a successional seqeunce.
- Particles of type i die at rate δ_i, give birth at rate β_i.
- A particle of 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.

Mean field ODE

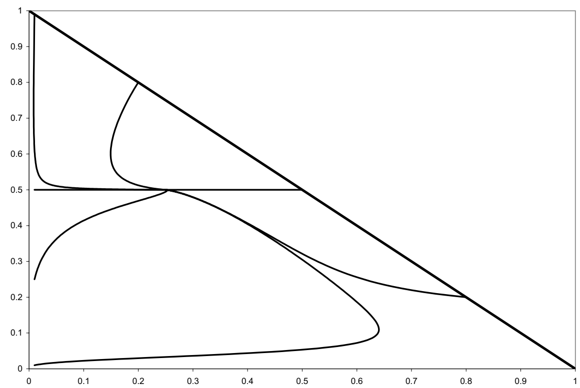
$$\frac{du_1}{dt} = \beta_1 u_1(1-u_1-u_2) - \delta_1 u_1 - \beta_2 u_2 u_1$$
$$\frac{du_2}{dt} = \beta_2 u_2(1-u_1) - \delta_2 u_2$$

If $\beta_2 > \delta_2$, $u_1^* = (\beta_2 - \delta_2)/\beta_2$.
If the 1's can invade 2's in equilibrium, that is,

$$\beta_1 \cdot \frac{\delta_2}{\beta_2} > \delta_1 + \beta_2 \cdot \frac{\beta_2 - \delta_2}{\beta_2}$$

then $u_1^* > 0$. When $\delta_1 = \delta_2 = 1$, we want $\beta_1 > \beta_2^2 > 1$.

$\beta_1 = 4,\ \delta_1 = 1,\ \beta_2 = 2,\ \delta_2 = 1$



Results for large range

For simplicity suppose $\delta_1 = \delta_2 = 1$.

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.*

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

Durrett and Moller (1991) *prove a complete convergence theorem. In particular, if the 1's and the 2's do not die out then the process converges to μ_{12}.*

A general result

fast stirring: for each pair of nearest neighbors x and y, at rate ϵ^{-2} exchange the values $\xi_t(x)$ and $\xi_t(y)$

Theorem. *Suppose there is a convex function ϕ that decreases along solutions of the mean-field ODE, and $\to \infty$ when $\min_i u_i \to 0$. Then there is coexistence in the model with fast stirring.*

Durrett (2002) *Mutual invadability implies coexistence.*
Memoirs of the AMS, 740 (118 pages)

epidemics, predator-prey models, predator mediated coexistence, etc.

Sketch of Proof

1. Lyapunov function implies that for solutions of the PDE

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

$\min_i u_i(t,x) \ge \epsilon$ for $t \ge T$, $|x| \le ct$.

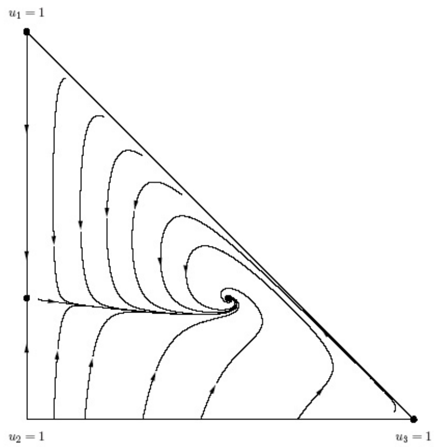
2. Particle system on $\epsilon\mathbb{Z}^d$ converges to PDE
3. Comparison with oriented percolation "block construction"

Host-pathogen models

It is known that predation can cause two competing species to coexistence. Durrett and Lanchier (2007) 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

$1 \to 2$	αf_2
$2 \to 1$	$\gamma_2(f_1 + f_2)$
$3 \to 1$	$\gamma_3(f_1 + f_2)$
$1 \to 3$	$\gamma_1 f_3$
$2 \to 3$	$\gamma_2 f_3$

Host-pathogen ODE



Theorem. *Suppose* $\gamma_1 < \gamma_3 < \gamma_2 < \alpha$ *and*

$$\gamma_1 \frac{\gamma_2}{\alpha} + \gamma_2 \left(1 - \frac{\gamma_2}{\alpha}\right) > \gamma_3$$

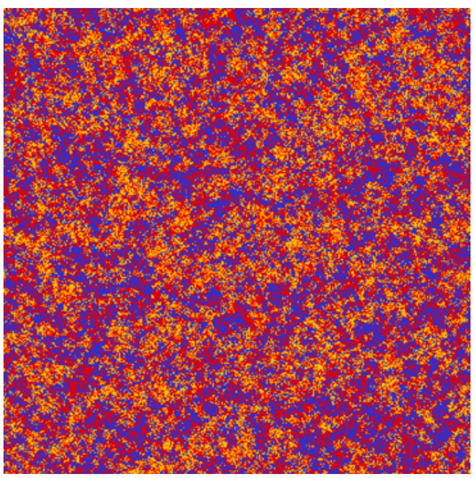
then there is coexistence for large range.

The displayed condition says that the 3's can invade the 1's and 2's in equilibrium.

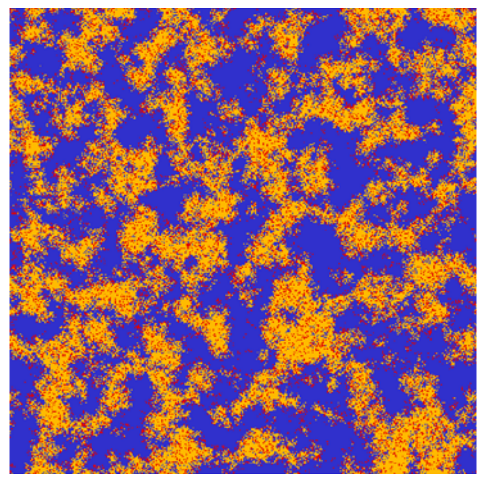
Problem 2. *Coexistence is not possible if* $\gamma_2 < \gamma_3 < \gamma_1$, *(mutualist).*

Once the invasion of the 3's starts the fraction of 2's gets smaller, and the 3's have an even bigger advantage.

Coexistence: 1= red, 2 = yellow, 3 = blue



No coexistence: 1= red, 2 = yellow, 3 = blue



Case 2: Two locally attracting fixed points

Outcome of competition is dictated
by sign of speed of traveling wave

Fast stirring results are available
IF you can handle the PDE

Sexual reproduction: Durrett-Neuhauser (1994)

$1 \to 0$ at rate 1

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

Mean field equation:

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

There are nontrivial fixed points $\rho_1 < \rho_2$ if and only if $\beta > 4$.
If $\beta = 4$, $1/2$ is a double root.

Let $\phi(u) = u(-1 + \beta u(1-u))$ and consider the PDE:

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

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.

sign of c = the sign of $\int_0^{\rho_2} \phi(u)\,du$ so $c > 0$ if and only if $\beta > 4.5$.

Theorem. *Introduce fast stirring: exchange the values at nearest neighbor sites at rate* ϵ^{-2}. *Then* $\beta_c \to 4.5$ *as* $\epsilon \to 0$.

Catalyst

States are 0 = vacant, $1 = CO$ (carbon monoxide), 2 = oxygen atom.

$0 \to 1$ 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).

Ziff et al. (1986) $r = \infty$, $q/2 = 1 - p$

Simulation shows coexistence for $0.389 \le p \le 0.525$. Otherwise converges to all 1's or all 2's.

Problem 3. Prove coexistence for $p \in (p_1, p_2)$.

Durrett and Swindle (1994)

Prove coexistence by introducing fast stirring. Mean-field PDE is:

$$\frac{\partial u_1}{\partial t} = \Delta u_1 + p(1 - u_1 - u_2) - r u_1 u_2$$
$$\frac{\partial u_2}{\partial t} = \Delta u_2 + q(1 - u_1 - u_2)^2 - r u_1 u_2$$

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

Existence of traveling wave requires finding a curve between two points in four dimensional space (u_1, u_1', u_2, u_2') using the Conley index theorem

Convergence theorem for PDE uses a monotonicty property of system $(u_1, -u_2)$.

Colicin

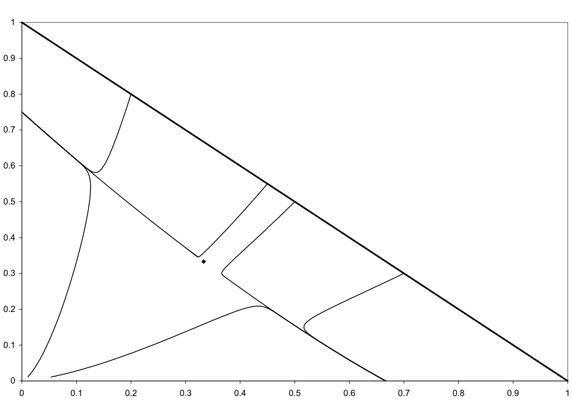
Durrett and Levin (1997) considered a competition between two types of *E. coli*, one of which produces colicin

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

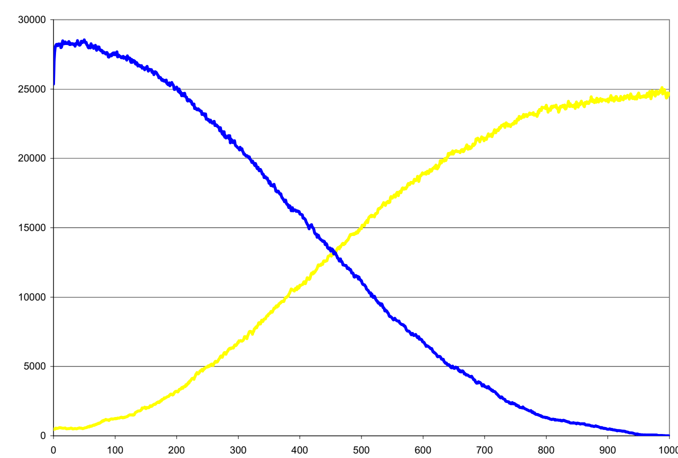
1's is a colicin producer, while 2 is colicin sensitive.

Suppose $\delta_1 = \delta_2 = 1$ and $\beta_1 < \beta_2$

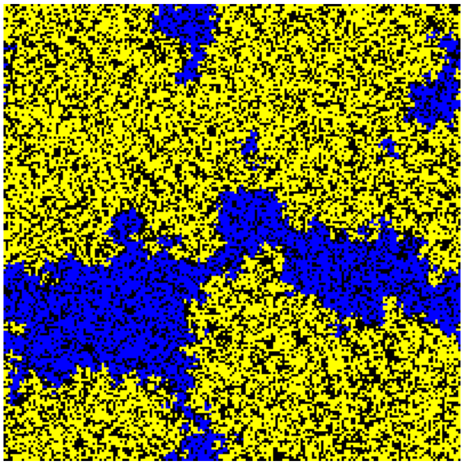
Mean-field ODE. Prove 4: no coexistence



(yellow producer $\beta_1 = 3$, $\gamma = 2.5$), $\beta_2 = 4$, $\delta_i = 1$



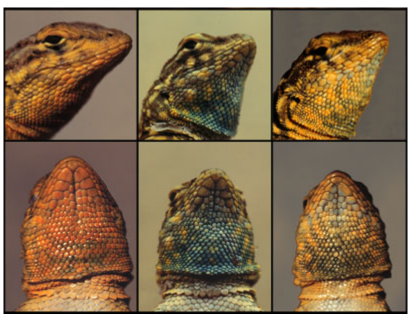
Time 600



Case 3 : Cyclic systems, Periodic orbits

Coexistence with significant spatial structure

Pretty pictures, hard problems



The sneaker strategy of yellow-throated males beats
the ultra-dominant polygynous orange-throated males beats
the more monogamous mate guarding blues who beat the yellow sneakers.

Silvertown's (1992) multitype biased voter model

States 1, 2, $\ldots k$. $i \to j$ at rate $\lambda_{ij} f_j$

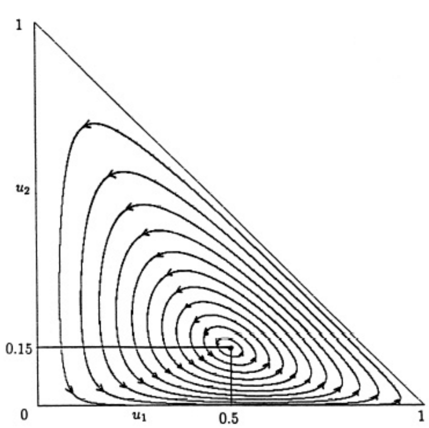
Durrett and Levin (1998) studied the cyclic case:
$\beta_1 = \lambda_{31}$, $\beta_2 = \lambda_{12}$, $\beta_3 = \lambda_{23}$

Mean field ODE: (arithmetic mod 3 in 1,2,3)

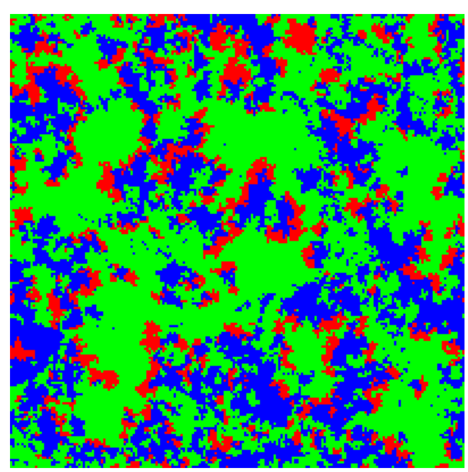
$$\frac{du_i}{dt} = u_i(\beta_i u_{i-1} - \beta_{i+1} u_{i+1})$$

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

$\beta_1 = 0.3$, $\beta_2 = 0.7$, $\beta_3 = 1.0$



Simulation. Problem 5: Prove coexistence.



Rock-Paper-Scissors

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

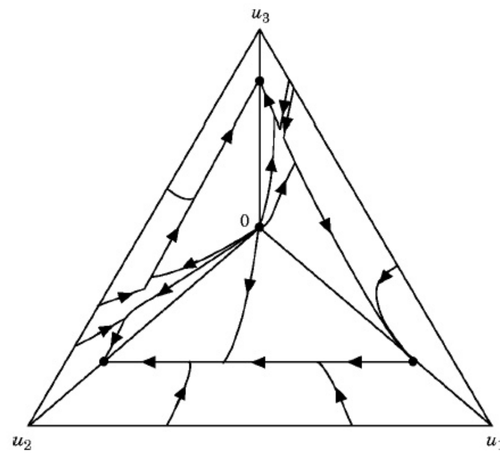
birth	rate	death	rate
$0 \to 1$	$\beta_1 f_1$	$1 \to 0$	δ_1
$0 \to 2$	$\beta_2 f_2$	$2 \to 0$	δ_2
$0 \to 3$	$\beta_3 f_3$	$3 \to 0$	$\delta_3 + \gamma_1 f_1 + \gamma_2 f_2$

1's and 2's are colicin producers, while 3 is colicin sensitive.

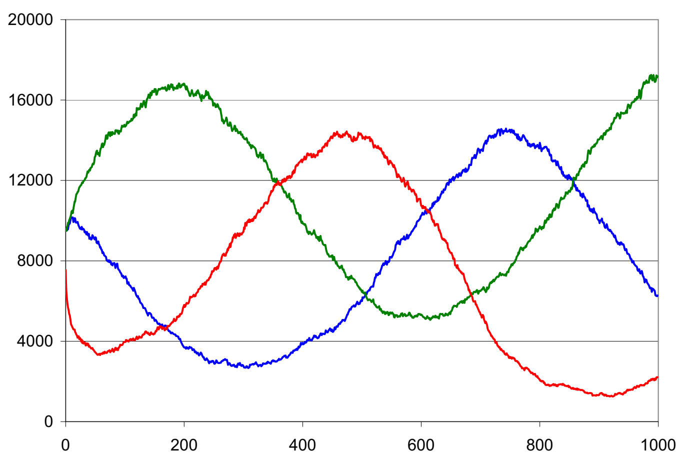
Coexistence was verified experimentally by Kirkup and Riley, Nature 2004.

Problem 6. Prove mathematically that coexistence can occur.

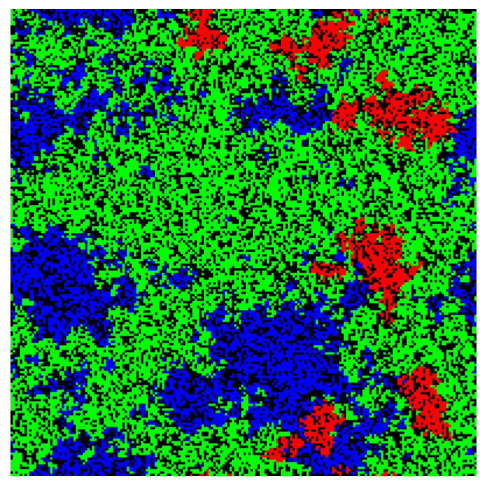
$\beta_1 = 3,\ \beta_2 = 3.2,\ \beta_3 = 4,\ \delta_i = 1,\ \gamma_1 = 3,\ \gamma_2 = 0.5$



$\beta_1 = 3,\ \beta_2 = 3.2,\ \beta_3 = 4,\ \delta_i = 1,\ \gamma_1 = 3,\ \gamma_2 = 0.5$



State at time 1000



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

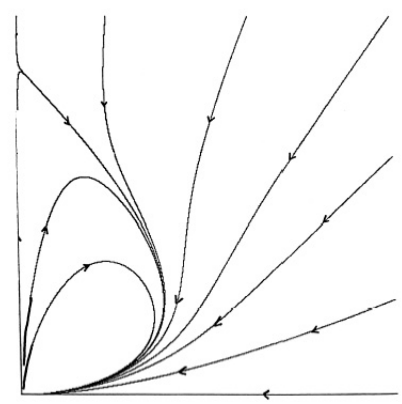
This time we allow multiple hawks $\eta_t(x)$ and doves $\zeta_t(x)$ at each site.

- *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 2×2 square centered at x. Hawks give birth (or death) at rate $ap_t(x) + b(1 - p_t(x))$, doves at rate $cp_t(x) + d(1 - p_t(x))$.

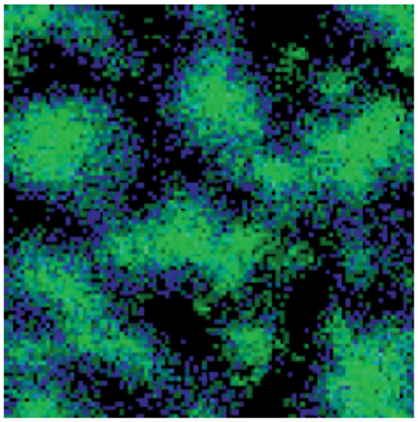
	H	D
H	$a = -0.6$	$b = 0.9$
D	$c = -0.9$	$d = 0.7$

The H strategy dominates D, but if there are only hawks then they die out.

Hawks-Doves ODE



Simulation. Problem 7: prove coexistence



Nowak and May (1992) Nature 359, 826–829

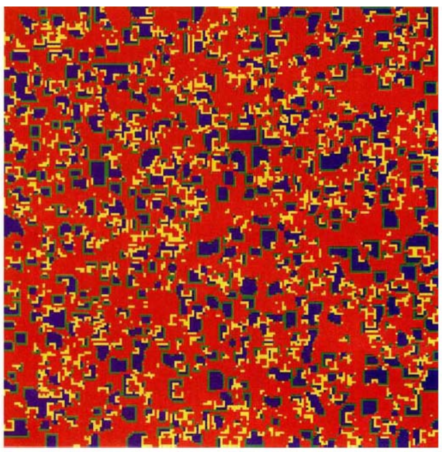
In these discrete time deterministic spatial game dynamics, each site is occupied by a cooperator or a defector. The payoff's to the first player in the game are

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

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.

They mostly consider the case $a = 1$, $c = 0$, $d = \epsilon$, very small.

$1.8 < b < 2$



$C \to C$ blue, $D \to D$ red, $D \to C$ green, $C \to D$ yellow

Since the possible values for a cooperator are $1 \le j \le 8$ and for a defector are jb where $1 \le j \le 8$, 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.

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

For the latter version see Nowak, Bonhoffer and May (1994) PNAS 91, 4877–4881