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 $0 = \text{vacant}$, 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 $\delta_i$, give birth at rate $\beta_i$.
- 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

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

$du_i/dt = 0$ when $(1 - u_1 - u_2) = \delta_i/\beta_i$, so null clines are parallel.
$\beta_1 = 4, \; \delta_1 = 1. \; \beta_2 = 2, \; \delta_2 = 1$
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

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

\(z_i\) 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 \(\leq\) 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 $0 = \text{grass}$, $1 = \text{bush}$, $2 = \text{tree}$. Biologists call this a successional sequence.
- Particles of type $i$ die at rate $\delta_i$, give birth at rate $\beta_i$.
- 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 \(\{x : 0 < \|x\| \leq L\}\) and $L$ is large, there is a stationary distribution $\mu_{12}$ 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 $\mu_{12}$. 
fast stirring: for each pair of nearest neighbors $x$ and $y$, at rate $\epsilon^{-2}$ exchange the values $\xi_t(x)$ and $\xi_t(y)$

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


epidemics, predator-prey models, predator mediated coexistence, etc.
Sketch of Proof

1. Lyapunov function implies that for solutions of the PDE

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

\[ \min_i u_i(t, x) \geq \epsilon \text{ for } t \geq T, \ |x| \leq ct. \]

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 coexist. 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 $\rightarrow$ 2 \quad \alpha f_2

2 $\rightarrow$ 1 \quad \gamma_2 (f_1 + f_2)

3 $\rightarrow$ 1 \quad \gamma_3 (f_1 + f_2)

1 $\rightarrow$ 3 \quad \gamma_1 f_3

2 $\rightarrow$ 3 \quad \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
1 → 0 at rate 1

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

**Theorem.** Introduce fast stirring: exchange the values at nearest neighbor sites at rate $\epsilon^{-2}$. Then $\beta_c \to 4.5$ as $\epsilon \to 0$. 
States are 0 = vacant, 1 = CO (carbon monoxide), 2 = oxygen atom.

0 → 1 at rate $p$.

A pair of neighboring 0’s → 22 at rate $q/4$.

Adjacent 12 → 00 at rate $r/4$ (reaction to form $CO_2$).

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

Simulation shows coexistence for $0.389 \leq p \leq 0.525$. 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:

\[
\frac{\partial u_1}{\partial t} = \Delta u_1 + p(1 - u_1 - u_2) - ru_1u_2
\]

\[
\frac{\partial u_2}{\partial t} = \Delta u_2 + q(1 - u_1 - u_2)^2 - ru_1u_2
\]

If \( p < q \), ODE has four fixed points: two stable \((1, 0)\) and \((\alpha, \beta)\) and two unstable: \((0, 1)\) and \((\beta, \alpha)\).

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 monotonicity property of system \((u_1, -u_2)\).
Durrett and Levin (1997) considered a competition between two types of *E. coli*, one of which produces colicin

<table>
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</thead>
<tbody>
<tr>
<td>0 → 1</td>
<td>$\beta_1 f_1$</td>
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</tr>
<tr>
<td>0 → 2</td>
<td>$\beta_2 f_2$</td>
<td>2 → 0</td>
<td>$\delta_2 + \gamma f_1$</td>
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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 \rightarrow 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.
Durrett and Levin (1997) considered an E. coli competition model with rates:

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<td>3 → 0</td>
<td>$\delta_3 + \gamma_1 f_1 + \gamma_2 f_2$</td>
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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 $\nu$ 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 $2 \times 2$ square centered at $x$. Hawks give birth (or death) at rate $ap_t(x) + b(1 - p_t(x))$, doves at rate $cp_t(x) + d(1 - p_t(x))$.

\[
\begin{array}{cccc}
 & H & D \\
H & a = -0.6 & b = 0.9 \\
D & c = -0.9 & d = 0.7 \\
\end{array}
\]

The $H$ strategy dominates $D$, but if there are only hawks then they die out.
Hawks-Doves ODE
Simulation. Problem 7: prove coexistence
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 $3 \times 3$ square that has the highest payoff.

They mostly consider the case $a = 1$, $c = 0$, $d = \epsilon$, very small.
$1.8 < b < 2$

$C \rightarrow C$ blue, $D \rightarrow D$ red, $D \rightarrow C$ green, $C \rightarrow D$ yellow
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 $8/7, 7/6, 6/5, 5/4, 8/6, 7/5, 3/2, 8/5, 5/3, 7/4, 9/5$.

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

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