Coexistence in Stochastic Spatial Models

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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 $i$.
- 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 vacant it changes to state $i$, otherwise nothing happens.
Mean field theory

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

\[
\begin{align*}
\frac{du_1}{dt} &= \beta_1 u_1 (1 - u_1 - u_2) - \delta_1 u_1 \\
\frac{du_2}{dt} &= \beta_2 u_2 (1 - u_1 - u_2) - \delta_2 u_2 \\
\end{align*}
\]

\( du_i/dt = 0 \) 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 $P(\xi_t(x) = 2) \to 0$.

**Conjecture.** The conclusion holds if the dispersal distributions are the same and $\beta_1/\delta_1 > \beta_2/\delta_2$. 
Competitive Exclusion Principle, Levin (1970)

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

\(z_i\) 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.
There is more diversity in nature than allowed by the competitive exclusion principle.
An example in which an inferior competitor $\beta_1/\delta_1 < \beta_2/\delta_2$ can coexist, because it is a better disperser and can colonize recently disturbed parts of the landscape. (Math imitates ecology.)

Models is a two type contact process in which:

- Particles of type $i$ die at rate $\delta_i$ and give birth at rate $\beta_i$.
- Dispersal kernel $p_1$ is a truncated powerlaw. $p_1(x) = c_1$ if $\|x\|_\infty = 1$, $c_2\|x\|_\infty^{-\rho}$ if $\|x\|_\infty \leq M$.
- Dispersal kernel $p_2$ has $p_2(x) = 1/8$ if $\|x\|_\infty = 1$, 0 otherwise.
- For each $x$, death to $\{y : \|x - y\|_\infty \leq F/2\}$ at rate $\delta_0$.

Deaths of the last type are due to “forest fires”.

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**Chan and Durrett (2006)**
Let $\lambda_c$ be the critical value of $\beta/\delta$ for the one type contact process with $p(x) = 1/8$ if $\|x\|_\infty = 1$, 0 otherwise.

**Theorem.** *Suppose that*

$$\frac{\beta_1}{\delta_1} > \lambda_c \quad \frac{\beta_2}{\delta_2} > (1 + \frac{\beta_1}{\delta_1}) \lambda_c$$

*We can choose $\delta_1$, $\delta_0$, $F$ and $M$ so that 1’s and 2’s coexist. That is there is a translation invariant stationary distribution which concentrates on configurations with infinitely many 1’s and 2’s.*

Two species can coexist because recently disturbed space is a second type of space.
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 → 2 $\alpha f_2$
2 → 1 $\gamma_2(f_1 + f_2)$
3 → 1 $\gamma_3(f_1 + f_2)$
1 → 3 $\gamma_1 f_3$
2 → 3 $\gamma_2 f_3$
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.

Conjecture. 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.
Host-pathogen ODE
Example with coexistence: 1 = red, 2 = yellow, 3 = blue
No coexistence: 1 = red, 2 = yellow, 3 = blue
Durrett and Levin (1997) considered an E. coli competition model with rates

\[
\begin{align*}
0 \rightarrow 1 & : \beta_1 f_1 \\
0 \rightarrow 2 & : \beta_2 f_2 \\
0 \rightarrow 3 & : \beta_3 f_3 \\
1 \rightarrow 0 & : \delta_1 \\
2 \rightarrow 0 & : \delta_2 \\
3 \rightarrow 0 & : \delta_3 + \gamma_1 f_1 + \gamma_2 f_2
\end{align*}
\]

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

Coexistence was verified experimentally by Kirkup and Riley, Nature 2004.
$\beta_1 = 3, \beta_2 = 3.2, \beta_3 = 4, \delta_i = 1, \gamma_1 = 3, \gamma_2 = 0.5$
\( \beta_1 = 3, \, \beta_2 = 3.2, \, \beta_3 = 4, \, \delta_i = 1, \, \gamma_1 = 3, \, \gamma_2 = 0.5 \)
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.
Theorem. *Any number of species can coexist on four resources.*

Part 1. Any number of species can coexist in a periodically changing environment.

Part 2. Smale (1976) has constructed a system of the type

\[ \frac{dx_i}{dt} = x_i f_i(x_1, x_2, x_3) \]

where almost all solution trajectories tend asymptotically to a single periodic orbit.
Two species contact process in which deaths occur at rate $\delta_i$ and births at rate $\beta_i(t)$ where

$$\beta_i(t) = \beta_{i1} \quad \text{for} \quad 2nD \leq t < (2n + 1)D$$

$$\beta_i(t) = \beta_{i2} \quad \text{for} \quad (2n + 1)D \leq t < (2n + 2)D$$

Contact process with two seasons.
Mean field calculation

One species by itself

\[ \frac{du_i}{dt} = \beta_i(t)u_i(1 - u_i) - \delta_i u_i \]

If \((\beta_{i1} + \beta_{i2})/2 > \delta_i\) then \(u_i(2nD + t) \to \bar{u}_i(t) > 0\).

**Theorem.** If \(\int_0^{2D} \beta_i(t)(1 - \bar{u}_{3-i}(t))\ dt > \delta_i\) for \(i = 1, 2\) then there is coexistence for large range.

One can state sufficient conditions in terms of the parameters and the densities \(\bar{u}_i(jD),\ i = 1, 2,\ j = 0, 1\).
Conjecture: 3 species can coexist in 2 season model

- Density of species 2 ($\beta_{21} = 1$ and $\beta_{22} = 3$)
- Density of species 1 ($\beta_{11} = 3$ and $\beta_{12} = 1$)
- Density of species 3 ($\beta_{31} = 2$ and $\beta_{32} = 2$)
Let $G_n$ be an $n$-vertex Bollobás-Chung small world. $i$ is adjacent to $i - 1$ and $i + 1 \pmod{n}$ and each $i$ has one long distance neighbor $\sigma(i)$ where $\sigma$ is a random pairing of $1, 2, \ldots, n$ ($n$ is even).

- State of each site is $0 = \text{vacant}$, $1 = \text{occupied}$.

- (Annual plants) At the end of the growing season, each occupied site has a Poisson mean $\beta > 1$ number of offspring (seeds) and sends them to locations chosen at random from the entire grid. A site receiving at least one seed is occupied by a plant at the beginning of the next growing season.

- (Epidemic) Each site becomes infected with probability $\epsilon_n \to 0$. The infection spreads to and kills all plants in the connected component of an infected plant in the graph.
Mean field equations

(Growth) Frequency of occupied sites $p \rightarrow f(p) = 1 - e^{-\beta p}$.

(Epidemic) Frequency

$$q \rightarrow g(q) = \begin{cases} q & \text{if } q \leq 1/2 \\ (1 - q)^{3}/q^2 & \text{if } q \geq 1/2 \end{cases}$$

Space looks locally like a tree in which each vertex has degree 3. Size of giant component can be computed using branching processes.

Let $a_0 = (\ln 2)/\beta$.

$$h(p) = g(f(p)) = \begin{cases} 1 - e^{-\beta p} & 0 \leq p \leq a_0 \\ \frac{e^{-3\beta p}}{(1 - e^{-\beta p})^2} & a_0 \leq p \leq 1 \end{cases}$$
Iterating $h(p)$
$h$ when $\beta = 2 \log 3$
$h^3$ when $\beta = 2 \log 3$.
Period three implies chaos. Li and Yorke (1975)
In some cases we have $|h'(x)| > 1$ for all $x$, so by Lasota and Yorke (1973) TAMS there is an absolutely continuous invariant measure.
These authors in a long term study demonstrate the existence of chaos in a food web isolated from the Baltic Sea which consists of bacteria, phytoplankton, herbivorous and predatory zooplankton, and detrivores.

“Our data show that chaotic fluctuations in species abundance may create temporal windows for more species to invade and survive in the system.”