Coexistence in locally regulated competing populations

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joint work with

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1. Introduction.

Classical (deterministic) model of two competing species: *Lotka Volterra* model

$N_1(t), N_2(t)$ total pop. size of species 1, 2, resp.

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - \alpha_{12}\frac{N_2}{K_1}\right),$$
$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - \alpha_{21}\frac{N_1}{K_2}\right),$$

r_i, K_i growth rates and carrying capacities, resp., α_{ij} determine the inter-specific competition.

Longterm coexistence?

Possible, if $K_1 > \alpha_{12}K_2, \quad K_2 > \alpha_{21}K_1.$

Drawbacks

no spatial structure, non-stochastic.

Chance matters
Stochastic logistic growth equation (single site):

$$dX_t = \Big[1 - X_t\Big] X_t \, dt + \sqrt{X_t} dB_t$$

hits zero after finite time! (compare to deterministic equation!)

Explicitly spatial and stochastic models?
Even in the single species case: Not obvious how to find appropriate stochastic models, usually difficult to treat them rigorously.

Most basic models are deficient
Galton-Watson process / Feller Diffusion / Branching Brownian motion / Super-Brownian motion:

die out / grow without bound / clump to arb. large extent

Way out: conditioning on total population size?

Kimura's (1953) *stepping stone model* forces the total population size to be constant at each site, but this does disguise important effects due to fluctuations in the population size

Role of space?

Population biologists:
Space facilitates coexistence ('competition-colonisation trade-off'). But: some recent results by Neuhauser/Pacala (1999) point in opposite direction.

A single species model

Spatial extension of the logistic growth model on the lattice $\mathbb{Z}^d$: for each site $i \in \mathbb{Z}^d$, let

$$dX_t(i) = \sum_j m_{ij}\Big[X_t(j) - X_t(i)\Big]dt + \alpha\left[M - \sum_j \lambda_{ij} X_t(j)\right] X_t(i)dt + \sqrt{X_t(i)}dB_t(i),$$

where

$\alpha > 0$	strength of local regulation,
$M > 0$	amount of resources at each site,
$\{m_{ij}\}$	finite range *migration* matrix,
$\{\lambda_{ij}\}$	finite range *interaction* matrix,
$\{B_t(i)\}$	independent Brownian motions.

Theorem (Etheridge 2003):

If the range of the migration $\geq$ range of interaction, and M large enough, then this system *survives* (without explosion) with positive probability (w.p.p.)

Question:

Is it possible (i.e. *with positive probability*) to obtain *coexistence for all times* in the case of *two competing* species?

2. Competing species model

Let $i \in \mathbb{Z}^d$. Species 1:

$$
\begin{aligned}
dX_t(i) = \sum_j m_{ij} \Big[X_t(j) - X_t(i) \Big] dt \\
+ \alpha \left[M - \sum_j \lambda_{ij} X_t(j) - \sum_j \gamma_{ij} Y_t(j) \right] X_t(i) dt \\
+ \sqrt{X_t(i)} dB_t(i),
\end{aligned}
$$

Species 2:

$$
\begin{aligned}
dY_t(i) = \sum_j m_{ij}^{'} \Big[Y_t(j) - Y_t(i) \Big] dt \\
+ \alpha^{'} \left[M^{'} - \sum_j \lambda_{ij}^{'} Y_t(j) - \sum_j \gamma_{ij}^{'} X_t(j) \right] Y_t(i) dt \\
+ \sqrt{Y_t(i)} dB_t^{'}(i).
\end{aligned}
$$

Here, let $\alpha, \alpha^{'}, M, M^{'} > 0$ and $\{m_{ij}\}, \{\lambda_{ij}\}$ be positive and of the *same finite range*, $\{\gamma_{ij}\}$ positive and of finite range (same holds for $\{m_{ij}^{'}\}, \{\lambda_{ij}^{'}\}, \{\gamma_{ij}^{'}\}$).

Theorem (B, Etheridge, Meredith (2004))

There exists a finite constant M_0, such that for each pair $M, M' > M_0 > 0$ there exists a pair $\gamma, \gamma' > 0$ and $\kappa^* > \kappa > 0$, such that if $\sum_j \gamma_{ij} < \gamma, \sum_j \gamma'_{ij} < \gamma'$, and

$$\kappa < X_i(0), Y_i(0) < \kappa^* \quad \text{for all } i \in \mathbb{Z}^d,$$

then

$$\mathbb{P}\left\{\forall_{t>0}\, \exists_{i,j\in\mathbb{Z}^d} \,:\, X_i(t), Y_j(t) > \kappa\right\} > 0.$$

Moreover,

$$\liminf_{t\uparrow\infty} \mathbb{P}\left\{X_0(t)Y_0(t) > \kappa^2\right\} > 0,$$

i.e. there is coexistence w.p.p.

Remarks

The fact that the range of migration must be at least as large as the range of intra-species interaction has already been suggested by Law, Murrell, Dieckmann (2003).

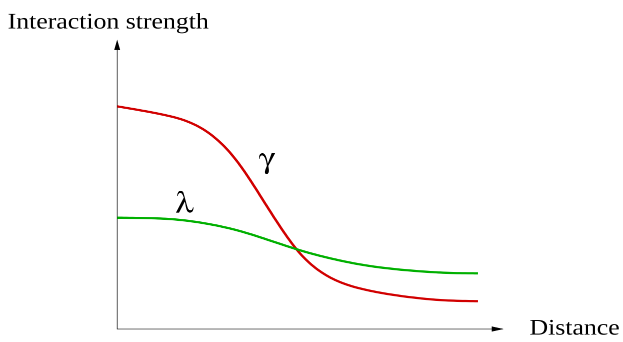
The fact we need them to be of the same range seems to be a technicality we would like to get rid of.

Murrell and Law (2003) suggest that coexistence in the competing species case should be possible under *'heteromyopia'*.

Heteromyopia

The name comes from the fact that the range over which individuals sense their competitors is shorter than the range over which they sense their con-specific neighbours.

More precisely, they use interaction *kernels*, where there is *heterozygous advantage* over large scales and *homozygous advantage* over short scales.



Conjecture

Our model admits coexistence under heteromyopia w.p.p., no coexistence under opposite effect possible.

Method of proof

First focus on X, evolving in a *random environment* (given by Y).

Find uniform bounds (in particular independent of X) of

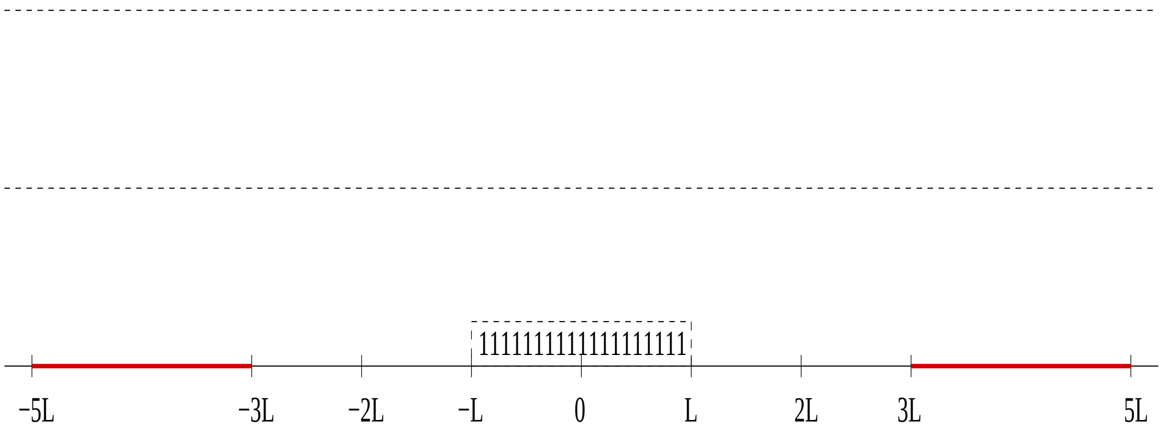
- the probability that the environment behaves badly at a given site i, i.e. takes large values and therefore kills lots of the X-population due to overcrowding,
- the speed at which the Y-population at an over-crowded site dies.

Compare the evolution of X to a *discrete time flip process* $\{\xi_i(n), i \in \mathbb{Z}^d, n \in \mathbb{Z}_+\}$ with values $\xi_i(n) \in \{0, 1\}$. At each site i, assume value 1 if the X-population at i is large; assume value 0 otherwise. Find bounds on the flip rates in the absence of nearby overcrowded sites.

Use a comparison to *(dependent) oriented percolation* to ensure that this flip process survives with probability greater than $1/2$.

Finally, use a symmetric argument for Y-population.

Comparison to oriented percolation



3. Duality

There is a useful duality between a related population model and *branching annihilating random walk*.

Recall that two stochastic processes $\{\eta_t\}, \{\zeta_t\}$ are *dual*, if there exists a function H, such that

$$\mathbb{E}_{\eta_0}\big[H(\eta_t, \zeta_0)\big] = \mathbb{E}_{\zeta_0}\big[H(\eta_0, \zeta_t)\big].$$

Branching annihilating random walk (BARW)

The Markov process $\{n_i(t), i \in \mathbb{Z}^d\}_{t \geq 0}$, in which $n_i(t) \in \mathbb{Z}_+$, with dynamics

$$
\begin{array}{lll}
\begin{cases} n_i \mapsto n_i - 1 \\ n_j \mapsto n_j + 1 \end{cases} & \text{at rate} & n_i m_{ij}, \\
n_i \mapsto n_i + 2 & \text{at rate} & s n_i, \\
n_i \mapsto n_i - 2 & \text{at rate} & \frac{1}{2} n_i (n_i - 1),
\end{array}
$$

is called a *branching annihilating random walk* with branching rate s.

N.B. Parity preservation!

A related population model

Let $p_i(t) \in [0,1]$ denote the proportion of the $X_i(t)$-population at site i. Fixing the total population size

$$X_i(t) + Y_i(t) = 1 \quad \text{for all } i, t,$$

we have

$$\begin{aligned} dp_i(t) = \sum_j m_{ij} \big[p_j(t) - p_i(t)\big]\, dt \\ + s p_i(t)\big[1 - p_i(t)\big]\big[1 - 2p_i(t)\big]\, dt \\ + \sqrt{p_i(t)\big[1 - p_i(t)\big]}\, dW_i(t). \end{aligned}$$

We are able to show that for s large enough there exists an $\varepsilon > 0$, such that

$$\mathbb{P}\big\{\forall t > 0 \ \exists\, i \in \mathbb{Z}^d : \varepsilon < p_i(t) < 1 - \varepsilon\big\} > 0,$$

and, moreover,

$$\liminf_{t\to\infty} \mathbb{P}\big\{\varepsilon < p_0(t) < 1 - \varepsilon\big\} > 0.$$

Now consider the process $x_i(t) = 1 - 2p_i(t)$. It turns out that we have the *moment duality*

$$\mathbb{E}\Big[\underline{x}(t)^{\underline{n}(0)}\Big] = \mathbb{E}\Big[\underline{x}(0)^{\underline{n}(t)}\Big].$$

From the *moment duality* and the fact that $p(t)$ *survives* (forcing $x_0(t)$ to stay inside $(-1, 1)$ w.p.p.), one can easily infer the following

Corollary

There exists an $s_0 \in [0, \infty)$, such that if $s > s_0$ the branching annihilating random walk with branching rate s, started from an even number of particles at time zero, will survive for all time w.p.p.

Conjecture

In dimension d=1, $s_0 > 0$, in dimension $d \geq 2$, $s_0 = 0$.

(based on results by Cardy/Täuber (1996), (1998)).