Learning Session
'Coexistence in competing species models'

moderated by Yu-Ting Chen & Matthias Hammer

Part II: Interacting diffusion models (Matthias Hammer)

Genealogies of Interacting Particle Systems
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BEM-Model II: A system of interacting diffusions

In [Blath-Etheridge-Meredith 2007], the authors consider the following model for the evolution of two competing populations on the lattice $\mathbb{Z}^d$, $d \in \mathbb{N}$:

$$\begin{aligned} dp_t(i) = & \sum_{j \in \mathbb{Z}^d} m_{ij} \left(p_t(j) - p_t(i) \right) dt \\ & + s\, p_t(i) \left(1 - p_t(i)\right) \left(1 - 2p_t(i)\right) dt \\ & + \sqrt{p_t(i)(1 - p_t(i))}\, dW_t(i), \qquad i \in \mathbb{Z}^d,\ t \geq 0, \end{aligned} \tag{1}$$

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for initial conditions $p_0(i) \in [0,1]$, $i \in \mathbb{Z}^d$.
Here $s \in \mathbb{R}$ selection parameter, $\{(W_t(i))_{t \geq 0} : i \in \mathbb{Z}^d\}$ a system of independent standard BMs, $m_{ij} \geq 0$, depending only on $\|i - j\|$, $m_{ij} = 0$ for $\|i - j\| > L$.

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Here $s \in \mathbb{R}$ selection parameter, $\{(W_t(i))_{t\geq 0} : i \in \mathbb{Z}^d\}$ a system of independent standard BMs, $m_{ij} \geq 0$, depending only on $\|i - j\|$, $m_{ij} = 0$ for $\|i - j\| > L$.
Remark: Existence and uniqueness of a strong $[0,1]^{\mathbb{Z}^d}$-valued solution follows from classical results (see [Shiga-Shimizu, 1980]).

Longterm coexistence

$$dp_t(i) = \sum_{j\in\mathbb{Z}^d} m_{ij}\,(p_t(j) - p_t(i))\;dt + s\,p_t(i)\,(1-p_t(i))\,(1-2p_t(i))\;dt \\ + \sqrt{p_t(i)(1-p_t(i))}\,dW_t(i).$$

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Problem: Longterm coexistence?
Remark:

- $s > 0 \rightsquigarrow$ *heterozygosity ('balancing') selection*
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Conjecture: There exists $s_0 \in \mathbb{R}$ such that we have coexistence for $s > s_0$, non-coexistence for $s < s_0$.

Coexistence for BEM-Model II

Problem: Longterm coexistence?

Definition 1

Say that the model exhibits *longterm coexistence* with positive probability if there exists $\kappa > 0$ such that

$$\liminf_{t\to\infty} \mathbb{P}\left(\kappa < p_t(0) < 1-\kappa\right) > 0.$$

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Theorem 2 (BEM 2007)

Fix $\varepsilon > 0$ small. Then there exists $s_0 \geq 0$ such that for all $s > s_0$ and all initial conditions p_0 with $p_0(i) \in (\varepsilon, 1-\varepsilon)$ for all $i \in \mathbb{Z}^d$, we have

$$\liminf_{t\to\infty} \mathbb{P}\left(\varepsilon < p_t(0) < 1-\varepsilon\right) > 0.$$

In particular, we have longterm coexistence with positive probability for this class of initial conditions.

Duality: Definition of the dual process

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Definition 3 (BARW)

The (double) branching annihilating random walk with branching rate $s > 0$ is the Markov process $(n_t)_t$ taking values $n_t \in (\mathbb{N}_0)^{\mathbb{Z}^d}$ starting from finitely many particles at time 0 and with transitions

$$
\begin{array}{lll}
\begin{cases} n(i) \to n(i) - 1 \\ n(j) \to n(j) + 1 \end{cases} & \text{at rate } m_{ij}\, n(i) & (\textit{migration}) \\
n(i) \to n(i) + 2 & \text{at rate } s\, n(i) & (\textit{branching}) \\
n(i) \to n(i) - 2 & \text{at rate } \frac{1}{2} n(i)(n(i) - 1) & (\textit{annihilation}).
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Note that $(n_t)_t$ is *parity-preserving*; in particular, it always survives if started with an odd number of particles.

A transformation

Exercise: The transformed process

$$x_t := 1 - 2p_t$$

taking values in $[-1, 1]$ solves the following system of SDEs:

$$\begin{aligned} dx_t(i) = \sum_{j \in \mathbb{Z}^d} m_{ij} \left(x_t(j) - x_t(i) \right) dt + \frac{s}{2} \left(x_t(i)^3 - x_t(i) \right) dt \\ + \sqrt{1 - x_t(i)^2} \, d\widetilde{W}_t(i). \end{aligned} \tag{2}$$

Moment duality

Proposition 1 (BEM 2007)

For each $s > 0$, the system $(x_t)_t$ of SDEs (2) is dual to the BARW $(n_t)_t$ with branching rate $s/2$, via the following moment duality: For each $x_0 \in [-1,1]^{\mathbb{Z}^d}$ and $n_0 \in \mathbb{N}_0^{\mathbb{Z}^d}$ with $\sum_{i\in\mathbb{Z}^d} n_0(i) < \infty$, we have

$$\mathbb{E}\left[\prod_{i\in\mathbb{Z}^d} x_t(i)^{n_0(i)}\right] = \mathbb{E}\left[\prod_{i\in\mathbb{Z}^d} x_0(i)^{n_t(i)}\right], \qquad t > 0. \tag{3}$$

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Proof: For $x \in [0,1]^{\mathbb{Z}^d}$ and $n \in (\mathbb{N}_0)^{\mathbb{Z}^d}$ with $\sum_i n(i) < \infty$ define

$$H(x,n) := \prod_{i\in\mathbb{Z}^d} x(i)^{n(i)}.$$

Let $\mathcal{L}$ denote generator of $(n_t)_t$, $\mathcal{A}$ denote generator of $(x_t)_t$. Then **(Exercise!)**

$$\mathcal{L}[H(x;\cdot)](n) = \mathcal{A}[H(\cdot;n)](x).$$

Linking coexistence and survival of the dual

Proposition 2

For all $s > 0$, the following are equivalent:

a) *For all initial conditions p_0 such that $p_0(i) \in (\varepsilon, 1-\varepsilon)$ for some small $\varepsilon > 0$, we have longterm coexistence of $(p_t)_t$ with positive probability, i.e. there exists $\kappa > 0$ with*

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b) *There exists some initial condition p_0 for which we have longterm coexistence of $(p_t)_t$ with positive probability.*

c) *The BARW with branching rate $s/2$ and started with exactly two particles at the origin at time zero survives for all time with positive probability, i.e.*

$$\mathbb{P}\left(\forall t > 0 : n_t \neq \underline{0}\right) > 0.$$

Method for proving coexistence

Idea:

- Compare $(p_t)_{t \geq 0}$ to a *discrete-time* spin system $(\zeta_n)_{n \in \mathbb{N}_0}$, $\zeta_n \in \{0,1\}^{\mathbb{Z}^d}$, such that coexistence for $(\zeta_n)_n$ implies coexistence for $(p_t)_t$.

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and there exists $\delta > 0$ such that, uniformly in $n \in \mathbb{N}_0$,

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Then clearly

$$\liminf_{t\to\infty} \mathbb{P}\left(\varepsilon < p_t(0) < 1 - \varepsilon\right) > 0,$$

and we have coexistence.

The second condition is checked via comparison to a suitable one-dimensional Wright-Fisher diffusion with drift. We have:

Lemma 4

For each $\varepsilon \in (0, 1/4)$ and $\delta \in (0, 1)$, there is a sufficiently large s_0 such that for all $s > s_0$ we have a uniform lower bound

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for all $i \in \mathbb{Z}^d$.

The first condition

$$\liminf_{n \to \infty} \mathbb{P}(\zeta_{2n}(0) = 1) > 0$$

is checked by a comparison to *oriented percolation*, again using Lemma 4.

Back to the classical LV model

Classical (deterministic, non-spatial) Lotka-Volterra model of two competing species:

$$dX_t = \alpha\,(M - \lambda X_t - \gamma Y_t)\,X_t\,dt,$$
$$dY_t = \alpha'\,(M' - \lambda' Y_t - \gamma' X_t)\,Y_t\,dt,$$

where $X_t, Y_t \geq 0$ denotes the total population size of the respective type at time t.

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- α, α' (intrinsic) growth rates
- M, M' carrying capacities
- λ, λ' *intraspecific* competition parameters
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In the symmetric case, we have coexistence (in the sense that there exists a nontrivial stable equilibrium) iff interspecific competition is less important than intraspecific competition, i.e. iff

$$\gamma < \lambda.$$

BEM-Model I: A stochastic spatial LV model

A system of interacting diffusions on $\mathbb{Z}^d$:

$$dX_t(i) = \sum_{j\in\mathbb{Z}^d} m_{ij}\left(X_t(j) - X_t(i)\right) dt$$

$$+ \alpha\left(M - \sum_{j\in\mathbb{Z}^d} \lambda_{ij} X_t(j) - \sum_{j\in\mathbb{Z}^d} \gamma_{ij} Y_t(j)\right) X_t(i)\, dt$$

$$+ \sqrt{X_t(i)}\, dB_t(i),$$

$$dY_t(i) = \sum_{j\in\mathbb{Z}^d} m'_{ij}\left(Y_t(j) - Y_t(i)\right) dt$$

$$+ \alpha'\left(M' - \sum_{j\in\mathbb{Z}^d} \lambda'_{ij} Y_t(j) - \sum_{j\in\mathbb{Z}^d} \gamma'_{ij} X_t(j)\right) Y_t(i)\, dt$$

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Remark: Existence is not covered by standard results; uniqueness is open!

Relationship between Model I and Model II

Write $N_t(i) := X_t(i) + Y_t(i)$ and

$$p_t(i) := \frac{X_t(i)}{N_t(i)} \in [0,1], \qquad i \in \mathbb{Z}^d,\ t \geq 0.$$

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Exercise: Use Ito's formula to show that $(p_t)_t$ solves

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where $s := \alpha(\lambda_{ii} - \gamma_{ii})$.

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where $s := \alpha(\lambda_{ii} - \gamma_{ii})$. If we *assume* $N_t(i) = 1$ for all $i \in \mathbb{Z}^d$, $t \geq 0$, we recover Model II.

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$$\liminf_{t\to\infty} \mathbb{P}\left(X_t(0), Y_t(0) > \kappa\right) > 0.$$

BEM-Model I: Assumptions for coexistence

- m_{ij}, m'_{ij}, λ_{ij}, λ'_{ij}, γ_{ij}, γ'_{ij} nonnegative, depending only on $\|i-j\|$, vanishing for $\|i-j\| > R$ (finite range of migration and interaction).

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- Same range of intraspecific competition and migration: There exists $c > 0$ such that

$$\frac{1}{c}\lambda_{ij} \leq m_{ij} \leq c\lambda_{ij}, \qquad \frac{1}{c}\lambda'_{ij} \leq m'_{ij} \leq c\lambda'_{ij}$$

with "$<$" whenever $m_{ij}, m'_{ij} \neq 0$.

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- m_{ij}, m'_{ij}, λ_{ij}, λ'_{ij}, γ_{ij}, γ'_{ij} nonnegative, depending only on $\|i-j\|$, vanishing for $\|i-j\| > R$ (finite range of migration and interaction).
- Same range of intraspecific competition and migration: There exists $c > 0$ such that

$$\frac{1}{c}\lambda_{ij} \leq m_{ij} \leq c\lambda_{ij}, \qquad \frac{1}{c}\lambda'_{ij} \leq m'_{ij} \leq c\lambda'_{ij}$$

  with "$<$" whenever $m_{ij}, m'_{ij} \neq 0$.
- m_{ij}, m'_{ij} are non-diagonal and of the same range, and $\lambda_{ii}, \lambda'_{ii} > 0$ for all $i \in \mathbb{Z}^d$.

Coexistence in BEM-Model I

Theorem 1 (BEM 2007)

Under the above assumptions, there exists a finite constant $0 < M_0 < \infty$ *such that the following holds: For all* $M, M' > M_0$ *there exist* $\gamma, \gamma' > 0$ *and constants* $0 < \kappa_1 < \kappa_2 < \infty$ *such that if*

$$\sum_{j \in \mathbb{Z}^d} \gamma_{ij} < \gamma \qquad \text{and} \qquad \sum_{j \in \mathbb{Z}^d} \gamma'_{ij} < \gamma'$$

and if the initial conditions satisfy

$$X_0(i), Y_0(i) \in [\kappa_1, \kappa_2] \qquad \text{for all } i \in \mathbb{Z}^d,$$

then we have longterm coexistence with positive probability, i.e. there is some $\kappa > 0$ *such that*

$$\liminf_{t \to \infty} \mathbb{P}\left(X_t(0), Y_t(0) > \kappa\right) > 0.$$

Oriented percolation

- Oriented percolation lives on the sub-lattice

$$\mathcal{L} := \{(x, n) \in \mathbb{Z}^2 : n \geq 0,\ x + n \text{ is even}\} \subset \mathbb{Z}^2$$

(see picture on blackboard).

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- Write $(x, m) \to (y, n)$ if there is a sequence $(x_k, k)_{k=m,\ldots,n}$ in $\mathcal{L}$ with $x_m = x$, $x_n = y$ such that $|x_k - x_{k-1}| = 1$ and $\omega(x_k, k) = 1$ for all $m \leq k \leq n$.

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- Given $\mathcal{W}_0 \subseteq 2\mathbb{Z}$, define a *percolation process* $(\mathcal{W}_n)_{n\in\mathbb{N}_0}$ by

$$\mathcal{W}_n := \{y \in \mathbb{Z} : \exists x \in \mathcal{W}_0 \text{ with } (x,0) \to (y,n)\}, \qquad n \in \mathbb{N}$$

('sites that are wet at time n').

M-dependence

Let $\theta \in (0,1)$ and $M \in \mathbb{N}$. Say that the percolation process

$$\mathcal{W}_n := \{y \in \mathbb{Z} : \exists x \in \mathcal{W}_0 \text{ with } (x,0) \to (y,n)\}$$

is *M-dependent with density at least* $1-\theta$ if the following holds: For any finite set I of indices and any sequence $(x_i, n_i)_{i \in I} \in \mathcal{L}$ such that

$$\|(x_i, n_i) - (x_j, n_j)\| > M \qquad \forall i \neq j \in I$$

we have

$$\mathbb{P}\left(\omega(x_i, n_i) = 0 \; \forall i \in I\right) \leq \theta^{|I|}.$$

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Theorem 2 (Durrett 1995)

Assume $\theta \leq 6^{-4(2M+1)^2}$. *If* $\mathcal{W}_0 = 2\mathbb{Z}$ *('all sites wet initially'), then*

$$\liminf_{n\to\infty} \mathbb{P}(0 \in \mathcal{W}_{2n}) \geq \frac{19}{20}.$$

Comparison assumption (for $d = 1$)

Say that $(\zeta_n)_n$ satisfies the *comparison assumption* (for θ and L) if for each initial configuration ζ_0 with

$$\zeta_0(i) = 1 \qquad \forall i \in [-L, L] \cap \mathbb{Z}$$

there exists a suitably measurable 'good event' G_{ζ_0} with $\mathbb{P}(G_{\zeta_0}) > 1 - \theta$ such that

$$\text{on } G_{\zeta_0} : \qquad \zeta_1(i) = 1 \qquad \forall i \in ([-3L, -L] \cup [L, 3L]) \cap \mathbb{Z}.$$

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Theorem 3 (Durrett 1995)

Suppose $(\zeta_n)_n$ satisfies the comparison assumption for some $\theta \in (0, 1)$ and $L \in \mathbb{N}$. Then there exists a coupling of $(\zeta_n)_n$ to an M-dependent oriented percolation process $(\mathcal{W}_n)_n$ with density at least $1 - \theta$ such that

$$\{0 \in \mathcal{W}_{2n}\} \subseteq \{\zeta_{2n}(i) = 1 \; \forall i \in [-L, L]\}.$$

Back to Model II: Checking the comparison assumption

Recall:

$$\zeta_n(i) = \begin{cases} 1 & \text{if } \varepsilon < p_n(i) < 1 - \varepsilon \\ 0 & \text{else.} \end{cases}$$

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Recall:

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By Lemma 4, there exists $s_0 > 0$ such that for $s > 0$ we have

$$\begin{aligned} &\mathbb{P}\Big(\zeta_1(i) = 1\ \forall i \in ([-3L, -L] \cup [L, 3L]) \cap \mathbb{Z}\Big) \\ &\geq \mathbb{P}\Big(\varepsilon < p_t(i) < 1-\varepsilon\ \forall t \in [0,2],\ i \in ([-3L, -L] \cup [L, 3L]) \cap \mathbb{Z}\Big) \\ &\geq (1 - (4L+2)\delta) \geq 1 - \theta, \end{aligned}$$

where we choose $\theta > 0$ small enough according to Theorem 2.

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