Coexistence in competing species models, II: Interacting diffusion models

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

$$
dp_t(i) = \sum_{j \in \mathbb{Z}^d} m_{ij} (p_t(j) - p_t(i)) \, dt \\
+ s p_t(i) (1 - p_t(i)) (1 - 2p_t(i)) \, dt \\
+ \sqrt{p_t(i)(1 - p_t(i))} \, dW_t(i), \quad i \in \mathbb{Z}^d, \, t \geq 0,
$$

(1)

for initial conditions $p_0(i) \in [0, 1], \, i \in \mathbb{Z}^d$. 

Remark: Existence and uniqueness of a strong $[0, 1] \times \mathbb{Z}^d$-valued solution follows from classical results (see [Shiga-Shimizu, 1980]).
**BEM-Model II: A system of interacting diffusions**

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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 $\|i - j\| > L$. 
BEM-Model II: A system of interacting diffusions

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**Remark:** Existence and uniqueness of a strong \([0, 1]^{\mathbb{Z}^d}\) -valued solution follows from classical results (see [Shiga-Shimizu, 1980]).
Longterm coexistence

\[ dp_t(i) = \sum_{j \in \mathbb{Z}^d} m_{ij} (p_t(j) - p_t(i)) \, dt + s \, p_t(i) (1 - p_t(i)) (1 - 2p_t(i)) \, dt \]

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**Remark:**
- \( s > 0 \) \( \rightarrow \) heterozygosity ('balancing') selection
- \( s < 0 \) \( \rightarrow \) homozygosity selection
- \( s = 0 \) \( \rightarrow \) neutral case, *stepping stone model*. 
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$$dp_t(i) = \sum_{j \in \mathbb{Z}^d} m_{ij} (p_t(j) - p_t(i)) \, dt + s p_t(i) (1 - p_t(i)) (1 - 2p_t(i)) \, dt$$

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**Remark:**
- $s > 0 \Rightarrow$ heterozygosity ('balancing') selection
- $s < 0 \Rightarrow$ homozygosity selection
- $s = 0 \Rightarrow$ neutral case, stepping stone model.

**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

$$\liminf_{t \to \infty} \mathbb{P} (\kappa < p_t(0) < 1 - \kappa) > 0.$$
Coexistence for BEM-Model II

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

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

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

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

In particular, we have longterm coexistence with positive probability for this class of initial conditions.
Duality: Definition of the dual process

It turns out that after transforming our process, we get a moment duality with a *branching annihilating random walk (BARW)*.
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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{align*}
    n(i) &\to n(i) - 1 & \text{at rate } m_{ij} n(i) \quad &\text{(migration)} \\
    n(j) &\to n(j) + 1 & \text{at rate } s n(i) \quad &\text{(branching)} \\
    n(i) &\to n(i) + 2 & \text{at rate } \frac{1}{2} n(i)(n(i) - 1) \quad &\text{(annihilation)}.
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Duality: Definition of the dual process

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\end{align*}
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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{align*}
    dx_t(i) &= \sum_{j \in \mathbb{Z}^d} m_{ij} (x_t(j) - x_t(i)) \ dt + \frac{s}{2} \left( x_t(i)^3 - x_t(i) \right) \ dt \\
    &+ \sqrt{1 - x_t(i)^2} \ d\bar{W}_t(i).
\end{align*}
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(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

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

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!)

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

$$\liminf_{t \to \infty} \mathbb{P}(\kappa < p_t(0) < 1 - \kappa) > 0.$$
Linking coexistence and survival of the dual

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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.
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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.

$$\mathbb{P}(\forall t > 0 : n_t \neq 0) > 0.$$
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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Definition of the spin system: Fix \(\varepsilon > 0\) and define

\[
\zeta_n(i) := \begin{cases} 
1 & \text{if } \varepsilon < p_n(i) < 1 - \varepsilon \\
0 & \text{else}.
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The strategy is to show the following two conditions:

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\liminf_{n \to \infty} \mathbb{P}(\zeta_{2n}(0) = 1) = \liminf_{n \to \infty} \mathbb{P}(\varepsilon < p_{2n}(0) < 1 - \varepsilon) > 0,
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and there exists \(\delta > 0\) such that, uniformly in \(n \in \mathbb{N}_0\),

\[
\mathbb{P}\left(\varepsilon < p_t(0) < 1 - \varepsilon \forall t \in [2n, 2(n+1)] \left| \varepsilon < p_{2n}(0) < 1 - \varepsilon\right.\right) \geq 1 - \delta.
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Suppose we can show the following two conditions:

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$$\mathbb{P}(\varepsilon < p_t(0) < 1 - \varepsilon \ \forall \ t \in [2n, 2(n+1)] \mid \varepsilon < p_{2n}(0) < 1 - \varepsilon) \geq 1 - \delta.$$

Then clearly

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

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*

$$\Pr\left( \varepsilon < p_t(i) < 1 - \varepsilon \quad \forall t \in [0, 2] \bigg| \varepsilon < p_0(i) < 1 - \varepsilon \right) \geq 1 - \delta$$

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

\[
\begin{align*}
    dX_t &= \alpha \left( M - \lambda X_t - \gamma Y_t \right) X_t \, dt, \\
    dY_t &= \alpha' \left( M' - \lambda' Y_t - \gamma' X_t \right) Y_t \, dt,
\end{align*}
\]

where \( X_t, Y_t \geq 0 \) denotes the total population size of the respective type at time \( t \).
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where \( X_t, Y_t \geq 0 \) denotes the total population size of the respective type at time \( t \). The parameters have the following interpretation:

- \( \alpha, \alpha' \) (intrinsic) growth rates
- \( M, M' \) carrying capacities
- \( \lambda, \lambda' \) *intraspecific* competition parameters
- \( \gamma, \gamma' \) *interspecific* 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 $\mathbb{Z}^d$:

$$
\begin{align*}
\text{d}X_t(i) &= \sum_{j \in \mathbb{Z}^d} m_{ij} \left( X_t(j) - X_t(i) \right) \text{d}t \\
&\quad + \alpha \left( M - \sum_{j \in \mathbb{Z}^d} \lambda_{ij} X_t(j) - \sum_{j \in \mathbb{Z}^d} \gamma_{ij} Y_t(j) \right) X_t(i) \text{d}t \\
&\quad + \sqrt{X_t(i)} \text{d}B_t(i), \\
\text{d}Y_t(i) &= \sum_{j \in \mathbb{Z}^d} m'_{ij} \left( Y_t(j) - Y_t(i) \right) \text{d}t \\
&\quad + \alpha' \left( M' - \sum_{j \in \mathbb{Z}^d} \lambda'_{ij} Y_t(j) - \sum_{j \in \mathbb{Z}^d} \gamma'_{ij} X_t(j) \right) Y_t(i) \text{d}t \\
&\quad + \sqrt{Y_t(i)} \text{d}B'_t(i), \quad i \in \mathbb{Z}^d.
\end{align*}
$$
BEM-Model I: A stochastic spatial LV model

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

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

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

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

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

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

$$+ \sqrt{Y_t(i)} \, dB'_t(i), \quad i \in \mathbb{Z}^d.$$  

Remark: Existence is 'non-standard'; uniqueness is open!
Relationship between Model I and Model II

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

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

Suppose 'symmetric' parameters and purely local interactions:

$$\lambda_{ij} = \lambda'_{ij} = \gamma_{ij} = \gamma'_{ij} = 0, \quad i \neq j.$$
Relationship between Model I and Model II

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Suppose 'symmetric' parameters and purely local interactions:

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

$$dp_t(i) = \sum_{j \in \mathbb{Z}^d} m_{ij} \frac{N_t(j)}{N_t(i)} (p_t(j) - p_t(i)) \, dt$$

$$+ s N_t(i) p_t(i) (1 - p_t(i)) (1 - 2p_t(i)) \, dt$$

$$+ \sqrt{N_t(i)^{-1}p_t(i)(1 - p_t(i))} \, dW_t(i),$$ 

where $s := \alpha(\lambda_{ii} - \gamma_{ii})$. 
Relationship between Model I and Model II

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

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$$+ s N_t(i) p_t(i) (1 - p_t(i)) (1 - 2p_t(i)) \ dt$$

$$+ \sqrt{N_t(i)^{-1} p_t(i) (1 - p_t(i))} dW_t(i),$$

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.
Longterm coexistence

**Problem:** Longterm coexistence?
Longterm coexistence

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Definition 5
Say that the model exhibits longterm coexistence with positive probability if there exists \( \kappa > 0 \) with

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\liminf_{t \to \infty} \mathbb{P} (X_t(0), Y_t(0) > \kappa) > 0.
\]
BEM-Model I: Assumptions for coexistence

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- \(m_{ij}, m'_{ij}\) 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

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

and if the initial conditions satisfy

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

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

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

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

(‘sites that are wet at time \(n\’).
M-dependence

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

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

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

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

we have

$$\mathbb{P}(\omega(x_i, n_i) = 0 \ \forall i \in I) \leq \theta^{|I|}.$$
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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 \(\theta\) and \(L\)) if for each initial configuration \(\zeta_0\) with

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

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

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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:

\[ \zeta_n(i) = \begin{cases} 
1 & \text{if } \varepsilon < p_n(i) < 1 - \varepsilon \\
0 & \text{else.} 
\end{cases} \]
Back to Model II: Checking the comparison assumption

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In our case, 'suitably measurable' means

$$G_{\zeta_0} \in \sigma\left( W_t(i) : i \in [-3L, 3L] \cap \mathbb{Z}, t \in [0, 2] \right),$$

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

$$\mathbb{P} \left( \zeta_1(i) = 1 \ \forall i \in ([-3L, -L] \cup [L, 3L]) \cap \mathbb{Z} \right)$$

$$\geq \mathbb{P} \left( \varepsilon < p_t(i) < 1 - \varepsilon \ \forall t \in [0, 2], i \in ([-3L, -L] \cup [L, 3L]) \cap \mathbb{Z} \right)$$

$$\geq (1 - (4L + 2)\delta) \geq 1 - \theta,$$

where we choose $\theta > 0$ small enough according to Theorem 2.
Introduction: Model II Duality Strategy for proving coexistence Model I Oriented percolation


