Genealogies for a biased voter model

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Joint with Rick Durrett

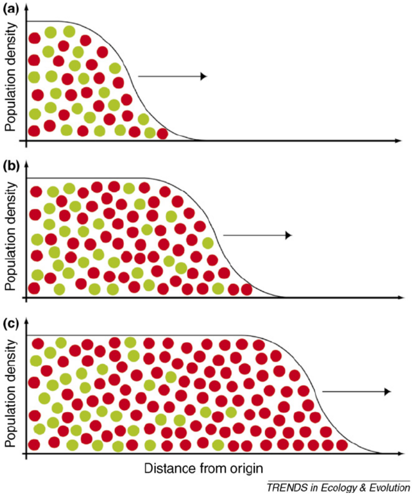
Frontier Probability Days 2016

University of Utah

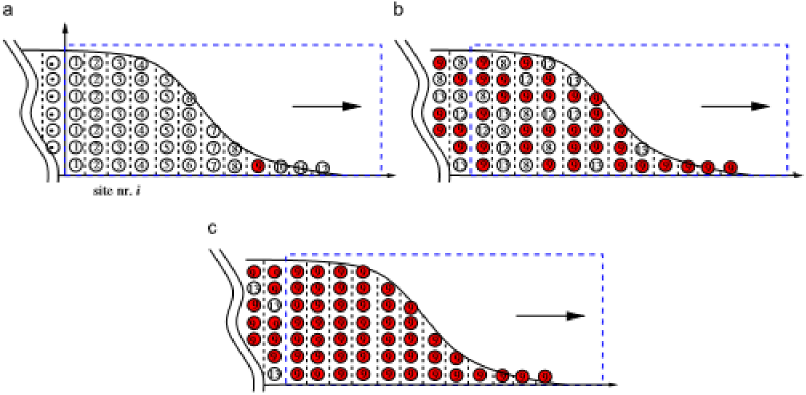
Expanding population

Picture from Duke Cancer Institute: http://sites.duke.edu/dukecancerinstitute/

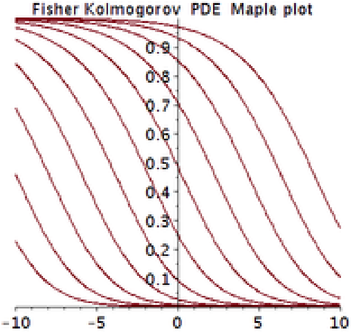
Expanding population



Expanding population

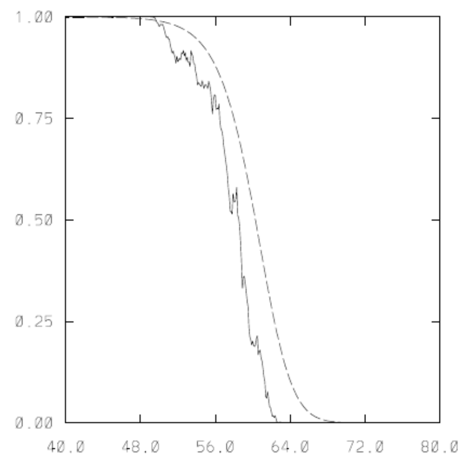


Hallatschek and Nelson, 2007



Fisher-Kolmogorov-Petrovsky-Piscounov (FKPP)

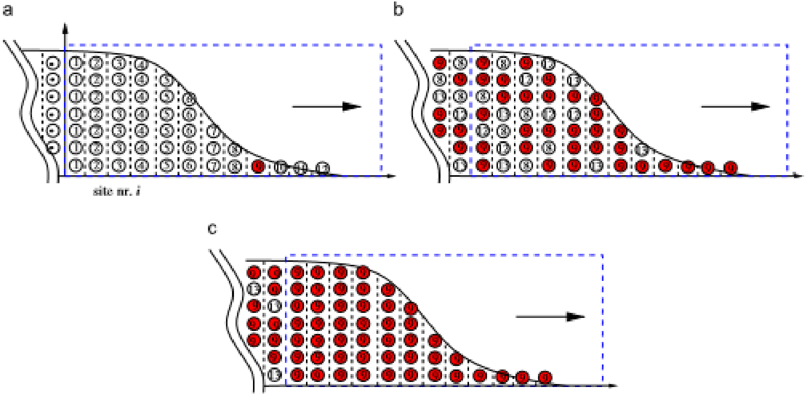
$$\partial_t u = \alpha\, \Delta u + \beta\, u(1-u)$$



(Figure from [Doering, Muller and Smereka 2003])
Stochastic FKPP

$$\partial_t u = \alpha \, \Delta u + \beta \, u(1-u) + |\gamma \, u(1-u)|^{1/2} \, \dot{W}$$

First question: FKPP or Stochastic FKPP ?

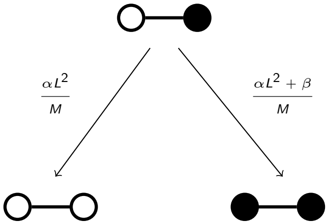


Biased Voter Model

BVM on

$$(L^{-1}\mathcal{Z}) \times \{1, \ldots, M\}.$$

$$(0-1) \quad \text{becomes} \quad \begin{cases} (0-0) & \text{at rate } \alpha L^2/M \\ (1-1) & \text{at rate } (\alpha L^2 + \beta)/M \end{cases}$$



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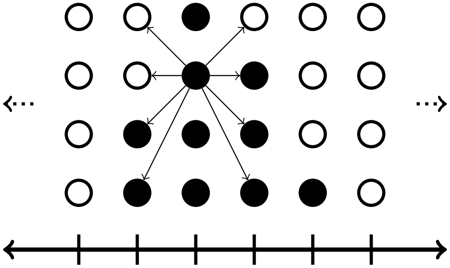

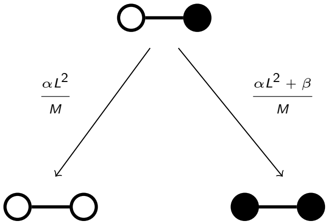

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Theorem (Durrett and Fan, 2016)

Suppose $L/M \to \gamma/(4\alpha) \in [0, \infty)$. Then density of type 1 converges to

$$\partial_t u = \alpha\, \Delta u + 2\beta\, u(1-u) + |\gamma\, u(1-u)|^{1/2}\, \dot{W}$$

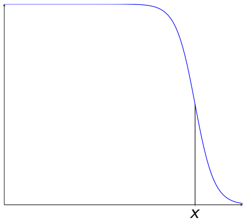
where $\alpha > 0$, $\beta \geq 0$ and $\gamma \geq 0$.

$\gamma = 0$ (deterministic FKPP)
$\gamma > 0$ (stochastic FKPP)

[Muller and Tribe 1995] (related to case $L = M = n^{1/2}$).

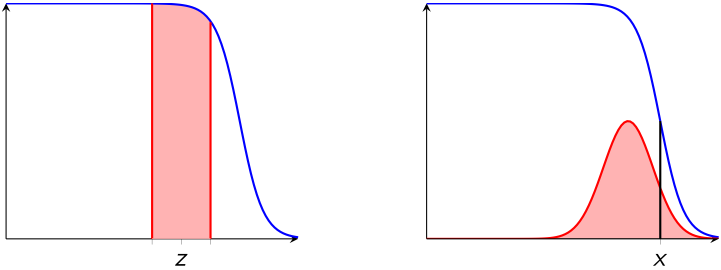
Lineage dynamics

1. Pick an individual at (t, x) and follow its ancestral line backward in time
2. What is the probability that it has an ancestor who lived at $(0, z)$?



Lineage dynamics

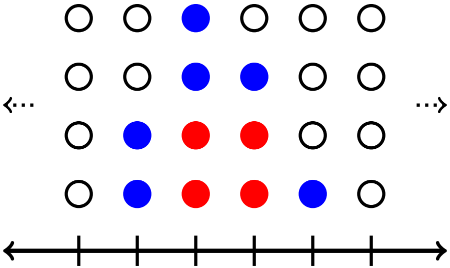
Let $G(\tau, z) := G(\tau, z|t, x)$ be probability density that an individual picked at (t, x) has an ancestor who lived at (τ, z).

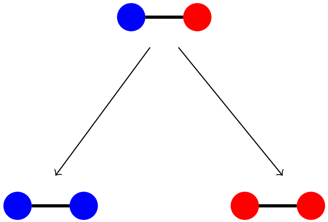


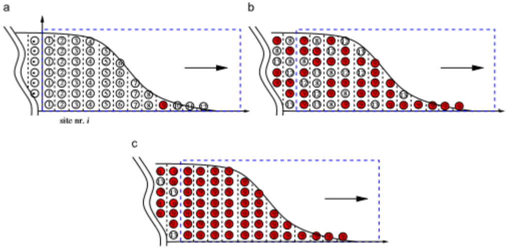
Then

$$G(0, z) = \lim_{\epsilon \to 0} \frac{1}{2\epsilon} \frac{\ell(t, x)}{u(t, x)}\Big|_{\ell_0 = u_0 \mathbf{1}[z-\epsilon, z+\epsilon]}$$

BVM with neutral mutations (labels)







Theorem (Durrett and Fan, 2016)

Under suitable scalings, the **pair** *of densities of type 1 and labeled type 1 converges in distribution to the coupled SPDE*

$$\partial_t u = \alpha \Delta u + 2\beta u(1-u) + |\gamma \ell (1-u)|^{1/2} \dot{W}^0 + |\gamma (u-\ell)(1-u)|^{1/2} \dot{W}^1$$

$$\partial_t \ell = \alpha \Delta \ell + 2\beta \ell \,(1-u) + |\gamma \ell (1-u)|^{1/2} \dot{W}^0 + |\gamma \ell \,(u-\ell)|^{1/2} \dot{W}^2$$

Applications: (i) lineage dynamics (ii) probability of gene surfing

Application: Lineage dynamics

Coupled SPDE suggests that $\rho = \ell/u$ satisfies

$$\partial_t \rho \;=\; \alpha\,\Delta\rho + 2\alpha\,\nabla_x \log u \cdot \nabla_x \rho \;+\; |4\gamma\,\rho\,(1-\rho)/u|^{1/2}\,\dot{W}.$$

with $\rho_0 = \delta_z$.

Implication:

For FKPP ($\gamma = 0$), **lineage dynamics is a Brownian motion with drift** and is independent of β.

Weak uniqueness of SPDE

Duality between sFKPP $\partial_t u = \alpha\Delta u + 2\beta u(1-u) + \sqrt{4\gamma u(1-u)}\dot{W}$ and the BCBM $(x_1(t), x_2(t), \cdots, x_{n(t)}(t))$:

$$\mathbb{E}\prod_{i=1}^{n(0)}(1-u_t(x_i(0))) = \mathbb{E}\prod_{i=1}^{n(t)}(1-u_0(x_i(t))).$$

1. Shiga and Uchiyama 1986
2. Shiga 1988
3. Athreya and Tribe 2000
4. Doering, Muller and Smereka 2003

This duality implies **weak uniqueness** of sFKPP.

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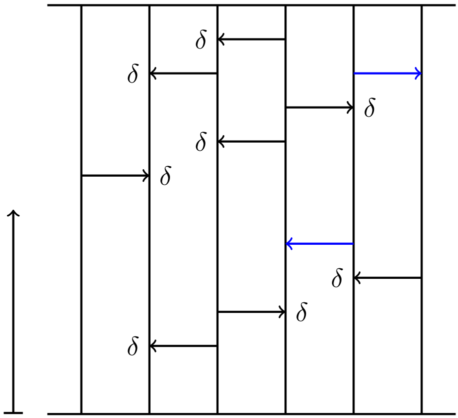


$\longrightarrow \delta$ at rate $\frac{\alpha L^2}{M}$

$\longrightarrow$ at rate $\frac{\beta}{M}$

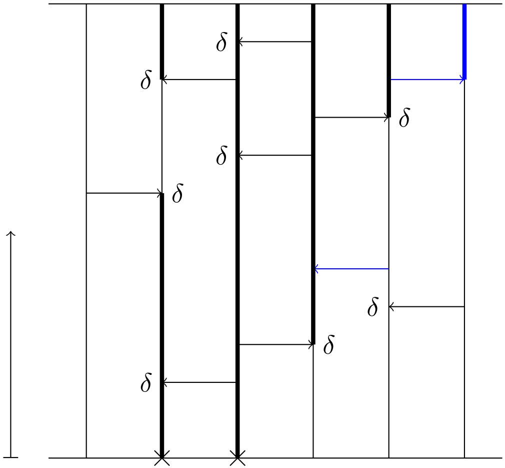


FIGURE: Biased voter model ξ_t

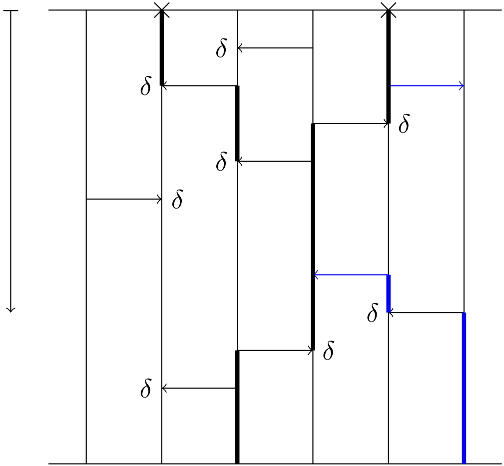
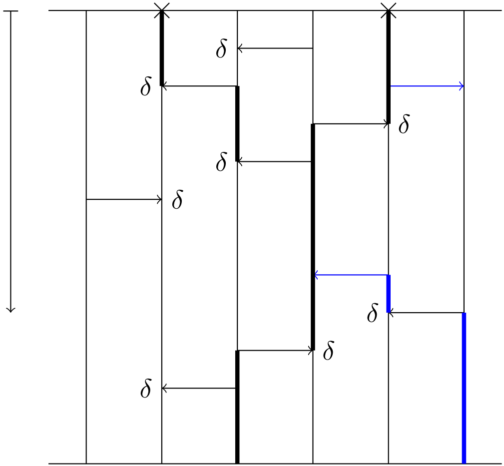


FIGURE: Dual of BVM: Branching Coalescing RW $(\zeta_s^t)_{s\in[0,t]}$



$$\{\xi_t^A \cap B \neq \emptyset\} = \{\zeta_t^{t,B} \cap A \neq \emptyset\}$$

Duality

BVM starting with A : ξ_t^A

Dual starting with B : $\zeta_t^B = \{x_i(t) : 1 \le i \le n(t)\}$

From Harris' graphical construction we have

$$\mathbb{P}(\xi_t^A \cap B = \emptyset) = \mathbb{P}(\zeta_t^B \cap A = \emptyset)$$
$$\mathbb{P}\big(\xi_t(x_i(0)) = 0,\ 1 \le i \le n(0)\big) = \mathbb{P}\big(\xi_0(x_i(t)) = 0,\ 1 \le i \le n(t)\big)$$
$$\mathbb{E}\prod_{i=1}^{n(0)}\big(1 - \xi_t(x_i(0))\big) = \mathbb{E}\prod_{i=1}^{n(t)}\big(1 - \xi_0(x_i(t))\big)$$

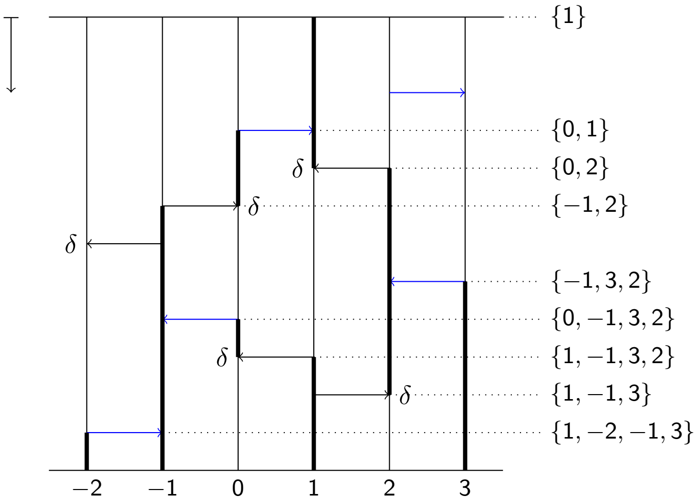
Formally $L, M \to \infty$ leads to **duality** between sFKPP and BCBM.

Duality

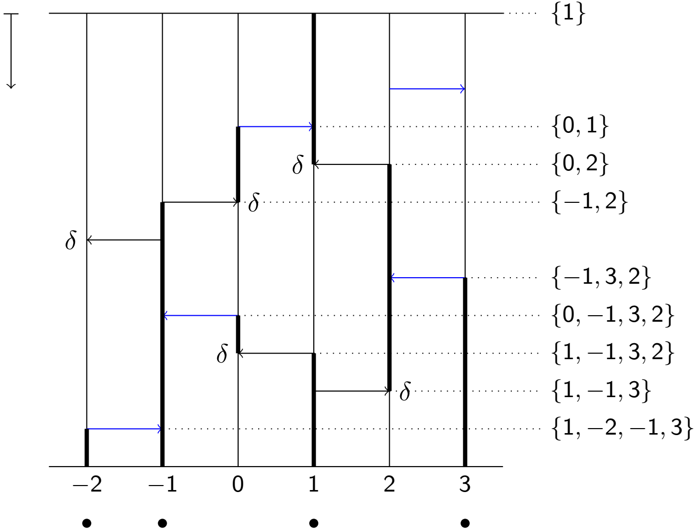
How about for the coupled SPDE?

$$\partial_t u = \alpha \Delta u + 2\beta u(1-u) + |\gamma \ell(1-u)|^{1/2}\,\dot{W}^0 + |\gamma(u-\ell)(1-u)|^{1/2}\,\dot{W}^1$$
$$\partial_t \ell = \alpha \Delta \ell + 2\beta \ell\,(1-u) + |\gamma \ell(1-u)|^{1/2}\,\dot{W}^0 + |\gamma \ell\,(u-\ell)|^{1/2}\,\dot{W}^2$$

Need an *ordered* BCBM $x_t = (x_1(t), x_2(t), \cdots, x_{n(t)}(t))$ such that the first occupied site is the ancestor.



Order the list so that the first occupied site is the ancestor.


{1}
{0, 1}
{0, 2}
{−1, 2}
{−1, 3, 2}
{0, −1, 3, 2}
{1, −1, 3, 2}
{1, −1, 3}
{1, −2, −1, 3}
δ
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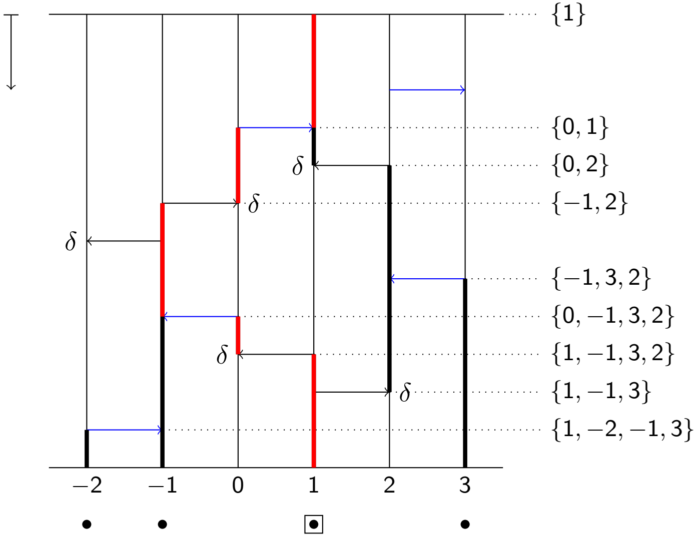
3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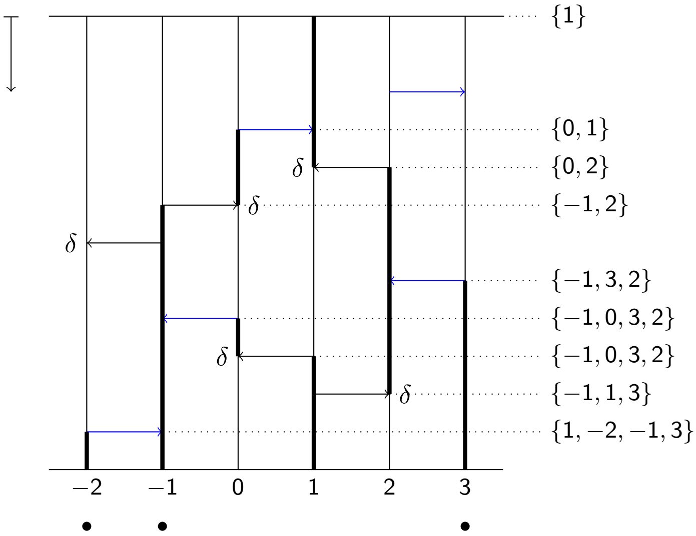
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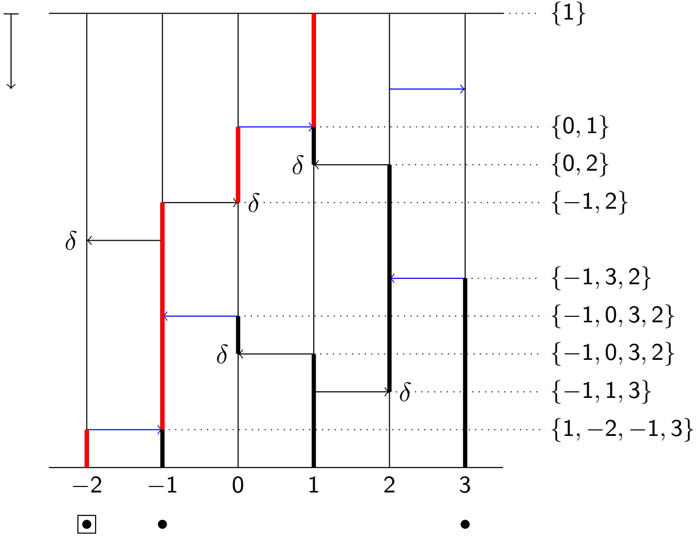
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δ
δ
δ
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2
3

Duality for coupled SPDE

BVM ξ_t, $\eta_t(x) = 1$ if the individual at x is labeled

Dual $\zeta_t = \{x_i(t) : 1 \le i \le n(t)\}$ *ordered*

Observe

$$\{\eta_t(x) = 1\} = \bigcup_{j=1}^{n(t)} \{\text{the first occupied site } j \text{ in the list is labeled}\}$$

Hence

$$\mathbb{P}(\eta_t(x) = 1) = \mathbb{E} \sum_{j=1}^{n(t)} \eta_0(x_j(t)) \prod_{i=1}^{j-1} (1 - \xi_0(x_i(t)))$$

Duality for coupled SPDE

$$\mathbb{P}(\eta_t(x) = 1) = \mathbb{E} \sum_{j=1}^{n(t)} \eta_0(x_j(t)) \prod_{i=1}^{j-1} (1 - \xi_0(x_i(t)))$$

Formally $L, M \to \infty$ leads to duality

$$\mathbb{E} F_1\big((u_t, \ell_t), (x_0, n(0))\big) = \mathbb{E} F_1\big((u_0, \ell_0), (x_t, n(t))\big)$$

where

$$F_1((u, \ell), (x, n)) = \sum_{1 \le j \le n} \ell(x_j) \prod_{i=1}^{j-1} \big(1 - u(x_i)\big).$$

Duality for coupled SPDE

Ordered BCBM $x_t = (x_1(t), x_2(t), \cdots, x_{n(t)}(t))$

Theorem (Durrett and Fan, 2016)

For $m \geq 1$, we have duality relations

$$\mathbb{E}F_m\big((u_t,\ell_t),(x_0,n(0))\big) = \mathbb{E}F_m\big((u_0,\ell_0),(x_t,n(t))\big)$$

where $$F_m((u,\ell),(x,n)) = \sum_{1\leq j_1<j_2<\cdots<j_m\leq n} \ell(x_{j_m})\cdots\ell(x_{j_1})\prod_{i=1}^{j_1-1}(1-u(x_i))$$

Corollary: **Weak uniqueness** of coupled SPDE holds.

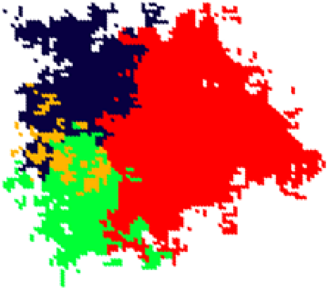
Related work

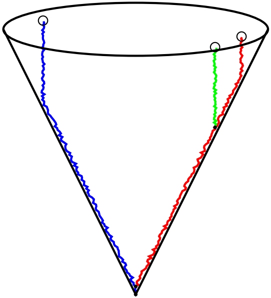
1. Neuhauser (1992)
2. Le Gall (1993)
3. Evans and Perkins (1998)
4. Donnelly and Kurtz (1996, 1999)
5. Durrett, Mytnik and Perkins (2005)

Ongoing work and open problems

1. Coupled SPDEs on graphs/trees
2. Multi-type advantageous/deleterious mutations

3. Long time behavior of coupled SPDEs and interacting superprocesses
4. Genealogies of BVM in higher dimensions





Thank you!