Ancestry in the face of competition

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Based on joint work with Jiří Černý,
Andrej Depperschmidt and Nina Gantert

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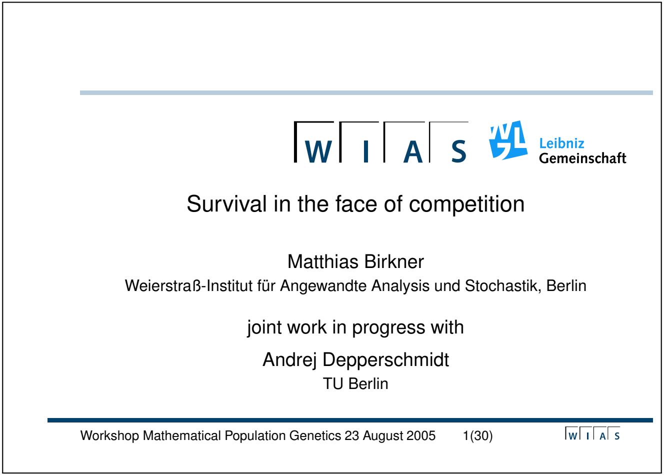
JOHANNES GUTENBERG UNIVERSITÄT MAINZ

Remark. The catchier part of the title is due to Steve Evans, who invented it in Oberwolfach in August 2005.



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Study/understand the space-time embedding of ancestral lineages in spatial models for populations with local density regulation (in particular, with non-constant local population sizes).

Outline

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1. Why local regulation?
2. Contact process (in discrete time) and directed percolation
3. Random walk on the cluster
   - A renewal structure
4. Locally regulated populations (and ancestral lineages)

A well-known problem with branching random walk

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Particles 'live' on $\mathbb{Z}^d$, produce offspring independently, offspring independently take a random walk step from mother's location.

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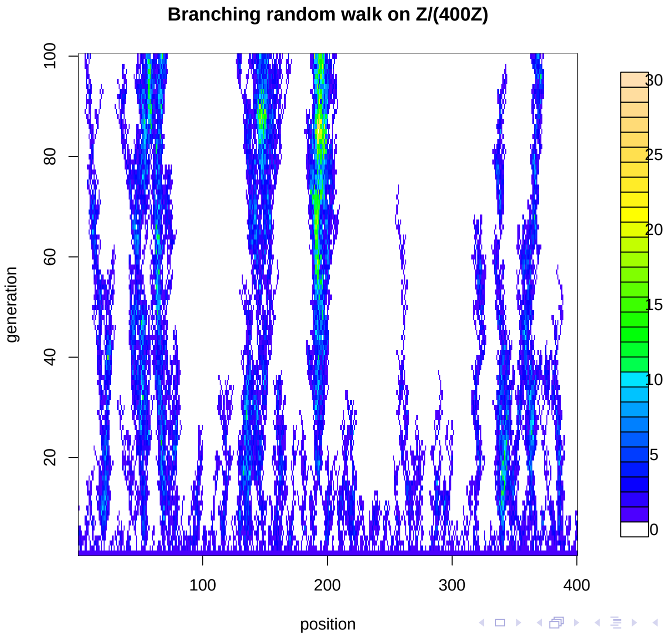
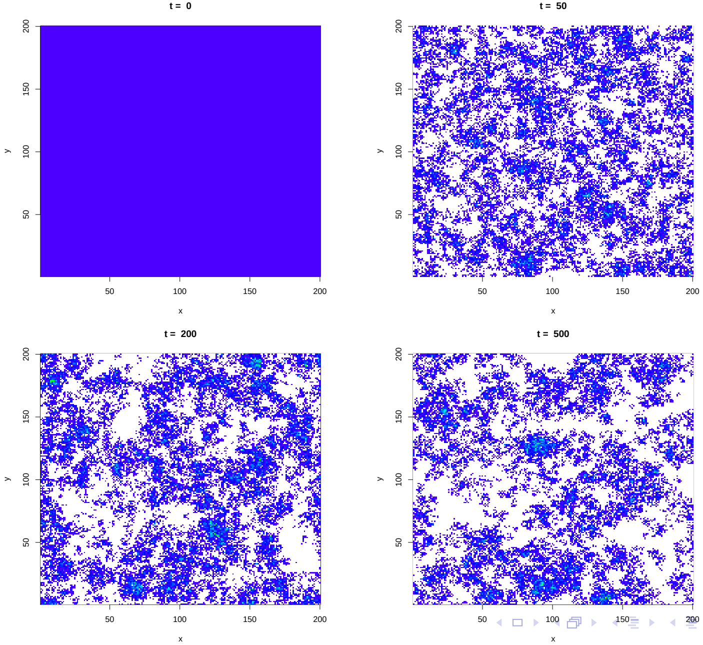
Problem: In $d = 1, 2$, under general second moment assumptions, there is no non-trivial equilibrium population (Kallenberg 1977).


Branching random walk on Z/(400Z)
generation
position
100
80
60
40
20
100
200
300
400
30
25
20
15
10
5
0

Branching random walk on $(\mathbb{Z}/(200\mathbb{Z}))^2$: Felsenstein's 'pain in the torus' (1975)



A customary 'solution' in population genetics:

Stepping stone model:

Condition on fixed local population size N in each patch

Pros:

- No local extinction
- Ancestral lineages are coalescing random walks, this makes detailed analysis feasible

Cons:

- An 'ad hoc' simplification, effects of local size fluctations no longer explicitly modelled
- N is an 'effective' parameter, relation to 'real' population dynamics is unclear

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Possible (and natural) extension: Branching random walk with local density-dependendent feedback

e.g. Bolker & Pacala (1997), Murrell & Law (2003), Etheridge (2004), Fournier & Méléard (2004), Blath, Etheridge & Meredith (2007), B. & Depperschmidt (2007), ...

Dynamics of ancestral lineages??

The discrete time contact process

$\eta_n(x)$, $n \in \mathbb{Z}_+$, $x \in \mathbb{Z}^d$, values in $\{0, 1\}$.
Site x is generation n is "inhabited" (or: "infected") if $\eta_n(x) = 1$.

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Dynamics: $U\big(= \{y \in \mathbb{Z}^d : ||y||_\infty \leq 1\big) \subset \mathbb{Z}^d$ finite, symmetric, $p \in (0, 1)$.
Given η_n, independently for $x \in \mathbb{Z}^d$,

$$\eta_{n+1}(x) = \begin{cases} 1 & \text{w. prob. } \; p \cdot \mathbf{1}(\eta_n(y) = 1 \text{ for some } y \in x + U) \\ 0 & \text{w. prob. } \; 1 - p \cdot \mathbf{1}(\eta_n(y) = 1 \text{ for some } y \in x + U) \end{cases}$$

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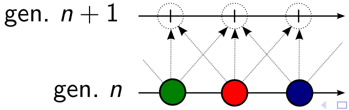
Interpretation:
In generation $n+1$, each site x is inhabitable with probability p.
If $\eta_n(y) = 1$ of some $y \in x + U$, the particle at y in gen. n puts an offspring at x.
If several y are eligible, one is chosen at random.



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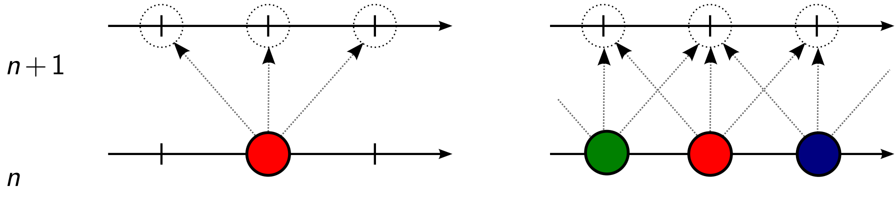
This is particularly evident in **multitype version**, where particles carry a *type*, e.g. from $(0,1)$, and offspring inherit parent's type.



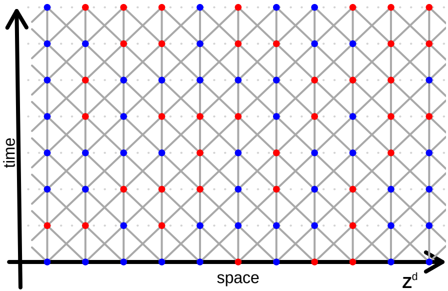
expected no. of red offspring: $3p > 1$

expected no. of red offspring: $3\frac{1}{3}p = p < 1$

Alternative view: Directed (site) percolation

$\omega(x,n)$, $x \in \mathbb{Z}^d$, $n \in \mathbb{Z}$, i.i.d. Bernoulli(p)

Interpretation: $\omega(x,n) = 1$: site (x,n) is inhabitable/open,
otherwise not inhabitable/closed



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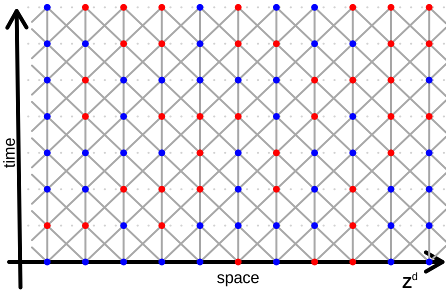

Open paths:

$m < n$, $x, y \in \mathbb{Z}^d$: $(x, m) \to (y, n)$ if there exist $x = x_0, x_1, \ldots, x_{n-m} = y$ such that $||x_i - x_{i-1}||_\infty \le 1$ and $\omega(x_i, m + i) = 1$ for $i = 1, \ldots, n - m$

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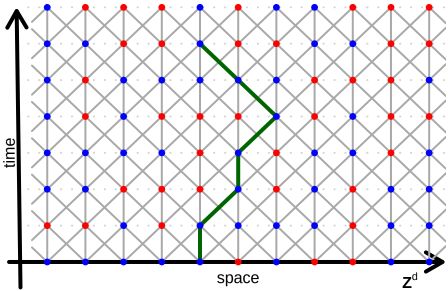

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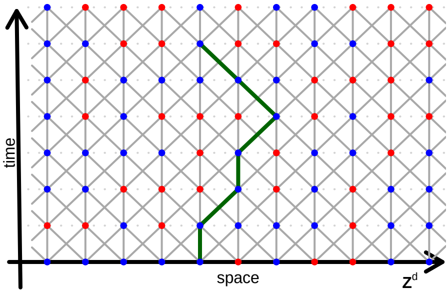

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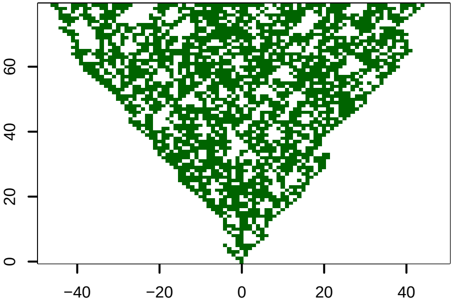
$\mathcal{C}_0 := \{(y,n) : y \in \mathbb{Z}^d, n \ge 0, (0,0) \to (y,n)\}$ is the (directed) cluster of the origin

Critical value



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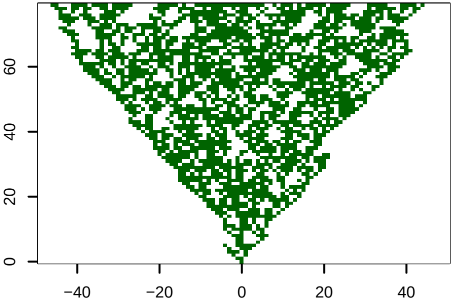

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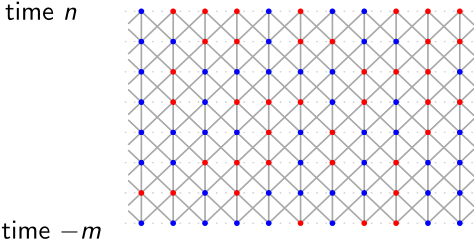
If $p > p_c$, $\mathbb{P}(\mathcal{C}_0 \text{ reaches height } n \mid |\mathcal{C}_0| < \infty) \leq Ce^{-cn}$ for some $c, C \in (0, \infty)$.

Stationary contact process and directed percolation

Assume $p > p_c$ (from now on).
Start with $\eta_{-m}(y) \equiv 1$ at time $-m < 0$, then $(n > -m)$

$$\eta_n(x) = 1 \quad \Longleftrightarrow \quad \exists\, y \in \mathbb{Z}^d \,:\, (y, -m) \to (x, n).$$



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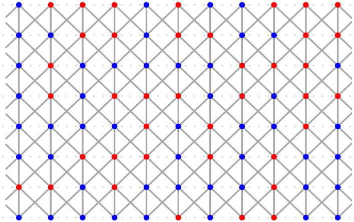


time $-m$

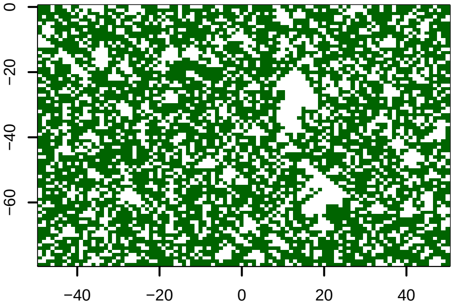
$m \to \infty$ yields $(\eta_n^{\mathrm{stat}})_{n \in \mathbb{Z}}$, the *stationary* (discrete time) contact process

$$\eta_n^{\mathrm{stat}}(x) = 1 \quad \text{“}\!\iff\!\text{”} \quad \mathbb{Z}^d \times \{-\infty\} \to (x, n)$$

(the law of η_0^{stat} is the upper invariant measure, the unique non-trivial ergodic stationary distribution)

An ancestral line in the stationary contact process

$(\eta_n^{\mathrm{stat}}(x), x \in \mathbb{Z}^d, n \in \mathbb{Z})$ stationary DCP, assume $\eta_0^{\mathrm{stat}}(0) = 1$.



Let X_n = position of the ancestor of the individual at the (space-time) origin n generations ago.

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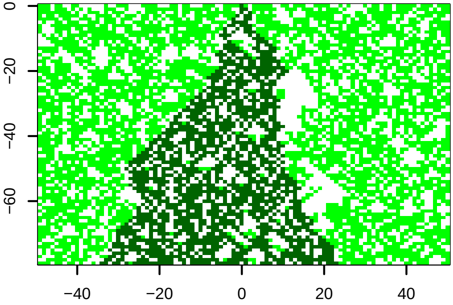

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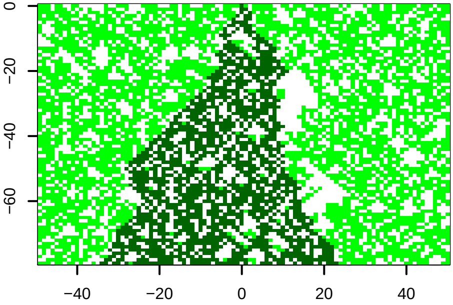

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To avoid lots of −-signs later, put $\xi_n(x) := \eta_{-n}^{\mathrm{stat}}(x)$, $x \in \mathbb{Z}^d, n \in \mathbb{Z}$.

Note: $\xi_n(x) = 1 \iff$ "$(x, n) \to \mathbb{Z}^d \times \{+\infty\}$"

Directed random walk on the supercritical directed cluster

$\omega(x, n)$, $x \in \mathbb{Z}^d$, $n \in \mathbb{Z}$, i.i.d. Bernoulli(p), $p > p_c$
$\xi_n(x)\ \big(= \xi_n(x; \omega)\big) = 1$ iff "$(x, n) \to \mathbb{Z}^d \times \{+\infty\}$"
Put $\mathcal{C} := \{(y, m) : \xi_m(y) = 1\}$, $U(x, n) := \{y : ||y - x||_\infty \leq 1\} \times \{n + 1\}$

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Let $X_0 = 0\,(\in \mathbb{Z}^d)$,

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Note:
For the voter model ($\approx$ contact process when no empty sites are allowed), ancestral lines are literally (coalescing) random walks.

Remark.

(X_n) is a random walk in space-time random environment (which is a function of $\xi = \xi(\omega)$).

Random walks in random environments and recently also random walks in dynamic (space-time) random environments have received considerable attention (see e.g. Firas Rassoul-Agha's homepage http://www.math.utah.edu/~firas/Research/)

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As far as we know, none of the general techniques developed so far in this context is applicable:

- (X_n) is not uniformly elliptic.
- ξ is complicated: not i.i.d., nor is $(\xi_n(x))_{n=0,1,\dots}$ for fixed x a Markov chain.
- The abstract conditions from Dolgopyat, Keller and Liverani (2008) appear very hard to verify.
- The cone-mixing condition from Avena, den Hollander and Redig (2010, 2011) is violated.
- The uniform coupling condition from Redig and Völlering (2011) does not hold.

A local construction of the walk

For $x \in \mathbb{Z}^d$, $n \in \mathbb{Z}$ let $\widetilde{\omega}(x,n) = \big(\widetilde{\omega}(x,n)[1], \widetilde{\omega}(x,n)[2], \dots, \widetilde{\omega}(x,n)[|3^d|]\big)$ an independent uniform permutation of $U(x,n) = (x+U) \times \{n+1\}$.

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For a space-time point (x,n) and $k \in \mathbb{N}$ define a (directed) path $\gamma_k^{(x,n)}$ of k steps that begin on open sites, choosing directions according to $\widetilde{\omega}$:

- $\gamma_k^{(x,n)}(0) = x$,
- if $\gamma_k^{(x,n)}(j) = y$ then $\gamma_k^{(x,n)}(j+1) = z$, where z is the element of

$$\left\{z' : ||z'-y||_\infty \le 1, (z', n+j+1) \to \mathbb{Z}^d \times \{n+k-1\}\right\}$$

with the smallest index in $\widetilde{\omega}(y, n+j)$

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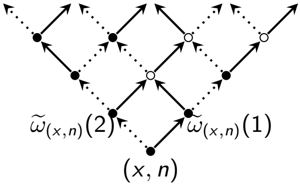

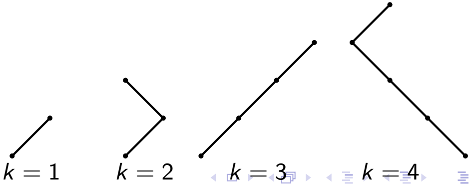

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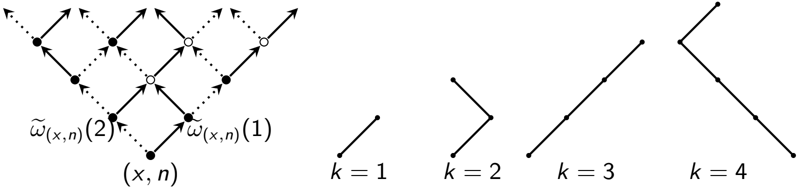
$\gamma_k^{(x,n)}(k)$ = endpoint of the local k-step construction
(interpretation: (potential) *ancestor* k generations ago of site (x,n))



For $(x,n) \in \mathcal{C}$, $\quad \gamma_\infty^{(x,n)}(j) := \lim_{k\to\infty} \gamma_k^{(x,n)}(j) \quad$ exists $\forall\, j$

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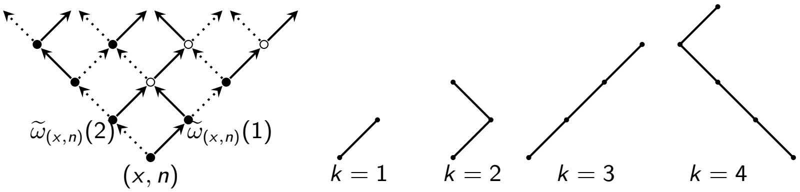

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Remarks. 1) Construction of $\gamma_k^{(x,n)}$ measurable w.r.t.
$\sigma\big(\omega(y,i), \widetilde{\omega}(y,i) : y \in \mathbb{Z}^d, n \le i < n+k\big)$

2) Randomised version of Kuczek's (1989) construction, morally a discrete time analogue of Neuhauser (1992)

Regeneration

On $B_0 := \{(0,0) \in \mathcal{C}\}$

$$X_k := \gamma_\infty^{(0,0)}(k), \ k = 0, 1, 2, \ldots$$

is (a version of) the directed random walk on $\mathcal{C}$,
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Regeneration times:

$T_0 := 0,\ Y_0 := 0,$

$T_1 := \min\big\{k > 0 : \xi_k\big(\gamma_k^{(0,0)}(k)\big) = 1\big\},\ Y_1 := \gamma_{T_1}^{(0,0)}(T_1) = X_{T_1}$,

then $T_2 := T_1 + \min\big\{k > 0 : \xi_{T_1+k}\big(\gamma_k^{(Y_1,T_1)}(k)\big) = 1\big\}$,

$Y_2 := \gamma_{T_2-T_1}^{(Y_1,T_1)}(T_2 - T_1) = X_{T_2}$, etc.

Proposition

$\big((Y_i - Y_{i-1}, T_i - T_{i-1})\big)_{i\geq 1}$ is i.i.d. under $\mathbb{P}(\cdot \mid B_0)$, Y_1 is symmetrically distributed. There exist $C, c \in (0,\infty)$, such that

$$\mathbb{P}(||Y_1|| > n \mid B_0),\ \mathbb{P}(\tau_1 > n \mid B_0) \leq Ce^{-cn} \quad \text{for } n \in \mathbb{N}.$$

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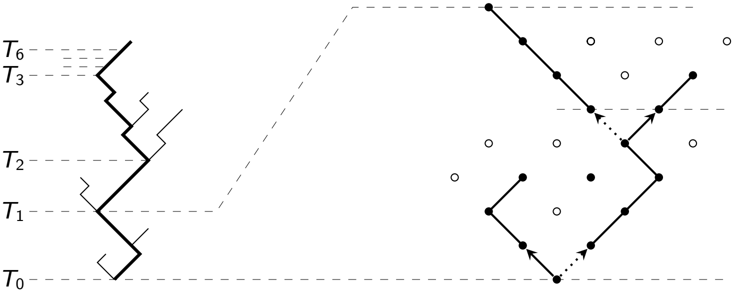

Tail bounds use the fact that finite clusters are small,

i.i.d. property follows from the fact that the local path construction uses disjoint time-slices.

LLN and annealed CLT for directed walk on the cluster

Corollary

$$\mathbb{P}\Big(\frac{1}{n}X_n \to 0 \,\Big|\, B_0\Big) = 1 \quad \text{and} \quad \mathbb{P}\Big(\frac{1}{n}X_n \to 0 \,\Big|\, \omega\Big) = 1 \quad \text{for } \mathbb{P}(\,\cdot \mid B_0)\text{-a.a. } \omega,$$

there exists $\sigma \in (0, \infty)$ s.th.

$$\lim_{n\to\infty} \mathbb{E}\Big[f\big(\tfrac{1}{\sigma\sqrt{n}}X_n\big) \,\Big|\, B_0\Big] = \mathbb{E}\big[f(Z)\big]$$

for any continuous bounded $f : \mathbb{R}^d \to \mathbb{R}$, where Z is d-dimensional standard normal.

A quenched CLT

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Note: Quenched CLT implies annealed CLT but yields much more information.
Extreme example: $\mathbb{P}\big(X_n = Z_n\,\big|\,\omega\big) = 1$ would be compatible with annealed CLT as long as $Z_n/\sqrt{n}$ is approximately normal.

Two walks on the same cluster

(X_n), (X'_n) two independent directed walks on the same supercritical directed cluster ξ (i.e. using the same ω's, but independent $\widetilde{\omega}$'s resp. $\widetilde{\omega}'$.)

Proposition

Let $d \geq 2$, $p > p_c$. There exists $b > 0$ s.th. for $f, g \in C_b(\mathbb{R}^d) \cap Lip(\mathbb{R}^d)$

$$\left| \mathbb{E}\left[f\left(\tfrac{1}{\sigma\sqrt{n}} X_n\right) g\left(\tfrac{1}{\sigma\sqrt{n}} X'_n\right) \,\Big|\, B_0 \right] - \mathbb{E}\big[f(Z)\big]\, \mathbb{E}\big[g(Z)\big] \right| \leq \frac{C_{f,g}}{n^b},$$

in particular $\mathbb{E}\left[f\left(\tfrac{1}{\sigma\sqrt{n}} X_n\right) \Big| \omega \right] \to \mathbb{E}\big[f(Z)\big]$ in $L^2\big(\mathbb{P}(\cdot \mid B_0)\big)$.

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Exponential mixing of ξ allows to couple with two walks on *independent* copies ξ and ξ' with high probability. (In $d = 2$ the two walks *do* meet $\approx \log n$ times up to time n, but with high probability not after time ϵn; in $d = 1$ we use a martingale decomposition)

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From Prop., obtain first quenched CLT for (X_n) along subsequence, then use additional concentration argument.

Back to ancestral lineages

Remarks

- Variation where (X_n) and (X'_n) coalesce upon meeting is of interest in mathematical population genetics:
  "Everything"[1] that is true for the neutral multi-type voter model is also true for the neutral multi-type discrete contact process.
- (Some) analogous arguments for the continuous-time case by Neuhauser (1992) and Valesin (2010).
- Diffusion rate $\sigma^2 = \sigma^2(p) = \mathbb{E}\big[Y_{1,1}^2\big]/\mathbb{E}[T_1] \in (0, \infty)$
  (no explicit formula, but in principle well-behaved for simulations since T_1, $Y_{1,1}$ have exponential tails)

  Effective coalescence probability still a "black box" (at least to me)
- Method also works for a variant with random carrying capacities and more general finite range, symmetric dispersal range U

[1] with a suitable interpretation of "everything".
Examples: Clustering of neutral types in $d = 1, 2$; multiype contact equilibria exists in $d \geq 3$, $\mathbb{P}\big(\text{two ind. sampled at distance } x \text{ have same type}\big) \sim C\, x^{2-d}$.

A spatial logistic model

Particles "live" in $\mathbb{Z}^d$ in discrete generations,
$\eta_n(x) = \#$ particles at $x \in \mathbb{Z}^d$ in generation n.

Given η_n,

each particle at x has $\mathrm{Poisson}\big(m - \sum_z \lambda_{z-x}\eta_n(z)\big)\big)_+$ offspring,
$m > 1$, $\lambda_z \geq 0$, $\lambda_0 > 0$, finite range.

Children take an independent random walk step to y with probability p_{y-x},
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$$\eta_{n+1}(y) \sim \mathrm{Poi}\Big(\sum_x p_{y-x}\eta_n(x)\Big(m - \sum_z \lambda_{z-x}\eta_n(z)\Big)_+\Big), \quad \text{independent}$$

Survival and complete convergence

Theorem (B. & Depperschmidt, 2007)

Assume $m \in (1,3)$, $0 < \lambda_0 \ll 1$, $\lambda_z \ll \lambda_0$ for $z \neq 0$.

(η_n) survives for all time globally and locally with positive probability for any non-trivial initial condition η_0.

Given survival, η_n converges in distribution to its unique non-trivial equilibrium.

Starting from any two initial conditions η_0, η_0', copies (η_n), (η_n') can be coupled such that if both survive, $\eta_n(x) = \eta_n'(x)$ in a space-time cone.

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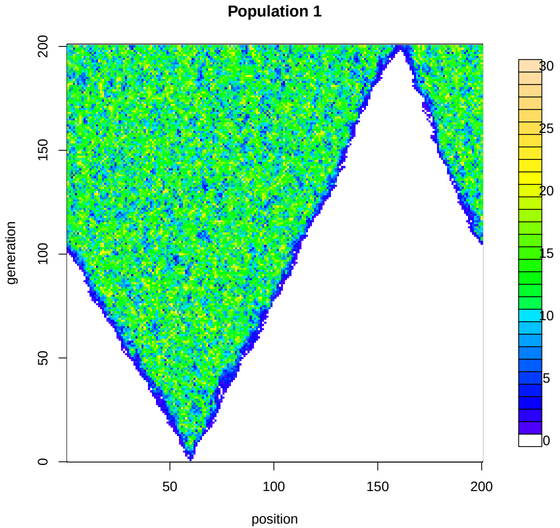
Proof uses that corresponding deterministic system

$$\zeta_{n+1}(y) = \sum_x p_{y-x}\zeta_n(x)\Big(m - \sum\nolimits_z \lambda_{z-x}\zeta_n(z)\Big)_+$$

has unique non-triv. fixed point

plus coarse-graining, lots of comparisons with directed percolation.

Coupling, survival and convergence



$m = 1.5,\ p = (1/3, 1/3, 1/3),\ \lambda = (0.01, 0.02, 0.01)$

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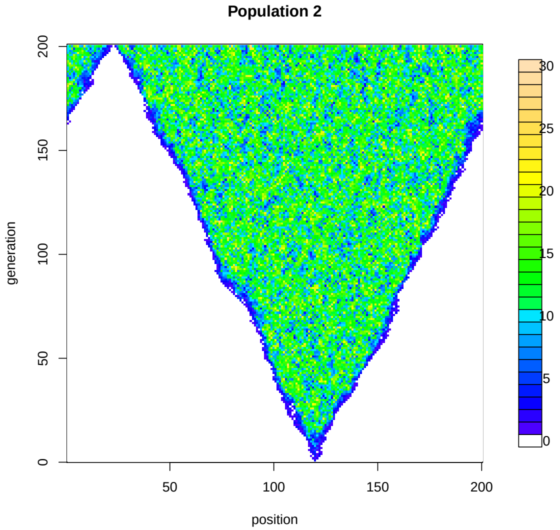

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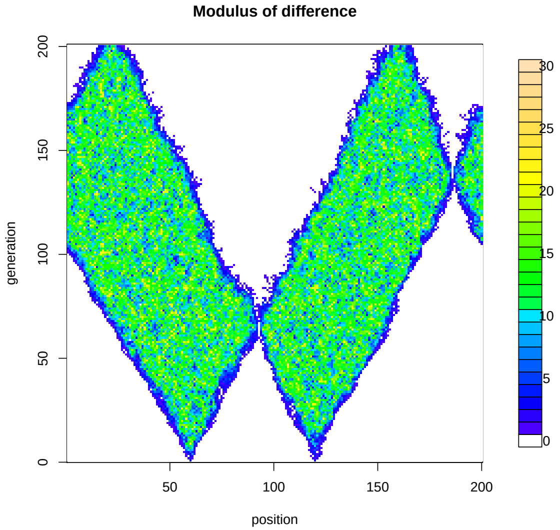

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Ancestral lines

Given stationary $(\eta_n^{\mathrm{stat}}(x), n \in \mathbb{Z}, x \in \mathbb{Z}^d)$, cond. on $\eta_0^{\mathrm{stat}}(0) > 0$, sample an individual from space-time origin $(0,0)$ (uniformly)

Let (X_n) position of her ancestor n generations ago:

Given η^{stat} and $X_n = x$, $X_{n+1} = y$ w. prob.

$$\frac{p_{x-y}\eta_{-n-1}^{\mathrm{stat}}(y)\big(m - \sum_z \lambda_{z-y}\eta_{-n-1}^{\mathrm{stat}}(z)\big)^+}{\sum_{y'} p_{x-y'}\eta_{-n-1}^{\mathrm{stat}}(y')\big(m - \sum_z \lambda_{z-y'}\eta_{-n-1}^{\mathrm{stat}}(z)\big)^+}$$

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Hopeful result in progress ...

If $m \in (1,3)$, $0 < \lambda_0 \ll 1$, $\lambda_z \ll \lambda_0$ for $z \neq 0$, there is a regeneration construction for (X_n).
This again yields LLN and CLT for the ancestral line of an individual drawn from equilibrium.

Thank you for your attention!