Ancestral lineages in locally regulated populations

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based on joint work, in part in progress, with
Jiří Černý, Andrej Depperschmidt, Nina Gantert and Sebastian Steiber

Spatial models in population genetics

University of Bath, 6–8 September 2017

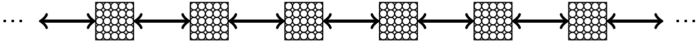
Outline

1. Introduction
2. Discrete time contact process and oriented percolation
   - Ancestral lines, RWDRE and a CLT
   - Central proof ingredient: Regeneration construction
3. Logistic branching random walks and 'relatives'
   - Long-time behaviour: Coupling and convergence
   - Ancestral lineages in the spatial logistic model

Outline

Stepping stone model (Kimura, 1953) (here, in discrete time)

Colonies of *fixed* size N are arranged in a geographical space, say $\mathbb{Z}^d$



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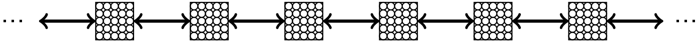

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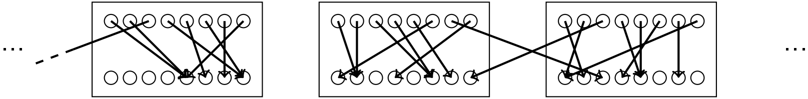
For each child: Assign a random parent in same colony with probability $1 - \nu$, in a neighbouring colony with probability ν



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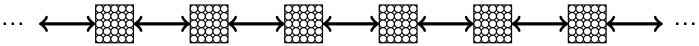

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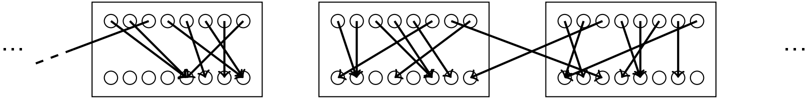

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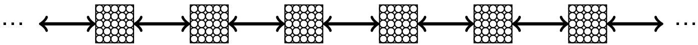

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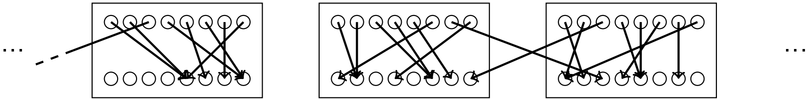

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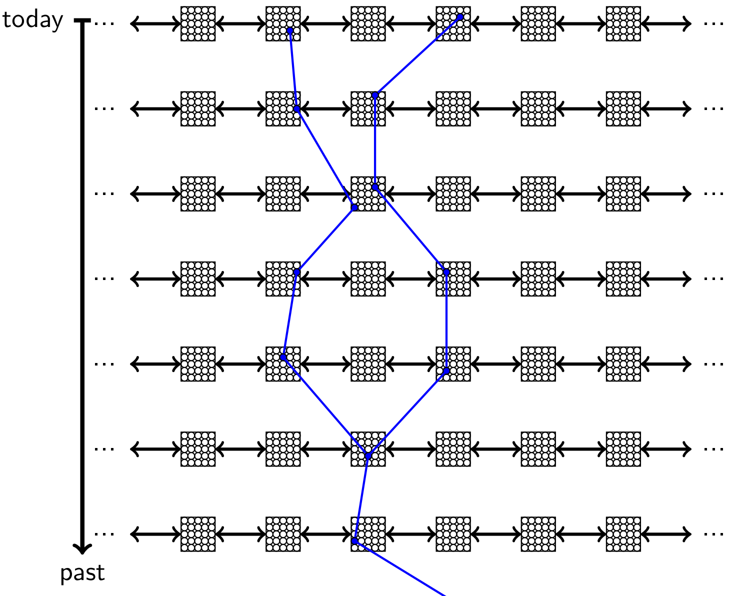
"Trivial" demographic structure, but paradigm model for evolution of *type distribution* in space

Stepping stone model: Ancestral lines



The stepping stone model

Fixed local population size N in each patch (arranged on $\mathbb{Z}^d$), patches connected by (random walk-type) migration

Pros:
+ Stable population, no local extinction, nor unbounded growth
+ Ancestral lineages are (delayed) coalescing random walks (in particular, well defined),

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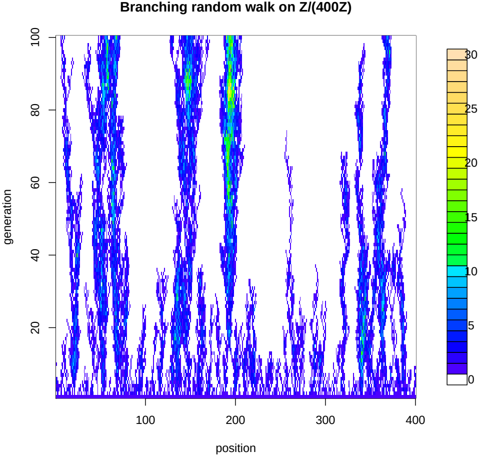
Cons:
- $-$ An ‘ad hoc’ simplification, effects of local size fluctations not explicitly modelled
- $-$ N is an ‘effective’ parameter, relation to ‘real’ population dynamics is unclear
- $-$ Grid not so realistic for most populations

Remark: A problem with branching random walk

(Critical) branching random walks, where particles move and produce offspring independently, explicitly model fluctuations in local population size, but do not allow stable populations in $d \leq 2$:



(Felsenstein's "pain in the torus" 1975; Kallenberg 1977)

Remark: A problem with branching random walk, 2

One could try to slow down the branching:

Self-catalytic critical branching random walks (in continuous time)

$a = (a_x)_{x \in \mathbb{Z}^d}$ ... a probability kernel

$b : \mathbb{N}_0 \to [0, \infty)$ ... branching rate function, $b(0) = 0$

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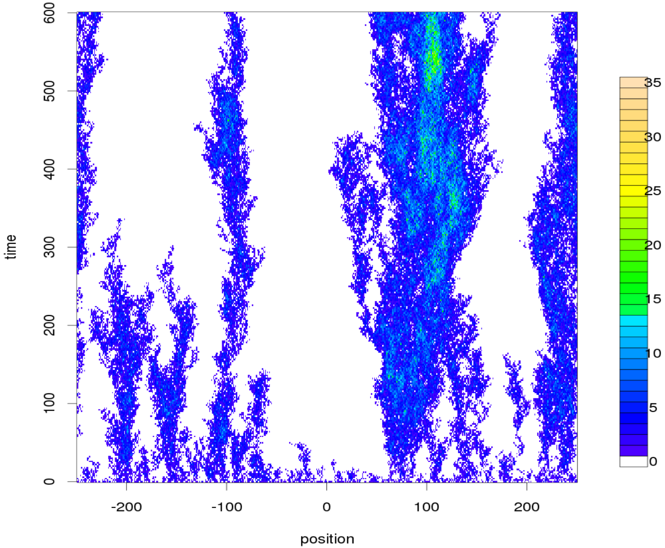
  disappears or doubles, each with prob. $\frac{1}{2}$
  note: each particle branches then at rate $b(k)/k$,
  $b(k) = c \cdot k$ corresponds to independent branching rw

Even $b(k) \ll k$ cannot prevent clustering

Self-catalytic branching rw, $b(k) = k^{1/10}$ in $d = 1$ (on $\mathbb{Z}/(500\mathbb{Z})$)



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assume $\sup_{x\in\mathbb{Z}^d} \mathbb{E}[\eta_x(0)] < \infty$

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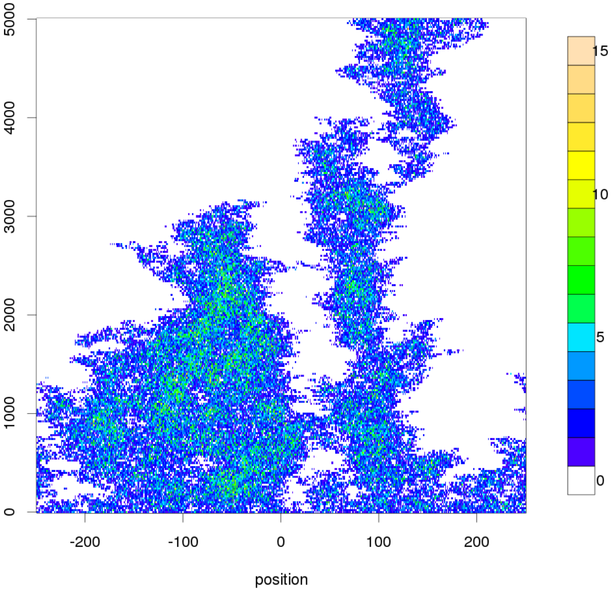
Theorem (B. & Sun, 2017)**.**
If $b(1) > 0$
and motion with the symmetrised kernel $\widehat{a_x} = (a_x + a_{-x})/2$ is recurrent
(e.g. finite variance and $d \leq 2$),

$$\lim_{t\to\infty} \mathbb{P}\big(\eta_x(t) = 0\big) = 1 \quad \text{for all } x \in \mathbb{Z}^d.$$

A simulation, $b(k) = \mathbf{1}_{\{k=1\}}$



Outline

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: $U \left(= \{y \in \mathbb{Z}^d : ||y||_\infty \leq 1\right) \subset \mathbb{Z}^d$ 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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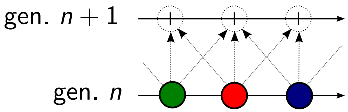
Interpretation:
In generation $n+1$, each site x is (independently) inhabitable with probability p.

If $\eta_n(y) = 1$ for some $y \in x + U$, the particle at y in generation n places an offspring at x.



If several y are eligible, one is chosen at random.

The discrete time contact process ...

... viewed as a locally regulated population model

Neighbours compete for inhabitable sites, so individuals in sparsely populated regions have on average higher reproductive success.

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... viewed as a locally regulated population model

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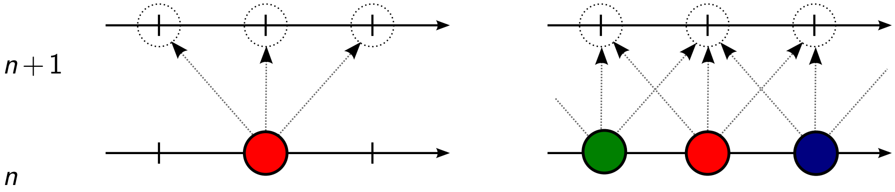
This is particularly evident in the **multitype version**, where particles carry a *type*, e.g. from $(0, 1)$, and offspring inherit parent's type.



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

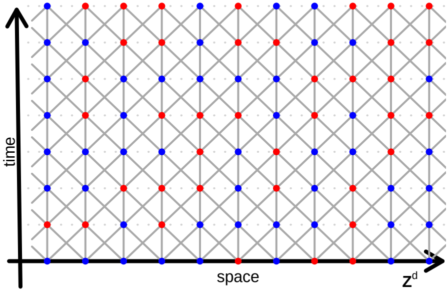
expected no. of red offspring: $3\frac{1}{3}p = p < 1$

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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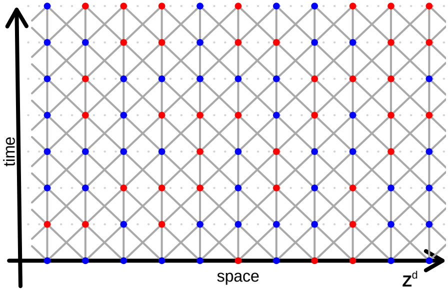

Open paths:

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

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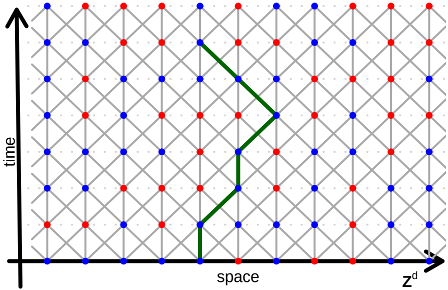

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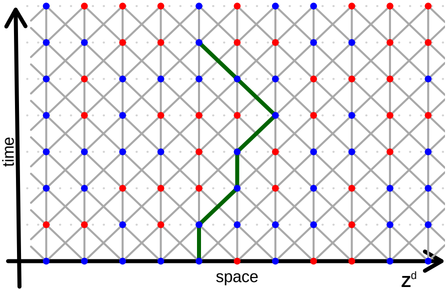

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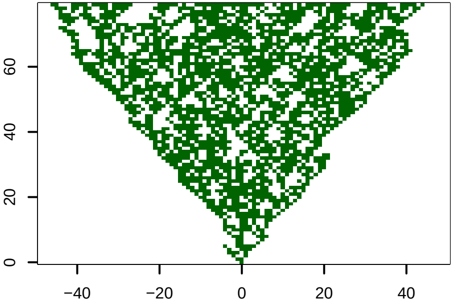
$\mathcal{C}_0 := \{(y, n) : y \in \mathbb{Z}^d, n \geq 0, (0,0) \to_\omega (y, n)\}$ is the (directed) cluster of the origin

Critical value



There exists $p_c \in (0, 1)$ such that

$$\mathbb{P}(|\mathcal{C}_0| = \infty) > 0 \quad \text{iff} \quad p > p_c.$$

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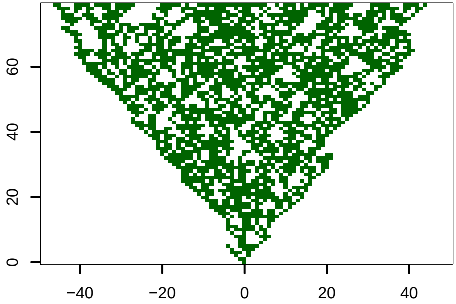

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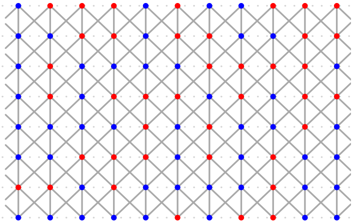
If $p > p_c$, $\mathbb{P}(\mathcal{C}_0 \text{ reaches height } n \mid |\mathcal{C}_0| < \infty) \leq Ce^{-cn}$ for some $c, C \in (0, \infty)$.

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 $(n > -m)$

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

time n



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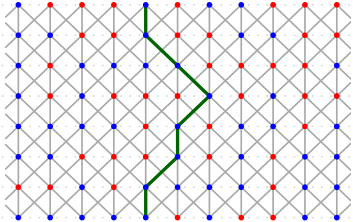

time $-m$

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

$$\eta_n^{\mathrm{stat}}(x) = 1 \quad \text{“}\!\Longleftrightarrow\!\text{''} \quad \mathbb{Z}^d \times \{-\infty\} \to_\omega (x, n)$$

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

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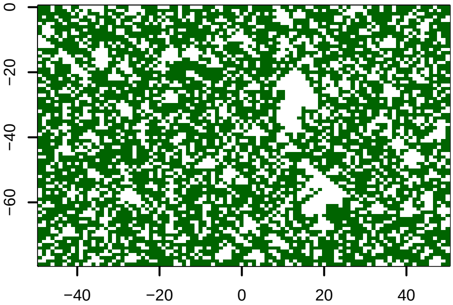
An ancestral line in the stationary contact process

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



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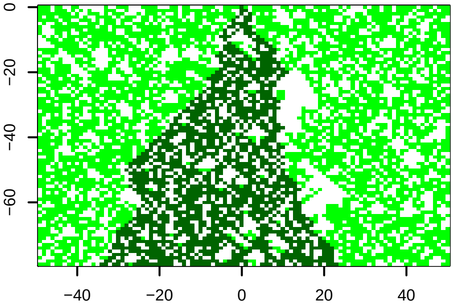

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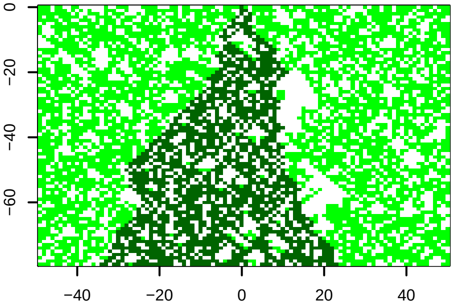

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To avoid lots of −-signs later, put $\xi_n(x) := \eta_{-n}^{\text{stat}}(x)$, $x \in \mathbb{Z}^d, n \in \mathbb{Z}$.

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

Directed random walk on the supercritical oriented cluster

$\omega(x,n)$, $x \in \mathbb{Z}^d$, $n \in \mathbb{Z}$, i.i.d. Bernoulli(p), $p > p_c$
$\xi(x,n) \big(= \xi(x,n;\omega)\big) = 1$ iff "$(x,n) \to_\omega \mathbb{Z}^d \times \{+\infty\}$"

Put $\mathcal{C} := \{(y,m) : \xi(y,m) = 1\}$ (the "backbone" of the oriented cluster, i.e. "dangling ends" are removed),
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Let $X_0 = 0 \,(\in \mathbb{Z}^d)$,

$$\mathbb{P}(X_{n+1} = y \mid \xi, X_n = x, X_{n-1} = x_{n-1}, \dots X_1 = x_1) = \frac{\mathbf{1}(y \in U(x,n) \cap \mathcal{C})}{|U(x,n) \cap \mathcal{C}|}$$

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It turns out: (X_n) is similar to "ordinary" random walk on large scales.

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It turns out: (X_n) is similar to "ordinary" random walk on large scales.

(It is a random walk in dynamic random environment, but somewhat non-standard from RWDRE point of view.)

LLN and CLT for directed walk on the oriented cluster

Theorem (B., Černý, Depperschmidt, Gantert 2013)**.**

Let $B_0 := \{(\mathbf{0},0) \in \mathcal{C}\}$, $p > p_c$.

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

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

$$\lim_{n\to\infty} \mathbb{E}\Big[f\big(\tfrac{1}{\sigma\sqrt{n}}X_n\big) \,\Big|\, \omega\Big] = \mathbb{E}\big[f(Z)\big] \quad \text{for } \mathbb{P}(\,\cdot \mid B_0)\text{-a.a. } \omega$$

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

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

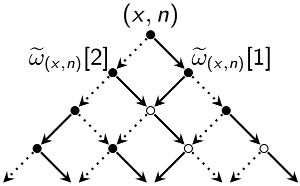
An invariance principle holds as well.

Outline

1. Introduction
2. Discrete time contact process and oriented percolation
   - Ancestral lines, RWDRE and a CLT
   - Central proof ingredient: Regeneration construction
3. Logistic branching random walks and ‘relatives’
   - Long-time behaviour: Coupling and convergence
   - Ancestral lineages in the spatial logistic model

Proof ingredient: 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 $U(x) = \{y : ||y-x||_\infty \le 1\}$.



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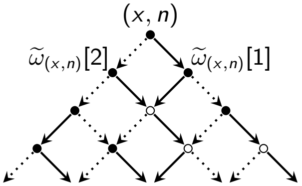

For a space-time point (x,n) and $k \in \mathbb{N}$ define a (directed) path $\gamma_k^{(x,n)}$ of k steps that *begin* on open sites, choosing directions according to $\widetilde{\omega}$:

- $\gamma_k^{(x,n)}(0) = x$,
- if $\gamma_k^{(x,n)}(j) = y$ then $\gamma_k^{(x,n)}(j+1) = z$, where z is the element of
$$\big\{z' : ||z'-y||_\infty \le 1, (z', n+j+1) \to_\omega \mathbb{Z}^d \times \{n+k-1\}\big\}$$
with the smallest index in $\widetilde{\omega}(y, n+j)$

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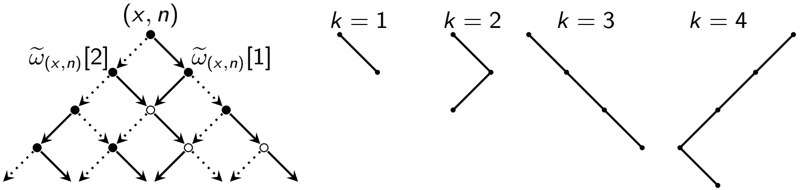

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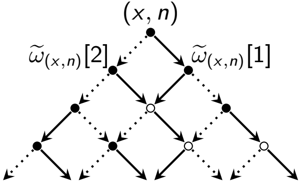
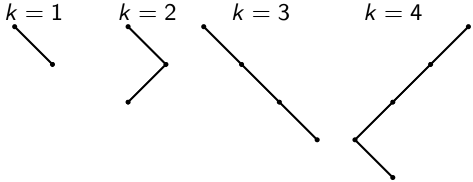
Local vs global construction of the walk

$\gamma_k^{(x,n)}(k)$ = endpoint of the local k-step construction





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

and $\gamma_k^{(x,n)}(k) = \gamma_\infty^{(x,n)}(k)$ if $\xi_{n+k}\big(\gamma_k^{(x,n)}(k)\big) = 1$.

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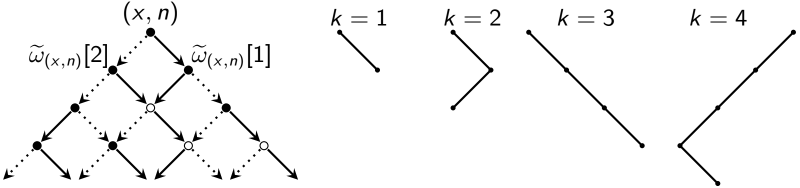

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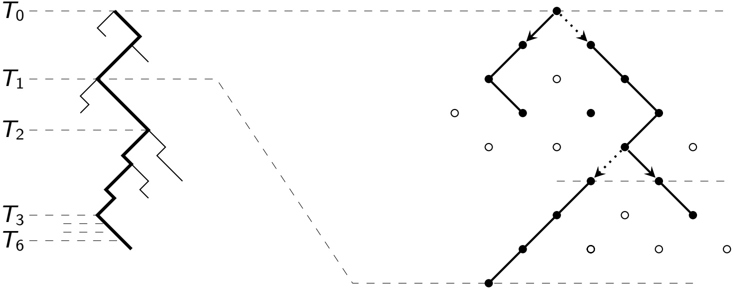
On $B_0 := \{(0,0) \in \mathcal{C}\}$,

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

is (a version of) the directed random walk on $\mathcal{C}$,
and $X_k = \gamma_k^{(0,0)}(k)$ if $\xi\big(\gamma_k^{(0,0)}(k), k\big) = 1$.

Regeneration times



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

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

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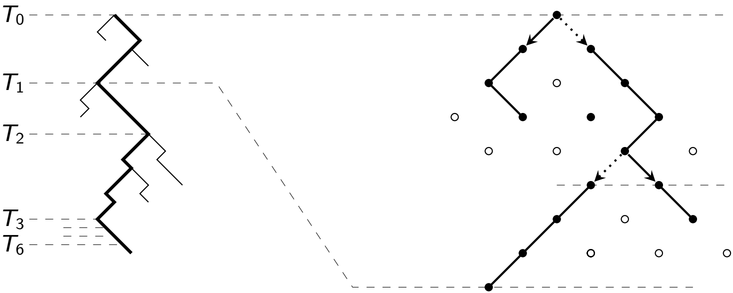

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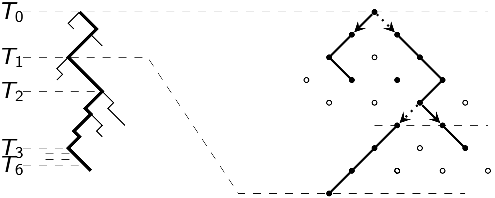
then $T_2 := T_1 + \min\left\{k > 0 : \xi\left(\gamma_k^{(Y_1,T_1)}(k), T_1 + k\right) = 1\right\},$

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

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

$$\mathbb{P}(||Y_1|| > n \mid B_0),\ \mathbb{P}(T_1 > n \mid B_0) \leq Ce^{-cn} \quad \text{for } n \in \mathbb{N}.$$



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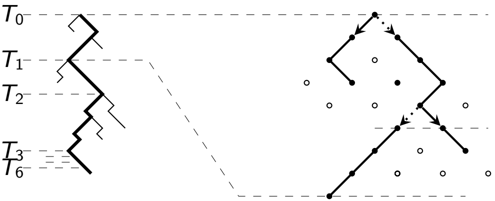

Tail bounds use the fact that finite clusters are small,
i.i.d. property follows from the fact that the local path construction uses disjoint time-slices.

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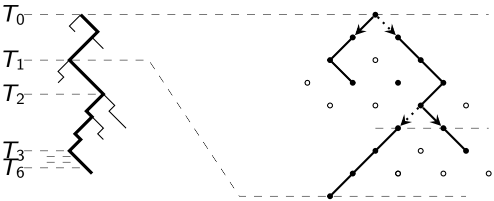

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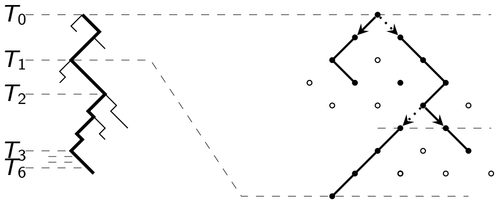

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Randomised version of Kuczek's (1989) construction, morally a discrete time analogue of Neuhauser (1992)

A.s. CLT uses variance estimates obtained from *joint* regeneration for two independent copies (X_n), (X_n') on the same ξ.

A "meta-theorem"

"Everything"[1] that is true for the neutral multi-type voter model is also true for the neutral multi-type contact process (and presumably for more general locally regulated models).

[1] with a suitable interpretation of "everything"

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Some "rigorous instances" (S. Steiber 2017)

- Start two walks on the cluster in $x_1 \neq x_2$ which coalesce when meeting (condition on $\xi(x_1, 0) = \xi(x_2, 0) = 1$), let T_{merge} = time until coalescence
  $T_{\mathrm{merge}} < \infty$ a.s. in $d = 1, 2$, $\mathbb{P}(T_{\mathrm{merge}} = \infty) > 0$ in $d \geq 3$
  (in particular, no neutral multi-type equilibria in $d \leq 2$)
- In $d = 1$, $\mathbb{P}(T_{\mathrm{merge}} \geq n) \asymp \dfrac{|x_1 - x_2|}{\sqrt{n}}$,
  start coalescing directed random walks on *every* site with $\xi(x, n) = 1$ and re-scale this set of paths diffusively:
  Obtain *Brownian web* as scaling limit.

[1] with a suitable interpretation of "everything"

Outline

Logistic branching random walks

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 Poisson$\big(\big(m - \sum_z \lambda_{z-x}\eta_n(z)\big)^+\big)$ offspring,
$m > 1$, $\lambda_z \geq 0$, $\lambda_0 > 0$, symmetric, finite range.

(Interpretation as local competition:
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$$\eta_{n+1}(y) \sim \mathrm{Poi}\Big(\sum_x p_{y-x}\eta_n(x)\big(m - \textstyle\sum_z \lambda_{z-x}\eta_n(z)\big)^+\Big), \quad \text{independent}$$

Remarks

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- For $\lambda \equiv 0$, (η_n) is a branching random walk.
- (η_n) is a spatial population model with local density-dependent feedback:
  Offspring distribution supercritical when there are few neighbours, subcritical when there are many neighbours
- System is in general *not* attractive.
- Conditioning[2] on $\eta_n(\cdot) \equiv N$ for some $N \in \mathbb{N}$ ("effective local population size") yields a discrete version of the stepping stone model
- Form of competetion kernel and Poisson offspring law are convenient but could be more general.

[2] and considering types and/or ancestral relationships

Outline

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.

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Proof uses

- corresponding deterministic system

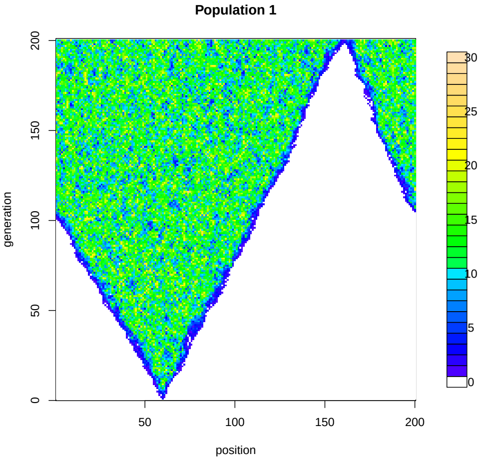
$$\zeta_{n+1}(y) = \sum_x p_{y-x} \zeta_n(x) \Big(m - \sum_z \lambda_{z-x} \zeta_n(z) \Big)^+$$

  has unique (and globally attracting) non-triv. fixed point
- strong coupling properties of η
- coarse-graining and comparison with directed percolation

Remarks

- Local extinction for $m \leq 1$ (domination by subcritical branching r.w.)
- Restriction to $m < 3$ in result "inherited" from logistic iteration $w_{n+1} = mw_n(1 - w_n)$
- Survival can be proved also for $m \in [3, 4)$ with analogous arguments, convergence not

Coupling: An essential proof ingredient



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

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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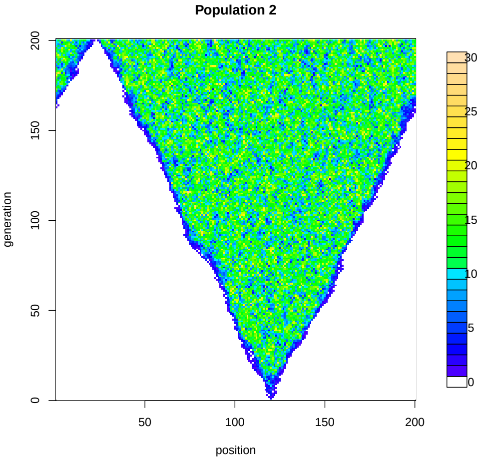

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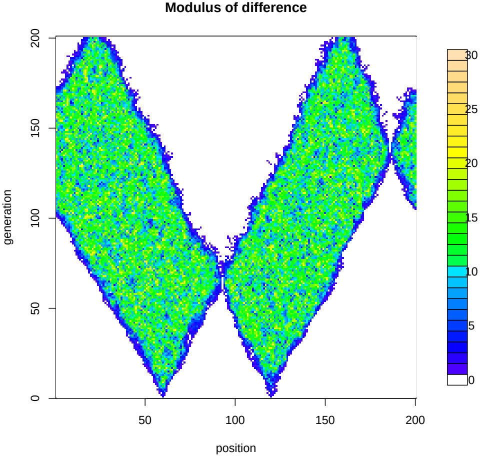

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Dynamics of an ancestral line

Given stationary $(\eta_n^{\mathrm{stat}}(x), n \in \mathbb{Z}, x \in \mathbb{Z}^d)$, cond. on $\eta_0^{\mathrm{stat}}(\mathbf{0}) > 0$ (and "enrich" suitably to allow bookkeeping of genealogical relationships), sample an individual from space-time origin $(\mathbf{0}, 0)$ (uniformly)

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Let X_n = position of her ancestor n generations ago:

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

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

(note: a Poisson vector conditioned on its total sum is multinomial)

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Note: (X_n) is close to ordinary rw in regions where relative variation of $\eta_{-n-1}(x)$ is small.

Large scale behaviour of an ancestral line

X_n = position of ancestor n generations ago of an individual sampled today at origin in equilibrium

Theorem (LLN and (averaged) CLT, B., Černý, Depperschmidt 2016).
If $m \in (1,3)$, $0 < \lambda_0 \ll 1$, $\lambda_z \ll \lambda_0$ for $z \neq 0$,

$$\mathbb{P}\Big(\frac{1}{n}X_n \to 0 \,\Big|\, \eta_0(0) \neq 0\Big) = 1 \;\text{ and }\; \mathbb{E}\Big[f\big(\tfrac{1}{\sqrt{n}}X_n\big) \,\Big|\, \eta_0(0) \neq 0\Big] \underset{n\to\infty}{\longrightarrow} \mathbb{E}\big[f(Z)\big]$$

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The proof uses a *regeneration* construction
(and *coarse-graining* and *coupling*, in particular with directed percolation):

Regeneration times $0 = T_0 < T_1 < T_2 < \cdots$, express $X_{T_k} = Y_1 + \cdots + Y_k$ with $Y_i := X_{T_i} - X_{T_{i-1}}$ and $(Y_i, T_i - T_{i-1})_{i\geq 1}$ ‘almost i.i.d.’

Spatial population models (η_n) and ancestral lineages (X_k): Abstract conditions

- *Local Markov structure*: $\eta_{n+1}(x)$ is a function of η_n in a finite window around x plus ‘local randomness’

  Given η, $(X_k)_{k=0,1,\dots}$ is a Markov chain, $\mathbb{P}(X_{k+1} = \cdot \,|\, \eta, X_k = x)$ depends on η_{-k}, η_{-k-1} in a finite window around x

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- *Good configurations and coupling propagation for η on coarse-grained scale $L_{\text{space}}\mathbb{Z}^d \times L_{\text{time}}\mathbb{Z}$*: With high probability,

  'good' blocks make neighbours good in L_{time} steps and

  η's with two different good local initial conditions become locally identical after L_{time} steps

Spatial population models (η_n) and ancestral lineages (X_k): Abstract conditions

- *Local Markov structure*: $\eta_{n+1}(x)$ is a function of η_n in a finite window around x plus 'local randomness'

  Given η, $(X_k)_{k=0,1,\dots}$ is a Markov chain, $\mathbb{P}(X_{k+1} = \cdot \,|\, \eta, X_k = x)$ depends on η_{-k}, η_{-k-1} in a finite window around x

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- *Good configurations and coupling propagation for η on coarse-grained scale $L_{\text{space}}\mathbb{Z}^d \times L_{\text{time}}\mathbb{Z}$*: With high probability,

  'good' blocks make neighbours good in L_{time} steps and

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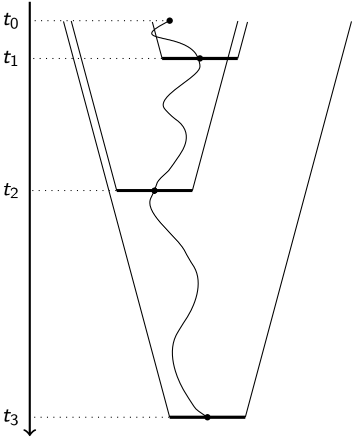
- *On good η blocks, the law of X is 'well behaved'*: close to a non-disorded symmetric finite range reference walk

- *Symmetry in distribution*

Idea for constructing regeneration times

Find time points along the path such that:

- a cone (with fixed suitable base diameter and slope)
  centred at the current space-time position of the walk covers the path and everything it has explored so far (since the last regeneration)
- configuration η^{stat} at the base of the cone is "good"
- "strong" coupling for η^{stat} occurs inside the cone



Then, the conditional law of future path increments is completely determined by the configuration η^{stat} at the base of the cone
(= a finite window around the current position)

Remarks

- Technique is robust (applies to many spatial population models in "high density" regime) but current result "conceptual" rather than practical
- Work in progress (so far in $d \geq 3$):
  A "joint regeneration" construction allows to analyse
  samples of size 2 (or even more) on large space-time scales
  (as for the contact process)
  and to derive an a.s. version of the CLT
- Meta-theorem (again): "Everything"[3] that is true for the neutral multi-type voter model is also true for the neutral multi-type spatial logistic model.

[3] with a suitable interpretation of "everything"

More details can be found in

M. B., A. Depperschmidt, Survival and complete convergence for a spatial branching system with local regulation, Ann. Appl. Probab. 17 (2007), 1777–1807

M. B., J. Černý, A. Depperschmidt, N. Gantert, Directed random walk on an oriented percolation cluster, Electron. J. Probab. 18 (2013), Article 80

M. B., J. Černý, A. Depperschmidt, Random walks in dynamic random environments and ancestry under local population regulation, Electron. J. Probab. 21 (2016), Article 38

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Thank you for your attention!