

Random walks in dynamic random environments and ancestry under local population regulation

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based on joint work, in part in progress, with
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General aim

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).

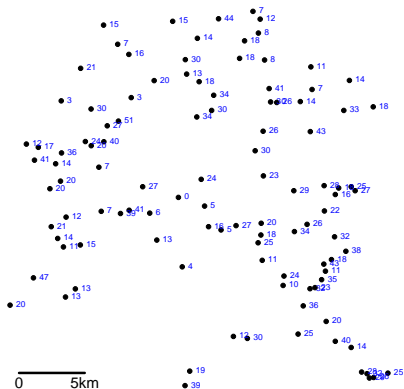
A step towards combining ecological and population genetics aspects in a stochastic spatial population model

Caveat: Most results so far are more of conceptual than practical interest.

Outline

- 1 Introduction
- 2 Logistic branching random walks and 'relatives'
 - Coupling
- 3 Spatial embedding of an ancestral line
- 4 Outlook

M. Lamotte's grove snail data (*cepaea nemoralis*)



Frequency of the $b+$ gene in 108 colonies in a region in Aquitaine, southwestern France

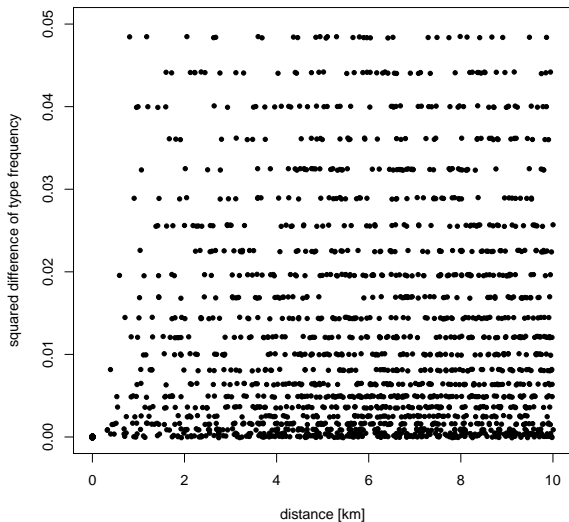


(c) Wikipedia user Mad Max

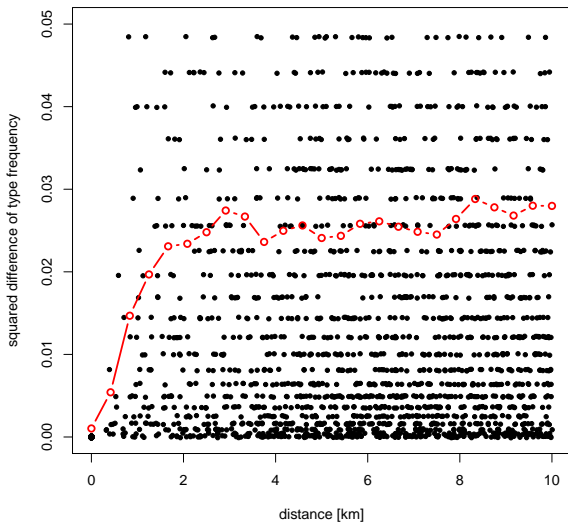


Maxime Lamotte, Recherches sur la structure génétique des populations naturelles du *Cepaea nemoralis*, Bulletin biologique de France et de Belgique, Suppl. 35, 1–239, (1951)

M. Lamotte's grove snail data



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Let $\eta(\mathbf{x})$ = frequency of gene $b+$ in colony at $\mathbf{x} \in \mathbb{R}^2$

Question: For population in homogeneous equilibrium,

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where

$\phi(\mathbf{x}, \mathbf{y}) = \text{Prob.}(\text{two individuals, sampled at } \mathbf{x} \text{ and at } \mathbf{y} \text{ have same type}).$

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Assuming stationarity, we can estimate $\mathbb{E}[\eta(\mathbf{x})^2] = \mathbb{E}[\eta(\mathbf{0})^2]$ and $\mathbb{E}[\eta(\mathbf{x})] = \mathbb{E}[\eta(\mathbf{0})]$ from the data, for $\phi(\mathbf{x}, \mathbf{y})$ we use *Malécot's formula* (assuming, in particular, small mutation rates).

Malécot's formula

$$\phi(\mathbf{x}, \mathbf{y}) = \phi(\mathbf{x} - \mathbf{y}) \approx \frac{1}{N + \log(\sigma/\kappa\sqrt{2\mu})} K_0(\sqrt{2\mu}\|\mathbf{x} - \mathbf{y}\|/\sigma)$$

with μ = mutation rate, σ = (backward) 'dispersal distance',
 N = 'neighbourhood size', κ = 'local scale'

[and $K_0(r) = \int_0^\infty \exp(-r^2t - 1/(4t)) \frac{dt}{t}$ is the modified Bessel function of the second kind of order 0]

(Malécot 1948, cf also Barton, Depaulis, Etheridge 2002)

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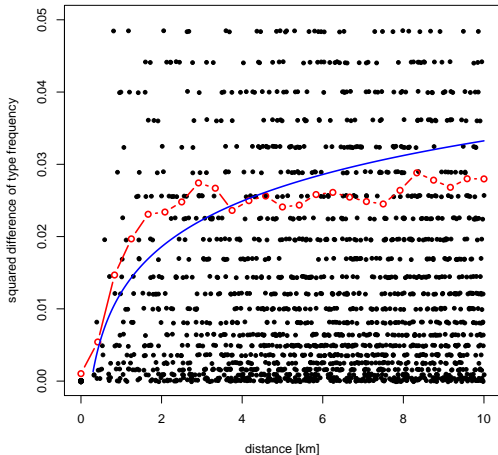
Obtained from recursive decomposition ('follow two lineages backwards')

$$\begin{aligned} \phi(\mathbf{z}) = (1 - \mu)^2 & \left(\frac{1 - \phi(\mathbf{0})}{\delta} \int_{\mathbb{R}^2} g(\mathbf{y})g(\mathbf{z} - \mathbf{y}) d\mathbf{y} \right. \\ & \left. + \int_{\mathbb{R}^2} \int_{\mathbb{R}^2} g(\mathbf{x})g(\mathbf{x}')\phi(\mathbf{z} + \mathbf{x} - \mathbf{x}') d\mathbf{x}d\mathbf{x}' \right) \end{aligned}$$

with $g(\cdot)$ an isotropic Gaussian density

[then solved e.g. via Fourier transform plus ad hoc assumption about behaviour near $\mathbf{z} = \mathbf{0}$]

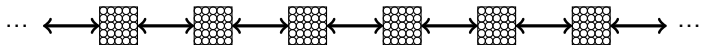
M. Lamotte's grove snail data again



A successful fit??? $\overline{\phi(\mathbf{0})} \approx 0.22$, $\overline{\phi(\mathbf{0})^2} \approx 0.06$, applying Malécot's formula with $\mu = 10^{-8}$, $\kappa = 0.3$, $N = 35$, $\sigma = 10^{28}$

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

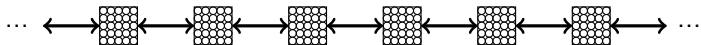
Colonies of *fixed* size N are arranged in a geographical space, say \mathbb{Z}^d



($d = 1$ in this picture)

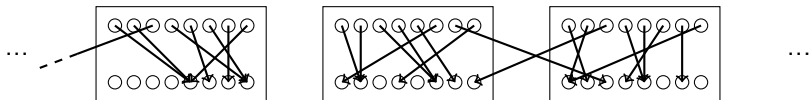
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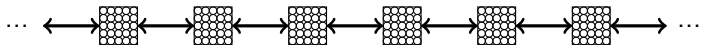
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For each child: Assign a random parent in same colony with probability $1 - \nu$, in a neighbouring colony with probability ν



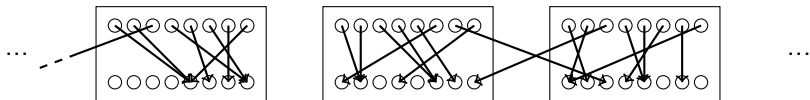
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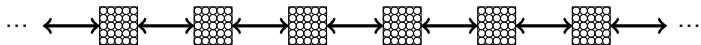
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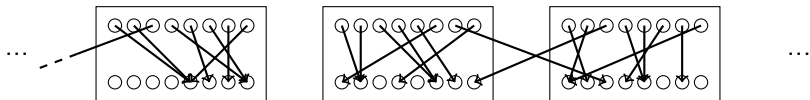
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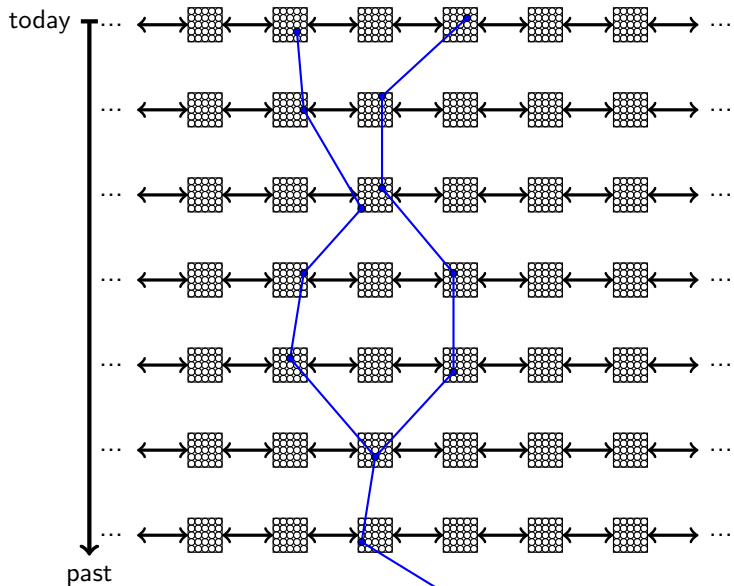
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“Trivial” demographic structure, but paradigm model for evolution of *type distribution* in space

Stepping stone model: Ancestral lines



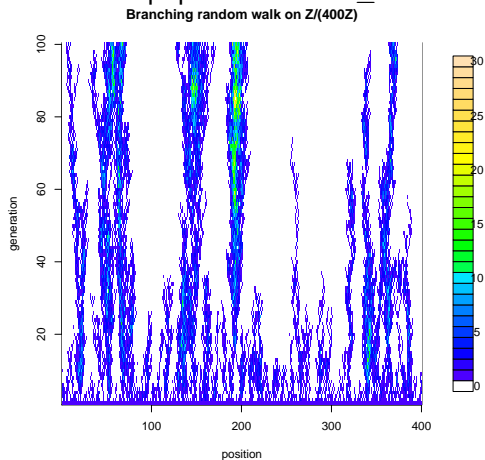
The stepping stone model (Kimura, 1953)

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),
this makes detailed analysis feasible, yields via duality:
long-time behaviour of (neutral) type distribution
- Cons:
- An 'ad hoc' simplification, effects of local size fluctuations 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 $d \leq 2$:



Branching random walk with local density-dependent feedback

- Possible and natural extension of the stepping stone model (and of branching random walks)
- Offspring distribution supercritical when there are few neighbours, subcritical when there are many neighbours

e.g. Bolker & Pacala (1997), Murrell & Law (2003), Etheridge (2004), Fournier & Méléard (2004), Hutzenthaler & Wakolbinger (2007), Blath, Etheridge & Meredith (2007), B. & Depperschmidt (2007), Pardoux & Wakolbinger (2011), Le, Pardoux & Wakolbinger (2013), ...

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Challenges:

- Mathematical analysis harder (population sizes are now a space-time random field; feedback mechanism makes different families dependent)
- Dynamics of ancestral lineages?

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

(Interpretation as local competition:

Ind. at z reduces average reproductive success of focal ind. at x by λ_{z-x})

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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.
- Conditioning¹ 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

¹and considering types and/or ancestral relationships

Remarks, 2

- Poisson offspring distribution is a somewhat artificial (though technically very convenient) choice, one could take any family $\nu(a) \in \mathcal{M}_1(\mathbb{Z}_+)$ parametrised by

$$a = \sum_k k \nu_k(a) \quad \text{satisfying} \quad \sum_k (k - a)^2 \nu_k(a) \leq \text{Const.} \times a$$

- Logistic term $x(1 - x)$ could be replaced by another suitable function $h(x)$, e.g. $h(x) = x \exp(a - bx)$.
- We have little “explicit” information on the system, e.g. no closed formulas for means, variances/covariances, etc.
- Related continuous-mass models (Etheridge 2004, Blath et al 2007) can be obtained as scaling limit

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

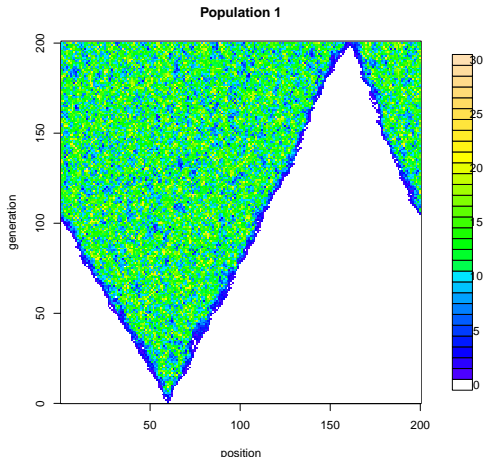
$$\zeta_{n+1}(y) = \sum_x p_{y-x} \zeta_n(x) \left(m - \sum_z \lambda_{z-x} \zeta_n(z) \right)^+$$

has unique (and globally attracting) non-triv. fixed point

- strong coupling properties of η
- coarse-graining and comparison with directed percolation

Restriction $m < 3$ is "inherited" from logistic iteration $w_{n+1} = mw_n(1 - w_n)$.

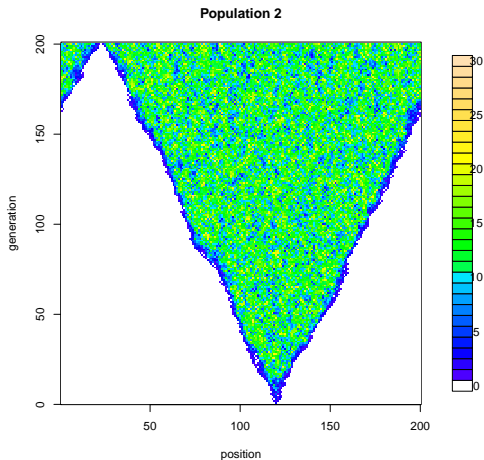
Coupling: An essential proof ingredient



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

Starting from any two initial conditions η_0, η'_0 , copies $(\eta_n), (\eta'_n)$ can be coupled such that if both survive, $\eta_n(x) = \eta'_n(x)$ in a space-time cone.

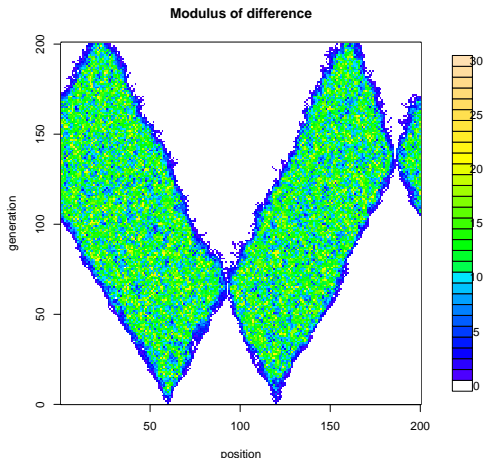
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Dynamics of an ancestral line

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

Let $X_n =$ position of her ancestor n generations ago:

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

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

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Question:

(X_n) is a random walk in a – relatively complicated – random environment. Is it similar to an ordinary random walk when viewed over large enough space-time scales?

Dynamics of an ancestral line

$$\begin{aligned} & \mathbb{P}(X_{n+1} = y \mid X_n = x, \eta^{\text{stat}}) \\ &= \frac{p_{x-y} \eta_{-n-1}^{\text{stat}}(y) (m - \sum_z \lambda_{z-y} \eta_{-n-1}^{\text{stat}}(z))^+}{\sum_{y'} p_{x-y'} \eta_{-n-1}^{\text{stat}}(y') (m - \sum_z \lambda_{z-y'} \eta_{-n-1}^{\text{stat}}(z))^+} \end{aligned}$$

Remarks

- Analysis of random walks in random environments (also in dynamic random environments) is today a major industry. Yet as far as we know, none of the general techniques developed so far in this context is applicable.
In particular: The natural “forwards” time direction for the walk is “backwards” time for the environment.
- Observation: (X_n) is close to ordinary rw in regions where relative variation of $\eta_{-n-1}(x)$ is small.

Large scale dynamics 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

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

$$\mathbb{P}\left(\frac{1}{n}X_n \rightarrow 0 \mid \eta_0(0) \neq 0\right) = 1 \quad \text{and} \quad \mathbb{E}\left[f\left(\frac{1}{\sqrt{n}}X_n\right) \mid \eta_0(0) \neq 0\right] \xrightarrow{n \rightarrow \infty} \mathbb{E}[f(Z)]$$

for $f \in C_b(\mathbb{R}^d)$, where Z is a (non-degenerate) d -dimensional normal rv.

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The proof uses a *regeneration* construction

(and *coarse-graining* and *coupling*, in particular with directed percolation):

Regeneration times $0 = T_0 < T_1 < T_2 < \dots$, express $X_{T_k} = Y_1 + \dots + Y_k$ 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, $\mathbb{P}(X_{k+1} = \cdot \mid \eta, X_k = x)$ depends on η_{-k}, η_{-k-1} in a finite window around x

[note reversal of time between η and 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 have to make neighbours good in L_{time} steps and η ’s with two different good local initial conditions become locally identical after L_{time} steps

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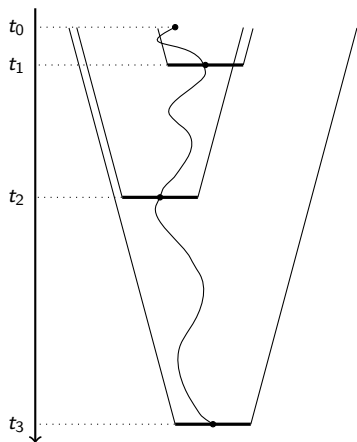
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- *On good η blocks, the law of X is ‘well behaved’*: e.g., close to a non-disordered symmetric finite range reference walk
- *Symmetry in distribution*

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)

Outlook

- Technique is robust (applies to many spatial population models in “high density” regime) but current result “conceptual” rather than practical
- We are hopeful that a “joint regeneration” construction can be implemented to analyse samples of size 2 (or even more) on large space-time scales.
- Meta-theorem: “Everything”² that is true for the neutral multi-type voter model is also true for the neutral multi-type spatial logistic model.
- Suitably controlled joint regeneration also allows to derive an a.s. version of the CLT, conditioned on a fixed realisation of η^{stat} .

²with a suitable interpretation of “everything”.

Examples: Clustering of neutral types in $d = 1, 2$; multi-type equilibria exist in $d \geq 3$,
 $\mathbb{P}(\text{two ind. sampled at distance } x \text{ have same type}) \sim C x^{2-d}$.

Outlook

- In fact, such a “joint regeneration” construction has been carried out for a simplified version of η^{stat} , the discrete time contact process. Then, (X_n) is a directed random walk on the “backbone” of an oriented percolation cluster.
- The diffusion rate $\sigma^2 = \sigma^2(p) = \mathbb{E}[Y_{1,1}^2] / \mathbb{E}[T_1] \in (0, \infty)$ is not very explicit (though in principle accessible by simulations), effective coalescence probability for two lineages still a “black box” (at least to me).

(Some) details can be found in

M. B., A. Depperschmidt, *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, [arXiv:1505.02791](https://arxiv.org/abs/1505.02791) (2015)

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M. B., A. Depperschmidt, *Ann. Appl. Probab.* 17 (2007), 1777–1807

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M. B., J. Černý, A. Depperschmidt, Random walks in dynamic random environments and ancestry under local population regulation, [arXiv:1505.02791](https://arxiv.org/abs/1505.02791) (2015)

Thank you for your attention!