Seed bank models in population genetics

Jochen Blath

Joint work with

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Maite Wilke Berenguer, Eugenio Buzzoni, Jere Koskela...

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Berlin Mathematical School

PROBABILISTIC STRUCTURES
IN EVOLUTION

DFG SPP 1590

Dormancy and seed banks in population genetics

- *Dormancy* is an adaptive trait that has independently evolved multiple times across the tree of life.
- For example, many microorganisms can enter a reversible state of *vanishing metabolic activity*. These dormant forms may stay inactive for extended periods of time.
- Dormancy allows a population to maintain a reservoir of genotypic and phenotypic diversity (i.e., a *seed bank*) that can contribute to the long-term survival of a population. This "bet hedging" strategy has long been of interest to ecologists.
- However, in population genetics, comparatively little is known about how dormancy influences the *evolutionary forces* of genetic drift, mutation, selection, recombination, and gene flow. See [LENNON & SHOEMAKER 2018] for a recent systematic overview.

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[Lennon & Jones, 2011] investigate dormancy in microbial communities:

- A large fraction of microorganisms in nature seems to be metabolically inactive.
- There is a variety of mechanisms for the initiation and termination of dormancy: Can be triggered by environmental cues (temperature, pH, resources, antibiotics treatment)...
- ... but also seems to happen spontaneously:

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Dormancy in microbial communities

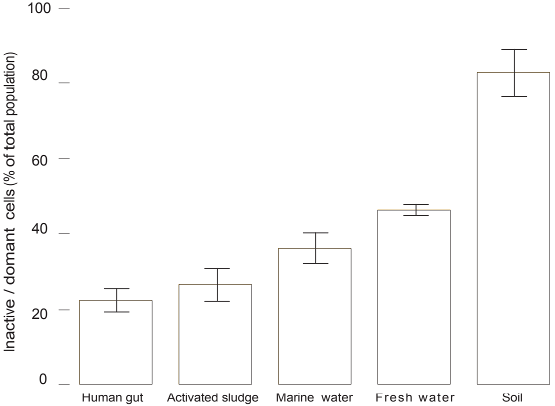

Figure: Percentage of inactive cells in microbial communities, data from [LENNON & JONES, 2011])

Mathematical modeling of seed-banks

Many (empirical) studies. Only relatively recently, systematic derivation of mathematical models. See e.g. (incomplete list)

- [KAJ, KRONE & LASCOUX 2001] (Wright-Fisher model with "weak seed bank"),
- [TELLIER, LAURENT, LAINER, PAVLIDIS, STEPHAN 2011] (inference of "seed bank parameters" in wild tomatoe species),
- [LENNON & JONES 2011] (overview and concepts for seed bank models in microbial communities),
- [BEGCKW 2015, BGCKW 2016,...] ("seed bank coalescent", "seed bank diffusion", some properties and evolutionary parameters),
- [KOOPMANN, MÜLLER, TELLIER, ŽIVKOVIĆ 2017] ("weak" seed banks and selection),
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Aims of this talk

- Review of known seed bank models in population genetics including "*seed bank coalescent / seed bank diffusion*" (introduced in previous Luminy talk in 2015), based on "spontaneous switching".
- Report progress in understanding of *boundary behaviour* of seed bank diffusion and the relation between "weak" and "strong" seed bank models via a *stochastic delay equation*.
- Separation of timescales: Provide an application of the *method of duality* to identify *degenerate diffusion limits*.
- *Statistical method* to select seed bank model based on IMS data.
- New seed bank model incorporating *responsive switching*, further extending the class of "*on/off coalescents*".

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Background: Classical Wright-Fisher model

Set-up: haploid population, discrete generations, fixed population size $N(=5)$

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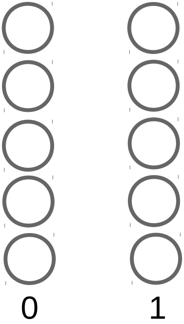

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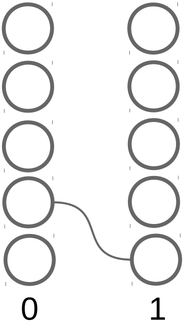

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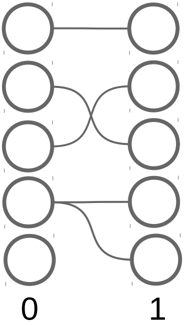

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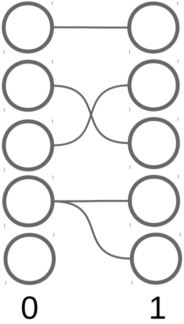

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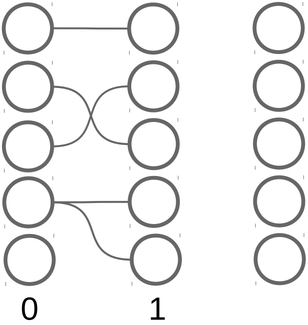

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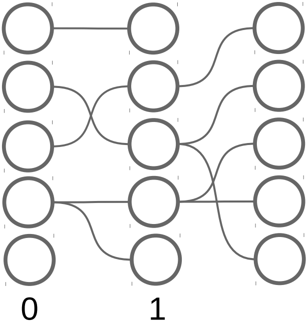

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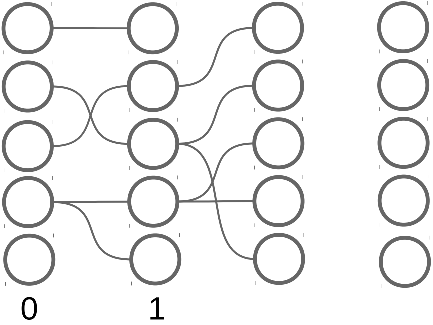

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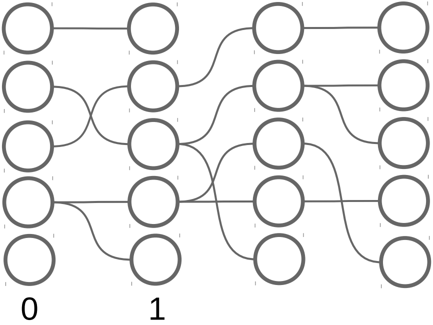

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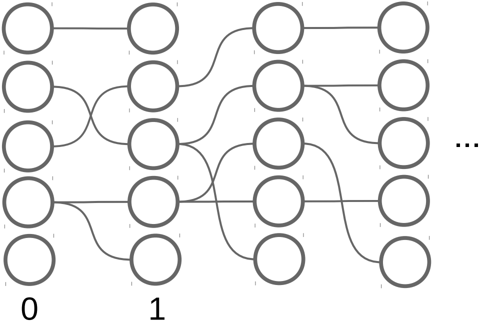

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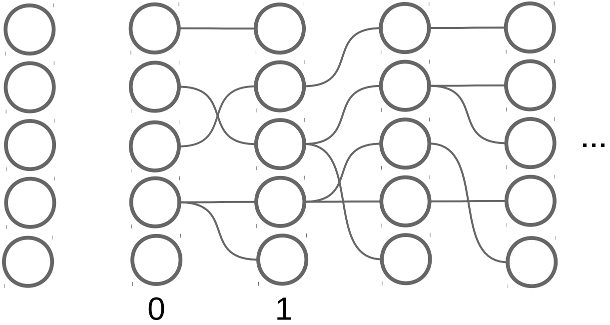

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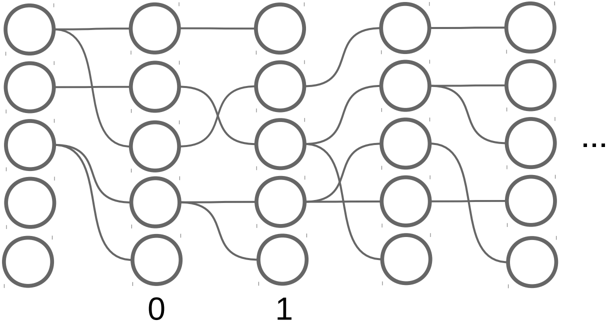

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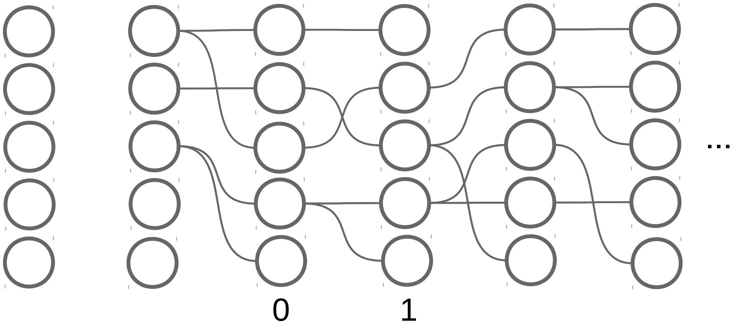

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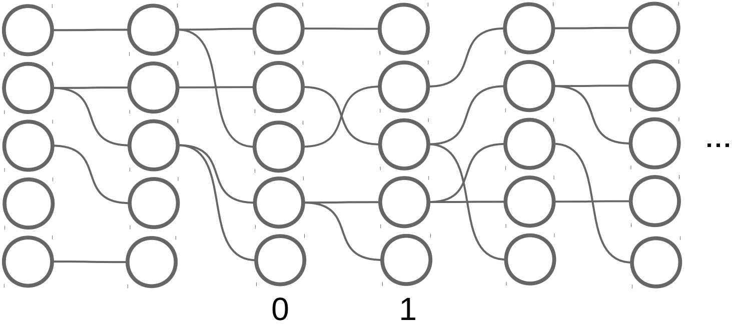

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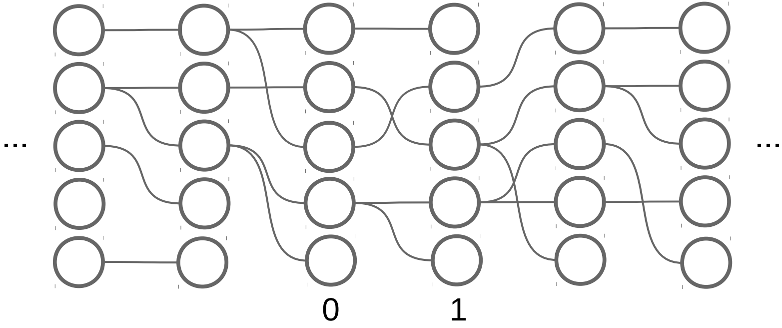
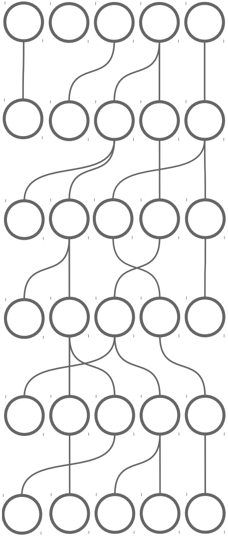


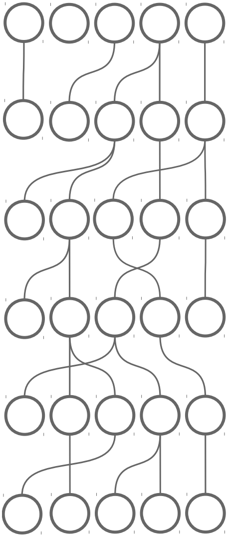
Ancestral graph

Forward – time – Backward

Types: {●, ○} → **Fraction of ●**



Genealogy of sample



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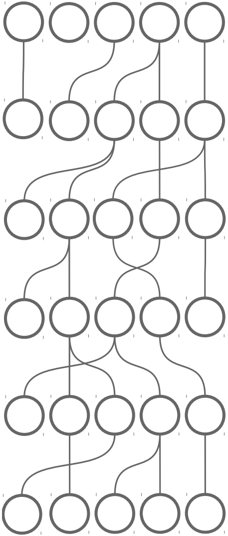

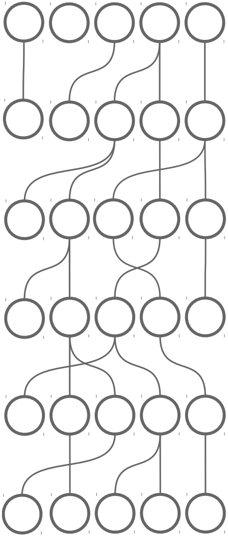

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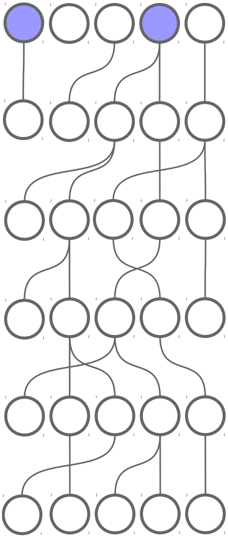

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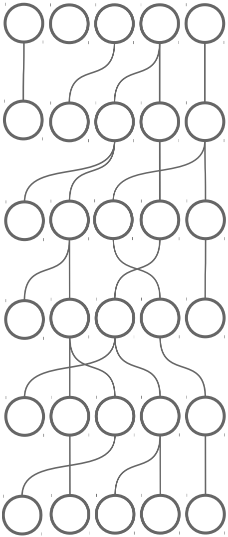

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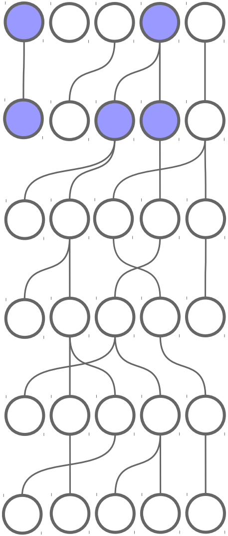

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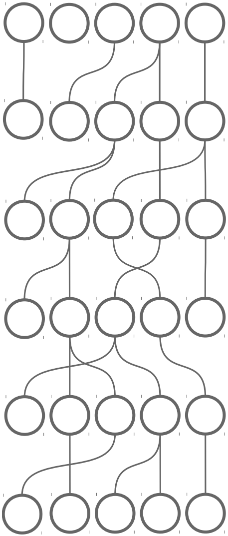

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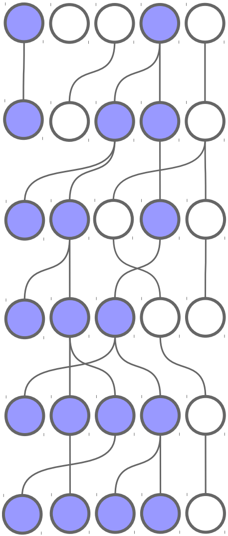

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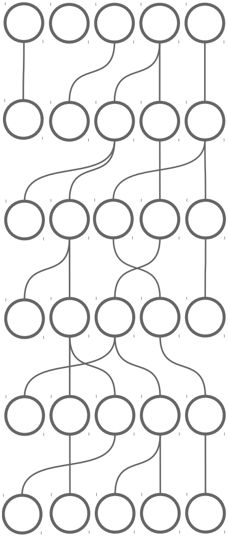

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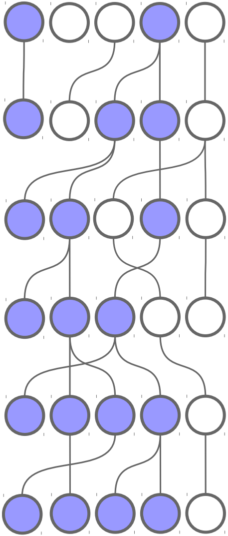

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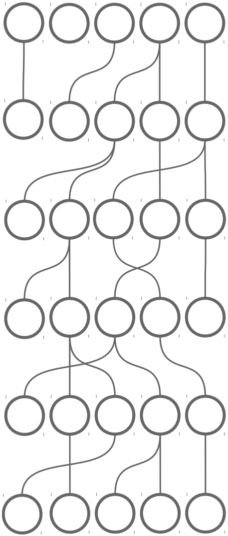

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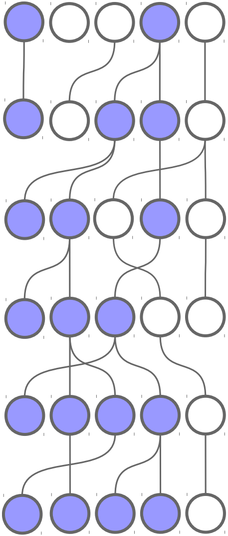

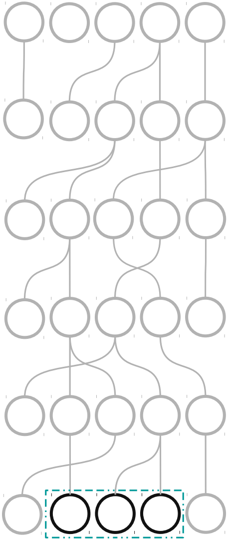

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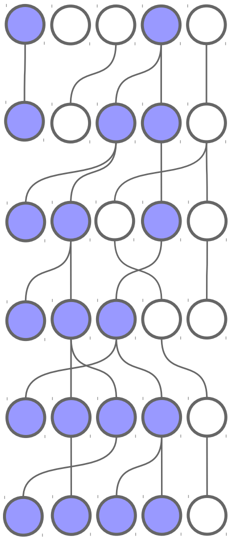

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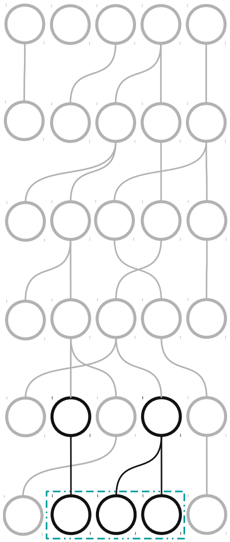

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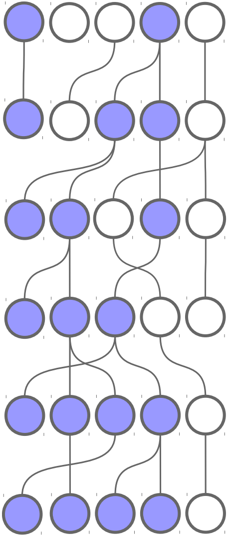

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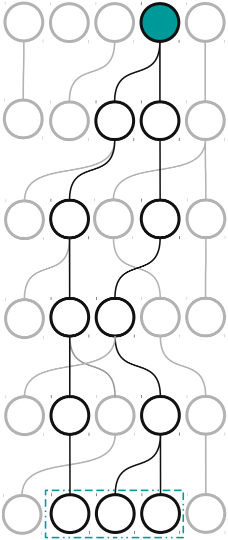

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Fraction X^N of ●

$$X_r^N := \frac{1}{N}\sum_{i\in[\![N]\!]} \mathbf{1}_{\{i \text{ in generation } r \text{ is } \bullet\}}$$

Theorem 1.1 (Wright '31, Feller '51,...)

$(X^N_{\lfloor Nt \rfloor})_{t\geq 0} \Rightarrow (X_t)_{t\geq 0}$
for $N \to \infty$ on $D_{[0,\infty)}([0,1])$, where

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Wright-Fisher diffusion

Genealogy Π^N of sample

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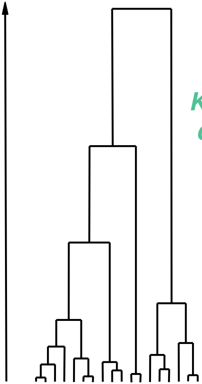

Kingman coalescent

Moment Duality

Fraction $\{X_t\}$ of ● Wright-Fisher diffusion,

Genealogy $\{\Pi_t\}$ of sample Kingman coalescent,

Block counting process $\{N_t\}$, given by $N_t = |\Pi_t|, t \geq 0$.

Theorem 1.3 (Moment Duality)

$$\mathbb{E}^n[x^{N(t)}] = \mathbb{E}_x[X(t)^n].$$

Here $H(x,n) := x^n$ is the “probability to sample n ● individuals if fraction is x”

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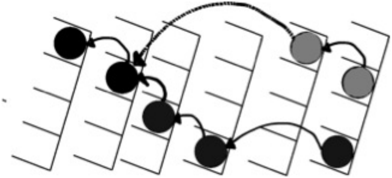
Seed bank models with ancestral jumps

[Kaj, Krone & Lascoux 2001]: One idea to introduce seed banks into a Wright-Fisher model is to allow individuals to pick parents from the $m \in \mathbb{N}$ *past generations* (and not only from previous generation):



Picture: Pop size $N = 4$. Generations $\overset{\uparrow}{-2}$ $\overset{\uparrow}{-1}$ $\overset{\uparrow}{0}$

Known results, I

- [Kaj, Krone & Lascoux 2001] show that if each individual independently picks a random $B \in \{1, \ldots, m\}$, and then its parent from B generations ago, then the ancestral process converges under the usual rescaling to a *time-changed Kingman coalescent*, where coalescence rates are multiplied by
$$\frac{1}{\mathbb{E}[B]^2} \le 1.$$
- This *decelerates* the coalescent, leading to an increase in the effective population size. Note that B and m do not scale with N.
- Since the overall coalescent tree structure is retained, this leaves the normalized site frequency spectrum (nSFS) in the IMS model unchanged. Hence, we speak of a *'weak' seed bank effect*.

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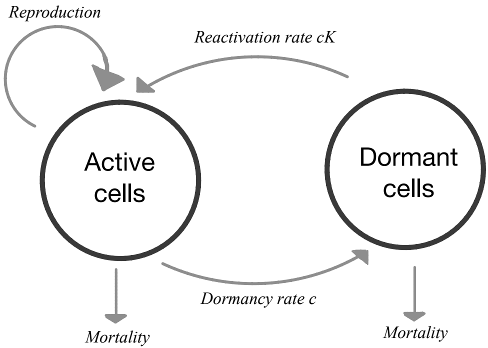
Seed banks in bacterial communities

Dormancy: Initiaton and resuscitation à la [Lennon & Jones 2011]



Spontaneous switching - *migration* between active and dormant population!

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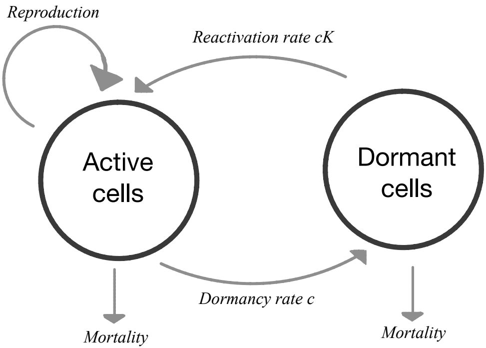
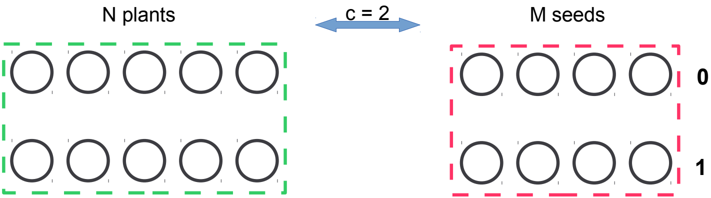


Spontaneous switching - *migration* between active and dormant population!

A Wrigth-Fisher model with seed bank

Set-up: WF-type model, active (size N) and dormant (size M) subpopulations



- N plants produce $N - c$ plants by multinomial sampling
- c seeds are selected uniformly to germinate: one plant each
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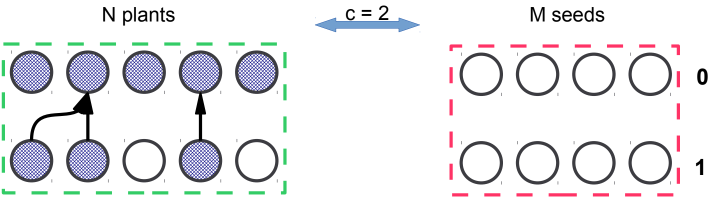

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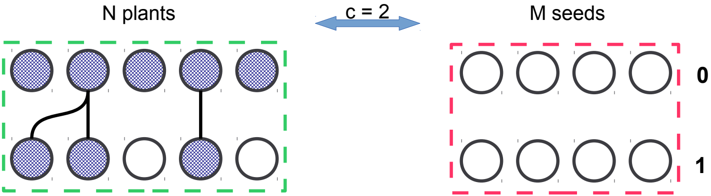

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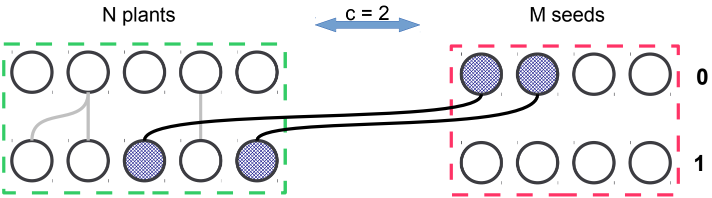

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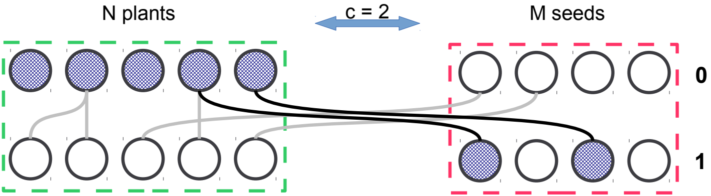

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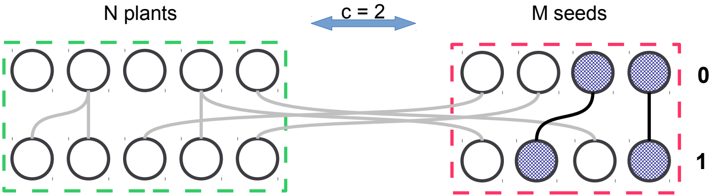

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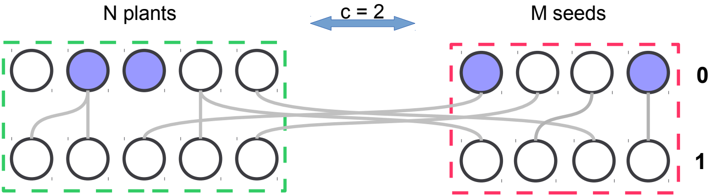

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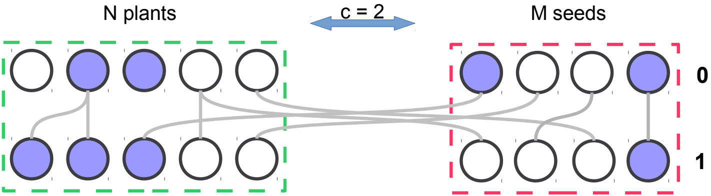

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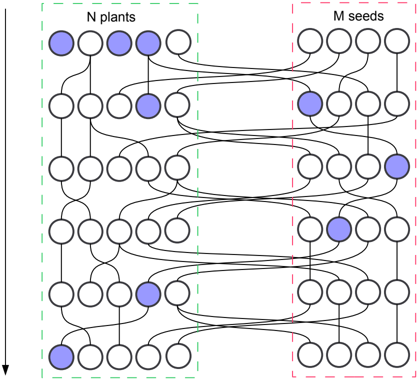
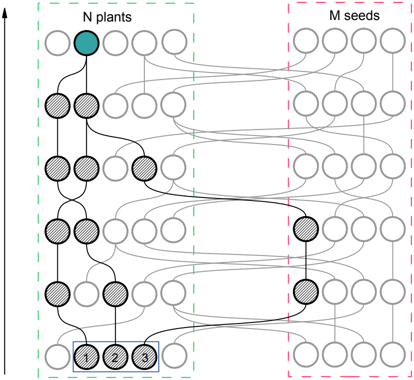
Forward and backward in time

Forward: trace fractions of purple type



Backward: trace sample to MRCA



Scaling limits

Forward: trace fractions of purple type

$$X_r^N := \frac{1}{N} \sum_{i \in [\![N]\!]} \mathbf{1}_{\{i \text{ in generation } r \text{ is purple}\}}$$

$$Y_r^M := \frac{1}{M} \sum_{j \in [\![M]\!]} \mathbf{1}_{\{j \text{ in generation } r \text{ is purple}\}}$$

Theorem 1.4 (BGKW '15)

$c, K > 0$, $M = M(N) = \lfloor KN \rfloor$

$$(X^N_{\lfloor Nt \rfloor}, Y^{M(N)}_{\lfloor Nt \rfloor})_{t \geq 0} \Rightarrow (X_t, Y_t)_{t \geq 0}$$

for $N \to \infty$ *on* $D_{[0,\infty)}([0,1]^2)$, *where*

$$\begin{cases} dX_t &= c(Y_t - X_t)dt + \sqrt{X_t(1-X_t)}dB_t, \\ dY_t &= cK(X_t - Y_t)dt. \end{cases}$$

Backward: trace sample to MRCA

Theorem 1.5 (BGKW '15)

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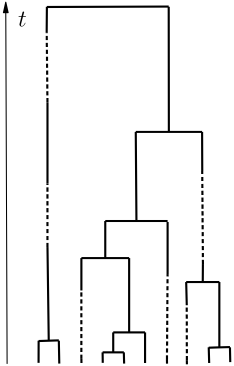

Adding bi-allelic mutation

Seed bank diffusion

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u_1, u_1': purple → white

u_2, u_2': white → purple

Seed bank: $\alpha' = 0$, $c' = cK$,

Two-island: $\alpha' > 0$

We are now interested in the *boundary behaviour* of these two-dim diffusions.

[KERMANY, ZHOU & HICKEY 2008] investigate the two island diffusion model, but whether boundaries are hit remained open.

Adding bi-allelic mutation

Seed bank diffusion with mutation

$$\begin{cases} \mathrm{d}X_t &= \left(-u_1 X_t + u_2(1-X_t) + c(Y_t - X_t)\right)\mathrm{d}t + \sqrt{X_t(1-X_t)}\,\mathrm{d}B_t, \\ \mathrm{d}Y_t &= \left(-u_1' Y_t + u_2'(1-Y_t) + cK(X_t - Y_t)\right)\mathrm{d}t. \end{cases} \tag{1}$$

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"Two-island diffusion"

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Boundary behaviour, known results

For the one-dimensional system (without seed bank),

$$\mathrm{d}X_t = \left[-u_1 X(t) + u_2(1 - X(t))\right]\mathrm{d}t + \sqrt{X_t(1 - X_t)}\,\mathrm{d}B_t, \tag{2}$$

classical *Feller boundary theory* (based on speed masure, scale funtion) shows that the boundary 1 (resp. 0) is hit *iff* $2u_1 < 1$ (resp. $2u_2 < 1$).

However, this method does not work in higher dimensions.

Comparison to the one-dim system (choosing $Y_t \equiv 0$ resp. $Y_t \equiv 1$) leaves open what happens in intervals of type $(u_1, u_1 + c)$.

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Boundary classification for the general model

Define

$$\tau_0^X := \inf\{t \geq 0 \mid X(t) = 0\} \qquad \text{(and likewise } \tau_1^X, \tau_0^Y, \tau_1^Y.\text{)}$$

Theorem 2.1 (BBGW17+)

Let $c, c' > 0$. For every initial distribution $\mu_0 = \mathcal{L}(X(0), Y(0))$ with $\mu_0((0,1)^2) = 1$

$$\mathbb{P}^{\mu_0}\left(\tau_0^X < \infty\right) = 0 \qquad \textit{iff} \qquad 2u_2 \geq \alpha^2,$$

i.e. X will never hit 0 from the interior if and only if $2u_2 \geq \alpha^2$.

Analogous results hold for all other boundaries.

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"⇒" Filipović and Larsson *Polynomial diffusions and applications in finance (2016)*

"⇐" Let $\mathcal{P} := \{x, 1-x, y, 1-y\}$, then $[0,1]^2 = \{(x,y) \in \mathbb{R}^2 \mid \forall p \in \mathcal{P} : p(x,y) \geq 0\}$.

Pick $p(x,y) = x$. Check via Ito's formula that for $u_2 \geq \frac{1}{2}\alpha^2$

$$M(s) := \log p(X(s), Y(s)) + \kappa_p s$$

is local submartingale on $[0, \tau_0^X[$ for some suitable constant $\kappa_p \geq 0$,

bounded from above on bounded intervals $[0, \tau_0^X[\cap [0, t]$.

Convergence Theorem: For every fixed t, we have $\lim_{s \to \tau_0^X} M(s \wedge t) \in \mathbb{R}$.

But there is explosion at τ_0^X, hence $\tau_0^X > t$ for every t and thus $\tau_0^X = \infty$ a.s.
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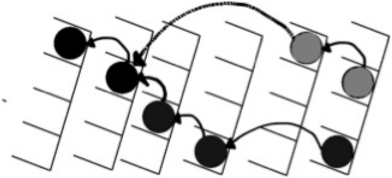
Weak vs strong seed banks: Delay representation

In the model of [KAJ, KRONE & LASCOUX 2001], there was no explicit seed bank (in form of an "island").

Instead, types of individuals have been directly chosen from the past "active" population:



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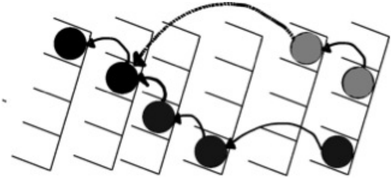

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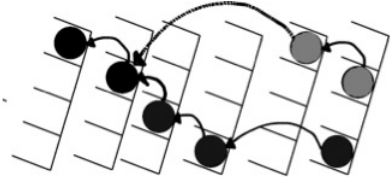

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An application of the integration by parts rule for semimartingales yields

Proposition 2.2 (BBGW18)

The seed bank diffusion solving (2) *with* $c = K = 1$*, started in* $X_0 = x = y = Y_0$*, agrees with the unique strong solution of the stochastic delay differential equations*

$$\begin{aligned} dX(t) &= \Big(xe^{-t} + \int_0^t e^{-(t-s)} X(s)\,ds - X(t)\Big)dt + \sqrt{X(t)(1-X(t))}\,dB(t), \\ dY(t) &= \Big(-ye^{-t} - \int_0^t e^{-(t-s)} X(s)\,ds + X(t)\Big)dt. \end{aligned} \tag{3}$$

Interpretation: The *type* of any “infinitesimal” resuscitated individual is determined by choosing an ancestor from the *active* pop an exp-distributed time ago (on the “evolutionary timescale”, with cutoff at 0).

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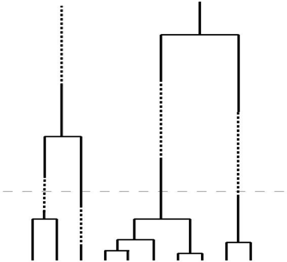
The seed bank coalescent

In the *seed bank coalescent* $\Pi_t, t \geq 0$, lines can be "*active*" (black lines) or "*dormant*" (dotted lines).



Transitions: If there are currently n active and m dormant lines, then

- Each pair of active lines merges at rate 1 (overall rate $\binom{n}{2}$)
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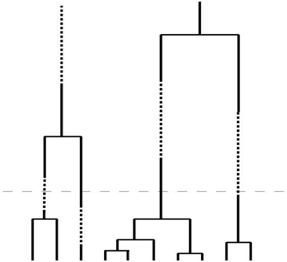

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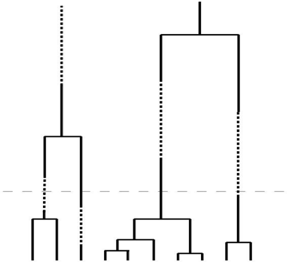

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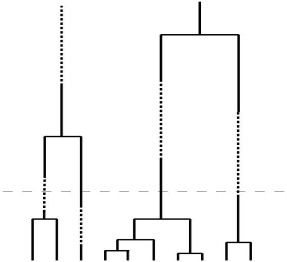

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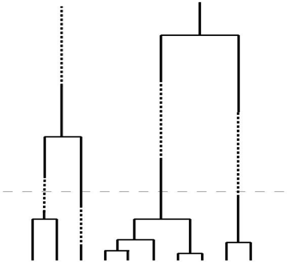

Its *block-counting process* (N_t, M_t) (active lines, dormant lines) satisfies the classical moment (sampling) duality with the seed bank diffusion (X_t, Y_t):

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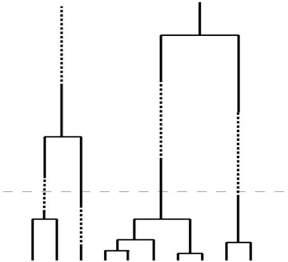

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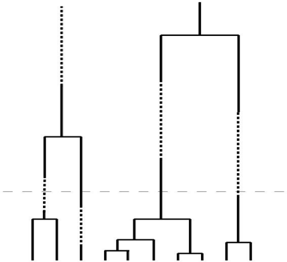

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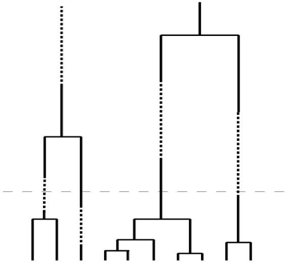

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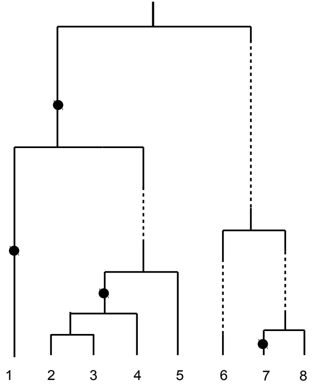
The seed bank coalescent with mutation

Mutations can be distributed on active branches, say with rate $u_1/2$.



Modeling choice whether mutations on dormant branches should be possible (perhaps at reduced rate $u_2/2$).

Inference and model selection

So far, we have encountered the following models:

- `K` *Kingman coalescent*. The standard model of genetic ancestry in the absence of a seed bank.
- `W` *Delayed Kingman coalescent*. Arises in [KKL 2001] model, “weak seed bank effect”’.
- `S` *Seed bank coalescent*, dual to seed bank diffusion, “strong seed bank effect”.
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Populations under `K` and `W` have same stationary distribution, tree topology identical. Estimate for mutation rates (Watterson’s estimate) will differ.

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Distinguishing the scenarios K, W, S, and TI

Apply Metropolis-Hastings type algorithm of [Andrieu & Roberts, 2009] for model selection and parameter inference simultaneously among $I = \{\mathtt{K}, \mathtt{S}, \mathtt{TI}\}$ in the IMS model. Target distributions is posterior π_I on model space I (and parameter space, omitted for simplicity).

Specifics of the method will be available in [BBKW18+] (in progress). For moderate sample size ($n = 100$) and $u = 10$, and flat prior on model space, we get

True model	$\pi_I(\mathtt{K}\vert\mathbf{t},\mathbf{n})$	$\pi_I(\mathtt{S}\vert\mathbf{t},\mathbf{n})$	$\pi_I(\mathtt{TI}\vert\mathbf{t},\mathbf{n})$
K	0.98	0.00	0.02
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True model can be recovered from a moderate amount of data, particularly in the case of K and S. Data generated under TI is also somewhat adequately explained by either of the other two model classes.

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Scaling limits and separation of timescales

Useful application of duality: Identify *degenerate* diffusion limits in certain scaling scenarios.

For example, for the seed bank diffusion (2), consider the following '*rare resuscitation regime*':

- Let the migration rate $c \to 0$,
- speed up time by a factor $1/c \to \infty$.

While exchange of ancestral lineages between active and dormant states thus becomes *rare* in the original timescale, in the new timescale, migration will happen at rate 1, while coalescences in the active population now occur "*instantaneously*" (with rate ∞).

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Rare resuscitation regime, on slow timescale (let $K = 1$ for simplicity):

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Seed bank diffusion

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Seed bank diffusion, sped up time by $\frac{1}{c}$, limit $c \to 0$, existence of scaling limit?

Scaling limits of the seed bank coalescent

To understand the limit, we work with the *dual* seed bank coalescent.

Rescaled dual seed bank coalescent as $c \to 0$, with time sped up by $\frac{1}{c}$:

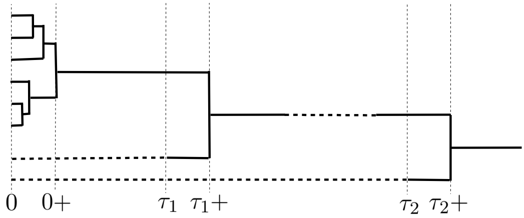

Figure: In the limit, at time $0+$ all lines in the active population have coalesced. At times τ_1 and τ_2 (with rate 1) a seed awakens and *immediately* coalesces.

Limit can be computed explicitly and has transition semigroup $\Pi(t) := Pe^{tG}, t > 0$, where P is a projection. P and G can easily be determined, see e.g. [Möhle & Notohara, 2016].

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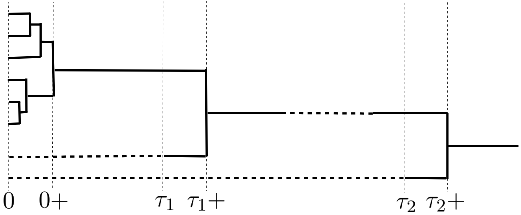

Figure: In the limit, at time $0+$ all lines in the active population have coalesced. At times τ_1 and τ_2 (with rate 1) a seed awakens and *immediately* coalesces.

Limit can be computed explicitly and has transition semigroup $\Pi(t) := Pe^{tG}, t > 0$, where P is a projection. P and G can easily be determined, see e.g. [MÖHLE & NOTOHARA, 2016].

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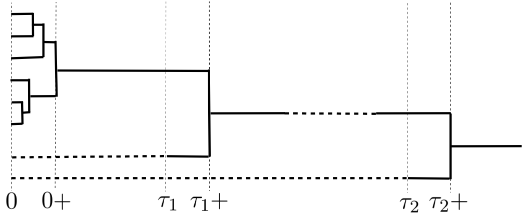

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Scaling limits of the seed bank diffusion

Convergence of the dual seed bank coalescent gives us convergence of the *finite dimensional distributions* of the corresponding seed bank diffusion:

$$\mathbb{E}_{x,y}\big[X_t^n, Y_t^m\big] = \mathbb{E}^{n,m}\big[x^{N_t} y^{M_t}\big] \xrightarrow{c\to 0} \mathbb{E}^{n,m}\Big[x^{N_t^\infty} y^{M_t^\infty}\Big].$$

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Identification of scaling limit?

Heuristically, the limiting process should be a *jump-diffusion* (X_t^∞, Y_t^∞) with dynamics as follows:

- X_t^∞ is a *pure jump process* between the states 0 and 1 with the seed-bank dependent rates Y_t^∞ for jumps from 0 to 1, and $(1 - Y_t^\infty)$ for jumps from 1 to 0.
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Scaling limits of the seed bank diffusion

Let

$$f(x,y)(n,m) := x^n y^m.$$

The generator of the candidate process is

$$\begin{aligned} Af(x,y)(n,m) &= (x-y)\frac{\partial f}{\partial y}(x,y)(n,m) + y(f(1,y)(n,m) - f(0,y)(n,m))1_{x=0} \\ &\quad + (1-y)(f(0,y)(n,m) - f(1,y)(n,m))1_{x=1}. \end{aligned}$$

Can be simplified to

$$Af(x,y)(n,m) = y^{m-1}mx^{n+1} - y^m(mx^n + nx) + ny^{m+1}.$$

Scaling limits of the seed bank diffusion

We need to check that this generator satisfies a duality relation with the limiting block counting process (N_t^∞, M_t^∞). Here, we choose the reduced form that already lives in the subspace $\{0,1\} \times \mathbb{N}_0$, with (effective) jump rates

$$\begin{gathered}(0,m) \to (1,m-1) \text{ rate } m,\\ (1,m) \to (1,m-1) \text{ rate } m,\\ (1,m) \to (0,m+1) \text{ rate } 1,\end{gathered}$$

We get

$$\begin{aligned} A^\infty f(x,y)(n,m) &= m(x^1y^{m-1} - x^0y^m)1_{n=0} + m(x^1y^{m-1} - x^1y^m)1_{n=1} \\ &\quad + (x^0y^{m+1} - x^1y^m)1_{n=1} \\ &= m(1-n)(xy^{m-1} - y^m) + mn(xy^{m-1} - xy^m) \\ &\quad + n(y^{m+1} - xy^m) \\ &= y^{m-1}mx - y^m(m(1-n+nx) + nx) + ny^{m+1} = Af(x,y)(n,m). \end{aligned}$$

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Technicalities

- Note that from duality we can only infer *fdd convergence* of the diffusion.
- The limit is a jump diffusion, hence we *cannot* have weak convergence wrt Skorohod topology (since this would yield continuity of paths of the limit - continuous paths from a closed subset of càdlàg paths).
- Claim: We have convergence in the *Meyer-Zheng topology*.
- Strictly speaking, we have checked duality of the limits only in *reduced statespaces* (but all mass concentrates there).

If available, duality seems to be a good tool to characterize limits in scenarios with “degenerate diffusion limits”.

Last part: Seed bank models with responsive switching

- So far, we have modeled our seed banks according to the *spontaneous switching regime* which amounts to continuous “migration” between resevoirs.
- However, dormancy seems to be intiated by to exogenous *trigger events* (change in temperature, pH, resources, antibiotics treatment etc.)
- Similarly, one could think about large-scale *simultaneous resuscitation* as result of mass extinction events (e.g. forest fires,...)

Hence one may wish to incorporate “discontinuous” large-scale simultaneous migration between active and dormant population.

We sketch this in a simple setup (to keep notation at a minimum). This is also work in progress.

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Seed bank models with responsive switching

Let $z_1, z_2 \in (0,1)$. Consider a Wright-Fisher model with seed bank as before.

- Assume that for *typical generations* (with prob. $1 - \frac{1}{N}$), reproduction occurs according to our previous mechanism.
- However, with probability $\frac{1}{2N}$, a *large-scale migration event* occurs: Each individual in the active population is replaced independently with probability z_1 by a uniformly chosen individual from the seed bank (with replacement).
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Forward in time

Consider two types (purple and white). Forward: again trace fractions of purple type:

$$\bar{X}_r^N := \frac{1}{N}\sum_{i\in[\![N]\!]} \mathbf{1}_{\{i \text{ in generation } r \text{ is purple}\}}, \quad \bar{Y}_r^M := \frac{1}{M}\sum_{j\in[\![M]\!]} \mathbf{1}_{\{j \text{ in generation } r \text{ is purple}\}}$$

Theorem 4.1 (BGKW18+)

$c > 0$, $M = M(N) = N$

$$(\bar{X}^N_{\lfloor Nt \rfloor}, \bar{Y}^{M(N)}_{\lfloor Nt \rfloor})_{t\geq 0} \Rightarrow (\bar{X}_t, \bar{Y}_t)_{t\geq 0}$$

for $N \to \infty$ *on* $D_{[0,\infty)}([0,1]^2)$*, with generator (including jumps!)*

$$\begin{aligned} Af(x,y) =& f(x+z_1(y-x),y) + f(x,y+z_2(x-y)) - 2f(x,y) \\ & + c(y-x)\frac{\partial}{\partial x}f(x,y) + c(x-y)\frac{\partial}{\partial y}f(x,y) + \frac{1}{2}x(1-x)\frac{\partial^2}{\partial x^2}f(x,y), \end{aligned}$$

Backward in time

Genealogy is gven by a seed bank coalescent with *simultaneous* initiation of / resuscitation from dormancy!

Theorem 4.2 (BGCK '18 (in progress))

We have

$$(\Pi^{(N,k)}_{[Nt]})_{t\geq 0} \Rightarrow (\Pi^k_t)_{t\geq 0}.$$

The corresponding block-counting process $(N_t, M_t)_{t\geq 0}$ *has transitions*

$$(n,m) \mapsto \begin{cases} (n-1, m+1) & \textit{at rate } (c + z_1(1-z_1)^{n-1})n, \\ (n-k, m+k) & \textit{at rate } \binom{n}{k} z_1^k (1-z_1)^{n-k}, 2 \leq k \leq n, \\ (n+1, m-1) & \textit{at rate } (c + z_2(1-z_2)^{m-1})m, \\ (n+l, m-l) & \textit{at rate } \binom{m}{l} z_2^l (1-z_2)^{m-k}, 2 \leq l \leq m, \\ (n-1, m) & \textit{at rate } \binom{n}{2}. \end{cases} \tag{5}$$

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Moment duality

Theorem 4.3

For every $(x,y) \in [0,1]^2$*, every* $n,m \in \mathbb{N}_0$ *and every* $t \geq 0$

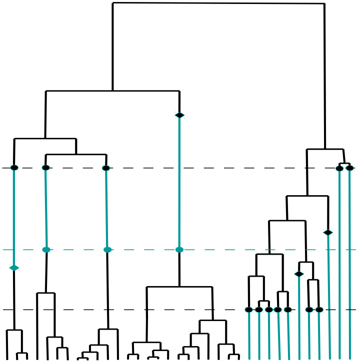
$$\mathbb{E}_{x,y}\left[X_t^n Y_t^m\right] = \mathbb{E}^{n,m}\left[x^{N_t} y^{M_t}\right]. \tag{6}$$

Proof: Let $f(x,y;n,m) := x^n y^m$. We get

$$\begin{aligned} Af(x,y) =& f(x+z_1(y-x),y) + f(x,y+z_2(x-y)) - 2f(x,y) \\ & + c(y-x)\frac{df}{dx}f(x,y) + \frac{1}{2}x(1-x)\frac{d^2f}{dx^2}f(x,y) + c(x-y)\frac{df}{dy}f(x,y) \\ =& \sum_{k=1}^{n}\binom{n}{k}z_1^k(1-z_1)^{n-k}(x^{n-k}y^{m+k} - x^n y^m) + \sum_{l=1}^{n}\binom{m}{l}z_2^l(1-z_2)^{n-l}(x^{m+l}y^{n-l} - x^n y^m) \\ & + cn(x^{n-1}y^{m+1} - x^n y^m) + \binom{n}{2}(x^{n-1}y^m - x^n y^m) + cm(x^{n+1}y^{m-1} - x^n y^m), \end{aligned}$$

as required.

The seed bank coalescent with simultaneous migration



A zoo of on/off coalescents

For people who like to investigate coalescent processes / ancestral influence graphs:

- Kingman coalescent with individual on/off events (seed bank coalescent / peripatric coalescent)
- Kingman coalescent simultaneous on/off events
- Λ-, Ξ-coalescents with individual on/off events
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Finally...

... thank you for your attention!

Talk mostly based on:

- B., ELDON, GONZÁLEZ CASANOVA, KURT, WILKE BERENGUER: Genetic variability under the seed bank coalescent, *Genetics* **200**, 2015
- B., GONZÁLEZ CASANOVA, KURT, WILKE BERENGUER: A new coalescent for seed bank models, *Annals of Applied Probability*, 2016
- B., BUZZONI, GONZÁLEZ CASANOVA, KURT, WILKE BERENGUER: The seed bank diffusion, and its relation to the two-island model, *SPP 1590 (p)reprint* **106**, 2017
- B., BUZZONI, WILKE BERENGUER, KOSKELA: Statistical tools for seed bank detection, *manuscript*, 2018
- B., GONZÁLEZ CASANOVA, KURT: The seed bank coalescent with large migration events, *manuscript*, 2018