Mutation, selection, and ancestry in the deterministic limit of the Moran model

Sebastian Hummel

based on joint work (in progress) with Ellen Baake and Fernando Cordero and thanks to many discussions with Anton Wakolbinger

Bielefeld University

Genealogies of Interacting Particle Systems

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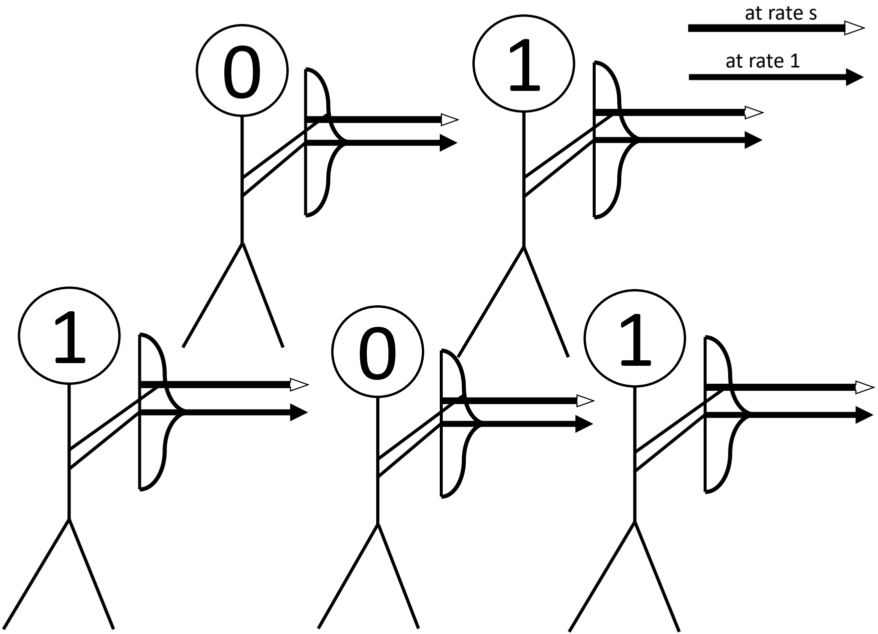
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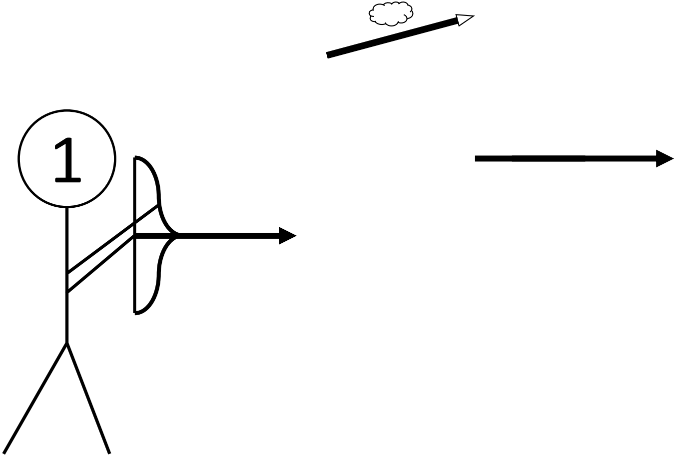
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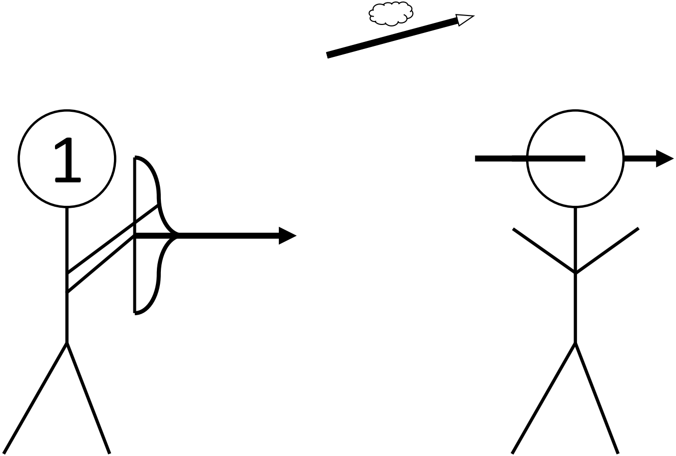
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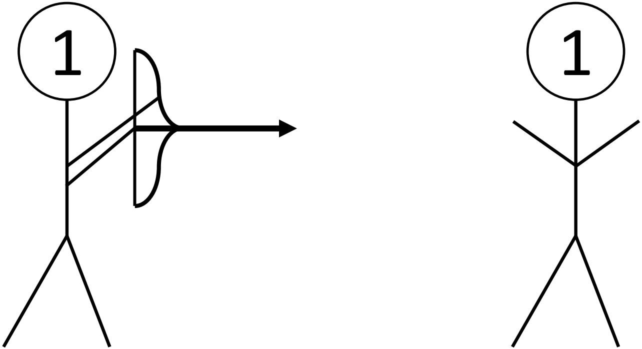
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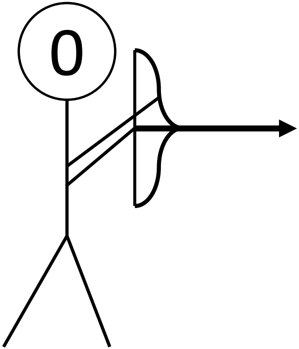
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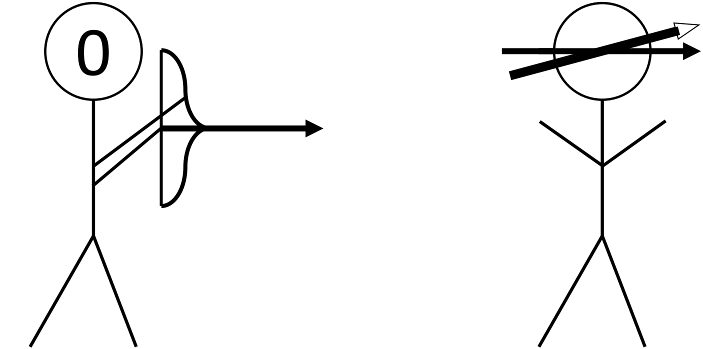
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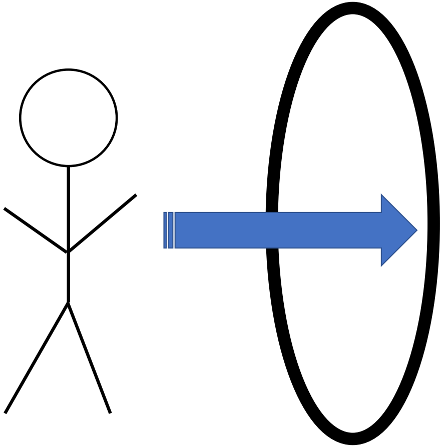
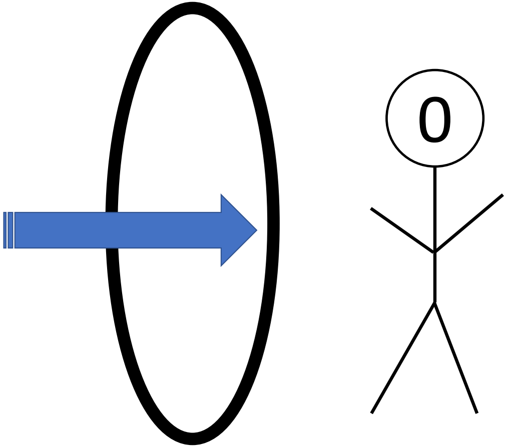
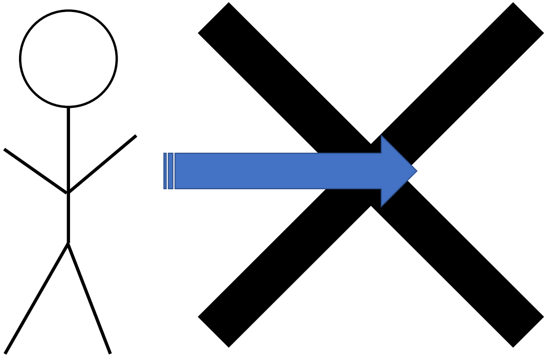


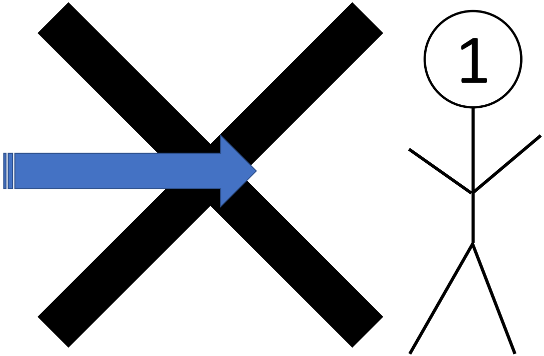
at rate uv_0



at rate uv_1



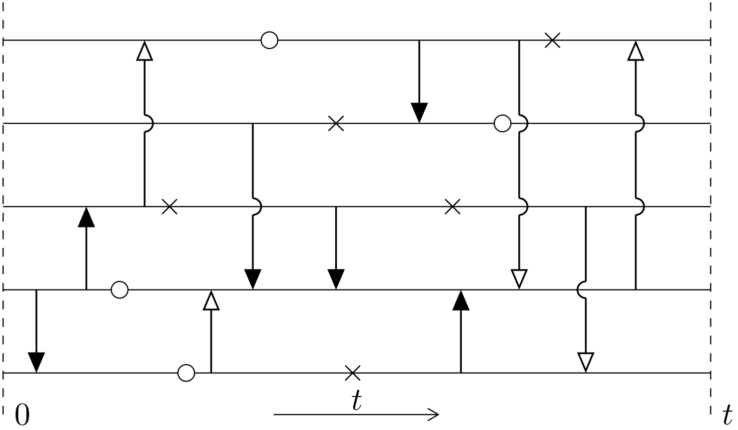
at rate uv_1



Moran model with 2-types

- Haploid population of fixed size N
- Types: 0 ('fit') and 1 ('unfit')
- Individuals of type 1 reproduce at rate 1
- Individuals of type 0 reproduce at rate $1 + s, \quad s \geq 0$
- Single offspring inherits parent's type and replaces uniformly chosen individual
- Parent-independent mutation at rate $u > 0$
- Resulting type: 0 with probability ν_0; 1 with probability ν_1

Graphical representation of 2-type Moran model



Type 0 ('fit') ○ Mutation to type 0 ▷ Selective arrow

Type 1 ('unfit') × Mutation to type 1 ▶ Neutral arrow

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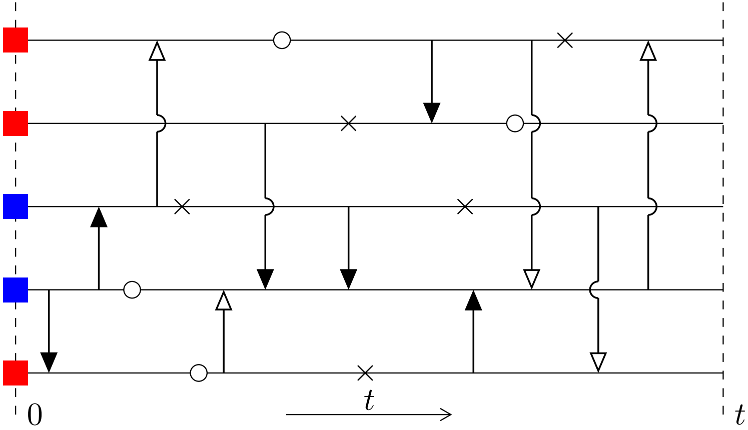

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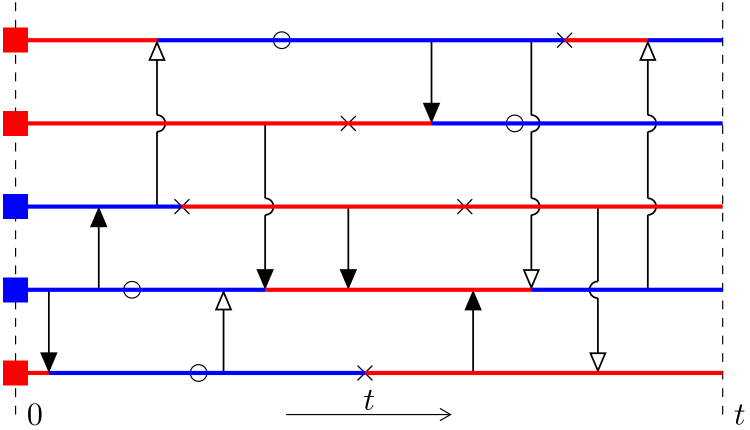

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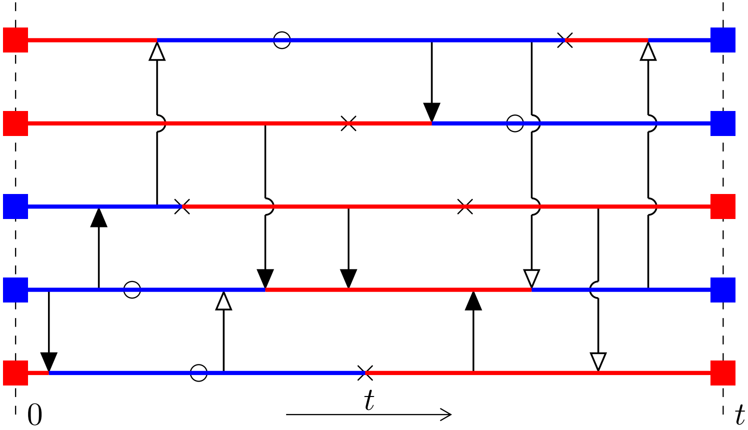

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Deterministic limit of the Moran model

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- If $\lim_{N\to\infty} Y_0^{(N)} = y_0$, then $\forall \varepsilon, T > 0$,

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- Convergence carries over to the stationary state $(t \to \infty)$
- Neither time nor parameters are rescaled

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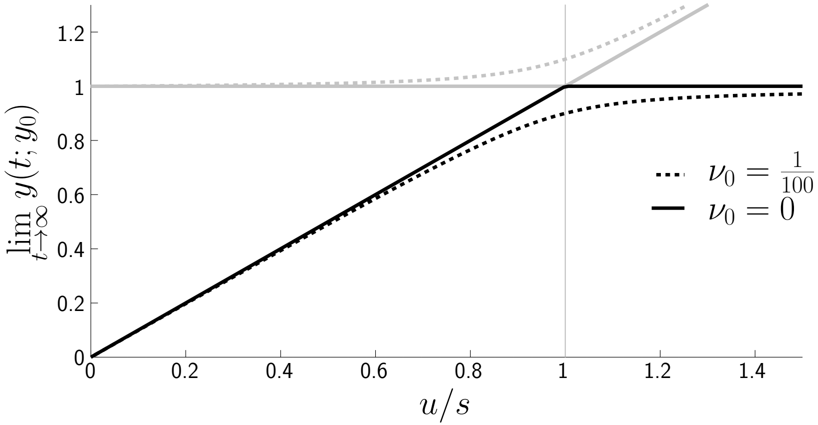
- If $\nu_0 = 0$,
  $\bar{y} = \min\left\{\frac{u}{s}, 1\right\} \rightarrow$ stable; $y^\star = \max\left\{1, \frac{u}{s}\right\} \rightarrow$ unstable

The equilibrium frequency



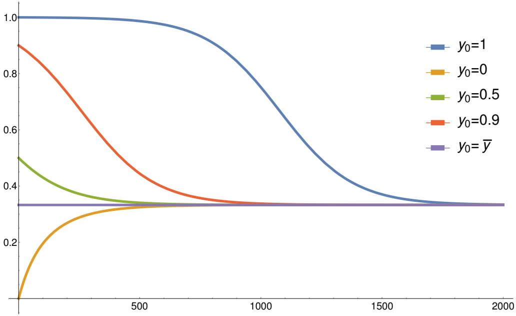
Black line: stable. Grey line: unstable.

- error threshold -

Properties of the deterministic limit $y(t;y_0)$

If $\bar{y} \in (0,1)$ and $y_0 \in (0,1)$, then

- if $y_0 < \bar{y} \;\Rightarrow y(t;y_0)$ monotonically increases to $\bar{y}$ as $t \to \infty$
- if $y_0 > \bar{y} \;\Rightarrow y(t;y_0)$ monotonically decreases to $\bar{y}$ as $t \to \infty$



Parameters: $s = \frac{1}{100},\; u = \frac{1}{300},\; \nu_0 = \frac{1}{1000},\; \nu_1 = 1 - \frac{1}{1000}$

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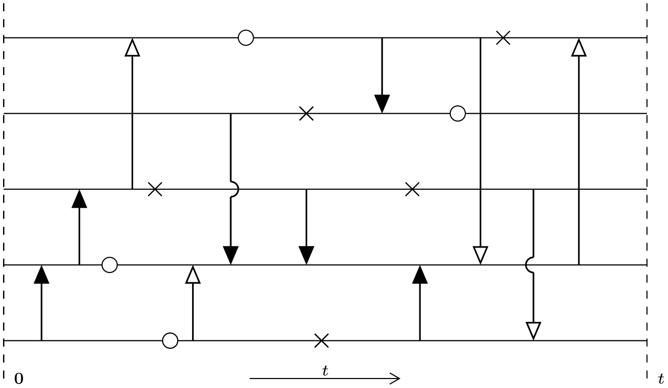
Ancestral selection graph (ASG)

Introduced by Krone and Neuhauser [1997]



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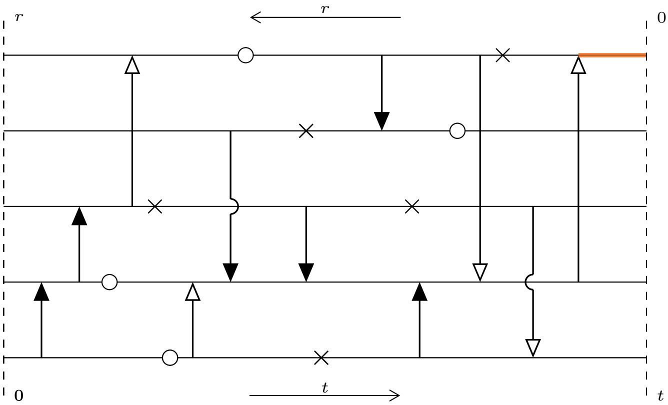

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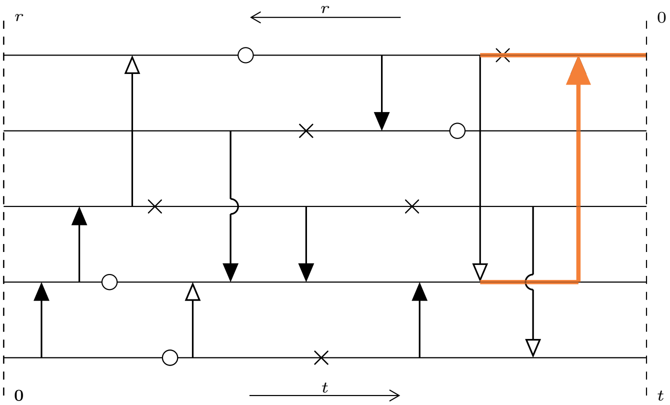

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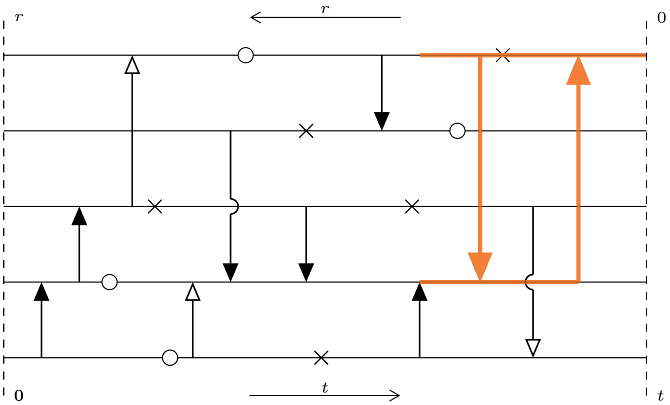

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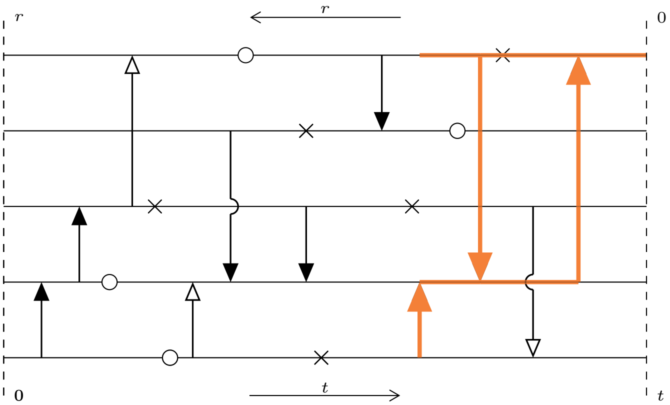

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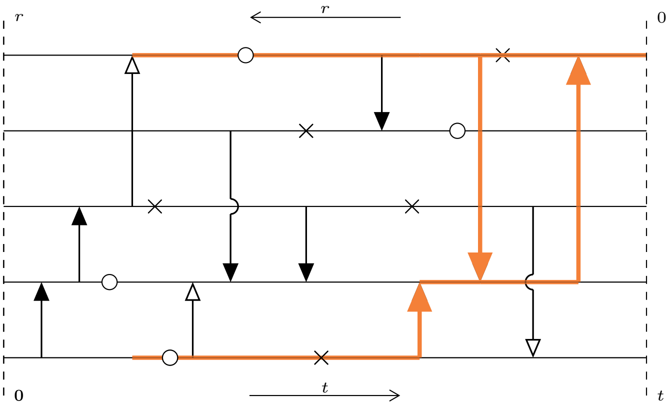

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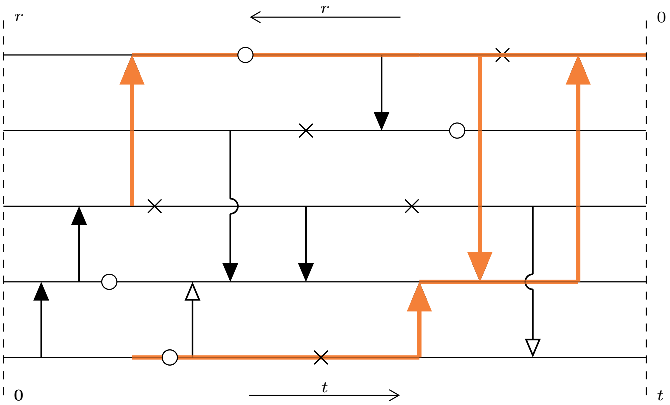

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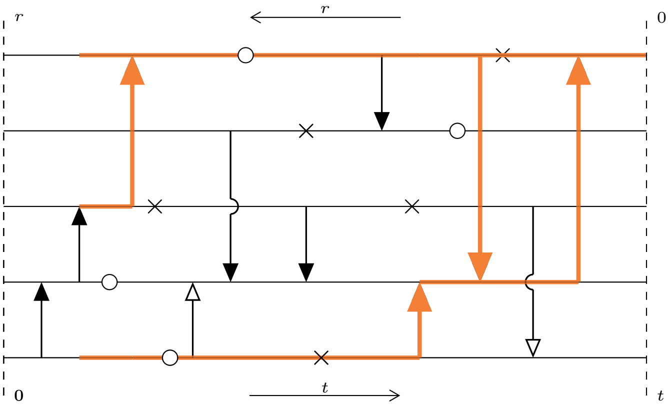

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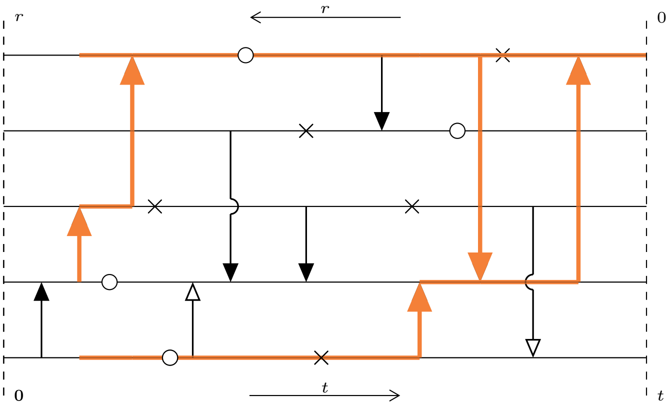

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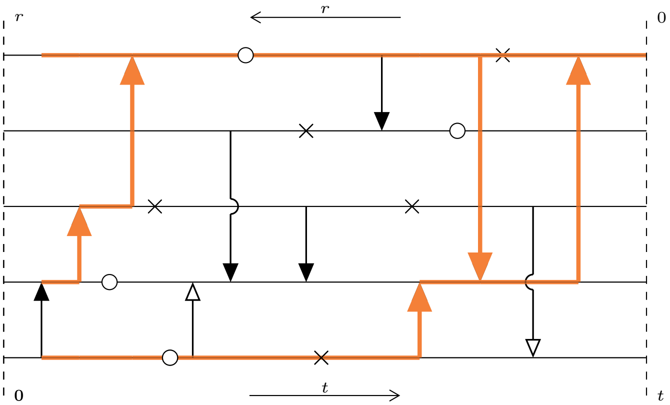

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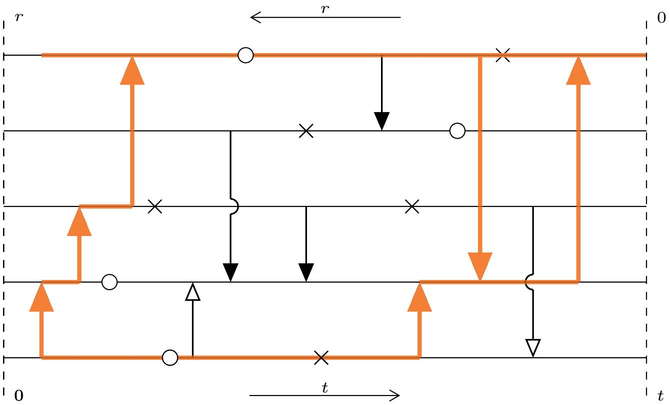

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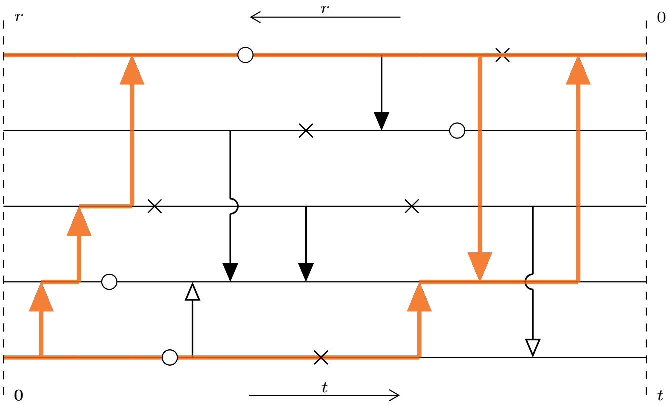

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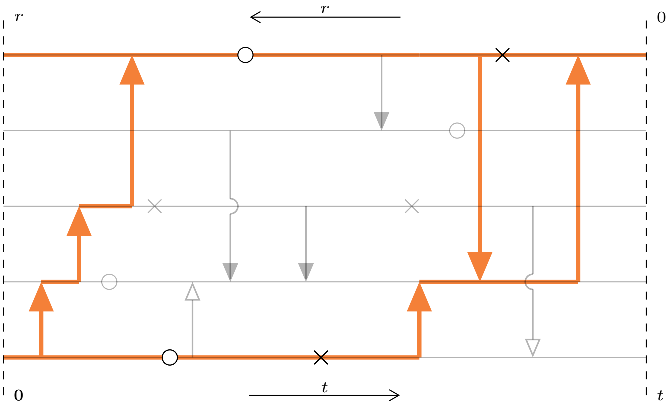
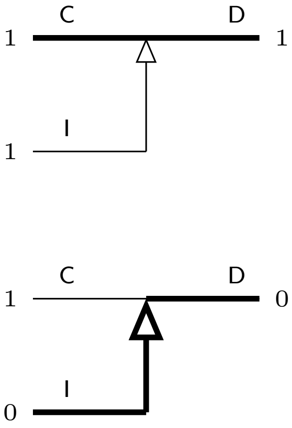


Pecking order

D=Descendant C=Continuing I=Incoming



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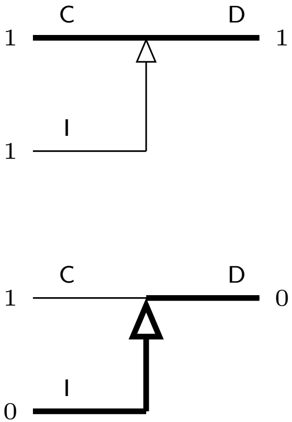
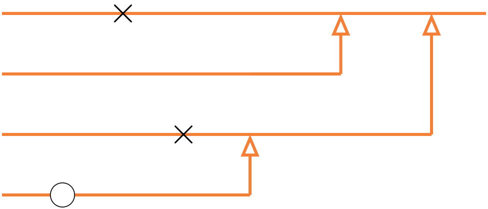


Descendant is of type $1 \Leftrightarrow$ all potential ancestors are of type 1

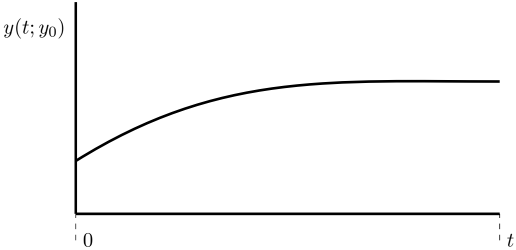
ASG in the deterministic limit

- No coalescence events, no collisions
- Branching at rate s per existing line
- Mutation to type 0 at rate $u\nu_0$ per existing line
- Mutation to type 1 at rate $u\nu_1$ per existing line

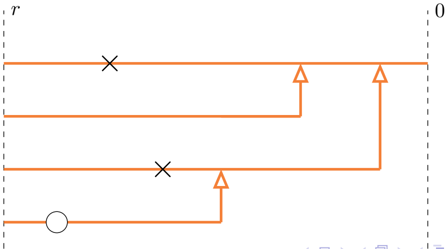


Type of uniformly chosen individual at time t

- Forward picture



- Backward picture?



The killed ASG

- Type of uniformly chosen individual?
- Count potential ancestors of a single individual
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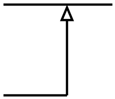

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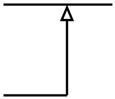

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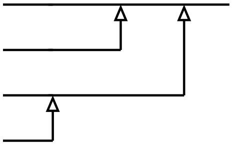

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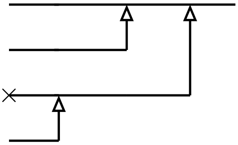

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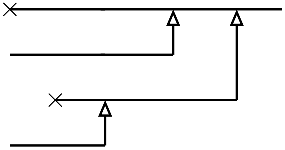

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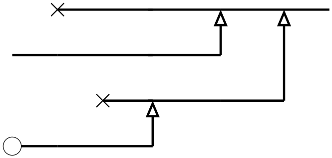

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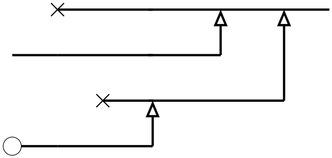
$$q_R(k, \Delta) = ku\nu_0$$



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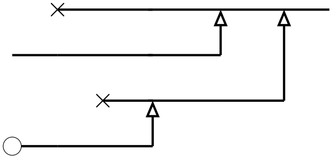

$\rightarrow$ $(R_r)_{r \geq 0}$ counts potential ancestors until type is known

Absorption states: 0 and Δ

Theorem

For $t \geq 0$,

$$y(t, y_0)^n = \mathbb{E}\Big[y_0^{R_t} \mid R_0 = n\Big] \qquad \forall n \in \mathbb{N}_0 \cup \{\Delta\},\ y_0 \in [0,1],$$

where $y^\Delta := 0$

$y(t, y_0)$*: proportion of type* 1

R_t*: number of potential ancestors until descendant's type is known*

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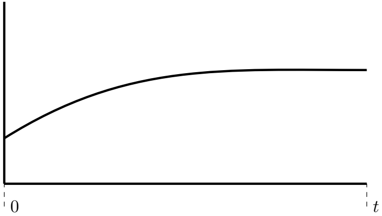

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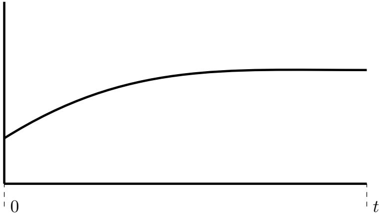
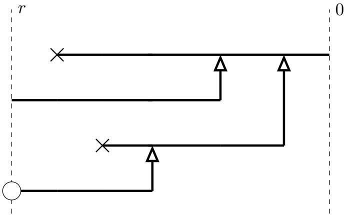
$$y(t, y_0)^n = \mathbb{E}\left[y_0^{R_t} \mid R_0 = n\right] \qquad \forall n \in \mathbb{N}_0 \cup \{\Delta\},\ y_0 \in [0,1],$$

where $y^{\Delta} := 0$

$y(t, y_0)$*: proportion of type* 1

R_t*: number of potential ancestors until descendant's type is known*





Absorption probabilities of R_r

- $w_n := P(\lim_{r\to\infty} R_r = 0 \mid R_0 = n)$
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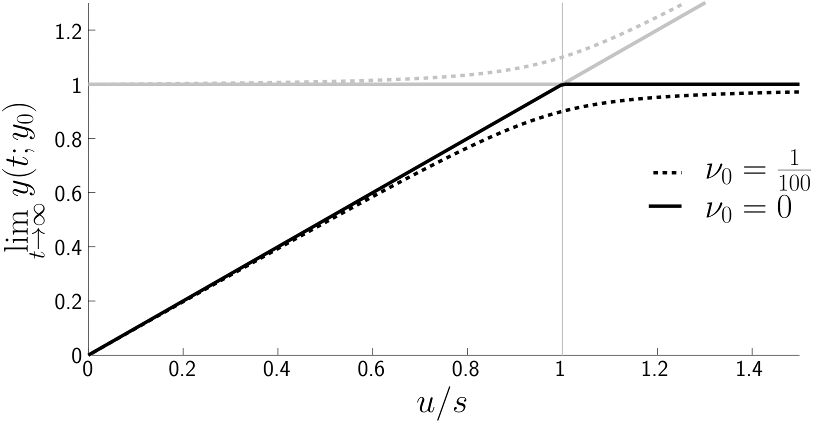
- Duality $\Rightarrow w_1 =$ proportion of 1 at stationarity $= \bar{y}$

The equilibrium frequency and absorption probability



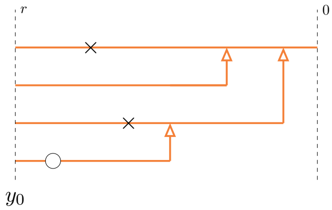
Black line: stable. Grey line: unstable.

- error threshold -

Representative ancestral type

Definition

The representative ancestral (RA) type at backward time r, denoted by $I_r \in \{0,1\}$, is the type of the ancestor at backward time r of an individual uniformly chosen at time 0.



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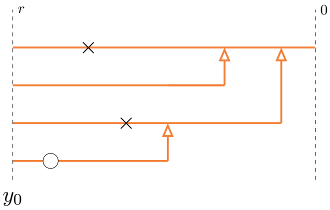
Quantities of interest

- $g(y_0, r) := P_{y_0}(I_r = 1)$
- $g_\infty(y_0) := \lim_{r\to\infty} g(y_0, r)$
  $\to$ conditional RA type distribution
- $g_\infty(\bar{y})$
  $\to$ RA type distribution in equilibrium



Pruned lookdown ASG (p-LD-ASG)

- In the diffusion case: Common ancestor type distribution Fearnhead [2002] and Taylor [2007] ⇒ analytic argument p-LD-ASG introduced by Lenz et al. [2015] ⇒ probabilistic argument
- Translation of p-LD-ASG to deterministic limit by Cordero [2017]

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Idea of p-LD-ASG:

- Count potential ancestors of a single individual
- Arrange potential ancestors in hierarchy
- Mutations rule out some potential ancestors

p-LD-ASG in deterministic limit

$$q_L(k, k+1) = ks$$

p-LD-ASG in deterministic limit

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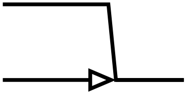

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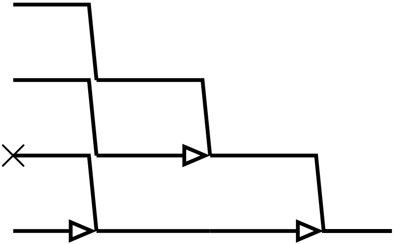

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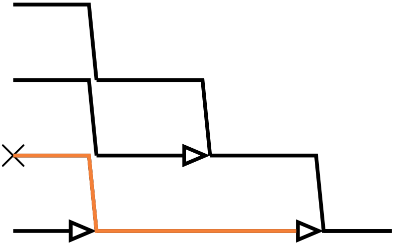

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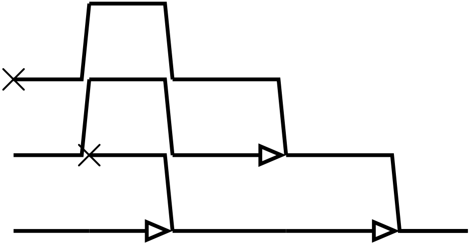

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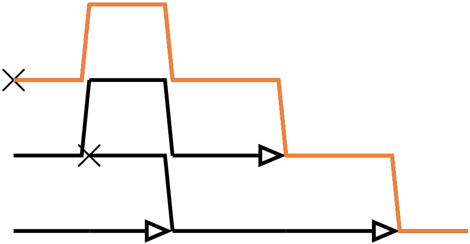

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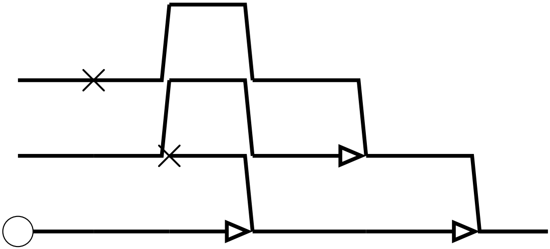

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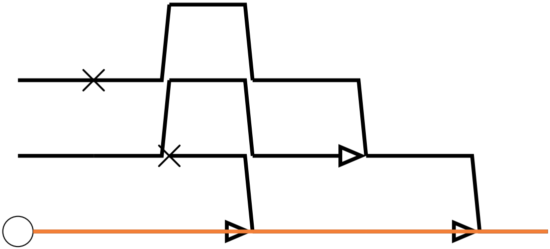

p-LD-ASG in deterministic limit

$$q_L(k,k+1) = ks$$
$$q_L(k,k-1) = (k-1)u\nu_1 + \mathbb{1}_{\{k>1\}}u\nu_0$$
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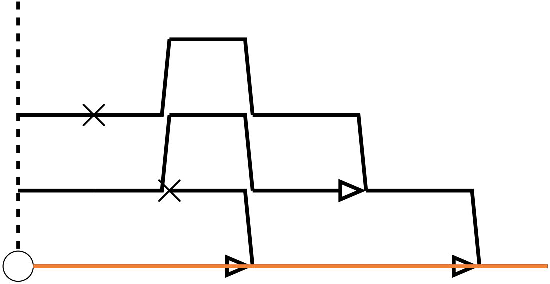

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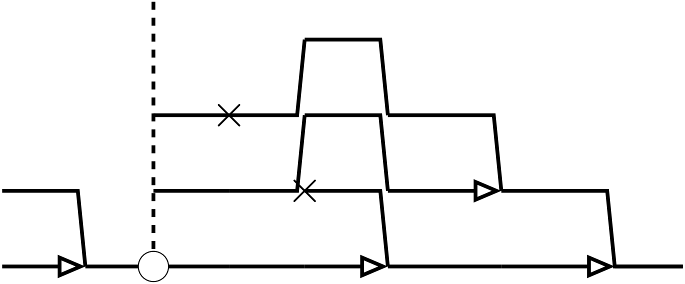

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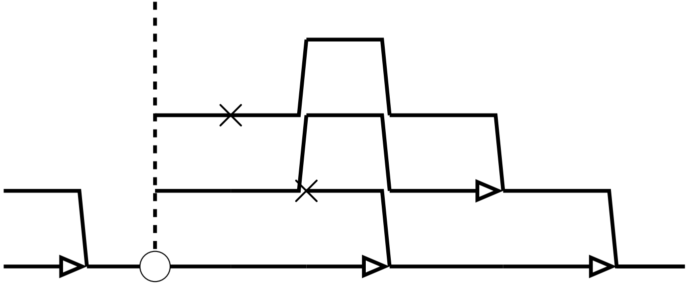

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$\Rightarrow$ ancestor of type 1 $\Leftrightarrow$ all potential ancestors in p-LD-ASG of type 1

p-LD-ASG - exploiting the hierarchy

- $$\begin{aligned}\Rightarrow g(y_0, r) &= \mathbb{E}[y_0^{L_r} \mid L_0 = 1] \\ &= 1 - (1 - y_0) \sum_{n \geq 0} P(L_r > n \mid L_0 = 1) y_0^n\end{aligned}$$

p-LD-ASG - exploiting the hierarchy

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  $$= 1 - (1 - y_0) \sum_{n \geq 0} P(L_r > n \mid L_0 = 1) y_0^n$$
- $g_\infty(y_0) := \lim_{r \to \infty} g(y_0, r)$??

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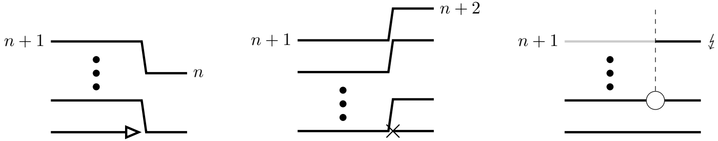
Proposition

1. *If* $s = 0$, L_r *absorbs in* 1 *almost surely*
2. *If* $u < s$ *and* $\nu_0 = 0$, L_r *is transient, so* $L_r \to \infty$ *a.s.* $(r \to \infty)$
3. *If* $u = s$ *and* $\nu_0 = 0$, L_r *is null recurrent*
4. *If* $u > s$ *or* $\nu_0 > 0$, L_r *is positive recurrent and the stationary distribution is geometric with parameter* $1 - p$, *where*

$$p = \begin{cases} \frac{s}{u\nu_1}\bar{y}, & \textit{if } \nu_1 > 0, \\ \frac{s}{u+s}, & \textit{if } \nu_1 = 0. \end{cases}$$

Intuition behind the geometric law

- Let $a_n := P(L_\infty > n)$



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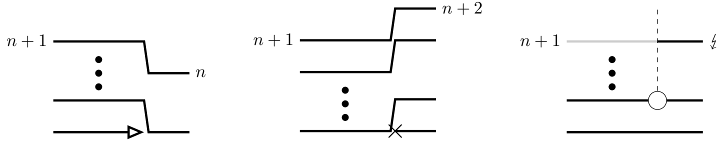

- Then,

$$a_n = \frac{s}{u+s} a_{n-1} + \frac{u\nu_1}{u+s} a_{n+1}$$

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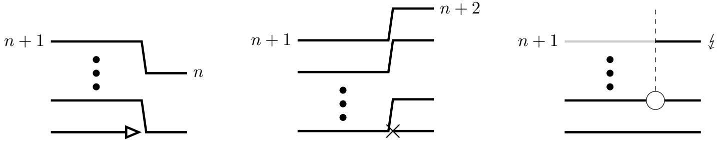

- Then,

$$a_n = \frac{s}{u+s} a_{n-1} + \frac{u\nu_1}{u+s} a_{n+1}$$

- $\Rightarrow$ lack of memory property

Recursion as FSA for absorption probabilities

Let D_t be the continuous-time Markov chain on $\mathbb{N} \cup \{\Delta\}$ with transition rates

$$q_D(d,j) = \begin{cases} (d-1)s, & \text{if } j = d-1, \\ (d-1)u\nu_1, & \text{if } j = d+1, \\ (d-1)u\nu_0, & \text{if } j = \Delta. \end{cases}$$

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Proposition

L_t and D_t are Siegmund dual, i.e. for $t \geq 0$,

$$P(m \leq L_t \mid L_0 = n) = P(D_t \leq n \mid D_0 = m), \quad \forall n \in \mathbb{N},\ m \in \mathbb{N} \cup \{\Delta\}.$$

Consequences of Siegmund duality

Corollary

$$P(D_\infty = 1 \mid D_0 = n+1) = \lim_{r\to\infty} P_1(L_r > n).$$

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Corollary (null recurrent case)

If $u = s$ *and* $\nu_0 = 0$,

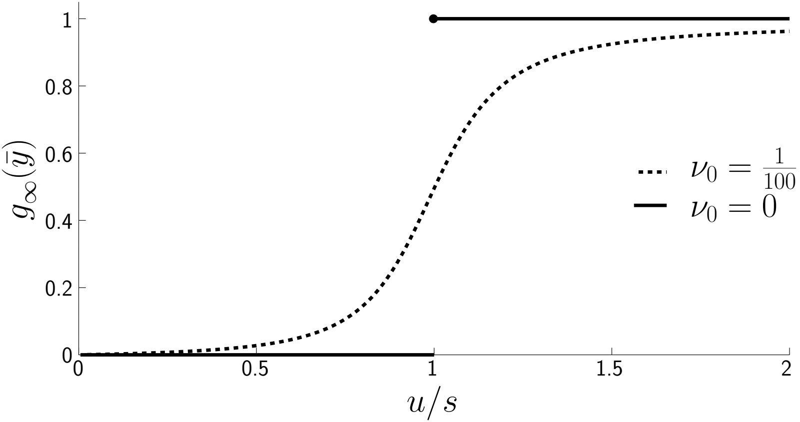
$$\lim_{r\to\infty} P(L_r > n \mid L_0 = 1) = 1.$$

Conditional RA type distribution

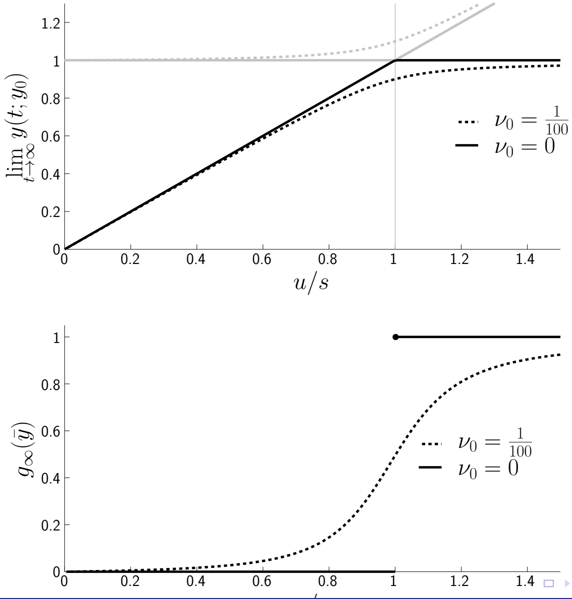
Theorem

1. *If* $s = 0$, $g_\infty(y_0) = y_0$ *for all* $y_0 \in [0,1]$.
2. *If* $u \leq s$ *and* $\nu_0 = 0$, $g_\infty(y_0) = \begin{cases} 0, & \textit{if } y_0 \in [0,1), \\ 1, & \textit{if } y_0 = 1. \end{cases}$
3. *If* $s > 0$ *and* $(u > s$ *or* $\nu_0 > 0)$, $g_\infty(y_0) = \frac{1-p}{1-py_0} y_0$.

RA type distribution in equilibrium

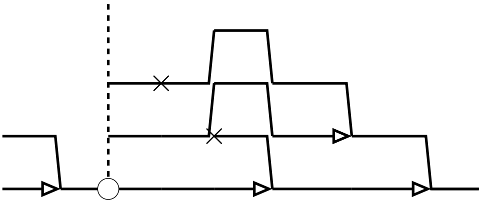


Properties of RA type distribution

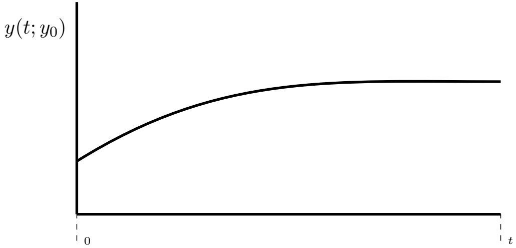


RA type at backward time r

- By means of non-absorbing $(L_r)_{r\geq 0}$



- Killed process? Absorption probability?



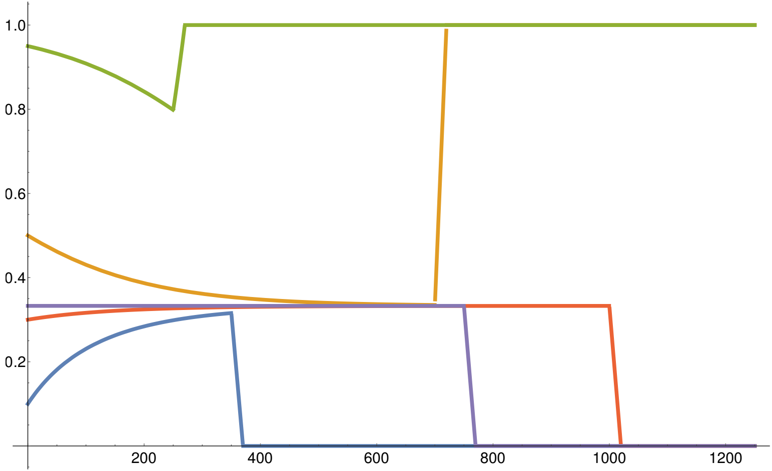
Piecewise-deterministic Markov process

- Inspired by Taylor [2007]
- $\tilde{Y}_t$ piecewise-deterministic Markov process on $[0,1]$ with generator

$$\begin{aligned}\mathcal{A}_{\tilde{Y}} f(y) = [-sy(1-y) - yu\nu_0 + u\nu_1(1-y)]\frac{\partial f}{\partial y} \\ + \frac{y}{1-y}u\nu_0\left[f(1) - f(y)\right] + \frac{1-y}{y}u\nu_1\left[f(0) - f(y)\right]\end{aligned}$$

  with $\lim_{y\to 1} \mathcal{A}_{\tilde{Y}} f(y) = \lim_{y\to 0} \mathcal{A}_{\tilde{Y}} f(y) = 0.$
- Absorbs in either 0 or 1

Piecewise-deterministic Markov process



Theorem

The piecewise-deterministic Markov processes $\tilde{Y}_t$ and the line-counting process of p-LD-ASG L_t are dual with respect to duality function y^n, and hence for $t \geq 0$,

$$\mathbb{E}\left[(\tilde{Y}_t)^n \mid \tilde{Y}_0 = y_0\right] = \mathbb{E}\left[y_0^{L_t} \mid L_0 = n\right] \qquad \forall y_0 \in [0,1],\ n \in \mathbb{N}.$$

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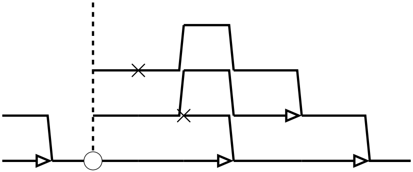

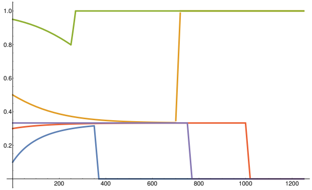

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Corollary

$$g_\infty(y_0) = \mathbb{E}\left[y_0^{L_\infty} \mid L_0 = 1\right] = P(\tilde{Y}_t \text{ absorbs in } 1 \mid \tilde{Y}_0 = y_0)$$

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Thank you for your attention!!!