A Siegmund dual for the line counting in a pruned ancestral selection graph

Ute Lenz

Goethe Universität Frankfurt

work in progress

joint with **Ellen Baake** (Bielefeld) and **Anton Wakolbinger** (Frankfurt)

1. Backward in time: ASG
2. pruned LD-ASG (with selection and mutation)
3. Forward in time: dual process

06.11.2014

PROBABILISTIC STRUCTURES IN EVOLUTION

DFG SPP 1590

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Universität Bielefeld

Wright-Fisher diffusion with mutation and selection

$$dX_t = \sqrt{2X_t(1-X_t)}\, dB_t \; + \; \Big[(1-X_t)\theta\nu_0 - X_t\theta\nu_1 + X_t(1-X_t)\sigma\Big]\, dt$$

$X_t,\ 1-X_t$	...	frequency type 0 ('good'), type 1 ('bad')
θ	...	mutation rate
$\nu_0,\ \nu_1$	...	mutation probability to type 0, 1, $\nu_0 + \nu_1 = 1$
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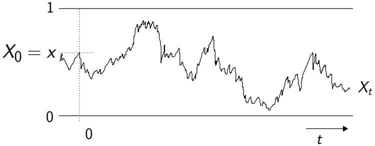

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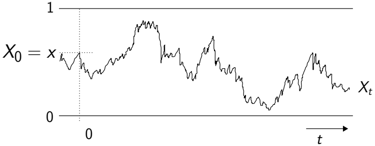

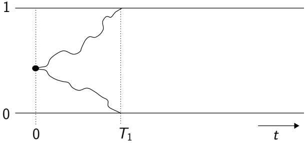

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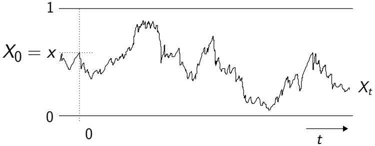

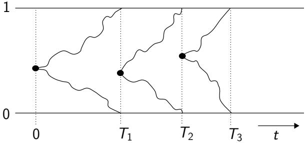

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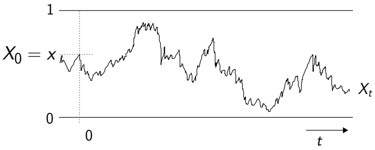

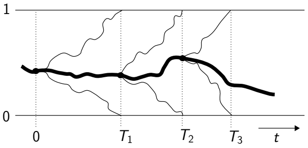

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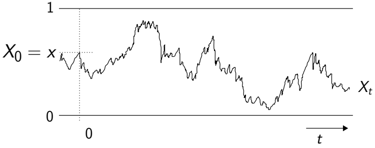

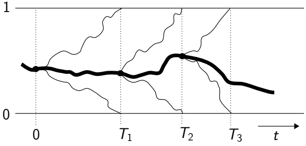

$$h(x) := \mathbb{P}\,(\text{'winner' at } t=0 \text{ is of type } 0 \mid X_0 = x)\}$$

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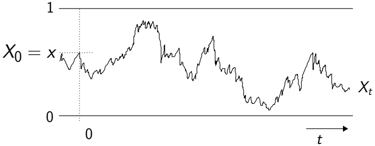
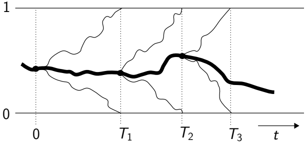




$$h(x) := \mathbb{P}\,(\text{'winner' at } t=0 \text{ is of type } 0 \mid X_0 = x)\} = \sum_{n\geq 0} a_{n-1}x(1-x)^{n-1}$$

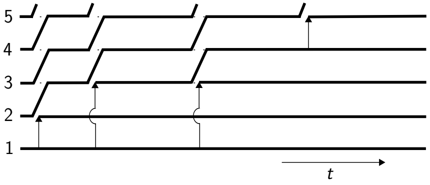
$$(n+1+\theta+\sigma)a_n = (n+1+\theta\nu_1)a_{n+1} + \sigma a_{n-1}$$ (Fearnhead 2002)

$$1 = a_0 \geq a_1 \geq \cdots, \qquad \lim_{n\to\infty} a_{n+1}/a_n = 0$$

Lookdown construction with selection

Wright-Fisher diffusion

$$dX_t = \sqrt{2X_t(1-X_t)}\; dB_t$$



Lookdown model

Donnelly & Kurtz 1999

N individuals on levels $\{1, 2, \ldots\}$,
types 0 ('good'), 1 ('bad')

X_t^N frequency of type-0 individuals at time t

$\longrightarrow$ neutral reproduction, rate 2
(for all individuals towards higher levels)

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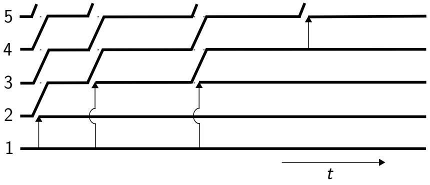

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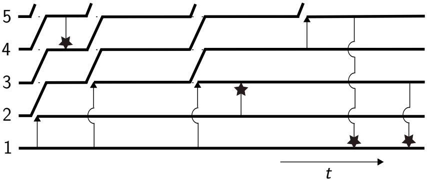

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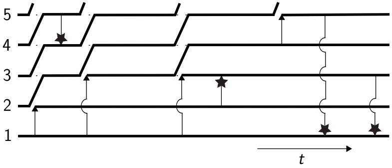
(for all individuals towards higher levels)

$\longrightarrow\!\!\star$ selective reproduction, rate s_N (for 0 individuals)
$(Ns_N \to \sigma)$

Lookdown construction with selection

assign types and let them evolve (forward in time)



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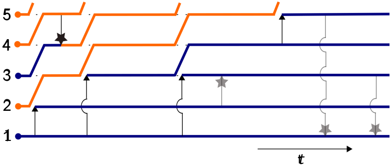
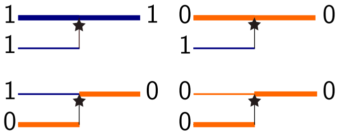
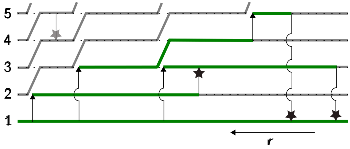


.... and keep in mind pecking order



ASG

backward in time: trace back all potential ancestors



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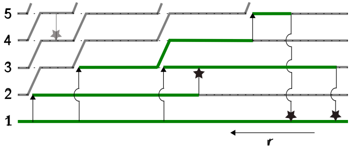
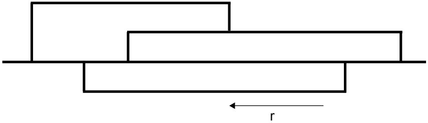


Ancestral Selection Graph (ASG) (Neuhauser and Krone 1997)



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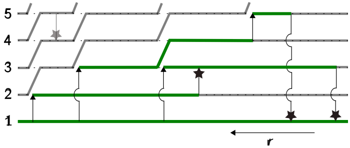

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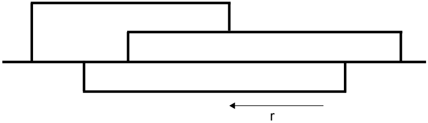

branching:
rate σ per line;

coalescence:
rate 2 per (unordered) pair

ASG

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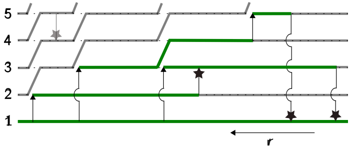

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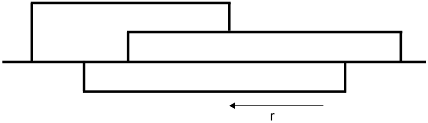

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$(K_r)_{r\geq 0}$ number of lines in ASG at time $r = -t$

birth-death process with rates

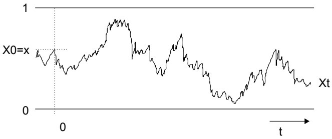
$$q_K(n, n-1) = n(n-1), \quad q_K(n, n+1) = n\sigma, \quad n \in \mathbb{N}$$

and (reversible) equilibrium distribution

$$\mathbb{P}(K_r = n) = \frac{\sigma^n}{(\exp(\sigma)-1)n!} \quad \text{(i.e., Poisson}(\sigma)\text{ conditioned to } \{1, 2, \ldots\})$$

Moment duality

Wright-Fisher diffusion with selection



forward in time

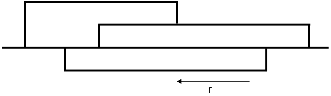
$(X_t)_{t\geq 0}$ frequency of type-0 individuals

$G_X f(x) =$

$x(1-x)f''(x) +$

$x(1-x)\sigma f'(x)$

ASG



backward in time

all potential ancestors of a sample

$(K_r)_{r=-t\geq 0}$ number of lines in ASG

$G_K f(n) =$

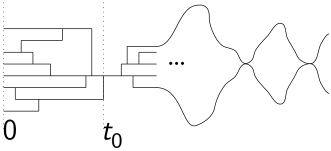
$n(n-1)\left[f(n-1)-f(n)\right] +$

$n\sigma\left[f(n+1)-f(n)\right]$

X and K are moment duals, i.e.

$$\mathbf{E}_x\left[(1-X_s)^n\right] = \mathbf{E}_n\left[(1-x)^{K_s}\right] \quad \forall\ s\geq 0,\ x\in[0,1],\ n\in\mathbb{N}_0$$

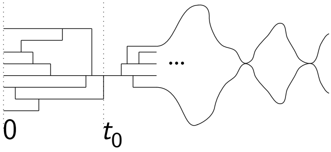
ASG



equilibrium ASG has bottlenecks

$\rightsquigarrow$ type 0 is ancestral iff at least one potential ancestor at $t = 0$ is of type 0 (Mano 2009; Pokalyuk and Pfaffelhuber 2013)

ASG



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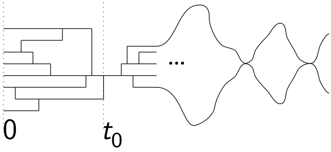
assign types by drawing iid according to X_0

$\rightsquigarrow$ $\mathbb{P}(\text{at least one potential ancestor is of type } 0 \mid X_0 = x) = 1 - (1-x)^{K_0}$, so

ASG



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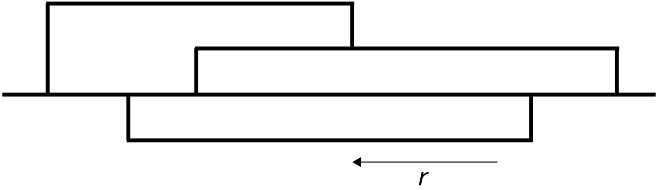
$$\begin{aligned} h(x) &= \sum_{n\geq 1} \left(1-(1-x)^n\right)\left[\mathbb{P}(K_0 \geq n) - \mathbb{P}(K_0 \geq n+1)\right] \\ &= \sum_{n\geq 1} \mathbb{P}(K_0 \geq n) x (1-x)^{n-1} \end{aligned}$$

ASG with mutations

step 1: backward, without types



(mutation: rates $\theta\nu_0, \theta\nu_1$ per line)

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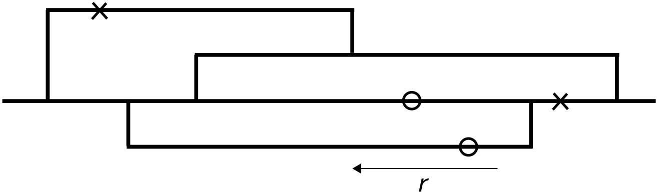

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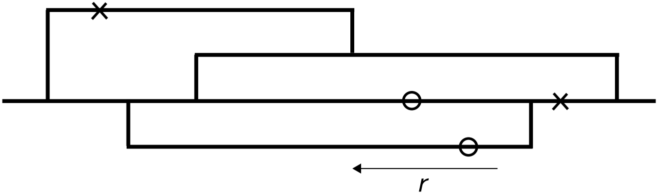

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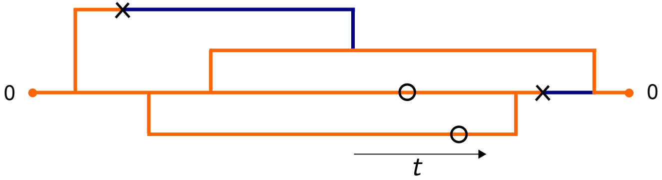
step 2: forward, with types



(resolve branching events)

ASG with mutations

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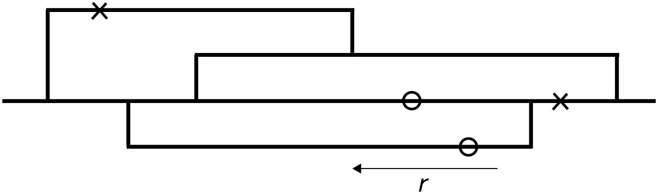

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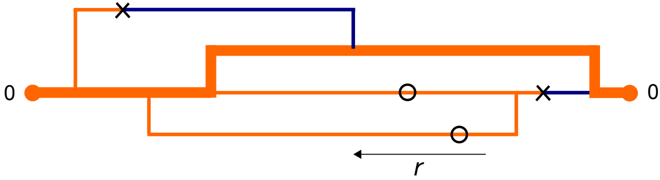
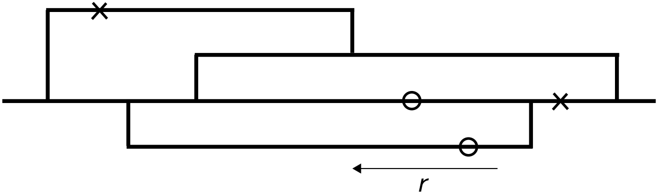


(identify ancestral line)

ASG with mutations

step 1: backward, without types



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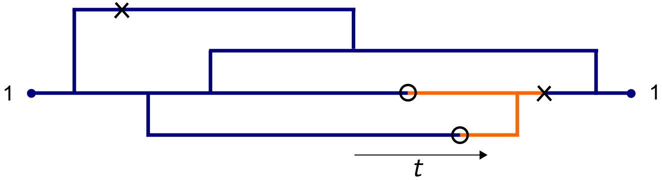

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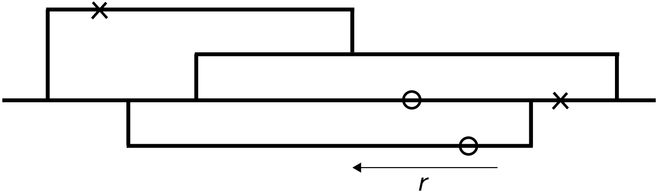

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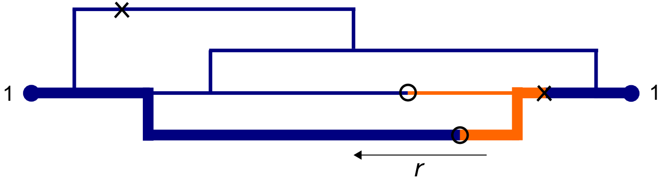

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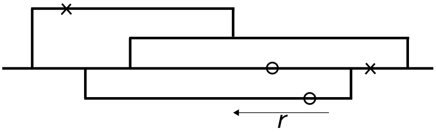
Ordering the ASG



ASG

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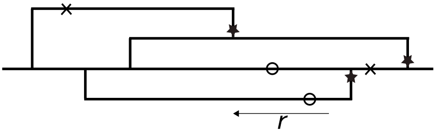

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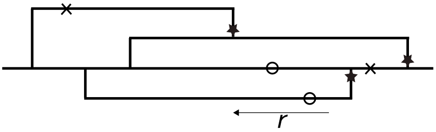
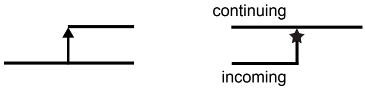


ASG

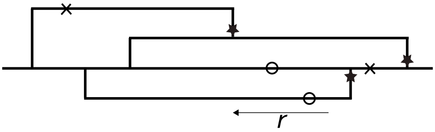
ordering convention:



coalescence

branching

Ordering the ASG



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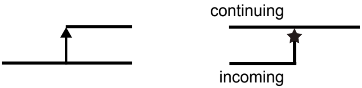
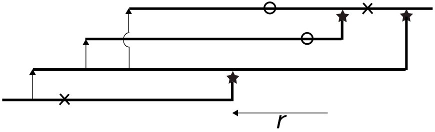
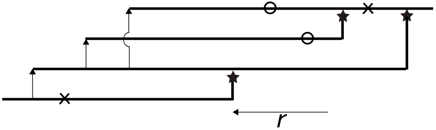


coalescence branching



ordered ASG

The Lookdown ASG



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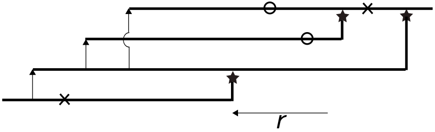
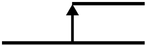


ordered ASG

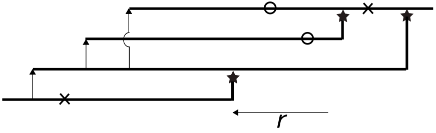
elements:



coalescence

branching

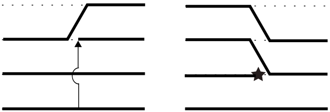
The Lookdown ASG



ordered ASG

elements:

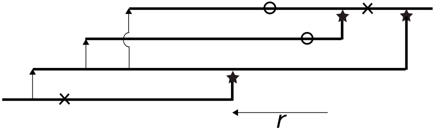
Lookdown elements:



coalescence

branching

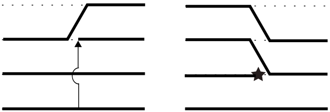
The Lookdown ASG



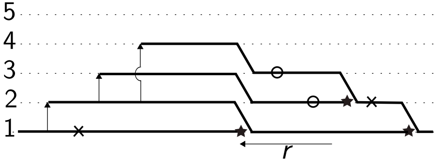
ordered ASG

elements:

Lookdown elements:



coalescence branching

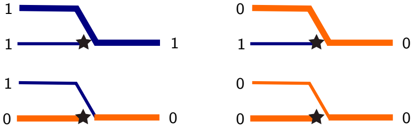


LD-ASG

LD-ASG with types

assign types (at $t = 0$ iid according to X_0)
$\rightsquigarrow$ type and level of immortal line?

branching: pecking order



LD-ASG with types

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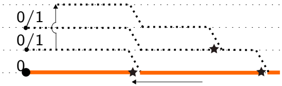
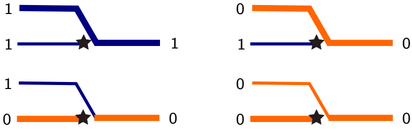


branching: pecking order



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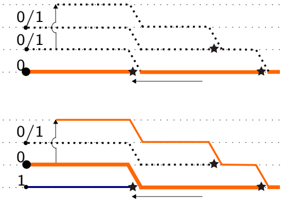
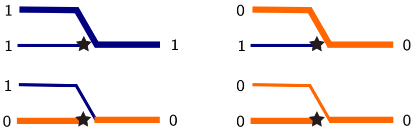


branching: pecking order



LD-ASG with types

assign types (at $t = 0$ iid according to X_0)
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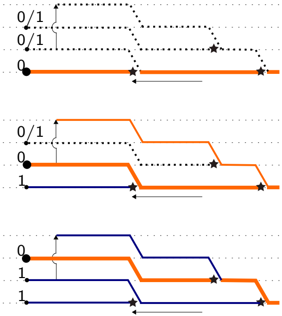

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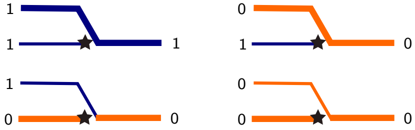

LD-ASG with types

assign types (at $t = 0$ iid according to X_0)

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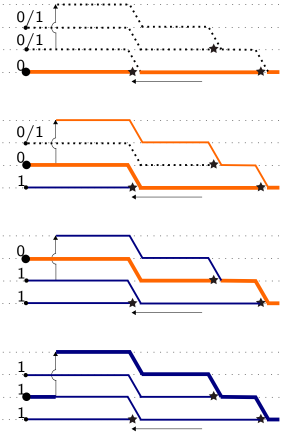
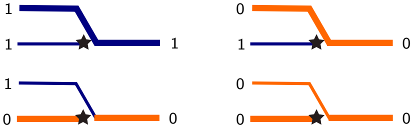


branching: pecking order



LD-ASG with types

assign types (at $t = 0$ iid according to X_0)
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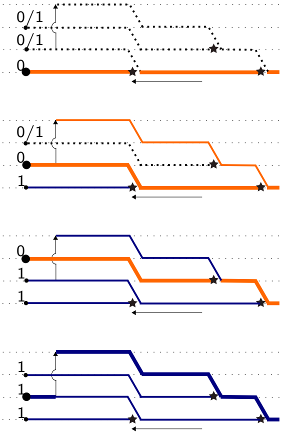
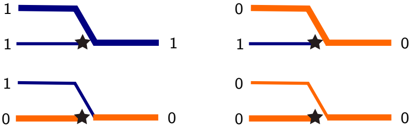


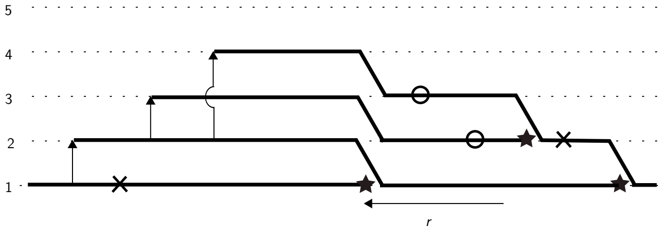
branching: pecking order



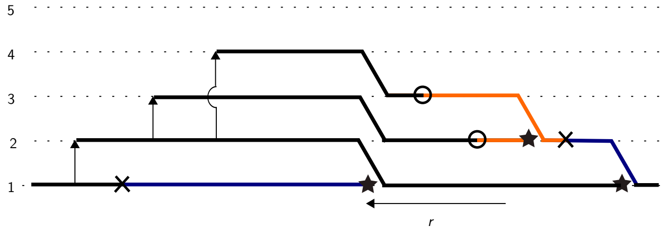
immune line
(:=immortal if all lines are of type 1)

- starts back from the bottleneck
- moves up at branching events $\rightsquigarrow$ follows continuing branch!
- follows coalescence events downwards

LD-ASG with mutations



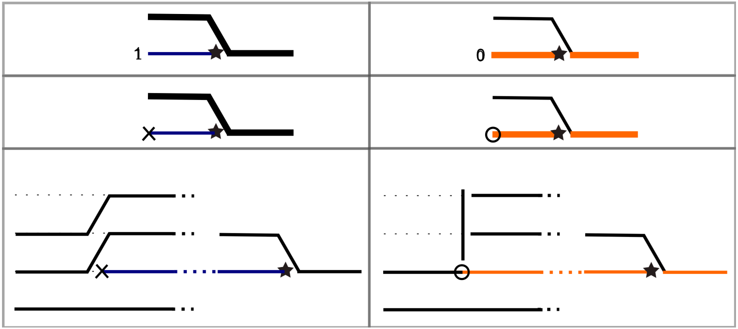
LD-ASG with mutations



some potential ancestors drop out
$\rightarrow$ erase lines and get a pruned LD-ASG

The pruned LD-ASG

Pruning procedure



mutation reduces number of potential ancestors

- (×) erase lines that carry the deleterious mutation
- (○) erase all lines above a beneficial mutation

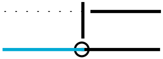
The pruned LD-ASG

Pruning procedure

But: immune line cannot be erased
(immune line at time t is immortal
if all lines at time t are assigned type 1)

- is not erased when hit by a cross
  but lines are rearranged

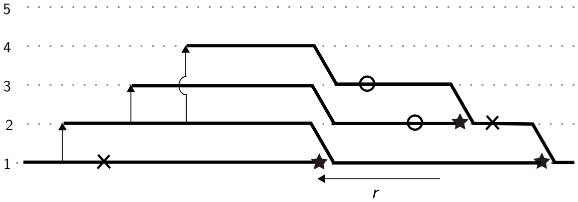
- jumps to the level of the circle at
  a beneficial mutation



The pruned LD-ASG

Construction from a given realisation of the LD-ASG

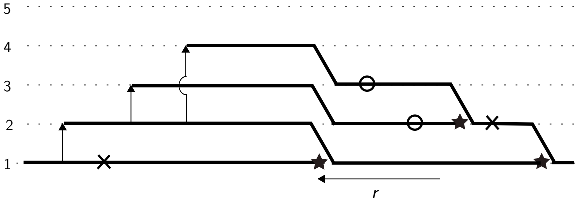
LD-ASG:



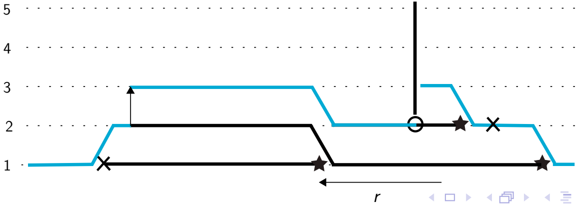
The pruned LD-ASG

Construction from a given realisation of the LD-ASG

LD-ASG:

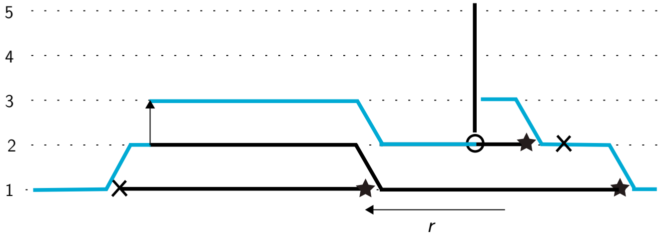


pruned LD-ASG:



The pruned LD-ASG

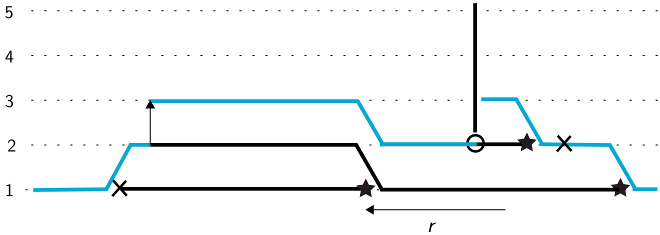
Markovian dynamics backward in time



$L_r :=$ highest occupied level (= number of lines) at time r

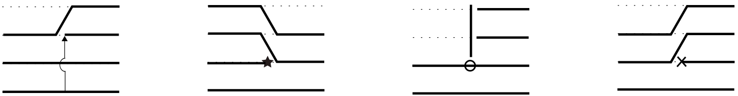
The pruned LD-ASG

Markovian dynamics backward in time



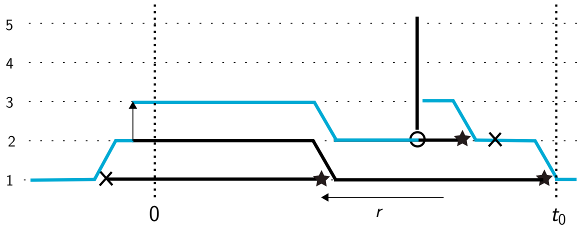
$L_r :=$ highest occupied level ($=$ number of lines) at time r

$(L_r)_{r\in\mathbb{R}}$ jump process with rates



$q_L^{\uparrow}(n, n-1) = n(n-1)$ $\quad$ $q_L^{*}(n, n+1) = n\sigma$ $\quad$ $q_L^{\circ}(n, n-\ell) = \theta\nu_0$ $\quad$ $q_L^{\times}(n, n-1) = (n-1)\theta\nu_1$

The pruned LD-ASG



realisation of pruned equilibrium LD-ASG

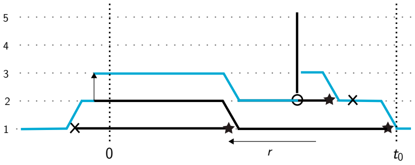
no mutations except on the immune line

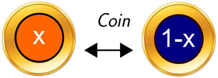
assign types at $t = 0$

Lemma (Type of the immortal line)

The immortal line at $t = 0$ in the pruned equilibrium LD-ASG with types assigned at $t = 0$ is of type 0 iff there is at least one line of type 0.

Common ancestor type distribution





$X_r :=$ frequency of type-0 individuals at time r

$I^k :=$ type of line on level $k \in \mathbb{N}_0$

$$
\begin{aligned}
h(x) &= \mathbb{P}\left(\text{immortal line has type 0 at } t = 0 \mid X_0 = x\right) \\
&= \mathbb{P}\left(\text{at least one line of type 0 at } t = 0 \mid X_0 = x\right) \\
&= \sum_{n \geq 1} \mathbb{P}\left(I^n = 0, I^1 = \ldots = I^{n-1} = 1, L_0 \geq n \mid X_0 = x\right) \\
&= \sum_{n \geq 1} x(1-x)^{n-1} \cdot \mathbb{P}(L_0 \geq n)
\end{aligned}
$$

Common ancestor type distribution

Theorem (main result)

1. $h(x) = \mathbb{P}\,(\text{immortal line has type } 0 \mid x)$ is the probability of at least one success when tossing L^{equ} times a coin with success probability x,

$$h(x) = \sum_{n \geq 1} x(1-x)^{n-1} \cdot a_{n-1}$$

2. The Fearnhead coefficients (a_n) are the tail probabilities of the stationary distribution of L, $a_{n-1} = \mathbb{P}(L^{equ} \geq n)$, determined by

$$(n+1+\theta+\sigma)a_n = (n+1+\theta\nu_1)a_{n+1} + \sigma a_{n-1}\ ,$$

$$1 = a_0 \geq a_1 \geq \cdots\ , \qquad \lim_{n\to\infty} a_{n+1}/a_n = 0\ .$$

Common ancestor type distribution

Theorem (main result)

1. $h(x) = \mathbb{P}$ (immortal line has type $0 \mid x$) is the probability of at least one success when tossing L^{equ} times a coin with success probability x,

$$h(x) = \sum_{n \geq 1} x(1-x)^{n-1} \cdot a_{n-1} \quad \checkmark$$

2. The Fearnhead coefficients (a_n) are the tail probabilities of the stationary distribution of L, $a_{n-1} = \mathbb{P}(L^{equ} \geq n)$, determined by

$$(n+1+\theta+\sigma)a_n = (n+1+\theta\nu_1)a_{n+1} + \sigma a_{n-1} ,$$

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Common ancestor type distribution

Theorem (main result)

1. $h(x) = \mathbb{P}\,(\text{immortal line has type } 0 \mid x)$ is the probability of at least one success when tossing L^{equ} times a coin with success probability x,

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2. The Fearnhead coefficients (a_n) are the tail probabilities of the stationary distribution of L, $a_{n-1} = \mathbb{P}(L^{equ} \geq n)$, determined by

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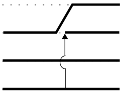
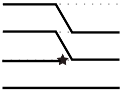
The processes L and D

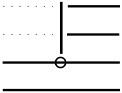
transition rates of L backward in time



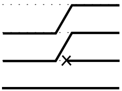
$q_L^{\uparrow}(\ell, \ell - 1)$
$= \ell(\ell - 1)$



$q_L^{*}(\ell, \ell + 1)$
$= \ell\sigma$



$q_L^{\circ}(\ell, \ell - m)$
$= \theta\nu_0$

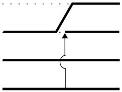


$q_L^{\times}(\ell, \ell - 1)$
$= (\ell - 1)\theta\nu_1$

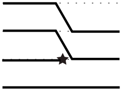
ignore on immune line

The processes L and D

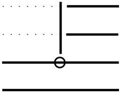
transition rates of L backward in time



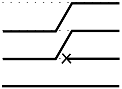
$q_L^{\uparrow}(\ell, \ell-1) = \ell(\ell-1)$



$q_L^{*}(\ell, \ell+1) = \ell\sigma$



$q_L^{\circ}(\ell, \ell-m) = \theta\nu_0$



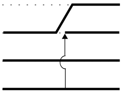
$q_L^{\times}(\ell, \ell-1) = (\ell-1)\theta\nu_1$

ignore on immune line

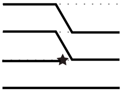
"transposed" rates forward in time

The processes L and D

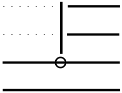
transition rates of L backward in time



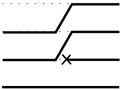
$q_L^{\uparrow}(\ell, \ell-1)$
$= \ell(\ell-1)$



$q_L^{*}(\ell, \ell+1)$
$= \ell\sigma$



$q_L^{\circ}(\ell, \ell-m)$
$= \theta\nu_0$



$q_L^{\times}(\ell, \ell-1)$
$= (\ell-1)\theta\nu_1$

ignore on immune line

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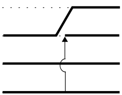
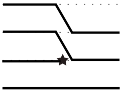
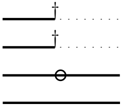


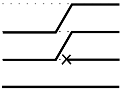
$q_D^{\uparrow}(n, n+1)$
$= n(n-1)$



$q_D^{*}(n, n-1)$
$= (n-1)\sigma$



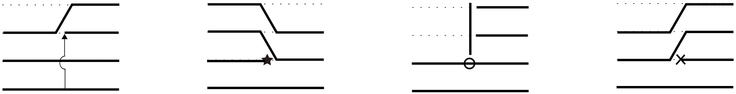
$q_D^{\circ}(n, \dagger)$
$= (n-1)\theta\nu_0$



$q_D^{\times}(n, n+1)$
$= (n-1)\theta\nu_1$

The processes L and D

transition rates of L backward in time



$q_L^{\uparrow}(\ell, \ell-1) = \ell(\ell-1)$

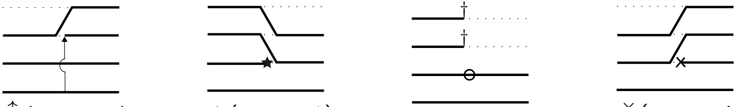
$q_L^{*}(\ell, \ell+1) = \ell\sigma$

$q_L^{\circ}(\ell, \ell-m) = \theta\nu_0$

$q_L^{\times}(\ell, \ell-1) = (\ell-1)\theta\nu_1$

ignore on immune line

"transposed" rates forward in time



$q_D^{\uparrow}(n, n+1) = n(n-1)$

$q_D^{*}(n, n-1) = (n-1)\sigma$

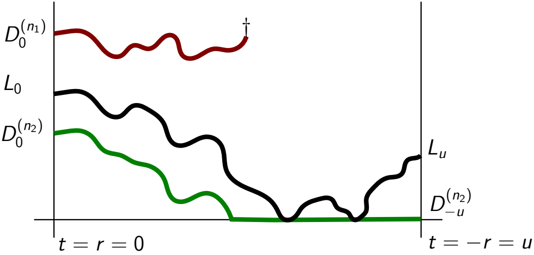
$q_D^{\circ}(n, \dagger) = (n-1)\theta\nu_0$

$q_D^{\times}(n, n+1) = (n-1)\theta\nu_1$

$\rightsquigarrow$ forward in time process $(D_t)_{t\geq 0}$:

- birth and death process
- absorbing states 1, $\dagger$, and ∞

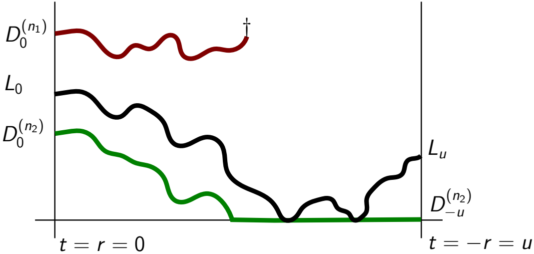
The processes L and D



Heuristics:

$$\mathbf{P}(L_0 \geq n) = \mathbf{P}(D^{(n)} \text{ eventually reaches level 1 forward in time})$$

The processes L and D

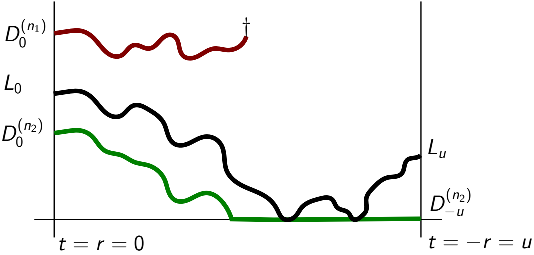


Heuristics:

$$\mathbf{P}(L_0 \geq n) = \mathbf{P}(D^{(n)} \text{ eventually reaches level 1 forward in time})$$

$\rightsquigarrow$ tail probabilities of L = absorption probabilities of D in 1

The processes L and D



Indeed,

Theorem (Siegmund duality)

L and D are Siegmund duals, i.e.

$$\mathbf{E}_\ell \left[\mathbf{I}_{\{L_s \geq n\}} \right] = \mathbf{E}_n \left[\mathbf{I}_{\{\ell \geq D_s\}} \right] \quad \forall s \geq 0, \ell \in \mathbb{N}_0, n \in \mathbb{N}_0 \cup \{\dagger\}$$

Proof:
Check calculation for the generators with duality function $\mathbf{I}_{\{L \geq D\}}$.

Siegmund duality

$$\mathbf{E}_\ell\left[\mathbf{I}_{\{L_s\geq n\}}\right] = \mathbf{E}_n\left[\mathbf{I}_{\{\ell\geq D_s\}}\right] \quad \forall \ell\in\mathbb{N}_0, n\in\mathbb{N}_0\cup\{\dagger\}$$
$$\Leftrightarrow \quad \mathbf{P}_\ell(L_s\geq n) = \mathbf{P}_n(\ell\geq D_s)$$

take $\ell = 1, s\to\infty$ (equilibrium situation)
(start L with one line in the far future)

$$\mathbf{P}(L^{equ}\geq n) = \mathbf{P}_n(1\geq D_\infty)$$

$$a_{n-1} = \mathbf{P}(L^{equ}\geq n) = \mathbf{P}_n(D_\infty = 1)$$

First step decomposition of the event 'absorption in one' yields

$$[n(n-1) + (n-1)\theta\nu_1 + (n-1)\sigma + (n-1)\theta\nu_0]\, a_{n-1}$$
$$= [n(n-1) + (n-1)\theta\nu_1]\, a_n \; + \; (n-1)\sigma a_{n-2} \; + \; (n-1)\theta\nu_0 a_\dagger$$

$$\Leftrightarrow [n+1+\theta+\sigma]\, a_n = [n+1+\theta\nu_1]\, a_{n+1} + \sigma a_{n-1}$$

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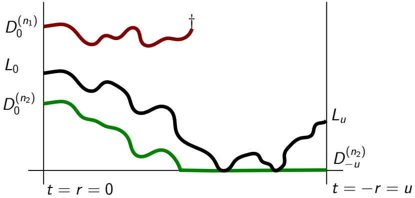
Siegmund duality

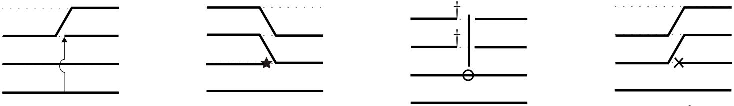
Siegmund duals are strongly pathwise duals:

We can find a version of the processes L and D, defined on a common probability space, such that $\forall \ell, n \in \mathbb{N}, s \geq 0$

$$\mathbf{1}_{\{L_s^{(\ell)} \geq n\}} = \mathbf{1}_{\{(\ell \geq D_s^{(n)}\}}$$



graphical representation of the underlying auxiliary process:



rate 2 per pair of levels

rate σ per level

rate $\theta\nu_0$ per level

rate $\theta\nu_1$ per level

ignore on immune line

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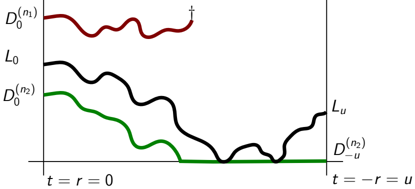
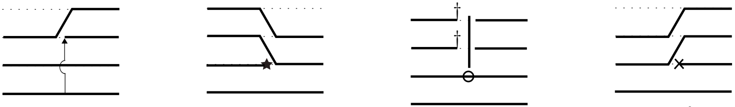


graphical representation of the underlying auxiliary process:



rate 2 per pair of levels | rate σ per level | rate $\theta\nu_0$ per level | rate $\theta\nu_1$ per level

~~ignore on immune line~~

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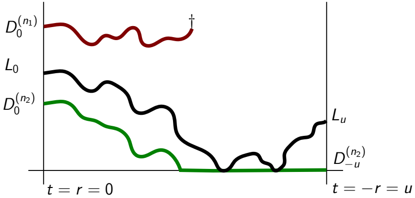

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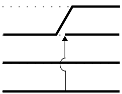
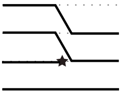
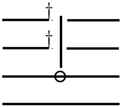


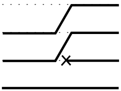
rate 2
per pair of levels



rate σ
per level



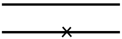
rate $\theta\nu_0$
per level



rate $\theta\nu_1$
per level

~~ignore on immune line~~

ignore on level 1

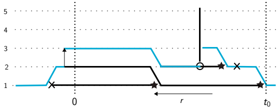


Conclusion

Two-type Wright-Fisher diffusion with mutation and selection

Backward in time:

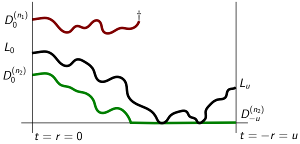
Transparent graphical method to identify all potential ancestors: pruned equilibrium LD-ASG (L top level)



arXiv:1409.0642

Forward in time:

Siegmund dual process D yields tail probabilities of L



Thank you!