# Lines of descent in a deterministic model with mutation and frequency dependent selection

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<sup>\*</sup>joint work (in progress) with E. Baake and S. Hummel

#### Structure of the talk

#### Models with mutation and frequency dependent selection

The deterministic model

The Moran model

Moran vs deterministic model

The ancestral selection graph (ASG)

Ancestral processes in the non-interactive deterministic limit

Ancestral processes in the frequency dependent deterministic limit

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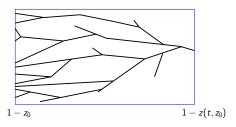
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- ▶ In the sequel, we focus on the case  $\beta > 0, \gamma \leq 0$ .

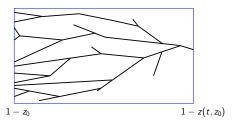
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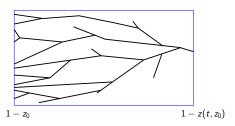
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- ▶ Prob. of sampling a 1-individual at time  $t \equiv 1 z(t, z_0)$ .
- Can we express this probability using an ancestral process (duality!)?



Population of size N, two types  $\{0,1\}$ .

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- ▶ Each individual mutates to type i at rate  $u_i$ ,  $i \in \{0, 1\}$ .

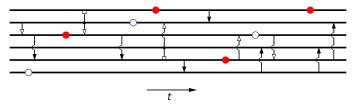
# The graphical representation $(\beta > 0, \gamma < 0)$

 $\longrightarrow$  = Neutral reproduction,  $\longrightarrow$  = Non-interactive selective reproduction,

□ → > = Interactive selective reproduction,

 $\bigcirc$  = Mutation to type 0,  $\bullet$  = Mutation to type 1,

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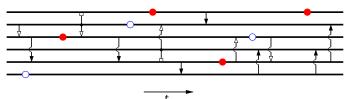
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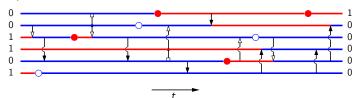
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#### Typed picture:



#### Dynamical law of large numbers

For  $t \ge 0$ , we denote by  $X_t^N$  the number of 0-individuals at time t in the Moran model of size N.

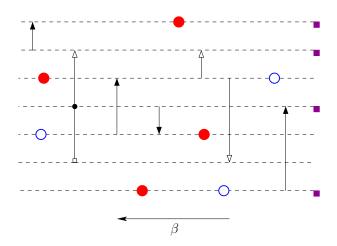
#### Proposition (Law of large numbers)

For  $z_0 \in [0,1]$ , let  $z(z_0,\cdot)$  be the solution of (1) with  $z(0,z_0)=z_0$ . Assume that  $\lim_{N\to\infty}\frac{X_0^N}{N}=z_0\in [0,1]$ . Then, for all  $\varepsilon>0$ , we have

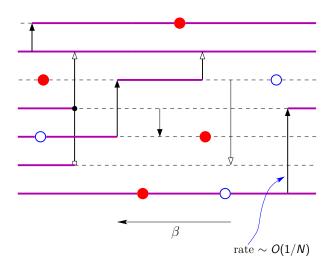
$$\lim_{N\to\infty} P\left(\sup_{t\le T}\left|\frac{X_t^N}{N}-z(t,z_0)\right|>\varepsilon\right)=0,$$

i.e.  $X^N/N$  converges to  $z(\cdot,z_0)$  uniformly in compacts in probability.

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#### Models with mutation and frequency dependent selection

Ancestral processes in the non-interactive deterministic limit

The case without mutation

The case with mutation

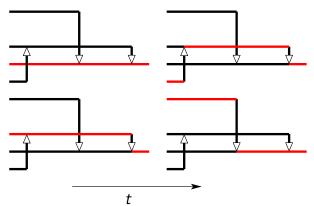
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# The asymptotic ASG $(\gamma = 0)$

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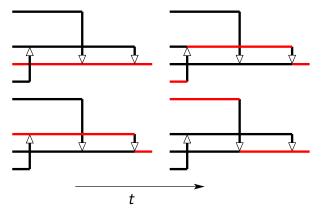
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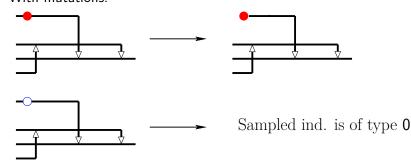
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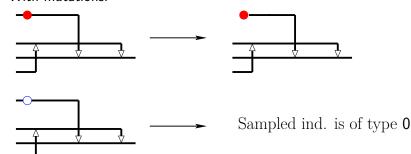
The probability of sampling an individual of type 0 at (forward) time t depends only on the number of lines in the ASG at time 0.



▶ With mutations:

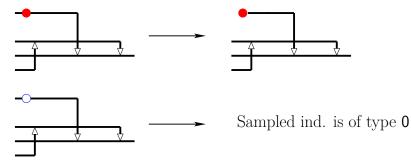


With mutations:



Mutation to type  $1 \rightarrow$  erase one line.

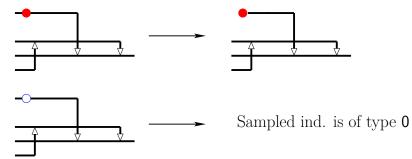
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Mutation to type  $0 \rightarrow \text{stop!}$  the sampled individual is of type 0.

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Killed ASG (E. Baake, U. Lenz, A. Wakolbinger)



#### **Duality**

Let  $R = (R_t)_{\geq 0}$  be the line-counting process in the killed-ASG, i.e. the continuous time Markov chain with rates

$$q_R(k,j) := \left\{ egin{array}{ll} ks & ext{if } j=k+1, \ & ku_1 & ext{if } j=k-1, \ & ku_0 & ext{if } j=\infty. \end{array} 
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#### Theorem (Duality)

For  $t \geq 0$  and  $z_0 \in (0,1)$ , we have

$$1-z(t,z_0):=E_1\left[(1-z_0)^{R_t}\right].$$

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▶ Duality  $\Rightarrow y_*$  is also the proportion of 1's at stationarity.



Models with mutation and frequency dependent selection

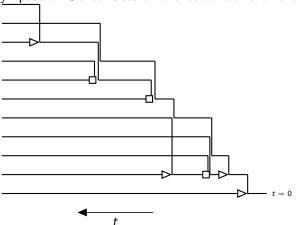
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Ancestral processes in the frequency dependent deterministic limit. The case without mutation

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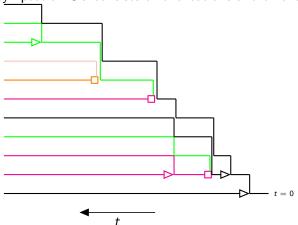
### The Asymptotic ASG with interactions and no mutations

The asymptotic ASG consists of bifurcations and trifurcations.

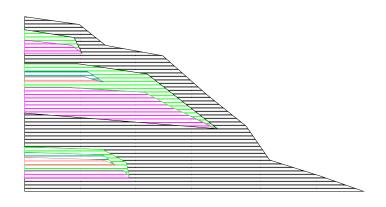


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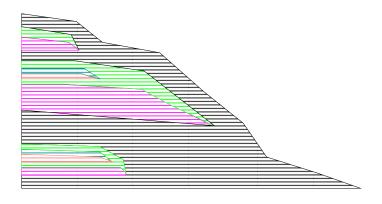
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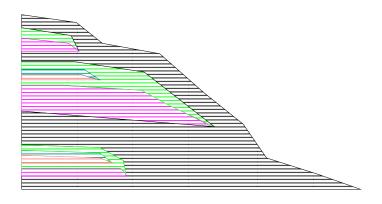


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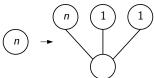
How to encode this information in order to determine the probability of sampling an individual of type 1? Ternary trees with marked leaves!

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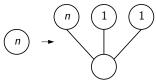
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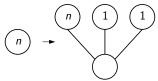
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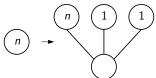


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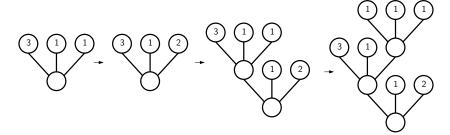


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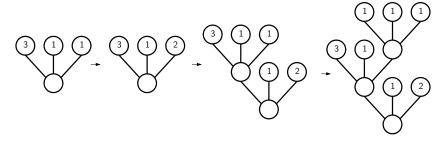
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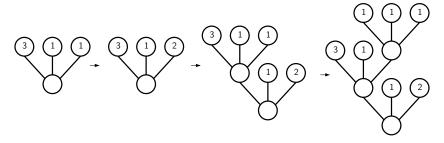


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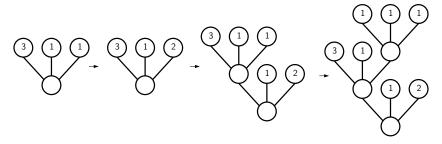
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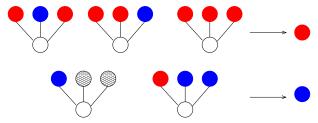
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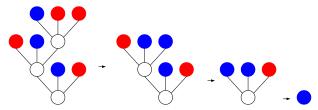
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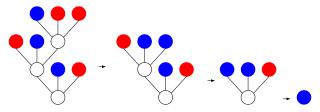
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3. The sampled ind. is of type 1 iff the root is colored red.



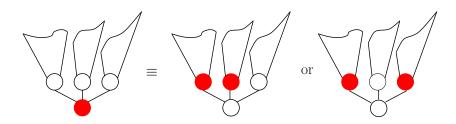
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- $\vdash H((n), y) = y^n.$
- ▶ If  $v_1, v_2, v_3$  are the left, middle and right children of the root:

$$H(\mathcal{T},y)\!=\!H(\mathcal{T}_{v_1},y)\left[H(\mathcal{T}_{v_2},y)+H(\mathcal{T}_{v_3},y)-H(\mathcal{T}_{v_2},y)H(\mathcal{T}_{v_3},y)\right].$$



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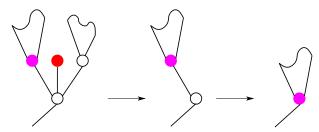
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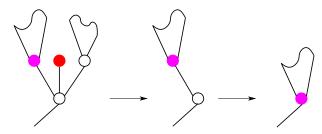
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This transition is denoted by  $\mathcal{T} \mapsto \mathcal{T}^{\bullet,\ell}$ .



Mutation to type 0 happens at a leaf  $\ell$  at rate  $u_0 m(\ell)$ .

# Pruning and grafting: mutation to type 0

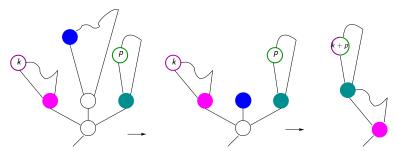
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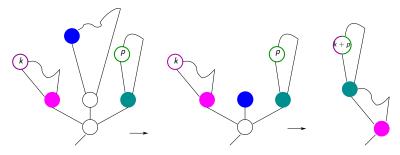
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# The line-counting tree

#### Definition

The line-counting tree process  $\mathcal{T}^*:=(\mathcal{T}^*(t))_{t\geq 0}$  is the jump process with values on  $\Upsilon\cup\{\bowtie\}$  starting at  $\widehat{1}$  and with the following transitions. If  $\mathcal{T}^*$  is currently in state  $\mathcal{T}:=(\tau,m)$ : for each  $\ell\in L_{\tau}$ ,

- 1.  $\mathcal{T} \longrightarrow \mathcal{T}^{\gamma,\ell}$  at rate  $\alpha\beta m(\ell)$ .
- 2.  $\mathcal{T} \longrightarrow \mathcal{T}^{\Psi,\ell}$  at rate  $\alpha |\gamma| m(\ell)$ .
- 3.  $\mathcal{T} \longrightarrow \mathcal{T}^{\bullet,\ell}$  at rate  $u_1 \ m(\ell)$ .
- 4.  $\mathcal{T} \longrightarrow \mathcal{T}^{\circ,\ell}$  at rate  $u_0 \ m(\ell)$ .

The states (0) and  $\bowtie$  are absorbing states of  $\mathcal{T}^*$ .

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Theorem (Duality)

For all t > 0 and  $z_0 \in (0,1)$ , we have

$$1 - z(t, z_0) = E_{1}[H(T^*(t), 1 - z_0)].$$

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Consider the det. Markov process  $y(\cdot, y_0) = 1 - z(\cdot, 1 - y_0)$ ,  $t \ge 0, y_0 \in (0, 1)$ .

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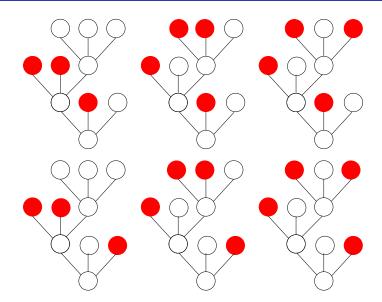
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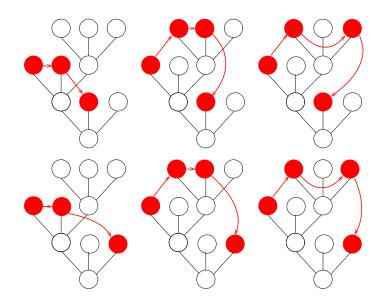
The result follows from classical duality results.

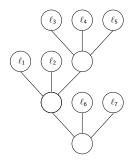


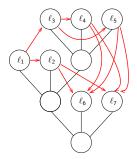
# Minimal red-colorings

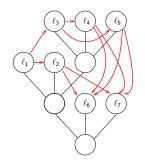


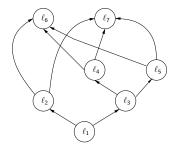
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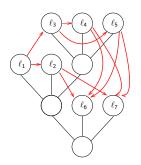


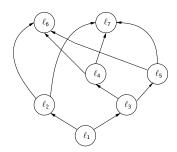




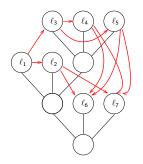


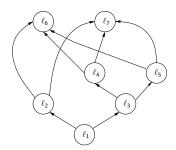




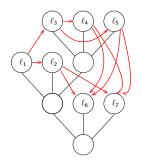


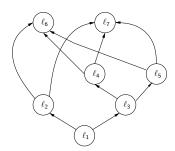
▶ Most left-leave  $\mapsto$  Source.



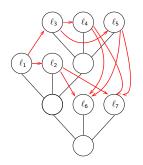


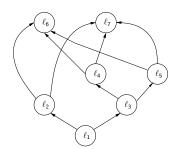
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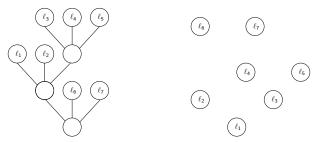


- ▶ Most left-leave → Source.
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- ► Marks on the leaves → Marks on the nodes.
- ▶ Minimal colorings  $\mapsto$  Strings (paths from source to a sink).

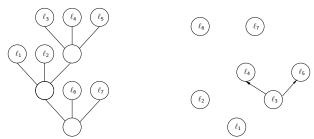
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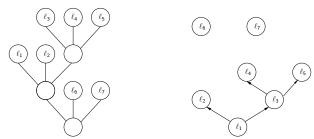
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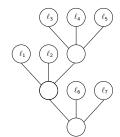
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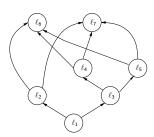


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#### Proposition

For each  $\mathcal{T} \in \Upsilon$  and  $y \in [0,1]$ , we have

$$H(\mathcal{T}, y) = \mathcal{H}(\rho(\mathcal{T}), y).$$

#### Definition

The line-counting digraph process is the continuous time Markov chain  $\mathcal{G}:=(\mathcal{G}(t))_{t\geq 0}$  with values in  $\Sigma_*\cup\{\bowtie\}$ , defined by  $\mathcal{G}(t)=\rho(\mathcal{T}^*(t)),\ t\geq 0.$ 

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Let  $T_{\odot}$  be the time to absorption of  $\mathcal{T}^*$  at  $\bigcirc$  and set  $a_0(t) = P(T_{\odot} \leq t)$ .

Let  $T_{\odot}$  be the time to absorption of  $\mathcal{T}^*$  at 0 and set  $a_0(t) = P(T_{\odot} \leq t)$ .

#### Corollary

For  $z_0 \in (0,1)$ , we have

$$1-z(t,z_0)=\sum_{k=0}^{\infty}a_k(t)(1-z_0)^k,$$

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$$\label{eq:hk} \textit{h}_{\textit{k}} := \textit{P}\left(\textit{T}_{\odot} < \infty | \mathcal{T}^*(0) = \overbrace{\textit{k}}\right), \quad \textit{k} \geq 1.$$

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$$\begin{split} (u + \alpha(\beta - \gamma))h_k &= \alpha\beta h_{k+1} + u\nu_1 h_{k-1} \\ &- \alpha\gamma P\left(T_{\odot} < \infty | \mathcal{T}^*(0) = \underbrace{k} \otimes \underbrace{1} \otimes \underbrace{1}\right). \end{split}$$

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• Duality  $\Rightarrow h_1 =$  stationary proportion of 1's in the forward model.



# Thank you for your attention!