The Moran model with selection revisited

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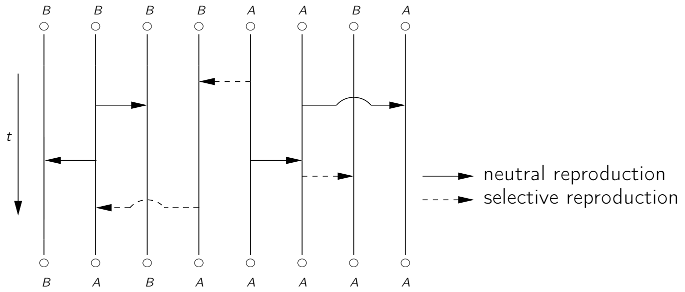
Outline

1) Moran model with selection and fixation probabilities
2) Connection to particle representation
   - labelled Moran model
   - defining events
   - simulation algorithm
3) Common ancestor type process

Moran model with selection

- N individuals
- Set of types: $S = \{A, B\}$
- Individuals of type A reproduce at rate $1 + s$, individuals of type B at rate 1
  Decomposition into neutral (types A and B, rate 1) and selective (just type A, rate s) reproductions (Krone/ Neuhauser 1997)

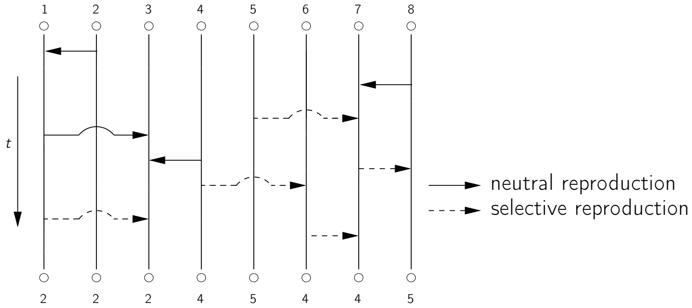


Moran model with selection

- $Z_t :=$ number of individuals of type A at time t, birth-death process with birth rates $\lambda_i = (1+s)i\frac{N-i}{N}$ and death rates $\mu_i = (N-i)\frac{i}{N}$
- $T_k := \min\{t \mid Z_t = k\}$
- Fixation probability:
  $h_i := \mathbb{P}(T_N < T_0 \mid Z_0 = i) = \frac{\sum_{j=N-i}^{N-1}(1+s)^j}{\sum_{j=0}^{N-1}(1+s)^j}$

Labelled Moran model

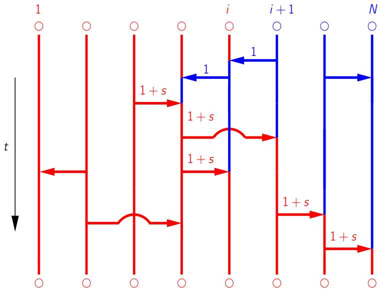
- N individuals, each characterised by label $i \in \{1, \dots, N\}$
- Offspring inherit parent's label
- Neutral arrows at rate $1/N$ (between every pair of labels), selective arrows at rate s/N (emanating from label i, pointing to label $j > i$)
- Spatial structure at time 0: Label i occupies position i



Ancestors and fixation probabilities

$I :=$ label that becomes fixed/ancestor

- $\mathbb{P}(I \leq i) = h_i$



Ancestors and fixation probabilities

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- $\mathbb{P}(I \leq i) = h_i$
- $\eta_i := \mathbb{P}(I = i) = (1+s)^{N-i}\eta_N$
  with $\eta_N := \mathbb{P}(I = N) = \frac{1}{\sum_{j=0}^{N-1}(1+s)^j}$

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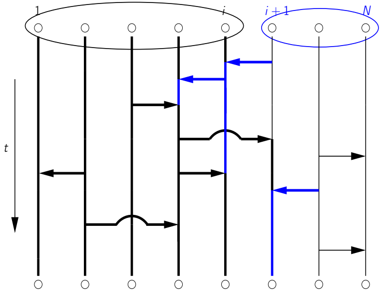
Based on particle *number* representation $\rightarrow$ decode particle representation

Particle representation behind $\eta_i = (1+s)^{N-i}\eta_N$

New descendants of labels in $\mathcal{S}$, $\mathcal{S} \subseteq \{1, \ldots, N\}$:

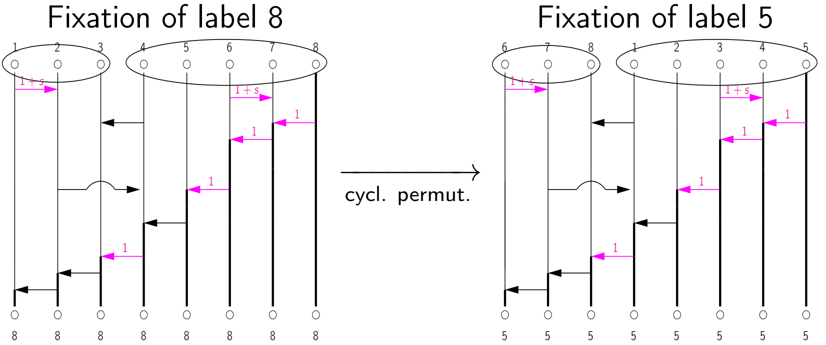
Descendants that increase the number of inidividuals in $\mathcal{S}$.

New descendants of labels in $\{i+1, \ldots, N\}$:



Particle representation behind $\eta_i = (1+s)^{N-i}\eta_N$

$N = 8, i = 5:$



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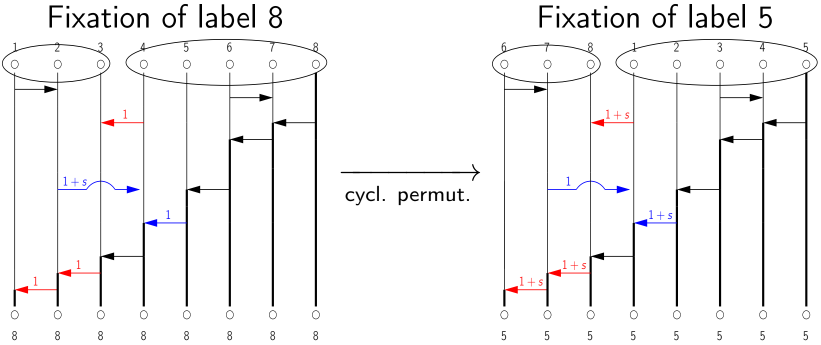
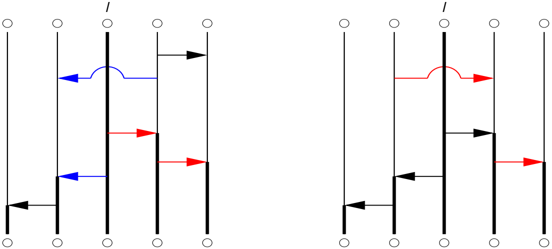


$$\eta_5 = \underbrace{\frac{1}{1+s}(1+s)}_{\text{new desc. of } \{6,7,8\}} \cdot \underbrace{(1+s)^3}_{\{6,7,8\}} \eta_8 = (1+s)^3 \eta_8$$

Definition

Let $I = i$.

Defining events:
Arrows emanating from labels $\{1, \dots, i\}$ and pointing to individuals with labels $\{i+1, \dots, N\}$ that are not new descendants of $\{i+1, \dots, N\}$.



defining event

Selective defining events

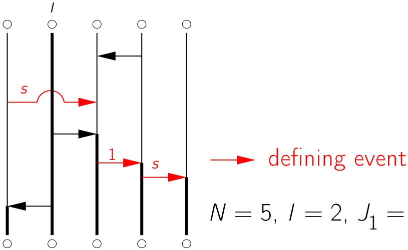
$Y :=$ number of selective defining events

- $\mathbb{P}(Y = n, I = i) = \binom{N-i}{n} s^n \eta_N$
- $\mathbb{P}(Y = n) = \sum_{i=1}^{N-n} \mathbb{P}(I = i, Y = n) = \binom{N}{n+1} s^n \eta_N$
- $h_i = \mathbb{P}(I \leq i) = \sum_{n=0}^{N-1} \mathbb{P}(I \leq i \mid Y = n)\mathbb{P}(Y = n)$

$$= \sum_{n=0}^{N-1} \left[\binom{N}{n+1} - \binom{N-i}{n+1} \right] s^n \eta_N$$

Targets of selective defining events

Let $Y = n$. Define $J_1, \ldots, J_n$ with $J_1 < \cdots < J_n$ as the (random) positions that are hit by selective defining events



$N = 5$, $I = 2$, $J_1 = 3$, $J_2 = 5$

- $\mathbb{P}(I = i, J_1 = j_1, \ldots, J_n = j_n \mid Y = n) = \frac{1}{\binom{N}{n+1}}$

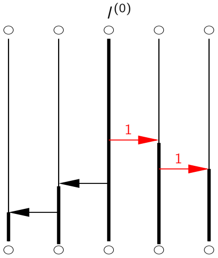
A simulation algorithm

Aim:
Generate $(I, J_1, \ldots, J_n)$

Generate Y. If $Y = n$ stop after step n.

Step 0: Generate $U^{(0)} \sim \mathcal{U}_{\{1,\ldots,N\}}$. Set $I^{(0)} := U^{(0)}$.

Genealogical interpretation:



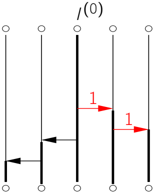
A simulation algorithm

Step 1: Generate $U^{(1)} \sim \mathcal{U}_{\{1,\dots,N\}\setminus U^{(0)}}$ independently of $U^{(0)}$.

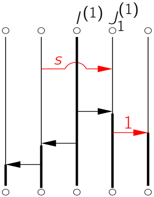
(a) If $U^{(1)} > I^{(0)}$:
Set $I^{(1)} := I^{(0)}$, $J_1^{(1)} := U^{(1)}$

(b) If $U^{(1)} < I^{(0)}$:
Set $I^{(1)} := U^{(1)}$, $J_1^{(1)} := I^{(0)}$

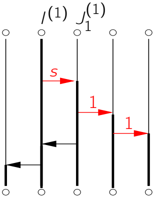
Step 0:



Step 1(a):



Step 1(b):



'shift to the left'

A simulation algorithm

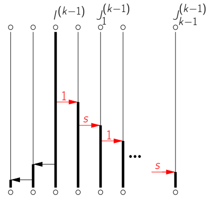
Step k: Generate

$U^{(k)} \sim \mathcal{U}_{\{1,\dots,N\}\setminus\{U^{(0)},\dots,U^{(k-1)}\}}$.

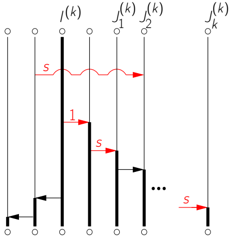
(a) If $U^{(k)} > I^{(k-1)}$: Set $I^{(k)} := I^{(k-1)}$

(b) If $U^{(k)} < I^{(k-1)}$: Set $I^{(k)} := U^{(k)}$

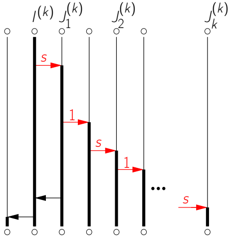
Step $k-1$:



Step k(a):



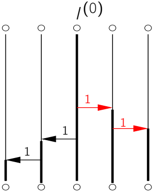
Step k(b):



'shift to the left'

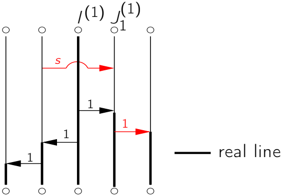
Relation to the ancestral selection graph

Step 0:



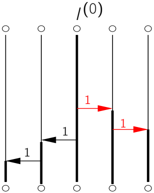
$\xrightarrow{\text{(a)}}$

Step 1:



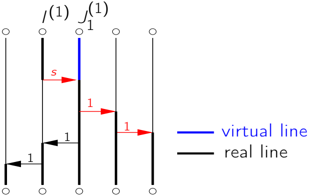
ASG without branching

Step 0:



$\xrightarrow{\text{(b)}}$

Step 1:



ASG with one branching event

Genealogical interpretation

$$
\begin{aligned}
h_i &= \mathbb{P}(I \leq i | Y = 0)\mathbb{P}(Y \geq 0) \\
&\quad + \sum_{n \geq 1} [\mathbb{P}(I \leq i | Y = n) - \mathbb{P}(I \leq i | Y = n-1)]\, \mathbb{P}(Y \geq n) \\
&= \mathbb{P}(I^{(0)} \leq i) + \sum_{n \geq 1} \left[\mathbb{P}(I^{(n)} \leq i) - \mathbb{P}(I^{(n-1)} \leq i)\right] \mathbb{P}(Y \geq n) \\
&= \mathbb{P}(I^{(0)} \leq i) + \sum_{n \geq 1} \mathbb{P}(I^{(n)} \leq i, I^{(n-1)} > i)\mathbb{P}(Y \geq n)
\end{aligned}
$$

Decomposition according to first step in which the ancestor has a label in $\{1, \ldots, i\}$.

Diffusion limit under weak selection ($Ns \xrightarrow{N\to\infty} \sigma$)

- $h_i \xrightarrow{\frac{i}{N}\to x} h(x) = \frac{1-e^{-\sigma x}}{1-e^{-\sigma}}$

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  - $1 - a_1 = \lim_{N\to\infty} \mathbb{P}(Y = 0) = \frac{\sigma}{\exp(\sigma)-1}$
  - $a_n - a_{n+1} = \lim_{N\to\infty} \mathbb{P}(Y = n) = \frac{\sigma}{n+1}(a_{n-1} - a_n)$

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  - $h_i = \mathbb{P}(I^{(0)} \leq i) + \sum_{n\geq 1} \mathbb{P}(I^{(n)} \leq i, I^{(n-1)} > i)\mathbb{P}(Y \geq n)$

$$\xrightarrow{\frac{i}{N}\to x} h(x) = x + \sum_{n\geq 1} x(1-x)^n a_n$$

$$= \frac{1}{\exp(\sigma)-1} \sum_{n\geq 1} \frac{1}{n!}(1-(1-x)^n)\sigma^n$$

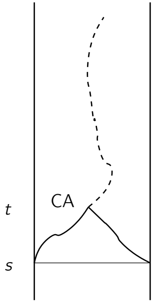
Common ancestor type process

Moran model with mutation and selection:

- N individuals
- Set of types: $S = \{A, B\}$
- Individuals of type A reproduce at rate $1 + s$, individuals of type B at rate 1
- mutations: $i \xrightarrow{u\nu_j} j$, $i, j \in S$
  here:
  - u general mutation rate with $Nu \xrightarrow{N\to\infty} \theta$
  - ν_j probability of mutations to type j ($\nu_A + \nu_B = 1$)
- Stationary density $\pi_X(x) = C(1-x)^{\theta\nu_B - 1} x^{\theta\nu_A - 1} \exp(\sigma x)$ (Wright's formula)

Common ancestor type process

- Population is stationary
- Common ancestor at time t:
  Unique individual (at time t) that is ancestral to the whole population at some time $s > t$
- I_t = type of common ancestor at time t
  $(I_t)_{t \geq 0}$ common ancestor type process



Stationary type distribution $\alpha = (\alpha_i)_{i \in S}$?

Taylor (2007)

- $(I_t, X_t)_{t \geqslant 0}$ with states (i, x), $i \in S$, $x \in [0,1]$
- $h(x) :=$ conditional probability that the common ancestor at time t is of type A, given that the frequency of type-A individuals at time t is x ($h(0) = 0$, $h(1) = 1$)
- Stationary distribution:

$$\pi_T(0, x) = h(x)\,\pi_X(x)$$
$$\pi_T(1, x) = (1 - h(x))\,\pi_X(x)$$

$\Rightarrow$ Stationary type distribution $\alpha_i = \int_0^1 \pi_T(i, x)dx$

Fearnhead (2002)

$$h(x) = x + x \sum_{n \geq 1} a_n (1-x)^n$$

Recursion of Fearnhead's coefficients a_n, $n \geq 0$:

$$(n + \theta\nu_1)\, a_n - (n + \sigma + \theta)\, a_{n-1} + \sigma a_{n-2} = 0, \quad n \geqslant 2,$$

with initial values $a_0 = 1$ and

$$a_1 = \frac{\sigma}{1+\theta\nu_1}(1-\tilde{x}), \text{where } \tilde{x} = \frac{\int_0^1 p^{\theta\nu_0+1}\,(1-p)^{\theta\nu_1}\exp(\sigma p)dp}{\int_0^1 p^{\theta\nu_0}\,(1-p)^{\theta\nu_1}\exp(\sigma p)dp}$$

Thank you for your attention!