Some problems with genealogies

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A question of genealogy

Our fundamental question

What does the ancestral family tree look like for a sample of individuals chosen from some population?

The question needs more precise formulation:

- a suitable model for the population's evolution (eg. fixed or randomly varying population size?)
- a sampling mechanism (eg. choose uniformly at random from entire population?)

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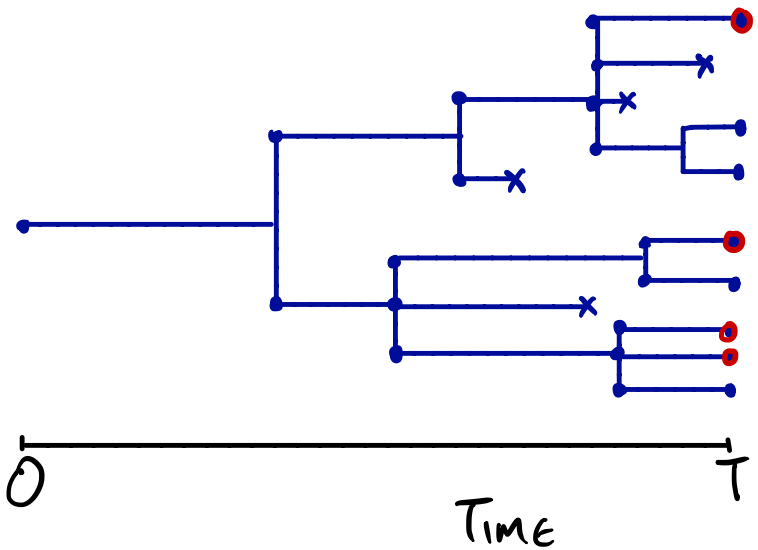

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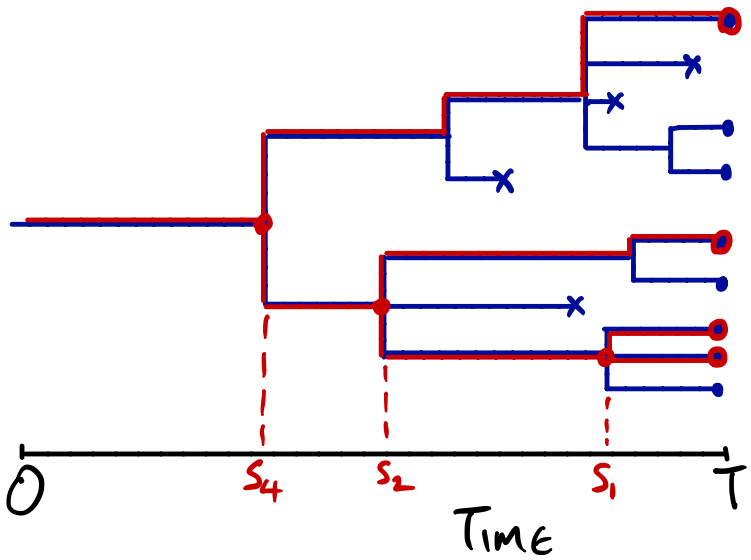
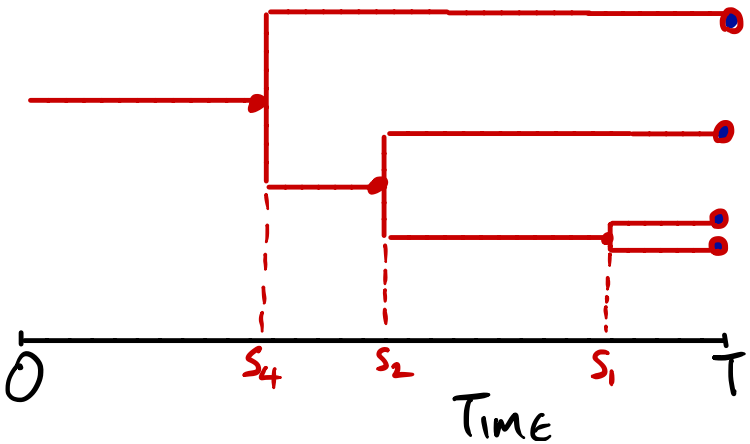
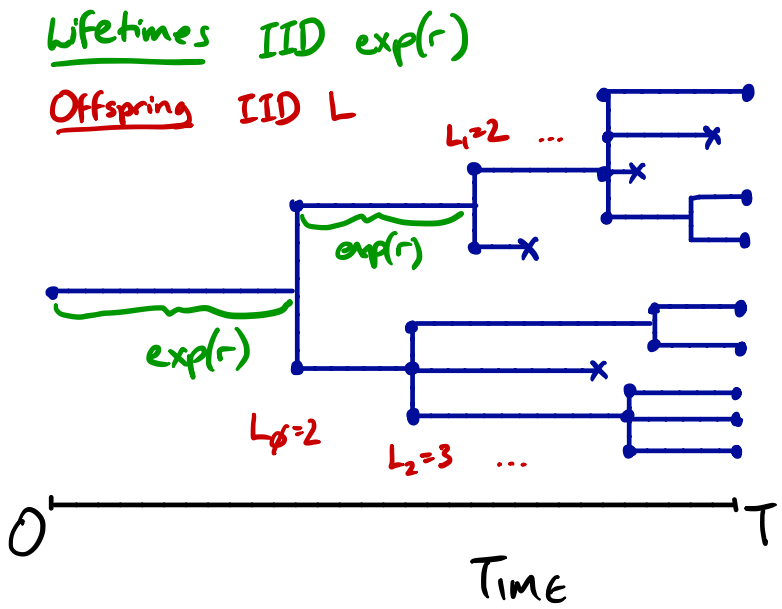




A population model

Offspring distribution. L is a random variable taking values in $\mathbb{Z}^+ := \{0, 1, 2, \dots\}$.

$$p_k := \mathbb{P}(L = k), \qquad m := \mathbb{E}(L) = \sum_{i=0}^{\infty} i p_i < \infty.$$



Continuous time Galton-Watson process

N_t represents the number of individuals in a population that are alive at time $t \geq 0$.

- any individual alive branches at rate $r > 0$, independently of others;
- when it branches, the parent dies and is replaced by a random number of offspring given by an independent realisation of offspring distribution L;
- once born, offspring evolve independently as above, and so on.

Some more basic properties of GW processes

Super-critical case ($m > 1$): Kesten-Stigum theorem. Suppose $1 < m < \infty$

If $E(L \log L) < \infty$, martingale $Z_t := e^{-r(m-1)t} N_t \to Z_\infty$ a.s. & in L^1 with $\mathbb{E}(Z_\infty) = 1$.
Further, $\{Z_\infty > 0\} = \{N_t \geq 1,\ \forall t \geq 0\}$ a.s., $\Rightarrow \mathbb{P}(\text{survival}) = \mathbb{P}(Z_\infty > 0) > 0$.
When the population survives it grows exponentially: $N_t \sim Z_\infty e^{r(m-1)t}$ a.s.

Critical case ($m = 1$): Conditioning on surviving a long time.

- $\mathbb{P}(N_t > 0) \sim \frac{c}{t} \to 0$
- *Critical Yaglom theorem.* Let $\sigma^2 := \mathbb{E}(L^2) - 1$. For each $x > 0$

$$\mathbb{P}\left(\frac{N_t}{t} > x \middle| N_t > 0\right) \to \exp\left(-\frac{2}{r\sigma^2} x\right) \quad \text{as } t \to \infty. \quad \textbf{Huge population} \approx \textbf{t}\times\textbf{RV}$$

Sub-critical case ($m < 1$): Conditioning on surviving a long time.

- $\mathbb{P}(N_t > 0) \sim c\mathbb{E}(N_t) = ce^{-r(1-m)t} \to 0$
- *Sub-critical Yaglom theorem.* For $\theta > 0$, for some RV Z taking values in $\mathbb{Z}^+$

$$\mathbb{E}(e^{-\theta N_t} | N_t > 0) \to E(e^{-\theta Z}) \quad \text{as } t \to \infty. \qquad \textbf{Finite population}$$

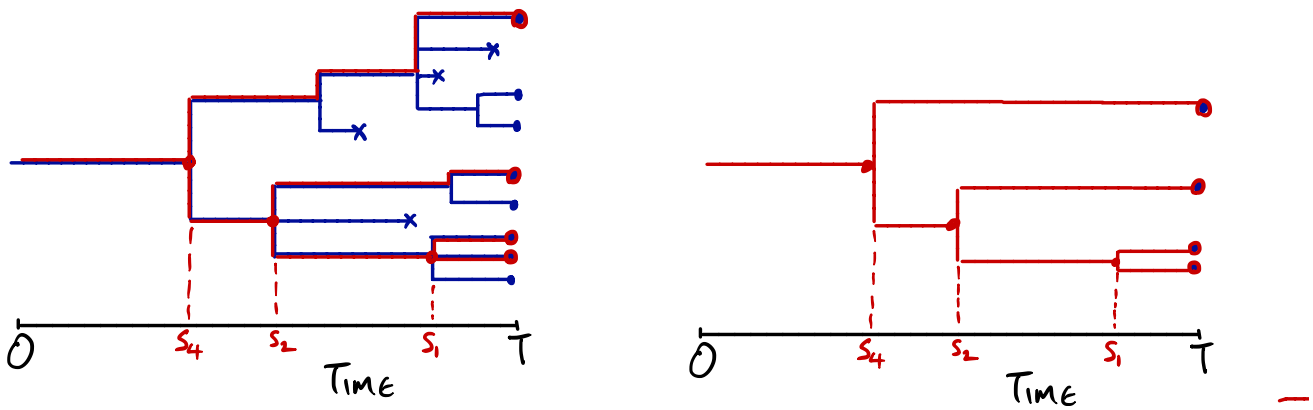
Uniform sampling from a Galton-Watson process

Our question

Consider a continuous time Galton-Watson process along with its genealogical tree.

- Fix a large time $T > 0$ (we will sometimes let $T \to \infty$)
- Condition on the event that at least k individuals are alive at time T.
- Choose k individuals uniformly at random (without replacement) from those alive at time T.

What does the ancestral tree drawn out by this sample of k individuals look like?



Existing literature. Critical case ($k = 2$): see Durrett (1978) and Athreya (2012). Near critical ($k = 2$), see O'Connell (1995). Also see related works by Aldous & Popovic (2005), Lambert & Stadler (2013), Lambert (2003, 2010 & recent...)

A small taste: birth-death process ($k = 2$)

Birth-death process: individuals branch into two at rate $\beta > 0$ and die at rate $\alpha > 0$

Offspring distribution $\mathbb{P}(L = 0) = \frac{\alpha}{\alpha+\beta}$, $\mathbb{P}(L = 2) = \frac{\beta}{\alpha+\beta}$

Branching rate $r := \alpha + \beta$ **Mean** $m := \mathbb{E}(L) = \frac{2\beta}{(\alpha+\beta)}$

Conditional on $\{N_T \geq 2\}$, let S_T be the **time of most recent common ancestor** of a pair of individuals $U_T, V_T \in N_T$ chosen *uniformly at random (without replacement)*.

Supercritical birth-death ($\beta > \alpha$) - related near start!

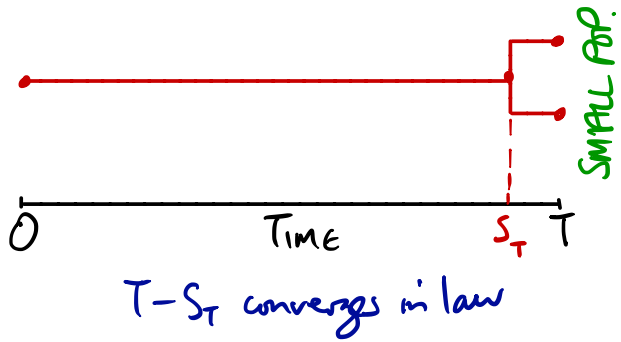
The law of S_T conditional on $N_T \geq 2$ converges to a non-trivial distribution as $T \to \infty$, with tail satisfying

$$\lim_{T\to\infty} \mathbb{P}(S_T \geq s \,|\, N_T \geq 2) \sim 2(\beta - \alpha)s\, e^{-(\beta-\alpha)s}$$

Sub-critical birth-death ($\beta < \alpha$) - related near end!

The law of $T - S_T$ conditional on $N_T \geq 2$ converges to a non-trivial distribution as $T \to \infty$, with tail satisfying

$$\lim_{T\to\infty} \mathbb{P}(T - S_T \geq s \,|\, N_T \geq 2) \sim \left(1 - \frac{2\beta}{3\alpha}\right) e^{-(\alpha-\beta)s}$$



A bigger taste: general critical GW process ($k = 2$)

General critical Galton-Watson process.

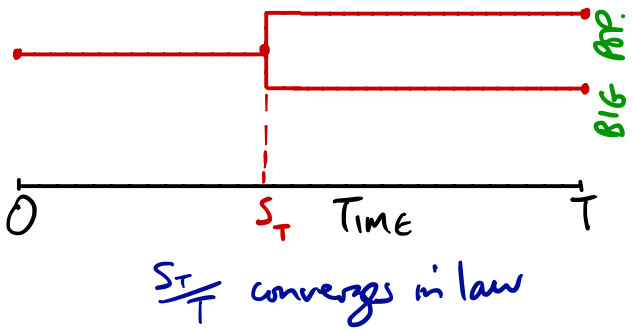
Assume **offspring distribution** L satisfies $m = \mathbb{E}(L) = 1$ and $\mathbb{E}(L^2) < \infty$.

On the event $\{N_T \geq 2\}$, let S_T be the **time of most recent common ancestor** of a pair of individuals $U_T, V_T \in N_T$ chosen *uniformly at random (without replacement)*.

Critical GW case ($m = 1$) - related anywhere!

The law of S_T/T conditional on $N_T \geq 2$ converges as $T \to \infty$ to a non-trivial distribution on $[0, 1]$ satisfying

$$\lim_{T\to\infty} \mathbb{P}\left(\frac{S_T}{T} \geq t \,\middle|\, N_T \geq 2\right) = \frac{2(1-t)}{t^2}\left(\log\left(\frac{1}{1-t}\right) - t\right)$$

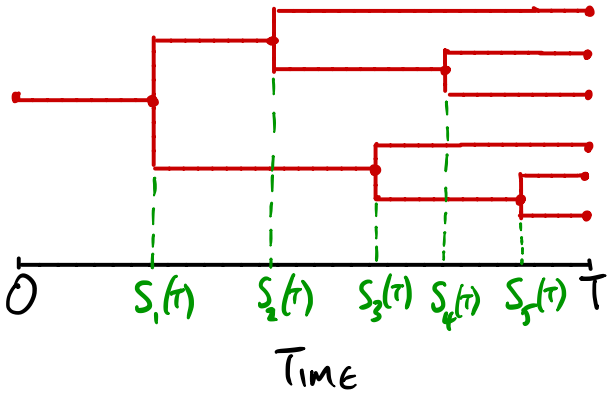


Harris-Johnston-Roberts (2017+) also give genealogy of k individuals explicitly for:

- super-critical birth-death processes at *fixed* times T
- general critical and *near*-critical GW processes as $T \to \infty$.

Further results: also see Johnston (2017+)

Genealogy of k individuals in critical GW at large times



Genealogy of uniform sample of k individuals:
We want to jointly characterise:

- *times of the $k-1$ mergers of family lines*, $(S_1^k(T), S_2^k(T), \ldots, S_{k-1}^k(T))$;
- *shape of the genealogical tree.*

Critical GW scaling limit: genealogy of k individuals Harris-Johnston-Roberts ('17)

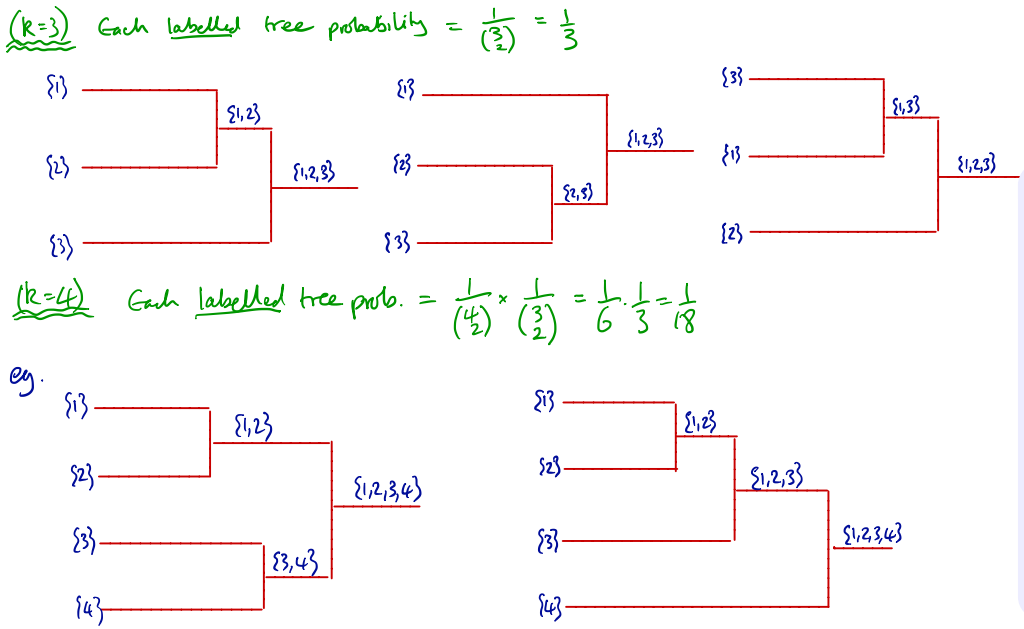
As $T \to \infty$, the **scaled merger times** $\left(\frac{S_1^k(T)}{T}, \ldots, \frac{S_{k-1}^k(T)}{T}\right)$ conditional on $N_T \geq k$, *converge in distribution* to $(S_1^k, \ldots, S_{k-1}^k)$ where, for any $0 \leq s_1 \leq \cdots \leq s_{k-1} \leq 1$,

$$\mathbb{P}(S_1^k \geq s_1, \ldots, S_{k-1}^k \geq s_{k-1}) = k! \prod_{i=1}^{k-1} \frac{s_i - 1}{s_i} - k! \sum_{j=1}^{k-1} \frac{1 - s_j}{s_j^2} \left(\prod_{\substack{i=1 \\ i \neq j}}^{k-1} \frac{1 - s_i}{s_j - s_i} \right) \log(1 - s_j)$$

As $T \to \infty$, the **shape of the tree** is *asymptotically independent* of the *merger times* where *each pair of family lines is equally likely to be the one to coalesce at the next merger time.*

IMPORTANT: as $\mathbb{E}L = 1$ and $\mathbb{E}L^2 < \infty$, *only pairwise mergers* observed in limit!

Genealogy of k individuals in critical GW at large times



NB. This is *same* tree topology as Kingman coalescent...

Kingman coalescent. Every pair of family lines merges at rate 1. That is, if there are currently i separate family lines, the next merger occurs at rate $i(i-1)/2$ and is equally likely to be any two of the family lines that merge.

In fact, to get the explicit distribution function we first found the following density.

Critical GW scaling limit: density for genealogy of k individuals

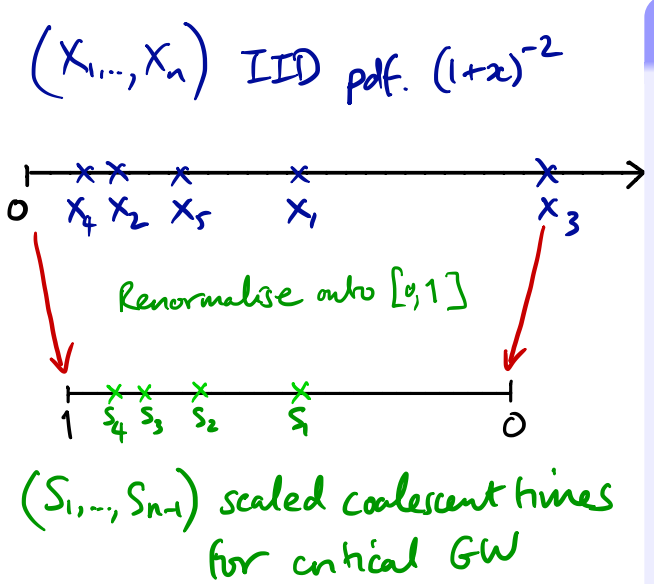
As $T \to \infty$, the **scaled merger times** $\left(\frac{S_1^k(T)}{T}, \ldots, \frac{S_{k-1}^k(T)}{T}\right)$ conditional on $N_T \geq k$, *converge in distribution* to $(S_1^k, \ldots, S_{k-1}^k)$ where, for any $0 \leq s_1 \leq \cdots \leq s_{k-1} \leq 1$,

$$\mathbb{P}(S_1^k \in \mathrm{d}s_1, \ldots, S_{k-1}^k \in \mathrm{d}s_{k-1}) = \int_0^\infty \frac{k}{(1+\theta)^2} \left(\prod_{i=1}^{k-1} \frac{\theta}{(1+\theta(1-s_i))^2} \, \mathrm{d}s_i \right) \mathrm{d}\theta$$

Genealogy of k individuals in critical GW at large times

Limiting coalescent times as a mixture of IID times:

First choose a mixture random variable M_k then, conditional on $M_k = \theta$, the $k-1$ coalescent times are IID on $[0,1]$ with a density depending on θ.



A construction of limiting coalescent times:

In fact, $(S_1^k, \ldots, S_{k-1}^k)$ can be constructed by:

- Let $X_1, X_2, \ldots, X_k$ be a sequence of IID RVs on $(0,\infty)$ with PDF $(1+x)^{-2}$.
- Renormalise $X_1, \ldots, X_k$ by the maximum $M_k := \max\{X_1, \ldots, X_k\}$
- Ignoring the maximum value 1, the remaining ordered $k-1$ renormalised RVs have the same distribution as $(1 - S_1^k, \ldots, 1 - S_{k-1}^k)$.

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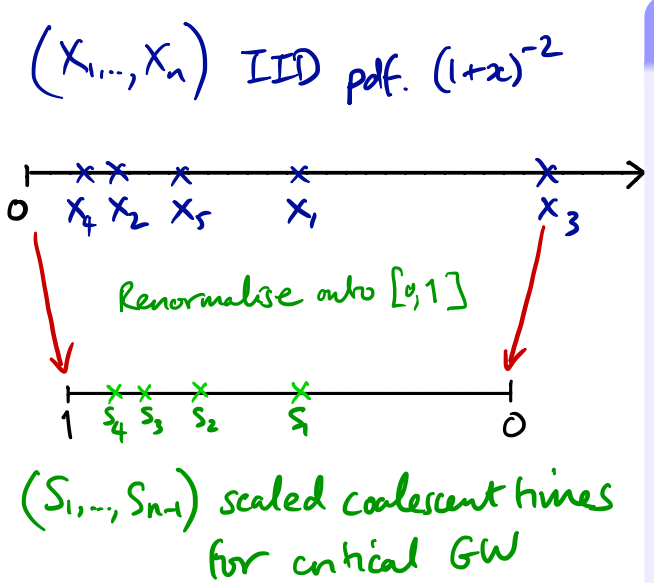

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Kingman coalescent often appears as limit when population is *constant*, but GW population size *varies* randomly...
A *'slow'* Kingman, with mergers *only* at rate $i-1$ when there are i individuals, would have coalescent times of k individuals given by $k-1$ IID exponentials.

Genealogy of uniform sample from a critical GW is like a mixture of time changed 'slow' Kingman coalescents. Interpret M_k like biologists' *effective population size*...

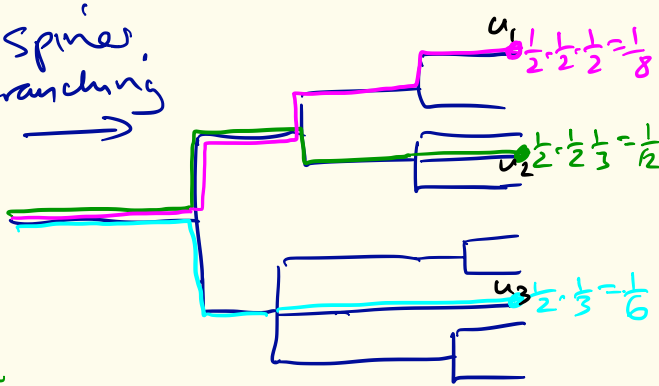
GW process with k spines

- GW process under $\mathbb{P}$
- Extend to GW tree with k spines under $\mathbb{P}^{(k)}$:

(i) Choose k spines independently

(ii) At birth events each spine follows path uniformly from offspring

uniform choice of k coalescence



e.g. $\mathbb{P}\left(u_1,u_2,u_3 \in \underset{\sim}{\xi}\left(\mathcal{T}_T\right)\right) = \frac{1}{8}\cdot\frac{1}{12}\cdot\frac{1}{6}$

$$\mathbb{P}\left(\underset{\sim}{u} \subset \underset{\sim}{\xi}\left(\mathcal{T}_T\right)\right) = \frac{1}{\prod_{i=1}^{k}\prod_{v<u_i} L_v}$$

$u_1,\dots,u_k$ are spines chosen

$v<u_i$: ancestors of u_i

L_v: # offspring at node v

Probabilities of spine choices

A useful change of measure

$$\left.\frac{d\mathbb{Q}_T^{(k)}}{d\mathbb{P}^{(k)}}\right|_{\mathcal{G}_T^{(k)}} = \frac{\mathbb{I}\{k \text{ spines alive \& distinct at time } T\} \prod_{\text{spines } \xi_1,\dots,\xi_k} \prod_{v \in \xi_i} L_v}{\mathbb{E}\left(N_T(N_T-1)\cdots(N_T-k+1)\right)} = \frac{Z_T}{\mathbb{E}(Z_T)}$$

$\mathcal{G}_T^{(k)}$ includes spine + GW information

Note:

- $\mathbb{E}^{(k)}\left(\mathbb{I}\{k \text{ spines distinct at time } T\} \prod_{i=1}^{k} \prod_{v<\xi_i} L_v \,\middle|\, \mathcal{G}_T\right)$ — Z_T; only GW information

$$= \sum_{u_1,\dots,u_k \in N_T} \mathbb{P}(u_1,\dots,u_k \in \xi \mid \mathcal{G}_T) \cdot \mathbb{I}\{u_1,\dots,u_k \text{ distinct \& alive}\} \prod_{i=1}^{k} \prod_{v<u_i} L_v \quad \cdots$$

$$= \frac{1}{\prod_{i=1}^{k} \prod_{v<u_i} L_v}$$

$\mathbb{P}(u_1,\dots,u_k \in \xi \mid \mathcal{G}_T) = 1$

$$= N_T(N_T-1)\cdots(N_T-k+1)$$

choices of k individuals from N_T without replacement

Important feature of $Q_T^{(k)}$

$$Q_T^{(k)}\left(\underset{\sim}{u} \in \underset{\sim}{\xi} \,\middle|\, \mathcal{H}_T\right) \propto P_T^{(k)}\left(\underset{\sim}{u} \in \underset{\sim}{\xi} \,\middle|\, \mathcal{H}_T\right) \times I\{\underset{\sim}{u} \text{ distinct, alive at time } T\} \prod_{i=1}^{k} \prod_{v \neq u_i} L_v$$

$= 1$ by careful choice

So,
$$Q_T^{(k)}\left(\underset{\sim}{u} \in \underset{\sim}{\xi} \,\middle|\, \mathcal{H}_T\right) = \frac{I\{u_1, \dots u_k \in N_T \text{ \& distinct}\}}{N_T(N_T-1)\dots(N_T-k+1)}$$

only GW info (no spine identity)

total # ways choosing k from N_T without replacement

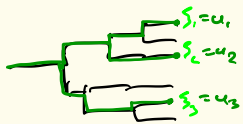
$\therefore$ under $Q_T^{(k)}$, at time T the spines are uniformly chosen without replacement from those alive at time T

Also find,

functional along spines (only)

functional along tree of particles $u_1, \dots, u_k$ (only)

$$Q_T^{(k)}\left(f(\underset{\sim}{\xi}) \,\middle|\, \mathcal{H}_T\right) = \frac{1}{N_T(N_T-1)\dots(N_T-k+1)} \sum_{\substack{u_1, \dots, u_k \in N_T \\ u_i \text{ distinct}}} f(\underset{\sim}{u})$$



Coalescent times for Uniform samples in critical GW

Let $\tau_1, \tau_2, \dots, \tau_{k-1}$ be the coalescent times of k particles chosen uniformly at random without replacement. Then:

$$\mathbb{P}\left(\tau_1 \in dt_1, \dots, \tau_{k-1} \in dt_{k-1} \,\middle|\, N_T \geq k \text{ and choose } k \text{ alive at time } T \text{ uniformly at random without replacement}\right)$$

$$= \mathbb{P}\left(\frac{1}{N_T(N_T-1)\cdots(N_T-k+1)} \sum_{\substack{u_1,\dots,u_k \in N_T \\ u_i \text{ distinct}}} I\left\{\tau_1^{u} \in dt_1, \dots, \tau_{k-1}^{u} \in dt_{k-1}\right\} \,\middle|\, N_T \geq k\right)$$

$$= Q_T^{(k)}\left(\frac{I\left\{\tau_1^{\Sigma} \in dt_1, \dots, \tau_{k-1}^{\Sigma} \in dt_{k-1}\right\}}{N_T(N_T-1)\cdots(N_T-k+1)}\right) \frac{\mathbb{E}\left(N_T(N_T-1)\cdots(N_T-k+1)\right)}{\mathbb{P}(N_T \geq k)}$$

$Q_T^{(k)}$: Can describe spine behaviour completely under $Q_T^{(k)}$

$\frac{\mathbb{E}\left(N_T(N_T-1)\cdots(N_T-k+1)\right)}{\mathbb{P}(N_T \geq k)}$: Easy using Yaglom

Application of Yaglom's theorem

Critical GW Offspring dist^n L, $\mathbb{E}L = 1$, $\sigma^2 := \mathrm{Var}(L) < \infty$, Branching rate r

$$\lambda := \frac{r\sigma^2}{2}$$

(a) $\mathbb{P}(N_T > 0) \sim \frac{\lambda}{T}$ as $T \to \infty$

(b) Conditional on $N_T > 0$, $\frac{N_T}{T} \xrightarrow{\text{law}} Z \sim \mathrm{Exp}(\lambda)$ as $T \to \infty$

- $\mathbb{E}\left(e^{-\theta \frac{N_T}{T}} \middle| N_T > 0\right) \to \mathbb{E}\left(e^{-\theta Z}\right) = \frac{\lambda}{\lambda + \theta}$ as $T \to \infty$
- $\mathbb{E}\left(\frac{N_T}{T}\left(\frac{N_T - 1}{T}\right)\cdots\left(\frac{N_T - k + 1}{T}\right) \middle| N_T > 0\right) \to \mathbb{E}(Z^k) = \frac{k!}{\lambda^k}$
- $\mathbb{P}(N_T \to \infty \mid N_T > 0) = 1$, so $\mathbb{P}(N_T \geq k) \sim \mathbb{P}(N_T > 0) \sim \frac{\lambda}{T}$

Hence, $$\mathbb{E}\left(N_T(N_T - 1)\cdots(N_T - k + 1) \middle| N_T \geq k\right) \sim T^k \frac{k!}{\lambda^k}$$

Understanding $\mathbb{Q}_T^{(k)}$ for large times

Total population size under $\mathbb{Q}_T^{(k)}$

- $$\mathbb{Q}_T^{(k)}\left(e^{-\theta \frac{N_T}{T}}\right) = \frac{\mathbb{E}\left(N_T(N_T-1)\dots(N_T-k+1)e^{-\theta \frac{N_T}{T}}\right)}{\mathbb{E}\left(N_T(N_T-1)\dots(N_T-k+1)\right)}$$

$$\to \frac{\mathbb{E}\left(Z^k e^{-\theta Z}\right)}{\mathbb{E}\left(Z^k\right)} = \left(\frac{\lambda}{\lambda+\theta}\right)^{k+1} \text{ since } \frac{N_T}{T} \Rightarrow Z \sim \text{Exp}(\lambda) \text{ under } \mathbb{P}$$

$\therefore$ $\frac{N_T}{T}$ under $\mathbb{Q}_T^{(k)}$ tends to $Z \sim \text{Gamma}(k+1, \lambda)$ under $\mathbb{Q}_\infty^{(k)}$

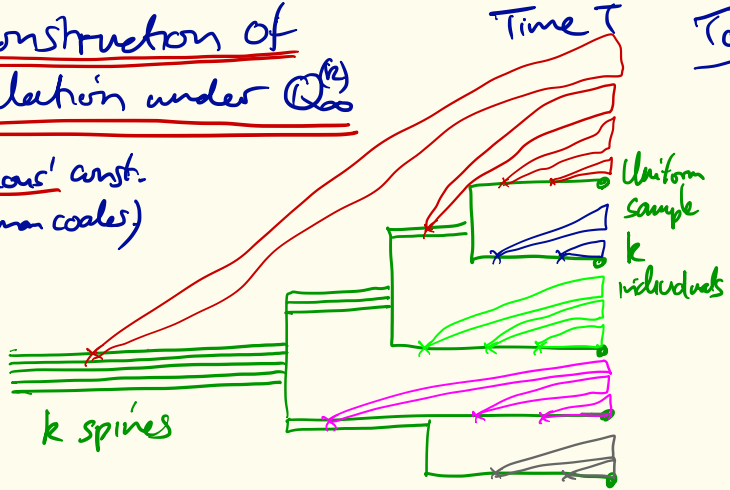
equivalently, a sum of $k+1$ independent $\text{Exp}(\lambda)$'s.

In particular, mass coming off single spine branch is $\Gamma(2, \lambda)$

$\Rightarrow$ We need joint distribution of (scaled) spine split times & (scaled) population size Z under $\mathbb{Q}_\infty^{(k)}$

A construction of population under $Q_\infty^{(k)}$

(c.f. Aldous' const. of Kingman coales.)



Total population under $Q_\infty^{(k)}$

$$\frac{N_T}{T} \to Z \sim \Gamma(k+1, \lambda)$$

Total population size:

$$Z = \dot{Z}_0 + \sum_{i=1}^{k-1} (1-\hat{\tau}_i)\dot{Z}_i$$

NB. Only splits into 2 groups in limit.

Coalescent times:

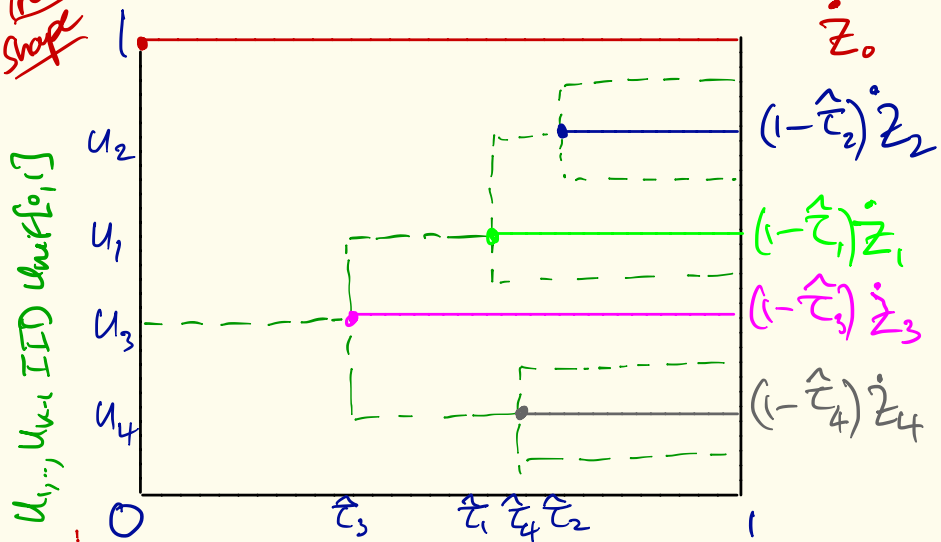
$\hat{\tau}_1, \hat{\tau}_2, \ldots, \hat{\tau}_{k-1}$ IID $\sim$ Unif$[0,1]$

Subpopulations:

$\dot{Z}_0, \dot{Z}_1, \ldots, \dot{Z}_{k-1}$ IID $\sim \Gamma(2, \lambda)$

NB. $(1-\hat{\tau})\dot{Z} \sim \text{Exp}(\lambda)$

Tell story



Calculating the $Q_\infty^{(k)}$ expectation

Then, as $T \to \infty$,

$$Q_T^{(k)}\left(\frac{T^k}{N_T(N_T-1)\cdots(N_T-k+1)} ; \frac{\tau_1^\xi}{T} \in dt_1 ; \ldots ; \frac{\tau_{k-1}^\xi}{T} \in dt_{k-1} \right)$$

$$\to Q_\infty^{(k)}\left(\frac{1}{Z^k} ; \hat{\tau}_1 \in dt_1 ; \ldots ; \hat{\tau}_{k-1} \in dt_{k-1} \right)$$

$$= \underbrace{Q_\infty^{(k)}\left(\hat{\underset{\sim}{\tau}} \in d\underset{\sim}{t} \right)}_{dt_1 . dt_2 \ldots dt_{k-1}} \int_0^\infty \frac{\theta^{k-1}}{(k-1)!} \underbrace{Q_\infty^{(k)}\left(e^{-\theta Z} \,\middle|\, \hat{\underset{\sim}{\tau}} = \underset{\sim}{t} \right)}_{Z = \dot{Z}_0 + \sum_{i=1}^{k-1} (1-t_i)\dot{Z}_i} d\theta$$

as $\tau_1, \ldots, \tau_{k-1}$ IID Unif$[0,1]$ $\quad \dot{Z}_0, \ldots, \dot{Z}_{k-1}$ IID $\Gamma(2,\lambda)$

$$= dt_1 . dt_2 \ldots dt_{k-1} \cdot \frac{1}{(k-1)!} \int_0^\infty \theta^{k-1} \left(\frac{\lambda}{\lambda+\theta} \right)^2 \prod_{i=1}^{k-1} \left(\frac{\lambda}{\lambda+\theta(1-t_i)} \right)^2 d\theta$$

Trick:

$$\frac{1}{2} = \int_0^\infty e^{-\theta 2} d\theta$$

$$\Rightarrow \frac{1}{2^k} = \int_0^\infty \frac{\theta^{k-1}}{(k-1)!} e^{-\theta 2} d\theta$$

Coalescent times for uniform sample in critical GW

$$\mathbb{P}\left(\frac{\tau_1}{T} \in dt_1, \dots, \frac{\tau_{k-1}}{T} \in dt_{k-1} \;\middle|\; \begin{array}{l}\text{uniform choice of}\\ k \text{ individuals at}\\ \text{time } T \text{ \& } N_T \geq k\end{array} \right)$$

Now order the coalescent times so $\tau_1 \leq \tau_2 \dots \leq \tau_{k-1}$

$$\to \mathbb{E}(Z^k)\, \mathbb{Q}_\infty^{(k)}\left(\frac{1}{Z^k} ; \hat{\tau}_1 \in dt_1; \dots; \hat{\tau}_{k-1} \in dt_{k-1} \right)$$

#orderings

$$= (k-1)!\, \frac{k!}{\lambda^k}\, dt_1 . dt_2 \dots dt_{k-1} \cdot \frac{1}{(k-1)!} \int_0^\infty \theta^{k-1} \left(\frac{\lambda}{\lambda+\theta}\right)^2 \prod_{i=1}^{k-1} \left(\frac{\lambda}{\lambda+\theta(1-t_i)}\right)^2 d\theta$$

$$= k! \int_{\theta=0}^{\infty} \frac{\lambda}{(\lambda+\theta)^2} \prod_{i=1}^{k-1} \frac{\theta\lambda}{(\lambda+\theta(1-t_i))^2}\, d\theta . dt_1 \dots dt_{k-1} \qquad (\theta = \lambda\varphi)$$

$$= k! \int_{\varphi=0}^{\infty} \frac{1}{(1+\varphi)^2} \prod_{i=1}^{k-1} \frac{\varphi}{(1+\varphi(1-t_i))^2}\, d\varphi . dt_1 \dots dt_{k-1} = \underline{\text{Can Compute Explicitly!}}$$

□