

MOST RECENT COMMON ANCESTORS AND POISSON CUT-OUTS

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Questions

- The **age of the most recent common ancestor (MRCA)** for some current population is **how far back in time** we have to go until we find an individual from whom **everyone is descended**.
- What is the **distribution** of the age of the MRCA for a given **genealogical model**?
- How does the age of the MRCA **evolve** as the **population moves into the future**?
- The dynamics for the **constant population Wright-Fisher model** were studied by Derrida and Simon (2006) and Pfaffelhuber and Wakolbinger (2006).

Critical continuous-time Galton-Watson branching process

- population of individuals
- individuals **die** at **rate** λ
- upon its death, each individual **gives birth** to a **random number of offspring** according to a **fixed distribution** with **mean** 1 and **variance** σ^2
- individuals behave **independently** of each other

Large populations and re-scaled time

Write $Z_t^{(n)}$ for the **number of individuals alive** at time $t \geq 0$ in a critical continuous-time Galton-Watson branching process with **branching rate** λ and **offspring variance** σ^2 .

Suppose that $Z_0^{(n)} \approx ny$ for some $y > 0$.

Put $Y_t^{(n)} = n^{-1}Z_{nt}^{(n)}$.

Note that

$$\mathbb{E} \left[Y_{t+\delta}^{(n)} - Y_t^{(n)} \mid Y_s^{(n)}, 0 \leq s \leq t \right] = 0$$

and

$$\mathbb{E} \left[\left(Y_{t+\delta}^{(n)} - Y_t^{(n)} \right)^2 \mid Y_s^{(n)}, 0 \leq s \leq t \right] \approx \lambda \sigma^2 Y_t^{(n)} \delta.$$

Feller's "continuous-state" branching process

If $Y_0^{(n)} \rightarrow y$ as $n \rightarrow \infty$, then $Y^{(n)}$ converges to a solution of the **stochastic differential equation**

$$Y_t = y + \int_0^t \sqrt{\lambda \sigma^2 Y_s} dB_s.$$

Suppose from now on that $\lambda \sigma^2 = 1$ (other values can be obtained by a linear time-change).

Conditioning on non-extinction

Write $\tau := \inf\{t \geq 0 : Y_t = 0\}$ for the **extinction time** of Y . We have $\mathbb{P}\{\tau > t \mid Y_0 = y\} = 1 - \exp(-2y/t)$, so

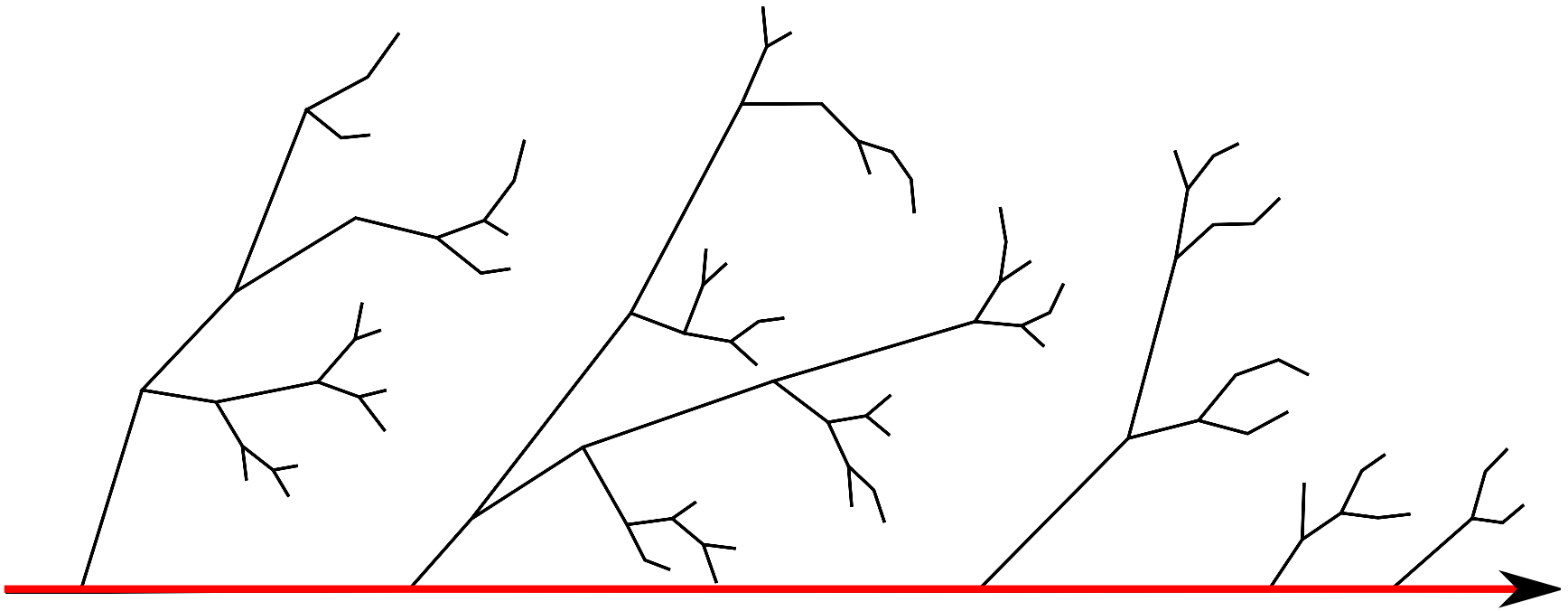
$$\lim_{T \rightarrow \infty} \mathbb{E}[f(Y_t) \mid Y_0 = y, \tau > T] = \frac{1}{y} \mathbb{E}[f(Y_t) Y_t \mid Y_0 = y].$$

If $Q_t(y', dy'') := \mathbb{P}\{Y_t \in dy'' \mid Y_0 = y'\}$ are the **transition probabilities** of Y , then there is a **Markov process** X with transition probabilities

$$P_t(x', dx'') = \mathbb{P}\{X_t \in dx'' \mid X_0 = x'\} = \frac{1}{x'} Q_t(x', dx'') x''.$$

The process X is Feller's process Y **conditioned on non-extinction** (an example of a **Doob h -transform**).

Immortal lineage I



Immortal lineage II

The conditioned process X consists of an immortal lineage that continually throws off independent sub-populations which evolve like Feller's process.

In particular, each sub-population dies out eventually.

Immortal lineage III

There is a σ -finite Markovian measure ν on

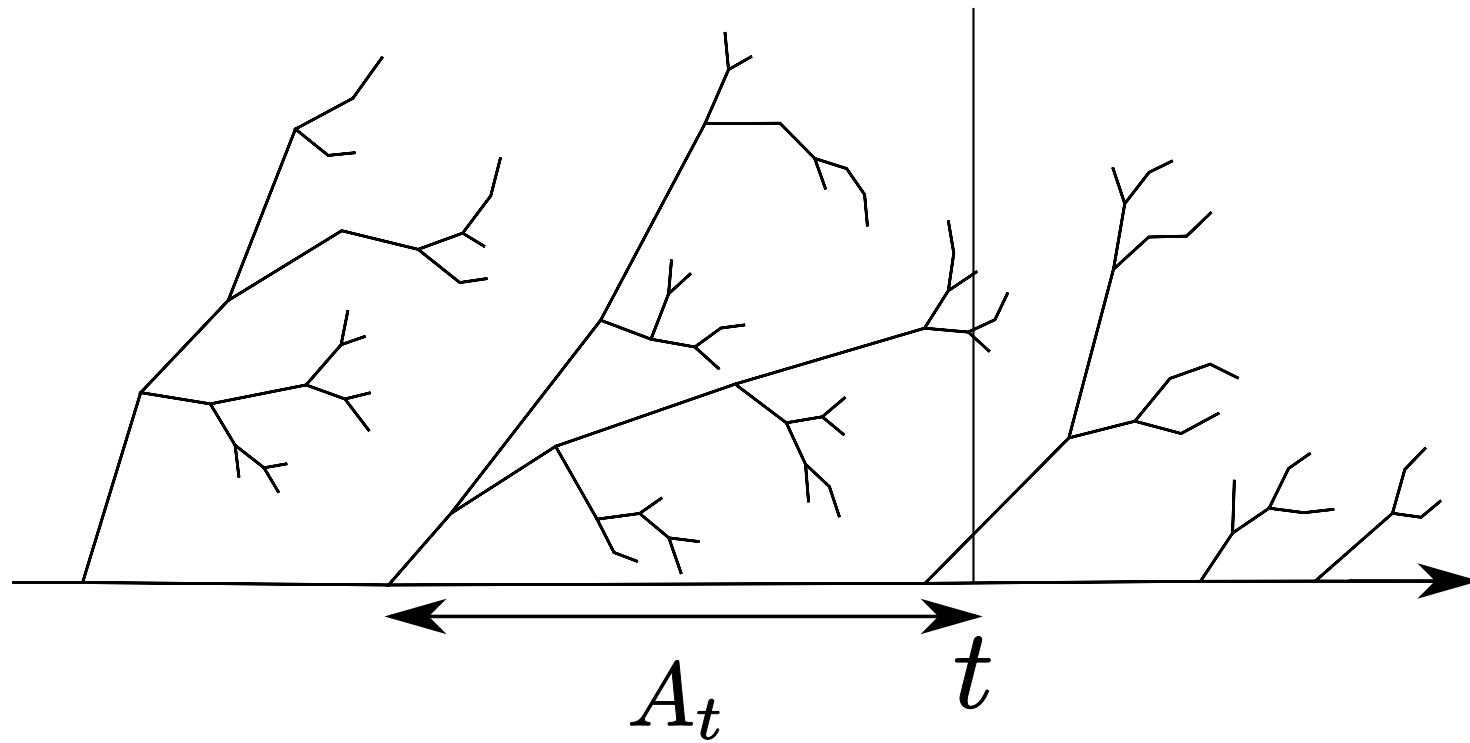
$$E := \{u \in C(\mathbb{R}_+, \mathbb{R}_+) : u_0 = 0 \text{ and } \exists g > 0 \text{ s.t. } u_t > 0 \\ \text{for } 0 < t < g \text{ and } u_t = 0 \forall t \geq g\}$$

with the same transition kernel Q as Feller's process Y such that if Π is a Poisson point process on $\mathbb{R}_+ \times E$ with intensity $\lambda \otimes \nu$ (where λ is Lebesgue), then the process

$$\sum_{(s,u) \in \Pi} u_{(t-s) \vee 0}, \quad t \geq 0,$$

has the same law as the conditioned process X started at $X_0 = 0$.

The most recent common ancestor I

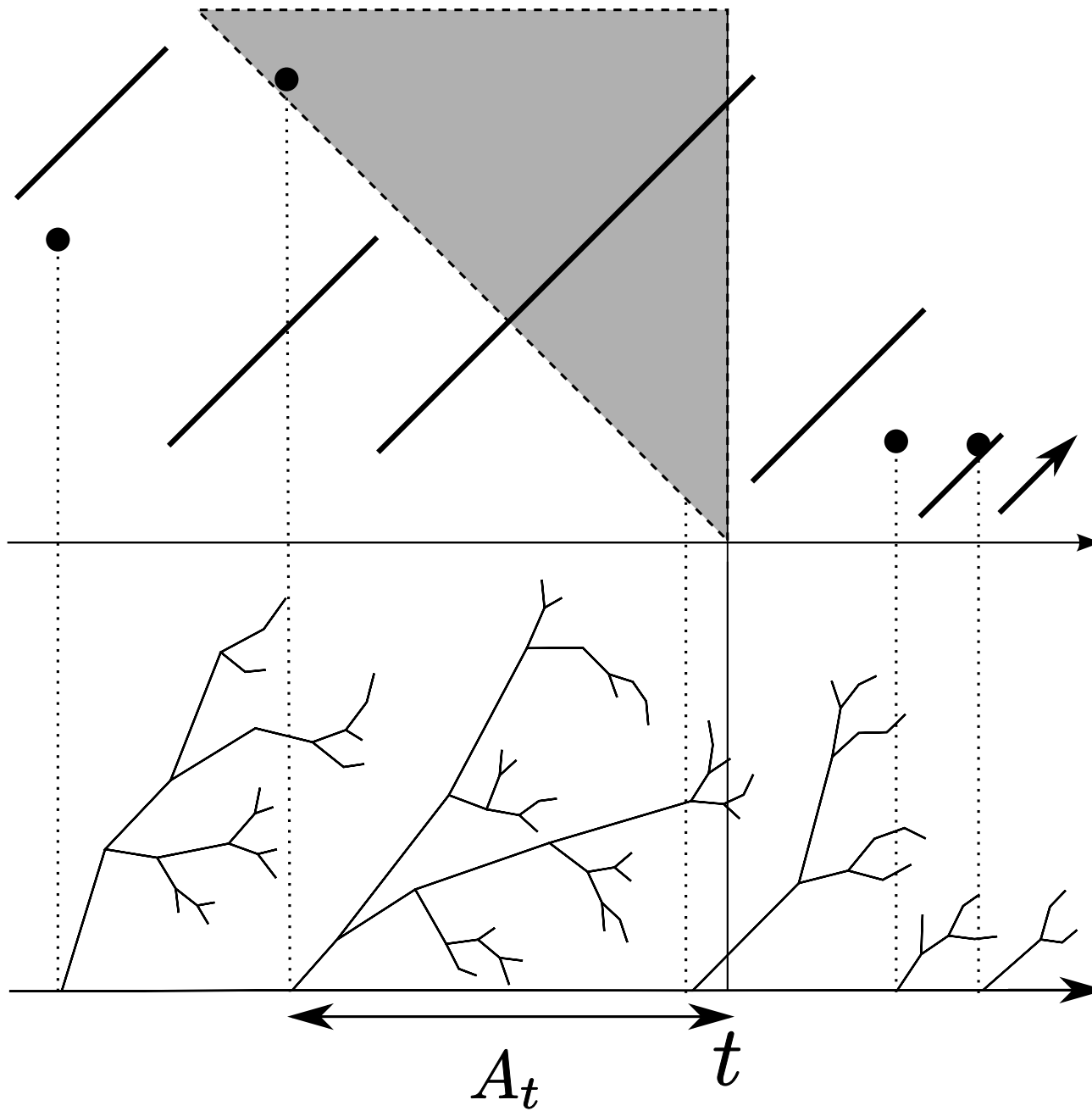


The most recent common ancestor II

The **time of the most recent common ancestor (MRCA)** of the population at time $t \geq 0$ is the largest time $0 \leq s \leq t$ such that **every individual** in the population at time t is **descended** from a **single individual** in the population at time s .

In the case of the conditioned process \mathbf{X} , this is the largest time s for which every “individual” alive at time t belongs to a sub-population that was thrown off by the immortal lineage at some time between s and t .

Write $A_t = t - s$ for the **age of the most recent common ancestor** of the population at time t .



The sub-population lifetime point process

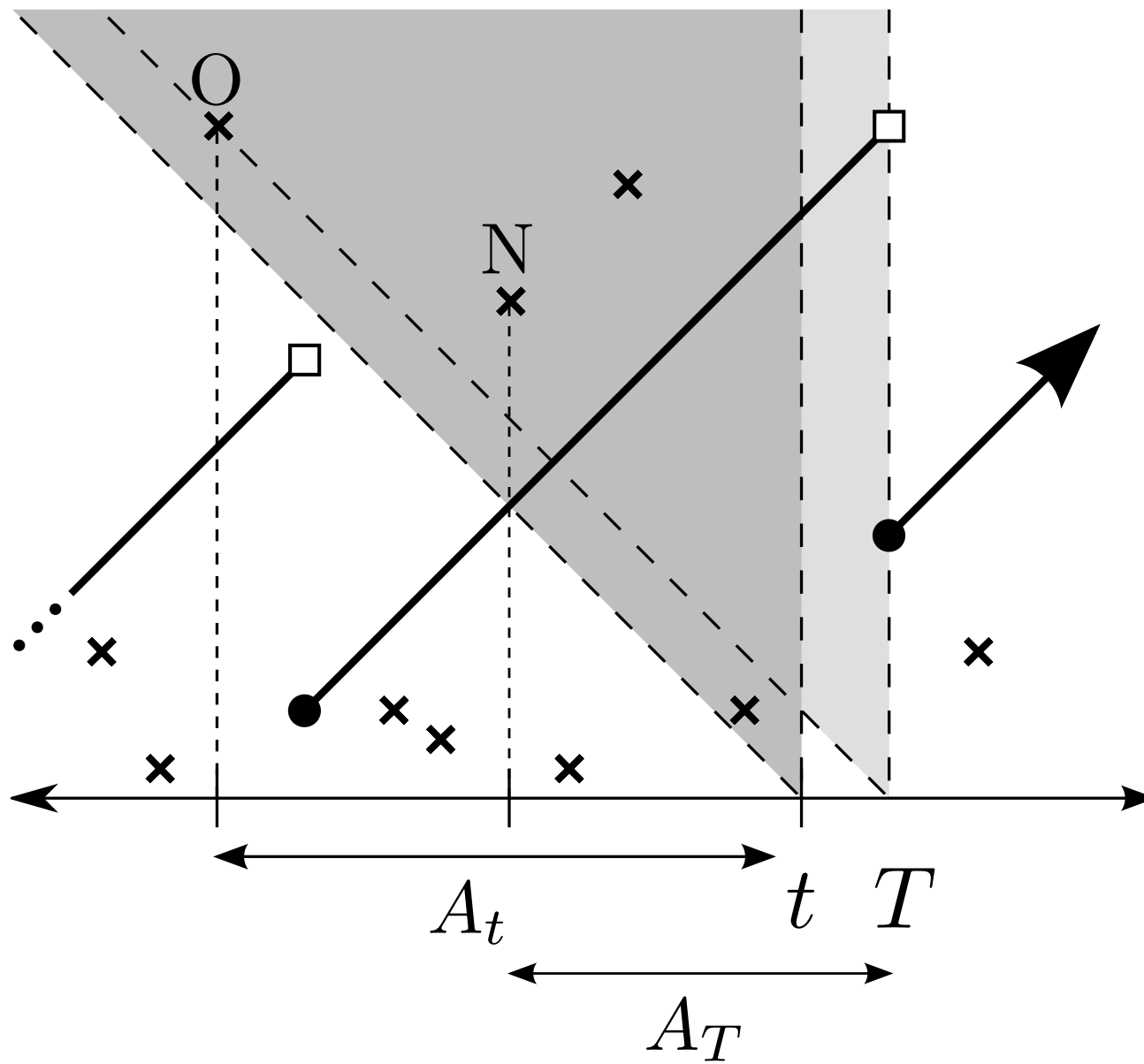
Given $u \in E$, write

$$\gamma(u) := \inf\{s > 0 : u(t) = 0, \forall t > s\}$$

for the **lifetime** of the sub-population described by u .

In order to build A we **only need** the point process Λ consisting of points $(t, \gamma(u))$, where (t, u) is a point of Γ .

It can be shown that Λ is a **Poisson point process** on $\mathbb{R}_+ \times \mathbb{R}_+$ with **intensity** $\lambda \otimes \mu$, where $\mu([x, \infty)) = \frac{2}{x}$.



Generalizing the age construction

The construction of $(A_t)_{t \geq 0}$ from the Poisson point process Λ **still makes sense** if Λ is **any Poisson point process** on $\mathbb{R}_+ \times \mathbb{R}_+$ with **intensity** $\lambda \otimes \mu$ for a **general σ -finite measure** μ .

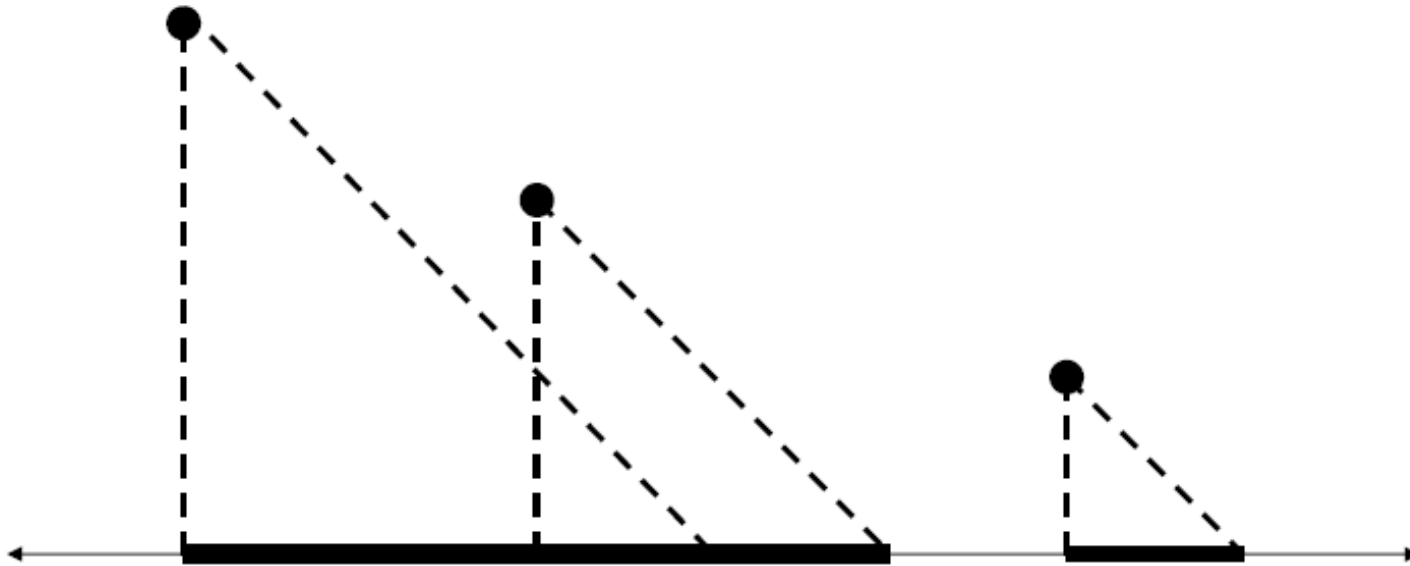
Assume **until further notice** that μ is any σ -finite measure on \mathbb{R}_+ with $\mu([x, \infty)) < \infty$ for all $x > 0$ and $\mu(dx) = m(x)\lambda(dx)$ (i.e. μ has **density** m).

The case $\mu([x, \infty)) = \frac{1+\beta}{\beta x}$ describes the **MRCA age** of the **conditioned $(1 + \beta)$ -stable continuous state branching process** studied by Etheridge and Williams (2003).

Does A ever return to zero?

Note that

$$\mathcal{Z} := \{t \geq 0 : A_t = 0\} = \mathbb{R}_+ \setminus \bigcup_{(t,x) \in \Lambda} [t, t+x).$$



Poisson cut-out fractals

Following a question by Mandelbrot, Shepp showed that $\mathcal{Z} = \{0\}$ if and only if

$$\int_0^1 \exp \left\{ \int_t^1 M(s) ds \right\} dt = \infty,$$

where $M(s) := \mu([s, \infty))$.

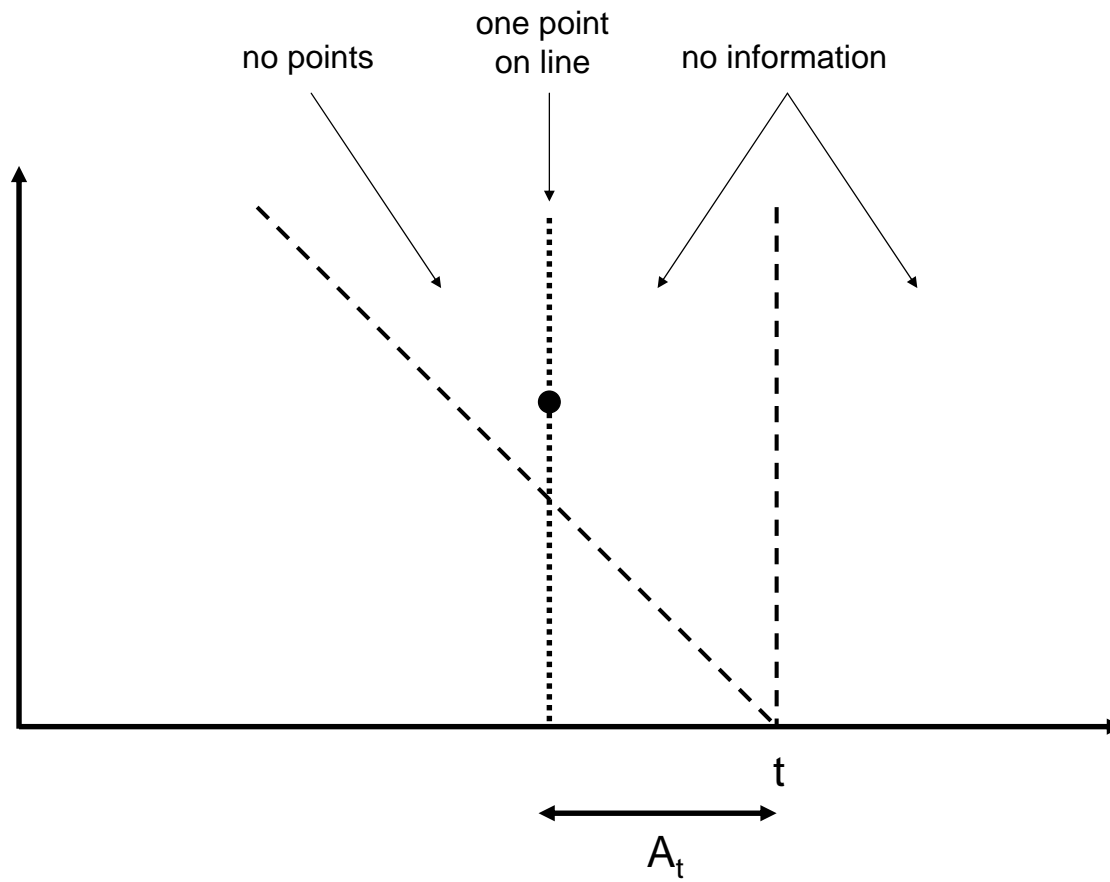
Fitzsimmons, Fristedt and Shepp showed that if $\mathcal{Z} \neq \{0\}$, then \mathcal{Z} is the **range** of non-trivial **subordinator** (with Laplace exponent given explicitly in terms of μ).

Example

If $\mu([s, \infty)) = \frac{\alpha}{s}$, then $\mathcal{Z} = \{0\}$ if and only if $\alpha \geq 1$.

Otherwise, \mathcal{Z} is the range of a $(1 - \alpha)$ -stable subordinator.

A is a Markov process



Transition probabilities

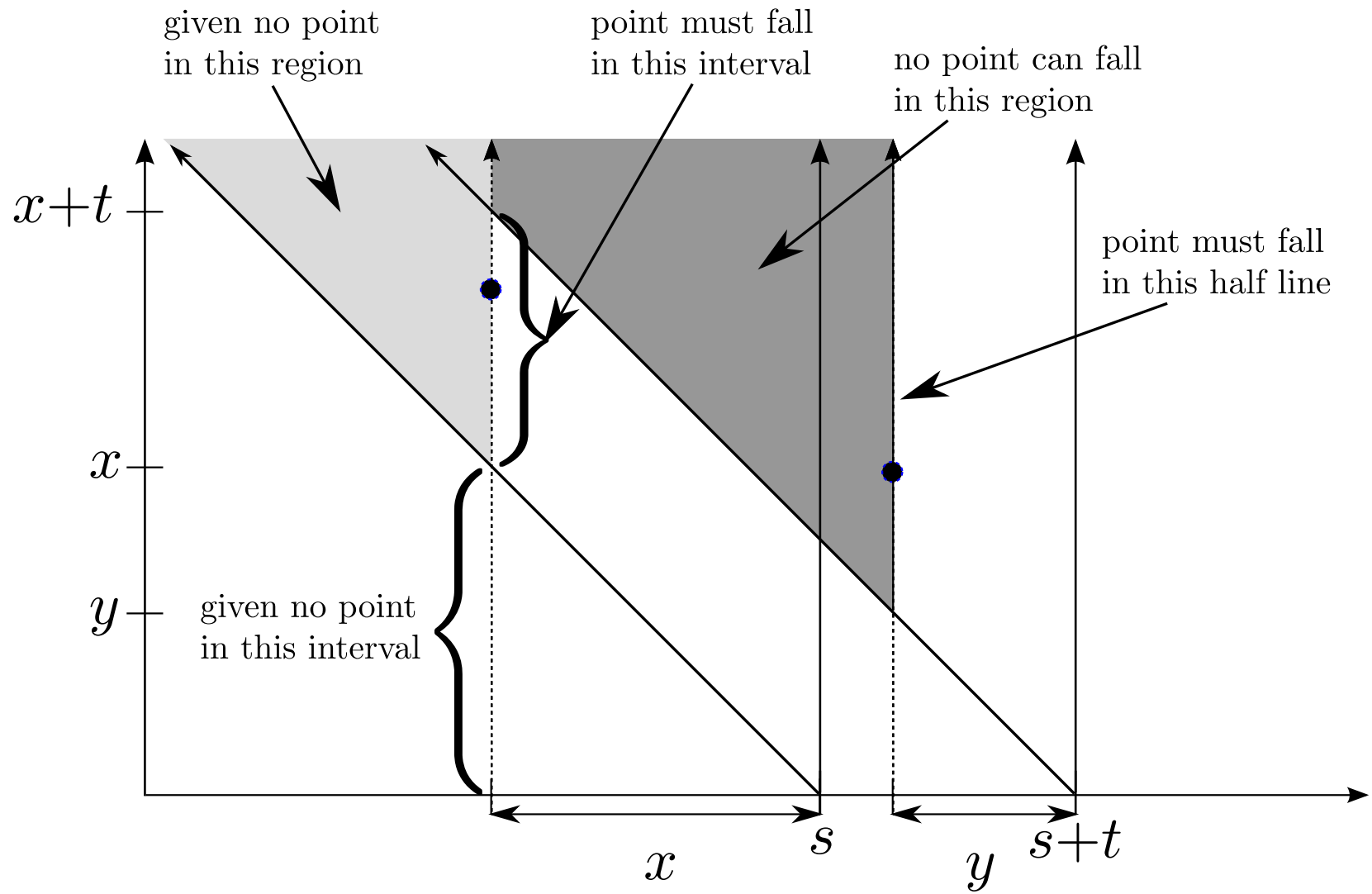
The process A is strong Markov with the following transition probabilities, where $M(x) := \mu([x, \infty))$.

For $y < x + t$,

$$\begin{aligned} & \mathbb{P}\{A_{s+t} \in dy \mid A_s = x\} \\ &= \frac{M(x) - M(x+t)}{M(x)} \exp\left\{-\int_y^{x+t} M(u) du\right\} M(y) dy, \end{aligned}$$

and

$$\mathbb{P}\{A_{s+t} = x + t \mid A_s = x\} = \frac{M(x+t)}{M(x)}.$$



Stationary distribution of A

We can try to construct a **stationary version** of A indexed by \mathbb{R} (rather than by \mathbb{R}_+) by replacing the Poisson point process Λ with an analogous process defined on $\mathbb{R} \times \mathbb{R}_+$ with intensity $\lambda \otimes \mu$.

This results in a finite-valued “age” process if and only if $\int_x^\infty M(u) du < \infty$ for all $x > 0$.

Thus, A has a **stationary distribution** π if and only if $\int_x^\infty M(u) du < \infty$ for all $x > 0$, in which case

$$\pi(dx) = M(x) \exp\left(-\int_x^\infty M(u) du\right) dx.$$

The “Ornstein-Uhlenbeck” transformation

If $\mu([x, \infty)) = \frac{\alpha}{x}$, then A does not have a stationary distribution.

The form of μ suggests we replace the time-scale t by a new one u given by $t = e^u$. If the MRCA at time t lived at time $t - a$ on the original scale, it lived at time $u - b$ on the new scale, where $t - a = e^{u-b}$.

The MRCA process on the new time scale is therefore the process B given by

$$e^{u-B_u} = t - A_t = e^u - A_{e^u}$$

so that

$$B_u = -\log(1 - e^{-u} A_{e^u}).$$

The “Ornstein-Uhlenbeck” process

The transformed process B is a stationary Markov process that comes from the “age” construction applied to the Poisson point process on $\mathbb{R} \times \mathbb{R}_+$ given by

$$\left\{ \left(\log s, \log \left(1 + \frac{x}{s} \right) \right) : (s, x) \in \Lambda \right\}$$

that has intensity $\lambda \otimes \nu$, where

$$\nu([x, \infty)) = \frac{\alpha}{e^x - 1}.$$

The “Ornstein-Uhlenbeck” marginals

The **one-dimensional marginal distributions** of B have **density**

$$\alpha e^{-x} (1 - e^{-x})^{\alpha-1},$$

and so $t^{-1}A_t$ has a $\text{Beta}(\alpha, 1)$ distribution for all $t > 0$ (when $A_0 = 0$).

The jump skeleton

- Return to general μ and suppose that $\int_x^\infty M(y) dy < \infty$ for all $x > 0$, so there is a stationary distribution.
- Take A to be in stationarity.
- Write $0 < T_0 < T_1 < \dots$ for the successive jump times.

Put $L_n := A_{T_n-}$ and $R_n := A_{T_n}$. These are the peaks and the troughs of the path of A that occur between the times 0 and $\sup_n T_n = \inf\{t > 0 : A_t = 0\} \in (0, \infty]$.

Classifying the jump skeleton

The processes $(L_n)_{n=0}^{\infty}$ and $(R_n)_{n=0}^{\infty}$ are **time-homogeneous Markov chains** with simple **transition kernels**.

- Both chains are **transient** if and only if

$$\int_0^1 \exp \left(\int_x^1 M(y) dy \right) dx < \infty.$$

- Both chains are **positive recurrent** if and only if

$$\int_0^1 m(x) \exp \left(- \int_x^1 M(y) dy \right) dx < \infty.$$

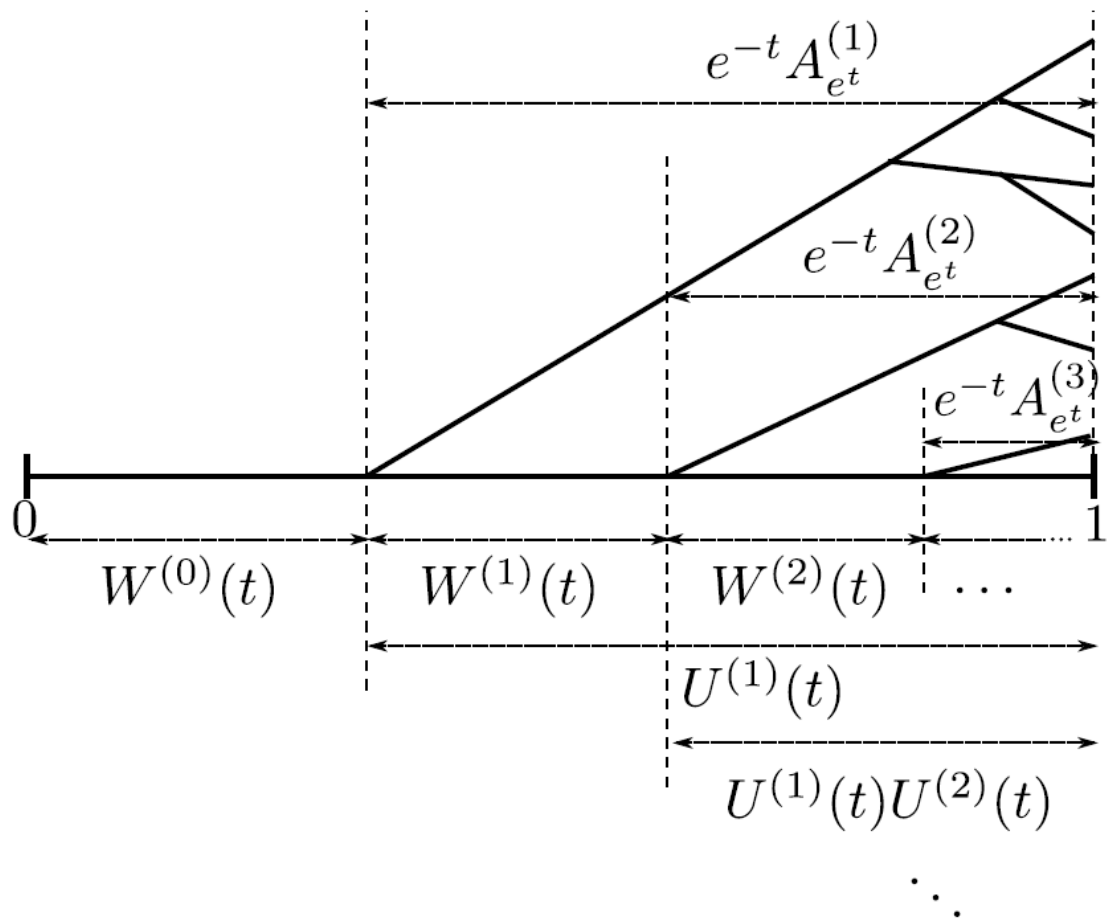
- Both chains are **null recurrent** if and only if both

$$\int_0^1 \exp \left(\int_x^1 M(y) dy \right) dx = \infty$$

and

$$\int_0^1 m(x) \exp \left(- \int_x^1 M(y) dy \right) dx = \infty.$$

Multiple split times for $M(x) = \mu([x, \infty)) = \frac{\alpha}{x}$



Stick breaking

Suppose that $A_0 = 0$ and $M(x) = \mu([x, \infty)) = \frac{\alpha}{x}$. Then,

$$(A_t^{(1)}/t, A_t^{(2)}/t, A_t^{(3)}/t, \dots)$$

has the same distribution as

$$((1 - U_1), (1 - U_1)(1 - U_2), (1 - U_1)(1 - U_2)(1 - U_3), \dots),$$

where the U_k are i.i.d. $\text{Beta}(\alpha, 1)$ r.v.

Thus,

$$(W_0, W_1, W_2, \dots)$$

has a $\text{GEM}(\alpha)$ distribution (that is, the distribution of the [size-biased ordering](#) of a $\text{Poisson} - \text{Dirichlet}(\alpha)$ sequence).