

Genealogy of catalytic branching models

Anita Winter, Erlangen

(with **Andreas Greven** & **Lea Popovic**)

“Probalistic models in evolutionary biology”

C.I.R.M. Marseille, 25.Mai 2009

Motivation

Branching Models - encoding the evolution of a population:

- > **population size**
- > **family forest** (genealogy/ancestral relationships)

Scaling Limits

- many individuals, each of small mass, rapid branching

Invariance Principles - general classes of models with same limit:

- > population - **continuous state branching processes (CSBP)**
- > genealogy - **continuum random trees (CRTs)**

Example: Independent Branching

critical Galton-Watson processes whose **offspring distribution** ...

- ... has **finite variance**:
 - population \Rightarrow **Feller diffusion** Feller '51
 - genealogy \Rightarrow **Aldous's CRT** Aldous '93
- ... is in the domain of attraction of an **α -stable distribution**:
 - population \Rightarrow **α -stable CSBP** Lamperti '67
 - genealogy \Rightarrow **α -stable CRT** Duquesne-LeGall '02

Our model: catalytic branching

- > the **catalyst** $(\eta_t)_{t \geq 0}$ is a critical binary GW with constant branching rate = 1
- > the **reactant** $(\xi_t)_{t \geq 0}$ is a critical binary GW with time-inhomogeneous branching rate **depending on** the current population size of the **catalyst**.

... and the scaling limit

In the n^{th} -rescaling step $(\tilde{\eta}^n, \tilde{\xi}^n)$ is a continuous time MC with $(\tilde{\eta}_0^n, \tilde{\xi}_0^n) = (1, 1)$ and

$$(\tilde{\eta}^n, \tilde{\xi}^n) \mapsto \begin{cases} (\tilde{\eta}^n \pm \frac{1}{n}, \tilde{\xi}^n), & \text{at rate } \frac{1}{2}n^2\tilde{\eta}^n, \\ (\tilde{\eta}^n, \tilde{\xi}^n \pm \frac{1}{n}), & \text{at rate } \frac{1}{2}n^2\tilde{\eta}^n\tilde{\xi}^n. \end{cases}$$

Fact. Greven, Klenke & Wakolbinger '99

$(\tilde{\eta}^n, \tilde{\xi}^n) \Rightarrow (X, Y)$ where

$$dX_t = \sqrt{X_t} dW_t^X$$

$$dY_t = \sqrt{X_t Y_t} dW_t^Y$$

A remark on extinction times

$$dX_t = \sqrt{X_t} dW_t^X$$

$$dY_t = \sqrt{X_t Y_t} dW_t^Y$$

and

$$\rho^0 := \inf \{t \geq 0 : X_t = 0\}, \quad \tau^0 := \inf \{t \geq 0 : Y_t = 0\}.$$

Basic Facts.

- $\rho^0 < \infty$, almost surely.
- The reactant gets absorbed in Y_{ρ^0} at time ρ^0 .
- Penssel '03

$$\mathbb{P}\{\rho^0 < \tau^0\} = \frac{1}{\sqrt{5}} \in (0, 1).$$

Problems we would like to answer ...

- from a **quenched view** (given the **catalyst mass process**):
 - establish **existence** of a limit **reactant** genealogy
 - **analytic characterizations** of the limit
- from an **annealed view**:
 - **joint convergence** of catalyst and reactant genealogies
 - **differences** in catalyst forest from Aldous's CRF

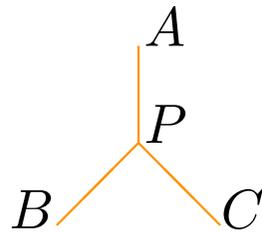
Existence of limit reactant genealogies

Rooted real trees

Dress (1984), Dress & Terhalle (1996)

A **rooted real tree** (T, r, ρ) is a

- **metric space** (T, r) ,
- **path-connected**,
- **0-hyperbolic**, i.e. $\forall A, B, C \in T \exists P \in [A, B]$ with $P \in [B, C] \cap [A, C]$



- with the **root** $\rho \in T$ distinguished.

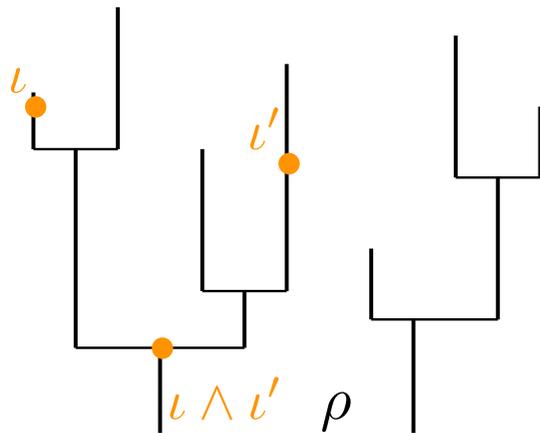
\mathbb{T} := (root invariant) isometry classes of **compact rooted \mathbb{R} -trees**

Coding finite forest as rooted \mathbb{R} -trees

$T := \bigcup_{t \in [0, \text{height}]} \text{all individuals alive time } t$

$d(\iota, \iota') := \text{generation of } (\iota) + \text{generation of } (\iota') - 2 \cdot \text{generation of } (\iota' \wedge \iota)$

$\rho := \text{glueing together all the trees' ancestors}$



Rule. At the height where the catalyst dies **cut off** the reactant forest

Hausdorff distance

Let (X, d) be a metric space.

Hausdorff distance:

For $A_1, A_2 \subseteq_{\text{closed}} X$,

$$d_H(A_1, A_2) := \inf\{\varepsilon > 0 : A_1 \subseteq A_2^\varepsilon \text{ and } A_2 \subseteq A_1^\varepsilon\},$$

where A^ε is the ε -neighborhood of A .

Gromov strong topology

$$(\mathbf{T}_N, \mathbf{d}_N, \rho_N) \xrightarrow{N \rightarrow \infty} (\mathbf{T}, \mathbf{r}, \rho)$$

iff $\{(T_N, d_N); N \in \mathbb{N}\}$ and (T, d) can be embedded via isometries $\{\varphi_N; N \in \mathbb{N}\}$ and φ , resp., in one and the same compact metric space $(\mathbf{Z}, \mathbf{d}_Z)$ on which

$$\varphi_N(\mathbf{T}_N) \xrightarrow{N \rightarrow \infty} \varphi(\mathbf{T}), \quad \varphi_N(\rho_N) \xrightarrow{N \rightarrow \infty} \varphi(\rho)$$

in the **Hausdorff topology on (\mathbf{Z}, \mathbf{d})** .

Existence of reactant limit forest

- let $(\tilde{\eta}^{\text{for},n}, \tilde{\xi}^{\text{for},n})$ be the pairs of \mathbb{R} -trees corresponding to the catalyst and reactant population in the n^{th} -approximation step

-

$(\cdot; \cdot) :=$ conditional law of **reactant** given a realization of the **catalyst**

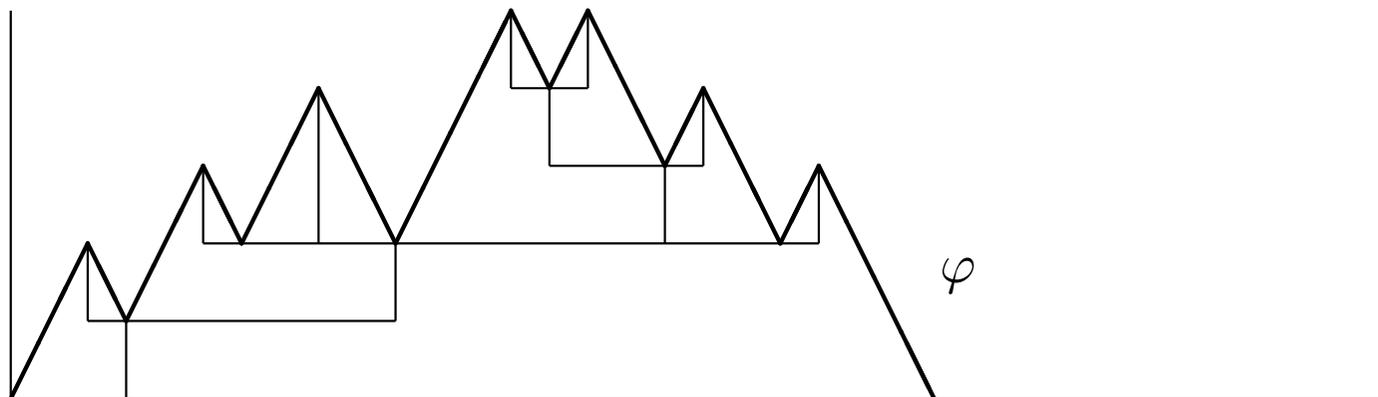
Proposition. Assume that $\sup_{t \leq T} |\tilde{\eta}_t^n - X_t| \rightarrow 0$ a.s. Then the family $\{(\tilde{\xi}^{\text{for},n}; \tilde{\eta}^n); n \in \mathbb{N}\}$ is relatively compact.

Characterization via excursions

Main example: Tree “below” an excursion

$\varphi \in C([0, L(\varphi)])$, $L(\varphi) \in (0, \infty)$, $\varphi|_{\{0, L(\varphi)\}} \equiv 0$, $\varphi|_{(0, L(\varphi))} > 0$

For $u, u' \in [0, L(\varphi)]$ put $u \equiv_{\varphi} u'$ iff **no minima** in between them.



$$\mathbf{T}_{\varphi} := \{[u]; u \in [0, L(\varphi)]\}, \quad \rho_{\varphi} := [0],$$

$$\mathbf{d}_{\varphi}([u], [u']) := \varphi(u) + \varphi(u') - 2 \inf_{s \in [u \wedge u', u \vee u']} \varphi(s).$$

Fact. $T|_{\varphi}$ is compact real tree.

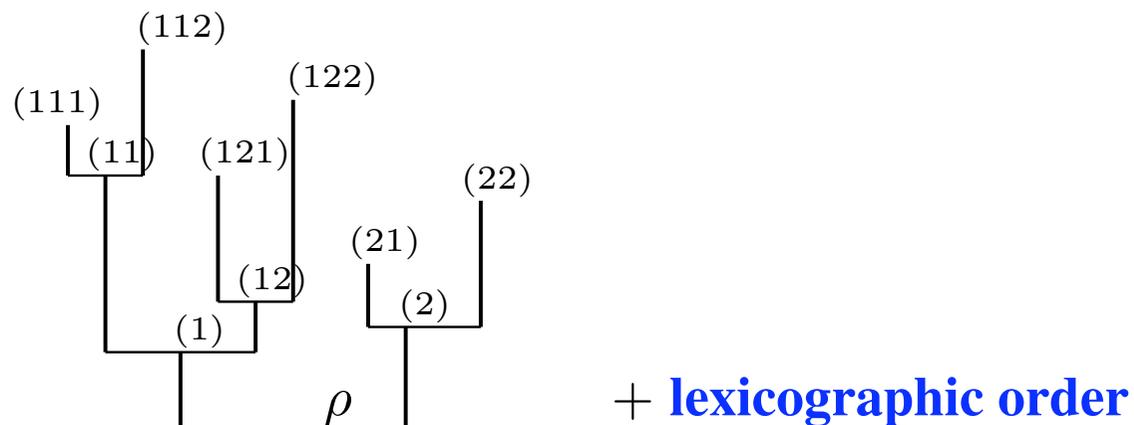
Example. Aldous’s CRT = tree “below” Brownian excursion

Planar embedding and linear order

Planar embedding requires a **linear ordering** which

- extends the partial order, and
- if x, y, x', y' are s.t. $x \leq^{\text{lin}} y$ and $x \wedge y \leq x' \wedge x$ and $x \wedge y \leq y' \wedge y$ then $x' \leq^{\text{lin}} y'$.

Example.



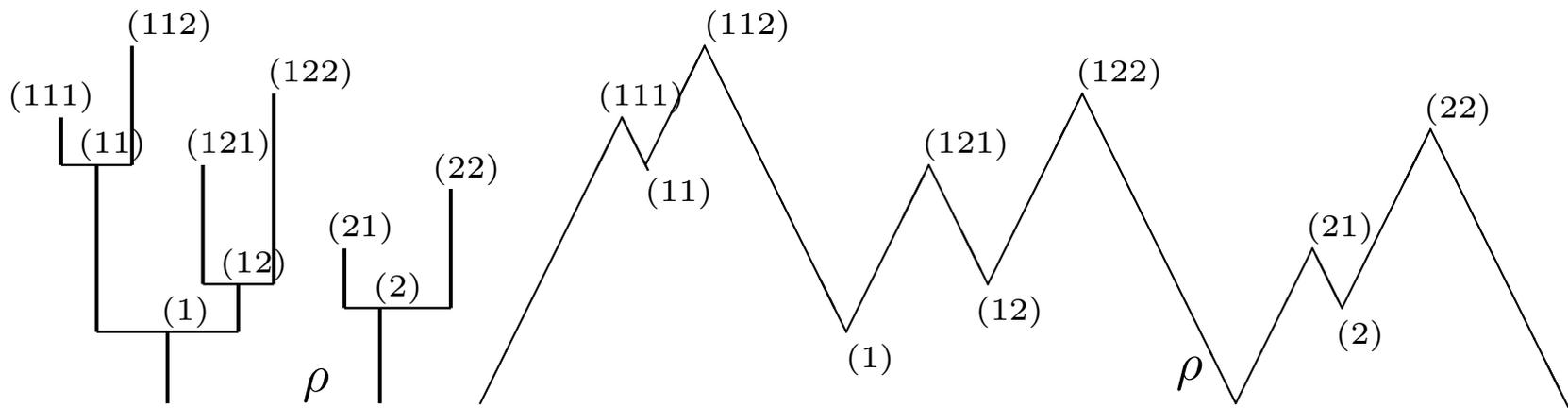
e.g., $x = (111)$, $y = (122)$, $x' = (112)$ and $y' = (12)$

The contour process of finite trees

(\mathbf{T}, ρ) : finite (linearly ordered) forest

σ : speed of traversal

$\mathcal{C}(T, \sigma)$: records height of the depth-first search around the forest



Lemma. In continuous time binary GW with **given** branching rate, $\mathcal{C}(T, \sigma)$ is a linear interpolation of an **alternating random walk**.

Re-scaling the contour

- Speeding up branching by n = rescaling **edges** by a factor $\frac{1}{n}$,
 - a GW-trees has height of order $\mathcal{O}(n)$ with probability $\mathcal{O}(\frac{1}{n})$
- ⇒ if we start initially with n -trees yields a **Poisson number** of trees each having height $\mathcal{O}(n)$
- given a GW-tree has height of order $\mathcal{O}(n)$ its **number of edges** is of order $\mathcal{O}(n^2)$

Since edges are of length $\mathcal{O}(\frac{1}{n})$, we choose in the n^{th} -approximation step

$$\sigma := n.$$

The catalyst contour

Obvious. [Brownian rescaling]

If $|\beta|$ is **reflected Brownian motion**, $\ell(|\beta|)$ its **local time** process, i.e.,

$$\ell(|\beta|)_t := \lim_{\varepsilon \rightarrow 0} \varepsilon^{-1} \int_0^t du \mathbf{1}\{|\beta|_u \in [0, \varepsilon]\},$$

and $\ell(|\beta|)^{-1}$ its **inverse**, i.e.,

$$\ell(|\beta|)^{-1}(s) := \inf \{t \geq 0 : \ell(|\beta|)_t = s\},$$

then

$$\mathcal{C}(\tilde{\eta}^{\text{for}, \mathbf{n}}; \mathbf{n}) \xrightarrow{\mathbf{n} \rightarrow \infty} \mathbf{2} \cdot |\beta|_{\cdot \wedge \ell_0^{-1}(1)}.$$

Random evolution and stochastic averaging (Kurtz '92)

$\delta > 0,$

$$\tilde{T}^{\delta,n} := \inf \{t \geq 0 : \tilde{\eta}_t^n \leq \delta\}.$$

Lemma.

Let $V_u := \frac{1}{2}\text{slope}(C_u)$ then $(C_u, V_u)_{u \geq 0}$ is a random evolution with

$$\tilde{\mathbf{A}}^{\delta,n} \mathbf{f}(\mathbf{c}, \mathbf{v}) = n\mathbf{v} \frac{\partial}{\partial \mathbf{c}} \mathbf{f}(\mathbf{c}, \mathbf{v}) + n^2 \tilde{\eta}_{\mathbf{c}}^n [\mathbf{f}(\mathbf{c}, -\mathbf{v}) - \mathbf{f}(\mathbf{c}, \mathbf{v})]$$

and domain

$$\mathcal{D}(\tilde{\mathbf{A}}^{\delta,n}) = \{\mathbf{f} \in \mathbf{C}^{1,0}(\mathbf{0}, \tilde{\mathbf{T}}^{\delta,n} \times \{-1, 1\}) : \partial_{\mathbf{c}} \mathbf{f}|_{\{\mathbf{0}, \tilde{\mathbf{T}}^{\delta,n}\} \times \{\mathbf{0}, 1\}} \equiv \mathbf{0}\}.$$

Limiting contour process

For $\delta > 0$, let $\tilde{\xi}^{\text{for},\delta,n} :=$ reactant tree **cut off** in height $\tilde{T}^{\delta,n}$ and

$$A^\delta f(c) := 2 \left(\frac{1}{X_c} f' \right)'(c)$$

on the domain

$$\mathcal{D}(A^\delta) := \left\{ f \in \mathcal{C}^2([0, \tau^\delta]) : \frac{1}{X} f' \in \mathcal{C}^1([0, \tau^\delta]), f'|_{\{0, \tau^\delta\}} = 0 \right\}.$$

Theorem The $(A^\delta, \mathcal{D}(A^\delta))$ -martingale problem is well-posed. If ζ^δ is the solution of the $(A^\delta, \mathcal{D}(A^\delta))$ -martingale problem, then

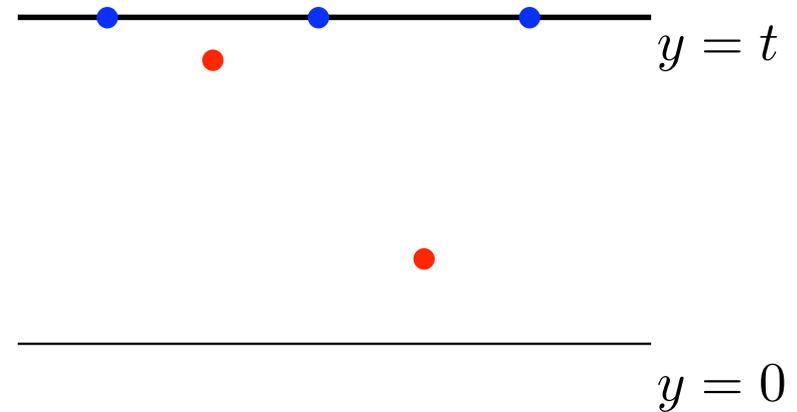
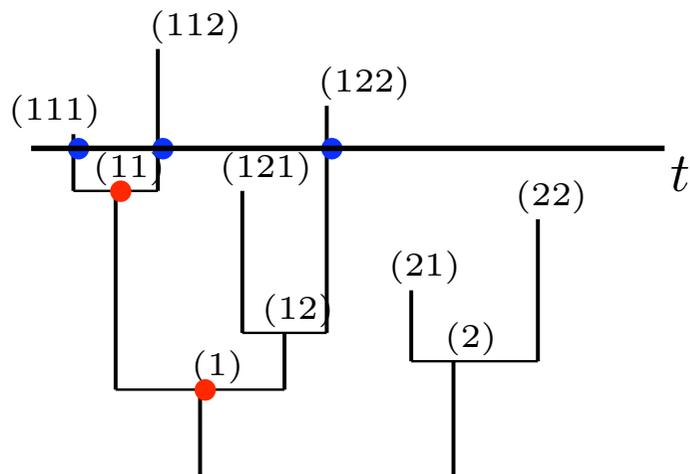
$$\left(\mathcal{C}(\tilde{\xi}^{\text{for},\delta,n}); \tilde{\eta}^n \right) \xrightarrow{n \rightarrow \infty} \left(\zeta^\delta; X \right).$$

.... but what if $\delta \downarrow 0$?

Yet another useful representation

Genealogical point process (Popovic '04)

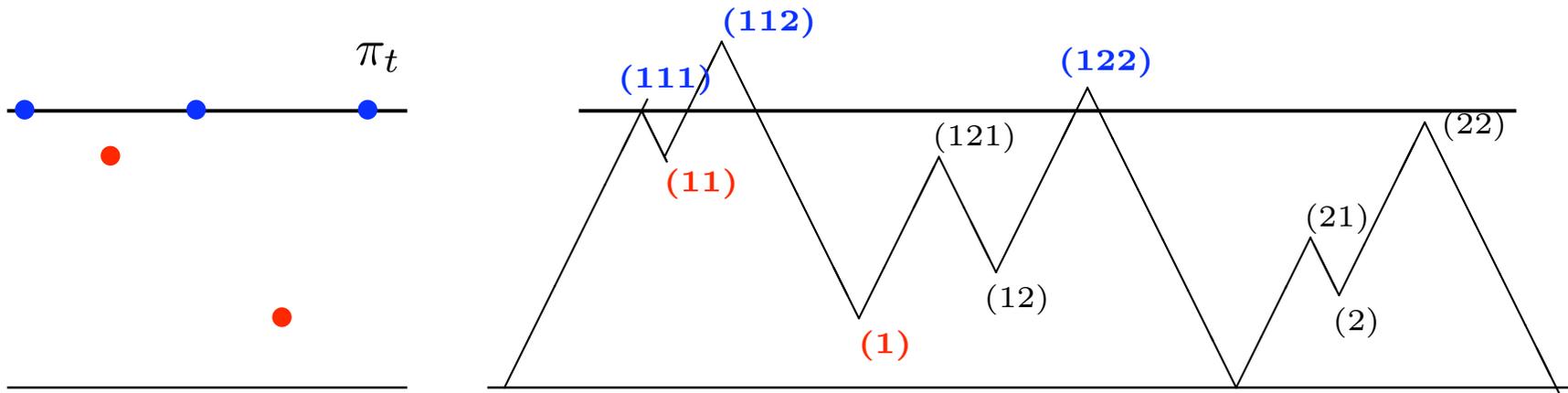
$\mathcal{P}(\mathbf{T}, \zeta) = \{\pi_t\}_{t \geq 0}$: collection of processes indexed by t ; each giving the ancestry of the population alive at time t



$\zeta :=$ spacing

Distribution of the point process

π_t are points of maximal depths of i.i.d. excursions below t



Lemma. For all $t > 0$, given a medium η , π_t is a simple point-process, $\{\tau_i\}_{i=0, \dots, (\xi_t-1)}$ are i.i.d. with

$$\mathbf{P}(\tau_i \in dh) = \frac{\eta_h}{\left(1 + \int_h^t \eta_s ds\right)^2} \frac{1 + \int_0^t \eta_s ds}{\int_0^t \eta_s ds}, \quad \mathbf{h} \in (0, t)$$

Rescaling the point process

Since after the rescaling of edge lengths we find at any height $t > 0$ a **Poisson number** of trees **each** having family size of order $\mathcal{O}(\mathbf{n})$, we choose in the n^{th} -approximation step

$$\zeta := \frac{1}{\mathbf{n}}.$$

Limit of the reactant genealogical point-process

Theorem. For any $t > 0$,

$$\left(\mathcal{P}^t(\tilde{\xi}^{\text{for}, \mathbf{n}}; \frac{\mathbf{1}}{\mathbf{n}}); \tilde{\eta}^{\mathbf{n}}\right) \Rightarrow (\pi^{\zeta, t}; \mathbf{X}),$$

where for given path of X the point process $\pi^{\zeta, t}$ consists of:

- Poisson point process on $\mathbb{R}^+ \times \mathbb{R}^+$ whose intensity measure is

$$\mathbb{N}^{\zeta, t} [d\ell \times d\mathbf{h}] = \mathbf{1}_{[0, \mathbf{Y}_t]}(\ell) d\ell \otimes \mathbf{1}_{(0, t \wedge \tau^0 \wedge \rho^0)}(\mathbf{h}) \frac{\mathbf{X}_{\mathbf{h}}}{\left(\int_{\mathbf{h}}^t \mathbf{X}_s ds\right)^2} d\mathbf{h}.$$

- rate $\left(\int_0^t \mathbf{X}_s ds\right)^{-1}$ Poisson point process at height 0 whose points separate distinct trees in the forest.

Remark. Result is δ -free!!!!

Properties of the Reactant Forest

Comparison with the constant rate branching forest:

- > differences in tree structure due to inhomogeneity of the random environment (evolving branching rates)
 - stretching of the tree metric
- > behavior of the forest Y^{for} at time τ^0 of extinction of the random environment (in the event the catalyst dies first)
 - infinite ℓ^2 -length of the tree tips!

Differences in the reactant forest due to inhomogeneous rates

$$\partial Q_t(Y, d, \rho) := \{u \in Y : d(\rho, u) = t\}.$$

Stretching Lemma. Let $(Z^{\text{for}}, d_{Z^{\text{for}}}, \rho)$ be the Brownian CRF and Y^{for} the reactant forest, and let $X : [0, \tau^0) \rightarrow \mathbb{R}_+$ be a given continuous function. For a fixed $t > 0$ define an increasing function $s_t^X : [0, t] \rightarrow [0, \int_0^t X_s ds]$ by

$$s_t^X(h) := \int_{t-h}^t X_s ds,$$

and let $(s_t^X)^{-1} : [0, \int_0^t X_s ds] \rightarrow [0, t]$ be its inverse. Then

$$\left((\partial Q_t(Y^{\text{for}}), d_{Y^{\text{for}}}, \rho); X \right) \stackrel{d}{=} \left(\partial Q_{s_t^X(t)}(Z^{\text{for}}), 2(s_t^X)^{-1} \left(\frac{1}{2} d_{Z^{\text{for}}}, \rho \right) \right)$$

Application of the stretching lemma

Theorem. [Comparing the probability to belong to different families]

Let Y^{for} be the reactant CRF and Z^{for} be Brownian CRF with the **same expected number of trees of a given height $t > 0$** . If $\mu^{t,Y}$ and $\mu^{t,Z}$ are the “uniform” distributions on $\partial Q_t(Y^{\text{for}})$ and $\partial Q_t(Z^{\text{for}})$, respectively, then

$$\begin{aligned} & \mathbb{E} \left[\int_{(\partial Q_t(Y^{\text{for}}))^2} (\mu^{t,Y})^{\otimes 2} (du, du') \mathbf{1}\{d_{Y^{\text{for}}}(u, u') = 2t\} \right] \\ & \leq \mathbb{E} \left[\int_{(\partial Q_t(Z^{\text{for}}))^2} (\mu^{t,Z})^{\otimes 2} (du, du') \mathbf{1}\{d_{Z^{\text{for}}}(u, u') = 2t\} \right]; \end{aligned}$$

Differences due to vanishing catalyst

Case. $\rho^0 < \tau^0$, i.e., reactant dies first

Proposition.

$$\lim_{\delta \downarrow 0} \langle \zeta^\delta, \zeta^\delta \rangle_{\ell^{-1}(\zeta^\delta)(\mathbf{1})} = \infty, \quad \mathbb{P}\text{-a.s.}$$

Note. With positive probability there does **not exist** a limiting diffusion ζ^0 describing the contour of the full forest Y^{for} including its highest tips.

Many thanks