Probabilistic Models of Evolutionary Biology

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Trees under attack: a genealogy in Feller's branching with logistic drift

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Joint work with Etienne Pardoux

Two beautiful genealogical structures

behind Feller's branching diffusion:

a) the subordinator representation

b) the Ray-Knight theorem

(Neveu, Pitman, Yor, Le Gall ...)

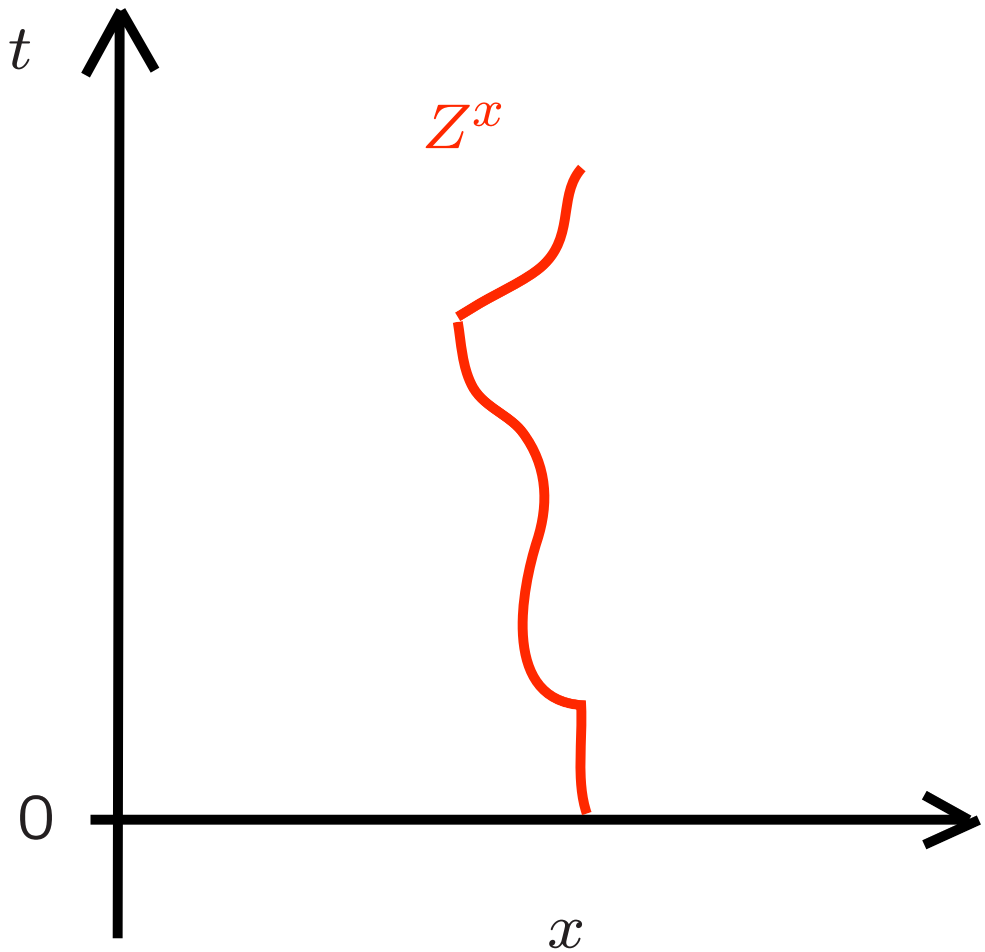
$$dZ_t^x = \sqrt{Z_t^x}\, dW_t^x, \quad Z_0^x = x$$

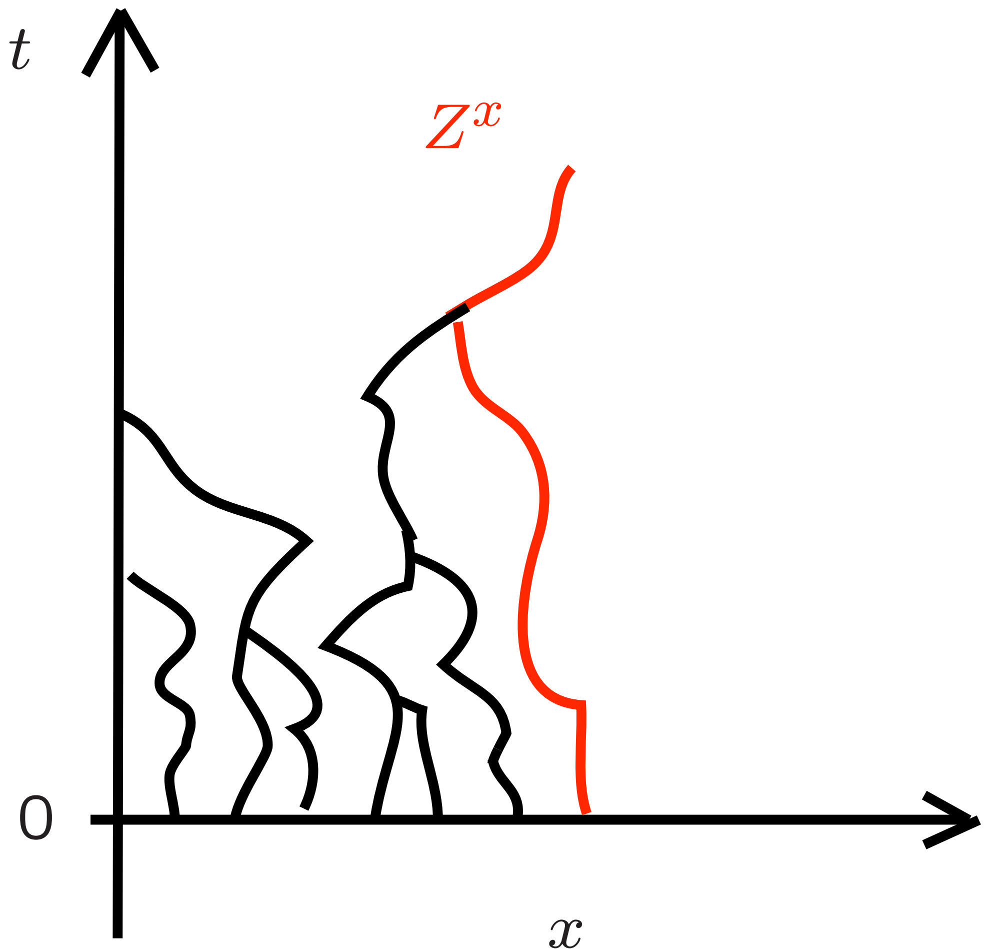
a) $$Z_t^x \stackrel{d}{=} \sum_{(a,\zeta):a\le x} \zeta_t, \quad t > 0,$$

where $((a, \zeta))$ is a Poisson point process on $\mathbb{R}_+ \times \mathcal{E}$ with intensity measure $\lambda \otimes Q$

and Q is a measure on the space $\mathcal{E}$ of excursions from 0:

$$Q(.) = \lim_{\varepsilon \to 0} \frac{1}{\varepsilon} \mathbf{P}_\varepsilon(Z \in (\cdot))$$


t
Z^x
0
x



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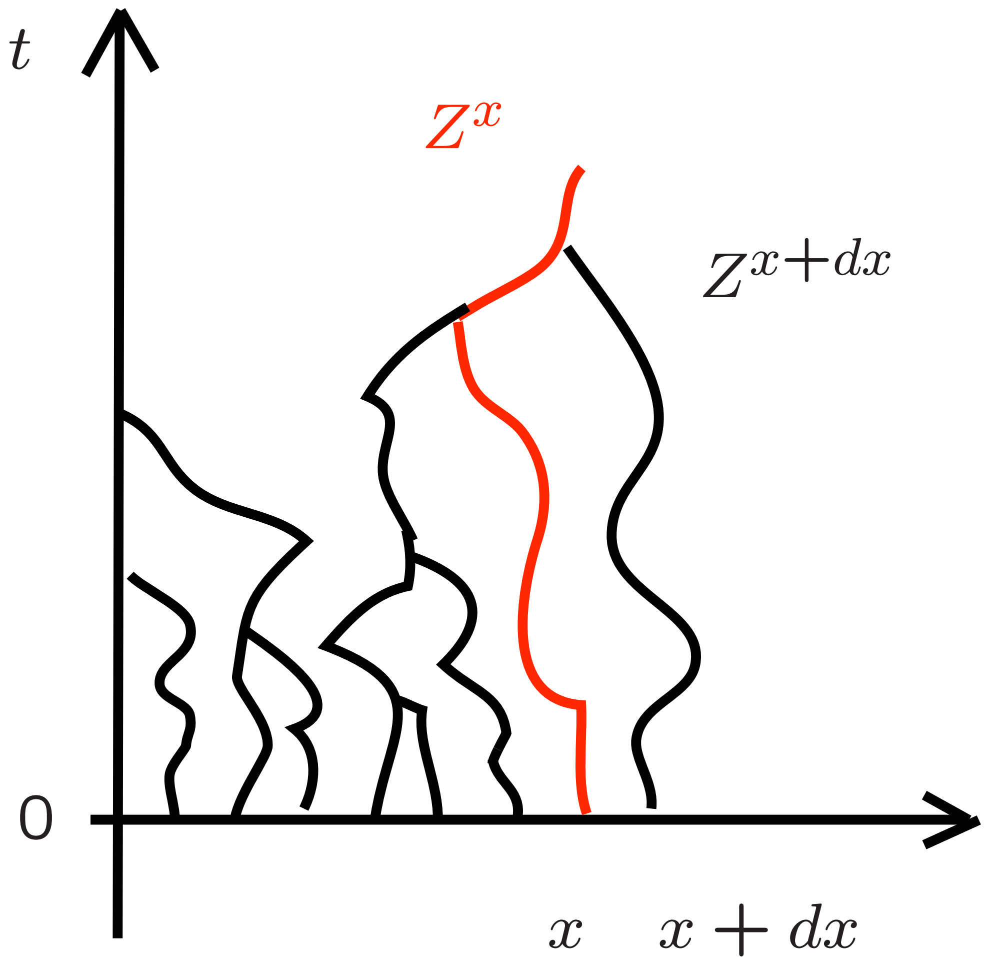

t
Z^x
Z^{x+dx}
0
x
$x + dx$

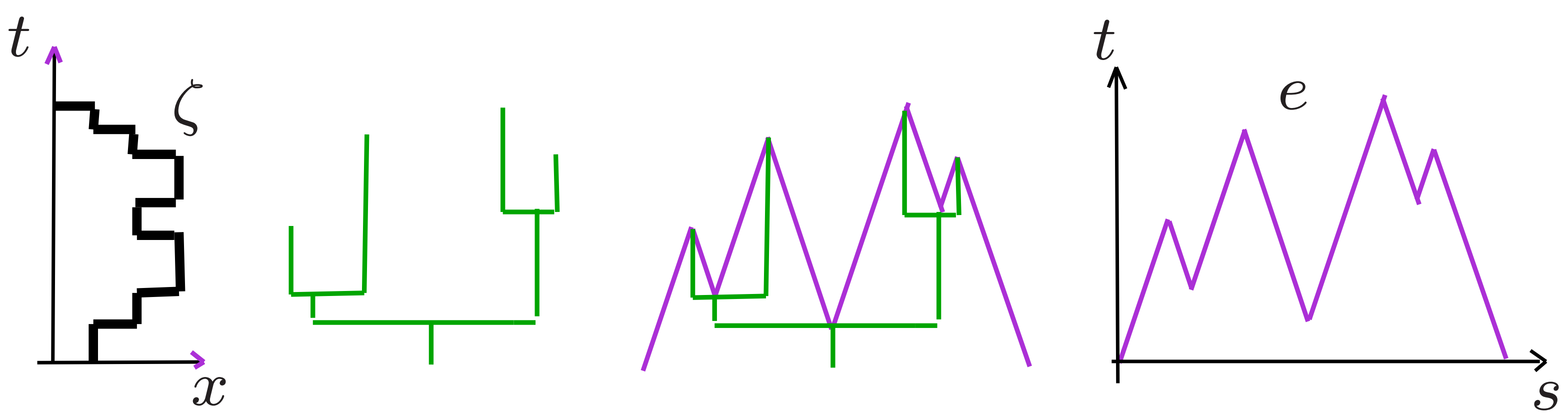
b) $\quad (Z_t^x)_{t\geq 0} \overset{d}{=} \big(L_{S_x}(H,t)\big)_{t\geq 0}$

where H is a Brownian motion reflected at 0,

$L_s(H,t)$ is its local time up to s at height t,

$S_x := \inf\{s > 0 : L_s(H,0) = x\}$.

Intuitive explanation: Every single “mass excursion” ζ
is the width profile of a (continuum) tree,
which is coded by its ***exploration path***.



The (mass) excursion measure Q is the image of the
Itô excursion measure under the mapping $e \mapsto (L_\infty(e,t))_{t>0}$

Extensions:

1. Supercritical branching:

$$dZ_t = KZ_t dt + \sqrt{Z_t}\, dW_t, \quad K > 0.$$

J.F. Delmas 06, *Height process for super-critical CSBP*:

The exploration excursions have an upward drift
and thus not necessarily return to 0.

Way out: Cutting the forest at $t_0 > 0$ induces a reflection
of the exploration process at height t_0,
and gives a projective system indexed by t_0.

2. Critical branching with time-dependent branching rate:

$dZ_t = \sqrt{Z_t}\,\sigma_t^2 dW_t$

A. Greven, L. Popovic, A. Winter 09, *Genealogy of catalytic branching models*:

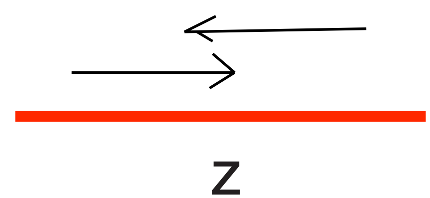
The exploration process has generator $Af(h) := (\frac{2}{\sigma^2}f')'(h)$ with reflection at $h = 0$.

3. Feller branching with logistic drift:

$$dZ_t = (KZ_t - \gamma Z_t^2)dt + \sqrt{Z_t}\,\sigma dW_t$$

The quadratic drift term $-\gamma Z_t^2$ destroys the independence of the branching.

Microscopic picture: Individuals attack each other (pairwise)



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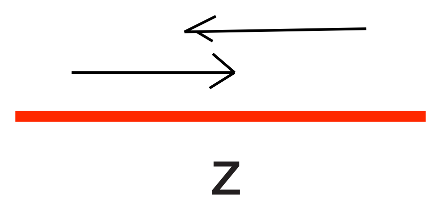
To introduce an order, let us distribute the death rate asymmetrically upon the individuals:



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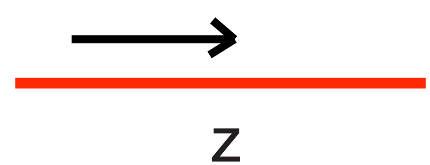
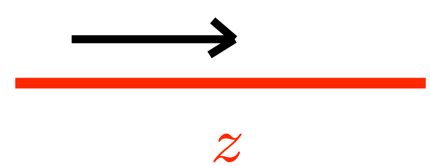


3. Feller branching with logistic drift:

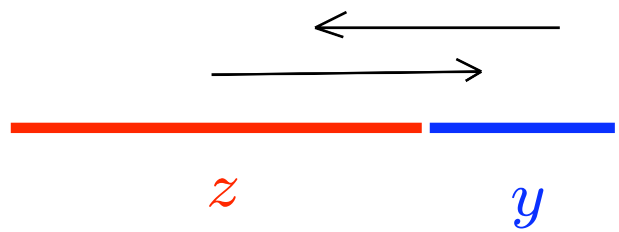
$$dZ_t = (KZ_t - \gamma Z_t^2)dt + \sqrt{Z_t}\,\sigma dW_t$$

Motto: those to the left attack those to the right

(this is of course not meant politically!)



For the sum of two populations:



Quadratic killing rate:

$$-(z + y)^2$$

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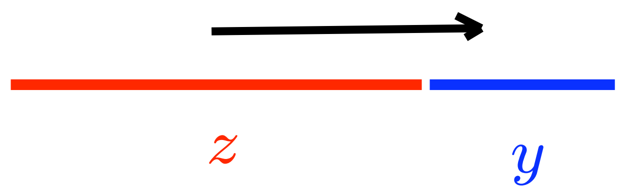


Quadratic killing rate:

$$-(z+y)^2 = -z^2 - 2zy - y^2$$

Fact: For $x > 0$ let Z^x be a solution of

$$dZ_t = Z_t(K - \gamma Z_t)dt + \sqrt{Z_t}\,\sigma\, dW_t^{(0,x)}, \quad Z_0 = x,$$

and for a given path $z = (z_t)$, and $\varepsilon > 0$,

let $Y^\varepsilon(z)$ be a solution of

$$dY_t = Y_t \left(K - \gamma(Y_t + 2z_t)\right) dt + \sqrt{Y_t}\,\sigma\, dW_t^{(x,x+\varepsilon)}, \quad Y_0 = \varepsilon$$

Then $Z^{x+\varepsilon} := Z^x + Y^\varepsilon(Z^x)$ solves

$$dZ_t = Z_t(K - \gamma Z_t)dt + \sqrt{Z_t}\,\sigma dW_t^{(0,x+\varepsilon)}, \quad Z_0 = x + \varepsilon.$$

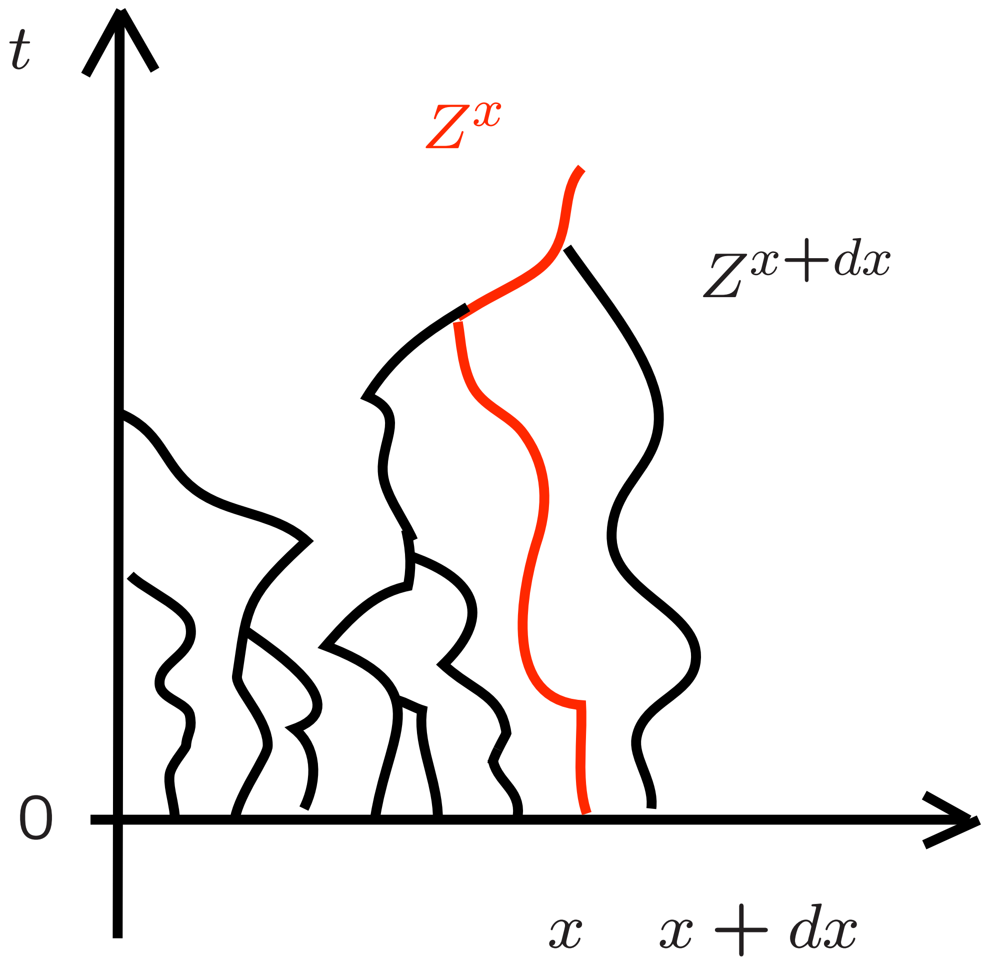
Corollary: $(Z^x)_{x>0}$ is a (path-valued) jump process with generator

$$\mathcal{L}f(z) := \lim_{\varepsilon \to 0} \frac{1}{\varepsilon} \mathbf{E}[f(z + Y^\varepsilon(z)) - f(z)]$$

$$=: \int (f(z+y) - f(z)) Q(z, dy).$$

For $f(z) = \exp(-\langle z, \varphi \rangle)$,

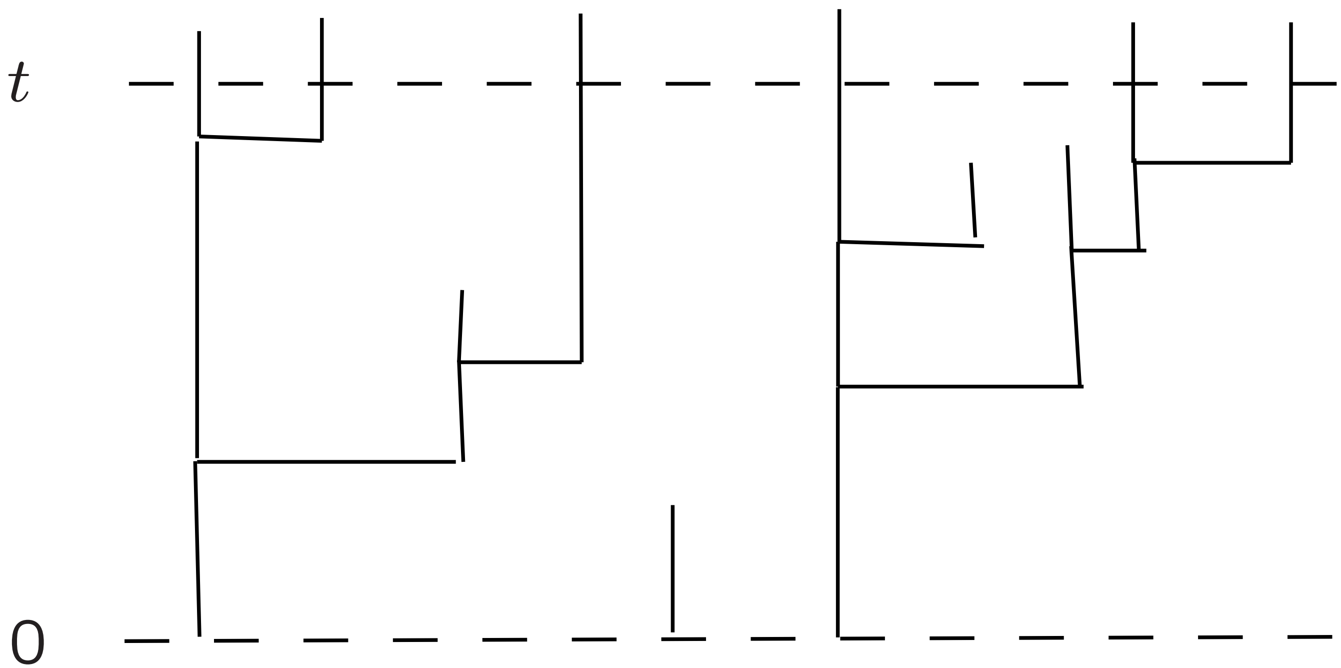
$$\mathcal{L}f(z) = \exp(-\langle z, \varphi \rangle) \int (\exp(-\langle y, \varphi \rangle) - 1)\, Q(z, dy).$$


t
Z^x
Z^{x+dx}
0
x
$x + dx$

So far this was on the level of “masses”, decomposed with respect to the ancestry from time 0.

Can we again understand the mass excursions as width profiles of continuum trees?

Let’s look at the limit of rescaled binary branching processes (with particles of mass $\frac{1}{N}$ in the N-th rescaling).



t
0

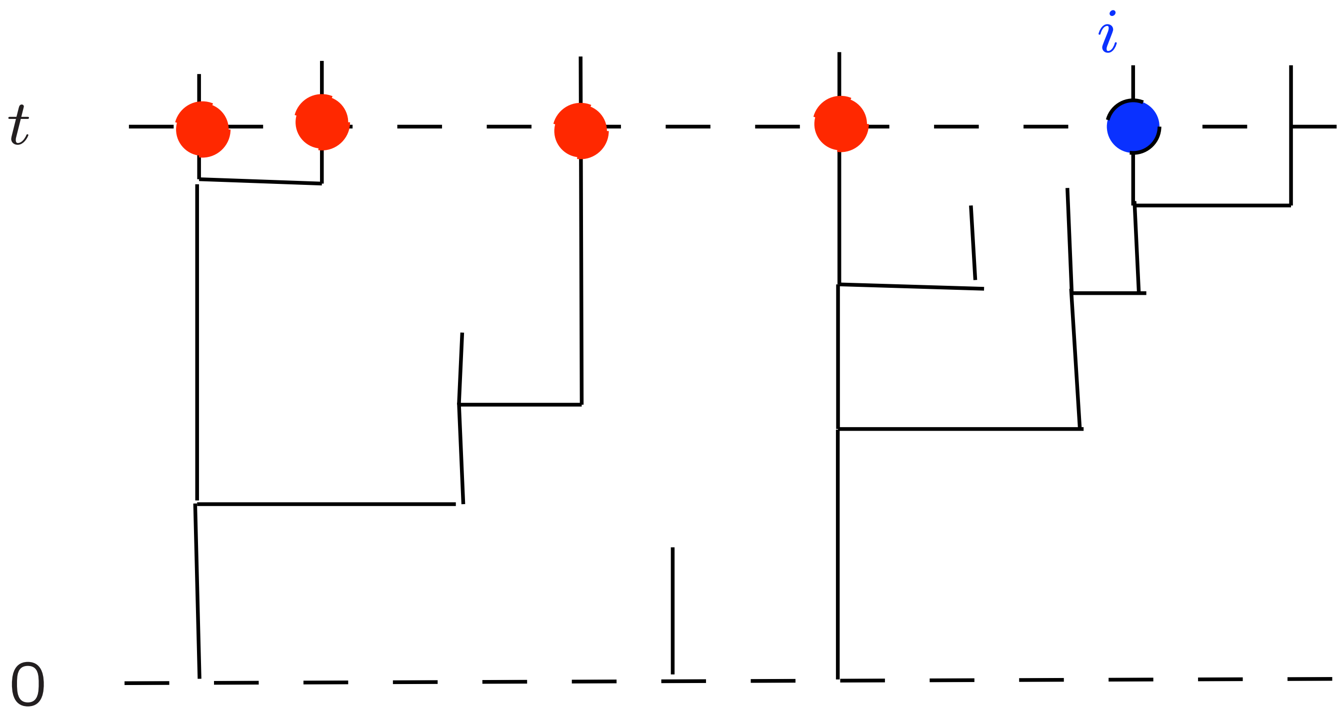
The growth of the forest in the N-th rescaling:

Along any branch:

Birth clock rings at rate $N\sigma^2/2 + K$

Death clock rings at rate $N\sigma^2/2 + \gamma 2 \Lambda_t(i)/N$, where

$\Lambda_t(i)$ is the number of individuals to the left of individual i


i
t
0

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$$\sum_{i=1}^{NZ_t^N} \gamma 2\Lambda_t(i)/N = \gamma N Z_t^N (N Z_t^N - 1)/N \sim N\gamma \cdot (Z_t^N)^2$$

is the jump rate from Z_t^N to $Z_t^N - 1/N$ induced by the killing

The exploration process in the N-th rescaling:

Exploration paths H^N have slope $\pm 2N$.

An individual $(s, H^N(s))$ is visited at exploration time s

and lives at real time $t = H^N(s)$.

Birth point of a branch $\leftrightarrow$ local minimum of H^N

Death point of a branch $\leftrightarrow$ local maximum of H^N

$$L_s(H^N, t) := \lim_{\varepsilon \to 0} \frac{1}{\varepsilon} \int_0^s \mathbf{1}_{\{t \le H_u^N < t+\varepsilon\}} \, du$$

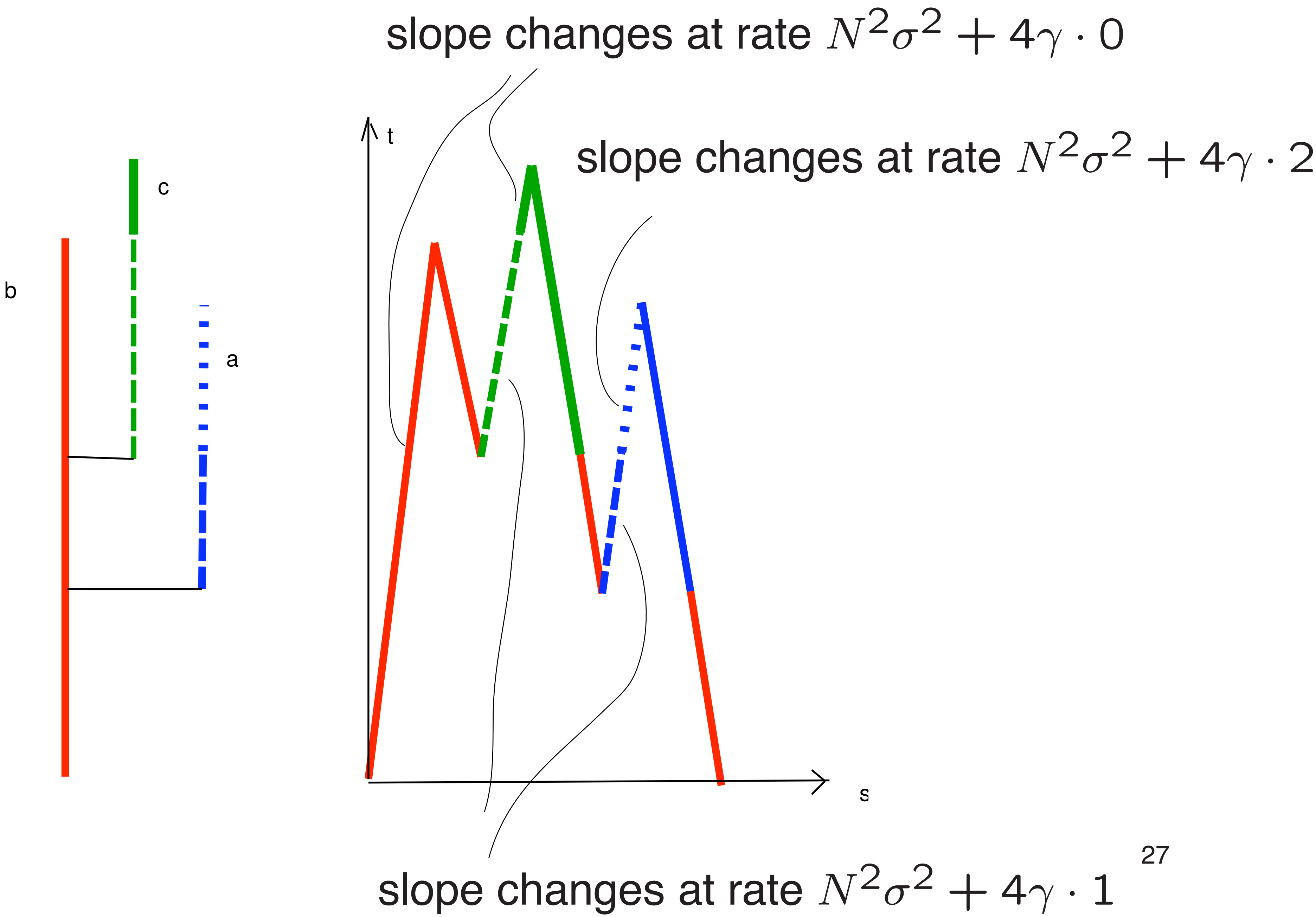
$N\, L_s(H^N, H_s^N) \sim$ # of individuals to the left of $(s, H^N(s))$

The dynamics of the exploration process in the N-th rescaling:

Multiplying the (real time) branch birth and death rates by $2N$ gives the slope change rates in the exploration time s:

Slope $-2N$ changes to $+2N$ at rate $N^2\sigma^2 + 2NK$
Slope $+2N$ changes to $-2N$ at rate $N^2\sigma^2 + 4\gamma N\ell$

where $h := H_s^N, \quad \ell := L_s^N := L_s(H^N, H_s^N)$.



slope changes at rate $N^2\sigma^2 + 4\gamma \cdot 0$
slope changes at rate $N^2\sigma^2 + 4\gamma \cdot 2$
slope changes at rate $N^2\sigma^2 + 4\gamma \cdot 1$
b
c
a
t
s

Theorem (with proof under construction)

As $N \to \infty$, the sequence of exploration processes of the rescaled forests of the “trees under attack” converge as $N \to \infty$ to the unique weak solution of

$$(*) \quad dH_s = \frac{2}{\sigma} dB_s + \frac{2}{\sigma^2}(K - 2\gamma L_s(H, H_s))\, ds$$

starting in $H_0 = 0$, reflected at $h = 0$ and stopped at $S_x := \inf\{s > 0 : L_s(H, 0) = x\}$.

Here, B is a standard Brownian motion and $L_s(H, h)$ is the local time of H at height h up to time s.

Elements of the proof:

Tightness issues

plus

identification of the limiting dynamics of H^N as $N \to \infty$

How to compensate $f(H_s^N)$ in order to get a martingale?

Perturbed test function method:

Consider the pair (H_s^N, V_s^N) with $\frac{dH_s^N}{ds} = 2NV_s^N$, $V_s^N = \pm 1$.

Instead of $f(H_s^N)$ compensate $f^N(H_s^N, V_s^N)$, where

$$f_N(h,v) = f(h) + \frac{v}{N\sigma_h^2} f'(h)$$

(In reminiscence of Anita Winter's talk
we allow here σ to depend on h.)

Expected rate of change of $f^N(H_s^N, V_s^N)$,

given $(H_s^N, V_s^N, L_s^N) = (h, v, l)$:

$$2Nvf'(h) + 2Nv\frac{v}{N}\left(\frac{f'}{\sigma^2}\right)'(h)$$

$$+(\mathbf{1}_{\{v=-1\}}(2N^2\sigma_h^2 + 4KN)$$

$$+\mathbf{1}_{\{v=+1\}}(-2N^2\sigma_h^2 - 8\gamma N\ell))\frac{1}{N\sigma_h^2}f'(h)$$

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$$2 N v \frac{v}{N} \left(\frac{f'}{\sigma^2} \right)' (h)$$

$$+ (\mathbf{1}_{\{v=-1\}} \qquad 4KN$$

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$$2\left(\frac{f'}{\sigma^2}\right)'(h)$$

$$+\left(\mathbf{1}_{\{v=-1\}}4K - \mathbf{1}_{\{v=+1\}}8\gamma\ell\right)\frac{1}{\sigma_h^2}f'(h)$$

In the limit $N \to \infty$, V_s^N is uniform on $\{-1, +1\}$,

leading to

$2\left(\frac{f'}{\sigma^2}\right)' + \frac{2}{\sigma^2}(K - 2\gamma\ell)f'$

Corollary (Ray-Knight representation of Feller's branching with logistic growth)

Let H be the solution of

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