A branching particle system as a model of FKPP fronts

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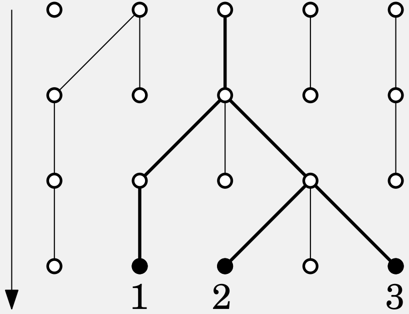
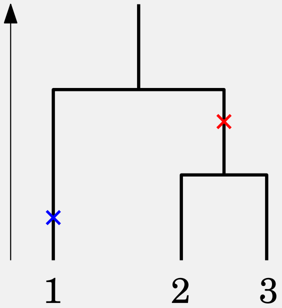
POPULATION GENETICS

GOAL: Unravel the complex genetic patterns that surround us

The genealogical approach



Population model



Genealogical structure

Sequence 1	A	T	C	C	T	T	T
Sequence 2	A	C	C	C	T	A	T
Sequence 3	A	C	C	C	T	A	T

DNA sequence alignment

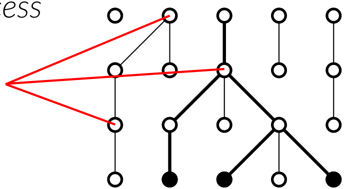
MOLECULAR CLOCK ASSUMPTION: **Genealogical structure $\Longleftrightarrow$ Genetic structure**

POPULATION GENETICS

Genetics in exchangeable (or neutral, unstructured) populations

equal chance of reproductive success

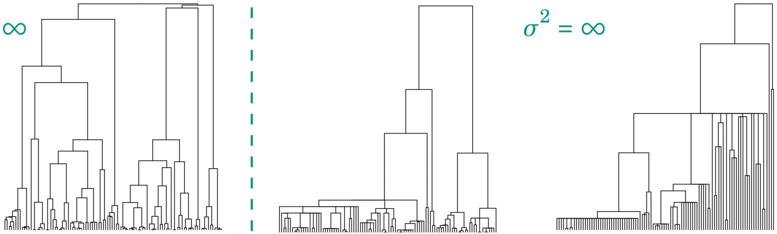
individuals are **exchangeable**



Universality class of genealogies: exchangeable coalescents

Λ-coalescents (non-simultaneous mergers)

$\sigma^2 < \infty$ $\quad$ $\sigma^2 = \infty$



Kingman $\quad$ Beta $\quad$ Bolthausen-Sznitman

skewed offspring distribution

Rich mathematical structure

- × Characterisation (Pitman, Sagitov '99)
- × Statistics (e.g. SFS)
- × Data (e.g. Steinruecken *et al.* '13)

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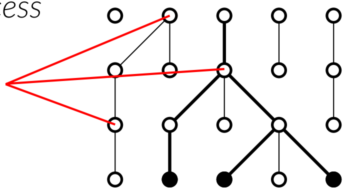


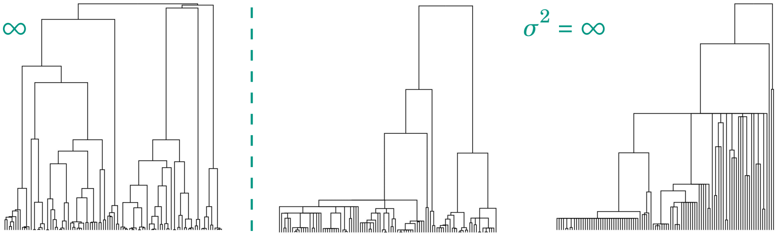
- × no selection
- × no spatial structure
- × no demography

⚠ **Key evolutionary forces**

Universality class of genealogies: exchangeable coalescents

Λ-coalescents (non-simultaneous mergers)

$\sigma^2 < \infty$ $\sigma^2 = \infty$



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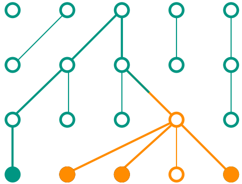
POPULATION GENETICS

Genetics in exchangeable (or neutral, unstructured) populations

equal chance of reproductive success

$\neq$ **structured populations**

each type has a different ability to reproduce: **structured coal. ?**



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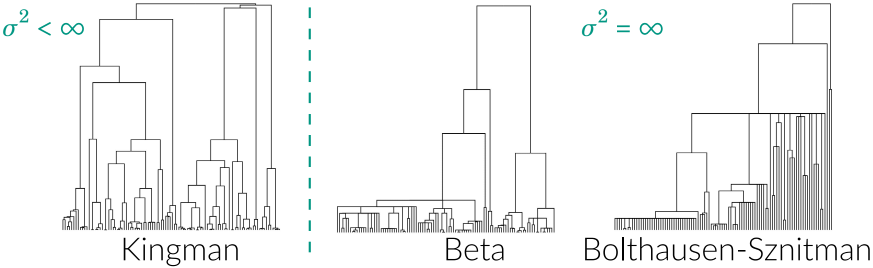

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POPULATION GENETICS

Genetics in exchangeable (or neutral, unstructured) populations

Universality beyond exchangeable models ?

Kingman (WF)
Effective population size
Charlesworth '09

Λ-coalescents
- expanding populations
- natural selection

Schweinsberg '17
Etheridge Pennington '22

Universality class of genealogies: exchangeable coalescents

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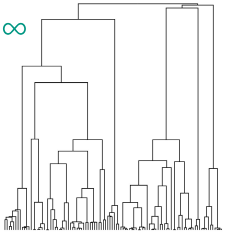
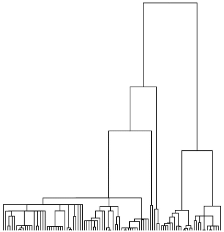
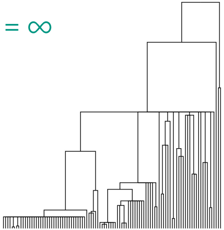


Kingman



Beta

$\sigma^2 = \infty$



Bolthausen-Sznitman

skewed offspring distribution

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F-KPP fronts with cooperation/Allee effects

Macroscopic dynamic

$$\partial_t u = \frac{1}{2}\partial_{xx} u + \frac{1}{2} u \overbrace{(1-u)}^{\text{local regulation}} \underbrace{(1+Bu)}_{\text{cooperation}}$$

$B > 0$ strength of cooperation

$u(t,x)$ = density of individuals at x at time $t > 0$

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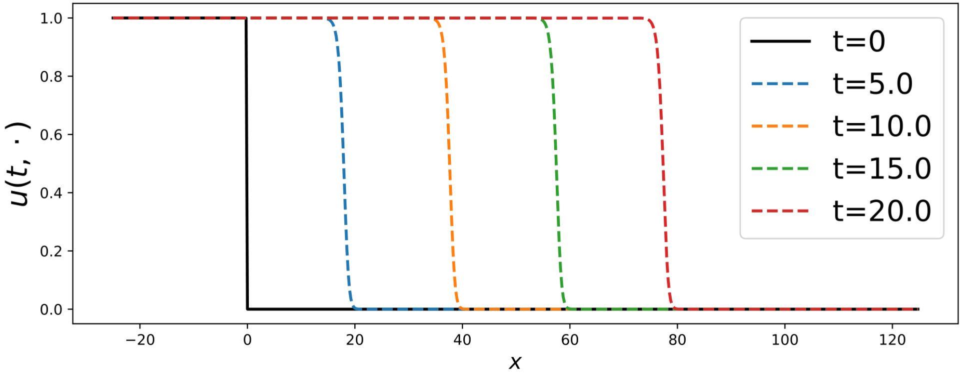
Travelling wave solutions

constant profile ϕ travelling

at constant speed $v \equiv v(B)$

$$u(t,x) = \phi(x - vt)$$



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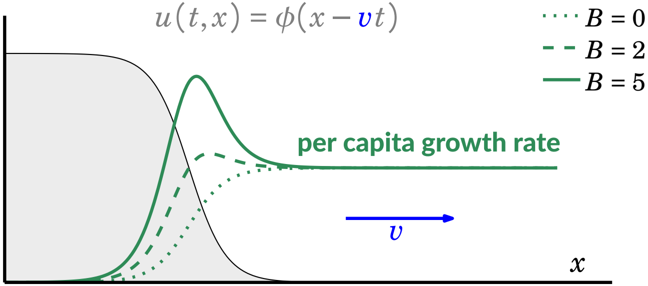
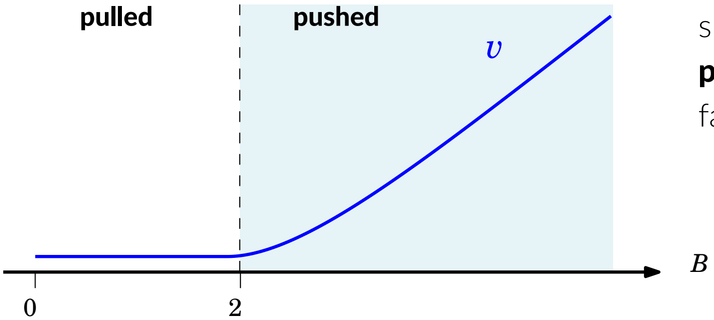


Two types of waves Stokes ’76



pulled

speed of the linearised equation $(u \approx 0)$

pushed

faster than the linearised equation

$$v(B) = \begin{cases} 1 & B \in [0,2] \\ \frac{1}{2}\sqrt{\frac{B}{2}}\left(1 + \frac{2}{B}\right) & B \geq 2 \end{cases}$$

F-KPP fronts with cooperation/Allee effects

Macroscopic dynamic

$$\partial_t u = \frac{1}{2}\partial_{xx} u + \frac{1}{2} u \overbrace{(1-u)}^{\text{local regulation}} \underbrace{(1+Bu)}_{\text{cooperation}} + \sqrt{\frac{u(1-u)}{N}}\, W$$

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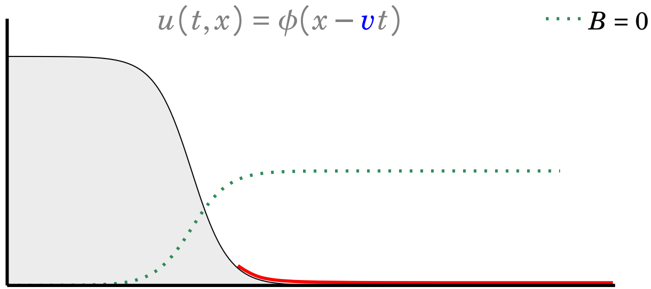

The case $B = 0$ (pulled waves)

physical (1) and **evolutionary** properties (2) are prescribed by the dynamics at the very tip of the front. They are '**pulled** by the individuals at the tip'.

simulations, conjectures and heuristics Brunet *et al.* '97, '06, '06, '07, '08

(1) Fluctuations of the invasion front

$$v - v_N \sim \frac{c}{\log(N)^2}$$

Mueller, Mytnik, Quastel '10

Bérard, Gouéré '12 Maillard '16

(2) Genealogy = Bolthausen-Sznitman

proved for a linear toy model (no interaction)

Berestycki, Berestycki, Schweinsberg, '13

F-KPP fronts with cooperation/Allee effects

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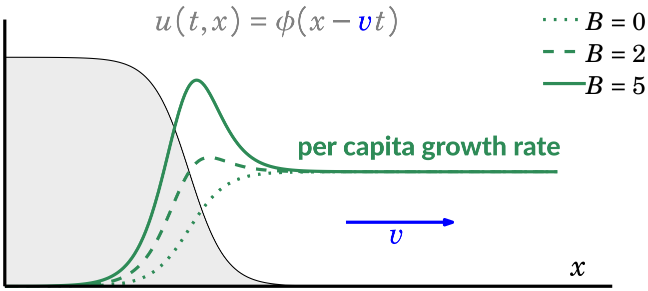


Recent breakthrough: conjectures by Birzu, Hallatschek, Korolev '18

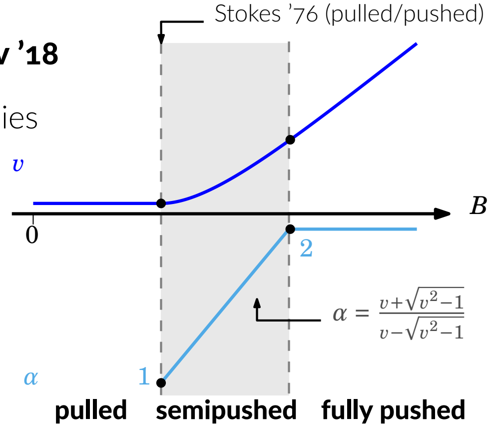
simulations: Wright-Fisher model with 2 neutral types and vacancies

N = local density of individuals → **genetic drift ?**

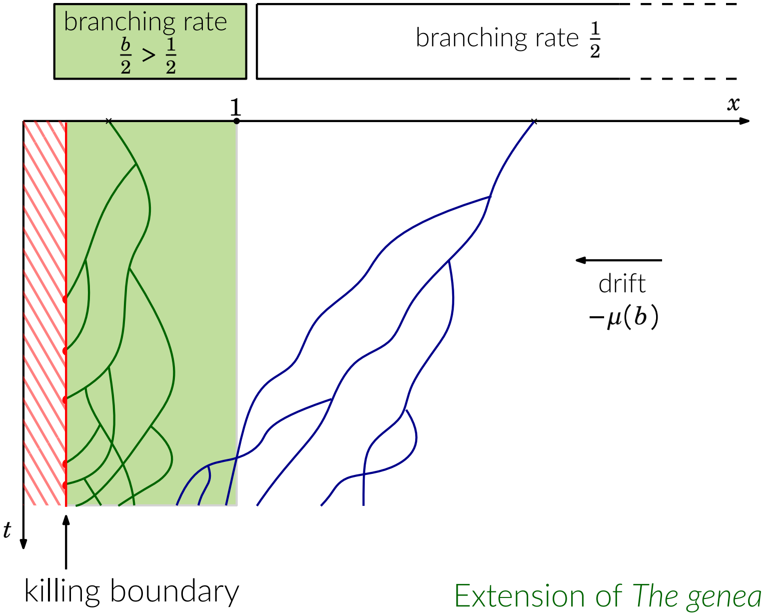
Heterozigocity

= proba. to sample $\mathbf{2}$ types at the tip

$$p_H(t) = e^{-\Lambda t}, \quad \Lambda = \begin{cases} \ln^{-3} N & B \in [0,2) \\ N^{1-\alpha} & B \in (2,4] \\ N^{-1} & B \geq 4 \end{cases}$$



A toy model to investigate the phase diagram



Dyadic branching Brownian motion with branching rate

$$r(x) = \frac{1}{2}[(b-1)\mathbf{1}_{x<1} + 1]$$

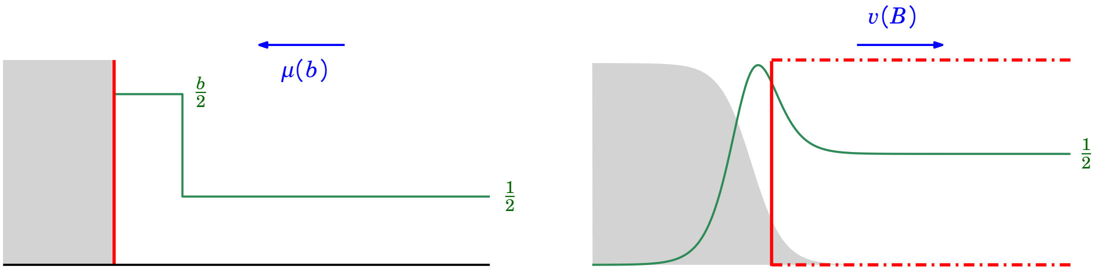
killing at $\mathbf{0}$

"critical" drift $-\mu(b)$

A model for travelling fronts ?

Extension of *The genealogy of branching Brownian motion with absorption*, Berestycki, Berestycki, Schweinsberg 2013 $(b = 1, \mu = 1)$

A toy model to investigate the phase diagram



Branching Brownian motion $\approx$ FKPP Travelling front

linearisation + approximation

Critical drift

Spectral decomposition of the critical operator $\mathcal{A}u = \frac{1}{2}u'' - \mu u' + r(x)u$ (λ_1, v_1) principal eigenv.

Many-to-one lemma $p_t(x,y) \approx c e^{\lambda_1 t} e^{(\frac{\mu^2}{2}-\frac{1}{2})t} e^{\mu x} v_1(x) e^{-\mu y} v_1(y) \Longrightarrow \mu = \sqrt{1+2\lambda_1}$

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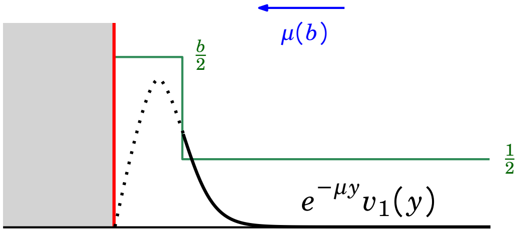
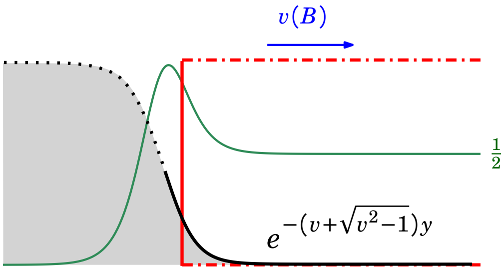


Branching Brownian motion

$\approx$



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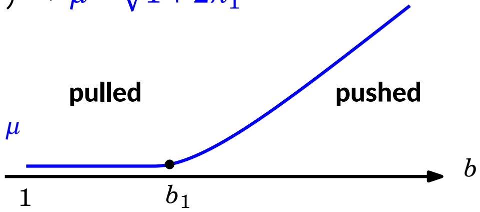
pulled/pushed regime: $\exists b_1 > 1$ such that

- if $b \in [1, b_1]$, $\lambda_1 = 0 \Longrightarrow \mu = 1$,
- if $b > b_1$, $\lambda_1 > 0$ and $\lambda_1 \nearrow b \Longrightarrow \mu > 1$, $\mu \nearrow b$

$\rightsquigarrow$ in this case $v_1(x) \propto e^{-\sqrt{\mu^2-1}x}$, $x \geq 1$



A toy model to investigate the phase diagram

$$p_t(x,y) \approx \cancel{c e^{\lambda_1 t} e^{(\mu^2-1)t}} e^{\mu(x-y)} v_1(x) v_1(y) =: h(x)\tilde{h}(y)$$

reproductive value at x

stable configuration

$\mu > 1$ (**pushed**) $\Rightarrow \Pi(x) \propto e^{-2\sqrt{\mu^2-1}x}$, $x \geq 1$

Spine = immortal particle $\Leftrightarrow$ h-transform

$\rightsquigarrow$ the **spine** is in the **bulk**

$$\mathcal{G}u = \frac{1}{2}\partial_{xx}u - \frac{v_1'(x)}{v_1(x)}\partial_x u$$

stationary measure $\Pi(x) = v_1(x)^2 = h(x)\tilde{h}(y)$

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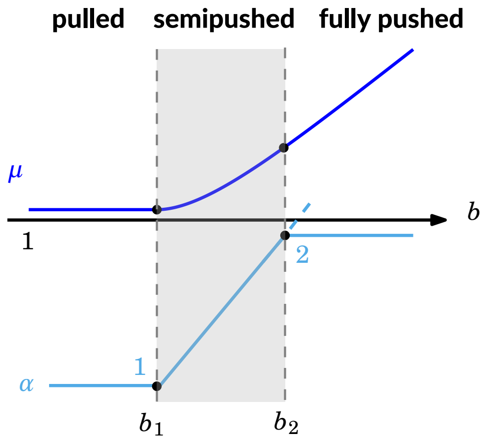
stationary measure $\Pi(x) = v_1(x)^2 = h(x)\tilde{h}(y)$

Let $\alpha := \frac{\mu+\sqrt{\mu^2-1}}{\mu-\sqrt{\mu^2-1}}$

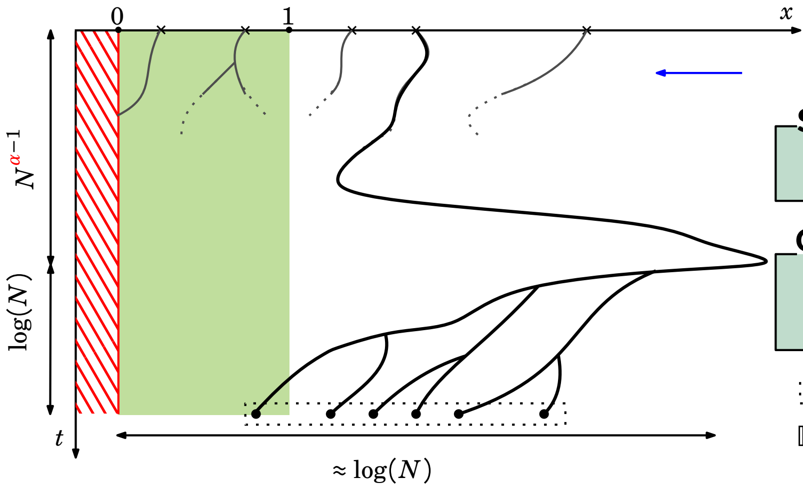
pulled/semipushed/fully pushed regime: $\exists b_2 > b_1$ **such that**

- for $b \in [1, b_1]$, $\mu = 1 \to \alpha = 1$,
- for $b > b_1$, $\alpha \nearrow b$, $\alpha(b_1) = 1$ and $\alpha(b_2) = 2$.



The semipushed regime $b \in (b_1, b_2)$

Start with N particles distributed according to $e^{-\mu y} v_1(y) dy$



Z_t = number of individuals

$N \to \infty$

SCALING LIMIT

$\left(\frac{1}{N} Z_{tN^{\alpha-1}}\right) \Rightarrow (\Xi_t)$ $\quad \Xi$ is an α-stable CSBP

GENEALOGY

The genealogy of the BBM converges to a Beta$(2-\alpha, \alpha)$-coalescent

• • • $\approx N$ descendants

$\mathbb{P}(\# \bullet > xN) \sim \frac{c}{x^\alpha}$

A branching particle system as a model of semi pushed fronts. T. 2024.

Convergence of spatial branching processes to alpha-stable CSBPs: Genealogy of semi-pushed fronts. Foutel-Rodier, Schertzer and T. 2025+.

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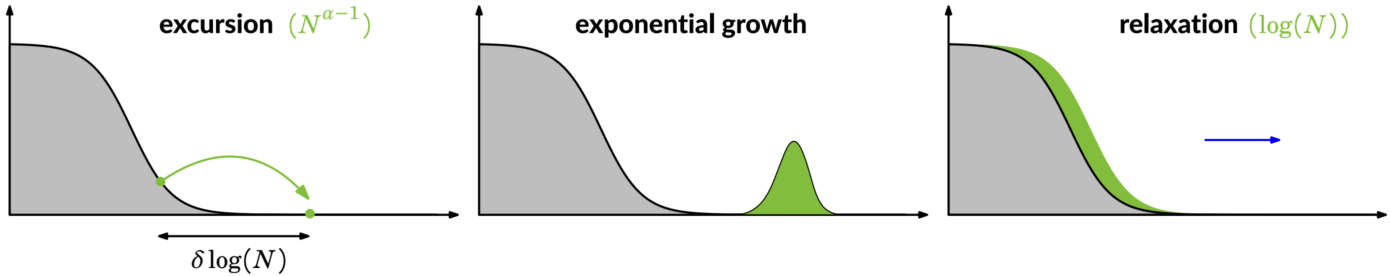
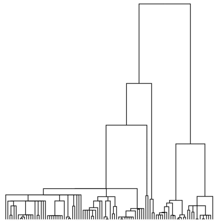
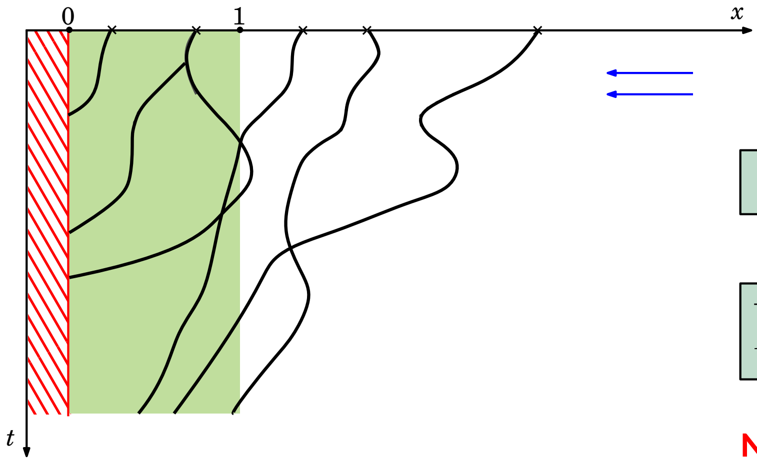


- The invasion is driven by **excursions** of particles
- These excursions generate **large subfamilies** in the associated genealogy, **diversity loss**
- Particles at the tip have a large reproductive value $\Rightarrow$ **large reproductive variance** (in some sense)
- fast relaxation $\Rightarrow$ collapse of structure



The fully pushed regime $b > b_2$

Start with N particles distributed according to $e^{-\mu y} v_1(y) dy$



Z_t = number of individuals

$N \to \infty$

SCALING LIMIT

$\left(\frac{1}{N} Z_{tN}\right) \Rightarrow (X_t)$ X is a Feller diffusion

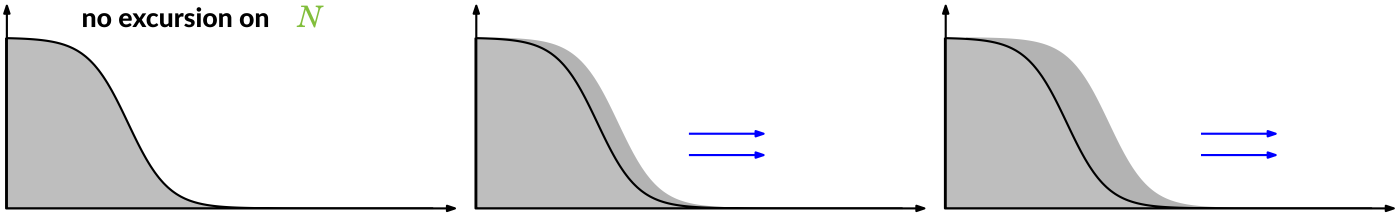
GENEALOGY

The genealogy of the BBM converges to the Kingman coalescent

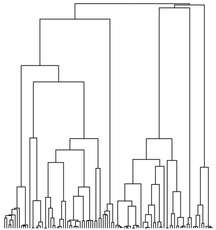
No excursion ! $\rightsquigarrow$ "CLT"/mean field

Spectral analysis and k-spine decomposition of inhomogeneous branching Brownian motions. Genealogies in fully pushed fronts. Schertzer and T. 2024.

The fully pushed regime $b > b_2$



- The invasion is pushed by the **growth** in the front
- This generates only **binary mergers** in the associated genealogy, **wide genetic diversity**
- The tip is not accessible $\Rightarrow$ **finite reproductive variance**



The method of moments Foutel-Rodier, Schertzer '22

The case $k = 1$: many-to-one

$\mathcal{N}_t$ = set of particles alive at t

X_v = position of v

$$\mathbb{E}_x\left[\sum_{v\in\mathcal{N}_t} f(X_v)\right] = \int_0^\infty f(x,y)p_t(x,y)$$

with $p_t(x,y) \approx e^{\mu x}v_1(x)e^{-\mu y}v_1(y) =: h(x)\tilde{h}(y)$

$$\approx h(x)\int_0^\infty f(x,y)\tilde{h}(y)dy$$

reproductive value

stable configuration

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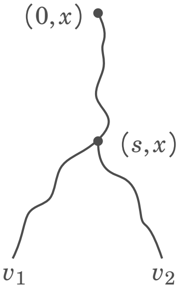
$$\approx \underbrace{h(x)}_{\text{reproductive value}} \int_0^\infty f(x,y) \underbrace{\tilde{h}(y)}_{\text{stable configuration}} dy$$

The case $k = 2$

$$\mathbb{E}_x\left[\sum_{v_1 \neq v_2 \in \mathcal{N}_t} f(X_{v_1}) g(X_{v_2})\right] = \int_0^\infty \int_0^t 2r(y) p_s(x,y) \left(\int_0^\infty f(z) p_{t-s}(y,z) dz\right)\left(\int_0^\infty g(z) p_{t-s}(y,z) dz\right) ds dy$$



$$\approx 2t h(x) \underbrace{\left(\int_0^\infty r(y) \tilde{h}(y)\, h(y)^2 dy\right)}_{=: \Sigma^2} \left(\int_0^\infty f(z) \tilde{h}(z) dz\right)\left(\int_0^\infty g(z) \tilde{h}(z) dz\right)$$

The method of moments

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with $p_t(x,y) \approx e^{\mu x} v_1(x) e^{-\mu y} v_1(y) =: h(x)\tilde{h}(y)$

$$\approx h(x) \int_0^\infty f(x,y)\tilde{h}(y) dy$$

reproductive value — stable configuration

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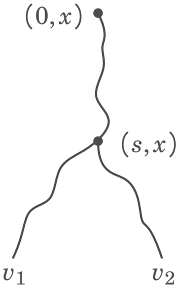
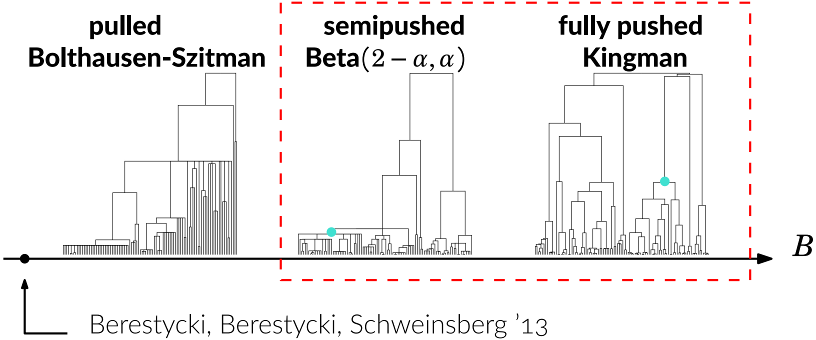


$\rightsquigarrow$ **position of the branching point**

$h(y)^2\tilde{h}(y) \propto e^{(\mu - 3\sqrt{\mu^2-1})y}$ and $\alpha \le 2 \iff \mu \ge 3\sqrt{\mu^2 - 1}$

$\alpha \le 2$	$\alpha > 2$
$\Sigma^2 = \infty$ **tip**	$\Sigma^2 < \infty$ **bulk**

F-KPP fronts with cooperation/Allee effects



lineages	at the tip	in the bulk	in the bulk
	at the tip	at the tip	in the bulk

Definition of a **toy model** for **pushed** fronts falling in the universality class of FKPP equation

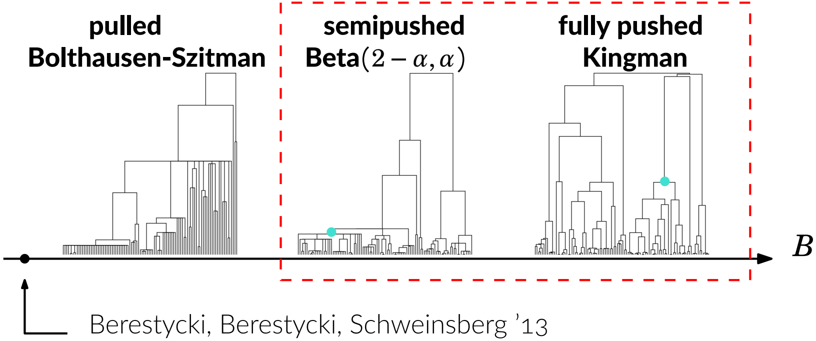
(1) phase diagram

in accordance with Birzu *et al.* '20

(2) internal mechanisms

speed of invasion ↭ **genetic composition**

F-KPP fronts with cooperation/Allee effects



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(2) **analytical criteria** for the emergence of exchangeable genealogies in structured models

spectral theory: fast mixing, reproductive variance

Tools

(1) extension of the **method of moments** to genealogies of branching diffusions

spinal decomposition

$\rightsquigarrow$ location of the ancestral lineages