

A particle system as a model of FKPP fronts

Julie Tourniaire

MOTIVATION

Population Genetics

- (?) Understand the complex genetic diversity around us
- (?) Identify the main forces that shaped our genetic landscape
ex: natural selection, spatial structure, demography, etc.

Sequence 1	A	T	C	C	T	T	T
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Figure: DNA sequence alignment

Why ?

wide genetic diversity



ability to **adapt** to changing environmental conditions

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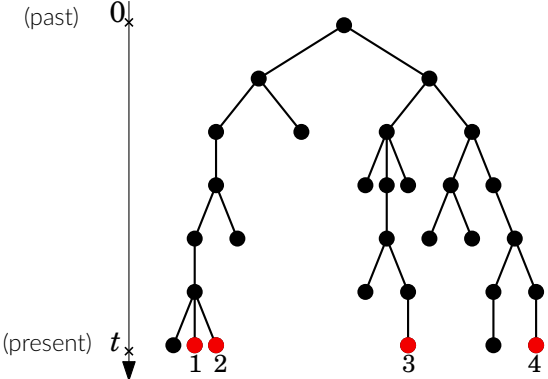
Genealogical approach

= reconstruct the typical genealogy of the population

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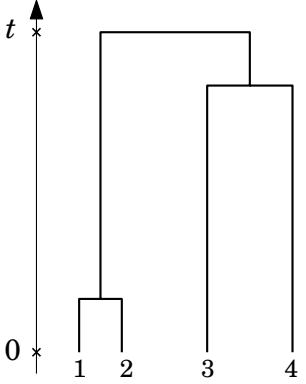
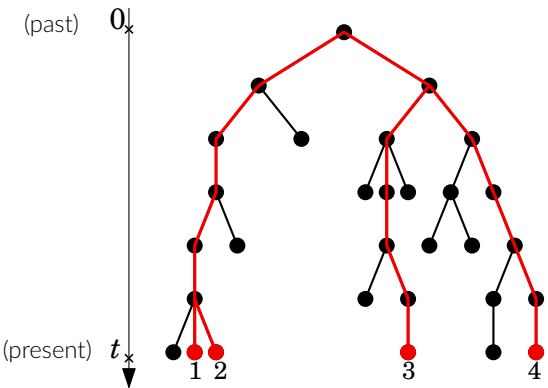
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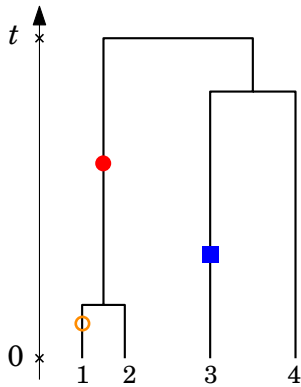
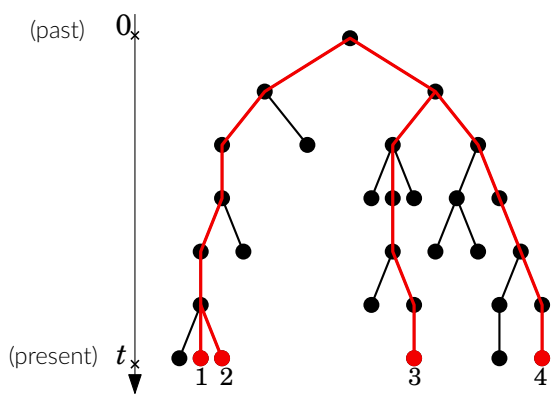
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How ?

Genealogical approach = reconstruct the typical genealogy of the population

Molecular clock: mutations appear at constant rate

GENEALOGICAL TREE \Leftrightarrow **GENETIC DIVERSITY**

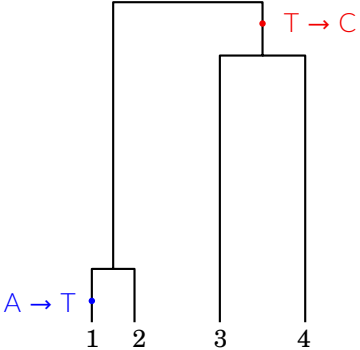


- Height of the tree
 \hookrightarrow number of mutations
 $\{ \bullet, \circ, \blacksquare \}$
- Shape of the tree
 \hookrightarrow mutational pattern

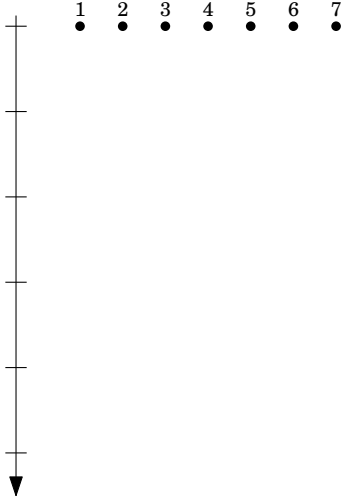
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MOTIVATION

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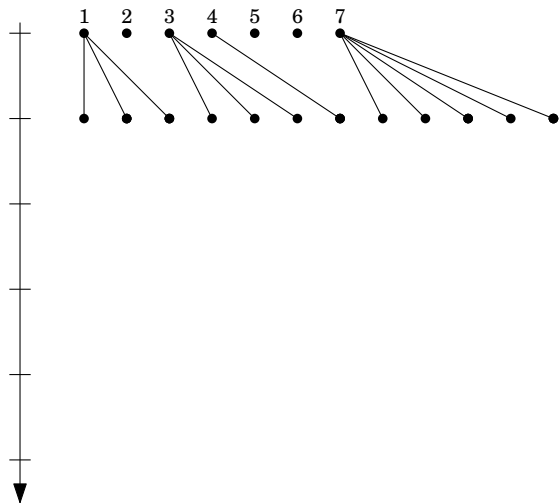
A MODEL IN POPULATION GENETICS (Schweinsberg 2003)



Discrete time (generations)

N (haploid) individuals

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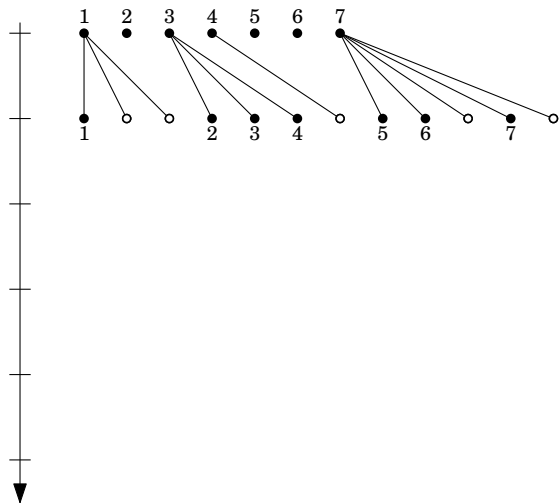
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X_i number of the children of the i -th individual

X_1, \dots, X_N are i.i.d. and $\mathbf{E}[X_1] > 1$

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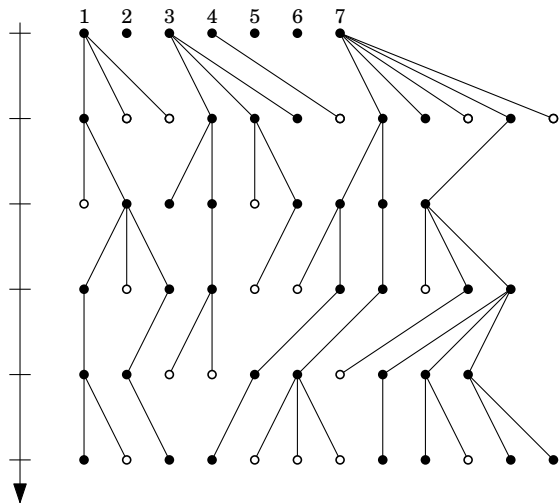
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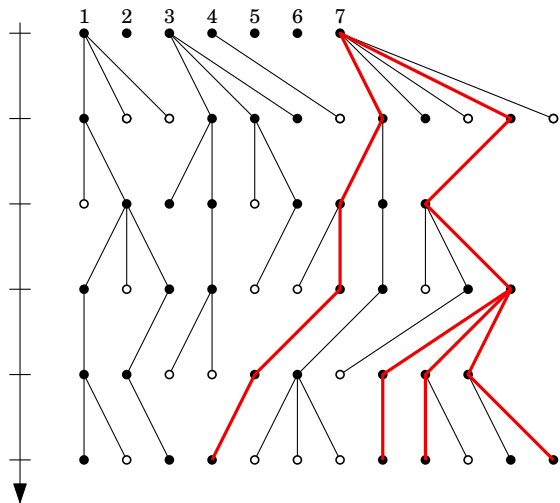
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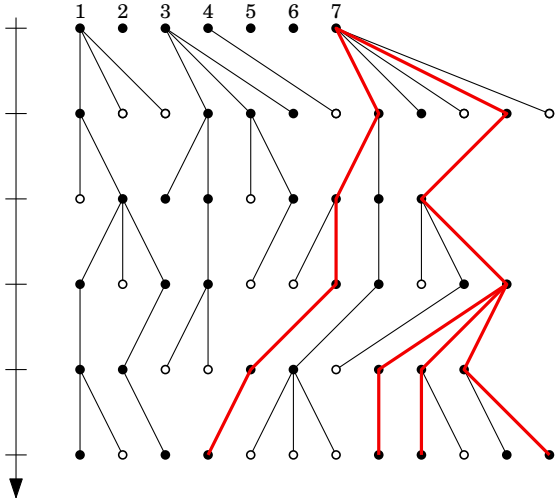
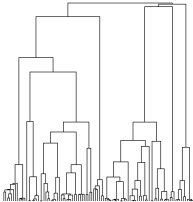
What can be said about the genealogy of this population ?

A MODEL IN POPULATION GENETICS (Schweinsberg 2003)

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Let N go to ∞

FINITE VARIANCE
if $\mathbf{E}[(X_1)^2] < \infty$,
the genealogy is given by
Kingman's coalescent
(a binary tree)



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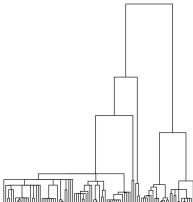
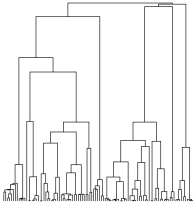
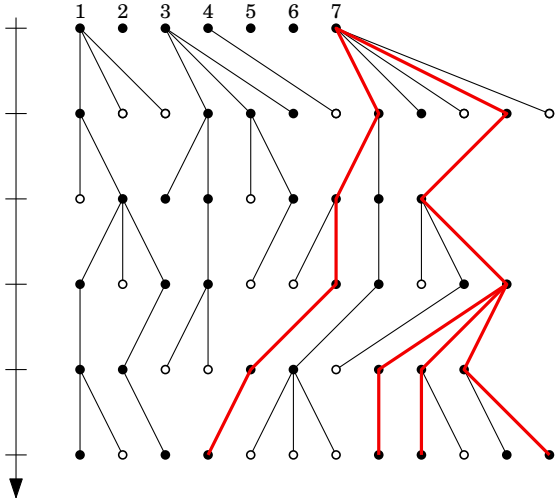
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HEAVY TAILS

if $\mathbf{P}(X_1 > x) \sim \frac{1}{x^\alpha}$,
 with $\alpha \in (1, 2)$,
 the genealogy is given by
 a **Beta(2 - α , α)-coalescent**



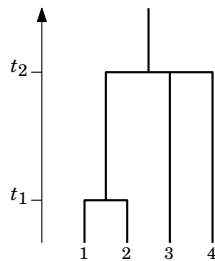
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A CLASS OF EXCHANGEABLE GENEALOGIES: BETA COALESCENTS

- coalescent process: continuous-time Markov process with values in the set of partitions of $\{1, \dots, n\}$

merging of blocks \Leftrightarrow merging of ancestral lines

- exchangeable coalescent: all the blocks play the same role



$$\Pi_{t_2} = \{\{1, 2, 3, 4\}\}$$

$$\Pi_{t_1} = \{\{1, 2\}, \{3\}, \{4\}\}$$

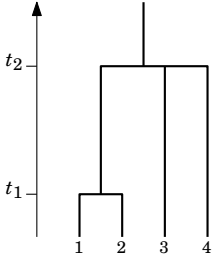
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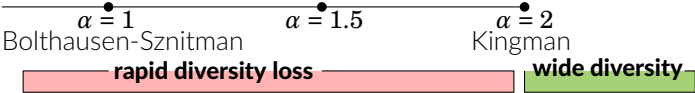
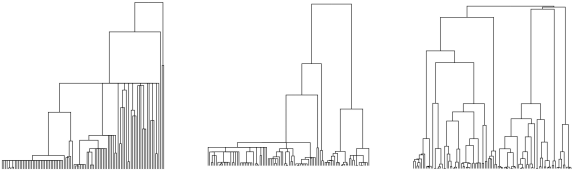
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rich mathematical structure (Pitman 99 and Sagitov 99)



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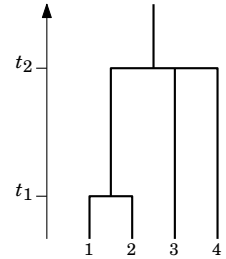
BETA-COALESCENTS

in a Beta($2 - \alpha, \alpha$)-coalescent, blocks merge at rates

$$\lambda_{b,k} = c_\alpha \int_0^1 x^{b-1-\alpha} (1-x)^{\alpha+k-b-1} dx$$


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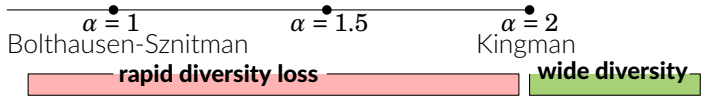
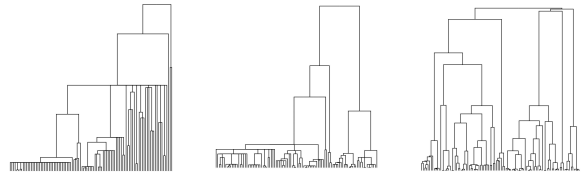
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LIMITATIONS

- *a priori* only suitable for neutral models
 - equal chances of reproductive success
 - **no selection, no structure**
- MAJOR FORCES IN EVOLUTION !**



A DETERMINISTIC MODEL FOR EXPANDING POPULATIONS: THE FKPP EQUATION

$$u_t = \frac{1}{2}u_{xx} + \frac{1}{2}u(1 - u)$$

$u(t, x)$ densité de population

□ saturation

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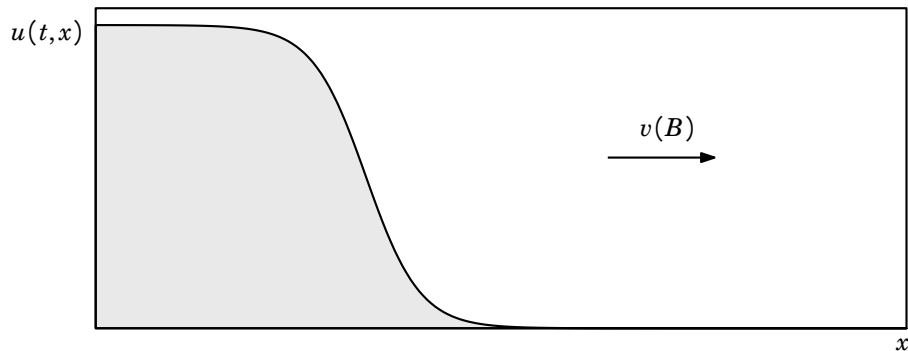
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Travelling front solutions:
constant profile travelling
at constant speed $v(B)$

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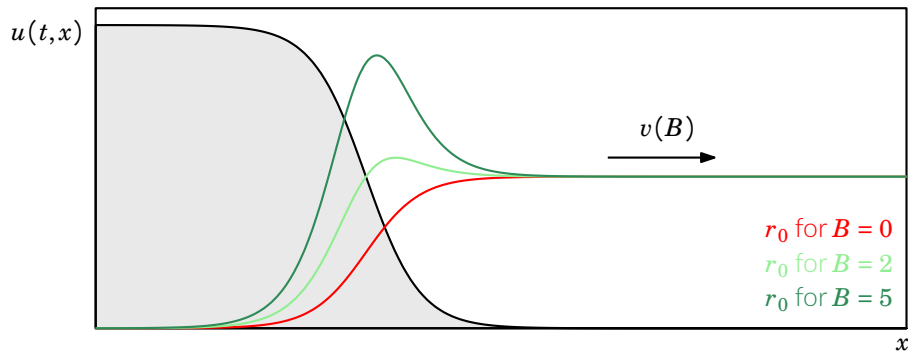
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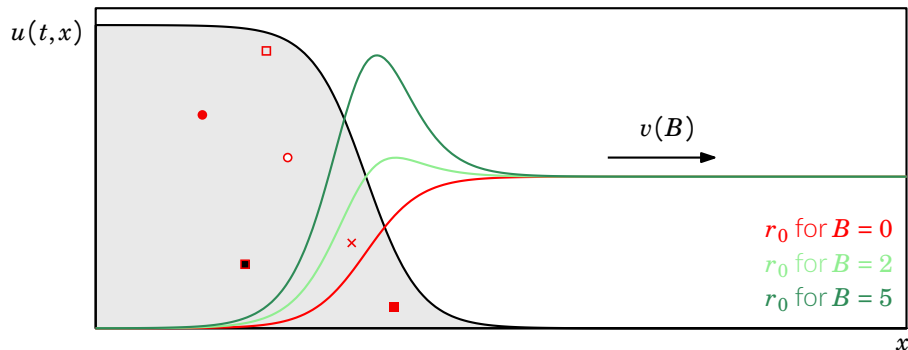
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Sample k individuals in the front

Genealogy ?

Position of the ancestors ?

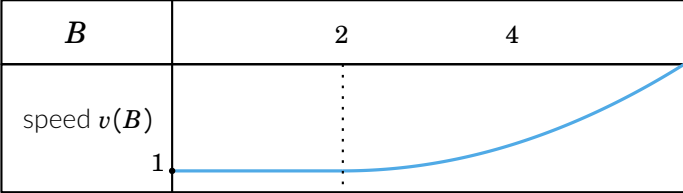
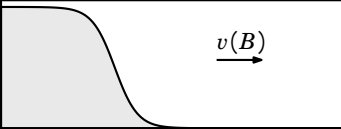
Phase transition ?

↔ **discrete model**

PULLED, SEMIPUSHED AND FULLY PUSHED FRONTS

FKPP Equation

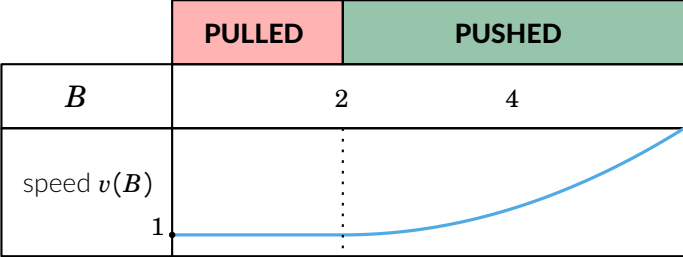
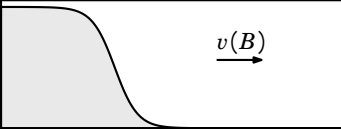
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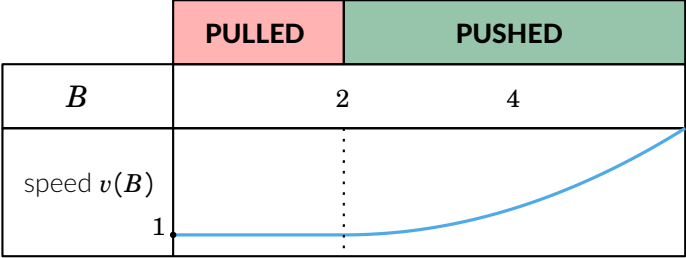
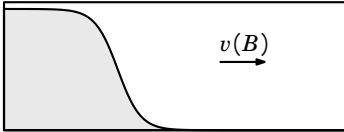
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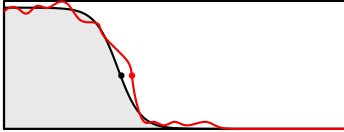
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Noisy FKPP Equation

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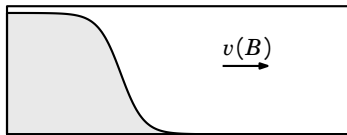
local density \nearrow
white noise \nearrow



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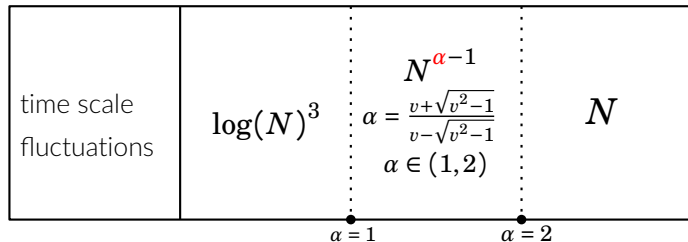
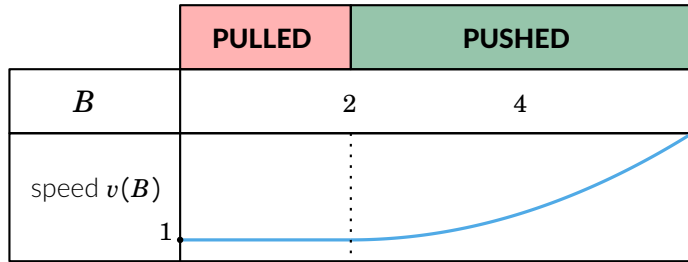
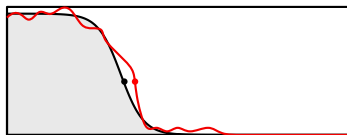
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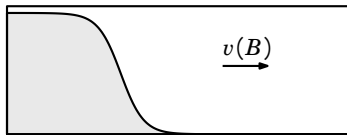


Heuristics and simulations: Birzu et al. '18
Fluctuations uncover a distinct class of traveling waves, PNAS

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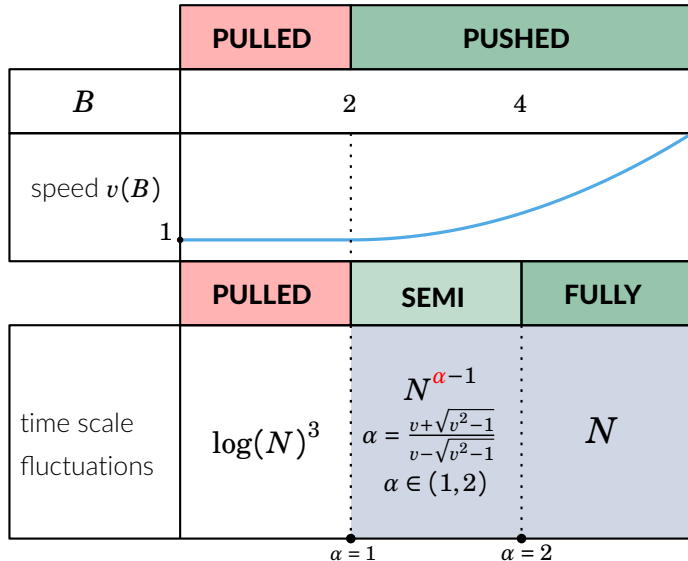
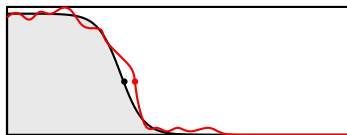
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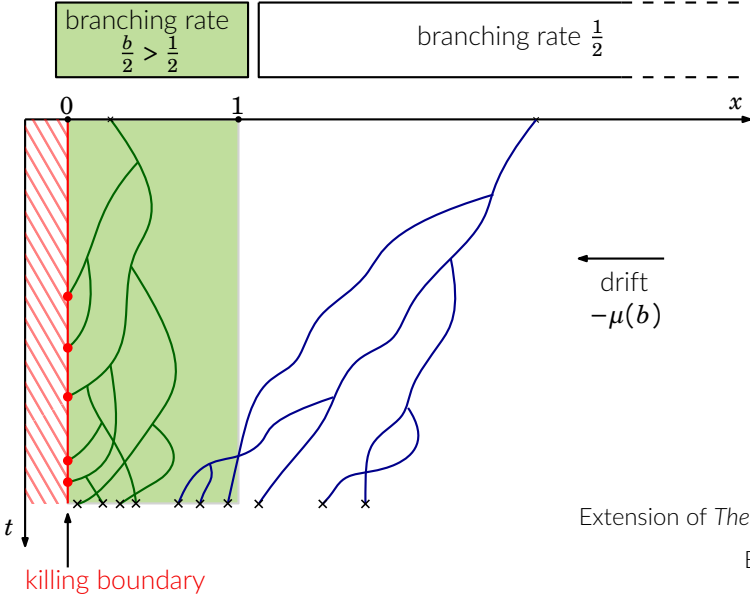
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A TOY MODEL TO INVESTIGATE THE PHASE DIAGRAM



Dyadic branching Brownian motion with branching rate

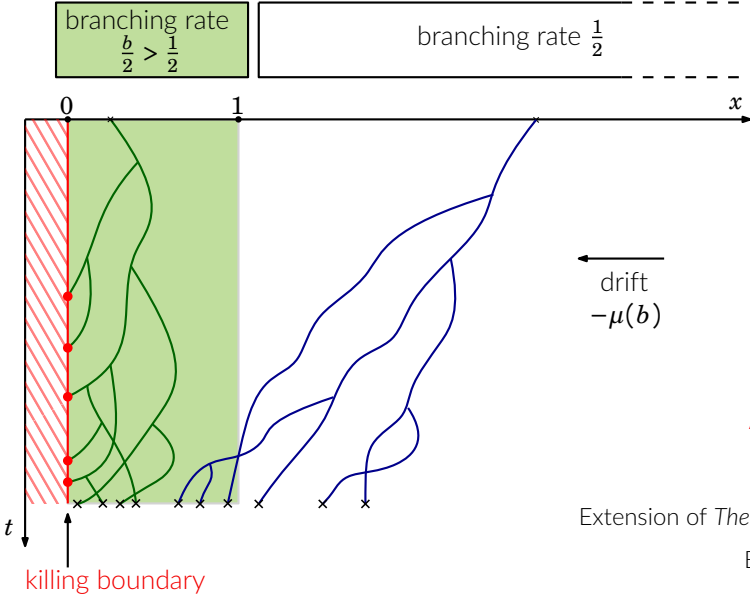
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killing at 0

“critical” drift $-\mu(b)$

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

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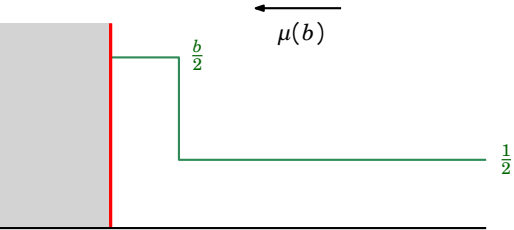
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A model for travelling fronts ?

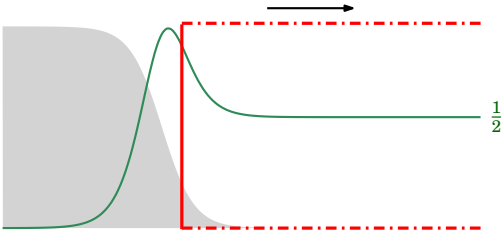
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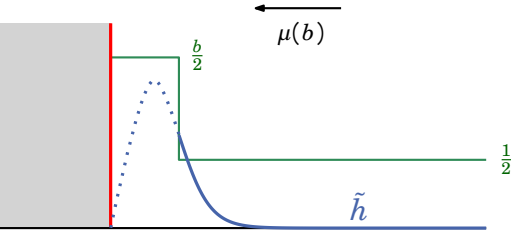
\approx



FKPP Travelling front

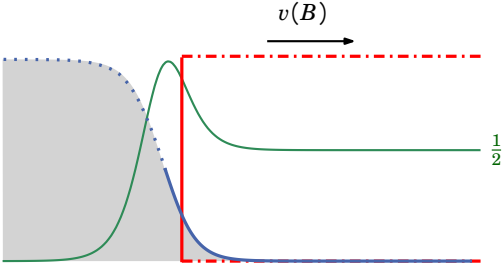
linearisation + approximation

A TOY MODEL TO INVESTIGATE THE PHASE DIAGRAM



Branching Brownian motion

≈



FKPP Travelling front

linearisation + approximation

Same macroscopic behaviours

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

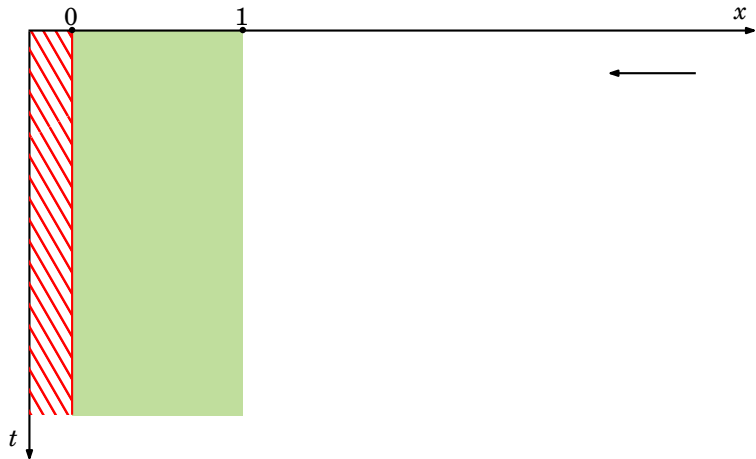
b	b_1
drift $\mu(B)$	
1	

critical = the number of particles is roughly constant

+

stable configuration: eigenvector \tilde{h} (Perron-Frobenius)

THE SEMIPUSHED REGIME



SEMIPUSHED REGIME

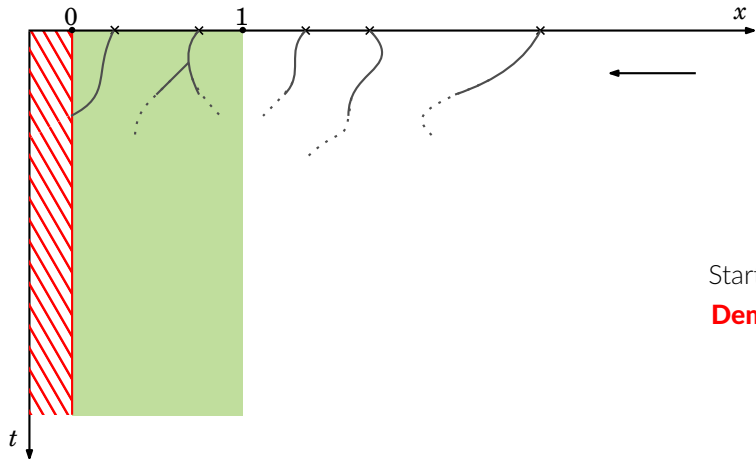
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$$\alpha(\mu) := \frac{\mu + \sqrt{\mu^2 - 1}}{\mu - \sqrt{\mu^2 - 1}} \in (1, 2)$$

for all $b \in (b_1, b_2)$.

↪ recall that $\alpha(v) = \frac{v + \sqrt{v^2 - 1}}{v - \sqrt{v^2 - 1}}$
time scale $N^{\alpha-1}$
 $\alpha(v) \in (1, 2)$

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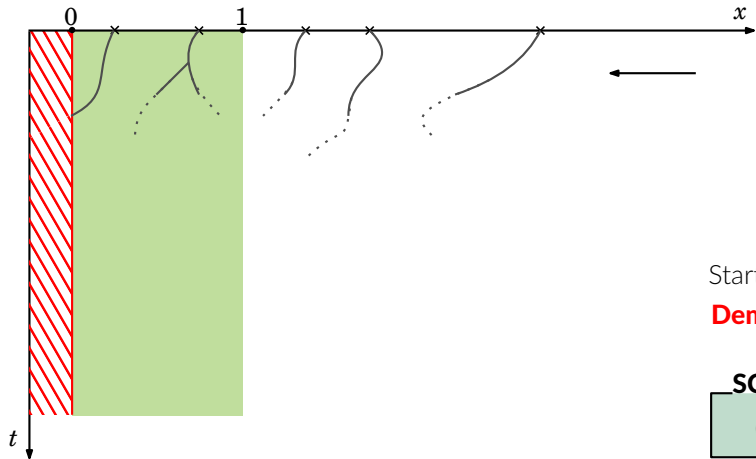
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Start with N particles distributed according to \tilde{h}

Demographic fluctuations ?

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SEMIPUSHED REGIME

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↪ recall that $\alpha(v) = \frac{v + \sqrt{v^2 - 1}}{v - \sqrt{v^2 - 1}}$
time scale $N^{\alpha-1}$
 $\alpha(v) \in (1, 2)$

Start with N particles distributed according to \tilde{h}

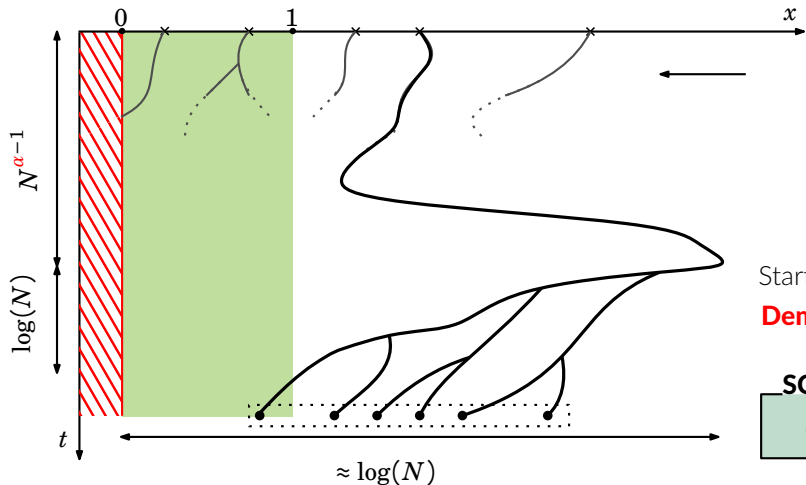
Demographic fluctuations ? Z_t = number of individuals

Let N goes to ∞

SCALING LIMIT

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

THE SEMIPUSHED REGIME



••• ≈ N descendants

SEMIPUSHED REGIME

There exists $b_2 > b_1$ such that

$$\alpha(\mu) := \frac{\mu + \sqrt{\mu^2 - 1}}{\mu - \sqrt{\mu^2 - 1}} \in (1, 2)$$

for all $b \in (b_1, b_2)$.

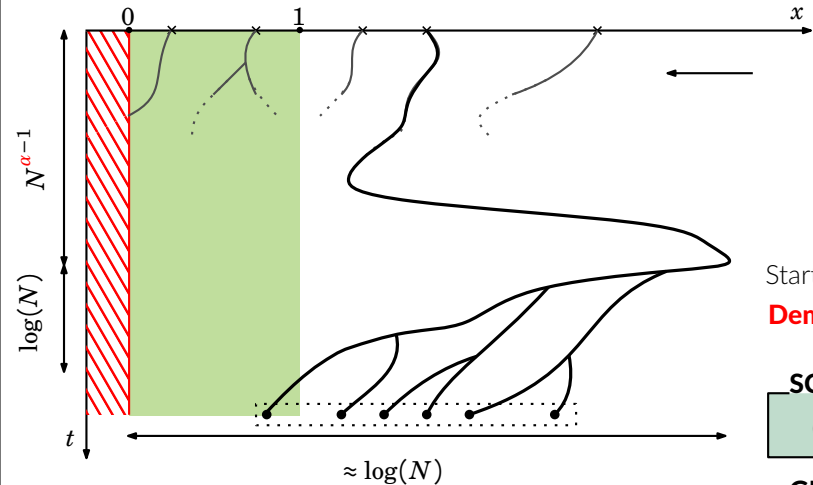
↪ recall that $\alpha(v) = \frac{v + \sqrt{v^2 - 1}}{v - \sqrt{v^2 - 1}}$
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Start with N particles distributed according to \tilde{h}
Demographic fluctuations? Z_t = number of individuals
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SCALING LIMIT

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

THE SEMIPUSHED REGIME



••••• $\approx N$ descendants

SEMIPUSHED REGIME

There exists $b_2 > b_1$ such that

$$\alpha(\mu) := \frac{\mu + \sqrt{\mu^2 - 1}}{\mu - \sqrt{\mu^2 - 1}} \in (1, 2)$$

for all $b \in (b_1, b_2)$.

\hookrightarrow recall that $\alpha(v) = \frac{v + \sqrt{v^2 - 1}}{v - \sqrt{v^2 - 1}}$
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Start with N particles distributed according to \tilde{h}

Demographic fluctuations? Z_t = number of individuals

Let N goes to ∞

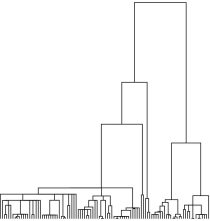
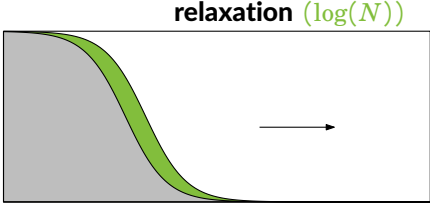
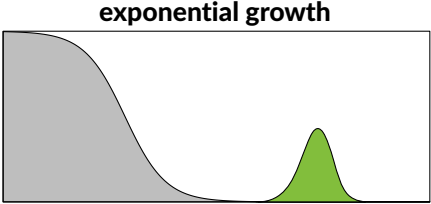
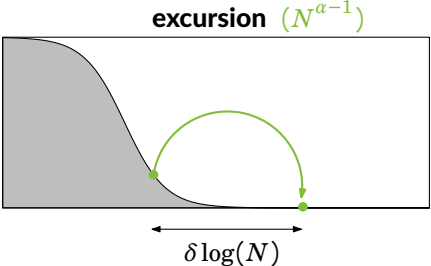
SCALING LIMIT

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

GENEALOGY

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

THE SEMIPUSHED REGIME $b \in (b_1, b_2)$



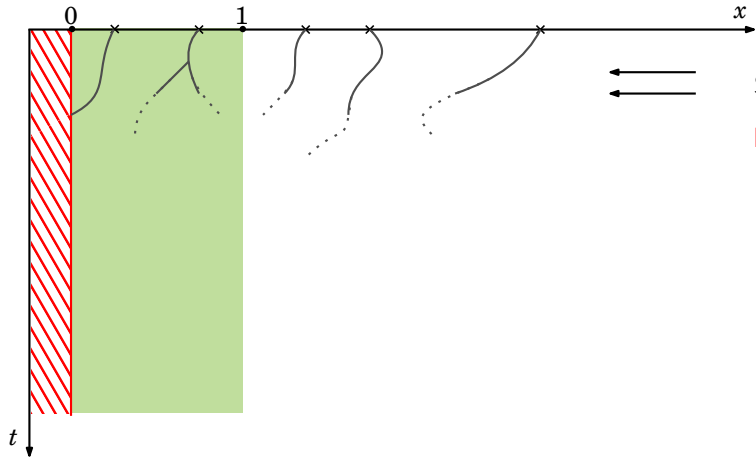
- The invasion is driven by **excursions** of particles
- These excursions generate **large subfamilies** in the associated genealogy, **diversity loss**
- Particles at the tip have a large reproductive value \Rightarrow **large reproductive variance**
- fast relaxation \Rightarrow collapse of structure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

A branching particle system as a model of semipushed fronts, T. (2024)

Convergence of spatial branching processes to α -stable CSBPs: Genealogy of semi-pushed fronts

Foutel-Rodier, Schertzer, T. (2024+)

THE FULLY PUSHED REGIME



FULLY PUSHED REGIME

For $b > b_2, \alpha > 2$

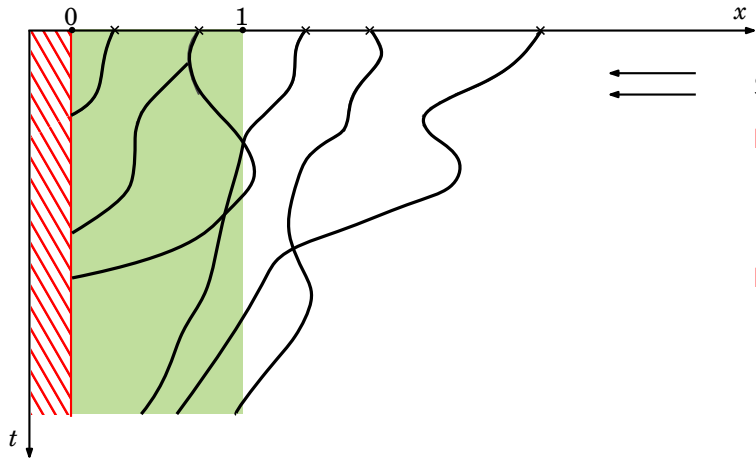
Start with N particles distributed according to \tilde{h}

Demographic fluctuations ?

Z_t = number of individuals

Let N goes to ∞

THE FULLY PUSHED REGIME



FULLY PUSHED REGIME

For $b > b_2, \alpha > 2$

Start with N particles distributed according to \tilde{h}

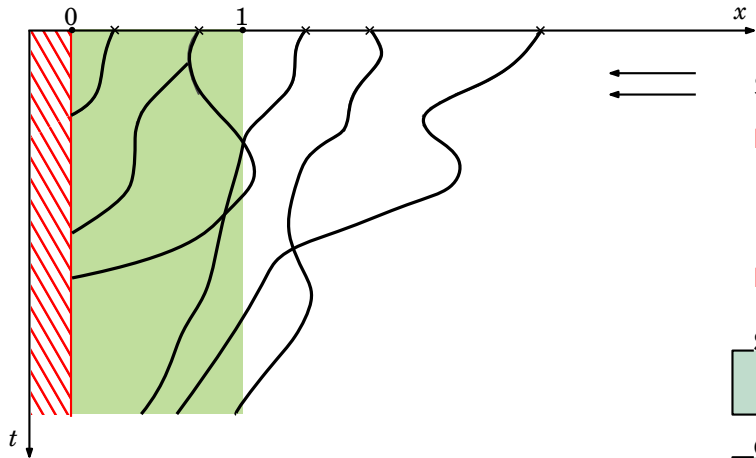
Demographic fluctuations ?

Z_t = number of individuals

Let N goes to ∞

No excursion !

THE FULLY PUSHED REGIME



FULLY PUSHED REGIME

For $b > b_2, \alpha > 2$

Start with N particles distributed according to \tilde{h}

Demographic fluctuations ?

Z_t = number of individuals

Let N goes to ∞

No excursion ! \leadsto "CLT"/mean field

SCALING LIMIT

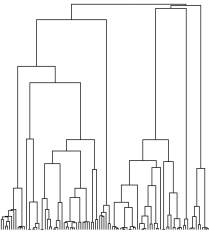
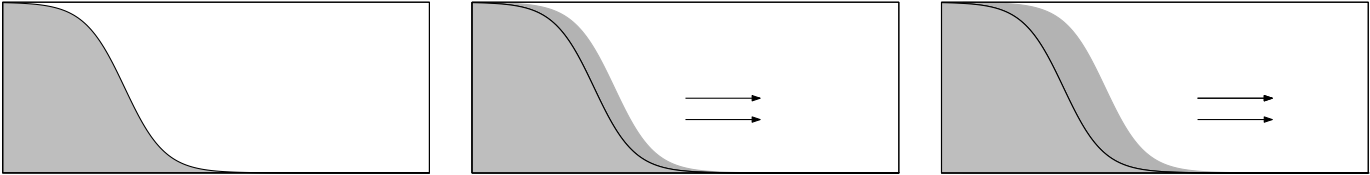
$(\frac{1}{N}Z_{tN}) \Rightarrow (X_t)$ X is a Feller diffusion

GENEALOGY

The genealogy of the BBM converges to Kingman's coalescent

THE FULLY PUSHED REGIME $b > b_2$

N



- 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**

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

CONCLUSION

		PULLED	SEMI	FULLY
FKPP	B	2		4
	speed $v(B)$			
	time scale fluctuations	$\log(N)^3$	$N^{\alpha-1}$	N
PARTICLE SYSTEM	b	b_1		b_2
	drift $\mu(b)$			
	time scale fluctuations	$\log(N)^3$ (?)	$N^{\alpha-1}$	N
	genealogy	(?)		

Besançon meeting on
**PROBABILITY
ECOLOGY
& EVOLUTION**

December 10th, 2024 @MSHE Besançon



Vincent BANSAYE
École Polytechnique

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University of Vienna

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