

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.

Why ?

wide genetic diversity



ability to **adapt** to changing environmental conditions

Sequence 1	A	T	C	C	T	T	T
Sequence 2	A	T	C	C	T	A	T
Sequence 3	A	C	C	C	T	A	T
Sequence 4	A	C	C	C	T	A	T

Figure: DNA sequence alignment

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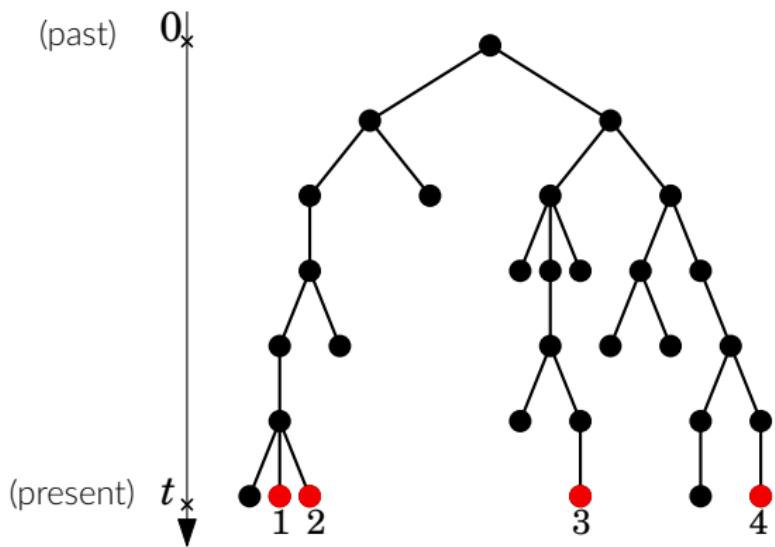
Genealogical approach

= reconstruct the typical genealogy of the population

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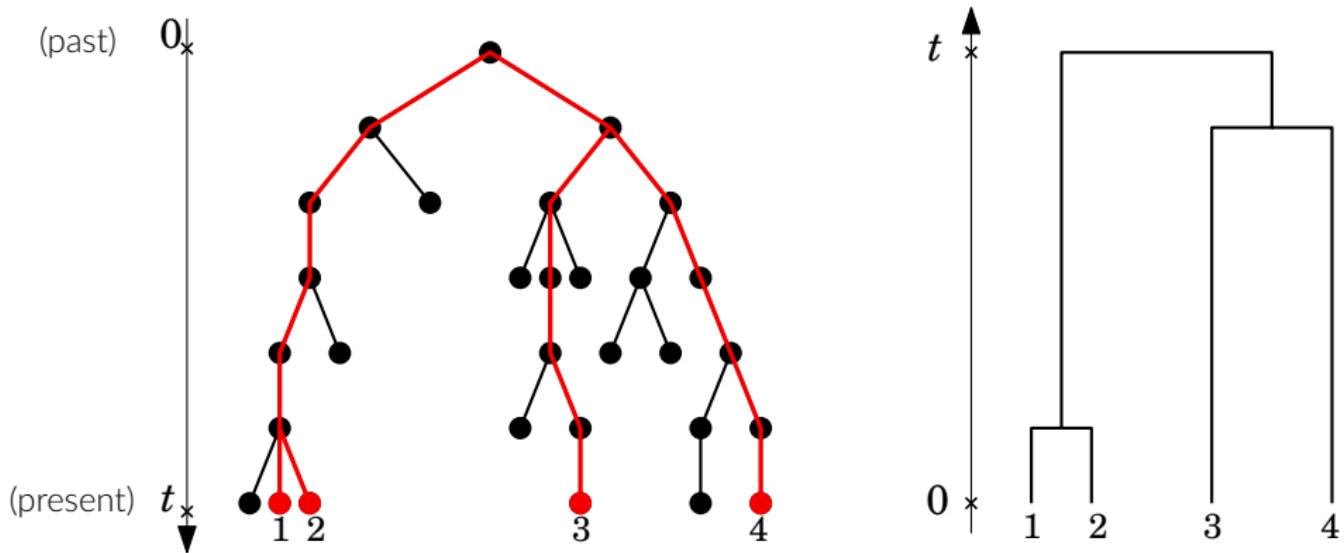
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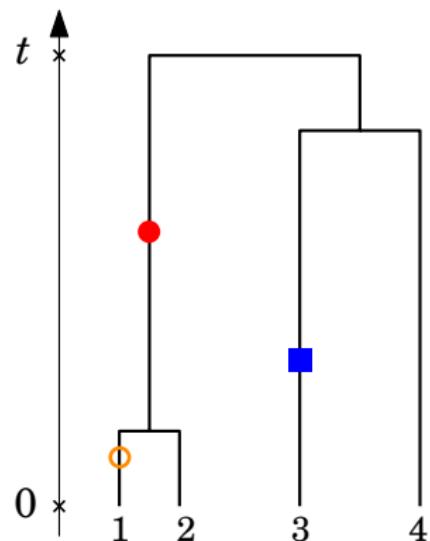
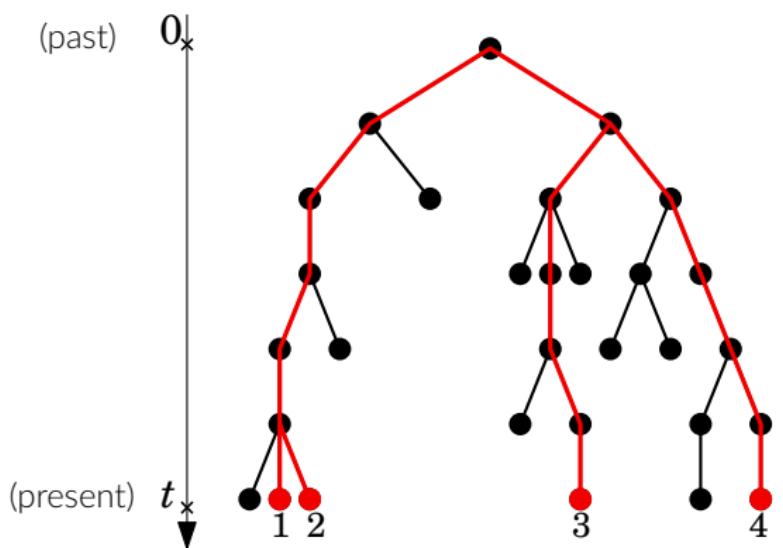
MOTIVATION

How ?

Genealogical approach = reconstruct the typical genealogy of the population

Molecular clock: mutations appear at constant rate

GENEALOGICAL TREE \Leftrightarrow GENETIC DIVERSITY



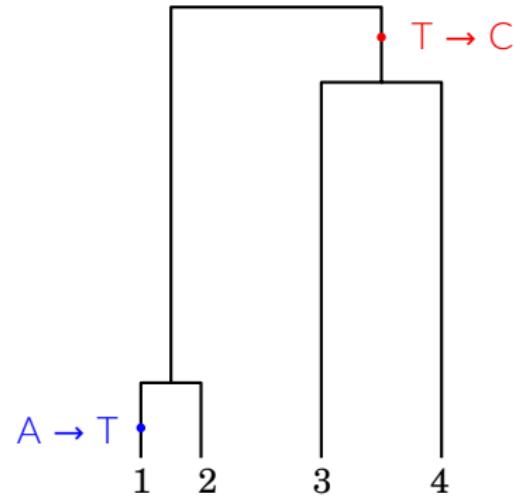
- Height of the tree
 \hookrightarrow number of mutations
 $\{ \textcolor{red}{\bullet}, \textcolor{orange}{\circ}, \textcolor{blue}{\blacksquare} \}$

- Shape of the tree
 \hookrightarrow mutational pattern

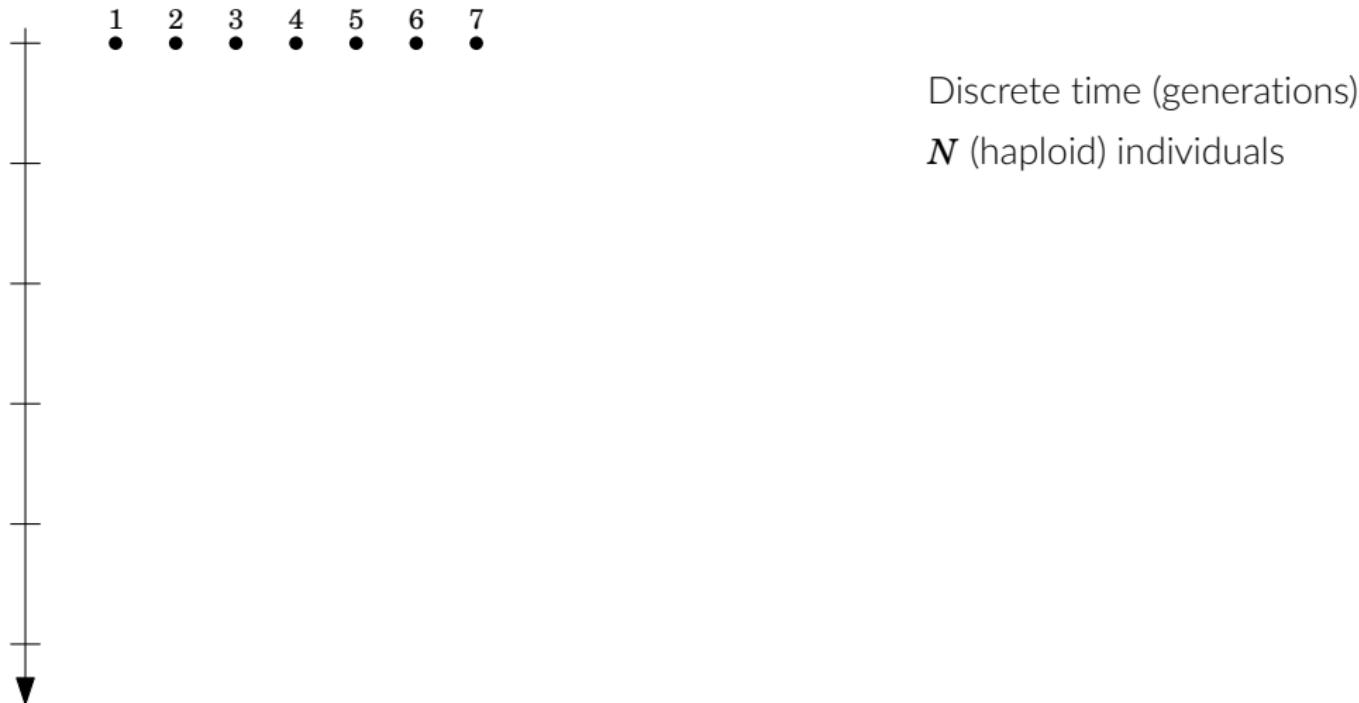
1	\bullet	\circ
2	\bullet	
3		\blacksquare
4		

MOTIVATION

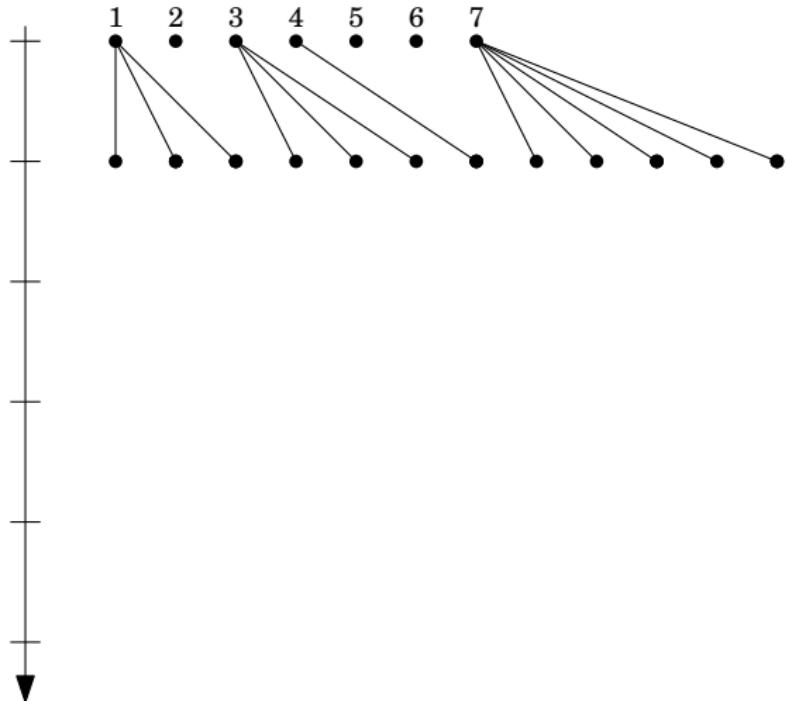
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A MODEL IN POPULATION GENETICS (Schweinsberg 2003)



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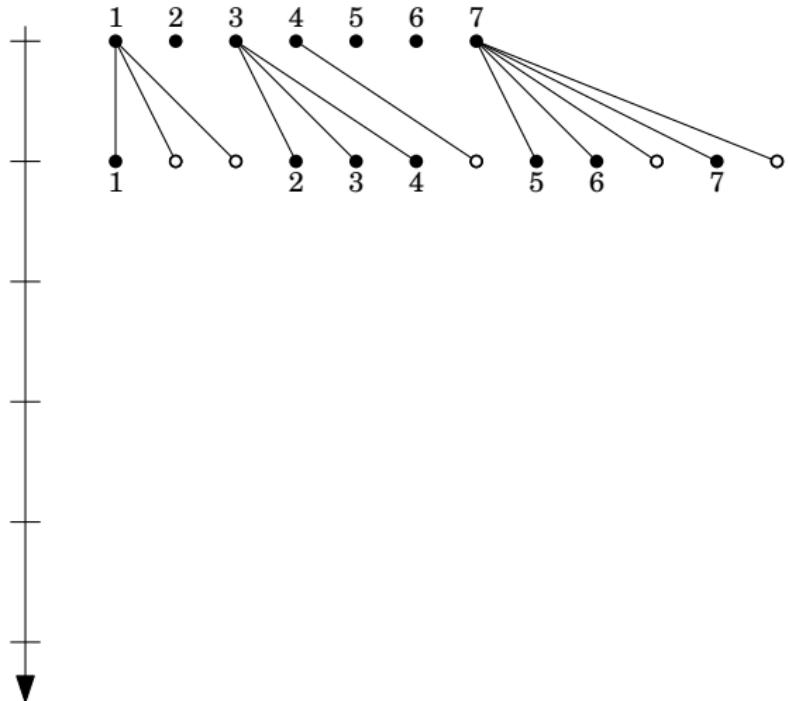
Discrete time (generations)

N (haploid) individuals

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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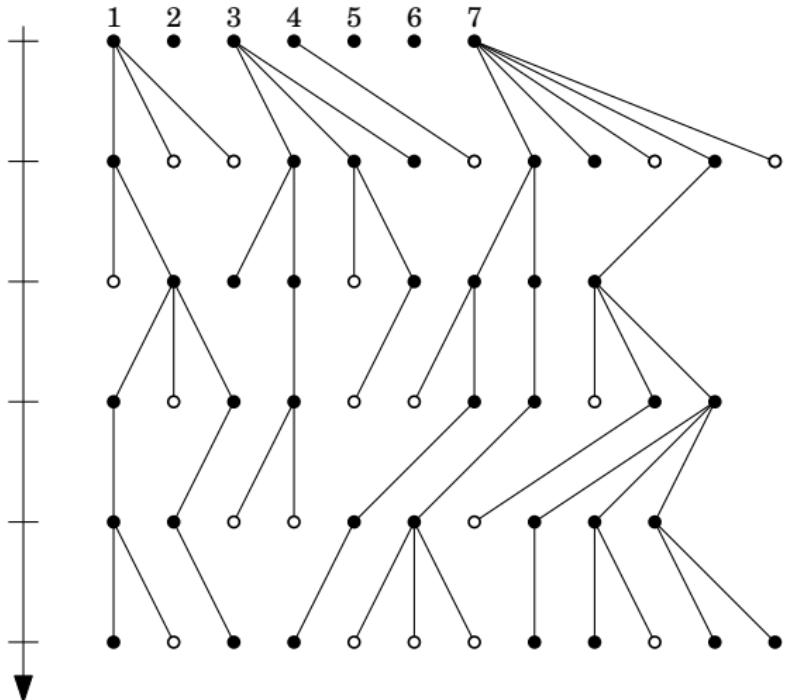
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Pick uniformly N newborns

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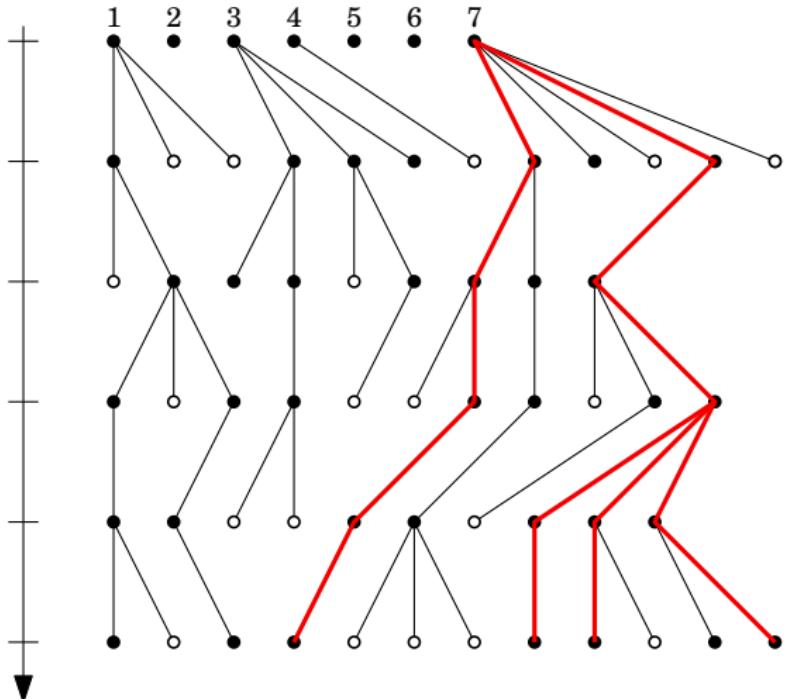
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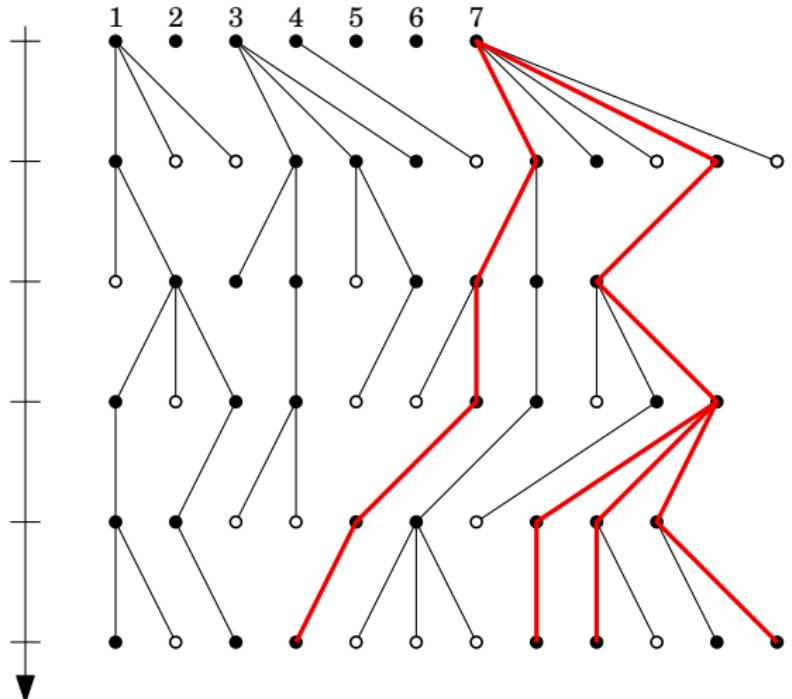
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What can be said about the genealogy of this population ?

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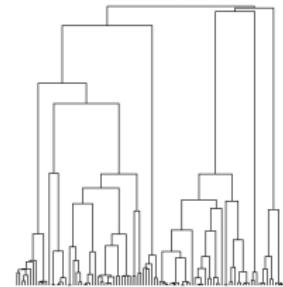
Let N go to ∞

FINITE VARIANCE

if $\mathbf{E}[(X_1)^2] < \infty$,
the genealogy is given by

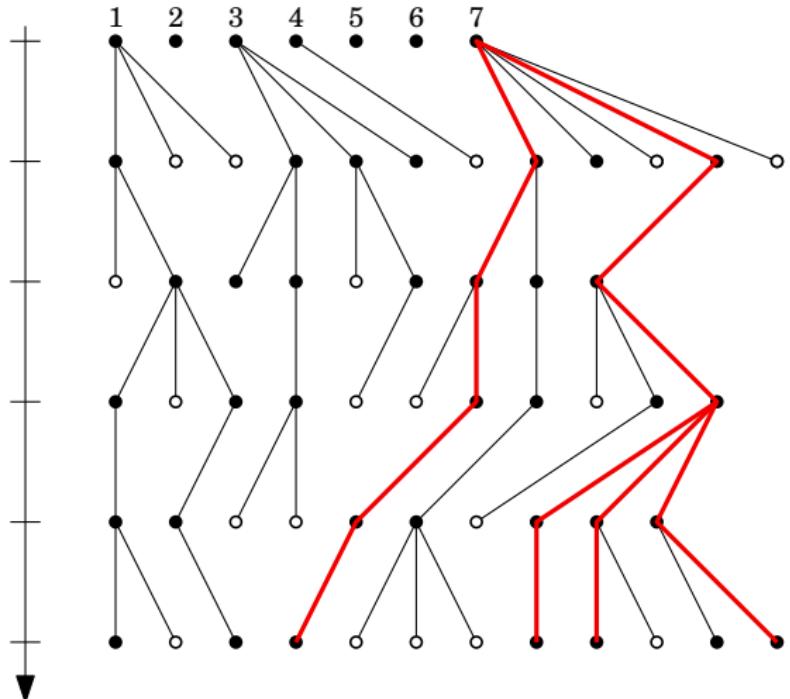
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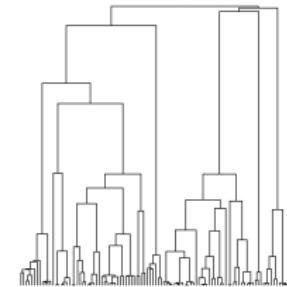
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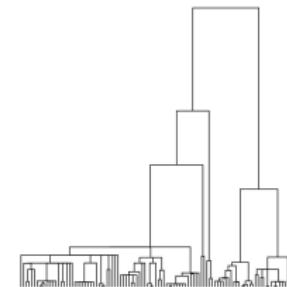
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HEAVY TAILS

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



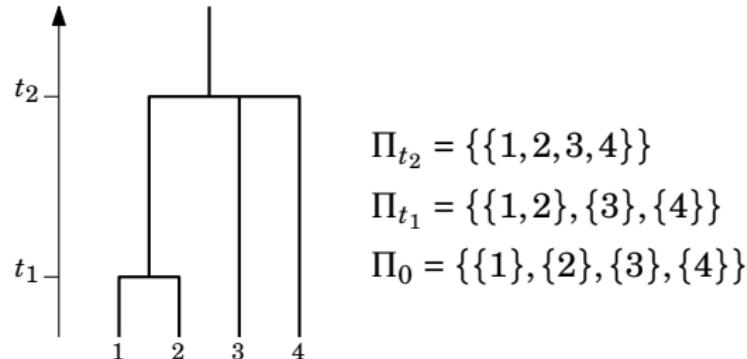
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A CLASS OF EXCHANGEABLE GENEALOGIES: BETA COALESCENTS

- 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

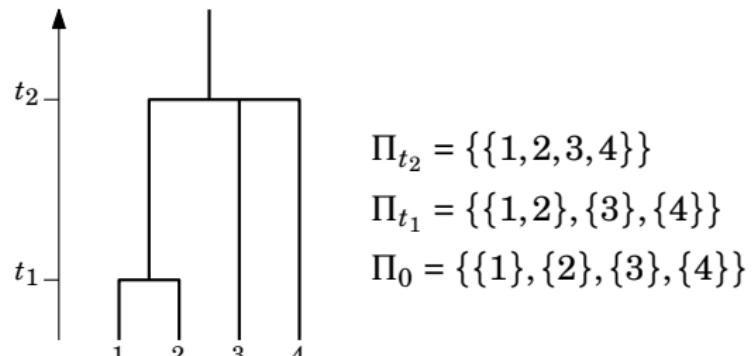


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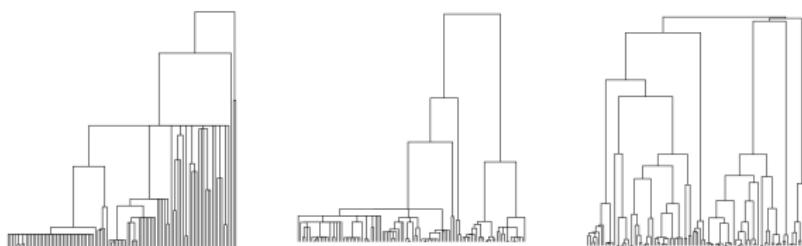
- exchangeable coalescent: all the blocks play the same role
rich mathematical structure (Pitman 99 and Sagitov 99)



BETA-COALESCENTS

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

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



$\alpha = 1$
Bolthausen-Sznitman

rapid diversity loss

$\alpha = 1.5$

$\alpha = 2$
Kingman

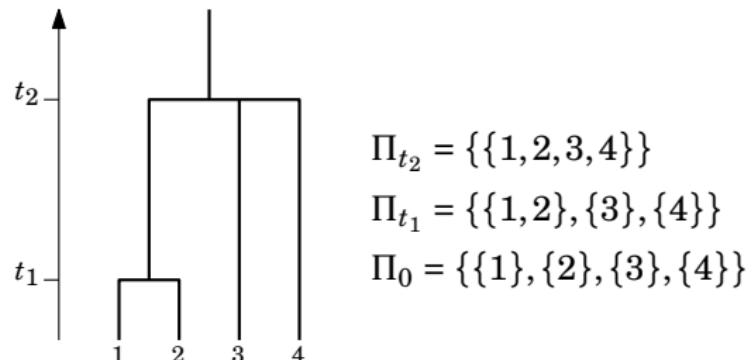
wide diversity

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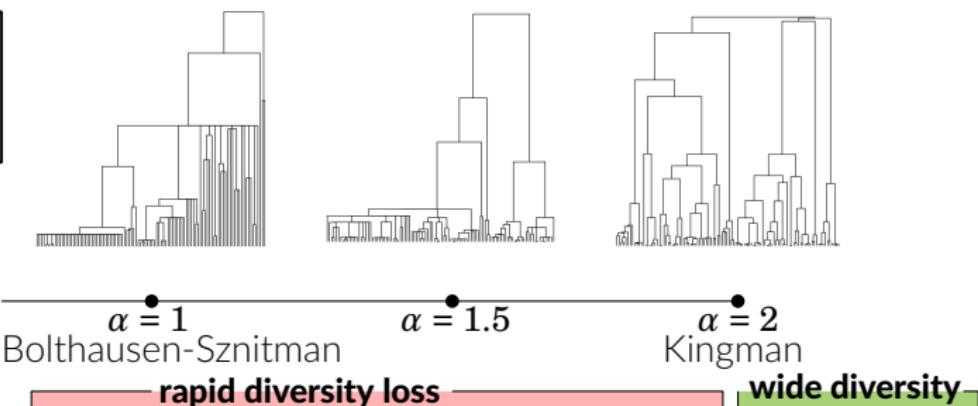
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LIMITATIONS

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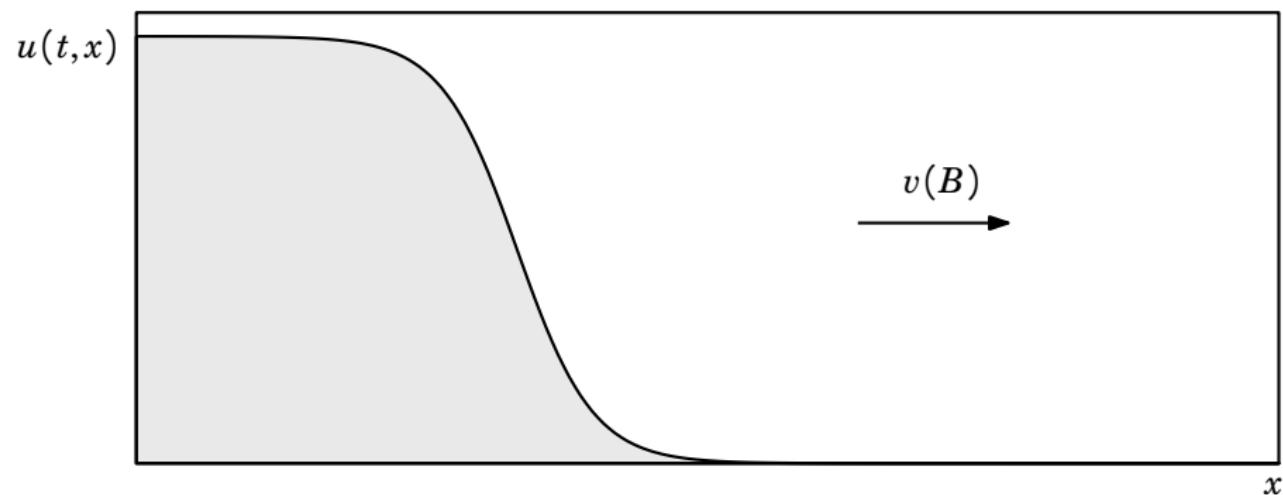
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Travelling front solutions:
constant profile travelling
at constant speed $v(B)$

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$$\begin{aligned} u_t &= \frac{1}{2}u_{xx} + \frac{1}{2}u(1-u)(1+Bu) \\ &= \frac{1}{2}u_{xx} + u \underbrace{r_0(u)}_{\text{per capita growth rate}} \end{aligned}$$

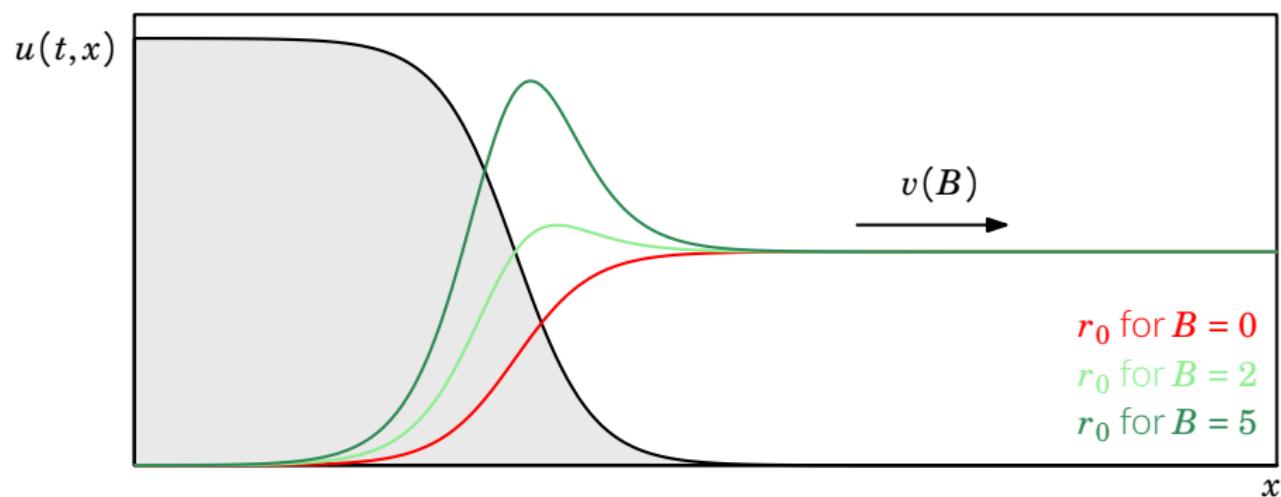
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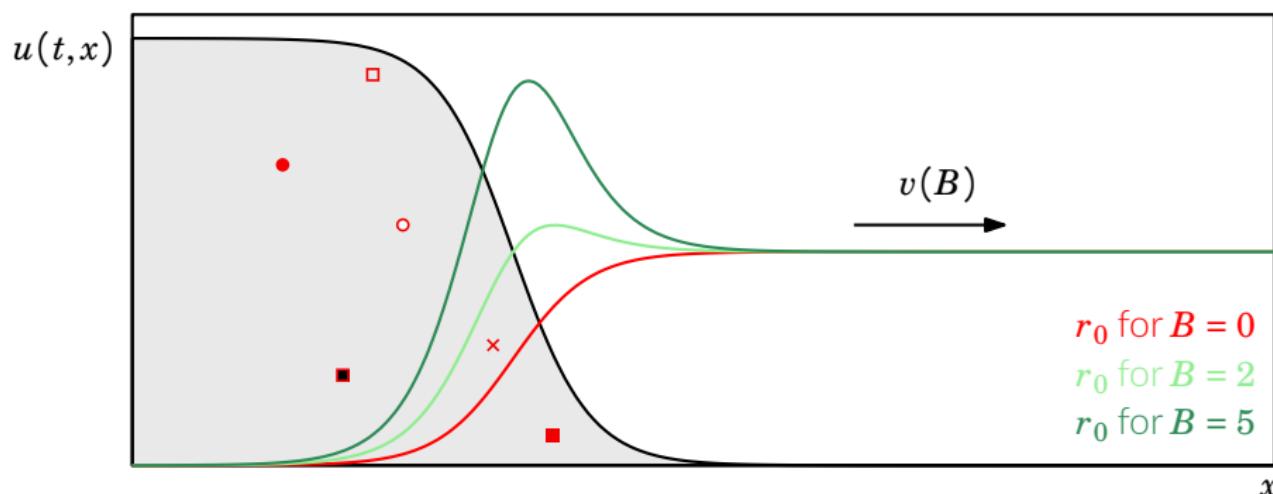
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r_0 for $B = 0$
 r_0 for $B = 2$
 r_0 for $B = 5$

Sample k individuals in the front

Genealogy ?

Position of the ancestors ?

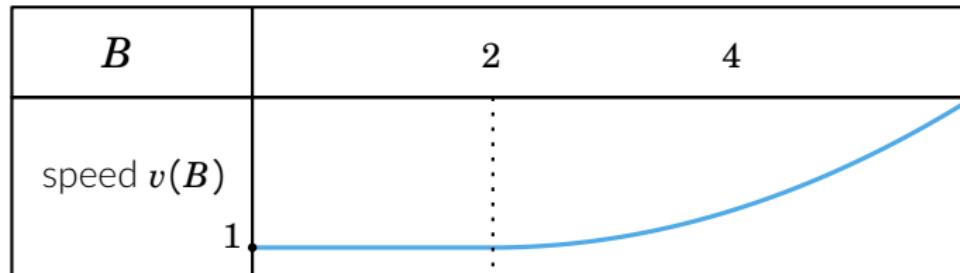
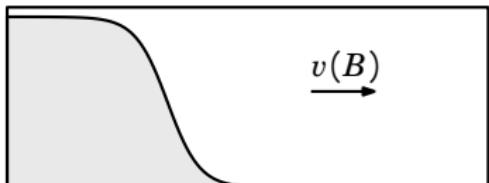
Phase transition ?

→ discrete model

PULLED, SEMIPUSHED AND FULLY PUSHED FRONTS

FKPP Equation

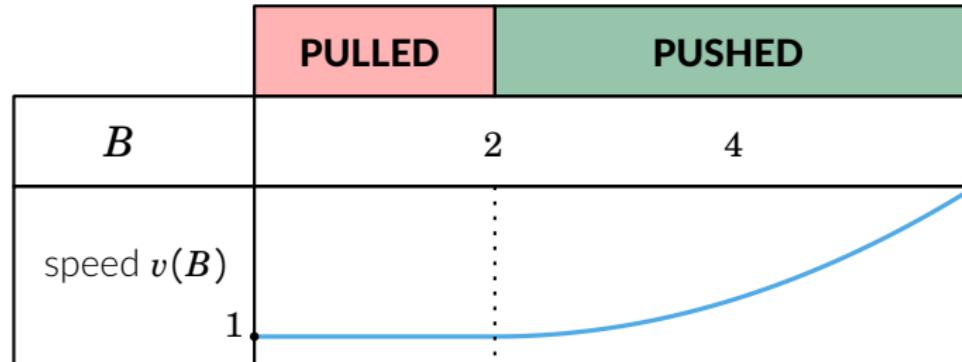
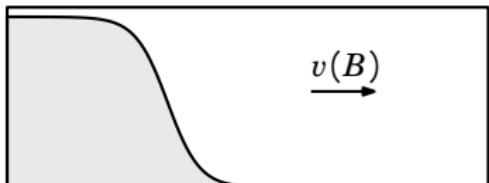
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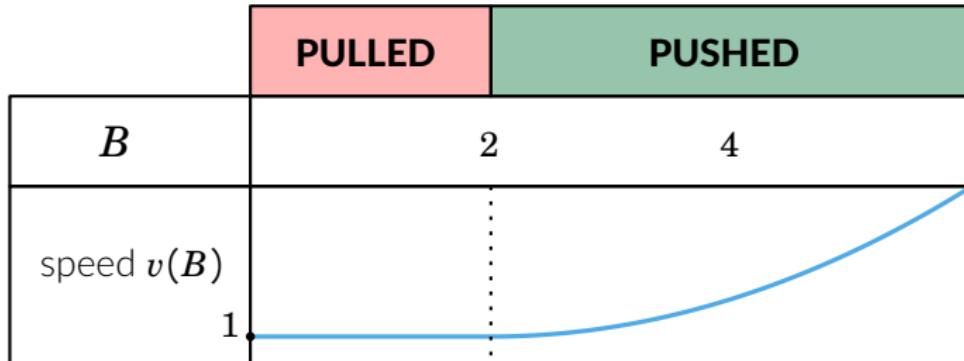
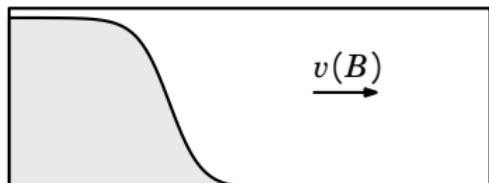
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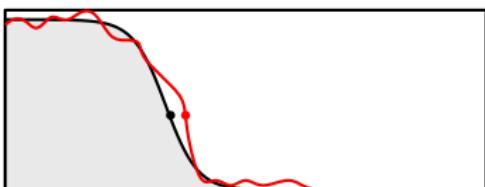
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Noisy FKPP Equation

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

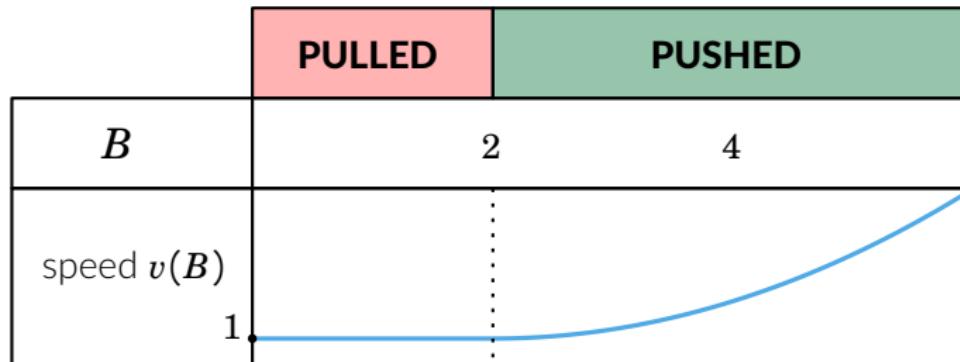
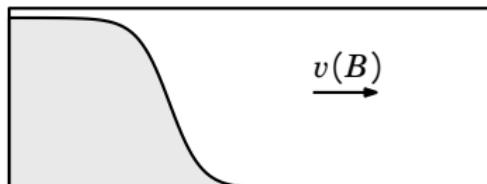
local density
white noise



PULLED, SEMIPUSHED AND FULLY PUSHED FRONTS

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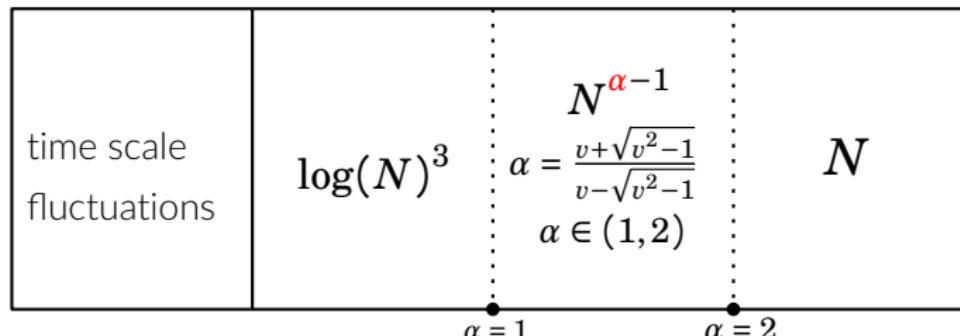
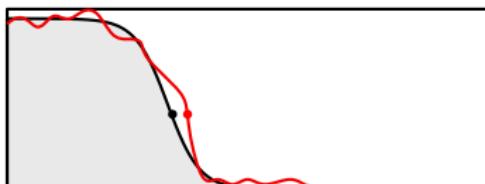
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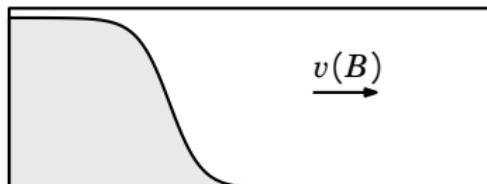


Heuristics and simulations: Birzu et al. '18
Fluctuations uncover a distinct class of traveling waves, PNAS

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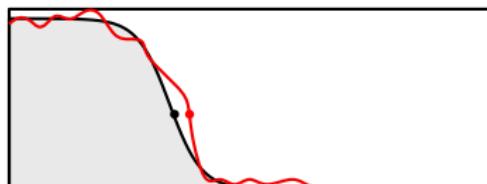
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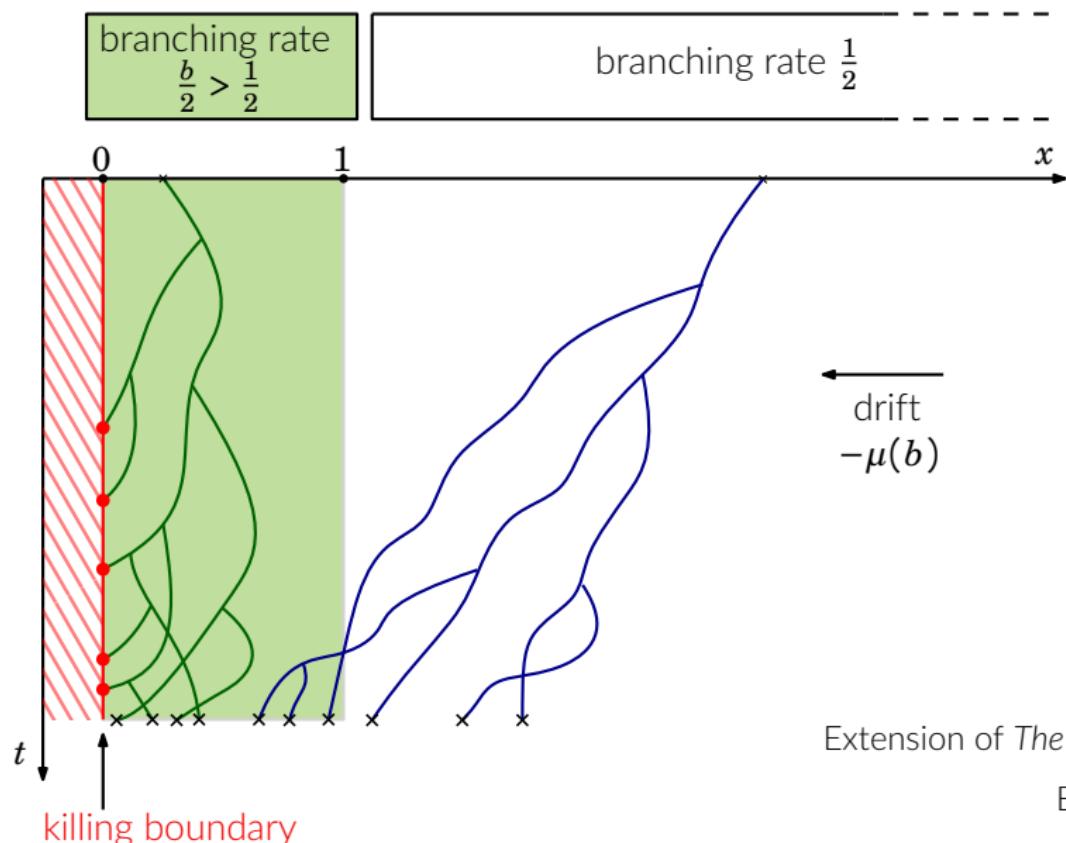
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	PULLED	PUSHED	
B	2	4	
speed $v(B)$	1		
	PULLED	SEMI	FULLY
time scale fluctuations	$\log(N)^3$	$N^{\alpha-1}$ $\alpha = \frac{v+\sqrt{v^2-1}}{v-\sqrt{v^2-1}}$ $\alpha \in (1, 2)$	N
	$\alpha = 1$	$\alpha = 2$	

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A TOY MODEL TO INVESTIGATE THE PHASE DIAGRAM



Dyadic branching Brownian motion
with branching rate

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

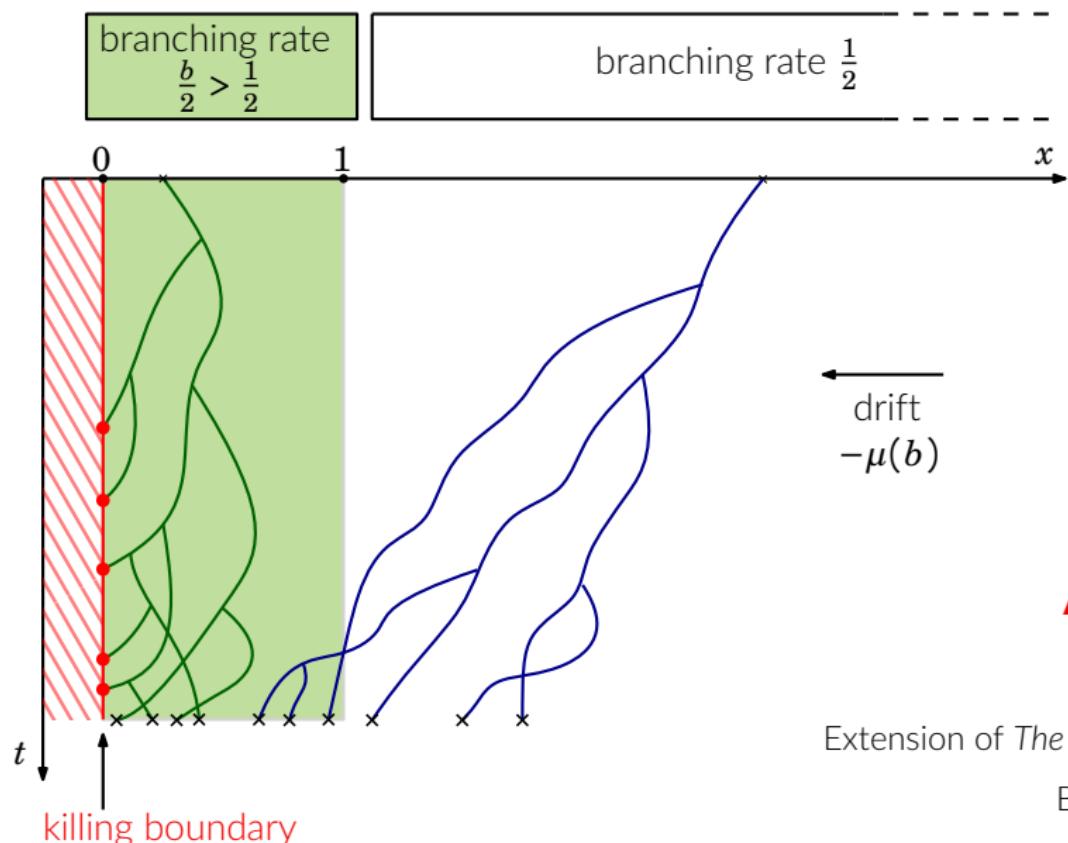
killing at 0

"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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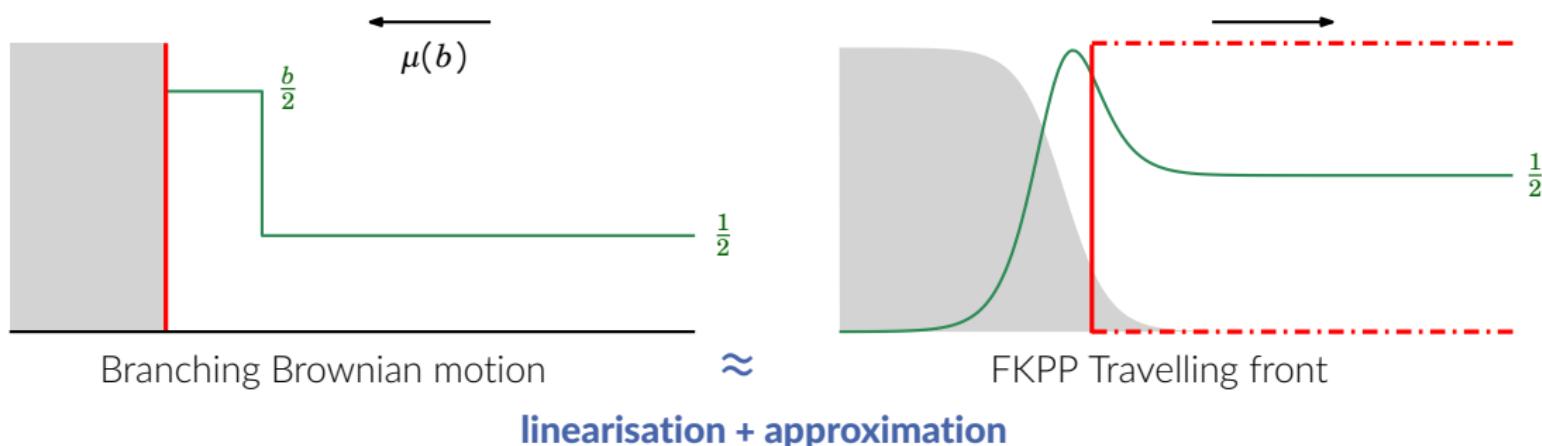


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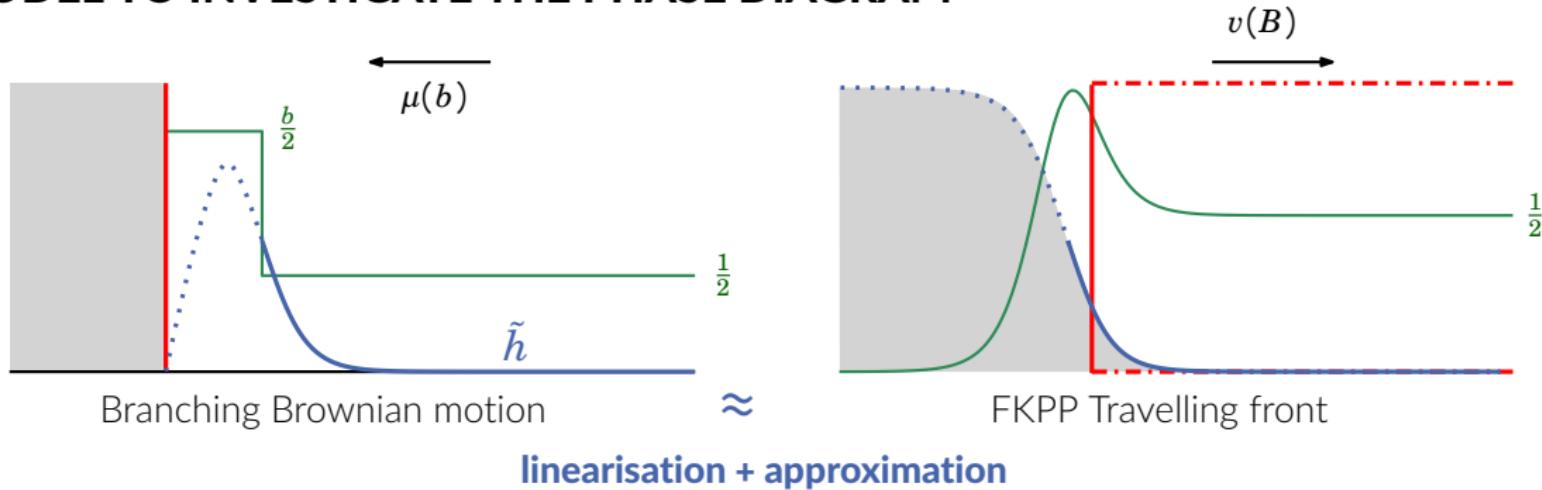
A model for travelling fronts ?

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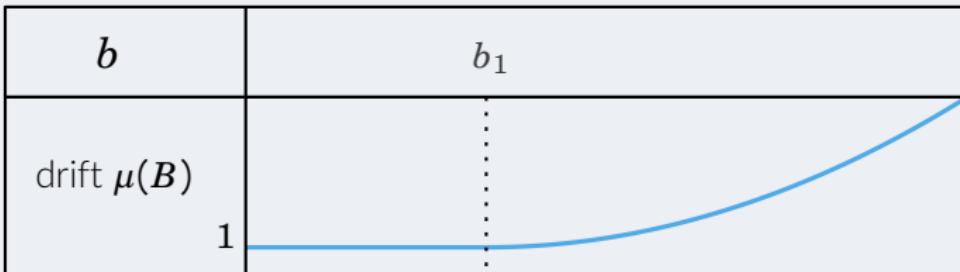
A TOY MODEL TO INVESTIGATE THE PHASE DIAGRAM



A TOY MODEL TO INVESTIGATE THE PHASE DIAGRAM



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

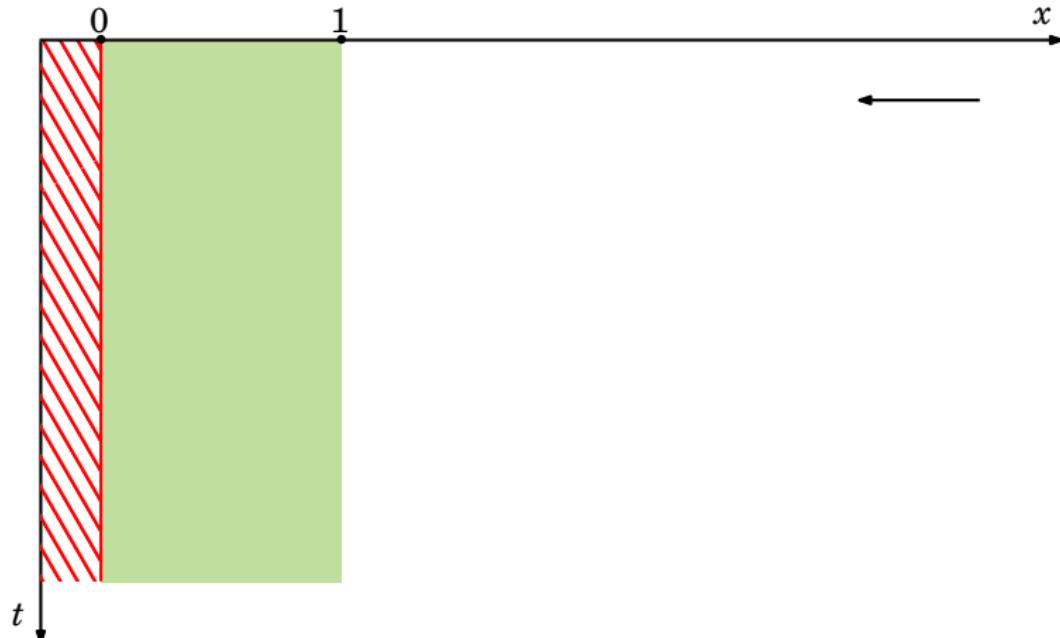


critical = the number of particles is roughly constant

+

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

THE SEMIPUSHED REGIME



SEMIPUSHED REGIME

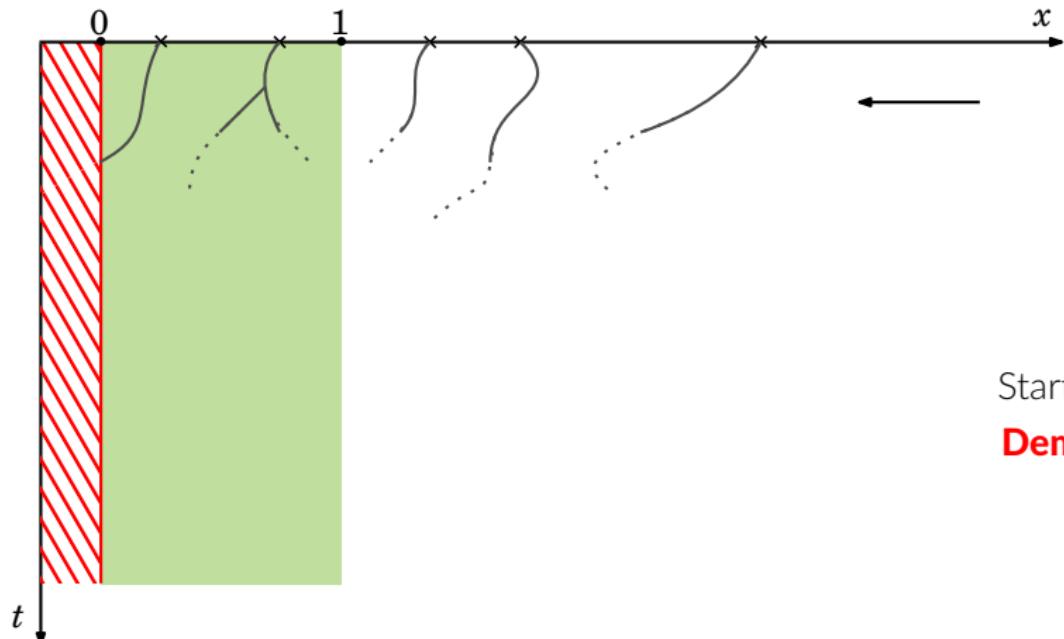
There exists $b_2 > b_1$ such that

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

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

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

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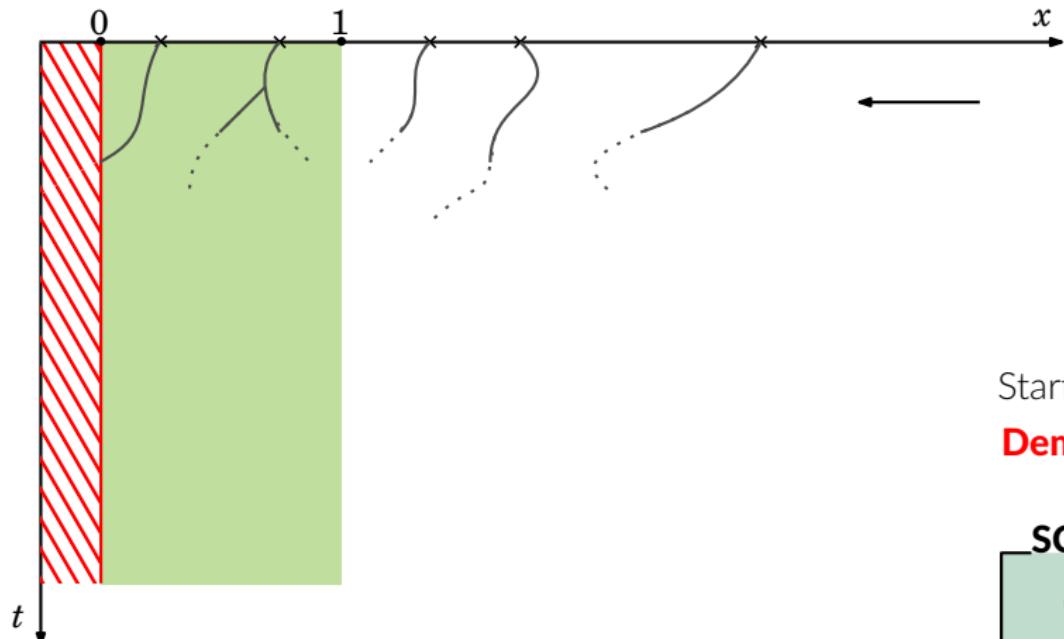
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Start with N particles distributed according to \tilde{h}

Demographic fluctuations ?

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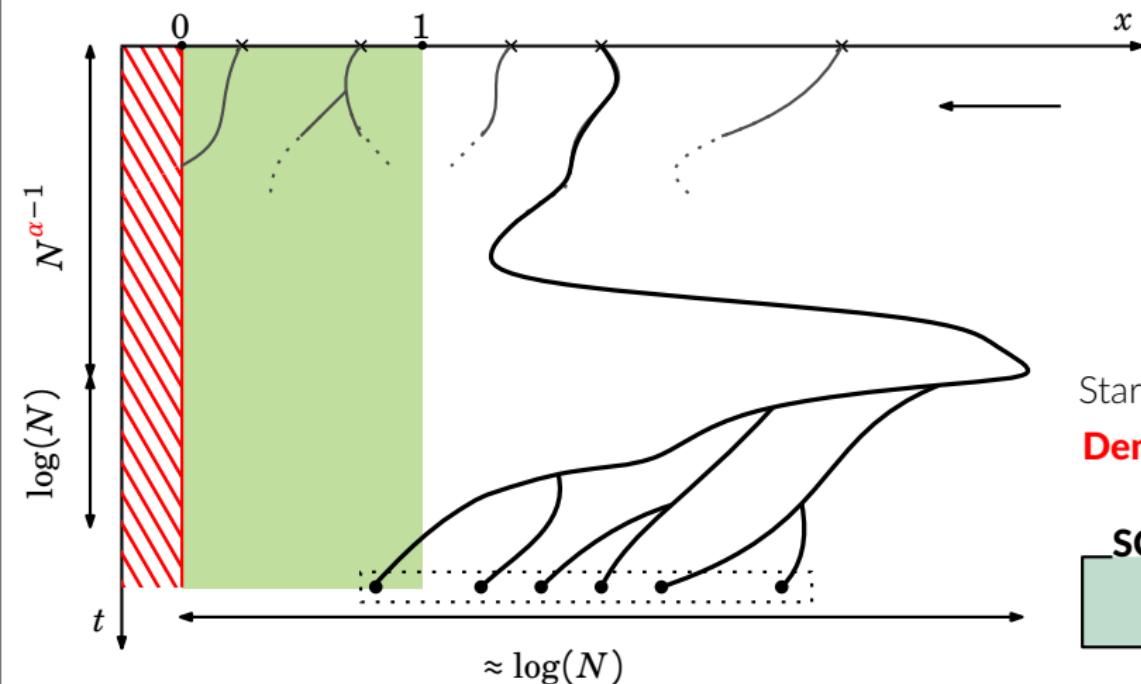
Demographic fluctuations ? Z_t = number of individuals

Let N goes to ∞

SCALING LIMIT

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

THE SEMIPUSHED REGIME



$\bullet \bullet \bullet \dots \approx N$ descendants

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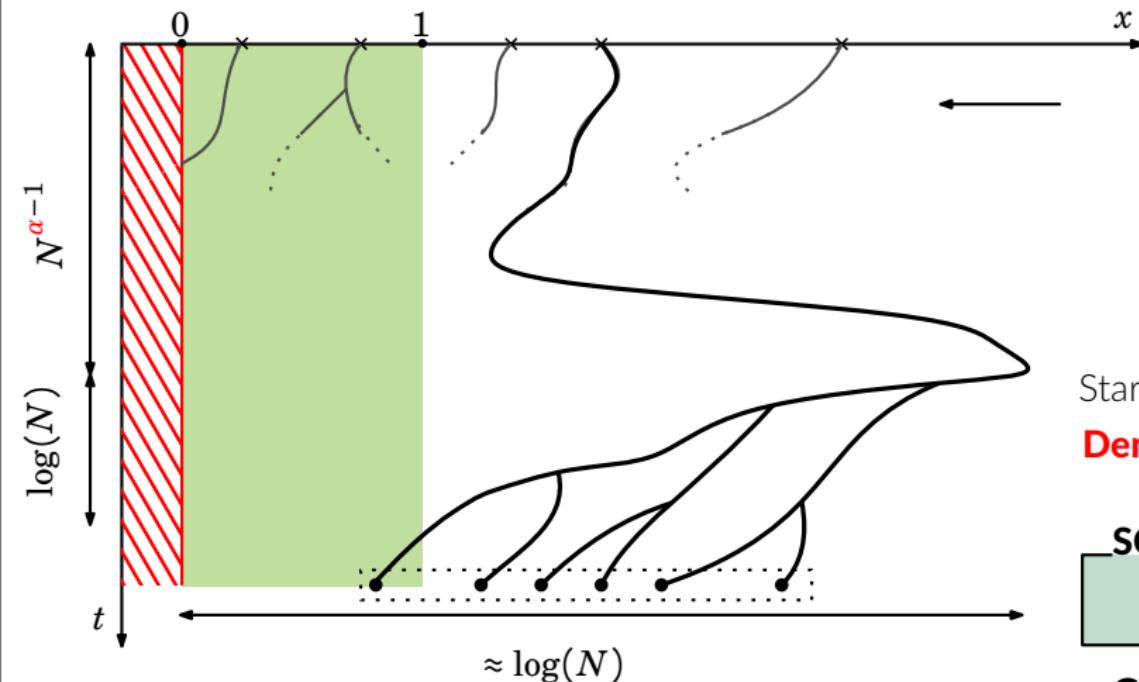
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$$(\frac{1}{N} Z_{tN^{\alpha-1}}) \Rightarrow (\Xi_t) \quad \Xi \text{ is an } \alpha\text{-stable CSBP}$$

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 $b \in (b_1, b_2)$.

↪ 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 ∞

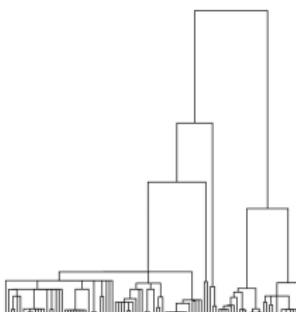
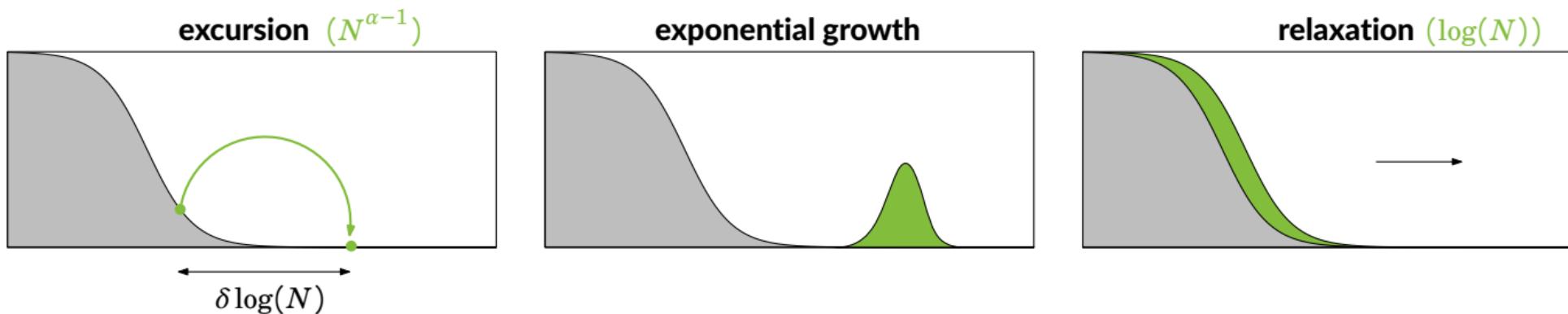
SCALING LIMIT

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

GENEALOGY

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

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

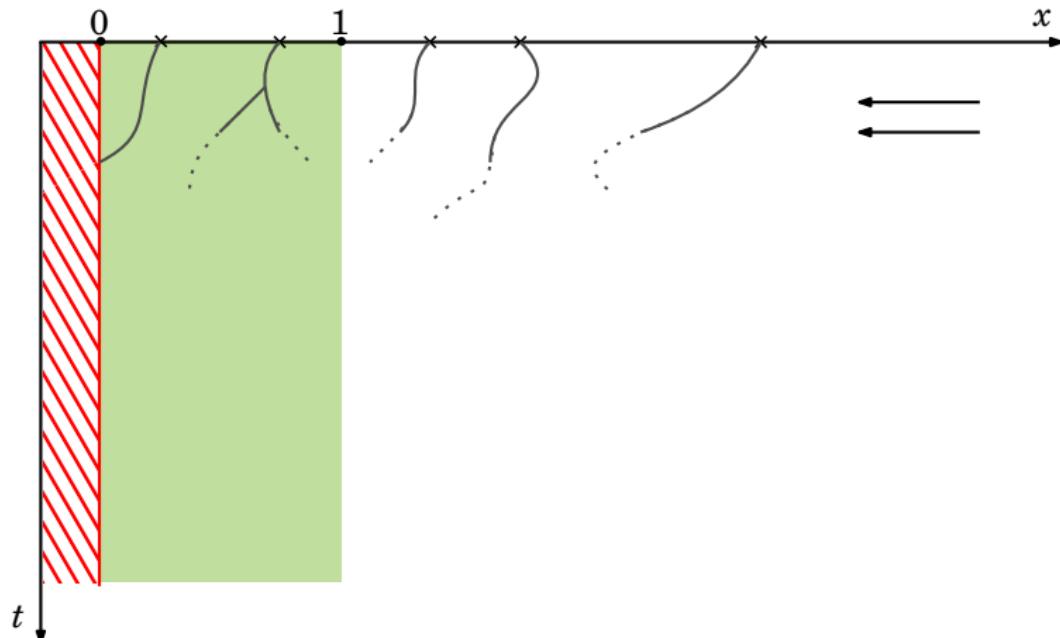


- The invasion is driven by **excursions** of particles
- These excursions generate **large subfamilies** in the associated genealogy, **diversity loss**
- Particles at the tip have a large reproductive value \Rightarrow **large reproductive variance**
(in some sense)
- fast relaxation \Rightarrow collapse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

*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 $b > b_2, \alpha > 2$

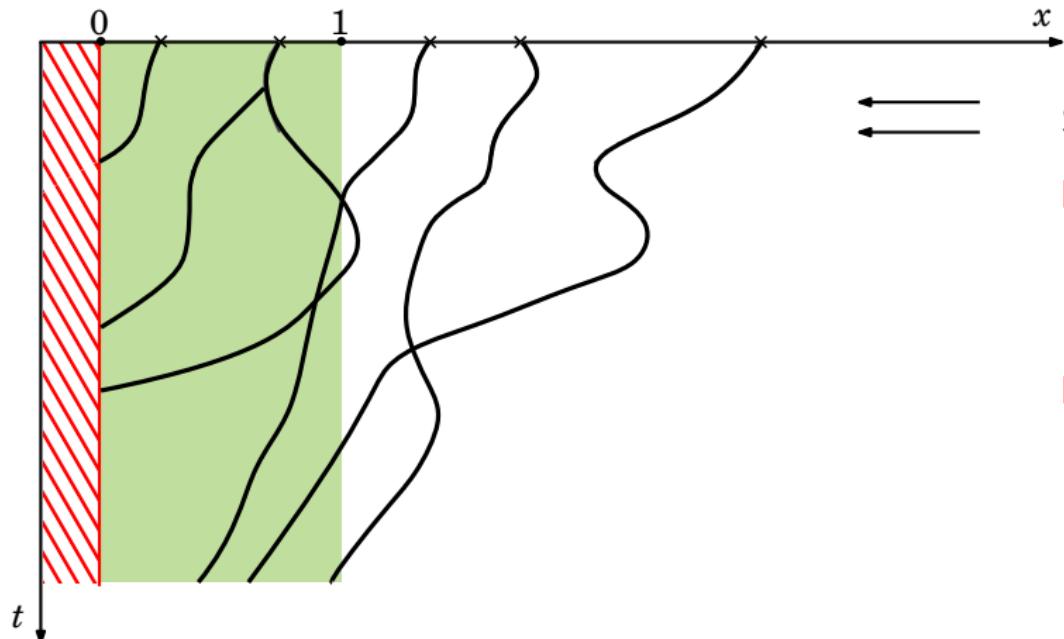
Start with N particles distributed according to \tilde{h}

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}

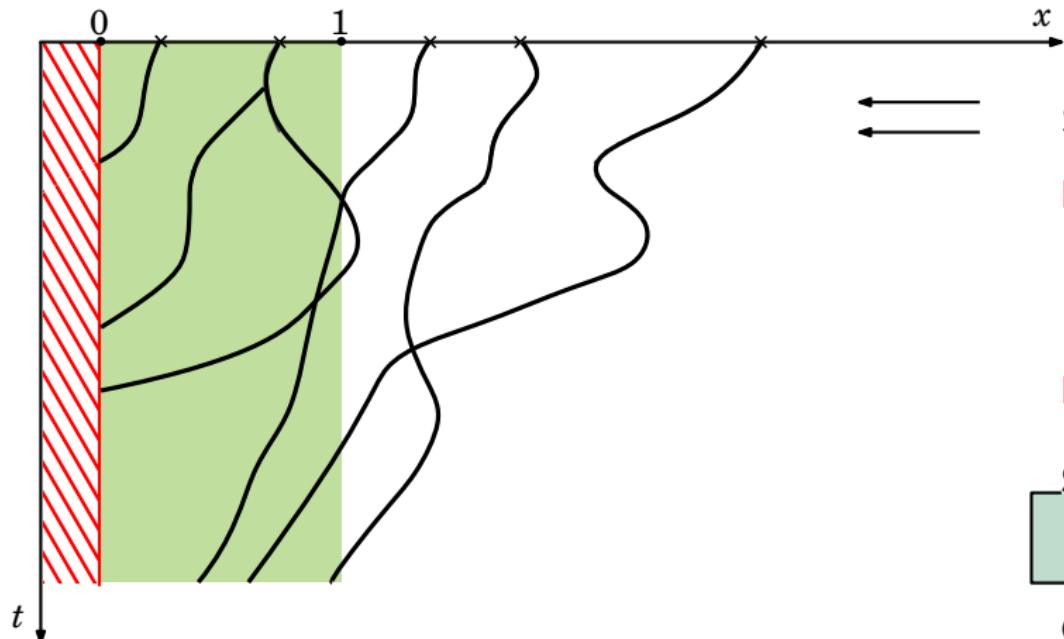
Demographic fluctuations ?

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 ! \rightsquigarrow "CLT"/mean field

SCALING LIMIT

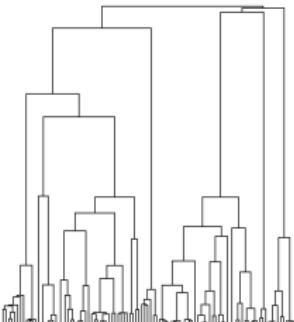
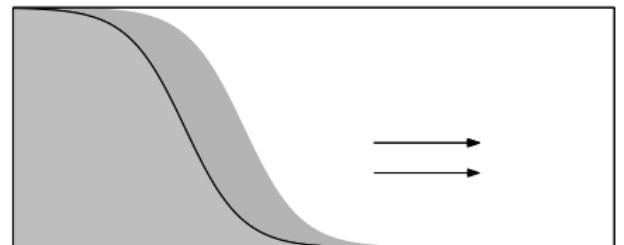
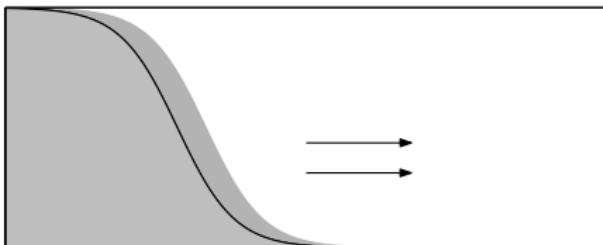
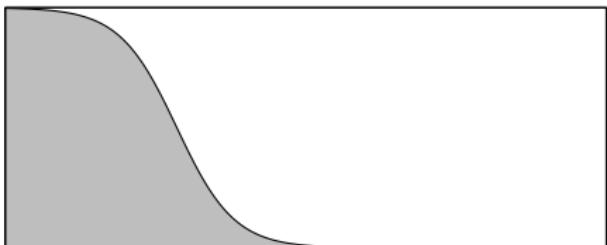
$$\left(\frac{1}{N} Z_{tN} \right) \Rightarrow (X_t) \quad X \text{ is a Feller diffusion}$$

GENEALOGY

The genealogy of the BBM converges to Kingman's coalescent

THE FULLY PUSHED REGIME $b > b_2$

N

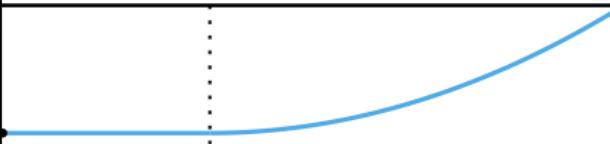
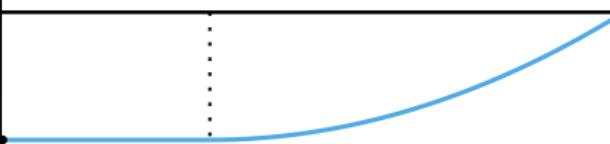
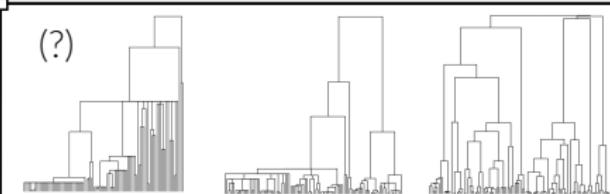


- The invasion is pushed by the **growth** in the front
- This generates only **binary mergers** in the associated genealogy, **wide genetic diversity**
- The tip is not accessible \Rightarrow **finite reproductive variance**

*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 $v(B)$	1		
PARTICLE SYSTEM	b	b_1	b_2
drift $\mu(b)$	1		
time scale fluctuations	$\log(N)^3$	$N^{\alpha-1}$	N
genealogy	(?)		

Besançon meeting on
**PROBABILITY
ECOLOGY
& EVOLUTION**

December 10th, 2024 @MSHE Besançon

