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
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Sequence 3	A	C	C	C	T	A	T
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Figure: DNA sequence alignment

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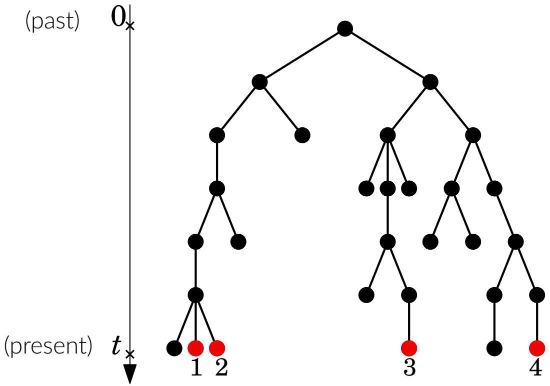

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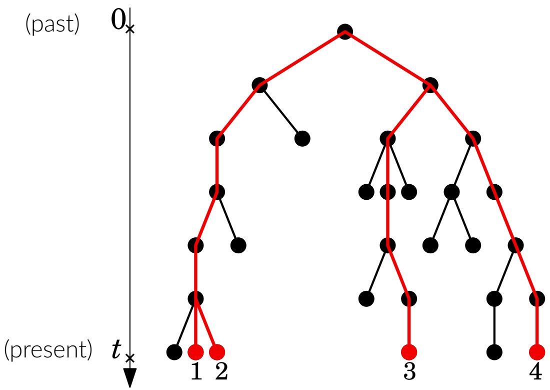
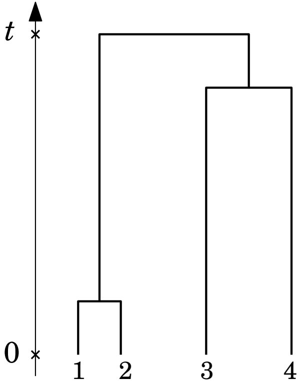




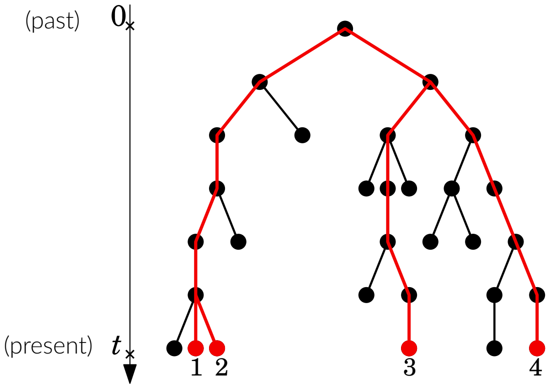
MOTIVATION

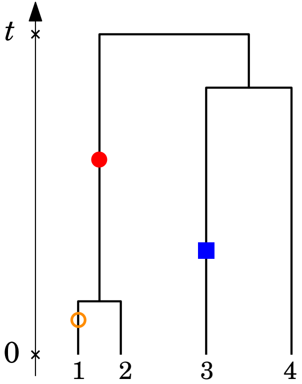
How ?

Genealogical approach = reconstruct the typical genealogy of the population

Molecular clock: mutations appear at constant rate

GENEALOGICAL TREE $\Leftrightarrow$ GENETIC DIVERSITY





- Heigh of the tree

  $\hookrightarrow$ number of mutations

  {●, ○, ■}

- Shape of the tree

  $\hookrightarrow$ mutational pattern

1	● ○
2	●
3	■
4	

MOTIVATION

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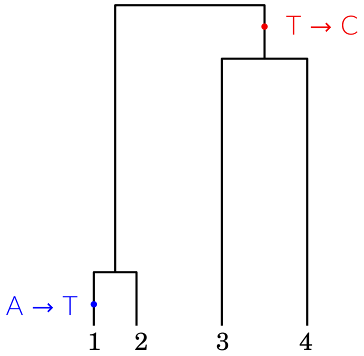
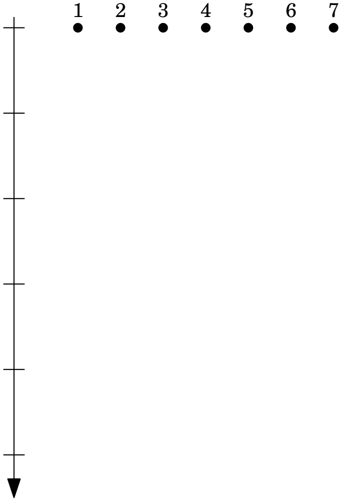


A MODEL IN POPULATION GENETICS (Schweinsberg 2003)



Discrete time (generations)

N (haploid) individuals

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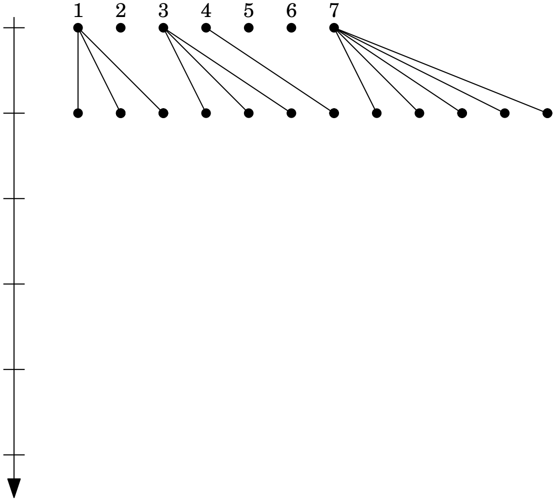

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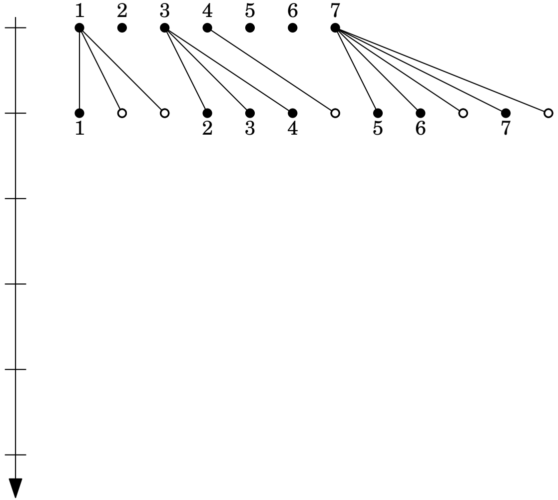

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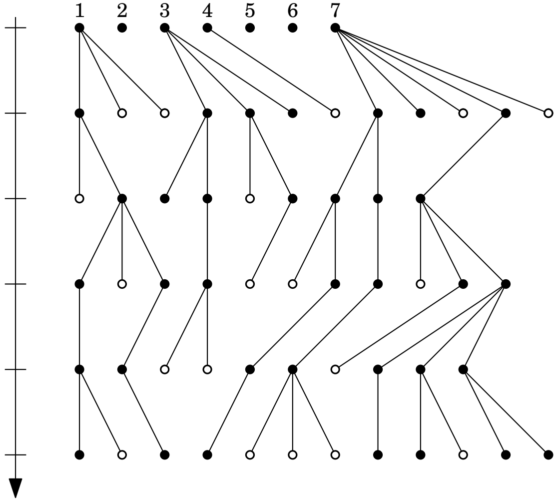

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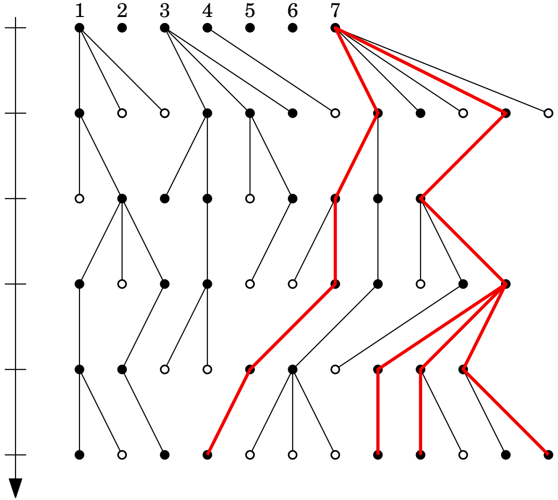

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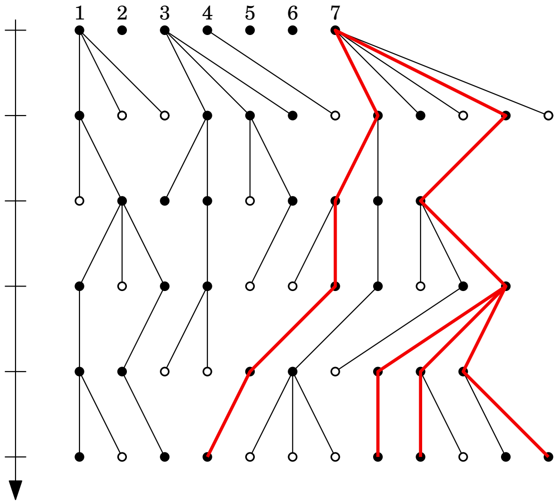


N (haploid) individuals

Let N go to ∞

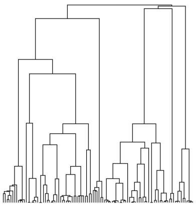
FINITE VARANCE

if $\mathbf{E}[(X_1)^2] < \infty$,

the genealogy is given by

Kingman's coalescent

(a binary tree)



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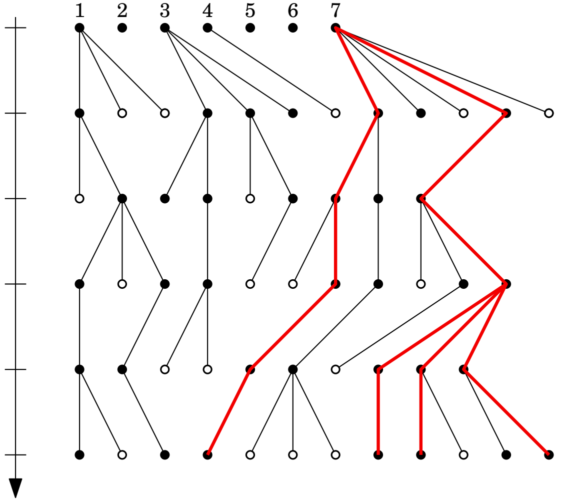

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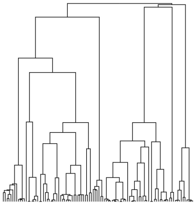


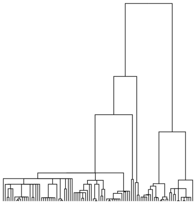
HEAVY TAILS

if $\mathbf{P}(X_1 > x) \sim \frac{1}{x^\alpha}$,

with $\alpha \in (1,2)$,

the genealogy is given by

a **Beta($2-\alpha,\alpha$)-coalescent**



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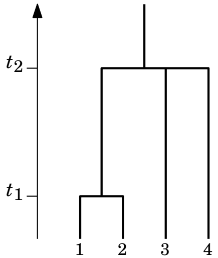
A CLASS OF EXCHANGEABLE GENEALOGIES: BETA COALESCENTS

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

  merging of blocks $\Leftrightarrow$ merging of ancestral lines

- exchangeable coalescent: all the blocks play the same role



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

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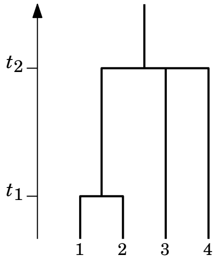

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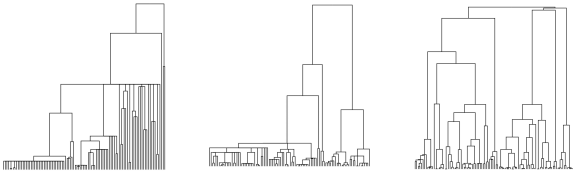
BETA-COALESCENTS

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

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



$\alpha = 1$ Bolthausen-Sznitman

$\alpha = 1.5$

$\alpha = 2$ Kingman

rapid diversity loss

wide diversity

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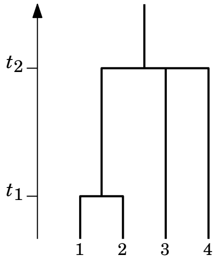

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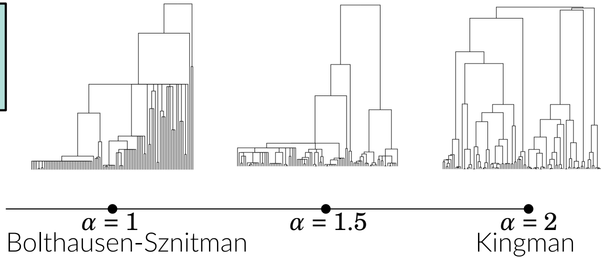
LIMITATIONS

- *a priori* only suitable for neutral models

  equal chances of reproductive success

- **no selection, no structure**

  MAJOR FORCES IN EVOLUTION !



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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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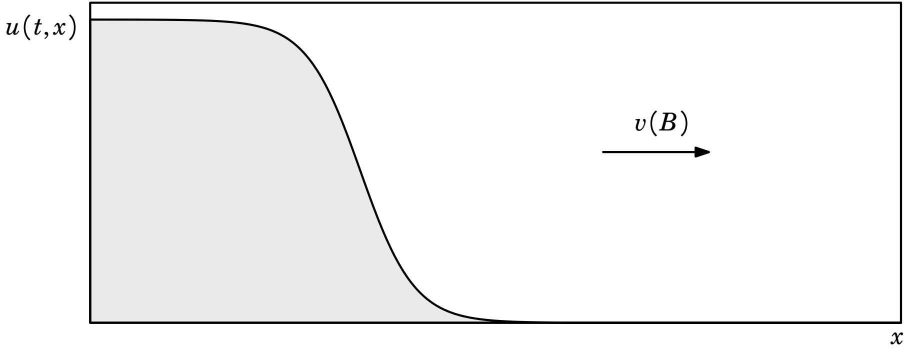

Travelling front solutions:

constant profile travelling at constant speed $v(B)$

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

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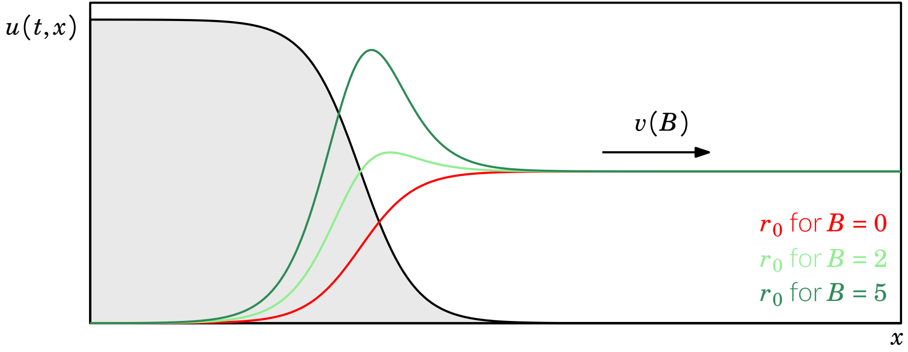

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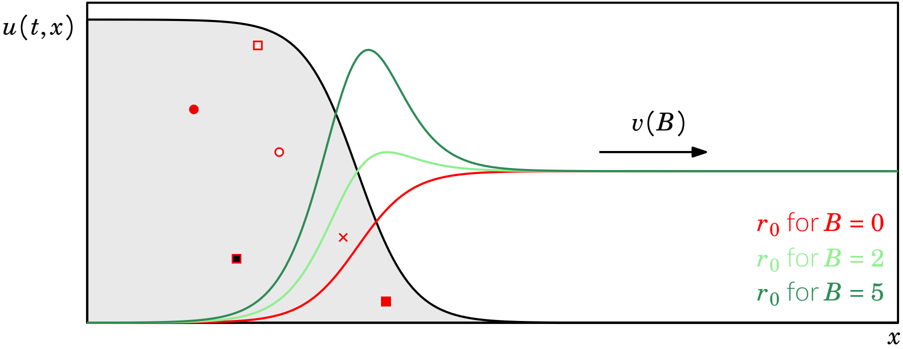

Travelling front solutions:

constant profile travelling at constant speed $v(B)$

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Sample k individuals in the front

Genealogy ?

Position of the ancestors ?

Phase transition ?

PULLED, SEMIPUSHED AND FULLY PUSHED FRONTS

FKPP Equation

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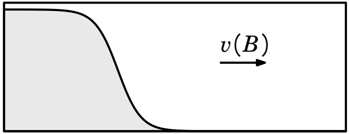

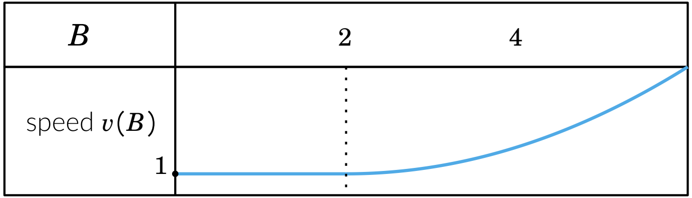

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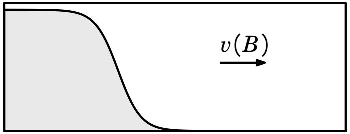

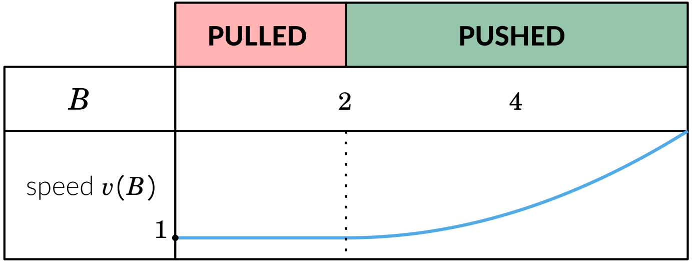

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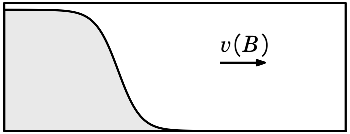
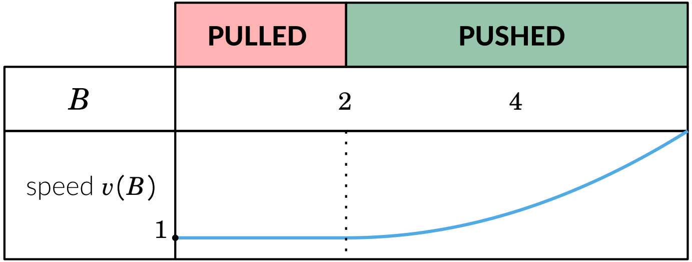


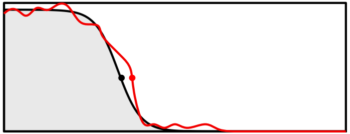


Noisy FKPP Equation

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

local density

white noise



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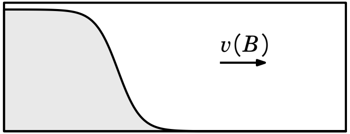

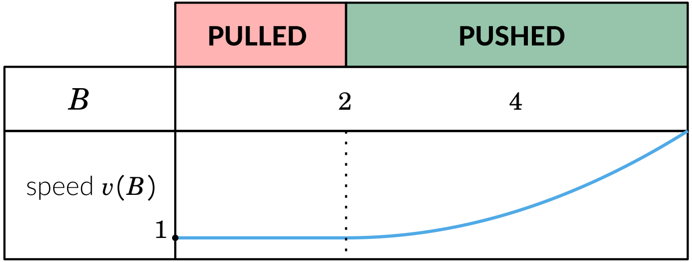

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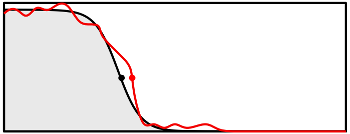

time scale fluctuations	$\log(N)^3$	$N^{\alpha-1}$ $\alpha = \frac{v+\sqrt{v^2-1}}{v-\sqrt{v^2-1}}$ $\alpha \in (1,2)$	N

$\alpha = 1$ $\quad$ $\alpha = 2$

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

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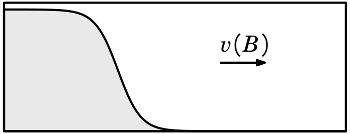

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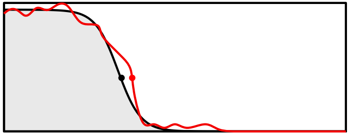

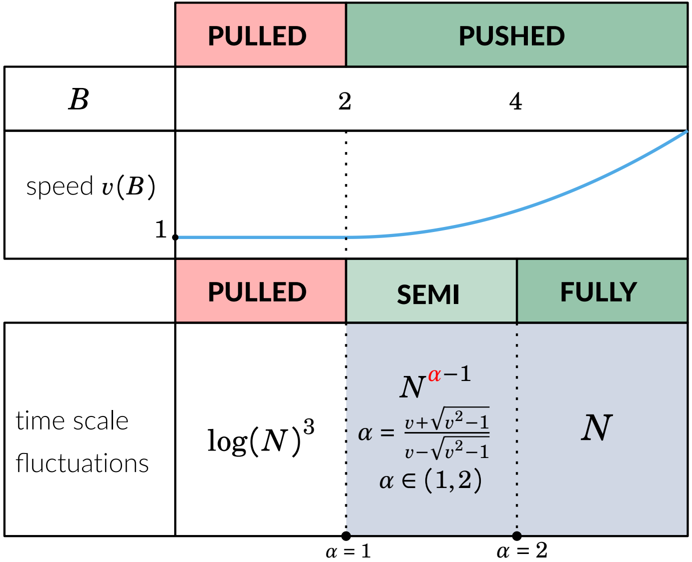

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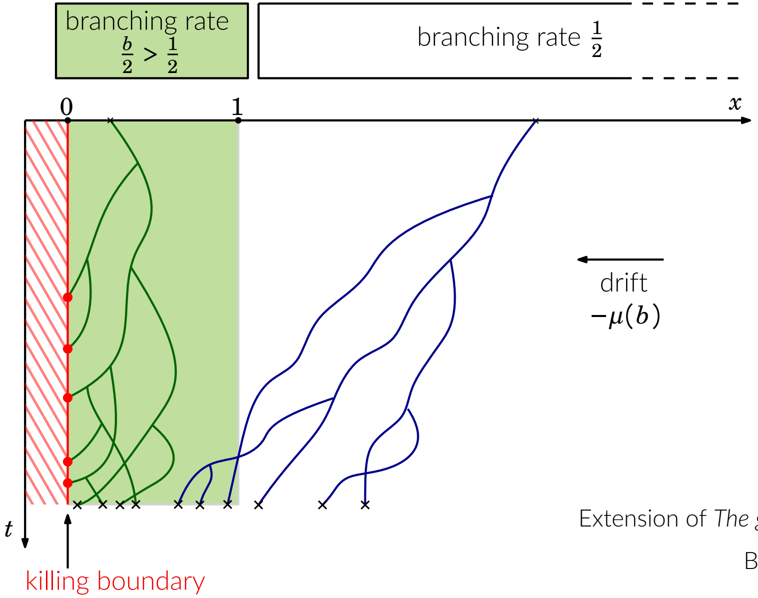
A TOY MODEL TO INVESTIGATE THE PHASE DIAGRAM



Dyadic branching Brownian motion with branching rate

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

killing at $\mathbf{0}$

“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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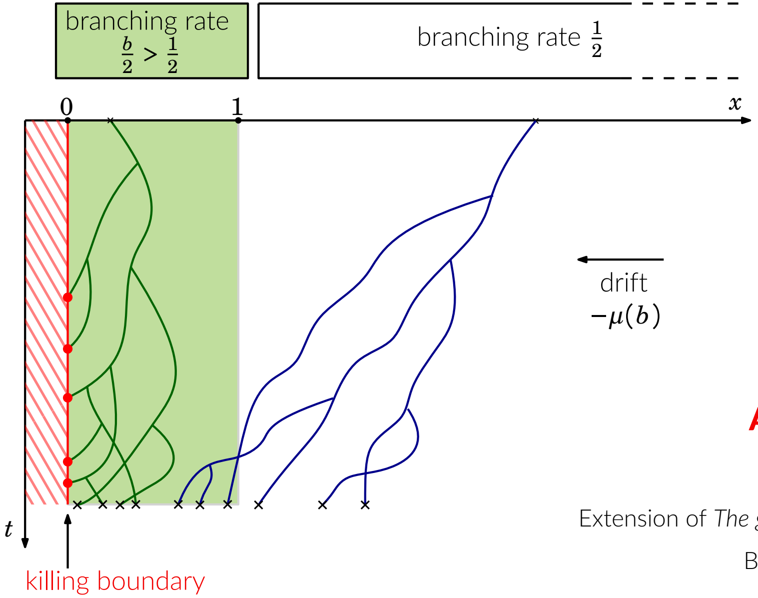

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A model for travelling fronts ?

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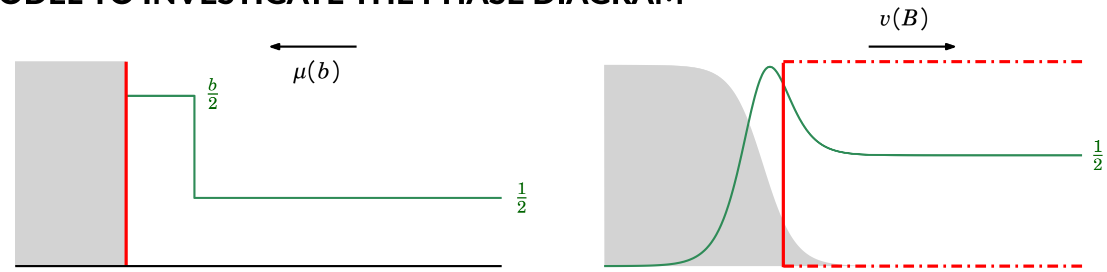

Branching Brownian motion $\approx$ FKPP Travelling front

linearisation + approximation

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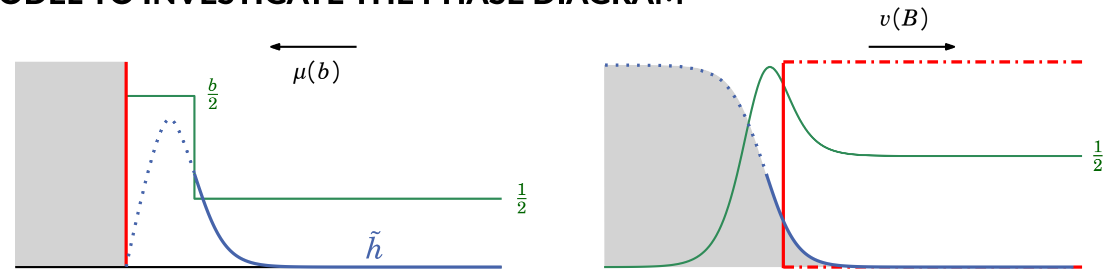

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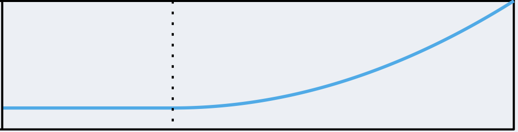
linearisation + approximation

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

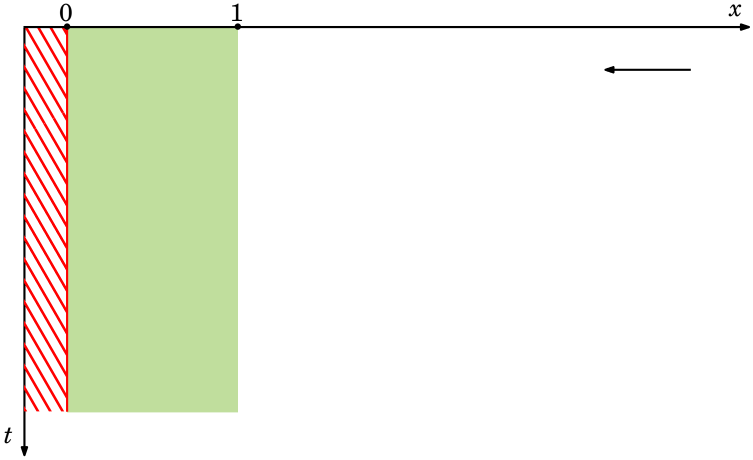
b	b_1
drift $\mu(B)$ 1	

critical = the number of particles is roughly constant

+

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

THE SEMIPUSHED REGIME



SEMIPUSHED REGIME

There exists $b_2 > b_1$ such that

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

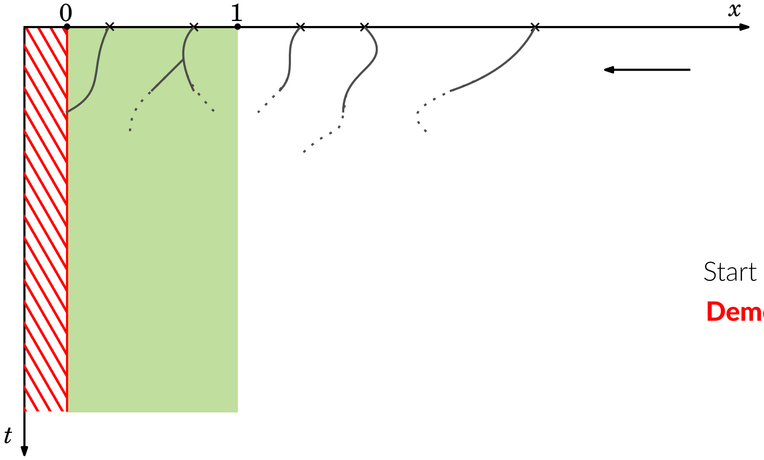
for all $b \in (b_1, b_2)$.

$\hookrightarrow$ recall that $\alpha(v) = \frac{v+\sqrt{v^2-1}}{v-\sqrt{v^2-1}}$

time scale $N^{\alpha-1}$

$\alpha(v) \in (1,2)$

THE SEMIPUSHED REGIME



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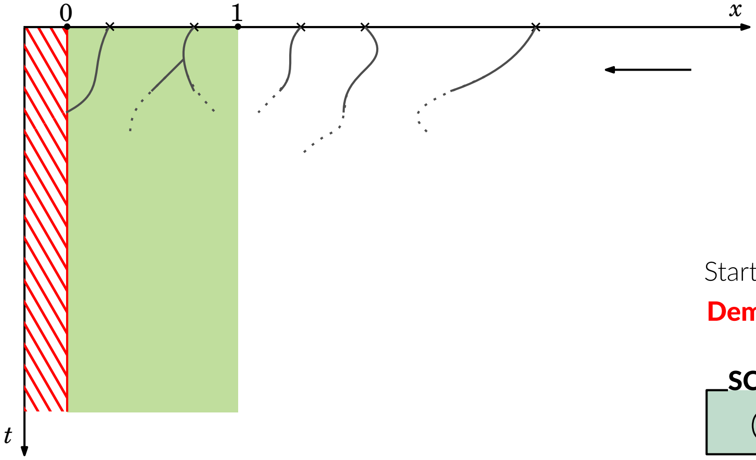
Start with N particles distributed according to $\tilde{h}$

Demographic fluctuations ?

THE SEMIPUSHED REGIME



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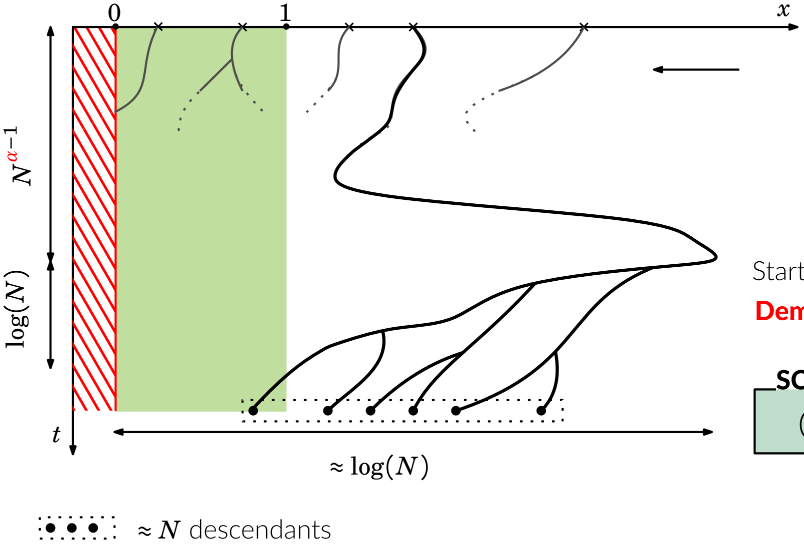
Demographic fluctuations ? Z_t = number of individuals

Let N goes to ∞

SCALING LIMIT

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

THE SEMIPUSHED REGIME



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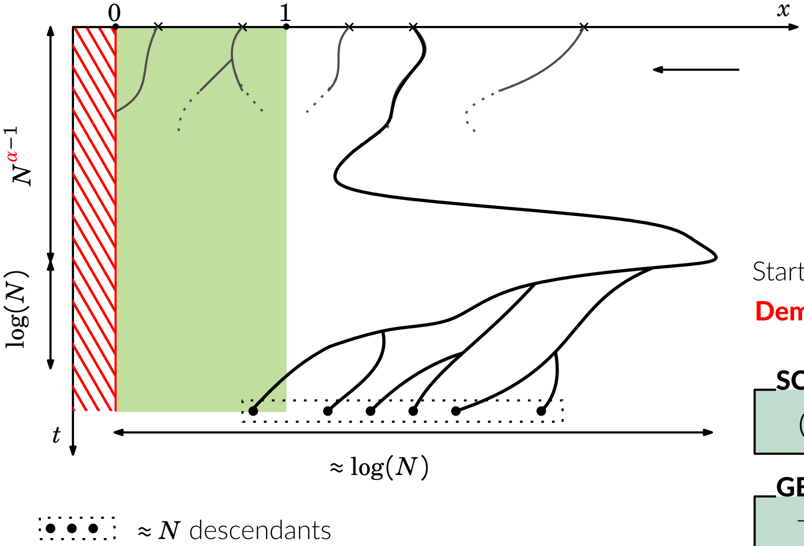

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SCALING LIMIT

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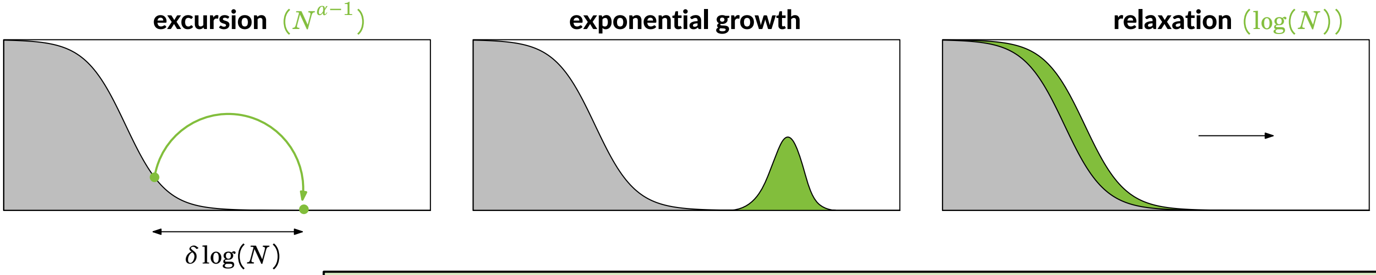
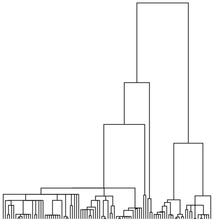
GENEALOGY

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

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





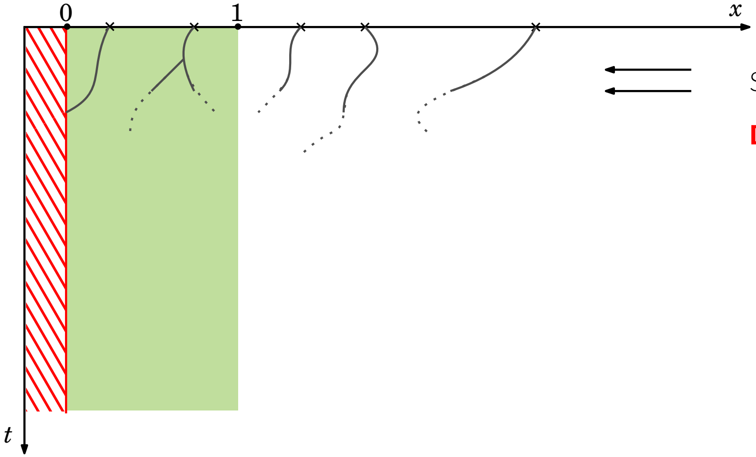
- The invasion is driven by **excursions** of particles
- These excursions generate **large subfamilies** in the associated genealogy, **diversity loss**
- Particles at the tip have a large reproductive value $\Rightarrow$ **large reproductive variance** (in some sense)
- fast relaxation $\Rightarrow$ 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 $b > b_2$, $\alpha > 2$

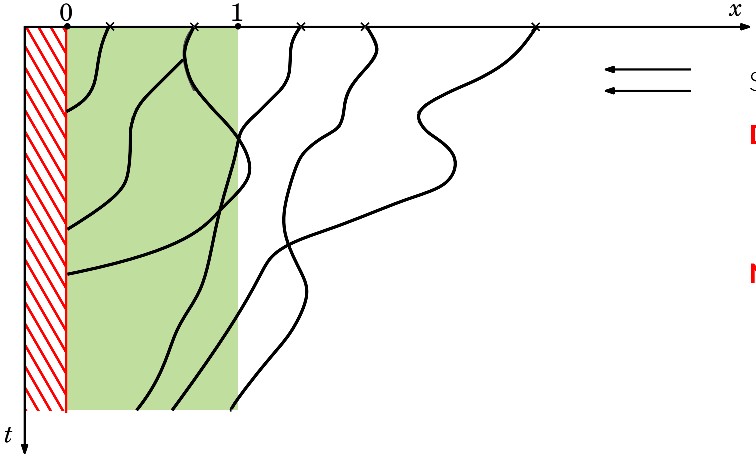
Start with N particles distributed according to $\tilde{h}$

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 $\tilde{h}$

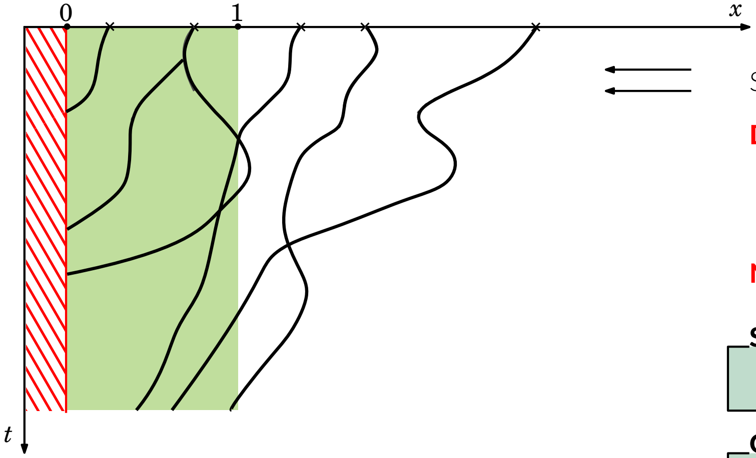
Demographic fluctuations ?

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

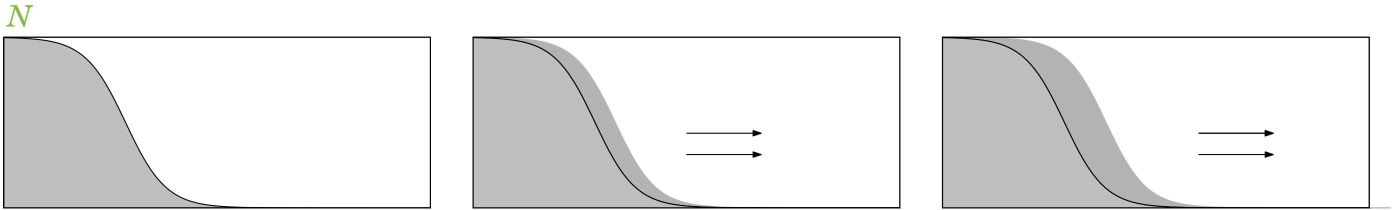
SCALING LIMIT

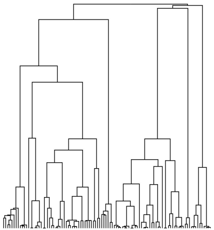
$(\frac{1}{N} Z_{tN}) \Rightarrow (X_t)$ X is a Feller diffusion

GENEALOGY

The genealogy of the BBM converges to Kingman's coalescent

THE FULLY PUSHED REGIME $b > b_2$

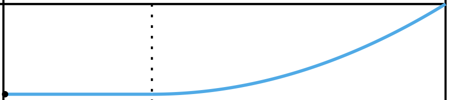
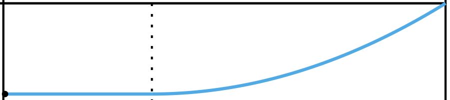
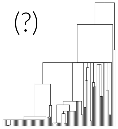
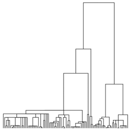
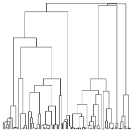




- The invasion is pushed by the **growth** in the front
- This generates only **binary mergers** in the associated genealogy, **wide genetic diversity**
- The tip is not accessible $\Rightarrow$ **finite reproductive variance**

Spectral analysis and $\boldsymbol{k}$-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			
	time scale fluctuations	$\log(N)^3$	$N^{\alpha-1}$	N
PARTICLE SYSTEM	b	b_1	b_2	
	drift $\mu(b)$ 1			
	time scale fluctuations	$\log(N)^3$ (?)	$N^{\alpha-1}$	N
	genealogy □	(?) 		

□ Berestycki, Berestycki, Schweinsberg 2013


Besançon meeting on
PROBABILITY
ECOLOGY
& EVOLUTION
December 10th, 2024 @MSHE Besançon
Vincent BANSAYE
École Polytechnique
Florin BOENKOST
University of Vienna
Céline BONNET
INRIA Lyon
Madeleine KUBASCH
Sorbonne Université
Martin MÖHLE
University of Tübingen
Nicolás ZALDUENDO
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