A branching particle system as a model of pushed fronts

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joint work with E. Schertzer and F. Foutel–Rodier

Motivation

⇝ **cooperating** population invading a 1D-habitat

competition	**cooperation** (or Allee effect)
individuals compete for resources	collective defence against predators difficulty to find a mate at low densities

⇝ **internal mechanisms** driving the invasion

cooperation vs. **competition** $\Rightarrow$ phase transition ?

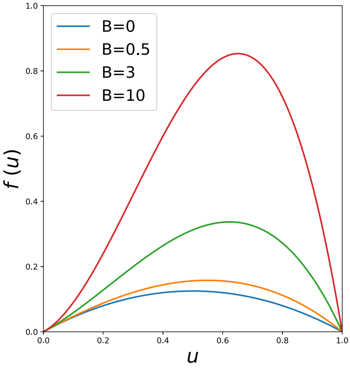
⇝ **genealogical structure of the population** ?

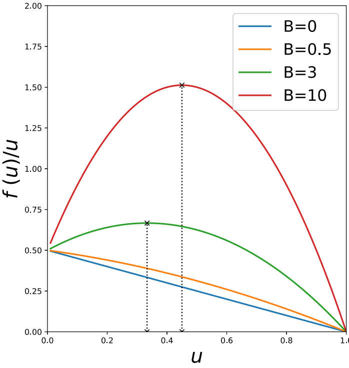
Monostable RD Equations: $u(t,x) \in [0,1]$ = density of individuals

$$u_t = \frac{1}{2}u_{xx} + f(u) \quad \text{with} \quad f(u) = \frac{1}{2}u(1-u)(1+Bu)$$

cooperation in the PDE

the per capita growth rate $\frac{f(u)}{u}$ is maximal at intermediate densities

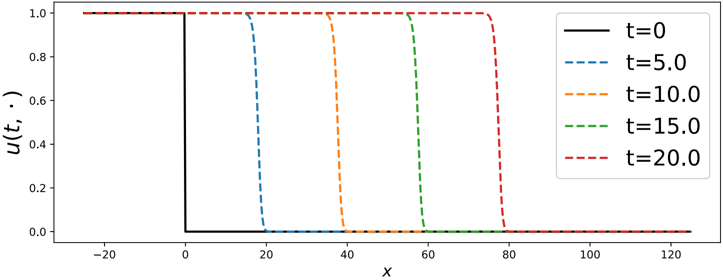




B= strength of the cooperation

Convergence to travelling wave solutions: if $u(0,x) = \mathbf{1}_{x<0}$, for $t \gg 1$

$$u(t,x) \approx \varphi(x - ct + x_0)$$



c speed of invasion

φ limiting profile of the invasion

Macroscopic dynamics of the invasion

Pulled and pushed fronts two classes of travelling fronts Stokes '76

$$u_t = \frac{1}{2} u_{xx} + f(u) \quad \text{with} \quad f(u) = \frac{1}{2} u(1-u)(1+Bu)$$

pulled fronts $c = \sqrt{2f'(0)}$

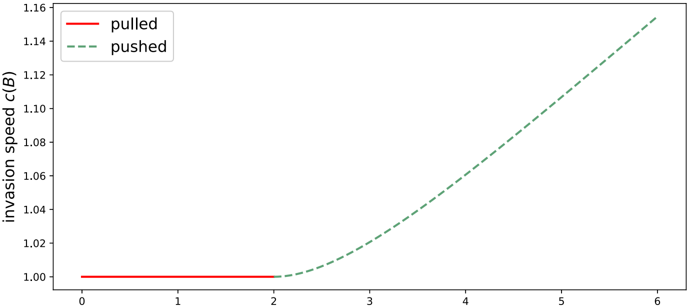
speed as the **linearised** equation

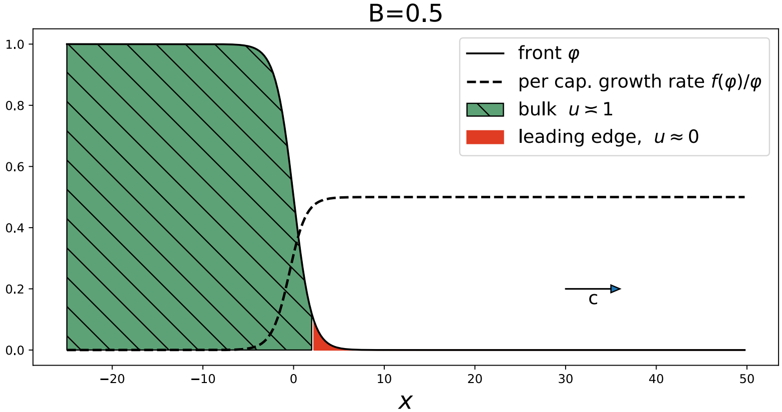
$$u_t = \frac{1}{2} u_{xx} + f'(0)u$$

pushed fronts $c > \sqrt{2f'(0)}$

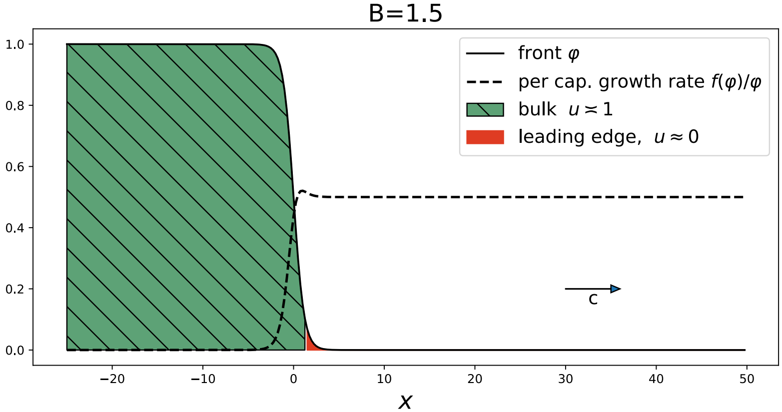
faster than pulled fronts

First phase transition: B large enough $\Rightarrow$ acceleration of the fronts





strength of the cooperation	$B \in (0, 2)$	$B > 2$
type of invasion	pulled	pushed
speed c	$c = \sqrt{2f'(0)}$	$c > \sqrt{2f'(0)}$



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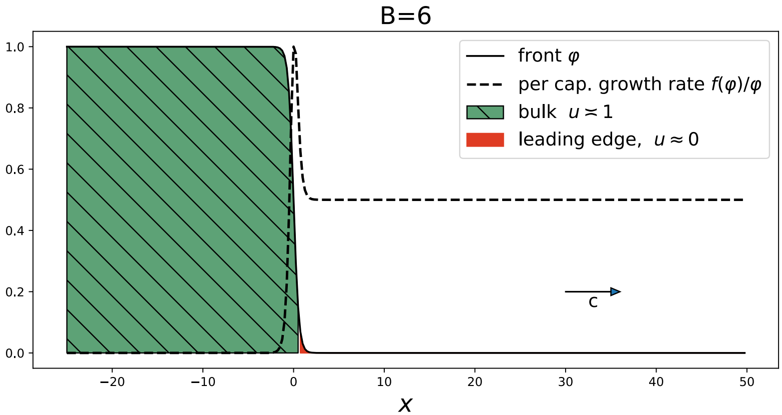


strength of the cooperation	$B \in (0,2)$	$B > 2$
type of invasion	pulled	pushed
speed c	$c = \sqrt{2f'(0)}$	$c > \sqrt{2f'(0)}$

Questions:

1. Where are the particles leading the invasion and thus the evolutionary dynamics ?
2. Sample an individual at the tip of the invasion front at time T. Where is its ancestor at time $T - t$?
3. Same question for two individuals sampled at time t and their MRCA.

(?) at the leading edge in **pulled** fronts,

(?) in the bulk for **pushed** fronts.

⇝ Not so simple !

4. Genealogical structure of k ind. sampled at the tip of the front ?

A third class of monostable invasions Birzu et al. '18

Effect of demographic fluctuations on the fronts arising from

$$u_t = \frac{1}{2} u_{xx} + \frac{1}{2} u(1-u)(1+Bu) + \overbrace{\sqrt{\frac{u}{N}} W(t,x)}^{\text{demographic fluctuations}} \;,$$

N: *local density* of individuals

X_t: position of the front

Numerical observations:

$$\langle (X_t - ct)^2 \rangle \approx \sigma^2(N) t$$

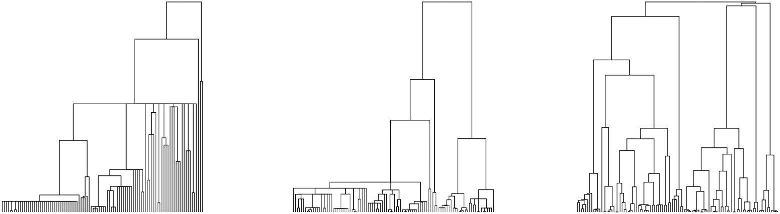
Allee effect	$B \in (0,2)$	$B \in (2,4)$	$B > 4$
in the PDE	pulled waves	pushed waves	
variance σ^2	$\log(N)^{-3}$	$N^{1-\tilde{\alpha}}$, $\tilde{\alpha} \in (1,2)$	N^{-1}
time scale	$\log(N)^3$	$N^{\tilde{\alpha}-1}$	N
in the SPDE	pulled	semi pushed	fully pushed
effect fluctuations	very sensitive		CLT

B=0 : Brunet, Derrida, Mueller, Munier '06

Microscopic model for invasion fronts capturing

(?) the internal mechanisms leading to this second phase transition ?

(?) the genealogical structure at the tip ?

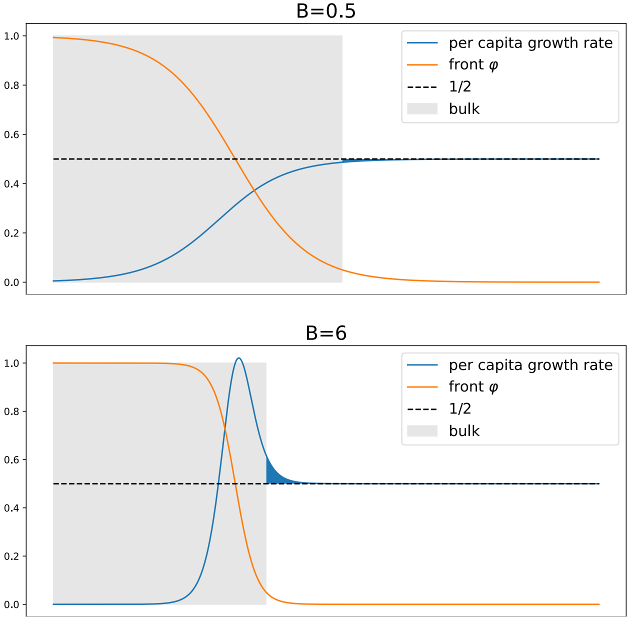


Bolthausen–Sznitman $\alpha = 1$	Beta$(2-\alpha, \alpha)$, $\alpha \in (1,2)$	Kingman $\alpha = 2$
(?) pulled	**(?)** semi pushed	**(?)** fully pushed
$B = 0$, Brunet, Derrida, Mueller, Munier '06		

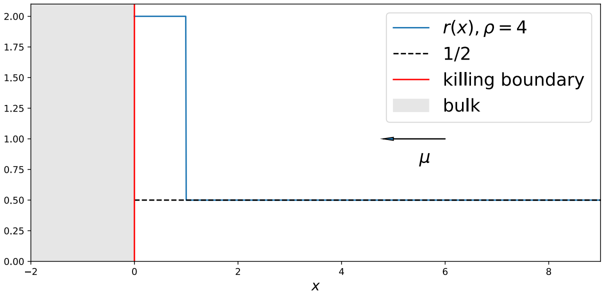
Picture by F. Boenkost

Birzu et al. '20

A toy model


B=0.5
1.0
0.8
0.6
0.4
0.2
0.0
per capita growth rate
front φ
1/2
bulk
B=6
1.0
0.8
0.6
0.4
0.2
0.0
per capita growth rate
front φ
1/2
bulk

A toy model



Dyadic branching Brownian motion with absorption at 0 with

- space-dependent branching rate $r(x)$:

$$r(x) = \frac{1}{2} + \frac{\rho - 1}{2} \mathbf{1}_{x \in [0,1]},$$

  ρ strength of the cooperation

- negative drift $-\mu(\rho)$ chosen such that the number of particles stays *roughly constant*

  μ speed of the wave

The case $\rho = 1$ (Berestycki, Berestycki, Schweinsberg '13)

For $\rho = 1$, $\mu = 1$ (speed of pulled waves)

Z_t = number of particles in the moving frame at time t

At $t = 0$, the system starts with $\approx N$ particles in a *stable* configuration

Let $\bar{Z}_t = Z_t / N$.

Theorem (demographic fluctuations)

$(\bar{Z}_{\log(N)^3 t})_{t>0}$ converges to **Neveu's Continuous-state branching process** (CSBP) as $N \to \infty$.

(i) time scale of the fluctuations for $B = 0$ in the SPDE.

(ii) Genealogy associated to Neveu's CSBP = Bolthausen–Sznitman coal. (Bertoin, Le Gall '00)

Theorem (genealogy)

The genealogy of the BBM is given by a **Bolthausen–Sznitman coalescent** on the time scale $\log(N)^3$

□ **Can we obtain a similar result on $\bar{Z}_t$ for $\rho > 1$?**

□ **Genealogy of the BBM ?**

The pulled and pushed regimes in the particle system

Density of particles in the system:

$$t \gg 1, \quad p_t(x,y)dy \approx e^{\mu(x-y)} \overbrace{e^{\left(\lambda_1 + \frac{1-\mu^2}{2}\right)t}}^{\text{mass loss}} v_1(x)v_1(y)dy,$$

where (λ_1, v_1) are the principal e.v. of the Sturm–Liouville problem

$$\frac{1}{2}u'' + \frac{\rho-1}{2}\mathbf{1}_{[0,1]}u = \lambda u, \quad u(0) = u(L) = 0, \ L \to \infty.$$

$\rightsquigarrow$ $\lambda_1 = \lambda_1(\rho)$ quantifies the growth of the system $\Rightarrow$ we set

$$\mu = \sqrt{1 + 2\lambda_1}$$

Pulled/pushed regime.

1. if $\rho < \rho_1$, $\lambda_1(\rho) = 0$ **(pulled)**
2. if $\rho > \rho_1$, $\lambda_1(\rho) > 0$ and $\lambda_1 \nearrow\nearrow$ w. r. t. ρ **(pushed)**

   in this case, $v_1(x) \propto e^{-\sqrt{\mu^2-1}\ x}$ as $x \to \infty$.

notation: $\beta := \sqrt{\mu^2 - 1}$ **(decay of the first e.v.)**

The semi pushed regime in the particle system

Assume that the system starts with N particles at 1.

$\bar{Z}_t = \frac{Z_t}{N}$ rescaled number of particles in the system

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

The semi-pushed regime (T. '22)

There exist $\rho_1 < \rho_2$ such that for all $\rho \in (\rho_1, \rho_2)$,

1. the exponent α is increasing and $\alpha(\rho_i) = i$
2. $(\bar{Z}_{N^{\alpha-1}t})_{t>0}$ converges (f.d.d.) to an α-**stable CSBP**.

Conjectures

if $\rho < \rho_1$ ($\mu = 1$, $\alpha = 1$), $(\bar{Z}_{\log(N)^3 t})_{t>0} \Rightarrow$ **Neveu**'s CSBP

if $\rho > \rho_2$ ($\mu > \frac{3}{4}\sqrt{2}$, $\alpha > 2$), $(\bar{Z}_{Nt})_{t>0} \Rightarrow$ **Feller** diffusion

Remark α-**stable CSBP** $\Leftrightarrow$ time changed Beta$(2-\alpha, \alpha)$-coalescent

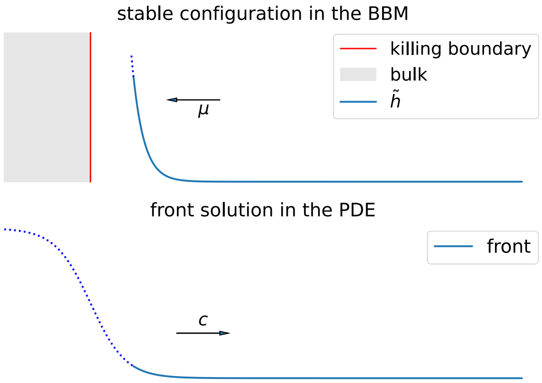
time change $T_t := \int_0^t (X_s)^{1-\alpha}$, $T^{-1}(t) = \inf\{s > 0 : T_s > t\}$ (X_s α-stab.)

(Birkner, Blath, Capaldo, Etheridge, Möhle, Schweinsberg, Wakolbinger' 05)

Remarks

$$p_t(x,y) \approx \underbrace{e^{\mu x} v_1(x)}_{\text{reproductive value } h(x)} \times \underbrace{e^{-\mu y} v_1(y)}_{\text{stable configuration } \tilde{h}(y)}$$

$$v_1(y) \approx e^{-\beta y}, \quad \beta = \sqrt{\mu^2 - 1}$$



	in the BBM	in the (S)PDE
stable configuration	$\tilde{h}(y) \propto e^{-(\mu+\beta)y}$	$\varphi(y) \sim e^{-(c+\sqrt{c^2-1})y}$
α semi pushed	$\alpha = \frac{\mu+\beta}{\mu-\beta}$	$\alpha = \frac{c+\sqrt{c^2-1}}{c-\sqrt{c^2-1}}$

Remarks

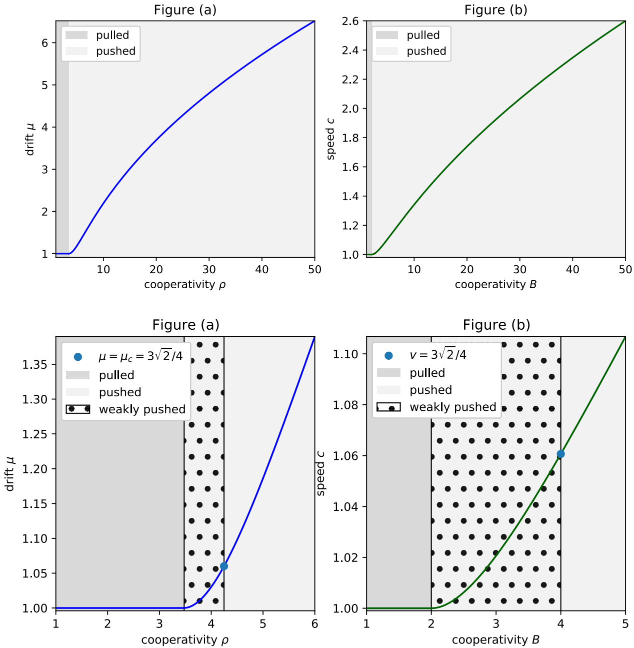
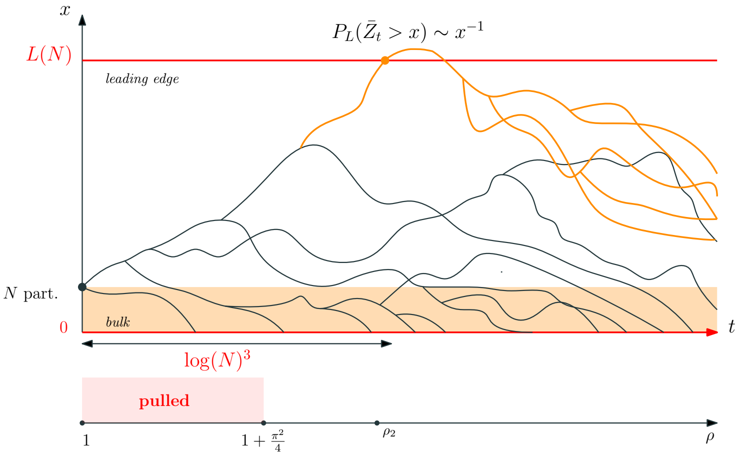


Figure (a)
pulled
pushed
drift μ
cooperativity ρ
Figure (b)
pulled
pushed
speed c
cooperativity B
Figure (a)
$\mu = \mu_c = 3\sqrt{2}/4$
pulled
pushed
weakly pushed
drift μ
cooperativity ρ
Figure (b)
$v = 3\sqrt{2}/4$
pulled
pushed
weakly pushed
speed c
cooperativity B

Idea of the proof:

Berestycki, Berestycki, Schweinsberg ($\rho = 1$) '13: Set $L(N)$ s.t. $\mathbb{E}_L[\bar{Z}_t] = 1$



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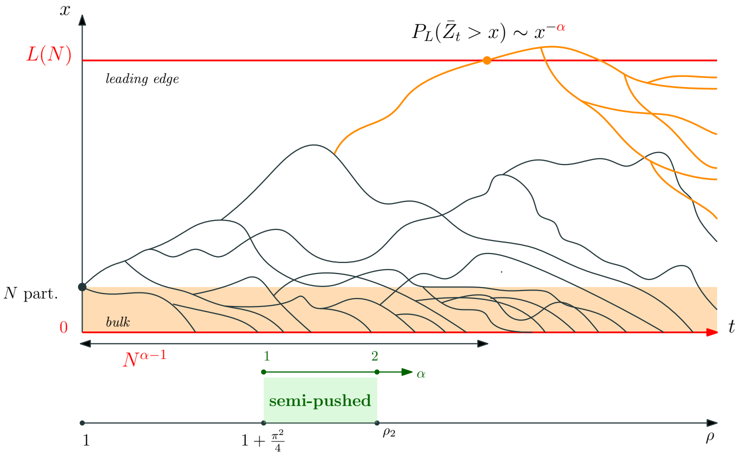

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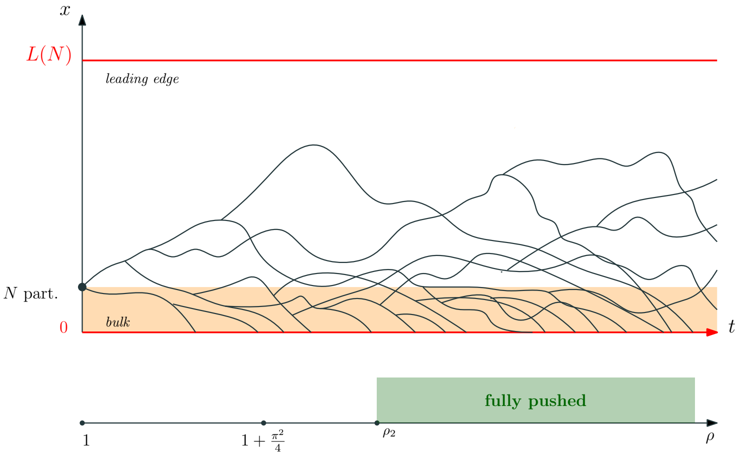

The fully pushed regime $\alpha > 2$

Method of moments (Foutel-Rodier, Schertzer '22)

Kolmogorov estimate (Schertzer-T. '23)

$$N\mathbb{P}_x(\bar{Z}_{Nt} > 0) \to \frac{2h(x)}{\Sigma^2(\rho)t}, \quad N \to \infty. \quad h(x) := e^{\mu x} v_1(x)$$

Remark $\approx$ Kolmogorov estimate for multi-type GW processes

$\mathbb{E}_x[\bar{Z}_t] \approx \frac{1}{N} h(x) \Rightarrow h(x)$ **reproductive value** of a part. located at x

$\Sigma^2(\rho)/2$ **"reproductive variance"**

Yaglom law (Schertzer-T. '23)

Starting from 1 part. at x, conditional on survival,

$\bar{Z}_{Nt} \Rightarrow \frac{\Sigma^2 t}{2} \mathcal{E}$ ($\mathcal{E}$ standard **exponential** distribution)

Remark multi-type GW, Feller diffusion

The fully pushed regime $\alpha > 2$

For 2 particles u, v alive at time t,

$$d_t(u, v) := \text{time to the MRCA } |v \wedge u|$$

At $t = 0$, the system starts with a single particle at $x > 0$.

Genealogy (Schertzer-T. '23)

Conditional on $\{Z_{tN} > 0\}$, sample k individuals in the BBM at time tN denoted by $(v_1, ..., v_k)$.
The distance matrix

$$\left(\frac{1}{N} d_{tN}(v_i, v_j)\right)_{i,j}$$

converges to that of a **critical GW process** with **finite variance** conditioned on surviving up to a large time.

Remark: only binary mergers

Moments of the BBM for $\alpha > 2$

spine = path of an immortal particle: stationary distribution $h\tilde{h} = (v_1)^2$

(Doob h-transform)

moments:

$$\mathbb{E}_x[\bar{Z}_t^{(K)}] \approx \frac{1}{N} h(x) K! t^{K-1} \left(\overbrace{\int r(z) h(z)^2 \tilde{h}(z) dz}^{=: \frac{\Sigma^2}{2}} \right)^{K-1} \underbrace{\left(\int \tilde{h} \right)^K}_{=1}$$

➤ **Reminder**: $v_1(z) \approx e^{-\beta z}$ $(z \gg 1)$, $h(z) = e^{\mu z} v_1(z)$ and $\alpha = \frac{\mu+\beta}{\mu-\beta}$.

(...) integral on the branching point of the genealogical tree

$$\Sigma^2 \propto \int e^{(\mu - 3\beta) z} dz < \infty \iff \mu < 3\beta \iff \alpha > 2.$$

Moments of the BBM for $\alpha > 2$

$$\mathbb{E}_x[\bar{Z}_t^{(K)}] \approx \frac{1}{N} h(x) K! t^{K-1} \left(\frac{\Sigma^2}{2}\right)^{K-1}$$

Kolmogorov estimate $\mathbb{P}_x\left(\bar{Z}_t > 0\right) \approx \frac{2}{\Sigma^2}\frac{h(x)}{tN}$

$$\mathbb{E}_x[\bar{Z}_t^{(K)} | \bar{Z}_t > 0] \approx K! \left(\frac{\Sigma^2 t}{2}\right)^{K}$$

$\Rightarrow$ moments of an exponential rv with parameter $\frac{\Sigma^2}{2} t$

The semi pushed regime $\alpha \in (1,2)$

$$\mathbb{E}_x[\bar{Z}_t^{(K)}] \approx \frac{1}{N} h(x) K! t^{K-1} \left(\overbrace{\int r(z) h(z)^2 \tilde{h}(z) dz}^{=: \frac{\Sigma^2}{2}} \right)^{K-1} \underbrace{\left(\int \tilde{h} \right)^K}_{=1}$$

(...) integral on the branching point of the genealogical tree

$$\Sigma^2 \propto \int e^{(\mu - 3\beta) z} dz < \infty \iff \mu < 3\beta \iff \alpha > 2.$$

- ☛ $\alpha > 2$**:** the branching points are concentrated around 0
- ☛ $\alpha \in [1,2)$**:** the branching points are at $+\infty$

Cut-off method Foutel-Rodier, Schertzer, T. 23+

The genealogy of the BBM coincides with that of an α-stable CSBP.

Conclusion

Questions: Sample an individual at the tip of the invasion front at time T. Where is its ancestor at time $T - t$? Same question for two individuals sampled at time t and their MRCA.

path of an immortal particle

☛ $\alpha > 1$ $(\mu > 1)$ **pushed regime**

stat. distribution $\boxed{q_t(x, y) \approx v_1(y)^2 \approx e^{-2\beta y}}$ with $\beta = \sqrt{\mu^2 - 1}$

➥ **in the bulk**

☛ $\alpha = 1$ $(\mu = 1)$ **pulled regime**

no stationary distribution ➥ **at the leading edge**

position of the branching points in the genealogical tree

☛ $\alpha > 2$ **fully pushed regime**

$\Sigma^2 < \infty$ ➥ **in the bulk**

☛ $\alpha \in [1, 2)$ **pulled and semi pushed regimes**

$\Sigma^2 = \infty$ ➥ **at the leading edge**

Conclusion

	pulled	semi-pushed	fully pushed
B	0	2	4
PDE	pulled	pushed	
invasion speed	$c = 1$	$c = c(B) > 1$	
time scale	$\log(N)^3$	$N^{\tilde{\alpha}-1}$	N
ρ	1	ρ_1	ρ_2
time scale	$\log(N)^3$	$N^{\alpha-1}$	N
drift	$\mu = 1$	$\mu = \mu(\rho) > 1$	
exponent	$\alpha = 1$	$\alpha \in (1, 2)$	$\alpha > 2$
limiting CSBP	Neveu (?)	α-stable	Feller
evolutionary dyn. driven by part....	at the **leading edge** $\Sigma^2 = +\infty$		in **the bulk** $\Sigma^2 < \infty$
path of an immortal part.	far to the **right** no stat. distribution	in the **bulk** $v_1^2(x) \sim e^{-2\beta x}$	