Go or Grow particles

joint work with M. Demircigil (U Aruzona)

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Outline

Motivatons

Stochastic model

Convergence of the model

Pushed or pulled

What's next

Travelling waves and Chemo-Aerotaxis

- Collective biased movement of cells in response to changing levels of **energy sources** (sugar) or **oxygen**.

- Experiments of Adler (1966): E. coli placed at one end of a capillary tube containing an energy source and oxygen migrate out into the tube in one or two bands.
  - Bacteria create a gradient of oxygen/energy source. Then, they **move preferentially** in the direction of the higher concentration of the chemical.
  - Consequence: bands of bacteria (or rings of bacteria in the case of agar plates) **form and move out**.

Travelling rings and self generated gradients

- Work of O. Cochet-Escartin, M. Demircigil, S. Hirose, B. Allais, P. Gonzalo, I. Mikaelian, K. Funamoto, C. Anjard, V. Calvez, J. Rieu (2021)
  Hypoxia triggers collective aerotactic migration in Dictyostelium discoideum

- Videos 1 and 3 here:
  https://elifesciences.org/articles/64731

Observations

- Traveling wave: stationnary profile at constant speed
- How to explain a collective movement as a wave?
- Two collective propagation phenomena:
  - Aerotaxis (through self-generated gradients)
  - Expansion by cell division (and diffusion) (as in F/KPP equation [1])
- How do these phenomena combine?

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[1] $\partial_t u - D\partial_{xx} u = ru(1-u)$ exhibits waves with speed $2\sqrt{rD}$

Go or Grow[2] Model of Demircigil and co-authors

- 1D Elementary Model:
  - doesn't aim at describing precisely the experiment
  - ingredients sufficient to trigger a traveling wave
- **Hypothesis**: cells ρ have two distinct behaviors:
  - *Go:* if $C < C_{\text{thresh}}$, cells move the gradient upward
  - *Grow:* if $C > C_{\text{thresh}}$, cells divide

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[2] by analogy to a model in Hatzikourou *et al.*, Math. Med. Biol. (2012)

[3] similar hypothesis in a model for chimotaxis in *E. coli*, Saragosti *et al.*, PNAS (2011)

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$$\begin{cases} \partial_t \rho = D\partial_{xx}\rho - \partial_x \left(\chi \mathbb{1}_{C<C_{\text{thresh}}} \text{sign}(\partial_x C)\rho\right) + r\mathbb{1}_{C>C_{\text{thresh}}}\rho \\ \partial_t C = d\partial_{xx} C - \rho C \end{cases}$$

- Equation is with piecewise constant coefficients [3]
- Coupling through $\bar{x}(t)$ $(C(t,\bar{x}(t)) = C_{\text{thresh}})$
  - $x < \bar{x}(t)$: GO
  - $x > \bar{x}(t)$: GROW.

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Existence of Traveling Waves

Solutions of the form

$$(\rho(t,x), C(t,x)) = (\tilde{\rho}(x-\sigma t), \tilde{C}(x-\sigma t))$$

for a velocity σ to be determined.

Proposition 1

For any $\sigma \geq \sigma^*$, there exists a corresponding traveling wave

- *Large (aerotactic) bias: If $\chi > \sqrt{rD}$, then $\sigma^* = \chi + \frac{rD}{\chi}$*
- *Small (aerotactic) bias: If $\chi \leq \sqrt{rD}$, then $\sigma^* = 2\sqrt{rD}$*

Note: result not depending on C!

Pulled Wave or Pushed Wave?

- Small bias $\chi \leq \sqrt{rD}$: wave is *pulled* by cells at the leading edge.
  Propagation by cell division and diffusion, $\sigma^* = 2\sqrt{rD}$. (like FKPP)

- Large bias $\chi > \sqrt{rD}$: wave is *pushed* by the whole cell profile.
  Propagation by aerotaxis and cell divison, $\sigma^* = \chi + \frac{rD}{\chi}$.

Note: A pulled wave is driven by growth and diffusion of the population at the edge of the front with negligible contribution from the overall population, whereas a pushed wave is subject to a significant contribution from the overall population to the net propagation.

Note: All the above is summarized in M. Demircigil thesis and preprint *When Self-Generated Gradients interact with Expansion by Cell Division and Diffusion. Analysis of a Minimal Model*. For pushed/pulled waves see J. Garnier et al. *Inside dynamics of pulled and pushed fronts*. JMPA (2012).

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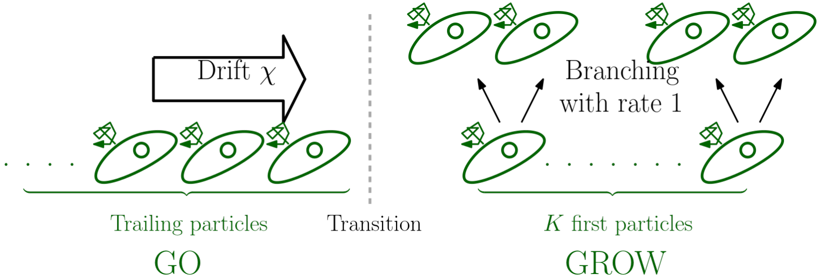
A stochastic twist on Go or Grow of Demircigil-T.

- Finite population of Brownian particles
- New *Go or Grow* Rule :
  - the first K particles : GROW (divide with rate 1)
  - the trailing particles : GO (advection with speed χ)



+ Brownian Motion

Crossroad of two classes of models

1. No brunching: mean-field models with rank based interactions and the famous Atlas model in finance (see e.g. Jourdain-Reygner, Stoch PDE: Anal Comp, 2013; EJP, 2014; Ichiba-Pal-Shkolnikov, PTRF 2013)
2. No drift: rank-dependent branching Brownian motions, e.g. N-BBM, (see e.g. Maillard, PTRF, 2016).

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2. No drift: rank-dependent branching Brownian motions, e.g. N-BBM, (see e.g. Maillard, PTRF, 2016).

Our goals:

- weighting individuals by $1/K$ show the convergence as $K \to \infty$ to a PDE with a new Go or Grow rule.
- explore the spreading properties of the stochastic model (K fixed).

Building the model

- **Spatial configuration** of our particles weighted by $\frac{1}{K}$ encoded by

$$\mu_t^K = \frac{1}{K} \sum_{i \in V_t^K} \delta_{X_t^i}, \quad t \geq 0 \tag{1}$$

where V_t^K is the label set of individuals alive at time t and X_t^i their positions. (labels with classical Ulam-Harris notation $\mathcal{U}$). State space is

$$\mathcal{M}_K := \left\{ \frac{1}{K} \sum_{i=1}^{n} \delta_{x_i}; \quad n \in \mathbb{N}, x_1, \ldots, x_n \in \mathbb{R} \right\}.$$

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- Total rate of **division** is always equal to K! Exponential clock with parameter K rings → choose uniformly among the K particles on the far right and add a new one in its place.

- Between the times of birth events $(T_m)_{m\geq 0}$, ($T_0 = 0$), **positions** evolve through the following SDE, for $i \in V_{T_m}, t \in (T_m, T_{m+1}]$,

  $$X_t^i = X_{T_m}^i + \chi \int_{T_m}^{t} \mathbb{1}\Big(\sum_{j \in V_{T_m}} \mathcal{H}(X_s^j - X_s^i) > K\Big) ds + \sqrt{2}(W_t^i - W_{T_m}^i),$$

  where $(W^i)_{i\in\mathcal{U}}$ are independent standard one-dimensional Brownian motions and $\mathcal{H}(x) = \mathbb{1}(x \geq 0)$.

Note: Given T_m and V_{T_m} this SDE admits unique strong solutions (bounded coeff, $d = 1$).

SDE for μ_t^K

For $\nu \in \mathcal{M}_K$ and $\mathcal{H}(x) = \mathbb{1}(x \geq 0)$ we note

$$a(x,\nu) = \mathbb{1}_{(\langle \nu, \mathcal{H}(\cdot - x)\rangle > 1)}, \;\; b(x,\nu) = \mathbb{1}_{(\langle \nu, \mathcal{H}(\cdot - x)\rangle \leq 1)}$$

$$\begin{aligned}
&\langle \mu_t^K, \phi_t \rangle - \langle \mu_0^K, \phi_0 \rangle - \int_0^t \left\langle \mu_s^K, \frac{\partial \phi_s}{\partial s} \right\rangle ds = \\
&\frac{1}{K} \int_0^t \sum_{i \in V_s^K} \left(\chi \frac{\partial \phi_s}{\partial x}(X_s^i) a(X_s^i, \mu_s^K) + \frac{\partial^2 \phi_s}{\partial x^2}(X_s^i) \right) ds + \frac{\sqrt{2}}{K} \int_0^t \sum_{i \in V_s^K} \frac{\partial \phi_s}{\partial x}(X_s^i) dW_s^i \\
&+ \int_0^t \int_{\mathcal{U}} \int_0^1 \mathbb{1}_{\left(i \in V_s^K, \theta \leq b(X_{s-}^i, \mu_{s-}^K)\right)} \frac{\phi_s(X_{s-}^i)}{K} \mathcal{N}(ds, di, d\theta) \\
&= \int_0^t \int \mathcal{L}_{\mu_s^K} \phi_s \mu_s^K(dx) ds + M_t^{K,\phi,W} + M_t^{K,\phi,\mathcal{N}}
\end{aligned}$$

with $M_t^{K,\phi,W}$, $M_t^{K,\phi,\mathcal{N}}$ martingales, and

$$\mathcal{L}_\nu \phi(x) := \chi \frac{\partial \phi}{\partial x}(x) a(x,\nu) + \frac{\partial^2 \phi}{\partial x^2}(x) + \phi(x) b(x,\nu)$$

Sending $K \to \infty$

- New *Go or Grow* Rule. Let $P(t,x) = \int_x^{+\infty} \rho(t,y)dy$:
  - *Grow:* if $P < 1$, cells divide with rate 1
  - *Go:* if $P \geq 1$, cells move to the right with drift χ.

$$\partial_t \rho = \partial_{xx}^2 \rho - \chi \partial_x \left(\mathbb{1}_{P \geq 1} \rho \right) + \mathbb{1}_{P<1} \rho$$

Sending $K \to \infty$

- New *Go or Grow* Rule. Let $P(t,x) = \int_x^{+\infty} \rho(t,y)dy$:
  - *Grow:* if $P < 1$, cells divide with rate 1
  - *Go:* if $P \geq 1$, cells move to the right with drift χ.

$$\partial_t \rho = \partial^2_{xx} \rho - \chi \partial_x \left(\mathbb{1}_{P \geq 1} \rho \right) + \mathbb{1}_{P<1} \rho$$

- The equation on P is useful:

$$\partial_t P = \partial^2_{xx} P - \chi \mathbb{1}_{P \geq 1} \partial_x P + \min\{1, P\}$$

- Traveling wave profile $u^\sigma(z)$, *i.e.* $u_t(x) = u^\sigma(x - \sigma t)$ is a solution if and only if $\sigma \geq \sigma^*$ where

$$\sigma^* = \begin{cases} \chi + \frac{1}{\chi} & \text{if } \chi > 1 \\ 2 & \text{if } \chi \leq 1 \end{cases} .$$

(u^{σ^*} explicit)

Recent preprint of C. Henderson and M. Demircigil.

- Let $\bar{x}(t)$ be the threshold, *i.e.* $P(t, \bar{x}(t)) = 1$.
  What is the asymptotic behavior of $\bar{x}(t)$?

	Asymptotic behavior of $\bar{x}(t)$
$\chi > 1$	$\bar{x}(t) = \left(\chi + \frac{1}{\chi}\right) t + O(1)$
$\chi < 1$	$\bar{x}(t) = 2t - \frac{3}{2}\ln(t) + O(1)$
$\chi = 1$	$\bar{x}(t) = 2t - \frac{1}{2}\ln(t) + O(1)$

- The logarithmic shift is called the Bramson shift
- Pushed/pulled wave characterized by absence/presence of a Bramson shift.

Simulation - speed of spreading over time

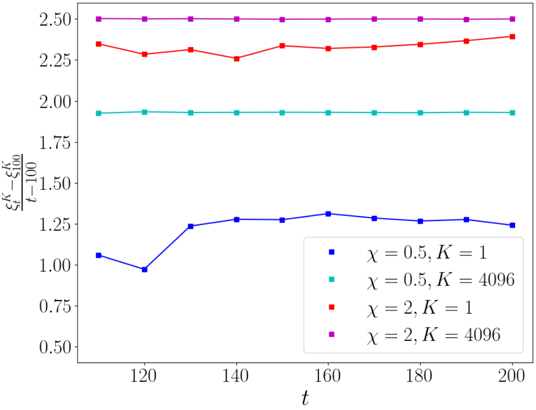

Figure: Graphic representation of $\frac{\xi_t^K - \xi_{100}^K}{t-100}$, where ξ_t^K is the position of the K-th particle at time t, for $K = 1$, $K = 4096$, $\chi = 2$, $\chi = \frac{1}{2}$

Simulation - Speed of spreading with K

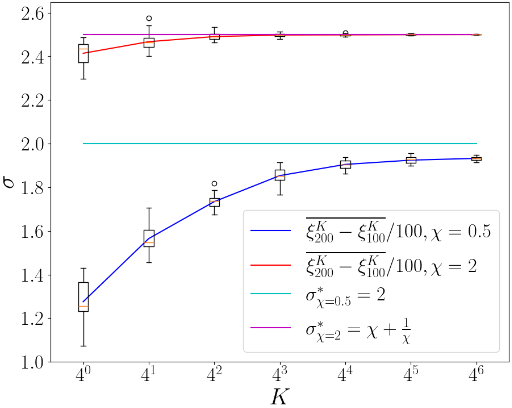

Figure: The average velocity of the K-th particle over the interval $[100, 200]$, *i.e.* $\frac{\xi^K_{200} - \xi^K_{100}}{100}$, where ξ^K_t is the position of the K-th particle at time t. As K increases, in average this estimator gets closer and closer to the deterministic traveling wave speed

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Convergence as $K \to \infty$

- Main issue: discontinuous drift coefficient and branching rate as we have rank based interactions!
- Fix: when you look at empirical CDF $\int_{\cdot}^{\infty} \mu_t^K(dx) =: \tilde{\mathcal{H}} * \mu_t^K(\cdot)$ your coefficients smooth out → discrete integration by parts inspired by Jourdain-Reygner.

Large-Population Limit ($K \to +\infty$)

Theorem 1

Let $T > 0$ and $(\mu_t^K)_{t \leq T}$, which satisfies the SDE above. Suppose

$$\mathbb{E}\left[|\langle \mu_0^K, 1\rangle|^3\right] < +\infty$$

and that μ_0^K converges , as $K \to \infty$, in probability in $M_F^w(\mathbb{R})$ to some deterministic $\mu_0 = \rho_0$.
Then $(\tilde{\mathcal{H}} * \mu_t^K)$ converges along subsequences as $K \to \infty$ to a weak solution of the PDE:

$$\partial_t P = \partial_{xx}^2 P - \chi \mathbb{1}_{P \geq 1} \partial_x P + \min\{1, P\}. \qquad (2)$$

Provided some **additional hypothesis** *on ρ_0, uniqueness holds and we can pass from the solution to (2), to the density PDE for ρ.*

Comment: **Additional hypothesis** needed for uniqueness, $\rho_0 \geq 0$, in $L^1 \cap L^\infty$, not all the particles are in the Grow regime, ρ_0 bounded from below in an open set around the threshold position.

Ideas of the proof of convergence

- First, show tightness of (μ_t^K) in vague topology (compactly supported test functions), using the Aldous-Rebolledo criterion.
- Then, extend tightness to weak topology (bounded test functions), using Roelly-Méléard criterion.
- The martingales $M_t^{K,\phi,W}, M_t^{K,\phi,\mathcal{N}} \to 0$ in L^2.
- To identify the limit, use $\phi_t = \mathcal{H} * \varphi_t$ as test functions. Some bits are obvious:

$$\left\langle \frac{\partial^2 \mathcal{H} * \varphi_t}{\partial x^2}, \mu_t^K \right\rangle = \left\langle \frac{\partial^2 \varphi_t}{\partial x^2}, \tilde{\mathcal{H}} * \mu_t^K \right\rangle$$

some are not

$$\left\langle \frac{\partial \mathcal{H} * \varphi_t}{\partial x} a(\cdot, \mu_t^K), \mu_t^K \right\rangle = \left\langle \frac{\partial \varphi_t}{\partial x}, A\left(\tilde{\mathcal{H}} * \mu_t^K(\cdot)\right) \right\rangle,$$

where $A(p) = \int_0^p \mathbb{1}_{s>1} ds$.

The not obvious bit

Let $H^i(\mu_s^K)$ denote the i-th particle in the system. Consider

$$
\begin{aligned}
&\left\langle \mu_s^K, \frac{\partial \phi_s}{\partial x} a(\cdot, \mu_s^K) \right\rangle \\
=&\frac{1}{K} \sum_{i=1}^{\langle \mu_s^K, K\rangle} \frac{\partial \phi_s}{\partial x}(H^i(\mu_s^K)) a(H^i(\mu_s^K), \mu_s^K) \\
=&\frac{1}{K} \sum_{i=1}^{\langle \mu_s^K, K\rangle} \int_{-\infty}^{H^i(\mu_s^K)} \frac{\partial \varphi_s}{\partial x}(x) dx a(H^i(\mu_s^K), \mu_s^K) \\
=&\int_{\mathbb{R}} \frac{\partial \varphi_s}{\partial x}(x) \frac{1}{K} \sum_{i=1}^{\langle \mu_s^K, K\rangle} \mathbb{1}_{\left(x \le H^i(\mu_s^K)\right)} a(H^i(\mu_s^K), \mu_s^K) dx \\
=&\int_{\mathbb{R}} \frac{\partial \varphi_s}{\partial x}(x) \sum_{i=1}^{\langle \mu_s^K, K\rangle} \mathbb{1}_{\left(x \le H^i(\mu_s^K)\right)} \frac{1}{K} \tilde{a}\left(\frac{i}{K}\right) dx,
\end{aligned}
$$

where $\tilde{a}(p) = \mathbb{1}_{p>1}$.

Observing next that $\tilde{a}(p)$ is constant on the intervals of the form $\left(\frac{i-1}{K}, \frac{i}{K}\right]$:

$$\frac{1}{K}\tilde{a}\left(\frac{i}{K}\right) = \int_{\frac{i-1}{K}}^{\frac{i}{K}} \tilde{a}\left(\frac{i}{K}\right) dp = \int_{\frac{i-1}{K}}^{\frac{i}{K}} \tilde{a}\left(p\right) dp = \int_{0}^{+\infty} \tilde{a}\left(p\right) \mathbb{1}_{\left(\frac{i-1}{K} < p \leq \frac{i}{K}\right)} dp.$$

This leads to

$$\begin{aligned} &\int_{\mathbb{R}} \frac{\partial \varphi_s}{\partial x}(x) \sum_{i=1}^{\langle \mu_s^K, K\rangle} \mathbb{1}_{\left(x \leq H^i(\mu_s^K)\right)} \frac{1}{K}\tilde{a}\left(\frac{i}{K}\right) dx \\ = &\int_{\mathbb{R}} \int_0^{+\infty} \frac{\partial \varphi_s}{\partial x}(x) \tilde{a}(p) \sum_{i=1}^{\langle \mu_s^K, K\rangle} \mathbb{1}_{\left(x \leq H^i(\mu_s^K)\right)} \mathbb{1}_{\left(\frac{i-1}{K} < p \leq \frac{i}{K}\right)} dp dx \end{aligned}$$

With a bit of mental gymnastics, you can see that

$$\sum_{i=1}^{\langle \mu_s^K, K\rangle} \mathbb{1}_{\left(x \leq H^i(\mu_s^K)\right)} \mathbb{1}_{\left(\frac{i-1}{K} < p \leq \frac{i}{K}\right)} = \mathbb{1}_{\left(p \leq \tilde{\mathcal{H}} * \mu_s^K(x)\right)} \qquad (3)$$

Hence

$$
\begin{aligned}
&\int_{\mathbb{R}}\int_0^{+\infty}\frac{\partial \varphi_s}{\partial x}(x)\tilde{a}(p)\sum_{i=1}^{\langle \mu_s^K,K\rangle}\mathbb{1}_{\left(x\leq H^i(\mu_s^K)\right)}\mathbb{1}_{\left(\frac{i-1}{K}<p\leq\frac{i}{K}\right)}dpdx\\
=&\int_{\mathbb{R}}\int_0^{+\infty}\frac{\partial \varphi_s}{\partial x}(x)\tilde{a}(p)\mathbb{1}_{(p\leq\tilde{\mathcal{H}}*\mu^K(x))}dpdx\\
=&\int_{\mathbb{R}}\frac{\partial \varphi_s}{\partial x}(x)A\left(\tilde{\mathcal{H}}*\mu^K(x)\right)dx
\end{aligned}
$$

Thus in conclusion, we have

$$
\left\langle \mu_s^K,\frac{\partial \phi_s}{\partial x}a(\cdot,\mu_s^K)\right\rangle=\left\langle \frac{\partial \varphi_t}{\partial x},A\left(\tilde{\mathcal{H}}*\mu_t^K(\cdot)\right)\right\rangle.
$$

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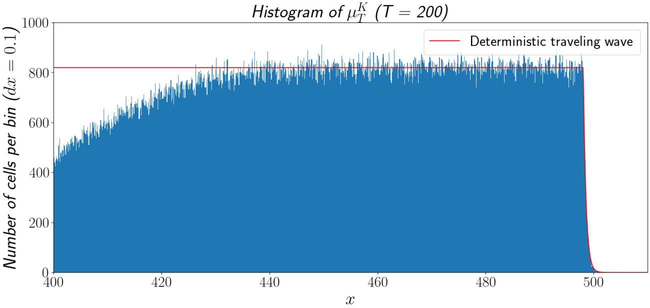
Another view on pushed vs pulled



- Gives rise to traveling waves
- We study the ancestral lineages (in the limit $K \to +\infty$)[11]

=> Gives an alternative viewpoint on pushed/pulled waves

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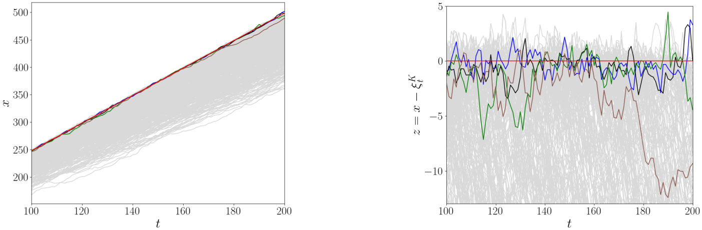
[11] Calvez, Henry, Méléard, Tran, 2022 (Annales Henri Lebesgue).
& Forien, Garnier, Patout, 2022 (Bull Math Biol.).

Where do the cells come from?

Consider a cell at a given time T, the ancestral lineage is the position of its ancestors for $t < T$.



(a) (b)

Figure: Graphical representation of the particle trajectories for $t \in [100, 200]$, with $\chi = 2, K = 256$. Figure (a) represents the trajectories in the stationary and Figure (b) in the moving frame.

According to Calvez *et al.* & Forien *et al.*, the ancestral lineage follows a simple SDE in the large-population limit $K \to +\infty$.

Where do the cells come from? $\chi > 1$

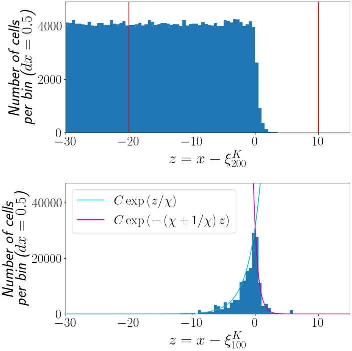


Figure: $\chi = 2, K = 4096$. Top: histogram of μ^K_T in the moving frame at $T = 200$. Bottom: histogram of the selected ancestors in the moving frame at $t = 100$. The number of selected particles is $n = 167686$ and the number of distinct ancestors is 2811.

For pushed waves, the ancestral lineage has a steady state.

Where do the cells come from? $\chi < 1$

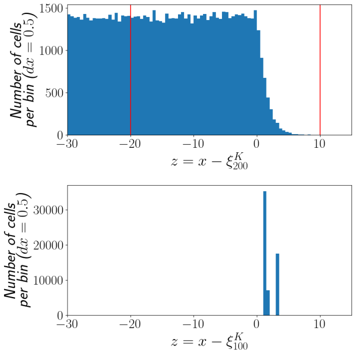


Figure: $\chi = \frac{1}{2}, K = 4096$. Top: histogram of μ^K_T in the moving frame at $T = 200$. Bottom: histogram of the selected ancestors in the moving frame at $t = 100$. The number of selected particles is $n = 59927$ and the number of distinct ancestors is 7.

For pulled waves, the ancestral lineage doesn't have a steady state.

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Next steps

1. For K fixed prove the spreading indeed is linear with the dichotomy in χ for the speed σ^K and that there is a stationary profile at least locally for
2. Prove that as $K \to \infty$ we have that $\sigma^K \to \sigma^*$
3. Formalize the pushed vs pulled analysis...

According to Calvez *et al.* & Forien *et al.*, the ancestral lineage follows a simple SDE in the large-population limit $K \to +\infty$.

$$dX_t = \beta(X_t)dt + dW_t,$$

where for $\chi \geq 1$

$$\beta(z) = \frac{1}{\chi} - \chi 1_{z \geq 0}$$

and $\chi \geq 1$

$$\beta(z) = \begin{cases} 2 - \chi, \text{if } z \leq 0 \\ 2\frac{1-\chi}{(1-\chi)z+1}, \text{if } z \geq 0 \end{cases}$$