Singular limits for models of selection and mutation with heavy-tailed mutation distribution

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Darwinian evolution of phenotypically structured populations under large mutation jumps

Mechanisms that we take into account:
- asexual reproduction: offsprings arise from a single organism
- heredity: transmission of the ancestral trait to the offsprings
- mutations: generates variability in the trait values
- competition leading to selection: individuals with better ability will spread through the population over time

Objective: to describe the dynamics of the trait density of the population while the mutations distribution has heavy tails
A fractional selection-mutation equation

We are interested in an asymptotic description of

\[
\begin{cases}
\partial_t n + (-\Delta)^\alpha n = n R(x, \rho(t)), & (t, x) \in \mathbb{R}^+ \times \mathbb{R}^d \\
n(t = 0, \cdot) = n^0(\cdot), & \rho(t) = \int_{\mathbb{R}^d} n(t, x) \, dx,
\end{cases}
\]

with \(0 < \alpha < 1\) and

\[
(-\Delta)^\alpha n(t, x) = \text{p.v.} \int_{\mathbb{R}^d} (n(t, x) - n(t, x + h)) \frac{dh}{|h|^{d+2\alpha}}.
\]

- \(x \in \mathbb{R}^d\): phenotypical trait
- \(n(t, x)\): density of trait \(x\)
- \(\rho(t)\): total population size
- \(R(x, \rho)\): growth rate
- \((-\Delta)^\alpha n\): mutation term
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Fractional laplacian: large mutation jumps with high rate

Derivation of the model: Jourdain–Méléard–Woyczynski (JMB-2012)
The choice of the growth rate

- $-C_1 \leq \frac{\partial R}{\partial \rho}(x, \rho) \leq -C_2 < 0$

- $0 < R(x, 0) < C$

- $\| R(\cdot, \rho) \|_{W^{2,\infty}(\mathbb{R}^d)} < K_2$
What do we expect?

Dynamics of the population’s density $n_\varepsilon$ with

$$R(x, \rho) = 1 + \exp\left(2 - \frac{x^2}{5}\right) - \rho$$

Classical diffusion:  

Fractional diffusion:

Colors: isolines of the phenotypic density $n_\varepsilon$
Concentration phenomenon: a classical selection-mutation model

\[
\begin{aligned}
\varepsilon \frac{\partial}{\partial t} n_\varepsilon - \varepsilon^2 \Delta n_\varepsilon &= n_\varepsilon R(x, \rho_\varepsilon), \\
n_\varepsilon(\cdot, t = 0) &= n_\varepsilon^0(\cdot), \quad \rho_\varepsilon(t) = \int_{\mathbb{R}^d} n_\varepsilon(t, x) dx.
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Concentration phenomenon: a classical selection-mutation model

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\begin{align*}
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n_\epsilon(\cdot, t = 0) &= n_0^\epsilon(\cdot), \quad \rho_\epsilon(t) = \int_{\mathbb{R}^d} n_\epsilon(t, x) dx.
\end{align*}
\]


\[
n_\epsilon(t, x) \xrightarrow{\epsilon \to 0} n(t, x) = \bar{\rho}(t) \delta(x - \bar{x}(t)).
\]

Dynamics of the dominant trait with:

\[R(x, \rho) = 1 + \exp\left(2 - \frac{x^2}{5}\right) - \rho\]

\[\epsilon = .01\]
How to rescale mutations to observe concentration?

In the case of a Laplace term or thin-tailed integral kernel:

\[ t \rightarrow t/\epsilon, \quad h \rightarrow \epsilon h, \quad h: \text{mutation step.} \]

Does not work for thick-tailed integral kernels.
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Proposed rescaling for fractional diffusion:

\[ t \to t/\varepsilon, \quad h = r\nu \to ((r + 1)\varepsilon - 1)\nu, \quad r = |h|, \quad \nu = \frac{h}{|h|}. \]
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Numerical resolution of the problem with this rescaling:

Dynamics of the dominant trait:

\[ R(x, \rho) = 1 + \exp\left(2 - \frac{x^2}{5}\right) - \rho \]

\[ \varepsilon = .01 \]
Some references on the asymptotic method based on Hamilton-Jacobi equations

- The study of propagation phenomena in reaction-diffusion equations: Freidlin, Evans, Souganidis, Barles,...
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- In **evolutionary biology** (nonlocal models):
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- The study of **propagation phenomena** in reaction-diffusion equations: Freidlin, Evans, Souganidis, Barles,…

- In **evolutionary biology** (nonlocal models):

  A large deviation type result in a model with an integral kernel with exponential tails: Brandle–Chasseigne (2013)
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3. Main results

4. Main elements of the proof of the convergence of $u_\epsilon$
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2 Where does this scaling come from?

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Where does this scaling come from? A toy model

\begin{equation}
\begin{cases}
\partial_t n + (-\Delta)^\alpha n = n(1 - n), \\
n(0, x) = n_0(x), \quad n_0 \text{ compactly supported.}
\end{cases}
\end{equation}


As $t \to \infty$, 
\begin{align*}
\{n(t, x) \to 0 \text{ in } A_\sigma = \{(t, x) \mid |x| \geq e^{\sigma t}\} \text{ if } \sigma > \frac{1}{d+2\alpha} \\
n(t, x) \to 1 \text{ in } B_\sigma = \{(t, x) \mid |x| \leq e^{\sigma t}\} \text{ if } \sigma < \frac{1}{d+2\alpha}
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\text{(KPP)} \\
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\end{cases}
\end{align*}
\]

A **long-time/long-range** rescaling keeping \( A_\sigma \) and \( B_\sigma \) invariant:

\[
t \to t/\varepsilon \implies x \to |x|^{1/\varepsilon} \nu, \quad \nu = x/|x|, \quad n_\varepsilon(t,x) = n(t/\varepsilon, |x|^{1/\varepsilon} \nu)
\]

**Theorem (Méléard–M, CPDE 2015)**

As \( \varepsilon \to 0 \),

\[
\begin{align*}
\begin{cases}
n_\varepsilon \to 0 & \text{in } A_\sigma \quad \text{if } \sigma > \frac{1}{d+2\alpha} \\
n_\varepsilon \to 1 & \text{in } B_\sigma \quad \text{if } \sigma < \frac{1}{d+2\alpha}
\end{cases}
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\]
Why this rescaling does not depend on $\alpha$?

- The ultimate speed of propagation is forced by the tails of the heat kernel: exponential, for the classical heat kernel, and algebraic, for the fractional heat kernel.
Where does this scaling come from?

Why this rescaling does not depend on $\alpha$?

- The ultimate speed of propagation is forced by the tails of the heat kernel: exponential, for the classical heat kernel, and algebraic, for the fractional heat kernel.

**Transition to constant speed of propagation as $\alpha \to 1$:**

- Coulon-Roquejoffre (CPDE-2012), Fractional KPP with $\alpha < 1$:
  
The position of the front scales ultimately as $e^{\frac{t}{d+2\alpha}}$ for $t_{\alpha} < t$. At intermediate times, it scales as $2t^{1/\alpha}$. As $\alpha \to 1$, $t_{\alpha} \to +\infty$, and the front will move ultimately as $2t$. 

An adapted rescaling for the selection-mutation model

The KPP rescaling $h = r\nu \to r^\epsilon\nu$ not relevant ($\nu = \frac{h}{|h|}$):
Mutation steps have to be reduced.
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The KPP rescaling $h = r\nu \to r^\varepsilon\nu$ not relevant ($\nu = \frac{h}{|h|}$):
Mutation steps have to be reduced.

An adapted rescaling: $h = r\nu \to ((r + 1)^\varepsilon - 1)\nu$

Change of variable: $r + 1 = e^k$

$$\varepsilon \partial_t n_\varepsilon(t, x) = \int_0^\infty \int_{S_{d-1}} (n_\varepsilon(t, x + (e^k - 1)\nu) - n_\varepsilon(t, x)) \frac{e^k dS dk}{|e^k - 1|^{1+2\alpha}}$$

$$+ n_\varepsilon(t, x) R(x, \rho_\varepsilon(t)).$$
An adapted rescaling for the selection-mutation model

The KPP rescaling $h = r\nu \to r^\varepsilon \nu$ not relevant ($\nu = \frac{h}{|h|}$):
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An adapted rescaling: $h = r\nu \to ((r + 1)^\varepsilon - 1)\nu$
Change of variable: $r + 1 = e^k$

$$
\varepsilon \partial_t n_\varepsilon(t, x) = \int_0^\infty \int_{S^d-1} \left( n_\varepsilon(t, x + (e^{\varepsilon k} - 1)\nu) - n_\varepsilon(t, x) \right) \frac{e^k dSd\kappa}{|e^k - 1|^{1+2\alpha}} \\
+ n_\varepsilon(t, x) R(x, \rho_\varepsilon(t)).$

• $(r + 1)^\varepsilon - 1 \approx \varepsilon \log(r + 1)$:
close to the classical rescaling for small $r$, slower growth for large $r$
• Mutation distribution has still algebraic tails but with large power
• The variance of the mutation distribution is of order $O(\varepsilon^2)$
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The Hamilton-Jacobi approach

Hopf-Cole transformation: \( n_\varepsilon = \frac{1}{(2\pi\varepsilon)^{d/2}} \exp \left( \frac{u_\varepsilon}{\varepsilon} \right). \)

The equation on \( u_\varepsilon \):

\[
\partial_t u_\varepsilon(t, x) = H_\varepsilon[u_\varepsilon] + R(x, \rho_\varepsilon(t)).
\]

\[
H_\varepsilon[u_\varepsilon] = \int_0^\infty \int_{S^{d-1}} \left( e^{\frac{u_\varepsilon(t, x + (e^k - 1)\nu) - u_\varepsilon(t, x)}{\varepsilon}} - 1 \right) \frac{e^k}{|e^k - 1|^{1+2\alpha}} dSdk.
\]
The Hamilton-Jacobi approach

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The equation on \( u_\varepsilon \):
\[
\partial_t u_\varepsilon(t, x) = H_\varepsilon[u_\varepsilon] + R(x, \rho_\varepsilon(t)).
\]

\[
H_\varepsilon[u_\varepsilon] = \int_0^\infty \int_{S^{d-1}} \left(e^\frac{u_\varepsilon(t, x) + (e^\varepsilon k - 1) \nu - u_\varepsilon(t, x)}{\varepsilon} - 1\right) \frac{e^k}{|e^k - 1|^{1+2\alpha}} dS dk.
\]

We expect that
\[
H_\varepsilon[u_\varepsilon] \rightarrow H(D_x u)
\]

The Hamiltonian for \( \alpha = .5 \)
\[
H(D_x u) = \int_0^\infty \int_{S^{d-1}} \left(e^{kD_x u \cdot \nu} - 1\right) \frac{e^k}{|e^k - 1|^{1+2\alpha}} dS dk
\]
Theorem (M, JMPA 2019)

As $\varepsilon \to 0$, along subsequences, $(\rho_{\varepsilon})_{\varepsilon}$ converges a.e. to $\rho \in BV_{\text{loc}}(\mathbb{R}^+)$ and $(u_{\varepsilon})_{\varepsilon}$ converges locally uniformly to $u \in C((0, \infty) \times \mathbb{R}^d)$, the minimal viscosity supersolution to

$$
\begin{aligned}
\partial_t u &= H(D_x u) + R(x, \rho), \\
\max_{x \in \mathbb{R}} u(t, x) &= 0, \\
u(0, x) &= u_0(x),
\end{aligned}
$$

satisfying for all $t > 0$ and $x, h \in \mathbb{R}^d$

$$
\|D_x u\|_{L^\infty((0, \infty) \times \mathbb{R}^d)} \leq 2\alpha, \quad u(t, x+h) - u(t, x) \leq 2\alpha \log(1+|h|).
$$

Moreover, $u$ is a viscosity subsolution of (1) in a weak sense.
Some remarks on the regularizing effect

\( H(D_x u) \)** blows up** when \( 2\alpha \leq |D_x u| \)

This leads to the first regularity result:

\[
\| D_x u \|_{L^\infty((0,\infty) \times \mathbb{R}^d)} \leq 2\alpha.
\]
Some remarks on the regularizing effect

$H(D_x u)$ blows up when $2\alpha \leq |D_x u|$

This leads to the first regularity result:

$$\|D_x u\|_{L^\infty((0,\infty) \times \mathbb{R}^d)} \leq 2\alpha.$$

The second regularity result, which is stronger:

$$u(t, x + h) - u(t, x) \leq 2\alpha \log(1 + |h|)$$

is a consequence of the original problem with $\varepsilon$.

These properties do not hold necessarily at the initial time $\Rightarrow$ strong regularizing effect
Is $u$ in general a viscosity solution to the HJ equation?

This is not necessarily the case:

- We find a HJ equation of the above type, which has a solution that does not satisfy the logarithmic decay property.
Is $u$ in general a viscosity solution to the HJ equation?

This is not necessarily the case:

- We find a HJ equation of the above type, which has a solution that does not satisfy the logarithmic decay property.
- The viscosity solution to such HJ equation is unique.
Is $u$ in general a viscosity solution to the HJ equation?

This is not necessarily the case:

- We find a HJ equation of the above type, which has a solution that does not satisfy the logarithmic decay property.

- The viscosity solution to such HJ equation is unique.

\[\implies\text{the logarithmic decay property is not an intrinsic property of such equation.}\] This indicates that $u$ may not be a viscosity solution to the above HJ equation.
Is $u$ in general a viscosity solution to the HJ equation?

Consider the following equation

$$\begin{cases} 
  \partial_t u(t, x) - \int_0^\infty \left( e^k \partial_x u(t, x) + e^{-k} \partial_x u(t, x) - 2 \right) \frac{e^k \, dk}{|e^k - 1|^{1+2\alpha}} = a(t, x) \\
  u(0, x) = 0, \quad x \in \mathbb{R},
\end{cases}$$

with

$$a(t, x) = \frac{-C \sqrt{1 + x^2}}{(1 + t)^2} - \int_0^\infty \left( e^{\frac{Ct}{(1+t)\sqrt{1+x^2}}} k + e^{\frac{-Ct}{(1+t)\sqrt{1+x^2}}} k - 2 \right) \frac{e^k \, dk}{|e^k - 1|^{1+2\alpha}},$$

and $0 < C < 2\alpha$. 
Is \( u \) in general a viscosity solution to the HJ equation?

Consider the following equation

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u(0,x) = 0, \quad x \in \mathbb{R},
\end{cases}
\end{aligned}
\]

with

\[
a(t,x) = -\frac{C \sqrt{1 + x^2}}{(1 + t)^2} - \int_0^\infty \left( e^{\frac{C t x}{(1+t)\sqrt{1+x^2}}} k + e^{\frac{-C t x}{(1+t)\sqrt{1+x^2}}} k - 2 \right) \frac{e^k dk}{|e^k - 1|^{1+2\alpha}},
\]

and \( 0 < C < 2\alpha \). One can verify that

\[
u(t,x) = -\frac{C t \sqrt{1 + x^2}}{1 + t},
\]

is a solution but \( u \) does not have logarithmic decay.
Concentration of the phenotypic density

The properties obtained for $u$ are still enough to capture the concentration phenomenon:

**Theorem (M, JMPA 2019)**

Along subsequences as $\varepsilon \to 0$, $n_\varepsilon \rightharpoonup n$ in the measure sense, and

$$\text{supp } n(t, \cdot) \subset \{u(t, \cdot) = 0\} \subset \{R(\cdot, \rho(t)) = 0\}, \text{ for a.e. } t$$

In particular, if $x \in \mathbb{R}$ and $R$ is monotonic with respect to $x$, then for a.e. $t$,

$$n(t, x) = \rho(t)\delta(x - \overline{x}(t)).$$
Where do the inclusion properties come from?

- \( \text{supp } n(t, \cdot) \subset \{ u(t, \cdot) = 0 \} \): From Hopf-Cole transformation:

\[
n_\varepsilon \approx \exp \left( \frac{u_\varepsilon}{\varepsilon} \right).
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Where do the inclusion properties come from?

- $\text{supp } n(t, \cdot) \subset \{ u(t, \cdot) = 0 \}$: From Hopf-Cole transformation:
  \[ n_\varepsilon \approx \exp \left( \frac{u_\varepsilon}{\varepsilon} \right). \]

- $\{ u(t, \cdot) = 0 \} \subset \{ R(\cdot, \rho(t)) = 0 \}$
  \[ u(t, \overline{x}) = 0 \quad \Rightarrow \quad (t, \overline{x}) \in \text{argmax } u \]
  \[ \Rightarrow \quad \partial_t u(t, \overline{x}) = 0, \quad \nabla u(t, \overline{x}) = 0. \]

If $u$ solution to HJ: $\partial_t u = H(D_x u) + R(x, \rho)$ then

\[ R(\overline{x}, \rho(t)) = 0. \]

Still holds for the minimal viscosity supersolution.
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Main difficulties

The main difficulties to prove the convergence of \((u_\varepsilon)_\varepsilon\):

- The Hamiltonian can take infinite values.
- The limit is not in general a viscosity solution to the HJ equation.
- \(\rho\) is only BV and potentially discontinuous.
The main elements of the proof

Convergence of $u_\varepsilon$:

$$\partial_t u_\varepsilon(t, x) = H_\varepsilon[u_\varepsilon] + R(x, \rho_\varepsilon(t)).$$

$$H_\varepsilon[u_\varepsilon] = \int_0^\infty \int_{\nu \in S^{d-1}} \left( e^{\frac{u_\varepsilon(t, x + (e^k - 1)\nu) - u_\varepsilon(t, x)}{\varepsilon}} - 1 \right) \frac{e^k}{|e^k - 1|^{1+2\alpha}} dS dk$$
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This equation converges formally to the HJ equation. The following properties allow to obtain the convergence of $H_\varepsilon[u_\varepsilon]$:

$$\|D_x u_\varepsilon\|_{L^\infty(\mathbb{R} \times \mathbb{R}^+)} < 2\alpha, \quad u_\varepsilon(t, x + h) - u_\varepsilon(t, x) < 2\alpha \log(1 + |h|).$$
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The following properties allow to obtain the convergence of $H_\varepsilon[u_\varepsilon]$:

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We prove these properties (with non-strict inequalities) and the convergence of $(u_\varepsilon)_\varepsilon$ simultaneously.
The main elements of the proof

To prove the convergence, we use the semi relaxed limits:

$$
\overline{u}(t, x) = \limsup_{(s, y) \to (t, x)} u_\varepsilon(s, y), \quad u(t, x) = \liminf_{(s, y) \to (t, x)} u_\varepsilon(s, y).
$$
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To prove the convergence, we use the semi relaxed limits:

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The classical method:

- \( \bar{u} \) is a viscosity subsolution to the HJ equation.
- \( u \) is a viscosity supersolution to the HJ equation.
- A strong comparison principle in the class of discontinuous viscosity solutions:

  $$\bar{u} \leq u.$$

  and hence \( \bar{u} = u \) which implies that \( (u_\varepsilon)_\varepsilon \) converges to \( u = \bar{u} = \underline{u} \).
The main elements of the proof

A difficulty in our case: the Hamiltonian takes infinite value

$\Rightarrow \bar{u}$ is not necessarily a viscosity subsolution.
The main elements of the proof

A difficulty in our case: the Hamiltonian takes infinite value
\[ \Rightarrow \overline{u} \text{ is not necessarily a viscosity subsolution.} \]

What we do (the main elements):

- We prove that \( u \) is a viscosity supersolution to HJ.
The main elements of the proof

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\[ \Rightarrow \bar{u} \text{ is not necessarily a viscosity subsolution.} \]

What we do (the main elements):

- We prove that \( u \) is a viscosity supersolution to HJ.
- We show that \( u \) has all the nice properties that we need.
The main elements of the proof

A difficulty in our case: the Hamiltonian takes infinite value
⇒ \( \bar{u} \) is not necessarily a viscosity subsolution.

What we do (the main elements):

- We prove that \( u \) is a viscosity supersolution to HJ.
- We show that \( u \) has all the nice properties that we need.
- We modify and regularize it and use it as a test function for \( \bar{u} \) to obtain a contradiction with the fact that \( \max \bar{u} - u > 0 \). We conclude that \( \bar{u} = u \) which means that \( (u_\varepsilon)_{\varepsilon} \) converges.
Thank you for your attention !