A large deviations approach to Hamilton-Jacobi scaling limits of PDE models of adaptive dynamics

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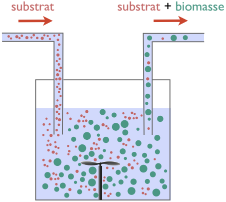
Introduction

Goal of the talk:

- Study general PDE models of evolution, describing the evolution of quantitative phenotypic traits.
- Apply as in the talk of B. Perthame on Monday a limit of "concentration" in order to describe the population dynamics as Dirac mass(es) evolving with time.
- Give an alternative description of the Hamilton-Jacobi limit using a probabilistic interpretation of the PDE.
- Discuss extensions of this approach, including the case of a finite trait space.

Chemostat example



PDE model with r resources: $u(t,x)$ is the density of population with trait $x \in \mathbb{R}$ at time $t \geq 0$

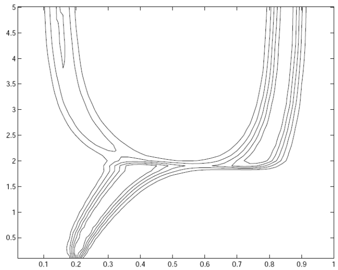
$$\partial_t u(t,x) = u(t,x)\Big(\underbrace{\sum_{i=1}^{r} v_i(t)\eta_i(x)}_{\text{growth}} - \underbrace{1}_{\text{outflow}} \Big) + \underbrace{\frac{1}{2}\Delta u(t,x)}_{\text{mutation}}$$

$$\dot{v}_i(t) = \underbrace{c_i}_{\text{inflow}} - \underbrace{v_i(t)}_{\text{outflow}} - \underbrace{v_i(t)\int_{\mathbb{R}} \eta_i(x)u(t,x)\,dx}_{\text{consumption}}$$

Accelerated resources dynamics

Putting resources dynamics at equilibrium, we obtain the PDE

$$\partial_t u(t,x) = \frac{1}{2}\Delta u(t,x) + u(t,x)\left(\sum_{i=1}^{r} \frac{c_i \eta_i(x)}{1+\int \eta_i(x) u(t,x)} - 1\right)$$



Competition for two resources

(Diekmann, Jabin, Mischler, Perthame, 2005)

General model

$$\partial_t u(t,x) = \frac{1}{2}\Delta u(t,x) + u(t,x) R\left(x, v_t\right), \quad x \in \mathbb{R}^d,\ t \geq 0,$$
$$v_t^i = \int_{\mathbb{R}^d} \eta_i(x) u(t,x) dx, \quad 1 \leq i \leq r,$$

where

- η_i $W^{2,\infty}$ with $M^{-1} \leq \eta_i(x) \leq M$,
- R $W^{2,\infty}$ with

$$-M \leq \partial_{v_i} R\left(x, v_1, \ldots, v_r\right) \leq -M^{-1}.$$

- $\min_{x\in\mathbb{R}^d} R(x,v) > 0$ as soon as $\|v\| <$ v_{min}, and $\max_{x\in\mathbb{R}^d} R(x,v) < 0$ as soon as $\|v\| > v_{max}$.

Scaling of small/rare mutations and large time

$$\partial_t u^\varepsilon(t,x) = \frac{\varepsilon}{2}\Delta u^\varepsilon(t,x) + \frac{1}{\varepsilon}u^\varepsilon(t,x)R\left(x, v_t^\varepsilon\right),$$

$$u^\varepsilon(0,x) = \exp - \frac{h_\varepsilon(x)}{\varepsilon},$$

$$v_t^{\varepsilon,i} = \int_{\mathbb{R}^d} \eta_i(x)u^\varepsilon(t,x)\,dx,$$

where h_ε are uniformly Lipschitz and converge to h in L^∞
Diekmann et al., 2005: defining (WKB ansatz)

$$u_\varepsilon(t,x) = \exp\left(\frac{\varphi_\varepsilon(t,x)}{\varepsilon}\right), \qquad \partial_t u_\varepsilon = \frac{u_\varepsilon}{\varepsilon}\partial_t\varphi_\varepsilon,\ \Delta u_\varepsilon = \frac{\Delta\varphi_\varepsilon}{\varepsilon}u_\varepsilon + \frac{|\nabla\varphi_\varepsilon|^2}{\varepsilon^2}u_\varepsilon,$$

the PDE becomes

$$\partial_t\varphi_\varepsilon(t,x) = R(x, v_t^\varepsilon) + \frac{1}{2}|\nabla\varphi_\varepsilon(t,x)|^2 + \frac{\varepsilon}{2}\Delta\varphi_\varepsilon$$

Hamilton-Jacobi limit with constraints

This suggests the convergence of φ_ε to a solution of

$$\partial_t \varphi(t,x) = R(x, v_t) + \frac{1}{2} |\nabla \varphi_\varepsilon(t,x)|^2,$$
$$\varphi(0,x) = -h(x), \quad v_t^i = \int_{\mathbb{R}^d} \eta_i(x) \mu_t(dx),$$

where $\mu_t(dx)$ is (in some sense) the limit of $u_\varepsilon(t,x)dx$.

Such a convergence and the limit equation were studied in lots of works (Diekmann, Jabin, Mischler, Perthame, 2005; Barles, Perthame, 2007, 2008; Barles, Mirrahimi, Perthame, 2009; C., Jabin, 2011; Lorz, Mirrahimi, Perthame, 2011; Mirrahimi, Roquejoffre, 2016...)

How to characterize μ_t?

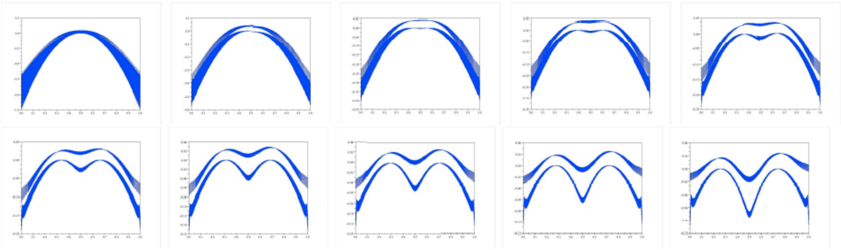
- The total population mass remains bounded $\rightsquigarrow$ $\max_x \varphi(t,x) = 0$ for all $t \geq 0$.
- The limit population density at time t is 0 except at the points x where $\varphi(t,x) = 0$ $\rightsquigarrow$ μ_t has support in $\{\varphi(t,\cdot) = 0\}$.
- The measure μ_t has to be metastable, i.e.
  - $R(x, v_t) \leq 0$ for all x such that $\varphi(t,x) = 0$,
  - $R(x, v_t) = 0$ for all x in the support of μ_t.

These properties are enough to characterize μ_t from $\{\varphi(t,\cdot) = 0\}$ in the case of a single resources, but it is only known in particular cases for two or more resources (chemostat example, cf. C., Jabin, 2011).

Well-posedness is a hard problem, only solved in general for a single resource (Mirrahimi, Roquejoffre, 2016).

For evolutionary branching to occur, we need $r \geq 2$.

Simulation of HJ in the chemostat example [T. Causseron]



Probabilistic interpretation of the PDE

We follow ideas from Freidlin (1987, 1992).

Feynman-Kac formula expresses solutions of linear PDEs as expectation of stochastic processes:

$$u^\varepsilon(t,x) = \mathbb{E}_x\left[\exp\left(-\varepsilon^{-1} h_\varepsilon(X_t^\varepsilon) + \frac{1}{\varepsilon}\int_0^t R\left(X_s^\varepsilon, v_{t-s}^\varepsilon\right) ds\right)\right],$$

where $X_t^\varepsilon = x + \sqrt{\varepsilon} B_t$ with B_t Brownian motion.

Strongly suggests to apply Varadhan's lemma!!

Computation

This can be proved applying Itô's formula between times 0 and t to

$$Y_s = u^\varepsilon(t-s, X_s^\varepsilon)\exp\left(-\frac{1}{\varepsilon}\int_0^s R(X_u^\varepsilon, v_{t-u}^\varepsilon)\,du\right).$$

Setting $\alpha(s,x) = R(x, v_s^\varepsilon)$, we obtain

$$\begin{aligned}
&u^\varepsilon(0, X_t^\varepsilon)\exp\left(\frac{1}{\varepsilon}\int_0^t \alpha(t-u, X_u^\varepsilon)\,du\right)\\
&= u^\varepsilon(t,x) + \int_0^t \nabla u^\varepsilon(t-s, X_s^\varepsilon)\exp\left(\frac{1}{\varepsilon}\int_0^s \alpha(t-u, X_u^\varepsilon)\,du\right)dX_s^\varepsilon\\
&+ \int_0^t \left(-\partial_s u^\varepsilon + \frac{\varepsilon}{2}\Delta u^\varepsilon + \frac{1}{\varepsilon}\alpha u^\varepsilon\right)(t-s, X_s^\varepsilon)\exp\left(\frac{1}{\varepsilon}\int_0^s \alpha(t-u, X_u^\varepsilon)\,du\right).
\end{aligned}$$

This gives the formula taking expectations.

Large deviations principle for Brownian paths

The process $X_t^\varepsilon = x + \sqrt{\varepsilon} B_t$ satisfies a LDP as $\varepsilon \to 0$ (Schilder's theorem):

$$\mathbb{P}_x\Big((X_s^\varepsilon)_{s\in[0,t]} \approx (\varphi_s)_{s\in[0,t]}\Big) \approx \exp\left(-\frac{1}{\varepsilon} I_t(\varphi)\right), \quad I_t(\varphi) = \frac{1}{2}\int_0^t \|\dot\varphi_s\|^2 \, ds.$$

More formally, for all $F \subset \mathcal{C}([0,t], \mathbb{R}^d)$,

$$-\inf_{\varphi\in \mathrm{int}(F)} I_t(\varphi) \le \liminf_{\varepsilon\to 0} \varepsilon \log \mathbb{P}_x(X^\varepsilon \in F)$$
$$\le \limsup_{\varepsilon\to 0} \varepsilon \log \mathbb{P}_x(X^\varepsilon \in F) \le -\inf_{\varphi\in \mathrm{adh}(F)} I_t(\varphi).$$

Varadhan's lemma

Varadhan's lemma is a version of Laplace's principle: for all $f : [0,1] \to \mathbb{R}$ continuous,

$$\int_0^1 e^{\frac{1}{\varepsilon} f(x)} dx \approx e^{\frac{1}{\varepsilon} \sup_{y\in[0,1]} f(y)},$$

or, more formally,

$$\lim_{\varepsilon\to 0} \varepsilon \log \int_0^1 e^{\frac{1}{\varepsilon} f(x)} dx = \sup_{y\in[0,1]} f(y).$$

Varadhan's lemma: if $F : \mathcal{C}([0,T], \mathbb{R}^d) \to \mathbb{R}$ is continuous,

$$\mathbb{E}_x\left(e^{\frac{1}{\varepsilon} F(X^\varepsilon)}\right) = \int e^{\frac{1}{\varepsilon} F(\varphi)} \mathbb{P}(X^\varepsilon \in d\varphi) \approx \int e^{\frac{1}{\varepsilon} F(\varphi)} e^{-\frac{1}{\varepsilon} I_t(\varphi)} d\varphi,$$

or

$$\lim_{\varepsilon\to 0} \varepsilon \log \mathbb{E}_x\left(e^{\frac{1}{\varepsilon} F(X^\varepsilon)}\right) = \sup_{\varphi \text{ s.t. } \varphi(0)=x} \left(F(\varphi) - I_t(\varphi)\right).$$

Application to our model

In our case,

$$F_\varepsilon(\varphi) = -h_\varepsilon(\varphi_t) + \int_0^t R(\varphi_s, v^\varepsilon_{t-s})\,ds.$$

Need it to converge as $\varepsilon \to 0$ to F continuous.

- $h_\varepsilon \to h$ in L^∞, h Lipschitz,
- to have a continuous limit of

$$\int_0^t R(\varphi_s, v^\varepsilon_{t-s})\,ds = \int_0^t \int_{\mathbb{R}^r} R(\varphi_s, y)\delta_{v^\varepsilon_{t-s}}(dy)\,ds,$$

  enough to look at weak convergence of measures: up to a subsequence ε_k,

$$\delta_{v_s^{\varepsilon_k}}(dy)\,ds \to \mathcal{M}_s(dy)\,ds.$$

Main result

Theorem

For all $x \in \mathbb{R}^d$ and $t \geq 0$,

$$V(t,x) := \lim_{k\to\infty} \varepsilon_k \log u^{\varepsilon_k}(t,x)$$

$$= \sup_{\varphi \ s.t.\ \varphi_t = x} \left\{ -h(\varphi_0) + \int_0^t \int_{\mathbb{R}^r} R(\varphi_s, y)\mathcal{M}_s(dy)\,ds - \frac{1}{2}\int_0^t \|\dot{\varphi}_s\|^2 ds \right\}$$

and $V(t,x)$ is locally Lipschitz in $\mathbb{R}_+ \times \mathbb{R}^d$.

Biologically, the optimal function φ may be thought of as the trait of the ancestors of the dominant individuals at time t.

Link with the HJ problem

When $r = 1$, using the results of Lorz, Mirrahimi, Perthame (2011), we deduce that $\mathcal{M}_t$ is a Dirac mass and $V(t,x) = \varphi(t,x)$, where

$$\partial_t \varphi(t,x) = \int_{\mathbb{R}} R(x,y)\mathcal{M}_t(dy) + \frac{1}{2}|\nabla \varphi(t,x)|^2.$$

This is the classical variational formulation of Hamilton-Jacobi problems.

Note that, in general, $t \mapsto \mathcal{M}_t$ is not continuous, so we cannot apply the standard results of this theory.

Extensions to other mutation models

Our method applies in general to any with mutation operators satisfying a large deviations principle. For example,

$$\partial_t u^\varepsilon(t,x) = \frac{1}{\varepsilon}\int_{\mathbb{R}^d} \left[u^\varepsilon(t,x+\varepsilon z) - u^\varepsilon(t,x)\right] K(z)dz + \frac{1}{\varepsilon} u^\varepsilon(t,x) R\left(x, v_t^\varepsilon\right),$$

where $K : \mathbb{R}^d \to \mathbb{R}_+$ satisfies

$$\int_{\mathbb{R}^d} zK(z)dz = 0 \quad \text{and} \quad \int_{\mathbb{R}^d} e^{a|z|} K(z)dz < \infty, \ \forall a > 0.$$

The rate function is

$$I_t(\varphi) = \int_0^t \int_{\mathbb{R}^d} \left(e^{\dot{\varphi}_s z} - 1\right) K(z)dz\, ds$$

In this case, the Hamilton-Jacobi limit was obtained in the chemostat example for any number of resources in C., Jabin (2011).

The case of finite trait space

In the case where the trait space E is finite, to have a large deviations principle for the mutation process, one needs mutations rates to be exponentially small:

$$\dot{u}^\varepsilon(t,i) = \sum_{j\in E} e^{-\frac{T(i,j)}{\varepsilon}}\left(u^\varepsilon(t,j) - u^\varepsilon(t,i)\right) + \frac{1}{\varepsilon}u^\varepsilon(t,i)R_i(v_t^\varepsilon),$$

$$u^\varepsilon(0,i) = \exp -\frac{h_\varepsilon(i)}{\varepsilon},$$

$$v_t^{k,\varepsilon} = \sum_{i\in E}\eta_k(i)u^\varepsilon(t,i),$$

where

$$T(i,j) > 0\ \forall i\neq j, \quad T(i,j)+T(j,k) > T(i,k),\ \forall i,j,k.$$

Feynman-Kac representation and LDP

We have as above

$$u^\varepsilon(t,i) = \mathbb{E}_i\left[\exp\left(-\frac{h_\varepsilon(X_t^\varepsilon)}{\varepsilon} + \frac{1}{\varepsilon}\int_0^t R(X_s^\varepsilon, v_{t-s}^\varepsilon)ds\right)\right],$$

where X_t^ε is a Markov jump process with $X_0^\varepsilon = i$ and jump rate $e^{-\frac{T(i,j)}{\varepsilon}}$ from i to j.

Thanks to the assumption $T(i,j) + T(j,k) > T(i,k)$, $\forall i,j,k$, the processes $(X^\varepsilon)_{\varepsilon>0}$ satisfy a LDP with rate function

$$\begin{aligned} I_t : \mathbb{D}([0,t],E) &\to \mathbb{R}_+ \\ \varphi &\mapsto \sum_{s\leq t} T(\varphi_{s-},\varphi_s), \end{aligned}$$

where we assume $T(i,i) = 0$ for all $i \in E$ and where $\mathbb{D}([0,t],E)$ is the set of right-continuous functions from $[0,t]$ to E admiting left limits at all positive times.

Variational problem

The rate function does not have compact level sets. However, it is possible to adapt Varadhan's lemma to prove

Theorem

For all $i \in E$ *and* $t \geq 0$,

$$V(t,i) := \lim_{k\to\infty} \varepsilon_k \log u^{\varepsilon_k}(t,x)$$

$$= \sup_{\varphi \text{ s.t. } \varphi_0 = i} \left\{ -h(\varphi_t) + \int_0^t \int_{\mathbb{R}^r} R(\varphi_s, y)\mathcal{M}_s(dy)\,ds - \sum_{s\leq t} T(\varphi_{s-}, \varphi_s) \right\}.$$

This problem is simpler to study than the previous one. In some cases, it is possible to characterize the limit.