Adaptive evolution: a population approach

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Adaptive dynamic : selection principle

\[
\begin{aligned}
\frac{d}{dt} n(x, t) &= n(x, t) R(x, \varrho(t)), \\
\varrho(t) &= \int_{\mathbb{R}^d} n(x, t) \, dx.
\end{aligned}
\]

- given \( \bar{x} \), \( \bar{n}(x) = \bar{\varrho} \, \delta(x - \bar{x}) \), \( R(\bar{x}, \bar{\varrho}) = 0 \), \( \bar{\varrho}(\bar{x}) \).

- They are stable by perturbation of the weight \( \bar{\varrho} \) (strong topology)

\[
\frac{d}{dt} \varrho(t) = \varrho(t) R(\bar{x}, \varrho(t)).
\]

- But they are unstable by approximation in measures (weak topology), and by mutation (structural)...
Adaptive dynamic: mutations

Off-springs undergo small mutations that change slightly the trait

\[
\begin{aligned}
\frac{\partial}{\partial t} n(x, t) - \Delta n &= n(x, t) R(x, \varrho(t)), \\
\varrho(t) &= \int_{\mathbb{R}^d} n(x, t) dx.
\end{aligned}
\]

\[
\begin{aligned}
\frac{\partial}{\partial t} n(x, t) &= n(x, t) R(x, \varrho(t)) + \int M(x, y) b(y) n(y, t) dy, \\
\varrho(t) &= \int_{\mathbb{R}^d} n(x, t) dx.
\end{aligned}
\]
Adaptive dynamic: mutations

Off-springs undergo small mutations that change slightly the trait

\[
\begin{align*}
\frac{\partial}{\partial t} n(x,t) - \Delta n &= n(x,t) R(x, \varrho(t)), \\
\varrho(t) &= \int \! n(x,t) dx.
\end{align*}
\]
Adaptive dynamic: mutations

Off-springs undergo small mutations that change slightly the trait

\[
\begin{aligned}
\frac{\partial}{\partial t} n(x,t) - \Delta n &= n(x,t) R(x, \varrho(t)), \\
\varrho(t) &= \int_{\mathbb{R}^d} n(x,t) dx.
\end{aligned}
\]

We assume that mutations are RARE and introduce a scale \( \varepsilon \) for 'small' mutations

\[
\begin{aligned}
\varepsilon \frac{\partial}{\partial t} n_\varepsilon(x,t) - \varepsilon^2 \Delta n_\varepsilon &= n_\varepsilon(x,t) R(x, \varrho_\varepsilon(t)), \\
\varrho_\varepsilon(t) &= \int_{\mathbb{R}^d} n_\varepsilon(x,t) dx.
\end{aligned}
\]
Population model of adaptive dynamics: mutations

This is not far from Fisher/KPP equation for invasion fronts/chemical reaction

\[ \varepsilon \frac{\partial}{\partial t} n_\varepsilon(x, t) - \varepsilon^2 \Delta n_\varepsilon = n_\varepsilon(x, t) \left( 1 - n_\varepsilon(x, t) \right), \]

WKB, large deviations, level sets, geometric motion

G. Barles, L. C. Evans, W. Fleming, P. E. Souganidis, S. Osher, J. Sethian...
Population model of adaptive dynamics: mutations

This is not far from Fisher/KPP equation for invasion fronts/chemical reaction

\[ \varepsilon \frac{\partial}{\partial t} n_\varepsilon(x,t) - \varepsilon^2 \Delta n_\varepsilon = n_\varepsilon(x,t)(1 - n_\varepsilon(x,t)), \]

\[ \{n_\varepsilon = 1\} \quad \{n_\varepsilon = 0\} \]

in the limit

\[ \bar{n}(x,t)(1 - \bar{n}(x,t)) = 0. \]
The situation is very different for the nonlocal equation

\[
\begin{cases}
\varepsilon \frac{\partial}{\partial t} n_\varepsilon(x, t) - \varepsilon^2 \Delta n_\varepsilon = n_\varepsilon(x, t) R(x, \varrho_\varepsilon(t)), \\
\varrho_\varepsilon(t) = \int_{\mathbb{R}^d} n_\varepsilon(x, t) dx.
\end{cases}
\]
The situation is very different for the nonlocal equation

\[
\begin{cases}
\varepsilon \frac{\partial}{\partial t} n_\varepsilon(x, t) - \varepsilon^2 \Delta n_\varepsilon = n_\varepsilon(x, t) R(x, \varrho_\varepsilon(t)), \\
\varrho_\varepsilon(t) = \int_{\mathbb{R}^d} n_\varepsilon(x, t) dx.
\end{cases}
\]

In the limit one can expect

\[
0 = n(x, t) R(x, \varrho(t)),
\]

\[
n(x, t) = \varrho \delta_{\Gamma(t)}, \quad \Gamma(t) \subset \{ R(\cdot, \varrho(t)) = 0 \}.
\]
**Asymptotic method**

**Question.** What tools to describe Dirac concentrations in PDEs?

\[ n_\varepsilon(x) = \frac{\bar{\varrho}}{(2\pi\varepsilon)^{d/2}} e^{-|x-x|^{2}/(2\varepsilon)} \xrightarrow{\varepsilon \to 0} \bar{\varrho}\delta(x-x) \]

\[ n_\varepsilon(x) = e^{-|x-x|^{2}+\varepsilon \ln O(\varepsilon))/(2\varepsilon)} \xrightarrow{\varepsilon \to 0} \bar{\varrho}\delta(x-x) \]

More generally (Hopf-Cole/WKB)

\[ n_\varepsilon(x) = e^{\varphi_\varepsilon(x)/\varepsilon} \xrightarrow{\varepsilon \to 0} \bar{\varrho}\delta(x-x) \]

with the conditions

\[ \varphi_\varepsilon \xrightarrow{\varepsilon \to 0} \varphi, \quad \max_x \varphi(x) = 0 = \varphi(\bar{x}) \]
Theorem  Suppose \( x \in \mathbb{R}, \, R_x > 0, \, R_\varrho < 0. \) Then, for subsequences

\[
\begin{align*}
n_\varepsilon(x, t) & \xrightarrow{\varepsilon_k \to 0} \varrho(t) \delta(x = \bar{x}(t)), \\
\varrho_\varepsilon & \xrightarrow{\varepsilon_k \to 0} \bar{\varrho}(t) = \int n(x, t)dx,
\end{align*}
\]

Can one give a law for the dynamics of \( \bar{x}(t) \)?
Asymptotic method

Theorem  Suppose $x \in \mathbb{R}$, $R_x > 0$, $R_\varrho < 0$. Then, for subsequences

$$n_\varepsilon(x, t) \xrightarrow[\varepsilon_k \to 0]{} \bar{\varrho}(t) \delta(x = \bar{x}(t)), \quad \varrho_\varepsilon \xrightarrow[\varepsilon_k \to 0]{} \bar{\varrho}(t) = \int n(x, t) dx,$$

and the 'fittest' trait $\bar{x}(t)$ is characterised by the Eikonal equation with constraints

$$\begin{align*}
\frac{\partial}{\partial t} \varphi(x, t) &= R(x, \bar{\varrho}(t)) + |\nabla \varphi(x, t)|^2 \\
\max_x \varphi(x, t) &= 0 = \varphi(t, \bar{x}(t))
\end{align*}$$

Definition  This situation is called monomorphism

Difficulty  Solutions to H.-J. eq. are not smooth
Asymptotic method

**Theorem** Suppose \( x \in \mathbb{R}, \ R_x > 0, \ R_\varrho < 0 \). Then, for subsequences

\[
n_{\varepsilon}(x, t) \xrightarrow{\varepsilon_k \to 0} \bar{\varrho}(t)\delta(x = \bar{x}(t)), \quad q_{\varepsilon} \xrightarrow{\varepsilon_k \to 0} \bar{\varrho}(t) = \int n(x, t)dx,
\]

and the 'fittest' trait \( \bar{x}(t) \) is characterised by the Eikonal equation with constraints

\[
\begin{cases}
\frac{\partial}{\partial t} \varphi(x, t) = R(x, \bar{\varrho}(t)) + |\nabla \varphi(x, t)|^2 \\
\max_x \varphi(x, t) = 0 = \varphi(t, \bar{x}(t))
\end{cases}
\]

However

\[
\frac{\partial}{\partial t} \varphi(\bar{x}(t), t) = 0 = \frac{\partial}{\partial x} \varphi(\bar{x}(t), t)
\]

\[
R(\bar{x}(t), \bar{\varrho}(t)) = 0 \quad \text{(Pessimism Principle)}
\]
**Asymptotic method**

This problem should be understood as follows

$$\max_x \varphi(x, t) = 0, \ \forall t$$ is a constraint,

$$\bar{\varrho}(t)$$ is a Lagrange multiplier.

This is not an obstacle problem!
Asymptotic method

**Theorem**  In $\mathbb{R}^d$, set

$$n_\varepsilon(x, t) = e^{\varphi_\varepsilon(x, t)/\varepsilon}.$$  

- After extraction, $\varphi_\varepsilon \rightarrow \varphi$ (locally uniformly), $\varrho_\varepsilon(t) \rightarrow \bar{\varrho}(t)$

\[
\begin{cases}
\frac{\partial}{\partial t} \varphi(x, t) = R(x, \bar{\varrho}(t)) + |\nabla \varphi(x, t)|^2 \\
\max_x \varphi(x, t) = 0 \quad \left( = \varphi(t, \bar{x}(t)) \right)
\end{cases}
\]

- And $n_\varepsilon(x, t) \rightharpoonup n(x, t)$ weakly in measures,

$$\text{supp}(n(t)) \subset \{\varphi(t) = 0\}.$$
Asymptotic method

Proof
1. $\varrho_\varepsilon(t)$ is BV (and converges after extraction) and its limit $\varrho(t)$ is non-decreasing

2. Because $n_\varepsilon(x,t) = e^{\varphi_\varepsilon(x,t)/\varepsilon}$ we have

$$\frac{\partial}{\partial t} \varphi_\varepsilon(x,t) = R(x, \varrho_\varepsilon(t)) + |\nabla \varphi_\varepsilon(x,t)|^2 - \varepsilon \Delta \varphi_\varepsilon$$

and $\varphi_\varepsilon$ is Lipschitz continous in $x$ (difficulty in $t$) (gives the H.-J. equation in viscosity sense)

3. $\varrho_m \leq \int n_\varepsilon(x,t) dx \leq \varrho_M$ (gives the constraint)
Asymptotic method

Conclusion:

\[ n_\epsilon \quad \phi_\epsilon \quad L^1 \quad C^0 \]
**Asymptotic method**

**Theorem (G. Barles, BP) Uniqueness** With reasonable assumptions there exist a unique lipschitz continuous solution \((\bar{\varrho}, \varphi)\) to the constraint H.-J. equation

\[
\begin{align*}
\frac{\partial}{\partial t} \varphi(x, t) &= b(x) - \bar{\varrho}(t)d(x) + |\nabla \varphi|^2, \\
\max_x \varphi(x, t) &= 0 \quad (= \varphi(t, \bar{x}(t)))
\end{align*}
\]

**Open question** Extend uniqueness to

\[
\frac{\partial}{\partial t} \varphi(x, t) = \frac{b(x)}{1 + \bar{\varrho}(t)} - \bar{\varrho}(t)d(x) + |\nabla \varphi|^2.
\]
Asymptotic method

Proof of uniqueness: the difficulty

The $L^\infty$ contraction property is lost! Define

$$M(t) := \max_x [\varphi_1(x, t) - \varphi_2(x, t)]$$

$$\frac{d}{dt} M(t) \leq R(x_M(t), \varphi_1(t)) - R(x_M(t), \varphi_2(t)) \leq C |\varphi_1(t) - \varphi_2(t)|$$

But the constraint cannot be used here to control $|\varphi_1(t) - \varphi_2(t)|$ by $M(t)$. 
Asymptotic method

Proof of uniqueness: idea. \[ R(x, \varrho) = b(x) - d(x) \varrho \]

Work on

\[ \psi(t) := \varphi(x, t) + d(x) \int_0^t \varrho(s) ds. \]

\[ \begin{cases} 
\frac{\partial}{\partial t} \psi(x, t) = b(x) + |\nabla \psi - \nabla d(x)| \int_0^t \varrho(s) ds|^2, \\
\max_x \varphi(x, t) = 0 \quad (= \varphi(t, \bar{x}(t))) 
\end{cases} \]

Define

\[ M(t) := \max_x [\psi_1(x, t) - \psi_2(x, t)] \]

\[ \frac{d}{dt} M(t) \leq |p_M - \nabla d(x_M)| \int_0^t \varrho_1(s) ds|^2 - |p_M - \nabla d(x_M)| \int_0^t \varrho_2(s) ds|^2 \]
Asymptotic method

\[ \frac{d}{dt} M(t) \leq |p_M - \nabla d(x_M) \int_0^t \varrho_1(s)ds|^2 - |p_M - \nabla d(x_M) \int_0^t \varrho_2(s)ds|^2 \]

Use that solutions are Lipschitz and the specific form of \( R \)

\[ \frac{d}{dt} M(t) \leq C \left| \int_0^t \varrho_1(s)ds - \int_0^t \varrho_2(s)ds \right| \]

But we may choose \( \varphi(t, x_1) = 0 \) and get

\[ M(t) \geq \psi_1(t, x_1) - \psi_2(t, x_1) \geq d(x_1) \left[ \int_0^t \varrho_1(s)ds - \int_0^t \varrho_2(s)ds \right] \]

The opposite inequality holds true similarly and thus

\[ \frac{d}{dt} M(t) \leq \bar{C} M(t). \]
Asymptotic method

Numerical tests: \( b(x) = 0.5 + x \)

Direct simulation (1500 points)  H.-J. solution (200 points)
Asymptotic method

Numerical tests: \( b(x) = 0.5 + x(2 - x) \)

Direct simulation (1500 points)  H.-J. solution (200 points)
Asymptotic method

Numerical tests: $\min(.45 + x^2, .55 + .4 \times x)$

Direct simulation (1500 points)  
H.-J. solution (200 points)
Next ingredient is the notion of survival threshold.

\[
\frac{\partial n(t, x)}{\partial t} - \varepsilon \Delta n(t, x) = \frac{n(t, x)}{\varepsilon} R(x, [n(t)]) - \frac{\sqrt{\bar{n}n(t, x)}}{\varepsilon}
\]

Motivated by

- Population really vanishes; some traits are not represented
- The notion of 'individual' is somehow included in the parameter \( \bar{n} \)
  because \( n(t, x) \) really vanishes at a level related to \( \bar{n} \)
Survival threshold

Next ingredient is the notion of survival threshold.

\[
\frac{\partial n(t, x)}{\partial t} - \varepsilon \Delta n(t, x) = \frac{n(t, x)}{\varepsilon} R(x, [n(t)]) - \frac{\sqrt{\bar{n} n(t, x)}}{\varepsilon}
\]

Motivated by

- Population really vanishes; some traits are not represented
- The notion of 'individual' is somehow included in the parameter \( \bar{n} \)
- A similar notion represents 'demographic stochasticity'
- Compatibility with Monte-Carlo simulations
Survival threshold

\[ \frac{\partial n(t, x)}{\partial t} - \varepsilon \Delta n(t, x) = \frac{n(t, x)}{\varepsilon} R(x, [n(t)]) - \frac{\sqrt{n} n(t, x)}{\varepsilon} \]

and choose a threshold of the form

\[ \bar{n} = e^{\varphi_{st}/\varepsilon}, \quad \varphi_{st} < 0 \] (constants).

The formal constrained H.-J. equation is a free boundary problem

\[
\begin{cases}
\frac{\partial \varphi}{\partial t} = |\nabla \varphi|^2 + R \quad \text{in} \quad \Omega(t) := \{(x, t), \ s.t. \ \varphi > -\varphi_{st}\}, \\
\varphi = -\infty \quad \text{in} \quad \overline{\Omega}^c, \\
\varphi \geq \varphi_{st} \quad \text{in} \quad \overline{\Omega}.
\end{cases}
\]

Open questions: prove it rigorously; other scales
\[
\frac{\partial n(t, x)}{\partial t} - \varepsilon \Delta n(t, x) = \frac{n(t, x)}{\varepsilon} R(x, [n(t)]) - \frac{\sqrt{n(t, x)}}{\varepsilon} n(t, x)
\]

\[
\bar{n} = e^{\varphi_{st}/\varepsilon}, \quad \varphi_{st} < 0 \quad \text{(constants)},
\]

Formal derivation \( n_\varepsilon = e^{\varphi_\varepsilon/\varepsilon} \), then

\[
\frac{\partial \varphi_\varepsilon}{\partial t} - \varepsilon \Delta \varphi_\varepsilon - |\nabla \varphi_\varepsilon|^2 = R(x, [n(t)]) - \frac{\sqrt{n(t, x)}}{\sqrt{n(t, x)}} \]

\[
\frac{\partial \varphi_\varepsilon}{\partial t} - \varepsilon \Delta \varphi_\varepsilon - |\nabla \varphi_\varepsilon|^2 = R(x, [n(t)]) - e^{\varphi_{st} - \varphi_\varepsilon}/2\varepsilon
\]

- when \( \varphi_{st} < \varphi_\varepsilon \) then \( e^{\varphi_{st} - \varphi_\varepsilon}/2\varepsilon \to 0 \) (disappears)
- when \( \varphi_{st} > \varphi_\varepsilon \) then \( e^{\varphi_{st} - \varphi_\varepsilon}/2\varepsilon \to \infty \) i.e. \( \varphi_\varepsilon \to -\infty \)
**Survival threshold**

**Theorem** Fix $R(x) \leq 0$ then

$$\varphi_{\varepsilon} \xrightarrow{\varepsilon \to 0} \varphi(t, x)$$

the free boundary problem

$$
\begin{cases}
\frac{\partial \varphi}{\partial t} = |\nabla \varphi|^2 + R(x) & \text{in} \quad \Omega(t) := \{(x, t), \text{s.t. } \varphi > -\varphi_{\text{st}}\}, \\
\varphi = -\infty & \text{in} \quad \overline{\Omega}^c, \\
\varphi \geq \varphi_{\text{st}} & \text{in} \quad \overline{\Omega}.
\end{cases}
$$

characterized by one of the equivalent statements

- it is the **minimal solution**
- the **Dirichlet boundary condition** should be satisfied
  $$\varphi = \varphi_{\text{st}} \quad \text{on} \quad \partial \Omega(t).$$
- $\varphi = $ is a truncation to $-\infty$ of the global solution in $\mathbb{R}^d$. 


Survival threshold

When \( R(x) \) changes sign.

- The previous truncation formula is wrong
- The additional Dirichlet boundary condition is not enough, one should maybe impose also a 'state constraint' boundary condition in \( \Omega(t) \)
- The semi-relaxed limits can be compared to two relatively close functions of 'optimal control type' (given by an iterative 'cleaning').

This implies at least that

- In opposition to the case \( R \leq 0 \), the solution is changed drastically (see numerics)
- The limit does not depend on the specific power \( \sqrt{n} \)
Survival threshold

\[
\frac{\partial n(t, x)}{\partial t} - \varepsilon \Delta n(t, x) = \frac{n(t, x)}{\varepsilon} R(x) - \frac{\sqrt{\bar{n}n(t, x)}}{\varepsilon}
\]

Related to another asymptotic (other scales):

Bernouilli problem (see Lorz, Markowich, BP)

\[
\begin{cases}
  -\Delta n(x) + n(x) = R(x) \geq 0, & x \in \Omega \\
  n(x) = 0 & x \in \partial \Omega, \quad \frac{\partial n}{\partial \nu} = \vec{n} & x \in \partial \Omega.
\end{cases}
\]
Numerical results

Effect of the survival threshold
Numerical results
Model with two nutrients: no survival threshold

\[ \rho_1(t) = \int \psi_1(x)n(x,t)dx, \quad \rho_2(t) = \int \psi_2(x)n(x,t)dx \]

See Champagnat and Jabin
Numerical results

And the dynamics looks like
Open questions

• Uniqueness for a general $R(x, \varrho)$
• Case of multiple nutrients (See Champagnat and Jabin)

\[ R := R(x, \varrho_1, \varrho_2, \ldots, \varrho_I), \quad \varrho_i = \int \psi_i(x)n(x, t)dx. \]

• Survival threshold ($R(x, \varrho)$, other scales)
• Explain branching