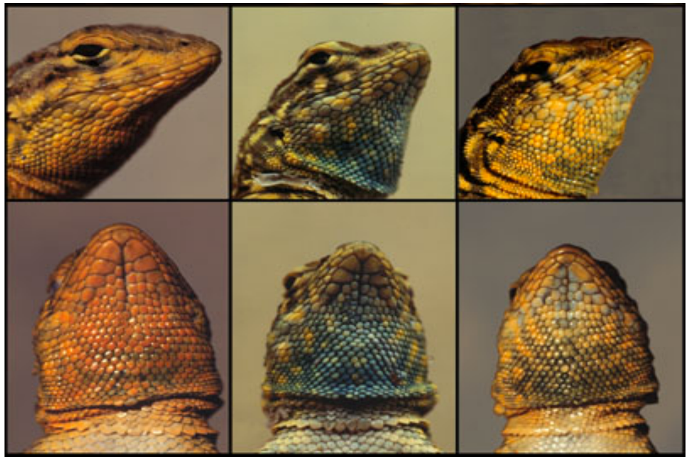
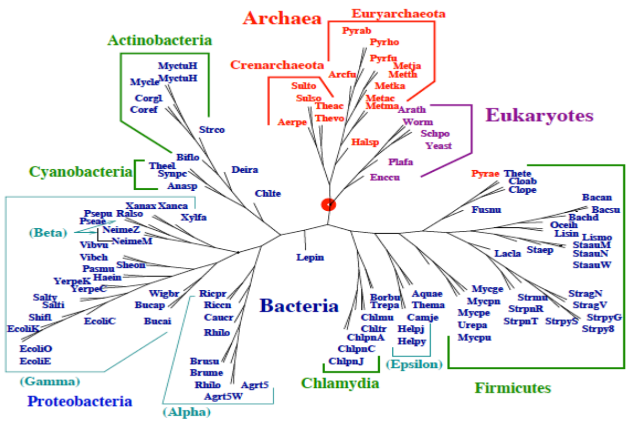
Adaptive evolution : a population approach

Benoît Perthame





Adaptive dynamic : selection principle

$$\begin{cases} \frac{d}{dt}n(x,t) = n(x,t)R\Big(x, \varrho(t)\Big), \\ \varrho(t) = \int_{\mathbb{R}^d} n(x,t)dx. \end{cases}$$

- 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

$$\begin{cases} \frac{\partial}{\partial t} n(x,t) - \Delta n = n(x,t) R\Big(x, \varrho(t)\Big), \\ \varrho(t) = \int_{\mathbb{R}^d} n(x,t)dx. \end{cases}$$

$$\begin{cases} \frac{\partial}{\partial t} n(x,t) = n(x,t) R\Big(x, \varrho(t)\Big) + \int M(x,y) b(y) n(y,t) dy, \\ \varrho(t) = \int_{\mathbb{R}^d} n(x,t)dx. \end{cases}$$

Adaptive dynamic : mutations

Off-springs undergo small mutations that change slightly the trait

$$\begin{cases} \frac{\partial}{\partial t} n(x,t) - \Delta n = n(x,t) R\Big(x, \varrho(t)\Big), \\ \varrho(t) = \int_{\mathbb{R}^d} n(x,t) dx. \end{cases}$$

Adaptive dynamic : mutations

Off-springs undergo small mutations that change slightly the trait

$$\begin{cases} \frac{\partial}{\partial t} n(x,t) - \Delta n = n(x,t) R\Big(x, \varrho(t)\Big), \\ \varrho(t) = \int_{\mathbb{R}^d} n(x,t)dx. \end{cases}$$

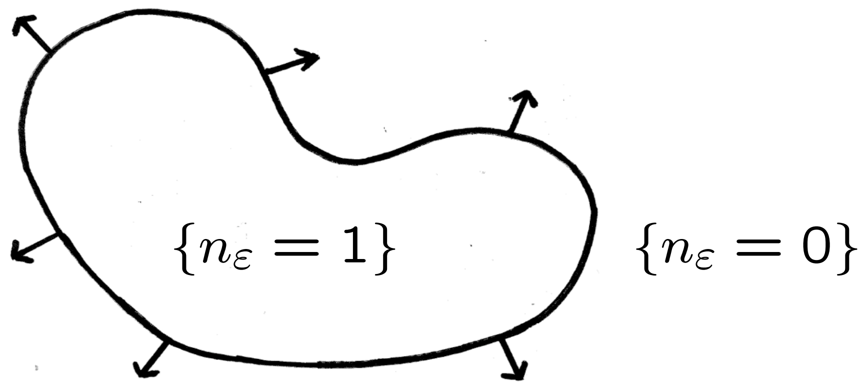
We assume that mutations are RARE and introduce a scale ε for 'small' mutations

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

Population model of adaptive dynamics : mutations

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

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



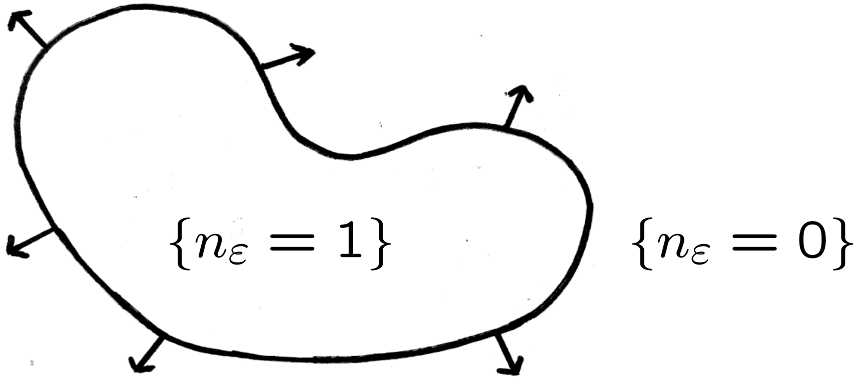
WKB, large deviations, level sets, geometric motion

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

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



in the limit

$$\bar{n}(x,t)(1 - \bar{n}(x,t) = 0.$$

Population model of adaptive dynamics : mutations

The situation is very different for the nonlocal equation

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

Population model of adaptive dynamics : mutations

The situation is very different for the nonlocal equation

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

In the limit one can expect

$$0 = n(x,t) R\Big(x, \varrho(t)\Big),$$

$$n(x,t) = \varrho \delta_{\Gamma(t)}, \qquad \Gamma(t) \subset \Big\{ R(\cdot, \varrho(t)) = 0 \Big\}.$$

Asymptotic method

Question. What tools to describe Dirac concentrations in PDEs ?

$$n_\varepsilon(x) = \frac{\bar\varrho}{(2\pi\varepsilon)^{d/2}} e^{-|x-\bar x|^2/(2\varepsilon)} \underset{\varepsilon\to 0}{\longrightarrow} \bar\varrho\delta(x-\bar x)$$

$$n_\varepsilon(x) = e^{-(|x-\bar x|^2+\varepsilon \ln O(\varepsilon))/(2\varepsilon)} \underset{\varepsilon\to 0}{\longrightarrow} \bar\varrho\delta(x-\bar x)$$

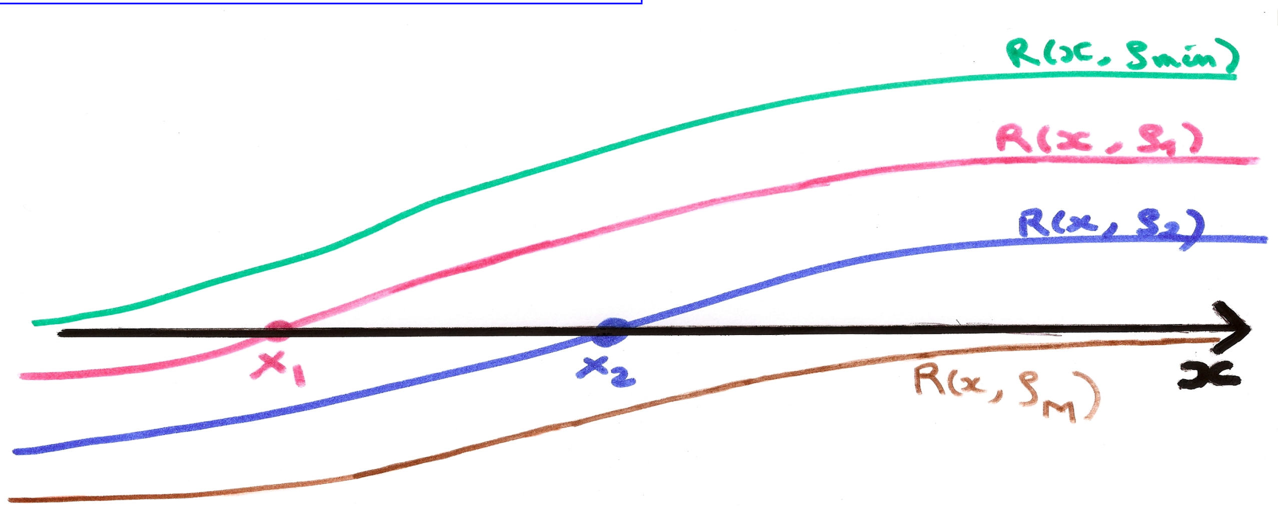
More generally (Hopf-Cole/WKB)

$$n_\varepsilon(x) = e^{\varphi_\varepsilon(x)/\varepsilon} \underset{\varepsilon\to 0}{\longrightarrow} \bar\varrho\delta(x-\bar x)$$

with the conditions

$$\varphi_\varepsilon \underset{\varepsilon\to 0}{\longrightarrow} \varphi, \qquad \max_x \varphi(x) = 0 = \varphi(\bar x)$$

Asymptotic method



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

$$n_\varepsilon(x,t) \underset{\varepsilon_k \to 0}{\longrightarrow} \bar{\varrho}(t)\delta(x = \bar{x}(t)), \qquad \varrho_\varepsilon \underset{\varepsilon_k \to 0}{\longrightarrow} \bar{\varrho}(t) = \int n(x,t)dx,$$

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

$$n_\varepsilon(x,t) \underset{\varepsilon_k \to 0}{\longrightarrow} \bar{\varrho}(t)\delta(x = \bar{x}(t)), \qquad \varrho_\varepsilon \underset{\varepsilon_k \to 0}{\longrightarrow} \bar{\varrho}(t) = \int n(x,t)dx,$$

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

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

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

$$n_\varepsilon(x,t) \underset{\varepsilon_k \to 0}{\longrightarrow} \bar{\varrho}(t)\delta(x = \bar{x}(t)), \qquad \varrho_\varepsilon \underset{\varepsilon_k \to 0}{\longrightarrow} \bar{\varrho}(t) = \int n(x,t)dx,$$

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

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

However $$\frac{\partial}{\partial t}\varphi\Big(\bar{x}(t), t\Big) = 0 = \frac{\partial}{\partial x}\varphi\Big(\bar{x}(t), t\Big)$$

$$R\Big(\bar{x}(t), \bar{\varrho}(t)\Big) = 0 \qquad \text{(Pessimism Principle)}$$

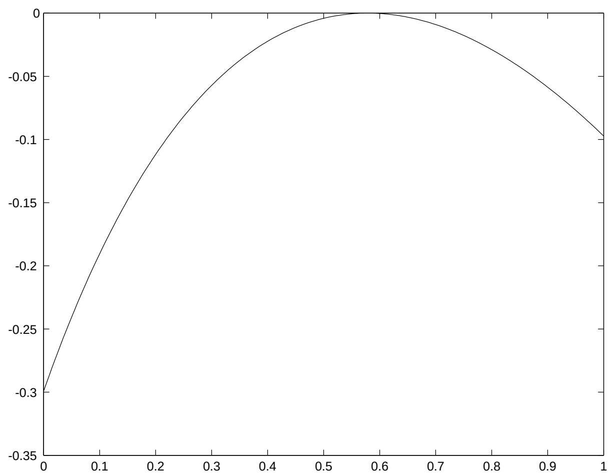
Asymptotic method

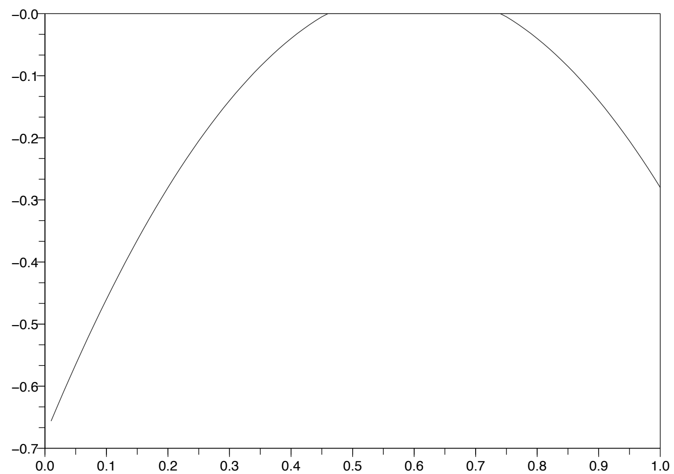
This problem should be understood as follows

$\max_x \varphi(x,t) = 0, \ \forall t$ 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, $\varphi_\varepsilon \underset{\varepsilon_k \to 0}{\longrightarrow} \varphi$ (locally uniformly), $\varrho_\varepsilon(t) \underset{\varepsilon_k \to 0}{\longrightarrow} \bar{\varrho}(t)$

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

- And $n_\varepsilon(x,t) \underset{\varepsilon_k \to 0}{\rightharpoonup} n(x,t)$ weakly in measures,

$$\text{supp}\Big(n(t)\Big) \subset \{\varphi(t) = 0\}$$

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

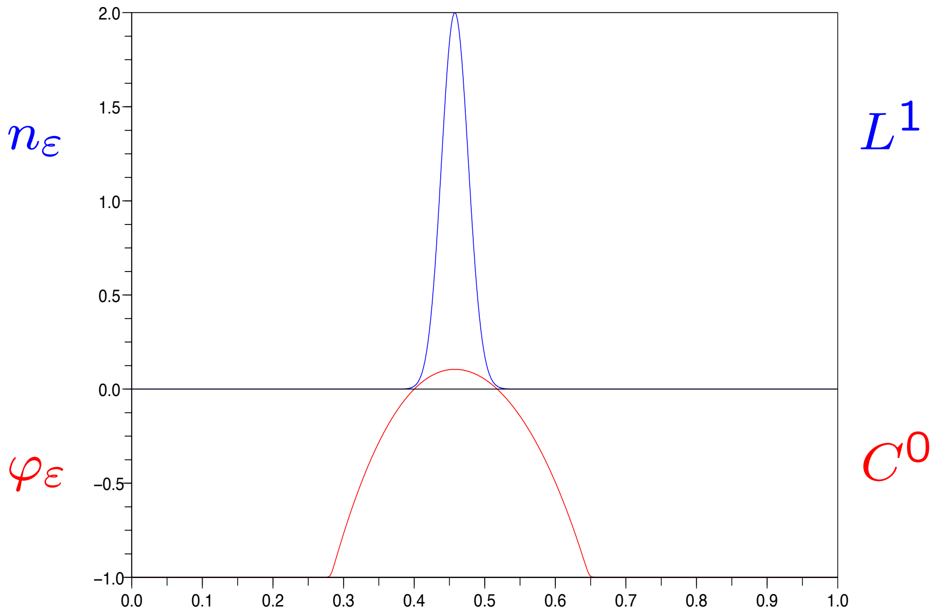
$$\frac{\partial}{\partial t}\varphi_\varepsilon(x,t) = R\Big(x, \varrho_\varepsilon(t)\Big) + |\nabla\varphi_\varepsilon(x,t)|^2 - \varepsilon\Delta\varphi_\varepsilon$$

and φ_ε 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 :



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

$$\begin{cases} \frac{\partial}{\partial t}\varphi(x,t) = b(x) - \bar{\varrho}(t)d(x) + |\nabla\varphi|^2, \\ \\ \max_x \varphi(x,t) = 0 \qquad \Big(= \varphi(t, \bar{x}(t)) \Big) \end{cases}$$

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^∞ contraction property is lost ! Define

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

$$\frac{d}{dt} M(t) \le R(x_M(t), \varrho_1(t)) - R(x_M(t), \varrho_2(t)) \le C|\varrho_1(t) - \varrho_2(t)|$$

But the constraint cannot be used here to control $|\varrho_1(t) - \varrho_2(t)|$ by $M(t)$.

Asymptotic method

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

Work on

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

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

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

$$\frac{d}{dt}M(t) \leq C\Big|\int_0^t \varrho_1(s)ds - \int_0^t \varrho_2(s)ds\Big|$$

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

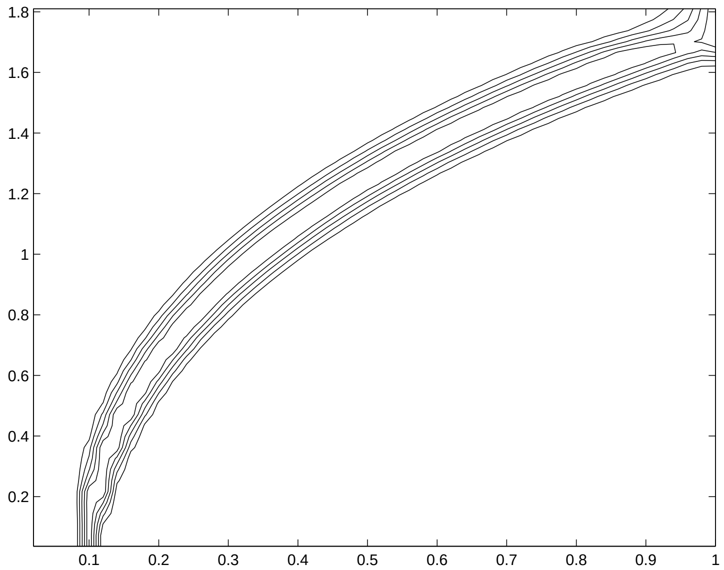
$$M(t) \geq \psi_1(t, x_1) - \psi_2(t, x_1) \geq d(x_1)\Big[\int_0^t \varrho_1(s)ds - \int_0^t \varrho_2(s)ds\Big]$$

The opposite inequality holds true similarly and thus

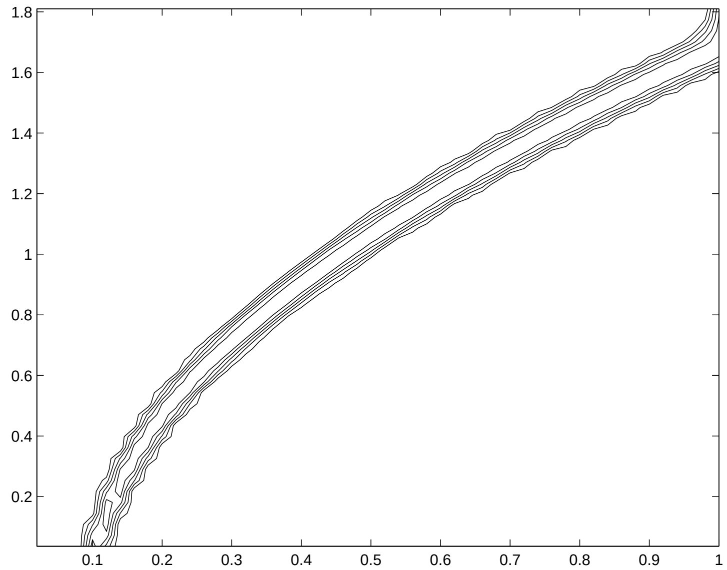
$$\frac{d}{dt}M(t) \leq \bar{C}M(t).$$

Asymptotic method

Numerical tests : $b(x) = .5 + x$



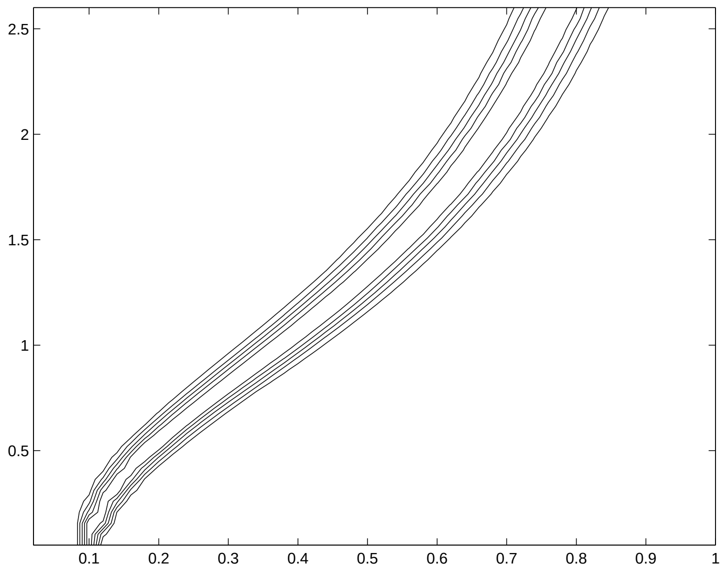
Direct simulation (1500 points)



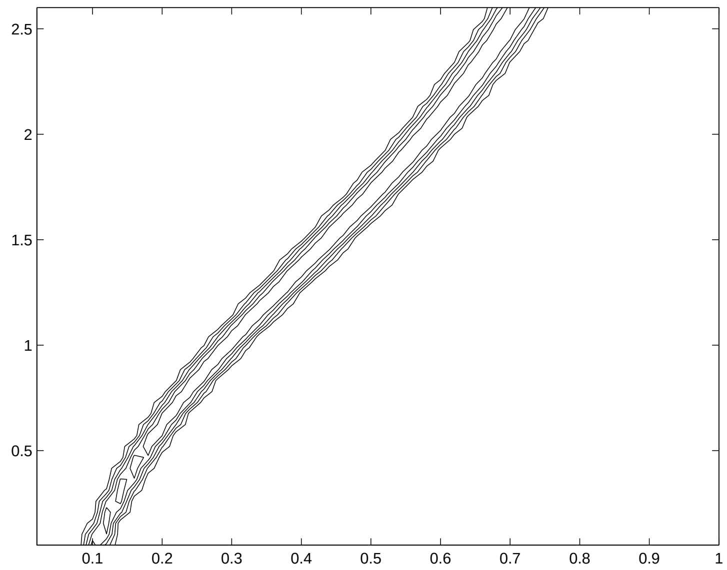
H.-J. solution (200 points)

Asymptotic method

Numerical tests : $b(x) = .5 + x(2 - x)$



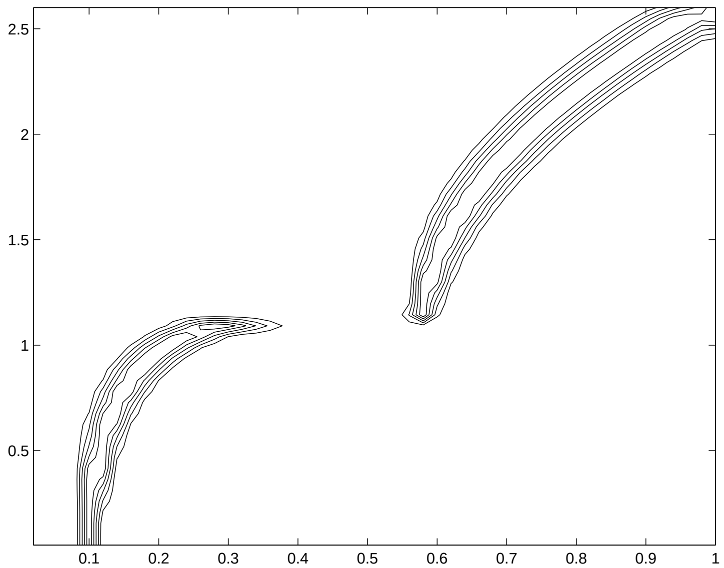
Direct simulation (1500 points)



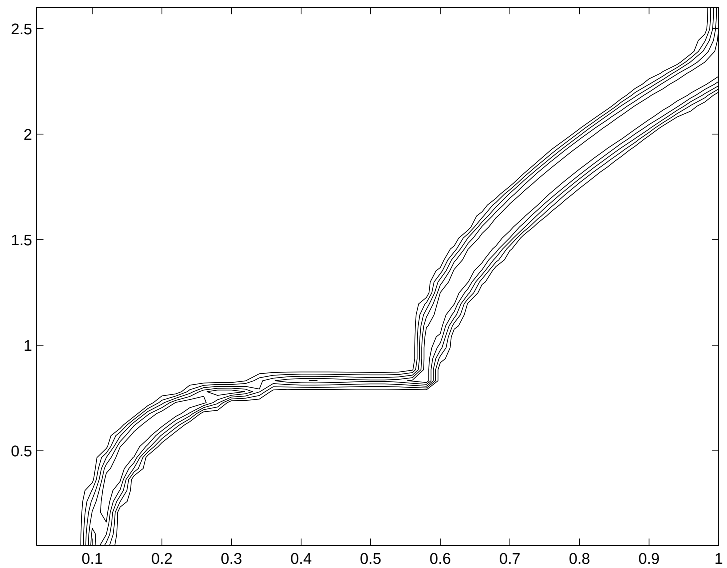
H.-J. solution (200 points)

Asymptotic method

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



Direct simulation (1500 points)



H.-J. solution (200 points)

Survival threshold

Next ingredient is the notion of survival threshold.

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

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.

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

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

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

and choose a threshold of the form

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

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

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

Open questions : prove it rigorously ; other scales

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

$$\bar{n} = e^{\varphi_{\text{st}}/\varepsilon}, \qquad \varphi_{\text{st}} < 0 \qquad\qquad \text{(constants)},$$

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

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

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

- when $\varphi_{\text{st}} < \varphi_\varepsilon$ then $e^{\frac{\varphi_{\text{st}} - \varphi_\varepsilon}{2\varepsilon}} \to 0$ (disappears)
- when $\varphi_{\text{st}} > \varphi_\varepsilon$ then $e^{\frac{\varphi_{\text{st}} - \varphi_\varepsilon}{2\varepsilon}} \to \infty$ i.e. $\varphi_\varepsilon \to -\infty$

Survival threshold

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

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

the free boundary problem

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

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

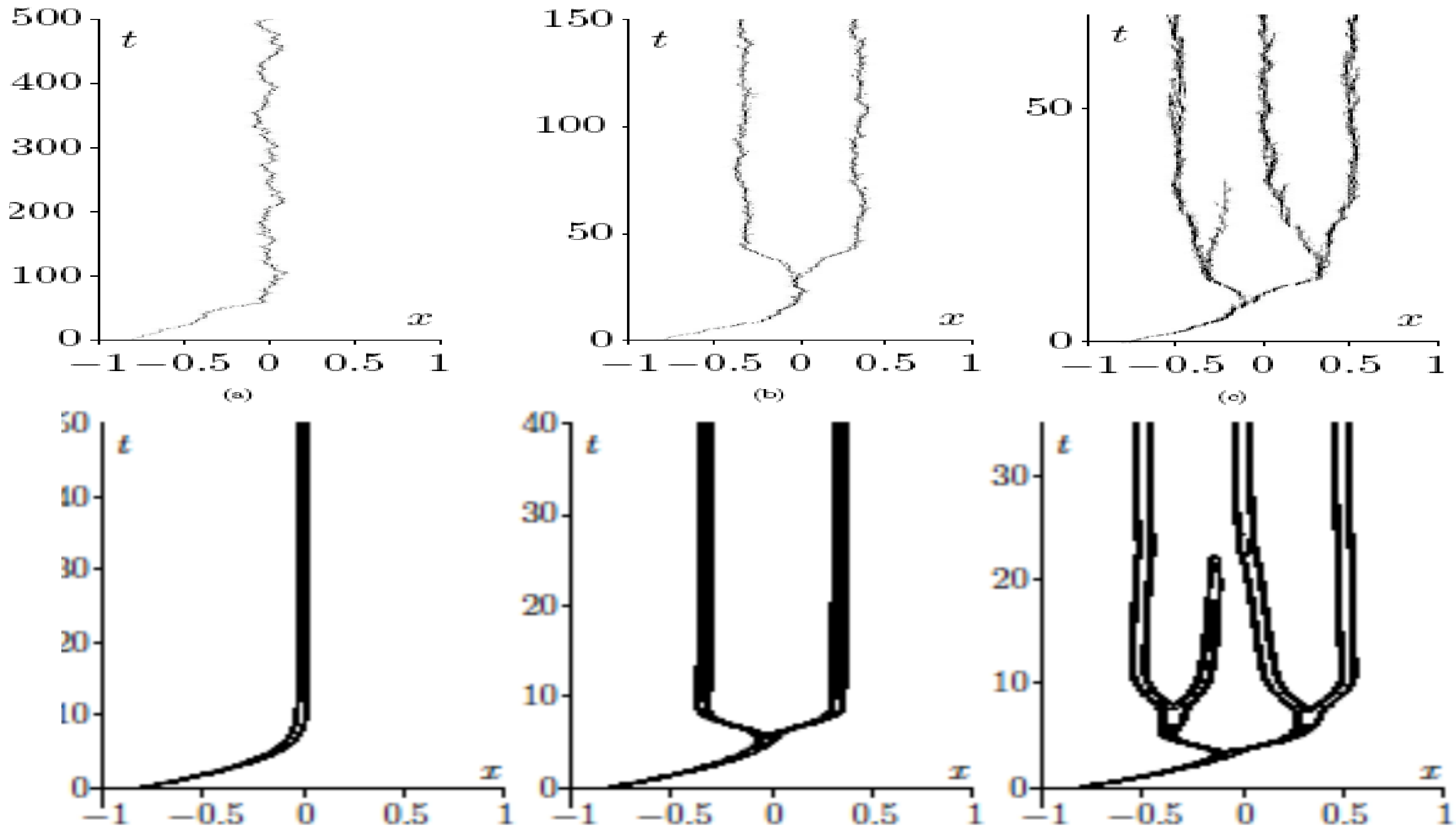
$$\frac{\partial n(t,x)}{\partial t} - \varepsilon \Delta n(t,x) = \frac{n(t,x)}{\varepsilon} R(x) - \frac{\sqrt{\bar{n} n(t,x)}}{\varepsilon}$$

Related to another asymptotic (other scales) :

Bernouilli problem (see Lorz, Markowich, BP)

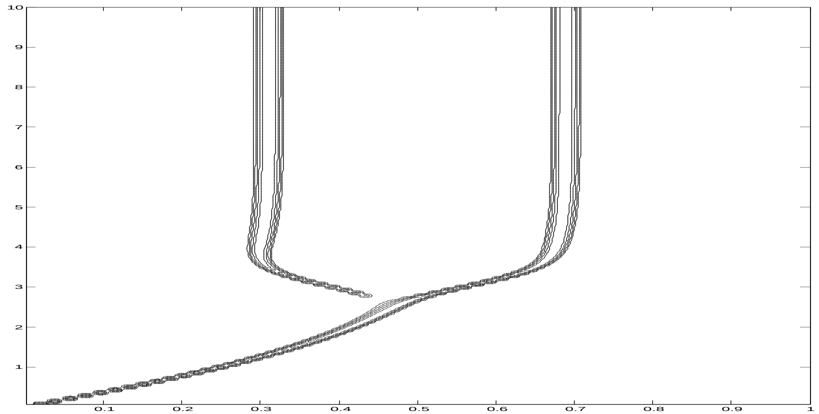
$$\begin{cases} -\Delta n(x) + n(x) = R(x) \geq 0, \quad x \in \Omega \\ n(x) = 0 \quad x \in \partial\Omega, \qquad \frac{\partial n}{\partial \nu} = \bar{n} \quad x \in \partial\Omega. \end{cases}$$

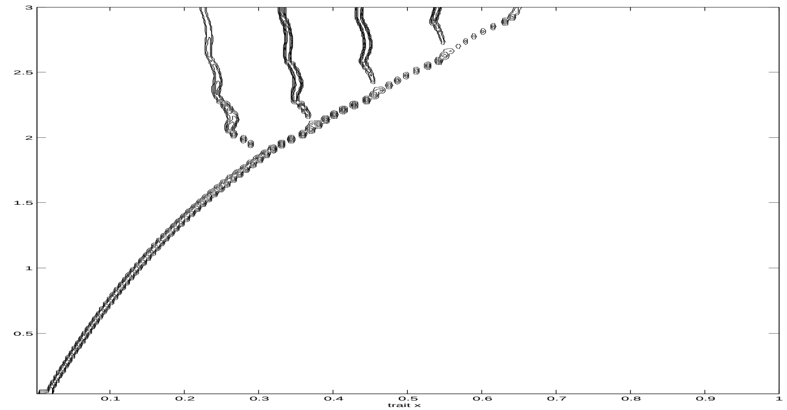
Numerical results

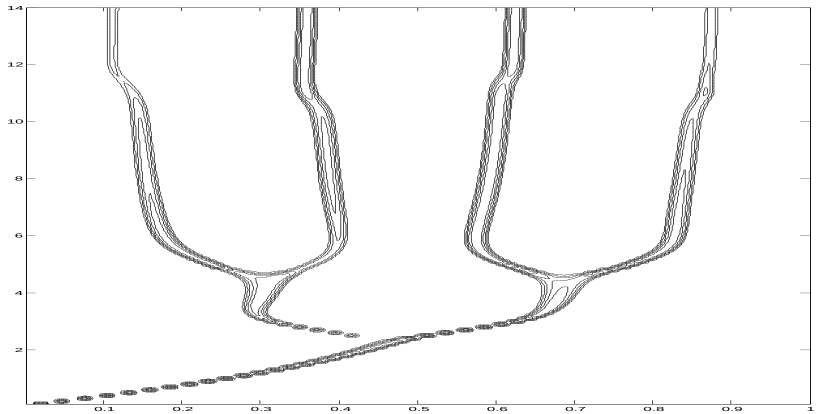


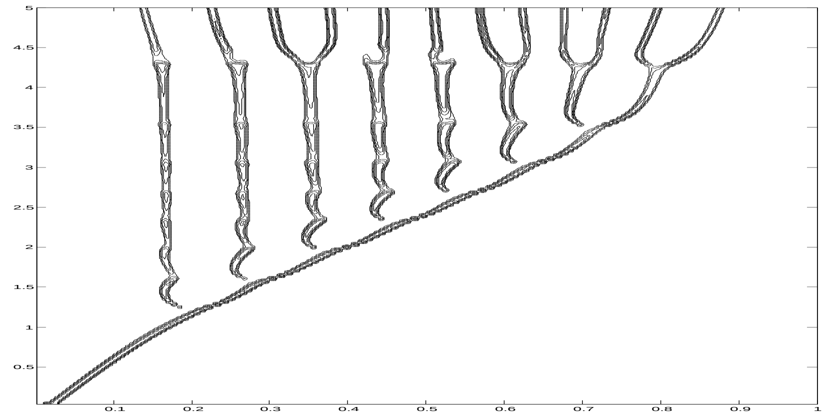
Effect of the survival threshold

Numerical results





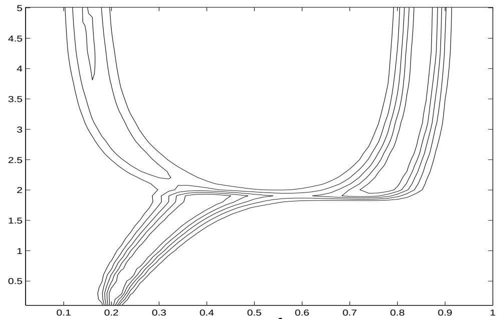




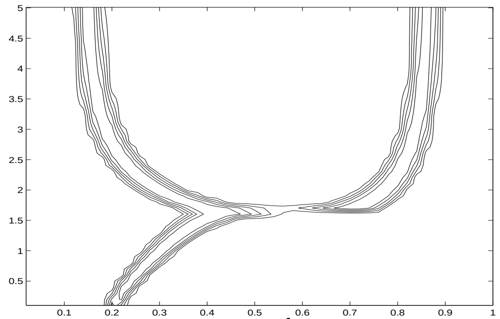
Model with two nutrients : no survival threshold

$$\varrho_1(t) = \int \psi_1(x) n(x,t) dx, \qquad \varrho_2(t) = \int \psi_2(x) n(x,t) dx$$

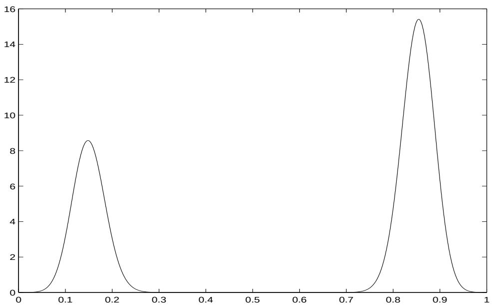
See Champagnat and Jabin



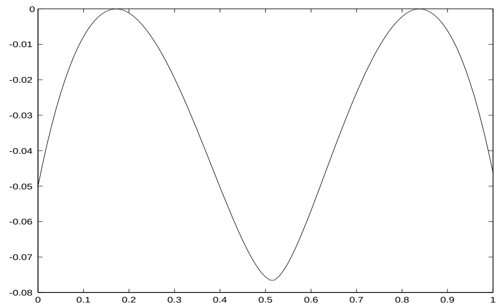
Direct simulation (1500 points)



H.-J. solution (200 points)



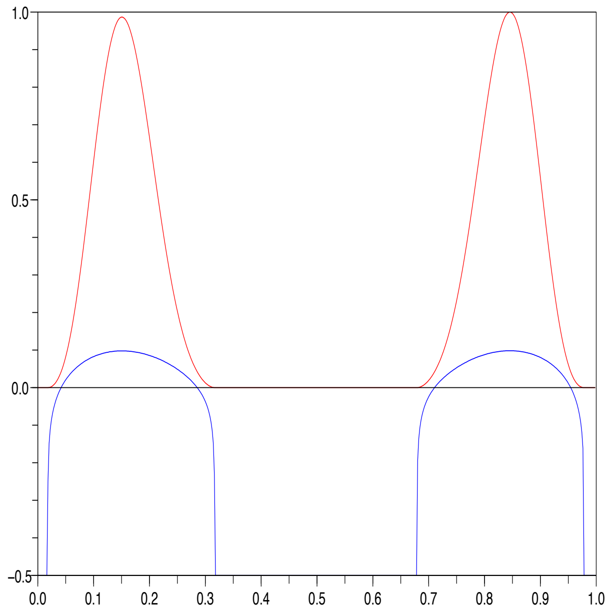
density n

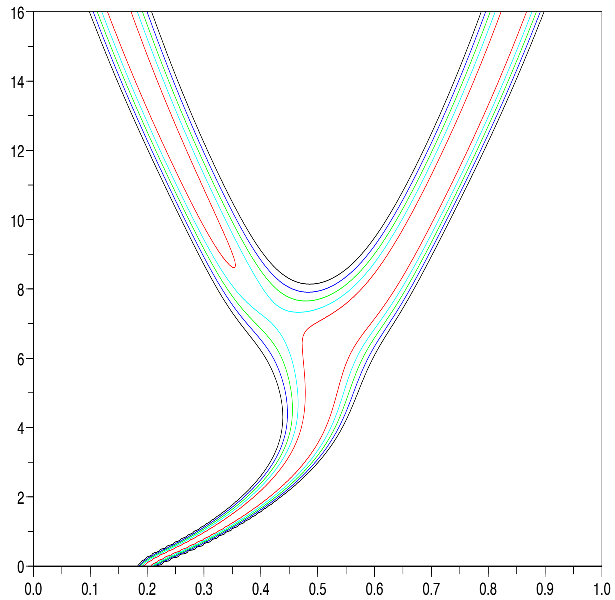


phase φ

Numerical results

And the dynamics looks like





Open questions

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

$$R := R(x, \varrho_1, \varrho_2, ..., \varrho_I), \qquad \varrho_i = \int \psi_i(x) n(x,t) dx.$$

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