Propagation in models of kinetic type in biology

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Presentation of the talk

- We focus on propagation phenomena arising in biology.
- Important feature : In all situations, it is noticed that the propagation is actively influenced by a microscopic **structure** of the population.

2 parts / 2 kind of structures :

1. **Reaction-kinetic models** inspired by bacterial dispersal,

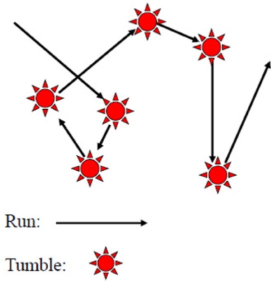
   $\Longrightarrow$ Structuring variable = velocity.

2. **Reaction-diffusion-mutation models** inspired by evolution in cane toads populations.

   $\Longrightarrow$ Structuring variable = phenotype.

Biologically quite far, but in fact **mathematically quite close !**

Motion of an individual bacteria



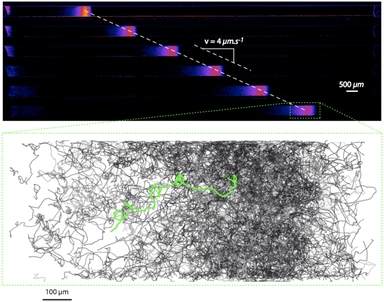
The bacteria E. Coli moves with a so-called *run and tumble* process :

straight swimming for $1s$
and
change of direction for $0.1s$.

$\Longrightarrow$ Ballistic trajectory.

Reference. Berg, H.C. ,*E. coli in Motion*, (2004).

Collective migration: Bacterial travelling pulses



Kinetic models are needed to describe accurately the pulses.

Question : Can we study mathematically propagation at the kinetic level ? Does it show new effects and makes a significant difference with macroscopic models ?

Reference. J. Saragosti *et al*, Directional persistence of . . . , (2011).

Propagation in kinetic models

1. Kinetic shock profiles (from physics)
    - Caflisch, Nicolaenko: Shock profiles solutions of the Boltzmann equation (1982),
    - Golse : Perthame-Tadmor profiles for scalar conservation laws (1998),
    - Liu, Yu : Boltzmann : Positivity of shock profiles (2004),
    - Cuesta, Schmeiser : Kinetic shock profiles for BGK equations (2006-2007-2009),

   (among others...)
2. Kinetic-reaction transport equations
    - Schwetlick : Travelling fronts for multidimensional nonlinear transport equations (2000),
    - Cuesta, Schmeiser, Hittmeir : Kinetic Fisher-KPP equation (2012),

Kinetic reaction transport equations

- Density of bacteria $f(t,x,v)$ at time t, position x and velocity v. Space density $\rho := \int_V f(v)dv$.
- The velocity set : $V = [-v_{\max}, v_{\max}]$, with $v_{max} \leq +\infty$.

The model (Schwetlick 2000 - Cuesta, Hittmeir, Schmeiser 2012):

$$\underbrace{\partial_t f + v\partial_x f}_{\text{Free run}} = \underbrace{(M(v)\rho - f)}_{\text{Tumbling}} + \underbrace{r\rho\,(M(v) - f)}_{\text{Growth with saturation}}$$

where M is a given distribution which satisfies

$$\int_V M(v)dv = 1, \qquad \int_V vM(v)dv = 0, \qquad \int_V v^2 M(v)dv = \theta.$$

Strong difference with the initial motivation :

Propagation is triggered by growth and not by bias of trajectories.

Reference. C. Cuesta *et al.*, Travelling Waves of a Kinetic Transport . . .(2012).

What we want to do :

→ Study qualitatively and quantitatively propagation phenomena in kinetic reaction-transport equations.

→ Are there special effects due to considering populations at the "mesoscopic" scale ?

We study the propagation from two points of view :

1. Study of (non-)existence of travelling wave solutions,
2. Geometric optics point of view.

Kinetic travelling waves

$$\partial_t f + v\partial_x f = (M(v)\rho - f) + r\rho\left(M(v) - f\right)$$

Definition

A travelling wave solution is of the form

$$f(t,x,v) = \mu\left(\xi = x - ct, v\right),$$

$$\text{Speed}: \ c \in \mathbb{R}^+, \qquad \text{Profile}: \ \mu \in \mathcal{C}^2\left(\mathbb{R}\times V, \mathbb{R}^+\right).$$

$$\text{Far field conditions}: \qquad \mu\left(-\infty,\cdot\right) = M, \qquad \mu\left(+\infty,\cdot\right) = 0.$$

Main equation :

$$(v - c)\partial_\xi \mu = (M(v)\nu - \mu) + r\nu\left(M(v) - \mu\right), \qquad \xi \in \mathbb{R},\ v \in V.$$

where ν is the macroscopic density associated to μ, that is $\nu\left(\xi\right) = \int_V \mu\left(\xi, v\right) dv$.

Why should we expect travelling waves ?

Macroscopic limit : We look at the situation when reorientations are much more frequent than reaction:

$$\mathbf{r} \mapsto \left(\mathbf{r}\varepsilon^{\mathbf{2}}\right).$$

M is unbiaised $\rightarrow$ Parabolic scaling $(t, x) \mapsto \left(\frac{t}{\varepsilon^{\mathbf{2}}}, \frac{x}{\varepsilon}\right)$:

$$\varepsilon^2 \partial_t f + \varepsilon v \partial_x f = (M(v)\rho - f) + r\varepsilon^2 \rho\, (M(v) - f)\,.$$

Then formally,

$$\lim_{\varepsilon \to 0} f^{\varepsilon}(t, x, v) = M(v)\rho(t, x),$$

The macroscopic limit is (at least formally) the **Fisher-KPP equation**

$$\partial_t \rho = \theta \partial_{xx} \rho + r\rho(1 - \rho)$$

Travelling waves for the Fisher-KPP equation (1937)

Combining **reaction** and **diffusion** creates propagation :

Theorem (Kolmogorov, Petrovsky, Piskunov, 1937)

- *There exists a minimal speed* $c^* := 2\sqrt{r\theta}$ *such that for all speed* $c \geq c^*$*, there exists a travelling wave solution (* $\rho(t,x) := \bar{\rho}(x - ct)$ *) of speed* c*.*
- *If the initial data has compact support then the front propagates with the minimal speed* c^**.*

(Fisher, KPP, Kanel, Fife and McLeod, Aronson and Weinberger ...)

The minimal speed c^* :
The front is created by small populations at the edge that reproduce almost exponentially. Seeking exponential decay in **the linearized equation** :

$$c(\lambda) = \theta\lambda + \frac{r}{\lambda} \geq 2\sqrt{r\theta} := c^* .$$

References. R.A. Fisher, *The advance of advantageous genes*, (1937),
D.G. Aronson *et al. Nonlinear diffusion in population genetics . . .* , 1975.
A.N. Kolmogorov *et al. Etude de l'équation de la diffusion . . .* , (1937).

Existence of travelling waves for the kinetic model

1. Perturbative approach in the parabolic limit $(t, x, r) \mapsto \left(\frac{t}{\varepsilon^2}, \frac{x}{\varepsilon}, r\varepsilon^2\right)$

Theorem (Cuesta, Hittmeir, Schmeiser)

Assume that V is compact. Let the wave speed satisfy $c \geq 2\sqrt{r\theta}$. For ε small enough, there exists a travelling wave solution of speed c.

2. Existence result in the kinetic regime:

Theorem (B., Calvez, Nadin)

Assume that V is compact. Suppose that M is continuous and positive.

1. *There exists a speed $c^* \in (0, v_{\max})$ such that there exists a travelling wave f solution of speed c for all $c \in [c^*, v_{\max})$.*
2. *The travelling wave is nonincreasing with respect to the space variable.*
3. *There exists no travelling wave of speed $c \in [0, c^*)$.*

Elements of proof

1. Find the minimal speed c^* : Given a spatial decay $\lambda \in \mathbb{R}^+$, we seek solutions of the linearized problem of type

$$f(t,x,v) = e^{-\lambda(x-c(\lambda)t)} Q_\lambda(v).$$

Associated speed : $c(\lambda) \in \mathbb{R}^+$, Expected profile at the edge : $Q_\lambda(v)$.

Proposition

We have $c^* = \min_{\lambda>0} c(\lambda)$, where $c(\lambda)$ is a solution of

$$\int_V \underbrace{\frac{(1+r)M(v)}{1+\lambda(c(\lambda)-v)}}_{=Q_\lambda(v)} \, dv = 1\,.$$

2. Key tool : Comparison principle.

   We can define, thanks to the dispersion relation, for $c \in (c^*, v_{max})$, an explicit couple of sub- and super- solutions.

Further properties

1. Spreading at finite speed (*a la* Aronson-Weinberger)
   1. For all $c > c^*$,

$$(\forall v \in V) \quad \lim_{t\to+\infty} \left(\sup_{x\geq ct} f(t,x,v) \right) = 0\,,$$

   2. For all $c < c^*$,

$$(\forall v \in V) \quad \lim_{t\to+\infty} \left(\sup_{x\leq ct} |M(v) - f(t,x,v)| \right) = 0\,,$$

2. Dynamical stability of the waves : *Rather explicit* weight $\phi(\xi, v)$ such that a travelling wave profile is *weakly linearly stable* in $L^2\left(e^{-2\phi(\xi,v)}d\xi dv\right)$.

Obstruction

The dispersion relation for $\lambda \in \mathbb{R}^+$

$$\int_V \frac{(1+r)M(v)}{1+\lambda(c(\lambda)-v)}\, dv = 1\,.$$

has **no solution** when V is unbounded ($v_{max} = +\infty$).

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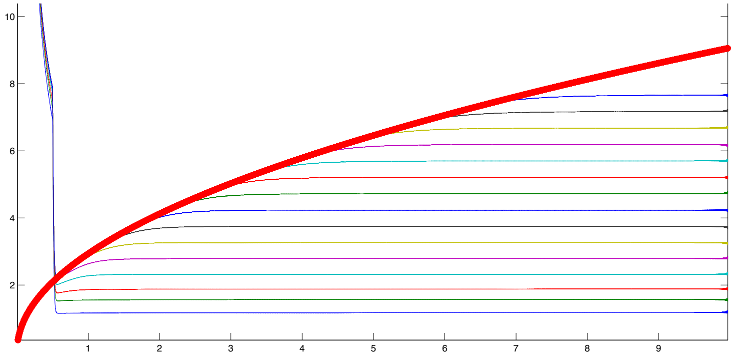
So what ?

Approximation of $v_{max} = +\infty$: speed as a function of time

$\rightarrow$ Gaussian equilibrium : $M(v) = C\left(v_{\max}\right)\exp\left(-\frac{v^2}{2}\right)\mathbf{1}_{|v|\leq v_{max}}$



Conjecture :

$$\mathbf{c(t) \approx \sqrt{t} \quad \Longrightarrow \quad x(t) \approx t^{\frac{3}{2}}}$$

Acceleration phenomena

→ Fisher-KPP with initial decay slower than exponential :
F. Hamel, L. Roques, *Fast propagation for KPP equations with slowly decaying initial conditions*, (2010).

→ Accelerated propagation in fractionnal diffusion equations :

- X. Cabré, J.-M. Roquejoffre, *Propagation de fronts dans les équations de Fisher–KPP avec diffusion fractionnaire*, (2009).
- X. Cabré, J.-M. Roquejoffre, *The influence of fractional diffusion in Fisher-KPP equations,* (2013).
- A.-C. Coulon, J.-M Roquejoffre, *Transition between linear and exponential propagation in Fisher-KPP type reaction-diffusion equations*, (2012).

→ Acceleration in integro-differential equations with slowly decaying kernel :
J. Garnier, *Accelerating solutions in integro-differential equations*, (2011).

Infinite speed of propagation

Assume that : $\forall v \in \mathbb{R}, \qquad M(v) > 0.$

Theorem (B., Calvez, Nadin)

Assume that there exists $\gamma \in (0,1)$ such that

$$\forall x \leq 0, \qquad f(0,x,v) \geq \gamma M(v).$$

Then, one has, for all $c > 0$,

$$\lim_{t \to +\infty} \sup_{x \leq ct} |M(v) - f(t,x,v)| = 0\,.$$

Sketch of proof.

$\lim_{v_{\max} \to +\infty} c^*(v_{\max}) = +\infty$ and a sub-solution using the truncated problem. □

Rate of acceleration when M is a Gaussian on $V = \mathbb{R}$

Theorem (B., Calvez, Nadin)

Let $M(v) = \frac{1}{\sqrt{2\pi}} \exp\left(-\frac{v^2}{2}\right)$. *Under suitable hypothesis on the initial data,*

1. ***Propagation bounded from above by*** $t^{\frac{3}{2}}$***:*** *There exists* C_1 *such that*

$$\lim_{t\to+\infty}\left(\sup_{x\geq C_1 t^{3/2}} \rho(t,x)\right) = 0\,.$$

2. ***Propagation bounded from below by*** $t^{\frac{3}{2}}$***:*** *There exists* C_2 *such that*

$$\lim_{t\to+\infty}\left(\inf_{x\leq C_2 t^{3/2}} \rho(t,x)\right) \geq \frac{1}{2}\,.$$

Conclusions

- Bounded velocities :
  - Minimal speed of propagation,
  - Profiles given by a spectral problem,
  - Linear spreading.

As for the Fisher-KPP equation.

- Unbounded velocities :
  - Accelerated propagation,
  - Almost exact rate in the Gaussian case ($\sim t^{\frac{3}{2}}$),

Unexpected result *since the diffusive limit is the Fisher-KPP equation.*

Hamilton-Jacobi approach

A method based on Hamilton-Jacobi equations has been used to study

1. Front propagation in models structured only by the space variable:

   Authors : Barles, Evans, Souganidis ... (89-94)

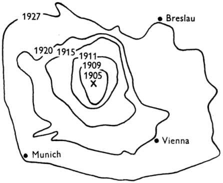
2. Dynamics of most favorable traits in populations structured only by a structural variable:

   Authors : Barles, Champagnat, Diekmann, Jabin, Lorz, Mirrahimi, Mischler, Perthame ...

Aim : Use this method to describe propagation phenomena in kinetic equations (populations structured by both space variable and velocity).

Geometric point of view - Fisher-KPP case

Hyperbolic scaling: $(t, x) \to \left(\frac{t}{\varepsilon}, \frac{x}{\varepsilon}\right)$:



$$(KPP_\varepsilon) \qquad \varepsilon\partial_t\rho^\varepsilon = \varepsilon^2\theta\partial_{xx}\rho^\varepsilon + r\rho^\varepsilon(1-\rho^\varepsilon)\,.$$

Hopf-Cole : $\rho^\varepsilon = \exp\left(-\frac{\varphi^\varepsilon}{\varepsilon}\right)$.

Equation for φ^ε :

$$\partial_t\varphi^\varepsilon + \theta|\partial_x\varphi^\varepsilon|^2 + r = \varepsilon\theta\partial_{xx}\varphi^\varepsilon + r\,\rho^\varepsilon.$$

When $\varepsilon \to 0$, the sequence φ^ε converges towards the **viscosity solution** of the following **constrained Hamilton-Jacobi equation**

$$\min\left(\partial_t\varphi^0 + \theta|\partial_x\varphi^0|^2 + r\,,\,\varphi^0\right) = 0\,.$$

The **nullset** of φ^0 gives the information about the propagation. Locally on

- $\mathrm{Int}\left(\varphi^0 = 0\right)$, $\qquad \lim_{\varepsilon\to 0}\rho^\varepsilon = 1.$
- $\mathrm{Int}\left(\varphi^0 > 0\right)$, $\qquad \lim_{\varepsilon\to 0}\rho^\varepsilon = 0.$

References. M.I. Freidlin, *Geometric optics approach . . .* , (1986)

L.C. Evans and P.E. Souganidis, *A PDE approach to geometric . . .* , (1989)

In the kinetic framework with bounded velocities.

Hyperbolic scaling : $(t, x, v) \to \left(\frac{t}{\varepsilon}, \frac{x}{\varepsilon}, v\right)$

$$\varepsilon \left(\partial_t f^\varepsilon + v \cdot \nabla_x f^\varepsilon\right) = L(f^\varepsilon) + r\rho^\varepsilon \left(M(v) - f^\varepsilon\right),$$

The *linear* operator L:

- Acts only on the velocity variable and is mass preserving,
- $\mathrm{Ker}(L) = \mathrm{Span}(M)$,
- Of the form

$$\forall v \in V, \qquad L(f)(v) = P(f)(v) - \Sigma(v) f(v),$$

where P satisfies a **maximum principle**.

Example

1. $L(f) = P(f) = \Delta f$, $\Sigma \equiv 0$.
2. $P(f) = \int_V K(v, v') f(v') dv'$ and $\Sigma(v) = \int_V K(v', v) dv'$.

By analogy with Fisher-KPP, our **kinetic WKB ansatz** writes

$$f^\varepsilon(t,x,v) = M(v)e^{-\frac{\varphi^\varepsilon(t,x,v)}{\varepsilon}}.$$

New equation for φ^ε :

$$\partial_t \varphi^\varepsilon + v\cdot\nabla_x\varphi^\varepsilon + r = -\frac{\mathcal{L}\left(M(v)e^{-\frac{\varphi^\varepsilon}{\varepsilon}}\right)}{M(v)e^{-\frac{\varphi^\varepsilon}{\varepsilon}}} + r\rho^\varepsilon,$$

where

$$\mathcal{L}(f) = L(f) + r\left(M(v)\rho - f\right).$$

$\rightarrow$ Can we pass to the limit ? Does it make a difference with the macroscopic case ?

Passing to the limit.

Theorem (B.)

Let $V = [-v_{\mathbf{max}}, v_{\mathbf{max}}]$. Suppose that the initial data is well-prepared,

$$\forall (x, v) \in \mathbb{R}^n \times V, \qquad \varphi^\varepsilon(0, x, v) = \varphi_0(x),$$

and that some structural hypothesis on $\mathcal{L}$ are satisfied. Then $(\varphi^\varepsilon)_\varepsilon$ converges locally uniformly towards φ^0, where φ^0 **does not depend on** *v. Moreover φ^0 is the unique viscosity solution of the constrained Hamilton-Jacobi equation*

$$\begin{cases} \min\left\{\partial_t \varphi^0 + \mathcal{H}\left(\nabla_x \varphi^0\right) + r, \varphi^0\right\} = 0, & \forall (t, x) \in \mathbb{R}_+^* \times \mathbb{R}^n, \\ \varphi^0(0, x) = \varphi_0(x), & x \in \mathbb{R}^n. \end{cases}$$

About the Hamiltonian.

- The Hamiltonian is obtained after solving a **spectral problem** in the velocity variable via a Krein-Rutman argument :
"For all $p \in \mathbb{R}^n$, there exists a unique $\mathcal{H}(p)$ such that there exists a positive normalized eigenvector $Q_p \in L^1(V)$ such that

$$\forall v \in V, \qquad \mathcal{L}(Q_p)(v) + (v \cdot p)\, Q_p(v) = \mathcal{H}(p) Q_p(v)."$$

- Looks like homogenization theory : x slow variable, v fast variable.

- **Striking conclusion :**
$\mathcal{H}$ is **Lipschitz** with respect to p : It keeps in mind the finite speed of propagation at the kinetic level. Performing the diffusion limit first gives $\theta|p|^2$.

- As an example, when $L(f) = M(v)\rho - f$ in one dimension :

$$M \equiv \frac{1}{2} \qquad \text{on} \qquad V = (-1, 1) \quad \Longrightarrow \qquad \mathcal{H}(p) = \frac{p}{\tanh\left(\frac{p}{1+r}\right)} - (1+r).$$

Why φ^0 is independent of v : Particular case

Assume for simplicity $L(f) = M(v)\rho - f$:

$$\partial_t \varphi^\varepsilon + v \cdot \nabla_x \varphi^\varepsilon + r = -(1+r) \int_V M(v) e^{\frac{\varphi^\varepsilon(v) - \varphi^\varepsilon(v')}{\varepsilon}} dv' + r\rho^\varepsilon,$$

1. Uniform Lipschitz estimates give the locally uniform convergence of φ^ε (up to extraction).
2. The boundedness of

$$\int_V M(v) e^{\frac{\varphi^\varepsilon(v) - \varphi^\varepsilon(v')}{\varepsilon}} dv'$$

implies the independence of v in the limit $\varepsilon \to 0$.

Viscosity super- solution step.

Let $\psi^0 \in \mathcal{C}^2\left(\mathbb{R}^+ \times \mathbb{R}^n\right)$ be a test function such that $\varphi^0 - \psi^0$ has a strict local minimum a (t^0, x^0) with $t^0 > 0$.

1. We define the **corrected test functions** :

$$\psi^\varepsilon(t,x,v) := \psi^0(t,x) - \varepsilon \ln\left(\frac{Q_{[\nabla_x \psi^0(t,x)]}(v)}{M(v)}\right).$$

2. Using the spectral problem and the **maximum principle** satisfied by $\mathcal{P}$:

$$\partial_t \psi^\varepsilon + \mathcal{H}\left(\nabla_x \psi^\varepsilon\right) + r \geq \frac{\mathcal{P}\left(Q_{p^\varepsilon}\right)}{Q_{p^\varepsilon}} - \frac{\mathcal{P}\left(Q_{\nabla_x \psi^0(t^\varepsilon, x^\varepsilon)}\right)}{Q_{\nabla_x \psi^0(t^\varepsilon, x^\varepsilon)}},$$

   at the point $(t^\varepsilon, x^\varepsilon, v^\varepsilon)$ (approximated minimas), with $p^\varepsilon = \nabla_x \psi^\varepsilon(t^\varepsilon, x^\varepsilon, v^\varepsilon)$.

3. The sequence v^ε is **bounded**, we pass to the limit.

References.

Crandall, M. G., *Some Properties of Viscosity Solutions of H-J Equations*, (1984),

Evans, L.C., *The perturbed test function method for viscosity solutions of nonlinear PDE*, (1989)

Conclusions and perspectives

- We can derive a limiting (macroscopic) Hamilton-Jacobi equation, the effective Hamiltonian is Lipschitz.
- We would like to do the same with $V = \mathbb{R}$, when $r = 0$, $L(f) = M(v)\rho - f$ and M is a Gaussian. The relevant equation to solve is

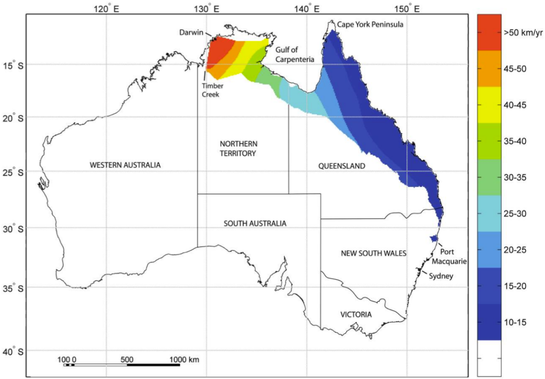
$$\partial_t \varphi^\varepsilon + v \cdot \nabla_x \varphi^\varepsilon = 1 - \frac{1}{\sqrt{2\pi\varepsilon}} \int_{\mathbb{R}^n} \exp\left(\frac{\varphi^\varepsilon(v) - \varphi^\varepsilon(v') - v^2/2}{\varepsilon} \right) dv',$$

The limit system when $\varepsilon \to 0$ shall be :

$$\begin{cases} \max\left(\partial_t \varphi^0 + v \cdot \nabla_x \varphi^0 - 1, \varphi^0 - \min_{w \in \mathbb{R}^n} \varphi^0 - \frac{v^2}{2} \right) = 0\,, \\ \partial_t \left(\min_{w \in \mathbb{R}^n} \varphi^0 \right) \leq 0\,, \\ \partial_t \left(\min_{w \in \mathbb{R}^n} \varphi^0 \right) = 0\,, \qquad \text{if} \quad \operatorname{argmin}(\varphi^0)(t,x) = \{0\}\ , \\ \varphi^0(0,x,v) = \varphi_0(x,v)\,. \end{cases}$$

This is work in progress ...

Evolution of dispersal in cane toads populations (*e.g.*)



- → Speed increased by 5.
- → At the edge, faster toads in majority.
- → **Spatial sorting** : Dynamic selection of traits along the invasion.

We need models with both space and dispersion variables.

Question : Can we study propagation in such models and recover biological conclusions ?

Reference. M. Urban *et al*, A toad more traveled: the heterogeneous ..., (2008).

Modelling the cane toads invasion

$t \in \mathbb{R}^+$: time, $x \in \mathbb{R}$: space variable, $\theta \in \Theta$: dispersal ability.

Mutations, Reproduction.

$$\begin{cases} \partial_t f = \theta \partial_{xx} f + \alpha \partial_{\theta\theta} f + r f (1-\rho), & (t,x,\theta) \in \mathbb{R}^+ \times \mathbb{R} \times \Theta, \\ \rho(t,x) = \int_\Theta f(t,x,\theta') \, d\theta', & (t,x) \in \mathbb{R}^+ \times \mathbb{R}. \end{cases}$$

with Neumann boundary conditions in $\theta \in \Theta := [\theta_{min} > 0, \theta_{max} < +\infty]$.

Crucial difference : No full **maximum/comparison principles available**.

References.

L. Desvillettes *et al.*, *Infinite dimensional reaction-diffusion ...*, (2004)

N. Champagnat *et al.*, *Invasion and adaptive evolution ...*, (2007)

O. Bénichou *et al.*, *Front acceleration ...*, (2012)

Edge of the front

Linear problem at infinity :

$$\text{Ansatz : } \mu(\xi,\theta) = \exp(-\lambda(x - c(\lambda)t))Q_\lambda(\theta),$$

$$(S)\begin{cases} \alpha\partial^2_{\theta\theta}Q_\lambda(\theta) + \left(-\lambda c(\lambda) + \theta\lambda^2 + r\right)Q_\lambda(\theta) = 0\,, \\ \partial_\theta Q_\lambda(\theta_{\min}) = \partial_\theta Q_\lambda(\theta_{\max}) = 0\,, \\ Q_\lambda(\theta) > 0\,. \end{cases}$$

Unique solution by the Krein-Rutman theorem iff Θ is bounded :

> For all $\lambda > 0$, there exists a unique $c(\lambda) \in \mathbb{R}^+$,
> such that there exists $Q_\lambda(\theta) > 0$
> satisfying (S).

The existence of waves is a theorem.

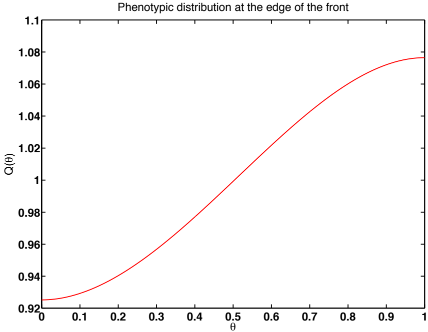
Spatial sorting at the edge of the front.

The eigenvector $Q_\lambda(\theta)$ gives the distribution of the motilities at the edge of the front going with speed $c(\lambda)$.

$Q_\lambda(\theta)$ is increasing ! $=$

At the edge of the front, more toads with the biggest dispersal ability.

$Q_\lambda(\theta)$ concentrates to $\delta_{\theta=\theta_{\mathbf{max}}}$ when $\alpha \to 0$.



Reference. R. Shine and al, *An evolutionary process that assembles phenotypes through space rather than through time*, (2011)

Prediction about unbounded $\Theta = (0, +\infty)$?

A WKB approach can (formally) show **an acceleration of the front** !

The only natural scaling to make is:

$$(t, x, \theta) \mapsto \left(\frac{t}{\varepsilon}, \frac{x}{\varepsilon^{\frac{3}{2}}}, \frac{\theta}{\varepsilon} \right)$$

The limit satisfies formally in the small population regime ($\min \varphi^0 > 0$):

$$\partial_t \varphi^0 + \theta |\partial_x \varphi^0|^2 + \alpha |\partial_\theta \varphi^0|^2 + r = 0\,.$$

Starting with a Dirac mass at $(x, \theta) = (0, 0)$, the point at the far edge satisfies

$$\boxed{x(t) \approx \frac{4}{3} \left(r^{3/4} \alpha^{1/4} \right) t^{3/2}}$$

Comparison with data.

Data from Urban et al. (Am. Nat. 2008): 1.63 ± 0.13.

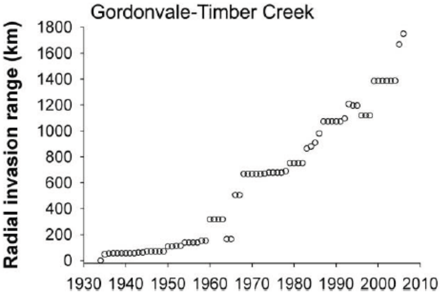


Figure : Position of the front with years - Section Gordonvale-Timber Creek, for which spatial sorting is presumably the main effect.

Reference. M. Urban *et al*, A toad more traveled: the heterogeneous . . . , (2008).

Thank you for your attention !