Étude de phénomènes de propagation pour des modèles cinétiques et structurés

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1. Introduction : Models of kinetic type in biology
   - Collective motion of bacteria
   - Modelling of Darwinian evolution

2. Travelling waves in kinetic equations.
   - Travelling waves when V is bounded
   - Front acceleration when V is unbounded

3. Hamilton-Jacobi limit of a structured population model
   - The problem
   - The WKB technique in the KPP case
   - Hamilton-Jacobi approach with θ as a "kinetic" variable

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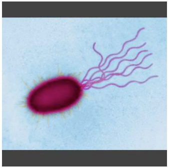
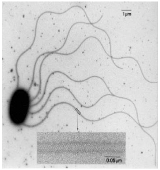
How do bacteria move ...

The bacteria E. Coli moves thanks to flagella :





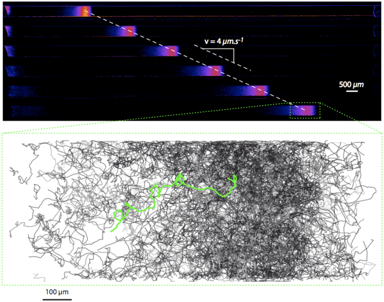
From Howard Berg's lab

and with a so-called *run and tumble* process :
straight swimming for $1s$
and
change of direction for $0.1s$.

Collective migration (1/2)

Collective migration (2/2)

Bacterial travelling pulses:



The kinetic point of view is the most relevant for this situation.

J. Saragosti, V. Calvez, N. Bournaveas, B. Perthame, A. Buguin and P. Silberzan, Directional persistence of chemotactic bacteria in a travelling concentration wave, PNAS (2011).

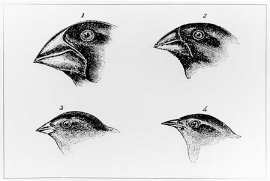
Darwinian evolution of populations

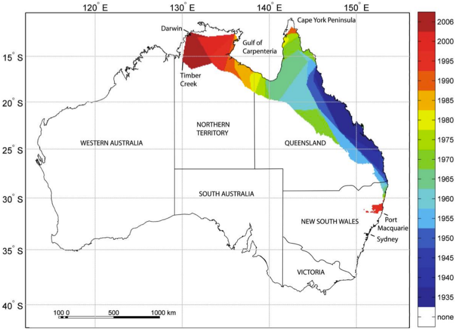
We study the

Darwinian evolution
of populations

which are structured by:

1. phenotypical traits,
2. position in space.





Some examples

Cane toads invasion

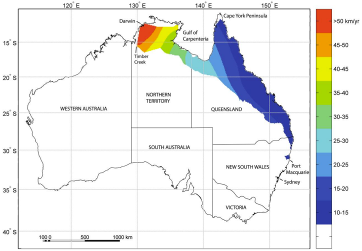


Figure : From Urban et al 2006

Evolution in fly wings

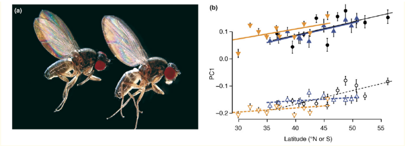


Figure : From Vellend et al 2007

With **Vincent Calvez** (ENS Lyon), **Grégoire Nadin** (Paris 6).

Kinetic equations

- Probability density of bacteria $f(t,x,v)$ at time t, position x and speed v. Total density $\rho := \int_V f(v)dv$.
- The velocity set V : symmetric, bounded or unbounded ; $v_{max} \leq +\infty$.

The model (Cuesta, Hittmeir, Schmeiser, 2010):

$$\underbrace{\partial_t f + v\partial_x f}_{\text{Free run}} = \underbrace{(M(v)\rho - f)}_{\text{Tumbling}} + \underbrace{r\rho\left(M(v) - f\right)}_{\text{Growth with saturation}} \qquad (1)$$

where the Maxwellian M on the space V satisfies

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

We assume here that $v_{max} < +\infty$.

Definition

We say that a function $f(t,x,v)$ is a travelling front solution of speed $c \in \mathbb{R}^+$ of equation (1) if it can be written $f(t,x,v) = \mu(\xi = x - ct, v)$, where *the profile* $\mu \in \mathcal{C}^2(\mathbb{R} \times V)$ is nonnegative, satisfies $\mu(-\infty, \cdot) = M$, $\mu(+\infty, \cdot) = 0$, and μ solves

$$(v - c)\partial_\xi \mu = (M(v)\nu - \mu) + r\nu\,(M(v) - \mu)\,, \qquad \xi \in \mathbb{R},\ v \in V. \tag{3}$$

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

Existence results

Parabolic limit result : (parabolic scaling) + ($r \to r\varepsilon^2$) :

Theorem (Cuesta, Hittmeir, Schmeiser)

Let the wave speed satisfy $s \geq 2\sqrt{rD}$. For ε small enough, there exists a travelling wave solution of speed s.

Existence result in the kinetic regime:

Theorem (B., Calvez, Nadin)

*Assume that $v_{max} < +\infty$. There exists a **minimal speed** $c^* \in (0, v_{max})$ such that **there exists a travelling wave solution of** (1) **of speed** c **for** $c \in [c^*, v_{max}]$. Moreover, the profile is **nonincreasing** with respect to ξ.*

Finding the speed : Dispersion relation

We look for solutions of the linearized problem of type $e^{-\lambda\xi}Q(v)$. Yields the following ***spectral problem*** :

For all λ, find $c(\lambda)$ such that there exists a Maxwellian Q_λ such that

$$\forall v \in V, \quad (1+\lambda\left(c(\lambda)-v\right))\, Q_\lambda(v) = (1+r)\int_V M(v)Q_\lambda(v)dv. \qquad (4)$$

Proposition

The minimal speed c^* is given by $c^* = \min_{\lambda>0} c(\lambda)$ where $c(\lambda)$ is for all λ a solution of the following **dispersion relation**:

$$(1+r)\int_V \frac{M(v)}{1+\lambda(c(\lambda)-v)}\,dv = 1\,. \qquad (5)$$

No solution when V is unbounded ($v_{max} = +\infty$)

Remarks on the results

1. The existence result is proved using a sub- and super-solutions technique (see e.g. Berestycki and Hamel).
2. One can recover the Fisher-KPP equation :

$$\text{(parabolic scaling)} + (r \to r\varepsilon^2).$$

Proposition

Assume that $v_{max} < +\infty$, then $c^* \underset{\varepsilon \to 0}{\longrightarrow} 2\sqrt{rD} := c_{\text{KPP}}$.

Approximation of $v_{max} = +\infty$: Numerical simulations

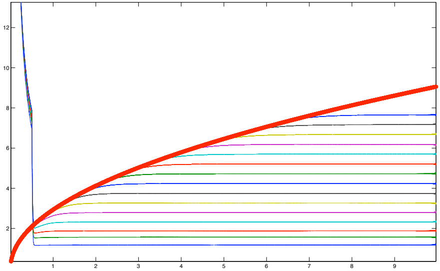


Figure : Evolution of the speed of the front for different values of the maximal speed. The Maxwellian here is a Gaussian : $M(v) = C\,(V_{max})\exp\left(-\frac{v^2}{2}\right)$. "Bell" initial condition.

With **Sepideh Mirrahimi** (Inst. Math. Toulouse).

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 phenotypical traits:

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

Aim : Use this method to describe space-trait interactions in populations structured by space variable and phenotypical traits.

A structured population model

$t \in \mathbb{R}^+$: time, $x \in \mathbb{R}^n$: space variable, $\theta \in \Theta$: phenotypical trait.

- Space diffusion with a constant rate D.
- Phenotypical mutations = diffusion with a constant rate α.
- When reproducing, an individual gives his trait to his offspring, the fitness is heterogeneous: $r\,a(x,\theta)$.
- Competition for resources : *local* in space, *nonlocal* in trait.

The model writes :

$$\begin{cases} \partial_t f - D\Delta_x f - \alpha\Delta_\theta f = r\,f\left(a(x,\theta) - \rho\right), & (t,x,\theta) \in \mathbb{R}^+ \times \mathbb{R} \times \Theta, \\ \rho(t,x) = \int_\Theta f(t,x,\theta')\,d\theta', & (t,x) \in \mathbb{R}^+ \times \mathbb{R}. \end{cases}$$

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

Issues/Discussion

- We expect a propagation behavior in space, with finite speed.

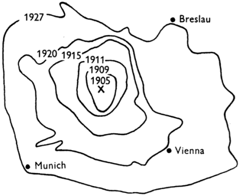
  Among others, in Alfaro and al. (2013), they show existence of travelling wave solutions in the case

  $$a(x,\theta) := a(x \cdot e - \theta),$$

  for larger speeds than some c^*.
- The population attains some certain trait distribution during the propagation phenomena.

Geometric point of view - The WKB approach for the front propagation in the Fisher-KPP case (1)

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



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

Equivalent to $D \to \varepsilon D$ (small diffusion) and $r \to r/\varepsilon$ (large reaction).

The fondamental solution of the linearized equation is

$$K_\varepsilon(t,x) = \frac{1}{(4\pi\varepsilon D t)^{\frac{1}{2}}} \exp\left(\frac{rt}{\varepsilon} - \frac{x^2}{4\varepsilon D t}\right) .$$

This says that we should perform the following WKB / Hopf-Cole transformation

$$\rho^\varepsilon = \exp(-u^\varepsilon/\varepsilon) .$$

Hamilton - Jacobi limit - The WKB approach for the front propagation in the Fisher-KPP case (2)

Equation for u^ε :

$$\partial_t u^\varepsilon + D|\partial_x u^\varepsilon|^2 + r = \varepsilon D \partial_{xx} u^\varepsilon + r\,\rho^\varepsilon\,, \quad \rho^\varepsilon = \exp(-u^\varepsilon/\varepsilon)\,.$$

In the limit $\varepsilon \to 0$, the solution is the **viscosity solution** of the following **constrained Hamilton-Jacobi equation**

$$\min\left(\partial_t u^0 + D|\partial_x u^0|^2 + r\,,\; u^0\right) = 0\,.$$

To study the front propagation, one should study the **nullset** of u^0:

- On every subcompact of Int $\left(u^0 = 0\right)$, $\lim_{\varepsilon\to 0} \rho^\varepsilon = 1$.
- On every subcompact of Int $\left(u^0 > 0\right)$, $\lim_{\varepsilon\to 0} \rho^\varepsilon = 0$.

References. M.I. Freidlin, *Geometric optics approach to reaction-diffusion equations*, SIAM J. Appl. Math. (1986)

L.C. Evans et P.E. Souganidis, *A PDE approach to geometric optics for...*, Indiana Univ. Math. J. (1989)

WKB transformation in the "kinetic" case

We want to use this Hamilton - Jacobi approach in a pretty general setting.

Hyperbolic scaling :

$$(t, x, \theta) \to \left(\frac{t}{\varepsilon}, \frac{x}{\varepsilon}, \theta\right).$$

WKB transformation :

$$f^\varepsilon(t, x, \theta) := \exp\left(-\frac{u^\varepsilon(t, x, \theta)}{\varepsilon}\right).$$

The model becomes:

$$\partial_t u^\varepsilon + D|\nabla_x u^\varepsilon|^2 = \varepsilon D \Delta_x u^\varepsilon + \underbrace{\frac{\alpha}{\varepsilon}\Delta_\theta u^\varepsilon - \frac{\alpha}{\varepsilon^2}|\nabla_\theta u^\varepsilon|^2 - ra(x,\theta)}_{\text{How to handle this terms ?}} + r\rho^\varepsilon$$

Heuristics - First ingredient.

$$\partial_t u^\varepsilon + D|\nabla_x u^\varepsilon|^2 = \varepsilon D \Delta_x u^\varepsilon + \frac{\alpha}{\varepsilon}\Delta_\theta u^\varepsilon - \frac{\alpha}{\varepsilon^2}|\nabla_\theta u^\varepsilon|^2 - ra(x,\theta) + r\rho^\varepsilon$$

Formal expansion of u^ε :

$$u^\varepsilon(t,x,\theta) = u^0(t,x,\theta) + \varepsilon\eta(t,x,\theta) + \mathcal{O}(\varepsilon^2).$$

This gives at order ε^{-2} for all (t,x,θ) :

$$\boxed{|\nabla_\theta u^0(t,x,\theta)|^2 = 0 \quad \Longrightarrow \quad u^0(t,x,\theta) = u^0(t,x)}$$

Now keeping terms of order 0 :

$$\alpha\left(\Delta_\theta \eta - |\nabla_\theta \eta|^2\right) - r\,a(x,\theta) = \underbrace{\partial_t u^0 + D|\nabla_x u^0|^2 - r\rho^0}_{\text{depends on } t,x \text{ only}}.$$

Setting $Q := e^{-\eta}$,

Second ingredient : Spectral problem

we obtain:

$$(S)\begin{cases} \alpha\Delta_\theta Q(\theta) + (r\,a(x,\theta) + H(x))\,Q(\theta) = 0\,, \\ \frac{\partial Q}{\partial \mathbf{n}} = 0\,, \qquad on \qquad \partial\Theta \\ Q(\theta) > 0\,. \end{cases}$$

Unique solution by the Krein-Rutman theorem :

> For all $x \in \mathbb{R}^n$, there exists a unique $H(x) \in \mathbb{R}$,
>
> such that there exists $Q(\theta) > 0$
>
> satisfying (S).

Third ingredient : the Hamilton - Jacobi equation

We now have formally

$$f^\varepsilon(t,x,\theta) \sim Q(x,\theta) e^{-\frac{u^0(t,x)}{\varepsilon}} \quad \Longrightarrow \quad \rho^\varepsilon(t,x) \sim e^{-\frac{u^0(t,x)}{\varepsilon}}.$$

and

$$\partial_t u^0 + D|\nabla_x u^0|^2 - r\rho^0 = -H(x).$$

- If $u^0(t,x) > 0$ then $\rho^0(t,x) = 0$, so that
$$\partial_t u^0 + D|\nabla_x u^0|^2 + H(x) = 0.$$
- If $u^0(t,x) = 0$ then $r\rho^0 = H(x)$ and thus $n^\varepsilon \to \frac{H(x)}{r} Q(x,\theta)$.

And thus u^0 solves

$$\boxed{\min\left(\partial_t u + D|\nabla_x u|^2 + H, u\right) = 0}$$

Convergence result for u_ε

Theorem

(i) *The family* $(u^\varepsilon)_\varepsilon$ *converges locally uniformly to* $u : [0,\infty) \times \mathbb{R}^d \to \mathbb{R}$ *the unique viscosity solution of*

$$\begin{cases} \min\left(\partial_t u + D|\nabla_x u|^2 + H, u\right) = 0, & \text{in } (0,\infty)\times\mathbb{R}^d, \\ u(0,\cdot) = u_0(\cdot) \quad \text{in } \mathbb{R}^d. \end{cases}$$

(ii) *Uniformly on compact subsets of* $\mathrm{Int}\{u<0\}\times\Theta$, $\quad \lim_{\varepsilon\to 0} n^\varepsilon = 0$,

(iii) *There exists* $\overline{C} > 1$ *such that, uniformly on compact subsets of* $\mathrm{Int}\left(\{u(t,x)=0\}\cap\{H(x)>0\}\right)$,

$$\liminf_{\varepsilon\to 0} \rho^\varepsilon(t,x) \geq \frac{H(x)}{r\overline{C}}.$$

Steps of the proof and difficulties

(0) Uniform bound for ρ^ε.

(1-a) Uniform bounds on u^ε.

(1-b) Sufficient Lipschitz estimate in θ to ensure the independence in the limit $\varepsilon \to 0$.

(2) Viscosity procedure

(2-a) Relaxed semi-limits method [Barles, Perthame ..].

(2-b) Definition of corrected tests function [Lions ..] thanks to the spectral problem.

- Technical difficulty: Lack of maximum principle for the full problem.

Coming back to the spectral problem ... (1/2)

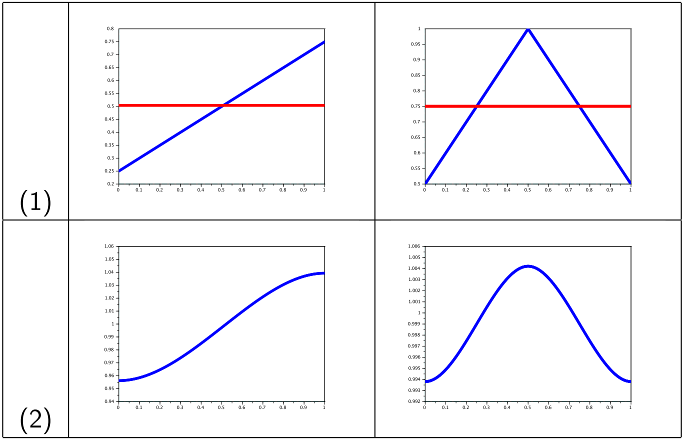
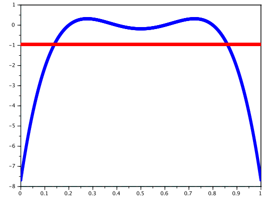
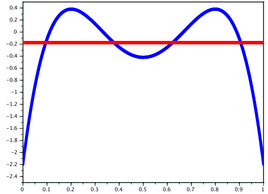
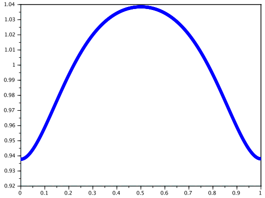
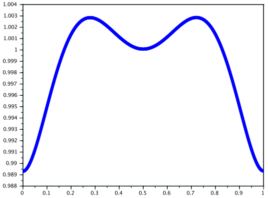


Table : (1): Fitness a (in blue) and principal eigenvalue H (in red); (2): Renormalized principal eigenfunction Q.

Coming back to the spectral problem ... (2/2)

(1)		
(2)		

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Numerics of the full problem (1/2)

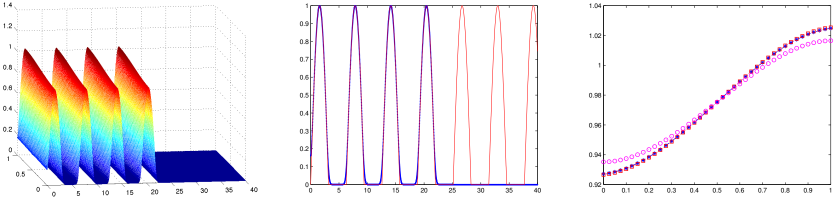

Figure : Numerical resolution with the fitness $a_2(x,\theta) = a_1(\theta) + \left(\sin(x) - \frac{1}{2}\right)$.

$$\alpha = 1, \qquad r = 2, \qquad D = 1, \qquad \varepsilon = 0.1.$$

Numerics of the full problem (2/2)

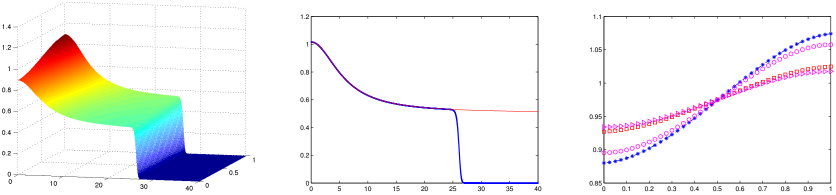

Figure : Numerical resolution with the fitness $a_3(x,\theta) = a_1(\theta)\left(1 + \frac{1}{1+0.05x^2}\right)$ and using the initial data and the parameters .

$$\alpha = 1, \qquad r = 2, \qquad D = 1, \qquad \varepsilon = 0.1.$$

Extensions and Complements

- Cane toads model

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

- Hamilton - Jacobi approach for kinetic equations, via the kinetic ansatz:

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

- Front acceleration via Hamilton - Jacobi:

  Fancy scalings - Formulation of the limit problem can be tricky.

Thank you for your attention !