Propagation in structured models from biology

Emeric Bouin

Université Paris-Dauphine

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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.

We will discuss two kinds of models/structures :

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

$$\Longrightarrow \text{Structuring variable} = \text{velocity.}$$

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

$$\Longrightarrow \text{Structuring variable} = \text{phenotype.}$$

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

1. Presentation of the talk
2. Introduction : Propagation phenomena in biology
3. Part 1 - Kinetic reaction-transport equations.
4. Part 2 - Study of dispersal evolution.

Propagation phenomena

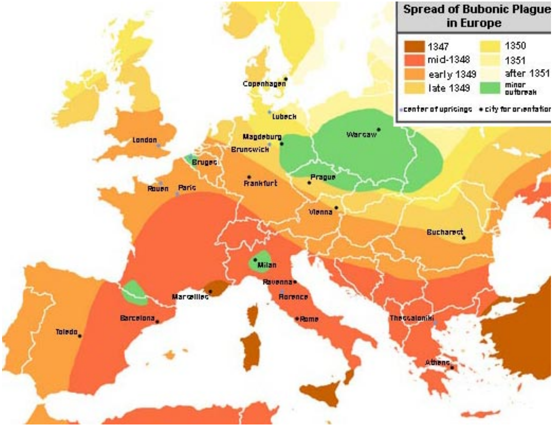


Figure: Spread of plague (Black Death) in Europe in the 14th century.

Propagation phenomena

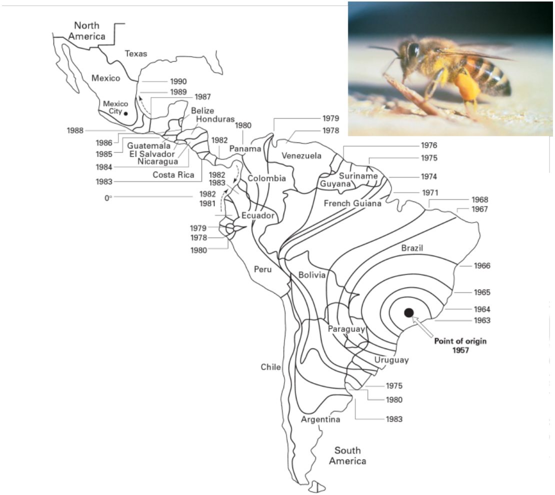
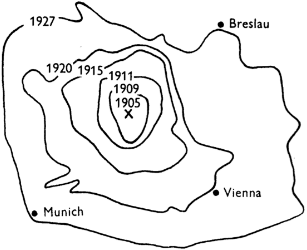


Figure: Invasion of South-America by the Africanized honey bee between its introduction in Brazil in 1957 and 1990.

Propagation phenomena



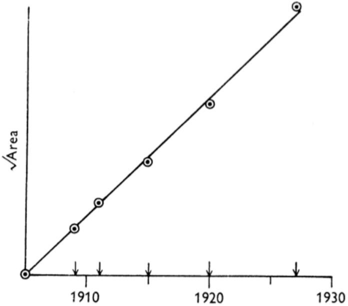


Figure: Spread of muskrats around Prague after Skellam and Elton (1951 & 1958).

The Fisher-KPP equation (1937)

Denote by $u(t,x)$ the population at time $t \in \mathbb{R}^+$ and position $x \in \mathbb{R}$. We assume

- The individuals can invade with diffusivity θ (no biais -> diffusion),
- The population can grow with a saturation due to a locally finite amount of food.

This gives the Fisher-KPP equation.

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

A travelling wave solution of speed c is a translated profile U,

$$\rho(t,x) = U(x - ct)\,,$$

with the natural limit conditions

$$\begin{cases} U(-\infty) = 1 & \text{stable equilibrium,} \\ U(+\infty) = 0 & \text{unstable equilibrium.} \end{cases}$$

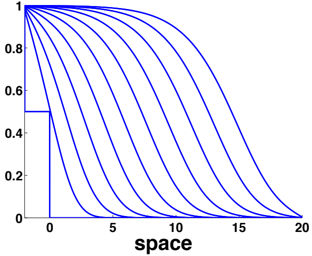


Figure: KPP fronts.

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^*.*

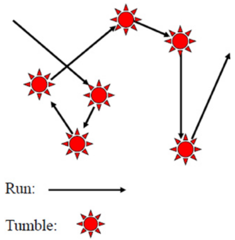
(Fisher, KPP, Kanel, Fife and McLeod, Aronson and Weinberger ...)

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).

Motion of an individual bacteria



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

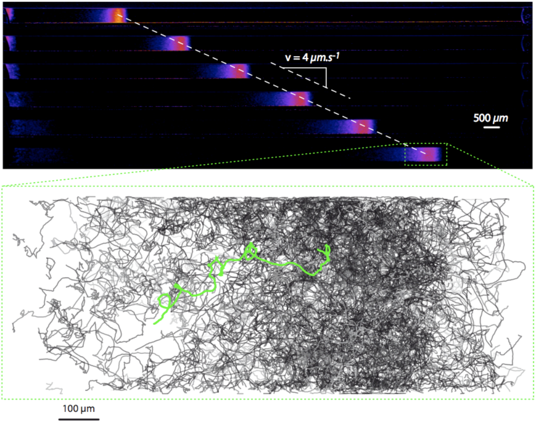
straight swimming for $1s$
and
change of direction for $0.1s$.

$\Longrightarrow$ Ballistic trajectory.

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

Bacterial travelling pulses

Collective migration: Bacterial travelling pulses



Kinetic models are needed to describe accurately the pulses.

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

Kinetic reaction-transport equations

Kinetic density $f(t,x,v)$: time t, position x and velocity v.

Space density

$$\rho := \int_V f(v)dv,$$

Set of velocities

$$V = [-v_{\max}, v_{\max}],$$

$\boxed{\text{with } v_{max} \leq +\infty}$.

3 ingredients :

- Run at velocity v = transport operator: $\partial_t + v\partial_x$,
- Tumbling events = velocity jump process: $\frac{1}{\tau}(M(v)\rho - f)$,
- Growth of the population = monostable nonlinearity: $r\rho(M(v) - f)$.

Altogether,

$$\partial_t f + v\partial_x f = \frac{1}{\tau}(M(v)\rho - f) + r\rho(M(v) - f)$$

Here, 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.

What we want to do :

$\rightarrow$ Study qualitatively and quantitatively propagation phenomena in kinetic reaction-transport equations.

$\rightarrow$ Are there special effects due to considering populations at the "mesoscopic" scale ?

We study the propagation from the point of view **of (non-)existence of travelling wave solutions**.

A la recherche d'ondes progressives ...

$$\partial_t f + v\partial_x f = \frac{1}{\tau}\left(M(v)\rho - f\right) + r\rho\left(M(v) - f\right)$$

The equilibrium states: 0 and $M(v)$.

Definition

A travelling wave solution is of the form

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

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

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

Main equation :

$$(v - c)\partial_\xi \mu = \frac{1}{\tau}\left(M(v)\nu - \mu\right) + r\nu\left(M(v) - \mu\right), \qquad \xi \in \mathbb{R},\ v \in V.$$

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

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 $\to$ 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**

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

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 ($v_{max} = +\infty$).

Obstruction

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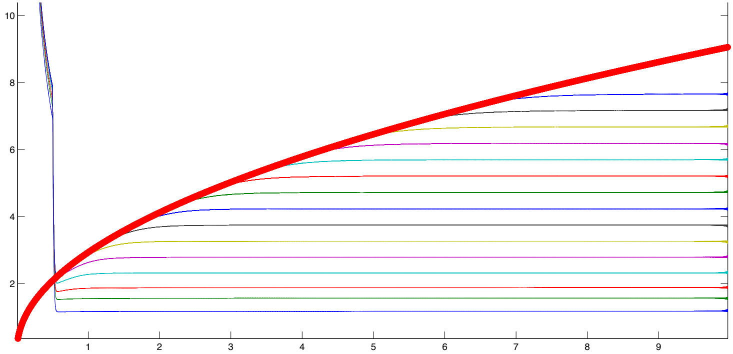
$\boxed{\text{has } \textbf{no solution} \text{ when } V \text{ is unbounded } (v_{max} = +\infty).}$

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 :

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

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*

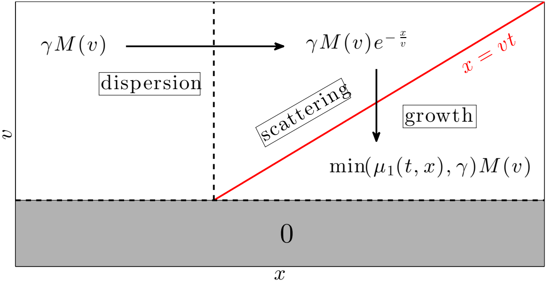
$$\lim_{t\to+\infty} \left(\sup_{x \geq C_1 t^{3/2}} \rho(t,x) \right) = 0\,.$$

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

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

Construction of the sub-solution

→ Idea : The free transport operator sends very few particles with very high velocity at the edge of the front. They are redistributed, and their density grows exponentially fast.



Reference. J. Garnier, *Accelerating solutions in integro-differential equations*, (2011).

Spreading : Estimation of μ_2 and then μ_1

Lemma

The following estimate holds true,

$$\mu_2(t,x) \geq \frac{1}{r_2(x)} \exp\left(-\frac{3}{2}x^{2/3}\right), \quad \textit{if} \quad x < t^{3/2}.$$

We define the zone

$$\mathcal{Y}_t = \left\{x \,:\, x \leq (\alpha t)^{3/2}\right\}.$$

Estimation of μ_1 for $x \in \mathcal{Y}_t$:

$$\mu_1(t,x) \gtrsim \frac{1}{\sqrt{t}} \exp\left(-\frac{3}{2}\left((\alpha t)^{3/2}\right)^{2/3}\right) e^{r(1-\alpha)t}.$$

For suitable α, for large times, the front has already passed through $\mathcal{Y}_t$.

Conclusions

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

As for the Fisher-KPP equation.

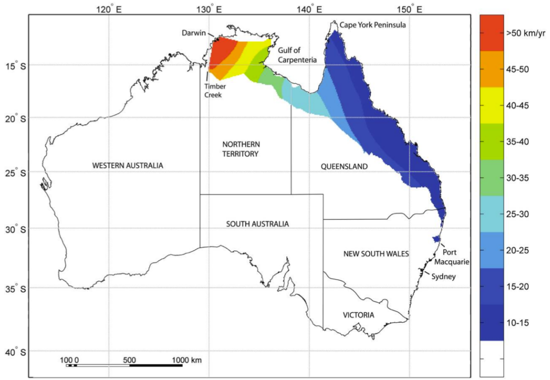
- Unbounded velocities :
    - Accelerated propagation,
    - Almost exact rate in the Gaussian case ($\sim t^{\frac{3}{2}}$),

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

Bufo Marinus (e.g.)

Julien is so cute !

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.

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.

Existence of cane toads waves

Theorem (B., Calvez)

Let Θ be ***bounded*** *and* $\mathbf{c^*} = \inf_{\lambda>0} c(\lambda)$. *There exists a traveling wave solution of the cane toads model of speed* $\mathbf{c^*}$.

We use **a Leray-Schauder type argument.**

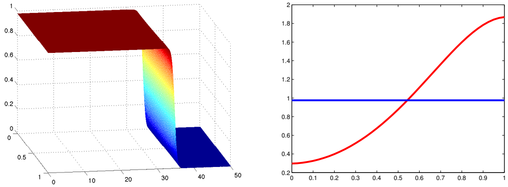


Figure: The front for $\alpha = 1$ and $r = 20$ (left). Trait profiles (right).

Reference. M. Alfaro and al, *Travelling waves in a nonlocal reaction-diffusion ...*, CPDE (2013).

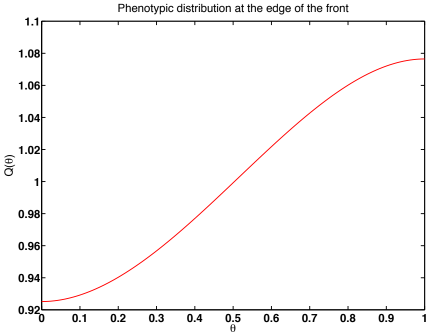
Spatial sorting at the edge of the front.

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 ! $\quad =$

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

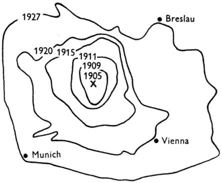
$Q_\lambda(\theta)$ concentrates to $\delta_{\theta=\theta_{\mathbf{max}}}$ when $\alpha \to 0$.



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

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)

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

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

The only natural scaling to make is:

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

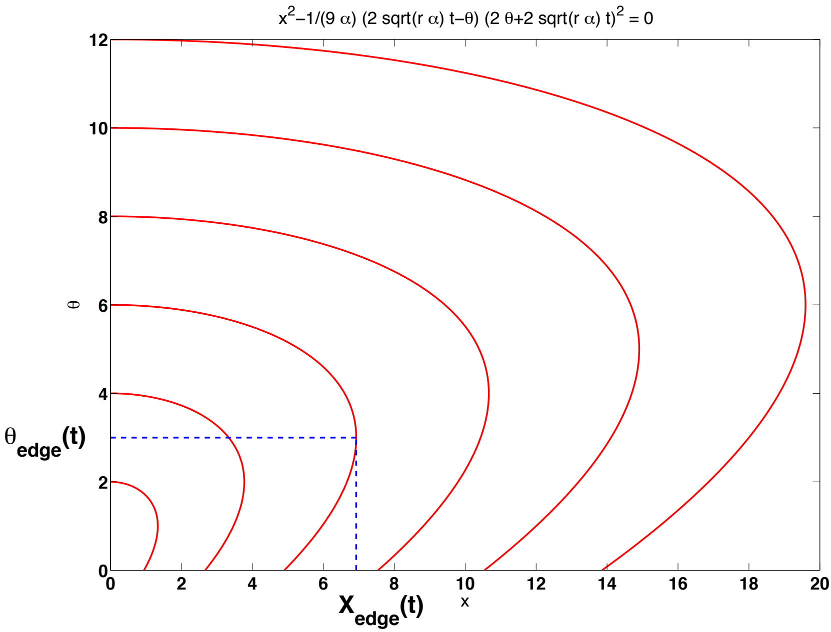
The limit satisfies formally in the small population regime ($\min \varphi^0 > 0$):

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

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

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

Note : The HJ limit has been rigorously justified in the bounded case by Turanova (2014), but the unbounded case is still formal.


x^2−1/(9 α) (2 sqrt(r α) t−θ) (2 θ+2 sqrt(r α) t)^2 = 0
θ
θedge(t)
Xedge(t)
x
0
2
4
6
8
10
12
14
16
18
20

Comparison with data.

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

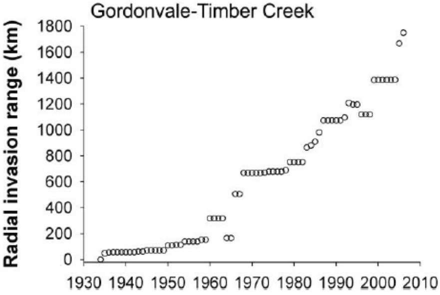


Figure: Position of the front with years - Section Gordonvale-Timber Creek, for which spatial sorting is presumably the main effect.

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

Following the Lagrangian trajectories of the HJ equation, we can prove a sharp spreading rate :

Theorem (B., Calvez, Henderson, Ryzhik)

Let u the unique solution of the LOCAL cane toads equation. Fix any constant $m \in (0,1)$.

$$\lim_{t \to \infty} \frac{\max\{x \in \mathbb{R} : \exists \theta \in \Theta, u(t,x,\theta) = m\}}{t^{3/2}} = \frac{4}{3}\alpha^{1/4} r^{3/4}.$$

We can also prove a weak propagation result for the non-local equation.

Thank you for your attention !