Travelling waves for models of kinetic type in biology

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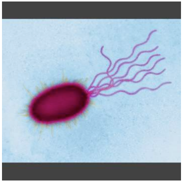
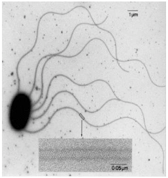
1. Modelling issue : Structured models in biology.
2. Reminder on reaction-diffusion fronts (Fisher-KPP equation).
3. Travelling waves and accelerating fronts in kinetic equations.
4. Travelling waves for the cane toads model.

Collective motion of bacteria

The bacteria E. Coli moves thanks to flagella :

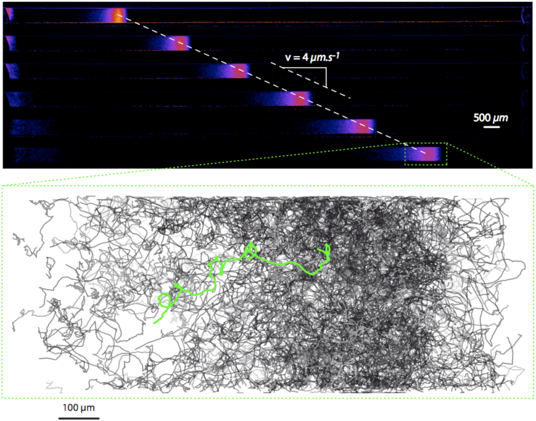




From Howard Berg's lab

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

Collective migration: Bacterial travelling pulses



The kinetic point of view is the most relevant for this situation (population structured by the **velocity**).

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

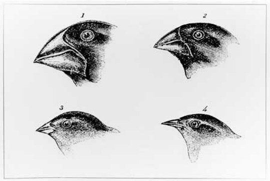
Modelling of Darwinian evolution

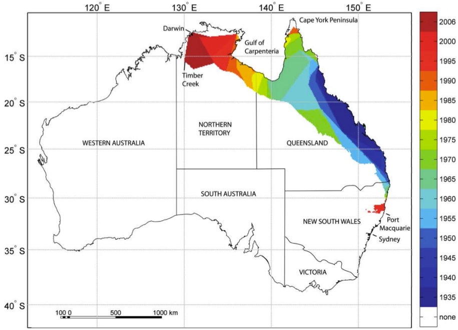
We study the

Darwinian evolution
of populations

which are structured by:

1. phenotypical traits,
2. position in space.





Interaction between invasion and evolution

Cane toads invasion

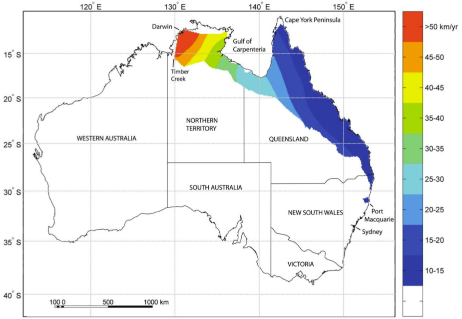


Figure : From Urban et al 2006

Spatial sorting : **Dynamic selection** of traits along the invasion.

1. Other examples : Tumor growth, age structured populations ...
2. Common feature : Propagation phenomena with local diversity.

Aim of this talk : Study qualitatively and quantitatively propagation effects in structured models (speed, shape of the front).

Here, study of 2 types of models:

- Kinetic reaction-transport equations (after the bacteria motivation),
- Reaction-diffusion-mutation equations (darwinian evolution motivation).

The Fisher-KPP equation (1937)

(Only space)

$$\partial_t \rho = \underbrace{D\partial_{xx}\rho}_{\text{unbiaised movement = diffusion}} + \underbrace{r\rho(1-\rho)}_{\text{Reproduction + saturation effect = logistic growth}} \qquad \text{(Fisher)}$$

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

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

with the natural limit conditions

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

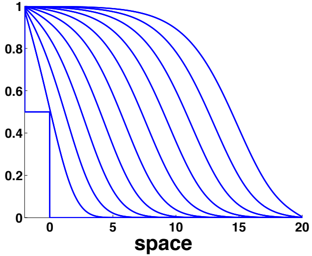


Figure : KPP fronts.

The possible speeds for the fronts

Theorem (Kolmogorov, Petrovsky, Piskunov, 1937)

There exists a minimal speed $c^* := 2\sqrt{rD}$ such that for all speed $c \geq c^*$, there exists a travelling wave solution of speed c. If the initial data has compact support then the front propagates with the minimal speed c^*.

Heuristic:

Speed given by the linearized equation at the edge ($\rho \ll 1$) **(pulled front).**

$$\partial_t \rho = D\partial_{xx}\rho + r\rho \,,$$

We seek **exponential decay** : $\rho(t,x) = \exp(-\lambda(x - c(\lambda)t))$ ($\lambda > 0$).

Dispersion relation $\quad c\lambda = D\lambda^2 + r.$

Minimal speed c^* $\quad c(\lambda) = D\lambda + \frac{r}{\lambda} \geq 2\sqrt{rD} := c^* \,.$

Kinetic reaction transport equations

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

The model (Schwetlick 2000 - Cuesta, Hittmeir, Schmeiser 2010):

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

where the distribution M on the space V satisfies

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

This is a kinetic analogous to the **Fisher-KPP equation**

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

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

Definition

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

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 :

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

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

Existence of travelling waves for bounded speeds

1. Parabolic limit : $(t, x, r) \mapsto (\varepsilon^{-2}t, \varepsilon^{-1}x, r \to r\varepsilon^2)$:

   The scaling limit is the Fisher-KPP equation.

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.

2. Existence result in the kinetic regime:

Theorem (B., Calvez, Nadin)

Assume that $v_{max} < +\infty$. There exists travelling front solutions for all $c \geq c^*$.

Remark: $c^* \leq 2\sqrt{rD}$.

Finding the speed : Dispersion relation

Solutions of the linearized problem of type $e^{-\lambda(x-c(\lambda)t)}Q_\lambda(v)$.
Spectral problem :

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

$$\forall v \in V, \quad (1+\lambda(c(\lambda)-v))\,Q_\lambda(v) = (1+r)\int_V M(v)Q_\lambda(v)dv. \tag{4}$$

Proposition

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

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

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

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

Here $M(v) = C\left(V_{max}\right)\exp\left(-\frac{v^2}{2}\right)\mathbf{1}_{|v|\leq V_{max}}$.

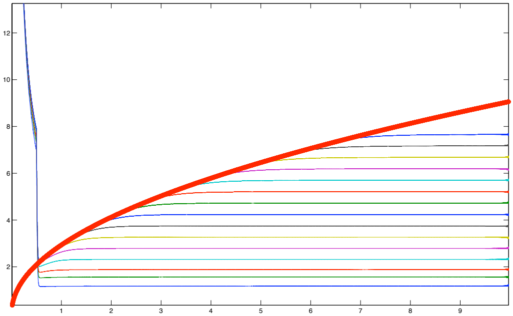


Figure : Speed as a function of time.

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

Infinite speed of propagation

Theorem (B., Calvez, Nadin)

We suppose that $M(v) > 0$, for all $v \in \mathbb{R}$. With a suitable initial data, one has, for all $c > 0$,

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

Front acceleration when V is unbounded

With a suitably constructed pair of sub- and super- solutions,

Theorem (B., Calvez, Nadin)

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

1. ***Propagation bounded from above by*** $t^{\frac{3}{2}}$***:*** *For all* $\varepsilon > 0$, *one has*

$$\lim_{t\to+\infty} \sup_{|x|\geq(1+\varepsilon)\sigma\sqrt{2r}(t+1)^{3/2}} \rho(t,x) \to 0\,.$$

2. ***Propagation bounded from below by*** $t^{\frac{3}{2}}$***:*** *For all* $\gamma > 0$, $\varepsilon > 0$, *we have*

$$\lim_{t\to+\infty} \left(\sup_{x\leq(1-\varepsilon)\sigma(\frac{r}{r+2}t)^{3/2}} \rho(t,x) \right) \geq 1-\gamma\,.$$

References. J. Garnier, Accelerating solutions in integro-differential equations, SIAM Journal on Mathematical Analysis. 43(4) (2011)

Conclusions

- Bounded velocities : Minimal speed of propagation, Profiles given by a spectral problem : *As for Fisher-KPP*.

- Unbounded velocities : Accelerated propagation, (almost) exact rate in the Gaussian case ($\sim t^{\frac{3}{2}}$) : *Even if the diffusive limit is Fisher-KPP*.

The cane toads model

"Kinetic" type of model : density of toads $f(t,x,\theta)$.

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

Space Diffusion, 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 $\theta \in \Theta := [\theta_{min} > 0, \theta_{max} < +\infty]$.

References.

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

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

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

Travelling waves

Definition

We say that a function $f(t,x,\theta)$ is a travelling front solution of speed $c \in \mathbb{R}^+$ if it can be written

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

where *the profile* $\mu \in \mathcal{C}^2\left(\mathbb{R} \times \Theta\right)$ is nonnegative, satisfies

$$\liminf_{\xi \to -\infty} \mu\left(\xi, \cdot\right) > 0, \qquad \lim_{\xi \to +\infty} \mu\left(\xi, \cdot\right) = 0,$$

and solves

$$\begin{cases} -c\partial_\xi \mu = \theta \partial_{\xi\xi}\mu + \alpha \partial_{\theta\theta}\mu + r\mu(1-\nu), & (\xi,\theta) \in \mathbb{R} \times \Theta, \\ \partial_\theta \mu(\xi, \theta_{\min}) = \partial_\theta \mu(\xi, \theta_{\max}) = 0, & \xi \in \mathbb{R}. \end{cases}$$

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

Edge of the front

Linear problem at infinity :

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

We plug this ansatz in ...

$$\begin{cases} -c\partial_\xi \mu = \theta \partial_{\xi\xi}\mu + \alpha \partial_{\theta\theta}\mu + r\mu, & (\xi,\theta) \in \mathbb{R}\times\Theta, \\ \partial_\theta \mu(\xi,\theta_{\text{min}}) = \partial_\theta \mu(\xi,\theta_{\text{max}}) = 0, & \xi \in \mathbb{R}. \end{cases}$$

Spectral problem

and we obtain:

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

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).

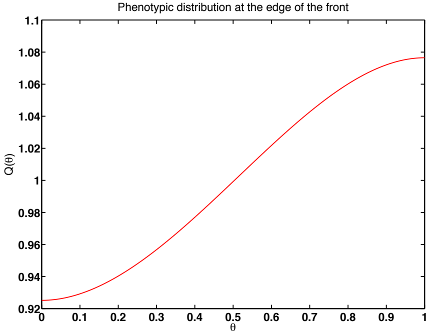
Spatial sorting at the edge of the front.

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 ! $=$

More toads with the biggest legs at the edge of the front.

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



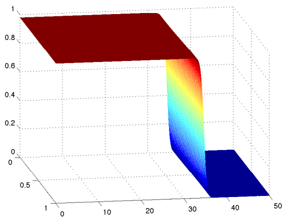
Reference. R. Shine and al, *An evolutionary process that assembles phenotypes through space rather than through time*, PNAS (2011)

Existence of cane toads waves

Theorem

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

$$-c^* \partial_\xi \mu = \theta \partial_{\xi\xi} \mu + \alpha \partial_{\theta\theta} \mu + r\mu(1-\nu), \qquad (\xi,\theta) \in \mathbb{R} \times \Theta,$$



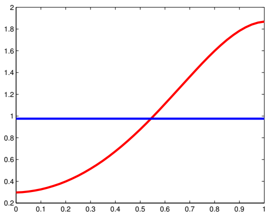


Figure : The front for $\alpha = 1$ and $r = 20$ (left). Trait profiles (right).

A Leray-Schauder type argument

No maximum principle : Abstract homotopy argument.

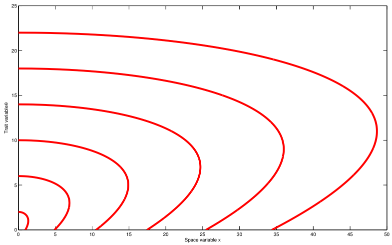
Three main ingredients :

1. Spectral problem,
2. An homotopy to come back to a constant diffusivity $g_\tau(\theta) = \theta + \tau(\theta - \theta_{\min})$,
3. Energy estimate to get the a priori bound on the fixed points.

Reference. M. Alfaro and al, *Travelling waves in a nonlocal reaction-diffusion equation as a model for a population structured by a space variable and a phenotypical trait*, CPDE (to appear)

What about unbounded Θ ?

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



New scaling :

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

$$\Downarrow$$

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

Data from Urban et al. (Am. Nat. 2008): 1.63 ± 0.13 (Gordonvale-Timber Creek, for which spatial sorting is presumably the main effect).

Thank you for your attention !

Figure : Female cane toad. Rick Shine's lab (University of Sydney).