Spatial sorting and invasion in models of kinetic type from biology

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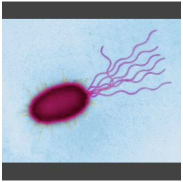
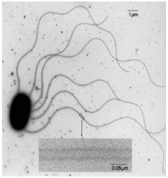
INVENTEURS DU MONDE NUMÉRIQUE

Collective motion of bacteria

The bacteria E. Coli moves thanks to flagella :

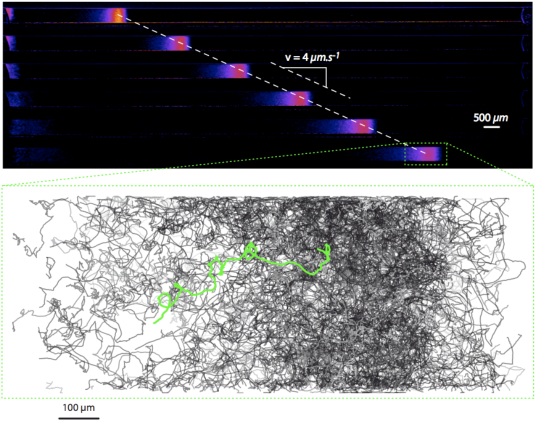




From Howard Berg's lab

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).

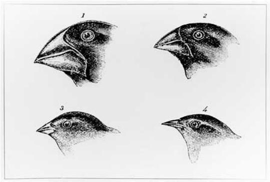
Modelling of Darwinian evolution

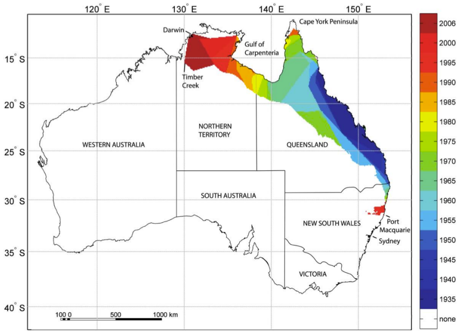
We study the

Darwinian evolution
of populations

which are structured by:

1. phenotypical traits,
2. position in space.





Interaction between invasion and evolution

Cane toads invasion

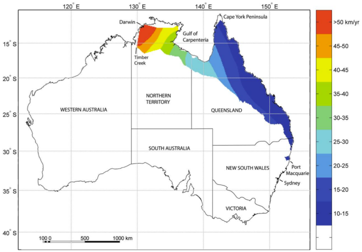


Figure : From Urban et al 2006

Evolution in fly wings

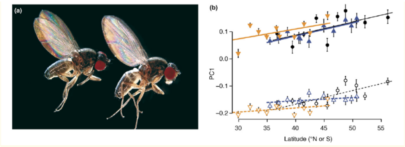


Figure : From Vellend et al 2007

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

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

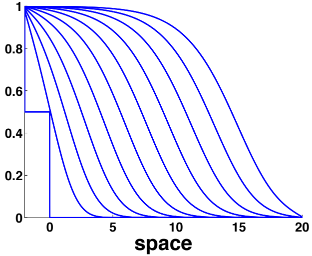


Figure : KPP fronts.

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 traveling wave solution of speed c. If the initial data has compact support then the front propagates with the minimal speed c^*.

Heuristic (pulled front). The speed of the front is given by the linearized equation at the edge of the front $(\rho \ll 1)$.

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

Exponential decay : $\rho(t,x) = \exp(-\lambda(x - ct))$ $(\lambda > 0)$.

We obtain **the dispersion relation**,

$$c\lambda = D\lambda^2 + r$$

giving **the minimal speed**

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

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):

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

where the distribution M on the space V satisfies

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

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

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

Existence of travelling waves for bounded speeds

1. 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.

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

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

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

$$\forall v \in V, \quad (1+\lambda\left(c(\lambda)-v\right))\,Q_\lambda(v) = (1+r)\int_V M(v)Q_\lambda(v)dv. \tag{3}$$

Proposition

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

$$(1+r)\int_V \frac{M(v)}{1+\lambda(c(\lambda)-v)}\,dv = 1\,. \tag{4}$$

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

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

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

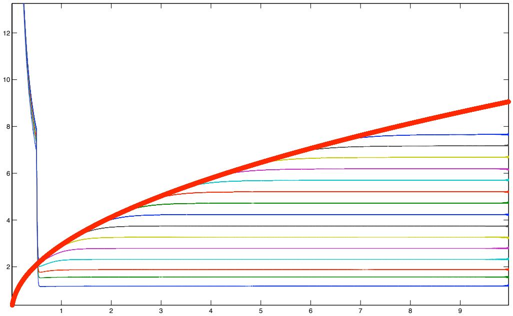


Figure : Speed as a function of time.

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

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

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*

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

The model

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

$t \in \mathbb{R}^+$: time, $x \in \mathbb{R}$: space variable, $\theta \in \Theta$: length of legs.

- The motility of the toads is heterogeneous = The space diffusion depends on θ.
- When reproducing, a toad gives his trait to his offspring, up to small variability.
- Phenotypical variability = diffusion with a constant rate α.
- Competition for resources : *local* in space, *nonlocal* in trait.

The model : Reaction-diffusion equation

The model writes :

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

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

References. L. Desvillettes, R. Ferrière et C. Prévost, *Infinite dimensional reaction-diffusion for population dynamics*, preprint CMLA (2004)

N. Champagnat et S. Méléard, *Invasion and adaptive evolution for individual-based spatially structured populations*, J. Math. Biol. (2007)

O. Bénichou, V. Calvez, N. Meunier, and R. Voituriez, *Front acceleration by dynamic selection in Fisher population waves*, 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 ...

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

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).

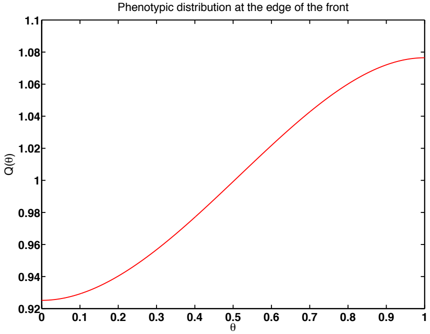
Spatial sorting at the edge of the front.

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

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

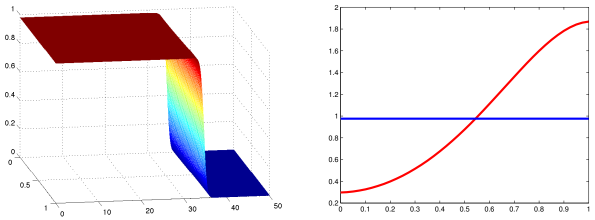


Figure : The front for $\alpha = 1$ and $r = 20$ (left). Trait profiles (right).

A Leray-Schauder type argument

No maximum principle : Abstract homotopy argument.

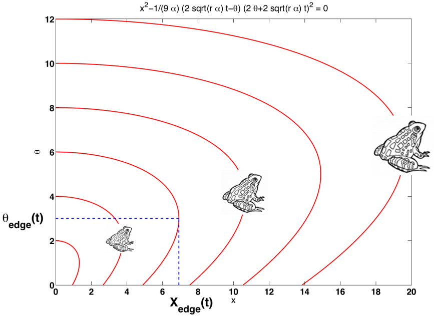
Two main ingredients :

1. $g_\tau(\theta) = \theta + \tau\,(\theta - \theta_{\mathrm{min}})$,
2. 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)

Advertisement : What about unbounded Θ ?

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



Thank you for your attention !