The inside dynamics of traveling waves

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Part I

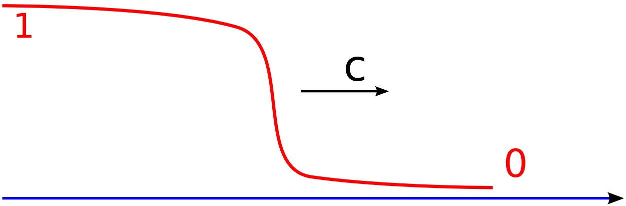
Traveling waves: known facts

Basic reaction-diffusion model in 1D

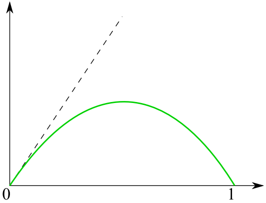
- Reaction-diffusion equation

$$u_t = u_{xx} + f(u),\ \ t > 0, x \in \mathbb{R}$$

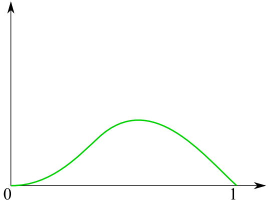
- A traveling wave (with $f(0) = f(1) = 0$): $\boxed{u(t,x) = U(x - ct)}$



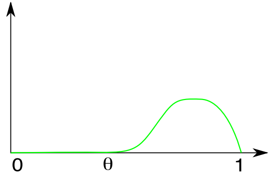
Nonlinearities f



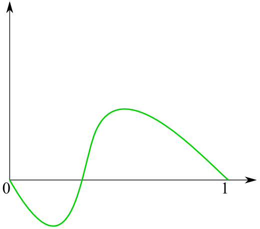
(a) monostable KPP



(b) monostable



(c) ignition



(d) bistable, with $\int_0^1 f > 0$

Existence results

- KPP (Kolmogorov, Petrovskii, Piskunov): $\{c\} = [c^*, +\infty)$ with $c^* = 2\sqrt{f'(0)}$
- Monostable case: $\{c\} = [c^*, +\infty)$ with $c^* \geq 2\sqrt{f'(0)}$ and $c^* > 0$
- Ignition and bistable: there is a unique speed c and $c > 0$

[Aronson and Weinberger, Fife and McLeod, Kanel']

Uniqueness of the profile U (up to shifts) for each speed c, and $U' < 0$

Stability for the Cauchy problem with

$$u_0 = U + \text{perturbation}$$

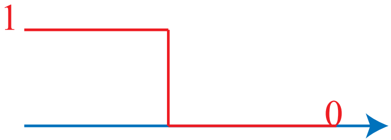
[Bramson, Eckmann and Wayne, Fife and McLeod, Kametaka, Kanel', Lau, McKean, Sattinger, Uchiyama...]

Asymptotic speed of propagation (spreading speed)

Cauchy problem:

$$\begin{cases} u_t = u_{xx} + f(u), & t > 0,\ x \in \mathbb{R}, \\ u(0,x) = u_0(x), & x \in \mathbb{R}. \end{cases}$$

Initial condition:



Asymptotic speed of propagation w^* ($= c^*$, the minimal speed of the fronts)

$$\begin{cases} u(t, x + c\,t) \to 0 & \text{for all } c > w^*, \\ u(t, x + c\,t) \not\to 0 & \text{for all } c < w^*. \end{cases}$$

Part II

Inside structure of traveling waves. Applications to population genetics.

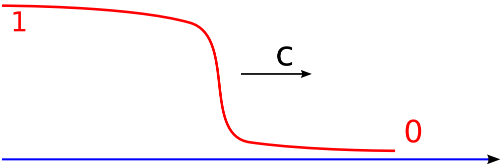
The model

- Same model for the total population:

$$u_t = u_{xx} + f(u), \;\; t > 0, x \in \mathbb{R}$$

Here, $u(t,x)$ =density of the population of genes

- A traveling front (with $f(0) = f(1) = 0$, KPP, monostable, combustion or bistable)

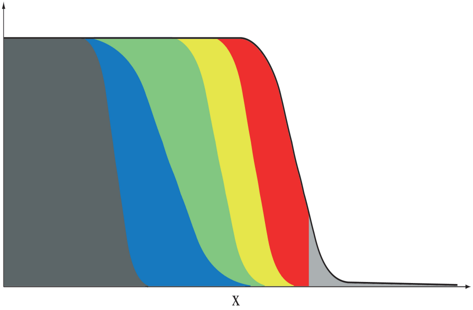


Decomposition of the front

$$u(t,x) = U(x - ct)$$

is the sum of neutral genetic fractions at initial time:

$$u(0,x) = U(x) = \sum_{i \in I} v_0^i(x), \quad 0 \leq\not\equiv v_0^i(x) \leq U(x)$$



All fractions v^i are neutral and share identical characteristics:

- Same diffusion rate, equal to 1
- Same per capita growth rate as the global front, equal to

$$g(u(t,x)) = \frac{f(u(t,x))}{u(t,x)}$$

[Hallatschek and Nelson, 2008, 2009], [Vlad, Cavalli-Sforza and Ross, 2004]

Questions:

- Evolution of the spatial genetic structure as time runs?
- Loss of diversity along the front?
- Gene surfing?

Each fraction $\upsilon^i(t,x)$ satisfies the linear equation

$$\begin{cases} \upsilon^i_t = \upsilon^i_{xx} + g(u(t,x))\,\upsilon^i, & t>0, \quad x \in \mathbb{R}, \\ 0 \leq\not\equiv \upsilon^i_0(x) \leq U(x), & x \in \mathbb{R} \end{cases}$$

Can also be derived from a system governing the genotype densities [Aronson and Weinberger, 1975]

By uniqueness:

$$u(t,x) = \sum_{i \in I} \upsilon^i(t,x) \quad \text{and} \quad g(u(t,x)) = g\Big(\sum_{i\in I} \upsilon^i(t,x)\Big)$$

Comparison principle:

$$0 < \upsilon^i(t,x) \leq u(t,x) = U(x-ct), \quad t>0, \quad x \in \mathbb{R}$$

Space-time heterogeneity with a forced speed c

Main question: Can υ^i follow the global front?

Results, KPP case

Theorem (KPP case)

Assume that f is of KPP-type.

Assume that v_0 converges to 0 faster than U as $x \to +\infty$:

$$\int_0^{+\infty} e^{cx}\, v_0(x)^2 dx < +\infty,$$

then

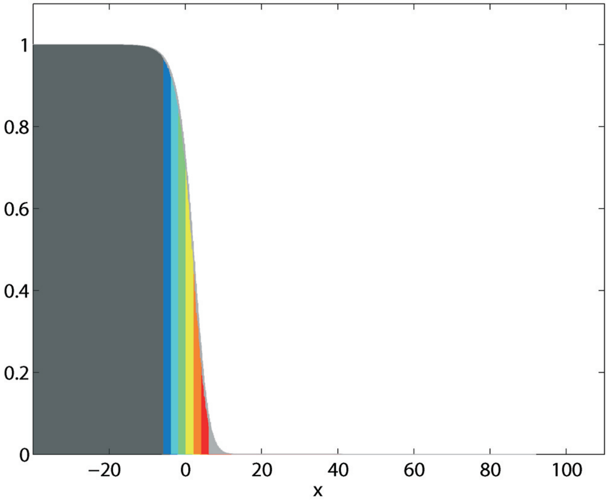
$$\forall\, \varepsilon > 0, \quad \max_{x \geq \varepsilon t} v(t,x) \to 0 \text{ as } t \to +\infty.$$

Furthermore, if $v_0(-\infty)=0$, then $v(t,\cdot)\to 0$ as $t\to+\infty$ uniformly in $\mathbb{R}$.

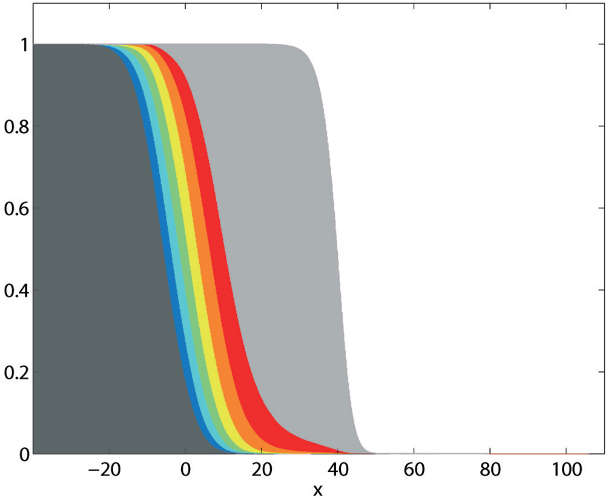
Consequences, KPP case

- If υ_0 is compactly supported, or supported in $(-\infty, a)$ then the right spreading speed of υ is equal to 0.
- If $\upsilon_0 = U \cdot \mathbb{1}_{[\alpha,\infty)}$, for some $\alpha > 0$, then $\upsilon(t,x)$ converges to $U(x - c\,t)$ in any moving half-line $[A + c\,t, \infty)$.
  $\rightarrow$ The fraction υ manages to "surf" on the front.
  $\rightarrow$ The propagation is due to the leading edge of the front.
- Strong erosion of diversity due to the demographic advantage of isolated individuals ahead of the colonization front.

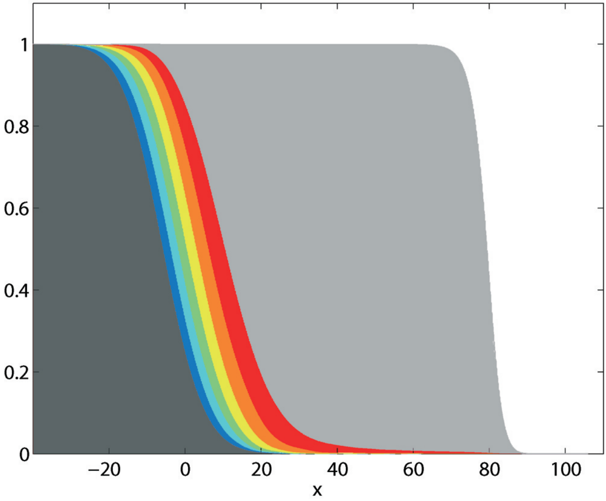
$t = 0$



$t = 20$ (speed=2)



$t = 40$ (speed=2)



Theorem (Allee case=Bistable)

Bistable = strong Allee effect: negative growth rate at low densities.

Then there is $p = p[v_0] \in (0,1]$ such that

$$v(t, x+ct) \to p\, U(x) \text{ as } t \to +\infty \text{ locally uniformly in } x \in \mathbb{R}.$$

The proportion $p[v_0]$ can be computed explicitly:

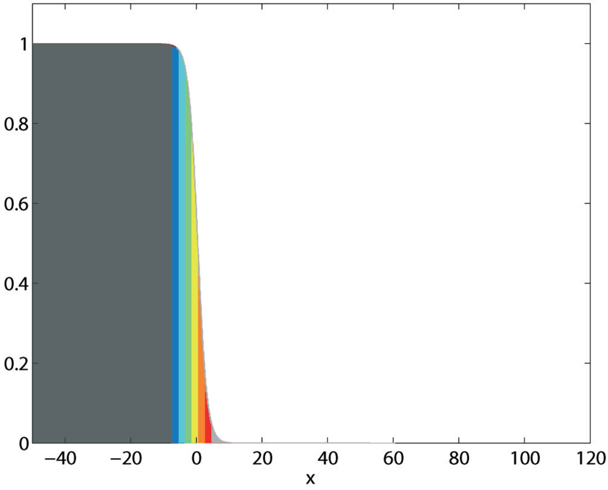
$$p[v_0] = \frac{\displaystyle\int_{-\infty}^{+\infty} v_0(x)\, U(x)\, e^{c\,x}\, dx}{\displaystyle\int_{-\infty}^{+\infty} U^2(x)\, e^{c\,x}\, dx} \in [0,1].$$

Consequences, Allee case

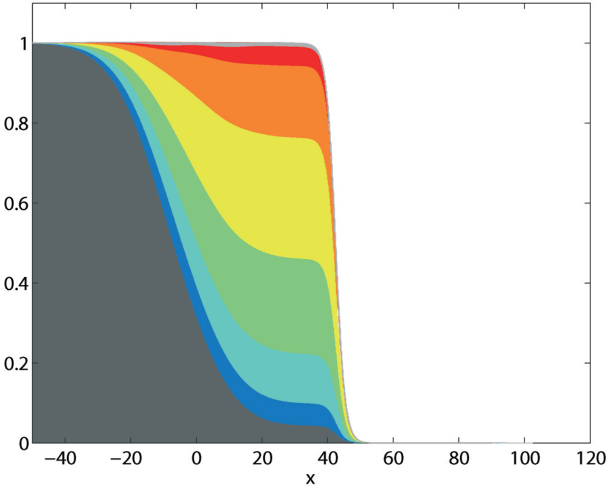
- The right spreading speed of any fraction υ is c.
- Every fraction υ contributes to a positive proportion of the global front (even if it is initially compactly supported).
- All of the genetic diversity is conserved in the colonization front.

Strong contrast with the KPP case.

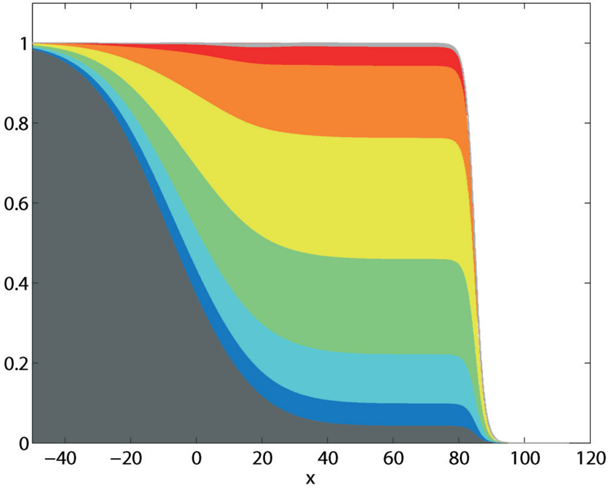
$t = 0$



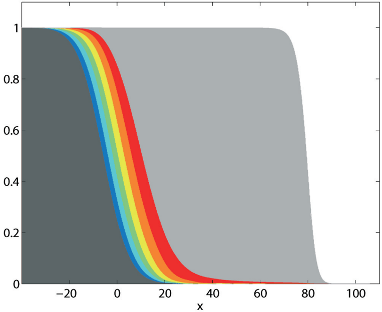
$t = 20$ (speed=2)



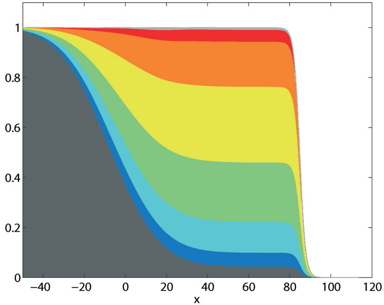
$t = 40$ (speed=2)



$t = 40$ (speed=2)



(e) KPP case



(f) Allee case

Notions of Pulled and pushed fronts

In the monostable case [Stokes, 1976]

- Pulled front:
  - *Either* a critical front with $c = c^* = 2\sqrt{f'(0)}$

    Same speed as the solution of the linearized problem
  - *Or* any super-critical front, that is $c > c^*$

- Pushed front: a critical front with $c = c^* > 2\sqrt{f'(0)}$

Theorem (Pulled case)

Assume f is monostable and (c, U) is a pulled front, that is

either $c = c^* = 2\sqrt{f'(0)}$ or $c > c^*$.

If

$$\int_0^{+\infty} e^{cx}\, v_0(x)^2 dx < +\infty,$$

then

$v(t, x + ct) \to 0$ as $t \to +\infty$ locally uniformly in $x \in \mathbb{R}$

and, more precisely,

$$\limsup_{t\to+\infty} \left(\max_{x\geq\alpha\sqrt{t}} v(t, x) \right) \to 0 \text{ as } \alpha \to +\infty.$$

Furthermore, if $v_0(-\infty) = 0$, then $v(t, \cdot) \to 0$ as $t \to +\infty$ uniformly in $\mathbb{R}$.

Theorem (Pushed case)

Assume f is monostable with $c = c^* > 2\sqrt{f'(0)}$ (pushed front) or ignition or bistable.

Then there is $p = p[v_0] \in (0, 1]$ such that

$$v(t, x + ct) \to p\,U(x) \text{ as } t \to +\infty \text{ locally uniformly in } x \in \mathbb{R}.$$

More precisely,

$$\limsup_{t\to+\infty} \Big(\max_{x\geq\alpha\sqrt{t}} \big|v(t, x) - p\,U(x - ct)\big| \Big) \to 0 \text{ as } \alpha \to +\infty.$$

Observations:

- All the pulled fronts share the same inside structure as KPP fronts, when $c = c^* = 2\sqrt{f'(0)}$ *or* when $c > c^*$.

  $\rightarrow$ The propagation is due to the leading edge of the front.

- The bistable and ignition fronts have the same inside structure as pushed monostable fronts.

  $\rightarrow$ All of the genetic diversity of the population is conserved in the colonization front.

New interpretation of the mathematical notions of pulled and pushed fronts.

Notions of pulled and pushed generalized transition fronts

$$u_t = \mathcal{D}(u) + f(t,x,u)$$

Assume $f(t,x,0) = 0$ and there is a solution $p^+(t,x) > 0$.
Generalized transition fronts connecting 0 and $p^+(t,x)$ [Berestycki, Hamel]:

$$\begin{cases} u(t,x) - p^+(t,x) & \to & 0 \text{ as } x - x_t \to -\infty, \\ u(t,x) & \to & 0 \text{ as } x - x_t \to +\infty. \end{cases}$$

Pulled transition front: for all $0 \leq\not\equiv v_0 \leq u(0,\cdot)$, the solution v of

$$\begin{cases} v_t & = & \mathcal{D}(v) + g(t,x,u(t,x))\, v, \\ v(0,\cdot) & = & v_0 \text{ (compactly supported)} \end{cases}$$

where $g(t,x,u) = f(t,x,u)/u$, satisfies

$$\forall\, M \geq 0, \quad \sup_{|x - x_t| \leq M} v(t,x) \to 0 \text{ as } t \to +\infty.$$

Pushed transition front: there is $M \geq 0$ such that

$$\limsup_{t\to+\infty} \left(\sup_{|x-x_t|\leq M} v(t,x) \right) > 0.$$

Conclusions and perspectives

- Pulled and pushed solutions can be defined based on the inside structure of the solutions.

  $\rightarrow$ More intuitive than previous notions of pulled/pushed fronts

  $\rightarrow$ Adaptable to more complex models that do not necessarily admit traveling front solutions.

- Existence of an Allee effect leads to a maintenance of genetic diversity.

  $\rightarrow$ The Allee effect not only have adverse consequences.

Conclusions and perspectives

Further work: identify the pulled/pushed nature of the solutions of other types of equations, such as

- Integro-differential equations including long distance dispersal events [Garnier 2011]:

$$u_t = J \star u - u + f(u) \;\rightarrow\; \upsilon_t = J \star \upsilon - \upsilon + \upsilon \, \frac{f(u)}{u}.$$

- Equations with nonlinear diffusion, e.g., porous media equations:

$$u_t = \Delta(u^2) + f(u) \;\rightarrow\; \upsilon_t = \Delta(u\,\upsilon) + \upsilon \, \frac{f(u)}{u}.$$

Thank you for your attention.

References:

Garnier, Giletti, Hamel, Roques (2012) Inside dynamics of pulled and pushed fronts. *Journal de Mathématiques Pures et Appliquées*, in press

Roques, Garnier, Hamel, Klein (2012) Allee effect promotes diversity in traveling waves of colonization. *Proceedings of The National Academy of Sciences of the USA*, vol 109 (23) pp. 8828-8833