# Pulled and pushed waves
# Causes and consequences

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# Introduction

# PDE models in population ecology. Main idea

The dynamics of a population is governed by two main forces:

dispersion and growth (births - deaths).

General form (1D):

$$\partial_t u(t,x) = \mathcal{D}[u](t,x) + \mathcal{F}[u](t,x), \ \ t > 0, x \in \mathbb{R}.$$

# Single species ODE models

**Goal:** to describe the dynamics of a population under the effect of growth only.

**Equation:**

$$\begin{cases} U'(t) = f(U(t)), \ t \in [0, T[, \\ U(0) = U_0 \geq 0, \end{cases}$$

**Meaning of $U(t)$:** population size at time $t \geq 0$.

**Initial condition:** $U_0$ = the initial population size.

**Growth term:** $f \in C^1(\mathbb{R})$.

# Derivation of the growth term

Dynamics of the population size $U(t)$ between $t$ and $t+\delta t$ :

$$U(t+\delta t)-U(t)=\text{(nb births-nb deaths) during } \delta t.$$

Birth rate $a$, death rate $b$.

$$U(t+\delta t)-U(t)=a\,U\,\delta t-b\,U\,\delta t.$$

Letting $\delta t\to 0$ :

$$\boxed{U'=a\,U-b\,U.}$$

The growth term is:

$$f(U)=(a-b)\,U.$$

# Malthusian growth (Malthus 1798)

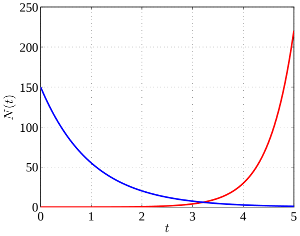
$$f(U) = (a - b)\,U$$

**Assumption :** $a$ and $b$ are constant.

Solution of $U' = f(U)$ :

$$U(t) = U_0 e^{r\,t},$$

with $r = a - b$, the growth rate.




*Red line:* $U_0 = 0.01$ and $r = 2$ ;
*Blue line:* $U_0 = 150$ and $r = -1$.

→ exponential growth for $r > 0$ (or decay, if $r < 0$).

# Logistic growth (Verhulst 1838)

**Assumption:** the death rate $b$ is a linear increasing function of the population size: $b(U) = b_0 + b_1 U$, with $b_1 > 0$.

Letting $r = a - b_0$ and $K = \dfrac{a - b_0}{b_1}$, we get:

$$U'(t) = f(U) = rU\left(1 - \frac{U}{K}\right),\ t \geq 0.$$

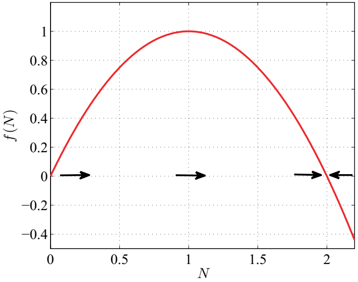
**Definitions:**

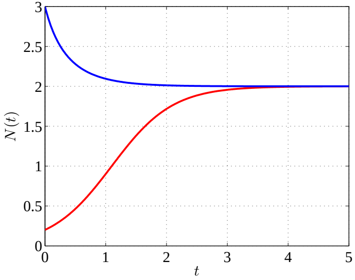
- $r$: intrinsic growth rate;
- $K$: carrying capacity;
- $U^*$ s.t $f(U^*) = 0$: stationary state (here, $0$ and $K$).

# Logistic growth, stability of the stationary states

$$U' = f(U) = rU\left(1 - \frac{U}{K}\right)$$

Here, $r = 2$, $K = 2$



# Allee effect

**Definition:** *per capita* growth rate $g(U) = f(U)/U$.

**Logistic case:** $g(U) = f(U)/U = r(1 - U/K) \rightarrow g(U)$ is a decreasing function of $U$.

**Allee effect:** $g(U)$ does not reach its maximum at $U = 0$. Some kind of "cooperation". Possible causes:

- difficulty of finding mates at low pop. density;
- inbreeding depression (consanguinité);
- isolated indiviuals are less robust to extreme climate events (pine processionary moth, emperor penguin...).

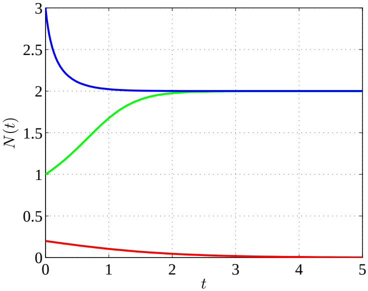
**Definitions:**

- *strong Allee effect*: $f(U) < 0$ when $U$ is small (death rate>birth rate when $U$ is small);
- *weak Allee effect*: $f(U) \geq 0$, but $g(U) = f(U)/U$ does not reach its maximum at $U = 0$.

# ODE model with Allee effects: some examples

Weak Allee effect: $f(U) = U^2(1 - \frac{U}{K})$.

Strong Allee effect: $f(U) = U(1 - \frac{U}{K})(U - \rho)$, with $\rho \in ]0, K[$.

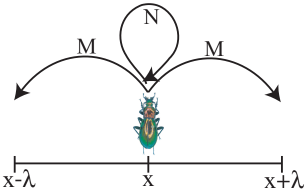



Strong Allee effect, with $r = 2$, $K = 2$ et $\rho = 0.5$. *Red line:* $U_0 = 0.2$ ; *green line*: $U_0 = 1$ ; *blue line:* $U_0 = 3$.

$\rightarrow$ the final state depends on the initial condition. fig

# Random walks and diffusion equation

Population of $U$ independent individuals. Random walk:




Time step $\tau << 1$ space step $\lambda << 1$.

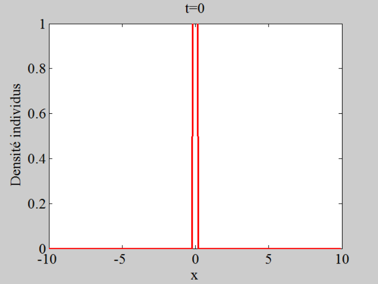
The expected population density (normalised by $U$) $u(t,x)$ converges towards the solution of:

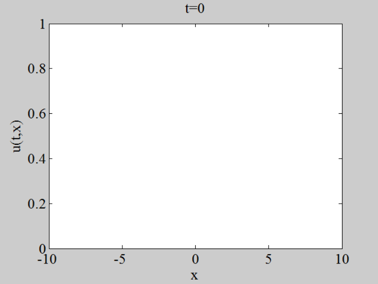
$$\boxed{\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2},}$$

with $D := \lim_{\tau\to 0, \lambda\to 0} M\frac{\lambda^2}{\tau} > 0$.

# Random walk model vs diffusion equation: numerical illustration

Population density ($10^4$ indiv.) Diffusion eq. $\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2}$

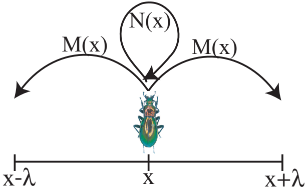



Here, $\tau = 2.5\,10^{-3}$, $\lambda \simeq 0.08$, $M = 0.4$ and $D = M\lambda^2/\tau = 1$.

# Diffusion in heterogeneous media

Population of $U$ independent individuals. Random walk:



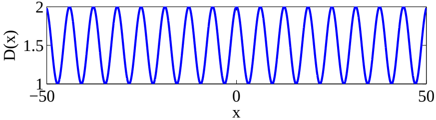

Time step $\tau << 1$ space step $\lambda << 1$.

The expected population density (normalised by $U$) $u(t,x)$ converges towards the solution of the Fokker-Planck equation :

$$\boxed{\frac{\partial u}{\partial t} = \frac{\partial^2 (D(x)\, u)}{\partial x^2},}$$

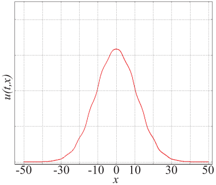
with $D(x) := \lim_{\tau \to 0, \lambda \to 0} M(x) \frac{\lambda^2}{\tau} > 0$.

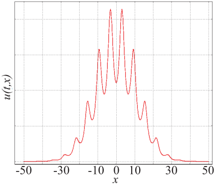
# Heterogeneous diffusion: Fick vs Fokker-Planck




Fick equation *vs* Fokker-Planck equation

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left(D(x)\frac{\partial u}{\partial x}\right) \quad vs \quad \frac{\partial u}{\partial t} = \frac{\partial^2 (D(x)\, u)}{\partial x^2}$$




Heat, pollutants ... *vs* Individuals, propagules, ...

# Reaction-dispersion models: general form

General form (1D):

$$\partial_t u(t,x) = \mathcal{D}[u](t,x) + \mathcal{F}[u](t,x), \;\; t>0, x\in\mathbb{R}.$$

Description of the dynamics of a concentration $u(t,x)$ under the effect of:

- a linear dispersion term $\mathcal{D}[u](t,x)$;
- a growth term (reaction) $\mathcal{F}[u](t,x)$;

# Reaction-dispersion models: examples

**Reaction-diffusion equations:**

$$\partial_t u(t,x) = \underbrace{\partial_x(D(x)\partial_x u - v\,u)}_{\text{dispersion}} + \underbrace{f(t,x,u)}_{\text{growth}},\ t>0, x\in\mathbb{R}.$$

**Delayed reaction-diffusion equations:**

$$\partial_t u(t,x) = \underbrace{\partial_x(D(x)\partial_x u - v\,u)}_{\text{dispersion}} + \underbrace{f(t,x,u,u(t-\tau,x))}_{\text{growth}},\ t>0, x\in\mathbb{R}.$$

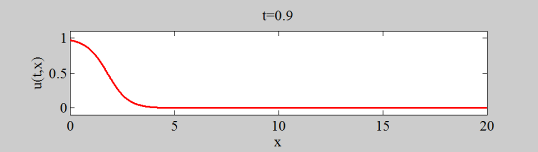
**Integro-differential equations:**

$$\partial_t u(t,x) = \underbrace{\int_{\mathbb{R}} J(|x-y|)\,(u(t,y)-u(t,x))\,dy}_{\text{dispersion}} + \underbrace{f(t,x,u)}_{\text{growth}}.$$

# Traveling waves solutions

Solutions with constant speed $c$ and a constant profile $U > 0$ :

$$u(t, x) = U(x - c\,t).$$



# Traveling waves: standard results for $\partial_t u = \partial_{xx} u + f(u), \ t > 0, x \in \mathbb{R}$

**Existence results**

- KPP case: $\{c\} = [c^*, +\infty)$ with $c^* = 2\sqrt{f'(0)}$
- Monostable case: $\{c\} = [c^*, +\infty)$ with $c^* \geq 2\sqrt{f'(0)}$ and $c^* > 0$
- Bistable case: 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 $u_0 = U +$ perturbation

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

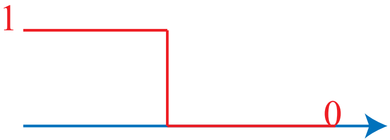
# Spreading properties

## The importance of the wave with minimal speed

Cauchy problem:

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

Initial condition:




Convergence (in some sense) to the wave with minimal speed $c^*$.

# Pulled and pushed waves: the notion of inside dynamics

# Inside dynamics of a solution: main idea

**Assumption:** $u$ is made of several components $\mu^i \geq 0$ ($i \in I \subset \mathbb{N}$):

$$u(t,x) = \sum_{i \in I} \mu^i(t,x).$$

**Interpretation:** $u$ is a density of genes inside a population.

**Objective:** to understand the dynamics of the $\mu^i$'s $\rightarrow$ dynamics of genetic diversity in a population.

# Inside dynamics of a solution: the equations

**Initial condition:** $u(0,x)=\sum_{i\in I}\mu_0^i(x), \quad x\in\mathbb{R}.$

**Neutrality assumption:** dispersion and growth abilities are the same in all the $\mu^i$'s.

$$\begin{cases} \partial_t\mu^i(t,x) &= \mathcal{D}[\mu^i](t,x)+\dfrac{\mu^i}{u}\mathcal{F}[u](t,x), \quad t>0,\ x\in\mathbb{R},\\ \mu^i(0,x) &= \mu_0^i(x), \qquad\qquad\qquad\qquad\qquad x\in\mathbb{R}. \end{cases}$$

**Well-posedness:** check that

$$u(t,x)=\sum_{i\in I}\mu^i(t,x) \text{ for all } t\geq 0,\ x\in\mathbb{R}.$$

$w=\sum_{i\in I}\mu^i(t,x)$ and $u$ are solutions of the linear equation:

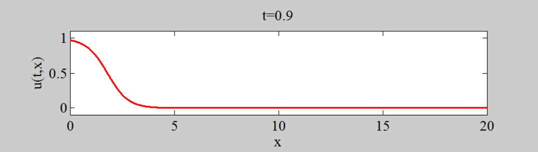
$$\partial_t w(t,x)=\mathcal{D}[w](t,x)+\frac{w}{u}\mathcal{F}[u](t,x),\ t>0, x\in\mathbb{R}.$$

Assumptions on $\mathcal{D},\mathcal{F}$: guarantee the uniqueness of the solution $w$.

# Inside dynamics of traveling waves

Solutions with constant speed $c$ and a constant profile $U > 0$ :

$$u(t,x) = U(x - c\,t).$$



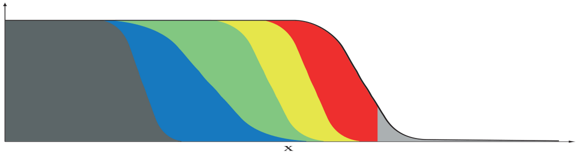

**Usual questions:** existence, uniqueness, stability, minimal speed ...

**New problem:** to study the inside dynamics of $U(x - c\,t)$.

# Inside dynamics of traveling waves

Solutions with constant speed $c$ and a constant profile $U > 0$ :

$$u(t, x) = U(x - c\,t).$$




**Usual questions:** existence, uniqueness, stability, minimal speed ...

**New problem:** to study the inside dynamics of $U(x - c\,t)$.

# Pulled and pushed waves: Stokes'definitions (1976)

**Monostable case:**

$$\partial_t u = d\,\partial_{xx} u + f(u), \text{ with monostable growth term } f$$ ▸ fig.

Existence of waves for all $c \geq c^* > 0$ (Aronson and Weinberger, 1975; 1978).

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

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

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

# Pulled and pushed waves: new definitions (2012)

## Definition (Pulled wave)

$u(t,x) = U(x-ct)$ is a pulled wave if, for any component $\mu$ such that $\mu_0(x) = 0$ for large $x$,

$$\mu(t, x+ct) \to 0 \text{ as } t \to +\infty, \text{ uniformly on compact sets.}$$

## Definition (Pushed wave)

$u(t,x) = U(x-ct)$ is a pushed wave if, for any component $\mu$ such that $\mu_0 \not\equiv 0$, there exists $M > 0$ such that

$$\limsup_{t\to+\infty} \sup_{x\in[-M,M]} \mu(t, x+ct) > 0.$$

## Application 1: Fisher-KPP growth terms

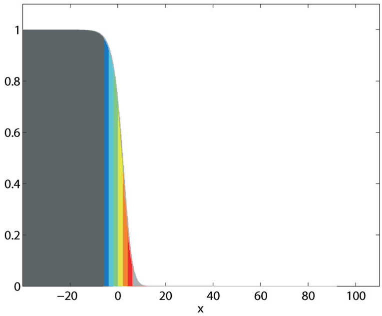
# KPP waves

- **Equation:** $\partial_t u = d\,\partial_{xx} u + f(u).$
- **Growth term:** $f(u) = u\,(1-u)$ (or other KPP growth terms). fig
- **Interpretation:** per capita growth rate is maximal at low density (competition effects).
- **Traveling waves:** $u(t,x) = U_c(x - c\,t)$ for all $c \geq c^* = 2\sqrt{f'(0)\,d}$ (Fisher, 1937; Kolmogorov et al, 1937)

# Inside dynamics of KPP waves

## Theorem [Garnier, Giletti, Hamel, Klein, R. 2012]

*All of the waves are pulled.*




Funder effects → strong erosion of diversity.
Same result for Stokes pulled waves.

# Application 2: bistable growth terms

# Bistable waves

- **Equation:** $\partial_t u = d\,\partial_{xx} u + f(u)$.

- **Growth term:** $f(u) = u\,(1-u)\,(u-\rho)$, $\rho \in (0, 1/2)$ (or other bistable growth terms). fig

- **Interpretation:** negative growth rate at low densities (Allee effect=cooperation between the individuals).

- **Traveling wave:** unique wave $u(t,x) = U_{c^*}(x - c^*\,t)$ (Aronson and Weinberger, 1975; Fife and McLeod, 1977).

# Inside dynamics of bistable waves

## Theorem [Garnier, Giletti, Hamel, Klein, R. 2012]

*The unique wave is pushed.*

Convergence to a positive proportion of the wave:

$$\mu(t, x + c^* t) \to p\, U(x) \text{ as } t \to +\infty, \text{ uniformly on compact sets,}$$

with

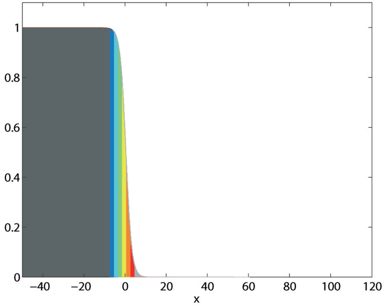
$$p = p[\mu_0] = \frac{\displaystyle\int_{-\infty}^{+\infty} \mu_0(x)\, U(x)\, e^{\frac{c^*}{d} x}\, dx}{\displaystyle\int_{-\infty}^{+\infty} U^2(x)\, e^{\frac{c^*}{d} x}\, dx} \in (0, 1].$$

Back

# Inside dynamics of bistable waves

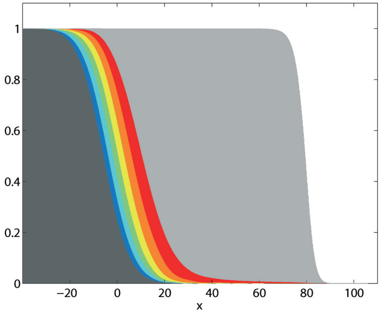
## Theorem [Garnier, Giletti, Hamel, Klein, R. 2012]

*The unique wave is pushed.*

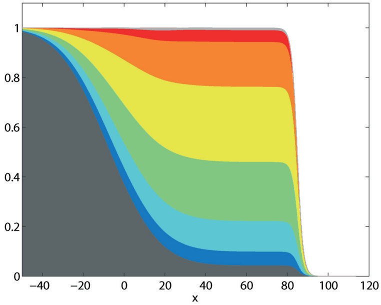



Higher mortality at low densities → maintenance of diversity.
Same result for Stokes pushed waves.

# Typical pulled and pushed profiles




Pulled profile
Diversity is lost




Pushed profile
Diversity is maintained

# Application 3: Lotka-Volterra competition models

# Traveling wave of LV competition systems

- **Equation:**

$$\begin{cases} \partial_t u = d\,\partial_{xx} u + u\,(1 - u - a_1 v), \\ \partial_t v = \partial_{xx} v + r\,v\,(1 - a_2\,u - v), \end{cases} \quad t > 0,\ x \in \mathbb{R},$$

$d,\ r,\ a_1,\ a_2$ are positive and $0 < a_1 < 1 < a_2$.

- **Growth term:** KPP-type (Fisher-KPP eq if $a_1 = 0$).

- **Traveling waves:** $u(t,x) = U(x - c\,t),\ v(t,x) = V(x - c\,t)$, with limiting conditions:

$$(U, V)(-\infty) = (1, 0) \text{ and } (U, V)(+\infty) = (0, 1).$$

Existence for all $c \geq c^* > 0$ (Kan-On, 1997).

# Traveling wave of LV competition systems

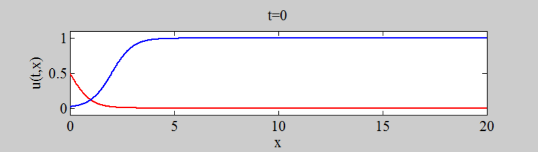
- **Equation:**

$$\begin{cases} \partial_t u = d\,\partial_{xx} u + u\,(1 - u - a_1 v), \\ \partial_t v = \partial_{xx} v + r\,v\,(1 - a_2 u - v), \end{cases} \quad t > 0,\ x \in \mathbb{R},$$

$d,\ r,\ a_1,\ a_2$ are positive and $0 < a_1 < 1 < a_2$.

- **Growth term:** KPP-type (Fisher-KPP eq if $a_1 = 0$).

- **Traveling waves:**




Existence for all $c \geq c^* > 0$ (Kan-On, 1997).

# Linear and nonlinear determinacy of the minimal speed

Comparison principle:

$$2\sqrt{d(1-a_1)} \leq c^* \leq 2\sqrt{d}.$$

- $c^*$ is *linearly determined* if $c^* = c_0 := 2\sqrt{d\,(1-a_1)}$;

  or
- *nonlinearly determined* if $c^* > c_0 := 2\sqrt{d\,(1-a_1)}$.

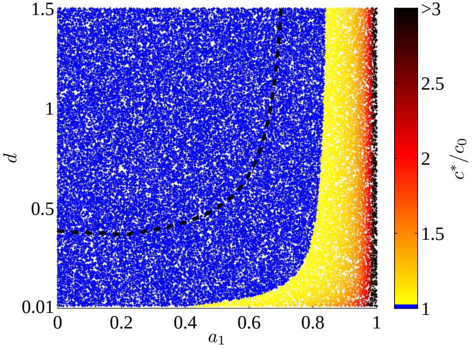
Natural conjecture: $c^*$ is always linearly determined (Okubo et al., 1989, Murray, 2002).

Other conjecture: $c^*$ is nonlinearly determined for $d << 1$ (Hosono, 2003).

Existence of nonlinear waves: $a_1 \to 1$ (Huang and Han, 2011), $d << 1$ (Holzer and Scheel, 2012).

# Linear and nonlinear determinacy of the minimal speed

Sufficient conditions for the linear determinacy: Lewis et al. 2002 and Huang 2010.

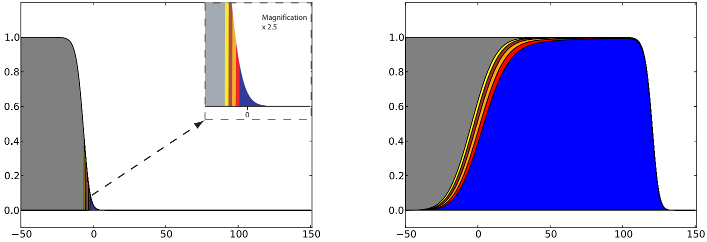



Ratio $c^*/c_0$, in terms of the parameters $a_1, d$ ($a_2 = 2$).
[Boivin, Bonnefon, Hosono, R. 2014]

# Inside dynamics of LV linear waves

## Theorem [Boivin, Bonnefon, Hosono, R. 2014]

*If* $c^*$ *is linearly determined, the wave* $u(t, x) = U(x - c^* t)$ *is pulled.*




(a) $a_1 = 0.4,\ d = 1,\ t = 0$

(b) $a_1 = 0.4,\ d = 1,\ t = 80$

Weak competitor ($a_1 << 1$)$\rightarrow$ erosion of diversity as in the scalar KPP case.

# Slow and fast-decay waves

## Definition (Slow-decay wave)

$u(t,x) = U(x-ct)$ is a *slow-decay wave* if $\ln[U(y)] \sim -\lambda\, y$ as $y \to +\infty$, for some $0 < \lambda \leq c/(2\,d)$.

## Definition (Fast-decay wave)

$u(t,x) = U(x-ct)$ is a *fast-decay* wave if $\ln[U(y)] \sim -\lambda\, y$ as $y \to +\infty$, for some $\lambda > c/(2\,d)$.

Denominator

**Monostable scalar case:**

$c^*$ is linearly determined $\Leftrightarrow u(t,x) = U(x - c^*\,t)$ is a slow-decay wave.

**Our conjecture:** also true for LV competition systems. fig.

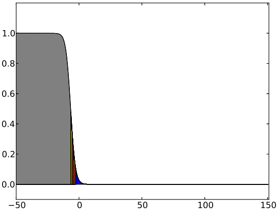
# Inside dynamics of LV nonlinear waves

## Theorem [Boivin, Bonnefon, Hosono, R. 2014]

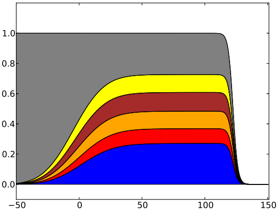
*If $c^*$ is nonlinearly determined:*

**1)** *if $u(t,x) = U(x - c^* t)$ is a fast-decay wave, then it is a pushed wave;*

**2)** *if $u(t,x) = U(x - c^* t)$ is a slow-decay wave, then it is a pulled wave.* *(should never occur)*




(c) $a_1 = 0.9,\ d = 1,\ t = 0$




(d) $a_1 = 0.9,\ d = 1,\ t = 175$

Strong competitor → maintenance of diversity.

# Application 4: delayed reaction-diffusion equations

# Traveling waves in delayed PDEs

- **Equation:** $\partial_t u = d\,\partial_{xx} u + \mathcal{F}[u]$.
- **Growth term:** $F(u(t-\tau,x),u(t,x)) = u(t-\tau,x)\,(1-u(t,x))$.
- **Interpretation:** non-reproductive and motionless juvenile stage.
- **Traveling waves:** $u(t,x) = U_c(x - c\,t)$ for all $c \geq c^*(\tau)$ (Schaaf, 1987)

# Slow vs fast decay at $+\infty$

Lemma [Bonnefon, Garnier, Hamel, R. 2013]

*There exists $\overline{c}(\tau) \in (c^*(\tau), +\infty)$ such that:*
*1) the waves with speeds $c \in (c^*(\tau), \overline{c}(\tau))$ are fast-decay waves;*

*2) the waves with speeds $c \geq \overline{c}(\tau)$ are slow-decay waves.*

# Inside dynamics of delayed waves

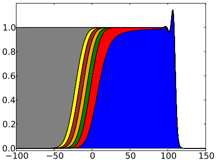
**Equation satisfied by the components of the wave:**

$$\begin{cases} \partial_t \mu(t,x) = \partial_{xx}\mu(t,x) + \dfrac{\mu(t-\tau,x)}{u(t-\tau,x)} F(u(t-\tau,x), u(t,x)), & t > 0, \\ \mu(t,x) = \mu_0(x-ct), & t \in [-\tau, 0]. \end{cases}$$

## Theorem [Bonnefon, Garnier, Hamel, R. 2013]

*All of the waves with speeds $c > c^*(\tau)$ are pulled.*

→ Same dynamics as in the non-delayed case.



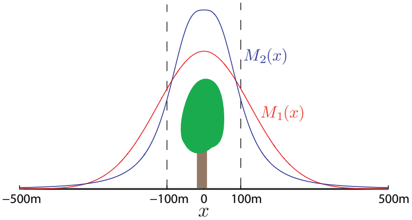
# Application 4: integro-differential equations
# The effect of long-distance dispersion

# Traveling waves and other solutions

- **Equation:** $\partial_t u = \mathcal{D}[u] + f(u).$
- **Growth term:** KPP or monostable (e.g. $f(u) = u(1-u)$).
- **Dispersion term:** $\mathcal{D}[u]$ : nonlocal linear operator

$$\mathcal{D}[u] = \mathcal{D}[u](t,x) = \int_{\mathbb{R}} J(|x-y|)\,(u(t,y) - u(t,x))\,dy.$$

Dispersion kernel $J(\lambda)$ : probability to move at a distance $\lambda$.



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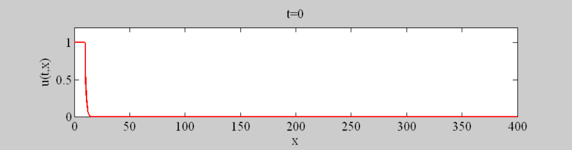


**Thin-tailed dispersion kernel: local dispersion $\rightarrow$ TW with constant speeds (Carr and Chmaj, 2004; Coville and Dupaigne, 2007)**

# Traveling waves and other solutions

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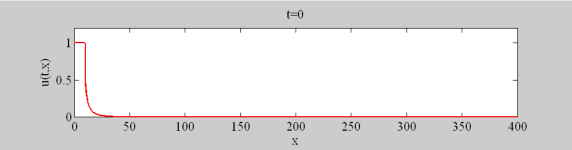



**Fat-tailed dispersion kernel: long-distance dispersion → acceleration (Garnier, 2011) and flattening [Garnier, Hamel, R., 2016].**

# Thin-tailed and fat-tailed kernels

**General assumptions:**

$$J \in \mathcal{C}^0(\mathbb{R}), \quad J \geq 0, \quad J(x) = J(-x), \quad \text{and} \quad \int_{\mathbb{R}} J(x)dx = 1.$$

## Definition (Thin-tailed dispersion kernels)

The dispersion kernel $J$ is a *thin-tailed* kernel if

$$\text{there exists} \quad \lambda > 0, \text{ such that } \int_{\mathbb{R}} J(x)e^{\lambda x}dx < \infty.$$

## Definition (Fat-tailed dispersion kernels)

The dispersion kernel $J$ is a *fat-tailed* kernel if

$$\text{for all} \quad \eta > 0, \quad \text{there exists} \quad x_\eta \in \mathbb{R} \quad \text{such that} \quad J(x) \geq e^{-\eta x} \quad \text{in} \quad [x_\eta, +\infty).$$

# Inside dynamics of traveling waves

## Theorem [Bonnefon, Coville, Garnier, R. 2014]

*If $J$ is a thin-tailed kernel and $f$ is of KPP type, all of the waves $u(t,x) = U(x - c\,t)$, with $c \geq c^*$, are pulled*

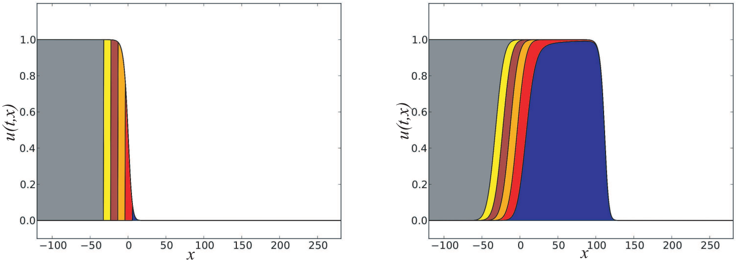



Figure: TW solution in the case of the thin-tailed kernel $J(x) = (1/2)\,e^{-|x|}$, at $t = 0$ (left) and $t = 40$

→ same dynamics as in the reaction-diffusion case (Fisher-KPP equation).

# Pulled/pushed accelerating solutions

**Level set:** for any level $\lambda \in (0,1)$ and $t > 0$:

$$E_\lambda(t) = \{x \in \mathbb{R},\ u(t,x) = \lambda\}.$$

Initial condition $u_0$ with support $(x_0^-, x_0^+)$.

## Definition (Pulled solution (to the right))

For any component $\mu$ with $\overline{Supp(\mu_0)} \subset [x_0^-, x_0^+)$, there holds

$$\sup_{x>0 \in E_\lambda(t)} \mu(t,x) \to 0, \quad \text{as } t \to +\infty, \quad \text{for any level } \lambda \in (0,1).$$

## Definition (Pushed solution to the right)

For all component $\mu$ such that $\overline{Supp(\mu_0)} \subset [x_0^-, x_0^+)$, there is a level $\lambda \in (0,1)$ such that

$$\limsup_{t \to +\infty} \sup_{x>0 \in E_\lambda(t)} \mu(t,x) > 0.$$

# Inside dynamics for very fat kernels

Consider the Cauchy kernel:

$$J(x) = \frac{\beta}{\pi(\beta^2 + x^2)} \text{ for some } \beta > 0,$$

and a monostable function $f$.

## Theorem [Bonnefon, Coville, Garnier, R. 2014]

*The solutions of the integro-differential equation* $\partial_t u = \int_{\mathbb{R}} J(|x-y|)\,(u(t,y) - u(t,x))\,dy + f(u)$ *are pushed in any direction:*

$$\frac{\mu(t,x)}{u(t,x)} \geq \alpha > 0 \ \text{ for all } t \geq \tau \text{ and } x \in \mathbb{R}.$$

# Inside dynamics for very fat kernels

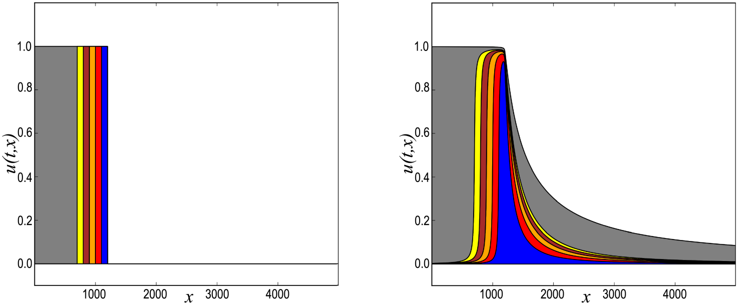



Figure: Solution starting from a step-function with $\beta = 1$, at $t = 0$ (left) and $t = 6$ (right).

Long-distance dispersion $\rightarrow$ better maintenance of diversity.

# Conclusions

Biological mechanisms have been identified as possible causes of pushed propagation waves:

- Allee effect;
- competition with a resident species;
- existence of moving climate barriers (Garnier and Lewis, 2016).

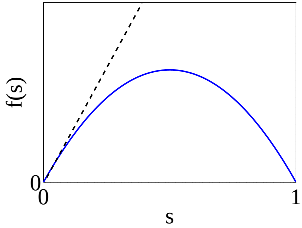
In all cases, they contribute to reduce the advantage of being in the leading edge of the wave.
Consequence: diversity is maintained during the colonization.

From a mathematical viewpoint:

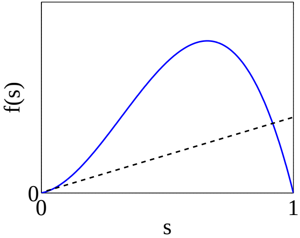
- new notions of pulled and pushed waves;
- these notions are consistent with previous notions, but more general;
- could be applied to other classes of equations, e.g. with nonlinear dispersion terms.

**Thank you for your attention!**

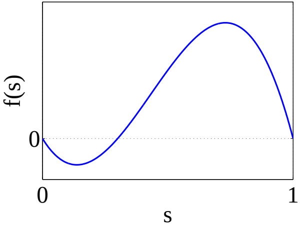
## Types of growth functions that we will consider in this talk: back




(a)KPP back




(b)Monostable back




(c)Bistable back

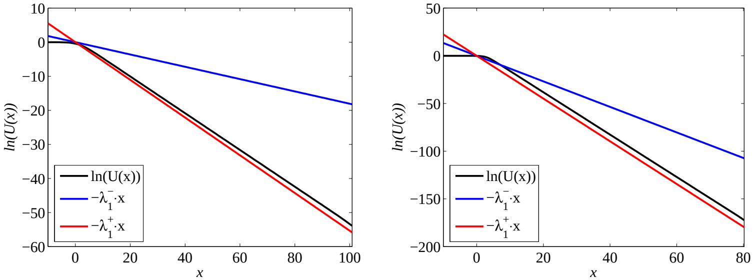



Figure: Comparison of $\ln(U(x))$ with $-\lambda_1^- x$ and $-\lambda_1^+ x$. Left: the parameter values are $a_1 = 0.9$, $a_2 = 2$ and $d = r = 1$, leading to $c^* \simeq 0.73 > c_0 \simeq 0.63$. Right: the parameter values are $a_1 = 0.7$, $a_2 = 2$, $d = 0.1$ and $r = 1$, leading to $c^* \simeq 0.358 > c_0 \simeq 0.346$.

with

$$\lambda_1^{\pm} = \frac{c^* \pm \sqrt{(c^*)^2 + 4\,d\,(a_1 - 1)}}{2\,d}.$$

back