Dynamique de la structure génétique spatiale au cours d'une invasion

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Introduction

Modèles d'EDP en écologie des populations, idée générale

Description de la dynamique d'une population sous l'effet de deux forces :

la dispersion et la croissance (naissances-décès).

Modalités de dispersion :

- locale : diffusion ;
- non locale : modèles à noyaux.

Modalités de croissance :

- logistique : densité-dépendance due à la compétition intra/inter ;
- effet Allee : coopération entre indiv. ;
- effets retards : phase juvénile.

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) $\mathcal{F}[u](t,x)$;

Traveling wave solutions

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

Traveling wave solutions

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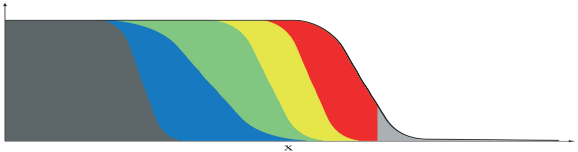
$$u(t, x) = U(x - c\,t).$$



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

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

Inside dynamics of a solution: main idea

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

$$u(0,x) = \sum_{i \in I} \mu^i(0,x).$$

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

Neutrality assumption: dispersion and growth abilities are the same in all the μ^i's.

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

Well-posedness: we can check that

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

Pulled and pushed waves: new definitions (2012)

Definition (Pulled wave)

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

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

→ Only the furthest forward component can follow the wave.

Definition (Pushed wave)

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

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

→ All of the components are maintained in the wave.

First mathematical definitions of pulled/pushed waves: Stokes (1976).

Application 1: logistic growth

Traveling waves – logistic case

- **Equation:** $\partial_t u = d\,\partial_{xx} u + f(u).$
- **Growth term:** $f(u) = u\,(1-u)$ (or other logistic – 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 the waves (logistic case)

Theorem 2012[1]

All of the waves are pulled.

Funder effects → strong erosion of diversity.

[1] Roques et al., PNAS 2012; Giletti et al., J Math Pures Appl, 2012

Application 2: bistable growth terms – strong Allee effect

Bistable waves : strong Allee effect

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

- **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 2012[2]

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

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

[2] Roques et al., PNAS 2012; Giletti et al., J Math Pures Appl, 2012

Inside dynamics of bistable waves

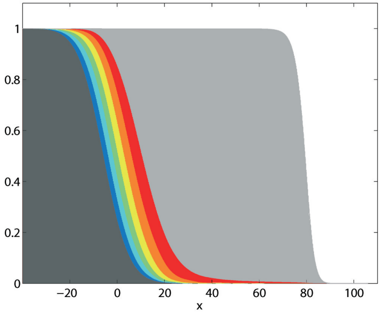
Theorem 2012[2]

The unique wave is pushed.

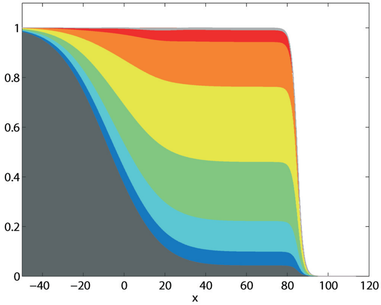
Higher mortality at low densities → maintenance of diversity.

[2] Roques et al., PNAS 2012; Giletti et al., J Math Pures Appl, 2012

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:** logistic-type (pure logistic 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:**

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- **Traveling waves:**

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

Linear and nonlinear determinacy of the minimal speed

Comparison principle:

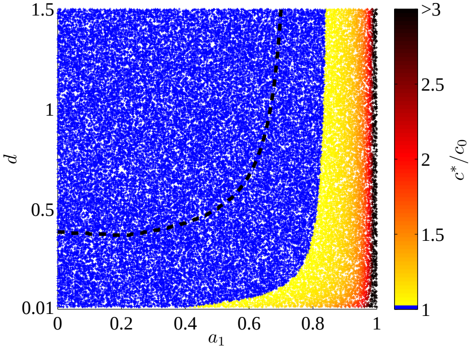
$$2\sqrt{d(1-a_1)} \leq c^* \leq 2\sqrt{d}.$$

- 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).

Linear and nonlinear determinacy of the minimal speed



Ratio c^*/c_0, in terms of the parameters a_1, d $(a_2 = 2)$[3]

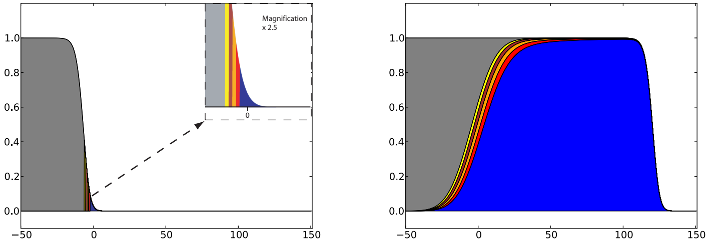
Existence of nonlinear waves: $a_1 \to 1$ (Huang and Han, 2011), $d << 1$ (Holzer and Scheel, 2012).

[3] Roques et al., J Math Biol 2014

Inside dynamics of LV linear waves

Theorem 2014[4]

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.

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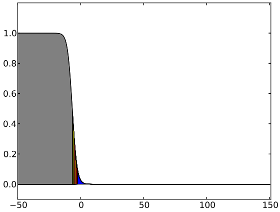
[4] Roques et al., J Math Biol 2014

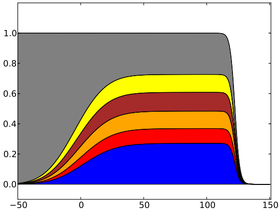
Inside dynamics of LV nonlinear waves

Theorem + conjecture [5]

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



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



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

Strong competitor → maintenance of diversity.

[5] Roques et al., J Math Biol 2014

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)

Inside dynamics of delayed waves

Theorem 2013[6]

All of the waves are pulled, although there exist some fast decay waves!

$\rightarrow$ Same large-time dynamics as in the non-delayed case. Numerical simulations show a “transient pushed stage".

[6] Bonnefon et al., Math Mod Nat Pheno, 2013

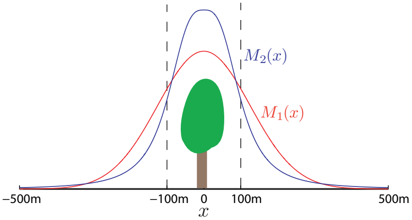
Application 5: integro-differential equations
The effect of long-distance dispersion

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 λ.



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

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Fat-tailed dispersion kernel: long-distance dispersion $\rightarrow$ acceleration (Garnier, 2011) and flattening (in preparation).

Thin-tailed kernels: inside dynamics

Theorem 2014 [7]

If J is a thin-tailed kernel and f is of KPP type, all of the waves are pulled

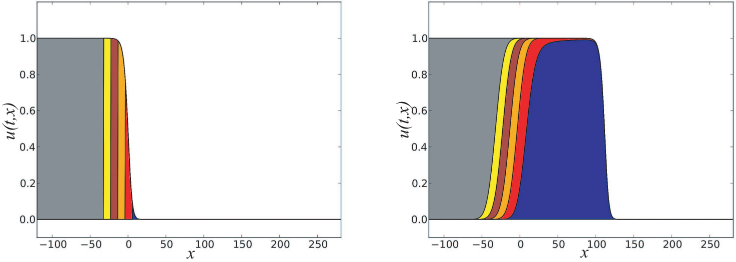


Figure: TW solution in the case of the thin-tailed kernel $J(x) = (1/2)\, e^{-|x|}$, at $t = 0$ (left) and $t = 40$

$\rightarrow$ same dynamics as in the diffusion case.

[7] Bonnefon et al., DCDS B, 2014

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 2014[8]

The solutions are pushed:

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

[8] Bonnefon et al., DCDS B, 2014

Inside dynamics for very fat kernels

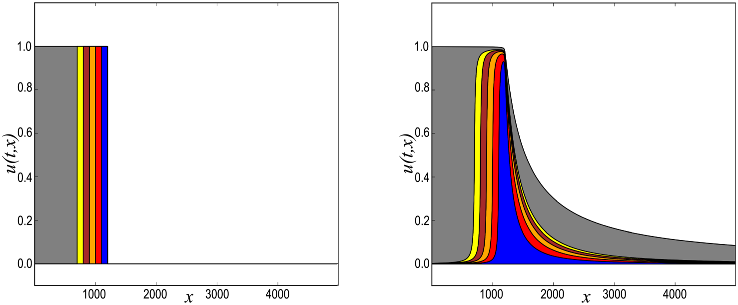


Figure: Solution starting from a step-function with $\beta = 1$, at $t = 0$ (left) and $t = 6$ (right).

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

Conclusions

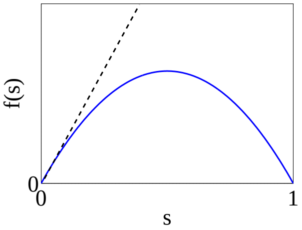
Ecological consequences:
Mechanisms which usually have adverse consequences can lead to a better maintenance of diversity:

- Allee effect (lower or negative growth rate at low densities);
- competition with a resident species;
- climatic constraints (Pluess, 2011, Garnier and Lewis, 2014).

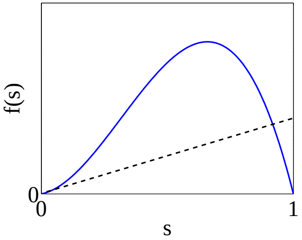
Next steps:

- check our results experimentally (collaboration with L Mailleret and E Vercken - demande thèse SPE);
- effect of density-dependent dispersal;
- include some feedback of diversity on population dynamics;
- estimate demographic parameters, based on genetic data (Emily's talk).

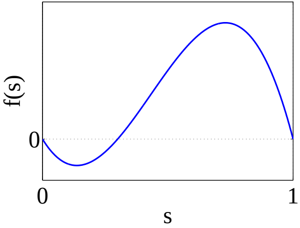
Thank you!



(a)KPP back



(b)Monostable back



(c)Bistable back