Sort d'une population affrontant un gradient environnemental translaté par le climat

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Talk based on collaborations with

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- Jérôme Coville (BIOSP, INRAE, Avignon)
- Gwenaël Peltier (IMAG, Univ. Montpellier)
- Gaël Raoul (CMAP, Ecole Polytechnique, Palaiseau)
- Ophélie Ronce (ISEM, Univ. Montpellier) for biological aspects.

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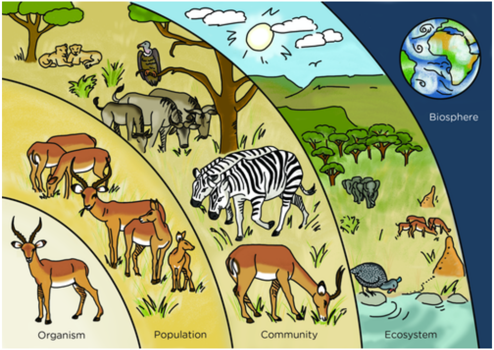
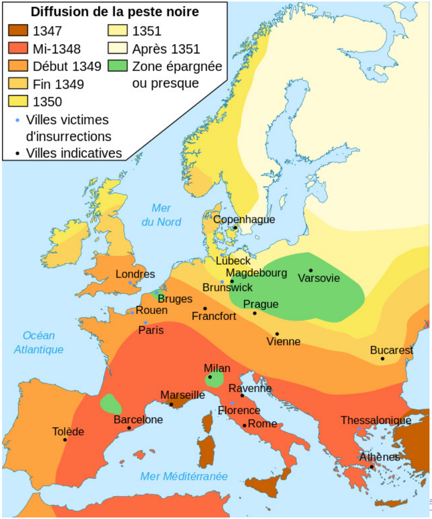
Ecology

Ecology: study of interactions of a population with another population and/or its environment.

Examples: prey-predator, epidemiology, chemotaxis, tumor growth...



Propagation of plague in Europe



Reaction-diffusion equation

$u(t,x) =$ density, at time $t \geq 0$, of a population structured in space $x \in \mathbb{R}^N$:

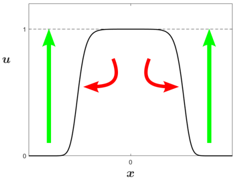
$$\left\{ \begin{array}{c} \text{density variation} \\ \text{of the population} \end{array} \right\} = \left\{ \begin{array}{c} \text{movement of} \\ \text{individuals} \end{array} \right\} + \left\{ \begin{array}{c} \text{birth and death} \\ \text{phenomena} \end{array} \right\}$$

$$\partial_t u = \underbrace{\Delta u}_{\text{diffusion}} + \underbrace{f(t,x,u)}_{\text{reaction}}.$$

Fisher-KPP equation

Fisher: "The wave of advance of advantageous gene" (1937) :

$$\partial_t u = \Delta u + ru(1-u)$$



Theorem (Begins with Kolmogorov, Petrovsky, Piskunov (1937))

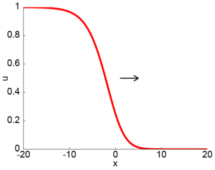
There is Hair Trigger Effect : any small amount of initial population drives the solution u towards 1 at large times, uniformly locally in space, i.e. invasion always occurs.

Traveling waves ($N = 1$)

Definition

A traveling wave is a speed c and a positive profile ϕ such that
$\phi(-\infty) = 1, \quad \phi(+\infty) = 0,$
$\phi(x - ct)$ *solves the PDE.*

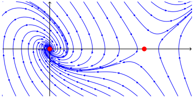
PDE: $\partial_t u = \partial_{xx} u + f(u) \rightarrow$ EDO: $-c\phi' = \phi'' + f(\phi)$.



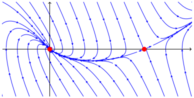
Necesseraly $c > 0$, meaning that $u \approx 1$ invades $u \approx 0$.

Phase plane analysis (Fisher-KPP equation)

- if $0 < c < c^* := 2\sqrt{r}$ then ϕ changes sign, i.e. NO TW.



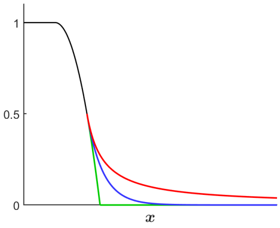
- if $c \geq c^*$ there is an appropriate trajectory, ie TW does exist.



▶ Critical speed c^*.

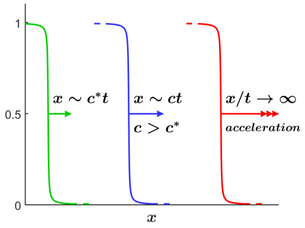
Spreading speed

Invasion speed depends only on the tail of u_0 (initial data).



$t = 0$

$\longrightarrow$



$t \to \infty$

▶ Fisher-KPP invasions are driven by individuals ahead of the front: pulled dynamics.

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Invasion requires evolution

Species invading new territories often face environmental gradients (temperature, luminosity, antibiotic chemicals...).

Experimentally, it is well documented that invasive species then evolve during their range expansion to adapt to local conditions.

Mutation and selection under our eyes

- From "Spatiotemporal microbial evolution on antibiotic landscapes" by Michael Baym, Tami D. Lieberman, Eric D. Kelsic, Remy Chait, Rotem Gross, Idan Yelin, Roy Kishony (2016):

Mutation/selection movie.

Accelerating invasion of cane toads

[1]

[1]Wikipédia.

Rather recent models

- Champagnat, Méléard 2007, Arnold, Desvillettes, Prevost 2012, Bouin, Calvez, Meunier, Mirrahimi, Perthame, Raoul, Voituriez 2012, Mirrahimi, Raoul 2013, Bouin, Calvez 2014, Turanova 2016, Djidjou-Demasse, Ducrot, Fabre 2017, Peltier 2019...
- Nonlocal effects, subtle interaction ecology/evolution...
- Well posedness, Hamilton-Jacobi approach, Traveling front, Finite spreading speed, Accelerating propagations...

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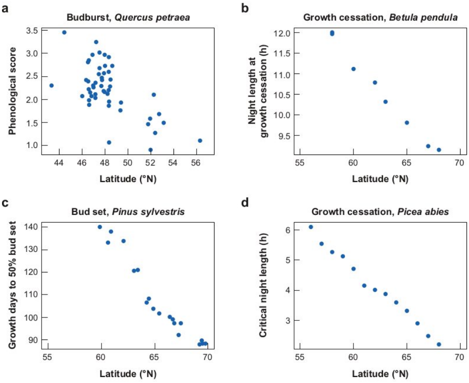
Phenotypic gradients

- Many traits related to timing of growth show clines over latitude:



[2]

[2]Savolainen et al, Annu. Rev. Ecol. Evol. Syst., 2007.

Asexual populations living in an environmental cline

To understand the speed, or even the success of an invasion, one should then consider the dispersion, birth and death processes, but should also take into account evolution.

$n(t, x, y)$: density of individuals

- at time $t \geq 0$
- at position $x \in \mathbb{R}$
- with a phenotypic trait $y \in \mathbb{R}$.

$$\partial_t n - \partial_{xx} n - \partial_{yy} n = \left(1 - A(y - Bx)^2 - \int_{\mathbb{R}} n(t,x,y')\,dy'\right) n.$$

- Reproduction is maximal along an optimal trait which depends on the location: $y = Bx$. Invasion in the direction of the environmental cline requires evolution.

- Logistic regulation is nonlocal in the trait, i.e. the intra-specific competition (for e.g. food) at each location takes place with all individuals whatever their traits.

What is the dynamics?

$$\partial_t n - \partial_{xx} n - \partial_{yy} n = \left(1 - A(y - Bx)^2 - \int_{\mathbb{R}} n(t, x, y')\, dy'\right) n.$$

- Difficulties:
  - The sign of the reaction term can change.
  - The space of the traits is infinite.
  - The competition term is nonlocal.
  - $B > 0$ (when $B = 0$ a separation of variables trick is available, see Berestycki, Jin, Silvestre 2016).

Rescaling following the cline

- $z = y - Bx$ yields

$$\partial_t n - \mathcal{E}(n) = \left(1 - Az^2 - \int_{\mathbb{R}} n(t,x,y')\,dy'\right) n,$$

where

$$\mathcal{E}(n) = n_{xx} + (B^2+1)n_{zz} - 2Bn_{xz}.$$

Gaussian as principal eigenfunctions

- Linearize around $n \equiv 0$ and look at the eigenvalue problem:

$$-\mathcal{E}(\psi) - (1 - Az^2)\psi = \lambda\psi.$$

- $\Gamma_0 : z \mapsto \exp\left(-\sqrt{\frac{A}{B^2+1}}\frac{z^2}{2}\right)$ solves:

$$\begin{cases} -\mathcal{E}(\Gamma) - (1 - Az^2)\Gamma = (\sqrt{A(B^2+1)} - 1)\Gamma & \text{in } \mathbb{R}^2 \\ \Gamma > 0 & \text{in } \mathbb{R}^2. \end{cases}$$

- We expect that invasion occurs iff $\lambda_0 := \sqrt{A(B^2+1)} - 1 < 0$.

Extinction vs. invasion

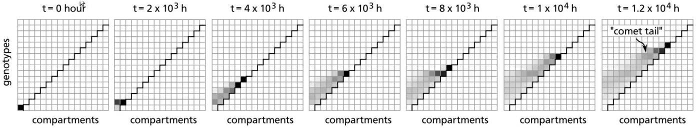
Theorem (A., Coville, Raoul 2012)

- *Assume* $\lambda_0 > 0$. *Then, extinction exponentially fast.*
- *Assume* $\lambda_0 < 0$. *Define* $c^* := 2\sqrt{\frac{-\lambda_0}{1+B^2}}$. *Then, for all* $c \geq c^*$, *there exists a TW* (c, u) *such that*

$$\nu \mathbf{1}_{\{(x,z)\in(-\infty,0]\times[-\nu,\nu]\}}(x,z) \leq u(x,z) \quad \text{"weak" behavior on the left,}$$

$$\|u(x,\cdot)\|_\infty \to_{x\to+\infty} 0 \quad \text{decay to zero on the right,}$$

$$u(x,z) \leq Ce^{-Kz^2} \quad \text{control of the z-tails.}$$



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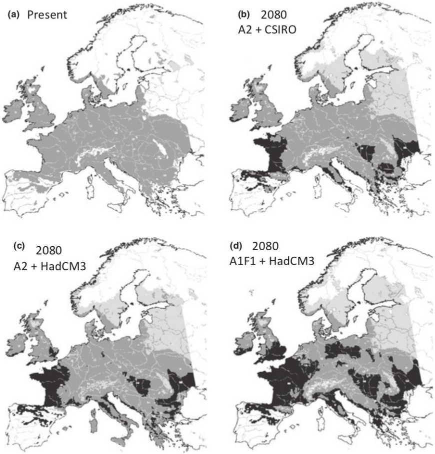
Fate of the oak in Europe?



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[3] Kremer *et al*, Ecology Letters, 2012.

Can a species keep pace with a shifting climate?

Berestycki, Diekmann, Nagelkerke and Zegeling 2009.

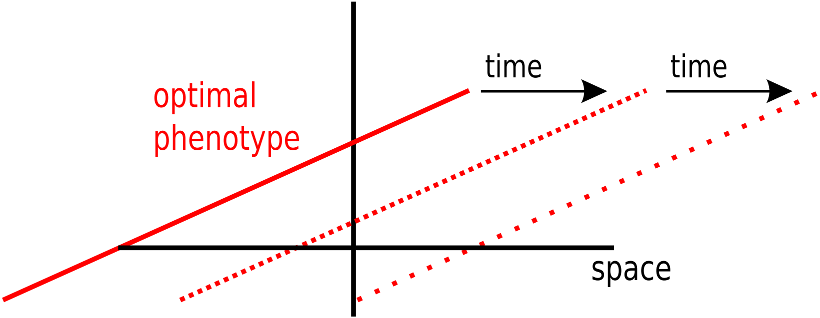
- The influence of Global Warming on the survival of a species.
- Evolutionary phenomena are neglected.
- However, species adapt to local conditions and in particular to the local temperatures.
- Again, we take evolution into account, and also consider nonlocal competition.

The considered equation

$$\partial_t n(t,x,y) \quad -\partial_{xx} n(t,x,y) - \partial_{yy} n(t,x,y) = \left(r(x-ct,y) - \int_{\mathbb{R}} n(t,x,y')\,dy' \right) n(t,x,y)$$

- The line of optimal trait is shifted by the climate, at a **GIVEN** forced speed $c \geq 0$.

$$r(x-ct,y)=1-A(y-B(x-ct))^2.$$



The critical speed

$$c^{**}_{unconf} := 2\sqrt{-\lambda_0 \frac{1+B^2}{B^2}}.$$

Theorem (A., Berestycki, Raoul 2017)

- *If $c > c^{**}_{unconf}$ then extinction.*
- *If $0 \leq c < c^{**}_{unconf}$ then survival and invasion, with the following propagation speeds*

$$\omega_x^- := -\sqrt{-\frac{4\lambda_0}{1+B^2} - \frac{B^2}{(1+B^2)^2}c^2} + \frac{B^2}{1+B^2}c \quad (\textit{towards south})$$

$$\omega_x^+ := \sqrt{-\frac{4\lambda_0}{1+B^2} - \frac{B^2}{(1+B^2)^2}c^2} + \frac{B^2}{1+B^2}c \quad (\textit{towards north}).$$

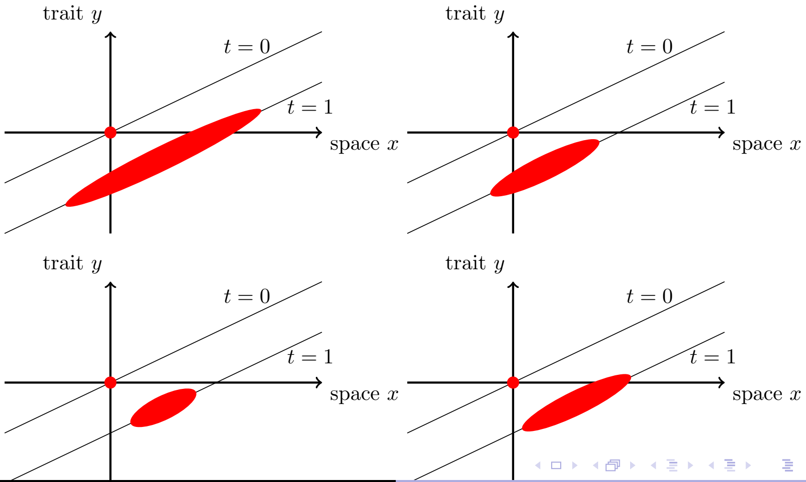
Following the climate shift?

- There is a critical speed c^*_{unconf} such that
  - $0 < c < c^*_{unconf}$ implies $\omega_x^+ > c$ meaning that the population is able to follow the climate shift.
  - $c^*_{unconf} < c < c^{**}_{unconf}$ implies $\omega_x^+ < c$ meaning that the population survives despite its inability to follow the climate change: it only survives because it is also able to evolve to become adapted to the changing climate.

Spreading towards south?

- There is a critical speed $c^\sharp_{unconf}$ for "propagation towards south":
  - $0 < c < c^\sharp_{unconf}$ implies $\omega_x^- < 0$ meaning that the population will spread to the entire environment.
  - $c^\sharp_{unconf} < c < c^{**}_{unconf}$ implies $\omega_x^- > 0$ meaning that, although the population will survive and grow in size globally, it will shift towards $+\infty$, and thus disappear from any given location after some time.

Four invasion scenarios



For equation $\partial_t n - \frac{\sigma^2}{2}\partial_{xx} n - \frac{\mu^2}{2}\partial_{yy} n = \dots$

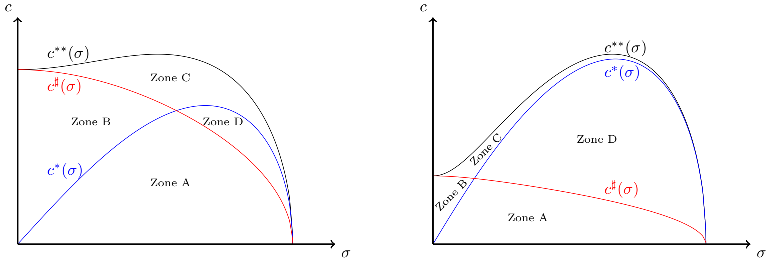


Figure: Left: μ large. Right: μ small.

c^{**}: critical speed for survival

c^{*}: critical speed for "following the climate" (north).

$c^{\sharp}$: critical speed for "total spreading" (south).

Population's range

In this model, during invasion the size increases at a speed

$$\omega_x^+ - \omega_x^- = \frac{2B}{1+B^2}\sqrt{(c_{unconf}^{**})^2 - c^2}$$

which enables to estimate the robustness of the population w.r.t. an increase of the climate speed.

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Facing a nonlinear obstacle

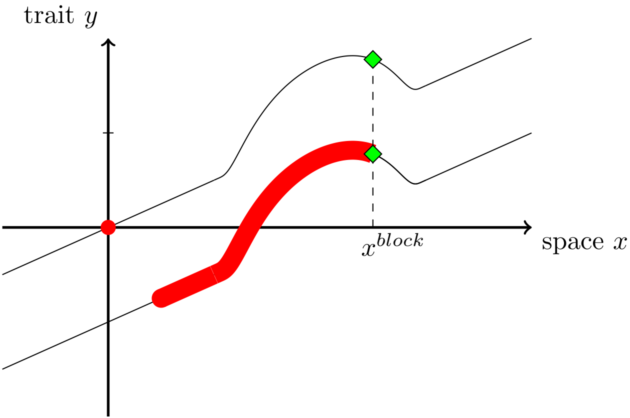
We consider a growth function $1 - A(y - y_{opt}(t,x))^2$, where

$$y_{opt}(t,x) := \underbrace{B(x-ct)}_{\text{unconfined}} + \varphi(x),$$

with φ compactly supported in $(0, M)$: there is a geographical obstacle in $(0, M)$ which induces a perturbation, via φ, of the optimal trait.

- We linearize around the northern position of the front.
- Using our previous results on the unconfined case, we derive the instantaneous speed of the front, and so an ODE for the position.
- It turns out that:

if there is x^{block} such that $\varphi'(x^{block})$ is large enough then propagation towards north is blocked.


trait y
x^{block}
space x

Effect of a natural reserve

- Without refuge: Movie

- With refuge: in a localized region, the conditions for survival are artificially ameliorated. The growth function is

$$1+\psi(x) - A(y - B(x - ct))^2,$$

with $\psi \geq 0$ compactly supported in $(0, M)$. Movie

Multidimensional versions

Previously $x \in \mathbb{R}$ was the position. Now we consider $x = (x_1, x_2) \in \mathbb{R}^2$ with x_1 the latitude, x_2 the longitude.

We consider a growth function $1 - A(y - y_{opt}(t,x))^2$, where

$$y_{opt}(t,x) = y_{opt}(t,x_1) = \underbrace{B(x_1 - ct)}_{\text{unconfined w.r.t. latitude}} .$$

As above, when $0 \leq c < c^{**}$, there is invasion.

- In which direction does the population spread the faster?

It turns out that

- For $c = 0$ invasion is faster along a parallel.
- When c increases from 0 to c^* the faster direction changes continuously until being along a meridian.
- When c increases from c^* to c^{**} then the faster direction remains along a meridian, but the invasion speed decreases until touching 0.

Very new rigorous results

$$\partial_t n - \partial_{xx} n - \partial_{yy} n = \left(1 - A(y - \varepsilon\theta(x))^2 - \int_{\mathbb{R}} n(t,x,y')\,dy'\right) n.$$

Theorem (A., Peltier 2020)

Assume $\lambda_0 < 0$. Assume $\theta \in C_b(\mathbb{R})$ or $\theta \in C_{per}(\mathbb{R})$. Then, for $|\varepsilon| \ll 1$, there is a steady state $n^\varepsilon(x,y)$ such that

$$n^\varepsilon(x,y) = n^0(y) + \varepsilon\, A(\rho_A * \theta)(x)\, y n_0(y) + \cdots,$$

where $n^0(y) := \frac{-\lambda_0}{\|\Gamma_0\|_{L^1}} \Gamma_0(y)$, and with the probability density $\rho_A(x) := \frac{1}{2}\sqrt{2A} e^{-\sqrt{2A}|x|}$.

Theorem (A., Peltier 2020)

Assume $\lambda_0 < 0$. Assume $\theta \in C_{per}(\mathbb{R})$. Then, for $|\varepsilon| \ll 1$, there is a pulsating front $u^\varepsilon(z := x - c_\varepsilon t, x, y)$ such that

$$u^\varepsilon(z,x,y) = U(z)n^\varepsilon(x,y) + \cdots, \quad c_\varepsilon = c_0 + o(\varepsilon),$$

where $U = U(z)$ is a Fisher-KPP front[a] connecting 1 to 0 and traveling at speed $c_0 \geq c^* := 2\sqrt{-\lambda_0}$.

[a] solving $U'' + c_0 U' - \lambda_0 U(1-U) = 0$.

- Careful application of the implicit function theorem in rather intricate function spaces.
- To deal with the trait variable y we use a Hilbert basis of $L^2(\mathbb{R})$ made of eigenfunctions of an underlying Schrödinger operator.
- To deal with the space variable x we use the Fourier series expansions.

Thanks for your attention.