Accelerating invasions along an environmental gradient

Gwenaël Peltier – Institut Montpelliérain Alexander Grothendieck

under the supervision of Matthieu Alfaro

1 – The Fisher-KPP equation

Before introducing our model, we present first a setting without evolution and mutation. The population, of density $u(t,x)$, is only structured in space $x \in \mathbb{R}$:

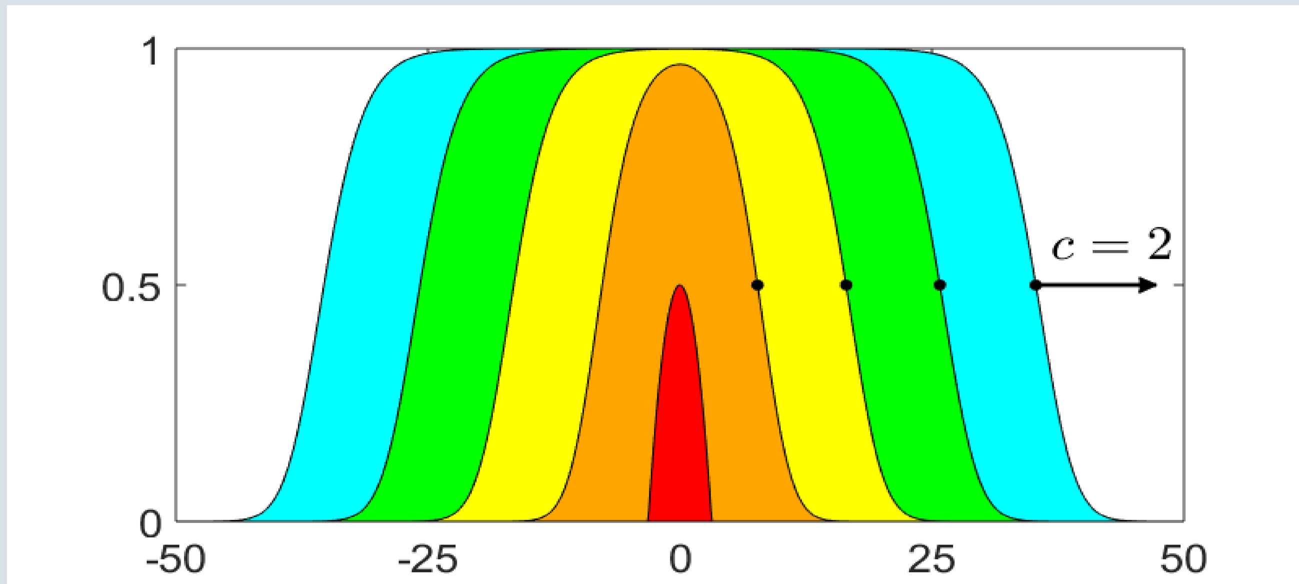
$$\partial_t u = \underbrace{\partial_{xx} u}_{\text{migrations}} + \underbrace{u(1-u)}_{\text{birth and death}}, \qquad (1)$$

with initial data $u_0(x) \in [0,1]$.

The environment is thus assumed *homogeneous*: the birth and death term does not depend on the position x.

2 – Accelerating invasions (Fisher-KPP) [3, 5]

Whenever $u_0 \not\equiv 0$, the population survives and spreads to the whole space.



Invasion for compactly supported u_0 (in red). $u(t,x)$ is represented every 5 seconds.

To quantify the invasion speed, we look at the point $x_{1/2}(t) \in \mathbb{R}_+$ for which $u(t,x_{1/2}) = 1/2$ (the value $1/2$ is arbitrary).

The invasion speed depends only on the behavior of $u_0(\cdot)$ at $+\infty$:

- If u_0 is compactly supported, the invasion occurs at speed 2: $x_{1/2}(t) \sim 2t$.
- If $u_0(x) \underset{+\infty}{\sim} Ce^{-\alpha x}$, then $x_{1/2}(t) \sim c_\alpha t$ with $c_\alpha \in [2,+\infty)$.
- If $u_0(x) \underset{+\infty}{\sim} Cx^{-\alpha}$, then $x_{1/2}(t) \sim C' \exp(t/\alpha)$.
- More generally, if u_0 displays a *heavy tail* (i.e. decreases more slowly than any $e^{-\alpha x}$), then $x_{1/2}(t)$ is super-linear, thus acceleration of the invasion.

3 – Evolutionary model in heterogeneous environment

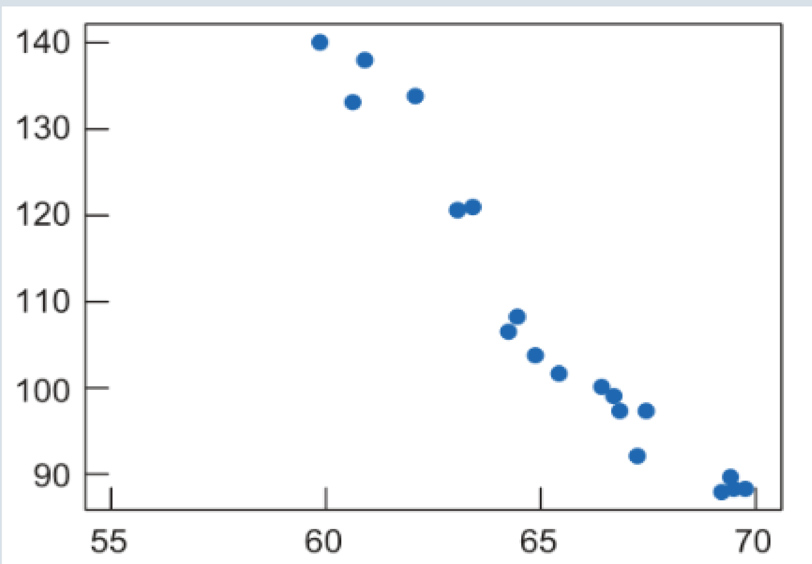
Now, we consider a population $n(t,x,y)$ structured by a space variable $x \in \mathbb{R}$, and a phenotypical trait $y \in \mathbb{R}$, which affects its survival.

$$\partial_t n = \underbrace{\partial_{xx} n}_{\text{migrations}} + \underbrace{\partial_{yy} n}_{\text{mutations}} + \left[\underbrace{r(x,y)}_{\text{growth}} - \underbrace{\int_{\mathbb{R}} n(t,x,y')dy'}_{\text{competition}}\right] n, \qquad (2)$$

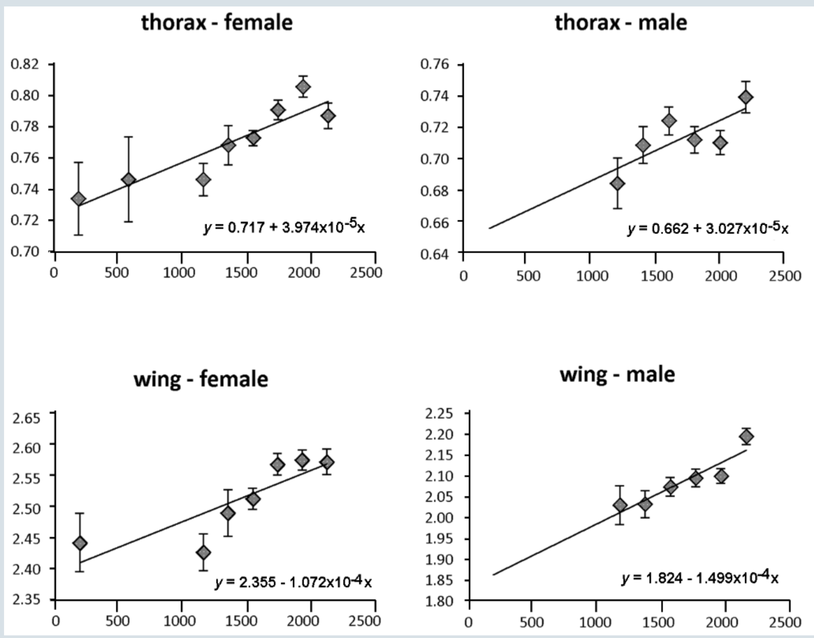
where $r(x,y) = 1 - A(y-Bx)^2$, with $A, B > 0$. The optimal trait for survival is thus $y_{opt}(x) = Bx$. This is called an *environmental gradient* (here linear). To invade the whole space, the population has to adapt.

Objective: find a "heavy tail" condition on $n_0(x,y)$, as general as possible, that leads to an accelerating invasion (in space).

4 – Examples of linear environmental gradients



Duration of bud growth of the Scotch pine tree, with respect to the North latitude.
Source: Savolainen et al. 2017.



Wing and thorax size of flies w.r.t. altitude.
Source: Tantowijoyo, Hoffmann, 2011.

5 – When $n_0(x,y)$ is compactly supported [1]

For the evolution model (2), survival or extinction of the population depends on the sign of the principal eigenvalue, denoted λ_0, of the differential operator

$$\mathcal{L}n := -\partial_{xx} n - \partial_{yy} n - r(x,y)n.$$

In our setting, there holds $\lambda_0 = \sqrt{A(1+B^2)} - 1$. If $\lambda_0 \geq 0$, the population goes extinct. When $\lambda_0 < 0$ and $n_0 \not\equiv 0$, it survives and invades the whole space. In what follows, we always assume the latter case.

We are interested in the spreading speed of the population in space, regardless of the trait. Therefore, we set $N(t,x) = \int_{\mathbb{R}} n(t,x,y)dy$ and $x_\delta(t)$ the point(s) where $N(t, x_\delta(t)) = \delta$.

When n_0 is compactly supported, the invasion speed is finite: $x_\delta(t) \sim 2t\sqrt{\frac{-\lambda_0}{1+B^2}}$ for levels δ small enough. Moreover, the population remains concentrated around the optimal trait as it invades, since $n(t,x,y) \leq C\exp(-k|y-Bx|)$ with $C, k > 0$.

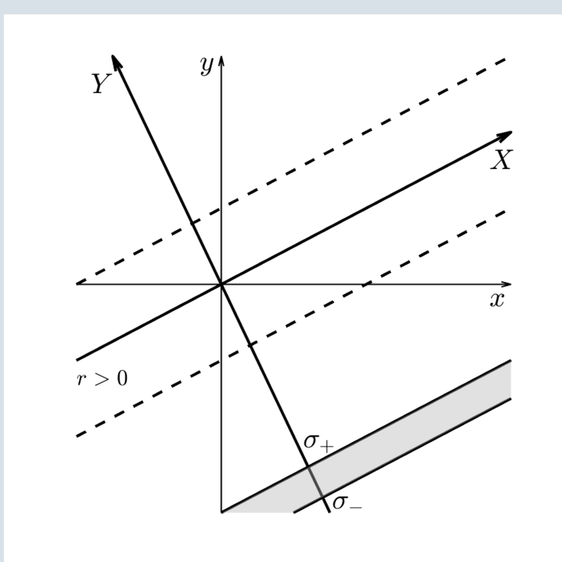
6 – Acceleration for "heavy tail" n_0

We rotate the coordinate system, and denote (X,Y) the new coordinates, so that X is directed along $y = Bx$ (see figure below).

Theorem: assume $n_0(x,y) \geq u_0(X)\mathbf{1}_{[\sigma_-,\sigma_+]}(Y)$ with heavy tail u_0 and $\sigma_- < \sigma_+$. Then there is acceleration: $x_\delta(t)/t \to +\infty$ for δ small enough, and there holds

$$x_\delta(t) \geq \frac{1}{\sqrt{1+B^2}} \min u_0^{-1}\left(e^{(\lambda_0^R+\varepsilon)t}\right), \qquad \text{for t large enough,}$$

with $\varepsilon > 0$ and $\lambda_0^R < 0$ the principal eigenvalue $\mathcal{L}^R := -\partial_{YY} - r(Y)$ defined for $Y \in [-R,R]$. R is large enough so that $\lambda_0^R < 0$ (since $\lambda_0^R \to \lambda_0 < 0$ as $R \to +\infty$).



In grey, the domain where $n_0(x,y) \geq u_0(X)$.

The proof involves the construction of a subsolution $\underline{n}$ satisfying $\underline{n} \leq n$ and spreads by accelerating. Several obstacles had to be overcome:

- The integral term in (2) prevents the application of the maximum principle. An argument based on a refinement of a Harnack inequality leads to an upper bound of this term.
- To construct an accelerating subsolution, we used a principal eigenfunction of $\mathcal{L}^R$. To do that, we needed to show that $n(t_0,x,y) \geq Cu_0(X)\mathbf{1}_{[-R,R]}(Y)$ for some $t_0 > 0$, which we achieved thanks to an intermediate subsolution.

7 – Remarks and continuations

Our heavy tail condition on n_0 does not require any other assumption on $\sigma_\pm$. The support may be as narrow and as far (from the optimal trait) as desired.

However, it is crucial that the support is oriented in the direction $X \to +\infty$. Otherwise, the invasion speed is identical to the case n_0 compactly supported.

In the continuation of this work, several paths are possible:

- The convergence of the "back" of the front towards a steady state.
- Include some Allee effect, which tends to slow invasion, and determine a possible trade-off with the heaviness of the initial tail.
- Change $\partial_{yy} n$ into a fractional laplacian or a convolution $J * n - n$, which were already studied in non-evolutionary models [2, 4].
- Consider nonlinear environmental gradients: $r(x,y) = 1 - A(y - \varphi(x))^2$.

8 – References

[1] M. Alfaro, H. Berestycki, and G. Raoul, *The effect of climate shift on a species submitted to dispersion, evolution, growth, and nonlocal competition*, SIAM Journal on Mathematical Analysis, 49 (2017), pp. 562–596.

[2] X. Cabré and J.-M. Roquejoffre, *The influence of fractional diffusion in fisher-kpp equations*, Communications in Mathematical Physics, 320 (2013), pp. 679–722.

[3] R. A. Fisher, *The wave of advance of advantageous genes*, Annals of eugenics, 7 (1937), pp. 355–369.

[4] J. Garnier, *Accelerating solutions in integro-differential equations*, SIAM Journal on Mathematical Analysis, 43 (2011), pp. 1955–1974.

[5] F. Hamel and L. Roques, *Fast propagation for KPP equations with slowly decaying initial conditions*, Journal of Differential Equations, 249 (2010), pp. 1726–1745.