Accelerating invasions in an evolutionary ecology model

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Overview

1. Motivations
2. Fisher-KPP equation – Acceleration
3. An evolutionary ecology model
4. Acceleration in the evolutionary model
5. Remarks and conclusion

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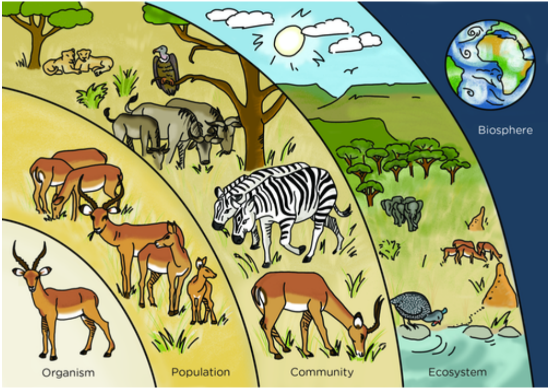
Ecology

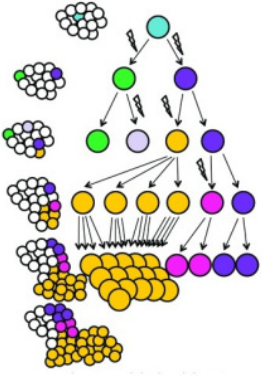
Ecology: study of interactions of a population with another population and/or its environment.

Model examples:
prey-predator, epidemiology, chemotaxis, tumor growth...



Evolution aspect is often neglected (rare mutations, etc.)

Evolutionary Biology



- Natural selection
- Gene inheritance
- Mutations

Model examples: branching process, evolutionary rescue, source-sink...

Ecology aspect is often neglected (homogeneous environment, no interaction with other populations, etc.)

Invasions : ecological + evolutionary effects

Context: (spatial) invasion of a population in a heterogeneous environment. Therefore the population must adapt during its migration.

$\Rightarrow$ **eco + evo effects**.

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Reaction-diffusion equation

$u(t,x)$: density of a population structured in time $t \geq 0$ and space $x \in \mathbb{R}$.

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

$$\partial_t u = \underbrace{\partial_{xx} u}_{\text{diffusion}} + \underbrace{f(x,u)}_{\text{reaction}}$$

The Fisher-KPP equation [4, 6]

$$\begin{cases} \partial_t u = \partial_{xx} u + ru(1-u), & r > 0, \\ u(0,x) = u_0(x), & 0 \le u_0 \le 1. \end{cases}$$

Maximum principle
$\Longrightarrow u(t,x) \in [0,1]$.

If $u_0 \not\equiv 0$, there is survival and invasion of the population :

$$\forall x \in \mathbb{R} \qquad u(t,x) \underset{t\to+\infty}{\longrightarrow} 1.$$

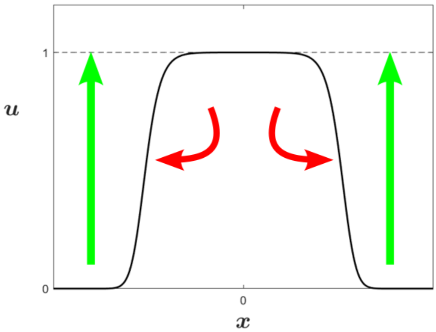

Figure: Form of the solution $u(t,x)$.

Invasion speed

Invasion speed depends only on the behavior of u_0 at infinity [3].

If u_0 displays a *heavy tail* at $+\infty$, i.e. if u_0 decreases more slowly than any exponential, then there is **acceleration** of the front [5].

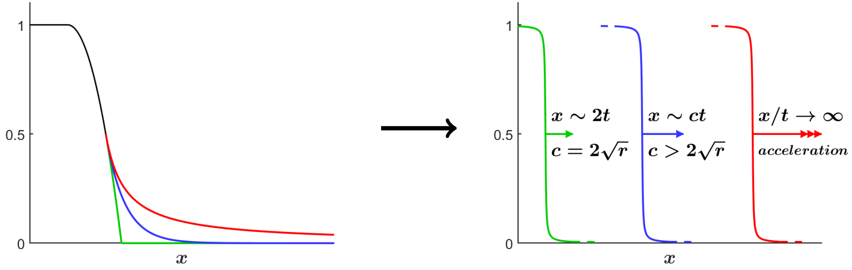

Figure: Three profiles of initial data, and the asymptotical speed of the front. Green : compact support. Blue : exponential tail. Rouge : heavy tail.

Location of level sets

We define the λ-level set of u with $\lambda \in (0,1)$

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

Theorem 1: *Hamel, Roques [5]*

Assume u_0 satisfies

- u_0 is *front-like* $\quad (\liminf_{-\infty} u_0 > 0, \quad u_0 > 0, \quad \lim_{+\infty} u_0 = 0)$,
- u_0 displays a heavy tail,
- $\exists \xi \in \mathbb{R}$ such that u_0 is C^2 and decreasing in $[\xi, +\infty)$,
- $u_0''(x) = o(u_0(x))$ when $x \to +\infty$,

Then for all $\lambda \in (0,1)$ and $\varepsilon \in (0,r)$, there exists T such that

$$E_\lambda(t) \subset \left[u_0^{-1}(e^{-rt+\varepsilon t}),\, u_0^{-1}(e^{-rt-\varepsilon t})\right], \qquad \forall t \geq T.$$

A few examples

$$E_\lambda(t) \subset \left[u_0^{-1}(e^{-rt+\varepsilon t}),\, u_0^{-1}(e^{-rt-\varepsilon t})\right], \qquad \forall t \geq T.$$

$$u_0(x) \underset{+\infty}{\sim} Ce^{-bx^a}, \quad 0 < a < 1 \qquad \Longrightarrow \quad E_\lambda(t) \sim \left(\frac{r}{b}\right)^{1/a} t^{1/a},$$

$$u_0(x) \underset{+\infty}{\sim} Cx^{-\alpha} \qquad \Longrightarrow \quad \ln E_\lambda(t) \sim \frac{r}{\alpha} t,$$

$$u_0(x) \underset{+\infty}{\sim} C(\ln x)^{-\alpha} \qquad \Longrightarrow \quad \ln \ln E_\lambda(t) \sim \frac{r}{\alpha} t.$$

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Model overview

$n(t,x,y)$: density of a population structured in time t, space $x \in \mathbb{R}$, and a phenotypical trait $y \in \mathbb{R}$.

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

where $r(x,y) = 1 - A(y - Bx)^2$, with $A, B > 0$.

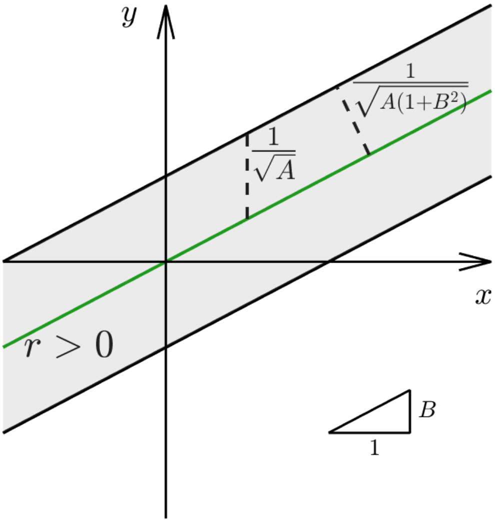
Optimal trait depends on the position in space: $y_{opt}(x) = Bx$. This is called a *linear environmental gradient*.

Does the population survive ? If yes, is there invasion ? At which speed ?

Intuition on parameters A and B

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

We expect that, if $A(1+B^2)$ is too large, the band $r > 0$ is too narrow, which leads to extinction.



Linear env. gradients

Example: tree population, where x is the latitude, proportional to the duration of sunshine and y a trait linked to the growth by photosynthesis.

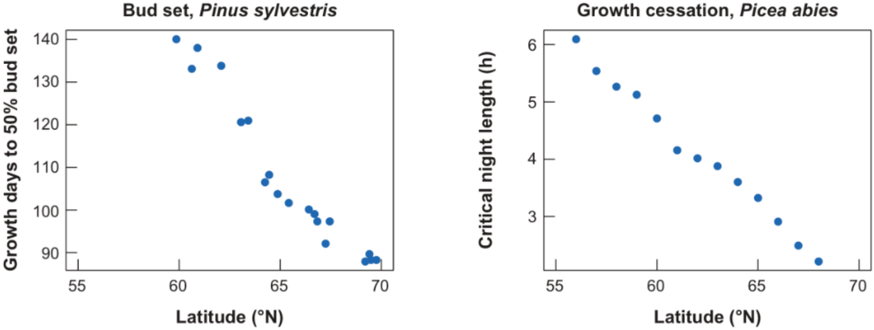


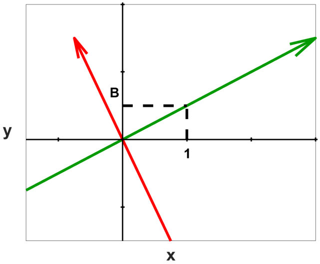
Figure: *Image from Savolainen et al. 2017.*

A change of variables

$$X = \frac{x + By}{\sqrt{1+B^2}}, \qquad Y = \frac{y - Bx}{\sqrt{1+B^2}}.$$

In green, the direction $X \to +\infty$.

In red, the direction $Y \to +\infty$.



If we set $v(t,X,Y) = n(t,x,y)$ and $\tilde{r}(Y) := 1 - A(1+B^2)Y^2$, then

$$\partial_t v - \partial_{XX} v - \partial_{YY} v = \left(\tilde{r}(Y) - \int_{\mathbb{R}} (\dots)\right) v.$$

A bit of spectral theory

For $w(Y)$ any function defined for $Y \in \mathbb{R}$, we set the operator $\mathcal{L}w := -w'' - \tilde{r}(Y)w$.

Proposition 1

The eigenvalues of $\mathcal{L}$ are real and satisfy $\lambda_0 < \lambda_1 \leq \dots$
There exists a unique eigenfunction Γ_0 such that

$$\mathcal{L}\Gamma_0 = \lambda_0 \Gamma_0, \qquad \Gamma_0 > 0, \qquad \|\Gamma_0\|_\infty = 1.$$

For our choice of $r(x, y)$:

$$\lambda_0 = \sqrt{A(1+B^2)} - 1, \quad \Gamma_0(Y) = \exp\left(-\frac{1}{2}\sqrt{A(1+B^2)}\,Y^2\right), \quad Y \in \mathbb{R}.$$

Survival or extinction depends only on the sign of λ_0.

Survival and invasion if $\lambda_0 < 0$, extinction otherwise

$\lambda_0 \geq 0 \Leftrightarrow$ extinction [2].
$\lambda_0 < 0 \Leftrightarrow$ survival and invasion [1].

We look at the *total* population in (t, x), and its μ-level set with $\mu > 0$

$$N(t,x) := \int_{\mathbb{R}} n(t,x,y)dy, \qquad E_\mu^n(t) := \{x \in \mathbb{R} \mid N(t,x) = \mu\}.$$

Theorem 2: *Alfaro, Berestycki, Raoul [1]*

Assume $\lambda_0 < 0$ and $n_0 \not\equiv 0$ compactly supported. Then

$$\exists \beta > 0, \quad \forall \mu \in (0,\beta), \qquad E_\mu^n(t) \sim \omega^* t, \qquad \omega^* := 2\sqrt{\frac{-\lambda_0}{1+B^2}} > 0.$$

Invasion in the direction $y = Bx$

No propagation in the direction Y: $v(t, X, Y) \leq C_1\, e^{-C_2|Y|}$.

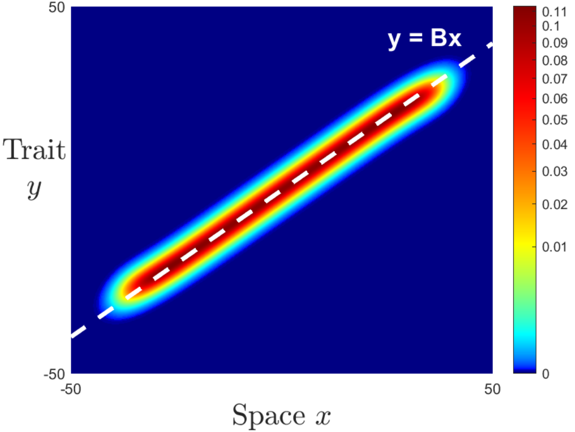


Figure: $n(t, \cdot, \cdot)$ for $t = 30s$, compactly supported n_0, $A = 0,02$ and $B = 0,8$.

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The main questions

$$\partial_t u - \partial_{xx} u = ru(1-u) \qquad \begin{cases} \text{Supp}\, u_0 \text{ compact} & \Longrightarrow E_\lambda(t) \sim c^* t \\ \text{heavy tail } u_0 & \Longrightarrow E_\lambda(t)/t \to +\infty \end{cases}$$

$$\partial_t n - \partial_{xx} n - \partial_{yy} n = \dots \qquad \begin{cases} \text{Supp}\, n_0 \text{ compact} & \Longrightarrow E_\mu^n(t) \sim \omega^* t \\ \text{"heavy tail" } n_0 & \Longrightarrow E_\mu^n(t)/t \to \textbf{???} \end{cases}$$

- Q1: condition on n_0 that leads to acceleration?
- Q2: bounds on $E_\mu^n(t)$ as in Theorem 1?

A "coarse" condition for acceleration

Proposition 2

Assume $\lambda_0 < 0$ *and* $v_0(X,Y) = n_0(x,y)$ *satisfies*

$$v_0(X,Y) \geq \underline{u}_0(X)\Gamma_0(Y),$$

with $\underline{u}_0$ front-like *displaying a* heavy tail*. Then there is acceleration:*

$$\exists \beta > 0, \quad \forall \mu \in (0,\beta), \quad E_\mu^n(t)/t \to +\infty.$$

Proof

Goal: construct a function $\underline{v}(t,X,Y)$ so that $v \geq \underline{v}$ for all (t,X,Y), and all the level sets of $\underline{v}$ are accelerating.

As a consequence, for levels $\mu < \beta = \|\underline{v}\|_\infty$, we have the result.

Let $0 < \varepsilon < -\lambda_0$ and $u(t,X)$ solve $\begin{cases} \partial_t u - \partial_{XX} u = (-\lambda_0 - \varepsilon) u(1-u), \\ u(0,X) = \underline{u}_0(X). \end{cases}$

Set $\underline{v}(t,X,Y) := \rho u(t,X)\Gamma_0(Y)$ with $\rho < 1$. Since $\underline{u}_0$ has a heavy tail, we have acceleration for u, thus for $\underline{v}$.

By assumption, $v(0,X,Y) > \underline{v}(0,X,Y)$. Assume by contradiction, that $v(t,\cdot,\cdot) \not> \underline{v}(t,\cdot,\cdot)$ for some $t > 0$, and define

$$t_0 = \min\left\{ t \geq 0 \mid \exists (X_0, Y_0) \in \mathbb{R}^2,\ v(t, X_0, Y_0) = \underline{v}(t, X_0, Y_0) \right\},\ t_0 > 0.$$

The function $\underline{v} - v$ reaches a local maximum at (t_0, X_0, Y_0), thus

$$\mathcal{D}[\underline{v} - v](t_0, X_0, Y_0) \geq 0, \qquad \mathcal{D} := \partial_t - \partial_{XX} - \partial_{YY} - \tilde{r}(Y).$$

We will get a contradiction by proving $\mathcal{D}[\underline{v} - v](t_0, X_0, Y_0) < 0$.

$$\begin{aligned}\mathcal{D}[\underline{v}] &= (\partial_t - \partial_{XX} - \partial_{YY} - \tilde{r}(Y))[\underline{v}] \\ &= \rho(\partial_t u - \partial_{XX} u)\Gamma_0 + \rho u \left(-\Gamma_0'' - \tilde{r}(Y)\Gamma_0\right) \\ &\leq \rho(-\lambda_0 - \varepsilon)u\Gamma_0 + \rho u(\lambda_0\Gamma_0) = -\varepsilon \underline{v}.\end{aligned}$$

Meanwhile, $\mathcal{D}[v]$ is equal to the integral term, and we get an upper bound thanks to a refinement of a Harnack inequality:

$$\begin{aligned}-\mathcal{D}[v](t_0, X_0, Y_0) &= v(t_0, X_0, Y_0) \int_{\mathbb{R}} (\dots) \\ &\leq v(t_0, X_0, Y_0) \left(Cv(t_0, X_0, Y_0) + \frac{\varepsilon}{3} \right).\end{aligned}$$

Selecting ρ small enough, there holds $\underline{v} = \rho u \Gamma_0 \leq \frac{\varepsilon}{3C}$, so that

$$\mathcal{D}[\underline{v} - v](t_0, X_0, Y_0) \leq \underline{v}(t_0, X_0, Y_0) \left(-\varepsilon + \frac{\varepsilon}{3} + \frac{\varepsilon}{3} \right) < 0. \quad \square$$

Good, but not good enough!

A little bit more spectral theory

Let $R > 0$. For $w(Y)$ a function defined for $Y \in [-R, R]$ and satisfying $w(\pm R) = 0$, we set the operator $\mathcal{L}^R w := -w'' - \tilde{r}(Y)w$.

Proposition 3

The eigenvalues of $\mathcal{L}^R$ are real and satisfy $\lambda_0^R < \lambda_1^R \leq \dots$
There exists a unique eigenfunction Γ_0^R such that

$$\begin{cases} \mathcal{L}^R \Gamma_0^R = \lambda_0^R \Gamma_0^R \\ \Gamma_0^R > 0 & \text{on } (-R, R), \\ \Gamma_0^R(\pm R) = 0 \\ \|\Gamma_0^R\|_\infty = 1. \end{cases}$$

Additionally, $\lambda_0^R > \lambda_0$ and $\lambda_0^R \to \lambda_0$ when $R \to +\infty$.

The "refined" condition for acceleration

In fact, we still have acceleration if $v_0(X, Y) \geq \underline{u}_0(X)\Gamma_0^R(Y)$ with $R > 0$ large enough so that $\lambda_0^R < 0$.

The proof is similar: just change $-\lambda_0$ to $-\lambda_0^R$. But we can do even better!

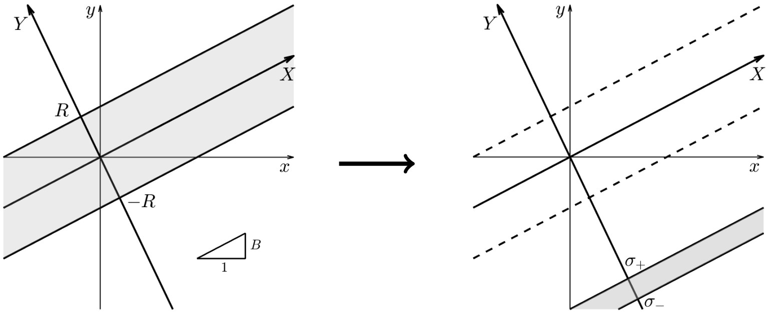

Figure: In grey, the domain where $v_0(X, Y) \geq \underline{u}_0(X)$ to obtain acceleration.

The "refined" condition for acceleration

Theorem 3: ***Peltier [7]***

Assume $\lambda_0 < 0$ and $v_0(X, Y) = n_0(x, y)$ satisfies

$$\exists \sigma_- < \sigma_+, \qquad v_0(X, Y) \geq \underline{u}_0(X) \mathbf{1}_{[\sigma_-, \sigma_+]}(Y)$$

with $\underline{u}_0$ front-like displaying a heavy tail. Then there is acceleration:

$$\exists \beta > 0, \quad \forall \mu \in (0, \beta), \quad E^n_\mu(t)/t \to +\infty.$$

To prove it, construct $\underline{\underline{v}}$ such that $\begin{cases} v(t, X, Y) \geq \underline{\underline{v}}(t, X, Y), \\ \underline{\underline{v}}(1, X, Y) \geq \rho u_0(X) \Gamma_0^R(Y). \end{cases}$

Location of $E^n_\mu(t)$ (1/2)

Definition 1

A function $q \in L^\infty(\mathbb{R})$ is said to satisfy condition (Q) if:

- *q is front-like* $(\liminf_{-\infty} q > 0, \quad q > 0, \quad \lim_{+\infty} q = 0)$,
- *q displays a heavy tail,*
- *$\exists \xi \in \mathbb{R}$ such that q is C^2 and decreasing in $[\xi, +\infty)$,*
- *$q''(x) = o(q(x))$ when $x \to +\infty$.*

Condition for the location of $E^n_\mu(t)$

$$\exists \sigma_- < \sigma_+, \qquad \underline{u}_0(X)\mathbf{1}_{[\sigma_-,\sigma_+]}(Y) \leq v_0(X,Y) \leq \overline{u}_0(X)\Gamma_0(Y), \quad \text{(LOC)}$$

where $\underline{u}_0$ and $\overline{u}_0$ satisfy (Q).

Location of $E_\mu^n(t)$ (2/2)

Theorem 4: *Peltier [7]*

Assume $\lambda_0 < 0$ and $v_0(X, Y) = n_0(x, y)$ satisfies (LOC).
Let $R > 0$ large enough such that $\lambda_0^R < 0$. Then:

$$\exists \beta > 0, \quad \forall \mu \in (0, \beta), \quad \forall \varepsilon \in (0, -\lambda_0^R), \quad \exists T \geq 0, \quad \forall t \geq T,$$

$$E_\mu^n(t) \subset \frac{1}{\sqrt{1+B^2}} \left[\min \underline{u}_0^{-1} \left(e^{-(-\lambda_0^R - \varepsilon)t} \right), \max \overline{u}_0^{-1} \left(e^{-(-\lambda_0 + \varepsilon)t} \right) \right].$$

Trade-off: if $R \to +\infty$, then $\lambda_0^R \searrow \lambda_0$, thus a more precise lower bound, but $\beta = \beta(R) \to 0$, therefore the levels localised are getting lower.

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Heavy tail along another direction

Initial heavy tail in the favorable direction $X \to +\infty \Rightarrow$ acceleration.
What if the heavy tail is in another direction, like $x \to +\infty$?

Theorem 5: *Peltier [7]*

Assume $\lambda_0 < 0$ and

$$\exists \sigma_- < \sigma_+, \qquad 0 \not\equiv n_0(x,y) \leq C\,\mathbf{1}_{[\sigma_-,\sigma_+]}(y).$$

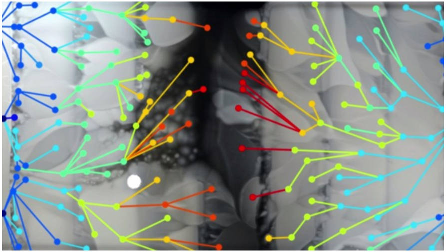
Then the asymptotic speed of propagation is the same as when n_0 is compactly supported: $E^n_\mu(t) \sim \omega^* t$.

Same for all directions $X' \neq X$.

Next steps

- Study the convergence towards a steady state. On numerical simulations, it seems that $v(t, X, Y) \to \text{Cst}\, \Gamma_0(Y)$ for all X.
- For more biological sense, change the mutation term $-\partial_{YY}$ to a convolution-type term $J * u - u$.
- Consider non-linear environmental gradients: $r(x, y) = 1 - A(y - \phi(x))^2$.

Thank you for your attention !



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