Non-cooperative Fisher–KPP systems: traveling waves and long-time behavior

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Introduction

A few models from mathematical biology

Diffusion equations and population dynamics

Two-dimensional diffusion equation (Fourier, 1822)

$$\partial_t n - d_x \partial_{xx} n - d_y \partial_{yy} n = 0$$

n is a pop. density diffusing in a 2D space of coordinates (x, y) (Brownian motion at the microscopic level). If d_x is a function of y, then the longitudinal diffusion depends on the latitude (e.g.: colder temperatures slow down individuals).

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With $y = \theta$ and $d_x(\theta) = \theta$

$$\partial_t n - \theta \partial_{xx} n - d_\theta \partial_{\theta\theta} n = 0$$

n is a pop. density which is diffusing in a 1D space of coordinate x and whose individuals are subjected to random mutations which affect their mobility and whose effect, at the macroscopic level, is a diffusion in phenotypical trait $\theta > 0$ at rate d_θ. At the microscopic level, the effect of the mutations is a Brownian jump in the phenotypical space: *local* mutations.

Logistic growth and population dynamics

Malthusian growth (Malthus, 1798)

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Logistic growth (Verhulst, 1838)

$$n'(t) = rn(t) - \frac{r}{K}n(t)^2 = rn(t)\left(1 - \frac{n(t)}{K}\right)$$

Incorporates a "friction" effect: at the microscopic level, when two individuals collide, one of them dies with a certain probability. If $n(0) > 0$, then $n(t) \to K$ as $t \to +\infty$: the parameter $K > 0$ is the carrying capacity.

Logistic growth with a phenotypical trait $\theta \in [\underline{\theta}, \overline{\theta}]$

$$\partial_t n(t,\theta) = rn(t,\theta) \left(1 - \frac{\int_{\underline{\theta}}^{\overline{\theta}} n\left(t,\theta'\right) \mathrm{d}\theta'}{K} \right)$$

$\int_{\underline{\theta}}^{\overline{\theta}} n\left(t,\theta'\right) \mathrm{d}\theta'$: total population at time t. When two individuals collide, one of them dies with a certain probability independent of their traits θ and θ': *non-local* competition.

Mutation–competition–diffusion model with local mutations and logistic growth

Continuous trait model:

Cane toads equation with non-local competition (Bénichou–Calvez–Meunier–Voituriez, 2012)

$$\begin{cases} \partial_t n - \theta\partial_{xx} n - \alpha\partial_{\theta\theta} n = n(t,x,\theta)\left(r - \int_{\underline{\theta}}^{\overline{\theta}} n(t,x,\theta')\,\mathrm{d}\theta'\right) \\ \partial_\theta n(t,x,\underline{\theta}) = \partial_\theta n\left(t,x,\overline{\theta}\right) = 0 \text{ for all } (t,x)\in\mathbb{R}^2 \end{cases}$$

n function of (t,x,θ), $\theta\in\left[\underline{\theta},\overline{\theta}\right]$ motility trait, α mutation rate, r growth rate and $\int_{\underline{\theta}}^{\overline{\theta}} n(t,x,\theta')\,\mathrm{d}\theta'$ total population present at (t,x).

Discrete trait model with N traits $(\theta_i)_{i\in[N]} = (\underline{\theta} + (i-1)\delta\theta)_{i\in[N]}$, $\delta\theta = \frac{\overline{\theta}-\underline{\theta}}{N-1}$, and N corresponding phenotypes $(u_i)_{i\in[N]}$:

$$\partial_t n - \theta\partial_{xx} n = \alpha\partial_{\theta\theta} n + rn - \left(\int_{\underline{\theta}}^{\overline{\theta}} n\left(t,x,\theta'\right) \mathrm{d}\theta'\right) n$$

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$$\partial_t \mathbf{u}$$

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$$\partial_t \mathbf{u} - \mathrm{diag}\boldsymbol{\theta}\partial_{xx}\mathbf{u} = \frac{\alpha}{\delta\theta^2}\mathbf{M}_{Lap}\mathbf{u}$$

with $\mathbf{M}_{Lap}$ the discrete Neumann Laplacian

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with $\mathbf{M}_{Lap}$ the discrete Neumann Laplacian and $\mathbf{1}_{N,1}$ the vector full of ones.

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L–V mutation-competition-diffusion system with step-wise mutations

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Mutation–competition–diffusion model with long-range mutations and logistic growth

Continuous trait model:

Doubly non-local cane toads equation (Arnold–Desvillettes–Prévost, 2012)

$$\partial_t n - d(\theta)\,\partial_{xx} n = r(\theta)\,n(t,x,\theta) + \int_{\underline{\theta}}^{\overline{\theta}} n(t,x,\theta')\,K(\theta,\theta')\,\mathrm{d}\theta' - n(t,x,\theta)\int_{\underline{\theta}}^{\overline{\theta}} n(t,x,\theta')\,C(\theta,\theta')\,\mathrm{d}\theta'.$$

Discrete trait model:

L–V mutation–competition–diffusion system with long-range mutations

$$\partial_t \mathbf{u} - \mathbf{D}\partial_{xx}\mathbf{u} = \mathbf{L}\mathbf{u} - (\mathbf{C}\mathbf{u}) \circ \mathbf{u},$$

with:

$$\mathbf{D} = \mathrm{diag}\left(d\left(\theta_i\right)\right)_{i\in[N]},$$

$$\mathbf{L} = \mathrm{diag}\left(r\left(\theta_i\right)\right)_{i\in[N]} + \delta\theta\left(K\left(\theta_i,\theta_j\right)\right)_{(i,j)\in[N]^2},$$

$$\mathbf{C} = \delta\theta\left(C\left(\theta_i,\theta_j\right)\right)_{(i,j)\in[N]^2},$$

and $\circ$ the Hadamard product.

An important remark on mutation–competition–diffusion systems

Alternative derivation (e.g., Dockery–Hutson–Mischaikow–Pernarowski, 1998)

Consider the standard Lotka–Volterra competition–diffusion system and add linear mutations.

Step-wise and long-range mutations are particular cases.

Transport equations and population dynamics

One-dimensional transport equation

$$\partial_t n + \partial_a n = 0$$

If the initial condition is $n_0(a)$, solution of the form $n(t,a) = n_0(a-t)$: transport at speed 1 of the initial condition.

n is a pop. density subjected to aging, a is the age variable.

E.g.: $n_0(a) = \mathbf{1}_{[0,1]}$ means that at $t = 0$ there are no individuals of age $a < 0$ or $a > 1$ whereas individuals of age $a \in [0,1]$ are uniformly distributed; at time t, there are no individuals of age $a < t$ or $a > t+1$ whereas individuals of age $a \in [t, t+1]$ are uniformly distributed.

With linear births and deaths and no immortal individuals

$$\begin{cases} \partial_t n + \partial_a n = -m(a)\, n \\ n(t,0) = \int_{A_m}^{A} n(t,a')\, K(a')\, \mathrm{d}a' \text{ for all } t > 0 \\ n(t,A) = 0 \text{ for all } t > 0 \end{cases}$$

$a \in [0, A]$, $A_m \geq 0$ maturation age, $A > A_m$ maximal age, m mortality rate, K birth rate.

Age-structured model with diffusion in space and overcrowding effect

Continuous age model:

Non-linear age-structured equation (Gurtin–MacCamy, 1977)

$$\begin{cases} \partial_t n + \partial_a n - d(a)\,\partial_{xx} n = -\left(m(a) + \int_0^A n(t,x,a')\,C(a,a')\,\mathrm{d}a'\right) n \\ n(t,x,0) = \int_{A_m}^A n(t,x,a')\,K(a')\,\mathrm{d}a' \text{ for all } (t,x)\in\mathbb{R}^2 \\ n(t,x,A) = 0 \text{ for all } (t,x)\in\mathbb{R}^2 \end{cases}$$

n function of (t,x,a), $a \in [0,A]$ age variable, $A_m \geq 0$ maturation age, $A > A_m$ maximal age, d diffusion rate, m mortality rate, C competition kernel and K birth rate.

Discrete age model:

Non-linear age-structured system

$$\partial_t \mathbf{u} - \mathbf{D}\partial_{xx}\mathbf{u} = \mathbf{L}\mathbf{u} - (\mathbf{C}\mathbf{u}) \circ \mathbf{u}$$

with

$$\mathbf{D} = \mathrm{diag}\left(d\left(a_i\right)\right)_{i\in[N]},$$

$$\mathbf{L} = \mathbf{L}_{mortality} + \mathbf{L}_{birth} + \mathbf{L}_{aging},$$

$$\mathbf{C} = \delta a\left(C\left(a_i, a_j\right)\right)_{(i,j)\in[N]^2}.$$

Detail of $\mathbf{L}$:

$$j_m = \min\left\{j \in [N] \mid a_j \geq A_m\right\},$$

$$\mathbf{L}_{mortality} = -\mathsf{diag}\left(m\left(a_i\right)_{i\in[N]}\right),$$

$$\mathbf{L}_{birth} = \delta a \begin{pmatrix} 0 & \dots & 0 & K\left(a_{j_m}\right) & \dots & K\left(a_N\right) \\ 0 & & & \dots & & 0 \\ \vdots & & & & & \vdots \\ 0 & & & \dots & & 0 \end{pmatrix},$$

$$\mathbf{L}_{aging} = \frac{1}{\delta a} \begin{pmatrix} 0 & 0 & \dots & \dots & 0 \\ 1 & -1 & \ddots & & \vdots \\ 0 & \ddots & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & 0 \\ 0 & \dots & 0 & 1 & -1 \end{pmatrix}.$$

Structural similarities of all these examples

Common factors

- Parabolic systems;

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- $\mathbf{C}$ positive.

General system

Non-cooperative KPP system

General system

$$\partial_t \mathbf{u} - \mathbf{D}\partial_{xx}\mathbf{u} = \mathbf{L}\mathbf{u} - \mathbf{C}\mathbf{u}\circ\mathbf{u}.$$

Unknown:

$$\mathbf{u} : \begin{array}{ccc} \mathbb{R}^2 & \to & \mathbb{R}^N \\ (t,x) & \mapsto & (u_i(t,x))_{i\in[N]} \end{array}.$$

Fixed parameters:
$\mathbf{D} = \operatorname{diag}\mathbf{d}$ with $\mathbf{d}$ positive, $\mathbf{L}$ essentially nonnegative and irreducible, $\mathbf{C}$ positive.
Stationary problem:

$$-\mathbf{D}\mathbf{u}'' = \mathbf{L}\mathbf{u} - \mathbf{C}\mathbf{u}\circ\mathbf{u}.$$

Nonnegativity, positivity, etc., of matrices are understood component-wise.

The crucial observation

Structure of the right-hand side

$\mathbf{Lu} - \mathbf{Cu} \circ \mathbf{u}$ is a form of multidimensional logistic growth!

Reminder: the (scalar) logistic growth is given by

$$ru - K^{-1}u^2.$$

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Literature

In homogeneous media:

- Barles–Evans–Souganidis, 1990 (viscosity approach);
- Elliott–Cornell, 2012 (numerics and conjectures for $N = 2$) (review: Cosner, 2014);
- Griette–Raoul, 2016 (steady states and traveling waves for $N = 2$, $d_1 = d_2$, weak mutations and a particular competitive regime; weak mutation limit);
- Moris–Börger–Crooks, 2017 (steady states, traveling waves and anomalous speeds for $N = 2$, $d_1 < d_2$, weak mutations and another particular competitive regime; weak mutation limit).

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In heterogeneous media:

- Dockery et al., 1998 (steady states for another particular competitive regime and in the weak mutation limit);
- Hei–Wu, 2005 (steady states for $N = 2$ and large mutations);
- Alfaro–Griette, 2016 (steady states and pulsating fronts in space-periodic media for $N = 2$ and $d_1 = d_2$).

The scalar KPP equation

Definition

The Fisher–KPP equation

Fisher, Kolmogorov–Petrovski–Piskunov (1937)

$$\partial_t u - d\Delta_x u = f(u) \text{ for all } (t,x) \in \mathbb{R} \times \mathbb{R}^n$$

with

- $f'(0) > 0$,
- $f'(0)u \geq f(u)$ for all $u \geq 0$,
- existence of $M > 0$ such that $f(u) < 0$ for all $u \geq M$.

Prototype: $f(u) = ru(1-u)$ with $r > 0$.

Well-known results

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Provided the initial condition u_0 satisfies $0 \leq u_0 \leq 1$, then so does the associated solution u for all $t > 0$.

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Stability of the steady states

$u = 0$ is unstable, $u = 1$ is stable.

In various senses, here focusing on *generalized principal eigenvalues* (Berestycki–Nirenberg–Varadhan, 1994).

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Persistence property

Asymptotically in time and locally uniformly in space, any nonnegative nonzero solution u converges to 1.

Well-known results: traveling waves

In order to fix the ideas, $x \in \mathbb{R}$.

Traveling waves

For any *speed* $c \geq c^\star = 2\sqrt{dr}$, there exists a unique, up to translation, *profile* $\phi_c \in \mathscr{C}^2(\mathbb{R})$ such that:

- $u : (t,x) \mapsto \phi_c(x-ct)$ is a positive entire solution;
- $\phi_c(-\infty) = 1$;
- $\phi_c(+\infty) = 0$.

ϕ_c is decreasing and satisfies:

$$-d\phi_c'' - c\phi_c' - r\phi_c(1-\phi_c) = 0 \text{ in } \mathbb{R}.$$

Furthermore, for all $c \in [0, c^\star)$, there exists no such profile.

$c^\star$ is the *minimal wave speed*.

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Strong connection with the linearized equation

$$-d\phi_c'' - c\phi_c' - r\phi_c = 0.$$

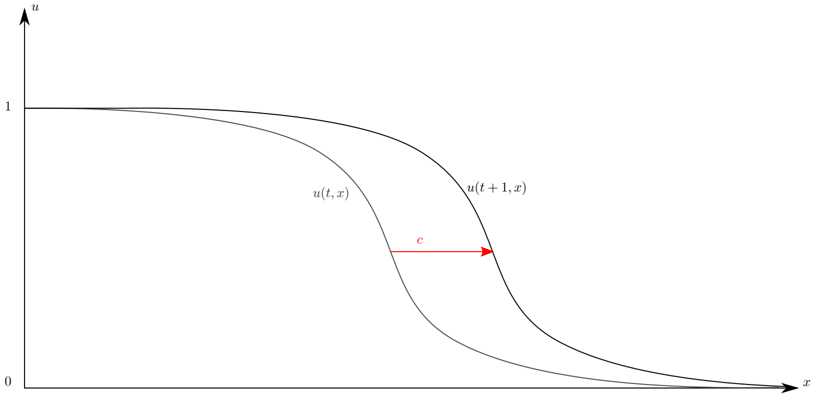

Figure: Traveling wave for the scalar KPP equation

Well-known results: spreading speed

Spreading speed

Let $x_0 \in \mathbb{R}$ and $v \in \mathscr{C}_b(\mathbb{R}, [0,1])$ be nonnegative nonzero.
Then $c^\star$ coincides with the spreading speed associated with the Cauchy problem with the "front-like initial condition" $u_0(x) = H(x_0 - x)v(x)$.

In the following sense:

$$\lim_{t\to+\infty} \sup_{x\in(y,+\infty)} u\left(t, x+ct\right) = 0 \text{ for all } c \in \left(c^\star, +\infty\right) \text{ and all } y \in \mathbb{R},$$

$$\lim_{t\to+\infty} \inf_{x\in[-R,R]} u\left(t, x+ct\right) = 1 \text{ for all } c \in \left[0, c^\star\right) \text{ and all } R > 0.$$

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Remark

Much more precise results exist (convergence to the critical traveling wave, Bramson shift, etc.).

The non-cooperative KPP system

My results (on arXiv, accepted for publication in Nonlinearity)

Strong positivity

Theorem

For all nonnegative classical solutions $\mathbf{u}$ of the Cauchy problem, if $x \mapsto \mathbf{u}(0, x)$ is nonnegative nonzero, then $\mathbf{u}$ is positive in $(0, +\infty) \times \mathbb{R}$.

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For all nonnegative classical solutions $\mathbf{u}$ of the Cauchy problem, if $x \mapsto \mathbf{u}(0,x)$ is nonnegative nonzero, then $\mathbf{u}$ is positive in $(0,+\infty)\times\mathbb{R}$. Consequently, all stationary nonnegative nonzero classical solutions are positive.

Absorbing set and upper estimates

Theorem

There exists a positive and continuous function $\mathbf{g}$, component-wise nondecreasing, such that all nonnegative classical solutions $\mathbf{u}$ of the Cauchy problem satisfy

$$\mathbf{u}(t,x) \leq \left(g_i\left(\sup_{x\in\mathbb{R}} u_i(0,x)\right)\right)_{i\in[N]} \quad \text{for all } (t,x)\in[0,+\infty)\times\mathbb{R}$$

and furthermore, if $x\mapsto \mathbf{u}(0,x)$ is bounded, then

$$\left(\limsup_{t\to+\infty}\sup_{x\in\mathbb{R}} u_i(t,x)\right)_{i\in[N]} \leq \mathbf{g}(0).$$

Absorbing set and upper estimates

Theorem

There exists a positive and continuous function $\mathbf{g}$, component-wise nondecreasing, such that all nonnegative classical solutions $\mathbf{u}$ of the Cauchy problem satisfy

$$\mathbf{u}(t,x) \leq \left(g_i \left(\sup_{x\in\mathbb{R}} u_i(0,x) \right) \right)_{i\in[N]} \quad \text{for all } (t,x) \in [0,+\infty) \times \mathbb{R}$$

and furthermore, if $x \mapsto \mathbf{u}(0,x)$ is bounded, then

$$\left(\limsup_{t\to+\infty} \sup_{x\in\mathbb{R}} u_i(t,x) \right)_{i\in[N]} \leq \mathbf{g}(0).$$

Consequently, all stationary bounded nonnegative classical solutions $\mathbf{u}$ satisfy

$$\mathbf{u} \leq \mathbf{g}(0).$$

Persistence or extinction dichotomy

Theorem

1. Assume $\lambda_{PF}(\mathbf{L}) \leq 0$. Then all bounded nonnegative classical solutions of the Cauchy problem converge asymptotically in time and uniformly in space to $\mathbf{0}$. If $\lambda_{PF}(\mathbf{L}) < 0$, the convergence is exponential.

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2. Conversely, assume $\lambda_{PF}(\mathbf{L}) > 0$. Then there exists $\nu > 0$ such that all bounded positive classical solutions $\mathbf{u}$ of the Cauchy problem satisfy, for all bounded intervals $I \subset \mathbb{R}$,

$$\left(\liminf_{t\to+\infty} \inf_{x\in I} u_i(t,x)\right)_{i\in[N]} \geq \nu \mathbf{1}_{N,1}.$$

   Consequently, all stationary bounded nonnegative classical solutions are valued in

$$\prod_{i=1}^{N} [\nu, g_i(0)].$$

Existence of steady states

Theorem

Assume $\lambda_{PF}(\mathbf{L}) > 0$. Then there exists a constant positive solution.

Traveling waves

Definition

A *traveling wave solution* is a profile–speed pair $(\mathbf{p}, c) \in \mathscr{C}^2\left(\mathbb{R}, \mathbb{R}^N\right) \times [0, +\infty)$ which satisfies:

1. $\mathbf{u} : (t, x) \mapsto \mathbf{p}\,(x - ct)$ is a bounded positive classical entire solution;
2. $\left(\liminf\limits_{\xi \to -\infty} p_i\,(\xi)\right)_{i \in [N]}$ is positive;
3. $\lim\limits_{\xi \to +\infty} \mathbf{p}\,(\xi) = \mathbf{0}$.

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The traveling wave satisfies:

$$-\mathbf{D}\mathbf{p}'' - c\mathbf{p}' = \mathbf{L}\mathbf{p} - \mathbf{C}\mathbf{p} \circ \mathbf{p} \text{ in } \mathbb{R}.$$

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2. All profiles $\mathbf{p}$ satisfy

$$\mathbf{p} \leq \mathbf{g}\left(0\right) \text{ and } \left(\liminf_{\xi \to -\infty} p_i\left(\xi\right)\right)_{i \in [N]} \geq \nu \mathbf{1}_{N,1}.$$

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3. All profiles are component-wise decreasing in a neighborhood of $+\infty$.

Furthermore,

$$c^\star = \min_{\mu>0} \frac{\lambda_{PF}\left(\mu^2\mathbf{D}+\mathbf{L}\right)}{\mu}$$

and this minimum is uniquely attained.

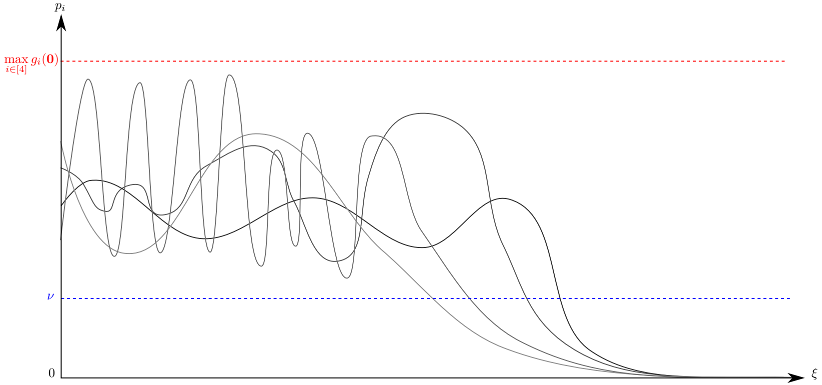

Figure: Profile of traveling wave for the KPP system $(N = 4)$

Spreading speed

Theorem

Assume $\lambda_{PF}(\mathbf{L}) > 0$.
Let $x_0 \in \mathbb{R}$ and $v \in \mathscr{C}_b\left(\mathbb{R}, \mathbb{R}^N\right)$ be nonnegative nonzero.
Then $c^\star$ coincides with the spreading speed associated with the Cauchy problem with the "front-like initial condition" $u_0(x) = H(x_0 - x)v(x)$.

In the following sense:

$$\left(\lim_{t\to+\infty} \sup_{x\in(y,+\infty)} u_i(t, x+ct)\right)_{i\in[N]} = \mathbf{0} \text{ for all } c \in (c^\star, +\infty) \text{ and } y \in \mathbb{R},$$

$$\left(\liminf_{t\to+\infty} \inf_{x\in[-R,R]} u_i(t, x+ct)\right)_{i\in[N]} \text{ is positive for all } c \in [0, c^\star) \text{ and } R > 0.$$

What about the proofs?

Main difficulty: non-cooperativity (lack of maximum principle).

- Positivity and a priori estimates are obtained standardly.
- Steady states are constructed with an easy fixed point argument.
- The extinction property is obtained by comparison with the linearized system. The persistence property has an interesting proof using both a comparison with another linear system and a Harnack inequality, due to Foldes–Polacik (2009), for linear weakly and fully coupled parabolic systems.
- Traveling waves for $c \geq c^\star$ are constructed with a refined super- and sub-solution method, due to Berestycki–Nadin–Perthame–Ryzhik (2009). The linearization of the system at the edge of the front yields the minimality of $c^\star$ and the monotonicity.
- Spreading properties are obtained by comparison with the linearized system and by repeating the persistence proof after a change of variables.

Open questions and perspectives

- The very big, very bad problem: the wake of the front. No hope for a general result. Results established in very particular cases:
  - weak selection: sufficiently close to $\mathbf{D} = \mathbf{I}$, $\mathbf{Cu} = (\mathbf{b}^T\mathbf{u})\mathbf{1}_{N,1}$;
  - two-component system with weak mutations;
- Heterogeneous spacetime.
- Continuous limit $N \to +\infty$ (requires entirely new estimates).
- Application to a model for the co-evolution of altruism and dispersal.

The end

Thank you for your attention!

Figure: A cane toad