Infinite-dimensional reaction-diffusion equations: modeling and analysis

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We present results obtained in collaboration with

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- √ S. Cuadrado (Barcelona)
- √ R. Ferrières (ENS Ulm)
- √ P.-E. Jabin (Nice)
- √ S. Mischler (Paris 9)
- √ C. Prévost (Orléans)
- √ G. Raoul (Cambridge)

Structured populations with respect to a quantitative trait

Quantitative trait: y belonging to an interval of $\mathbb{R}$.

Unknown: number density $f(t, y) \geq 0$ of individuals having the trait y.

That is: $f(t, y)\,dy$ is the number of individuals with trait in $[y, y + dy]$,

Example of evolution of the population

Assumptions: Evolution based on the processes of births and deaths including selection and competition/cooperation. Birth and death are local with respect to the trait, except for the term of (logistic) competition.

$$\frac{\partial f}{\partial t}(t,y) = \left(a(y) - \int b(y,y')\, f(t,y')\, dy' \right) f(t,y).$$

Typical assumption for competition: b is nonnegative and biggest when $y \sim y'$.

Natural question: what is the behavior of this equation when $t \longrightarrow +\infty$ [what are the stable equilibria]?

Steady solutions to linear/quadratic equations

A function of the form

$$f(y) = \sum_{j=1}^{N} \rho_j \, \delta_{y_j}(y)$$

(where $\rho_1 > 0, ..\rho_N > 0$) is a steady solution of eq.

$$\frac{\partial f}{\partial t}(t,y) = \left(a(y) - \int b(y,y')\, f(t,y')\, dy' \right) f(t,y)$$

if and only if

$$a(y_i) = \sum_{j=1}^{N} \rho_j \, b(y_i, y_j). \qquad i = 1, .., N.$$

Linear stability of the steady solutions to linear/quadratic equations, link with adaptive dynamics

Starting from a perturbation of the function of the form

$$f(y) = \varepsilon\, \delta_s(y) + \sum_{j=1}^{N} \rho_j\, \delta_{y_j}(y)$$

with $\varepsilon > 0$ and $s \neq y_1, .., y_N$, the linear stability analysis (that is, when $O(\varepsilon^2)$ is neglected) leads to the “global” condition of linear stability :

$$a(s) < \sum_{j=1}^{N} \rho_j\, b(s, y_j), \qquad s \neq y_1, .., y_N.$$

Linear stability of the steady solutions to linear/quadratic equations, corresponding local condition

$$a(y_i) = \sum_{j=1}^{N} \rho_j \, b(y_i, y_j). \qquad i = 1, .., N.$$

$$a'(y_i) = \sum_{j=1}^{N} \rho_j \, \frac{\partial b}{\partial 1}(y_i, y_j), \qquad i = 1, .., N,$$

$$a''(y_i) \leq \sum_{j=1}^{N} \rho_j \, \frac{\partial^2 b}{\partial 1^2}(y_i, y_j), \qquad i = 1, .., N.$$

An example

$$a(y) = A - y^2, \qquad b(y,z) = \frac{1}{1+(y-z)^2}.$$

Case $N = 1$
By symmetry:

$$y_1 = 0, \qquad \rho_1 = \frac{a(0)}{b(0,0)} = A.$$

Moreover:

$$a''(y_1) - \rho_1 \frac{\partial^2 b}{\partial 1^2}(y_1, y_1) = 2\,(A-1),$$

so that $f_1(y) = A\,\delta_{y=0}$ is linearly stable [for local (and in fact global) perturbations which are Dirac masses] if and only if $0 \le A \le 1$.

An example (2)

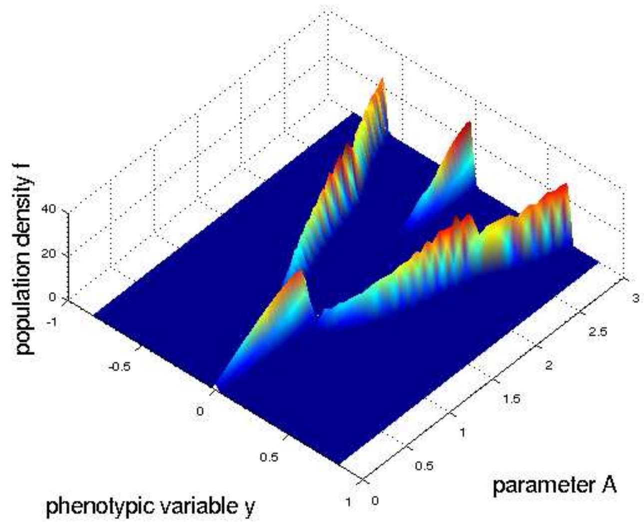
Case $N = 2$
By symmetry $y_1 = -y_2$, $\rho_1 = \rho_2$; then

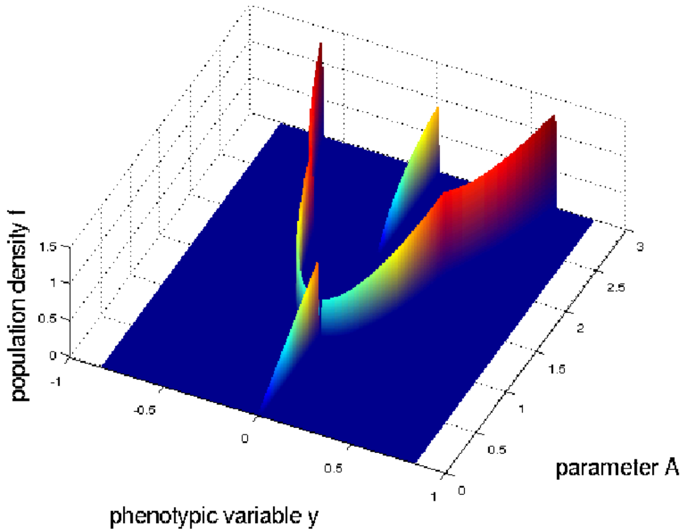
$$y_1 = \frac{1}{4}\sqrt{-7 + \sqrt{17 + 32\,A}}, \qquad \rho_1 = \frac{13 + 16\,A - 3\sqrt{17 + 32\,A}}{16}.$$

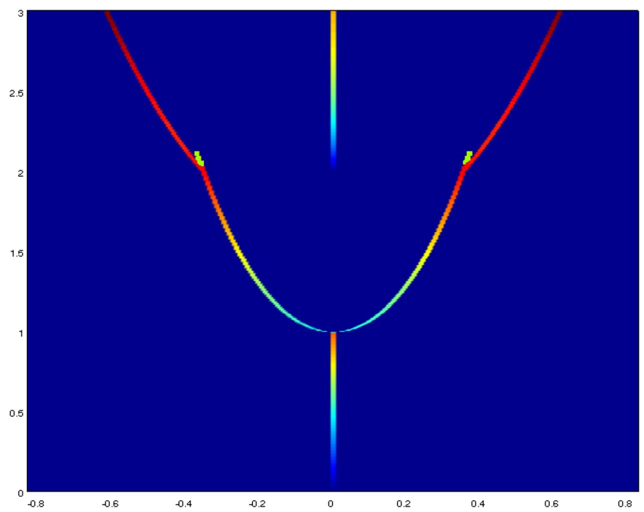
The state $f_2(y) = \rho_1\,(\delta_{y=y_1} + \delta_{y=-y_1})$ is linearly stable with respect to local perturbations if $A \in [1, \frac{13+\sqrt{17}}{8} \sim 2.13]$ and linearly stable with respect to global perturbations if $A \in [1, 2]$.

Case $N = 3$
A steady state of the form $f(y) = \rho_1\,\delta_{y=y_1} + \rho_2\,\delta_{y=0} + \rho_1\,\delta_{y=-y_1}$ is linearly stable with respect to global perturbations when $A \in [2, 3]$.

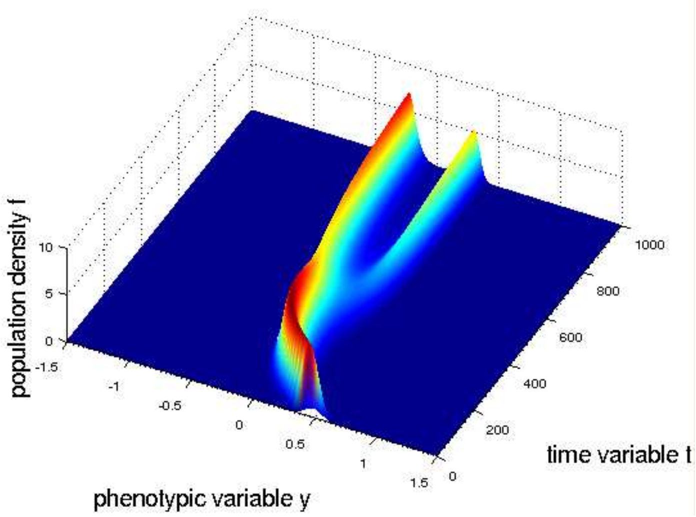
Figures (f w.r.t. y and the parameter)

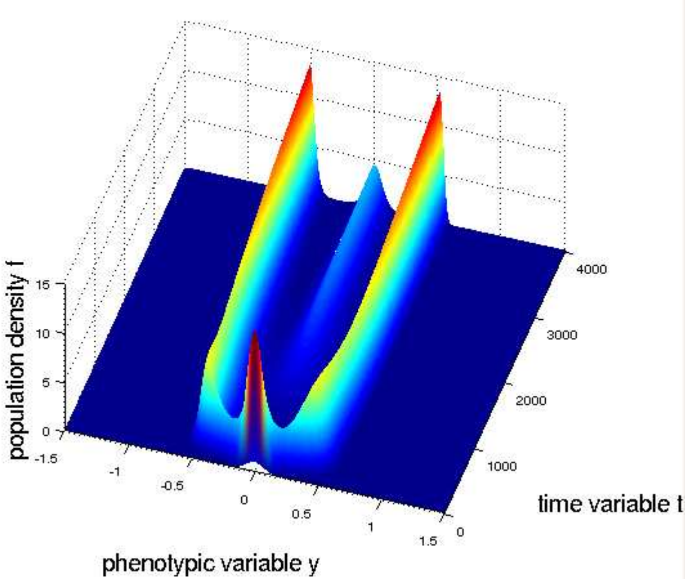






Figures (f w.r.t. y and time)





Large time behavior for linear/quadratic equations

Equation:

$$\partial_t f(t,y) = s[f(t,\cdot)](y)\, f(t,y),$$

with

$$s[f](y) = a(y) - \int b(y,y')\, f(y')\, dy'.$$

Rescaling:

$$\partial_t f_\varepsilon(t,y) = \frac{1}{\varepsilon}\, s[f_\varepsilon(t,\cdot)](y)\, f_\varepsilon(t,y).$$

Definition:

$$R_\varepsilon(t,y) := \int_0^t s[f_\varepsilon(\sigma,.)](y)\, d\sigma$$

General result for the large time behavior

Theorem[LD, P.-E. Jabin, S. Mischler, G. Raoul]: We assume that $a \in W^{1,\infty}(Y)$, $\mathcal{O} := \{y; a(y) > 0\} \neq \emptyset$, $b \in W^{1,\infty}(Y \times Y)$, $\inf_{y,y' \in Y} b(y, y') > 0$. Then if f_ε is the unique solution to the rescaled equation with $f_\varepsilon(0, \cdot) = f_{in}$, one can find $f \in L^\infty(]0, T[, M^1(Y))$ such that (up to a subsequence)

$$f_\varepsilon \rightharpoonup f \quad L^\infty(w*]0, T[; \sigma(M^1, C_b)(Y))$$

and

$$R_\varepsilon \to R \quad \text{uniformly in} \quad [0, T] \times \overline{Y},$$

where

$$R_\varepsilon(t, y) := \int_0^t s_\varepsilon[f(\sigma, .)](y)\, d\sigma, \qquad R(t, y) := \int_0^t s[f(\sigma, .)](y)\, d\sigma$$

and

$$\forall\, t \in [0, T] \qquad \max_{y \in \overline{Y}} R(t, y) = 0.$$

$$Supp\,(f(t, \cdot)) \neq \emptyset, \quad Supp\,(f(t, \cdot)) \subset \{R(t, \cdot) = 0\} \quad (\text{for a.e. } t \in [0, T]).$$

Example

$$s[f](y) = a(y) - \int_Y b(y-y')\, f(y')\, dy'$$

where

i) $a \in C^1(Y)$ takes its unique maximum at point 0, and for some constants $A, C > 0$,

$$\forall y \in Y, \qquad a(y) \leq C, \qquad |a'(y)| \geq A\,|y|$$

ii) $b \in C^1([-2,2])$ takes its unique maximum at point 0, and for some constants $D, E > 0$,

$$\forall y \in Y, \qquad b(y) \geq D, \qquad |b'(y)| \leq E\,|y|.$$

iii) $2\,C\,E < A\,D$.

Then, if $\frac{C}{D} \geq f_{in} > 0$ a.e., the measure f given by the theorem is

$$f(t, y) = \frac{a(0)}{b(0)} \, \delta_0(y).$$

As a consequence there is global nonlinear stability of this state.

Local nonlinear stability of evolutionary attractors (1)

We still consider

$$s[f] = a(y) - \int_Y b(y-y')\, f(y')\, dy'.$$

We define an Evolutionary Attractor as a linear combination of Dirac masses

$$\bar{f} = \sum_{j=1}^{N} \bar{\rho}_j \delta_{\bar{x}_j}$$

such that

i)

$$\forall i, \quad s[\bar{f}](x_i) = 0, \quad \partial_x s[\bar{f}](x_i) = 0, \quad \partial^2_{xx} s[\bar{f}](x_i) < 0,$$

Local nonlinear stability of evolutionary attractors (2)

ii)

$$\text{diag}\left(\left(\frac{1}{-\partial_{xx}^2 s[\sum_{j=1}^n \bar\rho_j \delta_{\bar x_j}]}(\bar x_i)\right)_i\right) DG((\bar x_i)_i) > 0,$$

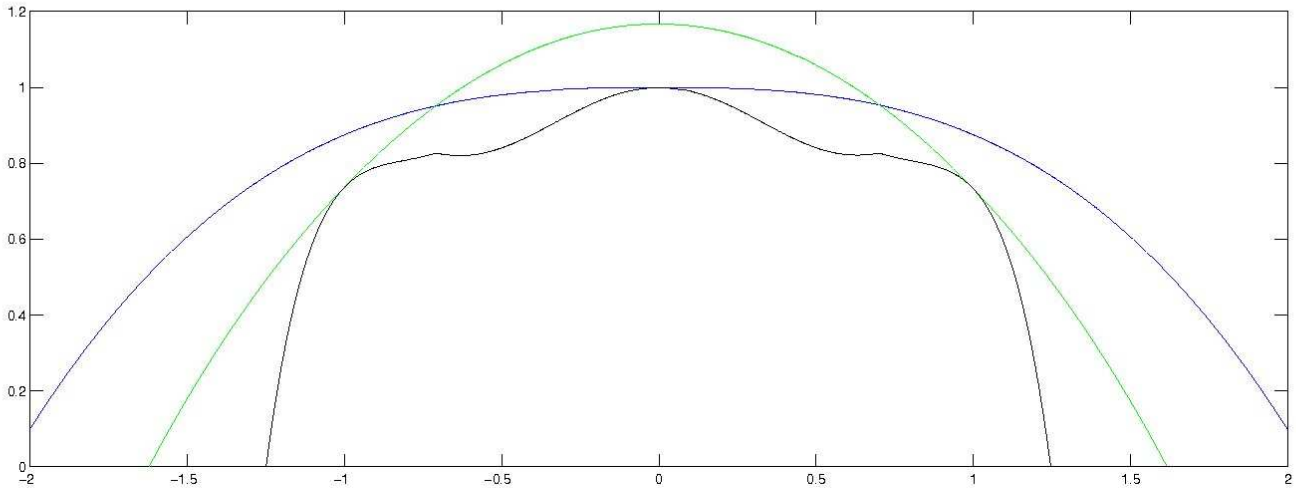
where DG is the Jacobian matrix of the application

$$G(x_1, x_2, .., x_N) = \left(\partial_x s[\sum_{j=1}^N \bar\rho_j \delta_{\bar x_j}](x_i)\right)_{i=1,\dots,n}.$$

Theorem (G. Raoul): If $\bar f$ is an Evolutionary Attractor, $f_{in} \in L^1(\mathbb{R})$ is close to $\bar f$ in $M^1(X)$ and $supp\, f_{in} = \cup_i B(\bar x_i, \lambda)$ for $\lambda > 0$ small enough, then the asymptotic limit f of f_ε is $\bar f$.

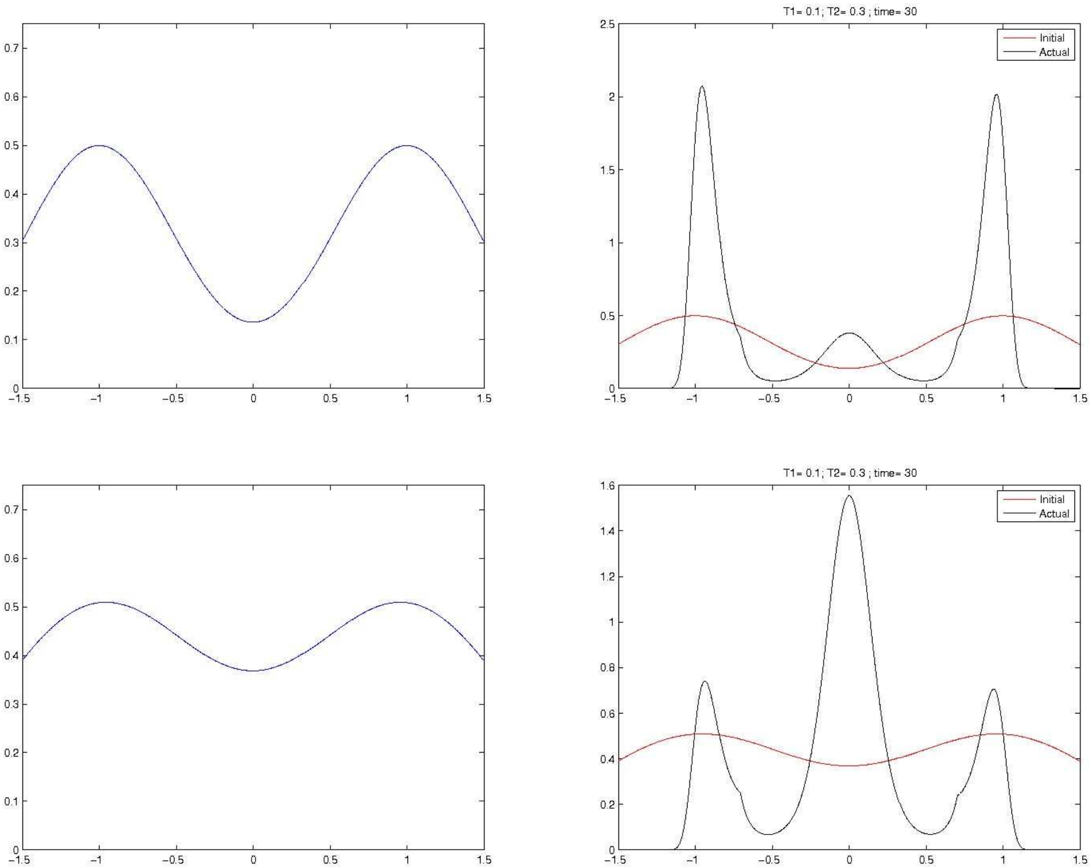
Case of local but non global nonlinear stability

$$s_{g(t,\cdot)}(x) = a(x) - \int_{\mathbb{R}} b(x-y)g(t,y)\,dy$$



a in black, b in blue, and $\frac{2}{3}\left(b(\cdot-1)+b(\cdot+1)\right)$ in green

Local but non global nonlinear stability: Numerical simulation



Continuous stable steady states (1)

Example:

$$a(y) = \frac{1}{\sqrt{2\pi(T_1+T_2)}} e^{-\frac{y^2}{2(T_1+T_2)}}, \quad b(y,y') = \frac{1}{\sqrt{2\pi T_1}} e^{-\frac{(y-y')^2}{2T_1}},$$

where $T_1,\, T_2 > 0$.
Steady state

$$\bar{f}(y) = \frac{1}{\sqrt{2\pi T_2}}\, e^{-\frac{y^2}{2T_2}}.$$

Proposition [P.-E. Jabin, G. Raoul]: This steady state is globally stable (for initial data strictly positive), and structurally stable in a weak norm.

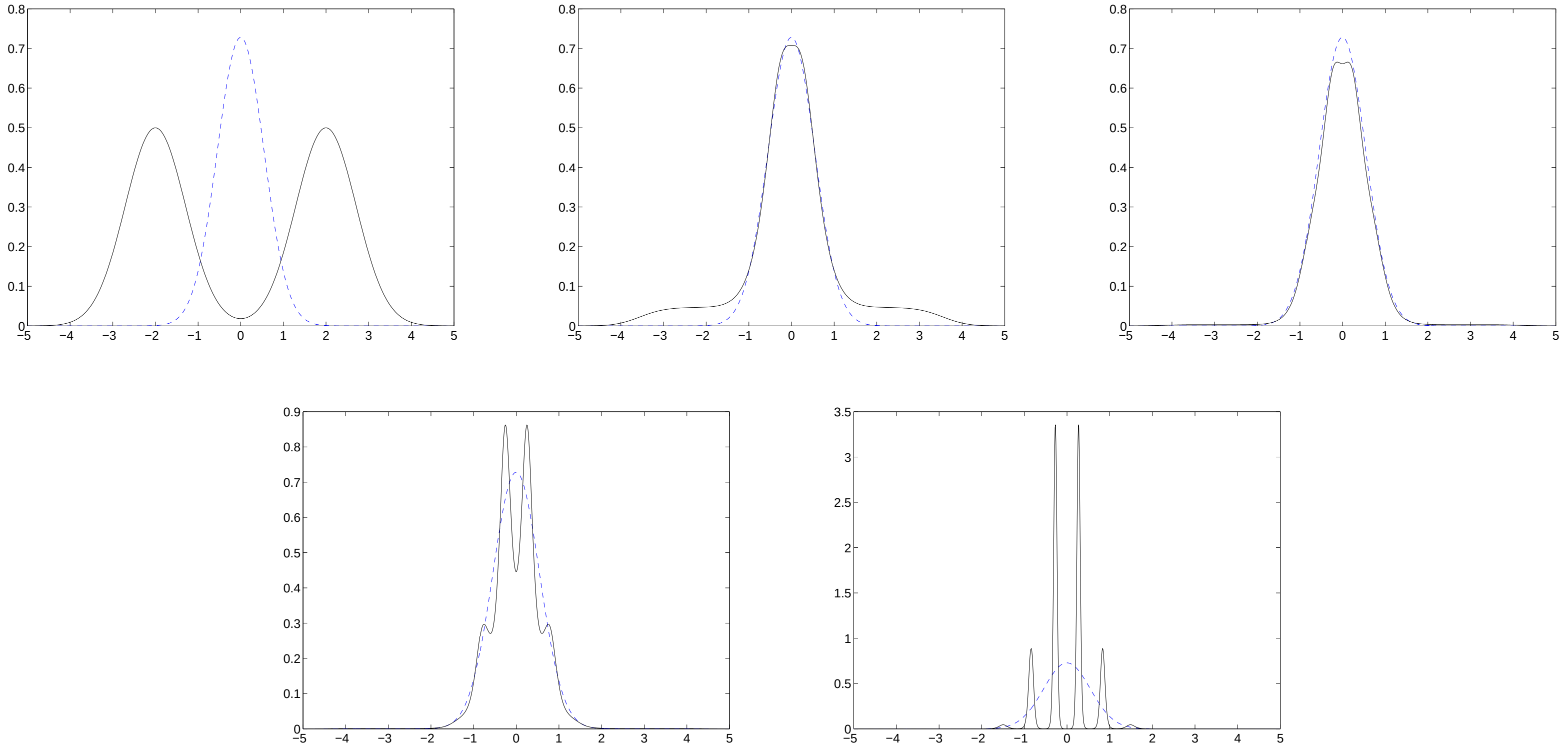
It is a particular case of a general theorem which uses a Lyapounov function in the case when b is a convolution kernel with nonnegative Fourier transform.

A case studied by Genieys, Volpert and Auger with a "non positive everywhere" Fourier transform of b, shows that $\bar{f}(y) := 1$ is unstable for $a(y) := 1$.

Continuous stable steady states (2)

There is a negative result for structural stability "in strong norm" by Gyllenberg and Meszena: When a and b are analytic, they show that if a solution $\bar{f}$ exists such that $Supp(\bar{f})$ has an accumulation point, then for arbitrary small perturbations of a and b, it does not admit any steady solution $\tilde{f}$ such that $Supp(\tilde{f})$ has an accumulation point.

Perturbations of the parameters of a Gaussian steady state: numerical simulation



Simulation for $T_1 = 0.1,\ T_2 = 0.3$, a Gaussian and $b(y, y_1) := \frac{1}{\sqrt{2\pi T_1}} e^{-\frac{(y-y_1)^{2.2}}{2T_1}}$,
at times $t = 0,\ 20,\ 300,\ 1\,000,\ 2\,000$.

Presence of a small number of large mutations

We consider the equation of selection/competition/mutation:

$$\Big((1-\varepsilon)\, b(y) - d_0(y)\Big)\, f^{\varepsilon}(y) - \Big(\int_X d(y,y')\, f^{\varepsilon}(y')\, dy'\Big)\, f^{\varepsilon}(y) + \varepsilon \int_X m(x,y) f^{\varepsilon}(y) = 0.$$

Assumption: b, d_0, d smooth, $b'(0) = d_0'(0) = 0$, and for some $1 > \bar{\varepsilon} > 0$,

$$\max_{x\in X} \max\big(b''(x), (1-\bar{\varepsilon})b''(x)\big) - \min_{x\in X} d_0''(x)$$

$$+ \frac{\max(b - d_0) + \bar{\varepsilon} \max_{y\in X} \|m(\cdot, y)\|_{L^1(X)}}{\min d} \|\partial_{11}^2 d\|_{\infty} \leq -\delta < 0.$$

$$\forall x \in X, \quad \partial_1 d(x,x) = 0.$$

$$m \geq 0,\ \min_{X\times X} m > 0,\ m \in C^1(X\times X) \cap L^{\infty}(X\times X).$$

Theorem (A. Calsina, S. Cuadrado, LD, G. Raoul): For $\varepsilon \in (0, \bar{\varepsilon})$ small enough, any solution f^ε of the equation writes (for some $\bar{x}^\varepsilon = O(\varepsilon^{-1/3})$)

$$\varepsilon f^\varepsilon(\varepsilon(\bar{x}^\varepsilon + x)) =$$

$$\frac{m(0,0)\frac{a_0(0)}{d(0,0)} + O(\sqrt{\varepsilon}) + O(\varepsilon x)}{\frac{2(m(0,0)\pi)^2}{-[a_0''(0) - \frac{a_0(0)}{d(0,0)}\partial_{11}^2 d(0,0)]} + O(\sqrt{\varepsilon}) + \frac{1}{2}\left(-[a_0''(0) - \frac{a_0(0)}{d(0,0)}\partial_{11}^2 d(0,0)] + O(\sqrt{\varepsilon}) + O(\varepsilon x)\right) x^2}$$

Adding the space variable: abstract of a paper about toads

Invasion and the evolution of speed in toads Nature 439, 803 (16 February 2006)

Benjamin L. Phillips, Gregory P. Brown, Jonathan K. Webb, Richard Shine

Cane toads (Bufo marinus) are large anurans (weighing up to 2 kg) that were introduced to Australia 70 years ago to control insect pests in sugar-cane fields. But the result has been disastrous because the toads are toxic and highly invasive.

Here we show that the annual rate of progress of the toad invasion front has increased about fivefold since the toads first arrived; we find that toads with longer legs can not only move faster and are the first to arrive in new areas, but also that those at the front have longer legs than toads in older (long-established) populations.

Over many generations, rates of invasion will be accelerated owing to rapid adaptive change in the invader, with continual ’spatial selection’ at the expanding front favouring traits that increase the toads’ dispersal.

Phenomena to take into account

- Migration (diffusion in the x variable)

- Selection (exponential growth rate depending upon y)

- Competition (logistic correction)

- Mutation (linear kernel in y variable)

Modeling by PDE

Equation satisfied by $f := f(t,x,y)$:

$$\partial_t f(t,x,y) - y\,\Delta_x f(t,x,y) = f(t,x,y)\left[r(y) - \int_{y'\in\mathbb{R}} C(y,y')\,f(t,x,y')\,dy'\right]$$

$$+ \int_{y'\in\mathbb{R}} m(y,y')\,f(t,x,y')\,dy'.$$

Formal analogy with coagulation/fragmentation/diffusion equations:

$$\partial_t f(t,x,y) - \nu(y)\,\Delta_x f(t,x,y) = -a(y)\,f(t,x,y) + \int_y^\infty a(y')\,q(y,y')\,f(t,x,y')\,dy'$$

$$-\int_0^\infty b(y,y')\,f(t,x,y')dy'\,f(t,x,y) + \frac{1}{2}\int_0^y b(y',y-y')\,f(t,x,y')\,f(t,x,y-y')\,dy'.$$

Those equations can be called “*Infinite dimensional (continuous) reaction-diffusion systems*”

Here, we take $x \in [0, L]$ and $y \in \mathbb{R}$;

$$r(y) = cst_1 - cst_2\, y,$$

$$m(y, y') = cst_3\, \exp(-cst_4\, (y - y')^2),$$

$$C(y, y') = \frac{cst_5}{1 + cst_6\, (y - y')^2}.$$

We add Neumann boundary conditions

$$\forall y \in \mathbb{R}, \qquad \nabla_x f(0, y) = \nabla_x f(L, y) = 0.$$

Cf. LD; R. Ferrières; C.Prevost

Numerical analysis and simulations

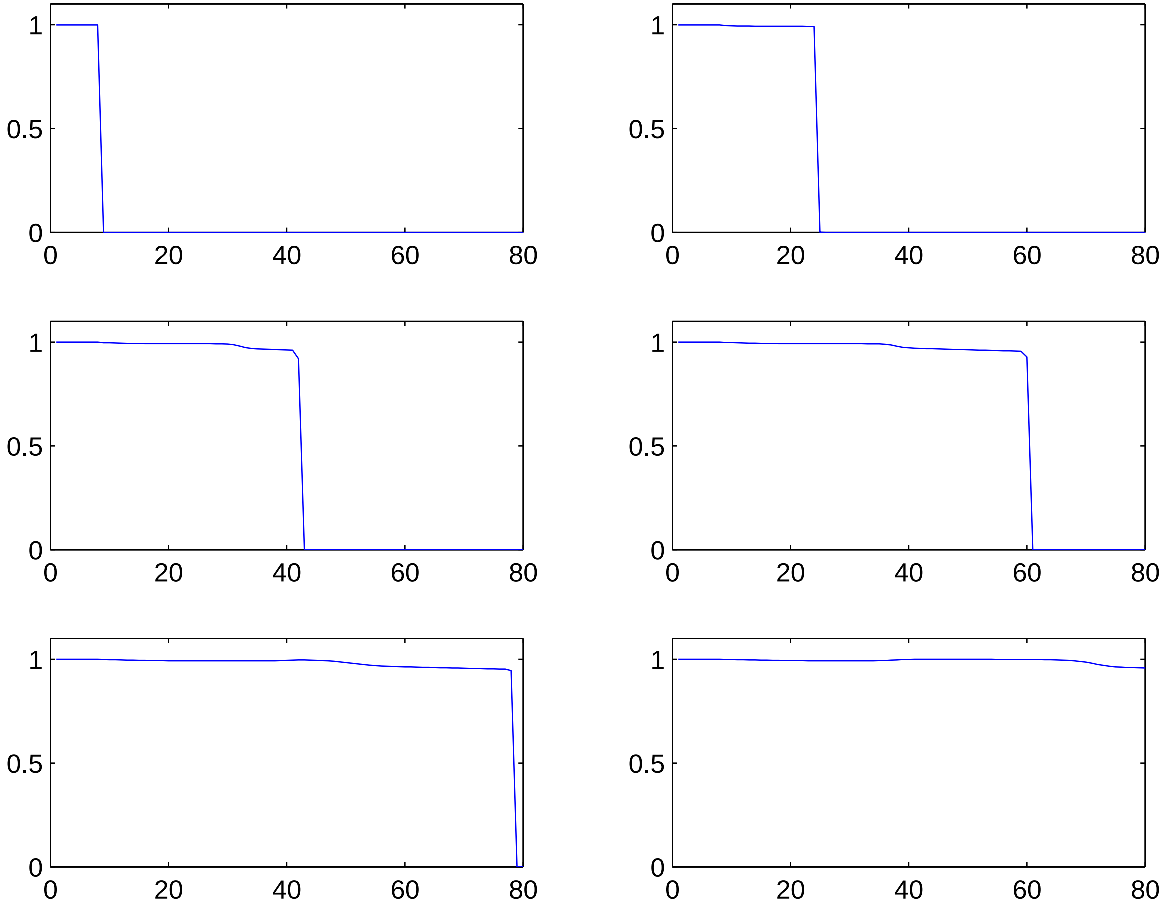
Computation thanks to an explicit finite difference scheme ($1D$ in x and $1D$ in y).

- Necessity to satisfy various CFL conditions

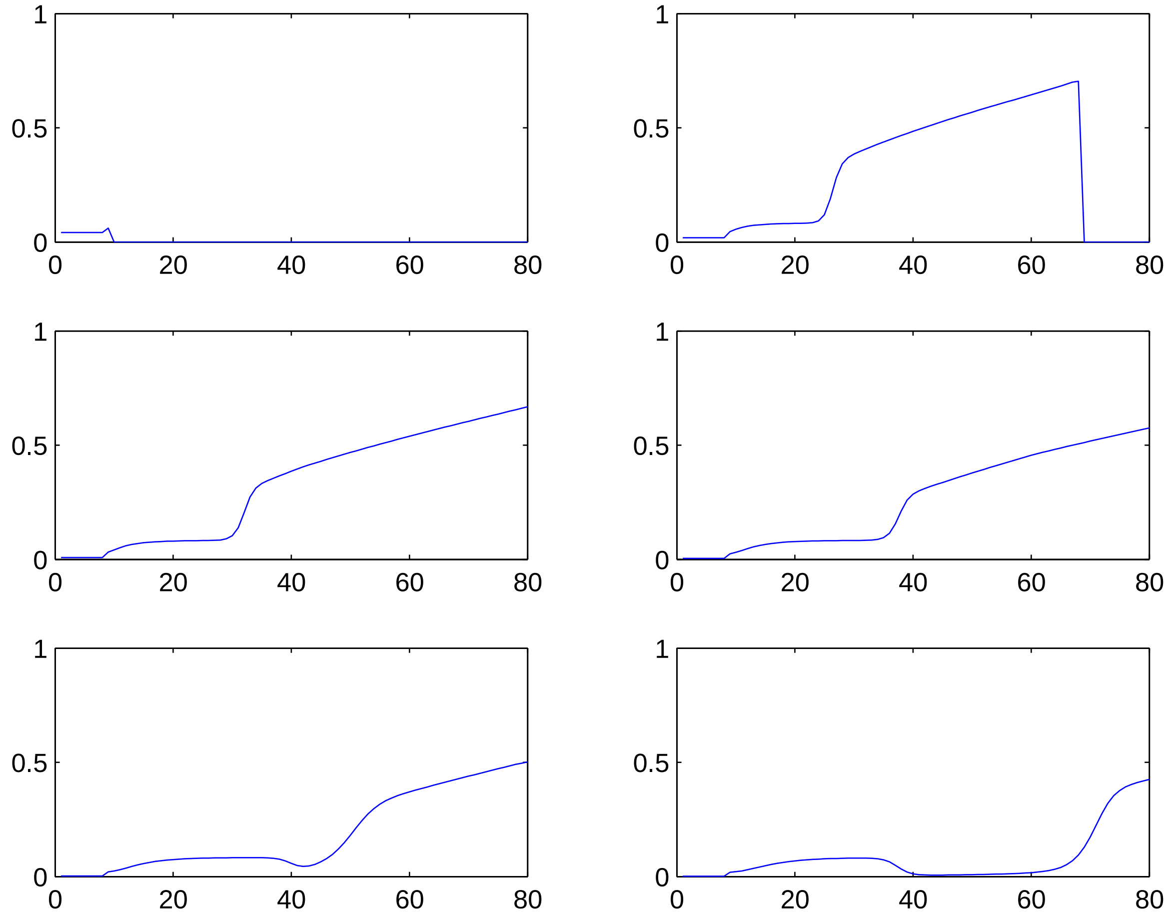
- Expensive because of the kernels in y

- Programmation in **c**; post-treatment in **matlab**; run time $\sim$ 10 min.

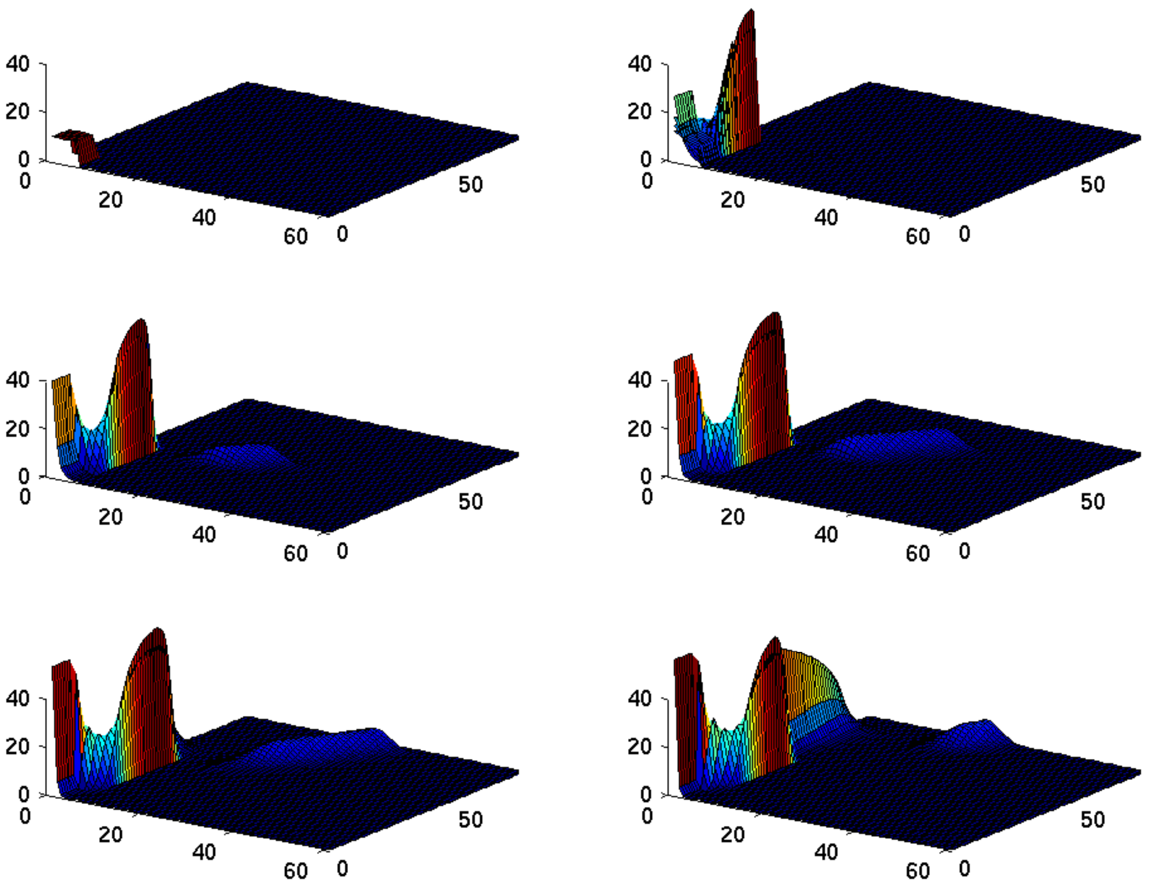
Results: number of individuals



Results: diffusion rate of individuals



Results: phase space distribution of individuals



Confrontation with data: conclusion

- Qualitatively OK

- Robust with respect to change of order of magnitude of parameters

Steady states

The steady states of

$$\frac{\partial f}{\partial t}(t,x,y)-\nu(y)\Delta_x f(t,x,y) = k^*(x,y)\, f(t,x,y)+\int_0^1 K^*(x,y,y')\, f(t,x,y')dy'$$

$$-f(t,x,y)\int_0^1 C^*(x,y,y')\, f(t,x,y')\, dy',$$

(where $x \in \Omega$, $v \in [0,1]$) are solutions of

$$-\Delta_x f(x,y) = k(x,y)\, f(x,y) + \int_0^1 K(x,y,y')\, f(x,y')\, dy'$$

$$-f(x,y)\int_0^1 C(x,y,y')\, f(x,y')\, dy'$$

(with $k(x,y) := k^*(x,y)/\nu(y)$, $K(x,y,y') := K^*(x,y,y')/\nu(y)$, and $C(x,y,y') := C^*(x,y,y')/\nu(y)$.)

Existence result

Theorem (A. Arnold, LD, C. Prevost): We assume that k, K, C are continuous and

$$\exists \kappa_+, \kappa_- > 0 : \quad \forall x \in \Omega,\ y \in [0,1], \quad \kappa_- \leq k(x,y) + \int_0^1 K(x,y,y')\, dy' \leq \kappa_+,$$

$$\exists C_-, C_+ > 0 : \quad \forall x \in \Omega,\ y, y' \in [0,1], \quad C_- \leq C(x,y,y') \leq C_+.$$

Then there exists a solution in $L^\infty(\Omega_x; M^1([0,1]))$ to

$$-\Delta_x f(x,y) = k(x,y)\, f(x,y) + \int_0^1 K(x,y,y')\, f(x,y')\, dy'$$

$$-f(x,y) \int_0^1 C(x,y,y')\, f(x,y')\, dy'$$

$$\forall x \in \partial\Omega,\ \forall y \in [0,1], \qquad \nabla_x f(x,y) \cdot n(x) = 0.$$

Simulations