On mutation-selection dynamics

Laurent Desvillettes

CMLA, ENS Cachan, 61, avenue du Président Wilson, 94235 Cachan Cedex, France

e-mail: desville@cmla.ens-cachan.fr

Pierre-Emmanuel Jabin

Lab. Dieudonné, Université de Nice Sophia-Antipolis, Parc Valrose - F-06108 Nice Cedex 02,France.

e-mail: jabin@unice.math.fr

Stéphane Mischler

Ceremade, Université Paris Dauphine, Place du Maréchal de Lattre de Tassigny F-75775 Paris Cedex 16

e-mail: mischler@ceremade.dauphine.fr

Gaël Raoul

CMLA, ENS Cachan, 61, avenue du Président Wilson, 94235 Cachan Cedex, France

e-mail: raoul@cmla.ens-cachan.fr

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1 Introduction

We are concerned with nonlinear mutation/selection-competition models aiming to describe at a mesoscopic level a population structured with respect to a quantitative trait. We are able to observe a process of speciation for those models. Or more precisely from many sub-populations with different traits, a few traits (typically a finite number of them) will be selected while the others will go extinct.

The individuals interact between themselves as their reproduction rate may for instance depend on the total population, or through competition with individuals having a close enough trait. An individual's offsprings share the same trait with possible mutation. More precisely, we represent a population by its density $f := f(t, y) \geq 0$ of individuals (fully) characterized by a trait $y \in Y$ (here, Y will always be an open interval of $\mathbb{R}$, for example we may choose $Y =]0, 1[$, $\mathbb{R}_+^*$ or $\mathbb{R}$) at time $t \geq 0$. We assume that the evolution of the density is given by the following selection-mutation integro-differential equation

$$\frac{\partial f}{\partial t} = s[f]\, f + m[f], \tag{1.1}$$

where $s[f]$ stands for the selection rate (or selective pressure) and $m[f]$ the mutation source term.

Typical examples of selection rate we have in mind, and that we shall consider in the sequel of the paper, are of logistic type :

$$s[f](y) = a(y) - \int_Y b(y,y')\, f(y')\, dy'. \tag{1.2}$$

If $m[f] \equiv 0$ (that is, no mutations are present in the dynamics of the individuals), eq. (1.1) becomes then

$$\frac{\partial f}{\partial t}(t,y) = \left(a(y) - \int_Y b(y,y')\, f(t,y')\, dy' \right) f(t,y). \tag{1.3}$$

In particular, the case $b \equiv 1$ corresponds to individuals which are in competition with each other, this competition not depending on the value of the trait y.

For the mutation, we shall consider integral operators like

$$m[f](y) = \int_Y c(y,y')\, f(y')\, dy.$$

Although (1.1) is our starting point, it can be derived from a dynamic where a finite number of individuals may randomly die or produce an offspring with a rate depending on the competition (or cooperation) between themselves. Taking the limit of an infinite number of individuals with the correct time scale, one recovers (1.1). We refer the interested reader to the paper [4].

We are interested in the limit for large times of (1.1). Without mutations (that is, when $m[f] \equiv 0$), the limit will logically be an evolutionarily stable strategy or ESS of the selection process $s[f]$. Evolutionarily stable strategies have been extensively studied for a finite number of traits (typically one resident and one invading traits) but also in some cases like ours for an infinite number of them (see [2] for instance). In the situation that we study, the stable strategy does not generally have only one dominant trait but several coexist (as in [9]).

Let us also point out another interesting limit of (1.1), namely the limit for $\varepsilon \to 0$ of the solutions f_ε to

$$\frac{\partial f_\varepsilon}{\partial t} = \frac{1}{\varepsilon} s[f_\varepsilon]\, f_\varepsilon + m[f_\varepsilon]. \tag{1.4}$$

In this last equation the time scales of the selection and mutation are separated or in other words the mutations are rare. If the stable strategy had always only one dominant trait this procedure should lead to the canonical equation of adaptive dynamic as it was obtained in [3] (we refer for reader to [5] or [8] for more on the rich subject of adaptive dynamic). If several traits may coexist, then the situation is more complicated as it was proved in [7]. Note in addition that the technique developed in this last paper cannot be applied for (1.4) with the forms of $s[f]$ that we have in mind, making this program somewhat ambitious.

2 A general existence result

In order to formalize the biologically coherent idea that $s[f] < 0$ when the population is large (like in the logistic model), we make the following

Assumption 1 :

$$f \mapsto s[f] \quad \text{is continuous in} \quad L^1(Y); \tag{2.1}$$

$$\int_Y s[f](y)\, f(y)\, dy \le (B_1 - B_2\, \rho)\, \rho.$$

Here and in the sequel, $\rho \equiv \rho(t)$ is defined by $\rho(t) = \int_Y f(t,y)\, dy$.

In order to obtain uniqueness (and stability with respect to initial data), we introduce the

Assumption 2 : $f \mapsto s[f]$ is bounded and Lipschitz continuous from $L^1(Y)$ to $L^\infty(Y)$, i.-e. there exists $K > 0$ such that

$$\forall f, g \in L^1(Y), \qquad ||s[f]||_{L^\infty(Y)} \le K\,(1 + ||f||_{L^1(Y)}),$$

$$||s[f] - s[g]||_{L^\infty(Y)} \le K\, ||f - g||_{L^1(Y)}.$$

We now present the

Theorem 2.1 *:*

1. We suppose that assumption 1 holds, that $f \mapsto m[f]$ *is linear and continuous in* $L^1(Y)$*, and that* $m[f] \ge 0$*. Then, for any nonnegative* $f_{in} \in L^1(Y)$*, there exists a nonnegative* $f \in C([0,+\infty[; L^1(Y))$ *which solves (1.1) together with* $f(0,\cdot) = f_{in}$*. Furthermore,*

$$\forall t \ge 0, \qquad \rho(t) \le \max\left(\frac{B_1 + |||m|||_{L^1(Y)}}{B_2}, \rho(0)\right).$$

2. If moreover assumption 2 holds, then

$$\forall t \in [0,T], \qquad ||f(t,\cdot) - g(t,\cdot)||_{L^1(Y)} \le e^{L_T\, t}\, ||f(0,\cdot) - g(0,\cdot)||$$

for any two solutions f, g *of (1.1) in* $C([0,+\infty[; L^1(Y))$*. Here,*

$$L_T = K\left(1 + \sup_{t\in[0,T]} ||f(t,\cdot)||_{L^1(Y)} + \sup_{t\in[0,T]} ||g(t,\cdot)||_{L^1(Y)}\right) + |||m|||_{L^1(Y)}.$$

In particular, if $f(0,\cdot) = g(0,\cdot)$*, then* $f(t,\cdot) = g(t,\cdot)$ *for all* $t > 0$*, so that uniqueness holds.*

3. Finally, if we assume that (still under assumption 2)

- $f_{in} \not\equiv 0$ *a.e. and (* $g \not\equiv 0$ *a.e* $\Longrightarrow m[g] > 0$ *a.e.),*

  or

- $f_{in} > 0$ *a.e.,*

then $f(t,\cdot) > 0$ *a.e. for any* $t > 0$*.*

Proof : Let us first prove the basic a priori estimates, under assumption 1 only. We begin by noting that any (smooth) solution to eq. (1.1) is nonnegative, thanks to the minimum principle. Then, integrating (1.1) with respect to Y, we see that any (smooth) solution satisfies

$$\partial_t \rho \le (B_1 - B_2\,\rho)\,\rho + |||m|||_{L^1(Y)}\,\rho,$$

so that

$$\rho(t) \le \max(\rho(0), B),$$

with

$$B = \frac{B_1 + |||m|||_{L^1(Y)}}{B_2}.$$

Existence can then be proven thanks to the inductive scheme

$$\begin{cases} f_0(t,y) = f_{in}(y), \\ \partial_t f_{n+1} = s[f_n]\, f_{n+1} + m[f_n], \qquad f_{n+1}(0) = f_{in}, \end{cases} \tag{2.2}$$

which respects the a priori estimates above (minimum principle for f_n and maximum principle for ρ_n).

We now suppose that assumptions 1 and 2 are satisfied. We compute, for $t \in [0,T]$,

$$\frac{d}{dt}||f-g||_{L^1(Y)}(t) = \int_Y (s[f]\,f - s[g]\,g)\,sgn(f-g)\,dy + \int_Y (m[f]-m[g])\,sgn(f-g)\,dy$$

$$\le \int_Y s[f]\,|f-g|\,dy + \int_Y |s[f]-s[g]|\,g\,dy + \int_Y |m[f]-m[g]|\,dy$$

$$\le ||s[f]||_{L^\infty(Y)}\,||f-g||_{L^1(Y)} + ||s[f]-s[g]||_{L^\infty(Y)}\,||g||_{L^1(Y)} + |||m|||_{L^1(Y)}\,||f-g||_{L^1(Y)}$$

$$\le \left[K\left(1 + \sup_{t\in[0,T]}||f(t,\cdot)||_{L^1(Y)} + \sup_{t\in[0,T]}||g(t,\cdot)||_{L^1(Y)}\right) + |||m|||_{L^1(Y)}\right]||f-g||_{L^1(Y)}.$$

We conclude thanks to Gronwall's lemma.

We finally turn to the question of the strict positivity of $f(t,\cdot)$. We suppose first that $f_{in} > 0$ a.e. We observe that

$$\begin{aligned} \partial_t f(t,y) &\ge s[f](t,y)\,f(t,y) \\ &\ge -K\,(1 + ||f(t,\cdot)||_{L^1(Y)})\,f(t,y) \\ &\ge -K\,(1 + \max(\rho(0),B))\,f(t,y), \end{aligned}$$

so that

$$f(t,y) \ge f(0,y)\,e^{-K\,(1+\max(\rho(0),B))\,t},$$

and consequently $f(t,\cdot) > 0$ a.e.

Assuming now that $f \not\equiv 0$, and that ($g \not\equiv 0 \implies m[g] > 0$ a.e.), we observe that $\frac{\partial f}{\partial t}(0,\cdot) \ge m[f(0,\cdot)] > 0$ a.e., so that $f(t,\cdot) > 0$ for $t > 0$ small enough. We can therefore use the proof of the previous case, starting from this time t instead of starting from time 0.

3 A general result on the large time asymptotic

We now restrict ourselves to a class of selection/competition models without mutations given by formula (1.3), and, more precisely, satisfying the

Assumption 3 : We take for Y a bounded open interval of $\mathbb{R}$. We assume then that the selection rate s, given by formula (1.2), is such that $a \in W^{1,\infty}(Y)$, $b \in C(\overline{Y} \times \overline{Y}, \mathbb{R}_+^*)$, and $\frac{\partial b}{\partial 1} \in L^\infty(Y)$.

Our aim is to investigate the qualitative large time behavior of the solution f to eq. (1.3) under assumption 3. Making the change of variables $t' = t/\varepsilon$, that is equivalent to consider the family of equations (after having renamed by t the rescaled time t')

$$\partial_t f_\varepsilon(t,y) = \frac{1}{\varepsilon}\, s[f_\varepsilon(t,\cdot)](y)\, f_\varepsilon(t,y) \quad \text{on} \quad]0,T[\times Y, \qquad f_\varepsilon(0,y) = f_{in}(y). \tag{3.1}$$

We define

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

so that f_ε is given by the formula

$$f_\varepsilon(t,y) = e^{\frac{1}{\varepsilon} R_\varepsilon(t,y)}\, f_{in}(y).$$

Theorem 3.1 *let $f_{in} \geq 0 \in L^1(Y)$ and s satisfy assumption 3. Then, there exists a unique solution f_ε to eq. (3.1) for any $\varepsilon > 0$. Moreover, there exists $f \in L^\infty(]0,T[, M^1(\overline{Y}))$, $R \in W^{1,\infty}(]0,T[\times Y)$ and a subsequence of (f_ε) and (R_ε) (still denoted by (f_ε) and (R_ε)), such that*

$$f_\varepsilon \rightharpoonup f \quad L^\infty(w*]0,T[;\sigma(M^1,C_b)(\overline{Y})) \quad \textit{and} \quad R_\varepsilon \to R \quad \textit{uniformly in} \quad [0,T]\times\overline{Y},$$

where $R(t,y) := \int_0^t s[f(\sigma,.)]\, d\sigma$.

Finally, when $f_{in} > 0$ a.e., f and R satisfy

$$\forall\, t \in [0,T] \qquad \sup_{y\in\overline{Y}} R(t,y) \leq 0 \quad \textit{and} \quad Supp\, f \subset \{(t,y) \in [0,T]\times\overline{Y};\, R(t,y) = 0\}.$$

More precisely, this last property means the following : if one has $R(t_*,y_*) < 0$ at some point $(t_*,y_*) \in [0,T]\times\overline{Y}$, then there exists $\delta > 0$ such that

$$\int_{[0,T]\cap[t_*-\delta,t_*+\delta]} \int_Y \phi(y)\, f(t,y)\, dydt = 0$$

for all smooth function $\phi : \mathbb{R} \to \mathbb{R}$ such that Supp $\phi \subset [y_* - \delta, y_* + \delta]$.

Proof of Theorem 3.1. We first observe that thanks to assumption 3, the quantity s/ε satisfies assumptions 1 and 2, with

$$B_1 = \frac{1}{\varepsilon}\, ||a||_{L^\infty(Y)}; \qquad B_2 = \frac{1}{\varepsilon} \inf_{y,y'\in\overline{Y}} b(y,y');$$

$$K = \frac{1}{\varepsilon} \max \Big(||a||_{L^\infty(Y)}, ||b||_{L^\infty(Y\times Y)} \Big).$$

Then, thanks to theorem 2.1, we know that

$$\forall t \in [0,T], \qquad 0 \le \rho_\varepsilon(t) \le D := \frac{\inf_{y,y' \in \overline{Y}} b(y,y')}{||a||_{L^\infty(Y)}}. \tag{3.2}$$

Therefore, up to extraction,

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

We recall that

$$R_\varepsilon(t,y) = a(y)\,t - \int_0^t \int_Y b(y,y')\, f_\varepsilon(\sigma,y')\, dy'\, d\sigma.$$

Since

$$\frac{\partial R_\varepsilon}{\partial t} = a(y) - \int_Y b(y,y')\, f_\varepsilon(t,y')\, dy',$$

and

$$\frac{\partial R_\varepsilon}{\partial y} = a'(y)\,t - \int_0^t \int_Y \frac{\partial b}{\partial 1}(y,y')\, f_\varepsilon(\sigma,y')\, dy'\, d\sigma,$$

We see that

$$\Big| R_\varepsilon \Big| \le T\,||a||_{L^\infty} + D\,T\,||b||_{L^\infty},$$

$$\left| \frac{\partial R_\varepsilon}{\partial t} \right| \le ||a||_{L^\infty} + D\,||b||_{L^\infty},$$

and

$$\left| \frac{\partial R_\varepsilon}{\partial y} \right| \le T\,||a'||_{L^\infty} + D\,T\,||\frac{\partial b}{\partial 1}||_{L^\infty}.$$

Therefore, R_ε is bounded in $W^{1,\infty}(]0,T[\times Y)$.

Then, we observe that since $f_\varepsilon \rightharpoonup f$ in $L^\infty(w*]0,T[;\sigma(M^1,C_b)(\overline{Y}))$, we have for all $t \in [0,T]$ and $y \in \overline{Y}$ the convergence of $\int_0^t \int_Y b(y,y')\, f_\varepsilon(\sigma,y')\, dy'\, d\sigma$ towards $\int_0^t \int_Y b(y,y')\, f(\sigma,y')\, dy'\, d\sigma$. As a consequence, $R_\varepsilon(t,y)$ converges toward $R(t,y)$ for all $t \in [0,T]$ and $y \in \overline{Y}$.

Thanks to the boundedness in $W^{1,\infty}(]0,T[\times Y)$ of R_ε, we obtain that R_ε converges to R uniformly on $[0,T] \times \overline{Y}$.

We now suppose that $f_{in} > 0$ a.e. Then, if $R(t_*,y_*) > 0$ at a certain point $(t_*,y_*) \in [0,T]\times Y$, we see that $R_\varepsilon(t,y) \ge \delta$ for some $\delta > 0$, as soon as $|t - t_*| \le \delta$, $|y - y_*| \le \delta$ and $0 < \varepsilon \le \delta$.

We can estimate

$$\rho_\varepsilon(t) \ge \int_Y e^{R_\varepsilon(t,y)/\varepsilon}\, f_{in}(y)\, dy \ge \int_{B(y_*,\delta)} e^{\delta/\varepsilon}\, f_{in}(y)\, dy \to_{\varepsilon\to 0} +\infty.$$

This contradicts the conclusion of estimate (3.2).

We now consider a point $(t_*, y_*) \in [0,T] \times \overline{Y}$ where $R(t_*, y_*) < 0$. Then , for some $\delta > 0$, we see that $R_\varepsilon(t,y) \le -\delta$ as soon as $|t - t_*| \le \delta$, $|y - y_*| \le \delta$ and $0 < \varepsilon \le \delta$. We consider a smooth test function $\chi : \mathbb{R} \to \mathbb{R}$ such that $1_{B(y_*, \delta/2)} \le \chi \le 1_{B(y_*,\delta)}$; Then,

$$\int_{t_*-\delta}^{t_*+\delta} \int_Y \chi(y)\, f(t,y)\, dy\, dt = \lim_{\varepsilon \to 0} \int_{t_*-\delta}^{t_*+\delta} \int_Y \chi(y)\, f_\varepsilon(t,y)\, dy\, dt$$

$$\le \lim_{\varepsilon \to 0} \int_{t_*-\delta}^{t_*+\delta} \int_{B(y_*,\delta)} e^{R_\varepsilon(t,y)/\varepsilon} f_{in}(y)\, dydt$$

$$\le 2\,\delta \lim_{\varepsilon \to 0} e^{-\delta/\varepsilon} \int_{B(y_*,\delta)} f_{in}(y)\, dy = 0.$$

We see therefore that Supp $f \subset \{(t,y) \in [0,T] \times \overline{Y};\, R(t,y) = 0\}$.

4 Some particular cases

In a few situations, it is possible to completely identify the limit given by theorem 3.1, and show the nonlinear global stability of a unique steady state.

We begin with the :

Example 4.1 *:*
Assume that Y is a bounded interval of $\mathbb{R}$, and that $s[f](y) = a(y) - \int_Y f(y')\, dy'$, where a is a $W^{1,\infty}$ function from Y to R_+^* which has a maximum reached at a unique point $y^* \in \overline{Y}$. Then, if $f_{in} > 0$ a.e. lies in $L^1(Y)$, the measure f given by theorem 3.1 is

$$f(t,y) = a(y_*)\, \delta_{y=y_*},$$

Proof : The quantity R defined by thm. 3.1 satisfies in this example the following identity:

$$R(t,y) = a(y)\, t - \int_0^t \int_Y f(\sigma, y')\, dy' d\sigma.$$

But by assumption, $a(y_*) < a(y)$ for all $y \ne y_*$, so that (for any $t \in [0,T]$) the unique possible point y of $\overline{Y}$ where $R(t,y) = 0$ is $y = y_*$. According to theorem 3.1, we know that for any smooth function ϕ such that $\phi \equiv 0$ in a neighborhood of y_*,

$$\int_0^T \int_Y \phi(y)\, f(\sigma, y)\, dy d\sigma = 0. \tag{4.3}$$

Then, we observe that

$$\partial_t \rho_\varepsilon \ge \frac{\rho_\varepsilon}{\varepsilon} \left(\inf_{y \in \overline{Y}} a(y) - \rho_\varepsilon \right),$$

so that

$$\forall t \in [0,T], \qquad \rho_\varepsilon(t) \ge E := \min \left(\rho(0), \inf_{y \in \overline{Y}} a(y) \right).$$

Passing to the limit in this estimate when $\varepsilon \to 0$ and using identity (4.3), we observe that for any $\delta > 0$, $t \in [0,T]$ and any smooth function χ such that $1_{B(y_*,\delta/2)} \le \chi \le 1_{B(y_*,\delta)}$,

$$\int_{[0,T]\cap[t-\delta,t+\delta]} \int_Y \chi(y)\, f(\sigma,y)\, dy d\sigma = \int_{[0,T]\cap[t-\delta,t+\delta]} \int_Y f(\sigma,y)\, dy d\sigma$$
$$\ge E\,\delta.$$

Using thm. 3.1, we deduce from this estimate that (for any $t \in [0,T]$), $R(t,y_*) = 0$, so that (for any $t \in [0,T]$)

$$a(y_*)\, t = \int_0^t \int_Y f(\sigma,y')\, dy' d\sigma,$$

and (using identity (4.3)), for any smooth function $\phi : \mathbb{R} \to \mathbb{R}$ such that $\phi \equiv 1$ in a neighborhood of y_*,

$$a(y_*)\, t = \int_0^t \int_Y \phi(y)\, f(\sigma,y')\, dy' d\sigma.$$

This can be seen as a weak formulation of the identity $f(t,y) = a(y_*)\, \delta_{y=y_*}$.

This situation can be somewhat generalized to cases when a still has a unique maximum (which, without loss of generality, can be taken at point 0), and its convexity at point 0 is large compared to the convexity of b at point 0, where $b(y,y') \equiv b(y-y')$ in (1.2). This situation is well-known in adaptive dynamics : it corresponds to a situation when the competition does not lead to a branching. We state a precise result :

Example 4.2 *Assume that* $Y =]-1,1[$ *and* $s[f] = a(y) - \int_Y b(y-y')\, f(y')\, dy'$. *We suppose that* $a \in C^1(\overline{Y};\mathbb{R}_+^*)$ *takes its unique maximum at point* 0, *and such that for some constants* $A, C > 0$,

$$\forall y \in Y, \qquad a(y) \le C, \qquad |a'(y)| \ge A\,|y|,$$

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

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

Finally, we suppose that

$$2\,C\,E < A\,D. \tag{4.4}$$

Then, if $\frac{C}{D} \ge f_{in} > 0$ *a.e., the measure* f *given by theorem 3.1 is* $f(t,y) = \frac{a(0)}{b(0)}\, \delta_0(y)$.

Proof : In order to show this result, we begin by observing that because of the maximum principle, $||f(t,\cdot)||_{L^1} \le \frac{C}{D}$.

Then, we denote by Q the set $\{y, \quad \exists t \in]0,T], (t,y) \in \text{ Supp } f\}$. Suppose that $y_* \in Q$. Then, we know that (for some $t \in]0,T]$) the function $y \mapsto R(t,y)$ admits a maximum at point y_*, and that $R(t,y_*) = 0$.

The assumption that b is C^1 ensures that $y \mapsto R(t,y)$ is also C^1, so that $\partial_y R(t,y_*) = 0$, which can be rewritten

$$t\, a'(y_*) = \int_0^t \int_{z \in Q} b'(y-z)\, f(s,z)\, dz ds.$$

Then

$$t\, |a'(y_*)| \le \int_0^t \int_{z \in Q} |b'(y-z)|\, |f(s,z)|\, dz ds$$

$$\le ||b'||_{L^\infty(Q-Q)} \int_0^t \int_{z \in Q} |f(s,z)|\, dz ds$$

$$\le \frac{C}{D}\, t\, ||b'||_{L^\infty(Q-Q)},$$

where $Q - Q$ denotes the set of differences of two elements of Q.

Finally, we end up with the following estimate for Q

$$||a'||_{L^\infty(Q)} \le \frac{C}{D}\, ||b'||_{L^\infty(Q-Q)}.$$

Here, $Q - Q$ is the set of differences of two elements of Q. Since $Q \subset [-1, 1]$, one has for any $x \in Q$ the inequality

$$A\, |x| \le |a'(x)| \le \frac{C}{D}\, ||b'||_{L^\infty([-2,2])},$$

so that

$$|x| \le \frac{C}{D}\, 2\, E\, \frac{1}{A},$$

and finally $Q \subset [-\frac{2\,E\,C}{A\,D}, \frac{2\,E\,C}{A\,D}]$. Then, for any $x \in Q$,

$$A\, |x| \le |a'(x)| \le \frac{C}{D}\, ||b'||_{L^\infty([-\frac{4\,E\,C}{A\,D}, \frac{4\,E\,C}{A\,D}])},$$

and $Q \subset [-(\frac{2EC}{AD})^2, (\frac{2EC}{AD})^2]$. By induction, we end up with $Q \subset [-(\frac{2EC}{AD})^n, (\frac{2EC}{AD})^n]$ for all $n \in \mathbb{N}$.

Thanks to hypothesis (4.4), we see that $Q = \{0\}$, which shows the result. The rest of the proof is similar to the end of the proof of the first example.

We now turn to a situation in which it is not possible to identify in totality the limit, but it is at least possible to see that this limit is necessarily a finite sum of Dirac masses (and to bound the number of possible Dirac masses).

Example 4.3 *: We suppose that for some $k \in \mathbb{N}^*$,*

$$s[f](y) = a(y) - \int_Y b(y,y')\, f(y')\, dy', \tag{4.5}$$

where $a \in C^k(Y)$, $y \mapsto b(y,y') \in C^k(Y)$ for all $y' \in Y$, and

$$a^{(k)} \equiv 0 \quad on \quad Y \quad , \qquad \frac{\partial^k b}{\partial 1^k} > 0 \quad on \quad Y \times Y.$$

Then, if $f_{in} > 0$ a.e., the measure f given by theorem 3.1 takes the shape

$$f(t,y) = \sum_{i=1}^{k} \rho_i(t)\, \delta_{y=y_i(t)},$$

for some $y_i(t) \in \overline{Y}$ and $\rho_i(t) \geq 0$ $(i = 1,..,k)$.

Proof : In this case,

$$R(t,y) = a(y)\,t - \int_0^t \int_Y b(y,y')\, f(\sigma,y')\, dy' d\sigma.$$

Then, R is clearly in $C^k(Y)$ and

$$\frac{\partial^p R}{\partial y^p}(t,y) = a^{(p)}(y)\,t - \int_0^t \int_Y \frac{\partial^p b}{\partial 1^p}(y,y')\, f(\sigma,y')\, dy' d\sigma$$

for all $p \leq k$. In particular

$$\frac{\partial^k R}{\partial y^k}(t,y) = - \int_0^t \int_Y \frac{\partial^k b}{\partial 1^k}(y,y')\, f(\sigma,y')\, dy' d\sigma > 0,$$

so that (for any time $t \in [0,T]$), the function $R(t,\cdot)$ has at most k zeros on $\overline{Y}$. Thanks to theorem 3.1, we can conclude.

5 Linear stability

In many situations, it is not possible to prove the nonlinear global stability of a general steady state. It is however at least possible to explore the linear stability of some specific steady solutions of eq. (1.3), with respect to perturbations having a particular shape. This leads to computations similar to those appearing in adaptive dynamics. We begin with the analysis of the steady solutions to eq. (1.3) (with a and b smooth C^2 functions) which are finite sums of Dirac masses.

5.1 Stability of sums of Dirac masses

We begin by noticing that a function of the form

$$f(y) = \sum_{i=1}^{N} \rho_i\, \delta_{y_i}(y), \tag{5.6}$$

(where $\rho_1 > 0, ..\rho_N > 0$) is a steady solution of eq. (1.3) if and only if

$$a(y_i) = \sum_{j=1}^{N} \rho_j \, b(y_i, y_j). \qquad i = 1, .., N. \tag{5.7}$$

Starting from a perturbation of the function in (5.6) of the form

$$f(y) = \varepsilon \, \delta_s(y) + \sum_{i=1}^{N} \rho_i \, \delta_{y_i}(y) \tag{5.8}$$

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

$$a(s) < \sum_{j=1}^{N} \rho_j \, b(s, y_j), \qquad s \in Y, s \neq y_1, .., y_N. \tag{5.9}$$

Here, the term "global" means that there is stability with respect to a perturbation whose support is not necessarily localized around the support of the steady state.

Still under the condition that a and b are C^2, this "global" condition entails the "local" condition :

$$a'(y_i) = \sum_{j=1}^{N} \rho_j \, \frac{\partial b}{\partial 1}(y_i, y_j), \qquad i = 1, .., N, \tag{5.10}$$

$$a''(y_i) \leq \sum_{j=1}^{N} \rho_j \, \frac{\partial^2 b}{\partial 1^2}(y_i, y_j), \qquad i = 1, .., N. \tag{5.11}$$

Those formulas are similar to the equations obtained in adaptive dynamics.

The set of equations (5.7), (5.10) and (5.11) (for arbitrary $N \in \mathbb{N}_*$, $b_i > 0$ and $y_i \in \overline{Y}$) enables to find the steady locally linearly stable (with respect to perturbations which are Dirac masses) solutions of eq. (3.1) of the particular shape (5.6).

In next subsection, we present a computation (for $N \leq 3$) in a simple and typical case, where it is possible to obtain explictly all the constants appearing in the steady states.

5.2 An example : local and global linear stability

We study in this subsection the case when

$$a(y) = A - y^2, \qquad b(y, z) = \frac{1}{1 + (y - z)^2}, \tag{5.12}$$

where $A > 0$ is a parameter (the study can be performed either in $\mathbb{R}$ or in a bounded interval containing $[-\sqrt{A}, \sqrt{A}]$, since any solution of eq. (1.3) will decay exponentially fast towards 0 at any point y where $a(y) < 0$).

Note that a has its maximum at $y = 0$ and becomes nonpositive when $|y|$ is large enough, that is, individuals having a trait too far from the optimal trait will disappear even if the competition is not taken into account. The competition kernel b is at its maximum when $y = z$, that is when the traits of two individuals are closest, and it decreases with $|y - z|$. It remains however nonnegative whatever the values of y, z. In other words, there is always competition and never cooperation between the individuals.

Note also that the bigger the parameter A becomes, the higher is the interest for individuals to have differents traits. In other words, N should grow with A.

In the sequel, we look for the locally and globally linearly stable (with respect to perturbations which are Dirac masses) steady solutions of eq. (3.1) [with coefficients defined by (5.12)] of the form (5.6). Since the coefficients are symmetric with respect to 0, we only look for symmetric steady states.

5.2.1 $N = 1$

We start by searching the solutions for $N = 1$. We see that the set of equations

$$a(y_1) = \rho_1 \, b(y_1, y_1), \qquad a'(y_1) = \rho_1 \, \frac{\partial b}{\partial 1}(y_1, y_1),$$

has the only symmetric solution given by

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

Moreover,

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

so that $\bar{f}_1(y) = A\,\delta_{y=0}$ is locally linearly stable if and only if $0 \le A \le 1$.

Finally, we test the global linear stability by computing

$$a(s) - \rho_1 \, b(s, y_1) = A - s^2 - \frac{A}{1 + s^2} := \psi(s^2).$$

It is clear that $\psi(0) = 0$ and $\lim_{u \to +\infty} \psi(u) = -\infty$. Moreover, $\psi'(u) = -1 + \frac{A}{(1+u)^2}$. Therefore, when $0 < A < 1$, $\psi(u) < 0$ for $u > 0$. Finally, there is global linear stability of $\bar{f}(y) = A\,\delta_{y=0}$ if and only if $0 \le A \le 1$..

5.2.2 $N = 2$

We now look for the symmetric solutions of (5.7), (5.10) when $N = 2$, and with the data (5.12). That is, we wish to solve

$$a(y_1) = \rho_1 \, b(y_1, y_1) + \rho_2 \, b(y_1, y_2), \qquad a(y_2) = \rho_1 \, b(y_2, y_1) + \rho_2 \, b(y_2, y_2),$$

$$a'(y_1) = \rho_1 \frac{\partial b}{\partial 1}(y_1, y_1) + \rho_2 \frac{\partial b}{\partial 1}(y_1, y_2), \qquad a'(y_2) = \rho_1 \frac{\partial b}{\partial 1}(y_2, y_1) + \rho_2 \frac{\partial b}{\partial 1}(y_2, y_2),$$

with $\rho_1 = \rho_2 > 0$, $y_1 = -y_2 > 0$ (and $y_1 \neq y_2$). This system can be therefore rewritten as

$$A - y_1^2 = \rho_1 \left(1 + \frac{1}{1 + 4\, y_1^2}\right), \qquad 1 = \frac{2\, \rho_1}{(1 + 4\, y_1^2)^2}.$$

We look for $x = y_1^2$. Then, the previous system turns into the second degree equation

$$8\, x^2 + 7\, x + 1 = A.$$

When $0 < A \leq 1$, this equation has only nonpositive solutions. When $A > 1$, its only stricly positive solution is given by

$$x = \frac{-7 + \sqrt{17 + 32\, A}}{16}, \tag{5.13}$$

so that

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

Note that $\rho_1 \geq 0$ for all $A > 0$.

By symmetry, it is enough to test the local stability at y_1 in order to obtain it also at y_2. Therefore, we compute

$$\begin{aligned} & a''(y_1) - \rho_1 \frac{\partial^2 b}{\partial 1^2}(y_1, y_1) - \rho_2 \frac{\partial^2 b}{\partial 1^2}(y_1, y_2) \\ &= -2 - \rho_1 \left(-2 + \frac{24\, y_1^2 - 2}{(1 + 4\, y_1^2)^3} \right) \\ &= -2 + (1 + 4x^2)^2 + \frac{1 - 12\, x}{1 + 4\, x}. \end{aligned}$$

Then, this quantity is nonnegative if and only if $x\,(8\, x^2 + 6\, x - 1) \geq 0$, i.-e. $x \geq \frac{-3+\sqrt{17}}{8}$. Remembering (5.13), this means that $A \geq \frac{13+\sqrt{17}}{8} \sim 2.13$.

In other words, the steady state

$$\bar{f}_2(y) = \frac{13 + 16\, A - 3\sqrt{17 + 32\, A}}{16} \left(\delta_{y = \frac{1}{4}\sqrt{-7+\sqrt{17+32\, A}}} + \delta_{y = -\frac{1}{4}\sqrt{-7+\sqrt{17+32\, A}}} \right)$$

is locally linearly stable if and only if $A \in [1, \frac{13+\sqrt{17}}{8}]$.

Finally, we test the global stability of this steady state by computing (with $u = s^2$)

$$a(s) - \rho_1\, b(s, y_1) - \rho_2\, b(s, y_2) = A - s^2 - \rho_1 \left[\frac{1}{1 + (y_1 - s)^2} + \frac{1}{1 + (y_1 + s)^2} \right]$$

$$= A - u - \rho_1 \left[\frac{2 + 2\,u + 2\,x}{1 + 2\,u + 2\,x + x^2 + u^2 - 2\,x\,u} \right]$$
$$= - \frac{(u-x)^2\,(u+2-A)}{1 + 2\,u + 2\,x + (x-u)^2}.$$

This means that the global linear stability of $\bar f_2$ holds for $1 \le A \le 2$.

We see that there is a range of A (between 2 and 2.13..) where a "short range" mutation does not perturb the steady state, while a "long range" one can destroy it. This is related to the fact that if the transition between $A < 1$ and $A > 1$ is a branching, the transition between $A < 2$ and $A > 2$ consists instead in the appearance of a new trait (at $y = 0$) "coming out of nowhere".

5.2.3 $N = 3$

After the use of the symmetries, the system to solve in order to know if a sum of three Dirac masses (of the form $f(y) = \rho_1\,\delta_{y=y_1} + \rho_2\,\delta_{y=0} + \rho_1\,\delta_{y=-y_1}$) is a linearly stable steady solution of eq. (1.3) (that is, (5.7), (5.10)), can be rewritten under the form

$$\begin{cases} A - y_1^2 = \rho_1\,(1 + \frac{1}{1+4\,y_1^2}) + \rho_2\,\frac{1}{1+y_1^2}, \\ A = 2\,\rho_1\,\frac{1}{1+y_1^2} + \rho_2, \\ 1 = 2\,\rho_1\,\frac{1}{(1+4\,y_1^2)^2} + \rho_2\,\frac{1}{(1+y_1^2)^2}. \end{cases} \tag{5.14}$$

Still writing $x = y_1^2$, we see that

$$8\,x^2 + 31\,x + 14 - 9\,A = 0.$$

The only strictly positive solution of this equation is

$$x = \frac{-31 + \sqrt{513 + 288\,A}}{16}.$$

We see that $x \ge 0$ as soon as $A \ge \frac{14}{9}$.

Then (for $x \ge 0$),

$$\rho_1 = \frac{(A - 1 - 2x)\,(1+4x)^2}{(16x+10)\,x},$$

so that $\rho_1 \ge 0$ if and only if $A - 1 - 2x \ge 0$, i.-e. $(x+1)\,(8x+5) \ge 0$, which is always true. Finally,

$$\rho_2 = A - \frac{2\,\rho_1}{1+x},$$

and $\rho_2 \ge 0$ when $A \ge 2$ (i.-e. $x \ge \frac{1}{8}$).

In order to study the global linear stability, we compute (for $u = s^2$)

$$A - u - \frac{\rho_2}{1+u} - \frac{\rho_1\,(2 + 2x + 2u)}{1 + 2x + 2u + x^2 + u^2 - 2xu}$$

$$= \frac{u\,(x-u)^2\,(8x^2+31x-13-9u)}{9\,(1+u)\,(1+2x+2u+x^2+u^2-2xu)}$$

so that this is nonnegative if and only if

$$8x^2+31x-13-9u \geq 0,$$

i.-e. $A-3-u \geq 0$. This ensures that there is global stability of the steady state

$$\bar{f}_3(y) = \rho_1 \left(\delta_{y=\sqrt{x}} + \delta_{y=-\sqrt{x}}\right) + \rho_2\,\delta_{y=0},$$

with

$$x = \frac{-31+\sqrt{513+288\,A}}{16}, \qquad \rho_1 = \frac{(A-1-2x)\,(1+4x)^2}{(16x+10)\,x}, \qquad \rho_2 = A - \frac{2\,\rho_1}{1+x},$$

if and only if $2 \leq A \leq 3$.

It is easy to verify also that for $A > 3$, the condition of local linear stability is not fulfiled for the Dirac mass at point 0.

5.3 Another example: stability of a steady Gaussian solution

One may wonder whether there are stable steady states to eq. (1.3) which are not sums of Dirac masses. The following example does not answer to this question, but gives at least a situation in which the unstability of such a steady state seems to develop only after a very long time.

We consider the case of a and b Gaussian, as follows :

$$a(y) = \frac{1}{\sqrt{2\pi(T_1+T_2)}} e^{-\frac{y^2}{2(T_1+T_2)}}, \quad b(y) = \frac{1}{\sqrt{2\pi T_1}} e^{-\frac{y^2}{2T_1}}, \tag{5.15}$$

where T_1, $T_2 > 0$. This formula for a is not very satisfactory since it is not negative for $|y|$ large enough, but this example is nevertheless interesting since it gives rise to the obvious steady state $\bar{f}(y) = \frac{1}{\sqrt{2\pi T_2}}\, e^{-\frac{y^2}{2T_2}}$. The study of the linear stability of this solution is much more intricate than the study we performed in subsections 5.1 and 5.2. Let us just present a few basic facts.

Let $\varepsilon\, g(t=0)$ be a small perturbation of $\bar{f}$, such that $\bar{f} + \varepsilon\, g(t=0) \geq 0$. Then, eq. (1.3) becomes $\partial_t g = -(b*g)\,\bar{f} - \varepsilon\,(b*g)\,g$. Thus, $\bar{f}$ is linearly stable if and only if 0 is an attractive point for the linear integro-differential equation :

$$\partial_t g = -(b*g)\,\bar{f}.$$

Let us first note that if g has a constant sign, then $|g(\cdot,y)|$ decreases for each $y \in Y$, and so does $\int_{\mathbb{R}} |g(\cdot,y)|^2\,dy$. But, as we shall see, this property disappears if g does not have a constant sign. For example, taking

$$g(t=0) = (\sin(26.69\,x) - 202\,\sin(27.5\,x))\; e^{-0.75\,x^2}, \tag{5.16}$$

we see that

$$\partial_t \int_{\mathbb{R}} |g(t=0,y)|^2\, dy \approx 9.2.10^{-83} > 0,$$

and that $\bar{f} + \varepsilon\, g(t=0) \geq 0$ for $\varepsilon > 0$ small enough. Then, the L^2 norm is not a Liapounov fonctional for the problem, which suggests that $\bar{f}$ might be linearly unstable. Moreover, computations with other oscillating functions seem to lead most of the time to values of $\partial_t \int_{\mathbb{R}} |g(t=0,y)|^2\, dy$ which are negative, and sometimes, like in (5.16), very small. This suggests that this instability might take a long time to develop.

We present in next section numerical simulations which show that $\bar{f}$ seems indeed to attract rapidly most of the initial data, then remains stable for a very long time, before finally being destabilized and converge toward a (presumably) infinite sum of Dirac masses.

6 Numerical simulations

6.1 The numerical method

All simulations have been done for eq. (1.3), in the particular case when $Y = \mathbb{R}$ and $b(y,y') := b(y-y')$. We assume that f_{in}, a and b have a compact support (that is, a is replaced by 0 at the points where it is nonpositive, or (in the case of the Gaussian) when it is close enough to 0: this does not lead to difficulties when f_{in} takes the value 0 in those zones). After a rescaling, we can consider that the support of f is included in $[\frac{1}{4}, \frac{3}{4}]$ and that the convolution $b *_{\mathbb{R}} f$ can be seen as a convolution of periodic functions. This will allow us to use a spectral method to compute it.

We first discretize f in the space variable under the form of a finite sequence $(f_i)_{i=0\ldots N}$. The equation becomes (with $a_i := N \int_{[\frac{i}{N}, \frac{i+1}{N}]} a$ and $b_i := N \int_{[\frac{i}{N}, \frac{i+1}{N}]} b$):

$$\frac{\partial f_i}{\partial t} = \left(a_i - \left(\sum_{j=0}^{i} b_j\, f_{j-i+N} + \sum_{j=i+1}^{N} b_j\, f_{j-i} \right) \right), \quad \forall i = 0 \ldots N.$$

Then, we use a Runge-Kutta method (RK4) for the time discretization.

As we said, we use a spectral method to compute the convolution, based on the following formula of Fourier analysis:

$$\widehat{(b_i)_i * (f_i)_i} = \widehat{(b_i)}_i \cdot \widehat{(f_i)}_i.$$

Using a FFT algorithm to compute the Fourier transform, we recall that the complexity of each time step is of order $N\, log(N)$ instead of N^2.

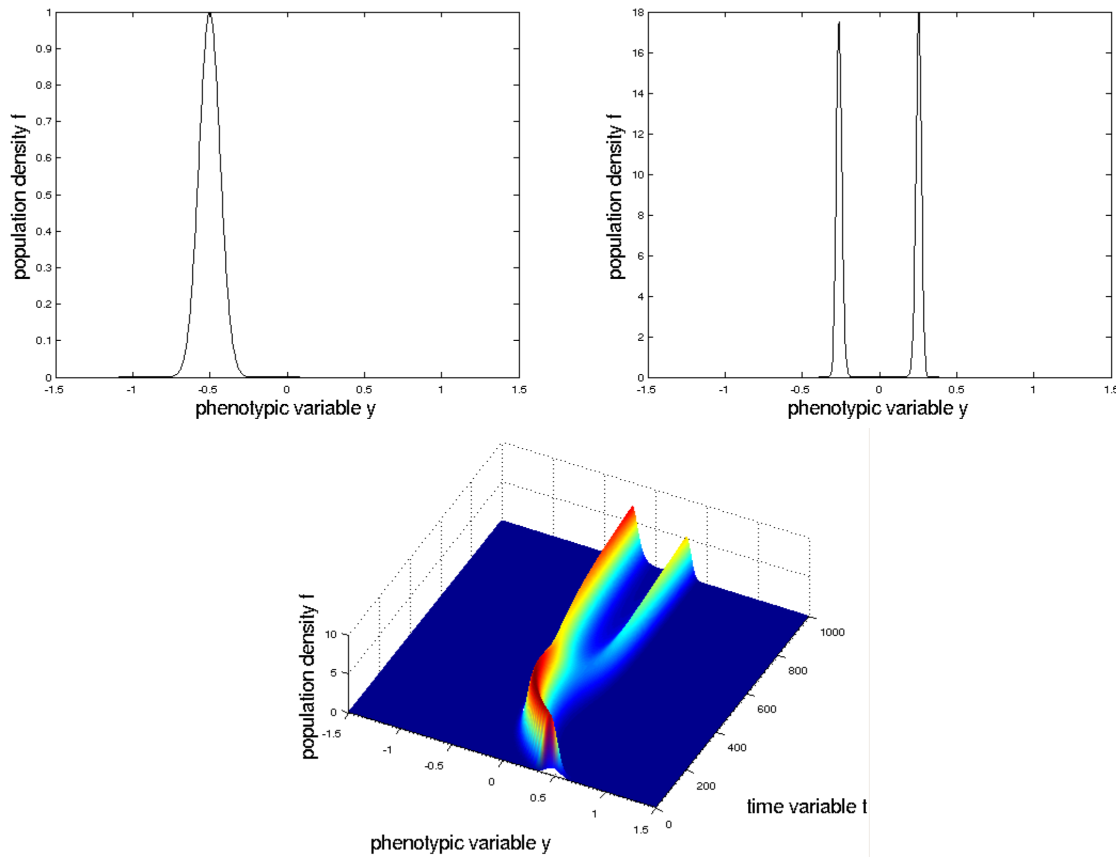

Figure 1: Simulation for $A = 1.5$ at times $t = 0$, $t = 10\,000$, and for $t \in [0, 1\,000]$.

6.2 Simulation for the example of subsection 5.2

In subsection 5.2, we found linearly stable steady solutions of eq. (1.3) with data (5.12) under the form of sums of Dirac masses. Thanks to the simulations, we observe that there is also most probably global nonlinear stability: for every initial condition $f_{in} > 0$ that we have tested, the solution numerically converges to the solution found theoretically when $A \in [0, 3]$

When $A \in [1, 3]$, the results can be interpreted a "speciation process". We observe two different types of such processes : in fig. 1 (corresponding to $A \in [1, 2]$), we observe a branching of the initial datum into two subspecies, while in fig. 2 (corresponding to $A \in [2, 3]$), the middle subspecies appears without any branching.

In fig. 3, we present the theoretical and numerical long-time limit of f (starting from a given initial condition $f_{in} > 0$ in the numerical simulation, but any other (strictly positive) initial datum that we have tested leads to the same result) for different values of the parameter A.

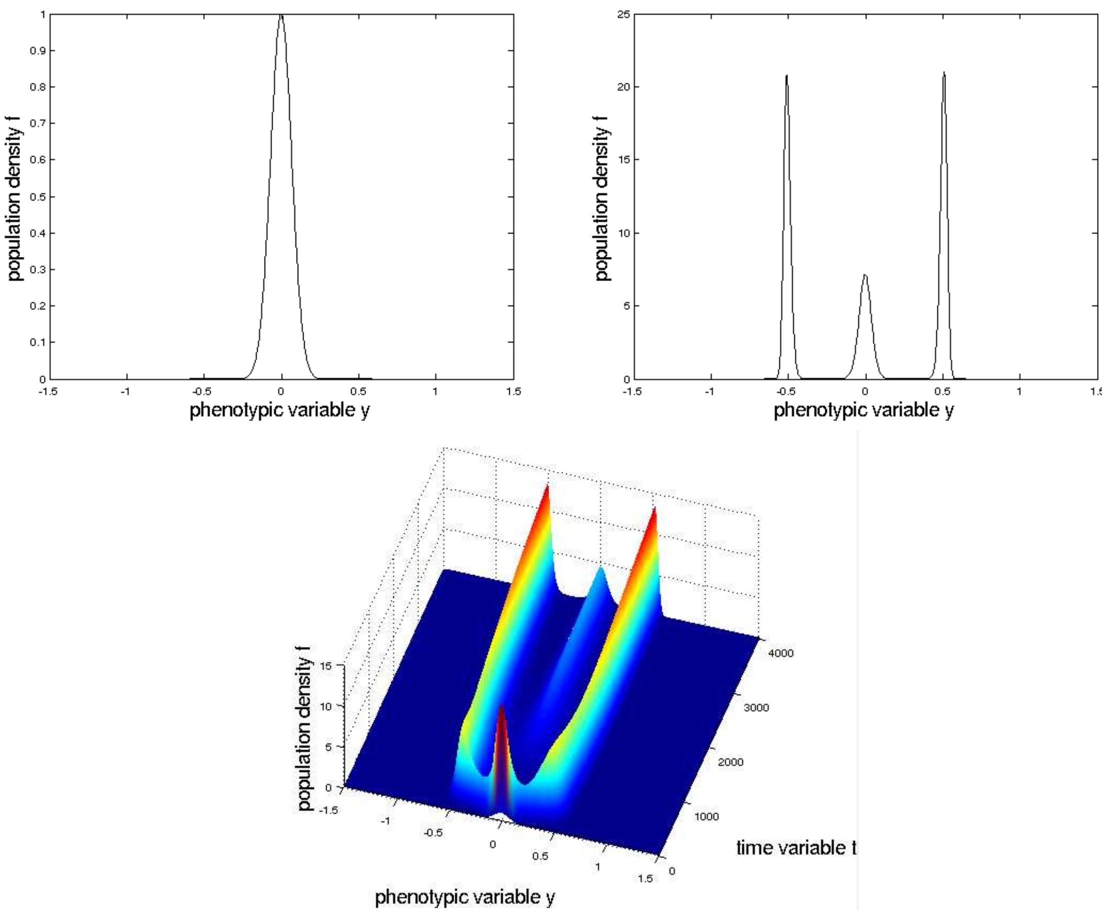

Figure 2: Simulation for $A = 2.5$, at times $t = 0$, $t = 10\,000$ and for $t \in [0, 4\,000]$.

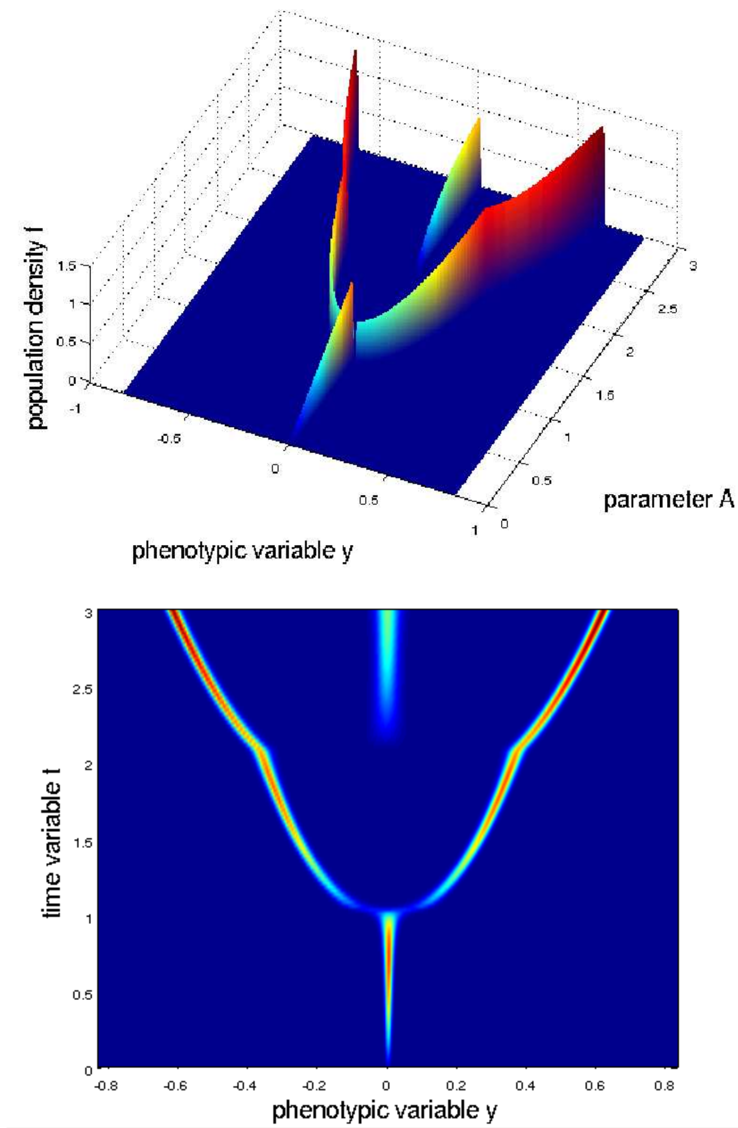

Figure 3: Theoretical asymptotic solution for $A \in [0,3]$, and numerical solutions $f(t = 20\,000)$ for $A \in [0,3]$.

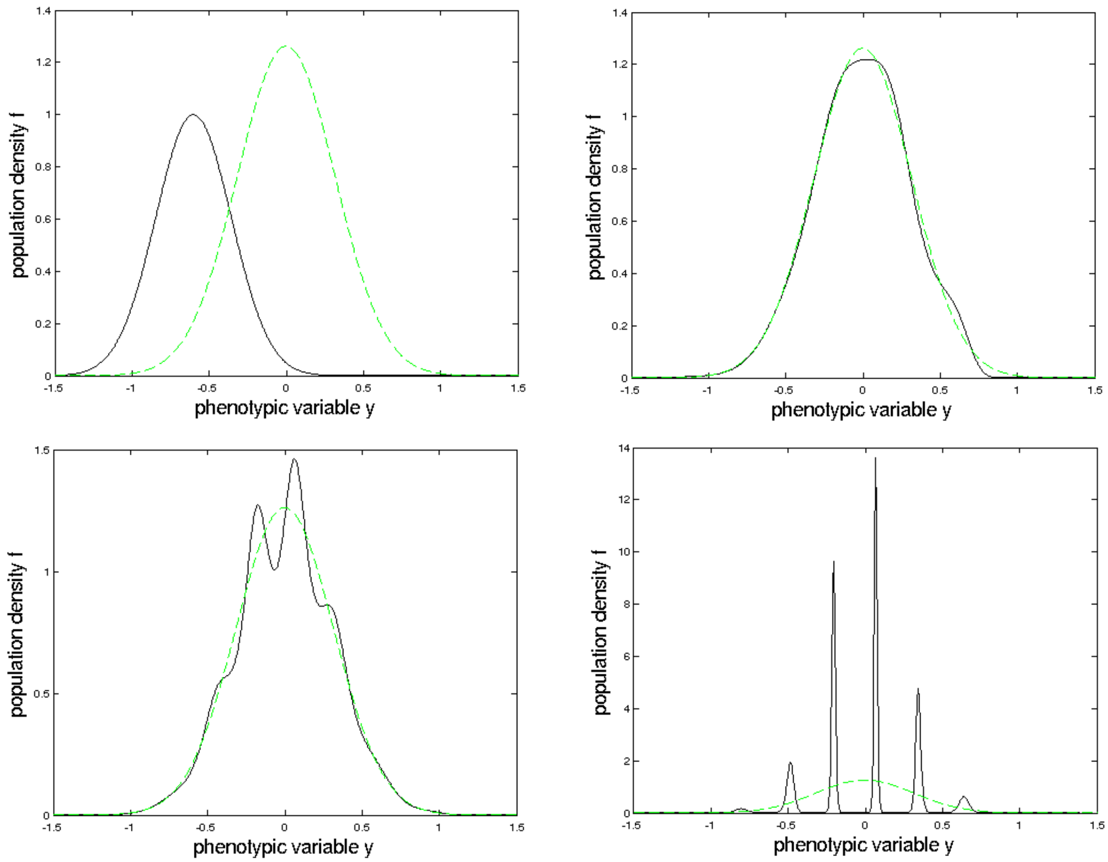

Figure 4: Simulation for $T_1 = 0.05$, $T_2 = 0.1$, at times $t = 0$, 500, 25 000, 50 000. f : continuous line, $\bar{f}$: dashed line

6.3 Simulation for the example of subsection 5.3

In subsection 5.3, we discussed the linear stability of a steady solution $\bar{f}$ of eq. (1.3) with data (5.15). By computing numerically for very large times the solution of this equation, we observe that $\bar{f}$ is not stable. It is however interesting to notice that for various initial conditions, f seems first to converge rather rapidly to $\bar{f}$, and then this steady state is destabilized much later, and turns into what looks to be an infinite sum of Dirac masses $\sum_{i \in \mathbb{Z}} \alpha_i \delta_{i\,h}$ (where h is a certain number). The shape of the solution of eq. (1.3) with data (5.15) at various times is presented in fig. 4.

References

[1] Bürger R., The Mathematical Theory of Selection, Recombination and Mutation. Wiley, New-York 2000.

[2] Calcina A., Cuadrado S., Small mutation rate and evolutionarily stable strategies in infinite dimensional adaptive dynamics. *J. Math. Biol.* **48**, 135–159 (2004).

[3] Champagnat N., Ferrière R., Ben Arous G., The canonical equation of adaptive dynamics: A mathematical view. *Selection* **2**, 71–81 (2001).

[4] Champagnat N., Ferrière R. et Méléard S., Unifying evolutionary dynamics: From individual stochastic processes to macroscopic models. *Theor. Popul. Biol.* to appear.

[5] Diekmann O., Beginner's guide to adaptive dynamics, vol. 63, Banach Center Publications, 47–86.

[6] Diekmann O., Gyllenberg M., Metz J.A.J., Steady states analysis of structured population models. *Theor. Popul. Biol.* **63**, 309–338, (2003).

[7] Diekmann O., Jabin P.E., Mischler S., Perthame B., The dynamics of adaptation: An illuminating example and a Hamilton-Jacobi approach. *Theor. Popul. Biol.* **67**, 257–271, (2005).

[8] Dieckmann U., Law R., The dynamical theory of coevolution: A derivation from a stochastic ecological processes. *J. Math. Biology* **34**, 579–612, (1996).

[9] Geritz S. A. H., Resident-invader dynamics and the coexistence of similar strategies. *J. Math. Biol.* **50**, 67–82, (2005).