# ON SELECTION DYNAMICS FOR CONTINUOUS STRUCTURED POPULATIONS\*

LAURENT DESVILLETTES<sup>†</sup>, PIERRE-EMMANUEL JABIN<sup>‡</sup>, STÉPHANE MISCHLER<sup>§</sup>, AND GAËL RAOUL¶

**Abstract.** In this paper, we provide results about the long time behavior of integrodifferential equations appearing in the study of populations structured with respect to a quantitative (continuous) trait, which are submitted to selection (or competition).

Key words. Selection-competition, population dynamics, long time asymptotics

AMS subject classifications. 45J05, 45M05, 92D15, 92D40

#### 1. Introduction

We are concerned with nonlinear selection (or competition) models aiming to describe a population structured with respect to a quantitative trait at an ecological time scale. We are able to observe a speciation-like process for those models. 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 become extinct.

The individuals interact between themselves through a competition with individuals having a close enough trait. An individual's offspring shares the same trait as its ancestor, so that all possible mutations are neglected.

More precisely, we represent a population by its density  $f := f(t,y) \ge 0$  of individuals (fully) characterized by a trait  $y \in Y$  (here Y will always be a compact interval of  $\mathbb{R}$ , except in subsection 5.3) at time  $t \ge 0$ . We assume that the evolution of the density is given by the following integro-differential equation

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

where s[f] stands for the selection rate (or selective pressure).

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

$$s[f](y) = a(y) - \int_{Y} b(y, y') f(y') dy', \qquad (1.2)$$

where  $a: Y \to \mathbb{R}$  is the birth rate and  $b: Y \times Y \to \mathbb{R}_+$  is the death rate. The case  $b \equiv 1$  corresponds to individuals that are in competition with each other, this competition being independent on the value of the trait y.

Although equation (1.1) is our starting point, it can be derived (with an additive mutation term) from a model in which a finite number of individuals may randomly

<sup>\*</sup>Received: February 19, 2008; accepted: July 23, 2008. Communicated by Francois Bouchut.

<sup>&</sup>lt;sup>†</sup>CMLA, ENS Cachan, CNRS & IUF, PRES UniverSud, 61, Avenue du Président Wilson, 94235 Cachan Cedex, France (desville@cmla.ens-cachan.fr).

<sup>&</sup>lt;sup>‡</sup>Lab. Dieudonné, Université de Nice Sophia-Antipolis, Parc Valrose - F-06108 Nice Cedex 02, France (jabin@unice.fr).

<sup>§</sup>Ceremade, Université Paris Dauphine, Place du Maréchal de Lattre de Tassigny F-75775 Paris Cedex 16, France (mischler@ceremade.dauphine.fr).

<sup>¶</sup>CMLA, ENS Cachan, CNRS, PRES UniverSud, 61, Avenue du Président Wilson, 94235 Cachan Cedex, France (raoul@cmla.ens-cachan.fr).

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) with this additive mutation term. We refer the interested reader to the paper [4].

We are interested in the limit for long times of (1.1). The limit should logically be an evolutionarily stable strategy or ESS of the selection process s[f], according to the theory of adaptive dynamics (we refer the reader to [13], [15], [9], [8], and to the comprehensive introduction [5] for more on the rich subject of adaptive dynamics). 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. Several traits can coexist (as in [12]).

Several theoretical questions naturally appear for this model, such as does the population really converge to an equilibrium? (Note that when the function b takes negative values, periodic behaviors of "predator-prey" type can appear). Is this equilibrium an ESS? Does this limit depend on the initial population distribution  $f(0,\cdot)$ ? This paper provides partial answers to those questions. We exhibit long time asymptotics of the population density, and we prove global stability of an ESS in various cases.

Remark 1.1. Let us also point out another interesting limit of (1.1), namely the limit for  $\varepsilon \to 0$  of the solutions  $f_{\varepsilon}$  to

$$\frac{\partial f_{\varepsilon}}{\partial t} = \frac{1}{\varepsilon} s[f_{\varepsilon}], f_{\varepsilon} + m[f_{\varepsilon}], \tag{1.3}$$

where  $m[f_{\varepsilon}]$  denotes a mutation term.

In this last equation the time scales of the selection and mutation are separated (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 dynamics as obtained in [3]. However, since several traits may coexist in our case, the situation can be much more complicated (as pointed out in [7]).

## 2. A general existence result

Most of our results will be obtained under the following

**Assumption 1** Y is a compact interval of  $\mathbb{R}$ , and the pressure operator  $s[f](y) = a(y) - \int_Y b(y, y') f(y') dy'$  satisfies:

- $a \in W^{1,\infty}(Y)$ ,  $\mathcal{O} := \{y; a(y) > 0\} \neq \emptyset$ ;
- $\bullet \ b \in W^{1,\infty}(Y \times Y), \quad \inf\nolimits_{y,y' \in Y} b(y,y') > 0.$

These conditions are sufficient to prove the following theorem of existence.

Theorem 2.1. We suppose that Assumption 1 holds. Then

1. 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) with  $f(0,\cdot) = f_{in}$ . Furthermore,

$$\forall t \ge 0, \qquad \|f(t,\cdot)\|_{L^1(Y)} \le \max\left(\frac{\|a\|_{L^{\infty}(Y)}}{\inf b}, \|f_{in}\|_{L^1(Y)}\right). \tag{2.1}$$

2. For any two nonnegative solutions f, g of (1.1) in  $C([0, +\infty[; L^1(Y)), one has$  the following stability property:

$$\forall t \in [0,T], \qquad ||f(t,\cdot) - g(t,\cdot)||_{L^1(Y)} \le e^{Lt} ||f(0,\cdot) - g(0,\cdot)||_{L^1(Y)}, \tag{2.2}$$

for some L>0 (depending on a, b,  $||f_{in}||_{L^1}$  and  $||g_{in}||_{L^1}$ ). 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, under the additional assumption that  $f_{in} > 0$  a.e. on a given measurable set  $U \subset Y$ , we have that  $f(t,\cdot) > 0$  a.e. on U for any t > 0.

*Proof.* Existence can be proven thanks to the inductive scheme

$$\begin{cases}
f_0(t,y) = f_{in}(y), \\
\partial_t f_{n+1} = s[f_n] f_{n+1}, & f_{n+1}(0) = f_{in}.
\end{cases}$$
(2.3)

Note that all  $f_n$  thus defined are nonnegative, and that  $||f_n||_{L^{\infty}([0,T];L^1(Y))} \le ||f_{in}||_{L^1(Y)}e^{||a||_{L^{\infty}(Y)}T}$  for any T>0. Then, by studying  $f_{n+1}-f_n$ , one can show that  $(f_n)_{n\in\mathbb{N}}$  is a Cauchy sequence in  $L^{\infty}([0,T];L^1(Y))$ , which converges towards a solution f of equation (1.1).

Then, integrating equation (1.1) with respect to  $y \in Y$ , we see that any solution satisfies

$$\partial_t \|f\|_{L^1(Y)} \leq \left( \|a\|_{L^\infty(Y)} - (\inf b) \|f\|_{L^1(Y)} \right) \|f\|_{L^1(Y)},$$

so that we get estimate (2.1) for  $||f||_{L^1(Y)}$ .

We next come to the stability and uniqueness of solutions (that is, Point 2. of our theorem). We compute, for  $t \in [0,T]$ ,

$$\begin{split} &\frac{d}{dt}||f-g||_{L^1(Y)}(t) \\ &= \int_Y (s[f]f-s[g]g)sgn(f-g)dy \\ &\leq \int_Y s[f]|f-g|dy + \int_Y |s[f]-s[g]|gdy \\ &\leq ||s[f]||_{L^\infty(Y)}||f-g||_{L^1(Y)} + ||s[f]-s[g]||_{L^\infty(Y)}||g||_{L^1(Y)} \\ &\leq \left( \|a\|_{L^\infty(Y)} + \|b\|_{L^\infty(Y\times Y)}||f||_{L^1(Y)} + \|b\|_{L^\infty(Y\times Y)}||g||_{L^1(Y)} \right) ||f-g||_{L^1(Y)}, \end{split}$$

and we obtain (2.2) thanks to Gronwall's lemma.

We finally turn to the question of the strict positivity of  $f(t,\cdot)$  (that is, Point 3. of our theorem). We observe that

$$\partial_t f(t,y) \ge -\left(\|a\|_{L^{\infty}(Y)} + \|b\|_{L^{\infty}(Y \times Y)} \|f\|_{L^1(Y)}\right) f(t,y)$$

so that

$$f(t,y) \geq f(0,y) e^{-\left(\|a\|_{L^{\infty}(Y)} + \|b\|_{L^{\infty}(Y \times Y)} \sup_{\sigma \in [0,t]} (||f(\sigma,\cdot)||_{L^{1}(Y)})\right)t}$$

and consequently  $f(t,\cdot) > 0$  a.e. on the set where  $f_{in} > 0$  a.e.

REMARK 2.2. Theorem 2.1 (or a variant of this result) still holds for many selection models which do not satisfy Assumption 1. Indeed, for example, we didn't use in the proof the assumption that a and b have one derivative in  $L^{\infty}$ . One can in fact check that the following abstract properties are sufficient to get a good theory of existence, stability and lower bounds for equation (1.1):

- $\forall r > 0, \exists K > 0, \forall f, g \in L^1(Y),$  $||f,g||_{L^1} \le r \quad \Rightarrow \quad ||s[f]-s[g]||_{L^\infty} \le$  $K \| f - g \|_{L^1}$ ,
- There exists  $A_1 > 0, A_2 : \mathbb{R}_+ \to \mathbb{R}, with A_2(z) \to \infty$  as  $z \to \infty$ , such that for all nonnegative  $f \in L^1(Y)$ ,  $\int_Y s[f] f \leq (A_1 - A_2(\int_Y f)) \int_Y f$ , •  $s[f](y) = s_1(y) - s_2[f](y)$ , where  $s_1 \in L^{\infty}(Y)$ ,  $s_2[y \mapsto 0] = 0$  and  $s_2[f] \geq 0$  for all
- nonnegative  $f \in L^1(Y)$ .

An example of a selection rate satisfying the properties above but not of the form (1.2) can be found in a model used to study the arising of cooperation behaviors in a population (it is a continuous version of the model used in [10]). The formula for s in this model is:

$$s[f](y) = a(y) + \int_{Y} (y-1)f(y)dy - \left(\int_{Y} yf(y)dy\right) \left(\int_{Y} k(y,y')f(y')dy'\right), \quad (2.4)$$

where Y = [0,1],  $a \in L^{\infty}(Y)$ ,  $k \in L^{\infty}(Y \times Y)$  and  $\inf k > 0$ .

However, we shall not in the sequel study equation (1.1) under these abstract assumptions because the crucial property (3.3) – (3.4) defined in next section does not seem to hold in this general setting.

## 3. A general result on the long time asymptotics

Our aim is to investigate the qualitative long time behavior of the solution f to equation (1.1). Making the change of variables  $t'=t/\varepsilon$ , it is equivalent to consider the family of equations (after having renamed by t the rescaled time t' and taken an arbitrarily T > 0

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

We define

$$R_{\varepsilon}(t,y) := \int_{0}^{t} s[f_{\varepsilon}(\sigma,\cdot)](y) d\sigma, \qquad (3.2)$$

so that  $f_{\varepsilon}$  is given by the formula

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

Theorem 3.1. We suppose that Assumption 1 holds.

Let  $0 \le f_{in} \in L^1(Y)$  such that  $f_{in}$  does not vanish a.e. on  $\mathcal{O}$  (the subset of Y on which a > 0), and consider the unique solution  $f_{\varepsilon}$  to equation (3.1) given by Theorem 2.1. Then, there exists  $f \in L^{\infty}([0,T],M^1(Y))$  and a subfamily of  $(f_{\varepsilon})$  and  $(R_{\varepsilon})$  (still denoted by  $(f_{\varepsilon})$  and  $(R_{\varepsilon})$ ), such that

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

$$(3.3)$$

where

$$(t,y) \mapsto R(t,y) := \int_0^t s[f(\sigma,.)](y) d\sigma \in W^{1,\infty}(]0,T[\times Y). \tag{3.4}$$

Moreover, R and f satisfy:

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

Finally, denote by  $\Omega(t)$  the set of traits  $y \in Y$  such that R(t,y) = 0, and denote by  $\omega(t)$  the support of the measure f(t,.) (which is defined a.e. on (0,T)),

$$\omega(t) \neq \emptyset$$
,  $\omega(t) \subset \Omega(t)$  (for a.e.  $t \in [0,T]$ ).

REMARK 3.2. More precisely, since R is a continuous function, the inclusion  $\omega(t) \subset \Omega(t)$  for a.e.  $t \in [0,T]$  means that if  $R(t_*,y_*) < 0$  at some point  $(t_*,y_*) \in [0,T] \times Y$ , then there exists  $\delta > 0$  such that

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

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

# Proof of Theorem 3.1.

Step 1. We first observe that the selection pressure operator  $s/\varepsilon$  satisfies Assumption 1, so that, thanks to Theorem 2.1, we know the existence and uniqueness of a nonnegative solution  $f_{\varepsilon} \in C([0,\infty); L^1)$  to equation (3.1) for any  $\varepsilon > 0$ . Moreover, the total number of individuals  $||f_{\varepsilon}(t,.)||_{L^1}$  satisfies the differential inequality

$$\partial_t \| f_{\varepsilon}(t,.) \|_{L^1} \leq \frac{1}{\varepsilon} (\|a\|_{L^{\infty}} - \|b\|_{L^{\infty}} \|f_{\varepsilon}(t,.)\|_{L^1}) \|f_{\varepsilon}(t,.)\|_{L^1}$$

so that (Cf. estimate (2.1))

$$\forall t \ge 0, \qquad \|f_{\varepsilon}(t,.)\|_{L^{1}} \le \max\left(\frac{\|a\|_{L^{\infty}(Y)}}{\inf b}, \|f_{in}\|_{L^{1}(Y)}\right).$$
 (3.5)

Therefore, up to extraction,

$$f_{\varepsilon} \rightharpoonup f \quad L^{\infty}(w*]0, T[; \sigma(M^1, C_b)(Y)).$$
 (3.6)

On the one hand, (3.6) leads to

$$\forall (t,y) \in \mathbb{R}_+ \times Y, \qquad R_{\varepsilon}(t,y) \to R(t,y),$$
 (3.7)

where R is given by formula (3.4).

On the other hand, thanks to the assumptions  $a \in W^{1,\infty}(Y)$ ,  $b \in W^{1,\infty}(Y \times Y)$ , the families  $(s[f_{\varepsilon}])$  and  $(\partial_y s[f_{\varepsilon}])$  are bounded in  $L^{\infty}((0,T) \times Y)$ . Thanks to (3.2) we have

$$\partial_t R_{\varepsilon} = s[f_{\varepsilon}], \quad \partial_y R_{\varepsilon} = \int_0^t \partial_y s[f_{\varepsilon}(\sigma, \cdot)] d\sigma,$$

and we can see that  $(R_{\varepsilon})$ ,  $(\partial_t R_{\varepsilon})$  and  $(\partial_y R_{\varepsilon})$  are bounded in  $L^{\infty}((0,T) \times Y)$ . We conclude that  $(R_{\varepsilon})$  is bounded in  $W^{1,\infty}((0,T) \times Y)$ , which is (strongly) compactly embedded in  $C([0,T] \times Y)$ , so that  $R_{\varepsilon} \to R$  uniformly on  $[0,T] \times Y$ .

Step 2. We prove that  $R \leq 0$  on  $(0,T) \times Y$ . First, notice that for any  $t \in (0,T)$  and any  $y \in Y \setminus \mathcal{O}$ , there holds

$$R(t,y) = \int_0^t s[f(\sigma,.)](y) d\sigma \le \int_0^t s[y \mapsto 0](y) d\sigma \le 0$$

with strict inequality if  $f \not\equiv 0$  a.e. on  $(0,t) \times Y$ . Let us then assume that  $R(t_*,y_*) > 0$  at a certain point  $(t_*,y_*) \in [0,T] \times Y$ . From the previous considerations, we see that  $y_* \in \mathcal{O}$ . Moreover, from the uniform convergence established in Step 1, there holds  $R_{\varepsilon}(t,y) \geq \delta$  for some  $\delta > 0$ , as soon as  $|t-t_*| \leq \delta$ ,  $|y-y_*| \leq \delta$  and  $0 < \varepsilon \leq \delta$ . As a consequence and because  $f_{in} > 0$  a.e. on  $\mathcal{O}$ ,  $B(y_*,\delta) \subset \mathcal{O}$ , and we have

$$\rho_{\varepsilon}(t) := \int_{Y} f_{\varepsilon}(t,y) \, dy \ge \int_{\mathcal{O}} e^{R_{\varepsilon}(t,y)/\varepsilon} f_{in}(y) \, dy \ge \int_{B(y_{\varepsilon},\delta)} e^{\delta/\varepsilon} f_{in}(y) \, dy \xrightarrow[\varepsilon \to 0]{} \infty.$$

This contradicts the conclusion of estimate (3.5).

Step 3. We prove that if  $R(t_*,y_*)<0$  at some point  $(t_*,y_*)\in[0,T]\times Y$ , then f vanishes in a neighborhood of that point. As a consequence, supp  $f\subset\{(t,y)\in[0,T]\times Y;R(t,y)=0\}$ , and if R(t,.)<0 on Y, then  $f(t,.)\equiv 0$  a.e. on Y. Let us indeed assume that  $R(t_*,y_*)<0$  at some point  $(t_*,y_*)\in[0,T]\times Y$ . There exists some  $\delta>0$  such that  $R_\varepsilon(t,y)\leq-\delta$  as soon as  $|t-t_*|\leq\delta, |y-y_*|\leq\delta$  and  $0<\varepsilon\leq\delta$ . We consider a smooth test function  $\chi:\mathbb{R}\to\mathbb{R}$  such that  $1_{B(y_*,\delta/2)}\leq\chi\leq 1_{B(y_*,\delta)}$  and we compute

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

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

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

Step 4. We prove that  $\max R(t,.) = 0$  for any  $t \in [0,T]$  and  $\|f(t,\cdot)\|_{L^1(Y)} > 0$  for a.e.  $t \in [0,T]$ . Assume indeed by contradiction that there exists a first time  $\tau \in [0,T]$  for which such a property is false, namely assume that  $\max R(t,.) = 0$  for any  $t \in [0,\tau]$ ,  $\|f(t,\cdot)\|_{L^1(Y)} > 0$  for a.e.  $t \in [0,\tau]$  and that  $\max R(t,.) < 0$  for any  $t \in (\tau,\tau+\varepsilon)$  or  $\rho(t) = 0$  for a.e.  $t \in (\tau,\tau+\varepsilon)$ , with  $\tau,\varepsilon \in \mathbb{R}$  such that  $0 \le \tau < \tau + \varepsilon \le T$ . Thanks to Step 3 we see that in both cases we have  $\|f(t,\cdot)\|_{L^1(Y)} = 0$  for a.e.  $t \in (\tau,\tau+\varepsilon)$ . Let consider  $y_* \in Y$  such that  $R(\tau,y_*) = 0$ . If  $\tau = 0$  we can of course choose  $y_* \in \mathcal{O}$  and if  $\tau > 0$  we must have  $y_* \in \mathcal{O}$  because of the first remark in Step 2 and the fact that f does not vanish a.e. on  $(0,\tau) \times Y$ . We then compute

$$R(\tau+\varepsilon,y_*) = R(\tau,y_*) + \int_{\tau}^{\tau+\varepsilon} s[f(t,.)](y_*) dt = \varepsilon s[y \mapsto 0](y_*) > 0,$$

which is in contradiction with the conclusions of Step 2. As a consequence, we see that  $||f||_{L^1(Y)} \not\equiv 0$  a.e. on  $(\tau, \tau + \varepsilon)$ , so that  $||f||_{L^1(Y)} > 0$  a.e. on  $(\tau, \tau + \varepsilon)$  and then also  $\max R(t, \cdot) = 0$  for any  $t \in (\tau, \tau + \varepsilon)$ .

## 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

Example 4.1. Assume that

$$s[f](y) = a(y) - b_1(y) \int_Y b_2(y') f(y') dy',$$

where  $a, b_i \in W^{1,\infty}(Y)$ ,  $\forall y \in Y$   $b_i(y) \ge b_m > 0$  and the function  $y \mapsto a(y)/b_1(y)$  has a positive maximum reached at some points  $y_1^*, ..., y_k^* \in Y$ ,  $k \in \mathbb{N}^*$ . Then, if  $f_{in} \in L^1(Y)$  with  $f_{in} > 0$  a.e. on Y, the measure f given by Theorem 3.1 is

$$f(t,y) = \sum_{j=1}^{k} \rho_j(t) \delta_{y=y_j^*}$$
 with  $\sum_{j=1}^{k} \rho_j(t) b_2(y_j^*) = \frac{a(y_1^*)}{b_1(y_1^*)}$ .

In particular, when k=1,

$$f(t,y) = \frac{a(y_1^*)}{b(y_1^*)} \delta_{y=y_1^*},$$

and the whole family  $(f_{\varepsilon})$  converges weakly  $\sigma(M^1, C_c)$  to f.

REMARK 4.2. et emphasize that we do not assume here the lower bound  $\inf a > 0$  (as it is done in [16]).

**Proof of the statement of Example 4.1**. The quantity R defined by Theorem 3.1 satisfies the following identity:

$$\frac{R(t,y)}{b_1(y)} = \frac{a(y)}{b_1(y)}t - \int_0^t \int_Y b_2(y')f(\sigma,y')\,dy'd\sigma.$$

Since the second term does not depend on the variable y and the first term reaches its maximum at the points  $y_1^*, ..., y_k^*$ , the conclusions of Theorem 3.1 state that R(t,.) is nonpositive and vanishes somewhere, implying here that

$$R(t,y) = 0 \text{ iff } y = y_i^* \text{ and } R(t,y) < 0 \text{ for any } y \notin \{y_1^*, ..., y_k^*\}.$$

This ensures that

$$f(t,y) = \sum_{j=1}^{k} \rho_j(t) \, \delta_{y=y_j^*}, \quad \rho_j(t) \ge 0,$$

and we get the condition on  $(\rho_j)$  by writing  $R(y_1^*) = 0$ . When k = 1, we can completely identify  $\rho_1(t)$  due to that equation.

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 case when the competition does not lead to a branching. We state a precise result:

EXAMPLE 4.3. Assume that Y = [-1,1] and  $s[f] = a(y) - \int_Y b(y-y') f(y') dy'$ . We suppose that  $a \in C^1(Y; \mathbb{R}_+^*)$  takes its unique maximum at point 0, and that for some constants A, C > 0,

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

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

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

Finally, we suppose that

$$2CE < AD. (4.1)$$

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.* We begin by observing that because of the maximum principle,  $||f(t,\cdot)||_{L^1} \leq \frac{C}{D}$ . We denote by Q the set  $\{y, \exists t \in ]0,T], (t,y) \in \text{Supp } f\}$ . 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 as

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

Then

$$\begin{split} t \, |a'(y_*)| &\leq \int_0^t \int_{z \in Q} |b'(y-z)| \, |f(s,z)| \, dz ds \\ &\leq ||b'||_{L^{\infty}(Q-Q)} \int_0^t \int_{z \in Q} |f(s,z)| \, dz ds \leq \frac{C}{D} \, t \, ||b'||_{L^{\infty}(Q-Q)}, \end{split}$$

and we end up with the following estimate

$$||a'||_{L^{\infty}(Q)} \le \frac{C}{D}||b'||_{L^{\infty}(Q-Q)}.$$
 (4.2)

Here, Q-Q is the set of differences of two elements of Q. Since  $Q \subset [-1,1]$ , one first has from (4.2) that

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

so that

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

and finally  $Q \subset \left[-\frac{2EC}{AD}, \frac{2EC}{AD}\right]$ . Then, repeating the argument, one next has from (4.2) that

$$\forall x \in Q, \qquad A|x| \le |a'(x)| \le \frac{C}{D} ||b'||_{L^{\infty}([-\frac{4EC}{AD}, \frac{4EC}{AD}])},$$

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 (4.1), we see that  $Q = \{0\}$ , which shows the result.

Remark 4.4. A local version of this result is the following:

If  $a \in C^2([-1,1])$ ,  $b \in C^2([-2,2])$ , 0 is a maximum for a and b,  $a''(0) - b''(0) \frac{a(0)}{b(0)} < 0$ , and  $\sup\{|x|; f_{in}(x) > 0\}$  is small enough, then  $f = \frac{a(0)}{b(0)} \delta_0$ .

Notice that the assumption  $a''(0) - b''(0) \frac{a(0)}{b(0)} < 0$  looks like the definition of an ESS (see 5.7), but is stronger.

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).

THEOREM 4.5. We suppose that Assumption 1 holds. Assume moreover that for some  $m', m'' \in \mathbb{N}^*, y \mapsto s[f](y) \in C^{m'}(Y)$  for any  $f \in M^1_+(Y)$  and either  $\partial_y^{m'} s[f](y)$  only vanishes on at most m'' points on Y for any  $f \in M^1_+(Y)$  or  $\partial_y^{m'} s[f](y) > 0$  on Y for any  $f \in M^1_+(Y)$  (resp.  $\partial_y^{m'} s[f](y) < 0$  on Y for any  $f \in M^1_+(Y)$ ). In the latter case we set m'' = 0.

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

$$f(t,y) = \sum_{i=1}^{m} \rho_i(t) \,\delta_{y=y_i(t)}, \quad m = m' + m''$$
(4.3)

for some  $y_i(t) \in Y$  and  $\rho_i(t) \ge 0$  (i = 1,...,m) with  $\rho_f = \rho_1 + ... + \rho_m > 0$  a.e. on [0,T].

*Proof.* In that case R is clearly in  $C^{m'}(Y)$  and for any time  $t \in [0,T]$ ,

$$\frac{\partial^{m'}R}{\partial y^{m'}}(t,y) = \int_0^t \frac{\partial^{m'}}{\partial y^{m'}} s[f(\sigma,\cdot)](y) \, d\sigma.$$

Under our assumptions, either  $\partial^{m'}R$  has a constant sign (always the same) or vanishes at most m'' times. In any cases the function  $y \mapsto R(t,y)$  has at most m zeros on Y and we conclude thanks to Theorem 3.1.

## 5. Linear stability

In many situations, it is very difficult to prove the nonlinear global stability of a general steady state. It is however at least possible to explore the linear stability (with respect to perturbations having a particuliar shape) of some specific steady solutions of equation (1.1) - (1.2), that is

$$\frac{\partial f}{\partial t}(t,y) = \left(a(y) - \int_Y b(y,y') f(t,y') dy'\right) f(t,y). \tag{5.1}$$

This leads to computations similar to those appearing in adaptive dynamics. We begin with the analysis of the steady solutions to equation (5.1) (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

$$f(y) = \sum_{i=1}^{N} \rho_i \, \delta_{y_i}(y), \tag{5.2}$$

(where  $\rho_1 > 0, ..., \rho_N > 0$ ) is a steady solution of equation (5.1) if and only if

$$a(y_i) = \sum_{j=1}^{N} \rho_j b(y_i, y_j). \qquad i = 1, ..., N.$$
 (5.3)

Starting from a perturbation of the function in (5.2) of the form

$$f(y) = \varepsilon \delta_s(y) + \sum_{i=1}^{N} \rho_i \delta_{y_i}(y)$$
(5.4)

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:

$$a(s) < \sum_{j=1}^{N} \rho_j b(s, y_j), \qquad s \in Y, s \neq y_1, ..., y_N.$$
 (5.5)

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.

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

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

$$(5.6)$$

$$a''(y_i) \le \sum_{j=1}^{N} \rho_j \frac{\partial^2 b}{\partial 1^2}(y_i, y_j), \qquad i = 1, ..., N.$$
 (5.7)

Those formulas are similar to the equations obtained in adaptive dynamics: (5.6) corresponds to singular strategies, and (5.7) corresponds to the Evolutionary Stable Strategies.

Equations (5.3), (5.6) and (5.7) (for arbitrary  $N \in \mathbb{N}_*$ ,  $b_i > 0$  and  $y_i \in Y$ ) enables to find the steady, locally linearly stable (with respect to perturbations which are Dirac masses) solutions of equation (3.1) of the particular shape (5.2).

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. In this subsection we study the case where

$$a(y) = A - y^2, b(y,z) = \frac{1}{1 + (y-z)^2},$$
 (5.8)

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 equation (5.1) 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|. However, it remains nonnegative whatever the values of y,z are. In other words, there is always competition and never cooperation between the individuals.

Note also that the bigger the parameter A becomes (that is, the wider the interval  $\{x; a(x) > 0\}$  is compared to  $b(\cdot)$ ), the higher is the interest for individuals to have different traits. In other words, N should grow with A.

In the following, we look for the locally and globally linearly stable (with respect to perturbations which are Dirac masses) steady solutions of equation (3.1) of the form (5.2), with coefficients defined by (5.8). Since the coefficients are symmetric with respect to 0, we only look for symmetric steady states.

**5.2.1.** N=1. We start by examining 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 only one symmetric solution given by

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

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 (5.3), (5.6) when N=2, and with a,b defined in (5.8). That is, we wish to solve

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

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

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

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

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

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

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

$$x = \frac{-7 + \sqrt{17 + 32A}}{16},\tag{5.9}$$

so that

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

Note that  $\rho_1 \ge 0$  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

$$a''(y_1) - \rho_1 \frac{\partial^2 b}{\partial 1^2} (y_1, y_1) - \rho_2 \frac{\partial^2 b}{\partial 1^2} (y_1, y_2)$$

$$= -2 - \rho_1 \left( -2 + \frac{24y_1^2 - 2}{(1 + 4y_1^2)^3} \right)$$

$$= -2 + (1 + 4x^2)^2 + \frac{1 - 12x}{1 + 4x}.$$

This quantity is nonnegative if and only if  $x(8x^2+6x-1) \ge 0$ , i.e.,  $x \ge \frac{-3+\sqrt{17}}{8}$ . Remembering (5.9), this means that  $A \ge \frac{13+\sqrt{17}}{8} \sim 2.13$ .

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  $u=s^2$ )

$$a(s) - \rho_1 b(s, y_1) - \rho_2 b(s, y_2) = A - s^2 - \rho_1 \left[ \frac{1}{1 + (y_1 - s)^2} + \frac{1}{1 + (y_1 + s)^2} \right]$$
(5.10)  

$$= A - u - \rho_1 \left[ \frac{2 + 2u + 2x}{1 + 2u + 2x + x^2 + u^2 - 2xu} \right]$$
(5.11)  

$$= -\frac{(u - x)^2 (u + 2 - A)}{1 + 2u + 2x + (x - u)^2}.$$
(5.12)

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 results 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 determine 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 equation (5.1) (that is, (5.3), (5.6)) can be rewritten in the form

$$\begin{cases}
A - y_1^2 = \rho_1 \left( 1 + \frac{1}{1 + 4y_1^2} \right) + \rho_2 \frac{1}{1 + y_1^2}, \\
A = 2 \rho_1 \frac{1}{1 + y_1^2} + \rho_2, \\
1 = 2 \rho_1 \frac{1}{(1 + 4y_1^2)^2} + \rho_2 \frac{1}{(1 + y_1^2)^2}.
\end{cases} (5.13)$$

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

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

The only strictly positive solution of this equation is

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

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

$$8x^2 + 31x - 13 - 9u > 0$$

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

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

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

It is also easy to verify that for A > 3, the condition of local linear stability is not fulfilled for a 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 equation (5.1) which are not sums of Dirac masses. Unfortunatly, we couldn't answer this question. A first case has been studied by Genieys, Volpert and Auger in [11], They show that in the case where a(x) = 1, the steady solution  $\bar{f} = 1$  is unstable as soon as the Fourier transform of b is not positive.

In the following, we study the case of a and b Gaussian. In order to keep the possibility of performing explicit computations, we take in this subsection  $Y = \mathbb{R}$  instead of a compact interval. The stability of the steady state remains unclear, but at least it seems that the steady state is unstable under slight modifications of the parameters a and b.

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

$$a(y) = \frac{1}{\sqrt{2\pi(T_1 + T_2)}} e^{-\frac{y^2}{2(T_1 + T_2)}}, \quad b(y) = \frac{1}{\sqrt{2\pi T_1}} e^{-\frac{y^2}{2T_1}}, \tag{5.14}$$

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 subsection 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  $\bar{f} + \varepsilon g(t=0) \ge 0$ . Then, equation (5.1) 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, if  $T_1 = 1$ ,  $T_2 = 1.33$  (but such perturbations g can be found for every  $T_1$ ,  $T_2$ ), taking

$$g(t=0) = (\sin(26.69x) - 202\sin(27.5x)) e^{-0.19x^2}, \tag{5.15}$$

we see that

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

and that  $\bar{f} + \varepsilon g(t=0) \ge 0$  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 (5.15), positive but very small. This suggests that this instability might take a long time to develop.

Another interesting notion of stability is the stability of steady-states of the equation (5.1) under perturbations of the coefficients a and b. This has been studied by Gyllenberg and Meszena in [14, Thms. 6 and 8]. 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 (5.1) does not admit any steady solution  $\tilde{f}$  such that  $supp(\tilde{f})$  has an accumulation point.

In the next section we present numerical simulations for a and b Gaussian. We cannot guess from those simulations whether  $\bar{f}$  is stable or not for the a, b given by (5.14), but we show that for slight perturbations of a or b, the populations seems to converge to a (presumably) infinite sum of Dirac masses.

## 6. Numerical simulations

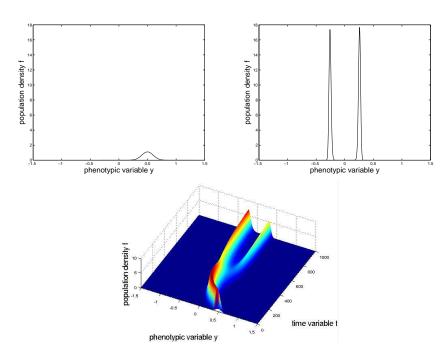


Fig. 6.1. Simulation for A = 1.5 at times t = 0, t = 10000, and for  $t \in [0, 1000]$ .

**6.1. The numerical method.** All simulations have been done for equation (5.1), in the case where b(y,y') := b(y-y'). We assume that  $f_{in}$ , a and b have 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  $\left[\frac{1}{4}, \frac{3}{4}\right]$  and that the convolution b\*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 of the form of a finite sequence  $(f_i)_{i=0...N}$ . The equation becomes (with  $a_i := N \int_{\left[\frac{i}{N}, \frac{i+1}{N}\right]} a$  and  $b_i := N \int_{\left[\frac{i}{N}, \frac{i+1}{N}\right]} b$ ):

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

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:

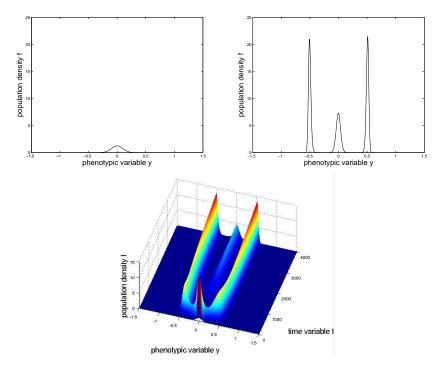


Fig. 6.2. Simulation for A = 2.5, at times t = 0, t = 10000 and for  $t \in [0,4000]$ .

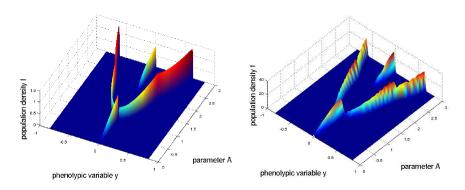


Fig. 6.3. Theoretical asymptotic solution for  $A \in [0,3]$ , and numerical solutions  $f(t=20\,000)$  for  $A \in [0,3]$ .

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

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  $N^2$ .

**6.2.** Simulation for the example of subsection 5.2. In subsection 5.2, we found linearly stable steady solutions of equation (5.1) with data (5.8) in the form

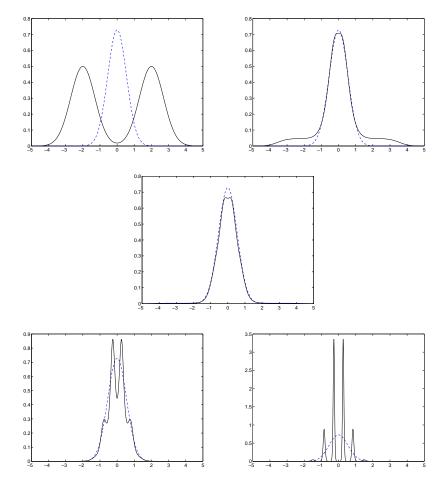


FIG. 6.4. Simulation for  $T_1 = 0.1, T_2 = 0.3$ , a given by (5.14), and  $b(y) = \frac{1}{\sqrt{2\pi T_1}}e^{-\frac{y^{2.2}}{2T_1}}$ , at times t = 0, 20, 300, 1000, 2000. f: continuous line,  $\bar{f}$ : dashed line.

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 Figure 6.1 (corresponding to  $A \in ]1,2]$ ), we observe a branching of the initial datum into two subspecies, while in Figure 6.2 (corresponding to  $A \in [2,3]$ ), the middle subspecies appears without any branching.

In Figure 6.3, 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.

**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 equation (5.1) with

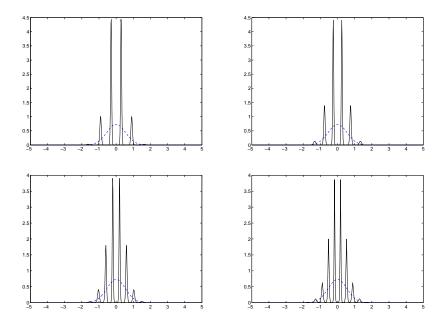


FIG. 6.5. Simulation for  $T_1 = 0.1, T_2 = 0.3$ , a given by (5.14), and  $b(y) = \frac{1}{\sqrt{2\pi}T_1}e^{-\frac{y^{(2+\varepsilon)}}{2T_1}}$ , where  $\varepsilon = 0.3, 10^{-1}, 10^{-2}, 10^{-3}$ , at times (respectively) t = 1500, 6000, 120000, 2000000.

data (5.14). We have led long time simulations for various initial conditions, and the solution always seem to converge to the Gaussian steady state  $\bar{f}$ .

For slight modifications of the parameters a or b, 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  $\sum_{i \in \mathbb{Z}} \alpha_i \delta_{(i+\frac{1}{2})h}$  where h > 0 is a certain number depending on a and b (see Figure 6.4). In Figure 6.5, we show the long-time shape of f for various perturbations of b. It is interesting to notice that

- the "destabilization time" where f ceases to be close to a Gaussian and begins to look like a sum of Dirac Masses increases as the perturbations of the coefficients become small,
- the quantity h seems to decrease to 0 as a and b get close to Gaussians (see Figure 6.5).

The first consequence of those observations is that one must be very careful while numerically studying the stability of a steady-state. Any numerically-induced perturbation of coefficients can drastically modify the behavior of the solution. The second consequence is that the Gaussian solution might be stable in a weak sense under perturbations of the coefficients, despite the results of [14].

### REFERENCES

- [1] R. Bürger, The Mathematical Theory of Selection, Recombination and Mutation, Wiley, New-York, 2000.
- [2] A. Calcina and S. Cuadrado, Small mutation rate and evolutionarily stable strategies in infinite dimensional adaptive dynamics, J. Math. Biol., 48, 135–159, 2004.

- [3] N. Champagnat, R. Ferrière and G. Ben Arous, *The canonical equation of adaptive dynamics:* a mathematical view, Selection, 2, 71–81, 2001.
- [4] N. Champagnat, R. Ferrière and S. et Méléard, Unifying evolutionary dynamics: From individual stochastic processes to macroscopic models, Theor. Popul. Biol., 69, 297–321, 2006.
- [5] O. Diekmann, Beginner's guide to adaptive dynamics, Banach Center Publications, 63, 47–86, 2004.
- [6] O. Diekmann, M. Gyllenberg and J.A.J. Metz, Steady states analysis of structured population models, Theor. Popul. Biol., 63, 309–338, 2003.
- [7] O. Diekmann, P.E. Jabin, S. Mischler and B. Perthame, The dynamics of adaptation: an illuminating example and a Hamilton-Jacobi approach, Theor. Popul. Biol., 67, 257–271, 2005.
- [8] U. Dieckmann and R. Law, The dynamical theory of coevolution: A derivation from a stochastic ecological processes, J. Math. Biol., 34, 579-612, 1996.
- [9] M. Durinx, J.A.J. Metz and G. Meszéna, Adaptive dynamics for physiologically structured population models, J. Math. Biol., 56(5), 673-742, 2008.
- [10] R. Ferrière, J.L. Bronstein, S. Rinaldi, R. Law and M. Gauduchon, Cheating and the evolutionary stability of mutualisms, Proc. Royal Soc. London Ser. B, 269, 773–780, 2002.
- [11] S. Genieys, V. Volpert and P. Auger, Pattern and waves for a model in population dynamics with nonlocal consumption of resources, Math. Model. Nat. Phenom., 1, 65–82, 2006.
- [12] S.A.H. Geritz, Resident-invader dynamics and the coexistence of similar strategies, J. Math. Biol., 50, 67–82, 2005.
- [13] S.A.H. Geritz, É. Kisdi, G. Meszéna and J.A.J. Metz, Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree, Evol. Ecol., 12, 35–57, 1998.
- [14] M. Gyllenberg, G. Meszna, On the impossibility of coexistence of infinitely many strategies, J. Math. Biol., 50, 133–160, 2005.
- [15] J.A.J. Metz, S.A.H. Geritz, G. Meszéna and F.J.A. Jacobs, Stochastic and Spatial Structures of Dynamical Systems, S. J. van Strien and S. M. Verduyn-Lunel eds, North Holland, Elsevier, 1996.
- [16] B. Perthame, Transport Equation in Biology, Frontiers in Mathematics series, Birkhäuser, 2005.