

## Mutation and recombination in a model of phenotype evolution

P. MAGAL

*Abstract.* A model of phenotype evolution incorporating mutation and recombination is investigated. The model consists of an ordinary differential equation for the population density with respect to a continuous variable representing phenotype diversity. We prove that each solution converges for the weak\* topology to a Radon measure.

### 1. Introduction

In this paper we investigate the following model for the evolution of a population with a continuously varying phenotype structure

$$\begin{cases} \frac{du}{dt} = \gamma[L(u(t)) - u(t)] + \tau[R(u(t)) - u(t)] + r(1 - \frac{1}{K} \int_0^1 u(t)(\widehat{y})d\widehat{y})u(t) \\ u(0) = u_0 \in L^1_+(0, 1), \end{cases} \quad (1)$$

where  $u(t)(y)$  is the density of population,  $\gamma \geq 0$  is the mutation rate,  $\tau > 0$  is the recombination rate,  $r > 0$  is the growth rate, and  $K > 0$  is the carrying capacity. The bounded linear operator  $L \in \mathcal{L}(L^1(0, 1), L^1(0, 1))$  is defined by

$$L(\varphi)(y) = \int_0^1 K_0(y, \widehat{y})\varphi(\widehat{y})d\widehat{y},$$

the nonlinear operator  $R : L^1_+(0, 1) \rightarrow L^1_+(0, 1)$  is defined by

$$R(\varphi)(y) = \begin{cases} \frac{\int_0^1 K_1(y, \widehat{y})\varphi(2y-\widehat{y})\varphi(\widehat{y})d\widehat{y}}{\int_0^1 \varphi(\widehat{y})d\widehat{y}}, & \text{if } \varphi \in L^1_+(0, 1) \setminus \{0\}, \\ 0 & \text{if } \varphi = 0. \end{cases}$$

The kernels are defined by

$$K_0(y, \widehat{y}) = \begin{cases} \frac{1}{1-\alpha} & \text{if } 0 < \widehat{y} < 1, \text{ and } \alpha\widehat{y} < y < \alpha\widehat{y} + 1 - \alpha, \\ 0 & \text{elsewhere,} \end{cases}$$

---

Received November 29, 2000; accepted August 30, 2001.

2000 *Mathematics Subject Classification*: 34A35, 47H20, 92D15.

*Key words*: Semigroups, asymptotic behavior, evolution, mutation, recombination.

with  $0 \leq \alpha < 1$ , and

$$K_1(y, \widehat{y}) = \begin{cases} 2 & \text{if } 0 \leq y \leq \frac{1}{2} \text{ and } 0 \leq \widehat{y} \leq 2y, \\ 2 & \text{if } \frac{1}{2} \leq y \leq 1 \text{ and } 2y - 1 \leq \widehat{y} \leq 1, \\ 0 & \text{elsewhere.} \end{cases}$$

In (1)  $u(t, y)$  is the density of a population with respect to a phenotype variable  $y \in (0, 1)$  at time  $t$ . The subpopulation of phenotypes at time  $t$  in the range  $[y_1, y_2] \subset [0, 1]$  is given by  $\int_{y_1}^{y_2} u(t, y) dy$ . The population is viewed as evolving over time due to the two separated processes of mutation, and recombination. In (1)  $\gamma$  represents the proportion of population which mutates, and the mutation process is represented by the kernel operator  $[L(u(t)) - u(t)]$ . Also,  $\tau$  represents the proportion involved in DNA exchange in phenotype evolution, which is represented by the term  $[R(u(t)) - u(t)]$ . The recombination operator  $R$  corresponds to the average rate at which two parent phenotypes  $y_1$  and  $y_2$  hybridize to yield offspring with phenotype  $\frac{y_1 + y_2}{2}$ . In (1) there is also a density dependent mortality independent of phenotype represented by the crowding term  $\mathcal{F}(u(t)) = \frac{r}{K} \int_0^1 u(t)(\widehat{y}) d\widehat{y}$ . Problem (1) thus models the evolution of phenotype structure from the initial phenotype distribution  $u_0 \in X = L^1(0, 1)$  at time 0 by these processes.

In [4] the asymptotic behavior of the model was studied when mutation is modeled by diffusion (with Neumann boundary conditions) and dominates recombination (i.e. when  $\tau$  is small). In this case it was shown in [4] that the distribution converges in  $X$  to a unique equilibrium independent of  $u_0 \in X_+ \setminus \{0\}$ . Here, in order to be able to investigate the asymptotic behavior when recombination dominates mutation, we simplify the model. First, we replace the diffusion operator  $d^2 \frac{\partial^2 u}{\partial x^2}$  in [4] by the kernel operator  $\gamma(L - Id)$ , and we assume that there is no natural selection (this assumption will be discussed in Section 5).

We now explain why the new model for the process of mutations is qualitatively similar to the previous one. The idea for this change is that we consider a kernel operator that: 1) has some convenient mathematical properties; and 2) generates a semigroup that asymptotically converges to the semigroup generated by the diffusion operator. More precisely, in both cases (i.e. diffusion operator and kernel operator) the semigroup has the property of asynchronous exponential growth (see [4], and Theorem 3.2 in Section 2 for this result). We have

$$T(t)\varphi \rightarrow \int_0^1 \varphi(\widehat{y}) d\widehat{y} \phi_0(y) \text{ as } t \rightarrow +\infty \text{ in } L^1(0, 1),$$

where  $\phi_0$  is a positive integrable function which is normalized, i.e.  $\int_0^1 \phi_0(\widehat{y}) d\widehat{y} = 1$ .

In the case of the diffusion operator (with Neumann boundary conditions) we have

$$\phi_0(y) = 1, \text{ a.e. in } (0, 1).$$

But for the kernel operator, when  $\alpha = 0$ , it is easy to see that  $L\phi_0 = \phi_0$ . So when  $\alpha = 0$ , both semigroups asymptotically coincide. Furthermore, when  $0 < \alpha < 1$ , one can see that  $L\phi_0 = \phi_0$  implies  $\phi_0(0) = \phi_0(1) = 0$  (since  $L(\varphi)(0) = L(\varphi)(1) = 0$  for any  $\varphi$  in  $L^1(0, 1)$ ). So, the case  $0 < \alpha < 1$  corresponds to a “diffusion” process with Dirichlet boundary conditions.

Making these simplifications, we obtain the convergence of all the moments of the distribution when time goes to infinity. More precisely, in Section 3 we will prove that if  $\gamma = 0$ , then

$$\begin{aligned} E_1(u(t)) &= E_1(u_0) \quad \forall t \geq 0, \\ E_k(u(t)) &\rightarrow E_1(u_0)^k \text{ as } t \rightarrow +\infty, \quad \forall k \geq 2, \end{aligned}$$

where

$$E_k(\phi) = \frac{\int_0^1 y^k \phi(y) dy}{\int_0^1 \phi(y) dy}, \quad \forall \phi \in L_+^1(0, 1) \setminus \{0\}, \quad \forall k \geq 1.$$

From this result we will deduce that

$$u(t) \rightharpoonup^* K\delta_{E_1(u_0)} \text{ as } t \rightarrow +\infty,$$

which is equivalent to the assertion

$$\int_0^1 f(y)u(t)(y)dy \rightarrow K\delta_{E_1(u_0)}(f) \text{ as } t \rightarrow +\infty, \quad \forall f \in C([0, 1], \mathbb{R}),$$

where  $\delta_c(\psi) = \psi(c)$ ,  $\forall c \in [0, 1]$ ,  $\forall \psi \in C([0, 1], \mathbb{R})$ . So, when there is no mutation the distribution of the population converges to a Dirac measure, and the limit distribution only depends on the mean of the initial value.

In Section 4, we will consider the case  $\gamma > 0$ . We will prove that

$$\begin{aligned} E_1(u(t)) &\rightarrow \frac{1}{2} \text{ as } t \rightarrow +\infty \\ E_k(u(t)) &\rightarrow \bar{E}_k \text{ as } t \rightarrow +\infty, \quad \forall k \geq 2, \end{aligned}$$

where  $\bar{E}_k$  does not depend on the initial distribution  $u_0 \in X_+ \setminus \{0\}$ . From this result we deduce the convergence of all solutions of (1) to a unique Radon measure (for the weak\* topology). It is important to note that when  $\gamma > 0$  the limit does not depend on the initial distribution  $u_0$ . Moreover, one can see that the smaller  $\gamma > 0$  is, the slower the speed of convergence to the limit. This result means that in the absence of natural selection, the asymptotic distribution of the population does not depend on the founding population, if there is some mutation. But when the mutation is weak (i.e. when  $\gamma$  is small), and when we start with two different founding populations, the differences in the observations may be only due to the speed of convergence to the limit.

An example of phenotype evolution (in which the phenotype is a continuous variable) is the colonization of *Helicobacter pylori*, a bacteria inhabiting the human stomach. This bacteria displays phenotype diversity in its expression of Lewis type antigen, which varies continuously through a range of optical density measurements. Experiments in [8] and [9] demonstrate that during the colonization of *Helicobacter pylori* the phenotype population migrates and stabilizes through successive generations subject to selection, mutation, and recombination process in the host.

## 2. Preliminary results

In the sequel, we denote

$$X = L^1(0, 1), X_+ = L^1_+(0, 1), \text{ and } S(0, r) = \{x \in X : \|x\| = r\}.$$

We start with some properties of the operator  $R$ .

**THEOREM 2.1.**  *$R$  is a nonlinear operator from  $X_+$  to  $X_+$  satisfying the following properties:*

- i)  $R$  is positive homogeneous, i.e.  $R(c\phi) = cR(\phi), \forall \phi \in X_+, \forall c \geq 0$ .
- ii)  $R$  is Lipschitz continuous in  $X_+$ .
- iii)  $R$  preserves norm in  $X_+$ , i.e.,  $\int_0^1 R(\phi)(y)dy = \int_0^1 \phi(y)dy, \forall \phi \in X_+$ .
- iv)  $\text{supp}(R(\phi))$  is contained in the closed convex hull of  $\text{supp}(\phi), \forall \phi \in X_+$ .
- v)  $R$  preserves mean in  $X_+$ , i.e., if  $\phi \in X_+ \setminus \{0\}$  and if  $E_1(\phi) := \int_0^1 y\phi(y)dy / \int_0^1 \phi(y)dy$ , then  $E_1(R(\phi)) = E_1(\phi), \forall \phi \in X_+$ .
- vi) If  $\phi \in L^2_+(0, 1) \setminus \{0\}$ , then

$$\lim_{n \rightarrow +\infty} R^n(\phi)(y) = \begin{cases} 0, & \text{if } y \neq E_1(\phi), \\ +\infty, & \text{if } y = E_1(\phi). \end{cases}$$

- vii)  $\forall k \geq 1, \forall \phi \in X_+ \setminus \{0\}$

$$\int_0^1 y^k R(\phi)(y)dy = \frac{1}{\|\phi\|} \left(\frac{1}{2}\right)^k \left[ \sum_{j=0}^k C_k^j \int_0^1 z^{k-j} \phi(z)dz \int_0^1 y^j \phi(y)dy \right],$$

$$\text{where } C_k^j = \frac{k!}{j!(k-j)!}.$$

*Proof.* We refer to Theorem 2.1 p. 223 in [4] for i)–vi). We now prove vii). Without loss of generality we can assume that  $\|\phi\| = 1$ . Let  $k \geq 1$ , then

$$\begin{aligned} \int_0^1 y^k R(\phi)(y) dy &= \int_0^1 y^k \int_0^1 K_1(y, \widehat{y}) \phi(2y - \widehat{y}) \phi(\widehat{y}) d\widehat{y} dy \\ &= \int_0^1 \int_{\frac{\widehat{y}}{2}}^{\frac{\widehat{y}+1}{2}} y^k \phi(2y - \widehat{y}) 2dy \phi(\widehat{y}) d\widehat{y} \\ &= \int_0^1 \int_0^1 \left(\frac{z+\widehat{y}}{2}\right)^k \phi(z) dz \phi(\widehat{y}) d\widehat{y} \\ &= \left(\frac{1}{2}\right)^k \int_0^1 \int_0^1 \sum_{j=0}^k C_k^j z^{k-j} \widehat{y}^j \phi(z) dz \phi(\widehat{y}) d\widehat{y}. \end{aligned}$$

□

We now consider the operator  $L$ .

**THEOREM 2.2.** *The bounded linear operator  $L \in \mathcal{L}(X, X)$  satisfies the following properties:*

- i)  $L$  is compact.
- ii) For each  $\phi \in X_+$ , one has

$$\begin{aligned} \int_0^1 L(\phi)(y) dy &= \int_0^1 \phi(y) dy, \\ \int_0^1 y L(\phi)(y) dy &= \alpha \int_0^1 y \phi(y) dy + \frac{(1-\alpha)}{2} \int_0^1 \phi(y) dy, \end{aligned}$$

and for each  $k \geq 1$ ,

$$\int_0^1 y^k L(\phi)(y) dy = \alpha^k \int_0^1 y^k \phi(y) dy + \sum_{j=0}^{k-1} a_j^k \int_0^1 y^j \phi(y) dy,$$

where

$$a_j^k = \frac{1}{k+1} C_{k+1}^{k+1-j} (1-\alpha)^{k-j} \alpha^j.$$

- iii)  $L$  is irreducible.
- iv) The spectrum of  $L$  is  $\sigma(L) = \{\alpha^k : k = 0, 1, 2, \dots\} \cup \{0\}$ , and  $\forall k \geq 0$  the eigenvalue  $\alpha^k$  is simple.

*Proof.* When  $\alpha = 0$ , assertions i), ii), iii), and iv) are trivially satisfied, because  $L$  is the one dimensional projector

$$L(\phi)(y) = \int_0^1 \phi(\widehat{y}) d\widehat{y}.$$

Now we assume that  $\alpha > 0$ . In this case, we have the formula

$$L(\phi)(y) = \int_{\max(0, \alpha^{-1}y - (\alpha^{-1}-1))}^{\min(1, \alpha^{-1}y)} \frac{1}{1-\alpha} \phi(\widehat{y}) d\widehat{y}.$$

Then the compactness of  $L$  follows from the fact that  $L$  is bounded from  $L^1(0, 1)$  to  $W^{1,1}(0, 1)$ , and from the fact that the imbedding from  $W^{1,1}(0, 1)$  to  $L^1(0, 1)$  is compact.

We now prove assertion ii). We remark that for all  $\varphi \in L^1(0, 1)$ , and for all  $k \in \mathbb{N}$ ,

$$\begin{aligned} \int_0^1 y^k L(\phi)(y) dy &= \int_0^1 y^k \int_0^1 K_0(y, \widehat{y}) \varphi(\widehat{y}) d\widehat{y} dy \\ &= \frac{1}{1-\alpha} \int_0^1 \int_{\alpha\widehat{y}}^{\alpha\widehat{y}+1-\alpha} y^k dy \varphi(\widehat{y}) d\widehat{y} \\ &= \frac{1}{1-\alpha} \int_0^1 \frac{1}{k+1} [(\alpha\widehat{y} + 1 - \alpha)^{k+1} - (\alpha\widehat{y})^{k+1}] \varphi(\widehat{y}) d\widehat{y} \\ &= \frac{1}{(1-\alpha)} \int_0^1 \frac{1}{k+1} [C_{k+1}^1 (\alpha\widehat{y})^k (1-\alpha) + C_{k+1}^2 \\ &\quad (\alpha\widehat{y})^{k-1} (1-\alpha)^2 + \dots + (1-\alpha)^{k+1}] \varphi(\widehat{y}) d\widehat{y}, \end{aligned}$$

so for all  $k \geq 1$

$$\int_0^1 y^k L(\phi)(y) dy = \alpha^k \int_0^1 y^k \phi(y) dy + \sum_{j=0}^{k-1} a_j^k \int_0^1 y^j \phi(y) dy,$$

where  $a_j^k = C_{k+1}^{k+1-j} \frac{1}{k+1} (1-\alpha)^{k-j} \alpha^j$ .

From this, we deduce that we can construct a unique (normalized) family of polynomials,

$$p_k(y) = y^k + \sum_{j=0}^{k-1} b_j^k y^j, \forall y \in [0, 1],$$

such that

$$\int_0^1 p_k(y) L(\phi)(y) dy = \alpha^k \int_0^1 p_k(y) \phi(y) dy, \forall \phi \in X, \forall k \in \mathbb{N},$$

This implies that  $\{\alpha^k : k \in \mathbb{N}\} \subset \sigma(L^*)$ , so  $\{\alpha^k : k \in \mathbb{N}\} \subset \sigma(L)$ . Furthermore, since  $L$  is compact, we have  $0 \in \sigma(L)$  in infinite dimensional spaces (see Brezis [1], Theorem VI.8 p. 95).

Assume now that there exists  $\lambda \in \sigma(L) \setminus \{0\}$ , and assume that  $\lambda \neq \alpha^k, \forall k \in \mathbb{N}$ . We assume that  $\lambda$  is real, the complex case being similar. From the spectral properties of compact linear operators, we know that there exists  $v_\lambda \in X \setminus \{0\}$  such that

$$Lv_\lambda = \lambda v_\lambda.$$

But then

$$\alpha^k \int_0^1 p_k(y) v_\lambda(y) dy = \int_0^1 p_k(y) L(v_\lambda)(y) dy = \lambda \int_0^1 p_k(y) v_\lambda(y) dy, \forall k \in \mathbb{N},$$

so,

$$\int_0^1 p_k(y) v_\lambda(y) dy = 0, \forall k \in \mathbb{N}.$$

But since  $v_\lambda = \frac{1}{\lambda}L(v_\lambda)$ ,  $v_\lambda$  also belongs to  $L^\infty(0, 1)$ . As the family  $\{p_k\}_{k \geq 0}$  generates the set of all polynomials, and as the set of polynomials is dense in  $L^1(0, 1)$ , we deduce that

$$\int_0^1 f(y)v_\lambda(y)dy = 0, \forall f \in L^1(0, 1) \Rightarrow v_\lambda = 0.$$

To prove iii) it is sufficient to remark that  $\forall \phi \in X_+$ ,  $\forall a, b \in (0, 1)$  with  $a < b$ , there exists an integer  $m \geq 1$ , such that  $[a, b] \subset \text{supp}(L^m(\phi))$ .

Let us now prove that each eigenvalue  $\alpha^k$  is simple. Let be  $k \in \mathbb{N}$ , and assume that there exists  $\phi_1, \phi_2 \in L^1(0, 1) \setminus \{0\}$  such that

$$L(\phi_i) = \alpha^k \phi_i, \forall i = 1, 2.$$

One can easily see that  $\int_0^1 p_l(y)\phi_i(y)dy = 0, \forall l \neq k$ . If  $\int_0^1 p_k(y)\phi_{i_0}(y)dy = 0$ , then as  $\phi_{i_0}$  is continuous, we have

$$\int_0^1 f(y)\phi_{i_0}(y)dy = 0, \forall f \in L^1(0, 1) \Rightarrow \phi_{i_0} = 0,$$

which gives a contradiction. So  $\int_0^1 p_k(y)\phi_i(y)dy \neq 0 \forall i = 1, 2$ , and by setting

$$w = \frac{\phi_1}{\int_0^1 p_k(y)\phi_1(y)dy} - \frac{\phi_2}{\int_0^1 p_k(y)\phi_2(y)dy},$$

then  $\langle p_l, w \rangle = 0, \forall l \in \mathbb{N}$  so  $w = 0$ . We deduce that  $\dim(\text{Ker}(\alpha^k \text{Id} - L)) = 1$ . The proof for  $\dim(\text{Ker}(\alpha^k \text{Id} - L)^2) = 1$  is similar.  $\square$

We are now interested in the linear part of equation (1). So, we consider the bounded linear operator

$$A = \gamma(L - \text{Id}).$$

From Theorem 2.2, the spectrum of  $A$  is

$$\sigma(A) = \{\gamma(\alpha^k - 1) : k = 0, 1, 2, \dots\} \cup \{-\gamma\}.$$

We denote

$$X_+^* = \{x^* \in X^* : x^*(x) \geq 0, \forall x \in X_+\}.$$

**THEOREM 2.3.** *The bounded linear operator  $A$  generates a uniformly continuous semi-group  $(T(t))_{t \geq 0}$  (see Pazy [7]) which satisfies the following properties:*

- i)  $\int_0^1 T(t)(\phi)(y)dy = \int_0^1 \phi(y)dy, \forall \phi \in X_+$ .
- ii)  $T(t) = e^{-\gamma t} \text{Id} + C(t)$ , where  $C(t) \in \mathcal{L}(X)$  is compact  $\forall t \geq 0$ .

iii)  $(T(t))_{t \geq 0}$  is irreducible, more precisely we have

$$x^*(T(t)x) > 0, \forall x \in X_+ \setminus \{0\}, \forall x^* \in X_+^* \setminus \{0\}, \forall t > 0.$$

iv)  $(T(t))_{t \geq 0}$  has the property of asynchronous exponential growth, that is,

$$\begin{aligned} P_0 T(t) &= T(t) P_0 = P_0, \forall t \geq 0, \\ \lim_{t \rightarrow +\infty} T(t)\phi &= P_0(\phi), \forall \phi \in X, \\ \text{and} \end{aligned}$$

$$\|T(t)P_1\phi\| \leq M e^{-\gamma(1-\alpha)t} \|P_1\phi\|, \forall \phi \in X,$$

for some  $M \geq 1$ , with  $P_0(\phi) = \int_0^1 \phi(y) dy \phi_0$ ,  $\forall \phi \in X$ , for some  $\phi_0 \in X_+ \setminus \{0\}$  (with  $\int_0^1 \phi_0(y) dy = 1$ ), and  $P_1 = Id - P_0$ .

REMARK. We have

$$T(t) = e^{\gamma(L-Id)t}, \forall t \geq 0,$$

so by changing the time scale, we see that  $M \geq 1$  is independent of  $\gamma$ .

*Proof.* Assertion i) is a simple consequence of the fact that

$$\int_0^1 A\phi(y) dy = 0, \forall \phi \in X.$$

Assertion ii) follows from the fact that  $L$  is compact, and from the variation of constants formula

$$T(t)\phi = e^{-\gamma t} \phi + \int_0^t e^{-\gamma(t-s)} \gamma L(T(s)\phi) ds, \forall t \geq 0.$$

So if we denote  $C(t) = \int_0^t e^{-\gamma(t-s)} \gamma L(T(s)\phi) ds = L(\int_0^t e^{-\gamma(t-s)} \gamma T(s)\phi ds)$ ,  $\forall t \geq 0$ , then it is clear that  $C(t)$  is a compact operator.

Assertion iii) is an immediate consequence of the fact that  $T(t) = e^{-\gamma t} e^{\gamma L t}$ ,  $\forall t \geq 0$ , and assertion iii) in Theorem 2.2.

From assertion ii) it is clear that  $(T(t))_{t \geq 0}$  is a quasi-compact semigroup (see Nagel [6], Definition 2.7, p. 214). Moreover,  $s(A) \stackrel{\text{def}}{=} \sup \{ \operatorname{Re} \lambda : \lambda \in \sigma(A) \} = 0$ , so we can apply Theorem 2.1, p. 343, and Remark (d), p. 344 in Nagel [6], and iii) and iv) follow.  $\square$

**THEOREM 2.4.** For each  $u_0 \in X_+$ , there exists  $u \in C^1(\mathbb{R}_+, L_+^1(0, 1))$  such that  $u$  is a solution of (1). Moreover, if  $u_0 \neq 0$ , then

$$\frac{d \|u(t)\|}{dt} = r \left( \|u(t)\| - \frac{1}{K} \|u(t)\|^2 \right),$$



so

$$\lim_{t \rightarrow +\infty} \|u(t)\| = K.$$

*Proof.* Let us denote by  $S(t)$  the nonlinear semigroup solution of

$$\begin{cases} \frac{dS(t)\phi}{dt} = \gamma(L - Id)S(t)\phi + \tau(R(S(t)\phi) - S(t)\phi) + rS(t), \\ S(0)\phi = \phi. \end{cases}$$

Then, since  $R$  is Lipschitzian, it is clear that  $S(t)\phi$  is defined for all  $t \geq 0$ . Now, by noting that for each  $t \geq 0$  the map  $\phi \rightarrow S(t)\phi$  (from  $X_+$  into  $X_+$ ) is homogeneous, one deduces that the solution of (1) is given by

$$u(t) = \frac{S(t)u_0}{1 + \int_0^t \mathcal{F}(S(s)u_0)ds}, \forall t \geq 0,$$

where

$$\mathcal{F}(\phi) = \frac{r}{K} \int_0^1 \phi(\hat{y})d\hat{y}.$$

Now by using iii) in Theorem 2.1, and ii) in Theorem 2.2 one immediately deduces that

$$\frac{d\|u(t)\|}{dt} = r \left( \|u(t)\| - \frac{1}{K} \|u(t)\|^2 \right), \forall t \geq 0. \quad \square$$

We are now interested in the existence of a nontrivial equilibrium.

**THEOREM 2.5.** *Assume that*

$$2 \frac{\tau}{\gamma + \tau} < 1.$$

*Then equation (1) admits a nontrivial equilibrium.*

*Proof.* The nontrivial fixed point problem associated to equation (1) is given by

$$\bar{u} = \frac{\gamma}{\gamma + \tau} L\bar{u} + \frac{\tau}{\gamma + \tau} R(\bar{u}) \text{ with } \bar{u} \in X_+ \cap S(0, K).$$

Dividing by  $\|\bar{u}\|$  this equation, we obtain the fixed point problem

$$v = \frac{\gamma}{\gamma + \tau} Lv + \frac{\tau}{\gamma + \tau} B(v, v) \stackrel{\text{def}}{=} F(v) \text{ with } v \in X_+ \cap S(0, 1),$$

where  $B(\phi_1, \phi_2)(y) = \int_0^1 K_1(y, \hat{y})\phi_1(2y - \hat{y})\phi_2(\hat{y})d\hat{y}, \forall \phi_1, \phi_2 \in X$ .

One can prove that

$$\|B(\phi_1, \phi_2)\| \leq \|\phi_1\| \|\phi_2\|, \forall \phi_1, \phi_2 \in X,$$

so

$$\|B(\phi_1, \phi_1) - B(\phi_2, \phi_2)\| \leq 2 \|\phi_1 - \phi_2\|, \forall \phi_1, \phi_2 \in X_+ \cap S(0, 1).$$

It is clear that  $F$  maps  $X_+ \cap S(0, 1)$  into itself. Since  $L$  is a compact linear operator, one deduces that  $2\frac{\tau}{\gamma+\tau} < 1$ , so that  $F$  is an  $\gamma$ -condensing map, and the result follows by applying Theorem 9.1, p. 71 in Deimling [2].  $\square$

Let us now set for each  $u_0 \in X_+ \setminus \{0\}$ ,

$$v(t) = \frac{u(t)}{\|u(t)\|},$$

then it is not difficult to prove that  $v(t)$  satisfies

$$\begin{cases} \frac{dv(t)}{dt} = \gamma(L - Id)v(t) + \tau(R(v(t)) - v(t)), \forall t \geq 0, \\ v(0) = v_0 = \frac{u_0}{\|u_0\|} \in S(0, 1) \cap X_+. \end{cases} \quad (2)$$

Henceforth, we denote by  $v(t)$  the solution of equation (2).

**THEOREM 2.6.** *Assume that*

$$M\tau(\|R\|_{Lip} + 1) < \gamma(1 - \alpha)$$

(where  $M \geq 1$  is the constant introduced in assertion iv) of Theorem 2.3). Then equation (1) has a unique nontrivial steady state  $\bar{u}_{\tau, \gamma} \in X_+$  with  $\|\bar{u}_{\tau, \gamma}\| = K$ . Moreover,  $\forall u_0 \in X_+ \setminus \{0\}$ , one has

$$\lim_{t \rightarrow +\infty} u(t) = \bar{u}_{\tau, \gamma},$$

and  $\bar{u}_{\tau, \gamma}$  is stable.

**REMARK.** We know that  $M \geq 1$  is independent of  $\gamma$  (see the remark following Theorem 2.3). So, the condition

$$M\tau(\|R\|_{Lip} + 1) < \gamma(1 - \alpha),$$

is satisfied when  $\frac{\tau}{\gamma}$  is small enough. So, the previous theorem says that when mutation is stronger than recombination, then the population globally stabilizes to a unique steady state.

*Proof.* Let be  $v_1^0, v_2^0 \in S(0, 1) \cap X_+$ , and for each  $i = 1, 2$ , let  $v_i(t)$  be the solution of equation (2) with initial value  $v_i^0$ . We have

$$v_i(t) = T(t)v_i^0 + \int_0^t T(t-s) [\tau(R(v_i(s))) - v_i(s)] ds, \forall t \geq 0.$$

Then

$$\begin{aligned} P_1(v_1(t) - v_2(t)) &= T(t)P_1(v_1^0 - v_2^0) \\ &+ \int_0^t T(t-s)P_1(\tau[R(v_1(s)) - R(v_2(s)) - v_1(s) + v_2(s)]) ds, \forall t \geq 0. \end{aligned}$$

Since

$$P_0(R(v_1(s)) - R(v_2(s))) = P_0(v_1(s) - v_2(s)) = 0,$$

we deduce that

$$\begin{aligned} &\|P_1(\tau[R(v_1(s)) - R(v_2(s)) - v_1(s) + v_2(s)])\| \\ &= \|\tau[R(v_1(s)) - R(v_2(s)) - v_1(s) + v_2(s)]\|, \end{aligned}$$

and we have

$$\begin{aligned} \|P_1(v_1(t) - v_2(t))\| &\leq Me^{-\gamma(1-\alpha)t} \|P_1(v_1^0 - v_2^0)\| \\ &+ M\tau(\|R\|_{Lip} + 1) \int_0^t e^{-\gamma(1-\alpha)(t-s)} \|P_1(v_1(s) - v_2(s))\| ds, \forall t \geq 0. \end{aligned}$$

We apply the Gronwall lemma to obtain

$$\|P_1(v_1(t) - v_2(t))\| \leq M \|P_1(v_1^0 - v_2^0)\| e^{(-\gamma(1-\alpha) + M\tau(\|R\|_{Lip} + 1))t}, \forall t \geq 0. \quad \square$$

### 3. Recombination

In this section we assume  $\gamma = 0$ . So, we consider the ordinary differential equation

$$\begin{cases} \frac{du}{dt} = \tau[R(u(t)) - u(t)] + r(1 - \frac{1}{K} \int_0^1 u(t)(\widehat{y})d\widehat{y})u(t), \\ u(0) = u_0 \in L_+^1(0, 1). \end{cases}$$

Let be  $u_0 \in L_+^1(0, 1) \setminus \{0\}$ . We denote

$$v(t) = \frac{u(t)}{\|u(t)\|}, \forall t \geq 0.$$

Then it is not difficult to show that

$$\begin{cases} \frac{dv}{dt} = \tau[R(v(t)) - v(t)], \forall t \geq 0, \\ v(0) = v_0. \end{cases} \quad (3)$$

Moreover, from Theorem 2.4, we know that

$$\frac{d \|u(t)\|}{dt} = r \left( \|u(t)\| - \frac{1}{K} \|u(t)\|^2 \right),$$

so

$$\lim_{t \rightarrow +\infty} \|u(t)\| = K.$$

In the sequel, we denote

$$E_k(\phi) = \frac{\int_0^1 y^k \phi(y) dy}{\int_0^1 \phi(y) dy}, \forall \phi \in X_+ \setminus \{0\}, \forall k \geq 1.$$

**THEOREM 3.1.** *Let be  $v_0 \in X_+ \setminus \{0\}$ , and let  $v(t)$  be the solution of equation (3) with initial value  $v_0$ . Then*

$$\frac{dE_1(v(t))}{dt} = 0,$$

and

$$\begin{aligned} \frac{dE_k(v(t))}{dt} = \tau & \left[ \left( \left( \frac{1}{2} \right)^{k-1} - 1 \right) E_k(v(t)) \right. \\ & \left. + \left( \frac{1}{2} \right)^k \sum_{j=1}^{k-1} C_k^j E_{k-j}(v(t)) E_j(v(t)) \right], \quad \forall k \geq 2, \end{aligned}$$

where

$$C_k^j = \frac{k!}{j!(k-j)!}.$$

Furthermore,

$$\lim_{t \rightarrow +\infty} E_1(v(t)) = E_1(v_0), \quad \lim_{t \rightarrow +\infty} E_k(v(t)) = E_1(v_0)^k, \quad \forall k \geq 1.$$

*Proof.* From Theorem 2.1 we deduce that

$$\begin{cases} \frac{dE_1(v(t))}{dt} = 0, \\ \frac{dE_k(v(t))}{dt} = \tau \left[ \left( \left( \frac{1}{2} \right)^{k-1} - 1 \right) E_k(v(t)) \right. \\ \left. + \left( \frac{1}{2} \right)^k \sum_{j=1}^{k-1} C_k^j E_{k-j}(v(t)) E_j(v(t)) \right], \quad \forall k \geq 2. \end{cases}$$

We consider

$$X_N(t) = \begin{pmatrix} E_1(v(t)) \\ E_2(v(t)) \\ \vdots \\ E_N(v(t)) \end{pmatrix}.$$

Then  $X_N(t)$  satisfies an ordinary differential equation of the following type:

$$\frac{dX_N(t)}{dt} = B_N X_N(t) + G_N(X_N(t)), \forall t \geq 0, \quad (4)$$

where the matrix  $B_N \in M_N(\mathbb{R})$ , and  $G_N : \mathbb{R}^N \rightarrow \mathbb{R}^N$  is lipschitzian on bounded sets.

Moreover, if

$$\bar{X}_N = \begin{pmatrix} \bar{E}_1 \\ \bar{E}_1 \\ \vdots \\ \bar{E}_N \end{pmatrix}$$

denotes the unique equilibrium solution of equation (4) which satisfies

$$\bar{E}_1 = E_1(v_0),$$

then we must have

$$\left\{ \begin{array}{l} \bar{E}_k = \frac{(\frac{1}{2})^k (\sum_{j=1}^{k-1} C_k^j \bar{E}_{k-j} \bar{E}_j)}{(1-s(\frac{1}{2})^{k-1})} \text{ for } k \geq 2, \\ \text{and} \\ \bar{E}_1 = E_1(v_0). \end{array} \right. \quad (5)$$

By induction on  $k$ , one deduces from (5) that

$$\bar{E}_k = E_1(v_0)^k, \forall k \geq 1.$$

Let us prove  $X_N(t) \rightarrow \bar{X}_N$  as  $t \rightarrow +\infty$ , by induction on  $N$ . For  $N = 1$ , it is clear that  $X_1(t) \rightarrow E_1(v_0)$  as  $t \rightarrow +\infty$ . Assume that for some  $l \geq 1$ ,  $X_l(t) \rightarrow \bar{X}_l$  as  $t \rightarrow +\infty$ . Since  $X_{l+1}(t)$  is the solution of equation (4), and

$$0 \leq E_{l+1}(v(t)) \leq E_l(v(t)) \leq \dots \leq E_2(v(t)) \leq E_1(v(t)),$$

the omega-limit set of  $X_{l+1}(t)$  is well defined by

$$\omega(X_{l+1}(0)) = \bigcap_{t \geq 0} \overline{\bigcup_{s \geq t} \{X_{l+1}(s)\}},$$

and we know (see Hale [3]) that  $\omega(X_k(0))$  is invariant by the flow of the ordinary differential equation (4). But, since we have assumed that  $X_l(t) \rightarrow \bar{X}_l$  as  $t \rightarrow +\infty$ , we deduce that

$$\omega(X_{l+1}(0)) \subset \left\{ \left( \begin{array}{c} \bar{E}_1 \\ \bar{E}_2 \\ \vdots \\ \bar{E}_l \\ E \end{array} \right), \text{ where } E \in [0, \bar{E}_l] \right\} \stackrel{\text{def}}{=} S.$$

But on  $S$  the  $(l+1)^{th}$  component of the solution of equation (4) satisfies the following linear ordinary differential equation

$$\begin{cases} \frac{dx(t)}{dt} = \tau\left(\left(\frac{1}{2}\right)^{k-1} - 1\right)(x(t) - \bar{E}_{l+1}), \\ x(0) \in [0, \bar{E}_l]. \end{cases}$$

By using the invariance of the omega-limit set, we deduce that  $S = \{\bar{X}_k\}$ .  $\square$

In the sequel we denote by  $P[0, 1]$  the space of polynomial functions on  $[0, 1]$ .

**THEOREM 3.2.** *Assume  $\gamma = 0$  in equation (1). Let be  $u_0 \in X_+ \setminus \{0\}$ , and let  $u(t)$  be the solution of equation (1) with initial value  $u_0$ . Then*

$$u(t) \xrightarrow{*} K\delta_{E_1(u_0)} \text{ as } t \rightarrow +\infty,$$

which is equivalent to the assertion

$$\int_0^1 f(y)u(t)(y)dy \rightarrow K\delta_{E_1(u_0)}(f) \text{ as } t \rightarrow +\infty, \forall f \in C([0, 1], \mathbb{R}).$$

*Proof.* From Theorem 2.4 we know that  $\forall k \geq 1$

$$E_k(v(t)) \rightarrow E_1(v_0)^k \text{ as } t \rightarrow +\infty.$$

Since  $E_k(v(t)) = E_k(u(t))$ ,  $\forall t \geq 0$ , we deduce that

$$\int_0^1 y^k u(t)(y)dy \rightarrow K E_1(u_0)^k \text{ as } t \rightarrow +\infty.$$

Now, by considering  $u(t)$  as an element of the dual space of  $C([0, 1], \mathbb{R})$ , we have

$$\langle u(t), f_k \rangle \stackrel{def}{=} \int_0^1 f_k(y)u(t)(y)dy \rightarrow K\delta_{E_1(u_0)}(f_k) \text{ as } t \rightarrow +\infty,$$

where  $f_k(y) = y^k$ ,  $\forall y \in [0, 1]$ . From this we deduce that for all  $p \in P[0, 1]$

$$\langle u(t), p \rangle \rightarrow K\delta_{E_1(u_0)}(p) \text{ as } t \rightarrow +\infty.$$

Let be  $\varepsilon > 0$ , and let be  $f \in C([0, 1], \mathbb{R})$ . By Weierstrass's theorem there exists  $p_\varepsilon \in P[0, 1]$  such that

$$\|f - p_\varepsilon\|_{\infty, [0, 1]} \leq \min\left(\frac{\varepsilon}{3K}, \frac{\varepsilon}{3 \max(\|u_0\|, K)}\right).$$

We now have

$$\begin{aligned} |\langle u(t), f \rangle - K\delta_{E_1(u_0)}(f)| &\leq |\langle u(t), f \rangle - \langle u(t), p_\varepsilon \rangle| + |\langle u(t), p_\varepsilon \rangle - K\delta_{E_1(u_0)}(p_\varepsilon)| \\ &\quad + |K\delta_{E_1(u_0)}(p_\varepsilon) - K\delta_{E_1(u_0)}(f)|, \\ &\leq \frac{2\varepsilon}{3} + |\langle u(t), p_\varepsilon \rangle - K\delta_{E_1(u_0)}(p_\varepsilon)|. \end{aligned}$$

So we deduce that there exists  $t_0 > 0$  such that

$$|\langle u(t), f \rangle - K\delta_{E_1(u_0)}(f)| \leq \varepsilon, \forall t \geq t_0. \quad \square$$

#### 4. Recombination and mutation

In this section we consider the case  $\gamma > 0$ . So, we consider the equation

$$\begin{cases} \frac{du}{dt} = \gamma [L(u(t)) - u(t)] + \tau [R(u(t)) - u(t)] + r(1 - \frac{1}{K} \int_0^1 u(t)(\widehat{y})d\widehat{y}) u(t) \\ u(0) = u_0 \in L_+^1(0, 1). \end{cases}$$

Let be  $u_0 \in L_+^1(0, 1) \setminus \{0\}$ . We denote

$$v(t) = \frac{u(t)}{\|u(t)\|}, \forall t \geq 0.$$

Then it is not difficult to show that

$$\begin{cases} \frac{dv}{dt} = \gamma [L(v(t)) - v(t)] + \tau [R(v(t)) - v(t)], \forall t \geq 0, \\ v(0) = v_0. \end{cases} \quad (6)$$

Moreover from Theorem 2.4 we know that

$$\frac{d\|u(t)\|}{dt} = r \left( \|u(t)\| - \frac{1}{K} \|u(t)\|^2 \right),$$

so

$$\lim_{t \rightarrow +\infty} \|u(t)\| = K.$$

**THEOREM 4.1.** *Assume  $\gamma > 0$ . Let be  $v_0 \in X_+ \setminus \{0\}$ , and let  $v(t)$  be the solution of equation (6) with initial value  $v_0$ . Then*

$$\lim_{t \rightarrow +\infty} E_k(v(t)) = \overline{E}_k, \forall k \geq 1,$$

where the constants  $\overline{E}_k > 0$  are independent of  $v_0$ , and are given by the following difference equation

$$\begin{cases} \overline{E}_k = \frac{\{\gamma \sum_{j=0}^{k-1} a_j^k \overline{E}_j + \tau (\frac{1}{2})^k \sum_{j=1}^{k-1} C_k^j \overline{E}_{k-j} \overline{E}_j\}}{[\gamma(1-\alpha^k) + \tau(1-(\frac{1}{2})^{k-1})]} \text{ for } k \geq 2, \\ \text{and} \\ \overline{E}_1 = \frac{1}{2}, \end{cases}$$

where

$$C_k^j = \frac{k!}{j!(k-j)!} \text{ and } a_j^k = \frac{1}{k+1} C_{k+1}^{k+1-j} (1-\alpha)^{k-j} \alpha^j.$$

**REMARK.** Let us now consider the problem of the speed of convergence. One can note that it depends on the scalar  $\gamma(1-\alpha)$  (see equations (7) and (4.)). Also, the smaller  $\gamma(1-\alpha)$  is, the weaker mutation is. So, from the previous theorem we also deduce that the weaker mutation is, the more time it takes for the distribution of the population to reach the steady state.

*Proof.* Let be  $v_0 \in X_+ \setminus \{0\}$ . Let  $v(t)$  be the solution of equation (6) with initial value  $v_0$ . By using assertion vii) in Theorem 2.1, and assertion iv) in Theorem 2.2, we deduce

$$\frac{dE_1(v(t))}{dt} = \gamma(1-\alpha) \left[ -E_1(v(t)) + \frac{1}{2} \right], \quad (7)$$

$$\begin{aligned} \frac{dE_k(v(t))}{dt} &= \gamma \left[ (\alpha^k - 1)E_k(v(t)) + \sum_{j=0}^{k-1} a_j^k E_j(v(t)) \right] \\ &+ \tau \left[ \left( \left( \frac{1}{2} \right)^{k-1} - 1 \right) E_k(v(t)) + \left( \frac{1}{2} \right)^k \sum_{j=1}^{k-1} C_k^j E_{k-j}(v(t)) E_j(v(t)) \right], \quad \forall k \geq 2. \end{aligned} \quad (8)$$

The result follows by using the arguments of the proof of Theorem 3.1.  $\square$

We are now interested in the convergence of the solutions  $v(t)$  of equation (6). We now prove the convergence (for the weak\* topology) of each solution to a Radon measure which does not depend of the initial value  $v_0$ .

**LEMMA 4.2.** *For each  $v_0 \in S(0, 1) \cap X_+$  and each  $f \in C([0, 1], \mathbb{R})$  there exists  $l_f \in \mathbb{R}$  such that*

$$\int_0^1 f(y)v(t)(y)dy \rightarrow l_f \text{ as } t \rightarrow +\infty.$$

*Proof.* Let be  $f \in C([0, 1], \mathbb{R})$ . We now prove that for each  $\varepsilon > 0$ , there exists  $t_0 > 0$  such that

$$\left| \int_0^1 f(y)v(t)(y)dy - \int_0^1 f(y)v(s)(y)dy \right| \leq \varepsilon, \quad \forall t, s \geq t_0.$$



Let be  $\varepsilon > 0$ . Then by Weierstrass's theorem there exists  $p_\varepsilon \in P[0, 1]$  such that

$$\|f - p_\varepsilon\|_{\infty, [0, 1]} \leq \frac{\varepsilon}{3}.$$

Moreover, by Theorem 4.1, we know that there exists  $t_0 > 0$  such that

$$\left| \int_0^1 p_\varepsilon(y)v(t)(y)dy - \int_0^1 p_\varepsilon(y)v(s)(y)dy \right| \leq \frac{\varepsilon}{3}, \forall t, s \geq t_0.$$

Then we have  $\forall t, s \geq t_0$

$$\begin{aligned} & \left| \int_0^1 f(y)v(t)(y)dy - \int_0^1 f(y)v(s)(y)dy \right| \leq \left| \int_0^1 (f(y) - p_\varepsilon(y))v(t)(y)dy \right| \\ & \quad + \left| \int_0^1 p_\varepsilon(y)v(t)(y)dy - \int_0^1 p_\varepsilon(y)v(s)(y)dy \right| \\ & \quad + \left| \int_0^1 (f(y) - p_\varepsilon(y))v(s)(y)dy \right|, \end{aligned}$$

and since  $\|v(t)\|_{L^1(0, 1)} = 1$ , we obtain

$$\left| \int_0^1 f(y)v(t)(y)dy - \int_0^1 f(y)v(s)(y)dy \right| \leq \varepsilon, \forall t, s \geq t_0.$$

□

LEMMA 4.3. *For each  $v_0 \in S(0, 1) \cap X_+$ , and each  $f \in C([0, 1], \mathbb{R})$ ,  $I_f$  is independent of the initial value  $v_0$ .*

*Proof.* Let be  $f \in C([0, 1], \mathbb{R})$  and let be  $v_1(t)$  and  $v_2(t)$  be two solutions of (6) with  $v_i(0) \in S(0, 1) \cap X_+$ ,  $\forall i = 1, 2$ . Let  $\varepsilon > 0$ , and  $p_\varepsilon \in P[0, 1]$  such that

$$\|f - p_\varepsilon\|_{\infty, [0, 1]} \leq \frac{\varepsilon}{2}.$$

Then

$$\begin{aligned} & \left| \int_0^1 f(y)v_1(t)(y)dy - \int_0^1 f(y)v_2(t)(y)dy \right| \leq \left| \int_0^1 (f(y) - p_\varepsilon(y))v_1(t)(y)dy \right| \\ & \quad + \left| \int_0^1 p_\varepsilon(y)(v_1(t)(y) - v_2(t)(y))dy \right| \\ & \quad + \left| \int_0^1 (f(y) - p_\varepsilon(y))v_2(t)(y)dy \right|. \end{aligned}$$

Since by Theorem 4.1 we have

$$\lim_{t \rightarrow +\infty} \left| \int_0^1 p_\varepsilon(y)(v_1(t)(y) - v_2(t)(y))dy \right| = 0,$$

we deduce that

$$\lim_{t \rightarrow +\infty} \sup \left| \int_0^1 f(y)v_1(t)(y)dy - \int_0^1 f(y)v_2(t)(y)dy \right| \leq \varepsilon,$$

and the result follows. □

LEMMA 4.4. *The map  $l : C([0, 1], \mathbb{R}) \rightarrow \mathbb{R}$  is linear and bounded and  $\|l\|_{C([0, 1], \mathbb{R})^*} \leq 1$ .*

*Proof.* It is clear that  $l$  is linear. Let us prove that  $l$  is bounded. Indeed, let  $v(t)$  be a solution of (6). Then

$$\begin{aligned} \left| \int_0^1 f_1(y)v(t)(y)dy - \int_0^1 f_2(y)v(t)(y)dy \right| &\leq \|f_1 - f_2\|_{\infty, [0, 1]} \|v(t)\|_{L^1(0, 1)} \\ &\leq \|f_1 - f_2\|_{\infty, [0, 1]}, \forall f_1, f_2 \in C([0, 1], \mathbb{R}), \forall t \geq 0, \end{aligned}$$

and the result follows by taking the limit in  $t$ .  $\square$

To summarize, we have the following theorem.

THEOREM 4.5. *Assume  $\gamma > 0$ . Let be  $u_0 \in X_+ \setminus \{0\}$ , let  $u(t)$  be the solution of equation (1) with initial value  $u_0$ . Then there exists a Radon measure  $l \in C([0, 1], \mathbb{R})^*$  (independent of  $u_0$ ) with  $\|l\|_{C([0, 1], \mathbb{R})^*} \leq 1$  such that*

$$u(t) \rightharpoonup^* Kl \text{ as } t \rightarrow +\infty,$$

which is equivalent to

$$\int_0^1 f(y)u(t)(y)dy \rightarrow Kl(f) \text{ as } t \rightarrow +\infty, \forall f \in C([0, 1], \mathbb{R}).$$

## 5. Concluding remarks

In this paper we have investigated a model for the evolution of a population when there is no selection. In particular, we have proved a new result concerning convergence of the population distribution when recombination dominates mutation. The model including the selection process takes the following form

$$\begin{cases} \frac{du}{dt} = \gamma [L(u(t)) - u(t)] + \beta u(t) + \tau [R(u(t)) - u(t)] \\ \quad + r(1 - \frac{1}{K} \int_0^1 u(t)(\hat{y})d\hat{y}) u(t), \\ u(0) = u_0 \in L_+^1(0, 1), \end{cases} \quad (9)$$

where  $\beta \in C([0, 1], \mathbb{R})$ . The function  $\beta(y)$  represents the fitness of individuals with respect to the phenotype. The assumption that  $\beta(y) = 0$  is equivalent to assume that the birth rate and the death rate do not depend on the phenotype expression.

We have concentrated our attention to the case where recombination dominates mutation. In fact, the results proved in [4] hold for equation (1). More precisely, by using a new approach it is proved in [5] that, when  $\beta$  is not necessarily equal zero and  $\gamma > 0$  is large enough, there exists a unique nontrivial equilibrium distribution that is a global attractor

for non zero initial distributions. Moreover, when  $\tau > 0$  is small enough, then under some (natural) additional assumptions, there exists a non trivial equilibrium which is globally stable.

The assumption that there is no natural selection (i.e.  $\beta(y) = 0, \forall y \in [0, 1]$ ) is strong. Nevertheless, this assumption is very convenient to investigate the global asymptotic behavior of the system. In a work in preparation, we investigate the case where  $\beta(y)$  is polynomial and  $\sup_{y \in [0, 1]} |\beta(y)|$  is small. Also for  $\gamma > 0$  fixed, when  $\sup_{y \in [0, 1]} |\beta(y)|$  is small enough, then there is a globally stable equilibrium in the space of Radon measures. It means that the behavior will remain the same for small selection, and only the shape of the asymptotic distribution will be modified by the selection. Moreover, when  $\tau > 0$  is large (with  $\sup_{y \in [0, 1]} |\beta(y)|$  non necessarily small), then the solutions asymptotically approach a small neighborhood of the Dirac measure  $c\delta_{1/2}$  for some constant  $c > 0$ . Finally the case where  $\gamma > 0, \tau > 0$  and  $\sup_{y \in [0, 1]} |\beta(y)|$  is large remains to be investigated. In this case, it would be interesting to find an example where one would find more complicated dynamics.

#### REFERENCES

- [1] BREZIS, H., *Analyse fonctionnelle*. Masson, 1983.
- [2] DEIMLING, K., *Nonlinear Functional Analysis*. Springer-Verlag, 1985.
- [3] HALE, J. K., *Asymptotic Behavior of Dissipative Systems*. Amer. Math. Soc., 1988.
- [4] MAGAL, P. and WEBB, G. F., *Mutation, selection, and recombination in a model of phenotype evolution*. *Discrete and Continuous Dynamical Systems* 6 (2000), 221–236.
- [5] MAGAL, P., *Dominant mutation and weak recombination in a model of phenotype evolution*. Preprint, 2001.
- [6] NAGEL, R., (editor) *One-parameter Semigroups of Positive Operators*. Lect. Notes in Math. 1184. Springer-Verlag, 1986.
- [7] PAZY, A., *Semigroup of Linear Operators and Applications to Partial Differential Equations*. Springer-Verlag, 1983.
- [8] PONCE, M. C., THAM, K. Y. and BLASER, M. J., *Helicobacter pylori lewis antigen expression in experimentally infected gerbils and mice*, to appear.
- [9] WIRTH, H. P., YANG, M., PEEK, R. M., HOOK-NIKANNE, J., FRIED, M. and BLASER, M. J., *Phenotypic diversity in Lewis expression of Helicobacter pylori isolates from the same host*, *J.Lab. Clin. Med.* 5 (1999), 488–500.

*P. Magal*  
*Unité de Biométrie*  
*INRA 78352*  
*Jouy-en-Josas*  
*France*  
*e-mail: magal.pierre@wanadoo.fr*



To access this journal online:  
<http://www.birkhauser.ch>

---