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# Asymptotic behavior of Eigen's quasispecies model

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## Abstract

We study Eigen's quasispecies model in the asymptotic regime where the length of the genotypes goes to  $\infty$  and the mutation probability goes to 0. A limiting infinite system of differential equations is obtained. We prove convergence of trajectories, as well as convergence of the equilibrium solutions. We give analogous results for a discrete-time version of Eigen's model, which coincides with a model proposed by Moran.

## 1 Introduction

In the early 1970s, Manfred Eigen proposed a mathematical model for the evolution of a population of replicating macromolecules, under the complementary forces of selection and mutation [7], as might have happened under prebiotic conditions. Let  $\mathcal{G}$  be the finite set of possible genotypes, along with a fitness function  $f : \mathcal{G} \rightarrow \mathbb{R}^+$  and a mutation matrix  $(M(u, v), u, v \in \mathcal{G})$ . The concentrations  $x_v(t)$  of individuals having genotype  $v$  in the population, evolve according to the system of differential equations

$$x'_v(t) = \sum_{u \in \mathcal{G}} x_u(t) f(u) M(u, v) - x_v(t) \sum_{u \in \mathcal{G}} x_u(t) f(u), \quad v \in \mathcal{G}.$$

These differential equations arise naturally when considering the proportions  $x_v(t) = N_v(t) / \sum_{u \in \mathcal{G}} N_u(t)$  associated to the simple linear model

$$N'_v(t) = \sum_{u \in \mathcal{G}} N_u(t) f(u) M(u, v), \quad v \in \mathcal{G},$$

where the number of individuals of type  $v$  grows exponentially due to the faithful replication of itself, as well as the erroneous replication of the other genotypes. Under the assumption that the matrix  $W = (f(u)M(u, v), u, v \in \mathcal{G})$  is primitive, it is well known [11, 17, 18] that the above system of differential equations has a unique stationary solution  $x^*$  and all the trajectories converge to  $x^*$ . Approximate formulas for  $x^*$  have been found under several approximation schemes, see [9] for an example. Eigen's model exhibits two phenomena of particular importance: an error threshold phenomenon and a

quasispecies distribution. In order to see what this means, let us fix  $\mathcal{G}$  to be the  $\ell$ -dimensional hypercube  $\{0, 1\}^\ell$ , and suppose that mutations arrive independently on each site of a chain with probability  $q$ . When the length of the genotypes  $\ell$  tends to infinity, there exists a critical mutation probability  $q^*$ , called the error threshold, separating two different regimes. For mutation probabilities above the error threshold, the population at equilibrium is totally random. For mutation probabilities below the error threshold, the population at equilibrium possesses a positive concentration of the fittest genotype, along with a cloud of mutants which are a few mutations away from the fittest genotype. This kind of distribution is referred to as a quasispecies. The concepts of error threshold and quasispecies, although they were originally meant to apply to prebiotic populations, rapidly found their place in explaining the behavior of more complex living populations, as viruses [6, 12], prions and bacteria [15], or even some sort of cancers [2, 16]. Explicit formulas for the distribution of the quasispecies have been found in [4], in the case of the sharp peak landscape, as well as in the case of class-dependent fitness landscapes. These formulas are obtained in the following asymptotic regime:

$$\ell \rightarrow \infty \quad q \rightarrow 0 \quad \ell q \rightarrow a \in ]0, +\infty[ ,$$

which arises when the genomes are considered to be long, the mutations rare, and the mean number of mutations per genome per generation is roughly  $a$ . Such an asymptotic regime is particularly well-suited for populations of RNA viruses, since their mutation rates are quite large compared to other organisms, and can acquire a magnitude of the order of the inverse genome length [8]. In this asymptotic regime, an infinite version of Eigen's system of differential equations  $(x^\infty)'(t) = F(x^\infty(t))$  is obtained, and the equations for the stationary solutions of the infinite system are explicitly solved. The solutions  $\mathcal{Q}(f, a)$  are called quasispecies distributions, and depend both on the fitness function  $f$  and the mean number of mutations per genome per generation  $a$ . The aim of this paper is to complete the picture by showing the following convergences:

$$\begin{array}{ccc}
 x(t) & \xrightarrow{t \rightarrow \infty} & x^* \\
 \downarrow \begin{array}{l} \ell \rightarrow \infty, q \rightarrow 0 \\ \ell q \rightarrow a \end{array} & & \downarrow \begin{array}{l} \ell \rightarrow \infty, q \rightarrow 0 \\ \ell q \rightarrow a \end{array} \\
 x^\infty(t) & \xrightarrow{t \rightarrow \infty} & \mathcal{Q}(f, a)
 \end{array}$$

We hope that this diagram may justify the approximation of Eigen's system by its infinite counterpart, and more importantly, that of the equilibrium

$x^*$  by the quasispecies distribution  $\mathcal{Q}(f, a)$ . Indeed, the Perron–Frobenius eigenvector  $x^*$  lacks an explicit representation, and cannot be calculated, in general, other than numerically, whereas for the quasispecies distribution we do have an explicit formula. We do wish to remark however, that in the long–chain regime, a system of ODEs might not be the best choice when modelling a finite population, even if its size is large; a stochastic model for a finite population would be a better option. Indeed, when a population is finite, say of size  $m$ , many of the concentrations obtained by the ODE will fall below  $1/m$ , which makes little sense. However, we believe that the ODE model is a necessary intermediate step in the understanding of a more pertinent model. There are at least two reasons for this:

1. Eigen’s quasispecies model can be linked to classical models in population genetics (Galton–Watson, Moran, Wright–Fisher), by performing infinite–population limits (see [5] for an example).
2. There are several fitness functions, in particular the class–dependent fitness functions that we will consider below, for which the ODE representation does make sense. Indeed, if many genotypes can be lumped together, many of the concentrations that were below  $1/m$  will be of a greater order. Of course, even in this case, the ODE representation will only work for sharply–peaked landscapes, and for the classes that contain those mutants that are close to the master sequence.

We also obtain analogous results for a closely related model. We keep the same framework as in Eigen’s model, but we consider the time to be discrete. The concentration  $x_v(n)$  of individuals having genotype  $v$  evolves according to the following dynamical system:

$$x_v(n+1) = \frac{\sum_{u \in \mathcal{G}} x_u(n) f(u) M(u, v)}{\sum_{u \in \mathcal{G}} x_u(n) f(u)}.$$

This model was first proposed by Moran [13,14], and it is not to be confused with the well–known Moran model, which is a stochastic model for the evolution of a finite population. We thus call this model the deterministic Moran model. It can be seen as the counterpart of Eigen’s model when the time is considered to be discrete, and the different generations do not overlap. We will show that a similar diagram holds for the deterministic Moran model. In particular, the unique fixed point of the above dynamical system is again  $x^*$ , and the distribution of the quasispecies found in the limit coincides with the distribution of the quasispecies for Eigen’s model.

## 2 Models and known results

Let  $\mathcal{A}$  be a finite alphabet of cardinality  $\kappa$ , and let  $\mathcal{A}^\ell$  be the set of sequences of length  $\ell \geq 1$  over  $\mathcal{A}$ . We will refer to  $\mathcal{A}^\ell$  as the set of genotypes; typical choices for  $\mathcal{A}$  are  $\{A, T, G, C\}$  for DNA sequences, the set of the twenty amino acids for proteins, or  $\{0, 1\}$  for binary sequences. The models we consider aim at modeling the evolution of a population, the individuals in the population having genotypes in  $\mathcal{A}^\ell$ . The evolution will be guided by two main forces, mutation and selection. Mutations occur during reproduction, independently on each site of the genotype, with probability  $q \in (0, 1)$ ; when a mutation occurs in a certain site, the letter present in it is replaced by one of the  $\kappa - 1$  remaining letters in the alphabet, chosen uniformly at random. The natural distance on  $\mathcal{A}^\ell$  is the Hamming distance, which counts the number of different digits between two chains, i.e.,

$$\forall u, v \in \mathcal{A}^\ell \quad d(u, v) = \text{card}\{1 \leq i \leq \ell : u(i) \neq v(i)\}.$$

The probability that a genotype  $u$  is transformed into a genotype  $v$  by mutation is given by

$$Q(u, v) = \left(\frac{q}{\kappa - 1}\right)^{d(u, v)} (1 - q)^{\ell - d(u, v)}.$$

Selection is defined via a fitness function. We make the following two assumptions on the selection mechanism of our model.

**Assumptions.** We suppose that:

- (A1) There exists a privileged sequence,  $w^* \in \mathcal{A}^\ell$  of strictly maximal fitness.
- (A2) All sequences at a same distance from  $w^*$  share the same fitness.

The privileged sequence  $w^*$  will be referred to as the master sequence. The second assumption can be rephrased by saying that the fitness is a function of the number of point mutations away from the master sequence. Formally, these assumptions mean that there is a function  $f : \mathbb{N} \rightarrow \mathbb{R}_+$  satisfying  $f(0) > f(k)$  for every  $k \geq 0$  and such that for every  $v \in \mathcal{A}^\ell$ , the fitness of  $v$  is given by the quantity  $f(d(v, w^*))$ . Note that in particular, this fitness landscape is frequency-independent. Under these assumptions, we can decompose the space of genotypes  $\mathcal{A}^\ell$  into Hamming classes with respect to the master sequence. We say that a genotype  $u \in \mathcal{A}^\ell$  belongs to the Hamming class  $k$  if  $d(u, w^*) = k$ . The set of Hamming classes is  $\{0, \dots, \ell\}$ ; the mutation matrix  $Q$  can be factorized through the Hamming classes. Indeed, for  $0 \leq i, k \leq \ell$ , the probability that a genotype in the class  $i$  mutates into a genotype in the class  $k$  is given by

$$M(i, k) = P(i - \text{Bin}(i, q/(\kappa - 1)) + \text{Bin}(\ell - i, q) = k),$$

where  $Bin(n, p)$  is the binomial law, and the two binomials in the formula are independent. The first binomial can be interpreted as follows: a genotype in the class  $i$  has  $i$  digits different to those of the master sequence, each of which independently mutates and becomes equal to that of the master sequence with probability  $q/(\kappa - 1)$ . The second binomial corresponds to the  $\ell - i$  remaining digits, which coincide with those of the master sequence, and change independently with probability  $q$ . Note that the mutation matrix is decomposable into Hamming classes because we only consider substitution-type mutations; the model would have to be adapted if we wanted to consider insertions and deletions too. Define  $\Delta^\ell$  to be the  $\ell$ -dimensional unit simplex:

$$\Delta^\ell = \{ x \in [0, 1]^{\ell+1} : x_0 + \dots + x_\ell = 1 \}.$$

**Eigen's model.** Let  $x_k(t)$  represent the proportion of individuals in the class  $k$  in a population at time  $t$ . The quantities  $x_k(t)$  evolve according to the following system of differential equations:

$$(Eig) \quad x'_k(t) = \sum_{i=0}^{\ell} x_i(t) f(i) M(i, k) - x_k(t) \sum_{i=0}^{\ell} x_i(t) f(i), \quad 0 \leq k \leq \ell.$$

Note that if  $x^0$  belongs to  $\Delta^\ell$ , then the solution  $(x(t), t \geq 0)$  of  $(Eig)$  with initial condition  $x(0) = x^0$  belongs to  $\Delta^\ell$  for all  $t \geq 0$ , which is a direct consequence of  $M$  being a stochastic matrix.

**The deterministic Moran model.** Let  $x_k(n)$  represent the proportion of individuals in the class  $k$  in generation  $n$ . The quantities  $x_k(n)$  evolve according to the following discrete-time dynamical system:

$$(DM) \quad x_k(n+1) = \frac{\sum_{0 \leq i \leq \ell} x_i(n) f(i) M(i, k)}{\sum_{0 \leq i \leq \ell} x_i(n) f(i)}, \quad 0 \leq k \leq \ell.$$

Again, if  $x^0 \in \Delta^\ell$ , then the solution  $(x(n), n \geq 0)$  of  $(DM)$  with initial condition  $x(0) = x^0$  belongs to  $\Delta^\ell$  for all  $n \geq 0$ .

Both of these models aim at explaining the evolution of simple population bound to selection and mutation forces. In Eigen's model, the generations are allowed to overlap, whereas in the deterministic Moran model they are not. If the evolution of a population is governed by any of these models for a very long time, it will eventually approach an equilibrium state, where the proportions of the different types will become constant. Moreover, as shown in the next theorem, the equilibrium solution will always be the same, regardless of the initial composition of the population. Let us define the matrix  $W$  by

$$\forall i, j \in \{0, \dots, \ell\} \quad W(i, j) = f(i) M(i, j).$$

The matrix  $W$  is strictly positive, and thus the Perron–Frobenius theorem applies. We have the following result.

**Proposition 2.1.** *Eigen’s system of differential equations (Eig) admits a unique stationary solution  $x^* \in \Delta^\ell$ . Moreover, for every  $x^0 \in \Delta^\ell$ , the solution  $(x(t), t \geq 0)$  of (Eig) with initial condition  $x(0) = x^0$  satisfies*

$$\lim_{t \rightarrow \infty} x(t) = x^* .$$

This result is well–known, and has been established by several authors, see for instance [1, 10, 11, 18]. A similar result holds for the deterministic Moran model, which has been proven by Moran himself in [13]. Both results can be proven in a similar way, by using the Perron–Frobenius theorem. In fact, the vector  $x^*$  is the same in both cases, and it is the left Perron–Frobenius eigenvector of the matrix  $W$ , normalized so that it belongs to  $\Delta^\ell$ . We also remark that the mean fitness of the population at equilibrium,

$$\lambda = \sum_{0 \leq i \leq \ell} x_i^* f(i) ,$$

is the Perron–Frobenius eigenvalue of the matrix  $W$ .

Unfortunately, proposition 2.1 gives little insight on what the composition of the population at equilibrium might be. Indeed, the calculation of the Perron–Frobenius eigenvector can only be done numerically in a case–by–case basis, except in special circumstances, such as, for exemple, in birth–death processes. There is, though, an appropriate asymptotic regime, which in addition to being biologically relevant [8], allows us to carry over some explicit computations. Let us suppose that the length of the genomes goes to  $\infty$  and the mutation probability goes to 0, while the mean number of mutations per genome per generation is approximately  $a > 0$ . I.e.,

$$\ell \rightarrow \infty , \quad q \rightarrow 0 , \quad \ell q \rightarrow a \in ]0, +\infty[ .$$

Recall that the mutation matrix  $M$  is given by the formula

$$M(i, k) = P(i - \text{Bin}(i, q/(\kappa - 1)) + \text{Bin}(\ell - i, q) = k) .$$

When considering the above asymptotic regime, the first of the binomial laws converges to a Dirac mass at 0, while the second one converges to a Poisson distribution of parameter  $a$ . Therefore, we obtain an infinite mutation matrix  $M_\infty$ , which is given by

$$\forall i, k \geq 0 \quad M_\infty(i, k) = \begin{cases} e^{-a} \frac{a^{k-i}}{(k-i)!} & \text{if } k \geq i , \\ 0 & \text{if } k < i . \end{cases}$$

In particular, the limit mutation matrix does not allow for back mutations, i.e., we can mutate away from the master sequence, but we cannot mutate towards the master sequence.

**Eigen's infinite system.** Let  $y_k(t)$  represent the proportion of individuals in the class  $k$  in a population at time  $t$ . The quantities  $y_k(t)$  evolve according to the following system of differential equations:

$$(Eig_\infty) \quad y'_k(t) = \sum_{i=0}^k y_i(t) f(i) e^{-a} \frac{a^{k-i}}{(k-i)!} - y_k(t) \sum_{i \geq 0} y_i(t) f(i), \quad k \geq 0.$$

**The infinite deterministic Moran model.** Let  $y_k(n)$  represent the proportion of individuals in the class  $k$  in generation  $n$ . The quantities  $y_k(n)$  evolve according to the following discrete-time dynamical system:

$$(DM_\infty) \quad y_k(n+1) = \frac{\sum_{0 \leq i \leq k} y_i(n) f(i) e^{-a} \frac{a^{k-i}}{(k-i)!}}{\sum_{i \geq 0} y_i(n) f(i)}, \quad k \geq 0.$$

We first look for the stationary solutions of  $(Eig_\infty)$ , which coincide with the fixed points of  $(DM_\infty)$ . We restrict our attention to the stationary solutions satisfying

$$\sum_{k \geq 0} y_k = 1.$$

Let  $I(f) \in \mathbb{N}$  be the set of indices  $i$  such that

$$f(i)e^{-a} > 1 \quad \text{and} \quad f(i) > f(j) \quad \forall j > i.$$

We have the following result.

**Proposition 2.2.** *The system  $(Eig_\infty)$  has as many stationary solutions as there are elements in  $I(f)$ . Moreover, for each  $i \in I(f)$ , the associated solution  $(\rho_k^i)_{k \geq 0}$  satisfies*

$$\rho_0^i = \dots = \rho_{i-1}^i = 0 \quad \text{and} \quad \rho_i^i > 0.$$

A similar statement holds for the fixed points of  $(DM_\infty)$ . This result has been proven in [4], where an explicit formula is found for the solutions  $\rho^i$ . Indeed, the solution  $\rho^i$  is given by: for all  $k \geq 0$ ,

$$\rho_{i+k}^i = \frac{\frac{1}{f(i)} 1_{k=0} + \frac{a^k}{f(i+k)} \sum_{\substack{1 \leq h \leq k \\ 0=i_0 < \dots < i_h=k}} \prod_{t=1}^h \frac{f(i+i_t)}{(i_t - i_{t-1})!(f(i) - f(i+i_t))}}{\frac{1}{f(i)} + \sum_{\substack{h \geq 1 \\ 0=i_0 < \dots < i_h}} \frac{a^{i_h}}{f(i+i_h)} \prod_{t=1}^h \frac{f(i+i_t)}{(i_t - i_{t-1})!(f(i) - f(i+i_t))}},$$

where an empty sum is taken to be equal to 0.

Before stating our results, we justify the existence and uniqueness of a global solution of the system  $(Eig_\infty)$  for a given initial condition. The facts stated below follow from the general theory of ODE's on Banach spaces (see for instance [3], part II, chapter 1). We denote by  $\ell^1$  the space of absolutely summable sequences  $(y_k)_{k \geq 0}$  and by  $\|\cdot\|$  their  $\ell^1$  norm, as well as the operator norm associated to it.

**Proposition 2.3.** *The Cauchy problem  $y'(t) = F(y(t))$  with initial condition  $y(0) \in \ell^1$  admits a unique maximal solution  $y : ]a, b[ \rightarrow \ell^1$  with  $-\infty \leq a < 0 < b \leq +\infty$ . Furthermore, the set*

$$E = \{ y \in \ell^1 : \forall k \geq 0 \ y_k \geq 0 \quad \text{and} \quad \|y\| = 1 \}$$

*is positively invariant, that is, if  $y(0) \in E$ , then for all  $t \geq 0$  we have  $y(t) \in E$ .*

*Proof.* Define the operator  $W_\infty : \ell^1 \rightarrow \ell^1$  by setting

$$\forall y \in \ell^1 \quad \forall k \geq 0 \quad (yW_\infty)_k = \sum_{i=0}^k y_i f(i) M_\infty(i, k).$$

In view of assumption (A), the operator  $W_\infty$  is bounded by  $f(0)$ . Moreover, we can rewrite the system of differential equations  $(Eig_\infty)$  in terms of the operator  $W_\infty$  as  $y'(t) = F(y(t))$  with

$$F(y) = yW_\infty - y \langle yW_\infty, 1 \rangle,$$

where for  $y \in \ell^1$  and  $(h_k)_{k \geq 0}$  a bounded sequence,  $\langle y, h \rangle = \sum_{i \geq 0} y_i h_i$ . Since the operator  $W_\infty$  is bounded, the mapping  $F : \ell^1 \rightarrow \ell^1$  is locally Lipschitz. Indeed, let  $y \in \ell^1$  and  $\delta > 0$ , for every  $z \in \ell^1$  such that  $\|y - z\| < \delta$ , we have

$$\|F(y) - F(z)\| \leq \|y - z\| \cdot \|W_\infty\| + \|y - z\| \cdot |\langle yW_\infty, 1 \rangle| + \|z\| \cdot |\langle (y - z)W_\infty, 1 \rangle|.$$

Note that for every  $u \in \ell^1$  we have  $|\langle uW_\infty, 1 \rangle| \leq \|u\| \cdot \|W_\infty\|$ . Thus,

$$\|F(y) - F(z)\| \leq \|W_\infty\| (1 + \|y\| + \|z\|) \|y - z\| \leq M(y, \delta) \|y - z\|,$$

with  $M(y, \delta) = \|W_\infty\| (1 + 2\|y\| + \delta)$ , so that  $F$  is locally Lipschitz. Indeed, if  $y(0)$  is a non-negative sequence, the fact that  $y_k(t) \geq 0$  for all  $k \geq 0$  and  $t \geq 0$  follows from lemma A.1 together with an inductive argument. Moreover, if  $y \in \ell^1$  is a non-negative sequence,

$$\frac{d}{dt} \|y(t)\| = \sum_{k \geq 0} y'_k(t) = \langle yW_\infty, 1 \rangle (1 - \|y(t)\|).$$

Thus,  $E$  is positively invariant. For every  $y \in E$  we have  $\|F(y)\| \leq 2\|W_\infty\|$ , therefore the solution  $y$  does not explode and  $b$  can be taken to be equal to  $\infty$ .  $\square$

In the sequel, we will only consider solutions of  $(Eig_\infty)$  such that  $y(0) \in E$ . In this case, the limit of  $y_k(t)$  when  $t$  goes to  $\infty$  is well defined for all  $k \geq 0$ . We now proceed to state our main results.

### 3 Main results

We begin by showing the convergence of the solutions of the system  $(Eig_\infty)$ . Contrary to Eigen's original system of differential equations  $(Eig)$ , the limiting system  $(Eig_\infty)$  admits several equilibrium solutions, and the long-time behavior of a population will now depend on the initial proportions of the different types. Assume that  $I(f) = \{i_1, \dots, i_N\}$ . Note that  $N$  might be equal to 0, in which case  $I(f)$  would be empty.

**Theorem 3.1.** *Let  $(y(t))_{t \geq 0}$  be a solution of  $(Eig_\infty)$ . For every  $k \geq 0$  and  $h \in \{1, \dots, N\}$ ,*

$$\lim_{t \rightarrow \infty} y_k(t) = \rho_k^{i_h}$$

*if and only if the initial condition satisfies*

$$y_0(0) = \dots = y_{i_{h-1}}(0) = 0 \quad \text{and} \quad \max_{i_{h-1} < i \leq i_h} y_i(0) > 0.$$

*In this case,  $y(t)$  converges to  $\rho^{i_h}$  in  $\ell^1$ . Otherwise,  $y_k(t)$  converges to 0 for all  $k \geq 0$ .*

This theorem will be proven in section 5. We have performed a formal passage to the limit in order to pass from Eigen's original system  $(Eig)$  to the system in the long chain regime  $(Eig_\infty)$ . The purpose of the next theorem is to show that this approximation goes beyond the formal one, by proving the convergence of the solutions of  $(Eig)$  to the solutions of  $(Eig_\infty)$  on finite time intervals.

**Theorem 3.2.** *Let  $(x(t))_{t \geq 0}$  and  $(y(t))_{t \geq 0}$  be solutions of  $(Eig)$  and  $(Eig_\infty)$  respectively, and assume that the initial conditions converge, i.e.,*

$$\forall k \geq 0, \quad \lim_{\substack{\ell \rightarrow \infty, q \rightarrow 0 \\ \ell q \rightarrow a}} x_k(0) = y_k(0).$$

*Then, for every  $T > 0$  and for every  $k \geq 0$ ,*

$$\lim_{\substack{\ell \rightarrow \infty, q \rightarrow 0 \\ \ell q \rightarrow a}} \sup_{0 \leq t \leq T} |x_k(t) - y_k(t)| = 0.$$

The proof of this theorem will be carried out in section 6. Finally, we study that the convergence of the unique stationary solution of  $(Eig)$ . Indeed, the system of ODE  $(Eig)$  has a unique equilibrium solution, while the limit system  $(Eig_\infty)$  might have several. The question thus arises so as to which of these equilibrium solutions is the one that best approximates the equilibrium of a population with long but finite genome. We answer this question in the next theorem.

**Theorem 3.3.** *Let  $x^* = (x_k^*)_{0 \leq k \leq \ell}$  be the unique stationary solution of  $(Eig)$ . We have the following dichotomy:*

- If  $f(0)e^{-a} \leq 1$ ,
 
$$\forall k \geq 0, \quad \lim_{\substack{\ell \rightarrow \infty, q \rightarrow 0 \\ \ell q \rightarrow a}} x_k^* = 0.$$

- If  $f(0)e^{-a} > 1$ ,
 
$$\forall k \geq 0, \quad \lim_{\substack{\ell \rightarrow \infty, q \rightarrow 0 \\ \ell q \rightarrow a}} x_k^* = \rho_k^0,$$

where  $(\rho_k^0)_{k \geq 0}$  is the unique stationary solution of  $(Eig_\infty)$  satisfying  $\rho_0^0 > 0$ .

We will prove this theorem in section 7. Even if the infinite system  $(Eig_\infty)$  possesses several equilibrium solutions, it is important to underline the relevance of the main equilibrium solution  $\rho^0$ . Indeed, the equilibrium  $\rho^0$  is locally stable, whereas all other equilibrium solutions have at least one direction in which they are unstable. Moreover, the importance of  $\rho^0$  is best seen thanks to this last theorem, since the system  $(Eig)$  is the one which is best suited to the biological reality, and the true equilibrium system is  $x^*$ . Analogous results to the previous ones hold for the discrete-time models  $(DM)$  and  $(DM_\infty)$ . The proofs are similar in both cases, and thus, in what follows, we will only deal with the continuous-time case. The next three sections prove each of the above results.

## 4 Eventually constant fitness functions

Suppose now that the fitness function  $f$  is eventually constant, i.e., there exists  $\kappa \in \mathbb{N}$  such that

$$f(\kappa - 1) \neq 1 = f(\kappa) = f(\kappa + 1) = \dots$$

In this case, in Eigen's system ( $Eig$ ), the mean fitness of a population  $x \in \mathcal{S}^\ell$  can be expressed as a function of  $x_0, \dots, x_\kappa$ . Indeed,

$$\phi_\kappa(x) = 1 + \sum_{i=0}^{\kappa} x_i(f(i) - 1).$$

Thus, replacing in the system ( $Eig$ ) and passing to the limit, we can now rewrite the infinite system as follows:

$$y'_k(t) = \sum_{i=0}^k y_i(t)f(i)e^{-a} \frac{a^{k-i}}{(k-i)!} - y_k\phi_\kappa(y) \quad k \geq 0.$$

For any  $K \geq \kappa$ , the system driving the evolution of  $(y_0(t), \dots, y_K(t))$  is a finite and autonomous system of differential equations, which we denote by ( $Eig_\infty^K$ ). Likewise, the analogous deterministic Moran model is rewritten, for  $K \geq \kappa$ , as follows

$$(DM_\infty^K) \quad y_k(n+1) = \phi_\kappa(y)^{-1} \sum_{i=0}^k y_i f(i) e^{-a} \frac{a^{k-i}}{(k-i)!} \quad 0 \leq k \leq K.$$

The system ( $Eig$ ) has  $|I(f)|$  stationary solutions, that correspond to the solutions of ( $Eig_\infty$ ) projected on the coordinates  $(0, \dots, K)$ . By an abuse of notation, for  $i \in I(f)$ , we still denote the projection of  $\rho^i$  onto the coordinates  $(0, \dots, K)$  by  $\rho^i$ . These are also the fixed points of ( $DM_\infty^K$ ).

**Theorem 4.1.** *If  $f(0)e^{-a} > 1$ , the point  $\rho^0$  is asymptotically exponentially stable, both as a stationary solution of ( $Eig_\infty^K$ ) and as a fixed point of ( $DM_\infty^K$ ). If  $f(0)e^{-a} < 1$ , the point 0 is asymptotically stable, both as a stationary solution of ( $Eig_\infty^K$ ) and as a fixed point of ( $DM_\infty^K$ ).*

We will prove this theorem in section 8.

## 5 Convergence to equilibrium

The aim of this section is to prove the theorem 3.1. We will only show that if  $i_1 = 0$  and  $y_0(0) > 0$ , then for every  $k \geq 0$ ,

$$\lim_{t \rightarrow \infty} y_k(t) = \rho_k^0,$$

where  $(\rho_k^0)_{k \geq 0}$  is the stationary solution of ( $Eig_\infty$ ) associated to 0. The remaining cases can be shown in a similar fashion. We denote by  $\phi_\infty(t)$  the mean fitness of the system ( $Eig_\infty$ ), i.e.,  $\phi_\infty(t) = \sum_{i \geq 0} y_i(t)f(i)$ . Let us note

first that if  $y_0(0) > 0$ , then  $y_0(t) > 0$  for all  $t \geq 0$ . Indeed, since for all  $t \geq 0$  we have  $\phi_\infty(t) \leq f(0)$ ,

$$y_0'(t) = y_0(t)f(0)e^{-a} - y_0(t)\phi_\infty(t) \geq y_0(t)f(0)(e^{-a} - 1).$$

Therefore, for all  $t \geq 0$ ,

$$y_0(t) \geq y_0(0)e^{-f(0)(1-e^{-a})t} > 0.$$

We can thus make the following change of variables: for all  $k \geq 0$ , we set  $z_k(t) = y_k(t)/y_0(t)$ . Differentiating, we obtain a new system of differential equations:

$$z_k'(t) = \sum_{i=0}^k z_i(t)f(i)e^{-a} \frac{a^{k-i}}{(k-i)!} - z_k(t)f(0)e^{-a}, \quad k \geq 1.$$

Thanks to this change of variables, we have managed to transform the original system of differential equations into a linear system. We will show by induction that for all  $k \geq 0$ ,  $z_k(t)$  converges to  $z_k^*$  when  $t$  goes to infinity, where  $z_k^* = \rho_k^0/\rho_0^0$ . The result is obvious for  $k = 0$ , since  $z_0(t) = 1$  for all  $t \geq 0$ . Let  $k \geq 1$  and suppose that  $z_i(t)$  converges to  $z_i^*$  for  $i \in \{0, \dots, k-1\}$ . We have

$$z_k'(t) = \sum_{i=0}^{k-1} z_i(t)f(i)e^{-a} \frac{a^{k-i}}{(k-i)!} - (f(0) - f(k))e^{-a}z_k(t).$$

We conclude that (appendix A):

$$\lim_{t \rightarrow \infty} z_k(t) = \frac{1}{f(0) - f(k)} \sum_{i=0}^{k-1} z_i^* f(i) \frac{a^{k-i}}{(k-i)!} = z_k^*.$$

This concludes the induction step. It remains to prove that

$$\lim_{t \rightarrow \infty} y_0(t) = \rho_0^0.$$

We have:

$$y_0(t) = \left( \sum_{k=0}^{\infty} z_k(t) \right)^{-1} \quad \text{and} \quad \rho_0^0 = \left( \sum_{k=0}^{\infty} z_k^* \right)^{-1}.$$

First, we will prove the convergence assuming that the fitness function  $f$  is eventually constant, and we will then use this fact to prove the general case. Let us suppose the existence of an  $N \geq 0$  such that the fitness function  $f$  is constant and equal to 1 for all  $n > N$ . In this case, the mean fitness  $\phi_\infty(t)$  is a function of  $y_0(t), \dots, y_N(t)$ ,

$$\phi_\infty(t) = \sum_{0 \leq k \leq N} y_k(t)(f(k) - 1) + 1 = y_0(t) \sum_{0 \leq k \leq N} z_k(t)(f(k) - 1) + 1.$$

Likewise, the mean fitness at equilibrium,  $\phi_\infty^*$ , is a function of  $\rho_0^0, \dots, \rho_N^0$ :

$$\phi_\infty^* = \sum_{0 \leq k \leq N} \rho_k^0 (f(k) - 1) + 1 = \rho_0^0 \sum_{0 \leq k \leq N} z_k^* (f(k) - 1) + 1.$$

Yet,  $\phi_\infty^* = f(0)e^{-a}$ . We conclude that

$$\sum_{0 \leq k \leq N} z_k^* (f(k) - 1) = \frac{f(0)e^{-a} - 1}{\rho_0^0} > 0.$$

Set

$$\begin{aligned} \alpha(t) &= \sum_{0 \leq k \leq N} z_k(t) (f(k) - 1), \\ \alpha^* &= \sum_{0 \leq k \leq N} z_k^* (f(k) - 1), \\ \beta &= f(0)e^{-a} - 1. \end{aligned}$$

The differential equation for  $y_0(t)$  can be rewritten as

$$y_0'(t) = y_0(t) (\beta - y_0(t) \alpha(t)).$$

We will show that  $y_0(t)$  converges to  $\beta/\alpha^* = \rho_0^0$ . Let  $\varepsilon > 0$  be small enough so that  $\alpha^* - \varepsilon > 0$ , and let  $T \geq 0$  be large enough so that

$$\forall t \geq T \quad |\alpha(t) - \alpha^*| < \varepsilon.$$

Then, for all  $t \geq T$ , the derivative  $y_0'(t)$  is strictly positive over  $]0, \beta/(\alpha^* + \varepsilon)[$  and strictly negative over  $] \beta/(\alpha^* - \varepsilon), 1[$ . We deduce the existence of a  $T_1 > T$  such that

$$\forall t \geq T_1 \quad \frac{\beta}{\alpha^* + \varepsilon} \leq y_0(t) \leq \frac{\beta}{\alpha^* - \varepsilon}.$$

Letting  $\varepsilon$  go to 0, we obtain the convergence of  $y_0(t)$  towards  $\rho_0^0$ . In particular, we get the convergence

$$\lim_{t \rightarrow \infty} \sum_{k \geq 0} z_k(t) = \sum_{k \geq 0} z_k^*.$$

If  $f$  is not eventually constant, we choose  $\varepsilon > 0$  small enough so that  $f(0)e^{-a} > 1 + \varepsilon$  and  $N \geq 0$  large enough so that

$$\forall n > N \quad f(n) < 1 + \varepsilon.$$

Let  $f_N : \mathbb{N} \rightarrow \mathbb{R}^+$  be the mapping defined by:

$$\forall n \geq 0 \quad f_N(n) = \begin{cases} f(n) & \text{if } n \leq N, \\ 1 + \varepsilon & \text{if } n > N. \end{cases}$$

Consider the system of differential equations

$$u'_k(t) = \sum_{0 \leq i \leq k} u_i(t) f_N(i) e^{-a} \frac{a^{k-i}}{(k-i)!} - u_k(t) f_N(0) e^{-a}.$$

Since  $f \leq f_N$  and  $f(0) = f_N(0)$ , if  $y_k(0) \leq u_k(0)$  for all  $k \geq 0$ , we have, thanks to the lemma A.2,

$$\forall k \geq 0 \quad \forall t \geq 0 \quad y_k(t) \leq u_k(t).$$

Moreover, since  $f_N$  is eventually constant, the series with general term  $u_k(t)$  converges to the series with general term  $u_k^*$ . We conclude that the same holds for the series with general term  $z_k(t)$ , as wanted. It remains to see that  $y(t)$  converges to  $\rho^0$  in  $\ell^1$ . Let  $\varepsilon > 0$  and choose  $N \geq 0$  large enough so that  $\rho_0^0 + \dots + \rho_N^0 > 1 - \varepsilon/4$ . It follows from the argument above that there exists  $T > 0$  such that

$$\forall k \in \{0, \dots, N\} \quad \forall t \geq T \quad |y_k(t) - \rho_k^0| < \frac{\varepsilon}{4(N+1)}.$$

In particular, for  $t \geq T$ ,

$$\sum_{k>N} y_k(t) = 1 - \sum_{k=0}^N y_k(t) \leq \left| 1 - \sum_{k=0}^N \rho_k^0 \right| + \sum_{k=0}^N |\rho_k^0 - y_k(t)| < \frac{\varepsilon}{2}.$$

Then, for all  $t \geq T$ ,

$$\|y(t) - \rho^0\| \leq \sum_{k=0}^N |y_k(t) - \rho_k^0| + \sum_{k>N} y_k(t) + \sum_{k>N} \rho_k^0 < \varepsilon,$$

which proves the  $\ell^1$  convergence.

## 6 Convergence of the trajectories

The aim of this section is to prove the theorem 3.2. Let  $\varepsilon, \delta, T > 0$  and let  $N$  be large enough so that

$$\forall n \geq N \quad |f(n) - 1| < \delta.$$

We will show that, for every  $n \geq N$  and  $t \leq T$ , asymptotically,

$$\sum_{k=0}^n |x_k(t) - y_k(t)| < \varepsilon.$$

Let  $n \geq N$ . Asymptotically, for every  $k \in \{1, \dots, n\}$ ,

$$\begin{aligned} \forall i \in \{0, \dots, k\}, & \quad |M_H(i, k) - M_\infty(i, k)| < \delta, \\ \forall i \in \{k+1, \dots, \ell\}, & \quad M_H(i, k) < \delta, \\ & \quad |x_k(0) - y_k(0)| < \delta. \end{aligned}$$

Moreover, denoting by  $\phi_H(t)$  and  $\phi_\infty(t)$  the mean fitness of the systems  $(Eig)$  and  $(Eig_\infty)$ , for every  $t \geq 0$ ,

$$\begin{aligned} \left| \phi_H(t) - \sum_{k=0}^N x_k(t)(f(k) - 1) - 1 \right| &= \left| \sum_{k=N+1}^{\ell} x_k(t)(f(k) - 1) \right| < \delta, \\ \left| \phi_\infty(t) - \sum_{k=0}^N y_k(t)(f(k) - 1) - 1 \right| &= \left| \sum_{k \geq N+1} y_k(t)(f(k) - 1) \right| < \delta. \end{aligned}$$

We have, for every  $k \geq 0$  and  $t \geq 0$ ,

$$\begin{aligned} x_k(t) &= x_k(0) + \int_0^t \left( \sum_{i=0}^{\ell} x_i(s)f(i)M_H(i, k) - x_k(s)\phi_H(s) \right) ds, \\ y_k(t) &= y_k(0) + \int_0^t \left( \sum_{i=0}^k y_i(s)f(i)M_\infty(i, k) - y_k(s)\phi_\infty(s) \right) ds. \end{aligned}$$

Thus, for every  $t \in [0, T]$ ,

$$\begin{aligned} |x_k(t) - y_k(t)| &\leq |x_k(0) - y_k(0)| + \\ &\quad \sum_{i=0}^k \int_0^t |x_i(s)f(i)M_H(i, k) - y_i(s)f(i)M_\infty(i, k)| ds + \\ &\quad \sum_{i=k+1}^{\ell} \int_0^t x_i(s)f(i)M_H(i, k) ds + \int_0^t |x_k(s)\phi_H(s) - y_k(s)\phi_\infty(s)| ds. \end{aligned}$$

The first term on the right is bounded by  $\delta$ . Adding and subtracting the quantity  $x_i(s)f(i)M_\infty(i, k)$  in each of the terms in the first sum, we see that the first sum is bounded by

$$\sum_{i=0}^k f(i)M_\infty(i, k) \int_0^t |x_i(s) - y_i(s)| ds + f(0)\delta T.$$

The second sum is bounded by  $f(0)\delta T$ , and for the last term, adding and subtracting  $y_k(s)\phi_H(s)$  inside the integral, we have

$$\begin{aligned} \int_0^t |x_k(s)\phi_H(s) - y_k(s)\phi_\infty(s)| ds &\leq \\ &\quad \int_0^t |x_k(s) - y_k(s)|\phi_H(s) ds + \int_0^t y_k(s)|\phi_H(s) - \phi_\infty(s)| ds. \end{aligned}$$

Noting that  $\phi_H(s) \leq f(0)$  and  $y_k(s) \leq 1$  for all  $s$ , we deduce from the bounds on  $\phi_H$  and  $\phi_\infty$  that the above expression is bounded by

$$f(0) \int_0^t |x_k(s) - y_k(s)| ds + 2\delta T + \sum_{i=0}^N |f(i) - 1| \int_0^t |x_i(s) - y_i(s)| ds.$$

Let  $C$  be the maximum of the  $|f(i) - 1|$  for  $1 \leq i \leq N$ , it follows that

$$\begin{aligned} |x_k(t) - y_k(t)| &\leq \delta(1 + 2(f(0) + 1)T) + \\ &\quad \sum_{i=0}^k f(0) M_\infty(i, k) \int_0^t |x_i(s) - y_i(s)| ds + \\ &\quad f(0) \int_0^t |x_k(s) - y_k(s)| ds + C \sum_{i=0}^N \int_0^t |x_i(s) - y_i(s)| ds. \end{aligned}$$

We sum for  $0 \leq k \leq n$  and we get

$$\begin{aligned} \sum_{k=0}^n |x_k(t) - y_k(t)| &\leq \delta(n+1)(1 + 2(f(0) + 1)T) + \\ &\quad \sum_{i=0}^n f(0) \left( \sum_{k=i}^n M_\infty(i, k) \right) \int_0^t |x_i(s) - y_i(s)| ds + \\ &\quad \sum_{k=0}^n f(0) \int_0^t |x_k(s) - y_k(s)| ds + (n+1)C \sum_{i=0}^n \int_0^t |x_i(s) - y_i(s)| ds. \end{aligned}$$

We deduce that

$$\sum_{k=0}^n |x_k(t) - y_k(t)| \leq \delta C_1 + C_2 \int_0^t \left( \sum_{k=0}^n |x_k(s) - y_k(s)| \right) ds,$$

where  $C_1, C_2$  positive constants that do not depend on  $\ell$  or  $q$ . We conclude thanks to Gronwall's lemma, by choosing  $\delta < \varepsilon C_1^{-1} e^{-C_2 T}$ .

## 7 Convergence of the stationary solution

Finally, we proceed to the proof of theorem 3.3. Let us recall that the matrix  $(W(i, j), 0 \leq i, j \leq \ell)$  is defined by

$$\forall i, j \in \{0, \dots, \ell\}, \quad W(i, j) = f(i) M_H(i, j).$$

The vector  $x^*$  solves the equation

$$\phi_H x_k^* = \sum_{i=0}^{\ell} x_i^* W(i, k), \quad 0 \leq k \leq \ell,$$

where

$$\phi_H = \sum_{i=0}^{\ell} x_i^* f(i),$$

is also the Perron–Frobenius eigenvalue of  $W$ . In particular,  $\phi_H \in ]0, f(0)[$ . Up to the extraction of a subsequence, we can suppose the existence of the limits

$$\phi_{\infty} = \lim_{\substack{\ell \rightarrow \infty, q \rightarrow 0 \\ \ell q \rightarrow a}} \phi_H, \quad y_k^* = \lim_{\substack{\ell \rightarrow \infty, q \rightarrow 0 \\ \ell q \rightarrow a}} x_k^*, \quad k \geq 0.$$

Writing down the  $k$ -th equation of the system  $(x^*)^T \phi_H = (x^*)^T W$ , we conclude that

$$\sum_{i=0}^k x_i^* f(i) M_H(i, k) < \phi_H x_k^* < \sum_{i=0}^k x_i^* f(i) M_H(i, k) + f(0) \max_{k < i \leq \ell} M_H(i, k).$$

In particular, if we take the left inequality with  $k = 0$ , and if we divide both sides by  $x_0^*$ , we get, passing to the limit, that  $\phi_{\infty} \geq f(0)e^{-a}$ . Passing to the limit in the above inequalities, we obtain the system of equations

$$\phi_{\infty} y_k^* = \sum_{i=0}^k y_i^* f(i) e^{-a} \frac{a^{k-i}}{(k-i)!}, \quad k \geq 0.$$

The zeroth equation reads  $\phi_{\infty} y_0^* = y_0^* f(0) e^{-a}$ . Since the sum of the components of the vector  $(x_k^*)_{k \geq 0}$  is equal to 1, the sequence  $(y_k^*)_{k \geq 0}$  satisfies

$$\sum_{k \geq 0} y_k^* \leq 1.$$

We know from [4] that this system of equations only admits the solution  $y_k^* = 0$  when  $f(0)e^{-a} < 1$ . On the other hand, if  $f(0)e^{-a} > 1$ , we see that necessarily  $y_0^* > 0$ : indeed, if  $K$  is the first index  $k \geq 0$  such that  $y_k^* > 0$ , it follows from a passage to the limit in the above inequalities that  $\phi_{\infty} \leq f(K)e^{-a}$ . In view of the constraints  $\phi_{\infty} \geq f(0)e^{-a}$  and  $f(0) > f(k)$  for all  $k \geq 1$ , we deduce that  $K$  must be equal to 0. Likewise, if  $y_k^* = 0$  for every  $k \geq 0$ , then taking  $N$  large enough so that, for all  $n \geq N$ ,  $|f(n) - 1| < \varepsilon$ , it follows that

$$\phi_H = \sum_{k=0}^{\ell} x_k^* f(k) \leq \sum_{k=0}^N x_k^* f(k) + (1 + \varepsilon).$$

We deduce from here that  $\phi_{\infty} \leq 1 + \varepsilon$ , which, for  $\varepsilon$  small enough is in contradiction with the fact that  $\phi_{\infty} \geq f(0)e^{-a}$ . Therefore,  $y_0^* > 0$  and  $\phi_{\infty} = f(0)e^{-a}$ . Summing over  $k \geq 0$  in the above system of equations, we see that

$$\phi_{\infty} \sum_{k \geq 0} y_k^* = \sum_{i \geq 0} y_i^* f(i) = \phi_{\infty}.$$

We conclude that the components of  $(y_k^*)_{k \geq 0}$  add up to 1, thus,  $(y_k^*)_{k \geq 0}$  must be equal to  $\rho^0$ .

## 8 Asymptotic stability

The aim of this section is to prove the theorem 4.1. We suppose thus that  $f$  is an eventually constant fitness function, and that  $\kappa$  is the last index such that  $f(\kappa) \neq 1$ . We show first that it is enough to prove the statement for the deterministic Moran model. Define the set  $\mathcal{D}^K$  by

$$\mathcal{D}^K = \left\{ y \in \mathbb{R}^{K+1} : y_0 \geq 0, \dots, y_K \geq 0 \text{ and } y_0 + \dots + y_K \leq 1 \right\}.$$

We define the mappings  $F, G : \mathcal{D}^K \rightarrow \mathcal{D}^K$  by

$$\forall k \in \{0, \dots, K\} \quad \forall y \in \mathcal{D}^K \quad F_k(y) = \sum_{i=0}^k y_i f(i) e^{-a} \frac{a^{k-i}}{(k-i)!} - y_k \phi_K(y).$$

and

$$\forall k \in \{0, \dots, K\} \quad \forall y \in \mathcal{D}^K \quad G_k(y) = \phi_K(y)^{-1} \sum_{i=0}^k y_i f(i) e^{-a} \frac{a^{k-i}}{(k-i)!}.$$

We can now rewrite the system ( $Eig_{\infty}^K$ ) as  $y'(t) = F(y(t))$  and the dynamical system ( $DM_{\infty}^K$ ) as  $y(n+1) = G(y(n))$ . Denote by  $J_F$  and  $J_G$  the Jacobian matrices of the mappings  $F$  and  $G$ . In order to prove the theorem 4.1, it is sufficient to show that if  $f(0)e^{-a} > 1$  all eigenvalues of  $J_F(\rho^0)$  have negative real part, and all eigenvalues of  $J_G(\rho^0)$  have a modulus smaller than 1. And if  $f(0)e^{-a} < 1$ , all eigenvalues of  $J_F(0)$  have negative real part, and all eigenvalues of  $J_G(0)$  have a modulus smaller than 1. Let us compute the jacobians of  $F$  and  $G$ . For  $0 \leq i, j \leq K$  we have

$$\frac{\partial F_i}{\partial y_j}(y) = \begin{cases} f(j)e^{-a} \frac{a^{j-i}}{(j-i)!} - y_i(f(j) - 1) & \text{if } j < i, \\ f(j)e^{-a} - \phi_K(y) - y_j(f(j) - 1) & \text{if } j = i, \\ -y_i(f(j) - 1) & \text{if } j > i. \end{cases}$$

and for  $G$ ,

$$\frac{\partial G_i}{\partial y_j}(y) = \begin{cases} \phi_K(y)^{-1} \left( f(j)e^{-a} \frac{a^{i-j}}{(i-j)!} - G_i(y)(f(j) - 1) \right) & \text{if } j \leq i, \\ -\phi_K(y)^{-1} G_i(y)(f(j) - 1) & \text{if } j > i. \end{cases}$$

In particular, if  $f(0)e^{-a} > 1$ , since  $\rho^0$  is a fixed point of  $G$ , and since  $\phi_K(\rho^0) = f(0)e^{-a}$ , we have

$$J_F(\rho^0) = f(0)e^{-a}(J_G(\rho^0) - I),$$

where  $I$  represents the identity matrix. Thus, if  $\lambda$  is an eigenvalue of  $J_F(\rho^0)$  and  $u$  an eigenvector of  $J_F(\rho^0)$  associated to  $\lambda$ , we have also

$$J_G(\rho^0)u = \left( \frac{\lambda}{f(0)e^{-a}} + 1 \right)u = \mu u.$$

In particular, if  $Re(\lambda) \geq 0$ , then the modulus of  $\mu$  is larger than 1. Thus, it suffices to show that  $J_G(\rho^0)$  has all its eigenvalues of modulus smaller than 1. Likewise, if  $f(0)e^{-a} < 1$ , then  $J_F(0) = J_G(0) - I$ , and we can reason as in the case  $f(0)e^{-a} > 1$ . In fact, if  $f(0)e^{-a} < 1$ , the matrix  $J_G(0)$  is a lower triangular matrix, the elements of the diagonal being

$$f(0)e^{-a}, \dots, f(K)e^{-a},$$

which proves that 0 is asymptotically exponentially stable. Let us now assume that  $f(0)e^{-a} > 1$ , and let us show that  $J_G(\rho^0)$  has all its eigenvalues of modulus smaller than one. Let  $U$  be an open neighborhood of  $\rho^0$ , and consider the mapping  $\iota : U \rightarrow \mathbb{R}_+^{K+1}$  given by

$$\forall r \in U \quad \iota(r) = \left( r_0, \frac{r_1}{r_0}, \dots, \frac{r_K}{r_0} \right).$$

Note that  $\iota$  is one-to-one, thus, we can define its inverse  $\iota^{-1}$  on the set  $V = \iota(U)$ . The inverse  $\iota^{-1} : V \rightarrow U$  is of course given by

$$\forall x \in V \quad \iota^{-1}(x) = (x_0, x_0x_1, \dots, x_0x_K).$$

Define the map  $H : \mathbb{R}_+^{K+1} \rightarrow \mathbb{R}^{K+1}$  by setting, for  $x \in \mathbb{R}_+^{K+1}$ ,

$$H_0(x) = \frac{x_0 f(0) e^{-a}}{1 + x_0 \left( f(0) - 1 + \sum_{h=1}^K x_h (f(h) - 1) \right)},$$

and for  $1 \leq k \leq K$ ,

$$H_k(x) = \frac{a^k}{k!} + \sum_{h=1}^k x_h \frac{f(h)}{f(0)} \frac{a^{k-h}}{(k-h)!}.$$

Then, for all  $r \in U$ , we have

$$\iota(G(r)) = H(\iota(r)).$$

Indeed, for  $r \in U$ , we have  $\iota_0(G(r)) = G_0(r)$ , and

$$\begin{aligned} H_0(\iota(r)) &= H_0\left(r_0, \frac{r_1}{r_0}, \dots, \frac{r_K}{r_0}\right) \\ &= \frac{r_0 f(0) e^{-a}}{1 + r_0 \left( f(0) - 1 + \sum_{h=1}^K \frac{r_h}{r_0} (f(h) - 1) \right)} = G_0(r). \end{aligned}$$

Likewise, for  $1 \leq k \leq K$ , we have

$$\iota_k(G(r)) = \frac{G_k(r)}{G_0(r)} = \frac{a^k}{k!} + \sum_{h=1}^k \frac{r_h f(h)}{r_0 f(0)} \frac{a^{k-h}}{(k-h)!} = H_k(\iota(r)).$$

Thus, the map  $H$  has a unique fixed point  $x^*$  in  $V$  and  $\iota(\rho^0) = x^*$ . Since  $G(\rho^0) = \iota^{-1}(H(\iota(\rho^0)))$ , we have

$$J_G(\rho^0) = J_{\iota^{-1}}(H(\iota(\rho^0)))J_H(\iota(\rho^0))J_{\iota}(\rho^0) = J_{\iota^{-1}}(x^*)J_H(x^*)J_{\iota}(\rho^0).$$

We compute next the three matrices appearing on the right hand-side. On one hand, we have,

$$J_{\iota^{-1}}(x^*) = \begin{pmatrix} 1 & 0 & 0 & \cdots & 0 & 0 \\ x_1^* & x_0^* & 0 & \cdots & 0 & 0 \\ x_2^* & 0 & x_0^* & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ x_{K+1}^* & 0 & 0 & \cdots & x_0^* & 0 \\ x_K^* & 0 & 0 & \cdots & 0 & x_0^* \end{pmatrix}.$$

On the other hand,

$$J_{\iota}(r) = \begin{pmatrix} 1 & 0 & 0 & \cdots & 0 & 0 \\ -r_1 & \frac{1}{r_0} & 0 & \cdots & 0 & 0 \\ \frac{r_0^2}{r_0^2} & r_0 & 0 & \cdots & 0 & 0 \\ -r_2 & 0 & \frac{1}{r_0} & \cdots & 0 & 0 \\ \frac{r_0^2}{r_0^2} & r_0 & r_0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ -r_{K-1} & 0 & 0 & \cdots & \frac{1}{r_0} & 0 \\ \frac{r_0^2}{r_0^2} & 0 & 0 & \cdots & r_0 & 0 \\ -r_K & 0 & 0 & \cdots & 0 & \frac{1}{r_0} \\ \frac{r_0^2}{r_0^2} & 0 & 0 & \cdots & 0 & r_0 \end{pmatrix}.$$

Thus, replacing  $r$  by  $\rho^0$  in the above matrix, and noting that  $\rho_0^0 = x_0^*$ , and  $\rho_k^0/\rho_0^0$  for  $1 \leq k \leq K$ , we can rewrite the above matrix in terms of  $x_0^*$  as follows.

$$J_{\iota}(\rho^0) = \begin{pmatrix} 1 & 0 & 0 & \cdots & 0 & 0 \\ -\frac{x_1^*}{x_0^*} & \frac{1}{r_0} & 0 & \cdots & 0 & 0 \\ \frac{x_0^*}{x_0^*} & r_0 & 0 & \cdots & 0 & 0 \\ -\frac{x_2^*}{x_0^*} & 0 & \frac{1}{x_0^*} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ -\frac{x_{K-1}^*}{x_0^*} & 0 & 0 & \cdots & \frac{1}{x_0^*} & 0 \\ \frac{x_0^*}{x_0^*} & 0 & 0 & \cdots & x_0^* & 0 \\ -\frac{x_K^*}{x_0^*} & 0 & 0 & \cdots & 0 & \frac{1}{x_0^*} \\ \frac{x_0^*}{x_0^*} & 0 & 0 & \cdots & 0 & x_0^* \end{pmatrix}.$$

We remark that, in particular,  $J_{l-1}(x^*)J_l(\rho^0) = J_l(\rho^0)J_{l-1}(x^*) = I$ . Finally, is a matrix of the following form, for which we have computed the diagonal:

$$J_H(x^*) = \begin{pmatrix} \frac{1}{f(0)e^{-a}} & * & * & \cdots & * & * \\ 0 & \frac{f(1)}{f(0)} & 0 & \cdots & 0 & 0 \\ 0 & * & \frac{f(2)}{f(0)} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & * & * & \cdots & \frac{f(K-1)}{f(0)} & 0 \\ 0 & * & * & \cdots & * & \frac{f(K)}{f(0)} \end{pmatrix}.$$

Here, the stars represent non zero quantities. Thus, the eigenvalues of the matrix  $J_H(x^*)$  are given by its diagonal, and all of them are real numbers smaller than 1. Note next that if  $\lambda$  is an eigenvalue of  $J_G$ , and  $u$  an eigenvector associated to  $\lambda$ , then

$$\lambda u = J_G(\rho^0)u = J_{l-1}(x^*)J_H(x^*)J_l(\rho^0)u \Rightarrow \lambda J_l(\rho^0)u = J_H(x^*)J_l(\rho^0)u.$$

So,  $J_l(\rho^0)u$  is an eigenvector of  $J_H(x^*)$  associated to  $\lambda$ . This shows that  $J_H(x^*)$  and  $J_G(\rho^0)$  have the same spectrum.

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## A Lemmas on linear ODEs

We give here some lemmas concerning linear ODEs, and specially their long time behavior.

**Lemma A.1.** *Let  $\alpha : [0, +\infty[ \rightarrow [0, +\infty[$  and  $\beta : [0, +\infty[ \rightarrow \mathbb{R}$  be Lipschitz functions and let  $(z(t), t \geq 0)$  be the solution of the differential equation*

$$z'(t) = \alpha(t) + \beta(t)z(t).$$

*If  $z(0) \geq 0$  then  $z(t) \geq 0$  for all  $t \geq 0$ .*

*Proof.* The trajectory  $(z(t), t \geq 0)$  is continuous. If there exists  $t^* \geq 0$  such that  $z(t^*) = 0$ , then

$$z'(t^*) = \alpha(t^*) \geq 0,$$

and thus  $z(t) \geq 0$  for all  $t \geq 0$ . □

**Lemma A.2.** *Let  $\alpha, \tilde{\alpha} : [0, +\infty[ \rightarrow [0, +\infty[$  and  $\beta, \tilde{\beta} : [0, +\infty[ \rightarrow \mathbb{R}$  be Lipschitz functions satisfying*

$$\forall t \geq 0, \quad \alpha(t) \leq \tilde{\alpha}(t), \quad \beta(t) \leq \tilde{\beta}(t).$$

*Let  $(y(t), t \geq 0)$  and  $(z(t), t \geq 0)$  be the solutions of the ODEs*

$$y'(t) = \alpha(t) + \beta(t)y(t), \quad z'(t) = \tilde{\alpha}(t) + \tilde{\beta}(t)z(t).$$

*If  $z(0) \geq y(0) \geq 0$  then  $z(t) \geq y(t)$  for all  $t \geq 0$ .*

*Proof.* We have

$$z'(t) - y'(t) = \tilde{\alpha}(t) - \alpha(t) + (\tilde{\beta}(t) - \beta(t))z(t) + \tilde{\beta}(t)(z(t) - y(t)).$$

From the previous lemma,  $z(t) \geq 0$  for all  $t \geq 0$ . Thus, applying the previous lemma once again,  $z(t) - y(t) \geq 0$  for all  $t \geq 0$ . □

**Lemma A.3.** Let  $\alpha, \beta : [0, +\infty[ \rightarrow [0, +\infty[$  be Lipschitz functions, and suppose that there exist  $\alpha^*, \beta^* \in ]0, +\infty[$  such that

$$\lim_{t \rightarrow \infty} \alpha(t) = \alpha^*, \quad \lim_{t \rightarrow \infty} \beta(t) = \beta^*.$$

Let  $(y(t), t \geq 0)$  be the solution of the differential equation

$$y'(t) = \alpha(t) - \beta(t)y(t).$$

Then, for every initial condition  $y(0) \in \mathbb{R}$ ,

$$\lim_{t \rightarrow \infty} y(t) = \frac{\alpha^*}{\beta^*}.$$

*Proof.* Let  $\varepsilon > 0$  be small enough so that  $\alpha^* - \varepsilon, \beta^* - \varepsilon > 0$ . Let  $T \geq 0$  be large enough so that

$$\forall t \geq T, \quad |\alpha(t) - \alpha^*| < \varepsilon, \quad |\beta(t) - \beta^*| < \varepsilon.$$

Let  $(\underline{y}(t), t \geq 0)$  and  $(\bar{y}(t), t \geq 0)$  be the solutions of the differential equations

$$\underline{y}'(t) = (\alpha^* - \varepsilon) - (\beta^* + \varepsilon)\underline{y}(t), \quad \bar{y}'(t) = (\alpha^* + \varepsilon) - (\beta^* - \varepsilon)\bar{y}(t),$$

with  $\underline{y}(0) = \bar{y}(0) = y(T)$ . From the previous lemma, for all  $t \geq 0$ ,

$$\underline{y}(t) \leq y(T+t) \leq \bar{y}(t).$$

Yet,  $\underline{y}(t)$  and  $\bar{y}(t)$  converge:

$$\lim_{t \rightarrow \infty} \underline{y}(t) = \frac{\alpha^* - \varepsilon}{\beta^* + \varepsilon}, \quad \lim_{t \rightarrow \infty} \bar{y}(t) = \frac{\alpha^* + \varepsilon}{\beta^* - \varepsilon}.$$

We conclude that

$$\frac{\alpha^* - \varepsilon}{\beta^* + \varepsilon} \leq \liminf_{t \rightarrow \infty} y(t) \leq \limsup_{t \rightarrow \infty} y(t) \leq \frac{\alpha^* + \varepsilon}{\beta^* - \varepsilon}.$$

We send  $\varepsilon$  to 0 and we obtain the desired result.  $\square$