

**Epidemiological modeling in  
a branching population with  
horizontal and vertical  
transmissions. Particular  
case of SIS diseases with  
two age classes**

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**Abstract**

This paper covers the elaboration of a general class of multitype branching processes for modeling, in a branching population, the evolution of a disease which may be transmitted both horizontally and vertically. The law governing a population's state of health can be used for studying the behavior of a disease in bounded populations. When the size of the population is large or not bounded, normalization must be carried out. As the initial size tends to infinity, the normalized model converges a.s. to a dynamical system resulting in the law of the state of health for an individual ancestors line. The latter is the generalization in an open population of the concept of individual in a closed population. The focal point of this study concerns the transient and asymptotical behavior of *SIS* diseases in branching populations with two age classes. We will compare the asymptotical probability of extinction for such diseases on the scale of a finite population and on the scale of an individual in an infinite population: when the rates of transmission are small compared to the rate of renewing the population of susceptibles, the two models lead to a.s. extinction, giving consistent results, which no longer applies to the opposite situation of important transmissions. In that case the size of the population plays a crucial role in the spreading of the disease.

*Key words:* Branching process; Discrete time; *SIS* model; Epidemiology; Vertical transmission; Horizontal transmission.

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## 1 Introduction

For diseases having epidemic behaviors over short periods compared to the hosts dynamics, the population under study can be considered as a closed population without immigration or offspring. In that case, stochastic epidemiological models are easily built from Markovian or semi-Markovian processes in a finite state space, either on the scale of the population's state of health by considering countings of individuals in every state, or on the scale of the individual by considering survival processes or more generally duration processes. When the disease is contagious or transmissible and may last over a long period compared to the population dynamics, as is the case for example for human diseases such as AIDS or animal diseases such as TSE (Transmissible Spongiform Encephalopathies), then there may be some interaction between the dynamics of the pathogenic agent and that of the host. In that case the modeling of the evolution of the disease also has to take into account the host population's dynamics.

In the second section we propose the elaboration of a general multitype size-dependent branching process for describing the evolution of a disease in an

open branching population, that is in a population with successive generations and with possible migrations. The disease is assumed to be transmissible both horizontally and vertically. The vertical transmission is the transmission from a mother to her newborns either *in utero* or at birth, and horizontal transmissions are the other ones. The modeling is considered here at discrete time but could be extended to continuous time. The probability law of the state of health of the population is solution of a dynamical system. In the frame of the branching process we first prove that if a healthy population remains healthy at every time, then the probability of extinction of the disease is positive and even equal to 1 in the particular case of a bounded population. When the size of the whole population remains bounded and not too large, the branching process may be considered as a classical Markovian or semi-Markovian process according to the assumptions made on the transitions between the states of health.

But should the branching population increase, what is much easier to study is rather the branching process normalized by the size of the population. In the third section we show that this process converges a.s., as the initial size of the population tends to infinity, to a dynamical system the solution of which is the law of the state of health of an individual ancestors line, generalization in an open population of the concept of individual for a closed population.

In the fourth section we finally give the example of *SIS* diseases, where the incubation period is considered as negligible and the infectives recover without immunity against reinfection. Vertical transmission from a mother to her newborns and horizontal transmission are both considered and general assumptions are made as regards the horizontal transmissions. The branching process is first built and the probability of extinction of the disease calculated: it is positive and even equal to 1 when the population is bounded, if the probability of recovery is nonnull and the vertical transmission probability is less than 1. Then the dynamical system which gives the proportion  $x_{n+1}$  of infectives at time  $n + 1$  as a function of  $x_n$  is derived as the limit of the normalized branching process:

$$(1 + \tilde{m})x_{n+1} = (1 - a(x_n))(1 - x_n) + (1 - p)x_n + \tilde{m}[(1 - b(x_n)) + b(x_n)(1 - \tilde{q})x_n], \quad (1)$$

where  $\tilde{m}$  is the mean number of newborns of every individual at every time,  $1 - b(x_n)$  is the horizontal transmission probability for a susceptible newborn to be infected by a proportion of  $x_n$  infectives other than his mother. The term  $(1 - a(x_n))(1 - x_n)$  represents the part of the previous susceptible population which is infected at time  $n + 1$ , and the quantity  $(1 - p)x_n$  represents the part of the previous infectious population which is still infectious at time  $n + 1$ . In (1), the infectives at time  $n + 1$  are made up not only of the existing population but also of the newborns who are immediately infected either by horizontal

transmission with probability  $(1 - b(x_n))$ , or by vertical transmission with probability  $b(x_n)(1 - \tilde{q})x_n$ ,  $1 - \tilde{q}$  representing the probability for a newborn to be infected by his mother when she is herself infectious. The functions  $a(\cdot)$  and  $b(\cdot)$  satisfy  $0 < a(\cdot) \leq 1$ ,  $0 < b(\cdot) \leq 1$  and  $a(0) = b(0) = 1$ . We assume either that  $a(x) = b(x) = 1$ , for all  $x \in [0, 1]$  (and in that case, we write  $a = b = 1$ ), or we assume either

$$a'(x) < 0, b'(x) < 0; a''(x) \geq 0, b''(x) \geq 0, \forall x \in [0, 1] \quad (2)$$

or

$$\begin{aligned} a'(x) + \tilde{m}b'(x) &< 0, a''(x) + \tilde{m}b''(x) \geq 0, \\ \tilde{q}(2a'(x) + xa''(x)) &\leq 0, \forall x \in [0, 1]. \end{aligned} \quad (3)$$

We summarize these sets of conditions by writing “ $a \neq 1$  or  $b \neq 1$ ”. In the particular case of a closed population ( $\tilde{m} = 0$ ), we set  $b = 1$  and  $\tilde{q} = 1$ . In this model, the death is not taken into account and there may be a transition  $p$  from  $I$  to  $S$ . This model is, for example, a suitable model for modeling the evolution of a disease in an animal breeding where an  $I$  animal either recovers or is replaced by a  $S$  animal coming from outside the breeding, with probability  $p$ , and a  $S$  animal who dies is immediately replaced by another  $S$  animal coming from outside.

The model (1) generalizes existing  $SIS$  models in closed populations. Many authors have already studied the asymptotical behavior of discrete time  $SIS$  models in closed populations. In his paper [1], Cooke studied a  $SIS$  model in a closed population under the Reed-Frost assumption and he assumed that the probability  $p$  of the transition for recovering is equal to 1; the Cooke’s model is a particular case of (1):

$$x_{n+1} = (1 - \exp(-Ax_n))(1 - x_n), x_n \in [0, 1]. \quad (4)$$

Longini compared the behavior of Cooke’s model with its stochastic counterpart on the population scale [2]. The Cooke’s approximate model where  $1 - \exp(-Ax_n)$  is replaced by  $Ax_n$  has been extensively studied in literature.

Allen and Burgin generalized the assumptions of model (4) concerning the probability for a susceptible in a closed population of size  $N$ , to be infected at every time in the following way [3]:

$$x_{n+1} = (1 - a(x_n))(1 - x_n) + (1 - p)x_n. \quad (5)$$

where  $1 - a(\cdot)$  is a concave increasing function such that  $a(0) = 1$ ,  $a'(0) = -\alpha/N$ ,  $1 - a(x) \leq \alpha x$ . This model is also a particular case of (1).

We study the temporal behavior of  $\{x_n\}_n$ , solution of (1). We show that the asymptotical behavior is either a globally stable persistence (corresponding to a nonnull fixed point of (1)) or a globally stable extinction (corresponding to a null fixed point of (1)) according to the value of the bifurcation parameter  $B = -a'(0) - \tilde{m}b'(0) - (p + \tilde{m}\tilde{q})$ . Since the quantity  $-a'(0)$  (resp.  $-b'(0)$ ) which is the first derivative of  $1 - a(x)$  (resp.  $1 - b(x)$ ) at  $x = 0$ , represents the increase of probability for a susceptible adult to be horizontally contaminated as soon as the population becomes contaminated, the term  $-a'(0) - \tilde{m}b'(0)$ , denoted  $HC$ , represents the capacity for the spreading of the disease (by horizontal transmission) as soon as the contamination appears. The term  $p + \tilde{m}\tilde{q}$ , denoted  $SC$ , represents the capacity to renew the population of susceptibles. The bifurcation parameter  $B = HC - SC$  therefore compares the spreading capacity with the renewal capacity. The theoretical results under the assumption  $HC > SC$  mean that the disease is asymptotically endemic and the endemicity level does not depend on the initial contamination whenever it is nonnull. Moreover, in the particular case  $SC = 0$ ,  $\{x_n\}$  increases until 1. When  $HC \leq SC$  with  $SC \neq 0$ , the disease always dies out in a monotonic way. Finally in the case  $HC = SC = 0$ ,  $\{x_n\}$  remains constant. The parameter  $R_0$  defined by  $R_0 = B[1 + \tilde{m}]^{-1} + 1$  is equal to the classical reproductive number which determines persistence or extinction of the disease in a neighborhood of the extinction and which is defined by the limit ratio  $\lim_{x_n \rightarrow 0} x_{n+1}/x_n$ , when (1) is approximate by its linearization around 0 (see for example [3]). The transient behaviors are also studied: we show, when the disease dies out, that the extinction occurs in a monotonic way, that is the probability to be infected is strictly decreasing until extinction, and when there is persistence, only three types of transient behavior are possible: either a strictly increasing behavior or a strictly decreasing one or damped oscillations around the limit. These results mean that epidemic transient behaviors may occur only when the asymptotical behavior is endemicity. The behavior of the system is also illustrated by simulations. From a methodological point of view, we establish the necessary and sufficient condition of existence of non trivial fixed points either by using Krasnoselskii's result ([4]) or in a more general way. Both methods lead, in the *SIS* model, to the same reasonable assumptions concerning  $a(\cdot)$  and  $b(\cdot)$ . We prove the global stability of the nonnull fixed point by a theorem, equivalent to Allen's theorem ([3]), a direct and original analytical proof of which, without using Coppel's theorem [5], is given in the appendix.

In the fifth section we compare the behavior of the *SIS* model on the scale of the state of health of a finite branching population and on the scale of the individual state of health in an infinite branching population. When the transmission probabilities are small enough compared to the probability of renewing the population of susceptibles ( $HC \leq SC$ ), the two models lead to a.s. extinction, giving consistent results. But this is no longer valid when the transmissions are too strong ( $HC > SC$ ). In that case the size of the population plays a crucial role for the propagation or the extinction of the

epidemics. In particular the asymptotical behavior of the disease will depend on whether the size of the population is finite or not.

All the results assume for simplification that the branching model is Markovian at first order. But the same results are proved exactly in the same way if the process is Markovian at  $k$ th order,  $k \geq 1$ . Such processes can be a good approximation in the case of semi-Markovian assumptions as is the case for example when the incubation time is not negligible.

## 2 General stochastic model for branching populations

We build here a general multitype size-dependent branching process for describing the evolution of a disease in an open branching population, that is in a population with successive generations and with possible migrations. Assume  $d$  different states which are either states of health or the latter, crossed with other factors, such as genetics, sex, . . . . The  $d$ th state will be generally the  $R$  state which means “removed” from the population under study. The individuals who die or who emigrate, go to the  $R$  state, and the individuals who immigrate come from the  $R$  state. Assume that the population is studied during the successive generations and that each individual can change state at each generation. Let  $\vec{N}_n = (N_n^1, \dots, N_n^d)^t$  be the number of individuals in each state at time  $n$ . Then  $\{\vec{N}_n\}_n$  can be modeled by a supercritical multitype size-dependent branching process :

$$N_{n+1}^k = \sum_{h=1}^d \sum_{i=1}^{N_n^h} (\delta_{a,n+1,i}^{h,k} + \sum_{j=1}^{\tilde{Y}_{n+1,i}^h} \delta_{b,n+1,i,j}^{h,k}), \forall k \in \{1, \dots, d\} \quad (6)$$

where

- The  $\{\delta_{a,n+1,i}^{h,k}\}_i$  are i.i.d. Bernoulli variables (independent and identically distributed) given  $F_{n+}$ , where  $F_{n+}$  is the  $\sigma$ -algebra generated by  $\{\vec{N}_k\}_{k \leq n}, \{\tilde{Y}_{n+1,i}^h\}_{i=1, \dots, N_n^h}\}_h$ , the  $\{\tilde{Y}_{n+1,i}^h\}_{i=1, \dots, N_n^h}$  being the offspring sizes of the  $i$  individual in the  $h$  state. We assume here that  $P(\delta_{a,n+1,1}^{h,k} = 1 | F_{n+})$  which represents the probability for an adult to be in the  $k$  state at time  $n+1$  after having been in the  $h$  state at time  $n$ , depends only on  $\vec{N}_n$ , and we write  $P(\delta_{a,n+1,1}^{h,k} = 1 | F_{n+}) \stackrel{\text{notation}}{=} P_a^{h,k}(\vec{N}_n)$ . Moreover  $\sum_k \delta_{a,n+1,i}^{h,k} = 1$ , for all  $i, h, n$ , implying  $\sum_k P_a^{h,k}(\vec{N}_n) = 1$ , for all  $h, n$ .
- The  $\{\delta_{b,n+1,i,j}^{h,k}\}_{i,j}$  are i.i.d. Bernoulli variables given  $F_{n+}$ . More precisely, they are defined by  $\delta_{b,n+1,i,j}^{h,k} = \sum_l \delta_{b,mh,n+1,i,j}^l \delta_{b,mh,n+1,i,j}^{l,k}$ , where  $\{\delta_{b,mh,n+1,i,j}^l\}_{i,j}$  are i.i.d. Bernoulli variables;  $\delta_{b,mh,n+1,i,j}^l = 1$  with parameter  $P_{b,mh}^l$ , if the  $j$  newborn of the individual  $i \in h$ , is in the  $l$  state at birth. The  $\{\delta_{b,mh,n+1,i,j}^{l,k}\}_{i,j}$

are i.i.d. Bernoulli variables with parameter  $P(\delta_{b,mh,n+1,1,1}^{l,k} = 1 | F_{n+}) \stackrel{\text{notation}}{=} P_{b,mh}^{l,k}(\vec{N}_n)$ . This probability represents the probability for a newborn with mother in the  $h$  state to change from  $l$  to  $k$ , at time  $n+1$ , and is supposed to depend only on  $\vec{N}_n$ . We denote  $P_b^{h,k}(\vec{N}_n) = \sum_l P_{b,mh}^l P_{b,mh}^{l,k}(\vec{N}_n)$ . Moreover  $\sum_k \delta_{b,n+1,i,j}^{h,k} = 1$ , for all  $i, j, h, n$ , implying  $\sum_k P_b^{h,k}(\vec{N}_n) = 1$ , for all  $h, n$ .

- The  $\{\tilde{Y}_{n+1,i}^h\}_i$  which represent the new offsprings at time  $n+1$  of each individual  $i$  belonging to the  $h$  population, are i.i.d.. Their law can depend on  $\vec{N}_n$  and they have bounded expectations  $\tilde{m}_{n+1}^h(\vec{N}_n)$  and variances  $\tilde{\sigma}_{n+1}^{h2}(\vec{N}_n)$  i.e. there exist  $\tilde{m}_{n+1}^h$  and  $\tilde{\sigma}_{n+1}^{h2}$  such that  $\tilde{m}_{n+1}^h(\vec{N}_n) \leq \tilde{m}_{n+1}^h$  and  $\tilde{\sigma}_{n+1}^{h2}(\vec{N}_n) \leq \tilde{\sigma}_{n+1}^{h2}$ .

The law of  $\{\vec{N}_{n+1}\}$  given  $F_n$ , where  $F_n$  is the  $\sigma$ -algebra generated by  $\{\vec{N}_k\}_{k \leq n}$ , is easily derived from (6) as a compound of independent multinomial laws allowing us to calculate the behavior of the population's state of health, especially when the size of the population is not too large.

We deal here more particularly with the extinction of the disease. We assume in the following proposition that a healthy population remains healthy at every time.

**Proposition 1** (1) *Assume that there is no incubation state and that  $P(N_n^I = 0 | N_{n-1}^I = 0) = 1$ , i.e.  $\theta$  is an absorbing state for the process  $\{N_n^I\}_n$ . For a given initial population  $\vec{N}_0$ , assume that there exists a positive and nonnull sequence  $\{\Psi_{n,N_0}\}$  such that*

$$P(N_n^I = 0 | N_{n-1}^I = l) \geq \Psi_{n,N_0}, \quad \forall l \neq 0, \forall n : P(N_{n-1}^I = l | \vec{N}_0) \neq 0. \quad (7)$$

Let  $\prod_{l=n+1}^n (1 - \Psi_{l,N_0}) = 1$ . Then

$$P(N_n^I = 0 | \vec{N}_0) \geq \sum_{k=1}^n \Psi_{k,N_0} \prod_{l=k+1}^n (1 - \Psi_{l,N_0}) \quad (8)$$

and  $\lim_n P(N_n^I = 0 | \vec{N}_0)$  exists and is not null.

Moreover, if  $\lim_n \Psi_{n,N_0} = \Psi_{N_0}$  with  $\Psi_{N_0} \neq 0$ , then  $\lim_n P(N_n^I = 0 | \vec{N}_0) = 1$ . In that case  $\theta$  is an asymptotically stable absorbing state for the process  $\{N_n^I\}_n$ , for every initial population of size  $N_0^0$ .

In the particular case of a homogeneous process in a closed population or a bounded population, there exists  $\Psi_{N_0}$  satisfying (7) implying  $\lim_n P(N_n^I = 0 | \vec{N}_0) = 1$  with the rate

$$1 - P(N_n^I = 0 | \vec{N}_0) \leq (1 - \Psi_{N_0})^{n-1}. \quad (9)$$

- (2) *Assume that there is an incubation state denoted  $E$ . The results of item 1 are still valid with  $N_n^I + N_n^E$  instead of  $N_n^I$  if in the assumptions,  $N_n^I$  is replaced by  $N_n^I + N_n^E$ .*

**PROOF.** We show only the first item, the second one being proved in the same way. 0 being an absorbing state for  $\{N_n^I\}_n$ ,

$$P(N_n^I = 0 | \vec{N}_0) = \sum_{l \neq 0} P(N_n^I = 0 | N_{n-1}^I = l) P(N_{n-1}^I = l | \vec{N}_0) + P(N_{n-1}^I = 0 | \vec{N}_0).$$

Write  $\alpha_n$  for  $P(N_n^I = 0 | \vec{N}_0)$ . Then according to (7)

$$\alpha_n \geq \Psi_{n, N_0} (1 - \alpha_{n-1}) + \alpha_{n-1} \quad (10)$$

that implies (8), by induction on  $n$ ; (10) also implies that  $\{\alpha_n\}_n$  is a bounded increasing sequence which therefore has a limit, as  $n \rightarrow \infty$ .

Now assume that  $\lim_n \Psi_{n, N_0} = \Psi_{N_0}$  and write  $\Psi$  for  $\Psi_{N_0}$ . Then, there exists  $N_\epsilon$  such that, for all  $n \geq N_\epsilon$ ,  $\Psi - \epsilon \leq \Psi_{n, N_0} \leq \Psi + \epsilon$ , implying  $1 - \Psi_{n, N_0} \geq (1 - \Psi)(1 - \xi)$ , where  $\xi = \epsilon(1 - \Psi)^{-1}$ . Consequently

$$\sum_{k=1}^n \Psi_{k, N_0} \prod_{l=k+1}^n (1 - \Psi_{l, N_0}) \geq (\Psi - \epsilon) \sum_{k=N_\epsilon}^n (1 - \Psi)^{n-k} (1 - \xi)^{n-k}$$

which becomes

$$\sum_{k=1}^n \Psi_{k, N_0} \prod_{l=k+1}^n (1 - \Psi_{l, N_0}) \geq \Psi \sum_{k=0}^{n-N_\epsilon} (1 - \Psi)^k (1 - \xi)^k - \epsilon \sum_{k=0}^{n-N_\epsilon} (1 - \Psi)^k (1 - \xi)^k$$

*i. e.*

$$\begin{aligned} & \sum_{k=1}^n \Psi_{k, N_0} \prod_{l=k+1}^n (1 - \Psi_{l, N_0}) \geq \\ & \Psi \frac{(1 - \Psi)^{n-N_\epsilon+1} (1 - \xi)^{n-N_\epsilon+1} - 1}{(1 - \Psi)(1 - \xi) - 1} - \epsilon \frac{(1 - \Psi)^{n-N_\epsilon+1} (1 - \xi)^{n-N_\epsilon+1} - 1}{(1 - \Psi)(1 - \xi) - 1}. \end{aligned}$$

So finally

$$\lim_n \alpha_n \geq \frac{\Psi}{\Psi + \epsilon} - \frac{\epsilon}{\Psi + \epsilon}$$

which implies the result by taking the limit as  $\epsilon \rightarrow 0$ .

In the particular case of a homogeneous process in a population with a bounded size, we can take  $\Psi_{N_0} = \inf_{l \in L_{N_0}} P(N_n^I = 0 | N_{n-1}^I = l)$ , where  $L_{N_0} = \{l \neq 0 : P(N_{n-1}^I = l | \vec{N}_0) \neq 0\}$ .

### 3 Pseudo Markov chain on ancestors lines and dynamical systems

We are interested not only by the extinction possibility but also by the general behavior of the multitype size-dependent branching process  $\{\vec{N}_n\}_n$  given by (6). Klebaner [6] studied the asymptotical behavior of Markovian multitype size-dependent processes, as  $n \rightarrow \infty$ , under some assumptions on the size-dependence. He assumed in particular that the expectation matrix  $M(\vec{N}_n)$  defined here by

$$\begin{aligned} M(\vec{N}_n)[h, k] &= E([\delta_{a,n+1,1}^{h,k} + \sum_{j=1}^{\tilde{Y}_{n+1,1}^h} \delta_{b,n+1,1,j}^{h,k}] | F_n) \\ &= P_a^{h,k}(\vec{N}_n) + \tilde{m}_{n+1}^h(\vec{N}_n) P_b^{h,k}(\vec{N}_n) \end{aligned}$$

converges a.s. to a limit  $M$ , as the whole size of the surviving population tends to infinity. This assumption is not valid *a priori* here since  $M(\vec{N}_n)$  depends on  $N_n^I$ , the asymptotical behavior of which is unknown. So we will rather study the behavior of the multitype branching process as the initial population size tends to  $\infty$ . This will allow us to study not only its asymptotical behavior but also its transient behavior.

Denote  $\vec{N}_n(N)$  a value of the branching process at time  $n$  starting from  $\vec{N}_0$  such that  $N_0^0 = N$ , where  $N_n^0 = \sum_h N_n^h$  is the total size of the population at any time  $n$ , including the  $R$  individuals. In the following we will denote  $\vec{N}_n$  as well as  $\vec{N}_n(N)$  and  $N_n^0$  as well as  $N_n^0(N)$ .

Let  $\vec{P}_n = \vec{N}_n / N_n^0$ . From now on, for all  $h, k, n$ , we assume that

$$\begin{aligned} P_a^{h,k}(\vec{N}_n) &= P_a^{h,k}(\vec{P}_n), \quad P_b^{h,k}(\vec{N}_n) = P_b^{h,k}(\vec{P}_n), \\ \tilde{m}_{n+1}^h(\vec{N}_n) &= \tilde{m}_{n+1}^h(\vec{P}_n), \quad \tilde{\sigma}_{n+1}^{h2}(\vec{N}_n) = \tilde{\sigma}_{n+1}^{h2}(\vec{P}_n). \end{aligned}$$

We write  $m_{n+1}^h(\vec{P}_n) = 1 + \tilde{m}_{n+1}^h(\vec{P}_n)$  and  $\vec{P}_n = (P_n^1, \dots, P_n^d)^t$ , where  $P_n^k = \lim_{N \rightarrow \infty} N_n^k / N_n^0$ ,  $k = 1, \dots, d$ , when these limits exist.

In an open population starting from  $N$  individuals at generation 0, the population evolves throughout the generations and can be represented by  $N$  trees starting each from a single individual. We introduce here the notion of ancestors line. The ancestors line of an individual  $i_n$  at time  $n$ , is defined by the individual  $i_n$  himself and all his ancestors in the tree. The previous ancestor of an individual can be either the individual himself or his mother if he is a newborn. There is a bijective mapping between the set of lines  $i_n$  and the leaves of the tree, stopped at generation  $n$ . A closed population can be considered as a

particular case of an open population in which any tree starting from a single individual is reduced to a single ancestors line  $i$  which remains the same one with time. Let  $E_k(i_n)$ , the state of health at time  $k \leq n$  of the ancestors line  $i_n$ . More generally, let  $X_k(i_n)$  be the value of the variable  $X$  at time  $k \leq n$  of the ancestors line  $i_n$ .

In figure 1, an ancestors line is represented by a thick line.

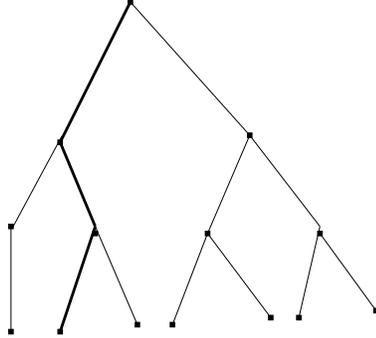


Fig. 1. Ancestors line in a tree stopped at generation  $n$

Denote  $Q_{n+1}(\vec{P}_n)$  the normalized matrix

$$\begin{aligned} Q_{n+1}(\vec{P}_n)[h, k] &= \frac{M(\vec{P}_n)[h, k]}{m_{n+1}^h(\vec{P}_n)} \\ &= \frac{[P_a^{h,k}(\vec{P}_n) + \tilde{m}_{n+1}^h(\vec{P}_n)P_b^{h,k}(\vec{P}_n)]}{m_{n+1}^h(\vec{P}_n)}. \end{aligned} \quad (11)$$

Then  $Q_{n+1}(\vec{P}_n)$  is a stochastic matrix *i.e.*  $Q_{n+1}(\vec{P}_n)[h, k] \geq 0$ , for all  $(h, k)$  and  $\sum_{k=1}^d Q_{n+1}(\vec{P}_n)[h, k] = 1$ , for all  $h$ .

In the particular case of a closed population,  $m_{n+1}^h(\vec{P}_n) = 1$ , for all  $h, n$  and  $Q_{n+1}(\cdot)$  is reduced to  $Q(\vec{P}_n)[h, k] = P_a^{h,k}(\vec{P}_n), \forall (h, k)$ .

**Proposition 2** *Assume the existence of  $\vec{P}_0$ . Assume moreover that  $\tilde{m}_{n+1}^h(\cdot)$ ,  $P_a^{h,k}(\cdot)$  and  $P_b^{h,k}(\cdot)$  are continuous functions, for all  $h, k, n$ . Then  $\{\vec{P}_n\}_n$  exists and is solution of the following dynamical system:*

$$P_{n+1}^k = \sum_h Q_{n+1}(\vec{P}_n)[h, k] \frac{m_{n+1}^h(\vec{P}_n)P_n^h}{\sum_l m_{n+1}^l(\vec{P}_n)P_n^l}, \quad k \in \{1, \dots, d\}, \quad n \geq 0. \quad (12)$$

Moreover the  $\{E_n(i_n)\}_{i_n}$  are identically distributed with

$$\lim_N P(E_n(i_n) = k | \vec{N}_0(N)) = P_n^k, \quad k = 1, \dots, d. \quad (13)$$

Moreover if  $d = R$ , let  $\tilde{P}_n^h = P_n^h[1 - P_n^R]^{-1}$ ,  $h \neq R$ , and let  $Q_{R,n+1}$  be the matrix  $Q_{n+1}$  restricted to the non removed states ( $d-1$  first lines and columns of  $Q_{n+1}$ ). If in that case,  $Q_{n+1}(\vec{P}_n) = Q_{n+1}(\vec{P}_n)$  with  $Q_{n+1}(\vec{P}_n)[d, k] = 0$ , for  $k \leq d-1$ , then, for  $k \in \{1, \dots, d\}$ ,  $n \geq 0$ ,

$$\tilde{P}_{n+1}^k = \frac{\sum_{h \leq d-1} Q_{R,n+1}(\vec{P}_n)[h, k] m_{n+1}^h(\vec{P}_n) \tilde{P}_n^h [\sum_l m_{n+1}^l(\vec{P}_n) \tilde{P}_n^l]^{-1}}{\sum_{k \leq d-1} \sum_{h \leq d-1} Q_{R,n+1}(\vec{P}_n)[h, k] m_{n+1}^h(\vec{P}_n) \tilde{P}_n^h [\sum_l m_{n+1}^l(\vec{P}_n) \tilde{P}_n^l]^{-1}} \quad (14)$$

According to (13),  $\tilde{P}_n^h$  is the probability for an individual to be in the  $h$  state among the non removed population. It is more interesting to study this probability than  $P_n^h$  when there is no return from  $R$  to  $\{1, \dots, d\}$ , i.e. no immigration.

The proof of the proposition is given in the appendix.

**Corollary 3** *In the particular case where the offspring distribution is independent of the process, then  $Q_{n+1}(\cdot) = Q(\cdot)$  and*

$$\lim_{N \rightarrow \infty} \frac{\vec{N}_n}{(\prod_{k=1}^n m_k) N} \stackrel{a.s.}{=} \vec{P}_n, \text{ where } \vec{P}_{n+1}^t = \vec{P}_n^t Q(\vec{P}_n). \quad (15)$$

Moreover if  $d = R$  and if  $Q(\vec{P}_n) = Q(\vec{P}_n)$  with  $Q(\vec{P}_n)[d, k] = 0$ , for  $k \leq d-1$ , then

$$\vec{P}_{n+1}^t = \vec{P}_n^t \frac{Q_R(\vec{P}_n)}{\vec{P}_n^t Q_R(\vec{P}_n) \vec{\Gamma}},$$

where  $\vec{\Gamma}$  is a vector of 1 of dimension  $d-1$ .

**PROOF.** In the particular case  $\tilde{m}_{n+1}^h(\vec{P}_n) = \tilde{m}_{n+1}$ , for all  $h, n$ , the first relationship of (15) comes directly from the relationship

$$\frac{\vec{N}_n}{(\prod_1^n m_k) N} = \frac{\vec{N}_n}{N_n^0 (\prod_1^n m_k) N}$$

and the strong law of large numbers applied to

$$\frac{N_n^0}{(\prod_1^n m_k)N} = \frac{1}{N} \sum_{i=1}^N \frac{N_{n,i}^0}{\prod_1^n m_k},$$

where the  $\{N_{n,i}^0(\prod_1^n m_k)^{-1}\}_i$  are i.i.d. with expectation 1 and bounded variances. The other results are straightforwardly deduced from the proposition.

**Remark 4** *In the frame of a closed population,  $m_{n+1}^h(\vec{P}_n) = 1$ , for all  $h, n$ , which implies that the sequence  $\{\vec{P}_n\}_n$  satisfies the recurrence (15). Therefore in that case, according to the Markov property of the branching model,  $\{E_n(i)\}_n$  is an inhomogeneous Markov chain with transition matrix  $Q(\vec{P}_n)$  which is density dependent. This idea can be generalized to branching populations. We call the process  $\{E_n(i_n)\}_n$ , an inhomogeneous “pseudo-Markov chain” on ancestors lines, the term “pseudo” coming from the fact that the individual  $i_n$  changes with time and cannot be replaced by  $i_\infty$  which is not defined.*

## 4 SIS model in branching populations

### 4.1 SIS branching process

Assume only two different states of health, the  $S$  and  $I$  states. Assume for simplification that each newborn is in the  $S$  state at birth. Then the stochastic SIS branching process is given by

$$\begin{aligned} N_{n+1}^S &= \sum_{i=1}^{N_n^S} [\delta_{a,n+1,i}^{S,S} + \sum_{j=1}^{\tilde{Y}_{n+1,i}^S} \delta_{b,mS,n+1,i,j}^{S,S}] + \sum_{i=1}^{N_n^I} [\delta_{a,n+1,i}^{I,S} + \sum_{j=1}^{\tilde{Y}_{n+1,i}^I} \delta_{b,mI,n+1,i,j}^{S,S}] \\ N_{n+1}^I &= \sum_{i=1}^{N_n^S} [(1 - \delta_{a,n+1,i}^{S,S}) + \sum_{j=1}^{\tilde{Y}_{n+1,i}^S} (1 - \delta_{b,mS,n+1,i,j}^{S,S})] \\ &\quad + \sum_{i=1}^{N_n^I} (1 - [\delta_{a,n+1,i}^{I,S} + \sum_{j=1}^{\tilde{Y}_{n+1,i}^I} (1 - \delta_{b,mI,n+1,i,j}^{S,S})]). \end{aligned} \quad (16)$$

We assume that  $\tilde{m}_n^S(\vec{P}_n) = \tilde{m}_n^I(\vec{P}_n) = \tilde{m}$ , that the probability for an adult not to be infected is  $P_a^{S,S}(\vec{P}_n) = a(\hat{P}_n^I)$ , and that the recovering probability is  $P_a^{I,S}(\vec{P}_n) = p$ . We also assume that each newborn can be infected either by his mother by vertical transmission (when she is herself infected) with a probability  $1 - \tilde{q}$  or by the other individuals according to horizontal transmission  $1 - b(\hat{P}_n^I)$ , that is

$$P_{b,m_S}^{S,S}(\vec{P}_n) = \tilde{q}b(\hat{P}_n^I); \quad P_{b,m_S}^{S,S}(\vec{P}_n) = b(\hat{P}_n^I).$$

$a(\cdot)$  and  $b(\cdot)$  are supposed to satisfy either  $a = b = 1$ , or  $a \neq 1$  or  $b \neq 1$ , defined in the introduction.

**Example.** Assume that the horizontal transmissions are of the Reed-Frost type  $a(\hat{P}_n^I) = q_a^{v(N_n^I)}$ , where  $q_a$  is the probability for a  $S$  adult of not being infected by a given  $I$  and  $v(N_n^I)$  is the number of infectives who are in a neighborhood of  $S$  at time  $n$ . If  $d_n$  denotes the spatial density at time  $n$  of the  $N_n^0 = N_n^S + N_n^I$  individuals, then we can assume that  $v(N_n^I)$  is proportional to  $\hat{P}_n^I$  and  $d_n$ . Moreover if we assume that  $d_n = d$ , for all  $n$ , then we can write  $v(N_n^I) = v\hat{P}_n^I d$ . Denote  $a = q_a^{vd}$ . Then  $a(\hat{P}_n^I) = a\hat{P}_n^I$ .

Let  $c(u) = (p\tilde{q}^L)^u a(u)^{(1-u)} b(u)^L$ ,  $L \geq 0$ ,  $u \in [0, 1]$ ,  $\gamma_{n-1} = (L+1)^{n-1} N_0^0$ ,  $u_0 = \arg \min c(u)$ .

**Proposition 5** Assume that  $\tilde{Y}_{n,i}^h \stackrel{a.s.}{\leq} L$ , for all  $i, n, h$ .

- (1) Assume  $p\tilde{q} \neq 0$ . Then the process  $\{N_n^I\}_n$  converges to extinction, as  $n \rightarrow \infty$ , with a positive probability  $P(N_n^I = 0 | \vec{N}_0) \geq \sum_{k=1}^n \Psi_{k,N_0} \prod_{l=k+1}^n (1 - \Psi_{l,N_0})$ , where  $\Psi_{n,N_0} = c(u_0)^{\gamma_{n-1}} > 0$ . In the particular case of a closed population,  $\lim_n P(N_n^I = 0 | \vec{N}_0) = 1$  with the convergence rate  $1 - P(N_n^I = 0 | \vec{N}_0) \leq (1 - \Psi_{N_0})^{N_0^0}$ .
- (2) Assume  $p = 0$ . Then  $P(N_n^I = 0 | \vec{N}_0) = 0$ , for all  $n$ , if  $N_0^I \neq 0$ , and  $P(N_n^I = 0 | \vec{N}_0) = 1$ , for all  $n$ , if  $N_0^I = 0$ .

## PROOF.

- (1) Assume  $p\tilde{q} \neq 0$ . Then

$$P(N_n^I = 0 | F_{n-1}^+) = p^{N_{n-1}^I} a(\hat{P}_{n-1}^I)^{N_{n-1}^S} \left( \tilde{q}b(\hat{P}_{n-1}^I) - \frac{1}{N_{n-1}^0} \right) \sum_{i=1}^{N_{n-1}^I} \tilde{Y}_{n,i}^I b(\hat{P}_n^I) \sum_{i=1}^{N_{n-1}^S} \tilde{Y}_{n,i}^S \quad (17)$$

implying first  $P(N_n^I = 0 | N_{n-1}^I = 0) = 1$ . Moreover since  $b(\cdot)$  is decreasing and  $\tilde{Y}_{n,i}^h \leq L$ , for all  $i, h, n$ ,

$$P(N_n^I = 0 | F_{n-1}^+) \geq p^{N_{n-1}^I} a(\hat{P}_{n-1}^I)^{N_{n-1}^0 - N_{n-1}^I} \tilde{q}^{LN_{n-1}^I} b(\hat{P}_{n-1}^I)^{LN_{n-1}^0}$$

implying

$$P(N_n^I = 0 | N_{n-1}^I = l) \geq c(u_0)^{\gamma_{n-1}}$$

where  $c(u) = (p\tilde{q}^L)^u a(u)^{(1-u)} b(u)^L$ ,  $\gamma_{n-1} = (L+1)^{n-1} N_0^0$ ,  $u_0 = \arg \min c(u)$ ;  $c(u)$  satisfies

$$\begin{aligned}
c(u) &\geq (p\tilde{q}^L)^u a(u)b(u)^L \\
&\geq (p\tilde{q}^L)a(1)b(1)^L \\
&> 0
\end{aligned}$$

implying  $c(u_0) > 0$ .

- (2) According to (17), if  $p = 0$ , then  $P(N_n^I = 0 | N_{n-1}^I = l) = 0$  if  $l \neq 0$  and  $P(N_n^I = 0 | N_{n-1}^I = 0) = 1$ .

## 4.2 SIS model on an individual ancestors line in an infinite branching population

### 4.2.1 Dynamical system

Let  $\vec{P}_n = (P_n^S, P_n^I)^t$ , where  $P_n^h$  is the probability at time  $n$  for an individual to be in the  $h$  state. Then according to section 3,  $\{\vec{P}_n\}$  is solution of system (15), where the transition probabilities matrix is derived from (16):

$$Q(\vec{P}_n) = \frac{1}{m} \begin{pmatrix} a(P_n^I) + \tilde{m}b(P_n^I) & m - a(P_n^I) - \tilde{m}b(P_n^I) \\ p + \tilde{m}\tilde{q}b(P_n^I) & m - p - \tilde{m}\tilde{q}b(P_n^I) \end{pmatrix} \quad (18)$$

**Remark 6** In the more general case where the newborn can be infected in utero with a probability  $P_{b,mI}^I = 1 - \tilde{q}_1$  and at birth by his mother with a probability  $1 - \tilde{q}_2$ , Then  $Q(\vec{P}_n)$  remains the same with  $p = p_a + \tilde{m}(1 - \tilde{q}_1)p_b$  and  $\tilde{q} = \tilde{q}_1\tilde{q}_2$ ,  $p_a$  and  $p_b$  being the respective probabilities for recovering for an adult and a newborn.

### 4.2.2 Transient and asymptotical behavior

Since  $P_n^S + P_n^I = 1$ , we replace the system (15) with the transition matrix given by (18) by a univariate equation, where  $x_n = P_n^I$ , for all  $n$ :

$$1 - x_{n+1} = m^{-1}[(1 - x_n)(a(x_n) + \tilde{m}b(x_n)) + x_n(p + \tilde{m}\tilde{q}b(x_n))] \quad (19)$$

i.e. writing  $x_{n+1} = T(x_n)$ ,

$$\begin{aligned}
T(x_n) &= \\
& m^{-1}[(m - a(x_n) - \tilde{m}b(x_n)) - x_n(p - \tilde{m}b(x_n)(1 - \tilde{q}) - a(x_n))] \quad (20)
\end{aligned}$$

We investigate the convergence of a sequence  $\{x_n\}_n$ . We denote  $x_*$  its limit, when it exists. Then  $x_*$  is solution of one or the other equivalent following

equations deduced from (19) or (20):

$$(1 - x_*)(m - a(x_*) - \tilde{m}b(x_*)) = x_*(p + \tilde{m}\tilde{q}b(x_*)) \quad (21)$$

$$\begin{aligned} x_* &= m^{-1}[(m - a(x_*) - \tilde{m}b(x_*)) - x_*(p - \tilde{m}b(x_*)(1 - \tilde{q}) - a(x_*))] \\ &= T(x_*). \end{aligned} \quad (22)$$

Since the previous equivalent equations (21) or (22) are nonlinear equations, the number of their solutions is unknown *a priori*. We will determine them in paragraph 4.2.2.1, and study their stability in paragraph 4.2.2.2.

The stability study concerns the asymptotical behavior. We will also study the transient (or short-term) behavior by using the following iteration. According to (20), on  $]0, 1]$ ,

$$\begin{aligned} m(x_{n+1} - x_n) &= \\ (m - a(x_n) - \tilde{m}b(x_n))(1 - x_n) - x_n(p + \tilde{m}\tilde{q}b(x_n)) &= \end{aligned} \quad (23)$$

$$(m - a(x_n) - \tilde{m}b(x_n))h(x_n), \quad \text{if } a \neq 1 \text{ or } b \neq 1, \quad (24)$$

where

$$h(x_n) = 1 - x_n - x_n \frac{p + \tilde{m}\tilde{q}b(x_n)}{m - a(x_n) - \tilde{m}b(x_n)}.$$

#### 4.2.2.1 Existence and determination of fixed points of $T$

**Proposition 7** *Let  $\{x_n\}_n$  defined by  $x_{n+1} = T(x_n)$  with  $x_n \in [0, 1]$ , for all  $n$ , and  $T$  continuous. We may always assume that  $T(x) - x$  can be factorized in the following way:  $T(x) - x = g(x)h(x)$ , where  $\lim_{x \rightarrow 0} g(x)x^{-1} > 0$ . Assume moreover that  $h(1) \leq 0$ . Then a sufficient condition for the existence of a nonnull fixed point of  $T$  is*

$$(C) : T'(0) > 1 \iff \lim_{x \rightarrow 0} h(x) > 0.$$

*Moreover if  $T$  is concave, or if  $h$  is either decreasing or convex, then (C) is also a necessary condition, and the nonnull fixed point is unique,*

The condition “ $T'(0) > 1$ ” is due to Krasnoselskii ([4]) and the remainder of the proof is straightforwardly deduced from the factorization of  $T(x) - x$ . This

proposition allows, *via* the function  $h$ , other properties for  $T$  than the concave one.

Let  $B = -a'(0) - \tilde{m}b'(0) - [p + \tilde{m}\tilde{q}]$ .

**Proposition 8**  $0$  is a fixed point of  $T$ . Moreover

- (1) Assume  $a = b = 1$ . Then if  $p + \tilde{m}\tilde{q} \neq 0$ , the only fixed point is  $0$ , and if  $p + \tilde{m}\tilde{q} = 0$ ,  $x_n = x_0$ , for all  $n$ .
- (2) Assume  $a \neq 1$  or  $b \neq 1$ . Then a necessary and sufficient condition for the existence of a non null fixed point  $x_*$  is the following:

$$(C): B > 0$$

Moreover, under this condition, the nonnull fixed point is unique. In the particular case  $p + \tilde{m}\tilde{q} = 0$ ,  $x_* = 1$ .

**Remark 9** (1) Item 1 means that in absence of horizontal transmission, the disease always dies out as soon as  $p + \tilde{m}\tilde{q} \neq 0$ .

- (2) When  $p + \tilde{m}\tilde{q} \neq 0$ , the parameter  $R_0 = B[1 + \tilde{m}]^{-1} + 1$  is the generalization of the classical reproductive number (see for example [3]).
- (3) We can summarize the results of proposition 8 in the following way:  $0$  is a fixed point. Moreover
  - (a) If  $B > 0$ , which can occur only in presence of horizontal transmission, then there exists a unique nonnull fixed point  $x_*$ ;
  - (b) If  $B < 0$ , which is possible only if  $p + \tilde{m}\tilde{q} \neq 0$ , or if  $B = 0$  with  $a \neq 1$  or  $b \neq 1$ , then  $0$  is the unique fixed point;
  - (c) If  $B = 0$  with  $a = b = 1$ , then  $x_n = x_0$ , for all  $n$  and  $x_0$ .
- (4) SI model is a particular case of SIS model, in which  $p = 0$ . The previous results show that for a SI model which satisfies  $\tilde{m}\tilde{q} = 0$ , apart from  $0$ , either  $x_n = x_0$ , for all  $n$ , or  $x_* = 1$ . The first case occurs when there is no horizontal transmission ( $B = 0$ ) and the second case occurs as soon as there is an horizontal transmission ( $B > 0$ ).

**PROOF.**

- (1) Assume  $a = b = 1$ .

Then, when  $p + \tilde{m}\tilde{q} \neq 0$ , the only solution of (21) is  $0$ , and if  $p + \tilde{m}\tilde{q} = 0$ , then we cannot determinate the fixed points from (21) or (22). But using (23), we obtain  $x_{n+1} = x_n$ , for all  $n$ .

- (2) Assume  $a \neq 1$  or  $b \neq 1$ .

Then  $0$  is a solution of (21). Assume first that  $p + \tilde{m}\tilde{q} = 0$ . It is obvious from (21) that  $1$  is the unique nonnull fixed point.

Assume now  $p + \tilde{m}\tilde{q} \neq 0$ . If they exist, the nonnull fixed points are, from (21) and (24), the nonnull solutions of the equation  $h(x) = 0$ , where

$h(x) = 1 - x - xf(x)g^{-1}(x) = m(T(x) - x)g^{-1}(x)$ , the functions  $f$  and  $g$  being defined on  $]0, 1]$  by

$$f(x) = p + \tilde{m}\tilde{q}b(x), \quad g(x) = m - a(x) - \tilde{m}b(x).$$

According to proposition 7, a sufficient condition for the existence of nonnull fixed points is, in an equivalent way, given either by  $T'(0) > 1$  or  $\lim_{x \rightarrow 0} h(x) > 0$ . Moreover if  $T'' < 0$  or if  $h$  is a decreasing or convex function, then the condition is also a necessary one. So first calculate  $T'$  and  $T''$ :

$$mT'(x) = -a'(x) - \tilde{m}b'(x) + a(x) - p + \tilde{m}b(x)(1 - \tilde{q}) + x[a'(x) + \tilde{m}b'(x)(1 - \tilde{q})] \quad (25)$$

$$mT''(x) = -a''(x)(1 - x) - \tilde{m}b''(x)(1 - x(1 - \tilde{q})) + 2(a'(x) + \tilde{m}b'(x)(1 - \tilde{q})). \quad (26)$$

$$= -(1 - x(1 - \tilde{q}))(a''(x) + \tilde{m}b''(x)) + 2(1 - \tilde{q})(a'(x) + \tilde{m}b'(x)) + \tilde{q}(2a'(x) + xa''(x)) \quad (27)$$

$T''$  is strictly negative under  $a \neq 1$  or  $b \neq 1$ , except in the particular case ( $P$ ):  $a = 1$ ,  $b(x) = 1 - \beta x$ ,  $\beta > 0$ ,  $\tilde{q} = 1$ , where  $T'' = 0$ . Therefore, except in that case, a necessary and sufficient condition for the existence of a nonnull fixed point, is  $T'(0) > 1$  *i.e.*  $B > 0$ . In the particular case ( $P$ ),  $B \leq 0$  and  $x_{n+1} = x_n[\tilde{m}\beta + (1 - p)]m^{-1}$  implying that  $\{x_n\}_n$  is strictly decreasing until extinction.

Now, use the function  $h$ . We first show that  $h$  is a strictly decreasing function on  $]0, 1]$ . The first derivative of  $h$  is

$$h'(x) = \frac{u(x)}{g^2(x)}, \quad \text{where}$$

$$u(x) = -g^2(x) - f(x)g(x) - x[f'(x)g(x) - f(x)g'(x)]$$

$$f'(x) = \tilde{m}\tilde{q}b'(x), \quad g'(x) = -a'(x) - \tilde{m}b'(x).$$

The sign of  $h'$  is the same as the sign of  $u$ . So study the function  $u$ :

$$u'(x) = -2g(x)[g'(x) + f'(x)] - x[f''(x)g(x) - f(x)g''(x)] \quad (28)$$

$$f''(x) = \tilde{m}\tilde{q}b''(x), \quad g''(x) = -a''(x) - \tilde{m}b''(x)$$

implying

$$u'(x) = 2g(x)(1 - \tilde{q})(a'(x) + \tilde{m}b'(x)) - x(f(x) + \tilde{q}g(x))(a''(x) + \tilde{m}b''(x)) + \tilde{q}g(x)(2a'(x) + xa''(x)) \quad (29)$$

$u'$  is strictly negative, except in the case ( $P$ ). Consequently, except in the case ( $P$ ),  $u$  is a strictly decreasing function, implying  $u(x) < u(0) = 0$  and  $h$  strictly decreasing. Under ( $P$ ),  $h(x) = 1 - (\tilde{m} + p)(\tilde{m}\beta)^{-1}$  which

is strictly negative. In this particular case there is no solution to the equation  $h(x) = x$ .

We also have  $h(1) = -f(1)g^{-1}(1) = -(p + \tilde{m}\tilde{q}b(1))(m - a(1) - \tilde{m}b(1))^{-1}$  which is strictly negative. Consequently there will exist exactly one non-null root of  $h(x) = 0$ , if and only if  $\lim_{x \rightarrow 0} h(x) > 0$  (which cannot be satisfied in the particular case  $(P)$ ). Since

$$\lim_{x \rightarrow 0} h(x) = 1 - \lim_{x \rightarrow 0} xf(x)g^{-1}(x)$$

we study  $\lim_{x \rightarrow 0} xf(x)g^{-1}(x)$  by considering the Taylor development at the first order of  $a(x)$  and  $b(x)$  in a neighborhood of 0. We obtain

$$\lim_{x \rightarrow 0} \frac{xf(x)}{g(x)} = \frac{p + \tilde{m}\tilde{q}}{-a'(0) - \tilde{m}b'(0)}$$

and

$$\lim_{x \rightarrow 0} h(x) > 0 \iff 1 - \frac{p + \tilde{m}\tilde{q}}{-a'(0) - \tilde{m}b'(0)} > 0 \iff B > 0.$$

Comparing (26) and (28), on one hand, and (27) and (29), on the other hand, we obtain the same reasonable assumptions on  $a(\cdot)$  and  $b(\cdot)$  for obtaining  $T'' < 0$  and  $u' < 0$ . Some more complicated assumptions leading to  $u' < 0$  could be found. But it would not have any epidemiological meaning.

#### 4.2.2.2 Stability of the fixed points and transient behavior

**Proposition 10** *Consider the general SIS model (1).*

- (1) *Assume  $B < 0$ , or  $B = 0$  together with  $a \neq 1$  or  $b \neq 1$ . Then 0 is globally stable on  $[0, 1]$  and  $x_{n+1} < x_n$ , for all  $n$  such that  $x_n > 0$ ;*
- (2) *Assume  $B > 0$ . Then 0 is unstable and the unique nonnull fixed point  $x_*$  is globally stable on  $]0, 1]$ . Moreover*

$$x_n < x_* \iff x_{n+1} > x_n \text{ and } x_n > x_* \iff x_{n+1} < x_n. \quad (30)$$

*In the particular case  $p + \tilde{m}\tilde{q} = 0$ ,  $\{x_n\}$  increases until 1.*

**Remark 11** *According to these results, when there is extinction, i.e. when  $B < 0$  or  $B = 0$  with  $a \neq 1$  or  $b \neq 1$ , the extinction occurs in a monotonic way, that is the probability to be infected is strictly decreasing until extinction, thus prohibiting any transient epidemic behavior. Such behavior is possible only under  $B > 0$ . In that case the asymptotical behavior is always persistence.*

To prove unstability or local stability, we will use the classical stability theorem based on the sign of  $|T'(x_*)| - 1$  [7]:

$$\text{If } |T'(x^*)| < 1, \text{ then } x^* \text{ is an asymptotically stable point;} \quad (31)$$

$$\text{If } |T'(x^*)| > 1, \text{ then } x^* \text{ is unstable.} \quad (32)$$

For proving the global stability of  $x_* \neq 0$ , we will use the following general proposition based on simple properties of  $T'$ , a similar version of which is described in [3]. Allen *et al.* give a direct proof using Coppel's theorem [5], which is based on the roots of  $T^{(2)}(x) = x$ . We give here in the appendix a direct analytical proof of this proposition without the use of Coppel's theorem.

**Proposition 12** *Let  $\{x_n\}_n$  defined by  $x_{n+1} = T(x_n)$  with  $x_n \in [0, 1]$ , for all  $n$  and  $T$  continuous. Let the following assumptions:*

- (1)  $T$  has only two fixed points, 0 and  $x_* \neq 0$ ;
- (2)  $T$  has a continuous and strictly decreasing derivative  $T'$ , and  $T'(0) > 1$ ,  $|T'(1)| < 1$ .

*Then, 0 is unstable and  $x_*$  is globally stable on  $]0, 1]$ .*

*Moreover, we obtain, for all  $x_n \in ]0, 1]$ , the properties :*

$$x_n < x_* \Leftrightarrow x_{n+1} > x_n \quad \text{and} \quad x_n > x_* \Leftrightarrow x_{n+1} < x_n \quad (33)$$

The proof of proposition (12) is given in the appendix.

**Remark 13** *Concerning the proof which uses Coppel's theorem [5], it is sufficient to assume  $T'(x) > -1$  on  $[0, 1]$  that is  $T'(1) > -1$  (instead of  $|T'(1)| < 1$ ) when  $T'$  is decreasing. However, the assumption  $T'(1) < 1$  is automatically satisfied when  $T'(0) > 1$  because  $T$  is a contracting function: indeed assume that  $T'(1) \geq 1$ . Then since  $T'(0) > 1$  and  $T'$  being decreasing, this implies  $T'(x) > 1$ , for all  $x \in [0, 1]$ . Consequently  $\int_0^1 T'(x)dx > 1$ . But  $\int_0^1 T'(x)dx = T(1) - T(0)$ . Consequently  $T(1) - T(0) > 1$  which is impossible, since by construction  $T$  is defined on  $[0, 1]$ .*

**Proof of proposition 10** According to (25),

$$mT'(0) = m - [a'(0) + \tilde{m}b'(0) + p + \tilde{m}\tilde{q}] \quad (34)$$

$$mT'(1) = a(1) - p + \tilde{m}[b(1)(1 - \tilde{q}) - b'(1)\tilde{q}]. \quad (35)$$

According to (26) or (27),  $T'' < 0$  under (2) or (3), *i.e.*, under  $a \neq 1$  or  $b \neq 1$ , except under (P), implying that  $T'$  is a strictly decreasing function when there exists a nonnull fixed point.

- (1) Assume  $B < 0$ , or  $B = 0$  together with  $a \neq 1$  or  $b \neq 1$ .

- (a) Transient behavior. Assume first  $a \neq 1$  or  $b \neq 1$ . According to (24),  $x_{n+1} - x_n < 0$  if and only if  $h(x_n)$  is strictly negative. But under  $B \leq 0$ ,  $\lim_{x \rightarrow 0} h(x) \leq 0$  and since  $h$  is a strictly decreasing function, except under (P) and since  $h$  is strictly negative under (P), then  $h(x) < 0$ , for all  $x \in ]0, 1]$ . Now if  $B < 0$  with  $a = b = 1$ , then, from (23),  $x_{n+1} - x_n < 0$ , for all  $x_n > 0$ .
- (b) Asymptotical behavior. Assume first  $B < 0$ . According to proposition 8, 0 is the unique fixed point. Moreover we see on (34) since  $B \geq -p - \tilde{m}\tilde{q} \geq -m$  that, under  $B < 0$ ,  $0 < T'(0) < 1$ . So according to the previous theorem [7], 0 is asymptotically stable. Moreover since  $\{x_n\}_n$  is a decreasing sequence (cf the transient behavior) in  $]0, 1]$ , whatever be  $x_0$ , then  $\{x_n\}_n$  has a limit in  $[0, 1]$  which is necessarily the only fixed point 0, implying that 0 is globally stable on  $[0, 1]$ . Now if  $B = 0$  with  $a \neq 1$  or  $b \neq 1$ , according to the transient behavior, whatever be  $x_0$ ,  $\{x_n\}_n$  is a decreasing sequence, which therefore converges to the unique fixed point, 0.
- (2) Assume  $B > 0$ . Assume first the particular case  $p + \tilde{m}\tilde{q} = 0$  with  $a \neq 1$  or  $b \neq 1$ . Then according to (23),

$$m(x_{n+1} - x_n) = (m - a(x_n) - \tilde{m}b(x_n))(1 - x_n)$$

which is strictly positive on  $]0, 1[$ . Consequently  $\{x_n\}_n$  is an increasing sequence which necessarily converges to the unique fixed point 1, whatever be  $x_0$ , implying that 1 is globally stable on  $]0, 1]$ .

In the general case, we saw in 4.2.2.1 that, under (C),  $T$  has exactly two fixed points, 0 and  $x_* \neq 0$ . Moreover according to (34) and (35),  $T'(0) > 1$  and  $T'(1) > -pm^{-1} \geq -1$ . Next according to (26),  $T'$  is strictly decreasing and finally, since  $T$  is contracting,  $|T'(1)| < 1$ .

Consequently, under (C) the assumptions of proposition 12 are satisfied. We conclude that  $x_*$  is globally stable on  $]0, 1]$ , and 0 is unstable and the transient behavior satisfies (33); (33) can also be directly shown using (24) since  $h$  is decreasing with  $h(x_*) = 0$ .

#### 4.2.2.3 Conclusion : existence of a parameter of bifurcation

A bifurcation corresponds to an asymptotical behavior change. According to propositions 8 and 10,  $B$  is a bifurcation parameter.

When  $B < 0$ , or  $B = 0$  together with  $a \neq 1$  or  $b \neq 1$ , 0 is the only fixed point and it is globally stable. Under this condition, the disease dies out in a monotonic way.

When  $B > 0$ , the disease is asymptotically endemic and according to (30), when  $p + \tilde{m}\tilde{q} \neq 0$ , its short-term behavior is either a monotonic behavior or presents damped oscillations around the limit (cf paragraph 4.2.2.4). In the

particular case  $p + \tilde{m}\tilde{q} = 0$ , all the population is asymptotically infected and the probability to become infected increases during time.

When  $B = 0$  with  $a = b = 1$  ( $SI$  model without any horizontal transmission, either in a closed population or in an open population with systematic vertical transmission ( $\tilde{q} = 0$ )), the disease remains the same one as at the initial time.

**4.2.2.4 Simulations** We illustrate the previous results by some simulations under the model  $a(x) = a^x$  and  $b(x) = b^x$ , first in the case of extinction and then in the case of persistence. We assume  $\tilde{m} = 1$ .

- (1) Assume  $B < 0$ . Let  $P_0^I = 0.1$ ,  $a = 1$ ,  $b = 0.8$ ,  $\tilde{q} = 0.9$  and  $p = 0.3$ . Then  $P_n^I$  is decreasing until extinction (fig. 2):

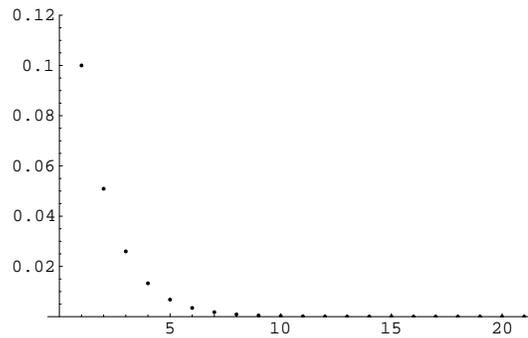


Fig. 2. Evolution of  $P_n^I$  during the first twenty iterations

- (2) Assume  $B > 0$ .  
(a) Let  $P_0^I = 0.01$ ,  $a = 1$ ,  $b = 0.3$ ,  $\tilde{q} = 0.7$  and  $p = 0.3$ . Then  $P_n^I$  increases to  $\Pi^I = 0.206$  (fig. 3):

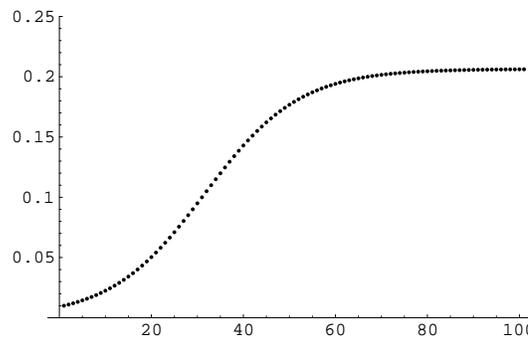


Fig. 3. Evolution of  $P_n^I$  during the first hundred iterations

- (b) Let  $P_0^I = 0.8$ ,  $a = 0.01$ ,  $b = 0.01$ ,  $\tilde{q} = 0.01$  and  $p = 0.99$ . Then  $P_n^I$  tends to  $\Pi^I = 0.67$  with damped oscillations around the limit (fig. 4):

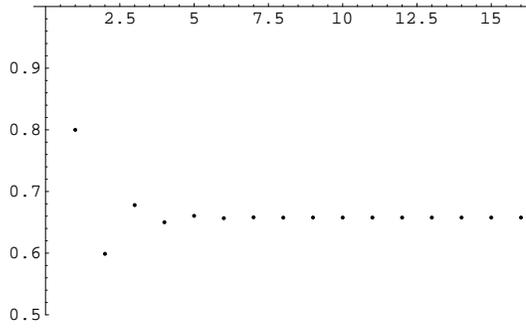


Fig. 4. Evolution of  $P_n^I$  during the first hundred iterations

## 5 Conclusion

The quantity which is studied in the frame of the model relative to the individual state of health is  $P_n^I = \lim_{N_0^0} N_n^I [N_n^0]^{-1}$  whereas on the scale of the population, it is the law of  $\{N_n^I\}$ . According to Lebesgue's dominated convergence theorem,

$$\begin{aligned} \lim_{N_0^0} E(\hat{P}_n^I | \vec{N}_0) &= E(\lim_{N_0^0} \hat{P}_n^I | \vec{N}_0) \\ &= P_n^I \end{aligned}$$

which implies

$$\lim_n \lim_{N_0^0} E(\hat{P}_n^I | \vec{N}_0) = \lim_n P_n^I. \quad (36)$$

Then we proved, according to (36), that

$$\lim_n \lim_{N_0^0} E(\hat{P}_n^I | \vec{N}_0) = 0, \text{ when } B \leq 0, \text{ except if } HC = SC = 0 \quad (37)$$

$$\lim_n \lim_{N_0^0} E(\hat{P}_n^I | \vec{N}_0) > 0, \text{ when } B > 0. \quad (38)$$

In addition, on the scale of a closed finite population, we showed that

$$\begin{aligned} \lim_n E(\hat{P}_n^I | \vec{N}_0) &\leq \lim_n P(\hat{P}_n^I > 0 | \vec{N}_0) \\ &= 0 \end{aligned}$$

implying

$$\lim_{N_0^0} \lim_n E(\hat{P}_n^I | \vec{N}_0) = 0. \quad (39)$$

In the particular case  $HC = SC = 0$ , the transmission is deterministic and therefore the proportion of infectives remains constant in both models. In the other cases, (37) and (39) show that under  $B \leq 0$ , *i.e.* when the transmission probabilities are smaller than the probability of renewing the population of susceptibles, then the two models which lead to extinction, are consistent, at least in a closed population. This result means that the limit in  $n$  and the limit in  $N_0^0$  can be exchanged. But it is no longer valid when the transmission probabilities are larger than the probability of renewing the population of susceptibles ( $B > 0$ ). In that case the size of the population,  $N_0^0$ , plays a central role for the extinction or the propagation of the disease. The asymptotical behavior is no more uniform according to the initial population size implying that the two limits cannot be exchanged.

We also notice that in a closed population, the sequence  $\{\overline{N}_n^I\}_n$  defined by  $\overline{N}_n^I = E(N_n^I | N_{n-1}^I = \overline{N}_{n-1}^I)$  is also solution of the system (1). This implies that  $B$  is also the bifurcation parameter for this conditional mean trajectory in a finite population. the divergence of results between the asymptotic behavior of this particular trajectory and that of the branching process means that this particular trajectory is not representative of the behavior of the branching process when  $B > 0$ .

## 6 Appendix

**Proof of proposition 2** . Write  $\tilde{m}_{n+1}^h$  and  $m_{n+1}^h$  for  $\tilde{m}_{n+1}^h(\vec{P}_n)$  and  $m_{n+1}^h(\vec{P}_n)$ . Let  $\Omega_n = \{\vec{N}_n(N)\}_N$ . Using (6) we will iteratively show on  $\Omega_{n-1}$ :

$$\lim_{N \rightarrow \infty} \frac{N_n^k}{N_n^0} \stackrel{a.s.}{=} \sum_h Q(\vec{P}_{n-1})[h, k] \frac{m_{n+1}^h P_{n-1}^h}{\sum_l m_{n+1}^l P_{n-1}^l}, \quad k \in \{1, \dots, d\} \quad (40)$$

$$\stackrel{a.s.}{=} \lim_{N \rightarrow \infty} P(E_n(i_n) = k | F_n). \quad (41)$$

Since (40) determines in a unique way the sequence  $\{\vec{P}_n\}_n$  from  $\vec{P}_0$ , we will finally obtain (12) and (13) on  $\{\lim_{N \rightarrow \infty} \vec{N}_0(N)N^{-1} = \vec{P}_0\}$ .

So assume (40) at  $n$  and prove it at  $n + 1$ , that is  $\lim_N A_{n+1}^k(N) \stackrel{a.s.}{=} 0$ , for all  $k$ , on  $\Omega_n$ , where

$$A_{n+1}^k(N) = \sum_h \sum_{i=1}^{N_n^h} \frac{\delta_{a,n+1,i}^{h,k} + \sum_{j=1}^{\tilde{Y}_{n+1,i}^h} \delta_{b,n+1,i,j}^{h,k}}{N_{n+1}^0} - \sum_h M(\vec{P}_n)[h, k] \frac{P_n^h}{\sum_l m_{n+1}^l P_n^l}.$$

We can decompose  $A_{n+1}^k(N)$  in the following way:

$$A_{n+1}^k(N) = A_{a,n+1}^k(N) + A_{b,n+1}^k(N),$$

where

$$A_{a,n+1}^k(N) = \sum_h \sum_{i=1}^{N_n^h} \frac{\delta_{a,n+1,i}^{h,k}}{N_{n+1}^0} - \sum_h P_a^{h,k}(\vec{P}_n) \frac{P_n^h}{\sum_l m_{n+1}^l P_n^l}$$

and

$$A_{b,n+1}^k(N) = \sum_h \sum_{i=1}^{N_n^h} \sum_{j=1}^{\hat{Y}_{n+1,i}^h} \frac{\delta_{b,n+1,i,j}^{h,k}}{N_{n+1}^0} - \sum_h \tilde{m}_{n+1}^h P_b^{h,k}(\vec{P}_n) \frac{P_n^h}{\sum_l m_{n+1}^l P_n^l}.$$

Further

$$\begin{aligned} A_{a,n+1}^k(N) &= \sum_h \sum_{i=1}^{N_n^h} \frac{\delta_{a,n+1,i}^{h,k} - P_a^{h,k}(\vec{P}_n)}{N_{n+1}^0} + \sum_h [P_a^{h,k}(\vec{P}_n) - P_a^{h,k}(\widehat{\vec{P}}_n)] \frac{N_n^h}{N_{n+1}^0} \\ &\quad + \sum_h P_a^{h,k}(\vec{P}_n) \left[ \frac{N_n^h}{N_{n+1}^0} - \frac{P_n^h}{\sum_l m_{n+1}^l P_n^l} \right] \end{aligned}$$

and

$$\begin{aligned} A_{b,n+1}^k(N) &= \sum_h \sum_{i=1}^{N_n^h} \frac{\sum_{j=1}^{\hat{Y}_{n+1,i}^h} \delta_{b,n+1,i,j}^{h,k} - \tilde{m}_{n+1}^h P_b^{h,k}(\vec{P}_n)}{N_{n+1}^0} \\ &\quad + \sum_h \tilde{m}_{n+1}^h [P_b^{h,k}(\widehat{\vec{P}}_n) - P_b^{h,k}(\vec{P}_n)] \frac{N_n^h}{N_{n+1}^0} \\ &\quad + \sum_h \tilde{m}_{n+1}^h P_b^{h,k}(\vec{P}_n) \left[ \frac{N_n^h}{N_{n+1}^0} - \frac{P_n^h}{\sum_l m_{n+1}^l P_n^l} \right]. \end{aligned}$$

On  $\Omega_n$ ,  $\{N_n^h(N)\}_N$  can be either bounded or can increase to infinity as  $N \rightarrow \infty$ . On  $\{\lim_N N_n^h(N) = \infty\}$ ,

$$\sum_{i=1}^{N_n^h} \frac{\delta_{a,n+1,i}^{h,k} - P_a^{h,k}(\vec{P}_n)}{N_{n+1}^0} = \sum_{i=1}^{N_n^h} \frac{\delta_{a,n+1,i}^{h,k} - P_a^{h,k}(\vec{P}_n)}{N_n^h} \frac{N_n^h}{N_{n+1}^0}.$$

According to the strong law of large numbers for i.i.d. variables  $X_i = \delta_{a,n+1,i}^{h,k} - P_a^{h,k}$  with bounded variances  $\text{var}(X_i | \vec{N}_n) \leq 2$  ([8]), we have on  $\Omega_n$

$$\lim_N \sum_{i=1}^{N_n^h} \frac{\delta_{a,n+1,i}^{h,k} - P_a^{h,k}(\vec{P}_n)}{N_n^h} \stackrel{a.s.}{=} 0.$$

Since  $N_n^h/N_{n+1}^0 \leq 1$ , then  $\lim_N [\sum_{i=1}^{N_n^h} \delta_{a,n+1,i}^{h,k} - P_a^{h,k}(\vec{P}_n)] [N_{n+1}^0]^{-1} \stackrel{a.s.}{=} 0$ . In the same way, since

$$\begin{aligned} & \text{var} \left( \sum_{j=1}^{\tilde{Y}_{n+1,i}^h} \delta_{b,n+1,i,j}^{h,k} - \tilde{m}_{n+1}^h P_b^{h,k}(\vec{P}_n) \mid \vec{N}_n \right) = \\ & \tilde{m}_{n+1}^h P_b^{h,k}(\vec{P}_n) (1 - P_b^{h,k}(\vec{P}_n)) + (P_b^{h,k}(\vec{P}_n))^2 \tilde{\sigma}_{n+1}^{2h} \leq \tilde{m}_{n+1} + \tilde{\sigma}_{n+1}^2, \end{aligned}$$

the quantity

$$\begin{aligned} & \sum_{i=1}^{N_n^h} \frac{\sum_{j=1}^{\tilde{Y}_{n+1,i}^h} \delta_{b,n+1,i,j}^{h,k} - \tilde{m}_{n+1}^h P_b^{h,k}(\vec{P}_n)}{N_{n+1}^0} = \\ & \sum_{i=1}^{N_n^h} \frac{\sum_{j=1}^{\tilde{Y}_{n+1,i}^h} \delta_{b,n+1,i,j}^{h,k} - \tilde{m}_{n+1}^h P_b^{h,k}(\vec{P}_n)}{N_n^h} \frac{N_n^h}{N_{n+1}^0} \end{aligned}$$

converges a.s. to 0, as  $N \rightarrow \infty$ .

Now when  $\{N_n^h(N)\}_N$  remains bounded, there exists  $M$  for such a sequence, such that  $N_n^h(N) \leq M$ , for all  $N$ , implying, since  $N_{n+1}^0 \geq N$ ,

$$\left| \sum_{i=1}^{N_n^h} \frac{\delta_{a,n+1,i}^{h,k} - P_a^{h,k}(\vec{P}_n)}{N_{n+1}^0} \right| \leq 2 \frac{M}{N}$$

which tends to 0, as  $N \rightarrow \infty$ . In the same way

$$\left| \sum_{i=1}^{N_n^h} \frac{\sum_{j=1}^{\tilde{Y}_{n+1,i}^h} \delta_{b,n+1,i,j}^{h,k} - \tilde{m}_{n+1}^h P_b^{h,k}(\vec{P}_n)}{N_{n+1}^0} \right| \leq \frac{\sum_{i=1}^M [\tilde{Y}_{n+1,i}^h + \tilde{m}_{n+1}^h]}{N}.$$

Since  $\text{var}(\tilde{Y}_{n+1,i}^h \mid \vec{N}_n) \leq \tilde{\sigma}_{n+1}^2$ , then by Borel-Cantelli's lemma and Bienaymé-Tshebychev inequality, the right member of the inequation above converges a.s. to 0, as  $N \rightarrow \infty$  on  $\Omega_n$  (use  $\sum_N P(X_i N^{-1} > N^{-1/4}) \leq \sup_i \text{var}(X_i) \sum_N N^{-3/2} < \infty$ , where  $X_i = \sum_{i=1}^M [\tilde{Y}_{n+1,i}^h + \tilde{m}_{n+1}^h]$ ).

Moreover, since  $P_a^{h,k}(\cdot)$  and  $P_b^{h,k}(\cdot)$  are continuous functions, and since  $\lim_N \vec{P}_n \stackrel{a.s.}{=} \vec{P}_n$ , then

$$\lim_N [P_a^{h,k}(\vec{P}_n) - P_a^{h,k}(\vec{P}_n)] \stackrel{a.s.}{=} 0$$

and the same is true concerning  $P_b^{h,k}(\cdot)$ .

Finally

$$\frac{N_n^h}{N_{n+1}^0} - \frac{P_n^h}{\sum_l m^l P_n^l} = \frac{N_n^h}{N_n^0} [1 + \sum_h \sum_{i=1}^{N_n^h} \frac{\tilde{Y}_{n+1,i}^h}{N_n^h} \frac{N_n^h}{N_n^0}]^{-1} - \frac{P_n^h}{\sum_l m^l P_n^l}$$

According to the same arguments as previously, this quantity converges a.s. to 0, as  $N \rightarrow \infty$ .

Finally it remains to prove (41) at  $n + 1$ .

So let  $C(i_{n+1})$  the variable taking the values  $a$  or  $b$  according to whether the ancestors line  $i_{n+1}$  is an adult or a newborn at time  $n + 1$ . We have

$$\begin{aligned} & P(E_{n+1}(i_{n+1}) = k | F_{n+}) = \\ & \sum_h [P(E_{n+1}(i_{n+1}) = k | C(i_{n+1}) = a, E_n(i_{n+1}) = h, F_{n+}) \cdot \\ & P(C(i_{n+1}) = a | E_n(i_{n+1}) = h, F_{n+}) + \\ & P(E_{n+1}(i_{n+1}) = k | C(i_{n+1}) = b, E_n(i_{n+1}) = h, F_{n+}) \cdot \\ & P(C(i_{n+1}) = b | E_n(i_{n+1}) = h | F_{n+})] P(E_n(i_{n+1}) = h | F_{n+}). \end{aligned}$$

By definition,

$$P(C(i_{n+1}) = b | E_n(i_{n+1}) = h, F_{n+}) = P(i_{n+1} \in \cup_i \{\tilde{Y}_{n+1,i}^h\} | F_{n+}). \quad (42)$$

Since in branching processes, the individuals are all considered equivalent, we can assume that  $i_{n+1}$  follows a uniform law, that is the probability above is equal to the percentage of newborns at time  $n + 1$ :

$$P(C(i_{n+1}) = b | E_n(i_{n+1}) = h, F_{n+}) = \frac{\sum_{i=1}^{N_n^h} \tilde{Y}_{n+1,i}^h}{\sum_{i=1}^{N_n^h} (1 + \tilde{Y}_{n+1,i}^h)}.$$

In the same way

$$P(E_n(i_{n+1}) = h | F_{n+}) = \frac{\sum_{i=1}^{N_n^h} (1 + \tilde{Y}_{n+1,i}^h)}{\sum_l \sum_{i=1}^{N_n^l} (1 + \tilde{Y}_{n+1,i}^l)}.$$

Moreover using the definitions and assumptions concerning  $\delta_{a,n+1,1}^{h,k}$  and  $\delta_{b,n+1,1}^{h,k}$ , we have

$$\begin{aligned} P(E_{n+1}(i_{n+1}) = k | C(i_{n+1}) = a, E_n(i_{n+1}) = h, F_{n+}) = \\ P(\delta_{a,n+1,i_{n+1}}^{h,k} = 1 | F_{n+}) = P_a^{h,k}(\vec{P}_n). \end{aligned}$$

The same is true concerning  $P(E_{n+1}(i_{n+1}) = k | C(i_{n+1}) = b, E_n(i_{n+1}) = h, F_{n+})$ .

So finally

$$\begin{aligned} P(E_{n+1}(i_{n+1}) = k | F_{n+}) = \\ \sum_h [P_a^{h,k}(\vec{P}_n) \frac{N_n^h}{\sum_{i=1}^{N_n^h} (1 + \tilde{Y}_{n+1,i}^h)} + P_b^{h,k}(\vec{P}_n) \frac{\sum_{i=1}^{N_n^h} \tilde{Y}_{n+1,i}^h}{\sum_{i=1}^{N_n^h} (1 + \tilde{Y}_{n+1,i}^h)}] \\ \frac{\sum_{i=1}^{N_n^h} (1 + \tilde{Y}_{n+1,i}^h)}{\sum_l \sum_{i=1}^{N_n^l} (1 + \tilde{Y}_{n+1,i}^l)}. \end{aligned}$$

Taking the limit as  $N \rightarrow \infty$ , we obtain (41). The relationship (14) is straightforwardly deduced from (12).

**Proof of proposition 12** We will first prove that 0 is unstable and  $x_*$  is asymptotically stable. Then, we will study the convergence of the sequence  $\{x_n\}_n$  to  $x_*$  and we will show that  $x_*$  is globally stable.

According to theorem ([7]), 0 is unstable. Next, concerning  $x_*$ , we are going to show that  $|T'(x_*)| < 1$ . Since  $-1 < T'(1) < 1$ ,  $T'(0) > 1$  and  $T'$  is a decreasing function, it is clear that there exists  $c1 \in ]0, 1[$  which satisfies  $T'(c1) = 1$  and moreover  $|T'(x)| < 1$ , for all  $x > c1$ . To conclude that  $x_*$  is asymptotically stable, it is sufficient to show that  $x_* > c1$  since this inequality implies  $|T'(x_*)| < 1$ . Let  $k(x) = T(x) - x$ ,  $x \in [0, 1]$ ;  $x_*$  satisfies  $k(x_*) = 0$ . Since  $T'$  is strictly decreasing, it is straightforward to show that  $k'$  is strictly decreasing and  $k'(x) > 0$  for all  $x \in [0, c1[$  and  $k'(x) \leq 0$  for all  $x \in [c1, 1]$ . Thus the function  $k$  is first increasing on  $[0, c1]$  and then decreasing on  $[c1, 1]$  with  $k(0) = T(0) - 0 = 0$  and  $k(1) = T(1) - 1 \leq 0$  (because  $T$  is an application from  $[0, 1]$  to  $[0, 1]$ ).

To show that  $x_* > c1$ , using  $k(x_*) = 0$ , it is sufficient to prove that  $k(x) > 0$ , for all  $x \in ]0, c1]$ . This property is directly deduced from  $k(0) = 0$  and  $k$  strictly increasing on  $[0, c1]$ .

We get the table of variation of  $k$ :

x	0	c1	$x_*$	1
Sign of $k'(x)$	+	0	-	-
Variation of $k(x)$	0	↗	↘	↘

After that considering  $x = x_n$ , we have  $T(x) = x_{n+1}$  and we can deduce the properties (33) from the table of variation.

Moreover according to the properties  $c1 < x_*$ ,  $T'(c1) = 1$  and  $T'$  is a decreasing function on  $[0, 1]$  with  $T'(1) > -1$ , then  $|T'(x_*)| < 1$ . Thus, according to theorem [7],  $x_*$  is locally asymptotically stable.

Now, consider the convergence of a sequence  $\{x_n\}_n$  defined by  $x_{n+1} = T(x_n)$ . Since the function  $T'$  is decreasing with  $T'(0) > 1$  and  $T'(1) > -1$ , we separate the study in two cases: either  $T$  is assumed increasing (*i.e.*  $T'(1) \geq 0$ ) or  $T$  is assumed first increasing and then decreasing ( $T'(1) < 0$ ).

- (1) Assume that  $T$  is increasing. Then the sequence  $\{x_n\}_n$  is monotonic and bounded. Consequently it converges and its limit  $l$  satisfies  $l = T(l)$ . Since 0 is a unstable fixed point, then necessarily  $l = x_*$ , when  $x_0 \in ]0, 1]$  and  $l = 0$  when  $x_0 = 0$ . Consequently  $x_*$  is globally stable on  $]0, 1]$ .
- (2) Assume that  $T$  is first increasing and then decreasing. Then there exist  $c2 \in [0, 1]$  which satisfies  $T'(c2) = 0$  with necessarily  $c2 > c1$  because  $T'$  is decreasing and  $T'(c1) = 1$ .

The table of variation of  $T'$  has the form:

x	0	c1	c2	1
Sign of $T'$	+	0	-	
Variation of $T$	0	↗	↘	

The following result will be used.

Let  $x_n \in ]c1, 1]$ . Then

$$|x_{n+1} - x_*| < |x_n - x_*|. \quad (43)$$

This result is shown using Taylor's formula:

$$T(x_n) = T(x_*) + (x_n - x_*)T'(\tilde{x}), \tilde{x} \in ]0, 1[$$

Since  $T(x_n) = x_{n+1}$  and  $T(x_*) = x_*$ , then

$$x_{n+1} - x_* = (x_n - x_*)T'(\tilde{x}). \quad (44)$$

Moreover for all  $\tilde{x} \in ]c1, 1]$ ,  $|T'(\tilde{x})| < 1$ , which implies the result.

Since (43) is valid only on  $]c1, 1]$ , let us denote  $I = ]c1, 1]$  and  $I^c = [0, c1]$ . We will consider the two cases : either  $x_0 \in I$  or  $x_0 \in I^c$ .

(a) Let  $x_0 \in I = ]c1, 1]$

We first define the largest interval  $I_s \subset I$  which is stable by  $T$  *i.e.*  $T(I_s) \subset I_s$ . Denote  $I_{-s} = I \setminus I_s$ . Then we will study the case  $x_0 \in I_s$  followed by the case  $x_0 \in I_{-s}$ .

(i) Determination of  $I_s$  such that  $T(I_s) \subset I_s$

$T$  being increasing on  $[c1, c2] \subset I$  and since  $T([0, 1]) \subset [0, 1]$  and  $T(c1) > c1$  (cf the table of variation of  $k$ ), then  $1 \geq T(x) > T(c1) > c1$ , for all  $c1 < x \leq c2$  which implies  $T(x) \in I$ , for all  $c1 < x \leq c2$ .

Now, the function  $T$  being decreasing on  $[c2, 1]$ , then  $T(x) \geq T(1)$ , for all  $c2 \leq x \leq 1$ . We consider the two cases : either  $T(1) > c1$  or  $T(1) \leq c1$ .

- Assume  $T(1) > c1$  (fig. 5).

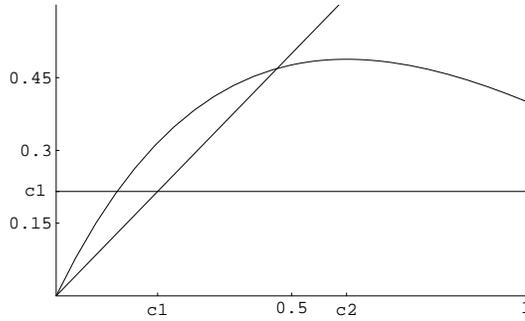


Fig. 5. Example of graph of  $T$  when  $T(1) > c1$

Since  $T$  is increasing on  $[0, c2]$  and  $T(c1) > c1$ , then, for all  $x \in ]c1, c2]$ ,  $T(x) > c1$  and since the function  $T$  is decreasing on  $[c2, 1]$ , then, for all  $x \in [c2, 1]$ ,  $T(x) \geq T(1) > c1$ . Consequently  $\forall x \in I$ ,  $T(x) \in I$  *i.e.*  $I_s = I$ .

- Assume  $T(1) \leq c1$ . Then there exists  $c3 > c1$  such that  $T(c3) = c1$ . Using (33) and  $T(c3) = c1 < c3$ , we have  $c3 > x_*$ . Moreover, we saw previously that, for all  $x \in [c1, c2]$ ,  $T(x) > c1$ . Consequently since  $T(c3) = c1$ , we have necessarily  $c3 \notin [c1, c2]$ .

We are going to show now that  $I_s = ]c1, c3[$ . So let  $I_* = ]c1, c3[$ . We must check that  $T(I_*) \subset I_*$ . According to the previous results, for all  $x \in [c1, c2]$ ,  $T(x) > T(c1) > c1$ .

Now  $T$  being decreasing on  $[c2, c3[$ , then for all  $x \in [c2, c3[$ ,  $T(x) > T(c3) = c1$ . Consequently, for all  $x \in I_*$ ,  $T(x) > c1$ . To conclude that  $T(I_*) \subset I_*$ , we need to show that  $\sup\{T(x); x \in ]c1, c3[ \} < c3$ . According to the table of variation of  $T$ ,  $\sup\{T(x); x \in ]c1, c3[ \} = T(c2)$ . Consequently it remains to show that  $T(c2) < c3$ .

Two cases can be considered, depending on the position of  $c2$  compared to  $x_*$ .

- Assume  $c2 \geq x_*$  (fig. 6). Then according to the definition of  $c3$  and using (33),  $T(c2) \leq c2 < c3$ . Hence  $\sup\{T(x); x \in ]c1, c3[ \} < c3$ . Consequently  $T(I_*) \subset I_*$ .

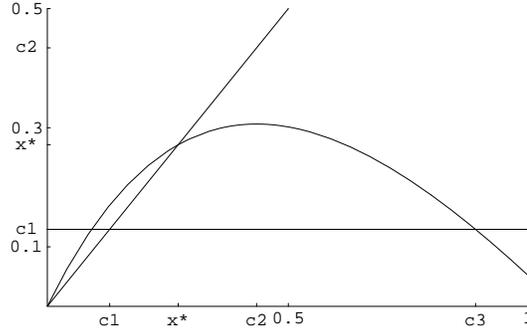


Fig. 6. Example of graph of  $T$  when  $T(1) \leq c1$  and  $c2 \geq x_*$

- Assume  $c2 < x_*$  (fig. 7); (33) implies  $T(c2) > c2$ . Now assume that  $T(c2) \geq c3$  and show that this is not possible.

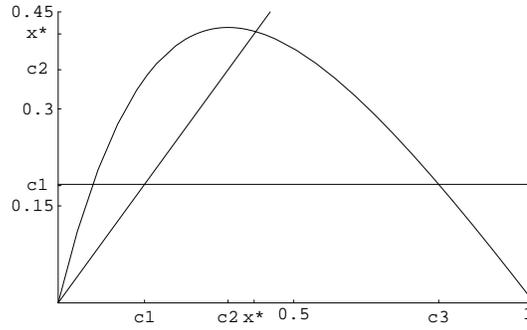


Fig. 7. Example of graph of  $T$  when  $T(1) \leq c1$  and  $c2 < x_*$

Let  $x_n = c2$ ,  $x_{n+1} = T(c2)$  and  $x_{n+2} = T(x_{n+1}) = T(T(c2))$ .

Since  $c2 \in ]c1, 1]$ , then according to (43),

$$|x_{n+1} - x_*| < |x_n - x_*| \quad (45)$$

Since  $T(c2) \in [c3, 1] \subset ]c1, 1]$ , using (43)

$$|x_{n+2} - x_*| < |x_{n+1} - x_*| \quad (46)$$

From (45) and (46), we deduce

$$|x_{n+2} - x_*| < |x_n - x_*| \quad (47)$$

Moreover since  $x_n = c2$  and  $c2 < x_*$ , then

$$|x_n - x_*| = x_* - x_n$$

Since  $T$  is decreasing on  $[c2, 1] \supset [c3, 1]$  and according to the assumption  $x_{n+1} \geq c3$ , then  $T(x_{n+1}) \leq T(c3) = c1$  and since  $c1 < x_*$ , then

$$|x_{n+2} - x_*| = x_* - x_{n+2}.$$

Consequently (47) is equivalent to

$$x_* - x_{n+2} < x_* - x_n$$

implying

$$x_{n+2} > x_n = c2. \quad (48)$$

But using  $T(c2) \geq c3$  and  $T$  decreasing on  $[c2, 1]$ , we have  $T(T(c2)) \leq T(c3) = c1$ , where  $c1 < c2$ , implying  $x_{n+2} \leq c2$ , which leads together with (48) to a contradiction.

Consequently  $T(c2) < c3$ , *i.e.*  $\sup\{T(x); x \in ]c1, c3[ \} < c3$ , implying  $T(I_*) \subset I_*$ . So define  $I_s = I_*$ . In the paragraph iii we will show that  $I_s$  is the largest stable interval in  $I$ .

(ii) Let  $x_0 \in I_s$ .

Since  $T(I_s) \subset I_s$  and using (43), the sequence  $\{|x_n - x_*|\}_n$  is a monotonic decreasing sequence in a compact, implying that this sequence converges to a limit.

Since  $|x_n - x_*| = x_n - x_*$  or  $-x_n + x_*$ , either  $\lim_n x_n$  exists with

$$\begin{aligned} \lim_n x_n &= \lim_n T(x_n) \\ &= T(\lim_n x_n) \end{aligned} \quad (49)$$

implying  $\lim_n x_n = x_*$ .

Or there exists two infinite different subsequences  $\{x_{n_i}\}$  and  $\{x_{n_j}\}$  such that  $|x_{n_i} - x_*| = x_{n_i} - x_*$  and  $|x_{n_j} - x_*| = -x_{n_j} + x_*$ . Therefore using the existence of  $\lim_n |x_n - x_*|$ , we have

$$\lim_{n_i} (x_{n_i} - x_*) + \lim_{n_j} (x_{n_j} - x_*) = 0$$

*i.e.*

$$\lim_{n_i} x_{n_i} + \lim_{n_j} x_{n_j} = 2x_*. \quad (50)$$

Let  $x_{(1)} = \lim_{n_i} x_{n_i}$  and  $x_{(2)} = \lim_{n_j} x_{n_j} = \lim_{n_j} T(x_{n_j-1})$ .

Now, either  $x_{n_j-1}$  belongs to  $\{x_{n_i}\}$ , for all  $n_j$  large enough. Or for all  $n_i$  and  $n_j$  large enough,  $x_{n_j-1} \neq x_{n_i}$ . In this latter case,  $x_{n_j-1}$  belongs to  $\{x_{n_j}\}$ , for any  $n_j$  large enough implying  $\lim_{n_j} x_{n_j} = \lim_{n_j} x_{n_j-1} = \lim_{n_j} T(x_{n_j-1}) = T(\lim_{n_j} x_{n_j-1})$  *i.e.*  $x_{(2)}$  is a fixed point (belonging to  $I_s$ ). Therefore  $x_{(2)} = x_*$ ; and the same is true for  $x_{(1)}$ :  $x_{(1)} = x_*$ . In the first case

$$\begin{aligned} \lim_{n_j} T(x_{n_j-1}) &= \lim_{n_i} T(x_{n_i}) \\ &= T(\lim_{n_i} x_{n_i}) \end{aligned}$$

Hence

$$x_{(2)} = T(x_{(1)}). \quad (51)$$

Using (50),  $x_{(1)}$  satisfies

$$x_{(1)} + T(x_{(1)}) = 2x_*. \quad (52)$$

So we study the function  $S(x) = x + T(x) - 2x_*$ . According to (52),  $S(x_{(1)}) = 0$ . Moreover  $S(x_*) = 0$ . Therefore if we show that the equation  $S(x) = 0$  has a unique root in  $I_s$ , we will have  $x_{(1)} = x_*$ . According to (51),  $x_{(2)} = T(x_*) = x_*$ .  $T'$  being decreasing on  $[0, 1]$  with  $T'(1) > -1$ , then, for all  $x \in [0, 1]$ ,  $T'(x) > -1$  which implies  $S'(x) > 0$ , hence  $S$  is strictly increasing. Therefore there exists at most a unique solution  $x^* \in I_s$  with  $S(x^*) = 0$ . Consequently  $x^* = x_* = x_{(1)}$  and  $\lim_n x_n = x_*$ .

(iii) Let  $x_0 \in I_{\neg s} = [c3, 1]$

From the definition of  $c3$ ,  $T(c3) = c1$  and since  $T$  is decreasing on  $[c2, 1] \supset I_{\neg s}$ , then, for all  $x \in I_{\neg s}$ ,  $0 \leq T(x) < T(c3) = c1$ . Consequently  $x_0 \in I_{\neg s}$  implies  $x_1 \in I^c$ , which proves moreover that  $I_s$  is the largest stable interval in  $I$ .

(b) Let  $x_0 \in I^c = [0, c1]$

If  $x_0 = 0$ , then  $x_n = 0$ , for all  $n$ . So assume now  $x_0 \in ]0, c1]$ . Then  $x_0 < x_*$  which implies according to (33) that  $x_0 < x_1$ .

(i) Assume that for all  $n$ ,  $x_n \in ]0, c1]$ . Since  $T$  is increasing on  $]0, c1]$ , the sequence  $\{x_n\}_n$  is increasing and bounded by  $c1$ . Therefore this sequence has a limit  $l \in I^c$ . But the unique fixed point in  $I^c$  being 0 which is unstable, this case is impossible.

(ii) There exists  $N$  such that  $x_N \in I = I_s \cup I_{\neg s}$ .

- Assume that  $x_N \in I_s$ . Then from the previous results concerning  $x_0 \in I_s$ , we have  $\lim_n x_n = x_*$ .

- Assume that  $x_N \in I_{\neg s}$ . We show that this case is not possible:
  - If  $T(1) > c1$ , then  $I_{\neg s} = \emptyset$ ;
  - If  $T(1) \leq c1$ ,  $T$  being increasing on  $[0, c2]$ , with  $c2 > c1$ , then  $T(x_0) < T(c2)$ . But  $T(c2) < c3$  which implies  $T(x_0) = x_1 < c3$ . Consequently  $x_1 \in I^c \cup I_s$  i.e.  $x_1 \notin I_{\neg s}$ . and iteratively,  $x_N \notin I_{\neg s}$ .

Consequently, for  $x_0 \in ]0, c1]$ , the sequence  $\{x_n\}_n$  converges and  $\lim_n x_n = x_*$ .

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