

# Quasi-stationary distributions for population processes

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## Abstract

*Key-words:* population dynamics, quasi-stationarity, Yaglom's limit, birth and death process, logistic Feller diffusion.

## 1 Introduction

We are interested in the long time behavior of regulated (density-dependent) and isolated biological populations. Competition for limited resources impedes these natural populations without immigration to grow indefinitely. Then, they are doomed to become extinct. When the population's size is zero, and without immigration, nothing happens and the population's size process stays at zero. This point 0 is thus an absorbing point for the process. Nevertheless, the time of extinction can be large compared to human time scale and it is common that population sizes fluctuate for large amount of time before extinction actually occurs. For example, it has been observed that in populations of endangered species, as for the Arizona ridge-nose rattlesnakes studied in Renault-Ferrière-Porter [29], the statistics of some biological traits seem to stabilize. To capture this phenomenon, we will study the long time behavior of the process conditioned to non extinction and the related notion of **quasi-stationarity**. We refer to the introduction of Steinsaltz-Evans [33] for a nice discussion of this notion in relationship with various biological observations (mortality plateaus).

In all the following we will assume that the population's size process  $(Z_t, t \geq 0)$  is a Markov process which almost surely goes to extinction. We are interested in looking for characteristics of the process that give more detailed information than the fact that absorption is certain. One way to approach this problem is to study the "quasi-limiting distribution" (QLD) of the process (if it exists), that is the limit, as  $t \rightarrow +\infty$ , of the

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distribution of  $Z_t$  conditioned on non-absorption up to time  $t$ . This distribution, which is also called Yaglom's limit, provides particularly useful information if the time scale of absorption is substantially larger than the one of the quasi-limiting distribution. In that case, the process relaxes to the quasi-limiting regime after a relatively short time, and then, after a very much long period, absorption will eventually occur. Thus the quasi-limiting distribution bridges gap between the known behavior (extinction) and the unknown time-dependent behavior of the process.

There is another quasi-stationary limit point of view. A quasi-stationary distribution for the process  $(Z_t, t \geq 0)$  denotes any proper initial distribution on the non-absorbing states which is such that the distribution of  $Z_t$  conditioned on non-extinction up to time  $t$  is independent of  $t, t \geq 0$ . If the distribution of  $Z_0$  is chosen to be any QSD, then the corresponding QLD exists and equals this QSD. Hence, any quasi-stationary distribution is a quasi-stationary limit, but the converse is not always true.

In Section 2 of this course, we will introduce the different notions of QSD and state some elementary properties. In Section 3, we will study the simple case of QSD for processes in continuous time with finite state space. Thus we will concentrate on QSD for several stochastic population models corresponding to different scaling. We will underline the importance of spectral theory as mathematical tool for the research of QSD, in these different contexts. In Section 4, we will consider birth and death processes and we will especially focus on the logistic case. We will show that in that case, the process goes almost surely to extinction. We will state the results obtained by Van Doorn [12], giving explicit conditions on the coefficients ensuring the existence and uniqueness (or not) of a QSD. We will show that in the logistic case, there is a unique QSD, which coincides with the unique QLD.

When the initial population size is very large, the logistic birth and death process takes very large values and it is interesting to study some well chosen renormalizations. In section 5, we show that the rescaled process converges as the initial size tends to infinity, to the unique solution of the famous deterministic logistic equation. In that case the solution converges as time tends to infinity to a nontrivial limit called carrying capacity. This model describes stable large populations whose size stays essentially constant. Another asymptotics consists in accelerating the birth and death rates as the initial population size increases. Then one shows that the re-scaled logistic birth and death process is close to the solution of a stochastic differential equation which generalizes the Feller diffusion with a density-dependent term. The randomness due to the accumulation of a large number of birth and death events is modeled by a Brownian term and usually called "demographic stochasticity" by the ecologists. We prove that in this case, there is also a unique QSD, equal to the Yaglom's limit, obtained as re-scaled eigenmeasure of the adjoint operator of the killed semi-group. The existence proof is not constructive and cannot be quantitatively exploited. It is useful to construct an algorithmic method to simulate it. At this end, we will give the main ideas of a work of Villemonais ([36]), describing a stochastic particle method based on Fleming-Viot systems.

## 2 Quasi-stationary distributions

### 2.1 Different notions of long time behavior conditioned on non extinction

We consider a stochastic Markov process  $(X_t, t \geq 0)$  with continuous time and with values in a metric space  $E$ . Let  $G$  be a subset of  $E$  which models a trap. Namely, if a trajectory arrives in  $G$  then the process is killed.

There are several natural questions associated with this situation.

(i) Given an initial distribution  $\mu$  on  $E^*$  (for example a Dirac measure), what is the probability that a trajectory has survived up to time  $t > 0$ ? In other words, if  $T_G$  denotes the entrance time of the process in  $G$ , a first question to study is the asymptotic behavior of the quantity

$$\mathbb{P}_\mu(T_G > t). \quad (2.1)$$

(ii) Let us fix  $t > 0$  and assume now that a trajectory initially distributed with  $\mu$  has survived up to time  $t > 0$ . We are interesting in knowing the conditional distribution of  $X_t$ . The mathematical quantity of interest is thus, for any Borel subset  $A$  of  $E \setminus G$ ,

$$\mathbb{P}_\mu(X_t \in A | T_G > t) = \frac{\mathbb{P}_\mu(X_t \in A; T_G > t)}{\mathbb{P}_\mu(T_G > t)}. \quad (2.2)$$

We want to study the asymptotic behavior of this conditional probability, when  $t$  tends to infinity. If the limit exists, it will be called the quasi-limiting distribution (QLD) of the measure  $\mu$ , or the Yaglom limit for  $\mu$ , in reference to Yaglom who wrote the first paper on this subject [37]. A main difficulty of this notion is that it may depend on the initial distribution  $\mu$ .

One will say that  $\alpha$  is the Yaglom limit (without reference to a measure), if for any initial point  $x \in E$ , and any Borel set  $A \subseteq E \setminus G$ ,

$$\alpha(A) = \lim_{t \rightarrow \infty} \frac{\mathbb{P}_x(X_t \in A; T_G > t)}{\mathbb{P}_x(T_G > t)}. \quad (2.3)$$

(iii) As in the ergodic case we can ask if this Yaglom limit has a conditional stationary property. More precisely we will define a quasi-stationary distribution (QSD) as a measure  $\alpha$  such that for all  $t > 0$ , for all  $A$  Borel set of  $E \setminus G$ ,

$$\frac{\mathbb{P}_\alpha(X_t \in A; T_G > t)}{\mathbb{P}_\alpha(T_G > t)} = \alpha(A). \quad (2.4)$$

The main questions are existence and uniqueness of these QSD. We will see examples where QSD does not exist, or where there is an infinity of QSD, or where there is a unique QSD. The latter will happen in the case of the size process of a density-dependent population. We will also see that the relation between QSD and QLD is not so easy, except when  $E$  is a finite space.

(iv) The fourth mathematical quantity related to this conditioning point of view is trajectorial. We are interested in describing the distribution of the trajectories who never attain the trap. We will prove that the new process defined by this distribution is ergodic, and that its stationary distribution is absolutely continuous with respect to the QSD (but not equal).

The study of quasi-stationarity is a long standing problem: see Pollett [28] for a regularly updated extensive bibliography and [14], [17], [32] for the Markov chain case. For Kolmogorov diffusions, the theory started with Mandl's paper [25] and was then developed by many authors, see in particular [9], [26], [34].

## 2.2 Our framework - Definitions

In the following, we will exclusively concentrate on population dynamics. Individuals can reproduce or die, and the size  $(Z_t, t \geq 0)$  of the population will be modelled by a Markov process in continuous time and taking values in  $\mathbb{N}$  or in  $\mathbb{R}_+$ . If the population is isolated, namely if there is no immigration, then the state 0, which describes the extinction of the population, is a trap. Indeed, if there are no more individuals, no reproduction can occur and the specie disappears. Thus if the system reaches 0, it stays there forever, that is, if  $Z_t = 0$  for some  $t$ , then  $Z_s = 0$  for any  $s \geq t$ .

We denote by  $T_0$  the (extinction) stopping time

$$T_0 = \inf\{t > 0, Z_t = 0\}. \quad (2.5)$$

We assume that the process goes almost surely to extinction, whatever the initial state is, namely, for all  $z \in E$ ,

$$\mathbb{P}_z(T_0 < \infty) = 1. \quad (2.6)$$

Before being extinct, the process takes its values in the space

$$E^* = E \setminus \{0\}. \quad (2.7)$$

Any long time distribution of the process conditioning on non-extinction will be supported by  $E^*$ .

### Notation:

1) for a probability measure  $\mu$ , we will denote as usual

$$\mathbb{P}_\mu = \int_E \mathbb{P}_z \mu(dz).$$

2) Let us denote by  $\mathcal{P}^*$  the set of probability measures on  $E^*$ .

3)  $C([0, T], E)$  will denote the space of continuous functions from  $[0, T]$  into  $E$ .

Let us now introduce rigorously our framework.

**Definition 2.1** 1) A probability measure  $\alpha$  on  $E^*$  is a quasi-stationary distribution (QSD) if and only if for all Borel set  $A \subseteq E^*$ , for all  $t > 0$ ,

$$\mathbb{P}_\alpha(Z_t \in A | T_0 > t) = \alpha(A). \quad (2.8)$$

Remark that  $\alpha$  is thus a fixed point for the conditional evolution from  $\mathcal{P}^*$  into itself:

$$\nu \rightarrow \mu_t(\nu) = \mathbb{P}_\nu(Z_t \in A | T_0 > t).$$

2) A quasi-limiting distribution (QLD) for  $\mu \in \mathcal{P}^*$  is a probability measure  $\nu$  on  $\mathcal{P}^*$ , such that

$$\lim_{t \rightarrow \infty} \mathbb{P}_\mu(Z_t \in A | T_0 > t) = \nu(A),$$

for any  $t > 0$  and  $A \subseteq E^*$ .

3) The Yaglom limit is the probability measure  $\pi$  on  $\mathcal{P}^*$  defined as

$$\pi(A) = \lim_{t \rightarrow 0} \mathbb{P}_z(Z_t \in A | T_0 > t), \quad (2.9)$$

for any  $t > 0$ ,  $A \subseteq E^*$  and  $z > 0$ , provided that this limit exists and is independent of  $z \in E^*$ .

4) The distribution  $Q_z$  is the law of the process  $Z$  issued from  $z$  and conditioned to never attain 0. When it exists, it is defined as follows: for  $s \geq 0$  and for any Borel set  $B \subset C([0, s], E)$ ,

$$Q_z(Z \in B) = \lim_{t \rightarrow 0} \mathbb{P}_z(Z \in B | T_0 > t). \quad (2.10)$$

This limit procedure defines the law of a diffusion that never reaches 0 called the  $Q$ -process.

## 2.3 First Properties

1 - Survival decay.

**Theorem 2.2** Let us consider a Markov process  $Z$ , with absorbing point  $\{0\}$  satisfying (2.6). Assume that  $\alpha$  is a QSD for the process.

Then there exists a positive real number  $\theta(\alpha)$  depending on the QSD such that

$$\mathbb{P}_\alpha(T_0 > t) = e^{-\theta(\alpha)t}. \quad (2.11)$$

This theorem shows us that starting from a QSD, the extinction time has an exponential distribution. The **extinction rate of survival**  $\theta(\alpha)$  is thus given by

$$\theta(\alpha) = -\frac{\ln \mathbb{P}_\alpha(T_0 > t)}{t},$$

which is independent of  $t$ .

**Proof** By the Markov property, we have

$$\begin{aligned}
\mathbb{P}_\alpha(T_0 > t + s) &= \int_{E^*} \mathbb{E}_z(\mathbf{1}_{T_0 > t} \mathbb{E}_z(\mathbf{1}_{T_0 > t+s} | \mathcal{F}_t)) \alpha(dz) \\
&= \int_{E^*} \mathbb{E}_z(\mathbf{1}_{T_0 > t} \mathbb{E}_{Z_t}(\mathbf{1}_{T_0 > s})) \alpha(dz) \\
&= \mathbb{E}_\alpha(\mathbf{1}_{T_0 > t} f(Z_t)),
\end{aligned}$$

where  $f(z) = \mathbb{E}_z(\mathbf{1}_{T_0 > s})$ .

In addition, by definition of a QSD, we get for any Borel bounded function  $f$  defined on  $E^*$ ,

$$\mathbb{E}_\alpha(f(Z_t) \mathbf{1}_{T_0 > t}) = \int_{E^*} f(z) \alpha(dz) \mathbb{P}_\alpha(T_0 > t),$$

from which we deduce that

$$\mathbb{P}_\alpha(T_0 > t + s) = \int_{E^*} f(z) \alpha(dz) \mathbb{P}_\alpha(T_0 > t).$$

But

$$\int_{E^*} f(z) \alpha(dz) = \int_{E^*} \mathbb{E}_z(T_0 > s) \alpha(dz) = \mathbb{P}_\alpha(T_0 > s).$$

Hence we obtain that for all  $s, t > 0$ ,

$$\mathbb{P}_\alpha(T_0 > t + s) = \mathbb{P}_\alpha(T_0 > s) \mathbb{P}_\alpha(T_0 > t).$$

Let us denote  $g(t) = \mathbb{P}_\alpha(T_0 > t)$ . The Borel function  $g$  is non-increasing. Because of (2.6) and since  $Z$  is non zero, it takes values in  $[0, 1]$  and tends to 0 as  $t$  tends to infinity. An elementary proof allows us to conclude that there exists a real number  $\theta(\alpha) > 0$  such that

$$\mathbb{P}_\alpha(T_0 > t) = e^{-\theta(\alpha)t}.$$

□

## 2- QSD and exponential moments

The existence of QSD is mainly related to the existence of exponential moments for the process  $Z$ .

**Proposition 2.3** *A necessary condition to obtain that  $\alpha$  is a QSD is that for any  $0 < \gamma < \theta(\alpha)$ , there exists  $z > 0$ , such that*

$$\mathbb{E}_z(e^{\gamma T_0}) < +\infty. \tag{2.12}$$

**Proof** From (2.11), we deduce that

$$\int_{E^*} \mathbb{P}_z(T_0 > t) \alpha(dz) \leq e^{-\theta(\alpha)t}. \tag{2.13}$$

In another way, a simple computation shows that for all  $\gamma > 0$ ,

$$\begin{aligned}\mathbb{E}_z(e^{\gamma T_0}) &= \mathbb{E}_z\left(\int_0^{T_0} \gamma e^{\gamma u} du + 1\right) \\ &= 1 + \int_{\mathbb{R}_+} \mathbb{P}_z(T_0 \geq u) \gamma e^{\gamma u} du.\end{aligned}$$

Since  $\gamma < \theta(\alpha)$  and using (2.13), the integral  $\int_{E^*} \mathbb{E}_z(e^{\gamma T_0}) \alpha(dz)$  is finite, and so is  $\mathbb{E}_z(e^{\gamma T_0})$  for at least one  $z > 0$ . The proposition is proved.  $\square$

### 3 - QSD and Yaglom limit.

These notions, although they are close, are not identical. In the next proposition, we will see the Yaglom limit is a QSD. The converse is not true in general, and they are processes with an infinity of QSD, although the Yaglom limit is uniquely defined. We will see below that in some cases we will be interested in, corresponding to logistic (density dependent) population processes, there is a unique QSD which is equal to the Yaglom limit.

Let us show the

**Proposition 2.4** *Assume that the Yaglom limit of the process  $Z$  exists and is equal to the probability measure  $\pi$  on  $E^*$ , then it is also a QSD.*

**Proof** By hypothesis, there exists a probability measure  $\mu$  on  $E^*$  (a Dirac measure) such that

$$\pi(\cdot) = \lim_{t \rightarrow \infty} \mathbb{P}_\mu(Z_t \in \cdot | T_0 > t).$$

Thus, for all measurable and bounded function  $f$  on  $E^*$ ,

$$\begin{aligned}\lim_{t \rightarrow \infty} \mathbb{P}_\mu(f(Z_t) | T_0 > t) &= \lim_{t \rightarrow \infty} \frac{\mathbb{P}_\mu(f(Z_t); T_0 > t)}{\mathbb{P}_\mu(T_0 > t)} \\ &= \int_{E^*} f(z) \pi(dz).\end{aligned}$$

Applying the latter with  $f(z) = \mathbb{P}_z(T_0 > s)$ , we get by Markov property

$$\lim_{t \rightarrow \infty} \frac{\mathbb{P}_\mu(T_0 > t + s)}{\mathbb{P}_\mu(T_0 > t)} = \mathbb{P}_\pi(T_0 > s).$$

Let us denote by  $g(s)$  this last quantity. We can show that  $g$  is bounded, nonzero, non-increasing and satisfies  $g(s + s') = g(s)g(s')$ . Indeed, if we define  $(f_{s'}(z) = \mathbb{E}_z(T_0 > s')$ ,

$$\begin{aligned}g(s + s') &= \lim_{t \rightarrow \infty} \frac{\mathbb{E}_\mu(T_0 > t + s, f_{s'}(Z_{t+s}))}{\mathbb{P}_\mu(T_0 > t + s)} \frac{\mathbb{P}_\mu(T_0 > t + s)}{\mathbb{P}_\mu(T_0 > t)} \\ &= \mathbb{P}_\pi(T_0 > s') \lim_{t \rightarrow \infty} \frac{\mathbb{P}_\mu(T_0 > t + s)}{\mathbb{P}_\mu(T_0 > t)} \\ &= \mathbb{P}_\pi(T_0 > s') \mathbb{P}_\pi(T_0 > s).\end{aligned}$$

Thus there exists  $0 < a < \infty$  such that  $g(s) = \mathbb{P}_\pi(T_0 > s) = e^{-as}$ . Let us now consider  $f(z) = \mathbb{P}_z(Z_s \in A, T_0 > s)$ , with  $A \subset E^*$ . By the Markov property, we can show that

$$\begin{aligned} \mathbb{P}_\pi(Z_s \in A; T_0 > s) &= \lim_{t \rightarrow \infty} \frac{\mathbb{P}_\mu(Z_{t+s} \in A; T_0 > t+s)}{\mathbb{P}_\mu(T_0 > t)} \\ &= \lim_{t \rightarrow \infty} \frac{\mathbb{P}_\mu(Z_{t+s} \in A; T_0 > t+s)}{\mathbb{P}_\mu(T_0 > t+s)} \frac{\mathbb{P}_\mu(T_0 > t+s)}{\mathbb{P}_\mu(T_0 > t)}. \end{aligned}$$

The term  $\frac{\mathbb{P}_\mu(T_0 > t+s)}{\mathbb{P}_\mu(T_0 > t)}$  tends to  $e^{-as}$  when  $t$  tends to infinity as showed in the first part of the proof. The term  $\frac{\mathbb{P}_\mu(Z_{t+s} \in A; T_0 > t+s)}{\mathbb{P}_\mu(T_0 > t+s)}$  tends to  $\pi(A)$  by definition. Thus, we have proved that for any Borel set  $A$  of  $E^*$ , and any  $s > 0$ ,

$$\pi(A) = \mathbb{P}_\pi(Z_s \in A | T_0 > s).$$

The probability measure  $\pi$  is then a QSD.  $\square$

## 2.4 A spectral point of view

Let us denote by  $(P_t)$  the semi-group of the process  $Z$  killed at 0. More precisely, for any  $z > 0$  and  $f$  measurable and bounded on  $\mathbb{R}_+^*$ , one defines

$$P_t f(z) = \mathbb{E}_z(f(Z_t) \mathbf{1}_{t < T_0}). \quad (2.14)$$

As defined above, a QSD  $\alpha$  is a probability measure on  $E^*$  such that for every Borel set  $A \subseteq E^*$ ,

$$\begin{aligned} \alpha(A) &= \frac{\mathbb{P}_\alpha(Z_t \in A; T > t)}{\mathbb{P}_\alpha(T_0 > t)} = \frac{\int_{E^*} P_t(\mathbf{1}_A)(z) \alpha(dz)}{\int_{E^*} P_t(\mathbf{1})(z) \alpha(dz)} \\ &= \frac{P_t^* \alpha(\mathbf{1}_A)}{P_t^* \alpha(\mathbf{1})}, \end{aligned}$$

where  $P_t^* \alpha$  is the measure on  $\mathbb{R}_+^*$  defined for  $f$  measurable and bounded by

$$P_t^* \alpha(f) = \int_{E^*} P_t f(z) \alpha(dz).$$

But we have seen in Theorem 2.11 that there exists  $\theta > 0$  such that for each  $t > 0$ ,

$$\mathbb{P}_\alpha(T_0 > t) = e^{-\theta t}.$$

Then, for every Borel set  $A \subseteq E^*$ , we get

$$\int_{E^*} P_t(\mathbf{1}_A)(z) \alpha(dz) = P_t^* \alpha(\mathbf{1}_A) = e^{-\theta t} \alpha(A). \quad (2.15)$$

Thus the probability measure  $\alpha$  is an eigenvector for the operator  $P_t^*$  (defined on the signed measure vector space), associated with the eigenvalue  $e^{-\theta t}$ .

To fix ideas, let us assume that  $E$  is finite and let us consider the generator  $Q^*$  associated with the semi-group  $(P_t^*)$ . Recall that  $P_t^* = e^{Q^* t}$ . The generator  $Q$  is given by a matrix  $Q = ((q_{ij}))$  and  $Q^*$  is the adjoint matrix given by  $q_{ij}^* = q_{ji}$ . It is easy to show that



**Proposition 2.5** *Any eigenvalue of  $P_t^*$  writes  $e^{\lambda t}$ , where  $\lambda$  is an eigenvalue of  $Q^*$  and conversely. Moreover, for any eigenvalue  $\lambda$  of  $Q^*$  and any associated eigenvector  $\alpha$ , one has*

$$\alpha Q = \lambda \alpha \Leftrightarrow Q^* \alpha = \lambda \alpha \Leftrightarrow P_t^* \alpha = e^{\lambda t} \alpha \Leftrightarrow \alpha P_t = e^{\lambda t} \alpha.$$

Thus  $\alpha$  is a right eigenvector of  $Q^*$ , (resp.  $P_t^*$ ) and a left eigenvector of  $Q$ , (resp.  $P_t$ ). We will show in the next section that this property characterizes the QSD in this finite space case.

**Main Remark:** In the general case, the proof of the existence of a QSD will often firstly consists in proving the existence of a positive number  $\theta$  and of a probability measure  $\alpha$  on  $E^*$  such that

$$L^* \alpha = -\theta \alpha,$$

where  $L^*$  is the dual of the generator  $L$  of the killed process with values in  $E^*$ . Therefore, the first step in proving the existence of a QSD usually consists in studying the spectral properties of  $L^*$ .

### 3 QSD in the finite case

Let us now detail the case of a finite state space  $E$ . For this part, we may refer to Darroch and Seneta ([10] and [11]).

Let  $X$  be a Markov process with values in a finite space  $E$ . We assume that 0 is an absorbing point that is attained almost surely. Let  $P_t$  be the semi-group of the process killed at 0 and  $Q$  the associated generator. The operators  $Q$  and  $P_t$  are matrices and a probability measure on the finite space  $E^*$  is thus a vector of non-negative entries whose sum is equal to 1. Taking  $A = \{i\}$  in (6.5), we obtain that

$$P_t^* \alpha(i) = e^{-\theta t} \alpha_i.$$

Then the QSD  $\alpha$  is an eigenvector with positive entries for the operator  $P_t^*$  associated with the eigenvalue  $e^{-\theta t}$ .

In this matrix framework, the Perron-Frobenius Theorem gives a complete description of the spectral properties of  $P_1$  (or  $P_t$ ) and brings us a complete answer to the research of quasi-stationary distributions. The main point is that the matrix  $P_1$  has non-negative entries. For the proof, we refer to Gantmacher [?] or Serre [?]. Let us

**Theorem 3.1** (*Perron-Frobenius Theorem*). *Let us assume that there exists  $n_0 \in \mathbb{N} \setminus \{0\}$  such that the entries of  $P_1^{n_0}$  are positive. This is equivalent to the fact that the  $\mathbb{R}_+$ -valued process with semi-group  $P_t$  is irreducible and aperiodic. Thus, there exists a unique positive eigenvalue  $\rho$ , which is equal to the maximum of the modulus of the eigenvalues, and there exists a unique left eigenvector  $\alpha$  such that  $\alpha_i > 0$  ;  $\sum_i \alpha_i = 1$ , and there exists a unique right eigenvector  $\pi$  such that  $\pi_i > 0$  ;  $\sum_i \alpha_i \pi_i = 1$ , satisfying*

$$\alpha P_1 = \rho P_1 ; P_1 \pi = \rho \pi.$$

In addition, since  $(P_t)$  is a sub-Markovian semi-group, thus  $\rho < 1$  and there exists  $\theta > 0$  such that  $\rho = e^{-\theta}$ . Therefore,

$$P_t = e^{-\theta t} A + \vartheta(e^{\chi t}), \quad (3.1)$$

where  $A$  is the matrix defined by  $A_{ij} = \pi_i \alpha_j$ , and  $\chi < -\theta$  and  $\vartheta(e^{\chi t})$  denotes a matrix such that none of the entries exceeds  $C^{te} e^{\chi t}$ , for some constant  $C^{te}$ .

Let us remember that in this finite framework, a left eigenvector of  $P_t$  is a right eigenvector of  $P_t^*$  (easy computation) and thus a right eigenvector of  $Q^*$ , associated with the eigenvalue  $-\theta$ .

Now we can state our main theorem.

**Theorem 3.2** *Assume that  $E$  is finite and that the semi-groupe  $(P_t)$  of the killed process (defined on  $E^*$ ) corresponds to an irreducible and aperiodic process.*

1) *There exists a unique QSD obtained as the unique eigenvector  $\alpha$  of  $Q^*$  satisfying*

$$\alpha_i > 0 ; \sum_i \alpha_i = 1.$$

*The corresponding eigenvalue  $-\theta$ ,  $\theta > 0$  is such that*

$$\mathbb{P}_\alpha(T_0 > t) = e^{-\theta t}.$$

2) *The measure  $\alpha$  is the Yaglom limit. For any  $i, j \in E^*$ ,  $\lim_{t \rightarrow \infty} \mathbb{P}_i(X_t = j | T_0 > t) = \alpha_j$ .*

3) *For any  $i, j \in E^*$ ,  $\lim_{t \rightarrow \infty} e^{\theta t} \mathbb{P}_i(X_t = j) = \pi_i \alpha_j$ .*

4) *For any  $i, j \in E^*$ ,  $s, t > 0$   $\lim_{t \rightarrow \infty} \frac{\mathbb{P}_i(T_0 > t+s)}{\mathbb{P}_j(T_0 > t)} = \frac{\pi_i}{\pi_j} e^{-\theta s}$ .*

**Proof** 1) The first part of the theorem is an immediate application of the Perron-Frobenius theorem. Remark that  $\alpha$  is the unique eigenvector of  $Q^*$ , associated with  $\ln \rho = -\theta$ , with  $\theta > 0$ . It is a QSD for the process and the convergence rate to extinction is given by  $\theta$ . If there is another QSD, then by (3.1), its convergence rate is also  $-\theta$ , and by uniqueness of the associated eigenvector, it is equal to  $\alpha$ .

2) Taking the  $i$ -th coordinate in (3.1), we get that  $\mathbb{P}_i(T_0 > t) = e^{-\theta t} \pi_i + \vartheta(e^{\chi t})$ , and then

$$\lim_{t \rightarrow \infty} \mathbb{P}_i(T_0 > t) e^{\theta t} = \pi_i. \quad (3.2)$$

Again from (3.1), it follows that

$$\mathbb{P}_i(X_t = j | T_0 > t) = \frac{\mathbb{P}_i(X_t = j)}{\mathbb{P}_i(T_0 > t)} \xrightarrow{t \rightarrow \infty} \alpha_j.$$

Thus there is a Yaglom limit equal to  $\alpha$  which is a QSD, by Proposition (2.4).

3) It is immediate that  $\lim_{t \rightarrow \infty} e^{\theta t} \mathbb{P}_i(X_t = j) = \lim_{t \rightarrow \infty} e^{\theta t} P_{ij}(t) = \pi_i \alpha_j$ .

4) This is an immediate consequence of (3.2). □

Let us now study the  $Q$ -process.

**Theorem 3.3** For any  $i_0, i_1, \dots, i_k \in E^*$ , any  $0 < s_1 < \dots, s_k < t$ , the limit  $\lim_{t \rightarrow \infty} \mathbb{P}_{i_0}(X_{s_1} = i_1, \dots, X_{s_k} = i_k | T_0 > t)$ , exists.

Let  $(Y_t, t \geq 0)$  be the process starting from  $i_0 \in E^*$  and defined by its finite dimensional distributions

$$\mathbb{P}_{i_0}(Y_{s_1} = i_1, \dots, Y_{s_k} = i_k) = \lim_{t \rightarrow \infty} \mathbb{P}_{i_0}(X_{s_1} = i_1, \dots, X_{s_k} = i_k | T_0 > t). \quad (3.3)$$

Then  $Y$  is a Markov process with values in  $E^*$  and transition probabilities given by

$$\mathbb{P}_{i_0}(Y_s = j) e^{\theta s} \frac{\pi_i}{\pi_j} P_{ij}(s).$$

It is conservative, and has a unique stationary probability measure  $(\alpha_j \pi_j)_j$ .

**Proof** Let  $i_0, i_1, \dots, i_k \in E^*$  and  $0 < s_1 < \dots < s_k < t$ . Let us introduce the filtration  $\mathcal{F}_s = \sigma(X_u, u \leq s)$ . Then

$$\begin{aligned} \mathbb{P}_{i_0}(X_{s_1} = i_1, \dots, X_{s_k} = i_k ; T_0 > t) &= \mathbb{P}_{i_0}(X_{s_1} = i_1, \dots, X_{s_k} = i_k ; \mathbb{E}(T_0 > t | \mathcal{F}_{s_k})) \\ &= \mathbb{P}_{i_0}(X_{s_1} = i_1, \dots, X_{s_k} = i_k ; \mathbb{E}_{i_k}(T_0 > t - s_k)) \\ &\quad (\text{ by Markov property}). \end{aligned}$$

Thus

$$\begin{aligned} \lim_{t \rightarrow \infty} \mathbb{P}_{i_0}(X_{s_1} = i_1, \dots, X_{s_k} = i_k | T_0 > t) &= \mathbb{P}_{i_0}(X_{s_1} = i_1, \dots, X_{s_k} = i_k) \lim_{t \rightarrow \infty} \frac{\mathbb{P}_{i_k}(T_0 > t - s_k)}{\mathbb{P}_{i_0}(T_0 > t)} \\ &= \mathbb{P}_{i_0}(X_{s_1} = i_1, \dots, X_{s_k} = i_k) \frac{\pi_{i_k}}{\pi_{i_0}} e^{\theta s_k}, \end{aligned}$$

by using Theorem 3.2 (4). Let us now show that  $Y$  is a Markov process. We have

$$\begin{aligned} \mathbb{P}_{i_0}(Y_{s_1} = i_1, \dots, Y_{s_k} = i_k, Y_t = j) &= e^{\theta t} \frac{\pi_j}{\pi_{i_0}} \mathbb{P}_{i_0}(X_{s_1} = i_1, \dots, X_{s_k} = i_k, X_t = j) \\ &= e^{\theta(t-s_k)} e^{\theta s_k} \frac{\pi_j}{\pi_{i_k}} \frac{\pi_{i_k}}{\pi_{i_0}} \mathbb{P}_{i_0}(X_{s_1} = i_1, \dots, X_{s_k} = i_k) \mathbb{P}_{i_0}(X_{t-s_k} = j) \\ &\quad (\text{ by Markov property}) \\ &= \mathbb{P}_{i_0}(Y_{s_1} = i_1, \dots, Y_{s_k} = i_k) \mathbb{P}_{i_k}(Y_{t-s_k} = j), \end{aligned}$$

and thus  $\mathbb{P}(Y_t = j | Y_{s_1} = i_1, \dots, Y_{s_k} = i_k) = \mathbb{P}_{i_k}(Y_{t-s_k} = j)$ .

In particular, we obtain that

$$\hat{P}_{ij}(t) = \mathbb{P}_i(Y_t = j) = \frac{\pi_j}{\pi_i} \mathbb{P}_i(X_t = j) e^{\theta t} \rightarrow \frac{\pi_j}{\pi_i} \alpha_j \pi_i = \alpha_j \pi_j.$$

Moreover let us compute the infinitesimal generator  $\hat{Q}$  of  $Y$ . We have for  $j \neq i$ ,

$$\hat{q}_{ij} = \lim_{s \rightarrow 0} \hat{P}_{ij}(s) = \frac{\pi_j}{\pi_i} q_{ij}.$$

For  $j = i$ ,

$$\begin{aligned}\hat{q}_{ii} &= -\lim_{s \rightarrow 0} \frac{1 - \hat{P}_{ii}(s)}{s} = -\lim_{s \rightarrow 0} \frac{1 - e^{\theta s} P_{ii}(s)}{s} \\ &= -\lim_{s \rightarrow 0} \frac{1 - e^{\theta s} + e^{\theta s}(1 - p_{ii}(s))}{s} = \theta + q_{ii}.\end{aligned}$$

Let us finish the proof by showing that the process  $Y$  is conservative.

$$\sum_{j \in E^*} \hat{q}_{ij} = \sum_{j \in E^*} \frac{\pi_j}{\pi_i} q_{ij} + \theta.$$

Since  $Q\pi = -\theta\pi$ , then  $\sum_{j \in E^*} \pi_j q_{ij} = -\theta\pi_i$  and thus  $\sum_{j \in E^*} \hat{q}_{ij} = 0$ .  $\square$

## 4 QSD for birth and death processes

We are describing the dynamics of isolated asexual populations, as for example populations of bacteria with cell binary division, in continuous time. Individuals may reproduce or die, and there is only one child per birth. The population size dynamics will be modelled by a birth and death process in continuous time. The individuals may interact, competing (for example) for resources and therefore the individual rate of death will depend on the total size of the population. We will mainly focus on the logistic case, which models linear density dependence. The death rate per capita (individual death rate) depends linearly on the population size. In this case the process will go almost surely to extinction, and our aim is thus to study the existence (and uniqueness) of quasi-stationary distributions. In a first part, we will recall and partially prove some results on the continuous time birth and death processes, and in a second part, we will study quasi-stationarity.

### 4.1 Birth and Death Processes

**Definition 4.1** *A birth and death process (B-D process), is a  $\mathbb{N}$ -valued pure jump Markov process, whose jump amplitudes are  $+1$  or  $-1$ , with transition rates given by:*

$$i \rightarrow i + 1 \quad \text{with rate} \quad \lambda_i ; \tag{4.1}$$

$$i \rightarrow i - 1 \quad \text{with rate} \quad \mu_i, \tag{4.2}$$

where  $\lambda_i$  and  $\mu_i$ ,  $i \in \mathbb{N}$ , are non-negative real numbers.

Knowing that the process is at state  $i$  at a certain time, the process will wait for an exponential time of parameter  $\lambda_i$  before jumping to  $i + 1$  or independently, will wait for an exponential time of parameter  $\mu_i$  before jumping to  $i - 1$ . The total jump rate for this individual is thus  $\lambda_i + \mu_i$ . We will assume in what follows that  $\lambda_0 = \mu_0 = 0$ . This condition ensures that 0 is an absorbing point, modelling the extinction of the population.

The most standard examples are the following ones.

1) **The Yule process.** For each  $i \in \mathbb{N}$ ,  $\lambda_i = \lambda i$  for a positive real number  $\lambda$ , and  $\mu_i = 0$ . There are no deaths. It's a fission model.

2) **The linear birth and death process, or binary branching process.** There exist positive numbers  $\lambda$  and  $\mu$  such that  $\lambda_i = \lambda i$  and  $\mu_i = \mu i$ . We assume that conditionally to the fact that the population size is equal to  $i$ , the  $i$  individuals reproduce and die independently. In this case, the individual birth rate is constant equal to  $\lambda$  and the individual death rate is equal to  $\mu$ .

3) **The logistic birth and death process.** We assume that every individual in the population has a constant birth rate  $\lambda$ . Moreover the individuals compete to share fixed resources, and each individual  $j \neq i$  creates a selection pressure on individual  $i$  with rate  $c > 0$ . Thus, given that the population size is  $i$  at a certain time, the individual death rate is given by  $c(i - 1)$  and the total death rate is

$$\mu_i = ci(i - 1).$$

Let us come back to the general birth and death processes. We will assume that  $\lambda_i >$  and  $\mu_i > 0$  for any  $i \in \mathbb{N}^*$ .

The process is defined by the sequence  $(\tau_n)_n$  of its jumps, either births or deaths. Let us first see under which conditions under the birth and death rates the process is well defined on  $\mathbb{R}_+$ , i.e.  $\tau = \lim_n \tau_n = +\infty$  a.s. . Indeed, if  $\tau = \lim_n \tau_n < \infty$  with a positive probability, the process would only be defined for  $t < \tau$  on this event. It would have an accumulation of (small) jumps near  $\tau$  and could increase until infinity. There is a necessary and sufficient condition ensuring that a birth and death process does not explode in finite time.

**Theorem 4.2** (*Anderson [2]*) *The life time of the birth and death process is finite if and only if*

$$\sum_{i \geq 1} \left( \frac{1}{\lambda_i} + \frac{\mu_i}{\lambda_i \lambda_{i-1}} + \dots + \frac{\mu_i \cdots \mu_2}{\lambda_i \cdots \lambda_2 \lambda_1} \right) = \infty.$$

The proof of this theorem is very hard and will not be reproduced in these notes. Let us remark that a consequence of Theorem 4.2 is that if the series  $\sum_i \frac{1}{\lambda_i} = +\infty$ , then the process is well defined on  $\mathbb{R}_+$ . There is a direct proof of this fact, that we state now. We remark that the BD-process is stochastically upper-bounded by a Yule process with the same birth rates. Indeed we consider the initial BD-process, and couple it with the Yule process as follows: both processes have the same initial value; at every birth time  $\tau_n$ , both processes jump together of  $+1$ ; at every death time, the BD-process jumps of  $-1$  and the Yule process stays at the same state. Then  $\omega$  by  $\omega$ , the BD-process is smaller than the Yule process, and the difference is a non-decreasing process. Therefore, the existence of the BD-process will be proved as soon as the one for the Yule process is showed.

**Proposition 4.3** *Let us consider a Yule process with birth rates  $(\lambda_i)_i$  and null death rates. Assume that the series*

$$\sum_{i \geq 1} \frac{1}{\lambda_i} = +\infty.$$

*Then the Yule process is well defined on  $\mathbb{R}_+$ .*

**Proof** Let us assume for simplicity that the Yule process starts from 1. Let us denote as before by  $(\tau_n)_n$  the sequence of jumps. Then

$$\tau_n = S_1 + \cdots + S_n,$$

where  $S_i$  is the inter-time between the  $(i-1)$ -th and the  $i$ -th jump. Since the initial condition is 1, the distribution of  $S_i$  is an exponential law with parameter  $\lambda_i$ . Thus,  $\mathbb{E}(S_i) = \frac{1}{\lambda_i}$ . Moreover, easily computation gives that  $\mathbb{E}(e^{-S_i}) = \frac{\lambda_i}{1+\lambda_i}$ .

a) We get

$$\begin{aligned} \sum_{i \geq 1} \frac{1}{\lambda_i} = +\infty &\Leftrightarrow \sum_i \mathbb{E}(S_i) < \infty \Leftrightarrow \mathbb{E}\left(\sum_i S_i\right) < \infty \Leftrightarrow \mathbb{E}(\lim_n \tau_n) < \infty \\ &\Rightarrow \lim \tau_n < \infty \quad \text{almost surely.} \end{aligned}$$

b) Assume that  $\sum_{i \geq 1} \frac{1}{\lambda_i} = +\infty$ . Then by Markov property,

$$\mathbb{E}(e^{-\tau_n}) = \prod_{i=1}^n \mathbb{E}(e^{-S_i}) = \prod_{i=1}^n \frac{\lambda_i}{1+\lambda_i} = \prod_{i=1}^n \left(1 - \frac{1}{1+\lambda_i}\right),$$

which tends to zero as  $n$  tends to infinity, by hypothesis. Thus  $\mathbb{E}(e^{-\tau_n})$  tends to zero and then the sequence  $\tau_n$  tends to infinity almost surely.  $\square$

**Corollary 4.4** *Let us consider a BD-process with birth rates  $(\lambda_i)_i$ . If there exists a constant  $\lambda > 0$  such that*

$$\lambda_i \leq \lambda,$$

*then the process is well defined until infinity.*

The proof is immediate. It turns out that the linear BD-process and the logistic process are well defined on  $\mathbb{R}_+$ .

Let us now study under which assumption the process goes to extinction almost surely.

**Proposition 4.5** *The BD-process goes almost-surely to extinction if and only if*

$$\sum_{k=1}^{\infty} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k} = \infty. \quad (4.3)$$

**Notation:** We will denote for each  $n$

$$\pi_1 = 1 ; \pi_n = \frac{\lambda_1 \cdots \lambda_{n-1}}{\mu_2 \cdots \mu_n}. \quad (4.4)$$

Then, the condition for explosion is given by

$$\sum_{n \geq 1} \frac{1}{\lambda_n \pi_n} = +\infty.$$

**Proof** Let us introduce the quantity

$$u_i := \mathbb{P}(\text{Extinction} | Z_0 = i) = \mathbb{P}_i(T_0 < \infty),$$

which is the probability to attain 0 in finite time, starting from  $i$ . We have denoted as before by  $T_0$  the extinction time. Then, using Markov property and the fact that the jumps have amplitude  $\pm 1$ , we have the induction formula: for each  $i \geq 1$ ,

$$\lambda_i u_{i+1} - (\lambda_i + \mu_i) u_i + \mu_i u_{i-1} = 0.$$

To resolve this equation, we firstly assume that the rates  $\lambda_i, \mu_i$  are nonzero until some fixed level  $I$  such that  $\lambda_I = \mu_I = 0$ . Let us define for each  $i$ ,

$$u_i^{(I)} := \mathbb{P}_i(T_0 < T_I).$$

Thus

$$u_i = \lim_{I \rightarrow \infty} u_i^{(I)}.$$

If we define

$$U_I := \sum_{k=1}^{I-1} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k},$$

an easy computation shows that for  $i \in \{1, \dots, I-1\}$ ,

$$u_i^{(I)} = (1 + U_I)^{-1} \sum_{k=i}^{I-1} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k}.$$

In particular,  $u_1^{(I)} = \frac{U_I}{1+U_I}$ . Hence, if  $(U_I)_I$  tends to infinity when  $I \rightarrow \infty$ , then any extinction probability  $u_i$  is equal to 1. If  $(U_I)_I$  converges to a finite limit  $U_\infty$ , then for  $i \geq 1$ ,

$$u_i = (1 + U_\infty)^{-1} \sum_{k=i}^{\infty} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k},$$

which is strictly less than 1. □

**Corollary 4.6** 1) *The linear BD-process with rates  $\lambda_i$  and  $\mu_i$  goes almost surely to extinction if and only if  $\lambda \leq \mu$ .*

2) *The logistic BD-process goes almost surely to extinction.*

**Proof** 1) If  $\lambda \leq \mu$ , i.e. when the process is sub-critical or critical, it is easy to show that the sequence  $(U_I)_I$  tends to infinity when  $I \rightarrow \infty$ . Thus, the process goes to extinction with probability 1. Conversely, if  $\lambda > \mu$ , the sequence  $(U_I)_I$  converges to  $\frac{\mu}{\lambda - \mu}$ , and an easy computation shows that  $u_i = (\lambda/\mu)^i$ .

2) Here we have

$$\lambda_i = \lambda i ; \mu_i = \mu i + ci(i-1). \tag{4.5}$$

It is easy to check that (4.3) is satisfied. □

## 4.2 Quasi-stationary distributions for birth and death processes

Let us now assume that the initial distribution of the process is a measure  $\alpha$  on  $\mathbb{N}^*$ . It is given by a sequence  $(\alpha_i)_{i \geq 1}$  of non-negative numbers such that  $\sum_i \alpha_i = 1$ . Let us consider the functions  $P_j(t)$  defined on  $\mathbb{R}_+^*$  by

$$P_j(t) = \sum_i \alpha_i P_{ij}(t),$$

where  $P_{ij}(t) = \mathbb{P}_i(Z_t = j | t < T_0)$ . Then the sequence  $P_j$  is solution of an infinite system of ordinary differential equations, called the backward Kolmogorov or Fokker-Planck equation (cf. for instance [3]). This equation involves the generator  $Q = (Q_{ij})$  of the killed process. It is given by

$$\begin{aligned} \frac{dP_j}{dt} &= \sum_{i \geq 1} P_i(t) Q_{ij} \\ &= P_{j-1}(t) Q_{j-1,j} + Q_{jj} P_j(t) + P_{j+1}(t) Q_{j+1,j} \\ &= \lambda_{j-1} P_{j-1}(t) - (\lambda_j + \mu_j) P_j(t) + \mu_{j+1} P_{j+1}(t); \\ \frac{dP_0}{dt} &= \mu_1 P_1(t). \end{aligned} \tag{4.6}$$

Let us now write the differential equation for  $q_j(t) = \frac{P_j(t)}{1 - P_0(t)}$ . We have

$$\frac{d}{dt} \left( \frac{P_j(t)}{1 - P_0(t)} \right) = \frac{1}{1 - P_0(t)} \frac{dP_j(t)}{dt} + P_j(t) \frac{dP_0(t)}{(1 - P_0(t))^2}.$$

Let us now assume that the probability measure  $q$  is a quasi-stationary distribution. Then the function  $\frac{P_j(t)}{1 - P_0(t)}$  does not depend on  $t$ . The equation above is thus equal to 0. Let us then replace  $\frac{dP_j(t)}{dt}$  by its value given in (4.6). We deduce

$$\frac{1}{1 - P_0(t)} (\lambda_{j-1} P_{j-1}(t) - (\lambda_j + \mu_j) P_j(t) + \mu_{j+1} P_{j+1}(t)) + \frac{P_j(t)}{(1 - P_0(t))^2} \mu_1 P_1(t) = 0,$$

which leads for  $j \geq 2$  to

$$\lambda_{j-1} q_{j-1} - (\lambda_j + \mu_j) q_j + \mu_{j+1} q_{j+1} + \mu_1 q_1 q_j = 0.$$

If  $j = 1$  we obtain

$$-(\lambda_1 + \mu_1) q_1 + \mu_2 q_2 + \mu_1 q_1^2 = 0.$$

These equations are in fact a necessary and sufficient condition to be a QSD.

**Theorem 4.7** *The sequence  $(q_j)_{j \geq 1}$  is a QSD if and only if*

1)  $q_j \geq 0$ ,  $\forall j \geq 1$ , and  $\sum_{j \geq 1} q_j = 1$ .

2)  $\forall j \geq 1$ ,

$$\begin{aligned} \lambda_{j-1} q_{j-1} - (\lambda_j + \mu_j) q_j + \mu_{j+1} q_{j+1} &= -\mu_1 q_1 q_j; \\ -(\lambda_1 + \mu_1) q_1 + \mu_2 q_2 &= -\mu_1 q_1^2. \end{aligned} \tag{4.7}$$



Let us remark that Equation (4.7) has the spectral form  $L^*q = -\theta q$ , with  $\theta = \mu_1 q_1$ .

**Proof** We have already proved that if  $q$  is QSD, then it satisfies 1) and 2). Let us now prove the converse.

Let be given a probability measure  $q$  on  $\mathbb{N}^*$  such that 1) and 2) are satisfied. Let us define the function  $t \rightarrow P_0(t)$  as solution of the ordinary differential equation

$$P_0(0) = 0 ; \quad \frac{dP_0(t)}{dt} = q_1 \mu_1 (1 - P_0(t)). \quad (4.8)$$

Then  $P_0(t) = 1 - e^{q_1 \mu_1 t}$ . Now, let us define for  $j \geq 1$  the function  $t \rightarrow P_j(t)$  by

$$P_j(t) = q_j (1 - P_0(t)). \quad (4.9)$$

Thus,

$$\sum_{j \geq 1} P_j(t) = \sum_{j \geq 1} q_j (1 - P_0(t)) = 1 - P_0(t),$$

thanks to 1). Then we obtain that  $\sum_{j \in \mathbb{N}} P_j(t) = 1$  and  $(P_j(t))_{j \geq 0}$  is a probability measure on  $\mathbb{N}$ . It is easy to check, using 2), that it satisfies the Backward Kolmogorov equation. Then there exists a Markov process  $(X_t, t \geq 0)$  on  $\mathbb{N}$ , such that

$$\begin{aligned} \mathbb{P}(X(0) = j) &= P_j(0) = q_j, \quad \forall j \geq 1 \\ \mathbb{P}(X(0) = 0) &= P_0(0) = 0. \end{aligned}$$

The probability measure  $q$  (with  $q_j = \frac{P_j(t)}{1 - P_0(t)}$ ), is by construction a QSD for the process  $X$  and the theorem is proved. Moreover we have for all  $j \geq 1$ ,

$$P_j(t) = q_j (1 - P_0(t)) = q_j e^{-q_1 \mu_1 t}.$$

□

Our aim now is to resolve (or to give an idea) of the resolution of the Equation (4.7) depending on the coefficients  $\lambda_i$  and  $\mu_i$ . (See Van Doorn [12] for details).

Let us define inductively the sequence of polynomials  $(H_n(x))_n$  as follows. We assume that  $H_1(x) = 1$  for all  $x \in \mathbb{R}$  and that

$$\begin{aligned} \text{For } n \geq 2, \quad \lambda_n H_{n+1}(x) &= (\lambda_n + \mu_n - x) H_n(x) - \mu_{n-1} H_{n-1}(x); \\ \lambda_1 H_2(x) &= \lambda_1 + \mu_1 - x. \end{aligned} \quad (4.10)$$

One can show by induction that for any  $n \geq 2$ , the polynomial  $H_n$  has  $n-1$  positive distinct zeros. Let us denote by  $x_{n_1}$  the smallest one. One can also prove that the sequence  $(x_{n_1})_n$  is decreasing and we denote

$$\xi_1 = \lim_{n \rightarrow \infty} x_{n_1}.$$

Thus it can be shown from (4.10) that

$$x \leq \xi_1 \iff H_n(x) > 0, \quad \forall n \geq 1.$$

**Proposition 4.8** *Recall that the sequence  $(\pi_n)_n$  is defined in (4.4). Any quasi-stationary distribution  $(q_j)_j$  satisfies for all  $j \geq 1$ ,*

$$q_j = q_1 \pi_j H_j(\mu_1 q_1).$$

**Proof** From 4.7 and 4.10, we get  $\lambda_1 H_2(x) = \lambda_1 + \mu_1 - x$  and

$$q_2 \mu_2 = (\lambda_1 + \mu_1 - q_1 \mu_1) q_1 = \lambda_1 H_2(q_1 \mu_1) q_1,$$

which leads to

$$q_2 = \frac{\lambda_1}{\mu_2} q_1 H_2(\mu_1 q_1) = \pi_2 q_1 H_2(\mu_1 q_1).$$

We thus proceed by induction to conclude. □

A main consequence is that since for any  $j$ ,  $q_j \geq 0$  and  $q_j > 0$  for at least one  $j$ , thus

$$H_j(\mu_1 q_1) \geq 0 \quad \forall j \geq 1 \iff 0 < \mu_1 q_1 \leq \xi_1.$$

We can immediately deduce from this property that if  $\xi_1 = 0$ , then there is no quasi-stationary distribution. In fact we may state now a complete description of the existence (or not) of QSD depending on the behavior of the coefficients. This theorem is proved in Van Doorn [12]. We introduce a series  $(S)$  which plays a crucial role, with general term  $S_n = \frac{1}{\lambda_n \pi_n} \sum_{i=n+1}^{\infty} \pi_i$ .

**Theorem 4.9** *1) We have*

$$\sum_{n=1}^{\infty} \frac{1}{\lambda_n \pi_n} \sum_{i=n+1}^{\infty} \pi_i \quad CV \iff \sum_{n=1}^{\infty} \pi_n \left( \frac{1}{\mu_1} + \sum_{i=1}^{n-1} \frac{1}{\lambda_i \pi_i} \right) \quad CV.$$

*2) If  $(S)$  diverges then*

- *If  $\xi_1 = 0$ , we have no QSD.*
- *If  $\xi_1 > 0$ , there is an infinity of QSD, given by the one parameter family*

$$\hat{q}_j(x) = \frac{1}{\mu_1} \pi_j x H_j(x),$$

*for  $0 < x \leq \xi_1$  (and  $\mu_1 q_1 = x$ ).*

*3) If  $(S)$  converges then  $\xi_1 > 0$  and there is a unique QSD defined for any  $j \geq 1$  by*

$$q_j = \frac{1}{\mu_1} \pi_j \xi_1 H_j(\xi_1).$$

Moreover, we can also describe the Yaglom's limit.

**Theorem 4.10** (cf. [12]) *If  $\xi_1 = 0$ , then*

$$\lim_{t \rightarrow \infty} \mathbb{P}_i(Z_t = j | T_0 > t) = 0.$$

2) *If  $\xi_1 > 0$ , then*

$$\lim_{t \rightarrow \infty} \mathbb{P}_i(Z_t = j | T_0 > t) = \frac{1}{\mu_1} \pi_j \xi_1 H_j(\xi_1).$$

The proof uses the spectral representation of the semi-group  $P_{ij}(t)$ . In fact the sequence  $(H_n)_n$  is a sequence of orthogonal polynomials with respect to the spectral measure.

The convergence of the series (S) thus characterizes the existence and uniqueness of the QSD, which is equal to the Yaglom's limit.

Let us now develop some examples.

**The linear case.** We assume  $\lambda_n = \lambda n$ ;  $\mu_n = \mu n$  and  $\lambda \leq \mu$ . An easy computation yields  $\xi_1 = \mu - \lambda$  and

$$\pi_n = \frac{\lambda^{n-1}}{\mu} \frac{1}{n},$$

and that the series (S) diverges. For  $\lambda < \mu$ ,  $\xi_1 > 0$  and there is an infinity of QSD. If  $\lambda = \mu$ ,  $\xi_1 = 0$  and there is no QSD.

**The logistic case.** We assume  $\lambda_n = \lambda n$ ;  $\mu_n = \mu n + cn(n-1)$ . We have

$$\begin{aligned} \sum_{i=n+1}^{\infty} \pi_i &\leq \sum_{i=n+1}^{\infty} \left(\frac{\lambda}{c}\right)^{i-1} \frac{1}{i!} = \sum_{p=0}^{\infty} \left(\frac{\lambda}{c}\right)^{n+p} \frac{1}{(n+p+1)!} \\ &\leq \left(\frac{\lambda}{c}\right)^n \frac{1}{(n+1)!} \sum_{p=0}^{\infty} \left(\frac{\lambda}{c}\right)^p \frac{1}{(p)!} = \left(\frac{\lambda}{c}\right)^n \frac{1}{(n+1)!} e^{\frac{\lambda}{c}}, \end{aligned}$$

since  $\frac{(n+1)!}{(n+p+1)!} \leq \frac{1}{p!}$ . Thus as  $\frac{1}{\pi_n} \leq Cte \left(\frac{c}{\lambda}\right)^{n-1} n!$ , we get

$$\frac{1}{\lambda_n \pi_n} \sum_{i=n+1}^{\infty} \lambda_i \pi_i \leq \frac{Cte}{c} \frac{1}{n(n+1)} e^{\frac{\lambda}{c}}.$$

Hence the series converges. In the logistic case, there exists a unique quasi-stationary distribution.

## 5 The logistic Feller diffusion process

### 5.1 A large population model

We are now considering a logistic birth and death process with a large population assumption. The way we model this hypothesis is the following one. We introduce a parameter  $K$  which will scale the population size, in the sense that we assume

$$Z_0^K = KX_0 \quad \text{with} \quad \mathbb{E}(X_0^3) < +\infty,$$

and  $K$  will tend to infinity. As  $K$  increases, the birth and death process issued from  $Z_0^K$  will jump more and more times with smaller and smaller jumps and it is suitable to obtain more tractable approximations.

Since we only have a finite number of jumps in a finite time interval, then for any time  $t$ ,  $Z_t^K$  will be of order  $K$ . Then we are led to study the asymptotic behavior of the re-scaled process  $(X_t^K, t \geq 0)$ , defined by

$$X_t^K = \frac{1}{K} Z_t^K \in \frac{\mathbb{N}}{K}.$$

The transitions of this process are the following ones:

$$\begin{aligned} \frac{i}{K} &\rightarrow \frac{i+1}{K} && \text{with rate } \lambda i = \lambda K \frac{i}{K}; \\ \frac{i}{K} &\rightarrow \frac{i-1}{K} && \text{with rate } \mu i + \frac{c}{K} i(i-1) = K \frac{i}{K} \left( \mu + c \left( \frac{i}{K} - \frac{1}{K} \right) \right). \end{aligned}$$

We assume in the following that  $\lambda > \mu$ .

**Remark 5.1** *Let us remark that the individual competition rate is assumed to be  $\frac{c}{K}$ . Indeed, since the total amount of resources is fixed, population increasing makes decrease the individual resources and thus the biomass of each individual.*

The pure jump Markov process  $(X_t^K, t \geq 0)$  defined by the transitions above is well defined. Its infinitesimal generator is given, for any measurable and bounded function  $\phi$ , by

$$L_K \phi(x) = \left( \phi\left(x + \frac{1}{K}\right) - \phi(x) \right) \lambda K x \tag{5.1}$$

$$+ \left( \phi\left(x - \frac{1}{K}\right) - \phi(x) \right) K(\mu x + cx(x-1)). \tag{5.2}$$

Hence, we deduce by Dynkin's theorem that

$$\phi(X_t^K) - \phi(X_0^K) - \int_0^t L_K \phi(X_s^K) ds \tag{5.3}$$

is a local martingale, and a martingale, as soon as each term in (5.3) is integrable. In particular, taking  $\phi(x) = x$ , one gets that  $(X_t^K, t \geq 0)$  is a semimartingale and that

$$X_t^K = X_0^K + M_t^K + \int_0^t X_s^K (\lambda - \mu - c \left( X_s^K - \frac{1}{K} \right)) ds. \tag{5.4}$$

Assuming that  $\mathbb{E}(X_0^2) < \infty$ , and with a localization argument, we deduce that  $\mathbb{E}(\sup_{t \leq T} (X_t^K)^2) < \infty$ . Moreover, taking  $\phi(x) = x^2$  applied to (5.3), and comparing with Itô's formula for the square of  $X_t^K$ , we deduce that  $(M^K)$  is a square-integrable martingale and that

$$\langle M^K \rangle_t = \frac{1}{K} \int_0^t (\lambda + \mu + c \left( X_s^K - \frac{1}{K} \right)) X_s^K ds. \tag{5.5}$$

**Theorem 5.2** *Assume that  $X_0 = x_0$ . The process  $(X_t^K, t \geq 0)$  converges in law in  $\mathbb{D}([0, T], \mathbb{R}_+)$  to the unique continuous (in time) deterministic function solution of*

$$x(t) = x_0 + \int_0^t (\lambda - \mu - cx(s))x(s)ds.$$

**Remark 5.3** *The function  $x$  is thus solution of the ordinary differential equation*

$$\dot{x} = (\lambda - \mu)x - cx^2 ; x(0) = x_0, \quad (5.6)$$

*called logistic equation. This equation has been historically the first macroscopic model introduced to describe populations regulated by competition between individuals. In the theorem above, we obtain a microscopic justification. Equation (5.6) has a unique stable equilibrium equal to  $x^* = \frac{\lambda - \mu}{c}$  and called charge capacity. One can easily prove that when  $t$  tends to infinity,  $x(t) \rightarrow x^*$  and the population stabilizes at this state.*

**Proof** The process  $t \rightarrow X_t^K$  is left limited and right-continuous from  $\mathbb{R}_+$  into  $\mathbb{R}_+$ . We want to study the convergence in law of the sequence  $(X^K)$ , when  $K$  tends to infinity. For any  $K$ , the law of  $X^K$  is a probability measure on the trajectory space. We need some topological properties of this space. For each  $T > 0$ , let us denote by  $\mathbb{D}_T = \mathbb{D}([0, T], \mathbb{R}_+)$  the space of left-limited and right-continuous functions from  $[0, T]$  into  $\mathbb{R}_+$ . This space is called the Skorohod space. The main point is to define a topology which makes  $\mathbb{D}_T$  a Polish state, that is a metrizable complete and separable space, which is not true if  $\mathbb{D}_T$  is endowed with the uniform topology. This topology, called Skorohod topology, is equivalent to the uniform topology for continuous functions. If there are jumps, two trajectories will be close if, when one of them is perturbed by a small time deformation, the news trajectories are close in the uniform topology sense. See Billingsley [5] for details.

The proof of convergence is obtained by a compactness-uniqueness argument. The uniqueness of (5.6) is immediate.

By a natural coupling, one may stochastically upperbound the birth and death process  $X^K$  by the Yule process  $Y^K$  issued from  $x_0$ , which jumps from  $x$  to  $x + \frac{1}{K}$ , at the same birth time than  $X^K$ . It is easy to show that  $\sup_K \mathbb{E}(\sup_{t \leq T} (Y_t^K)^3) < \infty$ , thus it turns out that

$$\sup_K \mathbb{E}(\sup_{t \leq T} (X_t^K)^3) < \infty. \quad (5.7)$$

From this uniform estimates, it is not hard to deduce the uniform tightness of the laws of  $X^K$  (as probability measures on  $\mathbb{D}_T$ ), using the Aldous criterion (cf. Aldous [1]). By Prokhorov's theorem, the compactness of the laws of  $(X^K)$  is thus proved. To get an intuition of the limit, we can firstly remark that

$$\sup_{t \leq T} |X_t^K - X_{t-}^K| \leq \frac{1}{K}.$$

Since the function  $x \mapsto \sup_{t \leq T} |x_t - x_{t-}|$  is continuous on  $\mathbb{D}_T$ , we may conclude that each limit value (in law) of the sequence  $(X^K)$  will be a process with continuous trajectories. In addition using (5.7), we easily show thanks to (5.5) that

$$\lim_{K \rightarrow \infty} \mathbb{E}(\langle M^K \rangle_t) = 0.$$

The random fluctuations disappear when  $K$  tends to infinity. The limit values will be deterministic functions. Now one has to show that they are solutions of (5.6). This identification step will be developed in the proof of Theorem 5.4 stated below.  $\square$

Let us now consider another scaling accelerating births and deaths. The birth rate  $\lambda$  of the process  $X^K$  will be replaced by  $\gamma K + \lambda$ , and the natural death rate  $\mu$  by  $\gamma K + \mu$ ,  $\lambda, \gamma, \mu$  being positive numbers with  $\lambda > \mu$ . The transitions of the process are given by

$$\begin{aligned} \frac{i}{K} &\rightarrow \frac{i+1}{K} && \text{with rate } \gamma K i + \lambda i = K(\gamma K + \lambda) \frac{i}{K}; \\ \frac{i}{K} &\rightarrow \frac{i-1}{K} && \text{with rate } \gamma K i + \mu i + \frac{c}{K} i(i-1) = K \frac{i}{K} \left( \gamma K + \mu + c \left( \frac{i}{K} - \frac{1}{K} \right) \right). \end{aligned} \quad (5.8)$$

Formula (5.4) giving the semi-martingale decomposition of  $X^K$  will stay true with a different martingale part  $N^K$  such that

$$\langle N^K \rangle_t = \frac{1}{K} \int_0^t (2\gamma K + \lambda + \mu + c \left( X_s^K - \frac{1}{K} \right)) X_s^K ds.$$

One immediately observes that a priori, the expectation of this quantity will not tend to zero as  $K$  tends to infinity. Hence the fluctuations will not disappear at infinity and the limit will be random. Let us now state the theorem.

**Theorem 5.4** *Consider the sequence of processes  $(X^K)$  with transitions (5.8) and initial condition  $X_0$  such that  $\mathbb{E}(X_0^3) < \infty$ . It converges in law in  $\mathcal{P}(\mathbb{D}_T)$  to the continuous process  $X$ , defined as unique solution of the stochastic differential equation*

$$dX_t = \sqrt{2\gamma X_t} dB_t + ((\lambda - \mu)X_t - cX_t^2) dt \quad (5.9)$$

issued from  $X_0$ .

When  $c = 0$ , the equation (5.9) is the Feller stochastic differential equation. In the general case where  $c \neq 0$ , it will be called logistic Feller stochastic differential equation following the terminology introduced par Etheridge [13] and Lambert [22]. Let us remark that the solutions will be non-negative, and that 0 will be an absorbing point.

**Remark 5.5** *Theorem 5.4 shows that the acceleration of births and deaths creates stochasticity, called demographic stochasticity.*

**Proof** As in the proof of Theorem 5.2, the proof will be based on a uniqueness-compactness argument.

(1) First step. For the uniqueness, we refer to Ikeda-Watanabe [19] Section IV-3 or to Karatzas-Shreve [21]. Let us recall their results. Let us define more generally a stochastic differential equation

$$dX_t = \sigma(X_t)dB_t + b(X_t)dt,$$

where  $\sigma$  and  $b$  are continuous on  $[0, +\infty)$  and of class  $C^1$  on  $(0, +\infty)$ . There is existence and pathwise uniqueness of the process until the explosion time  $T = T_0 \wedge T_\infty$ , where for each  $x \geq 0$ ,

$$T_x = \inf\{t \in \mathbb{R}_+, X_t = x\}.$$

This, one has to know the behavior of the process near the boundaries. Let us define for  $x > 0$  the function

$$Q(x) = - \int_1^x \frac{2b(y)}{\sigma^2(y)} dy.$$

Let us introduce two scale functions, defined for  $x > 0$  by

$$\Lambda(x) = \int_1^x \exp Q(z) dz ; \quad (5.10)$$

$$\kappa(x) = \int_1^x e^{Q(y)} \left( \int_1^y e^{-Q(z)} dz \right) dy. \quad (5.11)$$

We have

**Theorem 5.6** (cf. [19] Theorem IV-3.2). *The two propositions are equivalent.*

$$(i) \forall x > 0, \mathbb{P}_x(T_0 = T < T_\infty) = \mathbb{P}_x(\lim_{t \rightarrow \infty} X_{T \wedge t} = 0) = 1.$$

$$(ii) \Lambda(+\infty) = \infty ; \kappa(0^+) < +\infty.$$

*In that case, we have pathwise uniqueness of the process, and then uniqueness in law by Yamada's Theorem.*

In our case that, since the coefficients are

$$\sigma(x) = \sqrt{\gamma x} ; b(x) = (\lambda - \mu)x - cx^2,$$

the functions  $\Lambda$  and  $\kappa$  satisfy the assumptions of Theorem 5.6. Thus the existence and pathwise uniqueness of the solution of (5.9) are proved and the process goes to 0 almost surely (that is, extinction almost sure of the population).

(2) Second step. Let us assume that  $\mathbb{E}(X_0^3) < \infty$  and let us show that  $\sup_K \mathbb{E}(\sup_{t \leq T} (X_t^K)^3) < \infty$ . The generator of  $X^K$  is given by

$$\tilde{L}_K \phi(x) = \left( \phi\left(x + \frac{1}{K}\right) - \phi(x) \right) (\gamma Kx + \lambda x) K \quad (5.12)$$

$$+ \left( \phi\left(x - \frac{1}{K}\right) - \phi(x) \right) (\gamma Kx + \mu x + cx\left(x - \frac{1}{K}\right)) K. \quad (5.13)$$

With  $\phi(x) = x^3$ , we obtain that

$$\begin{aligned} (X_t^K)^3 &= X_0^3 + M_t^K + \int_0^t \gamma K^2 X_s^K \left[ \left( X_s^K + \frac{1}{K} \right)^3 - \left( X_s^K - \frac{1}{K} \right)^3 - (X_s^K)^3 \right] ds \\ &+ \int_0^t \lambda K X_s^K \left[ \left( X_s^K + \frac{1}{K} \right)^3 - (X_s^K)^3 \right] ds \\ &+ \int_0^t (\mu + c(X_s^K - 1)) K X_s^K \left[ \left( X_s^K - \frac{1}{K} \right)^3 - (X_s^K)^3 \right] ds, \end{aligned}$$

where  $M^K$  is a martingale. Using that

$$\left(X_s^K + \frac{1}{K}\right)^3 - \left(X_s^K - \frac{1}{K}\right)^3 - (X_s^K)^3 = 6 \frac{X_s^K}{K^2},$$

it is immediate to get

$$\mathbb{E}((X_t^K)^3) \leq \mathbb{E}(X_0^3) + C \int_0^t \mathbb{E}((X_s^K)^3) ds,$$

where  $C$  is independent of  $K$ . By Gronwall's lemma, we deduce that

$$\sup_{t \leq T} \sup_K \mathbb{E}(|X_t^K|^3) < \infty. \quad (5.14)$$

Now, thanks to this result and to Doob's inequality, we may deduce from the semi-martingale decomposition of  $(X_t^K)^2$  (obtained using  $\phi(x) = x^2$ ), that

$$\sup_K \mathbb{E}(\sup_{t \leq T} |X_t^K|^2) < \infty. \quad (5.15)$$

(3) Step 3. The uniform tightness of the laws of  $(X^K)$  is obtained using the Aldous criterion [1], thanks to (5.15). Then the sequence of laws is relatively compact and we have now to characterize its limit values.

(4) Step 4. As in the proof of Theorem 5.2, we remark that the limit values only charge the set of continuous trajectories, since  $\sup_{t \leq T} |\Delta X_t^K| \leq \frac{1}{K}$ . Let  $Q \in \mathcal{P}(C([0, T], \mathbb{R}_+))$  be a limit value of the sequence of laws of the processes  $X^K$ . We want to identify  $Q$  as the (unique) law of the solution of the logistic Feller stochastic differential equation. It will thus be uniquely defined, and the convergence will be proved. Let us denote  $C_T = C([0, T], \mathbb{R}_+)$  and define, for  $\phi \in C_b^2$ , and  $t > 0$  the function

$$\begin{aligned} \psi_t : C_T &\rightarrow \mathbb{R} \\ X &\mapsto \phi(X_t) - \phi(X_0) - \int_0^t (\gamma X_s \phi''(X_s) + ((\lambda - \mu)X_s - cX_s^2) \phi'(X_s)) ds. \end{aligned}$$

Then,  $X \mapsto \psi_t(X)$  is continuous  $Q$ -a.s.. We want to show that if  $X$  is the canonical process on  $C_T$ , then  $(\psi_t(X))_t$  is a  $Q$ -semi-martingale. We know that

$$\psi_t^K(X^K) = \phi(X_t^K) - \phi(X_0) - \int_0^t \tilde{L}_K \phi(X_s^K) ds$$

is a martingale, where  $\tilde{L}_K$  has been defined in (5.12). For  $x \in \mathbb{R}_+$ , we denote

$$L\phi(x) = \gamma x \phi''(x) + ((\lambda - \mu)x - cx^2) \phi'(x).$$

We have

$$\begin{aligned} |\tilde{L}_K \phi(x) - L\phi(x)| &= \gamma K^2 x \left| \phi\left(x + \frac{1}{K}\right) + \phi\left(x - \frac{1}{K}\right) - 2\phi(x) - \frac{1}{K^2} \phi''(x) \right| \\ &\quad + \lambda K x \left| \phi\left(x + \frac{1}{K}\right) - \phi(x) - \frac{1}{K} \phi'(x) \right| \\ &\quad + K (\mu x + cx(x-1)) \left| \phi\left(x - \frac{1}{K}\right) - \phi(x) + \frac{1}{K} \phi'(x) \right|. \end{aligned}$$



Using the Taylor expansion, we immediately deduce that

$$|\tilde{L}_K \phi(x) - L\phi(x)| \leq \frac{C}{K} (x^2 + 1), \quad (5.16)$$

where  $C$  doesn't depend on  $x$  and  $K$ . By (5.15), we deduce that

$$\mathbb{E} \left( |\tilde{L}_K \phi(X_t^K) - L\phi(X_t^K)| \right)$$

tends to 0 as  $K$  tends to infinity.

For  $s_1 < \dots < s_k < s < t$ , for  $g_1, \dots, g_k \in C_b$ , let us introduce the function  $H$  defined by

$$H(X) = g_1(X_{s_1}) \cdots g_k(X_{s_k}) (\psi_t(X) - \psi_s(X)).$$

Our aim is now to show that

$$\mathbb{E}_Q(H(X)) = 0, \quad (5.17)$$

which will imply that  $X$  is a  $Q$ -martingale. Since  $(\psi_t^K(X^K))_t$  is a martingale, we have

$$\mathbb{E} [g_1(X_{s_1}^K) \cdots g_k(X_{s_k}^K) (\psi_t^K(X^K) - \psi_s^K(X^K))] = 0.$$

In another way, this quantity is equal to

$$\begin{aligned} & \mathbb{E} [g_1(X_{s_1}^K) \cdots g_k(X_{s_k}^K) (\psi_t^K(X^K) - \psi_s^K(X^K) - \psi_t(X^K) + \psi_s(X^K))] \\ & + \mathbb{E} [g_1(X_{s_1}^K) \cdots g_k(X_{s_k}^K) (\psi_t(X^K) - \psi_s(X^K)) - g_1(X_{s_1}) \cdots g_k(X_{s_k}) (\psi_t(X) - \psi_s(X))] \\ & + \mathbb{E} [g_1(X_{s_1}) \cdots g_k(X_{s_k}) (\psi_t(X) - \psi_s(X))]. \end{aligned}$$

The first term is equal to

$$\mathbb{E} \left[ g_1(X_{s_1}^K) \cdots g_k(X_{s_k}^K) \int_0^t (\tilde{L}_K \phi(X_s^K) - L\phi(X_s^K)) ds \right].$$

(5.16) allows us to deduce that this term tends to 0.

The second term is equal to  $\mathbb{E}(H(X^K) - H(X))$ . Since  $X \mapsto H(X)$  is continuous and since  $H(X) \leq Cte \left(1 + \int_s^t (1 + X_u^2) du\right)$  and is therefore uniformly integrable by (5.14), this term tends to 0 as  $K$  tends to infinity.

Then we get (5.17) and thus the process  $\psi_t(X)$  is a  $Q$ -martingale. That means that for any  $\phi \in C_b^2$ ,

$$\phi(X_t) - \phi(X_0) - \int_0^t L\phi(X_s) ds$$

is a martingale.

(5) Step 5. The last step consists in proving that under  $Q$ , the process  $X$  is solution of the logistic Feller stochastic differential equation (5.9). Taking  $\phi(x) = x$  leads to  $X_t = X_0 + M_t + \int_0^t ((\lambda - \mu)X_s - cX_s^2) ds$ , where  $M$  is a martingale. Taking  $\phi(x) = x^2$  in one hand and applying Itô's formula for  $X_t^2$  in another hand allows us to identify

$$\langle M \rangle_t = \int_0^t \gamma X_s ds.$$

The last step consists in concluding that there exists a Brownian motion  $B$ , such that

$$M_t = \int_0^t \sqrt{\gamma X_s} dB_s.$$

This representation theorem can be found in [19] or in [21]. We introduce an auxiliary space  $\Omega'$  and a Brownian motion  $W$  on this space. The probability space will be  $(C_T \times \Omega', \mathcal{F}_t \otimes \mathcal{F}'_t, \mathbb{P} \otimes \mathbb{P}')$ . Then the process defined by

$$B_t(\omega, \omega') = \int_0^t \frac{1}{\sqrt{\gamma X_s(\omega)}} \mathbf{1}_{X_s(\omega) \neq 0} dM_s(\omega) + \int_0^t \mathbf{1}_{X_s(\omega) = 0} dW_s(\omega')$$

is a continuous square integrable martingale, and

$$\langle W \rangle_t = \int_0^t \frac{1}{\gamma X_s(\omega)} \mathbf{1}_{X_s(\omega) \neq 0} d\langle M \rangle_s(\omega) + \int_0^t \mathbf{1}_{X_s(\omega) = 0} ds = t.$$

Hence  $B$  is a Brownian motion on  $C_T \times \Omega'$ . We have

$$\mathbb{E} \left( \left( M_t - \int_0^t \sqrt{\gamma X_s} dB_s \right)^2 \right) = \mathbb{E} \left( \left( M_t - \int_0^t \mathbf{1}_{X_s \neq 0} dM_s \right)^2 \right) = \mathbb{E} \left( \int_0^t \mathbf{1}_{X_s = 0} d\langle M \rangle_s \right) = 0.$$

Hence,  $M_t = \int_0^t \sqrt{\gamma X_s} dB_s$ .

The conclusion of the theorem follows.  $\square$

## 6 QSD for logistic Feller diffusions

This part is developed in Cattiaux et al [8]. Let us consider the logistic Feller diffusion process defined as the unique pathwise solution of

$$dZ_t = \sqrt{Z_t} dB_t + (rZ_t - cZ_t^2)dt, \quad Z_0 > 0,$$

where the Brownian  $B$  and  $Z_0$  are given, and  $r$  and  $c$  are assumed to be positive. We study in this case the existence and uniqueness of a quasi-stationary distribution for the process  $Z$ .

Let us firstly state the main theorem of this part.

**Theorem 6.1** 1) *There exists a Yaglom limit  $\pi \in \mathcal{P}(\mathbb{R}_+^*)$  for the process  $Z$ . Then one has the existence of a QSD.*

2) *For any  $x > 0$ , the  $Q_x$ -process exists and converges, as  $t \rightarrow \infty$ , to its invariant probability measure which is absolutely continuous with respect to  $\pi$  (but not equal).*

3) *The QSD is unique.*

**Remark 6.2** *This theorem has to be related with the one concerning the logistic birth and death process (Section 4). In both cases we have existence and uniqueness of a QSD. Hence, the latter can be proposed as the interpretation of the mortality plateaus that biologists observed.*

The theory studying the quasi-stationary distributions for one-dimensional diffusion processes started with Mandl [25] and has been developed by many authors. See in particular [9], [26], [34]. Nevertheless in most of the papers, the diffusion and drift coefficients are regular and the "Mandl's condition"  $\kappa(+\infty) = \infty$  (see (5.11)) is assumed. These conditions are not satisfied in our case.

Let us remark that firstly the diffusion coefficient of the logistic Feller process can be zero, and secondly the drift term is quadratic and explodes at infinity. These two specificities lead to technical difficulties and new mathematical results.

Let us now give the ideas of the proof.

We firstly make a change a variable to obtain a Kolmogorov equation. Let us introduce the process  $(X_t; t \geq 0)$  defined by  $X_t = 2\sqrt{Z_t}$ . Of course,  $X$  is absorbing at 0 as  $Z$  and the research of QSD for  $Z$  will be easily deduced from the one obtained for  $X$ .

An elementary computation using Itô's formula shows that

$$dX_t = dB_t - q(X_t)dt, \quad (6.1)$$

where the function  $q(x)$  is given by

$$q(x) = \frac{1}{2x} - \frac{rx}{2} + \frac{cx^3}{8}.$$

Such a process  $X$  driven by a Brownian motion is called a Kolmogorov diffusion process. Let us remark that the function  $q$  is continuous on  $\mathbb{R}_+^*$  but explodes at 0 as  $\frac{1}{2x}$  and at infinity as  $\frac{c}{8}x^3$ . The strong cubic back strength at infinity will force the process to essentially live in compact sets. That will provide the uniqueness of the QSD, as seen below. This result is very different of the results obtained in case of smooth drifts or going slower to infinity. For example, Lambert [23], proves that if  $c = 0$  and  $r \leq 0$ , then either  $r = 0$  and there is no QSD, or  $r < 0$  and there is an infinite number of QSD. Lladser and San Martin [24] show that in the case of the Ornstein-Uhlenbeck process

$$dY_t = dB_t - Y_t dt,$$

killed at 0, the spectral equation  $L^*\psi = -\theta\psi$  can be realized with a non-negative and integrable function  $\psi$  for any  $\theta \in (0, 1]$ . It turns out that there is a continuum of QSD with decay rates  $\theta \in (0, 1]$ .

## 6.1 Existence of a QSD

Let us study the Kolmogorov diffusion process (6.1). As before we are interested in the semi-group of the killed process, that is, for any  $x > 0$ , for any  $t > 0$ , for any  $f \in C_b(\mathbb{R}_+^*)$ ,

$$P_t f(x) = \mathbb{E}_x(f(X_t)\mathbf{1}_{t < T_0}). \quad (6.2)$$

We have computed in the previous section the infinitesimal generator given for  $\phi \in C_c^2(0, +\infty)$  by

$$L\phi = \frac{1}{2}\phi'' - q\phi'. \quad (6.3)$$

We are led to develop a spectral theory for this generator. Firstly, we introduce the measure  $\mu$ , defined by

$$\mu(dy) = e^{-Q(y)} dy, \quad (6.4)$$

where  $Q$  is defined as before by

$$Q(y) = \int_1^y 2q(y)dy = \ln y + \frac{r}{2}(1 - y^2) + \frac{c}{16}(y^4 - 1).$$

Let us remark that in our case, the measure  $\mu$  is not finite. Nevertheless, through the unity function 1 does not belong to  $\mathbb{L}^2(\mu)$ , this space is the good functional space in which to work. The key point we firstly show is that, starting from  $x > 0$ , the law of the killed process at time  $t$  is absolutely continuous with respect to  $\mu$  with a density belonging to  $\mathbb{L}^2(\mu)$ . The first step of the proof is a Girsanov Theorem.

**Proposition 6.3** *For any Borel function  $F$  defined on  $\Omega = C([0, t], \mathbb{R}_+^*)$  it holds*

$$\mathbb{E}_x [F(\omega) \mathbf{1}_{t < T_0(\omega)}] = \mathbb{E}^{W_x} \left[ F(\omega) \mathbf{1}_{t < T_0(\omega)} \exp \left( \frac{1}{2} Q(x) - \frac{1}{2} Q(\omega_t) - \frac{1}{2} \int_0^t (q^2 - q')(\omega_s) ds \right) \right]$$

where  $\mathbb{E}^{W_x}$  denotes the expectation w.r.t. the Wiener measure starting from  $x$ .

**Proof** It is enough to show the result for  $F$  non-negative and bounded. Let  $\varepsilon \in (0, 1)$  and  $\tau_\varepsilon = T_\varepsilon \wedge T_{1/\varepsilon}$ . Let us choose some  $\psi_\varepsilon$  which is a non-negative  $C^\infty$  function with compact support included in  $] \varepsilon/2, 2/\varepsilon[$  such that  $\psi_\varepsilon(u) = 1$  if  $\varepsilon \leq u \leq 1/\varepsilon$ . For all  $x$  such that  $\varepsilon \leq x \leq 1/\varepsilon$  the law of the diffusion (6.1) coincides up to  $\tau_\varepsilon$  with the law of a similar diffusion process  $X^\varepsilon$  obtained by replacing  $q$  with the cutoff function  $q_\varepsilon = q\psi_\varepsilon$ . For the latter we may apply Novikov criterion (cf. [30] p.332), ensuring that the law of  $X^\varepsilon$  is given via Girsanov's formula. Hence

$$\begin{aligned} \mathbb{E}_x [F(\omega) \mathbf{1}_{t < \tau_\varepsilon(\omega)}] &= \mathbb{E}^{W_x} \left[ F(\omega) \mathbf{1}_{t < \tau_\varepsilon(\omega)} \exp \left( \int_0^t -q_\varepsilon(\omega_s) d\omega_s - \frac{1}{2} \int_0^t (q_\varepsilon)^2(\omega_s) ds \right) \right] \\ &= \mathbb{E}^{W_x} \left[ F(\omega) \mathbf{1}_{t < \tau_\varepsilon(\omega)} \exp \left( \int_0^t -q(\omega_s) d\omega_s - \frac{1}{2} \int_0^t q^2(\omega_s) ds \right) \right] \\ &= \mathbb{E}^{W_x} \left[ F(\omega) \mathbf{1}_{t < \tau_\varepsilon(\omega)} \exp \left( \frac{1}{2} Q(x) - \frac{1}{2} Q(\omega_t) - \frac{1}{2} \int_0^t (q^2 - q')(\omega_s) ds \right) \right] \end{aligned}$$

integrating by parts the stochastic integral. But  $\mathbf{1}_{t < \tau_\varepsilon}$  is non-decreasing in  $\varepsilon$  and converges almost surely to  $\mathbf{1}_{t < T_0}$  both for  $\mathbb{W}_x$  and for  $\mathbb{P}_x$  (since  $\mathbb{P}_x(T_0 < \infty) = 1$ ). Indeed, almost surely,

$$\lim_{\varepsilon \rightarrow 0} X_{\tau_\varepsilon} = \lim_{\varepsilon \rightarrow 0} X_{T_\varepsilon} = \lim_{\varepsilon \rightarrow 0} \varepsilon = 0$$

so that  $\lim_{\varepsilon \rightarrow 0} T_\varepsilon \geq T_0$ . But  $T_\varepsilon \leq T_0$  yielding the equality. It remains to use Lebesgue monotone convergence theorem to finish the proof.  $\square$

**Theorem 6.4** *For all  $x > 0$  and all  $t > 0$  there exists a density function  $r(t, x, \cdot)$  that satisfies*

$$\mathbb{E}_x [f(X_t) \mathbf{1}_{t < T_0}] = \int_0^{+\infty} f(y) r(t, x, y) \mu(dy)$$

for all bounded Borel function  $f$ .

If in addition there exists some  $C > 0$  such that

$$q^2(y) - q'(y) \geq -C \quad \text{for all } y > 0, \quad (6.5)$$

then for all  $t > 0$  and all  $x > 0$ ,

$$\int_0^{+\infty} r^2(t, x, y) \mu(dy) \leq (1/2\pi t)^{\frac{1}{2}} e^{Ct} e^{Q(x)}.$$

**Proof** Define

$$G(\omega) = \mathbf{1}_{t < T_0(\omega)} \exp \left( \frac{1}{2} Q(\omega_0) - \frac{1}{2} Q(\omega_t) - \frac{1}{2} \int_0^t (q^2 - q')(\omega_s) ds \right).$$

Denote by

$$e^{-v(t,x,y)} = (2\pi t)^{-\frac{1}{2}} \exp \left( -\frac{(x-y)^2}{2t} \right)$$

the density at time  $t$  of the Brownian motion starting from  $x$ . According to Proposition 6.3, we have

$$\begin{aligned} \mathbb{E}_x (f(X_t) \mathbf{1}_{t < T_0}) &= \mathbb{E}^{\mathbb{W}_x} \left( f(\omega_t) \mathbb{E}^{\mathbb{W}_x} (G|\omega_t) \right) \\ &= \int f(y) \mathbb{E}^{\mathbb{W}_x} (G|\omega_t = y) e^{-v(t,x,y)} dy \\ &= \int_0^{+\infty} f(y) \mathbb{E}^{\mathbb{W}_x} (G|\omega_t = y) e^{-v(t,x,y)+Q(y)} \mu(dy), \end{aligned}$$

because  $\mathbb{E}^{\mathbb{W}_x} (G|\omega_t = y) = 0$  if  $y \leq 0$ . In other words, the law of  $X_t$  restricted to non extinction has a density with respect to  $\mu$  given by

$$r(t, x, y) = \mathbb{E}^{\mathbb{W}_x} (G|\omega_t = y) e^{-v(t,x,y)+Q(y)}.$$

Hence

$$\begin{aligned} \int_0^{+\infty} r^2(t, x, y) \mu(dy) &= \int \left( \mathbb{E}^{\mathbb{W}_x} (G|\omega_t = y) e^{-v(t,x,y)+Q(y)} \right)^2 e^{-Q(y)+v(t,x,y)} e^{-v(t,x,y)} dy \\ &= \mathbb{E}^{\mathbb{W}_x} \left( e^{-v(t,x,\omega_t)+Q(\omega_t)} \left( \mathbb{E}^{\mathbb{W}_x} (G|\omega_t) \right)^2 \right) \\ &\leq \mathbb{E}^{\mathbb{W}_x} \left( e^{-v(t,x,\omega_t)+Q(\omega_t)} \mathbb{E}^{\mathbb{W}_x} (G^2|\omega_t) \right) \\ &\leq e^{Q(x)} \mathbb{E}^{\mathbb{W}_x} \left( \mathbf{1}_{t < T_0(\omega)} e^{-v(t,x,\omega_t)} e^{-\int_0^t (q^2 - q')(\omega_s) ds} \right), \end{aligned}$$

where we have used Cauchy-Schwarz's inequality. Since  $e^{-v(t,x,\cdot)} \leq (1/2\pi t)^{\frac{1}{2}}$ , the proof is completed.  $\square$

Thanks to Theorem 6.4, we can show, using the theory of Dirichlet forms (cf. Fukushima's theory [16]) that the infinitesimal generator  $L$  of  $X$ , defined for  $g \in C_c\infty(\mathbb{R}_+)$  by

$$Lg = \frac{1}{2} g'' - qg'$$

can be extended to the generator of a continuous symmetric semi-group of contractions of  $\mathbb{L}^2(\mu)$  denoted by  $(P_t)_{t \geq 0}$ . Then we can develop a spectral theory for  $L$  and  $P_t$  in  $\mathbb{L}^2(\mu)$ . In all what follows, and for  $f, g \in \mathbb{L}^2(\mu)$ , we will denote

$$\langle f, g \rangle_\mu = \int_{\mathbb{R}_+} f(x)g(x)\mu(dx).$$

The symmetry of  $P_t$  means that

$$\langle P_t f, g \rangle_\mu = \langle f, P_t g \rangle_\mu.$$

We can show

**Theorem 6.5** *Assume (6.5) and that  $\lim_{y \rightarrow \infty} q^2(y) - q'(y) = +\infty$ .*

*Then the operator  $-L$  has a purely discrete spectrum  $0 < \lambda_1 < \lambda_2 < \dots$ . Furthermore each  $\lambda_i$  ( $i \in \mathbb{N}$ ) is associated with a unique (up to a multiplicative constant) eigenfunction  $\eta_i$  of class  $C^2((0, \infty))$ , which satisfies the ODE*

$$\frac{1}{2}\eta_i'' - q\eta_i' = -\lambda_i\eta_i. \quad (6.6)$$

*The sequence  $(\eta_i)_{i \geq 1}$  is an orthonormal basis of  $\mathbb{L}^2(\mu)$  and  $\eta_1(x) > 0$  for all  $x > 0$ .*

*In addition, for each  $i$ ,  $\eta_i \in \mathbb{L}^1(\mu)$ .*

The proof of this theorem is based on a relation between the Fokker-Planck operator  $L$  and a Schrödinger's operator. Indeed, let us set for  $g \in L^2(dx)$ ,

$$\tilde{P}_t g = e^{-Q/2} P_t(g e^{Q/2}).$$

$\tilde{P}_t$  is a strongly semi-group on  $L^2(dx)$  with generator defined for  $g \in C_c^\infty(0, +\infty)$  by

$$\tilde{L}g = \frac{1}{2}\Delta g - \frac{1}{2}(q^2 - q')g.$$

The spectral theory for such Schrödinger's operator with potential  $\frac{(q^2 - q')}{2}$  on the line (or the half-line) is well known (see for example the book of Berezin-Shubin [4]), but the potential  $\frac{(q^2 - q')}{2}$  does not belong to  $L_{loc}^\infty$  as generally assumed. Nevertheless, Condition (6.5) ensures the compactness of these operators.

This theorem leads immediately to the following

**Corollary 6.6** *For  $f \in \mathbb{L}^2(\mu)$ ,*

$$P_t f =_{L^2} \sum_{i \in \mathbb{N}} e^{-\lambda_i t} \langle \eta_i, f \rangle_\mu \eta_i, \quad (6.7)$$

*then for  $f, g \in \mathbb{L}^2(\mu)$ ,*

$$\langle g, P_t f \rangle_\mu \sim_{t \rightarrow \infty} e^{-\lambda_1 t} \langle \eta_1, f \rangle_\mu \langle \eta_1, g \rangle_\mu. \quad (6.8)$$

**Proof** For  $f \in \mathbb{L}^2(\mu)$ ,

$$\begin{aligned} P_t f &= \sum_{i \in \mathbb{N}} \langle P_t f, \eta_i \rangle_\mu \eta_i \\ &= \sum_{i \in \mathbb{N}} \langle f, P_t \eta_i \rangle_\mu \eta_i \quad (\text{by symmetry}) \\ &= \sum_{i \in \mathbb{N}} e^{-\lambda_i t} \langle f, \eta_i \rangle_\mu \eta_i. \end{aligned}$$

The second assertion immediately follows.  $\square$

Let us now prove the existence of the Yaglom's limit. Let us assume for a while that the function identically equal to 1 belongs to  $\mathbb{L}^2(\mu)$  (which is false in our case since the total mass of  $\mu$  is infinite). We would have by (6.7) that

$$\begin{aligned} P_t \mathbf{1} &\sim_{t \rightarrow \infty} e^{-\lambda_1 t} \langle \eta_1, \mathbf{1} \rangle_\mu \eta_1 \\ P_t f &\sim_{t \rightarrow \infty} e^{-\lambda_1 t} \langle \eta_1, f \rangle_\mu \eta_1. \end{aligned}$$

Then, we would deduce (since  $\eta_1 > 0$ ) that

$$\mathbb{E}_x(f(X_t) | t < T_0) \sim_{t \rightarrow \infty} \frac{\langle \eta_1, f \rangle_\mu}{\langle \eta_1, \mathbf{1} \rangle_\mu}.$$

From this heuristics, we deduce that a good candidate to be a QSD is the probability measure

$$\frac{\eta_1}{\int \eta_1 d\mu} d\mu,$$

which is well defined since  $\eta_1 \in \mathbb{L}^1(\mu)$ .

Let us now state the main theorem of this section.

**Theorem 6.7** *Assume (6.5) and that  $\lim_{y \rightarrow \infty} q^2(y) - q'(y) = +\infty$ . Let us set*

$$\nu_1 = \frac{\eta_1}{\int \eta_1 d\mu} d\mu.$$

*Thus for any  $x > 0$ ,  $t > 0$  and  $A$  a Borel subset of  $(0, +\infty)$ , we have*

(i)  $\mathbb{P}_x(T_0 > t) \sim_{t \rightarrow \infty} e^{-\lambda_1 t} \eta_1(x)$ .

(ii)  $\nu_1$  is the Yaglom's limit:

$$\lim_{t \rightarrow \infty} \mathbb{P}_x(X_t \in A | T_0 > t) = \nu_1(A).$$

(iii)  $\nu_1$  is a QSD and  $\mathbb{P}_{\nu_1}(T_0 > t) = e^{-\lambda_1 t}$ .

(iv) We obtain the speed of convergence:

$$\lim_{t \rightarrow \infty} e^{-(\lambda_2 - \lambda_1)t} (\mathbb{P}_x(X_t \in A | T_0 > t) - \nu_1(A)) < +\infty.$$

For the complete proof we refer to [8]. Let us only give the mathematical trick which allows us to overtake the fact that  $\mathbf{1} \notin \mathbb{L}^2(\mu)$ . We use the Markov property and write for  $t > 1$

$$\begin{aligned}
\mathbb{E}_x(f(X_t)\mathbf{1}_{t < T_0}) &= \mathbb{E}_x(\mathbb{E}_x(f(X_t)\mathbf{1}_{t < T_0} | \mathcal{F}_1)) \\
&= \mathbb{E}_x(\mathbb{E}_{X_1}(f(X_{t-1})\mathbf{1}_{t-1 < T_0})) \\
&= \int \mathbb{E}_y(f(X_{t-1})\mathbf{1}_{t-1 < T_0}) r(1, x, y) \mu(dy) \\
&= \int P_{t-1}f(y) r(1, x, y) \mu(dy) = \int f(y) P_{t-1}r(1, x, y) \mu(dy) \\
&\underset{t \rightarrow \infty}{\sim} e^{-\lambda_1(t-1)} \langle \eta_1, f \rangle_\mu \langle \eta_1, r(1, x, \cdot) \rangle_\mu.
\end{aligned}$$

Here we have used that  $r(1, x, \cdot) \in \mathbb{L}^2(\mu)$  and the symmetry of  $P_{t-1}$ .

Now, noting that  $\langle \eta_1, r(1, x, \cdot) \rangle = P_1 \eta_1(x) = e^{-\lambda_1} \eta_1(x)$ , and proving boundedness estimates on the function  $r$ , we deduce that  $\frac{\eta_1}{\langle \eta_1, \mathbf{1} \rangle_\mu} d\mu$  is the Yaglom limit, and then a QSD.

## 6.2 Uniqueness of the QSD

**Theorem 6.8** *The QSD  $\nu_1$  is the unique QSD for the process  $X$ .*

The proof will be developed in several intermediary results. We will prove that  $\nu_1$  attracts all initial distributions  $\nu$  supported in  $(0, \infty)$ , that is

$$\lim_{t \rightarrow \infty} \mathbb{P}_\nu(X_t \in A | T_0 > t) = \nu_1(A), \quad (6.9)$$

for all Borel set  $A$ . This property implies that the uniqueness of the QSD. Indeed, take another QSD  $\nu_2$ . Then  $\mathbb{P}_{\nu_2}(X_t \in A | T_0 > t) = \nu_2(A)$  by definition and it is equal to  $\nu_1(A)$  by assumption.

Let us remark that the function  $Q$  satisfies that

$$\int_1^\infty e^{Q(y)} \left( \int_y^\infty e^{-Q(z)} dz \right) dy < \infty. \quad (6.10)$$

Tonelli's theorem ensures that (6.10) is equivalent to

$$\int_1^\infty e^{-Q(y)} \left( \int_1^y e^{Q(z)} dz \right) dy < \infty. \quad (6.11)$$

Let us show that his property is equivalent to the fact that the process  $X$  comes down from infinity: there exists  $y > 0$  and  $t > 0$  such that

$$\lim_{x \rightarrow \infty} \mathbb{P}_x(T_y < t) > 0.$$

Therefore  $\infty$  is an entrance boundary for  $X$  (see for instance [30]).

**Remark 6.9** *Property (6.10) is equivalent to the fact that the process  $X$  comes down from infinity.*



**Proof** Let us show that “ $\infty$  is an entrance boundary” and (6.11) are equivalent. This will follow from [20, Theorem 20.12,(iii)]. For that purpose consider  $Y_t = \Lambda(X_t)$ , where  $\Lambda(x) = \int_1^x e^{Q(y)} dy$ . Since  $\frac{1}{2}\Lambda'' - q\Lambda' = 0$  and  $\Lambda(\infty) = \infty$ , it is easy to show by Itô’s formula that  $(Y_t, t \geq 0)$  is a martingale and that

$$dY_t = \Lambda'(\Lambda^{-1}(Y_t))dB_t.$$

A standard computation shows that

$$\mathbb{P}_y(T_a^Y < T_b^Y) = \frac{b-y}{b-a},$$

where  $T_a^Y$  is the hitting time of  $a$  for the diffusion  $Y$ . Then,  $\infty$  is an entrance boundary for  $Y$  if and only if

$$\int_0^\infty y m(dy) < \infty,$$

where  $m$  is the speed measure of  $Y$ , which is given by

$$m(dy) = \frac{2 dy}{(\Lambda'(\Lambda^{-1}(y)))^2},$$

(see [21, formula (5.51)]).

After a change of variables we obtain

$$\int_0^\infty y m(dy) = \int_1^\infty e^{-Q(y)} \int_1^x e^{Q(z)} dz dx.$$

Therefore we have shown the equivalence between (6.11) and the fact that the process comes down from infinity.  $\square$

**Proposition 6.10** *For any  $a > 0$ , there exists  $y_a > 0$  such that  $\sup_{x > y_a} \mathbb{E}_x(e^{aT_{y_a}}) < \infty$ .*

**Proof** Let  $a > 0$ , and pick  $x_a$  large enough so that

$$\int_{x_a}^\infty e^{Q(x)} \int_x^\infty e^{-Q(z)} dz dx \leq \frac{1}{2a}.$$

Let  $J$  be the nonnegative increasing function defined on  $[x_a, \infty)$  by

$$J(x) = \int_{x_a}^x e^{Q(y)} \int_y^\infty e^{-Q(z)} dz dy.$$

Then check that  $J'' = 2qJ' - 1$ , so that  $LJ = -1/2$ . Set now  $y_a = 1 + x_a$ , and consider a large  $M > x$ . Itô’s formula gives

$$\mathbb{E}_x(e^{a(t \wedge T_M \wedge T_{y_a})} J(X_{t \wedge T_M \wedge T_{y_a}})) = J(x) + \mathbb{E}_x \left( \int_0^{t \wedge T_M \wedge T_{y_a}} e^{as} (aJ(X_s) + LJ(X_s)) ds \right).$$

But  $LJ = -1/2$ , and  $J(X_s) < J(\infty) \leq 1/(2a)$  for any  $s \leq T_{y_a}$ , so that

$$\mathbb{E}_x(e^{a(t \wedge T_M \wedge T_{y_a})} J(X_{t \wedge T_M \wedge T_{y_a}})) \leq J(x).$$

But  $J$  is increasing, hence for  $x \geq y_a$  one gets  $1/(2a) > J(x) \geq J(y_a) > 0$ . It follows that  $\mathbb{E}_x(e^{a(t \wedge T_M \wedge T_{y_a})}) \leq 1/(2aJ(y_a))$  and finally  $\mathbb{E}_x(e^{aT_{y_a}}) \leq 1/(2aJ(y_a))$ , by the monotone convergence theorem. So Proposition 6.10 is proved.  $\square$

Proving that  $\nu_1$  attracts all initial distribution requires the following estimates near 0 and  $\infty$ .

**Lemma 6.11** *Assume (H) holds, and  $\sup_{x \geq x_0} \mathbb{E}_x(e^{\lambda_1 T_{x_0}}) < \infty$ . For  $h \in L^1(\mu)$  strictly positive in  $(0, \infty)$  we have*

$$\lim_{\varepsilon \downarrow 0} \limsup_{t \rightarrow \infty} \frac{\int_0^\varepsilon h(x) \mathbb{P}_x(T_0 > t) \mu(dx)}{\int h(x) \mathbb{P}_x(T_0 > t) \mu(dx)} = 0 \quad (6.12)$$

$$\lim_{M \uparrow \infty} \limsup_{t \rightarrow \infty} \frac{\int_M^\infty h(x) \mathbb{P}_x(T_0 > t) \mu(dx)}{\int h(x) \mathbb{P}_x(T_0 > t) \mu(dx)} = 0 \quad (6.13)$$

**Proof** We start with (6.12). Using Harnack's inequality (to bound by below the density  $r(t, x, y)$ , see [35]), we have for  $\varepsilon < 1$  and large  $t$

$$\frac{\int_0^\varepsilon h(x) \mathbb{P}_x(T_0 > t) \mu(dx)}{\int h(x) \mathbb{P}_x(T_0 > t) \mu(dx)} \leq \frac{\mathbb{P}_1(T_0 > t) \int_0^\varepsilon h(z) \mu(dz)}{C \int_1^{3/2} h(x) \mu(dx) \mathbb{P}_1(T_0 > t-1)},$$

then

$$\begin{aligned} \limsup_{t \rightarrow \infty} \frac{\int_0^\varepsilon h(x) \mathbb{P}_x(T_0 > t) \mu(dx)}{\int h(x) \mathbb{P}_x(T_0 > t) \mu(dx)} &\leq \limsup_{t \rightarrow \infty} \frac{\mathbb{P}_1(T_0 > t) \int_0^\varepsilon h(z) \mu(dz)}{C \int_1^{3/2} h(x) \mu(dx) \mathbb{P}_1(T_0 > t-1)} \\ &= \frac{e^{-\lambda_1} \int_0^\varepsilon h(z) \mu(dz)}{C \int_1^{3/2} h(x) \mu(dx)}, \end{aligned}$$

and the first assertion of the lemma is proved.

For the second limit, we set  $A_0 := \sup_{x \geq x_0} \mathbb{E}_x(e^{\lambda_1 T_{x_0}}) < \infty$ . Then for large  $M > x_0$ , we have

$$\mathbb{P}_x(T_0 > t) = \int_0^t \mathbb{P}_{x_0}(T_0 > u) \mathbb{P}_x(T_{x_0} \in d(t-u)) + \mathbb{P}_x(T_{x_0} > t).$$

Using that  $\lim_{u \rightarrow \infty} e^{\lambda_1 u} \mathbb{P}_{x_0}(T_0 > u) = \eta_1(x_0) \langle \eta_1, 1 \rangle_\mu$  we obtain that  $B_0 := \sup_{u \geq 0} e^{\lambda_1 u} \mathbb{P}_{x_0}(T_0 > u) < \infty$ . Then

$$\begin{aligned} \mathbb{P}_x(T_0 > t) &\leq B_0 \int_0^t e^{-\lambda_1 u} \mathbb{P}_x(T_{x_0} \in d(t-u)) + \mathbb{P}_x(T_{x_0} > t) \\ &\leq B_0 e^{-\lambda_1 t} \mathbb{E}_x(e^{\lambda_1 T_{x_0}}) + e^{-\lambda_1 t} \mathbb{E}_x(e^{\lambda_1 T_{x_0}}) \leq e^{-\lambda_1 t} A_0 (B_0 + 1), \end{aligned}$$

and (6.13) follows immediately.  $\square$

Let us now prove that  $\nu_1$  attracts all initial distribution.

**Proof** [Proof of Theorem 6.8] Let  $\nu$  be any fixed probability distribution whose support is contained in  $(0, \infty)$ . We must show that the conditional evolution of  $\nu$  converges to  $\nu_1$ .

We begin by claiming that  $\nu$  can be assumed to have a strictly positive density  $h$ , with respect to  $\mu$ . Indeed, let

$$\ell(y) = \int r(1, x, y) \nu(dx).$$

Using Tonelli's theorem we have

$$\int \int r(1, x, y) \nu(dx) \mu(dy) = \int \int r(1, x, y) \mu(dy) \nu(dx) = \int \mathbb{P}_x(T_0 > 1) \nu(dx) \leq 1,$$

which implies that  $\int r(1, x, y) \nu(dx)$  is finite  $dy$ -a.s.. Finally, define  $h = \ell / \int \ell d\mu$ . Notice that for  $d\rho = h d\mu$

$$\mathbb{P}_\nu(X_{t+1} \in \cdot \mid T_0 > t + 1) = \mathbb{P}_\rho(X_t \in \cdot \mid T_0 > t),$$

showing the claim.

Consider  $M > \varepsilon > 0$  and any Borel set  $A$  included in  $(0, \infty)$ . Then

$$\left| \frac{\int \mathbb{P}_x(X_t \in A, T_0 > t) h(x) \mu(dx)}{\int \mathbb{P}_x(T_0 > t) h(x) \mu(dx)} - \frac{\int_\varepsilon^M \mathbb{P}_x(X_t \in A, T_0 > t) h(x) \mu(dx)}{\int_\varepsilon^M \mathbb{P}_x(T_0 > t) h(x) \mu(dx)} \right|$$

is bounded by the sum of the following two terms

$$\begin{aligned} I1 &= \left| \frac{\int \mathbb{P}_x(X_t \in A, T_0 > t) h(x) \mu(dx)}{\int \mathbb{P}_x(T_0 > t) h(x) \mu(dx)} - \frac{\int_\varepsilon^M \mathbb{P}_x(X_t \in A, T_0 > t) h(x) \mu(dx)}{\int \mathbb{P}_x(T_0 > t) h(x) \mu(dx)} \right| \\ I2 &= \left| \frac{\int_\varepsilon^M \mathbb{P}_x(X_t \in A, T_0 > t) h(x) \mu(dx)}{\int \mathbb{P}_x(T_0 > t) h(x) \mu(dx)} - \frac{\int_\varepsilon^M \mathbb{P}_x(X_t \in A, T_0 > t) h(x) \mu(dx)}{\int_\varepsilon^M \mathbb{P}_x(T_0 > t) h(x) \mu(dx)} \right|. \end{aligned}$$

We have the bound

$$I1 \vee I2 \leq \frac{\int_0^\varepsilon \mathbb{P}_x(T_0 > t) h(x) \mu(dx) + \int_M^\infty \mathbb{P}_x(T_0 > t) h(x) \mu(dx)}{\int \mathbb{P}_x(T_0 > t) h(x) \mu(dx)}.$$

Thus, from Lemma 6.11 we get

$$\lim_{\varepsilon \downarrow 0, M \uparrow \infty} \limsup_{t \rightarrow \infty} \left| \frac{\int \mathbb{P}_x(X_t \in A, T_0 > t) h(x) \mu(dx)}{\int \mathbb{P}_x(T_0 > t) h(x) \mu(dx)} - \frac{\int_\varepsilon^M \mathbb{P}_x(X_t \in A, T_0 > t) h(x) \mu(dx)}{\int_\varepsilon^M \mathbb{P}_x(T_0 > t) h(x) \mu(dx)} \right| = 0.$$

On the other hand we have

$$\lim_{t \rightarrow \infty} \frac{\int_\varepsilon^M \mathbb{P}_x(X_t \in A, T_0 > t) h(x) \mu(dx)}{\int_\varepsilon^M \mathbb{P}_x(T_0 > t) h(x) \mu(dx)} = \frac{\int_A \eta_1(z) \mu(dz)}{\int_{\mathbb{R}^+} \eta_1(z) \mu(dz)} = \nu_1(A),$$

independently of  $M > \varepsilon > 0$ , and the result follows.  $\square$

### 6.3 The $Q$ -process

Let us now describe the law of the trajectories conditioned to never attain 0.

**Theorem 6.12** *Let us fix a time  $s$  and consider  $B$  a measurable subset of  $C([0, s])$ . Then for any  $x \in \mathbb{R}_+^*$ ,*

$$\lim_{t \rightarrow \infty} \mathbb{P}_x(X \in B | t < T_0) = Q_x(B),$$

where  $Q_x$  is the law of a continuous process with transition probabilities given by  $q(s, x, y)dy$ , where

$$q(s, x, y) = e^{\lambda_1 s} \frac{\eta_1(y)}{\eta_1(x)} r(s, x, y) e^{-Q(y)}.$$

**Proof** Since  $r(s, x, y) e^{-Q(y)} dy$  is the law of  $X_s$  issued from  $x$ , we have to prove that

$$Q_x(B) = Q_x(X \in B) = \mathbb{E}_x \left( \mathbf{1}_B(X) \frac{\eta_1(X_s)}{\eta_1(x)} \mathbf{1}_{T_0 > s} \right).$$

We have

$$\frac{\mathbb{P}_x(X \in B; T_0 > t)}{\mathbb{P}_x(T_0 > t)} = \frac{\mathbb{P}_x(X \in B; T_0 > s; \mathbb{E}_{X_s}(T_0 > t - s))}{\mathbb{P}_x(T_0 > t)},$$

and we have proved that

$$\lim_{t \rightarrow \infty} \frac{\mathbb{P}_y(T_0 > t - s)}{\mathbb{P}_x(T_0 > t)} = e^{\lambda_1 s} \frac{\eta_1(y)}{\eta_1(x)}.$$

Then,

$$\lim_{t \rightarrow \infty} \frac{\mathbb{P}_x(X \in B; T_0 > t)}{\mathbb{P}_x(T_0 > t)} = \frac{e^{\lambda_1 s}}{\eta_1(x)} \mathbb{P}_x \left( \mathbf{1}_B(X) \frac{\eta_1(X_s)}{\eta_1(x)} \mathbf{1}_{T_0 > s} \right).$$

□

**Corollary 6.13** *For any Borel set  $A \subset (0, \infty)$  and any  $x$ ,*

$$\lim_{s \rightarrow \infty} Q_x(X_s \in A) = \int_A \eta_1^2(y) \mu(dy) = \langle \eta_1, \mathbf{1} \rangle_\mu \int_A \eta_1(y) \nu_1(dy).$$

**Proof**

Since  $\mathbf{1}_A \eta_1 \in L^2(\mu)$ , we have that

$$\eta_1(x) Q_x(X_s \in A) = \int \mathbf{1}_A(y) \eta_1(y) e^{\lambda_1 s} r(s, x, y) \mu(dy)$$

which converges to  $\eta_1(x) \int_B \eta_1^2(y) \mu(dy)$  as  $s \rightarrow +\infty$ , since  $e^{\lambda_1 s} r(s, x, \cdot)$  converges to  $\eta_1(x) \eta_1(\cdot)$  in  $L^2(d\mu)$ . □

**Remark 6.14** The stationary measure of the  $Q$ -process is absolutely continuous with respect to  $\nu_1$ , with Radon-Nikodym derivative  $\langle \eta_1, \mathbf{1} \rangle_\mu \eta_1$ , which is nondecreasing. In particular, the ergodic measure of the  $Q$ -process dominates stochastically the Yaglom limit.

## 7 Simulation: the Fleming-Viot system

The proof of the existence of the QSD  $\nu_1$  is based on spectral theory arguments and doesn't give quantitative information on this QSD. Thus it is very convenient to know how to approximate this QSD using simulable particle systems. We present here the main ideas of the work of Villemonais [36].

To avoid the problem of unboundedness of the drift at the boundaries, the first step consists in approximating the QSD  $\nu_1$  by a sequence of QSD  $(\nu^\varepsilon)_\varepsilon$  of diffusion processes with bounded drift. One defines  $\mathbb{P}^\varepsilon$  as the law of the process

$$dX_t = dB_t - q(X_t)dt ; X_0 \in (\varepsilon, \frac{1}{\varepsilon}), \quad (7.1)$$

killed when it hits  $\varepsilon$  or  $\frac{1}{\varepsilon}$ . Existence and uniqueness of the QSD  $\nu^\varepsilon$  for this process are easily obtained from Pinsky [27]. The first result stated by Villemonais is the

**Proposition 7.1** *The sequence  $(\nu^\varepsilon)_\varepsilon$  weakly converges to  $\nu_1$  as  $\varepsilon$  tends to 0.*

The proof is based on a compactness-uniqueness result and can be found in [36]. Then in a second step we fix  $\varepsilon > 0$  and we want to approximate the QSD  $\nu^\varepsilon$  by a particle system, which will be called Fleming-Viot particle system. Let us now describe this  $N$ -particle system.

Let us fix  $N$  initial data belonging to  $(\varepsilon, \frac{1}{\varepsilon})$ . The particles evolve from these data independently and following the law  $\mathbb{P}^\varepsilon$  of the solution of the Kolmogorov equation (7.1), until one of them hits the boundary  $\{\varepsilon, \frac{1}{\varepsilon}\}$ . At that time  $\tau_1$ , the killed particle jumps to the position at  $\tau_1$  of one of the  $N - 1$  remaining particles, chosen uniformly among them. Then the particles evolve independently until one of them attains the boundary (time  $\tau_2$ ), and so on. The sequence of jumps is denoted by  $(\tau_n)_n$ . This procedure defines a  $(\mathbb{R}_+)^N$ -valued diffusion process with jumps, denoted by  $(X_t^1, \dots, X_t^N)_{t \geq 0}$ . By coupling arguments, one can prove that there is no accumulation of jumps and that the process is well defined.

**Proposition 7.2** *The process  $(X_t^1, \dots, X_t^N)_t$  is well defined. That means that  $\lim_n \tau_n = \infty$ .*

Such systems have been introduced by Burdzy, Holyst, Ingerman, March in [6] and explored in [7] and in Grigorescu-Kang [18] for  $d$ -dimensional killed Brownian motions. Similar systems have also been studied by Ferrari-Maric [15] for continuous Markov chains in a countable state space.

From now,  $\varepsilon$  is fixed, and we forget it in the notation. We have now to study the  $N$ -Fleming Viot particle system when time  $t$  tends to infinity and then when  $N$  tends to infinity. By usual methods, it can be shown that the system is ergodic. More specifically we get

**Proposition 7.3** *The process  $(X_t^1, \dots, X_t^N)_t$  is exponentially ergodic, with a unique stationary distribution  $M^N$ .*

Let us now introduce the probability measure  $\chi^N$ , which is the empirical stationary measure of  $(X_t^1, \dots, X_t^N)_t$ . That means that  $\chi^N$  is the empirical measure of a random vector  $(x^1, \dots, x^N)$  distributed following the stationary distribution  $M^N$ .

Let us state the main theorem whose proof is given in [36].

**Theorem 7.4** *The sequence of random measures  $(\chi^N)_N$  converges in law, as  $N$  tends to infinity, to the deterministic measure  $\nu^\varepsilon$ , unique QSD of the killed Kolmogorov diffusion process defined in (7.1).*

Some simulations concerning the logistic Feller diffusion process are developed in [36] and show the quasi-stationary distribution of the process (5.9) for  $\gamma = 1$  and different values of  $\lambda - \mu$  and  $c$ .

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