ECOLE POLYTECHNIQUE

CENTRE DE MATHÉMATIQUES APPLIQUÉES
UMR CNRS 7641

Competitive or weak cooperative stochastic Lotka-Volterra systems conditioned to non-extinction

Patrick Cattiaux, Sylvie Méléard

R.I. N⁰ 644   *October 2008*

COMPETITIVE OR WEAK COOPERATIVE STOCHASTIC LOTKA-VOLTERRA SYSTEMS CONDITIONED TO NON-EXTINCTION

PATRICK CATTIAUX ♣ AND   SYLVIE MÉLÉARD ♠

♠ ECOLE POLYTECHNIQUE   ♣ UNIVERSITÉ DE TOULOUSE

ABSTRACT. We are interested in the long time behavior of a two-type density-dependent biological population conditioned to non-extinction, in both cases of competition or weak cooperation between the two species. This population is described by a stochastic Lotka-Volterra system, obtained as limit of renormalized interacting birth and death processes. The weak cooperation assumption allows the system not to blow up. We study the existence and uniqueness of a quasi-stationary distribution, that is convergence to equilibrium conditioned to non extinction. To this aim we generalize in two-dimensions spectral tools developed for one-dimensional generalized Feller diffusion processes. The existence proof of a quasi-stationary distribution is reduced to the one for a d-dimensional Kolmogorov diffusion process under a symmetry assumption. The symmetry we need is satisfied under a local balance condition relying the ecological rates. A novelty is the outlined relation between the uniqueness of the quasi-stationary distribution and the ultracontractivity of the killed semi-group. By a comparison between the killing rates for the populations of each type and the one of the global population, we show that the quasi-stationary distribution can be either supported by individuals of one (the strongest one) type or supported by individuals of the two types. We thus highlight two different long time behaviors depending on the parameters of the model: either the model exhibits an intermediary time scale for which only one type (the dominant trait) is surviving, or there is a positive probability to have coexistence of the two species.

Key words : Stochastic Lotka-Volterra systems, multitype population dynamics, quasi-stationary distribution, Yaglom limit, coexistence.

MSC 2000 : 92D25, 60J70, 37A60, 60J80.

1. Introduction.

Our aim in this paper is to study the long time behavior of a two dimensional stochastic Lotka-Volterra process $Z = (Z_t^1, Z_t^2)_{t \geq 0}$, which describes the size of a two-type density dependent population. It generalizes the one-dimensional logistic Feller diffusion process introduced in [7], [14] and whose long time scales have been studied in details in [3].

More precisely, let us consider the coefficients

$$\gamma_1, \gamma_2 > 0 \ , \ r_1, r_2 > 0 \ ; \ c_{11}, c_{22} > 0 \ ; \ c_{12}, c_{21} \in \mathbb{R}. \tag{1.1}$$

The process Z, called Stochastic Lotka-Volterra process (SLVP), takes its values in $(\mathbb{R}_+)^2$ and is solution of the following stochastic differential system:

$$dZ_t^1 = \sqrt{\gamma_1 Z_t^1} dB_t^1 + (r_1 Z_t^1 - c_{11}(Z_t^1)^2 - c_{12} Z_t^1 Z_t^2) \, dt,$$

$$dZ_t^2 = \sqrt{\gamma_2 Z_t^2} dB_t^2 + (r_2 Z_t^2 - c_{21} Z_t^1 Z_t^2 - c_{22}(Z_t^2)^2) \, dt, \quad\quad (1.2)$$

where B^1 and B^2 are independent standard Brownian motions independent of the initial data Z_0. The extinction of the population is modelled by the absorbing state $(0,0)$, and the mono-type populations by the absorbing sets $\mathbb{R}_+^* \times \{0\}$ and $\{0\} \times \mathbb{R}_+^*$.

This system (1.2) can be obtained as an approximation of a renormalized two-types birth and death process in case of large population and small ecological timescale. (The birth and death rates are at the same scale than the initial population size). This microscopic point of view has been developed in [3] concerning the logistic Feller equation and can be easily generalized to multi-type models. The coefficients r_1 and r_2 are the asymptotic growth rates of 1-type's and 2-type's populations. The positive coefficients γ_1 and γ_2 can be interpreted as demographic parameters describing the ecological timescale. The coefficients $c_{ij}, i, j = 1, 2$ represent the pressure felt by an individual holding type i from an individual with type j. In our case, the intra-specific interaction rates c_{11} and c_{22} are assumed to be negative, modelling a logistic intra-specific competition, while the inter-specific interaction rates given by c_{12} and c_{21} can be positive or negative. In case where $c_{12} > 0$, individuals of type 2 have a negative influence on individuals of type 1, while in case where $c_{12} < 0$, they cooperate. Our main results proved in this paper require two main assumptions. The first one is a symmetry assumption between the coefficients γ_i and c_{ij},

$$c_{12}\gamma_2 = c_{21}\gamma_1,$$

that we will call "balance condition" ((2.5)). It means that the global rates of influence of each species on the other one are equal. In particular, the coefficients c_{12} and c_{12} have both the same sign. The second main assumption ((2.8)) is required in the cooperative case (when $c_{12} > 0$ and $c_{21} > 0$) and is given by

$$c_{11}c_{22} - c_{12}c_{21} > 0,$$

which compares the intra-specific to the inter-specific interacting rates. This condition will be called the "weak cooperative case".

Because of the quadratic drift terms and of the degeneracy of the diffusion terms near 0, the SLVP can blow up and its existence has to be carefully studied. We prove the existence of solutions to (1.2) in the competition case and in the weak cooperative case. In the first case it results from a comparison argument with independent one-dimensional logistic Feller processes. In the general case, the existence of the process $(Z_t)_t$ and a non blow-up condition are less easy to prove. If (2.5) holds, a change of variable leads us to study a Kolmogorov process driven by a Brownian motion and the existence of the process is proved using a well chosen Lyapounov funtion. That can be done if (2.8) is satisfied and we don't know if this condition is also necessary to avoid the blow-up. Under conditions (2.5) and (2.8) we will also prove that $(0,0)$ is an absorbing point and that the process converges almost surely to this point. That means that population goes to extinction with probability one. We will show this property in two steps. We will firstly show that the process is attracted by one of

the boundaries $\mathbb{R}_+ \times \{0\}$ or $\{0\} \times \mathbb{R}_+$. Once the process has attained one of them, it behaves as the logistic Feller stochastic differential equation and tends almost surely to $(0,0)$ in finite time. Therefore, our main interest in this paper is to study the long time behavior of the process $(Z_t)_t$ conditioned to non-extinction, either in the competition case, or in the weak cooperative case, under the balance condition.

Let us outline that the long time behavior of the SLVP considerably differs from the one of the deterministic Lotka-Volterra system which corresponds to the case where $\gamma_1 = \gamma_2 = 0$. Indeed, a fine study shows that in this case, (cf. Istas [12]), the point $(0,0)$ is an unstable equilibrium and there are three possible non trivial strongly stable equilibria: either the remaining population is totally composed of individuals of type 1 (the trait 1 is dominant), or a similar situation holds for trait 2 or co-existence of the two types occurs. In particular, the population cannot goes to extinction.

In this paper, we want to describe the asymptotic behavior of the SLVP conditioned to non-extinction, thus generalizing the one-dimensional case studied in [3]. This question is of great importance in Ecology. Although the limited competition resources entail the extinction of the population, the extinction time can be large compared to human timescale and certain species may survive for long periods teetering on the brink of extinction before dying out. A natural biological question is which type will eventually survive conditionally to non-extinction. We will show that in the long-time limit, the two types do not always disappear at the same time scale in the population and that a transient mono-type state can appear. More precisely, we will give some conditions on parameters ensuring mono-type transient states (preserving a dominant trait in a longer time scale) or coexistence of the two traits. The main tool of our study will be spectral theory and the conditions will be obtained by comparing the smallest eigenvalues of different killed operators. Indeed, conditioning to non-extinction, the process can either stay inside the positive quadrant (coexistence of traits) or attain one of the boundary (extinction of the other trait). Let us remark that in a work in progress [4], Champagnat and Diaconis are studying a similar problem for two-types birth-and-death processes conditioned to non-extinction.

The approach we develop is based on the mathematical notion of quasi-stationarity (QSD) which has been extensively studied. (See [16] for a regularly updated extensive bibliography, [17, 20] for a description of the biological meaning, [8, 10, 19] for the Markov chain case and [3] for the logistic Feller one-dimensional diffusion). In the latter, the proofs are based on spectral theory, and the reference measure is the natural symmetric measure for the killed process. We will follow these basic ideas.

In our two-dimensional SLVP case, the existence of a symmetric measure will be equivalent to the balance condition and we are led to study the Kolmogorov equation obtained by change of variable. Before studying the conditioning to non-extinction, we will in a first step study the long time behavior of the population conditioned to the coexistence of the two types (the process stays in the interior of the quadrangle $(\mathbb{R}_+^*)^2$ as soon as coexistence between the two types holds). Our theoretical results, generalizing what has be done in [3] to any dimension are stated in the Appendix. The arguments implying the existence of a quasi-stationary distribution are mainly similar. The novelty will concern the uniqueness of the quasi-stationary distribution, which is shown to be related to the ultracontractivity of the killed process semi-group. We prove that the Kolmogorov process associated with the SLVP satisfies this setting and conclude to the existence and uniqueness of the QSD

for the Kolmogorov process conditioned to coexistence. To deduce a similar result for the process conditioned to non-extinction we need to carefully compare the boundaries hitting times, and the extinction time. That will give us our main theorem (Theorem 4.1) on the Kolmogorov system. Let us summarize here what does it means coming back to the stochastic Lotka-Volterra process.

Theorem 1.1. *1) Under assumptions (2.5) and (2.8), the SLVP is well defined on $\mathbb{R}_+$ and goes to extinction in finite time with probability one.*

2) The long-time behavior of its law conditioned to non-extinction depends on the starting point z and is given as follows.

- *For all $z^1 > 0$, if $z = (z^1, 0)$, then for all $A \subset \mathbb{R}_+^* \times \mathbb{R}_+$,*

$$\mathbb{P}_{(z^1,0)}(Z_t \in A | T_0 > 0) = (m^1 \otimes \delta_0)(A),$$

  where m^1 is the unique QSD of the logistic Feller process $(Y_t^1)_t$ defined in (2.1).
- *For all $z^2 > 0$, if $z = (0, z^2)$, then for all $A \subset \mathbb{R}_+ \times \mathbb{R}_+^*$,*

$$\mathbb{P}_{(0,z^2)}(Z_t \in A | T_0 > 0) = (\delta_0 \otimes m^2)(A),$$

  where m^2 is the unique QSD of $(Y_t^2)_t$ defined in (2.2).
- *There is a unique quasi-stationary distribution m on $(\mathbb{R}_+)^2 \backslash \{(0,0)\}$, such that for all $z = (z^1, z^2)$ with $z^1 > 0$, $z^2 > 0$, for all $A \subset (\mathbb{R}_+)^2 \backslash \{(0,0)\}$,*

$$\mathbb{P}_z(Z_t \in A | T_0 > 0) = m(A),$$

  where T_0 is the extinction time.
- *If λ_1, (resp. $\lambda_{1,1}$, $\lambda_{1,2}$) denotes the positive killing rates of the global population, (resp. the population of type 1, of type 2), we get*
  - ***Competition case***: *$\lambda_1 > \lambda_{1,1} + \lambda_{1,2}$ and m is given by*

$$m = \delta_0 \otimes m^2 + m^1 \otimes \delta_0.$$

  Furthermore when $\lambda_{1,2} > \lambda_{1,1}$ (resp. $<$), m^1 (resp. m^2) is equal to 0.
  In other words, the model exhibits an intermediary time scale when only one type (the dominant trait) is surviving.

  - ***Weak cooperation case***: *we have two different situations.*
    * *If $\lambda_1 > \lambda_{1,i}$ for $i = 1$ or $i = 2$, the conclusion is the same as in the competition case.*
    * *If $\lambda_1 < \lambda_{1,i}$ for $i = 1$ and $i = 2$, then*

$$m = \delta_0 \otimes m^2 + m^1 \otimes \delta_0 + m_D,$$

    where m_D is proportional to ν_1.
    We thus have a positive probability to have coexistence of the two species.

Let us remark that our analysis is not reduced to the 2-dimensional case, as it is made clear in the Appendix. All the machinery is still available in any dimension. However the explicit conditions on the coefficients are then more difficult to write down. That is why we restrict ourselves to the 2-dimensional setting.

4

2. Existence of the SLVP and boundary hitting times

Let us denote $D = (\mathbb{R}_+^*)^2$. Let us remark that ∂D, $\mathbb{R}_+ \times \{0\}$ and $\{0\} \times \mathbb{R}_+$ are absorbing sets for the process $(Z_t)_t$, as also $\{(0,0)\}$. We introduce

- T_0: the first hitting time of $\{(0,0)\}$,
- T_1: the first hitting time of $\mathbb{R}_+ \times \{0\}$,
- T_2: the first hitting time of $\{0\} \times \mathbb{R}_+$,
- $T_{\partial D}$: the first hitting time of ∂D (or the exit time of D).

Of course, some of these stopping times are comparable. For example

$$T_{\partial D} \le T_1 \le T_0 \; ; \; T_{\partial D} \le T_2 \le T_0.$$

On the other hand, T_1 and T_2 are not directly comparable.

Let us prove the existence of the SLVP in some cases.

Proposition 2.1. *If $c_{12} > 0$ and $c_{21} > 0$, then there is no blow-up and the process $(Z_t)_t$ is well defined on $\mathbb{R}_+$. In addition, for all $x \in (\mathbb{R}_+)^2$,*

$$\mathbb{P}_x(T_0 < +\infty) = 1$$

and there exists $\lambda > 0$ such that

$$\sup_{x \in (\mathbb{R}_+)^2} \mathbb{E}_x(e^{\lambda T_0}) < +\infty.$$

Proof. In this competition case, the existence of the SLVP is easy to show, by using a comparison argument (cf. Ikeda-Watanabe [11] Chapter 6 Thm 1.1), and the population process $(Z_t)_t$ does not blow up. Indeed, the coordinate $(Z_t^1)_t$, resp. $(Z_t^2)_t$) can be upper-bounded by the solution of the logistic Feller equation

$$dY_t^1 = \sqrt{\gamma_1 Y_t^1} dB_t^1 + (r_1 Y_t^1 - c_{11}(Y_t^1)^2) \, dt, \tag{2.1}$$

respectively

$$dY_t^2 = \sqrt{\gamma_2 Y_t^2} dB_t^2 + (r_2 Y_t^2 - c_{22}(Y_t^2)^2) \, dt. \tag{2.2}$$

These one-dimensional processes have been introduced in [7, 14] and studied in details in [3]. It's easy to deduce (by stochastic domination) that the processes Z^1 and Z^2 become extinct in finite time.

The a.s. finiteness of each T_i, hence of $T_{\partial D}$, thus follows. It has also been shown in [3] that the absorption times from infinity have exponential moments. $\square$

Let us now consider the general case. We reduce the problem by a change of variables.

Let us define $(X_t^1, X_t^2) = (2\sqrt{Z_t^1/\gamma_1}, 2\sqrt{Z_t^2/\gamma_2})$. We obtain via Itô's formula

$$
\begin{aligned}
dX_t^1 &= dB_t^1 + \left(\frac{r_1 X_t^1}{2} - \frac{c_{11}\gamma_1(X_t^1)^3}{8} - \frac{c_{12}\gamma_2 \, X_t^1 \, (X_t^2)^2}{8} - \frac{1}{2X_t^1} \right) dt \\
dX_t^2 &= dB_t^2 + \left(\frac{r_2 X_t^2}{2} - \frac{c_{22}\gamma_2(X_t^2)^3}{8} - \frac{c_{21}\gamma_1 \, X_t^2 \, (X_t^1)^2}{8} - \frac{1}{2X_t^2} \right) dt .
\end{aligned}
\tag{2.3}
$$

5

In all the following, we will focus on the symmetric case where X is a Kolmogorov diffusion, that is a Brownian motion with a drift in gradient form as

$$dX_t = dB_t - \nabla V(X_t)dt. \tag{2.4}$$

Indeed, all the results of spectral theory obtained in the Appendix have been stated for such processes. Obvious computation shows that it requires the following balance condition on the coefficients:

$$c_{12}\,\gamma_2 = c_{21}\,\gamma_1. \tag{2.5}$$

This relation is a symmetry assumption between the global interaction rate of type 2 on type 1 and of type 1 on type 2. (Recall that the coefficients γ_i describe the ecological timescales). If (2.5) holds, the coefficients c_{12} and c_{21} have the same sign, allowing inter-species competition (c_{12} and $c_{21} > 0$) or inter-species cooperation (c_{12} and $c_{21} < 0$).

Under this condition, the process X is called the stochastic Lotka-Volterra Kolmogorov process (SLVKP). The potential V is then equal to

$$V(x^1, x^2) = \frac{1}{2} \sum_{i=1,2} \left(\log(x^i) + \frac{c_{ii}\gamma_i(x^i)^4}{16} - \frac{r_i(x^i)^2}{2} \right) + \alpha(x^1)^2(x^2)^2, \tag{2.6}$$

where

$$\alpha = \frac{c_{12}\,\gamma_2}{16} = \frac{c_{21}\,\gamma_1}{16}. \tag{2.7}$$

Let us prove the existence of the SLVKP using the $\mathbb{L}^2$-norm as a Lyapunov function, under a weak cooperative assumption, that is if

$$\alpha < 0 \quad \text{and} \quad c_{11}c_{22} - c_{12}c_{21} > 0. \tag{2.8}$$

Theorem 2.2. *Assume balance condition (2.5), weak cooperative assumption (2.8), then there is no blow-up and the processes (X_t), and then (Z_t), are well defined on $\mathbb{R}_+$.*
In addition, for all $x \in D$,

$$\mathbb{P}_x(T_{\partial D} < +\infty) = 1,$$

for both X and Z.

Hence, under the assumptions of Theorem 2.2, Hypothesis (H1) of Definition A.3 in Appendix is satisfied, what we shall use later.

Proof. Let us compute

$$
\begin{aligned}
d\|X\|_t^2 &= d(X_t^1)^2 + d(X_t^2)^2 \\
&= 2(X_t^1 dB_t^1 + X_t^2 dB_t^2) + \sum_{i=1}^{2}(X_t^i)^2 \left(r_i - \frac{c_{ii}\gamma_i(X_t^i)^2}{4} - \frac{c_{ij}\gamma_j(X_t^j)^2}{4} \right) dt.
\end{aligned}
$$

The quartic function appearing in the drift term is thus $-q((x^1)^2, (x^2)^2)$, with

$$q(u, v) = c_{11}\gamma_1(u)^2 + c_{22}\gamma_2(v)^2 + 32\alpha uv.$$

Decomposing

$$q(u, v) = c_{11}\gamma_1 \left(u + \frac{16\alpha}{c_{11}\gamma_1}v \right)^2 + \frac{v^2}{c_{11}\gamma_1}(c_{11}c_{22} - c_{12}c_{21})\gamma_1\gamma_2,$$

6

and since $\alpha < 0$, a necessary and sufficient condition for $q(u,v)$ to be positive on the first quadrant ($u > 0, v > 0$), and to go to infinity at infinity, is thus $c_{11}c_{22} - c_{12}c_{21} > 0$. Hence the drift term in the previous S.D.E. is negative at infinity. It easily follows that

$$\sup_{t \in \mathbb{R}_+} \mathbb{E}(\|X_t\|^2) < +\infty,$$

ensuring that the processes (X_t), and then (Z_t) are well defined on $\mathbb{R}_+$.

Let us now study the hitting time of the boundary ∂D. We will compare (X_t^1, X_t^2) with the solution of

$$
\begin{aligned}
dU_t^1 &= dB_t^1 + \left(\frac{r_1 U_t^1}{2} - \frac{c_{11}\gamma_1 (U_t^1)^3}{8} - \frac{c_{12}\gamma_2 U_t^1 (U_t^2)^2}{8} \right) dt \qquad (2.9)\\
dU_t^2 &= dB_t^2 + \left(\frac{r_2 U_t^2}{2} - \frac{c_{22}\gamma_2 (U_t^2)^3}{8} - \frac{c_{21}\gamma_1 U_t^2 (U_t^1)^2}{8} \right) dt \,.
\end{aligned}
$$

Assuming (2.5) and (2.8), the diffusion process (U_t^1, U_t^2) exists and is unique in the strong sense, starting from any point. We consider now the solution built with the same Brownian motions as for X.

We shall see that, starting from the same (x^1, x^2) in the first quadrant, and for all $t < T_{\partial D}$, $X_t^1 \le U_t^1$ and $X_t^2 \le U_t^2$.

To this end we can make the following elementary reasoning. Fix ω and some $t < T_{\partial D}(\omega)$. Let us define $s \to W_s^i = X_s^i - U_s^i$ for $i = 1, 2$ and for $s \le t$. Of course $W_0^i = 0$. Due to the continuity of the paths, $s \mapsto W_s^i$ is of C^1 class and W^i solves an ordinary differential equation such that $\frac{d}{ds}(W_s^i)_{|s=0} = -\frac{1}{2x^i} < 0$.

Moreover we remark that if at some time $u \le t$, $W_u^i = 0$, then $\frac{d}{ds}(W_s^i)_{|s=u} = -\frac{1}{2X_u^i} < 0$. It follows that $W_s^i \le 0$ for $0 < s < t$, yielding the desired comparison result.

Denote $S_{\partial D}$ the hitting time of ∂D for the process U. We thus have $S_{\partial D} \ge T_{\partial D}$. It is thus enough to show that $S_{\partial D}$ is almost surely finite. But, remark that $d\nu = e^{-Q(x)}dx$, with

$$Q(x^1, x^2) = \sum_{i=1,2} \left(\frac{c_{ii}\gamma_i (x^i)^4}{16} - \frac{r_i (x^i)^2}{2} \right) + 2\,\alpha (x^1)^2 (x^2)^2, \qquad (2.10)$$

is an invariant (actually symmetric) bounded measure for U. The process U is thus positive recurrent and it follows that, starting from any point in the first quadrant D, $S_{\partial D}$ is a.s. finite. $\qquad\square$

These comparison arguments allow us to obtain other interesting properties of the process X, that we collect in the next proposition

Proposition 2.3. *Under the assumptions of Theorem 2.2, the following holds*

- *there exists $\lambda > 0$ such that $\sup_{x \in D} \mathbb{E}_x(e^{\lambda T_{\partial D}}) < +\infty$,*
- *for all $x \in D$, $\mathbb{P}_x(T_{\partial D} = T_i) > 0$ for $i = 1, 2$ (recall that T_i defined at the beginning of section 2 is the hitting time of each half axis), and $P_x(T_{\partial D} = T_0) = 0$ (recall that T_0 is the hitting time of the origin).*

Proof. The first point is an immediate consequence of the same moment controls for both Y and U, thanks to the comparison property. We already mentioned this property for Y in Proposition 2.1.

The same holds for U since U is known to be ultra-contractive (see definition B.4 in Appendix B2) under the hypotheses of theorem 2.2. The ultracontractivity property follows from the fact that the invariant measure $e^{-Q(x)}\,dx$ of the process U, (Q defined in (2.10)), satisfies the conditions of Corollary 5.7.12 of [21].

One sometimes says that X satisfies the *escape condition* from D.

In order to show the second point we shall introduce another process. Namely define for $i = 1, 2$, H^i as the solution of the following stochastic differential equation

$$dH_t^i = dB_t^i + \left(\frac{r_i H_t^i}{2} - \frac{c_{ii}\gamma_i (H_t^i)^3}{8} - \frac{1}{2H_t^i} \right) dt. \tag{2.11}$$

Of course H^1 and H^2 are independent processes, defined respectively up to the hitting time of the origin. We decide to stick H^i in 0 after it hits 0, as for X^i.

On the canonical space $\Omega_t = C([0, t], \bar{D})$ we denote by $\mathcal{P}^X$ and $\mathcal{P}^H$ the laws of the processes $(X_{s \wedge T_{\partial D}})_{s \leq t}$ and $(H_{s \wedge T_{\partial D}})_{s \leq t}$ starting from the same initial point x in D. We claim that $\mathcal{P}^X$ and $\mathcal{P}^H$ are equivalent. This is a consequence of an extended version of Girsanov theory as shown in [3] Proposition 2.2. One then have that for any bounded Borel function F defined on Ω_t,

$$\mathbb{E}^X \left[F(\omega)\, \mathbb{1}_{t < T_{\partial D}(\omega)} \right] = \mathbb{E}^H \left[F(\omega)\, \mathbb{1}_{t < T_{\partial D}(\omega)}\, e^{A(t)} \right]$$

where

$$
\begin{aligned}
A(t) &= \alpha\, (\omega_t^1)^2 (\omega_t^2)^2 - \alpha (x_1)^2 (x_2)^2 - \alpha \int_0^t \left(2\alpha\, (\omega_s^1)^2 (\omega_s^2)^2 \left((\omega_s^1)^2 + (\omega_s^2)^2 \right) - \left((\omega_s^1)^2 + (\omega_s^2)^2 \right) \right. \\
&\quad \left. - (r_1 + r_2)\, (\omega_s^1)^2 (\omega_s^2)^2 + \frac{1}{4}(c_{11}\gamma_1 + c_{22}\gamma_2)\, (\omega_s^1)^2 (\omega_s^2)^2 \left((\omega_s^1)^2 + (\omega_s^2)^2 \right) + \left((\omega_s^1)^2 + (\omega_s^2)^2 \right) \right) ds,
\end{aligned}
$$

and $\mathbb{E}^H$ (resp. $\mathbb{E}^X$) denotes the expectation w.r.t. to $\mathcal{P}^H$ (resp. $\mathcal{P}^X$). Remark that $A(t \wedge T_{\partial D})$ is well defined, so that the previous relation remains true without the $\mathbb{1}_{t < T_{\partial D}(\omega)}$ replacing $A(t)$ by $A(t \wedge T_{\partial D})$, i.e.

$$\mathbb{E}^X \left[F(\omega) \right] = \mathbb{E}^H \left[F(\omega)\, e^{A(t \wedge T_{\partial D})} \right].$$

This shows the claimed equivalence.

It thus remains to prove the second part of the proposition for the independent pair (H^1, H^2). But as shown in [3] Proposition 2.2 again, for each $i = 1, 2$,

$$\mathbb{E}^{H^i} \left[F(\omega)\, \mathbb{1}_{t < T_0(\omega)} \right] = \mathbb{E}^W \left[F(\omega)\, \mathbb{1}_{t < T_0(\omega)}\, e^{B(t)} \right]$$

for some almost surely finite $B(t)$, $\mathbb{E}^W$ being the expectation with respect to the Wiener measure starting at x^i. It follows that the $\mathcal{P}^{H^i}$ law of T_0 is equivalent to the Lebesgue measure on $]0, +\infty[$, since the same holds for the $\mathcal{P}^W$ law of T_0. The $\mathcal{P}^H$ law of (T_1, T_2) is thus equivalent to the Lebesgue measure on $]0, +\infty[\otimes]0, +\infty[$ yielding the desired result for H hence for X. $\qquad\square$

3. Existence and Uniqueness of the Quasi-Stationary Distribution for the Absorbing Set ∂D

We can define a quasi-stationarity notion associated with each absorbing set O, ∂D, $\mathbb{R}_+ \times \{0\}$, $\{0\} \times \mathbb{R}_+$. The results developed in Section 3 will refer to the absorbing set ∂D. Its complementary in $(\mathbb{R}_+)^2$ is D, which is an open connected subset of $\mathbb{R}^2$, conversely to the complementary of other absorbing sets.

Let us recall what a quasi-stationary distribution is. If F denotes an absorbing set for the $(\mathbb{R}_+)^2$-valued process Z and T_F the hitting time of this set, a quasi-stationary distribution (in short QSD) for Z and for this absorption event is a probability measure ν satisfying

$$\mathbb{P}_\nu(Z_t \in A \mid T_F > t) = \nu(A), \tag{3.1}$$

for any Borel set $A \subseteq \mathbb{R}_+{}^2 \setminus \{F\}$ and $t \geq 0$. A specific quasi-stationary distribution is defined, if it exists, as the limiting law, as $t \to \infty$, of Z_t conditioned on $T_F > t$, when starting from a fixed population. That is, if for a all $x \in \mathbb{R}_+{}^2 \setminus \{F\}$, the limit

$$\lim_{t \to \infty} \mathbb{P}_x(Z_t \in A \mid T_F > t)$$

exists and is independant of x, and defines a probability distribution on $\mathbb{R}_+{}^2 \setminus \{F\}$, then it is a QSD called quasi-limiting distribution, or (as we will do here) Yaglom limit.

It is thus well known, (see [8]), that there exists $\lambda_F > 0$ such that

$$\mathbb{P}_\nu(T_F > t) = e^{-\lambda_F t}.$$

This killing rate λ_F gives the velocity at which the process issued from the ν-distribution get to be absorbed.

Our aim is now to study the asymptotic behavior of the law of X_t conditioned on not reaching the boundary. All the material we need will be developed in Appendix. The later essentially extends to higher dimension the corpus of tools introduced in [3]. The spectral theory is developed for any Kolmogorov diffusion in $\mathbb{R}^d$, and for any dimension d. Then the existence of a quasi-stationary distribution is obtained. The novelty is the uniqueness result, since it is deduced from the ultracontractivity of the semigroup.

We will extensively refer to this Appendix, to study the problem of existence of a quasi-stationary distribution for the SLVKP, with the potential V defined in (2.6).
We introduce the reference measure, given by

$$\mu(dx^1, dx^2) = e^{-2V(x)}dx = \frac{1}{x^1 \, x^2} \, e^{-Q(x^1, x^2)} \, dx^1 \, dx^2$$

where Q is the symmetric polynomial of degree 4 given in (2.10).
It is the natural measure to deal with, since it makes the transition semi-group symmetric in $\mathbb{L}^2(\mu)$. One problem we have to face is that the measure μ has an infinite mass due to the behavior of its density near the axes. Remark that the density is integrable far from the axes, which is equivalent to

$$\int_D e^{-Q(x)}dx < +\infty. \tag{3.2}$$

This property is immediate in the competition case (c_{ii}, γ_i and α are positive) and has already been shown in the proof of Theorem 2.2, when (2.8) holds.

Proposition 3.1. *Assume (2.5) and (2.8). Then, there exists some $C > 0$ such that for all $x \in D$,*

$$|\nabla V|^2(x) - \triangle V(x) \geq -C. \tag{3.3}$$

We deduce that the semigroup P_t of the SLVKP killed at time $T_{\partial D}$, has a density with respect to μ, belonging to $\mathbb{L}^2(d\mu)$.

Proof. Under (2.5) and (2.8), we have seen that the explosion time ξ is infinite and thus (A.3) is satisfied. Then the conclusion of Theorem A.1 holds: one proves by Girsanov's theorem that the semigroup P_t of the SLVKP has a density with respect to μ.

Moreover, computation gives

$$|\nabla V|^2(x) - \triangle V(x) =$$
$$\left(-\frac{1}{2x^1} + r_1 \frac{x^1}{2} + c_{11} \frac{\gamma_1(x^1)^3}{8} + 2\alpha x^1(x^2)^2 \right)^2 + \left(-\frac{1}{2x^2} + r_2 \frac{x^2}{2} + c_{22} \frac{\gamma_2(x^2)^3}{8} + 2\alpha (x^1)^2 x^2 \right)^2$$
$$+ \frac{1}{2(x^1)^2} + \frac{r_1}{2} - c_{11} \frac{3\gamma_1(x^1)^2}{8} - 2\alpha(x^2)^2 + \frac{1}{2(x^2)^2} + \frac{r_2}{2} - c_{22} \frac{3\gamma_2(x^2)^2}{8} - 2\alpha(x^1)^2.$$

Hence, we observe that the terms in $|\nabla V|^2 - \triangle V$ playing a role near infinity are equal to $\frac{3}{4}\left(\frac{1}{x_1^2} + \frac{1}{x_2^2}\right)$ (when one of the coordinates is close to zero) and to

$$\left(\frac{c_{11}\gamma_1}{8}(x^1)^3 + 2\alpha x_1(x^2)^2 \right)^2 + \left(\frac{c_{22}\gamma_2}{8} x_2^3 + 2\alpha x_2(x^1)^2 \right)^2$$
$$= (x^1)^2 \left(-\frac{c_{11}\gamma_1}{8}(x^1)^2 + 2\alpha(x^2)^2 \right)^2 + (x^2)^2 \left(-\frac{c_{22}\gamma_2}{8}(x^2)^2 + 2\alpha(x^1)^2 \right)^2.$$

The two terms in factor of $(x^1)^2$ and $(x^2)^2$ in the first quantity will not be together equal to 0 as soon as $\alpha > 0$ or as the determinant of the system

$$\begin{cases} \frac{c_{11}\gamma_1}{8} Y_1 + 2\alpha Y_2 & = & 0 \\ 2\alpha Y_1 + \frac{c_{22}\gamma_2}{8} Y_2 & = & 0. \end{cases}$$

is non zero, what is satisfied under the condition (2.8). It follows that $|\nabla V|^2(x) - \triangle V(x)$ tends to $+\infty$ as $|x|$ tends to infinity. Since $|\nabla V|^2 - \triangle V$ is a smooth function in D, (3.3) follows. Then, we deduce from Theorem A.1 that for each $t > 0$, the density of P_t belongs to $\mathbb{L}^2(d\mu)$. $\square$

Let us now state our first main result.

Theorem 3.2. *Under Assumptions (2.5) and (2.8), that is if*

- $c_{12}\gamma_2 = c_{21}\gamma_1$,
- *if $\alpha < 0$, $c_{11}c_{22} - c_{12}c_{21} > 0$,*

there exists a unique quasi-stationary distribution ν_1 for the stochastic Lotka-Volterra Kolmogorov process X, which is the quasi-limiting distribution starting from any initial distribution.

10

In particular, there exists $\lambda_1 > 0$ such that for all $x \in D$, for all $A \subset D$,

$$\lim_{t \to \infty} e^{\lambda_1 t} \mathbb{P}_x(X_t \in A | T_{\partial D} > t) = \nu_1(A). \tag{3.4}$$

Proof. The proof is deduced from Appendices A and B. Standard results on Dirichlet forms (cf. Fukushima [9]) allow us to build a self-adjoint semigroup on $\mathbb{L}^2(\mu)$, which coincides with P_t for bounded functions belonging to $\mathbb{L}^2(\mu)$. Its generator L is non-positive and self-adjoint on $\mathbb{L}^2(d\mu)$, with $D(L) \supseteq C_0^\infty(D)$. Its restriction to $C_0^\infty(D)$ is equal to

$$Lg = \frac{1}{2}\Delta g - V.\nabla g \ , \quad g \in C_0^\infty(D).$$

We now develop a spectral theory for this semigroup (also called P_t), in $\mathbb{L}^2(d\mu)$.

We check that the hypotheses (H) introduced in Definition A.3 required to apply Theorem A.4 are satisfied under the assumptions (2.5) and (2.8). Indeed (H4) is obviously satisfied and (H1) and (H2) are deduced from Proposition 3.1. Furthermore, using for example polar coordinates, one easily shows that Condition (2.8) implies that

$$\bar{G}(R) = \inf\{|\nabla V|^2(x) - \triangle V(x); |x| \geq R \text{ and } x \in D\} \geq cR^6$$

for positive constant c. Thus (H3) holds.

Since Hypotheses (H) and $(H1)$ are satisfied, Theorem A.4 implies that $-L$ has a purely discrete spectrum of non-negative eigenvalues and the smallest one λ_1 is positive. Let us prove that the associated eigenfunction η_1 belongs to $L^1(d\mu)$. We have shown in Section B.2 that $\eta_1 e^{-V}$ is bounded. Thus

$$\int_D \eta_1(x)d\mu(x) = \int_D \eta_1(x)e^{-2V(x)}dx \leq \|\eta_1 e^{-V}\|_\infty \int_D e^{-V(x)}dx < +\infty,$$

since $e^{-V(x)} = \frac{1}{\sqrt{x^1 x^2}}e^{-\frac{1}{2}Q(x^1, x^2)}$.

Thus the eigenfunction η_1 belongs to $\mathbb{L}^1(d\mu)$ and therefore, as proved in Theorem B.2, the probability measure $\nu_1 = \frac{\eta_1 d\mu}{\int_D \eta_1 d\mu}$ is the Yaglom limit distribution.

In order to show the uniqueness of the quasi-stationary distribution, we apply Proposition B.12 relating this uniqueness property to the ultracontractivity of the semi-group P_t. Let us show that the sufficient conditions ensuring ultracontractivity stated in Proposition B.14 are satisfied by the SLVKP.

The function V is bounded from below in $D_\varepsilon = \{y \in D; d(y, \partial D) > \varepsilon\}$. In addition, Condition (2.8) implies that $\bar{V}(R) = \sup\{V(x), x \in FD, |x| \leq R\} \leq c'R^4$ and $\bar{G}(R) \geq cR^6$, for positive constants c' and c. Hence Condition (B.10) in Proposition B.14 is satisfied with $\gamma_k = k^{-3/2}$. Thus the killed semi-group P_t of the $SLVKP$ is ultracontractive and then the uniqueness of the quasi-stationary distribution holds (cf. Proposition B.12).

Hence existence and uniqueness of the quasi-stationary distribution holds for X. $\qquad\square$

Remark 3.3. *Since the laws of X_t and Z_t are related via an elementary change of variables formula, a similar result will be true for the stochastic Lotka-Volterra process Z.*

4. Explicit Quasi-stationary Equilibria - Mono-type transient states.

In the above Section we were concerned by conditioning to coexistence's event. Let us now come back to our initial question, that is the long time behavior of the process conditioned

to non-extinction. The SLVKP dynamics is particular in the sense that once hitting the boundary ∂D, the process will no more leave it. Hence, for $t \geq T_{\partial D}$ the process will stay on one half axis, and the dynamics on this axis is given by the process $(H_t^i)_t$ defined in (2.11), that has been extensively studied in [3]. Thus we know from [3] that for $i = 1, 2$, there is a positive killing rate $\lambda_{1,i} > 0$ and a unique quasi-stationary measure $\nu_{1,i}$ on the axis $x^j = 0$ characterized by the ground state $\eta_{1,i}$ (eigenfunction related to $\lambda_{1,i}$), which is a positive function, bounded and square integrable with respect to the corresponding symmetric measure μ^i on each axis. More precisely, we have

$$\nu_{1,i}(dx^i) = \eta_{1,i}(x^i)\,\mu^i(dx^i),$$

with

$$\mu_i(dx^i) = e^{-2\int_1^{x^i} q_i(u)du}dx^i \quad \text{and} \quad q_i(u) = \frac{1}{2u} - \frac{r_i u}{2} + \frac{c_{ii}\gamma_i}{8}.$$

In addition, $\forall A \subset \mathbb{R}_+^*$,

$$e^{\lambda_{1,i}t} \lim_{t \to \infty} \mathbb{P}_{x^i}(X_t^i \in A | T_i > t) = \nu_{1,i}(A), \tag{4.1}$$

We deduce from this study that for all $x^1 > 0$, for all $A \subset \mathbb{R}_+^* \times \mathbb{R}_+$, (resp. $x^2 > 0$ and $A \subset \mathbb{R}_+ \times \mathbb{R}_+^*$),

$$\mathbb{P}_{(x^1,0)}(X_t \in A | T_0 > t) = \nu_{1,1} \otimes \delta_0(A),$$

(resp. $\mathbb{P}_{(0,x^2)}(X_t \in A | T_0 > t) = \delta_0 \otimes \nu_{1,2}(A)$).

We are now led to study, for $x \in (\mathbb{R}_+^*)^2$ and for $A \subset (\mathbb{R}^2 \setminus \{(0,0)\})$, the asymptotic behavior of

$$\mathbb{P}_x(X_t \in A \,|\, T_0 > t) = \frac{\mathbb{P}_x(X_t \in A)}{\mathbb{P}_x(T_{\partial D} > t)} \frac{\mathbb{P}_x(T_{\partial D} > t)}{\mathbb{P}_x(T_0 > t)} \tag{4.2}$$

where T_0 is the hitting time of the origin. We have seen in the previous section that under (2.5) and (2.8), the hitting time $T_{\partial D}$ is almost surely finite and that for any $y \in \partial D$, T_0 is $\mathbb{P}_y$ almost surely finite too. Let us now study the asymptotic behavior of

$$\frac{\mathbb{P}_x(T_{\partial D} > t)}{\mathbb{P}_x(T_0 > t)}.$$

We will compare the three different killing rates λ_1, $\lambda_{1,1}$, $\lambda_{1,2}$ corresponding to the stopping times $T_{\partial D}$, T_1, T_2, (recall that T_i denotes the hitting time of the axis $x^j = 0$).

Notice that if $c_{1,2} = 0$, $(X^1, X^2) = (H^1, H^2)$, $\lambda_1 = \lambda_{1,2} + \lambda_{1,1}$, $\nu_1 = \nu_{1,1} \otimes \nu_{1,2}$. Indeed a standard (and elementary) result in QSD theory says that if ν is a QSD with absorbing set C, the $\mathbb{P}_\nu$-law of the hitting time T_C of C is an exponential law with parameter λ, where λ is exactly the killing rate. In addition, $\mathbb{P}_x(T_C > t)$ behaves like $e^{-\lambda t}$ for large t. Since the minimum of two independent exponential random variables with parameters $\lambda_{1,2}$ and $\lambda_{1,1}$ is an exponential variable of parameter $\lambda_{1,2} + \lambda_{1,1}$, we get $\lambda_1 = \lambda_{1,2} + \lambda_{1,1}$.

The following decomposition is the key point to prove our main theorem. For $x \in (\mathbb{R}_+)^2 \setminus \{(0,0)\}$

$$\mathbb{P}_x(T_0 > t) = \mathbb{P}_x(T_{\partial D} > t) + \sum_{i=1,2} \mathbb{P}_x\left(T_{\partial D} \leq t, X_{T_{\partial D}}^j = 0, \mathbb{P}_{(X_{T_{\partial D}}^i,0)}(T_0 > t - T_{\partial D})\right) \tag{4.3}$$

where $j = 1$ if $i = 2$ and conversely. We are interested in the asymptotic behavior of this quantity, i.e we have to compare the three killing rates λ_1, $\lambda_{1,1}$ and $\lambda_{1,2}$.

We obtain our main result.

12

Theorem 4.1. *Under (2.5) and (2.8), there exists a unique probability measure m such that for all $x \in D$, for all $A \subset (\mathbb{R}_+)^2 \backslash \{(0,0)\}$,*

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

In addition, we have the following description of ν.

- *Competition case (c_{12} and c_{21} positive). We have $\lambda_1 > \lambda_{1,1} + \lambda_{1,2}$, and the support of the QSD in included in the boundaries.*
  Furthermore when $\lambda_{1,2} > \lambda_{1,1}$ (resp. $<$), ν is given by $\nu_{1,1} \otimes \delta_0$ (resp. $\delta_0 \otimes \nu_{1,2}$).
  In other words, the model exhibits an intermediary time scale for which only one type (the dominant trait) is surviving.

- *Cooperation case (c_{12} and c_{21} negative). We have two different situations.*
  - *If $\lambda_1 > \lambda_{1,i}$ for $i = 1$ or $i = 2$, the conclusion is the same as in the competition case.*
  - *If $\lambda_1 < \lambda_{1,i}$ for $i = 1$ and $i = 2$, then*

$$\nu = \frac{1}{1 + \sum_{i,j=1}^2 \frac{c_j}{\lambda_{1,i} - \lambda_1}} \left(\frac{c_2}{\lambda_{1,1} - \lambda_1} \nu_{1,1} \otimes \delta_0 + \delta_0 \otimes \frac{c_1}{\lambda_{1,2} - \lambda_1} \nu_{1,2} + \nu_1 \right), \tag{4.4}$$

    where

$$c_j = \mathbb{P}_{\nu_1}(X^j_{T_{\partial D}} = 0).$$

    We thus have a positive probability to have coexistence of the two species.

Remark 4.2. The only remaining case is the one where $\lambda_1 = \lambda_{1,1} = \lambda_{1,2}$. However the proof of the theorem indicates that this situation is similar to the competition case, though we have no rigorous proof of it. In the discrete setting (as claimed in [4]), a fine analysis of Perron-Frobenius type is in accordance with our guess.

Proof. Our domination arguments allow us to compare the killing rates :

- **The competition case.** This is the case $c_{12} > 0$. In this case we can show with a similar argument as in the proof of Theorem 2.2 that starting from the same initial point, $X^i_t \le H^i_t$ for $i = 1, 2$. Hence $\lambda_1 \ge \lambda_{1,1} + \lambda_{1,2}$. Since the killing rates are positive, it follows that $\lambda_1 > \lambda_{1,i}$ for $i = 1, 2$. In particular $\mathbb{E}_x\left[e^{\lambda_{1,i} T_{\partial D}}\right] < +\infty$. Hence

$$\liminf_{t \to +\infty} e^{\lambda_{1,i} t} \mathbb{P}_x \left(T_{\partial D} \le t \,,\, X^j_{T_{\partial D}} = 0 \,,\, \mathbb{P}_{(X^i_{T_{\partial D}}, 0)}(T_0 > t - T_{\partial D}) \right) =$$

$$= \liminf_{t \to +\infty} \mathbb{E}_x \left(\mathbb{1}_{T_{\partial D} \le t} \, \mathbb{1}_{X^i_{T_{\partial D}} = 0} \, e^{\lambda_{1,i} T_{\partial D}} \, e^{\lambda_{1,i}(t - T_{\partial D})} \mathbb{P}_{(0, X^j_{T_{\partial D}})}(T_0 > t - T_{\partial D}) \right)$$

$$\ge \mathbb{E}_x \left(\mathbb{1}_{X^i_{T_{\partial D}} = 0} \, e^{\lambda_{1,i} T_{\partial D}} \, \eta_{1,i}(X^i_{T_{\partial D}}) \right) > 0 \quad (\text{ at least for one } i),$$

  according to Fatou's lemma, the positivity of the ground state and by Proposition 2.3. It follows that the rate of decay of $\mathbb{P}_x(T_0 > t)$ is at most $e^{-\lambda_{1,i} t}$, while the one of $P_x(T_{\partial D} > t)$ is $e^{-\lambda_1 t}$, hence as $t \to +\infty$,

$$\mathbb{P}_x(X_t \in A \,|\, T_0 > t) \to 0 \,,$$

  if $A \subset D$. Hence, the support of the quasi-stationary distribution will be included in the boundaries. Thanks to Proposition 2.3, we know that both terms in the sum

$\sum_{i=1,2}$ in (4.3) are positive, so that the leading term in the sum will be equivalent to $\mathbb{P}_x(T_0 > t)$. If $\lambda_{1,1} > \lambda_{1,2}$ this leading term is of order $e^{-\lambda_{1,2}t}$, the proof being exactly the same as before. The value of the quasi-stationary distribution follows.

- **The weak cooperative case.** This is the case if $c_{1,2} < 0$. Here a comparison argument gives $\lambda_1 \leq \lambda_{1,1} + \lambda_{1,2}$. But there is no a priori reason for λ_1 to be smaller than $\lambda_{1,i}$. In particular if $\lambda_1 > \lambda_{1,i}$ for $i = 1$ or 2, we are in the same situation as in the competition case, and the quasi-limiting distribution is supported by ∂D because one exits from D by hitting $x^j = 0$ with a positive probability as we mentioned in proposition 2.3.

It remains to look at the case $\lambda_1 \leq \lambda_{1,i}$ for $i = 1, 2$.

Denote by ψ_j the law of $T_{\partial D}$ when the process exits D by hitting $x^j = 0$. Denote by ζ_s^i the conditional law of $X_{T_{\partial D}}^i$ knowing $T_{\partial D} = s$ and $X_{T_{\partial D}}^j = 0$. Then

$$e^{\lambda_1 t} \, \mathbb{P}_x \left(T_{\partial D} \leq t \,,\, X_{T_{\partial D}}^j = 0 \,,\, \mathbb{P}_{(X_{T_{\partial D}}^i, 0)}(T_0 > t - T_{\partial D}) \right)$$

$$= \int_0^{+\infty} e^{\lambda_1 t} \, \mathbb{I}_{s<t} \, \mathbb{E}_{\zeta_s^i}(\mathbb{I}_{T_0 > t-s}) \, \psi_j(ds).$$

It has been proved in Corollary 7.9 of [3] that for any $\lambda < \lambda_{1,i}$,

$$\sup_{\theta^i} \mathbb{E}_{\theta^i}[e^{\lambda T_0^i}] < +\infty$$

where θ^i describes the set of all probability measures on $x^j = 0, x^i > 0$ and T_0^i is the first hitting time of 0 for the one dimensional logistic Feller diffusion H^i.

Hence $\mathbb{E}_{\zeta_s^i}(\mathbb{I}_{T_0 > t-s}) \leq C \, e^{-\lambda(t-s)}$ for some universal constant C and all s. It follows that, provided $\lambda_1 < \lambda_{1,i}$ (in which case we choose $\lambda_1 < \lambda < \lambda_{1,i}$), for all $T > 0$,

$$\lim_{t \to +\infty} \int_0^T e^{\lambda_1 t} \, \mathbb{I}_{s<t} \, \mathbb{E}_{\zeta_s^i}(\mathbb{I}_{T_0 > t-s}) \, \psi_j(ds) = 0 \,.$$

It remains to study

$$\lim_{t \to +\infty} e^{\lambda_1 t} \, \mathbb{P}_x \left(t \geq T_{\partial D} > T \,,\, X_{T_{\partial D}}^j = 0 \,,\, \mathbb{P}_{(X_{T_{\partial D}}^i, 0))}(T_0 > t - T_{\partial D}) \right) \,.$$

To this end we first remark that for T large enough we may replace $\mathbb{P}_x$ by $\mathbb{P}_{\nu_1}$. Indeed, denote

$$h(T, t, y) = \mathbb{P}_y \left(t - T \geq T_{\partial D} > 0 \,,\, X_{T_{\partial D}}^j = 0 \,,\, \mathbb{P}_{(X_{T_{\partial D}}^i, 0)}(T_0 > t - T - T_{\partial D}) \right) \,.$$

Since ν_1 is the Yaglom limit related to D and $0 \leq h(T, t, y) \leq 1$ for all $y \in D$ and all $T < t$, for $\varepsilon > 0$ one can find T large enough such that for all $t > T$,

$$\mathbb{P}_x \left(t \geq T_{\partial D} > T \,,\, X_{T_{\partial D}}^j = 0 \,,\, \mathbb{P}_{(X_{T_{\partial D}}^i, 0)}(T_0 > t - T_{\partial D}) \right) =$$

$$= \quad \mathbb{E}_x(\mathbb{I}_{T_{\partial D} > T} \, h(T, t, X_T))$$

$$\approx_\varepsilon \quad \mathbb{E}_{\nu_1}(\mathbb{I}_{T_{\partial D} > T} \, h(T, t, X_T))$$

$$= \quad \mathbb{P}_{\nu_1} \left(t \geq T_{\partial D} > T \,,\, X_{T_{\partial D}}^j = 0 \,,\, \mathbb{P}_{(X_{T_{\partial D}}^i, 0)}(T_0 > t - T_{\partial D}) \right)$$

where $a \approx_\varepsilon b$ means that the ratio a/b satisfies $1 - \varepsilon \leq a/b \leq 1 + \varepsilon$.

Now, since ν_1 is a quasi-stationary distribution, starting from ν_1, the law of $T_{\partial D}$ is the exponential law with parameter λ_1, so that $\psi_j(ds) = c_j \, \lambda_1 \, e^{-\lambda_1 s} ds$ where $c_j = \mathbb{P}_{\nu_1}(X^j_{T_{\partial D}} = 0)$ is the exit probability first hitting the half-axis j. In addition the conditional law ζ^i_s does not depend on s, we shall denote it by π^i from now on. This yields

$$e^{\lambda_1 t} \, \mathbb{P}_{\nu_1} \left(t \geq T_{\partial D} > T \, , \, X^j_{T_{\partial D}} = 0 \, , \, \mathbb{P}_{(X^i_{T_{\partial D}},0)}(T_0 > t - T_{\partial D}) \right)$$

$$= \; e^{\lambda_1 t} \int_T^t c_j \, \lambda_1 \, e^{-\lambda_1 s} \, \mathbb{P}_{\pi^i}(T_0 > t - s) \, ds$$

$$= \; c_j \, \lambda_1 \int_T^t e^{-(\lambda_{1,i} - \lambda_1)(t-s)} \left(e^{\lambda_{1,i}(t-s)} \, \mathbb{P}_{\pi^i}(T_0 > t - s) \right) ds \, .$$

Recall that $\nu_{1,i}$ is the unique Yaglom limit on axis i. As shown in [3], for any initial law π, in particular for π^i, $\lim_{t \to +\infty} e^{\lambda_{1,i} t} \, \mathbb{P}_\pi(T_0 > t) = 1$. Using Lebesgue bounded convergence theorem we thus obtain that for all $T > 0$,

$$\lim_{t \to +\infty} e^{\lambda_1 t} \, \mathbb{P}_{\nu_1} \left(t \geq T_{\partial D} > T \, , \, X^j_{T_{\partial D}} = 0 \, , \, \mathbb{P}_{(X^i_{T_{\partial D}},0)}(T_0 > t - T_{\partial D}) \right) = \frac{c_j \, \lambda_1}{\lambda_{1,i} - \lambda_1} \, .$$

Since the result does not depend upon T, we may use our approximation result of $\mathbb{P}_x$ by $\mathbb{P}_{\nu_1}$ for all ε hence finally obtain for all x,

$$\lim_{t \to +\infty} e^{\lambda_1 t} \, \mathbb{P}_x \left(t \geq T_{\partial D} > T \, , \, X^j_{T_{\partial D}} = 0 \, , \, \mathbb{P}_{(X^i_{T_{\partial D}},0)}(T_0 > t - T_{\partial D}) \right) = \frac{c_j \, \lambda_1}{\lambda_{1,i} - \lambda_1} \, .$$

Let us now consider $A \subset \mathbb{R}^2 \backslash \{(0,0)\}$. To compute $\mathbb{P}_x(X_t \in A, T_0 > t)$, we have to write $A = (A \cap D) + (A \cap \mathbb{R}^*_+ \times \{0\}) + (A \cap \{0\} \times \mathbb{R}^*_+)$ and we will compute separately the three terms. Let us first remark that Since ν_1 is the unique QSD related to the absorbing set ∂D, it is equal to the Yaglom limit and thus

$$\frac{\mathbb{P}_x(X_t \in A \cap D)}{\mathbb{P}_x(T_{\partial D} > t)} \to_{t \to +\infty} \nu_1(A \cap D).$$

Let us now write $A_1 = A \cap \mathbb{R}^*_+ \times \{0\}$. Thus

$$\frac{\mathbb{P}_x(X_t \in A_1)}{\mathbb{P}_x(T_{\partial D} > t)} = \frac{\mathbb{P}_x(X_t \in A_1)}{\mathbb{P}_x(T^1 > t, T^2 = T_{\partial D})} \frac{\mathbb{P}_x(T^1 > t, T^2 = T_{\partial D})}{\mathbb{P}_x(T_{\partial D} > t)} \, .$$

By a similar reasoning as previously, one can prove that $\frac{\mathbb{P}_x(X_t \in A_1)}{\mathbb{P}_x(T^1 > t, T^2 = T_{\partial D})} \to_{t \to +\infty}$ $\nu_{1,1}(A_1)$ and that $\frac{\mathbb{P}_x(T^1 > t, T^2 = T_{\partial D})}{\mathbb{P}_x(T_{\partial D} > t)} \to_{t \to +\infty} \frac{c_2 \lambda_1}{\lambda_{1,1} - \lambda_1}$. A similar result inverting indices 1 and 2 holds for the third term. That concludes the proof of (4.4), in the case where $\lambda_1 < \lambda_{1,i}$, for $i = 1, 2$.

This result together with the competition case indicates (but we do not have any rigorous proof of this) that if $\lambda_1 = \lambda_{1,i}$ for some i, then the QSD (conditioned to hitting the origin) is again supported by the axes.

$\square$

The conclusion of this study is partly intuitive. In the competition case, one of the species will kill the other one before dying. In the cooperation case, apparently, all can happen, including coexistence of the two types up to a common time of extinction. The problem is to know whether all situations for the killing rates are possible or not.

Here is an heuristic simple argument (to turn it in a rigorous one involves some technicalities): Fix all coefficients equal say to 1 except $c_{12} = c_{21} = -c$ with $c > 0$. Condition (2.8) reads $0 < c < 1$. In this situation $\lambda_{12} = \lambda_{11} = \lambda$ and both λ and λ_1 depend continuously on c. When $c \to 0$ (near the independent case) we know that ν concentrates on both axes. When $c \to 1$ the rate λ_1 of return from infinity decreases to 0 (this is the point to be carefully checked) so that there is some intermediate value c_c where the phase transition $\lambda = \lambda_1$ occurs.

APPENDIX A. **Killed Kolmogorov diffusion processes and their spectral theory.**

Let D be an open connected subset of $\mathbb{R}^d$, V a C^2 function defined on D. We introduce the stochastic differential equation

$$dX_t = dB_t - \nabla V(X_t)dt \quad , \quad X_0 = x \in D \,, \tag{A.1}$$

for which a pathwise unique solution exists up to an explosion time ξ. The law of the process starting from x will be denoted by $\mathbb{P}_x$, and for a non-negative measure ν on D we denote by $\mathbb{P}_\nu = \int \mathbb{P}_x \nu(dx)$.

For a subset A of the closure $\bar{D}$ of D and for $\varepsilon > 0$ we introduce

$$T_A^\varepsilon = \inf \{s \geq 0 \,; d(X_s, A) < \varepsilon\} \quad , \quad T_A = \lim_{\varepsilon \to 0} T_A^\varepsilon \,, \tag{A.2}$$

where $d(.,.)$ denotes the usual euclidean distance. T_A^ε and T_A are thus stopping times for the natural filtration. We shall be mainly interested to the cases when A is a subset of the boundary ∂D.

Our first hypothesis is that the process cannot explode unless it reaches the boundary i.e

$$\text{for all } x \in D, \, \xi \geq T_{\partial D} \,, \, \mathbb{P}_x \text{ almost surely.} \tag{A.3}$$

If D is bounded, (A.3) is automatically satisfied. If D is not bounded, it is enough to find some Lyapunov function. We shall make some assumptions later on implying that a specific function is a Lyapunov function, so the discussion on (A.3) will be delayed.

The peculiar aspect of gradient drift diffusion process as (A.1) is that the generator L defined for any function $g \in C^\infty$ by

$$L = \frac{1}{2} \Delta - \nabla V.\nabla \quad , \tag{A.4}$$

is symmetric w.r.t. the measure μ defined by

$$\mu(dx) = e^{-2V(x)} \, dx \,. \tag{A.5}$$

The following properties of the process can be proved exactly as Proposition 2.1, Theorem 2.2 and the discussion at the beginning of Section 3 in [3].

16

Theorem A.1. *Assume that (A.3) holds. Then there exists a self-adjoint semi-group (P_t) on $\mathbb{L}^2(\mu)$ such that for all bounded Borel function f,*

$$P_t f(x) := \mathbb{E}_x[f(X_t)\, \mathbb{1}_{t < T_{\partial D}}].$$

Moreover for any bounded Borel function F defined on $\Omega = C([0,t], D)$ it holds

$$\mathbb{E}_x\left[F(\omega)\, \mathbb{1}_{t < T_{\partial D}(\omega)}\right] = \mathbb{E}^{\mathbb{W}_x}\left[F(\omega)\, \mathbb{1}_{t < T_{\partial D}(\omega)} \exp\left(V(x) - V(\omega_t) - \frac{1}{2}\int_0^t (|\nabla V|^2 - \Delta V)(\omega_s)ds\right)\right]$$

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

It follows that for all $x \in D$ and all $t > 0$ there exists some density $r(t, x, .)$ that verifies

$$P_t f(x) = \int_D f(y)\, r(t, x, y)\, \mu(dy)$$

for all bounded Borel function f.

If in addition there exists some $C > 0$ such that $|\nabla V|^2(y) - \Delta V(y) \geq -C$ for all $y \in D$, then for all $t > 0$ and all $x \in D$, $r(t, x, \cdot) \in \mathbb{L}^2(\mu)$ with

$$\int_D r^2(t, x, y)\, \mu(dy) \leq (1/2\pi t)^{\frac{d}{2}} e^{Ct} e^{2V(x)}. \tag{A.6}$$

Remark A.2. If $V(x) \to +\infty$ as $x \to \infty$ in D, the condition $|\nabla V|^2(y) - \Delta V(y) \geq -C$ for all $y \in D$ is sufficient for (A.3) to hold. Just use Ito's formula with V as in [18] Theorem 2.2.19. $\diamond$

We thus have that for any measurable and compact subset $A \subset D$ and any $x \in D$,

$$\mathbb{P}_x(X_t \in A, T_{\partial D} > t) = \int \mathbb{P}_y(X_{t-1} \in A, T_{\partial D} > t-1)\, r(1, x, y)\, \mu(dy) \tag{A.7}$$

$$= \int P_{t-1}(\mathbb{1}_A)(y)\, r(1, x, y)\, \mu(dy)$$

$$= \int \mathbb{1}_A(y)\, (P_{t-1}r(1, x, .))(y)\, \mu(dy).$$

Hence, the long time behavior of the law of the killed process is completely described by $P_t r(1, ., .)$.

Since both $\mathbb{1}_A$ and $r(1, x, .)$ are in $\mathbb{L}^2(\mu)$, the $\mathbb{L}^2$ spectral theory of P_t is particularly relevant.

This spectral theory can be deduced from the much well known spectral theory for Schrödinger operators, thanks to the following standard transform: define for $f \in \mathbb{L}^2(D, dx)$ (resp. $f \in C_0^\infty(D)$)

$$\tilde{P}_t(f) = e^{-V} P_t(f\, e^V) \quad , \quad \tilde{L}f = \frac{1}{2}\Delta f - \frac{1}{2}(|\nabla V|^2 - \Delta V)f. \tag{A.8}$$

$\tilde{P}_t$ is then a self-adjoint strongly continuous semi-group on $\mathbb{L}^2(D, dx)$ whose generator coincides with $\tilde{L}$ on $C_0^\infty(D)$. Notice that $\tilde{P}_t$ has a stochastic representation as a Feynman-Kac semi-group, i.e.

$$\tilde{P}_t f(x) = \mathbb{E}^{\mathbb{W}_x}\left[f(\omega(t))\, \mathbb{1}_{t < T_{\partial D}} \exp\left(-\frac{1}{2}\int_0^t (|\nabla V|^2 - \Delta V)(\omega_s)ds\right)\right]. \tag{A.9}$$

The spectral relationship is clear: if λ is some eigenvalue for $\tilde{P}_t$ associated to ψ (i.e. $\tilde{P}_t(\psi) = e^{-\lambda t}\psi$), it is an eigenvalue of P_t associated with $\eta = e^V \psi$ and conversely.

For simplicity we shall impose conditions ensuring that the spectrum is discrete, in particular reduced to the pure point spectrum. Necessary and sufficient conditions for this property to hold have been obtained by Maz'ya and Shubin (see [15]) extending results by Molchanov in 1953. The criterion is written in terms of Wiener capacity, hence not very easy to directly read on the potential V. We shall here assume a less general but more tractable condition taken from the Euclidean case explained in chapter 3 of Berezin and Shubin [1]. To this end we now introduce our main hypotheses:

Definition A.3. (1) *We say that hypothesis (H1) is satisfied if (A.3) holds and if for all $x \in D$,*
$$\mathbb{P}_x(T_{\partial D} < +\infty) = 1 \,.$$

(2) *Hypothesis (H2) holds if*
$$G(y) = |\nabla V|^2(y) - \Delta V(y) \geq -C > -\infty$$
for all $y \in D$.

(3) *Hypothesis (H3) holds if*
$$\bar{G}(R) = \inf\{G(y); |y| \geq R \text{ and } y \in D\} \to +\infty \text{ as } R \to \infty \,.$$

(4) *We say that hypothesis (H4) holds if for all $R > 0$ one can find an increasing sequence of compact sets $K_n(R)$ such that the boundary of $K_n(R) \cap \bar{D}$ is smooth and $\bigcup_n (K_n(R) \cap \bar{D}) = \bar{B}(0,R) \cap \bar{D}$, where $\bar{B}(0,R)$ is the closed Euclidean ball of radius R.*

For simplicity we say that (H) holds when (A.3) and (H2)-(H4) are satisfied.

We may now state

Theorem A.4. *Assume that (H) is satisfied, then $-L$ has a purely discrete spectrum $0 \leq \lambda_1 < \lambda_2 < ....$ Each associated eigenspace E_i is finite dimensional. If (H1) holds, $\lambda_1 > 0$.*

Furthermore E_1 is one dimensional and we may find a (normalized) eigenfunction η_1 which is everywhere positive. In particular for all f, g in $\mathbb{L}^2(\mu)$,
$$\lim_{t \to +\infty} e^{\lambda_1 t} \langle g, P_t f \rangle_\mu = \langle g, \eta_1 \rangle \langle f, \eta_1 \rangle \,.$$

Proof. The proof of the first statement is similar to the one of Theorem 3.1 in [1], replacing $B(0,R)$ therein by $D \cap B(0,R)$. Hypothesis (H4) here is useful to show that the embedding $\mathbb{H}^1(B(0,R) \cap D) \hookrightarrow \mathbb{L}^2(B(0,R) \cap D)$ is compact. Indeed the result is known replacing $B(0,R)$ by $K_n(R)$ (due to the smoothness of the boundary). To get the compactness result, it is then enough to use a diagonal procedure.

$\lambda_1 \geq 0$ is obvious since $-L$ is a non-negative operator.

It directly follows from the representation formula in Theorem A.1 (or (A.9)) that the semi-group is positivity improving (i.e. if $f \geq 0$ and $f \neq 0$, $P_t f(x) > 0$ for all $x \in D$ and all $t > 0$). The proof of the second statement (non degeneracy of the ground state η_1) is thus similar to the one of Theorem 3.4 in [1].

Finally, as in [3] section 3, hypothesis (H1) implies that for $f \in \mathbb{L}^2(\mu)$, $P_t f$ goes to 0 in $\mathbb{L}^2(\mu)$ as $t \to +\infty$. This shows that $\lambda_1 > 0$. $\qquad\square$

Remark A.5. Contrary to the one dimensional case, for $i \geq 2$ the eigenspaces are not necessarily one dimensional.

APPENDIX B. **Quasi-stationary distributions and Yaglom limit in D.**

The aim of this section is to study the asymptotic behavior of the law of X_t conditioned on not reaching the boundary.

B.1. **The general result.** The first result is an immediate consequence of the spectral theory.

Proposition B.1. *Assume that hypothesis (H) is satisfied. If $A \subset D$ is such that $\mathbb{1}_A \in \mathbb{L}^2(\mu)$, then for all $x \in D$,*

$$\lim_{t \to +\infty} e^{\lambda_1 t} \, \mathbb{P}_x(X_t \in A \, , \, T_{\partial D} > t) \, = \, \langle \mathbb{1}_A, \eta_1 \rangle \, \eta_1(x) \, .$$

In particular if $\eta_1 \notin \mathbb{L}^1(\mu)$, $\lim_{t \to +\infty} \mathbb{P}_x(X_t \in A \,|\, T_{\partial D} > t) = 0$.

Proof. Recall (A.7), i.e. $\mathbb{P}_x(X_t \in A \, , \, T_{\partial D} > t) = \int \mathbb{1}_A(y) \, (P_{t-1} r(1, x, .))(y) \, \mu(dy)$. Since both $\mathbb{1}_A$ and $r(1, x, .)$ are in $\mathbb{L}^2(\mu)$ we may apply Theorem A.4 and get

$$\lim_{t \to +\infty} e^{\lambda_1(t-1)} \, \mathbb{P}_x(X_t \in A \, , \, T_{\partial D} > t) \, = \, \langle \mathbb{1}_A, \eta_1 \rangle \, \langle r(1, x, .), \eta_1 \rangle \, .$$

Since η_1 is an eigenfunction it holds

$$e^{\lambda_1} \, \langle r(1, x, .), \eta_1 \rangle = e^{\lambda_1} P_1 \eta_1(x) = \eta_1(x),$$

where equalities hold in $\mathbb{L}^2(\mu)$. Since η_1 satisfies $\tilde{L}\eta_1 = -\lambda_1 \, \eta_1$ in D, standard results in p.d.e.'s theory show that η_1 is regular (C^2) in D, hence these equalities extend to all $x \in D$. This yields the first statement.

For the second statement, choose some increasing sequence D_n of compact subsets of D, such that $\bigcup_n D_n = D$. It holds

$$\mathbb{P}_x(X_t \in A \,|\, T_{\partial D} > t) = \frac{\mathbb{P}_x(X_t \in A \, , \, T_{\partial D} > t)}{\mathbb{P}_x(X_t \in D \, , \, T_{\partial D} > t)} \leq \frac{\mathbb{P}_x(X_t \in A \, , \, T_{\partial D} > t)}{\mathbb{P}_x(X_t \in D_n \, , \, T_{\partial D} > t)}$$

so that according to what precedes for all n,

$$\limsup_{t \to +\infty} \mathbb{P}_x(X_t \in A \,|\, T_{\partial D} > t) \leq \frac{\langle \mathbb{1}_A, \eta_1 \rangle}{\langle \mathbb{1}_{D_n}, \eta_1 \rangle} \, .$$

The infimum over n on the right hand side is equal to 0 as soon as $\int_D \eta_1 d\mu = +\infty$, hence the result. $\qquad\square$

In view of what precedes, a non trivial behavior of the conditional law implies that $\eta_1 \in \mathbb{L}^1(\mu)$. Conversely this property is enough to get the following theorem whose statement and proof are the same as Theorem 5.2 in [3]. Observe that the only thing we have to do is to control $P_t \mathbb{1}_A$ for sets A of possible infinite μ mass.

19

Theorem B.2. *Assume that hypothesis (H) holds and that $\eta_1 \in \mathbb{L}^1(\mu)$.*
Then $d\nu_1 = \eta_1 d\mu / \int_D \eta_1(y)\mu(dy)$ is a quasi-stationary distribution, namely for every $t \geq 0$ and any Borel subset A of D,

$$\mathbb{P}_{\nu_1}(X_t \in A \mid T_{\partial D} > t) = \nu_1(A).$$

Also for any $x > 0$ and any Borel subset A of D,

$$\lim_{t \to +\infty} e^{\lambda_1 t} \, \mathbb{P}_x(T_{\partial D} > t) = \left(\int_D \eta_1(y)\mu(dy) \right) \eta_1(x), \tag{B.1}$$

$$\lim_{t \to +\infty} e^{\lambda_1 t} \, \mathbb{P}_x(X_t \in A, \, T_{\partial D} > t) = \left(\int_A \eta_1(y)\mu(dy) \right) \eta_1(x).$$

This implies that

$$\lim_{t \to +\infty} \mathbb{P}_x(X_t \in A \mid T_{\partial D} > t) = \nu_1(A),$$

and the probability measure ν_1 is the Yaglom limit distribution.

Remark B.3. The proof of Theorem 5.2 in [3] lies on the following estimate

$$r(t, x, y) \leq C(x) \, e^{-\lambda_1 t} \, \eta_1(y)$$

for all x, y in D ($(0, +\infty)$ in [3]), $t > 1$ and some function $C(x)$. This result is still true here and the proof based on the Harnack's inequality is similar. $\diamond$

B.2. **Ground state estimates.** We wish now to give tractable conditions for η_1 to be in $\mathbb{L}^1(\mu)$. Of course if μ is bounded there is nothing to do since $\eta_1 \in \mathbb{L}^2(\mu)$, so that this subsection is only interesting for unbounded μ. For simplicity of notation we assume that the origin $0 \in \bar{D}^c$ so that if $x \in D$, $|x| \geq \alpha > 0$. The results of this subsection are adapted from Section 4 in [3].

Recall that $\eta_1 = e^V \psi_1$ where ψ_1 is the ground state of $\tilde{L}$ (cf. (A.8)), i.e. the (positive and normalized) eigenfunction of $\tilde{L}$ associated to $-\lambda_1$. So in order to get some estimates on η_1 it is enough to get some estimates on ψ_1. Since $\psi_1 = e^{\lambda_1} \tilde{P}_1(\psi_1)$ it is interesting to prove contractivity properties for $\tilde{P}_1$.

Let us first recall the definition of ultracontractivity.

Definition B.4. *A semi-group of contractions $(Q_t)_{t \geq 0}$ is said to be ultracontractive if Q_t maps continuously $\mathbb{L}^2(\mu)$ in $\mathbb{L}^\infty(\mu)$ for any $t > 0$.*
Remark that by duality, and thanks to the symmetry of μ, Q_t also maps continuously $\mathbb{L}^1(\mu)$ to $\mathbb{L}^2(\mu)$.

Proposition B.5. *Assume that Hypothesis (H2) and (A.9) are satisfied. Then $\tilde{P}_t$ is ultracontractive. It follows that $\psi_1 = \eta_1 e^{-V}$ is bounded.*

Proof. We may compare the fundamental solution (kernel) of $\tilde{P}_t$ with the one of the Schrödinger equation with constant potential as in [1] by directly using the representation (A.9).
Introduce the Dirichlet heat semi-group in D i.e.

$$P_t^D f(x) = \mathbb{E}^{\mathbb{W}_x} \left[f(\omega(t)) \, \mathbb{1}_{t < T_{\partial D}} \right] = \int_D f(y) \, p_t^D(x, y) \, dy. \tag{B.2}$$

Hypothesis (H2) and (A.9) immediately imply that

$$\tilde{p}_t(x,y) \leq e^{Ct/2} p_t^D(x,y) \leq e^{Ct/2} (2\pi t)^{-d/2} e^{|x-y|^2/2t} \tag{B.3}$$

where $\tilde{p}_t$ denotes the (symmetric) kernel of $\tilde{P}_t$ w.r.t. the Lebesgue measure.

(B.3) shows that $\tilde{P}_t$ has a bounded kernel for all $t > 0$, and hence that $\tilde{P}_t$ is ultracontractive. In particular ψ_1 is bounded $\psi_1 = e^{\lambda_1} since \tilde{P}_1(\psi_1)$, hence $\eta_1 e^{-V}$ is bounded. More generally any eigenfunction ψ_k is bounded. $\qquad\square$

From the previous proposition, we deduce that $\eta_1 \in \mathbb{L}^1(\mu)$ as soon as $\int e^{-V(x)} dx < +\infty$. One can improve this result. Recall that p_1^D denotes the Dirichlet heat kernel defined in (B.2). Notice that $\int_D p_1^D(x,y) \, dy = \mathbb{W}_x(T_{\partial D} > t)$ goes to zero as x tends to the boundary.

Proposition B.6. *Assume that hypothesis (H) is fulfilled. Assume in addition that there exists some $R > 0$ such that the following is satisfied*

$$\int_{D \cap \{d(x,\partial D) > R\}} e^{-2V(x)} \, dx \; < \; +\infty \; and \; \int_{D \cap \{d(x,\partial D) \leq R\}} \left(\int_D p_1^D(x,y) \, dy \right) e^{-V(x)} \, dx \; < \; +\infty \,. \tag{B.4}$$

Then $\eta_1 \in \mathbb{L}^1(\mu)$. More generally any eigenfunction $\eta_k \in \mathbb{L}^1(\mu)$.

Proof. Since η_k is normalized,

$$\int_{D \cap \{d(x,\partial D)\}} \eta_k(x) \, d\mu \leq \left(\int_{D \cap \{d(x,\partial D)\}} e^{-2V(x)} \, dx \right)^{1/2} < +\infty \,.$$

Now

$$\begin{aligned}
\int_{D \cap \{d(x,\partial D) \leq R\}} \eta_k(x) \, d\mu &= \int_{D \cap \{d(x,\partial D) \leq R\}} \psi_k(x) \, e^{-V(x)} \, dx \\
&= \int_{D \cap \{d(x,\partial D) \leq R\}} \left(\int_D e^{\lambda_k} \psi_k(y) \, \tilde{p}_1(x,y) \, dy \right) e^{-V(x)} \, dx \\
&\leq e^{C/2} e^{\lambda_k} \parallel \psi_k \parallel_\infty \int_{D \cap \{d(x,\partial D) \leq R\}} \left(\int_D p_1^D(x,y) \, dy \right) e^{-V(x)} \, dx
\end{aligned}$$

and the result follows. $\qquad\square$

Remark B.7. Remark that we can replace p_1^D by any p_s^D with $s > 0$ in the previous proof.

B.3. **Rate of convergence.** According to the spectral representation we may decompose each function in $\mathbb{L}^2$. We introduce some notation.

Definition B.8. *We denote by E_2 the eigenspace associated with λ_2. We know that $dim(E_2) = n_2 < +\infty$ and we may choose an orthonormal basis of E_2, $(\eta_{2,1}, ..., \eta_{2,n_2})$. We denote by $pr^\perp$ the orthogonal projection onto the orthogonal of $\mathbb{R}\eta_1 \oplus E_2$.*

We thus have that

$$P_{t-1} r(1, x, .) = e^{-\lambda_1 t} \eta_1(x) \, \eta_1 + e^{-\lambda_2 t} \sum_{i=1}^{n_2} \eta_{2,i}(x) \, \eta_{2,i} + e^{-\lambda_3(t-1)} h(t, x, .) \tag{B.5}$$

where $h(t, x, .)$ is orthogonal to $\mathbb{R}\eta_1 \oplus E_2$ and such that $\| h(t, x, .) \|_{\mathbb{L}^2(\mu)} \leq \| pr^\perp r(1, x, .) \|_{\mathbb{L}^2(\mu)}$. Hence (recall (A.7)) if $\mathbb{1}_A \in \mathbb{L}^2(\mu)$,

$$
\begin{aligned}
\mathbb{P}_x(X_t \in A, \, T_{\partial D} > t) \; = \; & e^{-\lambda_1 t}\langle \mathbb{1}_A, \eta_1 \rangle \, \eta_1(x) + e^{-\lambda_2 t} \sum_{i=1}^{n_2} \eta_{2,i}(x) \, \langle \mathbb{1}_A, \eta_{2,i} \rangle \qquad \text{(B.6)} \\
& + \; e^{-\lambda_3(t-1)} \, \langle h(t, x, .), \mathbb{1}_A \rangle \,.
\end{aligned}
$$

If we could replace A by D we would obtain an expansion of the conditional probability $\mathbb{P}_x(X_t \in A \,|\, T_{\partial D} > t)$. But actually we have

Lemma B.9. *If (H) and (B.4) are satisfied, P_1 is a bounded operator from $\mathbb{L}^\infty(\mu)$ to $\mathbb{L}^2(\mu)$.*

Assume firstly the Lemma B.9. Then we may write

$$
\mathbb{P}_x(T_{\partial D} > t) = P_t(\mathbb{1}_D)(x) = P_{t-1}(P_1(\mathbb{1}_D))(x)
$$

with $P_1(\mathbb{1}_D) \in \mathbb{L}^2(\mu)$. Note that

$$
\langle P_1(\mathbb{1}_D), \eta_k \rangle = \int_D e^{-\lambda_k} \, \eta_k \, d\mu
$$

since (B.4) implies that each eigenfunction η_k is in $\mathbb{L}^1(\mu)$. We thus deduce the

Proposition B.10. *If (H) and (B.4) are satisfied then for all $x \in D$ and all measurable subset $A \subset D$ it holds*

$$
\lim_{t \to +\infty} e^{(\lambda_2 - \lambda_1)t} \, (\mathbb{P}_x(X_t \in A \,|\, T_{\partial D} > t) - \nu_1(A)) \; =
$$

$$
\frac{\sum_{i=1}^{n_2} \eta_{2,i}(x) \, (\langle \mathbb{1}_A, \eta_{2,i}\rangle\langle \mathbb{1}_D, \eta_1 \rangle - \langle \mathbb{1}_D, \eta_{2,i}\rangle\langle \mathbb{1}_A, \eta_1 \rangle)}{\eta_1(x) \, (\langle \mathbb{1}_D, \eta_1 \rangle)^2} \,.
$$

It remains to prove Lemma B.9. To this end let us first state an upperbound for $\tilde{p}_t$.

Lemma B.11. *If hypothesis (H) is fulfilled, there exist a constant M and a non-negative function B satisfying $\lim_{u \to +\infty} B(u) = +\infty$ such that for any x, y in D,*

$$
0 < \tilde{p}_1(x, y) \leq M \, e^{-|x-y|^2/4} \, e^{-B(|x| \vee |y|)} \,.
$$

Proof. We can obtain an upper bound for $\tilde{p}_t$, when hypothesis (H) is fulfilled. To this end, for a non-negative f but this time $\varepsilon = |x|/2$ we write

$$
\begin{aligned}
\int_D f(y) \tilde{p}_t(x, y) \, dy \; = \; & \mathbb{E}^{\mathbb{W}_x}\left[f(\omega(t)) \, \mathbb{1}_{t < \tau_x(\varepsilon)} \, \mathbb{1}_{t < T_{\partial D}} \exp\left(-\frac{1}{2} \int_0^t (|\nabla V|^2 - \Delta V)(\omega_s) ds \right) \right] \\
& + \; \mathbb{E}^{\mathbb{W}_x}\left[f(\omega(t)) \, \mathbb{1}_{T_{\partial D} > t \geq \tau_x(\varepsilon)} \exp\left(-\frac{1}{2} \int_0^t (|\nabla V|^2 - \Delta V)(\omega_s) ds \right) \right] \\
& \leq \; e^{-t \bar{G}(|x|/2)/2} \, \mathbb{E}^{\mathbb{W}_x}\left[f(\omega(t)) \, \mathbb{1}_{t < T_{\partial D})} \right] + e^{Ct/2} \, \mathbb{E}^{\mathbb{W}_x}\left[f(\omega(t)) \, \mathbb{1}_{T_{\partial D} > t \geq \tau_x(\varepsilon)} \right]
\end{aligned}
$$

The first term in the sum above is less than

$$
e^{-t \bar{G}(|x|/2)/2} \int f(y) \, p_t^D(x, y) \, dy \,.
$$

22

For the second term we shall assume that the support of f is included in the ball $B(x, \varepsilon/2)$. Recall that for a brownian motion starting at x, the exit distribution from $B(x, \varepsilon)$ is uniform on the sphere $S(x, \varepsilon)$. Hence

$$
\begin{aligned}
\mathbb{E}^{\mathbb{W}_x}\left[f(\omega(t))\,\mathbb{1}_{T_{\partial D} > t \geq \tau_x(\varepsilon)}\right] &\leq \mathbb{E}^{\mathbb{W}_x}\left[f(\omega(t))\,\mathbb{1}_{t \geq \tau_x(\varepsilon)}\right] \\
&\leq \int f(y)\,\mathbb{E}^{\mathbb{W}_x}\left[\mathbb{1}_{t \geq \tau_x(\varepsilon)}\left(\int_{S(x,\varepsilon)} \gamma_{t-\tau_x(\varepsilon)}(z,y)d_S z\right)\right]dy
\end{aligned}
$$

where γ is the ordinary heat kernel. Since $|z - y| > \varepsilon/2$ in the above formula,

$$
\begin{aligned}
\gamma_u(z, y) &= (2\pi u)^{-d/2}\,e^{|z-y|^2/2u} \\
&\leq (2\pi u)^{-d/2}\,e^{-\varepsilon^2/8u} \leq e^{-d/2}\left(\frac{\pi\,\varepsilon^2}{2d}\right)^{-d/2},
\end{aligned}
$$

the latter inequality being obtained by an easy optimization in u. Since $|x| \geq \alpha$ this quantity is bounded on D by some constant B. But

$$
\mathbb{E}^{\mathbb{W}_x}\left[\mathbb{1}_{t \geq \tau_x(\varepsilon)}\right] \leq K e^{-\varepsilon^2/8td}
$$

for some constant K depending on d only. So

$$
\mathbb{E}^{\mathbb{W}_x}\left[f(\omega(t))\,\mathbb{1}_{T_{\partial D} > t \geq \tau_x(\varepsilon)}\right] \leq B\,K\,e^{-|x|^2/32td}\int f(y)\,dy
$$

and gathering all the previous results we obtain

$$
\text{if } |x - y| \leq |x|/4\,;\; \tilde{p}_t(x, y) \leq M\left((2\pi t)^{-d/2}\,e^{-t\,\bar{G}(|x|/2)/2} + e^{-|x|^2/32td}\right), \tag{B.7}
$$

for some constant M. If $|x - y| \geq |x|/4$, (B.3) furnishes

$$
\tilde{p}_t(x, y) \leq e^{Ct/2}\,(2\pi t)^{-d/2}\,e^{-|x|^2/32t}.
$$

Define

$$
B(u) = \frac{1}{2}\,\min\left(\bar{G}(u/2)/2,\,(u^2/32d)\right). \tag{B.8}
$$

We have shown that there exists some constant M such that $\tilde{p}_1(x, y) \leq M\,e^{-2B(|x|)}$, but since $\tilde{p}_1$ is symmetric the same holds replacing $|x|$ by $|y|$ and finally $|x|$ by $\max(|x|, |y|)$. Taking the geometric average of this estimate and (B.3) ends the proof. $\qquad\square$

Proof. of Lemma B.9: let us consider a bounded function $\|g\|_\infty \leq 1$. Then $P_1 g(x) = e^{V(x)}\,\tilde{P}_1(e^{-V}g)(x)$. According to (B.4) and lemma B.11,

$$
\int_{D \cap \{d(x, \partial D) \leq R\}} |\tilde{P}_1(e^{-V}g)(x)|dx \leq
$$

23

$$
\leq \int_{D\cap\{d(x,\partial D)\leq R\}}\left(\int_{D\cap\{d(y,\partial D)>R\}} e^{-V(y)}\tilde{p}_1(x,y)dy\right)dx
$$

$$
+ M\int_{D\cap\{d(x,\partial D)\leq R\}}\left(\int_{D\cap\{d(y,\partial D)\leq R\}} e^{-V(y)}p_1^D(x,y)dy\right)dx
$$

$$
\leq M\left(\int_{D\cap\{d(y,\partial D)>R\}} e^{-2V(y)}dy\right)^{1/2}\times
$$

$$
\left(\int_{D\cap\{d(y,\partial D)>R\}}\left(\int_{D\cap\{d(x,\partial D)\leq R\}} e^{-|x-y|^2/4}\,e^{-B(|x|\vee|y|)}\,dx\right)^2 dy\right)^{1/2}
$$

$$
+ M\int_{D\cap\{d(y,\partial D)\leq R\}} e^{-V(y)}\left(\int_D p_1^D(x,y)\,dx\right)dy
$$

is finite (recall that $p_1^D(x,y) = p_1^D(y,x)$). Hence $\mathbb{1}_{d(x,\partial D)\leq R}\,\tilde{P}_1(e^{-V}g)\in L^1(dx)$. Since $\tilde{P}_t$ is ultracontractive, $\tilde{P}_1$ is a bounded map from $\mathbb{L}^1(dx)$ to $\mathbb{L}^2(dx)$. It follows that $\tilde{P}_1(\mathbb{1}_{d(x,\partial D)\leq R}\,\tilde{P}_1(e^{-V}g))\in L^2(dx)$.

In addition

$$
\int_{D\cap\{d(x,\partial D)>R\}} |\tilde{P}_1(e^{-V}g)(x)|^2 dx \leq \int_{D\cap\{d(x,\partial D)>R\}} e^{-2V(x)}dx < +\infty\,,
$$

i.e. $\mathbb{1}_{d(x,\partial D)>R}\,\tilde{P}_1(e^{-V}g)\in L^2(dx)$ so that $\tilde{P}_1(\mathbb{1}_{d(x,\partial D)>R}\,\tilde{P}_1(e^{-V}g))\in L^2(dx)$.

Summing up yields that $\tilde{P}_2(e^{-V}g)\in \mathbb{L}^2(dx)$.

Actually we may replace 1 by $s>0$ as remarked in remark B.7, thus replace 2 by 1 in the previous result. $\qquad\square$

B.4. **Uniqueness of the quasi-stationary distribution.** In [3] Theorem 7.2 we derived a necessary and sufficient condition for ν_1 to be the only quasi-limiting distribution, i.e. to satisfy $\lim_{t\to+\infty}\mathbb{P}_\nu(X_t\in A\,|\,T_{\partial D}>t) = \nu_1(A)$ for all initial distribution ν. In that case ν_1 is the only quasi-stationary distribution. (Recall that in [3], $D = \mathbb{R}^+$). This condition is very close to the ultracontractivity of the semi-group P_t.

We shall not try here to obtain such a criterion, but only a sufficient condition based on the previous remark.

Proposition B.12. *Assume that (H) and (B.4) are satisfied. If P_t is an ultracontractive semi-group, for all initial distribution ν and all Borel subset $A\subset D$*

$$
\lim_{t\to+\infty}\mathbb{P}_\nu(X_t\in A\,|\,T_{\partial D}>t) = \nu_1(A)\,.
$$

In particular ν_1 is the unique quasi-stationary distribution.

Proof. Since P_t is ultracontractive, it turns out, as proved in [6] Theorem 1.4.1, that $\mathbb{L}^1(\mu)\cap L^\infty(\mu)$ which is included into $\mathbb{L}^2(\mu)$, is invariant under P_t. So P_t extends as a contraction semi-group on all $\mathbb{L}^p(\mu)$.

Now, according to Theorem A.1 we know that $\mathbb{P}_\nu(X_t \in A\,,\,T_{\partial D} > t) = \int_A r_\nu(t,y)\mu(dy)$ with $r_\nu(t,.) = \int r(t,x,.)\nu(dx) \in \mathbb{L}^1(\mu)$ and $r_\nu(t+s,y) = P_s(r_\nu(t,.))(y)$. Hence for $t > 2$,

$$
\begin{aligned}
\mathbb{P}_\nu(X_t \in A\,,\,T_{\partial D} > t) &= \int_D \mathbb{1}_A\, P_{t-1}(r_\nu(1,.))\, d\mu \\
&= \int_D P_1(\mathbb{1}_A)\, P_{t-2}(r_\nu(1,.))\, d\mu\,.
\end{aligned}
$$

But thanks to Lemma B.9 and to ultracontractivity, both $P_1(\mathbb{1}_A)$ and $P_{t-2}(r_\nu(1,.))$ are in $\mathbb{L}^2(\mu)$. Furthermore $e^{\lambda_1(t-3)}\, P_{t-2}(r_\nu(1,.))$ converges strongly in $\mathbb{L}^2$ to $\langle P_1(r_\nu(1,.)),\eta_1\rangle\,\eta_1$ as $t \to +\infty$. Hence

$$
\lim_{t \to +\infty} \mathbb{P}_\nu(X_t \in A \,|\, T_{\partial D} > t) = \frac{\langle P_1(\mathbb{1}_A),\eta_1\rangle}{\langle P_1(\mathbb{1}_D),\eta_1\rangle} = \nu_1(A)
$$

since $\eta_1 \in \mathbb{L}^1(\mu)$. $\qquad\square$

It remains to give tractable conditions for P_t to be ultracontractive. To this end we shall use the ideas introduced in [13] and later developed in [2] in particular. The next lemma is the key

Lemma B.13. (see [13]) *Assume that (H) and (B.4) are satisfied. If for all $t > 0$ there exists $c(t)$ such that for all $x \in D$,*

$$
e^{V(x)}\, \mathbb{E}^{\mathbb{W}_x}\left[\mathbb{1}_{T_{\partial D} > t}\, e^{-\frac{1}{2}\int_0^t G(\omega_s)ds}\right] \leq c(t)\,, \tag{B.9}
$$

then P_t is ultracontractive. (Recall that $G(y) = |\nabla V|^2(y) - \triangle V(y)$).
Conversely this condition is necessary if we assume in addition that $\int_D e^{V(x)}\mu(dx) < +\infty$.

Proof. The proof is the same as in [13]. It is given for the sake of completeness.
Recall that the heat semi-group on D is ultracontractive, i.e. for all non-negative $f \in \mathbb{L}^2(dx)$,

$$
\sup_{x \in D} \mathbb{E}^{\mathbb{W}_x}\left[\mathbb{1}_{T_{\partial D} > t}\, f(\omega_t)\right] \leq (\pi t)^{-\frac{1}{4}}\,\|\,f\,\|_{\mathbb{L}^2(dx)}\,.
$$

For a non-negative $g \in \mathbb{L}^2(d\mu)$, $f = e^V g \in \mathbb{L}^2(dx)$ so that using Theorem A.1

$$
\begin{aligned}
P_t g(x) &= e^{V(x)}\, \mathbb{E}^{\mathbb{W}_x}\left[\mathbb{1}_{T_{\partial D} > t}\, f(\omega_t)\, e^{-\frac{1}{2}\int_0^t G(\omega_s)ds}\right] \\
&\leq e^{V(x)}\, \mathbb{E}^{\mathbb{W}_x}\left[\mathbb{1}_{T_{\partial D} > t/2}\, e^{-\frac{1}{2}\int_0^{t/2} G(\omega_s)ds}\, \mathbb{E}^{\mathbb{W}_{\omega_{t/2}}}\left[\mathbb{1}_{T_{\partial D} > t/2}\, f(\omega'_{t/2})\, e^{-\frac{1}{2}\int_0^{t/2} G(\omega'_s)ds}\right]\right] \\
&\leq e^{\frac{Ct}{4}}\, (\pi t)^{-\frac{1}{4}}\,\|\,g\,\|_{\mathbb{L}^2(d\mu)}\, e^{V(x)}\, \mathbb{E}^{\mathbb{W}_x}\left[\mathbb{1}_{T_{\partial D} > t/2}\, e^{-\frac{1}{2}\int_0^{t/2} G(\omega_s)ds}\right]\,.
\end{aligned}
$$

Hence if (B.9) is satisfied,

$$
P_t g(x) \leq c(t/2)e^{\frac{Ct}{4}}\, (\pi t)^{-\frac{1}{4}}\,\|\,g\,\|_{\mathbb{L}^2(d\mu)}
$$

for all $x \in D$, i.e. $P_t g$ is bounded and P_t is ultracontractive. (B.9) is thus a sufficient condition. It is also necessary once $e^V \in \mathbb{L}^1(\mu)$, since

$$
P_t(e^V)(x) = e^{V(x)}\, \mathbb{E}^{\mathbb{W}_x}\left[\mathbb{1}_{T_{\partial D} > t}\, e^{-\frac{1}{2}\int_0^t G(\omega_s)ds}\right]\,,
$$

as it can be observed in the Girsanov formula stated in Theorem A.1. $\qquad\square$

Papers [13] and [2] contain several methods to prove (B.9). The most adapted one to our situation is the " well method" based on the Girsanov transform (Theorem A.1).

To this end we shall introduce some notation :

- for $R > 0$, $A_R = D \cap \{|x| \le R\}$,
- $\bar{V}(R) = \sup_{x \in A_R} V(x)$ (be careful that there is no absolute value),
- for $\varepsilon > 0$, $D_\varepsilon = \{y \in D, d(y, \partial D) > \varepsilon\}$ and $S_\varepsilon = \inf\{t > 0, \omega(t) \in D_\varepsilon^c\}$,
- for $k \in \mathbb{N}^*$, $e_k = \inf\{t > 0, \omega(t) \in A_k\}$.

We then have the following analogue of Theorem 3.3 in [13]

Proposition B.14. *Assume that (A.3), (H2) and (H3) are satisfied. We shall also assume that for all $\varepsilon > 0$, V is bounded from below on D_ε. Let $a_k = \bar{G}(k)$, $b_k = \bar{V}(k)$ and γ_k be such that $\sum_{k=1}^\infty \gamma_k < +\infty$. P_t is ultracontractive as soon as the following holds:*

$$for \ all \ \beta > 0, \ \sum_{k=1}^\infty \exp\left(\frac{1}{2}\left(b_{k+1} - \beta \gamma_k a_k\right)\right) < +\infty. \tag{B.10}$$

Proof. The first step is to be convinced that Lemma 3.1 in [13] is still true i.e if $\tau_R = \inf\{t > 0, \omega_t \in A_R\}$ and $x \notin A_R$,

$$e^{V(x)} \mathbb{E}^{\mathbb{W}_x}\left[\mathbb{1}_{T_{\partial D} > \tau_R} e^{-\frac{1}{2}\int_0^{\tau_R} G(\omega_s)ds}\right] \le e^{\bar{V}(R)}.$$

Define $M_t = e^{-V(\omega_t) - \frac{1}{2}\int_0^t G(\omega_s)ds}$. Thanks to our hypothesis on V and (H2), $M_{t \wedge \tau_R \wedge S_\varepsilon}$ is actually a bounded martingale. The result follows by making successively t go to infinity and ε go to 0.

Once this is proved the rest of the proof is exactly the same as in [13] except that we have to replace the stopping times τ_j therein by $e_j \wedge S_\varepsilon$ and then make ε go to 0 again. $\qquad\square$

References

[1] F. A. Berezin and M. A. Shubin. *The Schrödinger equation.* Kluwer Academic Pub., Dordrecht, 1991.

[2] P. Cattiaux. Hypercontractivity for perturbed diffusion semi-groups. *Ann. Fac. des Sc. de Toulouse*, 14(4):609–628, 2005.

[3] P. Cattiaux, P. Collet, A. Lambert, S. Martinez, S. Méléard and J. San Martin. Quasi-stationarity distributions and diffusion models in population dynamics. *In revision for Ann. Prob., Preprint Ecole Polytechnique*, 616, 2007.

[4] N. Champagnat, P. Diaconis Two-types birth and death processes conditionned on non-extinction. *Private communication.*

[5] P. Collet, S. Martinez, and J. San Martin. Asymptotic laws for one dimensional diffusions conditioned to nonabsorption. *Ann. Prob.*, 23:1300–1314, 1995.

[6] E. B. Davies. *Heat kernels and spectral theory.* Cambridge University Press, 1989.

[7] A.M. Etheridge. Survival and extinction in a locally regulated population. *Ann. Appl. Prob.* 14:188-214, 2004.

[8] P. A. Ferrari, H. Kesten, S. Martínez, P. Picco. *Existence of quasi-stationary distributions. A renewal dynamical approach. Ann. Probab.*, 23:501–521, 1995.

[9] M. Fukushima. *Dirichlet Forms and Markov Processes.* Kodansha. North-Holland, Amsterdam, 1980.

[10] F. Gosselin. Asymptotic behavior of absorbing Markov chains conditional on nonabsorption for applications in conservation biology. *Ann. Appl. Prob.*, 11:261–284, 2001.

[11] N. Ikeda and S. Watanabe. *Stochastic differential equations and diffusion processes.* North-Holland, Amsterdam, 2nd edition, 1988.

[12] J. Istas. *Mathematical Modeling for the Life Sciences*. Universitext, Springer-Verlag, 2005.

[13] O. Kavian, G. Kerkyacharian, and B. Roynette. Some remarks on ultracontractivity. *J. Func. Anal.*, 111:155–196, 1993.

[14] A. Lambert. The branching process with logistic growth. *Ann. Appl. Prob.*, 15:1506–1535, 2005.

[15] V. Maz'ya and M. Shubin. Discreteness of spectrum and positivity criteria for Schrödinger operators. *Ann. Math.*, 162:919–942, 20005.

[16] P. K. Pollett.Quasi stationary distributions : a bibliography. Available at
http://www.maths.uq.edu.au/˜pkp/papers/qsds/qsds.html, regularly updated.

[17] O. Renault, R. Ferrière, and J. Porter. The quasi-stationary route to extinction. Private Communication.

[18] G. Royer. *Une initiation aux inégalités de Sobolev logarithmiques*. S.M.F., Paris, 1999.

[19] E. Seneta and D. Vere-Jones. *On quasi-stationary distributions in discrete-time Markov chains with a denumerable infinity of states. J. Appl. Prob.* 3:403–434, 1966.

[20] D. Steinsaltz and S. N. Evans. *Markov mortality models: implications of quasistationarity and varying initial distributions. Theo. Pop. Bio.* 65:319-337, 2004.

[21] F. Y. Wang. *Functional inequalities, Markov processes and Spectral theory*. Science Press, Beijing, 2004.

Patrick CATTIAUX,, Université Paul Sabatier Institut de Mathématiques. Laboratoire de Statistique et Probabilités, UMR C 5583, 118 route de Narbonne, F-31062 Toulouse cedex 09.

E-mail address: `cattiaux@math.univ-toulouse.fr`

Sylvie MÉLÉARD,, Ecole Polytechnique, CMAP, F- 91128 Palaiseau cedex, .

E-mail address: `meleard@cmapx.polytechnique.fr`