A STOCHASTIC LOTKA-VOLTERRA MODEL WITH KILLING

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Abstract. We study the long time behavior of a population which is modeled by a killed diffusion. The population evolves according to a stochastic version of a Lotka-Volterra equation with internal killing. The killing is chosen to be large when the population is small and small when the population is large. One possible biological interpretation is that when the population is small there is a higher chance of having a catastrophic event resulting in extinction. For this system we study the existence and uniqueness of quasistationary distributions. Quasistationary distributions give us insight regarding the convergence of the population, conditioned on non-extinction, to an equilibrium. The killed diffusion does not fall into any previously studied frameworks because both of the boundary points are inaccessible (that is, the diffusion cannot reach them in finite time). By studying the spectral properties of the generator of the killed diffusion we are able to prove that there exists a quasistationary distribution which attracts all compactly supported probability measures on $(0,\infty)$.

1. Introduction

We study the long time behavior of a stochastic one dimensional diffusion process $(N_t)_{t\geq 0}$ with internal killing. The unkilled process can be seen as describing the population abundance N_t at time t of a species and evolves according to a stochastic differential equation (SDE) of the following type

$$\begin{aligned} dN_t &= (\mu N_t - cN_t^2)\,dt + \sigma N_t dW_t,\ t>0 \\ N_0 &= x_0 > 0, \end{aligned} \tag{1.1}$$

where

- $\mu > 0$ is the mean per-capita growth rate,
- σ^2 is the 'infinitesimal' variance of fluctuations in the per-capita growth rate,
- $-cN_t^2$ for $c>0$ is due to competition for resources

and $(W_t)_{t\geq 0}$ is a standard Brownian motion. This model has been used in the literature, see Evans et al., Evans et al. [2013], Li and Mao [2009], Liu et al. [2011], and can be seen as a stochastic version of the logistic growth model (or a Lotka-Volterra process). It can be shown, see for example Evans et al., that this process never dies out, that is, that $N_t > 0$ for all $t \geq 0$. It is also standard to prove (see Evans et al.) that the process has a nontrivial stationary distribution on $(0,\infty)$ if and only if $\mu - \frac{\sigma^2}{2} > 0$.

Isolated populations with no immigration usually die out in nature in a finite time $T_\partial < \infty$. Therefore, it makes sense to introduce in our model an internal killing rate $\kappa : \mathbb{R}_+ \to \mathbb{R}_+$ and kill the population N_t at the rate $\kappa(N_t)$. The main killing rate we are interested in is $\kappa_0(x) := \frac{1}{x}$. One could intuitively pick this type of killing because when the population N_t gets small, individuals will have difficulty finding mates or defending themselves from predators, and therefore the killing rate $\kappa_0(N_t) = \frac{1}{N_t}$ will be large.

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Using killing rates is not new in biology and genetics. In Hanski and Ovaskainen [2000] a killing rate $\kappa_0(x) = \frac{1}{x}$ is used to model the rate of patch extinction in metapopulations.

Karlin and Tavaré [1983] study diffusion processes arising as scaling limits of discrete models of gene formation and detection in finite populations. The diffusions one gets are governed not only by their drift and diffusion terms but also by a state dependent killing rate, that corresponds to the formation of certain types of individuals.

Another interpretation of the killing rate in our model could also be the following: Similar to the model from Karlin and Tavaré [1983], one might be interested in detecting the first appearance of a non-native invasive species whose dynamics is governed by (1.1). In this case, a detection rate (which gives us the killing rate) proportional to the population density seems natural.

The natural question to ask in our setting is whether there exists a quasistationary distribution. That is, whether conditioned on not dying out (which we model by the absorption of N_t by a cemetery state ∂) there is convergence to equilibrium.

Quasistationary distributions have been studied extensively in population dynamics and demography. For example, Evans and Steinsaltz Steinsaltz and Evans [2004] were able to explain the mortality plateau phenomenon arising in Markov mortality models from demography using the concept of quasistationary distribution. Similarly, Cattiaux et al Cattiaux et al. [2009] study the existence and uniqueness of quasistationary distributions arising from the rescaling of some sequence of birth-death processes from population dynamics. Even though populations are expected to go extinct in finite time, the time to extinction can be large and it is common that population sizes fluctuate for large amounts of time before extinction occurs. The notion of quasistationarity captures such behavior. For an extensive bibliography of quasistationary distributions we refer the reader to Pollett.

2. Prelimiting model

Here we discuss how one can get the SDE (1.1) as a scaling limit of a discrete system. We follow parts of Section 2.4 from Lambert [2005]. First, define the Feller diffusion with logistic growth started at x by

$$\begin{aligned} dU_t &= (\mu U_t - cU_t^2)\, dt + \sqrt{\gamma U_t}\, dB_t \\ U_0 &= x > 0 \end{aligned} \tag{2.1}$$

where $\mu, c, \gamma \in \mathbb{R}_+$. Denote by $(U_t^{(n)}, t \geq 0)$ the Markov process living on $n^{-1}\mathbb{N}$, started at $n^{-1}\lceil nx \rceil$, stopped at 0 and with the following transition kernels

- $U_t^{(n)}$ goes up by $\frac{1}{n}$ at rate $(\frac{\gamma}{2}n + \lambda)n^2 U_t^{(n)}$,
- $U_t^{(n)}$ goes down by $\frac{1}{n}$ at rate $(\frac{\gamma}{2}n + \delta)n^2 U_t^{(n)}$,
- $U_t^{(n)}$ goes down by $\frac{1}{n}$ at rate $cn^2 U_t^{(n)}(U_t^{(n)} - n^{-1})$,

for positive constants $c, \delta, \gamma, \lambda$. Set $\mu = \lambda - \delta$. Then, as $n \to \infty$, the sequence $(U_t^{(n)}, t \geq 0)_n$ converges weakly to the Feller diffusion with logistic growth given by (2.1).

If we look at a random environment version, see Mytnik [1996], of the setup from above we can get the following SDE as a scaling limit of a finite system

$$\begin{aligned} dV_t &= (\mu V_t - cV_t^2)\, dt + \sigma V_t\, dW_t + \sqrt{\gamma V_t}\, dB_t \\ V_0 &= x > 0 \end{aligned} \tag{2.2}$$

where (W, B) is a standard two dimensional Brownian motion.

The basic observation is that in a branching process where the offspring distribution has mean μ and variance σ^2 and there are currently M individuals, the conditional distribution of the number of individuals in the next generation has mean

$$M\mu$$

and variance

$$M\sigma^2 = (\sqrt{M}\sigma)^2.$$

The $V_t dW_t$ type term comes from stochastic variations in the mean of the offspring distribution that every individual shares, whereas the $\sqrt{V_t} dB_t$ type term comes from the independent randomness around that common mean in the number of offspring that different individuals have.

If we now let $\gamma \downarrow 0$ in (2.2) we can recover, at least heuristically, our SDE

$$\begin{aligned} dN_t &= (\mu N_t - cN_t^2)\,dt + \sigma N_t dW_t,\ t > 0 \\ N_0 &= x > 0. \end{aligned}$$

Remark 2.1. If one has a finite population model then extinction is always possible if you are unlucky enough (with you needing to be less unlucky the smaller the population is), whereas in an ODE/PDE/SDE/SPDE scaling limit the population can get arbitrarily small and still recover. See for example Durrett and Levin [1994]. This is exactly what happens in our case, since the population given by (1.1) does not go extinct in finite time. Introducing the killing $\kappa(x)$ as we do seems like one way of "patching up" a scaling limit to incorporate the perils of extinction that arise in the finite population setting when the population is small.

3. The Model

Suppose Z is given by the SDE

$$\begin{aligned} dZ_t &= b(Z_t)\,dt + dW_t \\ Z_0 &= z_0 \in (-\infty, \infty). \end{aligned} \tag{3.1}$$

We assume throughout this paper that (3.1) has strong unique solutions. Next, we define some concepts which will play a key role in our arguments.

Definition 3.1. Let Z be given by (3.1) and suppose we have internal killing $\kappa : \mathbb{R} \to \mathbb{R}_+$. If U is a mean one exponential random variable that is independent of the diffusion Z we define the extinction time to be

$$T_\partial := \inf\left\{ t > 0 : \int_0^t \kappa(Z_s)\,ds > U \right\}. \tag{3.2}$$

Let $\mathbb{P}_\nu$ be the law of the process Z if Z_0 has distribution ν. A *quasistationary distribution* (or QSD) for Z is a probability measure ν supported on $(0, \infty)$ such that for any $t \geq 0$ and any Borel set $A \subset (0, \infty)$ one has

$$\mathbb{P}_\nu(Z_t \in A \mid T_\partial > t) = \nu(A). \tag{3.3}$$

Similarly, one can define a *Yaglom limit* π_ν as the limit in distribution

$$\pi_\nu(\bullet) = \lim_{t\to\infty} \mathbb{P}_\nu(Z_t \in \bullet \mid T_\partial > t), \tag{3.4}$$

if this limit exists. It is easy to show that the Yaglom limit is a quasistationary distribution (see Lemma 7.2 in Cattiaux et al. [2009]). We will show that a Yaglom limit exists in our setting, and thus that there exists a quasistationary distribution.

A distribution $\tilde{\nu}$ is said to *attract* all initial distributions ν compactly supported in $(0,\infty)$ if

$$\lim_{t\to\infty} \mathbb{P}_\nu(Z_t \in \bullet \mid T_\partial > t) = \tilde{\nu}(\bullet).$$

The unkilled diffusion Z given by (3.1) with $\kappa(x) = 0$ has the Feller semigroup

$$T_t f(x) := \mathbb{E}_x[f(X_t)]$$

with generator given by

$$-\mathcal{L} := \frac{1}{2}\frac{d^2}{dx^2} + b(x)\frac{d}{dx}. \tag{3.5}$$

If we add killing $\kappa(x)$ the Feller semigroup becomes

$$T_t^\kappa f(x) := \mathbb{E}_x[f(Z_t), T_\partial > t]$$

and the generator

$$-\mathcal{L}_\kappa := \frac{1}{2}\frac{d^2}{dx^2} + b(x)\frac{d}{dx} - k(x). \tag{3.6}$$

Note that we also have the heuristic relations

$$\begin{aligned} T_t &= e^{-t\mathcal{L}} \\ T_t^\kappa &= e^{-t\mathcal{L}_\kappa}. \end{aligned}$$

The operators $\mathcal{L}$ and $\mathcal{L}_\kappa$ will play an important role in our arguments. We next follow Chapter 3 from Lorenzi and Bertoldi [2010] and present the Feller classification of boundary points for diffusions with generators

$$\frac{1}{2}\frac{d^2}{dx^2} + b(x)\frac{d}{dx}$$

in an open interval (ℓ, r).

Definition 3.2. Let $c \in (\ell, r)$ be given and set

$$\rho = \exp\left(\int_0^x 2b(s)\,ds\right)$$

The point r is called *accessible*, if $\int_c^r \rho(x)^{-1} \int_c^x \rho(y)\,dy\,dx < \infty$, and otherwise *inaccessible*. If r is an accessible boundary point, then it is called *regular* if and only if $\int_c^r \rho(x) \int_c^x \rho(y)^{-1}\,dy\,dx < \infty$. If r is accesible and $\int_c^r \rho(x) \int_c^x \rho(y)^{-1}\,dy\,dx = \infty$ then r is called an *exit boundary*. If r is inaccesible, then it is an *entrance boundary*, if and only if $\int_c^r \rho(x) \int_c^x \rho(y)^{-1}\,dy\,dx < \infty$. If r is inaccesible and $\int_c^r \rho(x) \int_c^x \rho(y)^{-1}\,dy\,dx = \infty$ then r is called *natural*. A similar classification holds for ℓ.

Our main interest lies in the SDE

$$\begin{aligned} dN_t &= (\mu N_t - cN_t^2)\,dt + \sigma N_t dW_t,\ t > 0 \\ N_0 &= x_0 \in (0,\infty) \end{aligned} \tag{3.7}$$

together with a killing rate $\kappa : \mathbb{R} \to \mathbb{R}_+$. We want to make this be of type (3.1). The change of variables $X = \frac{\log N_t}{\sigma}$ combined with an easy application of Ito's formula yields

$$\begin{aligned} dX_t &= (A - ae^{\sigma X_t})\,dt + dW_t,\ t > 0 \\ X_0 &= \frac{\log x_0}{\sigma} \in (-\infty,\infty) \\ k(x) &= \kappa(e^{\sigma x}) \end{aligned} \tag{3.8}$$

where $k(x)$ is the new killing rate and

$$\begin{aligned} A &= \frac{1}{\sigma}\left(\mu - \frac{\sigma^2}{2}\right) \\ a &= \frac{c}{\sigma}. \end{aligned}$$

Note that in the case $\kappa_0(x) = \frac{1}{x}$ we get $k_0(x) = e^{-\sigma x}$. We will denote the drift of the SDE from (3.8) by

$$\tilde{b}(x) = (A - ae^{\sigma x}),$$

and the density of the speed measure Γ for the unkilled diffusion X by

$$\tilde{\rho}(x) = \exp\left(\int_0^x 2\tilde{b}(s)\,ds\right). \tag{3.9}$$

Instead of studying (3.7) we will concentrate on (3.8).

Quasistationary distributions for one dimensional diffusions have been studied extensively in Steinsaltz and Evans [2007], Cattiaux et al. [2009], Kolb and Steinsaltz [2012]. Our study does not fit in the setting of Cattiaux et al. [2009] because it has internal killing and the state space is $(-\infty, \infty)$ instead of $(0, \infty)$. Additionally, in Cattiaux et al. [2009] the authors assume that the diffusion gets absorbed a.s. in finite time at 0, while in our case $-\infty$ will be an inaccessible boundary point. We cannot make use of the general results from Steinsaltz and Evans [2007], Kolb and Steinsaltz [2012] because both of our boundary points $-\infty, \infty$ are inaccessible (that is, the diffusion X cannot reach the boundaries in finite time). More exactly, in our case, $-\infty$ is a natural boundary while ∞ is an entrance boundary. Our example shows that the study of a killed diffusion with two inaccessible boundary points can arise from the study of a biological system - it is not interesting only from an academic point of view.

Most studies regarding the existence of quasistationary distributions work with a diffusion on $(0, \infty)$ where 0 is a regular boundary and ∞ is a natural boundary. One exception is Chapter 3 from Kolb [2009] where the author considers the situation when 0 is an exit boundary. As explained in Kolb [2009], when the left boundary is not regular, the spectrum of the generator $\mathcal{L}_k$ does not always have multiplicity 1. For two inaccessible boundary points a spectral *matrix* might have to be used in the spectral representation. However, we are able to prove that in our setting $\mathcal{L}_k$ has multiplicity one. We actually show that $-\mathcal{L}_k$ has a discrete spectrum, $\sigma(-\mathcal{L}_k) = \{\lambda_0, \lambda_1, \dots\}$ with $\lambda_0 < \lambda_1 < \dots$ and that the bottom of the spectrum λ_0 has multiplicity 1. Finally, we prove that the eigenfunction ϕ_0 associated to λ_0 is strictly positive and that $\phi_0 \in L^1(\mathbb{R}, \rho(y)\,dy)$. These facts will then imply the existence of a Yaglom limit for our system.

4. Existence of the Yaglom limit

The next Theorem presents a general result regarding the existence of a quasistationary distribution for a diffusion with a natural and an entrance boundary.

Theorem 4.1. *Suppose Z is a diffusion living on $\mathbb{R}$ with generator*

$$-\mathcal{L} := \frac{1}{2}\frac{d^2}{dx^2} + b(x)\frac{d}{dx} = \frac{1}{2\rho}\frac{d}{dx}\rho\frac{d}{dx}$$

where, as in (3.9),

$$\rho = \exp\left(\int_0^x 2b(s)\,ds\right)$$

is the density of the speed measure of Z. Assume furthermore that $-\infty$ is a natural boundary, ∞ is an entrance boundary and that $\int_{\mathbb{R}} \rho\, dx < \infty$. Suppose Z^κ is the diffusion with generator

$$-\mathcal{L}_\kappa := \frac{1}{2}\frac{d^2}{dx^2} + b(x)\frac{d}{dx} - \kappa(x), \tag{4.1}$$

and that the killing rate $\kappa(x)$ satisfies

$$\lim_{x\to-\infty} q(x) = -\infty \tag{4.2}$$

where

$$q(x) := -\kappa(x) - \frac{1}{2}(|b(x)|^2 - b'(x)).$$

Then the process $(Z_t^\kappa)_{t\geq 0}$ has a quasistationary distribution π. Moreover, the quasistationary distribution π is a Yaglom limit and attracts all compactly supported probability measures on $(0,\infty)$.

Remark 4.2. Note that we looked at diffusions with diffusion coefficient equal to 1. The case of a general nondegenerate diffusion coefficient, i.e. a diffusion with generator

$$\frac{\sigma^2(x)}{2}\frac{d^2}{dx^2} + b(x)\frac{d}{dx}$$

can be reduced to the present case via a time change. Theorem 4.1 can be applied in the case of a general diffusion coefficient. We take $\sigma(x) = 1$ to simplify the computations.

Proof. The proof relies on some basic analytic properties which will be shown below. First, according to Lemma 4.3 the generator $\mathcal{L}_\kappa$ has compact resolvent and thus the spectrum $\sigma(\mathcal{L}_\kappa)$ is purely discrete. Standard theory implies that $\mathcal{L}_\kappa$ is negative definite and that the semigroup $(e^{-t\mathcal{L}_\kappa})_{t\geq 0}$ is positivity improving. Thus a direct application of standard results from functional analysis such as the Perron-Frobenius theorem (see e.g. Satz 17.13 in Weidmann [2003]) implies that the largest eigenvalue λ_0 of $\mathcal{L}_\kappa$ is strictly negative and has multiplicity 0. Moreover, the unique (modulo constants) eigenfunction $\phi_0 \in L^2(\rho)$ corresponding to λ_0 can be chosen to be strictly positive. The spectral theorem for selfadjoint operators implies that

$$e^{t\mathcal{L}_\kappa}\phi_0 = e^{\lambda_0 t}\phi_0.$$

The measure $\pi(dx) := \phi_0(x)\rho(dx)$ is therefore λ_0–invariant as for every $u \in L^2(\rho)$

$$\begin{aligned}\int \rho(dx)\phi_0(x)\mathbb{E}_x\big[u(Z_t), T_\partial > t\big] &= \langle \phi_0, e^{-t\mathcal{L}_\kappa}u\rangle_{L^2(\rho)} = \langle e^{t\mathcal{L}_\kappa}\phi_0, u\rangle_{L^2(\rho)} \\ &= e^{\lambda_0 t}\int \rho(dx)\phi_0(x)u(x)\end{aligned}$$

where $\langle\cdot,\cdot\rangle_{L^2(\rho)}$ denotes the inner product in $L^2(\rho)$. Thus we have

$$\int \pi(dx)\mathbb{P}_x\big(Z_t \in \cdot, T_\partial > t\big) = e^{\lambda_0 t}\pi(\cdot)$$

and it is therefore enough to show that π is a finite measure. Observe that in our situation the measure ρ is a finite measure since by assumption $\int_{\mathbb{R}} \rho\, dx < \infty$, and therefore $\phi_0 \in L^2(\rho) \subset L^1(\rho)$. As a result

$$\frac{\int \pi(dx)\mathbb{P}_x\big(Z_t \in \cdot, T_\partial > t\big)}{\int \pi(dx)\mathbb{P}_x\big(T_\partial > t\big)} = \frac{e^{\lambda_0 t}\pi(\cdot)}{e^{\lambda_0 t}\int \rho(dx)\phi_0(x)u(x)} = \frac{\pi(\cdot)}{\int \pi(dx)}$$

which shows that $\frac{\pi}{\int \pi(dx)}$ is a quasistationary distribution for Z.

Let us now show that all compactly supported initial distributions are attracted by the quasistationary distribution π. Fix $x_0 \in \mathbb{R}$, and $r > 0$. Pick any $f \in L^\infty(\rho) \subset L^1(\rho)$ and observe that for every $x \in (x_0 - r, x_0 + r)$ we have

$$\begin{aligned}\left|e^{-t\mathcal{L}_\kappa} f(x) - e^{\lambda_0 t}\phi_0(x)\right| &= \left|e^{-t\mathcal{L}_\kappa}(f - \phi_0)(x)\right| \\ &\leq C_{x_0,r}\left(\int_{\mathbb{R}} |f'(z)|^2 \rho(dz) + \int_{\mathbb{R}} \kappa(z)|f(z)|\rho(dz)\right)\end{aligned}$$

where $C_{x_0,r}$ is a finite real number. Therefore, we get

$$\sup_{x \in (x_0 - r, x_0 + r)} e^{\lambda_1 t}\left|e_\kappa^{-t\mathcal{L}} f(x) - e^{\lambda_0 t}\phi_0(x)\right| \to 0$$

as $t \to 0$ by the spectral theorem for selfadjoint operators. □

Lemma 4.3. *The operator $\mathcal{L}_\kappa$ from* (4.1) *has a compact resolvent.*

Proof. We will prove the assertion in three steps. First we show that one can consider the two boundaries ∞ and $-\infty$ separately and then we will use standard results in order to establish compactness. At the boundary ∞ the compactness will be due to the strong drift towards 0 and at $-\infty$ we use the fact that the killing rate is large.
Step 1: Let us denote by ${\mathcal{L}_\kappa}^+$ the selfadjoint realization of the operator $\mathcal{L}_\kappa$ in $L^2((0,\infty),\rho)$ with Dirichlet boundary condition at 0. Observe that the boundary ∞ is in the limit point case as shown in Lemma 3.1 of Kolb and Steinsaltz [2012] and thus no boundary condition has to be specified there. Similarly, let ${\mathcal{L}_\kappa}^-$ be the selfadjoint realization of the operator $\mathcal{L}_\kappa$ in $L^2((-\infty,0),\rho)$ with Dirichlet boundary condition at 0. Again, $-\infty$ is in the limit point case and thus ${\mathcal{L}_\kappa}^-$ has a unique selfadjoint realization. We identify

$$L^2((-\infty,\infty),\rho) = L^2((\infty,0),\rho) \oplus L^2((0,\infty),\rho)$$

and denote by ${\mathcal{L}_\kappa}^D$ the operator ${\mathcal{L}_\kappa}^+ \oplus {\mathcal{L}_\kappa}^-$. Arguing as in the proof of Lemma 3.3 in Kolb and Steinsaltz [2012] one concludes that the difference of the resolvents

$$(\mathcal{L}_\kappa - z)^{-1} - ({\mathcal{L}_\kappa}^D - z)^{-1}$$

for $z \in \mathbb{C} \setminus (\sigma(L_k) \cup \sigma(L_k^D))$ is a rank one operator and therefore in particular compact. By Weyl's result about the stability of essential spectra we conclude that it suffices to prove that the essential spectrum of L_k^D is empty. The essential spectrum of ${\mathcal{L}_\kappa}^D$ is empty if the essential spectra of ${\mathcal{L}_\kappa}^\pm$ are both empty.
Step 2: We consider the case ${\mathcal{L}_\kappa}^+$ first. Observe that ∞ is an entrance boundary. According to Theorem 3.16 in Kolb and Steinsaltz [2012] we conclude that ${\mathcal{L}_\kappa}^+$ is purely discrete and thus the essential spectrum is empty.
Step 3: In order to deal with the operator ${\mathcal{L}_\kappa}^-$ we use the following well known fact. If the continuous function $q : (-\infty, 0] \to \mathbb{R}$ satisfies

$$\lim_{x \to -\infty} q(x) = -\infty$$

then the spectrum of the operator $\frac{1}{2}\frac{d^2}{dx^2} + q$ in $L^2((-\infty,0),dx)$ with Dirichlet boundary condition at 0 is purely discrete. Using the unitary transformation U given by

$$U : L^2((-\infty,0),\rho(y)dy) \to L^2((\infty,0),dy), f \mapsto \sqrt{\rho} f$$

we see that the operator $-{\mathcal{L}_\kappa}^-$ is unitarily equivalent to the operator $\frac{1}{2}\frac{d^2}{dx^2} + q$ in $L^2((-\infty,0),dx)$ with

$$q(x) = -\kappa(y) - \frac{1}{2}\left(|b(y)|^2 - b'(y)\right).$$

Since by assumption $\lim_{x \to -\infty} q(x) = -\infty$ we are done. □

Let us collect some well known results about the unkilled diffusion $(N_t)_{t\geq 0}$ given by (1.1).

Proposition 4.4. *Assume $\mu - \frac{\sigma^2}{2} > 0$. The diffusion given by the SDE (1.1) is well defined and lives in $\mathbb{R}_{++} := (0,\infty)$, that is, for all $t \geq 0$ we have $N_t \in \mathbb{R}_{++}$. The boundary points 0 and ∞ are both inaccessible for the diffusion $(N_t)_{t\geq 0}$. More specifically, 0 is a natural boundary and ∞ is an entrance boundary. Furthermore, the process converges weakly to its unique stationary distribution which is a Gamma distribution with density $x \mapsto \frac{1}{\Gamma(\lambda)\theta^\lambda} x^{\lambda-1} e^{-\frac{x}{\theta}}$ having parameters $\theta := \frac{\sigma^2}{2c}$ and $\lambda := \frac{2\mu}{\sigma^2} - 1$.*

Proof. See Evans et al.. □

As an immediate consequence we get the following Corollary.

Corollary 4.5. *Suppose that $A, a, \sigma > 0$. The unkilled diffusion $(X_t)_{t\geq 0}$ given by (3.8) is well defined and lives in $\mathbb{R}$. The left boundary $-\infty$ is a natural boundary and the right boundary $+\infty$ is an entrance boundary. Moreover, $\int_{\mathbb{R}} \tilde{\rho}(x)\, dx < \infty$ since X has a nontrivial stationary distribution.*

Proof. Apply the results from proposition 4.4 together with the fact that $X_t = \log N_t$. □

As already mentioned in the introduction our main result concerns the existence of a quasistationary distribution for the process $(N_t)_{t\geq 0}$. Instead of proving this for N_t directly we first show X_t has a quasistationary distribution. It is then trivial to note that N_t also has a quasistationary distribution.

Corollary 4.6. *The killed diffusion given by*

$$\begin{aligned} dN_t &= (\mu N_t - c N_t^2)\, dt + \sigma N_t dW_t, \ t > 0 \\ N_0 &= x_0 \in (0,\infty) \\ \kappa(x) &= \frac{1}{x}. \end{aligned}$$

has a quasistationary distribution which attracts all compactly supported probability measures on $(0,\infty)$.

Proof. Note that since

$$\lim_{x\to-\infty} q(x) = \lim_{x\to-\infty} \left(-e^{-\sigma x} - \frac{1}{2}|A - a e^{\sigma x}|^2 + \frac{1}{2} a\sigma e^{\sigma x} \right) = -\infty$$

by Theorem 4.1 and Corollary 4.5 the process $(X_t)_{t\geq 0}$ with the killing rate $k(x) = \kappa(e^{\sigma x}) = e^{-\sigma x}$ has a quasistationary distribution which attracts all compactly supported probability measures on $(-\infty,\infty)$. It is then immediate that $N_t = e^{\sigma X_t}$ also has a quasistationary distribution which attracts all compactly supported probability measures on $(0,\infty)$. □

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References

P. Cattiaux, P. Collet, A. Lambert, S. Martínez, S. Méléard, and J. San Martín. Quasi-stationary distributions and diffusion models in population dynamics. *The Annals of Probability*, 37(5):1926–1969, 2009.

R. Durrett and S. Levin. The importance of being discrete (and spatial). *Theoretical Population Biology*, 46(3):363 – 394, 1994.

S. N. Evans, A. Hening, and S. J. Schreiber. Protected polymorphisms and evolutionary stability of patch-selection strategies in stochastic environments. *to appear in Journal of Mathematical Biology*. Available at http://arxiv.org/abs/1404.6759.

S. N. Evans, P. Ralph, S. J. Schreiber, and A. Sen. Stochastic population growth in spatially heterogeneous environments. *Journal of Mathematical Biology*, 66(3):423–476, 2013. ISSN 0303-6812.

I. Hanski and O. Ovaskainen. The metapopulation capacity of a fragmented landscape. *Nature*, 404(6779):755–758, 2000.

S. Karlin and S. Tavaré. A class of diffusion processes with killing arising in population genetics. *SIAM Journal on Applied Mathematics*, 43(1):31–41, 1983.

M. Kolb. On the large time behavior of diffusions. 2009. Dissertation, Kaiserslautern.

M. Kolb and D. Steinsaltz. Quasilimiting behavior for one-dimensional diffusions with killing. *The Annals of Probability*, 40(1):162–212, 2012.

A. Lambert. The branching process with logistic growth. *The Annals of Applied Probability*, 15(2):1506–1535, 2005.

X. Li and X. Mao. Population dynamical behavior of non-autonomous Lotka-Volterra competitive system with random perturbation. *Discrete and Continuous Dynamical Systems. Series A*, 24(2):523–545, 2009.

M. Liu, K. Wang, and Q. Wu. Survival analysis of stochastic competitive models in a polluted environment and stochastic competitive exclusion principle. *Bulletin of mathematical biology*, 73(9):1969–2012, 2011.

L. Lorenzi and M. Bertoldi. *Analytical methods for Markov semigroups*. CRC Press, 2010.

L. Mytnik. Superprocesses in random environments. *The Annals of Probability*, 24(4): 1953–1978, 1996.

P.K. Pollett. Quasi-stationary distributions: a bibliography. www.maths.uq.edu.au/~pkp/papers/qsds/qsds.pdf.

D. Steinsaltz and S. N. Evans. Markov mortality models: implications of quasistationarity and varying initial distributions. *Theoretical Population Biology*, 65(4):319–337, 2004.

D. Steinsaltz and S. N. Evans. Quasistationary distributions for one-dimensional diffusions with killing. *Transactions of the American Mathematical Society*, 359(3): 1285–1324, 2007.

J. Weidmann. *Lineare Operatoren in Hilbertraum: Teil 2 Anwendungen*. Vieweg Teubner Verlag, 2003.

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