# On the long time behaviour of the solution of an SDE driven by a Poisson Point Process 

Elma Nassar and Etienne Pardoux

January 18, 2016


#### Abstract

We study a stochastic differential equation driven by a Poisson point process, which models continuous changes in a population's environment, as well as the stochastic fixation of beneficial mutations that might compensate for this change. The fixation probability increases as the phenotypic lag between the population and the optimum grows larger, and successful mutations are assumed to fix instantaneously (leading to an adaptive jump). Our main result is that the process is transient (i.e., continued adaptation is impossible) if the rate of environmental change $v$ exceeds a parameter $m$, which can be interpreted as the rate of adaptation in case every beneficial mutation gets fixed with probability 1 . If $v<m$, the process is positive recurrent, while in the limiting case $m=v$, null recurrence or transience depends upon additional technical conditions. We show how our results can be extended to the case of a time varying rate of environmental change.


## 1 Introduction

We study the large time behaviour of the solution of a scalar stochastic differential equation of the type

$$
X_{t}=X_{0}-v(t)+\int_{[0, t] \times \mathbb{R} \times[0,1]} \alpha \varphi\left(X_{s^{-}}, \alpha, \xi\right) M(d s, d \alpha, d \xi)
$$

where $M$ is Poisson Point Process on $\mathbb{R}_{+} \times \mathbb{R} \times[0,1]$ with mean measure $d s \nu(d \alpha) d \xi$ and $\varphi(x, \alpha, \xi)=\mathbf{1}_{\{\xi \leq g(x, \alpha)\}}$. The goal of our work is to understand how a population can adapt to a deterioration of its fitness, due for instance to continuous
change in the climatic conditions, thanks to mutations which improve its adaptation to the new environment. $d s \nu(d \alpha)$ represents the rate of appearance of new mutations, while $g(x, \alpha)$ is the probability that a mutation $\alpha$, which is proposed while the population's fitness is given by $x$, gets fixed. We give a specific form to that probability. The important property, which is reasonable to assume in our case, is that whenever $x \rightarrow \pm \infty, g(x, \alpha) \rightarrow 1$ for each $\alpha$ such that $x \alpha<0$.

We start with the simple case $v(t)=v t$, with $v>0$. With the notation $m=$ $\int_{0}^{\infty} \alpha \nu(d \alpha)$, i.e. $m$ is the mean movement to the right per time unit produced by the positive mutations if all of them get fixed, which almost happens when $x<0$ is very large in absolute value, our first result says that the Markov process $X_{t}$ is positive recurrent if $m>v$, transient if $m<v$, with a speed of escape to infinity equal to $v-m$. The most interesting case is the limit situation $m=v$. We show that, depending upon the speed at which $m(x)=\int_{0}^{\infty} \alpha g(x, \alpha) \nu(d \alpha)$ converges to $m$ as $x \rightarrow-\infty$, the process can be either null recurrent or else transient with zero speed in case $m=v$.

We then generalize our results to the case where $v(t)$ is a more general (and even possibly random) function of time.

Note that Kersting (1986) has studied similar questions in discrete time. Similar resuts for a SDE driven by Brownian motion with coefficients which do not depend upon the time variable would be easy to obtain. Here we use stochastic calculus and several ad hoc Lyapounov functions. Note that the Itô formula for processes with jumps leads to less explicit computations than in the Brownian case. To circumvent this difficulty, for the treatment of the delicate case $m=v$, we establish a stochastic inequality for $C^{2}$ functions whose second derivative is either increasing or decreasing, see Lemma 3 in subsection 4.3 below.

The paper is organized as follows. We define our model in detail in section 2 , refering to models already studied in the biological literature. We establish existence and uniqueness of a solution to our equation in section 3 (the result is not immediate since we do not assume that the measure $\nu$ is finite). Section 4 is devoted to the large time behaviour of $X_{t}$ when $v(t)=v t$, successively with $m<v, m>v$, and $m=v$. Finally section 5 is devoted to the large time behaviour of $X_{t}$ when $v(t)$ takes a general form, but $\bar{v}=\lim _{t \rightarrow \infty} t^{-1} \int_{0}^{t} v(s) d s$ exists.

## 2 The Model

Our starting point is the model by Kopp and Hermisson (2009) of a population of constant size $N$ that is subject to Gaussian stabilizing selection, with a moving
optimum that increases linearly at rate $v$. That is, at time $t$, the phenotypic lag between an individual with trait value $z$ and the optimum equals $x=z-v t$, and the corresponding fitness is

$$
\begin{equation*}
\mathcal{W}(x)=\exp \left(-\sigma x^{2}\right) \tag{1}
\end{equation*}
$$

where $\sigma$ determines the strength of selection. For the adaptive-walk approximation, the population is assumed to be monomorphic at all times (i.e., its state is completely characterized by $x$ ). Mutations arise at rate $\Theta / 2=N \mu$ (where $\mu$ is the per-capita mutation rate and $\Theta=2 N \mu$ is a standard population-genetic parameter), and their phenotypic effects $\alpha$ are drawn from a distribution $p(\alpha)$. We neglect the possibility of fixation of deleterious mutations. Yet even beneficial mutations have a significant probability of being lost due to the effects of genetic drift. A mutation with effect $\alpha$ that arises in a population with phenotypic lag $x$ has a probability of fixation

$$
g(x, \alpha)=\left\{\begin{array}{l}
1-\exp (-2 s(x, \alpha)) \quad \text { if } s(x, \alpha)>0  \tag{2}\\
0 \text { otherwise }
\end{array}\right.
$$

where

$$
\begin{equation*}
s(x, \alpha)=\frac{\mathcal{W}(x+\alpha)}{\mathcal{W}(x)}-1 \approx-\sigma[|\alpha|(2|x|-|\alpha|)]^{+} \times \mathbf{1}_{\{x \alpha<0\}} \tag{3}
\end{equation*}
$$

is the selection coefficient. Formula (2) is a good approximation of the fixation probability derived under a diffusion approximation (Malécot 1952; Kimura 1962), which is valid when the population size $N$ is large enough. Note that Kopp and Hermisson (2009) used the even simpler approximation $g(x, \alpha) \approx 2 s(x, \alpha)$ (Haldane 1927, for more exact approximations for the fixation probability in changing environments, see Uecker and Hermisson 2011; Peischl and Kirkpatrick 2012). Once a mutation gets fixed, it is assumed to do so instantaneously, and the phenotypic lag $x$ of the population is updated accordingly. Three example realizations of the resulting adaptive walk are illustrated in Figure 1.
We now turn to a rigorous mathematical description of the above process. We introduce a stochastic equation driven by a Poisson point process that describes the evolution of the population, and we study whether the process is transient (leading to certain extinction of the population) or recurrent (at least potentially allowing survival). The key parameters are the maximal mean rate of adaptation, $m$, and the speed of the optimum, $v$. We prove that the process is transient when $m<v$ and recurrent when $m>v$. We then perform an in-depth analysis of the limiting case $m=v$, showing that transience or recurrence in this case depend on additional conditions. Next, we generalize the results to a model with variable speed of the optimum (i.e., $v$ becomes a random function of $t$ ).


Figure 1: Three example realizations of an adaptive walk, showing the evolution of the lag $X_{t}$ between the population phenotype $z$ and a linearly moving optimum $v t$, for three different values of $v$. In (A) and (B) the process is recurrent, whereas in (C), it is transient. Results were generated by drawing random mutations from a standard normal distribution $(\nu(\alpha) \sim$ $\mathcal{N}(0,1))$ at times drawn from an exponential distribution with intensity $\Theta / 2=0.5$ and accepting them (leading to an adaptive step) according to the fixation probability given by equation (2) with $\sigma=0.1$.

The evolution of the phenotypic lag of the population can be described by the following equation

$$
\begin{equation*}
X_{t}=X_{0}-v t+\int_{[0, t] \times \mathbb{R} \times[0,1]} \alpha \varphi\left(X_{s^{-}}, \alpha, \xi\right) M(d s, d \alpha, d \xi) . \tag{4}
\end{equation*}
$$

Here, $M$ is a Poisson point process (PPP) over $\mathbb{R}_{+} \times \mathbb{R} \times[0,1]$ with intensity

$$
\pi(d s, d \alpha, d \xi)=d s \nu(d \alpha) d \xi
$$

$\nu(d \alpha)$ is a $\sigma$-finite measure describing the distribution of new mutations up to a multiplicative constant, which satisfies

$$
\begin{equation*}
\int_{\mathbb{R}}|\alpha| \wedge 1 \nu(d \alpha)<\infty \tag{5}
\end{equation*}
$$

and

$$
\varphi(x, \alpha, \xi)=\mathbf{1}_{\{\xi \leq g(x, \alpha)\}},
$$

where the fixation probability $g(x, \alpha)$ (see formula (2)) of a mutation of size $\alpha$ that hits the population when the lag is $x$ can be expressed as

$$
g(x, \alpha)=\left(1-\exp \left(-2 \sigma\left[|\alpha|(2|x|-|\alpha|)^{+}\right]\right)\right) \times \mathbf{1}_{(x \alpha<0)} .
$$

The points of this PPP $\left(T_{i}, A_{i}, \Xi_{i}\right)$ are such that the $\left(T_{i}, A_{i}\right)$ form a PPP over $\mathbb{R}_{+} \times \mathbb{R}$ of the proposed mutations with intensity $d s \nu(d \alpha)$, and the $\Xi_{i}$ are i.i.d. $\mathcal{U}[0,1]$, globally independent of the PPP of the $\left(T_{i}, A_{i}\right) . T_{i}$ 's are the times when mutations are proposed and $A_{i}$ 's are the effect sizes of those mutations. The $\Xi_{i}$ are auxiliary variables determining fixation: a mutation gets instantaneously fixed if $\Xi_{i} \leq g\left(X_{T_{i}}, A_{i}\right)$, and is lost otherwise. Note that, in the model considered in Kopp and Hermisson (2009),

$$
\begin{equation*}
\nu(d \alpha)=\frac{\Theta}{2} p(\alpha) d \alpha, \tag{6}
\end{equation*}
$$

whereas here, we do not impose that $\nu$ has a density, nor that it is a finite measure. Also, the exact form of the function $g$ is not important for us. Our argument will rely only upon the fact that for all $\alpha>0, g(x, \alpha) \uparrow 1$ as $x \rightarrow-\infty$ while $g(x, \alpha)=0$ if $x \alpha>0$.

## 3 Existence and uniqueness

Define for all $x$

$$
\begin{align*}
m(x) & =\int_{\mathbb{R}} \alpha g(x, \alpha) \nu(d \alpha), \\
m & =\int_{\mathbb{R}_{+}} \alpha \nu(d \alpha),  \tag{7}\\
\psi(x) & =m(x)-v,  \tag{8}\\
V(x) & =\int_{\mathbb{R}^{2}} \alpha^{2} g(x, \alpha) \nu(d \alpha), \\
V & =\int_{\mathbb{R}_{+}} \alpha^{2} \nu(d \alpha) . \tag{9}
\end{align*}
$$

$m(x)$ is the mean speed towards zero induced by the fixation of random mutations while $X_{t}=x<0 . V(x)$ is related to the second moment of the distribution of these mutations. $m$ and $V$ are the limits of $m(x)$ and $V(x)$, respectively, in the case that all mutations with $\alpha>0$ go to fixation (as we will show later, this is the case if $x \rightarrow-\infty$ ). Note that our assumptions do not exclude cases where $m=\infty$ and/or $V=\infty$, unless stated otherwise. However, since $g(x, \cdot)$ has compact support, for each $x, m(x)<\infty$ and $V(x)<\infty$. The cases $m=\infty$ and $V=\infty$ correspond to a heavy tailed $\nu$. It would be quite acceptable on biological grounds to assume that $m<\infty$ and/or $V<\infty$. However, we refrain from adding unnecessary assumptions. We rewrite the SDE (4) as follows

$$
\begin{equation*}
X_{t}=X_{0}+\int_{0}^{t} \psi\left(X_{s}\right) d s+\mathcal{M}_{t} \tag{10}
\end{equation*}
$$

where the martingale

$$
\begin{equation*}
\mathcal{M}_{t}=\int_{0}^{t} \int_{\mathbb{R}_{+}} \int_{0}^{1} \alpha \varphi\left(X_{s^{-}}, \alpha, \xi\right) \bar{M}(d s, d \alpha, d \xi) \tag{11}
\end{equation*}
$$

with $\bar{M}(d s, d \alpha, \xi)$ being the compensated Poisson measure $M(d s, d \alpha, d \xi)-\pi(d s, d \alpha, d \xi)$.

Proposition 1. Equation (10) has a unique solution.
Proof. If $\nu$ is a finite measure, then $M$ has a.s. finitely many points in $[0, t] \times \mathbb{R}$ for any $t>0$. In that case, the unique solution is constructed explicitly by adding the successive jumps. In the general case, we choose an arbitrary compact set $K=[-k, k]$ (with $k>0$ ). There are finitely many jumps $\left(t_{i}, \alpha_{i}\right)$ of $M$ with $\alpha_{i} \notin K$. It suffices to prove existence and uniqueness between two such consecutive jumps.

In other words, it suffices to prove existence and uniqueness under the assumption $\nu\left(K^{c}\right)=0$, and hence from (5), we deduce that $\int\left(|\alpha|+\alpha^{2}\right) \nu(d \alpha)<\infty$, which we assume from now on. Define for each $t>0$

$$
\begin{equation*}
\Gamma_{t}(U)=x-v t+\int_{[0, t] \times \mathbb{R} \times[0,1]} \alpha \varphi\left(U_{s^{-}}, \alpha, \xi\right) M(d s, d \alpha, d \xi) \tag{12}
\end{equation*}
$$

A solution of equation (10) is a fixed point of the mapping $\Gamma$. Hence it suffices to prove that $\Gamma$ admits a unique fixed point. For $\lambda>0$,

$$
\begin{aligned}
\mathbb{E} e^{-\lambda t}\left|\Gamma_{t}(U)-\Gamma_{t}(V)\right|= & -\lambda \mathbb{E} \int_{0}^{t} e^{-\lambda s}\left|\Gamma_{s}(U)-\Gamma_{s}(V)\right| d s+\mathbb{E} \int_{0}^{t}|\alpha| e^{-\lambda t} d\left|\Gamma_{s}(U)-\Gamma_{s}(V)\right| \\
\leq & -\lambda \mathbb{E} \int_{0}^{t} e^{-\lambda s}\left|\Gamma_{s}(U)-\Gamma_{s}(V)\right| d s \\
& +\mathbb{E} \int_{[0, t] \times \mathbb{R} \times[0,1]}|\alpha| e^{-\lambda t}\left|\varphi\left(U_{s^{-}}, \alpha, \xi\right)-\varphi\left(V_{s^{-}}, \alpha, \xi\right)\right| M(d s, d \alpha, d \xi) .
\end{aligned}
$$

The above inequality follows readily from the fact that, for all $0<s<t$,

$$
\begin{aligned}
\left|\Gamma_{t}(U)-\Gamma_{t}(V)\right| & -\left|\Gamma_{s}(U)-\Gamma_{s}(V)\right| \\
& \leq \int_{(s, t) \times \mathbb{R} \times[0,1]}|\alpha| \times\left|\varphi\left(U_{r^{-}}, \alpha, \xi\right)-\varphi\left(V_{r^{-}}, \alpha, \xi\right)\right| M(d r, d \alpha, d \xi) .
\end{aligned}
$$

Thus,

$$
\begin{equation*}
\lambda \mathbb{E} \int_{0}^{t} e^{-\lambda s}\left|\Gamma_{s}(U)-\Gamma_{s}(V)\right| d s \leq \mathbb{E} \int|\alpha| e^{-\lambda t}\left|g\left(U_{s^{-}}, \alpha\right)-g\left(V_{s^{-}}, \alpha\right)\right| d s \nu(d \alpha) . \tag{*}
\end{equation*}
$$

For $0<u<v$ we have that

$$
\begin{aligned}
\int_{\mathbb{R}}|\alpha(g(u, \alpha)-g(v, \alpha))| \nu(d \alpha)= & \int_{\mathbb{R}-}\left|\alpha\left(e^{-2 \sigma|\alpha|(2|v|-|\alpha|)^{+}}-e^{-2 \sigma|\alpha|(2|u|-|\alpha|)^{+}}\right)\right| \nu(d \alpha) \\
= & \int_{-2 u}^{0}\left|\alpha\left(e^{-2 \sigma|\alpha|(2|v|-|\alpha|)}-e^{-2 \sigma|\alpha|(2|u|-|\alpha|)}\right)\right| \nu(d \alpha) \\
& +\int_{-2 v}^{-2 u}|\alpha|\left|e^{-2 \sigma|\alpha|(2|v|-|\alpha|))}-1\right| \nu(d \alpha) \\
\leq & 4 \sigma\left(\int_{-2 u}^{0} \alpha^{2} \nu(d \alpha)\right) \times|u-v| \\
& +2 \sigma \int_{-2 v}^{-2 u} \alpha^{2}(2 v+\alpha) \nu(d \alpha) \\
\leq & 4 \sigma\left(\int_{\mathbb{R}} \alpha^{2} \nu(d \alpha)\right) \times|u-v| .
\end{aligned}
$$

A similar estimate can easily be obtained for $v<u<0$. For $u<0<v$, we have
that

$$
\begin{aligned}
\int_{\mathbb{R}^{\prime}}|\alpha(g(u, \alpha)-g(v, \alpha))| \nu(d \alpha) & \leq \int_{\mathbb{R}_{-}}|\alpha g(v, \alpha)| \nu(d \alpha)+\int_{\mathbb{R}_{+}}|\alpha g(u, \alpha)| \nu(d \alpha) \\
& \leq 2 \sigma \int_{\mathbb{R}_{-}} \alpha^{2}(2 v+\alpha)^{+} \nu(d \alpha)+2 \sigma \int_{\mathbb{R}_{+}} \alpha^{2}(-2 u-\alpha)^{+} \nu(d \alpha) \\
& \leq 4 \sigma \int_{\mathbb{R}_{-}} \alpha^{2}|v| \nu(d \alpha)+4 \sigma \int_{\mathbb{R}_{+}} \alpha^{2}|u| \nu(d \alpha) \\
& \leq 4 \sigma\left(\int_{\mathbb{R}^{-}} \alpha^{2} \nu(d \alpha)\right) \times|u-v| .
\end{aligned}
$$

Let $T$ be arbitrary. Define for all $\lambda>0$ the norm on the Banach space $L^{1}(\Omega \times$ $[0, T]$ ),

$$
\|Z\|_{T, \lambda}=\mathbb{E} \int_{0}^{T} e^{-\lambda t}\left|Z_{t}\right| d t
$$

We choose $\lambda_{0}>c=4 \sigma \int_{\mathbb{R}} \alpha^{2} \nu(d \alpha)$. We deduce from *) that

$$
\mathbb{E}\|\Gamma(U)-\Gamma(V)\|_{T, \lambda_{0}} \leq \frac{c}{\lambda_{0}} \mathbb{E}\|U-V\|_{T, \lambda_{0}} .
$$

Since $c / \lambda_{0}<1, \Gamma$ has a unique fixed point such that $\Gamma_{t}(U)=U_{t}$ for all $0 \leq t \leq T$. Since $T$ is arbitrary, the result is proved.

## 4 Classification of the large-time behaviour

Proposition 2. If $X_{0}>0$, then $X_{t}$ becomes negative after a finite time a.s.
Proof. Let $T_{0}=\inf \left(t>0, X_{t}<0\right)$. Since $g(x, \alpha)=0$ for $x \alpha>0$,

$$
\begin{aligned}
X_{t \wedge T_{0}^{-}} & =X_{0}-v\left(t \wedge T_{0}\right)+\int_{0}^{t \wedge T_{0}^{-}} \int_{\mathbb{R}} \int_{0}^{1} \alpha \varphi\left(X_{s^{-}}, \alpha, \xi\right) M(d s, d \alpha, d \xi) \\
& \leq X_{0}-v\left(t \wedge T_{0}\right)
\end{aligned}
$$

hence

$$
t \wedge T_{0} \leq \frac{X_{0}-X_{t \wedge T_{0}^{-}}}{v}<\frac{X_{0}}{v}
$$

Let $t$ tend to $\infty$.

$$
T_{0} \leq \frac{X_{0}}{v}<\infty
$$

Whether the process $X_{t}$ is positive recurrent, nul recurrent or transient depends only upon its behavior while $X_{t}<0$. Hence, we only need to consider in detail the case when $X_{t}$ is negative, in which case only positive mutations ( $\alpha>0$ ) have a positive probability of fixation. Thus the fixation probability becomes

$$
g(x, \alpha)=(1-\exp (-2 \sigma \alpha(2|x|-\alpha))) \mathbf{1}_{[0,2|x|]} .
$$

Proposition 3. The functions $x \longmapsto m(x)$ and $x \longmapsto V(x)$ are of class $C^{1}$, strictly decreasing on $\mathbb{R}_{-}$and

$$
\begin{align*}
& m(x) \xrightarrow[x \rightarrow-\infty]{ } m,  \tag{13}\\
& V(x) \xrightarrow[x \rightarrow-\infty]{ } V
\end{align*}
$$

Proof. We prove this result for the function $x \longmapsto m(x)$. A similar argument applies to $V(x)$. Let

$$
\begin{aligned}
h: \mathbb{R}_{-} \times \mathbb{R}_{+} & \rightarrow \mathbb{R}_{+} \\
(x, \alpha) & \mapsto h(x, \alpha)=\alpha g(x, \alpha) .
\end{aligned}
$$

- $\forall \alpha \in \mathbb{R}_{+}, x \mapsto h(x, \alpha)$ is differentiable.
- $\forall x \in \mathbb{R}_{-}$, the functions $\alpha \mapsto h(x, \alpha)$ and $\alpha \mapsto \frac{\partial h}{\partial x}(x, \alpha)$ are piecewise continuous and integrable over $\mathbb{R}_{+}$since they have compact support.
- For each fixed $\alpha>0$, if $x_{n} \in \mathbb{R}_{-}$such that $x_{n} \rightarrow x$, and $y=\inf _{n \geq 1} x_{n}$,

$$
\left|\frac{\partial h}{\partial x}\left(x_{n}, \alpha\right)\right| \leq 4 \sigma \alpha^{2} \mathbf{1}_{[0,2|y|+1]}(\alpha) \in L^{1}(\nu) .
$$

Thus, for all $x \in \mathbb{R}_{-}$

$$
\frac{d m(x)}{d x}=-\int_{\mathbb{R}} 4 \sigma \alpha^{2} \exp (-2 \sigma \alpha(2|x|-\alpha)) \mathbf{1}_{[0,2|x|]}(\alpha) \nu(d \alpha)<0 .
$$

As a consequence, $x \longmapsto m(x)$ is a decreasing function. Moreover

$$
\begin{aligned}
& h(x, \alpha) \in L^{1}(\nu) \\
& \text { For each fixed } \alpha>0,0 \leq h(x, \alpha) \uparrow \alpha \text {, as } x \rightarrow-\infty
\end{aligned}
$$

By the monotone convergence theorem, we have that

$$
m(x)=\int_{\mathbb{R}} h(x, \alpha) \nu(d \alpha) \xrightarrow[x \rightarrow-\infty]{ } m
$$

To determine the large-time behavior of the process, we now consider successively, the three cases $v>m, v<m$ and $v=m$.

### 4.1 The case $v>m$

In particular, here $m=\int_{0}^{\infty} \alpha \nu(d \alpha)$ is finite. Let

$$
\mathcal{N}_{t}=\int_{[0, t] \times \mathbb{R} \times[0,1]} \alpha \varphi\left(X_{s^{-}}, \alpha, \xi\right) M(d s, d \alpha, d \xi)
$$

be the sum of all the jumps on the time interval $[0, t]$. We have that

$$
\mathcal{N}_{t}=\mathcal{N}_{t}^{(+)}+\mathcal{N}_{t}^{(-)} \leq \mathcal{N}_{t}^{(-)},
$$

where

$$
\begin{aligned}
& \mathcal{N}_{t}^{(+)}=1_{\left\{X_{s^{-}}>0\right\}} d \mathcal{N}_{s} \\
& \mathcal{N}_{t}^{(-)}=\mathbf{1}_{\left\{X_{s^{-}}<0\right\}} d \mathcal{N}_{s}
\end{aligned}
$$

Let $m^{(-)}(x)=\mathbf{1}_{\{x<0\}} m(x)$, hence

$$
\mathcal{M}_{t}^{(-)}=\mathcal{N}_{t}^{(-)}-\int_{0}^{t} m^{(-)}\left(X_{s}\right) d s
$$

Thus,

$$
X_{t} \leq X_{0}+\int_{0}^{t}\left(m^{-}\left(X_{s}\right)-v\right) d s+\mathcal{M}_{t}^{(-)}
$$

Lemma 1. If $m<\infty$, then

$$
\begin{equation*}
\lim _{t \rightarrow \infty} \frac{\mathcal{M}_{t}^{(-)}}{t}=0 \tag{14}
\end{equation*}
$$

Proof. $\mathcal{M}_{t}^{(-)}$is a square-integrable martingale, such that $\mathbb{E} \mathcal{M}_{t}^{(-)}=0$. Define $M^{0}$ as the Poisson random measure for new mutations i.e. a Poisson point process on $\mathbb{R}_{+} \times \mathbb{R}$ with intensity $d s \nu(d \alpha)$. For all $i \in \mathbb{N}^{*}$ and $n \in \mathbb{N}^{*}$, define

$$
\begin{aligned}
\xi_{i} & =\int_{i-1}^{i} \int_{0}^{\infty} \int_{0}^{1} \alpha \varphi\left(X_{s^{-}}, \alpha, \xi\right) M(d s, d \alpha, d \xi), \\
\omega_{i} & =\int_{i-1}^{i} m^{-}\left(X_{s}\right) d s \\
\eta_{i} & =\int_{i-1}^{i} \int_{0}^{\infty} \alpha M^{0}(d s, d \alpha), \\
Y_{i} & =\xi_{i}-\omega_{i} \\
\mathcal{M}_{n} & =\sum_{i=1}^{n} Y_{i},
\end{aligned}
$$

Note that for all $i \in \mathbb{N}^{*}, 0 \leq \xi_{i} \leq \eta_{i}$ and $0 \leq \omega_{i} \leq m$. We first establish

Lemma 2.

$$
\text { If } \quad \frac{\sum_{i=1}^{n} Y_{i}}{n} \underset{n}{\longrightarrow} 0, \quad \text { then } \quad \frac{\mathcal{M}_{t}^{-}}{t} \underset{t \rightarrow \infty}{\longrightarrow} 0
$$

Proof.

$$
\frac{\mathcal{M}_{t}^{-}}{t}=\frac{\mathcal{M}_{\lfloor t\rfloor}^{-}}{\lfloor t\rfloor} \times \frac{\lfloor t\rfloor}{t}+\frac{\tilde{\mathcal{M}}^{-} t}{t}
$$

where

$$
\begin{aligned}
\frac{\tilde{\mathcal{M}}_{t}^{-}}{t}= & \frac{1}{t}\left(\int_{\lfloor t\rfloor}^{t} \iint \alpha \varphi\left(X_{s^{-}}, \alpha, \xi\right) M(d s, d \alpha, d \xi)-\int_{\lfloor t\rfloor}^{t} m^{-}\left(X_{s}\right) d s\right) \\
& \leq \frac{1}{t}\left(\int_{\lfloor t\rfloor}^{\lceil t\rceil} \iint \alpha \varphi\left(X_{s^{-}}, \alpha, \xi\right) M(d s, d \alpha, d \xi)+\int_{\lfloor t\rfloor}^{\lceil t\rceil} m^{-}\left(X_{s}\right) d s\right) \\
& =\frac{1}{t}\left(\xi_{\lceil t\rceil}+\omega_{\lceil t\rceil}\right)=\frac{\lceil t\rceil}{t} \times \frac{1}{\lceil t\rceil}\left(Y_{\lceil t\rceil}+2 \omega_{\lceil t\rceil}\right) \underset{t \rightarrow \infty}{ } 0,
\end{aligned}
$$

since for all $n>0$,

$$
\frac{Y_{n+1}}{n+1}=\frac{\sum_{i=1}^{n+1} Y_{i}}{n+1}-\frac{\sum_{i=1}^{n} Y_{i}}{n} \times \frac{n}{n+1} \underset{n \rightarrow \infty}{ } 0
$$

and

$$
0 \leq \frac{\left|\omega_{n}\right|}{n} \leq \frac{m}{n}
$$

hence

$$
\frac{\omega_{n}}{n} \xrightarrow[n \rightarrow \infty]{ } 0
$$

Back to the proof of Lemma 1. We now define

$$
\begin{aligned}
A_{i} & =\left\{\eta_{i}>i\right\}, \\
\tilde{Y}_{i} & =Y_{i} \mathbf{1}_{\left\{\eta_{i} \leq i\right\}} .
\end{aligned}
$$

Since the $\left(\eta_{i}, i \in \mathbb{N}^{*}\right)$ are i.i.d, integrable and

$$
\mathbb{P}\left(\eta_{i}>i\right)=\sum_{i \geq 1} \mathbb{P}\left(\eta_{1}>i\right) \leq \mathbb{E} \eta_{1}<\infty,
$$

it follows from Borel Cantelli's Lemma that $\mathbb{P}\left(\lim \sup A_{i}\right)=0$. Hence, a.s. there exists $N(\alpha)$ such that for all $n>N(\alpha)$, we have $\tilde{Y}_{n}=Y_{n}$. But since $\mathbb{E}\left(\tilde{Y}_{n}\right) \rightarrow \mathbb{E}\left(Y_{1}\right)$ due to the dominated convergence theorem, it is sufficient to prove that

$$
\frac{\sum_{i=1}^{n}\left(\tilde{Y}_{i}-\mathbb{E}\left(\tilde{Y}_{i}\right)\right)}{n} \underset{n}{ } 0
$$

Due to corollary 3.22 in Breiman (1968) it is again sufficient to prove that

$$
\sum_{i=1}^{\infty} \frac{\mathbb{E}\left(\tilde{Y}_{i}^{2}\right)}{i^{2}}<\infty
$$

Indeed, we have that

$$
\sum_{i=1}^{\infty} \frac{\mathbb{E}\left(\tilde{Y}_{i}^{2}\right)}{i^{2}}<2 m
$$

The underlying calculation can be found in the proof of theorem 3.30 in Breiman (1968).

Remark 1. In the case $m<\infty$ and $X_{t} \rightarrow-\infty$, we have that

$$
\frac{1}{t} \mathcal{M}_{t}^{(+)} \rightarrow 0
$$

since eventually $X_{t}$ becomes negative. Furthermore, if we assume that $\int_{-\infty}^{0} \alpha \nu(d \alpha)>$ $-\infty$ then the previous Lemma implies that

$$
\frac{\mathcal{M}_{t}}{t} \rightarrow 0
$$

whether $X_{t} \rightarrow-\infty$ or not. But we refrain from adding any supplementary assumption on $\nu$.

Proposition 4. In the case $v>m, X_{t} \rightarrow-\infty$ with speed $v-m$ in the sense that

$$
\frac{X_{t}}{t} \xrightarrow{\text { a.s. }} m-v \text { as } t \rightarrow \infty .
$$

Proof.

$$
\frac{X_{t}}{t}=\frac{X_{0}}{t}-v+\frac{1}{t} \int_{0}^{t} m\left(X_{s}\right) d s+\frac{\mathcal{M}_{t}}{t} \leq \frac{X_{0}}{t}-v+m+\frac{\mathcal{M}_{t}}{t} .
$$

[^0]Hence

$$
\begin{equation*}
\limsup _{t \rightarrow \infty} \frac{X_{t}}{t} \leq-v+m \tag{15}
\end{equation*}
$$

On the other hand, it follows from (13) that

$$
\begin{equation*}
\forall \epsilon>0 \quad \exists K_{\epsilon}>0 \text { such that } x \leq-K_{\epsilon} \Rightarrow m(x)>m-\epsilon, \tag{16}
\end{equation*}
$$

and since $X_{t} \xrightarrow[t \rightarrow \infty]{ }-\infty$ by (15), we have

$$
\begin{equation*}
\forall \epsilon>0 \quad \exists t_{\epsilon}>0 \text { such that } \forall s \geq t_{\epsilon} \Rightarrow X_{s} \leq-K_{\epsilon} . \tag{17}
\end{equation*}
$$

Statements (16) and (17) combined give

$$
\forall \epsilon>0 \quad \exists t_{\epsilon} \text { such that } \forall s \geq t_{\epsilon} \Rightarrow m\left(X_{s}\right)>m-\epsilon .
$$

Then, $\forall \epsilon>0$ and $t>t_{\epsilon}$

$$
\begin{aligned}
\frac{X_{t}}{t} & \geq \frac{X_{t_{\epsilon}}}{t}+\frac{1}{t} \int_{t_{\epsilon}}^{t}\left(m\left(X_{s}\right)-v\right) d s+\frac{\mathcal{M}_{t}-\mathcal{M}_{t_{\epsilon}}}{t} \\
& \geq \frac{X_{t_{\epsilon}}}{t}+(m-\epsilon-v) \times \frac{t-t_{\epsilon}}{t}+\frac{\mathcal{M}_{t}-\mathcal{M}_{t_{\epsilon}}}{t} .
\end{aligned}
$$

Hence,

$$
\liminf _{t \rightarrow \infty} \frac{X_{t}}{t} \geq-v+m
$$

We conclude that $X_{t} \rightarrow-\infty$ with speed $v-m$.

### 4.2 The case $v<m$

The assumption is satisfied, in particular, when $m=\infty$.
Proposition 5. In the case $v<m, X_{t}$ is positive recurrent.
Proof. Since $x \longmapsto m(x)$ is continuous, strictly decreasing from $\mathbb{R}_{-}$to $\mathbb{R}_{+}$and $m(0)=0<v<m, \exists N>0$ such that $m(-N)=v$. We choose an arbitrary $K>N$, so that for all $x<-K$

$$
\psi(x)>m(-K)-v>0 .
$$

Assume that $X_{0}<-K$, and define the stopping time

$$
T_{K}=\inf \left\{t>0, X_{t} \geq-K\right\}
$$

We have

$$
\begin{aligned}
X_{t \wedge T_{K}} & =X_{0}+\int_{0}^{t \wedge T_{K}} \psi\left(X_{s}\right) d s+\int_{\left[0, t \wedge T_{K}\right] \times \mathbb{R}_{+} \times[0,1]} \alpha \varphi\left(X_{s^{-}}, \alpha, \xi\right) \bar{M}(d s, d \alpha, d \xi) \\
& >X_{0}+(m(-K)-v)\left(t \wedge T_{K}\right)+\mathcal{M}_{t \wedge T_{K}} .
\end{aligned}
$$

Thus,

$$
0>\mathbb{E}\left(X_{t \wedge T_{K}}\right)>X_{0}+(m(-K)-v) \mathbb{E}\left(t \wedge T_{K}\right)
$$

Now let $t$ tend to $\infty$. It follows by monotone convergence that

$$
\begin{equation*}
\mathbb{E}\left(T_{K}\right)<\frac{-X_{0}}{m(-K)-v}<\infty \tag{18}
\end{equation*}
$$

Given any fixed $T>0$, let $p$ denote the lower bound of the probability that, starting from any given point $x \in[-K, 0)$ at time $t_{0}, X$ hits $[0,+\infty)$ before time $T$. Clearly $p>0$. We now define a geometric random variable $\beta$ with success probability $p$. Let us restart our process $X$ at time $t_{0}=T_{K}$ from $x_{0} \in[-K, 0)$. If $X$ hits zero before time $T$, then $\beta=1$. If not, we look at the position $X_{T}$ of $X$ at time $T$. Two cases are possible:

- If $X_{T}<-K$, we wait until $X$ goes back above $-K$. Since $X_{T} \geq-(K+v T)$, the time $\alpha_{2}$ needed to do so satisfies

$$
\mathbb{E}\left(\alpha_{2}\right) \leq \frac{K+v T}{m(-K)-v} .
$$

This calculation is similar to (18).

- If $X_{T} \geq-K$, we start afresh from there, since the probability to reach zero in less than $T$ is greater than or equal to $p$.
So either at time $T$ or at time $T+\alpha_{2}$, we start again from a level which is above $-K$. If $[0,+\infty)$ is reached during the next time interval of length $T$, then $\beta=2$. If not, we repeat the procedure. A.s. one of the mutually independent trials is successful. We have that

$$
T_{0}<T_{K}+\sum_{i=1}^{\beta}\left(T+\alpha_{i}\right)
$$

where the random variables $\left(\alpha_{i}\right)_{i}$ are i.i.d, globally independent of $\beta$. Hence

$$
\left.\mathbb{E} T_{0}<\mathbb{E} T_{K}+\frac{1}{p}\left(T+\frac{K+v T}{m(-K)-v}\right)\right),
$$

and the process is positive recurrent.

### 4.3 The case $v=m$

We first state a lemma that we will apply several times in this section.
Lemma 3. Let $X_{t}$ be a FV càdlàg process.

1. If $\Phi \in C^{1}$, then
$\Phi\left(X_{t}\right)=\Phi\left(X_{0}\right)+\int_{0}^{t} \Phi^{\prime}\left(X_{s^{-}}\right) d X_{s}+\sum_{s \leq t, \Delta X_{s} \neq 0} \Phi\left(X_{s^{-}}+\Delta X_{s}\right)-\Phi\left(X_{s^{-}}\right)-\Phi^{\prime}\left(X_{s^{-}}\right) \Delta X_{s}$,
where $\Delta X_{s}=X_{s}-X_{s^{-}}, \forall s$.
2. Moreover, if $\Phi \in C^{2}$ such that $\Phi^{\prime \prime}$ is an increasing function and $\Delta X_{s} \geq 0$ for all s, then

$$
\Phi\left(X_{t}\right)-\Phi\left(X_{0}\right)-\int_{0}^{t} \Phi^{\prime}\left(X_{s^{-}}\right) d X_{s} \geq \frac{1}{2} \sum_{s \leq t, \Delta X_{s} \neq 0} \Phi^{\prime \prime}\left(X_{s}\right)\left(\Delta X_{s}\right)^{2} .
$$

If $\Phi \in C^{2}$ such that $\Phi^{\prime \prime}$ is a decreasing function and $\Delta X_{s} \geq 0$ for all $s$, then

$$
\Phi\left(X_{t}\right)-\Phi\left(X_{0}\right)-\int_{0}^{t} \Phi^{\prime}\left(X_{s^{-}}\right) d X_{s} \leq \frac{1}{2} \sum_{s \leq t, \Delta X_{s} \neq 0} \Phi^{\prime \prime}\left(X_{s^{-}}\right)\left(\Delta X_{s}\right)^{2}
$$

In particular, choosing $\Phi(x)=x^{2}$, we deduce that

$$
\begin{equation*}
X_{t}^{2}=X_{0}^{2}+2 \int_{0}^{t} X_{s^{-}} d X_{s}+\sum_{s \leq t}\left(\Delta X_{s}\right)^{2} \tag{19}
\end{equation*}
$$

Proof. The first part of this lemma is a well known result (see Protter 2005). We will only prove part 2 of the lemma. If $\Phi \in C^{2}$ then it follows from Taylor's formula that there exists a random function $\beta$ taking its values in $[0,1]$ such that for all $s$

$$
\Phi\left(X_{s}\right)-\Phi\left(X_{s^{-}}\right)-\Phi^{\prime}\left(X_{s^{-}}\right) \Delta X_{s}=\frac{1}{2} \Phi^{\prime \prime}\left(X_{s^{-}}+\beta_{s} \Delta X_{s}\right)\left(\Delta X_{s}\right)^{2} .
$$

If $\Phi^{\prime \prime}$ is an increasing function and $y \geq 0$ then

$$
\Phi^{\prime \prime}(x) \leq \Phi^{\prime \prime}\left(x+\beta_{s} y\right) \leq \Phi^{\prime \prime}(x+y)
$$

If $\Phi^{\prime \prime}$ is a decreasing function and $y \geq 0$ then

$$
\Phi^{\prime \prime}(x+y) \leq \Phi^{\prime \prime}\left(x+\beta_{s} y\right) \leq \Phi^{\prime \prime}(x)
$$

Note that $V \leq \infty$ and at this stage we do not assume that $V$ is finite. In the case $m=v$, the asymptotic behavior of the process $X_{t}$ depends on the asymptotic behavior of the mean net rate of adaptation $\psi(x)$ defined in (8) as $x \rightarrow-\infty$.

Proposition 6. We assume that $m=v$. If moreover

$$
\begin{equation*}
\limsup _{x \rightarrow-\infty}|x \psi(x)|<\frac{V}{2} \tag{20}
\end{equation*}
$$

then the process $X_{t}$ is null recurrent.
We first establish
Lemma 4. Under the condition $m<\infty$, we have that

$$
\lim _{x \rightarrow-\infty} \frac{V(x)}{|x|}=0
$$

Proof. Consider, for $x<x_{0}<0$,

$$
\begin{aligned}
\frac{V(x)}{|x|} & \leq \frac{1}{|x|} \int_{0}^{2|x|} \alpha^{2} \nu(d \alpha) \\
& =\frac{1}{|x|} \int_{0}^{2\left|x_{0}\right|} \alpha^{2} \nu(d \alpha)+\frac{1}{|x|} \int_{2\left|x_{0}\right|}^{2|x|} \alpha^{2} \nu(d \alpha) \\
& \leq \frac{1}{|x|} \int_{0}^{2\left|x_{0}\right|} \alpha^{2} \nu(d \alpha)+2 \int_{2\left|x_{0}\right|}^{\infty} \alpha \nu(d \alpha),
\end{aligned}
$$

hence

$$
\limsup _{x \rightarrow-\infty} \frac{V(x)}{|x|} \leq 2 \int_{2\left|x_{0}\right|}^{\infty} \alpha \nu(d \alpha)
$$

and our condition implies that the last right hand side tends to 0 , as $x_{0} \rightarrow-\infty$. The results follows.

We can now return to the
Proof of Proposition 6. First note that, since $m=v$ implies $\psi(x) \leq 0$ for all $x \leq 0$, condition (20) is equivalent to

$$
\liminf _{x \rightarrow-\infty}|x| \psi(x)>-\frac{V}{2}
$$

To prove recurrence under condition (20), we recall that

$$
\begin{equation*}
X_{t}=X_{0}+\int_{0}^{t} \psi\left(X_{s}\right) d s+\mathcal{M}_{t} \tag{21}
\end{equation*}
$$

We will apply Lemma 3 with $f(x)=\log |x|$, with $x<0$. Here $f^{\prime \prime}$ is decreasing. Hence as long as $X_{t}$ remains negative,

$$
\begin{aligned}
\log \left|X_{t}\right| & \leq \log \left|X_{0}\right|+\int_{0}^{t} \frac{\psi\left(X_{s}\right)}{X_{s}} d s+\int_{0}^{t} \frac{1}{X_{s^{-}}} d \mathcal{M}_{s}-\frac{1}{2} \sum_{s \leq t} \frac{\left(\Delta X_{s}\right)^{2}}{X_{s^{-}}^{2}} \\
& \leq \log \left|X_{0}\right|+\int_{0}^{t} \frac{\psi\left(X_{s}\right)}{X_{s}} d s+\int_{0}^{t} \frac{1}{X_{s^{-}}} d \mathcal{M}_{s} \\
& -\frac{1}{2} \int_{0}^{t} \int_{\mathbb{R}_{+}} \int_{0}^{1} \frac{\alpha^{2} \varphi\left(X_{s^{-}}, \alpha, \xi\right)}{X_{s^{-}}^{2}} \bar{M}(d s, d \alpha, d \xi)-\frac{1}{2} \int_{0}^{t} \frac{V\left(X_{s}\right)}{X_{s}^{2}} d s \\
& =\log \left|X_{0}\right|+\int_{0}^{t}\left(\frac{\psi\left(X_{s}\right)}{X_{s}}-\frac{V\left(X_{s}\right)}{2 X_{s}^{2}}\right) d s+\hat{\mathcal{M}}_{t}
\end{aligned}
$$

where $\hat{\mathcal{M}}$ is a martingale. For all $a<b<0$, define the stopping time

$$
S_{a, b}=\inf \left(t>0, X_{t} \leq a \text { or } X_{t} \geq b\right)
$$

It follows from our assumption that there exists $L>0$ such that

$$
\begin{equation*}
\inf _{x \leq-L}\left(|x| \psi(x)+\frac{V(x)}{2}\right)>0 \tag{22}
\end{equation*}
$$

For any $N>L$, from Doob's optional sampling theorem, if $-N<X_{0}<L$,

$$
\mathbb{E} \log \left|X_{t \wedge S_{-N,-L}}\right| \leq \log \left|X_{0}\right|+\mathbb{E} \int_{0}^{t \wedge S_{-N,-L}}\left(\frac{\psi\left(X_{s}\right)}{X_{s}}-\frac{V\left(X_{s}\right)}{2 X_{s}^{2}}\right) d s
$$

Letting $t$ tend to $\infty$,

$$
\mathbb{E} \log \left|X_{S_{-N,-L}}\right| \leq \log \left|X_{0}\right|
$$

Define the stopping times

$$
\begin{aligned}
T_{-L}^{\uparrow} & =\inf \left(t>0, X_{t} \geq-L\right) \\
T_{-N}^{\downarrow} & =\inf \left(t>0, X_{t} \leq-N\right) .
\end{aligned}
$$

It follows from the previous estimate that

$$
\log N \times \mathbb{P}\left(T_{-N}^{\downarrow}<T_{-L}^{\uparrow}\right)<\log \left|X_{0}\right|
$$

We deduce that $\mathbb{P}\left(T_{-N}^{\downarrow}<T_{-L}^{\uparrow}\right) \rightarrow 0$ as $N$ tend to $\infty$. We conclude that the process returns a.s. an infinite number of times above $-L$, hence also above 0 by a classical argument (see the proof of Proposition 5). Therefore, the process $X$ is recurrent.
Let now $X_{0}<-(L+1)$. For all $N>L$, multiplying (21) by -1 , we have

$$
\left|X_{t \wedge S_{-N,-L}}\right|=\left|X_{0}\right|-\int_{0}^{t \wedge S_{-N,-L}} \psi\left(X_{s}\right) d s-\int_{0}^{t \wedge S_{-N,-L}} d \mathcal{M}_{s},
$$

By Doob's theorem and letting $t$ tend to $\infty$, since again $\psi(x) \leq 0$ for $x \leq 0$

$$
\begin{aligned}
\mathbb{E}\left|X_{S_{-N,-L}}\right|=\left|X_{0}\right|-\mathbb{E} \int_{0}^{S_{-N,-L}} \psi\left(X_{s}\right) d s \geq\left|X_{0}\right|, \text { hence } \\
\quad L \mathbb{P}\left(T_{-L}^{\dagger}<T_{-N}^{\downarrow}\right)+N \mathbb{P}\left(T_{-N}^{\downarrow}<T_{-L}^{\uparrow}\right) \geq\left|X_{0}\right| .
\end{aligned}
$$

We have

$$
\begin{equation*}
\liminf _{N \rightarrow \infty} N \mathbb{P}\left(T_{-N}^{\downarrow}<T_{-L}^{\uparrow}\right) \geq\left|X_{0}\right|-L>0 \tag{23}
\end{equation*}
$$

It follows from Lemma 3 that

$$
X_{t}^{2}=X_{0}^{2}-\int_{0}^{t} 2\left|X_{s}\right| \psi\left(X_{s}\right) d s+\int_{0}^{t} 2 X_{s^{-}} d \mathcal{M}_{s}+\sum_{s \leq t}\left(\Delta X_{s}\right)^{2}
$$

On the other hand,

$$
\begin{aligned}
\sum_{s \leq t}\left(\Delta X_{s}\right)^{2} & =\int_{0}^{t} \int_{\mathbb{R}_{+}} \int_{0}^{1} \alpha^{2} \varphi\left(X_{s^{-}}, \alpha, \xi\right) \bar{M}(d s, d \alpha, d \xi) \\
& +\int_{0}^{t} \int_{\mathbb{R}_{+}} \alpha^{2} g\left(X_{s^{-}}, \alpha\right) \nu(d \alpha) d s
\end{aligned}
$$

Thus, from (22) and the monotonicity of $V(x)$

$$
X_{t \wedge S_{-N,-L}}^{2} \leq X_{0}^{2}+\int_{0}^{t \wedge S_{-N,-L}} 2 V(-N) d s+\tilde{\mathcal{M}}_{t \wedge S_{-N,-L}}
$$

where $\tilde{\mathcal{M}}_{\cdot \wedge S_{-N,-L}}$ is a martingale. Letting $t$ tend to $\infty$, we have for all $\epsilon>0$

$$
\begin{aligned}
\mathbb{E} X_{S_{-N,-L}}^{2} & \leq X_{0}^{2}+2 V(-N) \mathbb{E} S_{-N,-L}, \text { hence } \\
\mathbb{E} S_{-N,-L} & \geq \frac{L^{2} \mathbb{P}\left(T_{-L}^{\uparrow}<T_{-N}^{\downarrow}\right)+N^{2} \mathbb{P}\left(T_{-N}^{\downarrow}<T_{-L}^{\uparrow}\right)-X_{0}^{2}}{2 V(-N)}
\end{aligned}
$$

It follows by monotone convergence that

$$
\mathbb{E}\left(T_{-L}^{\dagger}\right)=\lim _{N \rightarrow \infty} \mathbb{E} S_{-N,-L} \geq \liminf _{N \rightarrow \infty}\left\{N \mathbb{P}\left(T_{-N}^{\downarrow}<T_{-L}^{\uparrow}\right) \times \frac{N}{2 V(-N)}-\frac{X_{0}^{2}}{2 V(-N)}\right\} .
$$

Combining this with Lemma 4 and (23), we deduce that $\mathbb{E} T_{-L}^{\uparrow}=\infty$ and the process is null recurrent.
Remark 2. Condition (20) is rather weak. It is satisfied as soon as both the measure $\nu$ and $V$ are finite. We give the proof below. It is also satisfied for some measures that don't have a second moment such as

$$
\nu(d \alpha) \approx \frac{d \alpha}{\alpha^{2+\delta}} \mathbf{1}_{\{\alpha \geq 1\}}, \quad \frac{1}{2}<\delta \leq 1
$$

Proposition 7. If $\nu$ is a finite measure and $V<\infty$ then (20) is satisfied.
Proof. Let for all $x$,

$$
\begin{aligned}
D(x)=|x \psi(x)|-\frac{V(x)}{2} & =|x| \int_{2 \mid x x}^{\infty} \alpha \nu(d \alpha)-\int_{0}^{2|x|} \frac{\alpha^{2}}{2} \nu(d \alpha) \\
& +\int_{0}^{2|x|}\left(|x| \alpha+\alpha^{2}\right) e^{-2 \sigma \alpha(2|x|-\alpha)} \nu(d \alpha) .
\end{aligned}
$$

It follows by dominated convergence that

$$
\int_{0}^{\infty} \alpha^{2} e^{-2 \sigma \alpha(2|x|-\alpha)} \mathbf{1}_{[0,2|x|]} \nu(d \alpha) \xrightarrow[x \rightarrow-\infty]{ } 0
$$

since,

$$
\begin{aligned}
& \quad \alpha^{2} e^{-2 \sigma \alpha(2|x|-\alpha)} \mathbf{1}_{[0,2|x|]} \xrightarrow[x \rightarrow-\infty]{a . s .} 0 \text { for all } \alpha>0, \\
& \text { and } \alpha^{2} e^{-2 \sigma \alpha(2|x|-\alpha)} \mathbf{1}_{[0,2|x|]} \leq \alpha^{2} \in L^{1}(\nu) .
\end{aligned}
$$

On the other hand,
$\int_{0}^{2|x|}|x| \alpha e^{-2 \sigma \alpha(2|x|-\alpha)} \nu(d \alpha)=\int_{0}^{|x|}|x| \alpha e^{-2 \sigma \alpha(2|x|-\alpha)} \nu(d \alpha)+\int_{|x|}^{2|x|}|x| \alpha e^{-2 \sigma \alpha(2|x|-\alpha)} \nu(d \alpha)$.
Note that if $0 \leq \alpha \leq|x|$ then $2|x|-\alpha \geq|x|$, thus

$$
e^{-2 \sigma \alpha(2|x|-\alpha)} \leq e^{-2 \sigma \alpha|x|}
$$

In addition the function

$$
\begin{aligned}
f_{\sigma}: \mathbb{R}_{+} & \rightarrow \mathbb{R}_{+} \\
z & \rightarrow f_{\sigma}(z)=z e^{-\sigma z}
\end{aligned}
$$

has a maximum for $z=\frac{1}{\sigma}$. It follows that

$$
\int_{0}^{|x|}|x| \alpha e^{-2 \sigma \alpha(2|x|-\alpha)} \nu(d \alpha) \leq \frac{2}{\sigma e} \int_{0}^{\infty} e^{-\sigma|x| \alpha} \nu(d \alpha) \xrightarrow[x \rightarrow-\infty]{ } 0,
$$

again by dominated convergence. The second term also goes to 0 when $x \rightarrow-\infty$. In fact,

$$
\int_{|x|}^{2|x|}|x| \alpha e^{-2 \sigma \alpha(2|x|-\alpha)} \nu(d \alpha) \leq \int_{0}^{\infty} \alpha^{2} e^{-2 \sigma \alpha(2|x|-\alpha)} \nu(d \alpha),
$$

and by the same argument as before the result follows since

$$
\begin{aligned}
& \quad \alpha^{2} e^{-2 \sigma \alpha(2|x|-\alpha)} \mathbf{1}_{[|x|, 2|x|]} \xrightarrow[x \rightarrow-\infty]{a . s .} 0 \text { for all } \alpha>0, \\
& \text { and } \alpha^{2} e^{-2 \sigma \alpha(2|x|-\alpha)} \mathbf{1}_{[|x|, 2|x|]} \leq \alpha^{2} \in L^{1}(\nu) .
\end{aligned}
$$

Furthermore, it follows from the fact that $V$ is finite that

$$
|x| \int_{2|x|}^{\infty} \alpha \nu(d \alpha) \leq \int_{2|x|}^{\infty} \frac{\alpha^{2}}{2} \nu(d \alpha) \xrightarrow[x \rightarrow-\infty]{ } 0
$$

Hence,

$$
\limsup _{x \rightarrow-\infty} D(x)=-\frac{V}{2}<0
$$

We now consider the case $m=v$ and $\liminf _{x \rightarrow-\infty}|x \psi(x)|>\frac{V}{2}$, which implies in particular that $V<\infty$.

Proposition 8. Assume that $m=v$ and

$$
\begin{equation*}
\liminf _{x \rightarrow-\infty}|x \psi(x)|>\frac{V}{2} \tag{24}
\end{equation*}
$$

If, moreover, there exist $0<p_{0}<1$ and $0<\beta_{0}<1$ such that for all $0<\beta<\beta_{0}$

$$
\begin{equation*}
|x|^{p_{0}+2} \int_{-\beta x}^{\infty} \alpha^{2} g(x, \alpha) \nu(d \alpha) \xrightarrow[x \rightarrow-\infty]{\longrightarrow} 0 \tag{25}
\end{equation*}
$$

then $X_{t}$ is transient, that is, $X_{t} \rightarrow-\infty$, and moreover $\frac{X_{t}}{t} \rightarrow 0$.
Remark 3. The conditions of Proposition 8 are satisfied in the case where both $\nu$ is infinite and its tail is thin enough. For example, if

$$
\nu(d \alpha)=\left(\frac{1}{\alpha^{1+\delta}} \mathbf{1}_{|\alpha|<1}+g(\alpha) \mathbf{1}_{|\alpha|>1}\right) d \alpha,
$$

where $g(\alpha) \leq C|\alpha|^{-\left(5+\delta^{\prime}\right)},|\alpha|>1$ for some $\delta, \delta^{\prime}>0$. Condition (24) follows from the fact that $V<\infty$ while $|x \psi(x)| \rightarrow \infty$ as $|x| \rightarrow \infty$, since, cf. proof of Proposition 7.

$$
\begin{aligned}
|x| \int_{0}^{1} \alpha e^{-2 \sigma \alpha(2|x|-\alpha)} \nu(d \alpha) & \geq|x| \int_{0}^{1} \alpha^{-\delta} e^{-4 \sigma \alpha|x|} d \alpha \\
& =|x|^{\delta} \int_{0}^{|x|} e^{-4 \sigma z} \frac{d z}{z^{\delta}} .
\end{aligned}
$$

Condition (25) is easy to check.

Proof. First note that condition (24) is equivalent to

$$
\limsup _{x \rightarrow-\infty}|x| \psi(x)<-\frac{V}{2}
$$

Hence there exist $K>0$ and $0<p \leq p_{0}$ such that

$$
\begin{equation*}
\sup _{x \leq-K}\left(|x| \psi(x)+(2 p+1) \frac{V(x)}{2}\right)<0 \tag{26}
\end{equation*}
$$

Let $f$ be the $C^{2}(\mathbb{R})$-function such that $f(-1)=1, f^{\prime}(-1)=p$, and

$$
f^{\prime \prime}(x)=\frac{p(p+1)}{|x|^{p+2}} \mathbf{1}_{\{x \leq-1\}}+p(p+1) \mathbf{1}_{\{x \geq-1\}},
$$

with $p$ being a real number in $(0,1)$ for which (26) holds. Then it follows from Lemma 3 applied to $f$, since $f^{\prime \prime}$ is an increasing function,
$f\left(X_{t}\right) \leq f\left(X_{0}\right)+\int_{0}^{t} \psi\left(X_{s}\right) f^{\prime}\left(X_{s}\right) d s+\frac{1}{2} \int_{0}^{t} \int_{0}^{\infty} f^{\prime \prime}\left(X_{s}+\alpha\right) \alpha^{2} g\left(X_{s}, \alpha\right) \nu(d \alpha) d s+\mathcal{N}_{t}$,
where the martingale $\mathcal{N}$ is defined by

$$
\mathcal{N}_{t}=\frac{1}{2} \int_{0}^{t} \int_{0}^{\infty} \int_{0}^{1}\left[f^{\prime}\left(X_{s^{-}}\right)+f^{\prime \prime}\left(X_{s^{-}}+\alpha\right) \alpha^{2}\right] \varphi\left(X_{s^{-}}, \alpha, \xi\right) \bar{M}(d s, d \alpha, d \xi)
$$

Let us admit for the moment:
Lemma 5. If (25) holds, then

$$
\lim _{x \rightarrow-\infty}|x|^{p+2} \int_{0}^{\infty} f^{\prime \prime}(x+\alpha) \alpha^{2} g(x, \alpha) \nu(d \alpha)=p(p+1) V .
$$

This implies that

$$
\lim _{x \rightarrow-\infty}|x|^{p+2} \int_{0}^{\infty} f^{\prime \prime}(x+\alpha) \alpha^{2} g(x, \alpha) \nu(d \alpha)<\lim _{x \rightarrow-\infty} p(2 p+1) V(x) .
$$

Hence, there exists $N \geq K$ such that for all $x \leq-N$,

$$
\int_{0}^{\infty} f^{\prime \prime}(x+\alpha) \alpha^{2} g(x, \alpha) \nu(d \alpha)<p(2 p+1) \frac{V(x)}{|x|^{p+2}}
$$

Thus, for all $k>0$ satisfying $-k N<X_{0}<-N$,

$$
\begin{aligned}
f\left(X_{t \wedge S_{-k N,-N}}\right) \leq & f\left(X_{0}\right)+\int_{0}^{t \wedge S_{-k N,-N}} \frac{p}{\left|X_{s}\right|^{p+1}}\left[\psi\left(X_{s}\right)+(2 p+1) \frac{V\left(X_{s}\right)}{2\left|X_{s}\right|}\right] d s \\
& +\mathcal{N}_{t \wedge S_{-k N,-N}} .
\end{aligned}
$$

Now if $k \geq 3$, letting $X_{0}=-2 N$, it follows from (26) that

$$
\mathbb{E}\left(f\left(X_{t \wedge S_{-k N,-N}}\right)\right) \leq \frac{1}{(2 N)^{p}} .
$$

Thus, if we let $t$ tend to $\infty$,

$$
\left.\frac{1}{N^{p}} \mathbb{P}\left(S_{-k N,-N}=T_{-N}^{\uparrow}\right)\right) \leq \mathbb{E} \frac{1}{\left|X_{S_{-k N,-N}}\right|^{p}} \leq \frac{1}{(2 N)^{p}}
$$

Now letting $k$ tend to $\infty$,

$$
\mathbb{P}\left(T_{-N}^{\uparrow}<\infty\right) \leq \frac{1}{2^{p}}
$$

Thus, the process is transient, which means

$$
X_{t} \xrightarrow[t \rightarrow \infty]{\longrightarrow}-\infty
$$

And since $m=v<\infty$, it follows from Lemma 1 that $\frac{\mathcal{M}_{t}}{t} \rightarrow 0$, hence

$$
\frac{X_{t}}{t} \xrightarrow[t \rightarrow \infty]{ } 0
$$

Proof of Lemma 4. For any $0<\beta<\beta_{0}<1$, if $x<-(1-\beta)^{-1}$,

$$
\begin{aligned}
|x|^{p+2} \int_{0}^{\infty} f^{\prime \prime}(x+\alpha) g(x, \alpha) \alpha^{2} \nu(d \alpha) & =|x|^{p+2} \int_{0}^{-\beta x} f^{\prime \prime}(x+\alpha) \alpha^{2} g(x, \alpha) \nu(d \alpha) \\
& +|x|^{p+2} \int_{-\beta x}^{\infty} f^{\prime \prime}(x+\alpha) \alpha^{2} g(x, \alpha) \nu(d \alpha) \\
& \leq \int_{0}^{-\beta x} \frac{p(p+1)}{(1-\beta)^{p+2}} \alpha^{2} g(x, \alpha) \nu(d \alpha) \\
& +|x|^{p+2} p(p+1) \int_{-\beta x}^{\infty} \alpha^{2} g(x, \alpha) \nu(d \alpha) .
\end{aligned}
$$

On the other hand,

$$
\begin{aligned}
|x|^{p+2} \int_{0}^{\infty} f^{\prime \prime}(x+\alpha) \alpha^{2} g(x, \alpha) \nu(d \alpha) & \geq p(p+1) \int_{0}^{-\beta x} \frac{|x|^{p+2}}{|x+\alpha|^{p+2}} \alpha^{2} g(x, \alpha) \nu(d \alpha) \\
& >p(p+1) \int_{0}^{-\beta x} \alpha^{2} g(x, \alpha) \nu(d \alpha)
\end{aligned}
$$

Letting $x \rightarrow-\infty$ in the two above inequalities, we deduce from (25), which holds with $p_{0}$ replaced by $p \leq p_{0}$,

$$
\begin{aligned}
p(p+1) V & \leq \liminf _{x \rightarrow-\infty}|x|^{p+2} \int_{0}^{\infty} f^{\prime \prime}(x+\alpha) \alpha^{2} g(x, \alpha) \nu(d \alpha) \\
& \leq \limsup _{x \rightarrow-\infty}|x|^{p+2} \int_{0}^{\infty} f^{\prime \prime}(x+\alpha) \alpha^{2} g(x, \alpha) \nu(d \alpha) \\
& \leq \frac{p(p+1)}{(1-\beta)^{p+2}} V .
\end{aligned}
$$

Thus, letting $\beta \rightarrow 0$, it follows that

$$
|x|^{p+2} \int_{0}^{\infty} f^{\prime \prime}(x+\alpha) \alpha^{2} g(x, \alpha) \nu(d \alpha) \underset{x \rightarrow-\infty}{ } p(p+1) V
$$

Remark 4. We have not been able to precise the large time behavior of the process $X_{t}$ when the measure $\nu$ is of the type

$$
\nu(d \alpha) \approx \frac{d \alpha}{\alpha^{2+\delta}} \mathbf{1}_{\{\alpha \geq 1\}}, \quad 0<\delta \leq \frac{1}{2}
$$

which still satisfies $m<\infty$. In this case, $V=\infty,|x \psi(x)| \rightarrow \infty$ as $|x| \rightarrow \infty$, and (25) also fails.

## 5 Generalization to the case of a time-variable speed

In the following, we treat the case where the speed of environmental change is a random function of time

$$
\begin{equation*}
v(t)=\int_{0}^{t} v_{1}(s) d s+\mathcal{R}_{t} \tag{27}
\end{equation*}
$$

where $v_{1}$ is a random function such that

$$
\frac{1}{t} \int_{0}^{t} v_{1}(s) d s \underset{t \rightarrow \infty}{ } \bar{v}
$$

and $\mathcal{R}$ is a stochastic process. The stochastic equation describing the evolution of phenotypic lag becomes

$$
\begin{equation*}
X_{t}=X_{0}-v(t)+\int_{0}^{t} m\left(X_{s}\right) d s+\mathcal{M}_{t} \tag{28}
\end{equation*}
$$

As above, we study three cases:

### 5.1 The case $\bar{v}>m$

Here we assume that $\mathcal{R}$ satisfies the condition

$$
\frac{\mathcal{R}_{t}}{t} \underset{t \rightarrow \infty}{ } 0
$$

This condition is verified by a Brownian motion for example. It is easy to see that results (13) and (14) hold in the new context of equation (28). Following the steps of the proof in section 1 , we can see that $X_{t} \rightarrow-\infty$ with speed $\bar{v}-m$.

### 5.2 The case $\bar{v}<m$

Define $\mathcal{T}$ as the set of bounded stopping times. Now we assume that there exists $0<c<\infty$ such that $\mathbb{E} \mathcal{R}_{T} \leq c$ for all $T \in \mathcal{T}$. This condition is verified for example by a process sum of a martingale and a bounded process. In this case, we will prove that the process $X_{t}$ is positive recurrent. We can see from (13) and (27) that there exist $M, N>0$ such that for $y<-M$ and $t>N$,

$$
m(x)-\frac{1}{t} \int_{0}^{t} v_{1}(s) d s>\frac{m-\bar{v}}{2} .
$$

We remind that

$$
T_{-M}^{\uparrow}=\inf \left\{t>0, X_{t} \geq-M\right\} .
$$

For the purpose of notation and without loss of generality, we denote $T_{-M}^{\dagger}$ by $T$. Assume that $X_{0}<-M$. It follows that for all $t>N$,

$$
\mathbb{E} \int_{0}^{t \wedge T}\left[m\left(X_{s}\right)-v_{1}(s)\right] d s<-X_{0}+\mathbb{E} \mathcal{R}_{t \wedge T}
$$

since $X_{s}<0$ for $s<T$. We have

$$
\begin{aligned}
\mathbb{E} \int_{0}^{t \wedge T}\left[m\left(X_{s}\right)-v_{1}(s)\right] d s & =\mathbb{E} \mathbf{1}_{T \geq N} \int_{0}^{t \wedge T}\left[m\left(X_{s}\right)-v_{1}(s)\right] d s \\
& +\mathbb{E} \mathbf{1}_{T<N} \int_{0}^{t \wedge T}\left[m\left(X_{s}\right)-v_{1}(s)\right] d s \\
& <-X_{0}+\mathbb{E} \mathcal{R}_{t \wedge T},
\end{aligned}
$$

and hence,

$$
\begin{aligned}
\frac{m-\bar{v}}{2} \mathbb{E}\left(\mathbf{1}_{T \geq N}(t \wedge T)\right) & \leq-X_{0}+\mathbb{E} \mathcal{R}_{t \wedge T}-\mathbb{E} \mathbf{1}_{T<N} \int_{0}^{t \wedge T}\left[m\left(X_{s}\right)-v_{1}(s)\right] d s \\
& \leq-X_{0}+\mathbb{E} \mathcal{R}_{t \wedge T}+\int_{0}^{N} v_{1}^{+}(s) d s
\end{aligned}
$$

Now let $t$ tend to $\infty$, yielding

$$
\mathbb{E}\left(\mathbf{1}_{T \geq N} T\right)<\frac{2}{m-\bar{v}}\left(-X_{0}+\int_{0}^{N} v_{1}^{+}(s) d s+c\right)<\infty .
$$

Thus, $\mathbb{E}(T)<N+\mathbb{E}\left(\mathbf{1}_{T \geq N} T\right)<\infty$. From here, it is not hard to prove that $\mathbb{E} X_{T_{0}^{\uparrow}}<\infty$. Thus, $X_{t}$ is positive recurrent.

### 5.3 The case $\bar{v}=m$

Here we assume that $\mathcal{R}_{t} \equiv 0$. Even in this case stronger assumptions need to be made. Define

$$
\begin{aligned}
v_{\text {sup }} & =\sup _{s} v_{1}(s), \\
v_{\text {inf }} & =\inf _{s} v_{1}(s), \\
\psi_{\text {sup }}(x) & =m(x)-v_{\text {sup }}, \\
\psi_{\text {inf }}(x) & =m(x)-v_{\text {inf }},
\end{aligned}
$$

We define two sets of assumptions:

## Assumptions A

- $v_{\text {sup }}<\infty$,
- $\liminf _{x \rightarrow-\infty}|x| \psi_{\text {sup }}(x)>-\frac{V}{2}$.


## Assumptions B

- $v_{\text {inf }}<\infty$,
- $\limsup _{x \rightarrow-\infty}|x| \psi_{\text {inf }}(x)<-\frac{V}{2}$.

Under the set of assumptions A, we can prove that the process is recurrent. We have, however, not been able to prove null recurrence in the case of non-constant $v$.

Ideas of Proof. Apply Lemma 3 to the process in equation (28) with $f(x)=\log |x|$, with $x<0$. Here $f^{\prime \prime}$ is decreasing. Hence, as long as $X_{t}$ remains negative,

$$
\begin{aligned}
\log \left|X_{t}\right| & \leq \log \left|X_{0}\right|+\int_{0}^{t}\left(\frac{\psi_{\sup }\left(X_{s}\right)}{X_{s}}-\frac{V\left(X_{s}\right)}{2 X_{s}^{2}}\right) d s+\int_{0}^{t} \frac{v_{\mathrm{sup}}-v_{1}(s)}{X_{s}} d s+\mathcal{M}_{t}^{\prime} \\
& <\log \left|X_{0}\right|+\int_{0}^{t}\left(\frac{\psi_{\sup }\left(X_{s}\right)}{X_{s}}-\frac{V\left(X_{s}\right)}{2 X_{s}^{2}}\right) d s+\mathcal{M}_{t}^{\prime}
\end{aligned}
$$

where $\mathcal{M}^{\prime}$ is a martingale. Then we continue the proof as for the case of constant speed.

Under the set of assumptions B and hypothesis (25), we can prove that

$$
X_{t} \underset{t \rightarrow \infty}{ }-\infty \quad \text { and } \quad \frac{X_{t}}{t} \xrightarrow[t \rightarrow \infty]{ } 0
$$

Ideas of Proof. We take the same function $f$ we constructed in the case of constant speed. We have $f^{\prime}>0$, and

$$
\begin{aligned}
f\left(X_{t}\right) & \leq f\left(X_{0}\right)+\int_{0}^{t} \psi_{\inf }\left(X_{s}\right) f^{\prime}\left(X_{s}\right) d s+\int_{0}^{t}\left(v_{\mathrm{inf}}-v_{1}(s)\right) f^{\prime}\left(X_{s}\right) d s \\
& +\frac{1}{2} \int_{0}^{t} \int_{0}^{\infty} f^{\prime \prime}\left(X_{s}+\alpha\right) \alpha^{2} g\left(X_{s}, \alpha\right) \nu(d \alpha) d s+\mathcal{N}_{t}^{\prime} \\
& \leq f\left(X_{0}\right)+\int_{0}^{t} \psi_{\inf }\left(X_{s}\right) f^{\prime}\left(X_{s}\right) d s+\frac{1}{2} \int_{0}^{t} \int_{0}^{\infty} f^{\prime \prime}\left(X_{s}+\alpha\right) \alpha^{2} g\left(X_{s}, \alpha\right) \nu(d \alpha) d s+\mathcal{N}_{t}^{\prime}
\end{aligned}
$$

where $\mathcal{N}^{\prime}$ is a martingale. Then we continue the proof as for the case of constant speed.

Acknowledgement The authors want to thank Michael Kopp for formulating the biological question which led us to this research, and for many stimulating discussions in the course of our work.

## References

Breiman L (1968) Probability. Addison-Wesley
Haldane JBS (1927) A mathematical theory of natural and artificial selection. Part V: selection and mutation. Proc Camb Philos Soc 23:838-844

Kersting G (1986) On recurrence and transcience of growth model. Journal of Applied Probability

Kimura M (1962) On the probability of fixation of mutant genes in a population. Genetics 47(6):713

Kopp M, Hermisson J (2009) The genetic basis of phenotypic adaptation II: The distribution of adaptive substitutions in the moving optimum model. Genetics 183:1453-1476

Malécot G (1952) Les processus stochastiques et la méthode des fonctions génératrices ou caractéristiques. Publications de l'institut de Statistiques de l'Université de Paris 1:1-16

Peischl S, Kirkpatrick M (2012) Establishment of new mutations in changing environments. Genetics

Protter PE (2005) Stochastic Integration and Differential Equations. SpringerVerlag, Heidelberg

Uecker H, Hermisson J (2011) On the fixation process of a beneficial mutation in a variable environment. Genetics 188(4):915-930


[^0]:    ${ }^{1}$ In the proof of this theorem, we replace Kolmogorov's inegality by Doob's inegality for martingales, and the result holds in our case.

