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Modèles Probabilistes de l'Evolution d'une Population dans un Environnement Variable

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Résumé

On étudie une équation différentielle stochastique animée par un processus ponctuel de Poisson, qui modélise un changement continu de l'environnement d'une population et la fixation stochastique de mutations bénéfiques pour compenser ce changement. La probabilité de fixation d'une mutation augmente dès que le retard phénotypique X_t entre la population et l'optimum augmente. On suppose que les mutations favorables se fixent instantanément induisant un saut adaptatif. En premier lieu, on a étudié le comportement à long terme de la solution de cette équation sachant qu'on ne considère qu'un seul trait phénotypique de la population et on a trouvé les conditions sous lesquelles X_t est récurrent (possibilité de survie) ou transient (extinction inévitable). Ensuite, on a généralisé nos résultats en considérant un vecteur de traits phénotypiques de la population, essentiellement dans $\mathbb{R}^2$. À la fin, on introduit une limite des petits sauts pour caractériser et comprendre le cas récurrent.

Mots clés : équation différentielle stochastique, processus ponctuel de Poisson, évolution, moving optimum, limite des petits sauts, transience, récurrence

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 of a given mutation increases as the phenotypic lag X_t between the population and the optimum grows larger, and successful mutations are assumed to fix instantaneously (leading to an adaptive jump). First, we study the large time behavior of the solution of this SDE taking into consideration one phenotypic trait of the population and we find the conditions under which X_t is recurrent (possibility of survival) or transient (doomed to exctinction).Then we generalize our results to the case of a phenotypic traits vector, essentially in $\mathbb{R}^2$. Finally, we introduce a small jumps limit to characterize and understand the recurrent case.

Keywords : stochastic differential equation, Poisson point process, evolution, moving optimum, small jumps limit, transience, recurrence

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> Je suis le chemin, la vérité et la vie.
>
> *(Jean 14 :6)*

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Introduction

Présentation

Face aux changements environnementaux imposés sur les populations vivantes, l'extinction devient un danger inévitable en absence de l'évolution. Des questions autour de l'adaptation surgissent de plus en plus ces derniers temps surtout que l'Homme devient plus conscient des effets notoires qu'il induit sur la nature autour de lui et des conséquences qui risquent de changer la vie telle qu'on la connaît jusqu'à présent. Mais d'abord comment modéliser de tels changements ? Et puis comment étudier l'adaptation d'une population à la lumière du modèle choisi ? Vu la complexité des phénomènes naturels, ces modèles se trouvent énormément simplifiés par rapport à la réalité. Dans ce travail, le modèle de l'optimum mobile, présenté ci-dessous, représente le modèle de base sous lequel on étudie les conditions de survie ou d'extinction d'une population qui subit un changement environnemental linéaire par rapport au temps. Inspiré de la littérature biologique, ce travail donne au modèle biologique un aspect mathématique rigoureux et vient complémenter et prouver certaines notions qu'on retrouve à partir de simulations, ou admises jusqu'à présent.

Le modèle

Le modèle unidimensionnel de l'optimum mobile

Le modèle présenté par Kopp and Hermisson (2009b) décrit l'évolution d'un trait phénotypique quantitatif d'une population de taille constante N qui subit une sélection Gaussienne stabilisante vers un optimum qui varie linéairement par rapport au temps avec une vitesse v. À l'instant t, le retard phénotypique entre un individu de trait z et l'optimum est $x = z - vt$. La fitness de cet individu définie par

$$\mathcal{W}(x) = \exp(-\sigma^{-2}x^2),$$

où σ^{-2} représente la force de sélection, et peut être envisagée comme la chance de survie de cet individu. Si le retard phénotypique augmente, la fitness diminue et par suite l'individu devient mal adapté par rapport à son environnement. La population est supposée monomorphique, c'est à dire le phénotype d'un seul individu caractérise le phénotype de la population entière. Les mutations apparaissent à un taux $\Theta/2 = N\mu$, où μ est le taux individuel de mutations, suivant une distribution $p(\alpha)$. On néglige la probabilité de fixation d'une mutation délétère, c'est à dire d'une mutation qui augmente le retard phénotypique. Une mutation de taille α qui apparaît dans la population quand le retard phénotypique vaut x possède une probabilité de fixation

$$g(x,\alpha) = \begin{cases} 1 - \exp(-2s(x,\alpha)) & \text{si } s(x,\alpha) > 0, \\ 0 \text{ sinon} \end{cases}$$

où

$$s(x,\alpha) = \frac{\mathcal{W}(x+\alpha)}{\mathcal{W}(x)} - 1 \approx -\alpha\sigma^{-2}(2x+\alpha)$$

est le coefficient de sélection. La dernière approximation est valide quand $\alpha\sigma^{-2}(2x+\alpha)$ est petit. Kopp and Hermisson (2009a) ont calculé une approximation analytique du temps de fixation d'une mutation favorable. Mais dans le cadre de ce travail, on suppose que ce temps est instantanné. Suite à une fixation, la taille α de la mutation s'ajoute à la valeur de x.

Le modèle multidimensionnel de l'optimum mobile

Le modèle décrit dans la partie précédente peut être facilement généralisé dans le cas de l'étude de d traits phénotypiques d'une population monomorphique évoluant dans un environnement variable. Comme présenté dans Matuszewski et al. (2014), la population est toujours soumise à une sélection stabilisante Gaussienne de matrice Σ et l'optimum varie linéairement par rapport au temps avec un vecteur vitesse v. À l'instant t, le vecteur retard phénotypique entre un individu, dont les d traits étudiés forment un vecteur z, et l'optimum est $x = z - vt$. La fitness de cet individu est donnée par

$$\mathcal{W}(x) = \exp(-x'\Sigma^{-1}x).$$

Dans le cas multidimensionnel, on suppose que les mutations apparaissent à un taux $\Theta/2$ suivant une distribution Gaussienne multivariée. Les mêmes hypothèses que celles du cas unidimensionnel sont supposées à propos du temps de fixation des mutations. La probabilité de fixation d'une mutation de taille α qui apparaît dans la population quand le retard phénotypique vaut x est donnée par l'expression

$$g(x,\alpha) = \begin{cases} 1 - \exp(-2s(x,\alpha)) & \text{si } s(x,\alpha) > 0, \\ 0 \text{ sinon} \end{cases}$$

où

$$s(x,\alpha) = \frac{\mathcal{W}(x+\alpha)}{\mathcal{W}(x)} - 1 \approx -(2x+\alpha)'\Sigma^{-1}\alpha$$

est le coefficient de sélection. Dans le cas particulier où $d = 2$, quand le retard phénotypique vaut x les mutations bénéfiques appartiennent à une ellipse de centre $-x$ passant par 0 et dont les axes sont dirigés par les vecteurs propres de la matrice Σ^{-1}.

1. Comportement à long terme de la solution d'une EDS animée par un processus ponctuel de Poisson

Dans le premier chapitre, on étudie l'évolution d'un trait phénotypique d'une population soumise à une dégradation de fitness provoquée par le changement linéaire continu de l'environnement. Cette population s'adapte grâce aux mutations bénéfiques qui réduisent le retard phénotypique. À partir du modèle unidimensionnel de l'optimum mobile décrit ci-dessus, on introduit une équation différentielle stochastique qui décrit l'évolution du retard phénotypique par rapport au temps :

$$X_t = X_0 - \int_0^t v(s)ds + \int_{[0,t]\times\mathbb{R}\times[0,1]} \alpha\varphi(X_{s^-},\alpha,\xi)M(ds,d\alpha,d\xi), \qquad (1.1)$$

où M est un processus ponctuel de Poisson sur $\mathbb{R}_+ \times \mathbb{R} \times [0,1]$ de mesure intensité $ds\ \nu(d\alpha)\ d\xi$ où ν vérifie la condition suivante

$$\int_{\mathbb{R}} |\alpha|\ \wedge\ 1\ \nu(d\alpha) < \infty,$$

et $\varphi(x,\alpha,\xi) = \mathbf{1}_{\{\xi \le g(x,\alpha)\}}$. On rappelle que $g(x,\alpha)$ est la probabilité de fixation d'une mutation de taille α qui apparaît quand le retard phénotypique vaut x. On suppose que $g(x,\alpha) \to 1$ quand $x \to \pm\infty$ pourvu que $x\alpha < 0$. On démontre que l'équation (1.1) admet une unique solution.

Le cas d'une vitesse constante $v(t) = vt$

D'abord on commence par le cas le plus simple où la vitesse du changement environnemental est constante. Ici, v peut être une constante quelconque, mais que l'on suppose positive pour fixer les idées. L'évolution du retard phénotypique se décrit par

$$X_t = X_0 + \int_0^t \psi(X_s)ds + \mathcal{N}_t,$$

où

$$\psi(x) = \int_{\mathbb{R}} \alpha g(x,\alpha)\nu(d\alpha) - v,$$
$$\text{et } \mathcal{N}_t = \int_{[0,t]\times\mathbb{R}\times[0,1]} \alpha\varphi(X_{s^-},\alpha,\xi)\bar{M}(ds,d\alpha,d\xi),$$

$\bar{M}$ étant le processus ponctuel de Poisson compensé correspondant à M. Le comportement asymptotique du processus étudié dépend en grande partie du signe de la limite de $\psi(x)$ quand $x \to -\infty$.

Proposition 1.1.
$$\psi(x) \xrightarrow[x\to-\infty]{} \bar{\psi} = \int_0^\infty \alpha\nu(d\alpha) - v.$$

Les trois cas qui se présentent sont les suivants :

Le cas $\bar{\psi} < 0$

Dans ce cas, le processus est transitoire. Le retard phénotypique augmente indéfiniment et l'extinction de la population est alors fatale.

Proposition 1.2. *Dans le cas où $\bar{\psi} < 0$,*

$$X_t \xrightarrow[t\to\infty]{} -\infty \text{ p.s.},$$
$$\text{et } \frac{X_t}{t} \xrightarrow[t\to\infty]{} \bar{\psi} \text{ p.s.}$$

Le cas $\bar{\psi} > 0$

En supposant une condition Lipschitz sur la probabilité de fixation g et dans le cas où la mesure ν vérifie

$$\int_{\mathbb{R}} |\alpha|\nu(d\alpha) < \infty, \tag{1.2}$$

on démontre dans ce cas que le processus est récurrent dans le sens de Harris. En plus, on prouve que X_t admet une unique mesure invariante de probabilité. En revanche, l'extinction n'est pas impossible même quand $\bar{\psi} > 0$ puisque on ne peut contrôler ni le temps de retour à zéro ni la valeur maximale que peut atteindre la valeur absolue du retard phénotypique.

Le cas $\bar{\psi} = 0$

Dans cette partie, la convergence obtenue dans la Proposition 1.1 ne suffit pas pour conclure. Afin de comprendre le comportement du processus étudié quand $\bar{\psi} = 0$, il faut considérer la vitesse de cette convergence. On définit d'abord le deuxième moment des mutations bénéfiques

$$V = \int_0^\infty \alpha^2 \nu(d\alpha). \tag{1.3}$$

Proposition 1.3. — *On suppose qu'il existe $K > 0$ tel que*

$$supp(\nu) \subset (-\infty, K]. \tag{1.4}$$

Si en outre

$$\limsup_{x \to -\infty} |x\psi(x)| < \frac{V}{2},$$

alors le processus est récurrent mais le temps de retour dans des compacts autour de zéro est d'espérance infinie.

— *Si*

$$\liminf_{x \to -\infty} |x\psi(x)| > \frac{V}{2},$$

et si en outre, il existe $0 < p_0 < 1$ et $0 < \beta_0 < 1$ tels que pour tout $0 < \beta < \beta_0$, on a

$$|x|^{p_0+2} \int_{-\beta x}^\infty \alpha^2 g(x, \alpha) \nu(d\alpha) \xrightarrow[x \to -\infty]{} 0,$$

alors le processus est transitoire, i.e. $X_t \xrightarrow[t \to \infty]{} -\infty$ p.s. et $\frac{X_t}{t} \xrightarrow[t \to \infty]{} 0$ p.s.

Le cas d'une vitesse $v(t)$ fonction du temps

On introduit dans cette partie les changements environnementaux non constants, voire aléatoires. On considère les fonctions vitesse de la forme

$$v(t) = \int_0^t v_1(s)ds + \mathcal{R}_t,$$

où v_1 est une fonction détérministe telle que

$$\frac{1}{t}\int_0^t v_1(s)ds \xrightarrow[t\to\infty]{} \bar{v},$$

et $\mathcal{R}$ est un process continu et F_t–progressivement measurable. La fonction ψ de la section précédente se définit désormais par rapport à la “vitesse moyenne limite” $\bar{v}$ comme suit

$$\psi(x) = \int_{\{x\alpha<0\}} \alpha g(x,\alpha)\nu(\alpha) - \bar{v}.$$

Donc

$$\bar{\psi} = \lim_{x\to-\infty}\psi(x) = \int_0^\infty \alpha\nu(d\alpha) - \bar{v}.$$

De nouveau trois cas se présentent :

Le cas $\bar{\psi} < 0$

En ajoutant l'hypothèse supplémentaire suivante

$$\frac{\mathcal{R}_t}{t} \xrightarrow[t\to\infty]{} 0,$$

on peut facilement démontrer que X_t est transitoire dans ce cas, i.e. $|X_t| \xrightarrow[t\to\infty]{} \infty$ p.s. et de plus que

$$\frac{X_t}{t} \xrightarrow[t\to\infty]{} \bar{\psi} \text{ p.s.}$$

Le cas $\bar{\psi} > 0$

On définit $\mathcal{T}$ comme étant l'ensemble des temps d'arrêts bornés. On suppose qu'il existe une constante $0 < c < \infty$ telle que $\mathbb{E}\mathcal{R}_T \leq c$, pour tout $T \in \mathcal{T}$. Dans ce cas, sous les conditions (1.2), on peut démontrer que le processus X_t est récurrent dans le sens de Harris et si $\mathcal{R} \equiv 0$ alors il admet une unique mesure invariante.

2. Modèle multidimensionnel du trait phenotypique

La deuxième partie de cette thèse porte sur la généralisation des résultats du premier chapitre pour l'évolution d'un vecteur de traits phénotypiques d'une population soumise à la dégradation de sa fitness provoquée toujours par un changement linéaire continu de l'environnement. À partir du modèle multidimensionnel de l'optimum mobile décrit ci-dessus, on introduit une équation différentielle stochastique qui décrit l'évolution du vecteur retard phénotypique par rapport au temps :

$$X_t = X_0 - vt + \int_{[0,t]\times\mathbb{R}^d\times[0,1]} \alpha g(X_{s^-}, \alpha) N(ds, d\alpha, d\xi), \tag{2.1}$$

où N est un processus ponctuel de Poisson sur $\mathbb{R}_+ \times \mathbb{R}^d \times [0,1]$ de mesure intensité $ds\ \nu(d\alpha)\ d\xi$, ν étant une mesure gaussienne multivariée de moyenne 0 et de matrice de variance covariance M et $\varphi(x, \alpha, \xi) = \mathbf{1}_{\{\xi \le g(x,\alpha)\}}$. On rappelle que $g(x, \alpha)$ est la probabilité de fixation d'une mutation de taille α qui apparaît quand le retard phénotypique vaut x. Dans le cas multidimensionnel, une mutation fixée est un vecteur qui s'ajoute au vecteur retard phénotypique et par suite affecte toutes ses composantes. On suppose que $g(x, \alpha) \to \mathbf{1}_{\{(x|\alpha)\le 0\}}$ quand $|x| \to \infty$. On démontre que l'équation (2.1) admet une unique solution. Dans la suite, on utilise les hypothèses suivantes sans perdre de généralité :

1. $\Sigma = \sigma^2 I_{\mathbb{R}^d}$,
2. $v = (v_1, 0, \dots, 0)$ où $v_1 > 0$,
3. la matrice M admet un détérminant égal à 1.

Par analogie au premier chapitre, on définit

$$\psi(x) = \int_{\mathbb{R}^d} \alpha g(X_s, \alpha)\nu(d\alpha) - v,$$
$$\bar{\psi}(x) = \int_{\{(x|\alpha)\le 0\}} \alpha\nu(d\alpha) - v.$$

On a effectué l'étude essentiellement dans le cas où $d = 2$ pour établir des résultats autour de la transience/récurrence de X généralisant les résultats du chapitre 1. Dans ce cas, l'optimum est fixé au point $(0, 0)$. On rappelle que la loi des nouvelles mutations est une gaussienne centrée de matrice de variance covariance

$$M = \begin{pmatrix} a & c \\ c & b \end{pmatrix},$$

a, b $\in \mathbb{R}_+^\star$ et $c \in \mathbb{R}$ tels que $ab - c^2 = 1$.

Le vecteur $\bar{\psi}(x)$ ne dépend que de la direction $u = \frac{x}{|x|}$ de x. Pour tout vecteur unitaire $u \in \mathbb{R}^2$, il existe $\beta \in [0, 2\pi]$ tel que

$$u = \begin{pmatrix} \cos\beta \\ \sin\beta \end{pmatrix}.$$

On définit $G(\beta) = \left(\bar{\psi}(u_\beta) \mid u_\beta\right)$ et $G_\perp(\beta) = \left(\bar{\psi}(u_\beta) \mid u_\beta^\perp\right)$ qui représentent les composantes de $\bar{\psi}$ par rapport au vecteur position. Ici, on peut calculer explicitement le vecteur $\bar{\psi}$ en fonction des coefficients de la matrice M et v_1.

Proposition 2.1. *Il existe deux angles $\bar{\theta}_v, \theta_2$, et $\theta_v \in \left[\frac{\pi}{2}, \frac{3\pi}{2}\right]$ tels que*

$$\bar{\psi}_1(u_{\bar{\theta}_v}) = 0, \ \ \bar{\psi}_2(u_{\theta_2}) = 0 \ \text{ et } \bar{\psi}(u_{\theta_v}) = |\bar{\psi}(u_{\theta_v})| u_{\theta_v}.$$

Donc le vecteur $\bar{\psi}$ est radial en u_{θ_v} qu'on appellera la direction limite. Notez que $\bar{\psi}_1$ est maximal en u_π.

En passant à l'écriture en coordonnées polaires du processus, on trouve les équations vérifiées par $\rho = \sqrt{X_1^2 + X_2^2}$ et $\beta = \arctan(\frac{X_2}{X_1})$:

$$\begin{aligned}\rho_t = \rho_0 &+ \int_0^t (\mathbf{u}_s \mid \psi(X_s))ds + \int_{[0,t]\times\mathbb{R}^2\times[0,1]} (|X_{s^-} + \alpha| - \rho_{s^-})\Gamma(X_{s^-}, \alpha, \xi)\bar{M}(ds, d\alpha, d\xi) \\ &+ \int_{[0,t]\times\mathbb{R}^2} (|X_s + \alpha| - \rho_s - (\mathbf{u}_s|\alpha))g(X_s, \alpha)\nu(d\alpha)ds,\end{aligned} \tag{2.2}$$

et

$$\begin{aligned}\beta_t &= \beta_0 + \int_0^t \rho_s^{-1}(\mathbf{u}_s^\perp|\psi(X_s))ds \\ &+ \int_{[0,t]\times\mathbb{R}^2\times[0,1]} \left[\arctan\left(\frac{X_{s^-}^2 + \alpha_2}{X_{s^-}^1 + \alpha_1}\right) - \beta_{s^-}\right]\Gamma(X_{s^-}, \alpha, \xi)\bar{M}(ds, d\alpha, d\xi) \\ &+ \int_{[0,t]\times\mathbb{R}^2} \left[\arctan\left(\frac{X_s^2 + \alpha_2}{X_s^1 + \alpha_1}\right) - \beta_s - \rho_s^{-1}(\mathbf{u}_s^\perp|\alpha))\right]\nu(d\alpha)ds.\end{aligned} \tag{2.3}$$

Transience : $\bar{\psi}_1(u_{\theta_2}) < 0$

Premier Cas :

Théorème 2.1. Dans le cas où $\bar{\psi}_1(u_\pi) < 0$, X_t, vérifiant (2.1), est transitoire. En outre,

$$\frac{X_t}{t} \xrightarrow[t\to\infty]{} \bar{\psi}(u_{\theta_v}) \text{ p.s.}$$

Dans le cas où le maximum de $\bar{\psi}$ est négatif, on démontre facilement que le processus X_t passe la plupart de son temps dans le demi espace

$$A^- = \{x \in \mathbb{R}^2; x_1 < 0\},$$

et qu'il franchit tous les cônes autour de la direction limite, jusqu'à ne plus en ressortir.

<u>Deuxième Cas :</u>

Théorème 2.2. Dans le cas où $\bar{\psi}_1(u_{\theta_2}) < 0$ et $\bar{\psi}_1(u_\pi) \geq 0$, le processus X_t est transitoire tel que

$$\frac{X_t}{t} \xrightarrow[t\to\infty]{} \bar{\psi}(u_{\theta_v}) \text{ p.s.}$$

La différence entre les deux cas est que dans le dernier le processus peut passer longtemps à osciller autour de l'optimum $(0,0)$ avant d'être absorbé par un cône autour de la direction limite u_{θ_v}.

Récurrence : $\bar{\psi}_1(u_{\theta_2}) > 0$

Proposition 2.2. *Dans le cas où $\bar{\psi}(u_{\theta_2}) > 0$, si*

$$G_{\text{sup}} = \sup_{\beta\in[0,2\pi]} G(\beta) < 0, \tag{2.4}$$

alors X_t est récurrent dans le sens où l'espérance du temps de retour dans des compacts autour de zéro est finie.

3. Limite des Petits Sauts

Le cas général

Les chapitres précédents présentent une étude complète du processus et une classification de son comportement suivant les conditions. Le but du chapitre 3 est d'approfondir notre étude dans le cas récurrent en utilisant l'approche des petits sauts d'abord à partir du modèle multidimensionnel puis unidimensionnel. Dans le cadre de ce chapitre, on suppose que

1. $v = (v_1, 0, \dots, 0)$,
2. $\Sigma = \sigma^2 I$,
3. la mesure ν est telle que $\int_{\mathbb{R}^d} |\alpha| \vee |\alpha|^3 \nu(d\alpha) < \infty$.

On traite le processus $X_t \in \mathbb{R}^d$ satisfaisant l'équation (2.1). On introduit le changement de variables suivant :

$$\tilde{\alpha} = \epsilon\alpha \ \text{ et } \ \tilde{s} = \frac{s}{\epsilon^2},$$

et on réécrit l'équation (2.1) :

$$X_t^\epsilon = X_0 - vt + \int_0^t \frac{1}{\epsilon^2} m_\epsilon(X_s^\epsilon) ds + \mathcal{M}_t^\epsilon,$$

où

$$\begin{aligned} m_\epsilon(x) &= \int_{\mathbb{R}^d} \epsilon\alpha g(x, \epsilon\alpha)\nu(d\alpha), \\ g(x, \epsilon\alpha) &= \left(1 - \exp\left(2\sigma^{-2}\left(2x + \epsilon\alpha \mid \epsilon\alpha\right)\right)\right) \times \mathbf{1}_{(2x+\epsilon\alpha|\epsilon\alpha)\leq 0)}, \end{aligned}$$

et la martingale

$$\mathcal{M}_t^\epsilon = \int_0^t \int_{\mathbb{R}^d} \int_0^1 \epsilon\alpha\varphi(X_{s^-}^\epsilon, \epsilon\alpha, \xi)\bar{M}_\epsilon(ds, d\alpha, d\xi),$$

où $\bar{M}_\epsilon(ds, d\alpha, d\xi) = M_\epsilon(ds, d\alpha, d\xi) - (1/\epsilon)ds\ \nu(d\alpha)\ d\xi$. On démontre que X^ϵ converge en probabilité vers $\bar{X}$ qui vérifie

$$\frac{d\bar{X}_t}{dt} = -v - 4\sigma^{-2}\bar{V}\bar{X}_t,$$

où

$$\bar{V} = \bar{V}(u) = \int_{\{(\alpha|u)\leq 0\}} \alpha \otimes \alpha\nu(d\alpha),$$

qui est une constante indépendante de u. Le comportement asymptotique de $\bar{X}_t$ se traduit par :

$$\bar{X}_t \xrightarrow[t\to\infty]{} \bar{X}_\infty = -\frac{1}{4\sigma^{-2}}\bar{V}^{-1}v. \tag{3.1}$$

On introduit ensuite le processus

$$U_t^\epsilon = \frac{X_t^\epsilon - \bar{X}_t}{\sqrt{\epsilon}},$$

et on démontre que U_t^ϵ converge en loi vers un processus d'Ornstein-Uhlenbeck U_t tel que

$$\begin{aligned} &dU_t = -4\sigma^{-2}\bar{V}U_t dt + \Lambda^{-\frac{1}{2}}(\bar{X}_t)dB_t, \\ &U_0 = 0, \end{aligned}$$

où B est un mouvement Brownien standard de dimension d et

$$\Lambda(x) = 4\sigma^{-2} \int_{\{(x|\alpha)\leq 0\}} |(x \mid \alpha)|\, \alpha \otimes \alpha\nu(d\alpha).$$

Par suite,

$$\mathbb{E}(U_t^2) = \int_0^t e^{-8\sigma^{-2}(t-s)\bar{V}} \Lambda(\bar{X}_s) ds.$$

Asymptotiquement, pour t grand, U_t vérifiera l'équation suivante :

$$dU_t = -4\sigma^{-2}\bar{V} U_t dt + \Lambda^{-\frac{1}{2}}(\bar{X}_\infty) dB_t.$$

Donc,

$$\mathbb{E}(U_t^2) \xrightarrow[t\to\infty]{} \bar{S}^2 = \frac{1}{8\sigma^{-2}} \bar{V}^{-1} \Lambda(\bar{X}_\infty). \tag{3.2}$$

Dans le cas particulier où la mesure ν est définie par

$$\nu(d\alpha) = \frac{\Theta}{2} p(\alpha) d\alpha,$$

telle que p est la densité d'une loi Gaussienne $\mathcal{N}(0, M)$ et en notant $\bar{\omega}^2 = \sqrt[d]{\det(M)}$, on réécrit (3.1) :

$$\bar{X}_\infty = -\gamma\bar{\omega} \left(\frac{M}{\bar{\omega}^2}\right)^{-1} e_1,$$

où $e_1 = (1, 0, \dots, 0)$ et

$$\gamma = \frac{v_1/\bar{\omega}}{\theta\sigma^{-2}\bar{\omega}^2}$$

le paramètre défini par Matuszewski et al. (2014) comme étant le taux relatif de changement environnemental qui réunit à la fois les facteurs mutationnels et environnementaux.

Le cas unidimensionnel

Dans le cas où X_t est récurrent ($\bar{\psi} > 0$), on introduit cette même approche des petits sauts. Si on approxime abusivement X_t par $\bar{X}_t + U_t$ alors les approximations asymptotiques de la moyenne et de la variance du processus données par les formules (3.1) et (3.2) deviennent :

$$\begin{aligned} \bar{X}_\infty &= -\frac{v}{4\sigma^{-2}V}, \\ S^2 &= \frac{v}{8\sigma^{-2}V^2} \int_{\mathbb{R}_+} |\alpha|^3 \nu(d\alpha). \end{aligned} \tag{3.3}$$

Dans le cas particulier où la mesure ν est donnée par :

$$\nu(d\alpha) = \frac{\Theta}{2} \frac{1}{\omega\sqrt{2\pi}} e^{-\frac{\alpha^2}{2\omega^2}} d\alpha,$$

on peut calculer $V = \frac{\Theta}{4}\omega^2$, où V est défini par (1.3). On retrouve la version unidimensionnelle du paramètre γ défini par Kopp and Hermisson (2009b) en écrivant $\bar{X}_\infty$ sous la forme suivante :

$$\bar{X}_\infty = -\frac{v}{\Theta\omega^2\sigma^{-2}} = -\omega\gamma, \tag{3.4}$$

où

$$\gamma = \frac{v/\omega}{\Theta\sigma^{-2}\omega^2}.$$

Pour le processus original avec des sauts de taille finie, les simulations ont montrées que (3.3) se révèle une bonne approximation si $\gamma \gtrsim 1$ (excellente pour $\gamma \gtrsim 10$) et sous la condition que v ne soit pas trop proche de m. Si l'une des deux conditions n'est pas vérifiée alors (3.3) surestime les vraies valeurs de la moyenne et de la variance du retard phénotypique.

Survie ou Extinction de la Population

On suppose que le risque d'extinction de la population devient très important une fois le retard phénotypique dépasse un seuil $X_{\text{crit}} = -\sqrt{\sigma^2 \ln n_{\text{off}}}$, où n_{off} détermine la capacité de reproduction de la population en question. On appelle temps d'extinction T_e le temps maximal passé au-dessus de X_{crit}. Ce temps dépend de la vitesse de changement environnemental v et on peut calculer un seuil critique à partir de (3.4) :

$$v_{\text{crit}} = \Theta\omega^2\sqrt{\sigma^{-2}\ln n_{\text{off}}}.$$

Suivant les valeurs de v, on peut trouver une approximation de T_e comme suit :

$$T_e \approx \begin{cases} |\bar{X}_\infty|/v + T_f & \text{si } v \leq v_{\text{crit}}, \\ |X_{\text{crit}}|/v & \text{si } v > v_{\text{crit}}. \end{cases}$$

où T_f est un temps aléatoire qui peut être approximé par le premier temps de passage du process $\bar{X}_\infty + U_t$ en dessous X_{crit} tel que

$$\mathbb{E}(T_f) = \frac{1}{2\lambda_{\text{OU}}}\sum_{k=1}^{\infty}\frac{\left(\sqrt{2}|\tilde{X}_{\text{crit}}|\right)^k}{k!}\Gamma\left(\frac{k}{2}\right)$$

et

$$\text{Var}(T_f) = \mathbb{E}(T_f)^2 - \frac{1}{2\lambda_{\text{OU}}^2}\sum_{k=1}^{\infty}\frac{\left(\sqrt{2}|\tilde{X}_{\text{crit}}|\right)^k}{k!}\Gamma\left(\frac{k}{2}\right)\left(\phi\left(\frac{k}{2}\right) - \phi(1)\right),$$

où $\tilde{X}_{\text{crit}} = (X_{\text{crit}} - \bar{X}_\infty)\frac{\sqrt{2\lambda_{\text{OU}}}}{\sigma_{\text{OU}}}$, $\phi(\,\cdot\,)$ est la fonction digamma et

$$\text{erf}(x) = \frac{2}{\sqrt{\pi}} \int_0^x e^{-t^2} dt$$

est la fonction d'erreur de Gauss. On peut s'assurer à partir des simulations que cette approximation est valide dès que $\gamma > 1$. En outre, pour des valeurs de v suffisamment inférieures à v_{crit}, T_e est approximativement exponentiel.

Conclusion

Ce travail présente une classification du comportement asymptotique du retard phénotypique $X_t \in \mathbb{R}^d$ où $d = 1, 2$.

Dans le cas $d = 1$, ce comportement dépend essentiellement de la vitesse du changement environnemental. En revanche, dans le cas $d = 2$, ce comportement est plus compliqué à analyser du fait qu'il ne suffit pas de distinguer entre récurrence/transience, mais de pouvoir identifier dans ce dernier, la direction asymptotique que prend le processus en s'éloignant de l'optimum. Cette direction est influencée non seulement par le vecteur vitesse du changement environnemental mais aussi par la matrice de variance covariance M de la loi normale des nouvelles mutations. Dans le cas transitoire, quand M est diagonale, le processus est entraîné par la direction du vecteur vitesse. Si la loi des nouvelles mutations est corrélée, cette direction limite est déviée de l'horizontale par l'effet des mutations bénéfiques qui tentent de freiner v. Cet effet est bien connu dans la littérature biologique sous le nom de "flying kite" ou effet du cerf-volant (Jones et al. (2004), Matuszewski et al. (2014)). Une question intéressante est de traiter le cas limite entre transience et récurrence ($\bar{\psi}(u_{\theta_2}) = 0$). Si on réussit à démontrer que G est négative pour tout β sauf un, qu'on appelle β_0 tel que $G(\beta_0) = 0$, alors intuitivement le processus tend à s'éloigner de l'optimum (l'origine) dans la direction u_{β_0}. Quant aux fluctuations, elles éloignent le processus de cette direction, qui se trouve dans une zone où la force de G le repousse vers l'origine. En outre, la question suivante qu'on peut traiter dans le futur est celle de la généralisation en dimension supérieure. Est-ce qu'il existera toujours une direction limite dans le cas transitoire ? Quel est l'effet de la dimension sur la classification du comportement asymptotique du processus ? En d'autres termes, est-ce qu'on peut démontrer mathématiquement que les populations complexes ont plus de difficulté à s'adapter ?

1. On the large time behaviour of the solution of an SDE driven by a Poisson point process

1.1. Introduction

When faced with environmental change, biological populations can increase their fitness by adaptive Darwinian evolution. While adaptation over short timescales often relies on frequency shifts of pre-existing standing genetic variation, long-term adaptation ultimately depends on the establishment and (frequently) fixation of new beneficial mutations, i.e. the entire population is composed of the progeny of the original mutant, which themselves arise in a stochastic manner (e.g. due to copying errors) independent of the current "needs" of the population. Several distinct mathematical frameworks have been developed to model adaptive evolution under various sets of simplifying assumptions. One such framework focuses on cases where fixations events are rare and clearly separated from one another, allowing adaptation to be modeled as a Markovian jump process, which has been called "adaptive walk" see Dieckmann and Law (1995), Kauffman and Levin (1987) or "trait substitution sequence" (TSS). For the links between TSS models and individual-based birth-death models (primarily for asexual populations) see Champagnat (2006).

Many traits of organisms are thought to be under stabilizing selection, such that fitness (i.e., the expected number of offspring of an individual with a certain trait value or phenotype) is maximal for intermediate values and declines monotonically with the distance to this optimum (a classical example is birth weight in humans, where infant mortality is increased for both very low and very high weights). Environmental change (e.g., climate change) can then be viewed as altering the value of the optimum, making a previously well-adapted population suffer a reduction in mean fitness. This so-called moving-optimum model has been widely used in the theoretical biology literature to investigate the effects of various kinds of environmental change (e.g., sudden, directional or fluctuating) on phenomena such as population extinction risk Bürger and Lynch (1995), the maintenance of genetic variation Bürger (1999), or the fixation probability Uecker and Hermisson (2011); Peischl and Kirkpatrick (2012), and fixation time Kopp and Hermisson (2009a); Uecker and Hermisson (2011) of beneficial mutations. Recently, Kopp and Hermisson Kopp and Hermisson (2009b) developed an adaptive-walk approximation for a model with a linearly moving optimum and used it to study the size-distribution of adaptive jumps by means of which the population phenotype follows the optimum. This model is the starting point for the present paper. The innovative idea here is to model the adaptive walk by means of a stochastic differential equation, allowing us to obtain results about the large-time behaviour of the solution, which have a precise meaning in biological terms. Our SDE is of the form

$$X_t = X_0 - V_t + \int_{[0,t]\times\mathbb{R}\times[0,1]} \alpha\varphi(X_{s-},\alpha,\xi)M(ds,d\alpha,d\xi),$$

where M is an $\mathcal{F}_t$–Poisson point process on $\mathbb{R}_+ \times \mathbb{R} \times [0,1]$ with mean measure $ds\ \nu(d\alpha)\ d\xi$ and $\varphi(x,\alpha,\xi) = \mathbf{1}_{\{\xi\le g(x,\alpha)\}}$, and the process V_t is right continuous with left limits at every point and $\mathcal{F}_t$–progressively measurable, satisfying $V_0 = 0$. X describes the evolution of the phenotypic lag and takes value in $\mathbb{R}$ depending whether the population lags above or below the optimal value 0. $ds\ \nu(d\alpha)$ represents the rate of appearance of new mutations of different size, while $g(x,\alpha)$ is the probability that a mutation of size α, which is proposed while the population's phenotypic lag is x, gets fixed. We assume that $g(x,\alpha) \to 1$ when $x \to \pm\infty$ provided that $x\alpha < 0$.

We start with the simple case $V_t = vt$, with $v > 0$ a real number. With the notation $m = \int_0^\infty \alpha\nu(d\alpha)$ – in other words, m is the mean movement to the right per time unit produced by the positive mutations if all of them get fixed – our first result says that under some additional assumption, the Markov process X_t is Harris recurrent if $m > v$, transient if $m < v$, with a speed of escape to infinity equal to $v - m$. The most difficult 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 $x \to -\infty$, the process can be either Harris recurrent or else transient with zero speed. 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. The same results for an SDE driven by Brownian motion with coefficients that 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, exploiting the fact that all jumps have the same sign, see Lemma 1.4.3 below.

The paper is organized as follows. We define our model in detail in section 1.2, referring to models already studied in the biological literature. We establish existence and uniqueness of a solution to our equation in section 1.3 (the result is not immediate, since we do not assume that the measure ν is finite). Section 1.4 is devoted to the large time behaviour of X_t when $V_t = vt$, successively with $m < v$, $m > v$, and $m = v$. Finally section 1.5 is devoted to the large time behaviour of X_t when V_t takes a more general form, but $\overline{v} = \lim_{t\to\infty} t^{-1}V_t$ exists and is deterministic.

1.2. The model

Our starting point is the model by Kopp and Hermisson Kopp and Hermisson (2009b), of which we subsequently relax several assumptions. Kopp and Hermisson modeled a population of constant size N that is subject to Gaussian stabilizing selection with a moving optimum that increases linearly at rate v. Therefore, an individual with phenotype z has a phenotypic lag $x = z - vt$ and fitness $\mathcal{W}(x) = e^{-\sigma^{-2}x^2}$, where σ^{-2} determines the strength of selection. The population is assumed to be monomorphic at all times (i.e., its state is completely characterized by x). Mutations appear at rate $\Theta/2 = N\mu$ (where μ is the *per-capita* mutation rate and $\Theta = 2N\mu$ is a standard population-genetic parameter), and their phenotypic effects α are drawn from a distribution with density $p(\alpha)$. In other words, mutations arise according to a Poisson point process with intensity $ds\ \nu(d\alpha)$, where

$$\nu(d\alpha) = \frac{\Theta}{2}p(\alpha)d\alpha. \tag{1.2.1}$$

A mutation that appears while the lag is x has selection coefficient

$$s(x,\alpha) = \left(\frac{\mathcal{W}(x+\alpha)}{\mathcal{W}(x)} - 1\right) \times \mathbf{1}_{\{x\alpha<0\}} \approx \sigma^{-2}[|\alpha|(2|x| - |\alpha|)]^+ \times \mathbf{1}_{\{x\alpha<0\}}, \tag{1.2.2}$$

where the approximation is valid as long as $\sigma^{-2}[|\alpha|(2|x| - |\alpha|)]^+$ is small. Even beneficial mutations have a considerable risk of being lost due to genetic drift (i.e., due to stochastic fluctuations while their frequency is low). The probability that a mutation escapes drift loss and instead goes to fixation is

$$g(x,\alpha) = \begin{cases} 1 - \exp(-2s(x,\alpha)) & \text{if } s(x,\alpha) > 0, \\ 0 \text{ otherwise} \end{cases} \tag{1.2.3}$$

This equation neglects the probability of fixation of deleterious mutations (with $s < 0$), and otherwise is a good approximation for 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 (2009b) used the even simpler approximation $g(x, \alpha) \approx 2s(x, \alpha)$ (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.

In the present work, we relax these assumptions in three respects : First, we consider a more general model of environmental change, such that, in the absence of evolution, the lag increases due to a random function V_t. Second, we only assume that mutations arise according to a Poisson point process with intensity $ds\, \nu(d\alpha)$ (which subsumes the mutation rate $\Theta/2$), but we do not impose that ν has a density, nor that it is a finite measure. This allows both for heavy-tailed mutational distributions, enabling very large jumps, and for an accumulation of infinitely many small jumps. Nore however that some of our results will require additional assumptions about the tail of ν. Third, we only make the following assumptions about the fixation probability : A mutation with effect α that arises in a population with phenotypic lag x has a probability of fixation $g(x, \alpha)$ that satisfies

1. $0 \leq g(x, \alpha) \leq \mathbf{1}_{\{\alpha x < 0\}} \times \mathbf{1}_{\{|\alpha| \leq 2|x|\}}$,
2. For all $\alpha \in \mathbb{R}$, $g(x, \alpha) \uparrow \mathbf{1}_{\{\alpha x < 0\}}$, as $|x| \to \infty$,
3. There exists a compact set $K \subset \mathbb{R}$ and $c_K > 0$ such that $\nu(K^c) < \infty$ and for all $x, y \in \mathbb{R}$

$$\int_K |\alpha| \times |g(x, \alpha) - g(y, \alpha)| \nu(d\alpha) \leq c_K |x - y|. \tag{1.2.4}$$

These items represent the basic mathematical assumptions, which will be assumed to hold throughout this paper. Condition 1 assures that only the beneficial mutations can be fixed, which is a reasonable slightly simplifying biological assumption. In reality, there is a small probability that a slightly deleterious mutation gets fixed through chance (i.e. genetic drift), but we neglect this possibility. Condition 2 means that when the phenotypic lag goes to infinity, the probability of fixation of any beneficial mutation tends to 1. This is quite reasonable : when the fitness of a population is very low, one may expect that any possible improvement will be taken by the population. Condition 3 is imposed for mathematical convenience but is required only in the case $\nu(\mathbb{R}) = \infty$.

The evolution of the phenotypic lag of the population can then be described by the following SDE already given in the introduction :

$$X_t = X_0 - V_t + \int_{[0,t] \times \mathbb{R} \times [0,1]} \alpha \varphi(X_{s-}, \alpha, \xi) M(ds, d\alpha, d\xi). \tag{1.2.5}$$

Here, M is a Poisson point process over $\mathbb{R}_+ \times \mathbb{R} \times [0,1]$ with intensity $ds\, \nu(d\alpha)\, d\xi$. $\nu(d\alpha)$ is a σ-finite measure on $\mathbb{R}$ which satisfies

$$\int_{\mathbb{R}} |\alpha| \wedge 1\, \nu(d\alpha) < \infty, \tag{1.2.6}$$

and

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

where the fixation probability $g(x, \alpha)$ has been defined above. The points of the Poisson point process M (T_i, A_i, Ξ_i) are such that the (T_i, A_i) form a Poisson point process over $\mathbb{R}_+ \times \mathbb{R}$ of the proposed mutations with intensity $ds\nu(d\alpha)$, and the Ξ_i are i.i.d. $\mathcal{U}[0,1]$, globally independent of the Poisson point process of the (T_i, A_i). T_i's are the times when mutations are proposed and A_i's are the effect sizes of those mutations. The Ξ_i are auxiliary variables determining fixation : a mutation gets instantaneously fixed if $\Xi_i \leq g(X_{T_i}, A_i)$, and is lost otherwise.

Finally, we define for all $x \in \mathbb{R}$

$$\begin{aligned} m(x) &= \int_{\mathbb{R}} \alpha g(x,\alpha)\nu(d\alpha), \\ m &= \int_{\mathbb{R}_+} \alpha\nu(d\alpha), \qquad (1.2.7) \\ V(x) &= \int_{\mathbb{R}} \alpha^2 g(x,\alpha)\nu(d\alpha), \\ V &= \int_{\mathbb{R}_+} \alpha^2\nu(d\alpha). \qquad (1.2.8) \end{aligned}$$

$m(x)$ 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, as $x \to -\infty$ or in other words, in the case that all mutations with $\alpha > 0$ go to fixation. 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 ν. It would be quite acceptable on biological grounds to assume that $m < \infty$ and/or $V < \infty$. However, we refrain from adding unnecessary assumptions.

In the case $V_t = vt$, X_t is a Markov process, whose generator $\mathcal{L}$ acts on a differentiable function f as

$$\mathcal{L}f(x) = f'(x)(m(x) - v) + \int_{\mathbb{R}} \left(f(x+\alpha) - f(x) - f'(x)\alpha\right) g(x,\alpha)\nu(d\alpha).$$

1.3. Existence and uniqueness

We rewrite the SDE (1.2.5) as follows

$$X_t = X_0 - V_t + \int_0^t m(X_s)ds + \mathcal{M}_t \tag{1.3.1}$$

where the martingale $\mathcal{M}_t$ is given as

$$\mathcal{M}_t = \int_0^t \int_{\mathbb{R}} \int_0^1 \alpha\varphi(X_{s-}, \alpha, \xi)\bar{M}(ds, d\alpha, d\xi), \tag{1.3.2}$$

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

Proposition 1.3.1. *Equation* (1.3.1) *has a unique solution.*

Proof. If ν 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 $k > 0$). Due to (1.2.6), there are finitely many jumps (t_i, α_i) 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 $\nu(K^c) = 0$ where K is chosen such that Condition 3 is satisfied, and hence from (1.2.6), we deduce that $\int (|\alpha| + \alpha^2)\, \nu(d\alpha) < \infty$, which we assume from now on. We shall also assume that there exists $C > 0$ such that

$$|V_t| \leq Ct, \quad \text{for all } t \geq 0. \tag{1.3.3}$$

Indeed, if that is not the case, we let $V_t^n = (V_t \wedge nt) \vee (-nt)$, and define $T_n = \inf\{t > 0, : |V_t| > nt\}$. Existence and uniqueness under the additional assumption (1.3.3) will provide a unique solution X_t^n associated to V_t^n. We will have that $X_t^m = X_t^n$ for $0 \leq t \leq T_n$ if $m > n$, and $T_n \uparrow \infty$ as $n \to \infty$. This clearly implies existence of a unique solution under our standing assumptions. Hence we assume for the rest of this proof that (1.3.3) is satisfied.

Define for each $t > 0$

$$\Gamma_t(U) = x - V_t + \int_{[0,t]\times K\times[0,1]} \alpha\varphi(U_{s-}, \alpha, \xi)M(ds, d\alpha, d\xi). \tag{1.3.4}$$

A solution of equation (1.3.1) is a fixed point of the mapping Γ a.s. . Hence it suffices to prove that Γ admits a unique fixed point a.s. . For $\lambda > 0$,

$$\begin{aligned} e^{-\lambda t}\left|\Gamma_t(U)-\Gamma_t(V)\right| =& -\lambda \int_0^t e^{-\lambda s}\left|\Gamma_s(U)-\Gamma_s(V)\right| ds + \int_0^t e^{-\lambda s} d\left|\Gamma_s(U)-\Gamma_s(V)\right| \\ \leq& -\lambda \int_0^t e^{-\lambda s}\left|\Gamma_s(U)-\Gamma_s(V)\right| ds \\ &+ \int_{[0,t]\times K\times[0,1]} |\alpha| e^{-\lambda s}\left|\varphi(U_{s-},\alpha,\xi)-\varphi(V_{s-},\alpha,\xi)\right| M(ds,d\alpha,d\xi). \end{aligned}$$

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

$$\begin{aligned} &|\Gamma_t(U)-\Gamma_t(V)| - |\Gamma_s(U)-\Gamma_s(V)| \\ &\qquad \leq \int_{(s,t)\times K\times[0,1]} |\alpha| \times |\varphi(U_{r-},\alpha,\xi)-\varphi(V_{r-},\alpha,\xi)| M(dr,d\alpha,d\xi). \end{aligned}$$

Thus,

$$\begin{aligned} \lambda \mathbb{E}\int_0^t e^{-\lambda s}\left|\Gamma_s(U)-\Gamma_s(V)\right| ds &\leq \mathbb{E}\int_0^t \int_K |\alpha| e^{-\lambda s}\left|g(U_s,\alpha)-g(V_s,\alpha)\right| \nu(d\alpha) ds \\ &\leq c_K \mathbb{E}\int_0^t e^{-\lambda s}|U_s - V_s| ds. \end{aligned} \tag{1.3.5}$$

The last inequality is due to the assumption (1.2.4). Let T be arbitrary. Define for all $\lambda > 0$ the norm on the Banach space $L^1(\Omega\times[0,T])$,

$$\|Z\|_{T,\lambda} = \mathbb{E}\int_0^T e^{-\lambda t}|Z_t| dt.$$

We choose $\lambda_0 > c_K$. We deduce from (1.3.5) that

$$\mathbb{E}\|\Gamma(U)-\Gamma(V)\|_{T,\lambda_0} \leq \frac{c_K}{\lambda_0}\mathbb{E}\|U-V\|_{T,\lambda_0}.$$

Since $c_K/\lambda_0 < 1$, Γ has a unique fixed point such that $\Gamma_t(U) = U_t$ a.s. for all $0 \leq t \leq T$. Since T is arbitrary, the result is proved. $\square$

We now prove that g given by (2.1.2) and (1.2.2) satisfies the assumption (1.2.4).

Lemma 1.3.1. *For any compact set $K \subset \mathbb{R}$ and for all $u, v \in \mathbb{R}$,*

$$\int_K |\alpha(g(u,\alpha)-g(v,\alpha))| \nu(d\alpha) \leq c_K |u-v|,$$

where $c_K = 4\sigma^{-2}\left(\int_K \alpha^2 \nu(d\alpha)\right)$.

Proof. For $0 < u < v$ we have that

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

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

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

□

1.4. Classification of the large-time behaviour in the case $V_t = vt$

We now consider the case $V_t = vt,\ v > 0$.

Proposition 1.4.1. *If $X_0 > 0$, then X_t becomes negative after a finite time a.s.*

Proof. Let $T_- = \inf(t > 0, X_t < 0)$. We have that

$$0 \leq X_{(t \wedge T_-)-} \leq X_0 - v(t \wedge T_-).$$

Hence

$$t \wedge T_- \leq \frac{X_0 - X_{(t\wedge T_-)-}}{v} < \frac{X_0}{v}, \text{ and } T_- \leq \frac{X_0}{v} < \infty.$$

$\square$

Proposition 1.4.2. *The functions $x \longmapsto m(x)$ and $x \longmapsto V(x)$ are continuous and decreasing on $\mathbb{R}_-$ and*

$$\begin{aligned} m(x) &\xrightarrow[x\to-\infty]{} m, \\ V(x) &\xrightarrow[x\to-\infty]{} V. \end{aligned} \tag{1.4.1}$$

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

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

We have that $h(x,\cdot) \in L^1(\nu)$, and $x \mapsto h(x,\alpha)$ is decreasing. For each fixed $\alpha > 0$, $0 \leq h(x,\alpha) \uparrow \alpha$, as $x \to -\infty$. By the monotone convergence theorem, it follows that

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

Continuity is proved similarly. $\square$

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

1. 4. 1. The case $v > m$

In particular, here $m = \int_0^\infty \alpha\nu(d\alpha)$ is finite. Let

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

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

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

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

$$\mathcal{M}_t^{(-)} = \mathcal{N}_t^{(-)} - \int_0^t m^{(-)}(X_s)ds.$$

Thus,

$$X_t \leq X_0 + \int_0^t (m^{(-)}(X_s) - v)ds + \mathcal{M}_t^{(-)}$$

Lemma 1.4.1. *If $m < \infty$, then*

$$\frac{\mathcal{M}_t^{(-)}}{t} \xrightarrow[t\to\infty]{} 0 \ a.s. \tag{1.4.2}$$

Proof. $\mathcal{M}_t^{(-)}$ is a square-integrable martingale, such that $\mathbb{E}\mathcal{M}_t^{(-)} = 0$. For all $i \in \mathbb{N}^*$ and $n \in \mathbb{N}^*$, define

$$\begin{aligned}
\xi_i &= \int_{i-1}^i \int_0^\infty \int_0^1 \alpha\varphi(X_{s-}, \alpha, \xi) M(ds, d\alpha, d\xi), \\
\omega_i &= \int_{i-1}^i m^{(-)}(X_s)ds, \\
\eta_i &= \int_{i-1}^i \int_0^\infty \int_0^1 \alpha M(ds, d\alpha, d\xi), \\
Y_i &= \xi_i - \omega_i, \\
\mathcal{M}_n^{(-)} &= \sum_{i=1}^n Y_i,
\end{aligned}$$

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 1.4.2. *The event*

$$\left\{ \frac{\sum_{i=1}^n Y_i}{n} \to 0 \quad as\ n \to \infty \right\}$$

entails the event

$$\left\{ \frac{\mathcal{M}_t^{(-)}}{t} \to 0 \quad as\ t \to \infty \right\}.$$

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

$$\begin{aligned}
\frac{\tilde{\mathcal{M}}_t^{(-)}}{t} =& \frac{1}{t}\left(\int_{\lfloor t\rfloor}^{t}\int\int \alpha\varphi(X_{s-},\alpha,\xi)M(ds,d\alpha,d\xi) - \int_{\lfloor t\rfloor}^{t} m^{(-)}(X_s)ds\right) \\
\leq& \frac{1}{t}\left(\int_{\lfloor t\rfloor}^{\lceil t\rceil}\int\int \alpha\varphi(X_{s-},\alpha,\xi)M(ds,d\alpha,d\xi) + \int_{\lfloor t\rfloor}^{\lceil t\rceil} m^{(-)}(X_s)ds\right) \\
=& \frac{1}{t}\left(\xi_{\lceil t\rceil} + \omega_{\lceil t\rceil}\right) = \frac{\lceil t\rceil}{t} \times \frac{1}{\lceil t\rceil}\left(Y_{\lceil t\rceil} + 2\omega_{\lceil t\rceil}\right) \xrightarrow[t\to\infty]{} 0,
\end{aligned}$$

since for all $n > 0$,

$$\frac{Y_{n+1}}{n+1} = \frac{\sum_{i=1}^{n+1} Y_i}{n+1} - \frac{\sum_{i=1}^{n} Y_i}{n} \times \frac{n}{n+1} \xrightarrow[n\to\infty]{} 0$$

and

$$0 \leq \frac{\omega_n}{n} \leq \frac{m}{n},$$

hence

$$\frac{\omega_n}{n} \xrightarrow[n\to\infty]{} 0.$$

□

Back to the proof of Lemma 1.4.1. We now define

$$\begin{aligned}
A_i &= \{\eta_i > i\}, \\
\tilde{Y}_i &= Y_i \mathbf{1}_{\{\eta_i \leq i\}}.
\end{aligned}$$

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

$$\sum_{i\geq 1} \mathbb{P}(\eta_i > i) = \sum_{i\geq 1} \mathbb{P}(\eta_1 > i) \leq \mathbb{E}\eta_1 < \infty,$$

it follows from Borel Cantelli's Lemma that $\mathbb{P}(\limsup A_i) = 0$. Hence, a.s. there exists $N(\alpha)$ such that for all $n > N(\alpha)$, we have $\tilde{Y}_n = Y_n$. But since $\mathbb{E}(\tilde{Y}_n) \to \mathbb{E}(Y_1) = 0$ due to the dominated convergence theorem, it is sufficient to prove that

$$\frac{\sum_{i=1}^{n}\left(\tilde{Y}_i - \mathbb{E}(\tilde{Y}_i)\right)}{n} \xrightarrow[n]{} 0.$$

Due to corollary 3.22 in Breiman (1968) [a], it is again sufficient to prove that

$$\sum_{i=1}^{\infty} \frac{\mathbb{E}(\tilde{Y}_i^2)}{i^2} < \infty.$$

a. In the proof of this Corollary, we replace Kolmogorov's inequality by Doob's inequality for martingales, and the result holds in our case.

Indeed, we have that

$$\sum_{i=1}^{\infty} \frac{\mathbb{E}(\tilde{Y}_i^2)}{i^2} \leq 2m.$$

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

Remark 1.4.1. In the case $m < \infty$ and $X_t \to -\infty$, we have that

$$\frac{1}{t}\mathcal{M}_t^{(+)} \to 0 \text{ a.s.} \quad \text{as } t \to \infty,$$

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

$$\frac{\mathcal{M}_t}{t} \to 0 \text{ a.s.} \quad \text{as } t \to \infty,$$

whether $X_t \to -\infty$ or not. But we refrain from adding any unnecessary assumption on ν.

Theorem 1.4.1. *In the case $v > m$, $X_t \to -\infty$ with speed $v - m$ in the sense that*

$$\frac{X_t}{t} \xrightarrow[t\to\infty]{} m - v \text{ a.s.}$$

Proof. We have that

$$\begin{aligned} X_t &= X_0 - vt + \int_{[0,t]\times\mathbb{R}\times[0,1]} \alpha\varphi(X_{s-}, \alpha, \xi) M(ds, d\alpha, d\xi) \\ &\leq X_0 - vt + \int_0^t m^{(-)}(X_s)ds + \mathcal{M}_t^{(-)}, \end{aligned}$$

since we have deleted negative jumps (recall the notation defined before Lemma 1.4.1). Hence

$$\frac{X_t}{t} = \frac{X_0}{t} - v + \frac{1}{t}\int_0^t m(X_s)ds + \frac{\mathcal{M}_t}{t} \leq \frac{X_0}{t} - v + m + \frac{\mathcal{M}_t^{(-)}}{t}.$$

It follows from Lemma 1.4.1 that

$$\limsup_{t\to\infty} \frac{X_t}{t} \leq -v + m \text{ a.s.}$$

In particular, $X_t \to -\infty$ a.s. as $t \to \infty$, and combined with (1.4.1), we deduce that

$$\forall \epsilon > 0 \quad \exists t_\epsilon \text{ such that } \forall s \geq t_\epsilon,\ m(X_s) > m - \epsilon.$$

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

$$\frac{X_t}{t} \geq \frac{X_{t_\epsilon}}{t} + (m - \epsilon - v) \times \frac{t - t_\epsilon}{t} + \frac{\mathcal{M}_t - \mathcal{M}_{t_\epsilon}}{t}.$$

Hence,

$$\liminf_{t\to\infty} \frac{X_t}{t} \geq -v + m \text{ a.s.}$$

We conclude that $X_t \to -\infty$ a.s. with speed $v - m$. □

1. 4. 2. The case $v < m$

Define for all $x \in \mathbb{R}$

$$\psi(x) = m(x) - v. \tag{1.4.3}$$

In this section, we assume that either $\nu(\mathbb{R}) < \infty$, or else the following mild growth condition on $g(x, \alpha)$ for small $x > 0$, which is satisfied in case g is given by (2.1.2) and (1.2.2) : for some $\delta > 0$, $c > 0$,

$$|g(x, \alpha)| \leq c|x|, \quad \text{for all } 0 < x \leq \delta. \tag{1.4.4}$$

Theorem 1.4.2. *In the case $v < m$, if (1.4.4) is satisfied and*

$$\int_{\mathbb{R}} |\alpha|\nu(d\alpha) < \infty, \tag{1.4.5}$$

then X_t is recurrent in the sense of Harris. Moreover, X_t possesses a unique invariant probability measure.

Proof. **Step 1 :** *X_t returns to $[-K, K]$ in finite time*

Since $x \longmapsto m(x)$ is continuous, 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 $x \leq -K$

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

On the other hand, if $x > 0$ we have that $\psi(x) < -v < 0$. Assume that $|X_0| > K$, and define the stopping time

$$T_K = \inf\{t > 0, |X_t| \leq K\}$$

We have

$$
\begin{aligned}
|X_t| = |X_0| + \int_0^t \operatorname{sign}(X_s)\psi(X_s)ds + \int_0^t \operatorname{sign}(X_{s-})d\mathcal{M}_s \\
+ \sum_{s\le t} \left(|X_{s-} + \Delta X_s| - |X_{s-}| - \operatorname{sign}(X_{s-}\Delta X_s)\right) \\
= |X_0| + \int_0^t \operatorname{sign}(X_s)\psi(X_s)ds + \int_0^t \operatorname{sign}(X_{s-})d\mathcal{M}_s \\
+ 2\sum_{s\le t} \mathbf{1}_{\{X_{s-}(X_{s-}+\Delta X_s)<0\}}|X_{s-} + \Delta X_s| \\
= |X_0| + \int_0^t \left(\operatorname{sign}(X_s)\psi(X_s) + \Phi(X_s)\right) ds + M_t^\star,
\end{aligned}
$$

where

$$
M_t^\star = \int_0^t \operatorname{sign}(X_{s-})d\mathcal{M}_s + 2\int_{[0,t]\times\mathbb{R}\times[0,1]} |X_{s-}+\alpha|\mathbf{1}_{\{\alpha X_{s-}<0\}}\varphi(X_{s-},\alpha,\xi)\bar{M}(ds,d\alpha,d\xi),
$$

and

$$
\Phi(x) = \begin{cases} 2\int_{-x}^{-2x} |x+\alpha|g(x,\alpha)\nu(d\alpha) & \text{if } x<0 \\ 2\int_{-2x}^{-x} |x+\alpha|g(x,\alpha)\nu(d\alpha) & \text{if } x>0 \end{cases}.
$$

Furthermore,

$$
\Phi(x) \le \begin{cases} 2|x|\nu([|x|,\infty)) & \text{if } x<0 \\ 2|x|\nu((-\infty,|x|]) & \text{if } x>0 \end{cases}.
$$

If condition (1.4.5) is satisfied, then $\Phi(x) \to 0$ as $|x| \to \infty$. Consequently there exists $c_1 > 0$ and K sufficiently large such that for all $|x| > K$,

$$
\operatorname{sign}(x)\psi(x) + \Phi(x) < -c_1.
$$

Hence

$$
\mathbb{E}|X_{t\wedge T_K}| \le |X_0| - c_1\,\mathbb{E}(t\wedge T_K),
$$

yielding

$$
\mathbb{E}T_K < \frac{|X_0|}{c_1} < \infty.
$$

Step 2 : *X_t visits $[0, K+vT]$ infinitely often*

Here $K' = K + vT$ where $T > 0$ and p is the lower bound of the probability that, starting from any given point $x \in [-K, 0)$ at time t_0, X hits $[0, K']$ before time $t_0 + T$. Clearly we can choose T such that $p > 0$. We now define a random variable β as follows :

If $X_{T_K} \in [0, K]$, then $\beta = 0$. Otherwise, we restart our process X at time $t_0 = T_K$ from $x_0 \in [-K, 0)$. If X hits $[0, K']$ 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 enters $[-K, K]$. Since $|X_T| \leq K'$, the time α_2 needed to do so satisfies (see Step 1)

$$\mathbb{E}(\alpha_2) \leq \frac{K'}{c_1}.$$

— If $-K \leq X_T < 0$, we start afresh from there, since the probability to reach $[0, K']$ in a time 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 position belonging to the interval $[-K, K]$. If $[0, K']$ 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

$$T^+_{K'} \leq T_K + \sum_{i=1}^{\beta} (T + \alpha_i)\,,$$

where $T^+_{K'} = \inf\{t > 0;\ X_t \in [0, K']\}$ and β is a stopping time associated with the sequence $(\alpha_i)_{i\geq 1}$. It follows from the martingale version of Wald's formula that

$$\mathbb{E}T^+_{K'} < \mathbb{E}T_K + \frac{1}{p}\left(T + \frac{K'}{c_1}\right),$$

since $\mathbb{P}(\beta > k) \leq (1-p)^k$, hence $\mathbb{E}\beta < 1/p$.

Step 3 : *X_t hits zero infinitely often*

If $\nu(\mathbb{R}_-) < \infty$, starting from any point in $(0, K']$ at time 0, there is a no jump of X_t before it hits 0 with probability

$$\exp\left(-\nu(\mathbb{R}_-)\frac{K'}{v}\right).$$

If $\nu(\mathbb{R}_-) = \infty$, we choose $0 < \delta < K'$ such that (1.4.4) is satisfied and

$$q = \frac{c\delta}{v}\int_{-\delta}^{0} |\alpha|\nu(d\alpha) < 1.$$

Let A_δ be the event that there is no jump of size $< -\delta$ before X_t hits $\mathbb{R}_-$.

$$\mathbb{P}(A_\delta) \leq \exp\left(-\nu(-\infty, -\delta)\frac{K'}{v}\right).$$

Moreover for $0 < x < \delta$

$$
\begin{aligned}
\mathbb{P}_x(X_t \text{ jumps over } 0 \mid A_\delta) &\leq \mathbb{E}\int_{[0,\frac{\delta}{v}]\times[-\delta,-X_{s-}]\times[0,1]} \mathbf{1}_{X_{s-}<0}\varphi(X_{s-},\alpha,\xi)M(ds,d\alpha,d\xi) \\
&= \mathbb{E}\int_0^{\frac{\delta}{v}} \mathbf{1}_{X_s<0}\int_{-\delta}^{-X_s} g(X_s,\alpha)\nu(d\alpha)ds \\
&\leq c\int_0^{\frac{\delta}{v}}\int_{-\delta}^{0}|\alpha|\nu(d\alpha)ds = q.
\end{aligned}
$$

If $p = \mathbb{P}(A_\delta^c)$ then, starting from any point in $(0, K']$,

$$
\mathbb{P}(X_t \text{ hits } \mathbb{R}_- \text{ without visiting } 0) \leq p + (1-p)q < 1.
$$

Since X_t visits $(0, K']$ infinitely often, and hits 0 with positive probability after any such visit, the same argument as above yields that for any $x \in \mathbb{R}$, $\mathbb{E}_x T_0 < \infty$, where $T_0 = \inf\{t > 0;\ X_t = 0\}$. In particular, the process is Harris recurrent, since it satisfies condition (b) on page 490 of Meyn and Tweedie Meyn and Tweedie (1993) with $\mu = \delta_0$.

Step 4 : *Existence of an invariant probability measure*

Let X_t start from $X_0 = 0$ and define

$$
T_+ = \inf\{t > 0;\ X_t \geq 0\}.
$$

We want to show that $T_+ > 0$ a.s. Let $\xi_t = \mathbf{1}_{\{T_+\leq t\}}$. We have

$$
\xi_t = \int_{[0,t]\times\mathcal{R}_+\times[0,1]} \mathbf{1}_{\{X_{s-}\leq 0\}}\mathbf{1}_{\{\alpha\geq -X_{s-}\}}\varphi(X_{s-},\alpha,\xi)M(ds,d\alpha,d\xi).
$$

Hence

$$
\begin{aligned}
\mathbb{E}\xi_t &= \mathbb{E}\int_0^t \mathbf{1}_{\{X_{s-}\leq 0\}}\int_{-X_s}^{-2X_s} g(X_s,\alpha)\,\nu(d\alpha)\,ds \\
&\leq c\,\mathbb{E}\int_0^t \mathbf{1}_{\{X_{s-}\leq 0\}}\int_{-X_s}^{-2X_s} |X_s|\,\nu(d\alpha)\,ds \\
&\leq c\ t\ \int_0^{2vt}\alpha\,\nu(d\alpha),
\end{aligned}
$$

where c is the constant defined by condition (1.4.4). Thus

$$
\mathbb{P}(T_+ \leq t) = \mathbb{P}(\xi_t = 1) = \mathbb{E}\xi_t \leq c\ t\ \int_0^{2vt}\alpha\,\nu(d\alpha),
$$

yielding $\mathbb{P}(T_+ > t) \to 1$ as $t \downarrow 0$. Since $T_0 = \inf\{t > 0;\ X_t = 0\} \geq T_+$, $T_0 > 0$ $\mathbb{P}_0$ a.s.

Define the measure μ on $(\mathbb{R}, \mathcal{B})$ by

$$\mu(A) = \mathbb{E}_0 \int_0^{T_0} \mathbf{1}_A(X_s)ds.$$

It follows from Step 3 that $\mu(\mathbb{R}) = \mathbb{E}_0(T_0) < \infty$, hence μ is a finite measure and we define the probability measure

$$\bar{\mu}(A) = \frac{\mu(A)}{\mu(\mathbb{R})}.$$

$\bar{\mu}$ is invariant under the semi group P_t associated to the Markov process X_t. Indeed for any t,

$$\mathbb{E}_0 \int_0^t \mathbf{1}_A(X_s)ds = \mathbb{E}_0 \int_{T_0}^{T_0+t} \mathbf{1}_A(X_s)ds.$$

Hence,

$$\begin{aligned}
\mathbb{E}_0 \int_0^{T_0} \mathbf{1}_A(X_s)ds &= \mathbb{E}_0 \int_t^{T_0+t} \mathbf{1}_A(X_s)ds \\
&= \mathbb{E}_0 \int_0^{T_0} \mathbf{1}_A(X_{t+s})ds \\
&= \int_0^\infty \mathbb{P}_0(X_{t+s} \in A,\ s < T_0)ds \\
&= \int_0^\infty \int_{\mathbb{R}} \mathbb{P}_0(X_s \in dz,\ s < T_0)\mathbb{P}_z(X_t \in A)ds \\
&= \int_{\mathbb{R}} \mathbb{P}_z(X_t \in A)\mu(dz).
\end{aligned}$$

Step 5 : *Uniqueness of the invariant probability measure*

Since an invariant probability measure exists, there exists an invariant ergodic probability measure which we again denote by $\bar{\mu}$. From the ergodic theorem, if f is continuous and bounded, as $t \to \infty$

$$\frac{1}{t} \int_0^t f(X_s)ds \to \int f(x)\bar{\mu}(dx) \ \mathbb{P}_{\bar{\mu}} \text{ a.s.}$$

Now, if $t > T_0$

$$\frac{1}{t} \int_0^t f(X_s)ds = \frac{1}{t} \int_0^{T_0} f(X_s)ds + \frac{1}{t} \int_{T_0}^t f(X_s)ds.$$

Consequently, as $t \to \infty$

$$\frac{1}{t} \int_{T_0}^t f(X_s)ds \to \int f(x)\bar{\mu}(dx).$$

Thus, if $\bar{\mu}'$ is another ergodic invariant probability measure,

$$\int f(x)\bar{\mu}(dx) = \int f(x)\bar{\mu}'(dx),$$

for all f continuous and bounded. Uniqueness of the ergodic invariant probability measure and hence of the invariant probability measure follows.

$\square$

Remark 1.4.2. Let us now discuss why the assumption (1.4.5) is not just imposed by our method of proof. Consider the example

$$\nu(d\alpha) = \mathbf{1}_{\{|\alpha|>1\}} \frac{d\alpha}{\alpha^{\delta}}, \ 1 < \delta < 2$$

and we assume that for some $c > 0$, $1 < a < 2$, $g(x, \alpha) \geq c\mathbf{1}_{\{\alpha x<0\}}\mathbf{1}_{\{|x|\leq|\alpha|\leq a|x|\}}$. Then, refering to the notations of Step 1 of the above proof, $\Phi(x) \to +\infty$, as $|x| \to \infty$. This implies that, while $|X_t|$ is large enough, $|X_t|$ is a submartingale, which then tends to increase. This may look strange, since the drift in the equation for X_t is opposite to that of X_t, provided $|X_t|$ is large enough, and the jumps cannot increase the distance to the origin. However, we believe that the intuitive explanation is as follows. First note that the fact that the change of sign between the drift of X_t and that of $|X_t|$ comes from $\Phi(X_t)$, which is due only to the jumps of X_t over 0. If the measure ν has a heavy tail, the jumps from far on the left push X_t far to the right, but may not decrease very much its distance to 0. This can very well result in $|X_t| \to +\infty$, while the sign of X_t does not remain constant.

There is a large class of Lévy processes which possess that property, which includes the scalar symmetric α–stable processes in case $0 < \alpha < 1$, see e.g. Theorem 17 in Chapter 1 of Bertoin (1996).

Remark 1.4.3. On the other hand, condition (1.4.4) is rather weak. It is hard to find an example of a g that would satisfy (1.2.4), but not (1.4.4). This new condition is not really necessary. It simplifies our proof, since it allows us to prove that 0 is visited infinitely many times. We have decided to adopt it, since it is not a serious restriction. At any rate, Steps 1 and 2 of our proof do not necessitate this assumption.

1. 4. 3. The case $v = m$

We first state a lemma that we will apply several times in this section.

Lemma 1.4.3. *Let X_t be a finite variation càdlàg process.*

1. *If $\Phi \in C^1$, then*

$$\Phi(X_t) = \Phi(X_0)+\int_0^t \Phi'(X_{s-})dX_s+\sum_{s\le t,\Delta X_s\neq 0} \Phi(X_{s-}+\Delta X_s)-\Phi(X_{s-})-\Phi'(X_{s-})\Delta X_s,$$

   where $\Delta X_s = X_s - X_{s-}$, $\forall s$.
2. *Moreover, if $\Phi \in C^2$ such that Φ'' is an increasing function and $\Delta X_s \ge 0$ for all s, then*

$$\Phi(X_t) - \Phi(X_0) - \int_0^t \Phi'(X_{s-})dX_s \le \frac{1}{2}\sum_{s\le t,\Delta X_s\neq 0} \Phi''(X_{s-} + \Delta X_s)(\Delta X_s)^2.$$

   If $\Phi \in C^2$ such that Φ'' is a decreasing function and $\Delta X_s \ge 0$ for all s, then

$$\Phi(X_t) - \Phi(X_0) - \int_0^t \Phi'(X_{s-})dX_s \le \frac{1}{2}\sum_{s\le t,\Delta X_s\neq 0} \Phi''(X_{s-})(\Delta X_s)^2.$$

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

$$X_t^2 = X_0^2 + 2\int_0^t X_{s-}dX_s + \sum_{s\le t} (\Delta X_s)^2 . \tag{1.4.6}$$

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 β taking its values in $[0, 1]$ such that for all s

$$\Phi(X_s) - \Phi(X_{s-}) - \Phi'(X_{s-})\Delta X_s = \frac{1}{2}\Phi''(X_{s-} + \beta_s\Delta X_s)(\Delta X_s)^2 .$$

If Φ'' is an increasing function and $y \ge 0$ then

$$\Phi''(x) \le \Phi''(x + \beta_s y) \le \Phi''(x + y).$$

If Φ'' is a decreasing function and $y \ge 0$ then

$$\Phi''(x + y) \le \Phi''(x + \beta_s y) \le \Phi''(x).$$

□

Note that $V \le \infty$ 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 (1.4.3) as $x \to -\infty$.

Theorem 1.4.3. *We assume that $m = v$ and that*

$$supp(\nu) \subset (-\infty, K], \ \textit{for some } K > 0. \tag{1.4.7}$$

If moreover

$$\limsup_{x\to-\infty} |x\psi(x)| < \frac{V}{2}, \tag{1.4.8}$$

then the process X_t is Harris recurrent but the mean return time to a compact is infinite.

Proof. First note that, since $m = v$ implies $\psi(x) \leq 0$ for all $x \leq 0$, condition (1.4.8) is equivalent to

$$\liminf_{x\to-\infty} |x|\psi(x) > -\frac{V}{2}.$$

To prove recurrence under condition (1.4.8), we recall that

$$X_t = X_0 + \int_0^t \psi(X_s)ds + \mathcal{M}_t. \tag{1.4.9}$$

We will apply Lemma 1.4.3 with $\Phi(x) = \log|x|$, with $x < 0$. Here Φ'' is decreasing. Hence as long as X_t remains negative,

$$\begin{aligned}
\log|X_t| &\leq \log|X_0| + \int_0^t \frac{\psi(X_s)}{X_s}ds + \int_0^t \frac{1}{X_{s-}}d\mathcal{M}_s - \frac{1}{2}\sum_{s\leq t}\frac{(\Delta X_s)^2}{X_{s-}^2} \\
&= \log|X_0| + \int_0^t \frac{\psi(X_s)}{X_s}ds + \int_0^t \frac{1}{X_{s-}}d\mathcal{M}_s \\
&- \frac{1}{2}\int_0^t\int_{\mathbb{R}_+}\int_0^1 \frac{\alpha^2\varphi(X_{s-},\alpha,\xi)}{X_{s-}^2}\bar{M}(ds,d\alpha,d\xi) - \frac{1}{2}\int_0^t \frac{V(X_s)}{X_s^2}ds \\
&= \log|X_0| + \int_0^t \left(\frac{\psi(X_s)}{X_s} - \frac{V(X_s)}{2X_s^2}\right)ds + \hat{\mathcal{M}}_t,
\end{aligned}$$

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

$$S_{a,b} = \inf(t > 0, X_t \leq a \text{ or } X_t \geq b).$$

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

$$\inf_{x\leq -L}\left\{|x|\psi(x) + \frac{V(x)}{2}\right\} > 0. \tag{1.4.10}$$

For any $N > L$, from Doob's optional sampling theorem, if $-N < X_0 < -L <$

$-K-1$,

$$\mathbb{E}\log|X_{t\wedge S_{-N,-L}}| \leq \log|X_0| + \mathbb{E}\int_0^{t\wedge S_{-N,-L}} \left(\frac{\psi(X_s)}{X_s} - \frac{V(X_s)}{2X_s^2}\right) ds.$$

Letting t tend to ∞,

$$\mathbb{E}\log|X_{S_{-N,-L}}| \leq \log|X_0|.$$

Define the stopping times

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

From (1.4.7) and the condition on L, $\log|X_{S_{-N,-L}}| > 0$. It follows from the previous estimate that

$$\log N \times \mathbb{P}(T_{-N}^{\downarrow} < T_{-L}^{\uparrow}) < \log|X_0|.$$

By the same argument as in the proof of Theorem 1.4.2, X_t will visit $[-L, L]$, thus also $(0, L)$ infinitely often, and also 0. Note that the process remains in $(-\infty, L]$ when starting there. Therefore, the process X is Harris recurrent.

Let now $X_0 < -(L+1)$. For all $N > L$, multiplying (1.4.9) by -1, we have

$$-X_{t\wedge S_{-N,-L}} = |X_0| - \int_0^{t\wedge S_{-N,-L}} \psi(X_s)ds - \int_0^{t\wedge S_{-N,-L}} d\mathcal{M}_s,$$

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

$$\begin{gathered} -\mathbb{E}X_{S_{-N,-L}} = |X_0| - \mathbb{E}\int_0^{S_{-N,-L}} \psi(X_s)ds \geq |X_0|, \text{ hence} \\ L\mathbb{P}(T_{-L}^{\uparrow} < T_{-N}^{\downarrow}) + N\mathbb{P}(T_{-N}^{\downarrow} < T_{-L}^{\uparrow}) \geq |X_0|, \end{gathered}$$

since $X_{S_{-N,-L}} = -N$ on the event $\left\{T_{-N}^{\downarrow} < T_{-L}^{\uparrow}\right\}$, and $X_{S_{-N,-L}} \geq -L$ on the complementary event. We have

$$\liminf_{N\to\infty} N\mathbb{P}(T_{-N}^{\downarrow} < T_{-L}^{\uparrow}) \geq |X_0| - L > 0. \tag{1.4.11}$$

It follows from Lemma 1.4.3 that

$$X_t^2 = X_0^2 - \int_0^t 2|X_s|\psi(X_s)ds + \int_0^t 2X_{s-}d\mathcal{M}_s + \sum_{s\leq t}(\Delta X_s)^2.$$

On the other hand, for $t \leq S_{-N,-L}$,

$$\sum_{s \leq t} (\Delta X_s)^2 = \int_0^t \int_{\mathbb{R}_+} \int_0^1 \alpha^2 \varphi(X_{s-}, \alpha, \xi) \bar{M}(ds, d\alpha, d\xi) + \int_0^t \int_{\mathbb{R}_+} \alpha^2 g(X_{s-}, \alpha) \nu(d\alpha) ds.$$

Thus, from (1.4.10) and the fact that from (1.4.7), $V(x) \leq V < \infty$,

$$X^2_{t \wedge S_{-N,-L}} \leq X_0^2 + 2V \times (t \wedge S_{-N,-L}) + \tilde{\mathcal{M}}_{t \wedge S_{-N,-L}},$$

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

$$\mathbb{E} X^2_{S_{-N,-L}} \leq X_0^2 + 2V\, \mathbb{E} S_{-N,-L}, \text{ hence}$$
$$\mathbb{E} S_{-N,-L} \geq \frac{N^2 \mathbb{P}(T^{\downarrow}_{-N} < T^{\uparrow}_{-L}) - X_0^2}{2V}.$$

It follows by monotone convergence that

$$\mathbb{E}(T^{\uparrow}_{-L}) = \lim_{N \to \infty} \mathbb{E} S_{-N,-L} \geq \liminf_{N \to \infty} \left\{ N \mathbb{P}(T^{\downarrow}_{-N} < T^{\uparrow}_{-L}) \times \frac{N}{2V} - \frac{X_0^2}{2V} \right\}.$$

Combining this with (1.4.11), we deduce that $\mathbb{E} T^{\uparrow}_{-L} = \infty$. In other words, the return times to compacts have infinite expectation. $\square$

Using similar arguments as in Step 4 of the proof of Theorem 1.4.2, one should be able to conclude that X_t has an infinite invariant measure, which is unique up to a multiplicative constant.

Remark 1.4.4. Condition (1.4.8) is rather weak. Under the current assumption on the support of ν, it can be shown to hold in particular if ν is finite and g given by (2.1.2) and (1.2.2). On the other hand, our very strong condition (1.4.7) on the support of ν may not be necessary. It might however very well be that in case $m = v$ a stronger condition on the tail of the law of ν than in case $m > v$ is necessary for recurrence. We do not know what is the optimal condition.

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

Theorem 1.4.4. *Assume that $m = v$ and*

$$\liminf_{x \to -\infty} |x\psi(x)| > \frac{V}{2}. \tag{1.4.12}$$

If, moreover, there exist $0 < p_0 < 1$ *and* $0 < \beta_0 < 1$ *such that for all* $0 < \beta < \beta_0$

$$|x|^{p_0+2} \int_{-\beta x}^{\infty} \alpha^2 g(x, \alpha) \nu(d\alpha) \xrightarrow[x \to -\infty]{} 0, \tag{1.4.13}$$

then X_t *is transient, that is* $X_t \to -\infty$ *a.s., and moreover* $\frac{X_t}{t} \to 0$ *a.s.*

Remark 1.4.5. The conditions of Theorem 1.4.4 are satisfied in the case where both ν is infinite and its tail is not too heavy, while g is given by (2.1.2) and (1.2.2). For example, if

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

where $\rho(\alpha) \leq C|\alpha|^{-(5+\delta')}$, $|\alpha| > 1$ for some $\delta, \delta' > 0$. Condition (1.4.12) follows from the fact that $V < \infty$ while $|x\psi(x)| \to \infty$ as $|x| \to \infty$.

Condition (1.4.13) is easy to check.

Proof. First note that condition (1.4.12) is equivalent to

$$\limsup_{x \to -\infty} |x|\psi(x) < -\frac{V}{2}.$$

Hence there exist $K > 0$ and $0 < p \leq p_0$ such that

$$\sup_{x \leq -K} \left\{ |x|\psi(x) + (2p+1)\frac{V(x)}{2} \right\} < 0. \tag{1.4.14}$$

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

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

with p being a real number in $(0, 1)$ for which (1.4.14) holds. Then it follows from Lemma 1.4.3 applied to f, since f'' is an increasing function, as long as $X_s \leq 0$ for $s \leq t$

$$f(X_t) \leq f(X_0) + \int_0^t \psi(X_s) f'(X_s) ds + \frac{1}{2} \int_0^t \int_0^{\infty} f''(X_s + \alpha)\alpha^2 g(X_s, \alpha)\nu(d\alpha)ds + \mathcal{N}_t,$$

where the martingale $\mathcal{N}$ is defined by

$$\mathcal{N}_t = \frac{1}{2} \int_0^t \int_0^{\infty} \int_0^1 \left[f'(X_{s-}) + f''(X_{s-} + \alpha)\alpha^2 \right] \varphi(X_{s-}, \alpha, \xi) \bar{M}(ds, d\alpha, d\xi).$$

Let us admit for the moment :

Lemma 1.4.4. *If* (1.4.13) *holds, then*

$$\lim_{x\to-\infty}|x|^{p+2}\int_0^\infty f''(x+\alpha)\alpha^2 g(x,\alpha)\nu(d\alpha)=p(p+1)V.$$

This implies that

$$\lim_{x\to-\infty}|x|^{p+2}\int_0^\infty f''(x+\alpha)\alpha^2 g(x,\alpha)\nu(d\alpha)<\lim_{x\to-\infty}p(2p+1)V(x).$$

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

$$\int_0^\infty f''(x+\alpha)\alpha^2 g(x,\alpha)\nu(d\alpha)<p(2p+1)\frac{V(x)}{|x|^{p+2}}.$$

Thus, for all $k>0$ satisfying $-kN<X_0<-N$,

$$\begin{aligned}f(X_{t\wedge S_{-kN,-N}}) &\leq f(X_0)+\int_0^{t\wedge S_{-kN,-N}}\frac{p}{|X_s|^{p+1}}\left[\psi(X_s)+(2p+1)\frac{V(X_s)}{2|X_s|}\right]ds\\ &\quad+\mathcal{N}_{t\wedge S_{-kN,-N}}.\end{aligned}$$

Now if $k\geq 3$, letting $X_0=-2N$, it follows from (1.4.14) that

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

Thus, if we let t tend to ∞,

$$\frac{1}{N^p}\mathbb{P}(S_{-kN,-N}=T^{\uparrow}_{-N}))\leq\mathbb{E}\frac{1}{|X_{S_{-kN,-N}}|^p}\leq\frac{1}{(2N)^p}.$$

Now letting k tend to ∞,

$$\mathbb{P}(T^{\uparrow}_{-N}<\infty)\leq\frac{1}{2^p}. \tag{1.4.15}$$

Let for all $k\geq 1$

$$B_k=\left\{T^{\uparrow}_{-N}\geq T^{\downarrow}_{-kN}\right\}$$

The $(B_k)_{k\geq 1}$ is a decreasing sequence of sets such that

$$\lim_k\mathbb{P}(B_k)=\mathbb{P}(B),$$

where $B=\{X_t \text{ hits } -kN \text{ before } -N \text{ for all } k\geq 1\}\subset\left\{X_t\xrightarrow[t\to\infty]{}-\infty\right\}$. It follows from (1.4.15) that

$$\mathbb{P}(X_t\xrightarrow[t\to\infty]{}-\infty)>\mathbb{P}(B)\geq 1-\frac{1}{2^p}.$$

On B^c, X_t enters $(-N, +\infty)$. The arguments from section 1. 4. 2 show that sooner or later the process X_t will hit $-2N$ again, and from there the probability of going to $-\infty$ is bounded from below by $1 - 1/2^p$ since this will happen each time the process gets above $-N$, hence

$$X_t \xrightarrow[t\to\infty]{} -\infty \text{ a.s.}$$

And since $m = v < \infty$, it follows from Lemma 1.4.1 and Remark 1. 4. 1 that $\frac{\mathcal{M}_t}{t} \to 0$, hence by the same arguments as in the proof of Therorem 2.4.1.

$$\frac{X_t}{t} \xrightarrow[t\to\infty]{} 0 \text{ a.s..}$$

$\square$

Proof of Lemma 1.4.4. For any $0 < \beta < \beta_0 < 1$, if $x < -(1-\beta)^{-1}$,

$$\begin{aligned}
|x|^{p+2} \int_0^\infty f''(x+\alpha) g(x,\alpha)\alpha^2 \nu(d\alpha) &= |x|^{p+2} \int_0^{-\beta x} f''(x+\alpha)\alpha^2 g(x,\alpha)\nu(d\alpha) \\
&\quad + |x|^{p+2} \int_{-\beta x}^\infty f''(x+\alpha)\alpha^2 g(x,\alpha)\nu(d\alpha) \\
&\le \int_0^{-\beta x} \frac{p(p+1)}{(1-\beta)^{p+2}} \alpha^2 g(x,\alpha)\nu(d\alpha) \\
&\quad + |x|^{p+2} p(p+1) \int_{-\beta x}^\infty \alpha^2 g(x,\alpha)\nu(d\alpha).
\end{aligned}$$

On the other hand,

$$\begin{aligned}
|x|^{p+2} \int_0^\infty f''(x+\alpha)\alpha^2 g(x,\alpha)\nu(d\alpha) &\ge p(p+1) \int_0^{-\beta x} \frac{|x|^{p+2}}{|x+\alpha|^{p+2}} \alpha^2 g(x,\alpha)\nu(d\alpha) \\
&> p(p+1) \int_0^{-\beta x} \alpha^2 g(x,\alpha)\nu(d\alpha).
\end{aligned}$$

Letting $x \to -\infty$ in the two above inequalities, we deduce from (1.4.13), which holds with p_0 replaced by $p \le p_0$,

$$\begin{aligned}
p(p+1)V &\le \liminf_{x\to-\infty} |x|^{p+2} \int_0^\infty f''(x+\alpha)\alpha^2 g(x,\alpha)\nu(d\alpha) \\
&\le \limsup_{x\to-\infty} |x|^{p+2} \int_0^\infty f''(x+\alpha)\alpha^2 g(x,\alpha)\nu(d\alpha) \\
&\le \frac{p(p+1)}{(1-\beta)^{p+2}} V.
\end{aligned}$$

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

$$|x|^{p+2} \int_0^{\infty} f''(x+\alpha)\alpha^2 g(x,\alpha)\nu(d\alpha) \xrightarrow[x\to-\infty]{} p(p+1)V.$$

$\square$

Remark 1.4.6. We have not been able to precise the large time behavior of the process X_t when the measure ν 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, $V = \infty$, $|x\psi(x)| \to \infty$ as $|x| \to \infty$, and (1.4.13) also fails.

1.5. 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 V_t, V_t being $\mathcal{F}_t$ progressively measurable, where again $\mathcal{F}_t$ is such that our Poisson Point Process M satisfies both that $M\big|_{[0,t]\times\mathbb{R}\times[0,1]}$ is $\mathcal{F}_t$ measurable and $M\big|_{(t,+\infty)\times\mathbb{R}\times[0,1]}$ is independent of $\mathcal{F}_t$. The stochastic equation describing the evolution of phenotypic lag becomes

$$X_t = X_0 - V_t + \int_0^t m(X_s)ds + \mathcal{M}_t. \tag{1.5.1}$$

As above, we study three cases :

1. 5. 1. The transient case

Here we assume that there exists a constant $\bar{v} \in \mathbb{R}$ such that

$$\lim_{t\to\infty} \frac{V_t}{t} = \bar{v} \text{ a.s.}$$

It is easy to see that results (1.4.1) and (1.4.2) hold in the new context of equation (1.5.1), provided $\bar{v} > m$. Following the steps of the proof in section 1. 4. 1, we can see that $X_t \to -\infty$ a.s. with speed $\bar{v} - m$.

1. 5. 2. The recurrent case

In this section we assume that

$$V_t = \int_0^t v_1(s)ds + \mathcal{M}_V(t),$$

where $\mathcal{M}_V(t)$ is a continuous $\mathcal{F}_t$–martingale, and that

$$v_1(t) \to \bar{v} \text{ a.s.}, \quad \text{as } t \to \infty.$$

Under the above conditions, together with $\bar{v} < m$ and (1.4.5), we will prove that the process X_t is Harris recurrent. We define again

$$T_K = \inf\{t > 0, |X_t| \leq K\}.$$

Assume that $|X_0| > K$. We rewrite the same inequality from Step 1 of the proof of Theorem 1. 4. 2 :

$$|X_t| \leq |X_0| + \int_0^t \Big\{\text{sign}(X_s)[m(X_s) - v_1(s)] + \Phi(X_s)\Big\}ds + \int_0^t \text{sign}(X_s)d\mathcal{M}_V(s) + M_t^\star,$$

where $M_t^\star$ is a martingale. We prove again that $\mathbb{E}T_K < \infty$. Then we prove that X_t visits $[0, M + (\bar{v} + 1)T]$ infinitely often using the same arguments as Step 2. The rest of the proof remains unchanged. Thus, X_t is Harris recurrent and the return time to $[-K, K]$ has finite expectation. If V_t is deterministic, then X_t is a Markov process and we again conclude the existence of a unique invariant probability measure.

1. 5. 3. The limiting case

Here we assume that

$$V_t = \int_0^t v_1(s)ds, \quad \text{and } v_1(t) \to \bar{v} \ \text{ a.s. as } t \to \infty.$$

Define moreover

$$\begin{aligned}
v_{\sup} &= \sup_s v_1(s), \\
v_{\inf} &= \inf_s v_1(s), \\
\psi_{\sup}(x) &= m(x) - v_{\sup}, \\
\psi_{\inf}(x) &= m(x) - v_{\inf},
\end{aligned}$$

We formulate two sets of assumptions :

Assumptions A

- $v_{\sup} < \infty$,
- $\liminf_{x \to -\infty} |x| \psi_{\sup}(x) > -\frac{V}{2}$.

Assumptions B

- $v_{\inf} < \infty$,
- $\limsup_{x \to -\infty} |x| \psi_{\inf}(x) < -\frac{V}{2}$.

Under the set of assumptions A and hypothesis (1.4.7), we can prove that the process is Harris recurrent. We have, however, not been able to prove that the return time to compacts has infinite expectation.

Ideas of Proof. Apply Lemma 1.4.3 to the process in equation (1.5.1) with $f(x) = \log |x|$, with $x < 0$. Here f'' is decreasing. Hence, as long as X_t remains negative,

$$\begin{aligned}\log |X_t| &\leq \log |X_0| + \int_0^t \left(\frac{\psi_{\sup}(X_s)}{X_s} - \frac{V(X_s)}{2X_s^2} \right) ds + \int_0^t \frac{v_{\sup} - v_1(s)}{X_s} ds + \mathcal{M'}_t \\ &< \log |X_0| + \int_0^t \left(\frac{\psi_{\sup}(X_s)}{X_s} - \frac{V(X_s)}{2X_s^2} \right) ds + \mathcal{M'}_t,\end{aligned}$$

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

Under the set of assumptions B and hypothesis (1.4.13), we can prove that

$$X_t \xrightarrow[t \to \infty]{} -\infty \quad \text{and} \quad \frac{X_t}{t} \xrightarrow[t \to \infty]{} 0.$$

Ideas of Proof. We take the same function f we constructed in the case of constant speed. We have $f' > 0$, and

$$\begin{aligned}f(X_t) &\leq f(X_0) + \int_0^t \psi_{\inf}(X_s) f'(X_s) ds + \int_0^t (v_{\inf} - v_1(s)) f'(X_s) ds \\ &+ \frac{1}{2} \int_0^t \int_0^\infty f''(X_s + \alpha) \alpha^2 g(X_s, \alpha) \nu(d\alpha) ds + \mathcal{N'}_t \\ &\leq f(X_0) + \int_0^t \psi_{\inf}(X_s) f'(X_s) ds + \frac{1}{2} \int_0^t \int_0^\infty f''(X_s + \alpha) \alpha^2 g(X_s, \alpha) \nu(d\alpha) ds + \mathcal{N'}_t,\end{aligned}$$

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

2. Model for a multidimensional phenotypic trait

2.1. Introduction

The model by Matuszewski et al. (2014) is set up as follows : A population of constant size N is subject to Gaussian stabilizing selection with a moving optimum that increases linearly with speed v. That is, at time t, the phenotypic lag between an individual with trait value z and the optimum equals $x = z - vt$, and the corresponding fitness is

$$\mathcal{W}(x) = \exp\left(-x'\Sigma^{-1}x\right), \tag{2.1.1}$$

where Σ describes the shape of the fitness landscape. 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 μ is the *per-capita* mutation rate and $\Theta = 2N\mu$ is a standard population-genetic parameter), and their phenotypic effects α are drawn from a distribution $p(\alpha)$. We neglect the possibility of fixation for deleterious mutations. Yet even beneficial mutations have a significant probability of being lost due to the effects of genetic drift while they are rare. A mutation with effect α that arises in a population with phenotypic lag x has a probability of fixation

$$g(x,\alpha) = \begin{cases} 1 - \exp(-2s(x,\alpha)) & \text{if } s(x,\alpha) > 0, \\ 0 \text{ otherwise} \end{cases} \tag{2.1.2}$$

where

$$s(x,\alpha) = \frac{\mathcal{W}(x+\alpha)}{\mathcal{W}(x)} - 1 \approx -(2x+\alpha)'\Sigma^{-1}\alpha \tag{2.1.3}$$

is the selection coefficient. Formula (2.1.2) is a good approximation of the fixation probability derived under a diffusion approximation (Kimura, 1962), as long as the population size N is not too small. Note that Matuszewski et al. (2014) used the even simpler approximation $g(x,\alpha) \approx 2s(x,\alpha)$ (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.

Our purpose is to study the large time behavior of X_t generalizing the asymptotic classification of the previous chapter. The principal result is that, in the transient case, the process goes far from the optimum in a direction that we identify. This effect is well known in the biological literature as the "flying kite" effect (Jones et al. (2004),Matuszewski et al. (2014)).

2.2. Generalities

Consider a probability space $(\Omega, \mathcal{F}, \mathbb{P})$ and a d-dimensional trait in $\left(\mathbb{R}^d, \langle \bullet, \bullet \rangle\right)$ for a monomorphic population undergoing a linear degradation with respect to time in the direction of the speed vector $-v$. We use the convention that A' is the transposed vector of A, and $A_i = (A \mid e_i)$ where $(e_i)_i$ is the canonic base of $\mathbb{R}^d$. We investigate the survival/extinction of such a population. Let ν be such that

$$\nu(d\alpha) = \frac{\Theta}{2} p(\alpha) d\alpha$$

where Θ is the mutation rate and $p(\alpha)$ is the density of a d-dimensional Gaussian measure $\mathcal{N}(0, M)$. Mutations appear according to a Poisson Point Process over $\mathbb{R}_+ \times \mathbb{R}^d$ with intensity $ds\nu(d\alpha)$. Given a positive-definite symmetric matrix Σ corresponding to selection, we define the quadratic form

$$\left\{ \begin{array}{llll} q: & \mathbb{R}^d & \to & \mathbb{R}_+ \\ & x & \mapsto & q(x) = x'\Sigma^{-1}x \end{array} \right.$$

The expression for the fixation probability of a mutation w that hits the population when the phenotypic lag is x is given by

$$g(x, \alpha) = 1 - \exp\left(-2\left[q(x) - q(x+\alpha)\right]^+\right)$$

Mutations that have a positive probability of fixation belong to an ellipse $\mathcal{E}_x = \{\alpha \in \mathbb{R}^d; q(x+\alpha) - q(x) \leq 0\}$.

Definition 2.2.1. *We define for all $x \in \mathbb{R}^d$*

$$m(x) = \int_{\mathbb{R}^d} \alpha g(x, \alpha) \nu(d\alpha),$$
$$\textit{and } \bar{m}(x) = \int_{\mathbb{R}^d} \alpha \mathbf{1}_{\{(x|\alpha) \leq 0\}} \nu(d\alpha).$$

Note that the asymptotic mean vector $\bar{m}(x)$ depends uniquely upon the direction of x.

The evolution of X over time can be described by the following equation

$$X_t = X_0 + \int_0^t (m(X_{s^-}) - v)\, ds + \int_0^t \int_{\mathbb{R}^d} \int_0^1 \alpha \Gamma(X_s, \alpha, \xi) \bar{N}(ds, d\alpha, d\xi)$$

where N is a PPP over $\mathbb{R}_+ \times \mathbb{R}^d \times [0,1]$ with intensity $ds\nu(d\alpha)d\xi$ and $\bar{N}$ is the corresponding compensated PPP and

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

From now on, we denote the last term by $\mathcal{N}_t$ and we rewrite the SDE as

$$X_t = X_0 + \int_0^t (m(X_s) - v)\, ds + \mathcal{N}_t \tag{2.2.1}$$

Definition 2.2.2. *We define the process $\langle\langle \mathcal{N} \rangle\rangle_t$ as the unique matrix valued predictable increasing process such that $\mathcal{N}_t \otimes \mathcal{N}_t - \langle\langle \mathcal{N} \rangle\rangle_t$ is a martingale and $\langle \mathcal{N} \rangle_t$ as the unique predictable increasing process such that $|\mathcal{N}_t|^2 - \langle \mathcal{N} \rangle_t$ is a martingale.*

Proposition 2.2.1. *We have that*

$$\sup_{|u|=1} (m(ru) - \bar{m}(u)) \xrightarrow[r\to\infty]{} 0. \tag{2.2.2}$$

Proof. For all $r > 0$ and all unit vector $u \in \mathbb{R}^d$

$$\begin{aligned} g(ru, \alpha) &= \left[1 - \exp\left(2(2ru + \alpha)'\Sigma^{-1}\alpha]\right)\right] \times \mathbf{1}_{\{(2ru+\alpha)'\Sigma^{-1}\alpha \leq 0\}} \\ &= \left[1 - \exp\left(4r(u + \frac{\alpha}{2r})'\Sigma^{-1}\alpha]\right)\right] \times \mathbf{1}_{\{\left(u+\frac{\alpha}{2r}\right)'\Sigma^{-1}\alpha \leq 0\}} \\ &\xrightarrow[r\to\infty]{} \mathbf{1}_{\{u'\Sigma^{-1}\alpha \leq 0\}}. \end{aligned}$$

On the other hand, $|\alpha g(ru, \alpha)| \leq |\alpha| \in L^1(\nu)$. Hence by the Lebesgue convergence theorem we have that for all unit vector $u \in \mathbb{R}^d$

$$m(ru) \xrightarrow[a\to\infty]{} \bar{m}(u).$$

□

In the following, we consider without loss of generality the following assumptions (see Matuszewski et al. (2014)) :

1. $\Sigma = \sigma^2\mathbf{I}$; $\mathbf{I}$ being the identity matrix,

2. $v = (v_1, 0, \dots, 0)$,
3. $\det(M) = 1$.

Lemma 2.2.1. *Define*

$$\begin{array}{rccc} L_x : & \mathbb{R}^d & \to & [0,1] \\ & l & \mapsto & L_x(l) = g(x, l - x). \end{array}$$

For all $l_1, l_2 \in \mathbb{R}^d$, if $|l_1| < |l_2|$ then $L_x(l_1) > L_x(l_2)$.

Proof. This is quite obvious to see since

$$L_x(l) = \Big(1 - \exp\Big[2\sigma^{-2}(|l|^2 - |x|^2)\Big]\Big) \times \mathbf{1}_{\{|l| \leq |x|\}}.$$

This means that the closer the mutation to the center $-x$ of the circle (C_{-x}) the more probable will it get fixed. Moreover for a given x, the subset of mutations that has the same fixation probability $0 < \tilde{g} < 1$ is a disk centered around $-x$ with radius

$$\sqrt{\frac{\sigma^2 \log(1 - \tilde{g})}{2} + \|x\|^2}.$$

□

Proposition 2.2.2. *We have the following proprieties : For all unit vector $u \in \mathbb{R}^d$ and $r > 0$,*
— $m(-ru) = -m(ru)$ *and* $\bar{m}(-u) = -\bar{m}(u)$,
— $(m(ru) - \bar{m}(u) \mid u) \geq 0$.

Proof. For all unit vetor $u \in \mathbb{R}^d$ and $r > 0$, introducing the change in variables $\tilde{\alpha} = -\alpha$,

$$m(-ru) = \int_{\mathbb{R}^2} \alpha g(-ru, \alpha) \nu(d\alpha)$$

and $g(-ru, \alpha) = (-2ru + \alpha \mid \alpha)\, \mathbf{1}_{(-2ru+\alpha|\alpha) \leq 0} = (2ru + \tilde{\alpha} \mid \tilde{\alpha})\, \mathbf{1}_{(2ru+\tilde{\alpha}|\tilde{\alpha}) \leq 0}$. Hence,

$$m(-ru) = -\int_{\mathbb{R}^2} \tilde{\alpha}^2 g(ru, \tilde{\alpha}) \nu(d\tilde{\alpha}) = -m(ru).$$

Similarly,

$$\begin{aligned} \bar{m}(-u) &= \int_{\{(-u|\alpha) \leq 0\}} \alpha \nu(d\alpha) = \int_{\{(u|-\alpha) \leq 0\}} \alpha \nu(d\alpha), \\ &= -\int_{\{(u|\tilde{\alpha}) \leq 0\}} \tilde{\alpha} \nu(d\tilde{\alpha}) = -\bar{m}(u). \end{aligned}$$

In addition, we have that

$$\begin{aligned}(m(ru) \mid u) &= \int_{\mathbb{R}^d} (\alpha \mid u)\, g(ru, \alpha)\nu(d\alpha) = \int_{\{(\alpha|u)\leq 0\}} (\alpha \mid u)\, g(ru, \alpha)\nu(d\alpha) \\ &\geq \int_{\{(\alpha|u)\leq 0\}} (\alpha \mid u)\, \nu(d\alpha) = (\bar{m}(u) \mid u)\,.\end{aligned}$$

□

Proposition 2.2.3. *We have that*

$$\frac{\mathcal{N}_t}{t} \xrightarrow[t\to\infty]{} 0. \tag{2.2.3}$$

Before giving the proof of Proposition 2.2.3 we first introduce a few Lemmas :

Lemma 2.2.2. *Let M be a square integrable martingale and let $\langle M\rangle_t$ be the process associated to it by Definition 2.2.2. On $\{\langle M\rangle_\infty < \infty\}$, M converges to a finite random variable M_∞.*

Proof. We will give a sketch of the proof since we didn't find a classical reference for this result. Let for each $n \geq 0$

$$T_n = \inf\{t > 0; \langle M\rangle_t \geq n\}.$$

For all n, T_n is a stopping time, and consequently from Doob's optional sampling theorem, $M^n = (M_{\cdot\wedge T_n})$ is a martingale such that

$$\mathbb{E}\langle M^n\rangle_\infty < \infty, \text{ hence } \sup_{t>0} \mathbb{E}(M_t^n)^2 < \infty.$$

Thus from the martingale convergence theorem M^n converges a.s. and in mean square to a finite random variable M_∞^n a.s. However

$$\{\langle M\rangle_\infty < \infty\} = \bigcup_n \{T_n = \infty\},$$

thus on the event $\{\langle M\rangle_\infty < \infty\}$, M converges to M_∞. □

Lemma 2.2.3 (Continuous Version of Kronecker's Lemma)**.** *Let $a : \mathbb{R}_+ \to \mathbb{R}_+$ be a measurable increasing function that diverges to ∞ and such that $a(0) = 0$, and $x : \mathbb{R}_+ \to \mathbb{R}_+$ a function of finite variation that converges to a finite limit x_∞ when $t \to \infty$. We have that*

$$\frac{1}{a_t}\int_0^t a_s dx_s \xrightarrow[t\to\infty]{} 0.$$

Proof. Let $y_t = x_\infty - x_t$. We have

$$\frac{1}{a_t}\int_0^t a_s dx_s = -\frac{1}{a_t}\int_0^t a_s dy_s$$

By integration by parts, we get

$$-\frac{1}{a_t}\int_0^t a_s dy_s = -y_t + \frac{1}{a_t}\int_0^t y_s da_s.$$

The first term $-y_t \to 0$ when $t \to \infty$. It follows that for all $\epsilon > 0$, there exists t_ϵ such that

$$\sup_{s>t_\epsilon} |y_s| \leq \epsilon.$$

Now we will prove that the second term of the above right hand side goes to 0 as well. Since a is an increasing function, if $t > t_\epsilon$

$$\begin{aligned}\left|\frac{1}{a_t}\int_0^t y_s da_s\right| &\leq \frac{1}{a_t}\int_0^t |y_s| da_s \\ &= \frac{1}{a_t}\int_0^{t_\epsilon} |y_s| da_s + \frac{1}{a_t}\int_{t_\epsilon}^t |y_s| da_s.\end{aligned}$$

Clearly,

$$\frac{1}{a_t}\int_0^{t_\epsilon} |y_s| da_s \xrightarrow[t\to\infty]{} 0,$$

and for all $\epsilon > 0$

$$\frac{1}{a_t}\int_{t_\epsilon}^t |y_s| da_s \leq \epsilon \times \frac{a_t - a_{t_\epsilon}}{a_t} \leq \epsilon,$$

Thus,

$$\frac{1}{a_t}\int_{t_\epsilon}^t |y_s| da_s \xrightarrow[t\to\infty]{} 0.$$

□

Lemma 2.2.4. *Let V be a predictable square-integrable finite variation process and M a square integrable FV martingale with the associated process $\langle M\rangle_t$ (See Definition 2.2.2). We have that $V_t \cdot M_t$ converges a.s. to 0 on the event*

$$\{\int_0^\infty V_s^2 d\langle M\rangle_s < \infty\} \bigcap \{V_t \textit{ decreases towards } 0 \textit{ as } t \to \infty\}.$$

In particular, on $\{\langle M\rangle_\infty = \infty\}$,

$$\left(\frac{M_t}{\langle M\rangle_t}\right) \textit{ converges to } 0 \textit{ a.s.}$$

Proof. Let $(V \cdot M)_t = \int_0^t V_{s^-} dM_s$. We have

$$\langle V \cdot M \rangle_t = \int_0^t V_s^2 d\langle M \rangle_s.$$

It follows form Lemma 2.2.2 that on $\{\langle V \cdot M \rangle_\infty < \infty\}$, $V \cdot M$ converges to a finite random variable. Applying Lemma 2.2.3 with

$$a_t = \frac{1}{V_t} \text{ and } x_t = \int_0^t V_{s^-} dM_s,$$

we deduce that if V_t decreases towards 0 we have that

$$V_t \int_0^t dM_s = V_t \cdot M_t \xrightarrow{a.s.} 0.$$

Choose

$$V_t = \frac{1}{1 + \langle M \rangle_t}.$$

We have that

$$\begin{aligned}\int_0^\infty V_t^2 d\langle M \rangle_t &= \int_0^\infty \frac{1}{(1 + \langle M \rangle_t)^2} d\langle M \rangle_t \\ &= \int_0^{\langle M \rangle_\infty} \frac{1}{(1+s)^2} ds \leq \int_0^\infty \frac{1}{(1+s)^2} ds < \infty.\end{aligned}$$

It follows that on the event $\{\langle M \rangle_\infty = \infty\}$

$$\frac{M_t}{\langle M \rangle_t} = \frac{M_t}{1 + \langle M \rangle_t} \times \frac{1 + \langle M \rangle_t}{\langle M \rangle_t} \xrightarrow[t \to \infty]{} 0 \ \ a.s.$$

□

Proof of Proposition 2.2.3. Consider the martingale defined in (2.2.1) :

$$\mathcal{N}_t = \int_{[0,t] \times \mathbb{R}^d \times [0,1]} \alpha \Gamma(X_{s^-}, \alpha, \xi) \bar{N}(ds, d\alpha, d\xi).$$

We have that

$$\langle \mathcal{N} \rangle_t = \int_{[0,t] \times \mathbb{R}^d} |\alpha|^2 g(X_{s^-}, \alpha) \nu(d\alpha) ds \leq \left(\int_{\mathbb{R}^d} |\alpha|^2 \nu(d\alpha) \right) \times t.$$

On $\{\langle \mathcal{N} \rangle_\infty = \infty\}$, it follows from Lemma 2.2.4 that

$$\frac{1}{\int_{\mathbb{R}^d} |\alpha|^2 \nu(d\alpha)} \times \frac{|\mathcal{N}_t|}{t} \leq \frac{|\mathcal{N}_t|}{\langle \mathcal{N} \rangle_t} \xrightarrow[t \to \infty]{} 0.$$

This implies that

$$\frac{\mathcal{N}_t}{t} \xrightarrow[t\to\infty]{} 0.$$

The same result holds on the event $\{\langle \mathcal{N} \rangle_\infty < \infty\}$ thanks to Lemma 2.2.2. $\square$

In the following, we provide an in-depth study of the process in $\mathbb{R}^2$. In this case, let

$$M = \begin{pmatrix} a & c \\ c & b \end{pmatrix},$$

for $a, b > 0,\ c \in \mathbb{R}$ such that $ab - c^2 = 1$. Thus the inverse of M is

$$M^{-1} = \begin{pmatrix} b & -c \\ -c & a \end{pmatrix}.$$

2.3. Existence and Uniqueness

Define for all $x \in \mathbb{R}^2$, $\bar{\psi}(x) = \bar{m}(x) - v$. It is clear that

$$\bar{\psi}(x) = \bar{\psi}\left(\frac{x}{|x|}\right). \tag{2.3.1}$$

First we establish the following Lemma :

Lemma 2.3.1. *Let u, w be two unit vectors of $\mathbb{R}^2$ such that $(u \mid w) = \cos\beta$, with $\beta \in [0, \pi]$. We have*

$$\beta \leq \frac{\pi}{2}|u - w|.$$

Proof. It follows from the definition of u and w that there exist $\rho_1, \rho_2 \in \mathbb{R}$ such that $u = e^{i\rho_1}$ and $w = e^{i\rho_2}$ and $\beta = |\rho_1 - \rho_2| \in [0, \pi]$. Thus,

$$|u - w| = \left|1 - e^{i\beta}\right| = \sqrt{(1 - \cos\beta)^2 + \sin^2\beta} = \sqrt{2\,(1 - \cos\beta)}.$$

Define for all $\beta \in]0, \pi]$

$$f(\beta) = \frac{\beta}{\sqrt{2\,(1 - \cos\beta)}}.$$

It remains to prove that for all $\beta \in]0, \pi]$, $f(\beta) \leq \frac{\pi}{2}$.

$$f'(\beta) = \frac{1}{(2(1 - \cos\beta))^{3/2}} \times (2 - 2\cos\beta - \beta\sin\beta)\,.$$

f' has the same sign as $\tilde{f}(\beta) = 2 - 2\cos\beta - \beta\sin\beta$.

$$\begin{aligned}\tilde{f}'(\beta) &= \sin\beta - \beta\cos\beta, \\ \tilde{f}''(\beta) &= \beta\sin\beta \geq 0 \text{ for } \beta \in [0,\pi].\end{aligned}$$

Thus, $\tilde{f}'$ is an increasing continuous function on $[0,\pi]$ with values in $[\tilde{f}'(0), \tilde{f}'(\pi)] = [0,\pi]$. This means that $\tilde{f}'(\beta) \geq 0$ for all $\beta \in [0,\pi]$. It follows that $\tilde{f}$ is an increasing continuous function on $[0,\pi]$ with values in $[\tilde{f}(0), \tilde{f}(\pi)] = [0,4]$. Consequently, $f'(\beta) > 0$ for all $\beta \in]0,\pi]$ implying that f is an increasing function on $]0,\pi]$ with values in $\left]\lim_{\beta\to 0} f(\beta), f(\pi)\right] = \left]1, \frac{\pi}{2}\right]$. □

Proposition 2.3.1. *The SDE as defined in* (2.2.1) *admits a unique solution.*

Proof. Since ν is a finite mesure, then N has a.s. finitely many points in $[0,t]\times\mathbb{R}^2\times[0,1]$ for any $t > 0$. The unique solution exists and can be constructed explicitly by adding the jumps. □

Proposition 2.3.2. *The ODE*

$$\frac{dY_t}{dt} = \bar{\psi}(Y_t) \tag{2.3.2}$$

admits a unique solution.

Proof. For all u, w unit vectors of $\mathbb{R}^2$, we have

$$\begin{aligned}\left|\bar{\psi}(u) - \bar{\psi}(w)\right| &= \left|\int_{\mathbb{R}^2} \alpha\left(\mathbf{1}_{\{(u|\alpha)\leq 0\}} - \mathbf{1}_{\{(w|\alpha)\leq 0\}}\right)\nu(d\alpha)\right| \\ &\leq \frac{\Theta}{4\pi}\int_{\mathbb{R}^2} |\alpha| \times \left|\mathbf{1}_{\{(u|\alpha)\leq 0\}} - \mathbf{1}_{\{(w|\alpha)\leq 0\}}\right| e^{-\frac{1}{2}\alpha' M^{-1}\alpha} d\alpha\end{aligned}$$

We have that

$$c_M = \inf_{|u|=1} u' M^{-1} u > 0,$$

since M is a symmetric definite positive matrix. Introduce the change to the polar coordinates $(r = |\alpha|, \gamma) \in \mathbb{R}_+ \times [\eta, \eta+\beta]$, where β is the positive angle between u and w and η is the positive angle between u and e_1. It follows that

$$\begin{aligned}\left|\bar{\psi}(u) - \bar{\psi}(w)\right| &\leq \frac{\Theta}{4\pi}\int_{\mathbb{R}^2} |\alpha| \times \left|\mathbf{1}_{\{(u|\alpha)\leq 0\}} - \mathbf{1}_{\{(w|\alpha)\leq 0\}}\right| e^{-\frac{1}{2}c_M|\alpha|^2} d\alpha \\ &\leq \frac{\Theta}{4\pi}\int_{\eta}^{\eta+\beta}\int_0^{\infty} r^2 e^{-\frac{1}{2}c_M r^2} dr d\gamma \leq \frac{\Theta}{8c_M}\sqrt{\frac{\pi}{2c_M}} \times |u - w|.\end{aligned}$$

The last inequality is due to Lemma 2.3.1. We proved that $\bar{\psi}$ is globally lipschitz which implies existence and uniqueness of the solution of Equation (2.3.2). □

2.4. Large time behaviour

For all $x \in \mathbb{R}^2$ there exist $r \geq 0,\ \beta \in [0, 2\pi]$ such that

$$x = ru_\beta \text{ where } u_\beta = \begin{pmatrix} \cos\beta \\ \sin\beta \end{pmatrix}. \tag{2.4.1}$$

In the following we study some proprieties of $\bar{m}(x)$ for all $x \in \mathbb{R}^2$. We remind that $\bar{m}(x)$ does not depend upon r, hence it remains to study $\bar{m}(u_\beta)$ for all $\beta \in [0, 2\pi]$. Furthermore, it follows from Proposition 2.2.2 that we can study the variations of $\bar{m}(u_\beta)$ on $\left[\frac{\pi}{2}, \frac{3\pi}{2}\right]$ and complete the study by symmetry entirely on $[0, 2\pi]$. Define

$$\mathcal{T}(\beta) = \tan\left(\beta + \frac{\pi}{2}\right).$$

Proposition 2.4.1. *In the two-dimensional case, the asymptotic mean vector can be derived explicitly :*

$$\bar{m}_1(u_\beta) = \begin{cases} -\frac{\Theta}{2\sqrt{2\pi}}\tilde{I}_\beta & \text{if } \beta \in \left[\frac{\pi}{2}, \pi\right] \\ \frac{\Theta}{2\sqrt{2\pi}}\tilde{I}_\beta & \text{if } \beta \in \left[\pi, \frac{3\pi}{2}\right] \end{cases},\ \bar{m}_2(u_\beta) = \begin{cases} -\frac{\Theta}{2a\sqrt{2\pi}}\left[I_\beta + c\tilde{I}_\beta\right] & \text{if } \beta \in \left[\frac{\pi}{2}, \pi\right] \\ \frac{\Theta}{2a\sqrt{2\pi}}\left[I_\beta + c\tilde{I}_\beta\right] & \text{if } \beta \in \left[\pi, \frac{3\pi}{2}\right] \end{cases}$$

where

$$\begin{aligned} I_\beta &= \sqrt{\frac{1}{b - 2c\mathcal{T}(\beta) + a(\mathcal{T}(\beta))^2}}, \\ \tilde{I}_\beta &= \frac{1}{\sqrt{a}}\left[\int_0^\infty \alpha \exp\left(-\frac{1}{2a}\alpha^2\right)[1 - 2\varphi_\beta(\alpha)]\, d\alpha\right], \\ \text{and} \quad \varphi_\beta(\alpha) &= \mathbf{\Phi}\left(\sqrt{a}\left(\mathcal{T}(\beta) - \frac{c}{a}\right)\alpha\right), \end{aligned}$$

$\mathbf{\Phi}$ *being the cumulative function of the standard normal distribution.*

Proof. We will write the detailed calculation for $\bar{m}_2(u_\beta)$ and it will be similar for $\bar{m}_1(u_\beta)$.

$$\begin{aligned} \bar{m}_2(u_\beta) &= \int_{\left\{\left(u_\beta|\alpha\right)\leq 0\right\}} \alpha_2 \nu(d\alpha) \\ &= \int_{\{\alpha_1\cos\beta + \alpha_2\sin\beta \leq 0\}} \alpha_2 \nu(d\alpha). \end{aligned}$$

For $\beta \in \left[\pi, \frac{3\pi}{2}\right]$ i.e. $\mathcal{T}(\beta) \leq 0$, we have that

$$
\begin{aligned}
\bar{m}_2(u_\beta) &= \frac{\Theta}{4\pi}\int_{\mathbb{R}} \exp\left(-\frac{1}{2a}\alpha_1^2\right)\int_{\mathcal{T}(\beta)\alpha_1}^{\infty} \alpha_2 \exp\left(-\frac{1}{2}a\left(\alpha_2 - \frac{c\alpha_1}{a}\right)^2\right) d\alpha_2 d\alpha_1 \\
&= \frac{\Theta}{4\pi}\int_{\mathbb{R}} \exp\left(-\frac{1}{2a}\alpha_1^2\right)\int_{\mathcal{T}(\beta)\alpha_1}^{\infty} \left(\alpha_2 - \frac{c\alpha_1}{a}\right) \exp\left(-\frac{1}{2}a\left(\alpha_2 - \frac{c\alpha_1}{a}\right)^2\right) d\alpha_2 d\alpha_1 \\
&+ \frac{\Theta}{4\pi}\int_{\mathbb{R}} \frac{c\alpha_1}{a} \exp\left(-\frac{1}{2a}\alpha_1^2\right)\int_{\mathcal{T}(\beta)\alpha_1}^{\infty} \exp\left(-\frac{1}{2}a\left(\alpha_2 - \frac{c\alpha_1}{a}\right)^2\right) d\alpha_2 d\alpha_1 \\
&= \frac{\Theta}{4\pi}\int_{\mathbb{R}} \exp\left(-\frac{1}{2a}\alpha_1^2\right)\left[-\frac{1}{a}\exp\left(-\frac{1}{2}a\left(\alpha_2 - \frac{c\alpha_1}{a}\right)^2\right)\right]_{\mathcal{T}(\beta)\alpha_1}^{\infty} d\alpha_1 \\
&+ \frac{\Theta}{4\pi}\sqrt{\frac{2\pi}{a}}\int_{\mathbb{R}} \frac{c\alpha_1}{a} \exp\left(-\frac{1}{2a}\alpha_1^2\right)\left(1 - \Phi\left(\sqrt{a}\left(\mathcal{T}(\beta) - \frac{c}{a}\right)\alpha_1\right)\right) d\alpha_1 \\
&= \frac{\Theta}{2a\sqrt{2\pi}}\left[I_\beta + c\tilde{I}_\beta\right].
\end{aligned}
$$

where

$$
\begin{aligned}
I_\beta &= \frac{1}{\sqrt{2\pi}}\int_{\mathbb{R}} \exp\left(-\frac{1}{2a}\alpha_1^2\right)\exp\left(-\frac{1}{2}a\left(\mathcal{T}(\beta) - \frac{c}{a}\right)^2\alpha_1^2\right) d\alpha_1 \\
&= \sqrt{\frac{1}{a(\mathcal{T}(\beta))^2 - 2c\mathcal{T}(\beta) + b}},
\end{aligned}
$$

since $ab - c^2 = 1$ and

$$
\begin{aligned}
\tilde{I}_\beta &= \frac{1}{\sqrt{a}}\int_{\mathbb{R}} \alpha \exp\left(-\frac{1}{2a}\alpha^2\right)\left(1 - \Phi\left(\sqrt{a}\left(\mathcal{T}(\beta) - \frac{c}{a}\right)\alpha\right)\right) d\alpha \\
&= \frac{1}{\sqrt{a}}\int_0^{\infty} \alpha \exp\left(-\frac{1}{2a}\alpha^2\right)\left(1 - 2\Phi\left(\sqrt{a}\left(\mathcal{T}(\beta) - \frac{c}{a}\right)\alpha\right)\right) d\alpha.
\end{aligned}
$$

In the case $\beta \in \left[\frac{\pi}{2}, \pi\right]$ i.e. $\mathcal{T}(\beta) \geq 0$, similar calculations give

$$
\bar{m}_2(u_\beta) = \int_{\mathbb{R}}\int_{\{\alpha_2 \leq \mathcal{T}(\beta)\alpha_1\}} \alpha_2 \nu(d\alpha) = -\frac{\Theta}{2a\sqrt{2\pi}}\left[I_\beta + c\tilde{I}_\beta\right].
$$

□

Proposition 2.4.2. *Define for any unit vector $u \in \mathbb{R}^2$,*

$$
\bar{V}(u) = \int_{\{(u|\alpha) \leq 0\}} \alpha \otimes \alpha \nu(d\alpha). \tag{2.4.2}
$$

We have that $\bar{V} = \bar{V}(u)$ is independent of u and

$$\bar{V} = \frac{\Theta}{4} M.$$

Proof. For all $\alpha \in \mathbb{R}^2$, let $\tilde{\alpha} = -\alpha$.

$$\begin{aligned}\bar{V}(u) &= \int_{\{(u|\alpha)\leq 0\}} \alpha \otimes \alpha \nu(d\alpha) = \int_{\{(u|\tilde{\alpha})\geq 0\}} \tilde{\alpha} \otimes \tilde{\alpha} \nu(d\tilde{\alpha}) \\ &= \frac{1}{2} \int_{\mathbb{R}^2} \alpha \otimes \alpha \nu(d\alpha) = \frac{\Theta}{4} \int_{\mathbb{R}^2} \alpha \otimes \alpha \; p(\alpha) d\alpha = \frac{\Theta}{4} M.\end{aligned}$$

□

Definition 2.4.1. *We define $\theta_1 \in \left[\frac{\pi}{2}, \pi\left[\bigcup\right]\pi, \frac{3\pi}{2}\right]$ as the angle that satisfies*

$$\mathcal{T}(\theta_1) = \mathcal{T}(\theta_1 + \pi) = \frac{c}{a}.$$

It follows that

$$\theta_1 = \begin{cases} \arctan\left(\frac{c}{a}\right) + \frac{\pi}{2} \text{ if } c > 0, \\ \arctan\left(\frac{c}{a}\right) + \frac{3\pi}{2} \text{ if } c < 0. \end{cases}$$

Proposition 2.4.3. *There exists a unique θ_2 such that $\bar{m}_2(u_{\theta_2}) = 0$. Furthermore, we have the following :*
- *If $c \geq 0$, then $\theta_2 \in [\theta_1, \pi] \subset \left[\frac{\pi}{2}, \pi\right]$;*
- *If $c \leq 0$, then $\theta_2 \in [\pi, \theta_1] \subset \left[\pi, \frac{3\pi}{2}\right]$.*

Remark 2.4.1. In the case $c = 0$, we can clearly see that $\theta_2 = \pi$. In other words, if the matrix M is diagonal then $\bar{m}(u_\pi)$ is horizontal.

Proof. For all $x \in \mathbb{R}$, define

$$\begin{aligned} h(x) &= x - \frac{c}{a}, \\ f(x) &= \begin{cases} -\sqrt{\frac{1}{b-2cx+ax^2}} & \text{if } x \geq 0 \\ \sqrt{\frac{1}{b-2cx+ax^2}} & \text{if } x \leq 0 \end{cases}, \\ j(x) &= \begin{cases} -\frac{c}{\sqrt{a}} \int_0^\infty \alpha \exp\left(-\frac{1}{2a}\alpha^2\right) \left[1 - 2\Phi(\sqrt{a}h(x)\alpha)\right] d\alpha & \text{if } x \geq 0 \\ \frac{c}{\sqrt{a}} \int_0^\infty \alpha \exp\left(-\frac{1}{2a}\alpha^2\right) \left[1 - 2\Phi(\sqrt{a}h(x)\alpha)\right] d\alpha & \text{if } x \leq 0 \end{cases}. \end{aligned}$$

First, we will present a Lemma that will be useful for the rest of the proof.

Lemma 2.4.1. *For all $x \neq 0$, j is differentiable and j' has the same sign as*

$$\begin{cases} c \text{ if } x > 0 \\ -c \text{ if } x < 0 \end{cases}.$$

Proof. Define the function $u : \mathbb{R} \times \mathbb{R}_+ \longrightarrow \mathbb{R}$ such that for all $(x, \alpha) \in \mathbb{R} \times \mathbb{R}_+$, $u(x, \alpha) = \alpha \exp\left(-\frac{1}{2a}\alpha^2\right) \mathbf{\Phi}\left(\sqrt{a}h(x)\alpha\right)$.

1. $u(x, \alpha)$ is a Lebesgue integrable function of α for all $x \in \mathbb{R}$.
2. For fixed α,

$$\frac{\partial u(x, \alpha)}{\partial x} = \alpha \exp\left(-\frac{1}{2a}\alpha^2\right) \frac{\partial \mathbf{\Phi}\left(\sqrt{a}h(x)\alpha\right)}{\partial x}.$$

   For fixed α, $x \mapsto \mathbf{\Phi}(x)$ are continuously differentiable functions with respect to x. Thus,

$$\frac{\partial \mathbf{\Phi}(\sqrt{a}h(x)\alpha)}{\partial x} = \frac{1}{\sqrt{2\pi}}\sqrt{a}\alpha \exp\left(-\frac{1}{2}a\left(h(x)\alpha\right)^2\right).$$

   Hence, $\frac{\partial u(x,\alpha)}{\partial x}$ exists for all $x \in \mathbb{R}$.
3. $$\left|\frac{\partial u(x, \alpha)}{\partial x}\right| \leq \sqrt{\frac{a}{2\pi}}\alpha^2 \exp\left(-\frac{1}{2a}\alpha^2\right) \in L^1, \text{ for all } x \in \mathbb{R}.$$

Consequently,

$$\frac{\partial j(x)}{\partial x} = \begin{cases} 2\frac{c}{\sqrt{2\pi}} \int_0^\infty \alpha^2 \exp\left(-\frac{1}{2}\left[ah^2(x) + \frac{1}{a}\right]\alpha^2\right) d\alpha & \text{if } x > 0 \\ -2\frac{c}{\sqrt{2\pi}} \int_0^\infty \alpha^2 \exp\left(-\frac{1}{2}\left[ah^2(x) + \frac{1}{a}\right]\alpha^2\right) d\alpha & \text{if } x < 0 \end{cases}.$$

□

Back to the proof of Proposition 2.4.3. We have that

$$\bar{m}_2(u_\beta) = \frac{\Theta}{2a\sqrt{2\pi}}(f + j)(\mathcal{T}(\beta)).$$

Take the case $c > 0$. The equation $h(\mathcal{T}(\beta)) = 0$ has a unique solution $\beta = \theta_1 \in \left[\frac{\pi}{2}, \frac{3\pi}{2}\right]$. Furthermore, $\bar{m}_2'(u_\beta)$ has the same sign as $(f' + j')(\mathcal{T}(\beta))$ since

$$\mathcal{T}'(\beta) > 0 \text{ on } \left[\frac{\pi}{2}, \pi\right[\bigcup \left]\pi, \frac{3\pi}{2}\right].$$

We can clearly see that $f'(\mathcal{T}(\beta))$ has the same sign of the following function

$$\begin{cases} h(\mathcal{T}(\beta)) & \text{if } \beta \in \left[\frac{\pi}{2}, \pi\right[\\ -h(\mathcal{T}(\beta)) & \text{if } \beta \in \left]\pi, \frac{3\pi}{2}\right] \end{cases}.$$

This combined with the result in Lemma 2.4.1 leads to the table of variations in Table 2.1. Since $\bar{m}_2$ is a continuous function on $\left[\frac{\pi}{2}, \frac{3\pi}{2}\right]$, strictly increasing on $[\theta_1, \pi]$ then based on Table 2.1, we deduce that there exists a unique $\theta_2 \in [\theta_1, \pi]$ such that $\bar{m}_2(\theta_2) = 0$. The proof is similar in the case $c \leq 0$ except that θ_2 exists and is unique on $[\pi, \theta_1]$. $\square$

β	$\frac{\pi}{2}$		θ_1		π		$\frac{3\pi}{2}$
$h(\mathcal{T}(\beta))$		$-$	0	$+$	$\|$	$-$	
$f'(\mathcal{T}(\beta))$		$-$	$\|$	$+$	$\|$	$+$	
$f(\mathcal{T}(\beta))$	$-\frac{1}{\sqrt{b}}$	$\searrow$	$-\sqrt{a}$	$\nearrow$	0	$\nearrow$	$\frac{1}{\sqrt{b}}$
$j'(\mathcal{T}(\beta))$		$+$	$\|$	$+$	$\|$	$-$	
$j(\mathcal{T}(\beta))$	(< 0)	$\nearrow$	0	$\nearrow$	$c\sqrt{a} > 0$	$\searrow$	(> 0)
$\bar{m}_1'(u_\beta)$		$+$	$\|$	$+$	$\|$	$-$	
$\bar{m}_1(u_\beta)$	(< 0)	$\nearrow$	0	$\nearrow$	$\frac{\Theta}{2}\sqrt{\frac{a}{2\pi}}$	$\searrow$	(> 0)
$\bar{m}_2'(u_\beta)$		$?$	$\|$	$+$	$\|$	$?$	
$\bar{m}_2(u_\beta)$		$-$	$-\frac{\Theta}{2\sqrt{2\pi a}} < 0$	$\nearrow$	$\frac{\Theta c}{2\sqrt{2\pi a}} > 0$	$+$	

β	0		θ_1		π		$\theta_1 + \pi$		2π
$\bar{m}_1(u_\beta)$		$\nearrow$	0	$\nearrow$		$\searrow$	0	$\searrow$	
$\bar{m}_2(u_\beta)$		$-$	$\|$	$\nearrow$	$\|$	$+$	$\|$	$\searrow$	

Table 2.1. – Tables of the variations of $\bar{m}_1(u_\cdot)$ and $\bar{m}_2(u_\cdot)$ first in the interval $\left[\frac{\pi}{2}, \frac{3\pi}{2}\right]$ then completed by symmetry on $[0, 2\pi]$ in the case $c \geq 0$. (see Proposition 2.2.2).

From now on, we will only consider the case $c > 0$. The other case $c < 0$ can be treated similarly.

2. 4. 1. The case $v_1 > \bar{m}_1(u_{\theta_2})$

2. 4. 1.1. Case 1 : The particular case $v_1 > \bar{m}_1(u_\pi)$

Lemma 2.4.2. *For all unit vector $u \in \mathbb{R}^2$ and $r > 0$, we have that $m_1(ru) \leq \bar{m}_1(u_\pi)$.*

Proof. For all unit vector $u \in \mathbb{R}^2$ and $r > 0$,

$$m_1(ru) = \int_{\mathbb{R}^2} \alpha_1 g(ru, \alpha)\nu(d\alpha) \leq \bar{m}_1^+(u),$$

where

$$\bar{m}_1^+(u) = \int_{\{(\alpha,u)\leq 0\}} \alpha_1 \mathbf{1}_{\{\alpha_1>0\}}\nu(d\alpha).$$

There exists $\beta \in [0, 2\pi]$ such that $u = \begin{pmatrix}\cos\beta \\ \sin\beta\end{pmatrix}$. For $\beta \in \left[\pi, \frac{3\pi}{2}\right] \cup \left[0, \frac{\pi}{2}\right]$,

$$\begin{aligned}\bar{m}_1^+(u) &= \frac{\Theta}{4\pi}\int_0^\infty \alpha_1 \exp\left(-\frac{1}{2a}\alpha_1^2\right)\int_{\mathcal{T}(\beta)\alpha_1}^\infty \exp\left(-\frac{1}{2}a\left(\alpha_2 - \frac{c\alpha_1}{a}\right)^2\right)d\alpha_2 d\alpha_1 \\ &= \frac{\Theta}{2\sqrt{2\pi a}}\int_0^\infty \alpha \exp\left(-\frac{1}{2a}\alpha^2\right)\left(1 - \Phi\left(\sqrt{a}\left(\mathcal{T}(\beta) - \frac{c}{a}\right)\alpha\right)\right)d\alpha,\end{aligned}$$

and for $\beta \in \left[\frac{\pi}{2}, \pi\right] \cup \left[\frac{3\pi}{2}, 2\pi\right]$,

$$\begin{aligned}\bar{m}_1^+(u) &= \frac{\Theta}{4\pi}\int_0^\infty \alpha_1 \exp\left(-\frac{1}{2a}\alpha_1^2\right)\int_{-\infty}^{\mathcal{T}(\beta)\alpha_1} \exp\left(-\frac{1}{2}a\left(\alpha_2 - \frac{c\alpha_1}{a}\right)^2\right)d\alpha_2 d\alpha_1 \\ &= \frac{\Theta}{2\sqrt{2\pi a}}\int_0^\infty \alpha \exp\left(-\frac{1}{2a}\alpha^2\right)\Phi\left(\sqrt{a}\left(\mathcal{T}(\beta) - \frac{c}{a}\right)\alpha\right)d\alpha.\end{aligned}$$

Study of the variations of $\bar{m}_1^+(u)$: Following the same steps of the proof of Proposition 2.4.1, we have that $\left(\bar{m}_1^+(u)\right)'$ exists and has the same sign as

$$\begin{cases} \sqrt{\frac{a}{2\pi}}\int_0^\infty \alpha^2 \exp\left(-\frac{1}{2a}\left(a^2\left(\mathcal{T}(\beta) - \frac{c}{a}\right)^2 + 1\right)\alpha^2\right)d\alpha & \text{if } \beta \in \left[\frac{\pi}{2}, \pi\right] \cup \left[\frac{3\pi}{2}, 2\pi\right] \\ -\sqrt{\frac{a}{2\pi}}\int_0^\infty \alpha^2 \exp\left(-\frac{1}{2a}\left(a^2\left(\mathcal{T}(\beta) - \frac{c}{a}\right)^2 + 1\right)\alpha^2\right)d\alpha & \text{if } \beta \in \left[\pi, \frac{3\pi}{2}\right] \cup \left[0, \frac{\pi}{2}\right] \end{cases}$$

Since $\bar{m}_1^+(u)$ is a continuous function for all unit vector $u \in \mathbb{R}^2$, we can clearly see that this function presents a maximum at π. Hence, for all unit vector $u \in \mathbb{R}^2$ and $r > 0$,

$$m_1(ru) \leq \bar{m}_1^+(u) \leq \bar{m}_1^+(u_\pi) = \frac{\Theta}{2\sqrt{2\pi a}}\int_0^\infty \alpha e^{-\frac{1}{2a}\alpha^2}d\alpha = \frac{\Theta}{2}\sqrt{\frac{a}{2\pi}} = \bar{m}_1(u_\pi).$$

□

Let $A^- = \{x \in \mathbb{R}^2$ such that $x_1 < 0\}$ and define the stopping time

$$T_0 = \inf\{t > 0, X_t \in A^-\}.$$

Proposition 2.4.4. *In the case $v_1 > \bar{m}_1(u_\pi)$, if $X_0 \notin A^-$ then T_0 is finite a.s. .*

Proof. Using Lemma 2.4.2, we have that

$$0 < X^1_{t\wedge T_0^-} < X^1_0 + (\bar{m}_1(u_\pi) - v_1) \times \left(t \wedge T_0^-\right) + \mathcal{N}^1_{t\wedge T_0^-}.$$

Thus letting t tend to ∞, we have

$$\mathbb{E}T_0 < \frac{X^1_0}{\bar{m}_1(u_\pi) - v_1} < \infty.$$

□

It follows from Proposition 2.4.4 that while $v_1 > \bar{m}_1(u_\pi)$ we can restrict our study on the half space A^- where the process X_t spends most of its time.

Lemma 2.4.3. *There exists $\theta_v \in \,]\theta_2, \pi]$ such that*

$$x_\theta = \bar{\psi}(x_{\theta_v}) = \left|\bar{\psi}(u_{\theta_v})\right| u_{\theta_v}$$

is the unique fixed point of $\bar{\psi}$ on A^-.

Proof. Define the vector orthogonal to u_β

$$u^\perp_\beta = \left(\begin{array}{c} -\sin\beta \\ \cos\beta \end{array} \right),$$

as well as the functions

$$G_\perp(\beta) = \left(\bar{\psi}(u_\beta) \mid u^\perp_\beta\right), \tag{2.4.3}$$

$$\text{and } G(\beta) = \left(\bar{\psi}(u_\beta) \mid u_\beta\right). \tag{2.4.4}$$

First, we write $G_\perp$ as a function of β :

$$G_\perp(\beta) = -(\bar{m}_1(u_\beta) - v_1)\sin\beta + \bar{m}_2(u_\beta)\cos\beta.$$

Proving that there exists a unique $\theta_v \in]\theta_2, \pi]$ that satisfies

$$\bar{\psi}(x_{\theta_v}) = x_{\theta_v},$$

is equivalent to proving that the equation $G_\perp(\beta) = 0$ has a unique solution $\theta_v \in]\theta_2, \pi]$ since $\bar{\psi}(x_{\theta_v}) = \bar{\psi}(u_{\theta_v})$ due to (2.3.1). $G_\perp$ is a continuous function such that

$$G_\perp(\theta_2) = -(\bar{m}_1(u_{\theta_2}) - v_1)\sin\theta_2 > 0$$
$$G_\perp(\pi) = -\bar{m}_2(u_\pi) < 0.$$

It follows from the Intermediate Value Theorem that $G_\perp$ has a root θ_v in the interval $]\theta_2, \pi]$. Moreover since for all $\beta \in]\theta_2, \pi]$

$$G'_\perp(\beta) = -\bar{m}'_1(u_\beta)\sin\beta - (\bar{m}_1(u_\beta) - v_1)\cos\beta + \bar{m}'_2(u_\beta)\cos\beta - \bar{m}_2(u_\beta)\sin\beta < 0, \quad (2.4.5)$$

using Tables 2.1 and 2.2. Hence $G_\perp$ is monotone on $]\theta_2, \pi]$. In addition, $G_\perp(\beta) > 0$ for all $\beta \in \left[\frac{\pi}{2}, \theta_2\right]$ and $G(\beta) < 0$ for all $\beta \in \left]\pi, \frac{3\pi}{2}\right]$. Consequently, θ_v is unique on A^-. $\square$

β	$\frac{\pi}{2}$ … θ_2	θ_2 … θ_v	θ_v … π	π … $\frac{3\pi}{2}$
$\bar{m}_1(u_\beta) - v$	$-$	$-$	$-$	$-$
$-\sin\beta$	$-$	$-$	$-$ 0	$+$
$\bar{m}_2(u_\beta)$	$-$ 0	$+$	$+$	$+$
$\cos\beta$	$-$	$-$	$-$	$-$
$G_\perp(\beta)$	$+$	$+$ 0	$-$	$-$

β	$\frac{\pi}{2}$ … ξ_1	ξ_1 … θ_2	θ_2 … π	π … ξ_2	ξ_2 … $\frac{3\pi}{2}$
$\bar{m}_1(u_\beta) - v_1$	$-$	$-$	$-$	$-$	$-$
$\cos\beta$	$-$	$-$	$-$	$-$	$-$
$\bar{m}_2(u_\beta)$	$-$	$-$ 0	$+$	$+$	$+$
$\sin\beta$	$+$	$+$	$+$ 0	$-$	$-$
$G(\beta)$	? 0	$+$	$+$	$+$ 0	?

Table 2.2. – Tables of sign of $G_\perp(\beta)$ and $G(\beta)$ for $\beta \in \left[\frac{\pi}{2}, \frac{3\pi}{2}\right]$ in the case $v_1 \geq \bar{m}_1(u_\pi)$.

Note that θ_v defined by Lemma 2.4.3 is in the interval $]\theta_2, \pi]$ which means in this case $\cos\theta_v < 0$ and $\sin\theta_v \geq 0$. In the case $c < 0$, $\theta_2 \in \left[\pi, \frac{3\pi}{2}\right]$ and $\theta_v \in [\pi, \theta_2]$. In the case $c = 0$, $\theta_2 = \theta_v = \pi$.

In order to gain some insight into the behavior of the stochastic process, we first study the corresponding deterministic process :

Proposition 2.4.5. *In the case $v_1 > \bar{m}_1(u_\pi)$, the ODE (2.3.2) is such that*

$$\frac{Y_t}{t} \xrightarrow[t\to\infty]{} \bar{\psi}(u_{\theta_v}) \ a.s.$$

Furthermore if

$$1 + \frac{G'_\perp(\theta_v)}{G(\theta_v)} < 0, \ \text{then } \left(Y_t \mid u^\perp_{\theta_v}\right) \xrightarrow[t\to\infty]{} 0.$$

But if

$$1 + \frac{G'_\perp(\theta_v)}{G(\theta_v)} > 0, \ \text{then } \left(Y_t \mid u^\perp_{\theta_v}\right) \xrightarrow[t\to\infty]{} \infty.$$

Proof. We write Y_t using its polar coordinates (r_t, η_t). Note that $\bar{\psi}(Y_t)$ depends only upon u_{η_t}.

$$\frac{dY_t}{dt} = \begin{pmatrix} \frac{dr_t}{dt}\cos\eta_t - r_t \sin\eta_t \frac{d\eta_t}{dt} \\ \frac{dr_t}{dt}\sin\eta_t + r_t\cos\eta_t \frac{d\eta_t}{dt} \end{pmatrix} = \bar{\psi}(u_{\eta_t}).$$

It follows that

$$\frac{dr_t}{dt} = \bar{\psi}_1(u_{\eta_t})\cos\eta_t + \bar{\psi}_2(u_{\eta_t})\sin\eta_t = \left(\bar{\psi}(u_{\eta_t}) \mid u_{\eta_t}\right) = G(\eta_t), \tag{2.4.6}$$

$$\text{and } r_t\frac{d\eta_t}{dt} = -\bar{\psi}_1(u_{\eta_t})\sin\eta_t + \bar{\psi}_2(u_{\eta_t})\cos\eta_t = \left(\bar{\psi}(u_{\eta_t}) \mid u_{\eta_t}^{\perp}\right) = G_{\perp}(\eta_t), \tag{2.4.7}$$

with G and $G_{\perp}$ defined in (2.4.4).

We have that

$$\frac{dY_t^1}{dt} < \bar{\psi}_1(u_\pi) < 0,$$

hence Y_t is transient such that

$$\frac{r_t}{t} > |\bar{\psi}_1(u_\pi)|.$$

We need to prove that η_t converges to θ_v. We assume in the contrary that for all

$$0 < \epsilon < \frac{(\theta_v - \xi_1) \wedge (\xi_2 - \theta_v)}{2}, \tag{2.4.8}$$

where ξ_1, ξ_2 are defined by Table 2.2 such that $G(\xi_1) = G(\xi_2) = 0$, there exists t_ϵ such that for all $t \geq t_\epsilon$, $|\eta_t - \theta_v| > \epsilon$. Without loss of generality, we consider $\eta_0 < \theta_v$. In this case, η is an increasing function. Thus, $\eta_0 < \eta_t < \theta_v$. We deduce from (2.4.6) that for all $t \geq t_\epsilon$,

$$r_t \leq r_{t_\epsilon} + \left(\sup_{\beta\in\left[\frac{\pi}{2},\theta_v-\epsilon\right]} G(\beta)\right)(t - t_\epsilon),$$

thus

$$\begin{aligned}
\eta_t &\geq \eta_{t_\epsilon} + G_{\perp}(\theta_v - \epsilon)\int_{t_\epsilon}^{t}\frac{1}{r_s}ds \\
&\geq \eta_{t_\epsilon} + \frac{G_{\perp}(\theta_v-\epsilon)}{\left(\sup_{\beta\in\left[\frac{\pi}{2},\theta_v-\epsilon\right]} G(\beta)\right)}\log\left(\frac{r_{t_\epsilon} + \left(\sup_{\beta\in\left[\frac{\pi}{2},\theta_v-\epsilon\right]} G(\beta)\right)(t-t_\epsilon)}{r_{t_\epsilon}}\right) \\
&\xrightarrow[t\to\infty]{} \infty,
\end{aligned}$$

contradicting the initial hypothesis. Hence $\eta_t \xrightarrow[t\to\infty]{} \theta_v$ yielding $\frac{r_t}{t} \xrightarrow[t\to\infty]{} G(\theta_v)$.

Until now we proved that in the case $v_1 > \bar{m}_1(u_\pi)$, the deterministic process Y_t is such that

$$\frac{Y_t}{t} \xrightarrow[t\to\infty]{} \bar{\psi}(u_{\theta_v}).$$

Another interesting question is about the behavior of $\left(Y_t \mid u_{\theta_v}^{\perp}\right)$ as t goes to ∞. We will see that this distance goes to 0 under a certain condition. Let $\hat{\eta}_t = \eta_t - \theta_v$. We already know that

$$\hat{\eta}_t \xrightarrow[t\to\infty]{} 0.$$

It follows that, for all $\epsilon > 0$ as defined in (2.4.8), there exists $t_\epsilon > 0$ such that for all $t \geq t_\epsilon$, $|\hat{\eta}_t| < \epsilon$. Again without loss of generality we assume that $\hat{\eta}_0 < 0$. First we give the following notations useful for the rest of the proof :

$$\begin{aligned}
\overline{G'_\perp}^{\epsilon} &= \sup_{\beta\in[\theta_v-\epsilon,\theta_v]} G'_\perp(\beta) < 0, \quad \underline{G'_\perp}^{\epsilon} = \inf_{\beta\in[\theta_v-\epsilon,\theta_v]} G'_\perp(\beta) < 0, \;\; (\text{See } (2.4.5))\\
\overline{G}_\epsilon &= \sup_{\beta\in[\theta_v-\epsilon,\theta_v]} G(\beta) > 0, \quad \underline{G}_\epsilon = \inf_{\beta\in[\theta_v-\epsilon,\theta_v]} G(\beta) > 0 \; (\text{See Table } 2.2).
\end{aligned}$$

The ODE satisfied by $\hat{\eta}_t$:

$$r_t \frac{d\hat{\eta}_t}{dt} = G_\perp(\eta_t) - G_\perp(\theta_v) = \hat{\eta}_t G'_\perp(\hat{\hat{\eta}}_t),$$

where $\theta_v - \epsilon < \hat{\hat{\eta}}_t < \theta_v$. It follows that for $t \geq t_\epsilon$,

$$r_{t_\epsilon} \underline{G}_\epsilon (t - t_\epsilon) \leq r_t \leq r_{t_\epsilon} \overline{G}_\epsilon (t - t_\epsilon),$$

and since $\hat{\eta}_t < 0$

$$\overline{G'_\perp}^{\epsilon} \frac{\hat{\eta}_t}{r_t} \leq \frac{d\hat{\eta}_t}{dt} \leq \underline{G'_\perp}^{\epsilon} \frac{\hat{\eta}_t}{r_t}.$$

Hence

$$\begin{aligned}
\hat{\eta}_{t_\epsilon} \exp\left(\frac{\overline{G'_\perp}^{\epsilon}}{\overline{G}_\epsilon} \log\left(\frac{r_{t_\epsilon} + \overline{G}_\epsilon (t - t_\epsilon)}{r_{t_\epsilon}} \right)\right) &\leq \hat{\eta}_t \leq \hat{\eta}_{t_\epsilon} \exp\left(\frac{\underline{G'_\perp}^{\epsilon}}{\underline{G}_\epsilon} \log\left(\frac{r_{t_\epsilon} + \underline{G}_\epsilon (t - t_\epsilon)}{r_{t_\epsilon}} \right)\right)\\
\hat{\eta}_{t_\epsilon} \left(\frac{r_{t_\epsilon} + \overline{G}_\epsilon (t - t_\epsilon)}{r_{t_\epsilon}} \right)^{\frac{\overline{G'_\perp}^{\epsilon}}{\overline{G}_\epsilon}} &\leq \hat{\eta}_t \leq \hat{\eta}_{t_\epsilon} \left(\frac{r_{t_\epsilon} + \underline{G}_\epsilon (t - t_\epsilon)}{r_{t_\epsilon}} \right)^{\frac{\underline{G'_\perp}^{\epsilon}}{\underline{G}_\epsilon}}.
\end{aligned}$$

On the other hand, we have that

$$\left(Y_t \mid u_{\theta_v}^{\perp}\right) = r_t \sin \hat{\eta}_t.$$

For all $t \geq t_\epsilon$, $\hat{\eta}_t < 0$ and we have

$$\hat{\eta}_t < \sin \hat{\eta}_t < \hat{\eta}_t - \frac{\hat{\eta}_t^3}{6} < \hat{\eta}_t \left(1 - \frac{\epsilon^2}{6}\right).$$

Hence,

$$\begin{aligned}
\hat{\eta}_{t_\epsilon} r_{t_\epsilon} \underline{G}_\epsilon \left(\frac{\frac{r_{t_\epsilon}}{t-t_\epsilon} + \overline{G}_\epsilon}{r_{t_\epsilon}} \right)^{\frac{\overline{G'_\perp}^\epsilon}{\overline{G}_\epsilon}} (t-t_\epsilon)^{1+\frac{\overline{G'_\perp}^\epsilon}{\overline{G}_\epsilon}} &\leq \left(Y_t \mid u_\theta^\perp\right) \\
&\leq \left(1 - \frac{\epsilon^2}{6}\right) \hat{\eta}_{t_\epsilon} r_{t_\epsilon} \overline{G}_\epsilon \left(\frac{\frac{r_{t_\epsilon}}{t-t_\epsilon} + \underline{G}_\epsilon}{r_{t_\epsilon}} \right)^{\frac{\underline{G'_\perp}^\epsilon}{\underline{G}_\epsilon}} (t-t_\epsilon)^{1+\frac{\underline{G'_\perp}^\epsilon}{\underline{G}_\epsilon}}.
\end{aligned}$$

If

$$1 + \frac{G'_\perp(\theta_v)}{G(\theta_v)} < 0, \text{ then } 1 + \frac{\underline{G'_\perp}^\epsilon}{\underline{G}_\epsilon} < 1 + \frac{G'_\perp(\theta_v)}{G(\theta_v)} < 0,$$

hence $\left(Y_t \mid u_\theta^\perp\right) \xrightarrow[t\to\infty]{} 0$. On the other hand, if

$$1 + \frac{G'_\perp(\theta_v)}{G(\theta_v)} > 0, \text{ then } 1 + \frac{\overline{G'_\perp}^\epsilon}{\overline{G}_\epsilon} > 1 + \frac{G'_\perp(\theta_v)}{G(\theta_v)} > 0,$$

hence $\left(Y_t \mid u_{\theta_v}^\perp\right) \xrightarrow[t\to\infty]{} \infty$. □

Theorem 2.4.1. *In the case $v_1 > \bar{m}_1(u_\pi)$, X_t, satisfying (2.2.1), is transient and we have that*

$$\frac{X_t}{t} \xrightarrow[t\to\infty]{} \bar{\psi}(u_{\theta_v}) \ a.s.$$

Proof. Let

$$\mathbf{u}_t = u_{\beta_t} = \begin{pmatrix} \cos \beta_t \\ \sin \beta_t \end{pmatrix} \text{ and } X_t = \rho_t \mathbf{u}_t.$$

Step 1 : *Transience of the process X_t :*

It follows from Lemma 2.4.2 that

$$\begin{aligned}
\frac{X_t^1}{t} &= \frac{X_0^1}{t} + \frac{1}{t}\int_0^t (m_1(X_s) - v_1)ds + \frac{\mathcal{N}_t^1}{t} \\
&\leq \frac{X_0^1}{t} + \frac{1}{t}\int_0^t (\bar{m}_1(u_\pi) - v_1)ds + \frac{\mathcal{N}_t^1}{t}.
\end{aligned}$$

Hence,

$$\limsup_{t\to\infty} \frac{X_t^1}{t} \leq \bar{m}_1(u_\pi) - v_1 < 0.$$

This means that X_t^1 goes to $-\infty$ when $t \to \infty$. Hence, X_t is transient and

$$\liminf_{t\to\infty} \frac{\rho_t}{t} \geq \liminf_{t\to\infty} \frac{|X_t^1|}{t} \geq |\bar{\psi}_1(u_\pi)|. \tag{2.4.9}$$

Hence there exists t_w such that for all $t \geq t_w$, we have that

$$\frac{\rho_t}{t} > \frac{|\bar{\psi}_1(u_\pi)|}{2}. \tag{2.4.10}$$

Step 2 : *Stochastic Differential Equations describing the evolution of ρ and β :*

Using the SDE describing the evolution of X_t :

$$X_t = X_0 + \int_0^t \psi(X_s)ds + \int_{[0,t]\times\mathbb{R}^2\times[0,1]} \alpha\Gamma(X_{s^-}, \alpha, \xi)\bar{M}(ds, \alpha, d\xi),$$

we apply the Itô formula for discontinuous processes to the following functions :

$$\begin{cases} \mathbb{R}^2 & \to \mathbb{R}^2 \\ x & \mapsto R(x) = \sqrt{x_1^2 + x_2^2}, \\ x & \mapsto \varphi(x) = \arctan(x_2/x_1). \end{cases}$$

Note that $\nabla R(x) = |x|^{-1}x = u$, with $u = x/|x|$. We denote by $u^\perp = (-u_2, u_1)$ the orthogonal vector to u and $\rho = |x|$. Hence, $\nabla\varphi(x) = u^\perp/|x| = u^\perp/\rho$.

For an arbitrary C^1 function f (see Pardoux (2016a), Therorem 6.2.1), we have that

$$
\begin{aligned}
f(X_t) &= f(X_0) + \int_0^t (\nabla f(X_s)|\psi(X_s))ds \\
&+ \int_{[0,t]\times\mathbb{R}^2\times[0,1]} (\nabla f(X_{s^-})|\alpha)\Gamma(X_{s^-},\alpha,\xi)\bar{M}(ds,d\alpha,d\xi) \\
&+ \int_{[0,t]\times\mathbb{R}^2\times[0,1]} \left[f(X_{s^-}+\alpha) - f(X_{s^-}) - (\nabla f(X_{s^-})|\alpha)\right]\Gamma(X_{s^-},\alpha,\xi)M(ds,d\alpha,d\xi) \\
&= f(X_0) + \int_0^t (\nabla f(X_s)|\psi(X_s))ds \\
&+ \int_{[0,t]\times\mathbb{R}^2\times[0,1]} (\nabla f(X_{s^-})|\alpha)\Gamma(X_{s^-},\alpha,\xi)\bar{M}(ds,d\alpha,d\xi) \\
&+ \int_{[0,t]\times\mathbb{R}^2\times[0,1]} \left[f(X_{s^-}+\alpha) - f(X_{s^-}) - (\nabla f(X_{s^-})|\alpha)\right]\Gamma(X_{s^-},\alpha,\xi)\bar{M}(ds,d\alpha,d\xi) \\
&+ \int_{[0,t]\times\mathbb{R}^2} \left[f(X_s+\alpha) - f(X_s) - (\nabla f(X_s)|\alpha)\right]g(X_s,\alpha)\nu(d\alpha)ds \\
&= f(X_0) + \int_0^t (\nabla f(X_s)|\psi(X_s))ds \\
&+ \int_{[0,t]\times\mathbb{R}^2\times[0,1]} \left[f(X_{s^-}+\alpha) - f(X_{s^-})\right]\Gamma(X_{s^-},\alpha,\xi)\bar{M}(ds,d\alpha,d\xi) \\
&+ \int_{[0,t]\times\mathbb{R}^2} \left[f(X_s+\alpha) - f(X_s) - (\nabla f(X_s)|\alpha)\right]g(X_s,\alpha)\nu(d\alpha)ds.
\end{aligned}
$$

Using the last identity, we write

$$
\begin{aligned}
\rho_t = R(X_t) = \rho_0 &+ \int_0^t (\mathbf{u}_s \mid \psi(X_s))ds + \int_{[0,t]\times\mathbb{R}^2} (|X_s+\alpha| - \rho_s - (\mathbf{u}_s|\alpha))g(X_s,\alpha)\nu(d\alpha)ds \\
&+ \int_{[0,t]\times\mathbb{R}^2\times[0,1]} (|X_{s^-}+\alpha| - \rho_{s^-})\Gamma(X_{s^-},\alpha,\xi)\bar{M}(ds,d\alpha,d\xi),
\end{aligned}
\tag{2.4.11}
$$

and

$$
\begin{aligned}
\beta_t = \arctan(X_t) = \beta_0 &+ \int_0^t \rho_s^{-1}(\mathbf{u}_s^\perp|\psi(X_s))ds \\
&+ \int_{[0,t]\times\mathbb{R}^2\times[0,1]} \left[\arctan\left(\frac{X_{s^-}^2+\alpha_2}{X_{s^-}^1+\alpha_1}\right) - \beta_{s^-}\right]\Gamma(X_{s^-},\alpha,\xi)\bar{M}(ds,d\alpha,d\xi) \\
&+ \int_{[0,t]\times\mathbb{R}^2} \left[\arctan\left(\frac{X_s^2+\alpha_2}{X_s^1+\alpha_1}\right) - \beta_s - \rho_s^{-1}(\mathbf{u}_s^\perp|\alpha)\right]\nu(d\alpha)ds.
\end{aligned}
\tag{2.4.12}
$$

Now introduce a few Lemmas that will be useful for the rest of the Proof. The proofs of these Lemmas can be found respectively in Appendices A, B, C and D.

Lemma 2.4.4. *For all unit vector $u \in A^-$, we have that*

$$\sqrt{r} \times \left|\psi(ru) - \bar{\psi}(u)\right| \xrightarrow[r \to \infty]{} 0.$$

In other words, there exists $K > 0$ such that for all $r > K$, we have that

$$\left|\psi(ru) - \bar{\psi}(u)\right| \leq \frac{1}{2\sqrt{r}}.$$

Lemma 2.4.5. *There exists a constant $C_1 > 0$ such that for all $x \in \mathbb{R}^2$, if $u = x/|x|$,*

$$\left|\int_{\mathbb{R}^2} [|x+\alpha| - |x| - (u|\alpha)]\, g(x,\alpha)\nu(d\alpha)\right| \leq \frac{C_1}{|x|}.$$

Lemma 2.4.6. *There exists $C_2 > 0$ such that*

$$\left|\int_{\mathbb{R}^2} \left[\arctan\left(\frac{x_2+\alpha_2}{x_1+\alpha_1}\right) - \arctan\left(\frac{x_2}{x_1}\right) - |x|^{-1}(u^\perp|\alpha)\right] g(x,\alpha)\nu(d\alpha)\right| \leq C_2\,|x|^{-2},$$

where we have used the notation $u = \frac{x}{|x|}$.

Lemma 2.4.7. *There exists $C_3 > 0$ such that*

$$\left|\int_{\mathbb{R}^2} \left[\arctan\left(\frac{x_2+\alpha_2}{x_1+\alpha_1}\right) - \arctan\left(\frac{x_2}{x_1}\right)\right]^2 g(x,\alpha)\nu(d\alpha)\right| \leq C_3\,|x|^{-2}.$$

Back to the Proof of Theorem 2.4.1. We have that for $t > t_w$ defined in (2.4.10),

$$\begin{aligned}\frac{\rho_t}{t} &= \frac{\rho_{t_w}}{t} + \frac{1}{t}\int_{t_w}^t G(\beta_s)ds + \frac{1}{t}\int_{t_w}^t \left(\psi(\rho_s\mathbf{u}_s) - \bar{\psi}(\mathbf{u}_s) \mid \mathbf{u}_s\right) ds \\ &\quad + \frac{1}{t}\int_{t_w}^t \int_{\mathbb{R}^2} (|X_s+\alpha| - \rho_s - (\mathbf{u}_s \mid \alpha))\, g(X_s,\alpha)\nu(d\alpha)ds + \frac{1}{t}\left(M_t^\rho - M_{t_w}^\rho\right),\end{aligned} \tag{2.4.13}$$

where

$$M_t^\rho = \int_{[0,t]\times\mathbb{R}^2\times[0,1]} (|X_{s^-}+\alpha| - \rho_{s^-})\Gamma(X_{s^-},\alpha,\xi)\bar{M}(ds,d\alpha,d\xi). \tag{2.4.14}$$

It follows from Lemma 2.4.4 and (2.4.10) that there exists $t_0 \geq t_w$ such that for all $t \geq t_0$,

$$|\psi(\rho_t\mathbf{u}_t) - \bar{\psi}(\mathbf{u}_t)| \leq \frac{1}{\sqrt{2t|\bar{\psi}_1(u_\pi)|}}. \tag{2.4.15}$$

Hence,

$$\begin{aligned}
&\frac{1}{t}\int_{t_w}^{t}\left|\left(\psi(\rho_s\mathbf{u}_s)-\bar{\psi}(\mathbf{u}_s)\mid \mathbf{u}_s\right)\right|ds\\
&\qquad\le \frac{1}{t}\int_{t_w}^{t_0}\left|\psi(\rho_s\mathbf{u}_s)-\bar{\psi}(\mathbf{u}_s)\right|ds+\frac{1}{t}\int_{t_0}^{t}\left|\psi(\rho_s\mathbf{u}_s)-\bar{\psi}(\mathbf{u}_s)\right|ds\\
&\qquad\le \frac{1}{t}\int_{t_w}^{t_0}\left|\psi(\rho_s\mathbf{u}_s)-\bar{\psi}(\mathbf{u}_s)\right|ds+\sqrt{\frac{2}{|\bar{\psi}_1(u_\pi)|}}\times\frac{\sqrt{t}-\sqrt{t_0}}{t}\xrightarrow[t\to\infty]{}0.
\end{aligned}$$

Furthermore,

$$\lim_{t\to\infty}\frac{1}{t}M_t^{\rho}=0,$$

due to the same argument used in the proof of Proposition 2.2.3. On the other hand, it follows from Lemma 2.4.5 that

$$\begin{aligned}
&\frac{1}{t}\int_{t_w}^{t}\int_{\mathbb{R}^2}\left(|X_s+\alpha|-\rho_s-(\mathbf{u}_s\mid\alpha)\right)g(X_s,\alpha)\nu(d\alpha)ds\\
&\qquad\le\frac{C_1}{t}\int_{t_w}^{t}\frac{ds}{\rho_s}=\frac{C_1}{t}\log\left(\frac{t}{t_w}\right)\xrightarrow[t\to\infty]{}0.
\end{aligned}$$

We deduce that

$$\limsup_{t\to\infty}\frac{\rho_t}{t}\le\sup_{\beta}G(\beta). \tag{2.4.16}$$

<u>**Step 3 :**</u> *About the asymptotic behavior of β_t :*

We introduce the time change

$$A_t=\int_0^t\frac{1}{\rho_s}ds\ \text{ and }\ \tau_t=A^{-1}(t)=\inf\{s>0,A_s>t\}, \tag{2.4.17}$$

yielding

$$\frac{d\tau_t}{dt}=\rho_{\tau_t}. \tag{2.4.18}$$

Let $\tilde{\beta}_t=\beta_{\tau_t}$. We have that for t_0 as defined by (2.4.15) :

$$\begin{aligned}
\tilde{\beta}_t&=\tilde{\beta}_{t_0}+\int_{t_0}^{t}G_\perp(\tilde{\beta}_s)ds+\int_{t_0}^{t}\left(\psi(X_{\tau_s})-\bar{\psi}\left(\mathbf{u}_{\tau_s}\right)\mid\mathbf{u}_{\tau_s}^{\perp}\right)ds\\
&+\int_{t_0}^{t}\rho_{\tau_s}^{-1}\left[\arctan\left(\frac{X_{\tau_s}^2+\alpha_2}{X_{\tau_s}^1+\alpha_1}\right)-\beta_{\tau_s}-\rho_{\tau_s}^{-1}(\mathbf{u}_{\tau_s}^{\perp}|\alpha)\right]\nu(d\alpha)ds\\
&+\mathbf{M}_t^{\beta}-\mathbf{M}_{t_0}^{\beta},
\end{aligned}\tag{2.4.19}$$

where

$$\mathbf{M}_t^{\beta} = \int_{[0,\tau_t]\times\mathbb{R}^2\times[0,1]} \rho_{s^-}^{-1}\left[\arctan\left(\frac{X_{s^-}^2+\alpha_2}{X_{s^-}^1+\alpha_1}\right)-\beta_{s^-}\right]\Gamma(X_{s^-},\alpha,\xi)\bar{N}(ds,d\alpha,d\xi) \tag{2.4.20}$$

We have that

$$\int_{t_0}^{t}\left(\psi(X_{\tau_s})-\bar{\psi}(\mathbf{u}_{\tau_s})\mid \mathbf{u}_{\tau_s}^{\perp}\right)ds \le \frac{1}{\sqrt{2|\bar{\psi}_1(u_\pi)|}}\int_{t_0}^{t}\frac{1}{\sqrt{\tau_s}}ds.$$

But for $t_0 \le s \le t$,

$$\rho_{\tau_s} = \frac{d\tau_s}{ds} \ge \frac{|\bar{\psi}_1(u_\pi)|\tau_s}{2}, \text{ hence } \tau_s \ge e^{\frac{|\bar{\psi}_1(u_\pi)|s}{2}}.$$

It follows that

$$\sup_{t\ge t_0}\int_{t_0}^{t}\left(\psi(X_{\tau_s})-\bar{\psi}(\mathbf{u}_{\tau_s})\mid \mathbf{u}_{\tau_s}^{\perp}\right)ds \le \sup_{t\ge t_0}\frac{1}{\sqrt{2|\bar{\psi}_1(u_\pi)|}}\int_{t_0}^{t}e^{-\frac{|\bar{\psi}_1(u_\pi)|s}{4}}ds \xrightarrow[t_0\to\infty]{} 0.$$

Moreover, using Lemma 2.4.6, we have that

$$\begin{aligned}
&\sup_{t\ge t_0}\int_{t_0}^{t}\rho_{\tau_s}\left[\arctan\left(\frac{X_{\tau_s}^2+\alpha_2}{X_{\tau_s}^1+\alpha_1}\right)-\beta_{\tau_s}-\rho_{\tau_s}^{-1}(\mathbf{u}_{\tau_s}^{\perp}|\alpha)]\right]\nu(d\alpha)ds\\
&\quad\le \sup_{t\ge t_0}\int_{t_0}^{t}\frac{C_2}{\rho_{\tau_s}}ds \le \sup_{t\ge t_0}\frac{1}{2|\bar{\psi}_1(u_\pi)|}\int_{t_0}^{t}e^{-\frac{|\bar{\psi}_1(u_\pi)|s}{2}}ds \xrightarrow[t_0\to\infty]{} 0.
\end{aligned}$$

Furthermore, we deduce from Lemma 2.4.7 that

$$\begin{aligned}
\langle\mathbf{M}^{\beta}\rangle_{t+r}-\langle\mathbf{M}^{\beta}\rangle_t &= \int_{\tau_t}^{\tau_{t+r}}\int_{\mathbb{R}^2}\rho_{\tau_s}^{-1}\left[\arctan\left(\frac{X_{\tau_s}^2+\alpha_2}{X_{\tau_s}^1+\alpha_1}\right)-\beta_{\tau_s}\right]^2 g(X_{\tau_s},\alpha)\nu(d\alpha)ds\\
&\le C_3\int_t^{t+r}\frac{1}{\rho_{\tau_s}^3}ds.
\end{aligned}$$

Now define the stopping time

$$T_\rho^t = \inf\left\{s>t;\rho_{\tau_s}<\frac{|\bar{\psi}_1(u_\pi)|}{2}\tau_s\right\}.$$

We have that

$$\left\{\sup_{0\le r\le s}|\mathbf{M}_{t+r}^{\beta}-\mathbf{M}_t^{\beta}|>\epsilon\right\}\subset\left\{T_\rho^t<\tau_{t+s}\right\}\bigcup\left\{\sup_{0\le r\le s}|\mathbf{M}_{(t+r)\wedge T_\rho^t}^{\beta}-\mathbf{M}_t^{\beta}|>\epsilon\right\}.$$

Hence,

$$\begin{aligned}
\mathbb{P}\left(\sup_{0\le r\le s}|\mathbf{M}^\beta_{t+r}-\mathbf{M}^\beta_t|>\epsilon\right) &\le \mathbb{P}(T^t_\rho<t+s)+\mathbb{P}\left(\sup_{0\le r\le s}|\mathbf{M}^\beta_{(t+r)\wedge T^t_\rho}-\mathbf{M}^\beta_t|>\epsilon\right)\\
&\le \mathbb{P}(T^t_\rho<t+s)+\frac{4}{\epsilon^2}\mathbb{E}\left(\langle\mathbf{M}^\beta\rangle_{(t+s)\wedge T^t_\rho}-\langle\mathbf{M}^\beta\rangle_t\right)\\
&\le \mathbb{P}(T^t_\rho<t+s)+\frac{4}{\epsilon^2}C_3\ \mathbb{E}\int_t^{(t+s)\wedge T^t_\rho}\frac{du}{\rho^3_{\tau_u}}\\
&\le \mathbb{P}(T^t_\rho<t+s)+\frac{32\ C_3}{\epsilon^2(\bar\psi_1(u_\pi))^3}\ \mathbb{E}\int_t^{t+s}\frac{du}{\tau_u^3}.
\end{aligned}$$

It follows that

$$\begin{aligned}
\mathbb{P}\left(\sup_{r<\infty}|\mathbf{M}^\beta_{t+r}-\mathbf{M}^\beta_t|>\epsilon\right) &= \lim_{s\to\infty}\mathbb{P}\left(\sup_{0\le r\le s}|\mathbf{M}^\beta_{t+r}-\mathbf{M}^\beta_t|>\epsilon\right)\\
&\le \mathbb{P}(T^t_\rho<\infty)+\frac{32\ C_3}{\epsilon^2(\bar\psi_1(u_\pi))^3}\ \mathbb{E}\int_t^{\infty}\frac{du}{\tau_u^3}.
\end{aligned}$$

The first term goes to zero as t goes to infinity due to condition (2.4.9). Using (2.4.18), we have that for $s\le T^t_\rho$

$$\rho_{\tau_s}=\frac{d\tau_s}{ds}\ge\frac{|\bar\psi_1(u_\pi)|}{2}\tau_s.$$

Hence,

$$\tau_s\ge\tau_t e^{\frac{|\bar\psi_1(u_\pi)|}{2}(s-t)}$$

and the second term of the last estimate goes to zero as well. We deduce that

$$\sup_{0\le r<\infty}|\mathbf{M}^\beta_{t+r}-\mathbf{M}^\beta_t|\xrightarrow[t\to\infty]{}0 \text{ in probability,}$$

implying that there exists a subsequence that converges almost surely. Therefore the whole sequence converges to 0 almost surely since we take the supremum over all values of r. Hence,

$$\tilde\beta_t=\tilde\beta_{t_0}+\int_{t_0}^t G_\perp(\tilde\beta_s)ds+\mathcal{A}_t-\mathcal{A}_{t_0},$$

where

$$\begin{aligned}
\mathcal{A}_t=&\int_0^t\left(\psi(X_{\tau_s})-\bar\psi\left(\mathbf{u}_{\tau_s}\right)\mid\mathbf{u}^\perp_{\tau_s}\right)ds\\
&+\int_{t_0}^t\rho^{-1}_{\tau_s}\left[\arctan\left(\frac{X^2_{\tau_s}+\alpha_2}{X^1_{\tau_s}+\alpha_1}\right)-\beta_{\tau_s}-\rho^{-1}_{\tau_s}(\mathbf{u}^\perp_{\tau_s}|\alpha)\right]\nu(d\alpha)ds+\mathbf{M}^\beta_t,
\end{aligned}$$

such that

$$\sup_{t\geq t_0}|\mathcal{A}_t-\mathcal{A}_{t_0}|\xrightarrow[t_0\to\infty]{}0. \tag{2.4.21}$$

<u>**Step 4 :**</u> *The limiting orientation of the process :*

We choose $t_0>1$ large enough to have

$$\sup_{t\geq t_0}|\mathcal{A}_t-\mathcal{A}_{t_0}|<-\sup_{\beta>\theta_v+\delta}G_\perp(\beta),$$

where

$$\sup_{\beta>\theta_v+\delta}G_\perp(\beta)<0.$$

Assume that $\tilde{\beta}_{t_0}>\theta_v$ and define for $\delta>0$ the stopping time

$$T_\delta=\inf\left\{t>t_0;\ \tilde{\beta}_s<\theta_v+\delta\right\}.$$

We have that

$$\theta_v+\delta\leq\tilde{\beta}_{t\wedge T_\delta^-}<\tilde{\beta}_{t_0}+\sup_{\beta>\theta_v+\delta}G_\perp(\beta)\left(t\wedge T_\delta^- -1\right).$$

Hence, by letting t go to ∞, we have that

$$T_\delta<\frac{\theta_v+\delta-\tilde{\beta}_{t_0}}{\sup\limits_{\beta>\theta_v+\delta}G_\perp(\beta)}+1<\infty.$$

The proof is similar if we take $\tilde{\beta}_{t_0}<\theta_v$. This implies that the process enters every cone around the direction u_{θ_v} in finite time. But does it stay close to this direction as t goes to ∞? In the following we will prove that for all $\delta>0$, there exists t_0 such that if $\left|\tilde{\beta}_{t_0}-\theta_v\right|\leq\delta$ then $\left|\tilde{\beta}_t-\theta_v\right|\leq 2\delta$, for all $t\geq t_0$.

We deduce from (2.4.21) that for all $\delta>0$, there exists t_0 such that

$$\sup_{t\geq t_0}|\mathcal{A}_t-\mathcal{A}_{t_0}|\leq\frac{\delta}{3}.$$

Define

$$S=\inf\left\{t>t_0;\ \left|\tilde{\beta}_s-\theta_v\right|>2\delta\right\},$$
$$\bar{S}=\sup\left\{t<S;\ \left|\tilde{\beta}_t-\theta_v\right|<\delta\right\}.$$

We have that

$$\left|\tilde{\beta}_{\bar{S}}-\theta_v\right|\leq\left|\tilde{\beta}_{t_0}-\theta_v\right|+\frac{\delta}{3}\leq\frac{4\delta}{3}.$$

Assume that $\mathbb{P}(S < \infty) > 0$. Without loss of generality, take $\theta_v + \delta \leq \tilde{\beta}_{\bar{S}} < \theta_v + 2\delta$. It follows that on the event $\{S < \infty\}$,

$$\tilde{\beta}_S - \tilde{\beta}_{\bar{S}} \leq \sup_{\beta > \theta_v + \delta} G_{\perp}(\beta)(S - \bar{S}) + \frac{\delta}{3} \leq \frac{\delta}{3},$$

which contradicts with the fact that

$$\tilde{\beta}_S - \tilde{\beta}_{\bar{S}} = \tilde{\beta}_S - \theta_v - (\tilde{\beta}_{\bar{S}} - \theta_v) \geq \frac{2\delta}{3}.$$

Hence, $\mathbb{P}(S = \infty) = 1$.

Step 5 : *Conclusion :*

We proved that in the case $v_1 > \bar{m}_1(u_\pi)$, the process X_t is transient and can enter every cone around the limiting direction defined by u_{θ_v}. In addition for all $\delta > 0$, if X_t enters a cone with a vertex angle $\mathcal{V}_\delta = \delta$ then it never leaves the cone of vertex angle $\mathcal{V}_{2\delta}$. Since δ is arbitrary, it follows that

$$\tilde{\beta}_t \xrightarrow[t\to\infty]{} \theta_v, \text{ yielding } \beta_t \xrightarrow[t\to\infty]{} \theta_v, \text{ and } \frac{r_t}{t} \xrightarrow[t\to\infty]{} G(\theta_v).$$

Hence,

$$\frac{X_t}{t} \xrightarrow[t\to\infty]{} \bar{\psi}(u_{\theta_v}).$$

□

2. 4. 1.2. Case 2 : The case $\bar{m}_1(u_{\theta_2}) < v_1 \leq \bar{m}_1(u_\pi)$

In this case, there exist $\bar{\theta}_v \in [\theta_2, \pi]$ and $\bar{\bar{\theta}}_v \in [\pi, \theta_2 + \pi]$ such that

$$\bar{m}_1(u_{\bar{\theta}_v}) = \bar{m}_1(u_{\bar{\bar{\theta}}_v}) = v_1.$$

Note that $\bar{\bar{\theta}}_v$ can either be in $\left[\pi, \frac{3\pi}{2}\right]$ or in $\left[\frac{3\pi}{2}, \theta_2 + \pi\right]$. Furthermore, there exists $\xi_1 \in \left[\frac{\pi}{2}, \theta_2\right]$ and $\xi_2 \in \left[\bar{\theta}_v, \pi\right]$ such that $G(\xi_1) = G(\xi_2) = 0$ and $G(\beta) \geq 0$ for all $\beta \in [\xi_1, \xi_2]$.

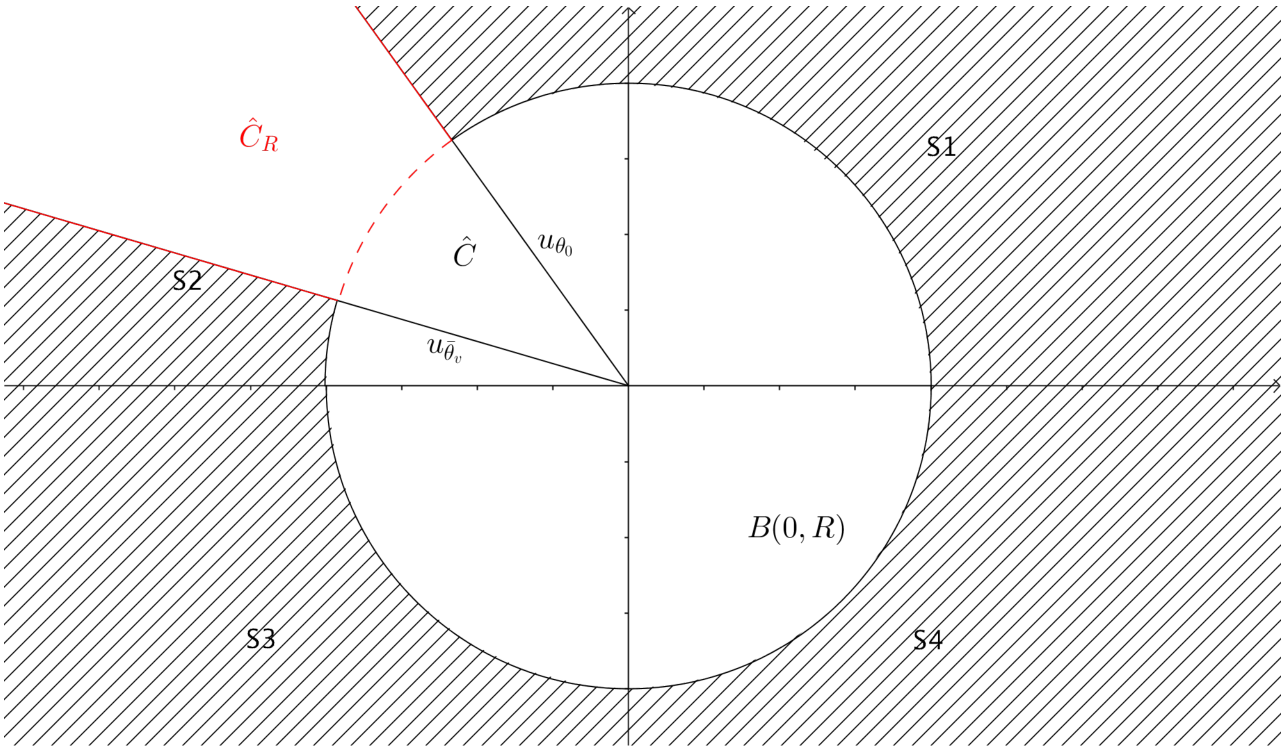

Figure 2.1. – Illustration of the different sectors defined in the present section. The hatched surface represents the space that the process quits in finite time a.s.

Theorem 2.4.2. *In the case $\bar{m}_1(u_{\theta_2}) < v_1 \leq \bar{m}_1(u_\pi)$, the process X_t is transient and*

$$\frac{X_t}{t} \xrightarrow[t\to\infty]{} \bar{\psi}(u_{\theta_v}) \ a.s.$$

Proof. First, we present some useful notations : (see Figure 2.1)

$$\begin{aligned}
S_1 &= \left\{x \in \mathbb{R}^2;\ x_1 > 0 \text{ and } x_2 > 0\right\},\\
S_2 &= \left\{x \in \mathbb{R}^2;\ x_1 < 0 \text{ and } x_2 > 0\right\},\\
S_3 &= \left\{x \in \mathbb{R}^2;\ x_1 < 0 \text{ and } x_2 < 0\right\},\\
S_4 &= \left\{x \in \mathbb{R}^2;\ x_1 > 0 \text{ and } x_2 < 0\right\},\\
\hat{C} &= \left\{x = r u_\beta;\ r > 0 \text{ and } \theta_2 < \beta < \bar{\theta}_v\right\},\\
\hat{C}_R &= \hat{C} \cap B(0,R)^c,\\
C(\beta_1,\beta_2) &= \{x = r u_\beta;\ r > 0 \text{ and } \beta_1 < \beta < \beta_2\}.
\end{aligned}$$

T_H always denotes the first time X_t hits the set H.

Step 1 : *The process hits $\hat{C} \cup B(0,R)$ in finite time.*

1. The case G strictly negative on $\mathbb{R}^2 \backslash S_2$.
   Assume that $X_0 \in S_2^c \cap B(0,R)^c$, then on the event that $t > T_{S_2} \wedge T_{B(0,R)}$, we have
   $$\frac{\rho_t}{t} \leq \frac{\rho_0}{t} - \left|\sup_\beta G(\beta)\right| + \frac{M_t^\rho}{t} + \varepsilon(R),$$
   where by choosing R large enough, we can achieve $\varepsilon(R) < \frac{c}{2}$. Clearly $T_{S_2} \wedge T_{B(0,R)} < \infty$ a.s. follows, since on the complementary event ρ_t would become negative, which is absurd.
   If X_t does not hit $\hat{C} \cup B(0,R)$ in finite time, either X_t spends infinite time in $S_2 \cap \hat{C}^c$, which is impossible from the identity
   $$\frac{\tilde{\beta}_t}{t} = \frac{\tilde{\beta}_{t_0}}{t} + \frac{1}{t}\int_{t_0}^t G_\perp(\tilde{\beta}_s)ds + \frac{\mathcal{A}_t - \mathcal{A}_{t_0}}{t},$$
   or X_t alternates infinitely often between $S_2^c \cap B(0,R)^c$ and $S_2 \cap \hat{C}^c \cap B(0,R)^c$. But each time X_t hits $S_2 \cap B(0,R)^c$, it then hits $\hat{C}$ in some fixed time with a uniformly positive probability (in fact this happens unless the "small" – if R is large – martingale term makes a very unprobable excursion). Hence a contradiction from the strong Markov property (see the argument in step 2 below).
2. Tables 2.3 and 2.4 reveal that the assumption made earlier about the sign of G might not be true as there exist sectors outside of S_2 where G might be positive.
   If $\bar{\bar{\theta}}_v \in \left[\frac{3\pi}{2}, 2\pi\right]$ (Table 2.4) and $X_0 \in C\left(\frac{3\pi}{2}, \bar{\bar{\theta}}_v\right) \cup C(\theta_2 + \pi, 2\pi)$, where the sign of G is unknown, we will show that the process hits $B(0,R)$ in finite time a.s. It follows from the continuity of G and $G_\perp$ that there exists $\delta > 0$ such that $G(\beta) < -\delta$ on $C(\bar{\bar{\theta}}_v - \delta, \theta_2 + \pi + \delta)$. On the other hand, $G_\perp$ is positive on $C\left(\frac{3\pi}{2}, \bar{\bar{\theta}}_v\right)$ and negative on $C(\theta_2 + \pi, 2\pi)$. By a similar argument to the one used in the strong transience case, if R is large enough, we can prove that the process is absorbed by the cone $C(\bar{\bar{\theta}}_v - \delta, \theta_2 + \pi + \delta)$ and thus it hits $B(0,R)$ in finite time a.s. from the first part of Step 1.
   If $\bar{\bar{\theta}}_v \in \left[\pi, \frac{3\pi}{2}\right]$ (Table 2.3), and $X_0 \in C\left(\bar{\bar{\theta}}_v, \frac{3\pi}{2}\right) \cup C(\theta_2 + \pi, 2\pi)$, where the sign of G is unknown, then by using a similar argument as above, it is easy to see that $G_\perp$ pushes the process either into a sector where G is negative, thus making $B(0,R)$ accessible in finite time, either into the cone $\hat{C}$. The particularity of this case is that $G_\perp$ is always negative in the corresponding sectors. In other words, if R is large enough the process has only two possible choices : returning to $B(0,R)$ or turning clockwise until hitting $\hat{C}$.

Conclusion : we have proved that, starting anywhere, $T_{\hat{C}} \wedge T_{B(0,R)} < \infty$ a.s.

Step 2 : *The process hits $\hat{C}_R$ in finite time.*

Basic claim : there exists $T > 0$ such that

$$\inf_{x \in B(0,R)} \mathbb{P}_x(T_{\hat{C}_R} < T) = p > 0.$$

This follows from the fact that there is a set of realizations of the Poisson Point Process with uniform positive probability which drives any $x \in B(0,R)$ into $\hat{C}_R$ in time less than T appropriately chosen.

Now starting anywhere, we have concluded in Step 1 that X_t hits $\hat{C} \cup B(0,R)$ at some finite time t_1. If X_t hits $B(0,R)$ before hitting $\hat{C}_R$, then with probability at least p, we hit $\hat{C}_R$ before time $t_1 + T$. If that is not the case, we are somewhere at time $t_1 + T$. From Step 1, at some time $t_2 \geq t_1 + T$, we hit again $\hat{C} \cup B(0,R)$. If by then we are in $B(0,R)$, we wait again a length of time T. If by time $t_2 + T$, we have not yet hit $\hat{C}_R$, we start again the procedure. The probability that we have not hit $\hat{C}_R$ at the end of the n–th step of the procedure is bounded above by $(1-p)^n$, which tends to zero as $n \to \infty$. This shows that X_t hits $\hat{C}_R$ in finite time.

Step 3 : *Staying forever in $\hat{C}_R$.*

If we leave the set $\hat{C}_R$ after having hit it, we will come back in it. Due to the arguments from the previous section, eventually we will stay in $\hat{C}_R$ for ever, and when in $\hat{C}_R$, the arguments of the previous section show that $\beta_t \to \theta_v$. $\square$

β	0		$\frac{\pi}{2}$		θ_2		θ_v		$\bar{\theta}_v$		π		$\bar{\bar{\theta}}_v$		$\frac{3\pi}{2}$		$\theta_2+\pi$		2π
$\bar{m}_1(u_\beta) - v_1$		$-$		$-$		$-$		$-$	0	$+$		$+$	0	$-$		$-$		$-$	
$-\sin\beta$		$-$		$-$		$-$		$-$		$-$	0	$+$		$+$		$+$		$+$	
$\bar{m}_2(u_\beta)$		$-$		$-$	0	$+$		$+$		$+$		$+$		$+$		$+$	0	$-$	
$\cos\beta$		$+$	0	$-$		$-$		$-$		$-$		$-$		$-$	0	$+$		$+$	
$G_\perp(\beta)$		?		$+$		$+$	0	$-$		$-$		?		$-$		?		$-$	

β	0		$\frac{\pi}{2}$		θ_2		θ_v		$\bar{\theta}_v$		π		$\bar{\bar{\theta}}_v$		$\frac{3\pi}{2}$		$\theta_2+\pi$		2π
$\bar{m}_1(u_\beta) - v_1$		$-$		$-$		$-$		$-$	0	$+$		$+$	0	$-$		$-$		$-$	
$\cos\beta$		$+$	0	$-$		$-$		$-$		$-$		$-$		$-$	0	$+$		$+$	
$\bar{m}_2(u_\beta)$		$-$		$-$	0	$+$		$+$		$+$		$+$		$+$		$+$	0	$-$	
$\sin\beta$		$+$		$+$		$+$		$+$		$+$	0	$-$		$-$		$-$		$-$	
$G(\beta)$		$-$		?		$+$		$+$		?		$-$		?		$-$		?	

Table 2.3. – Tables of sign of $G_\perp(\beta)$ and $G(\beta)$ in the case $\bar{m}_1(u_{\frac{3\pi}{2}}) < v_1 < \bar{m}_1(u_\pi)$ and $\bar{\bar{\theta}}_v \in [\pi, \frac{3\pi}{2}]$.

β	0	$\frac{\pi}{2}$	θ_2	θ_v	$\bar{\theta}_v$	π	$\frac{3\pi}{2}$	$\bar{\bar{\theta}}_v$	$\theta_2+\pi$ 2π
$\bar{m}_1(u_\beta)-v_1$	$-$	$-$	$-$	$-\ 0$	$+$	$+$	$+\ 0$	$-$	$-$
$-\sin\beta$	$-$	$-$	$-$	$-$	$-\ 0$	$+$	$+$	$+$	$+$
$\bar{m}_2(u_\beta)$	$-$	$-\ 0$	$+$	$+$	$+$	$+$	$+$	$+\ 0$	$-$
$\cos\beta$	$+\ 0$	$-$	$-$	$-$	$-$	$-\ 0$	$+$	$+$	$+$
$G_\perp(\beta)$	$?$	$+$	$+\ 0$	$-$	$-$	$?$	$+$	$?$	$-$

β	0	$\frac{\pi}{2}$	θ_2	θ_v	$\bar{\theta}_v$	π	$\frac{3\pi}{2}$	$\bar{\bar{\theta}}_v$	$\theta_2+\pi$ 2π
$\bar{m}_1(u_\beta)-v_1$	$-$	$-$	$-$	$-\ 0$	$+$	$+$	$+\ 0$	$-$	$-$
$\cos\beta$	$+\ 0$	$-$	$-$	$-$	$-$	$-\ 0$	$+$	$+$	$+$
$\bar{m}_2(u_\beta)$	$-$	$-\ 0$	$+$	$+$	$+$	$+$	$+$	$+\ 0$	$-$
$\sin\beta$	$+$	$+$	$+$	$+$	$+\ 0$	$-$	$-$	$-$	$-$
$G(\beta)$	$-$	$?$	$+$	$+$	$?$	$-$	$?$	$-$	$?$

Table 2.4. – Tables of sign of $G_\perp(\beta)$ and $G(\beta)$ in the case $\bar{m}_1(u_{\theta_2}) < v_1 < \bar{m}_1(u_{\frac{3\pi}{2}})$ and $\bar{\bar{\theta}}_v \in \left[\frac{3\pi}{2}, \theta_2+\pi\right]$.

2. 4. 2. The case $v_1 < \bar{m}_1(u_{\theta_2})$

In the case where $v_1 < \bar{m}_1(u_{\theta_2})$, there exists $\bar{\theta}_v \in]\theta_1, \theta_2[$ and $\bar{\bar{\theta}}_v \in]\pi, \theta_2+\pi[$ such that

$$\bar{m}_1(u_{\bar{\theta}_v}) = \bar{m}_1(u_{\bar{\bar{\theta}}_v}) = v_1, \tag{2.4.22}$$

since $\bar{m}_1(u_\cdot)$ is an increasing continuous function on $[0, 2\pi]$.

Proposition 2.4.6. *In the case $v < \bar{m}_1(u_{\theta_2})$, if moreover*

$$G_{\text{sup}} = \sup_{\beta\in[0,2\pi]} G(\beta) < 0, \tag{2.4.23}$$

then X_t is recurrent in the sense that the mean time to return into a compact around zero is finite.

Proof. We rewrite equation (2.4.11) as follows :

$$\begin{aligned}\rho_t = \rho_0 &+ \int_0^t G(\beta_s)ds + \int_{t_w}^t \left(\psi(\rho_s \mathbf{u}_s) - \bar{\psi}(\mathbf{u}_s) \mid \mathbf{u}_s\right) ds \\ &+ \int_{[0,t]\times\mathbb{R}^2} \left(|X_s+\alpha| - \rho_s - (\mathbf{u}_s \mid \alpha)\right) g(X_s,\alpha)\nu(d\alpha)ds + M_t^\rho,\end{aligned}$$

where M^ρ is defined by (2.4.14). We choose

$$\bar{K} > K \vee \left(\frac{1+\sqrt{1+8\,|G_{\text{sup}}|\,C_1}}{2\,|G_{\text{sup}}|}\right)^2, \tag{2.4.24}$$

β	0		$\frac{\pi}{2}$		$\bar{\theta}_v$		θ_2		π		$\frac{3\pi}{2}$		$\bar{\bar{\theta}}_v$		$\theta_2+\pi$		2π
$\bar{m}_1(u_\beta)-v_1$		$-$		$-$	0	$+$		$+$		$+$		$+$	0	$-$		$-$	
$-\sin\beta$		$-$		$-$		$-$		$-$	0	$+$		$+$		$+$		$+$	
$\bar{m}_2(u_\beta)$		$-$		$-$		$-$	0	$+$		$+$		$+$		$+$	0	$-$	
$\cos\beta$		$+$	0	$-$		$-$		$-$		$-$	0	$+$		$+$		$+$	
$G_\perp(\beta)$		?		$+$		?		$-$		?		$+$		?		$-$	

β	0		$\frac{\pi}{2}$		$\bar{\theta}_v$		θ_2		π		$\frac{3\pi}{2}$		$\bar{\bar{\theta}}_v$		$\theta_2+\pi$		2π
$\bar{m}_1(u_\beta)-v_1$		$-$		$-$	0	$+$		$+$		$+$		$+$	0	$-$		$-$	
$\cos\beta$		$+$	0	$-$		$-$		$-$		$-$	0	$+$		$+$		$+$	
$\bar{m}_2(u_\beta)$		$-$		$-$		$-$	0	$+$		$+$		$+$		$+$	0	$-$	
$\sin\beta$		$+$		$+$		$+$		$+$	0	$-$		$-$		$-$		$-$	
$G(\beta)$		$-$		?		$-$		?		$-$		?		$-$		?	

Table 2.5. – Tables of sign of $G_\perp(\beta)$ and $G(\beta)$ in the case $v_1 < \bar{m}_1(u_{\theta_2})$ and $\bar{\bar{\theta}}_v \in \left[\frac{3\pi}{2}, \theta_2+\pi\right]$.

where K is defined by Lemma 2.4.4 and C_1 by Lemma 2.4.5. Assume that $\rho_0 > \bar{K}$ and define the stopping time

$$\bar{T} = \inf\left\{t > 0;\ \rho_t \leq \bar{K}\right\}.$$

Hence,

$$\begin{aligned} 0 < \mathbb{E}\rho_{t\wedge\bar{T}} &< \rho_0 + \left(G_{\sup} + \frac{1}{2\sqrt{\bar{K}}} + \frac{C_1}{\bar{K}}\right)\mathbb{E}(t\wedge\bar{T}) \\ &< \rho_0 - \frac{|G_{\sup}|}{2}\mathbb{E}(t\wedge\bar{T}), \end{aligned}$$

due to the choice (2.4.24) of $\bar{K}$. Thus by letting t go to ∞,

$$\mathbb{E}\bar{T} < \frac{2\rho_0}{|G_{\sup}|} < \infty.$$

It follows that X_t is recurrent in the sense that the mean time to return into a compact around zero is finite. □

Remark 2.4.2. Condition (2.4.23) is satisfied for example if M is diagonal. In this case, $c = 0$ and $\theta_2 = \pi$. Hence for all $v_1 < \bar{m}_1(u_\pi)$, X_t is positive recurrent. However, it remains unclear whether or not $v_1 < \bar{m}_1(u_{\theta_2})$ implies $G_{\sup} < 0$ for any M. Tables 2.5 and 2.6 reveal the zones where G can perhaps become positive. In

β	0		$\frac{\pi}{2}$		$\bar{\theta}_v$		θ_2		π		$\bar{\bar{\theta}}_v$		$\frac{3\pi}{2}$		$\theta_2+\pi$		2π
$\bar{m}_1(u_\beta)-v_1$		$-$		$-$	0	$+$		$+$		$+$	0	$-$		$-$		$-$	
$-\sin\beta$		$-$		$-$		$-$		$-$	0	$+$		$+$		$+$		$+$	
$\bar{m}_2(u_\beta)$		$-$		$-$		$-$	0	$+$		$+$		$+$		$+$	0	$-$	
$\cos\beta$		$+$	0	$-$		$-$		$-$		$-$		$-$	0	$+$		$+$	
$G_\perp(\beta)$		?		$+$		?		$-$		?		$-$		?		$-$	

β	0		$\frac{\pi}{2}$		$\bar{\theta}_v$		θ_2		π		$\bar{\bar{\theta}}_v$		$\frac{3\pi}{2}$		$\theta_2+\pi$		2π
$\bar{m}_1(u_\beta)-v_1$		$-$		$-$	0	$+$		$+$		$+$	0	$-$		$-$		$-$	
$\cos\beta$		$+$	0	$-$		$-$		$-$		$-$		$-$	0	$+$		$+$	
$\bar{m}_2(u_\beta)$		$-$		$-$		$-$	0	$+$		$+$		$+$		$+$	0	$-$	
$\sin\beta$		$+$		$+$		$+$		$+$	0	$-$		$-$		$-$		$-$	
$G(\beta)$		$-$		?		$-$		?		$-$		?		$-$		?	

Table 2.6. – Tables of sign of $G_\perp(\beta)$ and $G(\beta)$ in the case $v_1 < \bar{m}_1(u_{\theta_2})$ and $\bar{\bar{\theta}}_v \in \left[\pi, \frac{3\pi}{2}\right]$.

this case, we study both β_t and the rescaled $\tilde{\beta}_t$ which satisfy

$$\begin{aligned}
\beta_t &= \beta_0 + \int_0^t \rho_s^{-1}(\mathbf{u}_s^\perp|\psi(X_s))ds \\
&\quad + \int_{[0,t]\times\mathbb{R}^2\times[0,1]} \left[\arctan\left(\frac{X_{s^-}^2+\alpha_2}{X_{s^-}^1+\alpha_1}\right) - \beta_{s^-}\right]\Gamma(X_{s^-},\alpha,\xi)\bar{M}(ds,d\alpha,d\xi) \\
&\quad + \int_{[0,t]\times\mathbb{R}^2} \left[\arctan\left(\frac{X_s^2+\alpha_2}{X_s^1+\alpha_1}\right) - \beta_s - \rho_s^{-1}(\mathbf{u}_s^\perp|\alpha)\right]\nu(d\alpha)ds, \\
\text{and} \quad \tilde{\beta}_t &= \tilde{\beta}_{t_0} + \int_{t_0}^t G_\perp(\tilde{\beta}_s)ds + \int_{t_0}^t \left(\psi(X_{\tau_s}) - \bar{\psi}\left(\mathbf{u}_{\tau_s}\right) \mid \mathbf{u}_{\tau_s}^\perp\right)ds \\
&\quad + \int_{t_0}^t \rho_{\tau_s}^{-1}\left[\arctan\left(\frac{X_{\tau_s}^2+\alpha_2}{X_{\tau_s}^1+\alpha_1}\right) - \beta_{\tau_s} - \rho_{\tau_s}^{-1}(\mathbf{u}_{\tau_s}^\perp|\alpha)\right]\nu(d\alpha)ds \\
&\quad + \mathbf{M}_t^\beta - \mathbf{M}_{t_0}^\beta,
\end{aligned}$$

where $\mathbf{M}^\beta$ is the martingale defined by (2.4.20). Fortunately, $G_\perp$ performs well in these cones where $G(\beta)$ may be positive pushing the process to a cone where G is negative (see Tables 2.5 and 2.6). Probably, Harris recurrence still holds in this case but we cannot say more about the expectation of the time of return to compacts. The reason is the presence of the factor ρ_t^{-1} in the drift of β_t, so that we can upper bound the expected time spent in the "bad" cones by the rescaled $\tilde{\beta}_t$ only.

3. Small Jumps Limit

3.1. Introduction

Natural populations living in changing environments may face extinction unless they manage to evolve and adapt to the new conditions. This issue is becoming particularly pressing in the light of global change, and an increasing number of theoretical studies are aimed at understanding the likelihood of rapid evolution and "evolutionary rescue" (e.g., Gonzalez et al., 2013; Kopp and Matuszewski, 2014), and more generally, the "mechanics" and genetic basis of adaptation (reviewed by Orr, 2005a). Given the enormous complexity of any real biological system, such models are necessarily simplified. One approach has been to focus exclusively on adaptation from new mutations, and to model the successive fixation of beneficial mutations as a stochastic "adaptive walk" (e.g., Gillespie, 1983; Orr, 1998). The basic idea is that mutations with random effects arrive in the population at random times and are fixed with a probability depending on their selective advantage at the time of appearance. Fixations are assumed to happen quasi-instantaneously, such that adaptation resembles a jump process. Such an approach ignores adaptation from standing genetic variation (e.g. Hermisson and Pennings, 2005; Barrett and Schluter, 2008) and is most appropriate under a scenario of "strong-selection-weak-mutation" (Gillespie, 1983). Initially, adaptive-walk models were mainly concerned with the distribution of adaptive substitutions after a sudden, one-time change in the environment (e.g. Gillespie, 1983; Orr, 1998, 2000, 2005a,b). More recent models have investigated adaptation to gradual environmental change (Bello and Waxman, 2006; Collins et al., 2007; Kopp and Hermisson, 2007; Sato and Waxman, 2008; Kopp and Hermisson, 2009a,b; Matuszewski et al., 2014), using the so-called "moving-optimum model" (Lynch and Lande, 1993; Bürger and Lynch, 1995; Bürger, 1999; Waxman and Peck, 1999; Jones et al., 2004), where one or more traits are under stabilizing selection with an optimum that changes linearly in time. The moving optimum not only might be more appropriate to understand the effects of gradual change such as global warming, but it also adds an increased ecological realism by introducing an additional time-scale that influences the rate of evolution (Kopp and Hermisson, 2007).

Kopp and Hermisson (2009b) developed an adaptive-walk approximation to describe adaptation in a one-dimensional moving-optimum model. While they derived a recurrence formula for the distribution of adaptive "jumps", their model does not allow to predict survival and extinction. Later, Matuszewski et al. (2014) generalized the results to a multidimensional moving-optimum model. As a minimal condition for survival, the adaptive walk needs to be recurrent, such that the lag between the population and the optimum does not become infinite. Kersting (1986) first studied this sort of question under transience and recurrence of growth models in discrete time. Then Klebaner (1990) gave a generalization of this study to multitype populations. In this chapter, we use the multidimensional model by Matuszewski et al. (2014) to conduct a small jumps limit approach leading to a better understanding of the recurrent case for an adaptive walk of a multidimensional trait in continuous time. Thereafter, we thoroughly study the unidimensional case using simulations.

3.2. The model

Based on the model in Chapter 2, we consider without loss of generality the following assumptions (see Matuszewski et al., 2014) :

1. v is a horizontal vector,
2. Σ is isotropic, i.e. $\Sigma = \sigma^{-2}\mathbf{I}_{\mathbb{R}^d}$.

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

$$X_t = x_0 - vt + \int_{[0,t]\times\mathbb{R}^d\times[0,1]} \alpha\Gamma(X_{s^-}, \alpha, \xi)N(ds, d\alpha, d\xi). \tag{3.2.1}$$

Here, N is a Poisson point process over $\mathbb{R}_+ \times \mathbb{R}^d \times [0,1]$ with intensity $ds\,\nu(d\alpha)\,d\xi$ where $\nu(d\alpha)$ is a σ-finite measure that satisfies

$$\int_{\mathbb{R}^d} |\alpha| \vee |\alpha|^3 \nu(d\alpha) < \infty, \tag{3.2.2}$$

and

$$\Gamma(x, \alpha, \xi) = \mathbf{1}_{\{\xi \le g(x,\alpha)\}},$$

where the fixation probability $g(x, \alpha)$ of a mutation of size α that hits the population when the lag is x, as defined by (2.1.2) and (2.1.3), can be expressed as

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

The points of this Poisson Point Process (T_i, A_i, Ξ_i) are such that the (T_i, A_i) form a Poisson Point Process over $\mathbb{R}_+ \times \mathbb{R}^d$ of the mutations that hit the population with intensity $ds\nu(d\alpha)$, and the Ξ_i are i.i.d. $\mathcal{U}[0,1]$, globally independent of the Poisson Point Process of the (T_i, A_i). T_i's are the times when mutations are proposed and A_i's are the effect sizes of those mutations. The Ξ_i are auxiliary variables determining fixation : a mutation gets instantaneously fixed if $\Xi_i \leq g(X_{T_i}, A_i)$, and is lost otherwise. Note that, in the model considered in Matuszewski et al. (2014),

$$\nu(d\alpha) = \frac{\Theta}{2} p(\alpha) d\alpha, \tag{3.2.3}$$

where p is the density of a multidimensional Gaussian distribution $\mathcal{N}(0, M)$.

3.3. Small Jumps Limit

In the following, we introduce the rescaling

$$\tilde{\alpha} = \epsilon\alpha \quad \text{and} \quad \tilde{s} = \frac{s}{\epsilon^2} \text{ with } \epsilon > 0$$

of phenotype and time, respectively, we rewrite our process (3.2.1) as

$$X_t^\epsilon = X_0 - vt + \int_0^t \int_{\mathbb{R}^d} \int_0^1 \epsilon\alpha\varphi(X_{s-}^\epsilon, \epsilon\alpha, \xi) M_\epsilon(ds, d\alpha, d\xi),$$

where the intensity measure of the Poisson Point Process M_ϵ is

$$\left(\frac{1}{\epsilon^2} ds\right) \times \nu(d\alpha) \times d\xi.$$

The process can be rewritten as

$$X_t^\epsilon = X_0 - vt + \int_0^t \frac{1}{\epsilon^2} m_\epsilon(X_s^\epsilon) ds + \mathcal{M}_t^\epsilon, \tag{3.3.1}$$

with

$$\begin{aligned} m_\epsilon(x) &= \int_{\mathbb{R}^d} \epsilon\alpha g(x, \epsilon\alpha)\nu(d\alpha), \\ \text{and} \quad g(x, \epsilon\alpha) &\leq 2\sigma^{-2} \left|(2x + \epsilon\alpha \mid \epsilon\alpha)\right| \mathbf{1}_{\{(2x+\epsilon\alpha|\epsilon\alpha)\leq 0\}} \\ &\leq 4\sigma^{-2}\epsilon \left|(x \mid \alpha)\right| \mathbf{1}_{\{(x|\alpha)\leq 0\}}, \end{aligned}$$

and the martingale

$$\mathcal{M}_t^\epsilon = \int_0^t \int_{\mathbb{R}^d} \int_0^1 \epsilon\alpha\varphi(X_{s-}^\epsilon, \epsilon\alpha, \xi) \bar{M}_\epsilon(ds, d\alpha, d\xi).$$

Thus we have that

$$\frac{1}{\epsilon^2} \left|m_\epsilon(X_t^\epsilon)\right| \leq 4|X_t^\epsilon|\sigma^{-2} \int_{\mathbb{R}^d} |\alpha|^2 \nu(d\alpha),$$

$$\langle\langle \mathcal{M}^\epsilon \rangle\rangle_t = \int_0^t \int_{\mathbb{R}^d} \alpha \otimes \alpha g(X_s^\epsilon, \epsilon\alpha)\nu(d\alpha)ds,$$

and

$$\begin{aligned}\langle \mathcal{M}^\epsilon \rangle_t &= \frac{1}{\epsilon^2}\int_0^t \int_{\mathbb{R}^d} |\epsilon\alpha|^2 g(X_s^\epsilon, \epsilon\alpha)\nu(d\alpha)ds \\ &\leq 4\sigma^{-2}\epsilon \int_0^t \int_{(\alpha|X_s^\epsilon)\leq 0} |\alpha|^2 \left|(\alpha \mid X_s^\epsilon)\right| \nu(d\alpha)ds \\ &\leq 4\sigma^{-2}\epsilon \left(\int_{\mathbb{R}^d} |\alpha|^3 \nu(d\alpha)\right) \int_0^t |X_s^\epsilon|\, ds.\end{aligned} \tag{3.3.2}$$

Moreover for all x, we have

$$\frac{1}{\epsilon^2}\left(m_\epsilon(x) \mid x\right) \leq 0$$

On the other hand,

$$|X_t^\epsilon|^2 = |X_0^\epsilon|^2 - 2\int_0^t (v \mid X_s^\epsilon)\, ds + \frac{2}{\epsilon^2}\int_0^t \left(m_\epsilon(X_s^\epsilon) \mid X_s^\epsilon\right) ds + 2\int_0^t X_{s^-} dM_s^\epsilon + \langle \mathcal{M}^\epsilon \rangle_t$$

Hence, for fixed T, we have for all $0 \leq t \leq T$

$$\begin{aligned}\mathbb{E}|X_t^\epsilon|^2 &\leq \mathbb{E}|X_0^\epsilon|^2 + 2v_1 \int_0^t \mathbb{E}|X_s^\epsilon| ds + \mathbb{E}\langle \mathcal{M}^\epsilon \rangle_t \\ &\leq \mathbb{E}|X_0^\epsilon|^2 + v_1\left(t + \int_0^t \mathbb{E}(X_s^\epsilon)^2 ds\right) + 2\epsilon \int_{\mathbb{R}^d} |\alpha|^3 \nu(d\alpha)\left(t + \int_0^t \mathbb{E}(X_s^\epsilon)^2 ds\right) \\ &\leq \mathbb{E}|X_0^\epsilon|^2 + \left(v_1 + 2\epsilon\int_{\mathbb{R}^d} |\alpha|^3\nu(d\alpha)\right)t + \left(v_1 + 2\epsilon\int_{\mathbb{R}^d} |\alpha|^3\nu(d\alpha)\right)\int_0^t \mathbb{E}(X_s^\epsilon)^2 ds \\ &\leq \left(\mathbb{E}|X_0^\epsilon|^2 + \left(v_1 + 2\epsilon\int_{\mathbb{R}^d}|\alpha|^3\nu(d\alpha)\right)T\right) e^{\left[v_1 + 2\epsilon\left(\int_{\mathbb{R}^d}|\alpha|^3\nu(d\alpha)\right)\right]T},\end{aligned} \tag{3.3.3}$$

since $2\mathbb{E}|X| \leq 1+\mathbb{E}X^2$. Thus the process X^ϵ is tight in $\mathbb{D}\left(\mathbb{R}_+, \mathbb{R}^d\right)$ due to Remark 14, part 2 in Pardoux (2016b) and

$$\langle \mathcal{M}^\epsilon \rangle_t \xrightarrow[\epsilon \to 0]{} 0 \text{ in probability.}$$

Furthermore we can extract a subsequence which we still denote X^ϵ by an abuse of notation such that $X^\epsilon \Rightarrow \bar{X}$, and we have the following result :

Proposition 3.3.1. *We have that*

$$\frac{1}{\epsilon^2} m_\epsilon(X_\cdot^\epsilon) \Rightarrow L(\bar{X}_\cdot) \quad \text{ in } D(\mathbb{R}_+, \mathbb{R}^d),$$

where

$$L(x) = 4\sigma^{-2}\int_{(x|\alpha)\leq 0} \alpha \left|(x \mid \alpha)\right| \nu(d\alpha) = -4\sigma^{-2}\bar{V}x,$$

and $\bar{V} = M\Theta/4$ as defined by 2.4.2.

Proof. Let for all $\epsilon > 0$ and $x, \alpha \in \mathbb{R}^d$

$$y_\epsilon = -2\sigma^{-2}\left(2x + \epsilon\alpha \mid \alpha\right) \text{ and } y = -4\sigma^{-2}\left(x \mid \alpha\right).$$

We have that

$$\frac{1 - e^{-\epsilon y_\epsilon}}{\epsilon}\mathbf{1}_{y_\epsilon \geq 0} - y\mathbf{1}_{y \geq 0} = \left(\frac{1 - e^{-\epsilon y_\epsilon}}{\epsilon}\mathbf{1}_{y_\epsilon \geq 0} - y_\epsilon \mathbf{1}_{y_\epsilon \geq 0}\right) + \left(y_\epsilon \mathbf{1}_{y_\epsilon \geq 0} - y\mathbf{1}_{y \geq 0}\right). \tag{3.3.4}$$

In addition,

$$-\epsilon\frac{y_\epsilon^2}{2}\mathbf{1}_{y_\epsilon \geq 0} \leq \frac{1 - e^{-\epsilon y_\epsilon}}{\epsilon}\mathbf{1}_{y_\epsilon \geq 0} - y_\epsilon \mathbf{1}_{y_\epsilon \geq 0} \leq 0, \tag{3.3.5}$$

since for all $z > 0$

$$z - \frac{z^2}{2} \leq 1 - e^{-z} \leq z.$$

Combining (3.3.5) with the fact that

$$y_\epsilon^2 \mathbf{1}_{y_\epsilon \geq 0} \leq y^2 \mathbf{1}_{y \geq 0} \leq 16\sigma^{-4}|x|^2|\alpha|^2,$$

we obtain

$$-8\sigma^{-4}\epsilon|x|^2|\alpha|^2 \leq \frac{1 - e^{-\epsilon y_\epsilon}}{\epsilon}\mathbf{1}_{y_\epsilon \geq 0} - y_\epsilon \mathbf{1}_{y_\epsilon \geq 0} \leq 0. \tag{3.3.6}$$

Moreover, $\{y_\epsilon \geq 0\} \subset \{y \geq 0\}$. It follows that

$$\begin{aligned} y_\epsilon \mathbf{1}_{y_\epsilon \geq 0} - y\mathbf{1}_{y \geq 0} &= (y_\epsilon - y)\mathbf{1}_{y \geq 0} - y_\epsilon \mathbf{1}_{y \geq 0 \setminus y_\epsilon \geq 0} \\ &= -2\sigma^{-2}\epsilon|\alpha|^2 \mathbf{1}_{y \geq 0} - y_\epsilon \mathbf{1}_{y \geq 0 \setminus y_\epsilon \geq 0}. \end{aligned} \tag{3.3.7}$$

Furthermore, $\{y \geq 0 \setminus y_\epsilon \geq 0\} = \{-\epsilon|\alpha|^2 < (2x \mid \alpha) < 0\}$. Thus,

$$0 < -y_\epsilon \mathbf{1}_{y \geq 0 \setminus y_\epsilon \geq 0} < 2\sigma^{-2}\epsilon|\alpha|^2 \mathbf{1}_{y \geq 0}. \tag{3.3.8}$$

Combining (3.3.7) and (3.3.8), we get

$$-2\sigma^{-2}\epsilon|\alpha|^2 \leq y_\epsilon \mathbf{1}_{y_\epsilon \geq 0} - y\mathbf{1}_{y \geq 0} \leq 0. \tag{3.3.9}$$

We deduce from (3.3.4), (3.3.6) and (3.3.9) that

$$-\epsilon\left(8\sigma^{-4}|x|^2 + 2\sigma^{-2}\right)|\alpha|^2 \leq \frac{1 - e^{-\epsilon y_\epsilon}}{\epsilon}\mathbf{1}_{y_\epsilon \geq 0} - y\mathbf{1}_{y \geq 0} \leq 0.$$

Hence,

$$\left|\alpha\left(\frac{1 - e^{-\epsilon y_\epsilon}}{\epsilon}\mathbf{1}_{y_\epsilon \geq 0} - y\mathbf{1}_{y \geq 0}\right)\right| \leq \epsilon\left(8\sigma^{-4}|x|^2 + 2\sigma^{-2}\right)|\alpha|^3. \tag{3.3.10}$$

By integrating (3.3.10) with respect to ν, we obtain

$$\left|\frac{1}{\epsilon^2}m_\epsilon(x) - L(x)\right| \leq \epsilon\left(8\sigma^{-4}|x|^2 + 2\sigma^{-2}\right)\int_{\mathbb{R}^d}|\alpha|^3\nu(d\alpha). \tag{3.3.11}$$

Consequently, for fixed t we have that for all $\delta, C > 0$, if ϵ is sufficiently small and due to condition (3.2.2),

$$\sup_{|x|\leq C}\left|\frac{1}{\epsilon^2}m_\epsilon(x) - L(x)\right| \leq \delta,$$

thus, for an arbitrary $T > 0$

$$\mathbb{P}\left(\sup_{t\leq T}\left|\frac{1}{\epsilon^2}m_\epsilon(X_t^\epsilon) - L(X_t^\epsilon)\right| > \delta\right) \leq \mathbb{P}\left(\sup_{t\leq T}|X_t^\epsilon| > C\right).$$

It follows that for all $\delta, C > 0$,

$$\limsup_{\epsilon\to 0}\mathbb{P}\left(\sup_{t\leq T}\left|\frac{1}{\epsilon^2}m_\epsilon(X_t^\epsilon) - L(X_t^\epsilon)\right| > \delta\right) \leq \sup_{\epsilon}\mathbb{P}\left(\sup_{t\leq T}|X_t^\epsilon| > C\right).$$

For all $\eta > 0$, we choose $C > 0$ such that

$$\sup_{\epsilon}\mathbb{P}\left(\sup_{t\leq T}|X_t^\epsilon| > C\right) \leq \eta.$$

This is possible since the sequence X^ϵ is proven to be tight. Hence for all $\delta, \eta > 0$

$$\limsup_{\epsilon\to 0}\mathbb{P}\left(\sup_{t}\left|\frac{1}{\epsilon^2}m_\epsilon(X_t^\epsilon) - L(X_t^\epsilon)\right| > \delta\right) \leq \eta.$$

Moreover $L(X^\epsilon) \Rightarrow L(\bar{X})$ in $\mathbb{D}(\mathbb{R}_+, \mathbb{R}^d)$ since L is continuous function. Consequently,

$$\frac{1}{\epsilon^2}m_\epsilon(X^\epsilon) = \frac{1}{\epsilon^2}m_\epsilon(X^\epsilon) - L(X^\epsilon) + L(X^\epsilon) \Rightarrow L(\bar{X}).$$

□

It follows that $X_t^\epsilon \xrightarrow[\epsilon\to 0]{} \bar{X}_t$ in probability, locally uniformly in t, where

$$\frac{d\bar{X}_t}{dt} = -v - 4\sigma^{-2}\bar{V}\bar{X}_t. \tag{3.3.12}$$

This is true for all subsequences of X_t^ϵ, and since $\bar{X}_t$ is uniquely determined, the whole process X_t^ϵ converges in probability towards $\bar{X}_t$. The differential equation (3.3.12) represents a deterministic approximation for the stochastic process $\bar{X}^\epsilon$

in the limit of small jumps. The large-time behavior of $\bar{X}_t$ is :

$$\bar{X}_t \xrightarrow[t\to\infty]{} \bar{X}_\infty = -\frac{1}{4\sigma^{-2}}\bar{V}^{-1}v. \tag{3.3.13}$$

As long as $p(\alpha)$ is symmetric (e.g., multivariate Gaussian), we can use the result from from Proposition 2.4.2 that

$$\bar{V} = \frac{\Theta}{4}M.$$

Defining $\bar{\omega}^2 = \sqrt[d]{\det(M)}$, $\bar{X}_\infty$ (see Matuszewski et al., 2014) and using the fact that $v = v_1 e_1$ (where e_1 is the unit vector $(1, 0, \ldots)$, see assumption 1), equation (3.3.13) can be rewritten as

$$\bar{X}_\infty = -\gamma\bar{\omega}\left(\frac{M}{\bar{\omega}^2}\right)^{-1} e_1, \tag{3.3.14}$$

where

$$\gamma = \frac{v_1/\bar{\omega}}{\theta\sigma^{-2}\bar{\omega}^2} \tag{3.3.15}$$

is the scaled rate of environmental change defined in Matuszewski et al. (2014). The term $(M/\bar{\omega}^2)^{-1}e_1$ corresponds to the first column of the inverse of the scaled mutation matrix. Its entries are related to the partial correlation coefficients between the effects of mutations on trait 1 (whose optimum value is directly affected by v) and each of the other traits (i.e., the partial correlation between trait 1 and trait i is given by $-m_{1i}^{-1}/\sqrt{m_{ii}^{-1}m_{11}^{-1}}$). Thus, the equilibrium mean lag depends only on γ and the structure of mutational correlations in the direction of the moving optimum.

To calculate the variance of the process in the small-jumps limit, we now consider the following process

$$U_t^\epsilon = \frac{X_t^\epsilon - \bar{X}_t}{\sqrt{\epsilon}}.$$

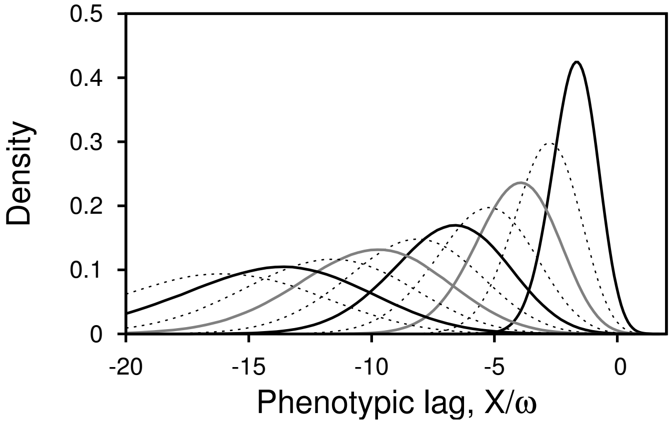

Figure 3.1. – The stationary distribution of the process in the recurrent case, assuming a Gaussian distribution of new mutations with variance ω^2. Results are from simulations of equation (1.3.1) with a Gaussian distribution of new mutations and $v(t) = vt$. To reduce the number of parameters, we focus (here and in the following Figures) on the variable X_t/ω, which depends only on the scaled rate of environmental change $v/(\omega\Theta)$ and the scaled strength of selection $\sigma^{-2}\omega^2$ (this can be shown by measuring the phenotype in units of ω and time in units of Θ^{-1}). Solid lines are for (from right to left) $v/(\omega\Theta) = 0.01, 0.03, 0.05, 0.07, 0.09$. Dotted lines are for (from right to left) $v/(\omega\Theta) = 0.02, 0.04, 0.06, 0.08, 0.1$. $\sigma^{-2}\omega^2$ was set to 0.01 (see Fig. 3.3D).

We have that

$$\begin{aligned}
U_t^\epsilon &= \int_0^t \frac{\epsilon^{-2} m_\epsilon(X_s^\epsilon) + 4\sigma^{-2}\bar{V}\bar{X}_s}{\sqrt{\epsilon}} ds + \frac{1}{\sqrt{\epsilon}} \mathcal{M}_t^\epsilon, \\
&= -4\sigma^{-2}\bar{V} \int_0^t \frac{X_s^\epsilon - \bar{X}_s}{\sqrt{\epsilon}} ds + \frac{1}{\sqrt{\epsilon}} \int_0^t \left(\frac{1}{\epsilon^2} m_\epsilon(X_s^\epsilon) - L(X_s^\epsilon) \right) ds + \frac{1}{\sqrt{\epsilon}} \mathcal{M}_t^\epsilon \\
&= -4\sigma^{-2}\bar{V} \int_0^t U_s^\epsilon ds + \frac{1}{\sqrt{\epsilon}} \int_0^t \left(\frac{1}{\epsilon^2} m_\epsilon(X_s^\epsilon) - L(X_s^\epsilon) \right) ds + \frac{1}{\sqrt{\epsilon}} \mathcal{M}_t^\epsilon,
\end{aligned}$$

where $\frac{1}{\sqrt{\epsilon}}\mathcal{M}^\epsilon$ are tight martingales by a similar argument as before since

$$\sup_{\{t>0,\ \epsilon\}} \int_{\mathbb{R}^2} |\alpha|^2 g(X_t^\epsilon, \epsilon\alpha)\nu(d\alpha) \leq \int_{\mathbb{R}^2} |\alpha|^2 \nu(d\alpha) < \infty.$$

Furthermore for any arbitrary $T > 0$,

$$\sup_{t \leq T} \left| \frac{1}{\sqrt{\epsilon}} \left(\mathcal{M}_t^\epsilon - \mathcal{M}_{t-}^\epsilon \right) \right| \xrightarrow[\epsilon \to 0]{} 0,$$

since the jumps are multiplied by ϵ. Hence every converging subsequence of

$\frac{1}{\sqrt{\epsilon}}\mathcal{M}^\epsilon$ converges to a continuous martingale $\mathcal{M}$ as ϵ goes to 0, and since

$$\langle\langle \frac{1}{\sqrt{\epsilon}}\mathcal{M}^\epsilon\rangle\rangle_t \underset{\epsilon\to 0}{\longrightarrow} \int_0^t \Lambda(\bar{X}_s)ds,$$

where

$$\Lambda(x) = 4\sigma^{-2}\int_{(x|\alpha)\leq 0} |\,(x \mid \alpha)\,|\alpha\otimes\alpha\nu(d\alpha),$$

it follows that

$$\langle\langle\mathcal{M}\rangle\rangle_t = \int_0^t \Lambda(\bar{X}_s)ds.$$

We deduce thanks to the Representation Theorem of continuous martingales that there exists a Brownian motion (B_t) such that

$$\mathcal{M}_t = \int_0^t \Lambda^{\frac{1}{2}}(\bar{X}_s)dB_s,\ t\geq 0.$$

This is true for any subsequence of $\frac{1}{\sqrt{\epsilon}}\mathcal{M}^\epsilon$ thus this limit is unique. On the other hand, we deduce from (3.3.11) that

$$\frac{1}{\sqrt{\epsilon}}\left|\frac{1}{\epsilon^2}m_\epsilon(X_t^\epsilon) - L(X_t^\epsilon)\right| \leq \sqrt{\epsilon}C(1+|X_t^\epsilon|^2).$$

Using a similar tightness criterion as before, along with (3.3.2) and (3.3.3), the process U^ϵ is tight and $U^\epsilon \Rightarrow U$, where U is an Ornstein-Uhlenbeck process :

$$\begin{aligned} dU_t &= -4\sigma^{-2}\bar{V}U_tdt + \Lambda^{\frac{1}{2}}(\bar{X}_t)dB_t, \\ U_0 &= 0, \end{aligned} \tag{3.3.16}$$

with B being a d-dimensional standard Brownian motion. Thus,

$$U_t = \int_0^t e^{-4\sigma^{-2}(t-s)\bar{V}}\Lambda^{\frac{1}{2}}(\bar{X}_s)dB_s.$$

It follows that

$$\mathbb{E}(U_t^2) = \int_0^t e^{-8\sigma^{-2}(t-s)\bar{V}}\Lambda(\bar{X}_s)ds. \tag{3.3.17}$$

For large t when $\bar{X}_t \sim \bar{X}_\infty$, the SDE (3.3.16) becomes

$$dU_t = -4\sigma^{-2}\bar{V}U_tdt + \Lambda^{\frac{1}{2}}\left(\bar{X}_\infty\right)dB_t.$$

Using (3.3.17), we deduce that

$$\mathbb{E}(U_t^2) \underset{t\to\infty}{\longrightarrow} \bar{S}^2 = \frac{1}{8\sigma^{-2}}\bar{V}^{-1}\Lambda\left(\bar{X}_\infty\right). \tag{3.3.18}$$

We can explicit the expression for $\bar{S}^2$ in the particular case where

$$\nu(d\alpha) = \frac{\Theta}{2} p(\alpha) d\alpha \tag{3.3.19}$$

such that p is the density of a Gaussian distribution $\mathcal{N}(0, M)$ with $M = \omega^2 \mathbf{I}_{\mathbb{R}^d}$. Using the result from Proposition 2.4.2, we have that

$$\begin{aligned} \Lambda(\bar{X}_\infty) &= \frac{4|v|}{\Theta\omega^2} \int_{\mathbb{R}^{d-1}} \int_0^\infty \alpha_1 \alpha \otimes \alpha \nu(d\alpha) \\ &= \frac{2|v|}{(2\pi)^{\frac{d}{2}} \omega^{d+2}} \int_{\mathbb{R}^{d-1}} \int_0^\infty \alpha_1 \alpha \otimes \alpha e^{-\frac{1}{2\omega^2} \sum\limits_{i=1}^{d} \alpha_i^2} d\alpha. \end{aligned} \tag{3.3.20}$$

The first element of this matrix is

$$\Lambda_{1,1}(\bar{X}_\infty) = \frac{2|v|}{\sqrt{2\pi}\omega^3} \int_0^\infty \alpha_1^3 e^{-\frac{\alpha_1^2}{2\omega^2}} d\alpha_1 = \frac{4|v|\omega}{\sqrt{2\pi}}. \tag{3.3.21}$$

For $i = 2, ..., d$,

$$\Lambda_{i,i}(\bar{X}_\infty) = \frac{2|v|}{2\pi\omega^4} \int_{\mathbb{R}} \alpha_i^2 e^{-\frac{\alpha_i^2}{2\omega^2}} d\alpha_i \int_0^\infty \alpha_1 e^{-\frac{\alpha_1^2}{2\omega^2}} d\alpha_1 = \frac{2|v|\omega}{\sqrt{2\pi}}.$$

For $2 \leq i < j \leq d$,

$$\Lambda_{i,j}(\bar{X}_\infty) = \Lambda_{j,i}(\bar{X}_\infty) = \frac{2|v|}{(2\pi)^{\frac{3}{2}}\omega^5} \int_{\mathbb{R}} \alpha_i e^{-\frac{\alpha_i^2}{2\omega^2}} d\alpha_i \int_{\mathbb{R}} \alpha_j e^{-\frac{\alpha_j^2}{2\omega^2}} d\alpha_j \int_0^\infty \alpha_1 e^{-\frac{\alpha_1^2}{2\omega^2}} d\alpha_1 = 0.$$

Similarly, for all $i \neq 1$,

$$\Lambda_{1,i}(\bar{X}_\infty) = \Lambda_{i,1}(\bar{X}_\infty) = 0.$$

Hence,

$$\Lambda(\bar{X}_\infty) = \frac{2|v|\omega}{\sqrt{2\pi}} \begin{pmatrix} 2 & 0 & 0 & ... & 0 \\ 0 & 1 & 0 & ... & 0 \\ 0 & 0 & 1 & ... & 0 \\ ... & ... & ... & ... & ... \\ 0 & 0 & 0 & ... & 1 \end{pmatrix}.$$

It follows that

$$\bar{S}^2 = \frac{|v|}{\sqrt{2\pi}\Theta\sigma^{-2}\omega} \begin{pmatrix} 2 & 0 & 0 & ... & 0 \\ 0 & 1 & 0 & ... & 0 \\ 0 & 0 & 1 & ... & 0 \\ ... & ... & ... & ... & ... \\ 0 & 0 & 0 & ... & 1 \end{pmatrix} = \frac{\omega^2\gamma}{\sqrt{2\pi}} \begin{pmatrix} 2 & 0 & 0 & ... & 0 \\ 0 & 1 & 0 & ... & 0 \\ 0 & 0 & 1 & ... & 0 \\ ... & ... & ... & ... & ... \\ 0 & 0 & 0 & ... & 1 \end{pmatrix},$$

because, for $M = \omega^2 \mathbf{I}_{\mathbb{R}^d}$, $\bar{\omega} = \omega$. Thus, the variance in the direction of the optimum is twice the variance in all other directions.

3. 3. 1. Back to the one dimensional case

We now proceed to a closer examination of these results in the unidimensional case. We remind that, in the first chapter, we classified the behavior of X_t in the univariate case as transient for $v > m$, Harris recurrent for $v < m$ and Harris recurrent or transient in the limiting case $v = m$. Here, we conduct a small jumps limit in the case $v < m$, where the distribution of X_t converges to a unique stationary distribution (i.e., an invariant probability measure) since ν given by (3.3.19) satisfies condition (1.4.5). Some simulated examples of this distribution are illustrated in Figure 3.1.

Evolution of the mean phenotypic lag : In analogy to (3.3.1), we write

$$X_t^\epsilon = X_0 - vt + \int_0^t \frac{1}{\epsilon^2} m_\epsilon(X_s^\epsilon) ds + \mathcal{M}_t^\epsilon,$$

with

$$m_\epsilon(x) = \begin{cases} \int_0^{\frac{-2x}{\epsilon}} \epsilon\alpha \left(1 - \exp\left(-2\sigma^{-2}\epsilon\alpha(2|x| - \epsilon\alpha)\right)\right) \nu(d\alpha) & \text{if } x < 0 \\ \int_{\frac{-2x}{\epsilon}}^0 \epsilon\alpha \left(1 - \exp\left(-2\sigma^{-2}\epsilon\alpha(2|x| - \epsilon\alpha)\right)\right) \nu(d\alpha) & \text{if } x > 0 \end{cases},$$

and the martingale term reads

$$\mathcal{M}_t^\epsilon = \int_0^t \int_{\mathbb{R}} \int_0^1 \epsilon\alpha\varphi(X_{s^-}^\epsilon, \epsilon\alpha, \xi) \bar{M}_\epsilon(ds, d\alpha, d\xi).$$

Equation (3.3.12) reduces to

$$\frac{d\bar{X}_t}{dt} = -v - 4\sigma^{-2} V \bar{X}_t, \tag{3.3.22}$$

with V as defined by (1.2.8). It follows immediately from (3.3.22) that the large-time behavior of $\bar{X}_t$ is :

$$\bar{X}_t \xrightarrow[t\to\infty]{} \bar{X}_\infty = -\frac{v}{4\sigma^{-2}V}. \tag{3.3.23}$$

The variance of the phenotypic lag : To calculate the variance in the small-jumps limit, we combine (3.3.16) and (3.3.20), yielding

$$dU_t = -4\sigma V U_t dt + 2\left(\sigma^{-2}\int_{\mathbb{R}_+} \alpha^3 \nu(d\alpha)\right)^{\frac{1}{2}} \sqrt{|\bar{X}_t|} dB_t, \qquad U_0 = 0, \tag{3.3.24}$$

with B being a standard Brownian motion. Thus,

$$U_t = 2\left(\sigma^{-2}\int_{\mathbb{R}_+} \alpha^3 \nu(d\alpha)\right)^{\frac{1}{2}} \int_0^t \exp\left(-4\sigma^{-2}V(t-s)\right) \sqrt{|\bar{X}_s|} dB_s.$$

It follows that

$$\mathbb{E}(U_t^2) = 4\sigma^{-2}\int_{\mathbb{R}_+} \alpha^3 \nu(d\alpha) \int_0^t \exp(-8\sigma^{-2}V(t-s))|\bar{X}_s| ds.$$

For large t when $\bar{X}_t \sim \bar{X}_\infty$, the SDE (3.3.24) becomes

$$dU_t = -4\sigma^{-2} V U_t dt + \left(\frac{v}{V}\int_0^\infty \alpha^3 \nu(d\alpha)\right)^{-\frac{1}{2}} dB_t \tag{3.3.25}$$

Using (3.3.23), we deduce that

$$\mathbb{E}(U_t^2) \xrightarrow[t\to\infty]{} S^2 = \frac{v}{8\sigma^{-2}V^2}\int_{\mathbb{R}_+} \alpha^3 \nu(d\alpha). \tag{3.3.26}$$

In consequence, for $\epsilon \ll 1$ and large t, $X_t^\epsilon \sim \bar{X}_t + \sqrt{\epsilon} U_t$, and hence,

$$X_t^\epsilon \sim \mathcal{N}\left(\bar{X}_\infty, \epsilon S^2\right).$$

Gaussian distribution of new mutations : We now consider the special case (3.2.3) where we assume that the distribution of new mutations is Gaussian with mean 0 and variance ω^2. In consequence the measure ν is given as

$$\nu(d\alpha) = \frac{\Theta}{2} \times \frac{1}{\omega\sqrt{2\pi}} \exp\left(-\frac{\alpha^2}{2\omega^2}\right) d\alpha, \tag{3.3.27}$$

and V as defined by (1.2.8) equals

$$V = \frac{\Theta}{2} \times \frac{1}{\omega\sqrt{2\pi}} \int_0^\infty \alpha^2 \exp\left(-\frac{\alpha^2}{2\omega^2}\right) d\alpha = \frac{\Theta}{4}\omega^2.$$

It follows that the ODE (3.3.22) becomes

$$\frac{d\bar{X}_t}{dt} = -v - \Theta\omega^2\sigma^{-2}\bar{X}_t. \tag{3.3.28}$$

For $\bar{X}_0 = 0$, its solution is

$$\bar{X}_t = -\frac{v}{\Theta\omega^2\sigma^{-2}}\left(1 - \exp(-\Theta\omega^2\sigma^{-2}t)\right), \tag{3.3.29}$$

which converges exponentially to

$$\bar{X}_\infty = -\frac{v}{\Theta\omega^2\sigma^{-2}} = -\omega\gamma. \tag{3.3.30}$$

Here

$$\gamma = \frac{v/\omega}{\Theta\sigma^{-2}\omega^2} \tag{3.3.31}$$

is the univariate version of (3.3.15) (see Kopp and Hermisson (2009b)) whose denominator can be interpreted as the "adaptive potential" of the population (see the second term on the r.h.s. of eq. (3.3.28)). We note that equation (3.3.28) is analogous to the "canonical equation" (Dieckmann and Law, 1996; Champagnat et al., 2002) of adaptive dynamics (which is also based on a small-jumps limit). In particular, the rate of adaptation (the second term on the right-hand side) is given by the product of the genetic variance created by new mutations per generation, $\Theta\omega^2/2$ and the selection gradient $|d\log(\mathcal{W}(X_t))/dX_t| = 2\sigma^{-2}X_t$ (the slope of the fitness landscape at X_t). Furthermore, equation (3.3.28) is structurally similar to a simplified version of the model by Lynch and Lande (1993) and Bürger and Lynch (1995), who used quantitative-genetics theory to study adaptation to a moving optimum from standing genetic variation.

Using (3.3.21), the Ornstein-Uhlenbeck process describing fluctuations around the long-term mean (3.3.16) becomes

$$dY_t = -\lambda_{\mathrm{OU}}Y_t + \sigma_{\mathrm{OU}}dB_t \tag{3.3.32a}$$

with parameters

$$\lambda_{\mathrm{OU}} = \Theta\sigma^{-2}\omega^2, \tag{3.3.32b}$$

$$\sigma^2_{\mathrm{OU}} = \frac{4v\omega}{\sqrt{2\pi}}. \tag{3.3.32c}$$

Here, λ_{OU} is the rate at which the process tends to revert to its mean, and σ^2_{OU} is the (infinitesimal) variance. Note that λ_{OU} is again given by the "adaptive potential" of the population (the denominator of γ in equation 3.3.31). In contrast, σ^2_{OU} captures the factors that drive the process away from the optimum, that is, the rate of environmental change and the typical size of mutations (leading to adaptation via discrete jumps). We note, however, that the limiting process (3.3.32) is symmetric (such that, e.g., λ_{OU} describes reversion to the mean from both above and below) and no longer reflects the inherent asymmetry of the original model (where X_t decreases due to environmental change and increases due to fixations). The variance around the long-term mean (see eq. 3.3.26) is given by $\sigma_{\mathrm{OU}}^2/(2\lambda_{\mathrm{OU}})$, which evaluates to

$$S^2 = \sqrt{\frac{2}{\pi}}\,\frac{v}{\Theta\sigma^{-2}\omega} = \sqrt{\frac{2}{\pi}}\,\omega^2\gamma. \tag{3.3.33}$$

Equation (3.3.33) can also be derived from the "fluctuation equation" of adaptive dynamics (Boettiger et al., 2010 ; in particular, their eq. 4).

For the original process with finite jumps, equations (3.3.30) and (3.3.33) (or, more generally, 3.3.23 and 3.3.26) are approximate predictions for the long-term mean and variance of the phenotypic lag X if we abusively approximate X_t by $\bar{X}_t + U_t$ (i.e., set $\epsilon = 1$). Figures 3.2A and B compare these predictions to the results from simulations. It can be seen that the predictions from the small-jumps limit are fairly accurate if $|\bar{X}_\infty|/\omega = \gamma \gtrsim 1$ (and very good if $\gamma \gtrsim 10$), provided v is not too close to m. In other words, the approximation is good if the mean lag is larger than the size of a typical mutation (such that adaptive jumps are small relative to the lag, see Fig. ??B), but $v - m$ is not too close to 0. For $\gamma \lesssim 1$ or $v \to m$, in contrast, (3.3.30) and (3.3.33) overestimate both the mean size of the lag and its variance, but the reasons are different in the two cases. For $v \to m$, the approximation does not capture the divergence of the phenotypic lag as the process approaches the transient case. The reason is that equation (3.3.28) assumes weak selection, and in particular, that the fixation probability $g(x,\alpha) \approx 2s(x,\alpha)$, whereas the real fixation probability of finitely-sized mutations is lower (see eq. 2.1.2) and saturates at 1 as $X_t \to -\infty$. For $\gamma \lesssim 1$, the small-jumps approximation is invalid because adaptive jumps are large relative to the mean lag (and often overshoot the optimum, leading to $X_t > 0$, see Fig. ??A). Indeed, simulations show that the mean lag is significantly larger than predicted by (3.3.30). The reason is that, for $\gamma \ll 1$, adaptive jumps are relatively rare (because only few mutations are beneficial), and the lag will continue to increase until a successful mutation arrives. Figure 3.2C shows, in addition, that for small γ the variance of the lag converges to the square of the mean, such that the coefficient of variation is close to 1 (Fig. 3.2D).

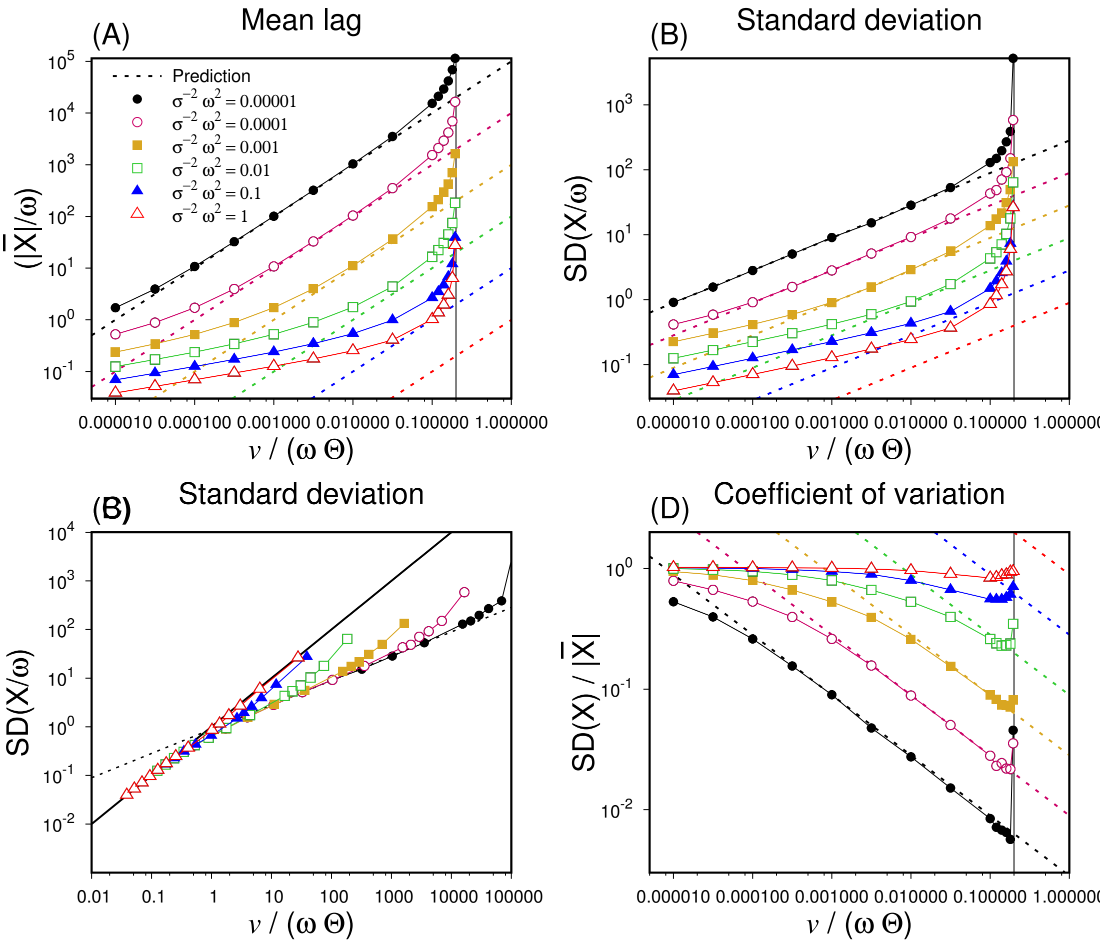

Figure 3.2. – Properties of the stationary distribution in the recurrent case (results from simulations of 10^6 adaptive steps). (A) The magnitude of the mean phenotypic lag $\mathbb{E}(|X|/\omega)$ (relative to the mutational standard deviation ω), as a function of the scaled rate of environmental change $v/(\omega\Theta)$ for various values of the scaled strength of selection $\sigma^{-2}\omega^2$. The dotted lines represent the analytical prediction from eq. (3.3.30) (from top to bottom for the same values of $\sigma^{-2}\omega^2$ as the simulation data). (B) The standard deviation of the scaled lag (same data as in A). The dotted lines represent the analytical predictions from eq. (3.3.33). (C) The standard deviation as a function of the mean lag. The dotted line marks the analytical prediction according to equations (3.3.30) and (3.3.33). The dashed line markes the main diagonal (CV = 1). (D) The coefficient of variation (standard deviation over mean) of the lag, with the dotted lines again marking the analytical predictions. The vertical line in (A), (B) and (D) marks the boundary between the recurrent and transiented cases ($v = m = \Theta\omega/\sqrt{8\pi} \Leftrightarrow v/(\omega\Theta) = 1/\sqrt{8\pi}$).

3. 3. 2. Population survival and extinction

A question of considerable interest to biologists is how much environmental change a population can compensate by adaptive evolution without going extinct (e.g., Bürger and Lynch, 1995; Kopp and Matuszewski, 2014). While our model does not directly include explicit population dynamics, a simple approach is to assume that extinction risk is strongly elevated once the phenotypic lag drops below a critical threshold X_{crit}. For example, if individuals that survive selection have, on average, $n_{\text{off}} > 1$ offspring, population size will start declining once the population (mean) fitness drops below $1/n_{\text{off}}$, that is, once $X_t < X_{\text{crit}}$, where

$$X_{\text{crit}} = -\sqrt{\sigma^2 \ln n_{\text{off}}}.$$

Extinction will usually follow rapidly (Bürger and Lynch, 1995), even though "evolutionary rescue" (Gonzalez et al., 2013) is still possible by the timely arrival and fixation of a beneficial mutation (Orr and Unckless, 2008; Uecker and Hermisson, 2011; Orr and Unckless, 2014). If the process is transient, it will reach the critical value after at most $X_{\text{crit}}/(m-v)$ generations. In contrast, if the process is recurrent, it may spend most of its time above X_{crit}. Note, however, that even in this case, eventual extinction is certain, because the process has a non-zero probability of reaching any arbitrarily low value. The key question is, therefore : How long will the process typically remain above X_{crit} ? Neglecting the possibility of evolutionary rescue, we will call this the "time to extinction" and denote it by T_e.

Obviously, the time to reach X_{crit} strongly depends on the rate of environmental change (Fig. 3.3). Typically, extinction risk is negligible if the mean lag is less than one mutational standard deviation ($\gamma < 1$, corresponding to $v/(\omega\Theta) < \sigma^{-2}\omega^2$ in Fig. 3.3), unless the fitness effect of a single mutation is very strong ($\sigma^{-2}\omega^2$ close to 1, Fig. 3.3E, F). For $\gamma > 1$, we can gain additionnal insights from the small-jumps approximation.

First, extinction risk should certainly be high if the long-term mean of the process $\bar{X}_\infty < X_{\text{crit}}$. Staying with assumption (3.2.3), it follows immediately from (3.3.28) that the "critical rate of environmental change" (Bürger and Lynch, 1995) satisfies

$$v_{\text{crit}} = \Theta\omega^2\sigma^{-2}|X_{\text{crit}}| = \Theta\omega^2\sqrt{\sigma^{-2}\ln n_{\text{off}}}. \tag{3.3.34}$$

If $v > v_{\text{crit}}$, the time to extinction might be estimated by setting the right-hand side of the deterministic approximation (3.3.29) equal to X_{crit} and solving for t (see Bürger and Lynch, 1995). However, the solution diverges as $v \downarrow v_{\text{crit}}$, and generally overestimates the real time to extinction, because it neglects stochastic fluctuations. Indeed, simulations show that, for $v > v_{\text{crit}}$, the time to extinction is typically of order X_{crit}/v, that is, it is only slightly prolonged by the fixation of beneficial mutations (see Fig. 3.3). If, on the contrary, $v < v_{\text{crit}}$, we can use the fact that the process converges to an Ornstein-Uhlenbeck process around $\bar{X}_\infty$ (eq. 3.3.32). The time to extinction can then be decomposed into the time for X_t to drop from 0 to $\bar{X}_\infty$ and the additional time from $\bar{X}_\infty$ to X_{crit}. Unless v is close to v_{crit}, the first part will be much shorter than the second and can be approximated (and slightly underestimated) by $|\bar{X}_\infty|/v$. The second part is highly stochastic and can be approximated by the first-passage time T_f of the process $\bar{X}_\infty + U_t$ by X_{crit} when starting at $\bar{X}_\infty$. Thus, in summary,

$$T_e \approx \begin{cases} |\bar{X}_\infty|/v + T_f & \text{if } v \leq v_{\text{crit}}, \\ |X_{\text{crit}}|/v & \text{if } v > v_{\text{crit}}. \end{cases} \tag{3.3.35}$$

Following Thomas (1975) and Ricciardi and Sato (1988, see also Finch, 2004), T_f has mean

$$\begin{aligned} \mathbb{E}(T_f) &= \frac{\sqrt{\pi/2}}{\lambda_{\text{OU}}} \int_0^{|\tilde{X}_{\text{crit}}|} \left(1 + \text{erf}\left(\frac{t}{\sqrt{2}}\right)\right) \exp\left(\frac{t^2}{2}\right) dt \\ &= \frac{1}{2\lambda_{\text{OU}}} \sum_{k=1}^{\infty} \frac{\left(\sqrt{2}|\tilde{X}_{\text{crit}}|\right)^k}{k!} \Gamma\left(\frac{k}{2}\right) \end{aligned} \tag{3.3.36}$$

and variance

$$\begin{aligned} \text{Var}(T_f) &= \frac{\sqrt{2\pi}}{\lambda_{\text{OU}}^2} \int_0^{|\tilde{X}_{\text{crit}}|} \int_{-\infty}^{t} \int_s^{|\tilde{X}_{\text{crit}}|} \left(1 + \text{erf}\left(\frac{r}{\sqrt{2}}\right)\right) \exp\left(\frac{r^2 + t^2 - s^2}{2}\right) dr\, ds\, dt - \mathbb{E}(T_f)^2 \\ &= \mathbb{E}(T_f)^2 - \frac{1}{2\lambda_{\text{OU}}^2} \sum_{k=1}^{\infty} \frac{\left(\sqrt{2}|\tilde{X}_{\text{crit}}|\right)^k}{k!} \Gamma\left(\frac{k}{2}\right) \left(\phi\left(\frac{k}{2}\right) - \phi(1)\right), \end{aligned} \tag{3.3.37}$$

where $\tilde{X}_{\text{crit}} = (X_{\text{crit}} - \bar{X}_\infty) \frac{\sqrt{2\lambda_{\text{OU}}}}{\sigma_{\text{OU}}}$, $\phi(\,\cdot\,)$ is the digamma function and

$$\text{erf}(x) = \frac{2}{\sqrt{\pi}} \int_0^x e^{-t^2} dt$$

is the Gauss Error Function. Figure 3.3 compares these predictions to results from simulations. As long as $\sigma^{-2}\omega^2 \leq 0.01$, the mean time to extinction is well approximated by (3.3.35) and (3.3.36), even though it is slightly underestimated in the region where $v \approx v_{\text{crit}}$ (because we neglect adaptive steps before X_t reaches $\bar{X}_\infty$ or X_{crit}, respectively) and for small values of $v/(\omega\Theta)$ (probably as a result of the finite intervals between jumps in our simulations). Similarly, the variance is well approximated by (3.3.35) and (3.3.37), as long as $v < v_{\text{crit}}$ (whereas we lack a prediction for the variance in the opposite case $v > v_{\text{crit}}$). Note that, in Figure 3.3, the predictions were improved (in particular for $\sigma^{-2}\omega^2 = 0.01$) by replacing the mean lag $\bar{X}_\infty$ according to (3.3.30) by the value found in simulations (see Fig. 3.2). Also note that, for small v, the mean and standard deviation of the time to extinction are nearly identical, suggesting that T_e follows an exponential distribution (which can be confirmed by histograms ; not shown). Finally, for $\sigma^{-2}\omega^2 > 0.01$, the approximation (3.3.35) breaks down, because $\gamma < 1$ even for large v and, hence, the small-jumps approximation does not apply. Extinction is nevertheless high, because even a small deviation from the optimum (relative to the mutational standard deviation) has dramatic fitness consequences. We note, however, that these extreme parameter values are probably unrealistic, because the fitness effects of single mutations for quantitative traits are usually small. For example, Bürger and Lynch (1995) assumed $\omega^2 = 0.05$ and considered values of σ^{-2} between 0.005 and 0.5, implying $\sigma^{-2}\omega^2$ between 0.00025 and 0.025 (or 0.0125 if selection is "diluted" by non-genetic phenotypic variation).

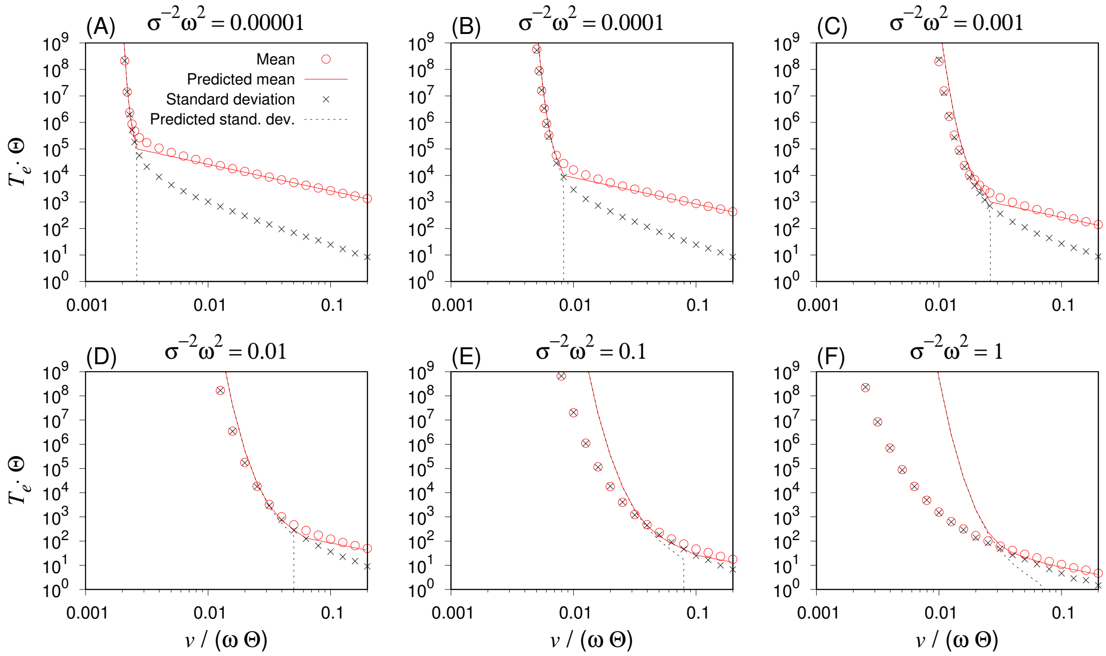

Figure 3.3. – The time T_e (relative to the mean interval between new mutations) until the population mean fitness $\mathcal{W}(X_t)$ drops below $1/2$ for the first time ("time to extinction "), as a function of the scaled rate of environmental change $v/(\omega\Theta)$ for various values of the scaled strength of selection $\sigma^{-2}\omega^2$. Open circles show the mean and red crosses the standard deviation from 1000 replicated simulations. The solid line shows the analytical prediction for the mean, (eq. 3.3.35 and 3.3.36, where $\bar{X}_\infty$ from eq. 3.3.30 has been replaced by the mean lag from simulations, see Fig. 3.2), and the dotted line the prediction for the standard deviation (square root of eq. 3.3.37). Note that the latter is 0 for $v > v_{\text{crit}}$ (eq. 3.3.34), because our approximation (3.3.35) considers stochasticity only after the process has reached its long-term mean $\bar{X}_\infty$ (and at this value, the population is already extinct).

Finally, some simple scaling relations can be obtained for $v < v_{\text{crit}}$ by applying a further approximation to the first-passage time T_f. Indeed, for $|\tilde{X}_{\text{crit}}| \gtrsim 1.5$, the mean $\mathbb{E}(T_f)$ (eq. 3.3.36) is well approximated by

$$\mathbb{E}(T_f) \approx \frac{\sqrt{2\pi}}{\lambda_{\text{OU}}|\tilde{X}_{\text{crit}}|} \exp\left(\frac{\tilde{X}^2_{\text{crit}}}{2}\right), \tag{3.3.38}$$

(Ricciardi and Sato, 1988) and the variance $\text{Var}(T_f)$ (eq. 3.3.37) by the square of this value (showing again that, for small v, T_e converges to an exponential distribution). For most values of $\tilde{X}_{\text{crit}}$, the estimate (3.3.38) is dominated by the exponential term

$$\begin{aligned}
\exp\left(\frac{\tilde{X}^2_{\text{crit}}}{2}\right) &= \exp\left[\frac{\lambda_{\text{OU}}}{\sigma^2_{\text{OU}}}(X_{\text{crit}} - \bar{X}_\infty)^2\right] \\
&= \exp\left[\frac{\sqrt{2\pi}\Theta\omega\sigma^{-2}}{4v}\left(\sqrt{\frac{\ln n_{\text{off}}}{\sigma^{-2}}} - \frac{v}{\Theta\omega^2\sigma^{-2}}\right)^2\right] \\
&= \exp\left[\frac{\sqrt{2\pi}}{4\gamma}\left(\frac{X_{\text{crit}}}{\omega} - \gamma\right)^2\right].
\end{aligned} \tag{3.3.39}$$

In particular, as long as $v \ll v_{\text{crit}}$, the difference $X_{\text{crit}} - \bar{X}_\infty$ (the squared term in the exponent) depends only weakly on v, Θ and ω. To a first approximation, therefore, the mean time to extinction in this case scales with $\exp(\Theta\omega/v)$ (second line of equation 3.3.39). In contrast, the dependence on σ^{-2} is more complex, since σ^{-2} affects both X_{crit} and $\bar{X}_\infty$, leading to a non-monotonic relation if v is intermediate (Fig. 3.4). The reason is that, for both low and high σ^{-2}, the mean time to extinction approaches the minimum X_{crit}/v. For small σ^{-2}, selection is so weak that, even though $|X_{\text{crit}}|$ is large, almost no mutations get fixed. For large σ^{-2}, $|X_{\text{crit}}|$ is so small that the population has a high probability of going extinct before the first fixation can occur. In contrast, for intermediate σ^{-2}, $|X_{\text{crit}}|$ is sufficiently large and selection sufficiently efficient to prevent population extinction over long periods due to the fixation of beneficial mutations. Finally, the last line of equation (3.3.39) shows that if $X_{\text{crit}} \ll \bar{X}_\infty$ is treated as a constant and is measured relative to ω then the time to reach this value scales with $\exp(\gamma^{-1})$.

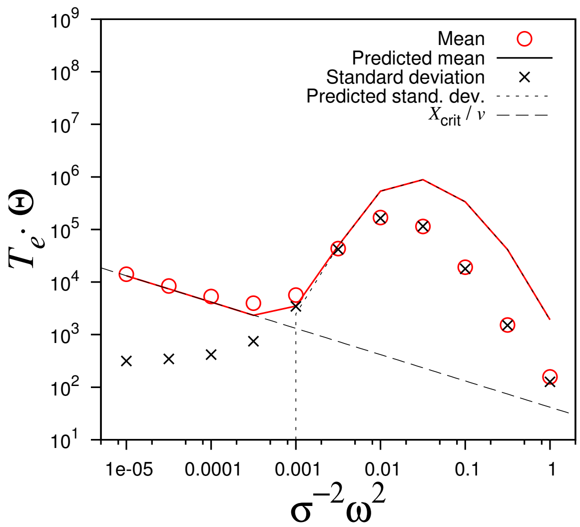

Figure 3.4. – The time T_e (relative to the mean interval between new mutations) until the population mean fitness $\mathcal{W}(X_t)$ drops below $1/2$ for the first time ("time to extinction"), as a function of the scaled strength of selection $\sigma^{-2}\omega^2$ for an intermediate rate of environmental change ($v/(\omega\Theta) = 0.02$). The dashed line marks the minimal time X_{crit}/v. For further details, see Fig. 3.3.

3. 3. 3. Discussion

We have studied a stochastic process describing an "adaptive-walk" of an evolving population following a moving phenotypic optimum via the quasi-instantaneous fixation of beneficial mutations. The process combines a continuous and deterministic increase of the phenotypic lag between a population and its environment (environmental change) with discrete and stochastic adaptive jumps (fixation of beneficial mutations), whose frequency and size increase with the magnitude of the lag. Despite its simplicity, this model captures essential aspects of adaptive evolution in a changing environment. It has previously been shown to provide accurate approximations for a much more detailed individual-based model over a large range of parameter values (Kopp and Hermisson, 2009b).

After establishing the basic mathematical properties of the process in the first two chapters, we aimed to gain further insight into its behavior in the recurrent case. For this purpose, we analysed a small-jumps limit, which allowed us to derive approximations for the mean and variance of the stationary distribution of the phenotypic lag. Even though valid only in part of parameter space, these approximations are highly instructive and allow us to place our results in the context of previous studies of the moving optimum model. In particular, both the mean and the variance in the small-jumps limit depend on the composite parameter γ (eq. 3.3.15, 3.3.31), whose key role in the moving-optimum model had already been shown by Kopp and Hermisson (2009a,b) and Matuszewski et al. (2014). This parameter can be interpreted as a scaled rate of environmental change, which relates the unscaled rate v/ω (measured in units of the mutational standard deviation ω) to the "adaptive potential" of the population ($\Theta\sigma^{-2}\omega^2$), which determines the rate of evolution towards the optimum in the small-jumps limit (eq. 3.3.28, 3.3.32) ; the latter combines the mutation rate Θ with the strength of selection towards the optimum (σ^{-2}, again relative to ω). Here, we show that, when the phenotypic lag in the univariate case is measured relative to ω, its mean in the small-jumps limit is simply equal to γ and that its variance is $\gamma\sqrt{2/\pi}$. In the multivariate case, the phenotypic lag depends furthermore on the structure of the mutational covariance matrix M. In particular, mutational correlations can create a lag also in directions perpendicular to the vector of environmental change ("flying kite effect" ; Jones et al., 2004; Matuszewski et al., 2014). Finally, in the absence of mutational correlations, we can show that the variance in the direction of the optimum is twice that in other directions.

Focusing on the univariate case, comparison to simulations shows that the predictions from the small-jumps limit perform reasonably well as long as $\gamma \gtrsim 1$, that is, as long as the mean lag exceeds the effect of a typical mutation (and, in addition, environmental change is not too close to the boundary of the transient case). This observation conforms nicely to the classification introduced in Kopp and Hermisson (2009b), who stated that for $\gamma \ll 1$, the adaptive process is "environmentally-limited", whereas for $\gamma \gg 1$, it is "genetically-limited". The idea is that for $\gamma \ll 1$, the mean lag is so small that large mutations are usually selected against (as they would overshoot the optimum by too much), and hence, which mutations are fixed depends primarily on the rate of environmental change. In contrast, for $\gamma \gg 1$, the mean lag is large, so most mutations with $\alpha > 0$ are positively selected most of the time and their rate of fixation depends primarily on genetic factors (i.e., the rate and distribution of new mutations ; for a discussion of the boundary between these two regimes, see Supporting Information 3 in Matuszewski et al., 2014). It is, thus, in the genetically-limited regime that the small-jumps approximation is accurate. We note, however, that the small-jumps approximation predicts that the stationary distribution of the lag is Gaussian (the stationary distribution of an Ornstein-Uhlenbeck process), whereas simulations show that the stationary distribution of our process with finite-sized mutations is typically negatively skewed (although this effect is weak in Fig. 3.1).

In the environmentally-limited regime ($\gamma \ll 1$), the small-jumps approximation fails, because most mutations are large relative to the phenotypic lag. Indeed, Kopp and Hermisson (2009b) proposed a different approximation for this case : Since most large mutations are selected against, the successful mutations resulting in adaptive jumps come from the center of the distribution of new mutations, which therefore can be approximated by a uniform distribution with density equal to $p(0)$, the value of the density at $\alpha = 0$. Under this approximation, equation (1.3.2) simplifies to

$$X_t = X_0 - vt - \frac{4}{3}\Theta p(0)\int_0^t \mathrm{sign}(X_s)(X_s)^4 ds + \mathcal{M}_t,$$

but unfortunately, this equation does not allow to directly calculate the long-term moments of the process. However, some qualitative insight can be gained using a result from Kopp and Hermisson (2009b), who showed that, if the distribution of new mutations is uniform, the mean lag immediately before the *first* adaptive jump equals $\Gamma(5/4)(3\gamma/p(0))^{1/4}$. While this value is different from the long-term mean $\bar{X}_\infty$, it shows the same scaling relation, as can be seem from the fact that, for small $v/(\omega\Theta)$ and $\sigma^{-2}\omega^2$, the graphs in Figure 3.2A have slope close to $1/4$. In addition, Figure 3.2C shows that, in the environmentally-limited regime, the standard deviation of the lag is almost identical to the mean, such that the coefficient of variation is very close to 1 (Fig. 3.2D). We do not have analytical results to explain this observation, but intuitively, it is likely linked to the fact that, if new advantageous mutations are approximately uniform, whenever the lag before a jump is x, the mean size of the jump will also be close to x.

Finally, we applied our results to investigate the time until the population reaches a dangerously high level of maladaptation, entailing a significant risk of extinction. In the context of a moving optimum, this question has previously been studied mainly in quantitative-genetics models (which assume adaptation from standing genetic variation). Following Lynch and Lande (1993) and Bürger and Lynch (1995), several authors have calculated "critical rate of environmental change" v_{crit}, beyond which the equilibrium phenotypic lag becomes too large for the population to tolerate (reviewed in Kopp and Matuszewski, 2014). Here, we have found an equivalent expression by using the small-jumps approximation. The result is very simple : The critical rate of environmental change equals the critical phenotypic lag times the adaptive potential of the population.

Indeed, our equation (3.3.34) is structurally similar to equation (10) from Bürger and Lynch (1995). It is tempting to use these results for a comparison of critical rates when adaptation is based on either new mutations or standing genetic variation. However, such a comparison is problematic due to the different assumptions and approximations underlying the two approaches (in particular, instantaneous fixation in our model, and constant genetic variance without new mutations in the model by Bürger and Lynch, 1995). Nevertheless, it is worth mentioning that the genetic variance that is "active" in our model (Θ/ω^2) is exactly half the standing genetic variance expected in the limit of weak selection ($\Theta\omega^2$). This suggests that, under weak selection, the presence of standing genetic variation might increase the critical rate of environmental change by about a factor of 2.

However, even below this critical rate, the population will ultimately go extinct due to stochastic fluctuations, but so far, the time until this event had been studied only by simulations. Here, we used the fact that, in the small-jumps limit, our process converges to an Ornstein-Uhlenbeck process around the expected mean lag. We then used known results on the first-passage time of this process to derive analytical predictions for the time to extinction. In particular, a simple approximation yields that the time to extinction is proportional to $\exp(\Theta\omega/v)$, that is, it is exponential in the mutation rate, mutational standard deviation and the inverse of the speed of environmental change. In contrast, the dependence on the strength of stabilizing selection is more complex and non-monotonic, since this parameter influences not only the adaptive potential but also the critical phenotypic lag. Finally, we find that the distribution of the time to extinction is approximately exponential if v is sufficiently below v_{crit}. These results are in qualitative agreement with the simulations in Bürger and Lynch (1995).

Our approximation is valid in the genetically-limited regime. In the environmentally-limited regime, extinction times are usually extremely high, unless selection is unrealistically strong. For very high $\sigma^{-2}\omega^2$ (Fig. 3.3E,F), extinction times from simulations also seem to be approximately exponential in $1/v$. Again, a potential explanation can be found in the results from Kopp and Hermisson (2009b), who showed that, in the environmentally-limited regime, the probability that the process reaches X_{crit} before the first jump (when starting at 0) is given by $\exp(-X_{\text{crit}}^4/(3\sqrt{2\pi\omega^2}\gamma))$, and hence, the time until this event occurs for the first time should arguably scale with $\exp(\gamma^{-1})$.

Future work should strive to extend our results about extinction times to the multivariate case. Indeed, in the small-jumps limit, the predicted lag in the direction on the optimum is independent of the total number of traits under selection, d (see eq. 3.3.14). However, the small-jumps approximation does not capture the fact that, for finite mutational effect sizes, the proportion of beneficial mutations decreases with d (the key argument from Fisher's geometric model ; Fisher, 1930), inducing a "cost of complexity" Orr (2000), which should be incorporated into an extended theory.

Appendices

A. Proof of Lemma 2.4.4

For $r > 0$ and for all unit vector $u \in A^-$,

$$\begin{aligned}
\sqrt{r} \times \left|\psi(ru) - \bar{\psi}(u)\right| &= \sqrt{r} \times \left|\int_{\mathbb{R}^2} \alpha \left(\mathbf{1}_{\{(u|\alpha)\leq 0\}} - g(ru,\alpha)\right) \nu(d\alpha)\right| \\
&\leq \sqrt{r}\left|\int_{\mathbb{R}^2} \alpha \left(\mathbf{1}_{\{(u|\alpha)\leq 0\}} - \mathbf{1}_{\{(2ru+\alpha|\alpha)\leq 0\}}\right) \nu(d\alpha)\right| \\
&+ \sqrt{r} \times \int_{\mathbb{R}^2} |\alpha| e^{2r\left(2u+\frac{\alpha}{r}|\alpha\right)} \mathbf{1}_{\{(2ru+\alpha|\alpha)\leq 0\}} \nu(d\alpha) \\
&\leq \frac{\Theta\sqrt{r}}{4\pi\sqrt{\det(M)}} \left|\int_{\mathbb{R}^2} \alpha \mathbf{1}_{\left\{0\geq(u|\alpha)\geq -\frac{|\alpha|^2}{2r}\right\}} e^{-\frac{1}{2}\alpha' M^{-1}\alpha} d\alpha\right| \\
&+ \sqrt{r} \times \int_{\mathbb{R}^2} |\alpha| e^{2(2ru+\alpha|\alpha)} \mathbf{1}_{\{(2ru+\alpha|\alpha)\leq 0\}} \nu(d\alpha).
\end{aligned} \tag{A.1}$$

Let us treat the first term of the last estimate of (A.1). Without loss of generality, we fix $u = (-1, 0)$. This is possible since a suitable planar rotation will bring us back to any unit vector of A^-. The transformation will affect the matrix M but the result of this Lemma remains unchanged since it is established for arbitrary M.

$$\sqrt{r}\left|\int_{\mathbb{R}^2} \alpha \mathbf{1}_{\left\{0\geq(u|\alpha)\geq -\frac{|\alpha|^2}{2r}\right\}} e^{-\frac{1}{2}\alpha' M^{-1}\alpha} d\alpha\right| = \sqrt{r}\left|\int_{\mathbb{R}^2} \alpha_1 \mathbf{1}_{\left\{0\geq(u|\alpha)\geq -\frac{|\alpha|^2}{2r}\right\}} e^{-\frac{1}{2}\alpha' M^{-1}\alpha} d\alpha\right|,$$

since the set $\left\{0 \geq (u \mid \alpha) \geq -\frac{|\alpha|^2}{2r}\right\}$ is symmetric around the x-axis. Furthermore, M is a positive definite matrix hence there exists $c_M > 0$ such that

$$c_M = \inf_{|u|=1} u' M^{-1} u > 0.$$

It follows that

$$\left|\int_{\mathbb{R}^2} \alpha \mathbf{1}_{\left\{0\geq(u|\alpha)\geq -\frac{|\alpha|^2}{2r}\right\}} e^{-\frac{1}{2}\alpha' M^{-1}\alpha} d\alpha\right| \leq \int_{B_R^c} |\alpha| e^{-\frac{c_M}{2}|\alpha|^2} d\alpha + \int_{B_R \bigcap C_r^c} \alpha_1 \mathbf{1}_{\{\alpha_1>0\}} e^{-\frac{c_M}{2}|\alpha|^2} d\alpha.$$

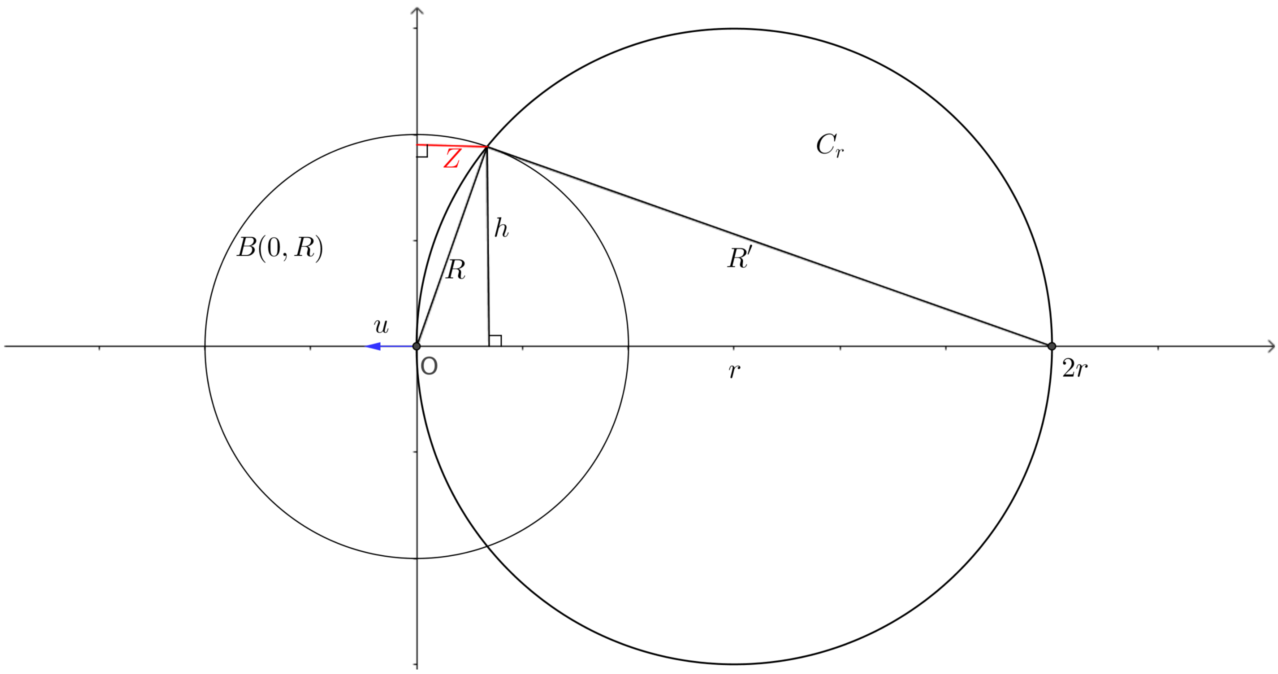

Figure .5. – Geometric insight for the first part of the proof of Lemma 2.4.4. C_r is the disk centered around $(r,0)$ with radius r.

We have that

$$\begin{aligned}\int_{B_R^c} |\alpha| e^{-\frac{c_M}{2}|\alpha|^2} d\alpha &\leq \int_0^{2\pi} \int_R^{\infty} \rho^2 e^{-\frac{c_M}{2}\rho^2} d\rho d\gamma \\ &\leq \frac{2\pi}{c_M} R e^{-\frac{c_M}{2}R^2} + \frac{1}{c_M} \int_R^{\infty} e^{-\frac{c_M}{2}\rho^2} d\rho \\ &\leq \frac{2\pi}{c_M} R e^{-\frac{c_M}{2}R^2} + \frac{1}{c_M} \sqrt{\frac{2\pi}{c_M}} e^{-(R+1)\sqrt{c_M}},\end{aligned}$$

since

$$\int_R^{\infty} e^{-\frac{c_M}{2}\rho^2} d\rho = \sqrt{\frac{2\pi}{c_M}} \mathbb{P}(X > R) = \sqrt{\frac{2\pi}{c_M}} \mathbb{P}\left(e^{X\sqrt{c_M}} > e^{R\sqrt{c_M}}\right) \leq \sqrt{\frac{2\pi}{c_M}} e^{-(R+1)c_M},$$

due to Bienaymé-Tchebychev inequality. On the other hand,

$$\int_{B_R \bigcap C_r^c} \alpha_1 e^{-\frac{c_M}{2}|\alpha|^2} d\alpha \leq \sqrt{\frac{2\pi}{c_M}} Z,$$

as shown in Figure .5 that reveals the following relations :

$$\begin{aligned}
&R^2 + (R')^2 = 4r^2,\\
&R \times R' = h \times 2r,\\
&Z^2 + h^2 = R^2.
\end{aligned}$$

Hence,

$$h^2 = \frac{R^2(R')^2}{4r^2} = \frac{R^2(4r^2 - R^2)}{4r^2} = R^2 - \frac{R^4}{4r^2},$$

yielding

$$Z^2 = \frac{R^2}{4r^2}.$$

Finally by choosing $R = r^{\frac{1}{4}}$ we have that

$$\sqrt{r}\left|\int_{\mathbb{R}^2}\alpha \mathbf{1}_{\left\{0\geq(u|\alpha)\geq-\frac{|\alpha|^2}{2r}\right\}} e^{-\frac{1}{2}\alpha' M^{-1}\alpha}d\alpha\right| \leq \frac{2\pi}{c_M} r^{\frac{3}{4}} e^{-\frac{c_M}{2}\sqrt{r}} + \frac{1}{c_M}\sqrt{\frac{2\pi r}{c_M}}\, e^{-(r^{\frac{1}{4}}+1)\sqrt{c_M}} + \sqrt{\frac{2\pi}{c_M}}\,\frac{1}{2r^{\frac{1}{4}}}.$$

Thus, the first term of the estimate (A.1) goes to 0 as r goes to ∞.

Now we treat the second term of the last estimate of (A.1) for all $u \in A^-$. Let

$$f_r(\alpha) = \sqrt{r}|\alpha| e^{2(2ru+\alpha|\alpha)}\mathbf{1}_{\{(2ru+\alpha|\alpha)\leq 0\}}.$$

It is clear that $f_r(\alpha) \neq 0$ iff $r \geq \frac{|\alpha|^2}{|(u|\alpha)|}$ and $f_r(\alpha) \xrightarrow[r\to\infty]{} 0$. Let $h(\alpha) = \sup_r f_r(\alpha) > 0$. We have that

$$\frac{\partial f_r(\alpha)}{\partial r} = \frac{|\alpha|}{2\sqrt{r}}\left(1 + 2r^2\,(u \mid \alpha)\right) e^{2(2ru+\alpha|\alpha)}\mathbf{1}_{\{(2ru+\alpha|\alpha)\leq 0\}}.$$

r		$\frac{1}{\sqrt{2\lvert(u\lvert\alpha)\rvert}}$	
$\frac{\partial f_r(\alpha)}{\partial r}$	$+$	0	$-$
$f_r(\alpha)$	$\nearrow$		$\searrow$

Hence,

$$h(\alpha) = \begin{cases} f_{\frac{|\alpha|^2}{|(u|\alpha)|}}(\alpha) & \text{if } \frac{|\alpha|^2}{|(u|\alpha)|} \geq \frac{1}{\sqrt{2|(u|\alpha)|}} \\ f_{\frac{1}{\sqrt{2|(u|\alpha)|}}}(\alpha) & \text{if } \frac{|\alpha|^2}{|(u|\alpha)|} \leq \frac{1}{\sqrt{2|(u|\alpha)|}} \end{cases}$$

It follows that

$$h(\alpha) \leq \frac{|\alpha|^2}{\sqrt{|(u \mid \alpha)|}} + \frac{|\alpha|^2}{(2\,|(u \mid \alpha)|)^{\frac{1}{4}}} \in L^1(\nu).$$

It follows from the dominated convergence theorem that

$$\int_{\mathbb{R}^2} f_r(\alpha)\nu(d\alpha) \xrightarrow[r\to\infty]{} 0.$$

Thus,

$$\sqrt{r} \times \left|\psi(ru) - \bar{\psi}(u)\right| \xrightarrow[r\to\infty]{} 0.$$

B. Proof of Lemma 2.4.5

With $f(x) = |x|$, there exists $0 \leq \theta = \theta(\alpha) \leq 1$ s.t.

$$\begin{aligned}
|x+\alpha| - |x| &= (\nabla f(x+\theta\alpha)|\alpha) \\
&= \left(\frac{x+\theta\alpha}{|x+\theta\alpha|}|\alpha\right), \\
|x+\alpha| - |x| - (u|\alpha) &= \left(\frac{x+\theta\alpha}{|x+\theta\alpha|} - \frac{x}{|x|}|\alpha\right) \\
&= (\nabla f(x+\theta\alpha) - \nabla f(x)|\alpha) \\
&= \theta\left(\partial^2 f(x+\theta'\alpha)\alpha|\alpha\right)
\end{aligned}$$

Applying the Intermediate Values Theorem is justified since the segment joining x and $x+\alpha$ does not pass by 0. We forget about the first θ which is unimportant, and write θ for θ'. The above quantity equals

$$\frac{|\alpha|^2}{|x+\theta\alpha|} - \frac{(x+\theta\alpha|\alpha)^2}{|x+\theta\alpha|^3},$$

whose absolute value is dominated by

$$2\frac{|\alpha|^2}{|x+\theta\alpha|}.$$

It thus remains to show that

$$|x|\int_{\mathbb{R}^2} \frac{|\alpha|^2}{|x+\theta\alpha|} g(x,\alpha)\nu(d\alpha)$$

remains bounded as $|x| \to \infty$. Note that the integrand is integrable on $\mathbb{R}^2$.

We split the integral in two pieces. The first piece is (recall that $0 \leq \theta \leq 1$, hence on the set $\{|\alpha| \leq |x|/2\}$, $|x + \theta\alpha| \geq |x|/2$)

$$|x| \int_{|\alpha| \leq |x|/2} \frac{|\alpha|^2}{|x+\theta\alpha|} g(x,\alpha)\nu(d\alpha) \leq 2 \int_{\mathbb{R}^2} |\alpha|^2 g(x,\alpha)\nu(d\alpha)$$
$$\leq 2 \int_{\mathbb{R}^2} |\alpha|^2 \nu(d\alpha),$$

which does not depend upon x. The second term reads

$$|x| \int_{|\alpha|>|x|/2} \frac{|\alpha|^2}{|x+\theta\alpha|} g(x,\alpha)\nu(d\alpha)$$
$$\leq |x| \left(\nu(|\alpha| > |x|/2)\right)^{1/4} \times \left(\int_{\mathbb{R}^2} |\alpha|^8 \nu(d\alpha)\right)^{1/4} \times \left(\int_{\mathbb{R}^2} \frac{1}{|x+\theta\alpha|}\nu(d\alpha)\right)^{1/2}.$$

It is plain that each of the three factors of this right hand side is bounded as a function of x. In particular the first factor tends to 0 as $|x| \to \infty$.

C. Proof of Lemma 2.4.6

Consider

$$A(x,\alpha) := \left| \arctan\left(\frac{x_2+\alpha_2}{x_1+\alpha_1}\right) - \arctan\left(\frac{x_2}{x_1}\right) - |x|^{-1}(u^\perp|\alpha)\right|$$

We want to show that (we get rid of the factor $g(x,\alpha)$, since $0 \leq g(x,\alpha) \leq 1$)

$$\int_{\mathbb{R}^2} A(x,\alpha)\nu(d\alpha) \leq C_2|x|^{-2}.$$

We split this integral into two parts, the first one being

$$\int_{|\alpha|>|x|/2} A(x,\alpha)\nu(d\alpha) \leq C\left(1 + \frac{1}{|x|}\right)\nu(|\alpha| > |x|/2),$$

which is easily seen to converge to 0 as $|x| \to \infty$ faster than any power of $|x|^{-1}$.

We now consider the integral

$$\int_{|\alpha| \leq |x|/2} A(x,\alpha)\nu(d\alpha).$$

For that sake, we note that the increment of the function $\varphi(x) = \arctan(x^2/x^1)$ can be expressed using the derivatives of that function at some intermediate point, so that for some $0 \leq \theta' = \theta'(\alpha) \leq \theta = \theta(\alpha) \leq 1$, since on the set $\{|\alpha| \leq$

$|x|/2\}$, $|x+\theta'\alpha|\geq |x|/2$,

$$\begin{aligned}
A(x,\alpha) &= \left|\frac{((x+\theta\alpha)^\perp|\alpha)}{|x+\theta\alpha|^2} - \frac{(x|\alpha)}{|x|^2}\right| \\
&= 2\theta\frac{\left|((x+\theta'\alpha)^\perp|\alpha)(x+\theta'\alpha|\alpha)\right|}{|x+\theta'\alpha|^4} \\
&\leq \frac{2^5}{|x|^4}\left|((x+\theta'\alpha)^\perp|\alpha)(x+\theta'\alpha|\alpha)\right| \\
&\leq \frac{2^6}{|x|^4}\left(|x|^2+|\alpha|^2\right)|\alpha|^2
\end{aligned}$$

We finally conclude that

$$\int_{|\alpha|\leq|x|/2} A(x,\alpha)\nu(d\alpha) \leq 2^6\left(|x|^{-2}\int_{\mathbb{R}^2}|\alpha|^2\nu(d\alpha) + |x|^{-4}\int_{\mathbb{R}^2}|\alpha|^4\nu(d\alpha)\right).$$

The result clearly follows.

D. Proof of Lemma 2.4.7

Using a similar argument as in the previous proof, there exists $0\leq\theta=\theta(\alpha)\leq 1$ such that

$$\begin{aligned}
\left|\arctan\left(\frac{x_2+\alpha_2}{x_1+\alpha_1}\right) - \arctan\left(\frac{x^2}{x^1}\right)\right|^2 g(x,\alpha) &= \left|\frac{\left((x+\theta\alpha)^\perp \mid \alpha\right)}{|x+\theta\alpha|^2}\right|^2 g(x,\alpha) \\
&\leq C\frac{(|x|^2+|\alpha|^2)|\alpha|^2}{|x+\theta\alpha|^4}.
\end{aligned}$$

It is clear that

$$|x|^2\int_{\{|\alpha|>|x|/2\}}\frac{(|x|^2+|\alpha|^2)|\alpha|^2}{|x+\theta\alpha|^4}\nu(d\alpha) \xrightarrow[|x|\to\infty]{} 0,$$

and

$$\begin{aligned}
\int_{\{|\alpha\leq|x|/2\}}\frac{(|x|^2+|\alpha|^2)|\alpha|^2}{|x+\theta\alpha|^4}\nu(d\alpha) &\leq 2^4\int_{\mathbb{R}^2}\frac{(|x|^2+|\alpha|^2)|\alpha|^2}{|x|^4}\nu(d\alpha) \\
&\leq 2^4\left(|x|^{-2}\int_{\mathbb{R}^2}|\alpha|^2\nu(d\alpha) + |x|^{-4}\int_{\mathbb{R}^2}|\alpha|^4\nu(d\alpha)\right) \\
&\leq 2^4|x|^{-2}\left(\int_{\mathbb{R}^2}|\alpha|^2\nu(d\alpha) + \int_{\mathbb{R}^2}|\alpha|^4\nu(d\alpha)\right),
\end{aligned}$$

provided $|x| \geq 1$. Hence, there exists $C_3 > 0$ such that

$$\int_{\mathbb{R}^2} \left| \arctan\left(\frac{x_2 + \alpha_2}{x_1 + \alpha_1}\right) - \arctan\left(\frac{x^2}{x^1}\right) \right|^2 g(x, \alpha)\nu(d\alpha) \leq C_3 |x|^{-2}.$$

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