



HAL
open science

Untangling the role of temporal and spatial variations in persistence of populations

Michel Benaïm, Claude Lobry, Tewfik Sari, Edouard Strickler

► **To cite this version:**

Michel Benaïm, Claude Lobry, Tewfik Sari, Edouard Strickler. Untangling the role of temporal and spatial variations in persistence of populations. 2021. hal-03453665v1

HAL Id: hal-03453665

<https://hal.science/hal-03453665v1>

Preprint submitted on 28 Nov 2021 (v1), last revised 6 Jul 2023 (v2)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Untangling the role of temporal and spatial variations in persistence of populations

Michel Benaïm¹, Claude Lobry², Tewfik Sari³, and Édouard Strickler⁴

¹ Institut de Mathématiques, Université de Neuchâtel, Switzerland

² C.R.H.I, Université Nice Sophia Antipolis, France

³ ITAP, University of Montpellier, INRAE, Institut Agro, Montpellier, France

⁴ Université de Lorraine, CNRS, Inria, IECL, Nancy, France

November 24, 2021

Abstract

We consider a population distributed between two habitats, in each of which it experiences a growth rate that switches periodically between two values, $1 - \varepsilon > 0$ or $-(1 + \varepsilon) < 0$. We study the specific case where the growth rate is positive in one habitat and negative in the other one for the first half of the period, and conversely for the second half of the period, that we refer as the (± 1) model. In the absence of migration, the population goes to 0 exponentially fast in each environment. In this paper, we show that, when the period is sufficiently large, a small dispersal between the two patches is able to produce a very high positive exponential growth rate for the whole population, a phenomena called inflation. We prove in particular that the threshold of the dispersal rate at which the inflation appears is exponentially small with the period. We show that inflation is robust to random perturbation, by considering a model where the values of the growth rate in each patch are switched at random times: we prove, using theory of Piecewise Deterministic Markov Processes (PDMP) that inflation occurs for low switching rate and small dispersal. Finally, we provide some extensions to more complicated models, especially epidemiological and density dependent models.

Keywords: Population dynamic, dispersal, periodic environment, random environment, switched systems, Piecewise Deterministic Markov Process, Epidemiology

Contents

Keywords: 1

1	Introduction	3
2	The (± 1) model.	4
2.1	The Klausmaier model.	4
2.2	The (± 1) model in periodic environment.	6
2.2.1	First observations	6
2.2.2	The (± 1) model in the variables (U, V)	8
	The switched system $F(m, T)$	9
	The switched system $S(\varepsilon, m, T)$	10
2.2.3	An explicit formula for $\Delta(\varepsilon, m, T)$	12
	Small and large values of m or T	12
	Threshold value of m for large T	14
2.2.4	Back to the variables x_1, x_2	14
2.3	The (± 1) model in stochastic environment	15
2.3.1	The Piecewise Deterministic Markov Processes (PDMP)	15
2.3.2	Link with the top Lyapunov exponent	19
2.3.3	A general stochastic (± 1) model	20
3	Some extensions to more complex situations.	22
3.1	Migration between different patches	22
	Comments on figure 13.	24
3.2	The case of non symmetric dispersal	24
3.3	The case of partial phase shift	25
3.4	Density dependent models	26
3.4.1	A density dependent stochastic model	27
3.5	The epidemic model of Holt and al.	28
4	Conclusion	31
A	The system $\Sigma(\varepsilon, m, T)$ for large m	33
B	The switched system $F(m, T)$ has a single globally stable periodic orbit	33
C	Qualitative properties of $S(\varepsilon, m, T)$	37
D	Explicit formula for $\Delta(\varepsilon, m, T)$	38
E	Asymptotics of $\Delta(\varepsilon, m, T)$ for large T	39
F	The randomly switched system $F(m, T)$ admits a unique stationary distribution	39
G	Asymptotic of $\Delta(\varepsilon, m, T)$	40
H	Stochastic Approximately Periodic Environment	43
I	Density dependent model	45
J	Connection between $\Delta(\varepsilon, m, T)$ and $\sigma(\varepsilon, m, T)$.	47

1 Introduction

In a paper [21] devoted to the popularization of Floquet theory among ecologists, Christopher Klausmeier gives a striking example of the interplay of dispersal and temporal variations in population dynamics. In this example a small dispersal between two patches, where populations experience similar, but out of phase, neutral (i.e. with nul average growth rate 0) environment is able to produce very high exponential growth rate for the whole population. He says that his example is a complement, in the multiple patches and continuous time, to the study of the phenomenon introduced by Holt ([10]) and his colleagues and coined by them as *inflation*.

In conservation biology the SLOSS debate, (i.e. what is better to maintain biodiversity, to have a *Single Large Or Several Small* habitats) has a very long standing history (see e.g. [13]). The exemple of a population living on two patches connected by dispersal has seen a revival of theoretical interest in recent years see [1], [2]. In these papers it is shown that even in the simplest case of the logistic model, the question "does dispersal increases or not the total carrying capacity ?" has not a definitive answer: it depends on the parameters of the model ; a complete discussion is given in the case of constant parameters. In the present paper we extend this discussion to the case of time varying parameters where we shall see that the Klausmeier example plays a central role.

In conservation biology one wants to maintain population abundances at the highest possible level and, in contrast, in epidemiology, one wants to maintain the population of some infectious agent at the lowest possible state. But at the theoretical level, this is the same problem. Thus it is not surprising that recently Holt and his colleagues [19] showed that this inflation phenomenon familiar to some ecologists could have dramatic effects in degrading pandemic control policies. Namely they made the conceptual point that efficient policies could become inefficient if they where implemented asynchronously on two places connected by migration. On the basis of numerical simulations they showed, with realistic parameters, how a small migration associated with the phase shift in policies produce high inflation in the number of cases.

In view of these important applications, the purpose of the present paper is to elucidate the respective roles of period, phase shift and migration on the persistance of populations living in multiple patches, in the presence of both migration and temporal variations in the environment.

An interesting feature of the paper [10] was the use of so called "square wave" growth rates $r(t)$ in the differential equation $\frac{dN}{dt} = r(t)N + d$, that is to say a piecewise constant periodic function in place of usually considered continuous periodic functions. This made possible explicit computations, which, in general, is not the case for periodic linear differential equations. The consideration of differential equations of the form :

$$\frac{dx}{dt} = f(x, u(t))$$

where $u(t)$ is a piecewise continuous function of time is not recent. It started in the early seventies, if not before, in the area of control systems and is now known as *geometric control theory* (see [17] for a comprehensive account).

If the number of possible values taken by $u(t)$ is a finite set, such systems can be viewed as a collection of differential systems where one switches from one system to another one according to some rules and are called "switched dynamical systems". The rules might be "deterministic", for instance switches occur periodically, or stochastic. About ten years after the development of the deterministic case, following a paper of M. Davis, [9] the notion of "*Piecewise Deterministic Markov Process*" (PDMP) started to be investigated and the particular case of randomly switched ODEs got much attention in the last decade (see e.g [4], [3] or [23] for general qualitative results and [5], [6], [14], [25] for applications in ecology, epidemiology and neuroscience). In a PDMP, the duration between two switches is a sequence of independent random variables exponentially distributed. In continuous time models of population dynamics, switched systems, either deterministic or stochastic, are suitable to model situations where changes in the environment can be considered instantaneous regarding the scale of growth rates, or, if it is not the case, suitable to provide a first conceptual exploration of the issue considered.

The paper is divided in two parts. In the first one we explore in details a model, which we call the " (± 1) model", inspired by the example of Klausmeier, from both points of view of the deterministic periodic switched system and its associate PDMP; in this part all the mathematical details and proofs are provided (details are given in the appendix) in a style readable by non professional mathematicians. In a second part we provide results for the case of more complex systems than the " (± 1) model" but, in order to keep a reasonable size to the paper, we only provide intuitive explanations and numerical evidences.

While we were in the final phase of writing this article, we took note of G. Katriel's recent¹ deposit on ArXiv [18]. This article looks at the same problem as the one we are considering but from a different point of view. While we focus on switched deterministic systems with a view to their extension to random models, [18] considers *continuously differentiable deterministic systems* and therefore its results cannot be applied directly to our model. Our article and [18] are complementary since they present two different points of view on the same question.

2 The (± 1) model.

2.1 The Klausmaier model.

In the paper [21] one considers a population living on two patches which abundances x_1 and x_2 on each patch obey to the system (notations are ours) :

$$\begin{aligned} \frac{dx_1}{dt} &= r(t)x_1 + m(x_2 - x_1) \\ \frac{dx_2}{dt} &= r(t + \varphi)x_2 + m(x_1 - x_2) \end{aligned} \tag{1}$$

We assume that $t \mapsto r(t)$ is a periodic function and $m \geq 0$ is a parameter measuring the strength of migration between the two patches. In [21] one

¹Submitted on 4 Apr 2021 (v1), last revised 10 Jul 2021.

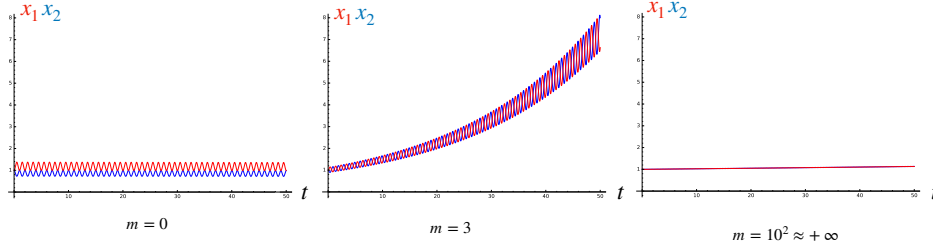


Figure 1: $r(t) = \sin(2\pi t)$

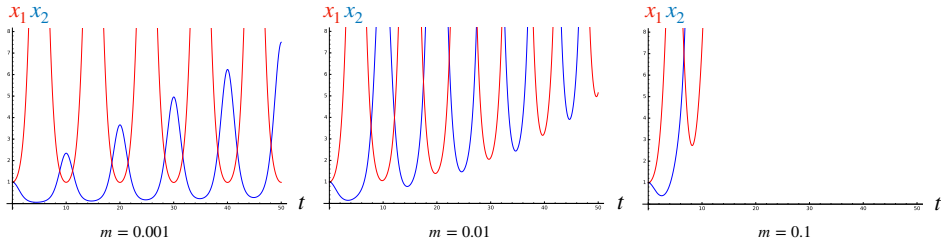


Figure 2: $r(t) = \sin(0.2\pi t)$

considers the specific case $r(t) = \sin(2\pi t)$ and $\varphi = \frac{1}{2}$ and, by the way, the system :

$$\begin{aligned} \frac{dx_1}{dt} &= \sin(2\pi t)x_1 + m(x_2 - x_1) \\ \frac{dx_2}{dt} &= -\sin(2\pi t)x_2 + m(x_1 - x_2) \end{aligned} \quad (2)$$

Simulations of this system, from the initial conditions $x_1(0) = 1$, $x_2(0) = 1$, are shown on fig. 1. The case $m = 0$ is easily understood : the two systems are uncoupled and each one has periodic solutions. In the case $m \approx +\infty$ (perfect mixing) it is easily proved that the solutions converge to $x_1(t) = 1$, $x_2(t) = 1$ (see Appendix A). In both cases the solutions are bounded by 2. Surprisingly a moderate migration makes $x_1(t)$ and $x_2(t)$ unbounded. Perhaps, more surprising, this effect is far more spectacular if, instead of $r(t) = \sin(2\pi t)$ which is of period 1, we simulate the case $r(t) = \sin(0.2\pi t)$ which is of period 10 and $\varphi = 5$ as is shown on fig. 2. This connection between period and dispersal is what we want to understand. In view of our interest in stochastic PDMP, we shall not address this question in the case of continuous $r(t)$ but piecewise constant ones, which has the advantage of permitting explicit calculations.

2.2 The (± 1) model in periodic environment.

Our idea is to understand the mathematics of the simplest possible model presenting the phenomenon of inflation on two patches and to complicate it thereafter. We consider the system :

$$\Sigma(\varepsilon, m, T) \quad \begin{cases} \frac{dx_1}{dt} &= (+u(t) - \varepsilon)x_1 + m(x_2 - x_1) \\ \frac{dx_2}{dt} &= (-u(t) - \varepsilon)x_2 + m(x_1 - x_2) \end{cases} \quad (3)$$

where $0 \leq \varepsilon \leq 1$, $0 \leq m$, $0 \leq T$ and the function $t \mapsto u(t)$ is periodic of period $2T$, with :

$$t \in [0, T[\Rightarrow u(t) = 1 \quad t \in [T, 2T[\Rightarrow u(t) = -1$$

We denote by $(x_1(t, (x_{1_0}, x_{2_0})), x_2(t, (x_{1_0}, x_{2_0})))$ the solutions of (3) with initial condition (x_{1_0}, x_{2_0}) . For $u(t) = +1$ we are integrating the system :

$$\Sigma^+(\varepsilon, m) \quad \begin{cases} \frac{dx_1}{dt} &= (+1 - \varepsilon)x_1 + m(x_2 - x_1) \\ \frac{dx_2}{dt} &= (-1 - \varepsilon)x_2 + m(x_1 - x_2) \end{cases} \quad (4)$$

while for $u(t) = -1$ we are integrating the system :

$$\Sigma^-(\varepsilon, m) \quad \begin{cases} \frac{dx_1}{dt} &= (-1 - \varepsilon)x_1 + m(x_2 - x_1) \\ \frac{dx_2}{dt} &= (+1 - \varepsilon)x_2 + m(x_1 - x_2) \end{cases} \quad (5)$$

Thus we are switching, each T units of time, from system $\Sigma^+(\varepsilon, m)$ to system $\Sigma^-(\varepsilon, m)$ and vice versa ; such system is called a *switched* systems.

From now and all along the section 2, the function $u(t)$ is periodic of period $2T$, taking alternatively the values $+1$ and -1 .

2.2.1 First observations

In the absence of migration ($m = 0$) system $\Sigma^+(\varepsilon, 0)$ reduces to :

$$\Sigma^+(\varepsilon, 0) \quad \begin{cases} \frac{dx_1}{dt} &= (+1 - \varepsilon)x_1 \\ \frac{dx_2}{dt} &= (-1 - \varepsilon)x_2 \end{cases} \quad (6)$$

which is a trivial system of two decoupled equations ; the same is true for $\Sigma^-(\varepsilon, 0)$ and one deduces immediately that the solutions are in this case :

$$x_1(2T, (x_{1_0}, x_{2_0})) = e^{T(-1-\varepsilon)} e^{T(+1-\varepsilon)} x_{1_0} = e^{-2T\varepsilon} x_{1_0}$$

$$x_2(2T, (x_{1_0}, x_{2_0})) = e^{T(+1-\varepsilon)} e^{T(-1-\varepsilon)} x_{2_0} = e^{-2T\varepsilon} x_{2_0}$$

For $\varepsilon > 0$ both $x_1(n2T, (x_{1_0}, x_{2_0}))$ and $x_2(n2T, (x_{1_0}, x_{2_0}))$ tend to 0 when n tends to infinity. For $\varepsilon = 0$, trajectories $t \mapsto ((x_1(t, (x_{1_0}, x_{2_0})), x_2(t, (x_{1_0}, x_{2_0}))))$ are portions of the same hyperbola traversed alternately from top to bottom then from bottom to top ; for small ε , trajectories are small deformations of hyperbolas "zig-zagging" as shown on the simulations of Figure 3.

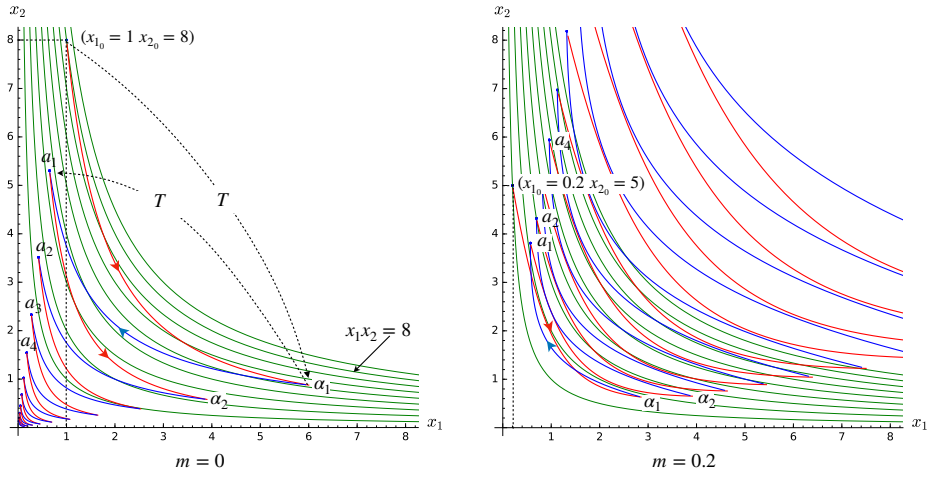


Figure 3: Trajectories of $\Sigma(\varepsilon, m, T)$: $\varepsilon = 0.1$; $T = 2$; $m = 0$ (left); $m = 0.2$ (right)

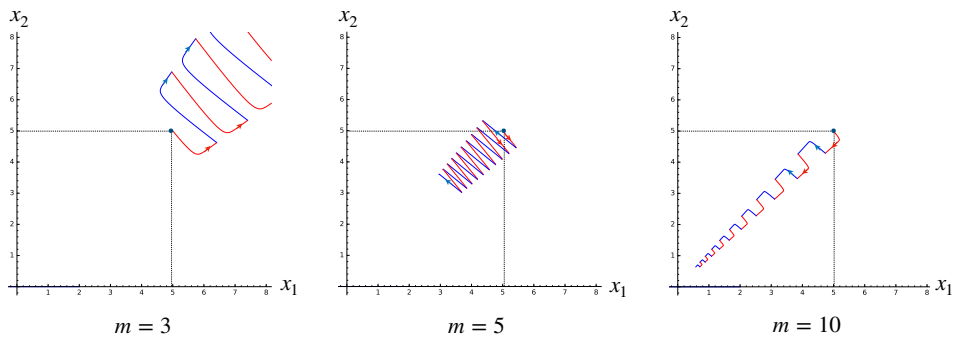


Figure 4: Trajectories of $\Sigma(\varepsilon, m, T)$ $\varepsilon = 0.1$ $T = 2$

Comments on Figure 3 The system $\Sigma(\varepsilon, m, T)$ is considered with $\varepsilon = 0.1$ and $T = 2$.

- On the left one considers the case $m = 0$. The initial condition is the point of coordinates $(1, 8)$ which is on the hyperbola $\{x_1, x_2 : x_1 x_2 = 8\}$. The hyperbolas $\{x_1, x_2 : x_1 x_2 = k; k = 1, 2, \dots\}$ are drawn in green. First one integrates the system $\Sigma^{+1}(\varepsilon, m, T)$ up to time $t = T = 2$ which gives the red trajectory up to point α_1 . Then one switches to system $\Sigma^{-1}(\varepsilon, m, T)$ which gives the blue trajectory which ends after T units of time at the point a_1 . One sees that at each step the product $x_1 x_2$ is smaller and, thus, the "zig-zag" tends to 0. This could easily be proved rigorously by differentiating the product $x_1(t)x_2(t)$ along the trajectories of $\Sigma(\varepsilon, 0, T)$ but we shall not do it since this fact will be a corollary of the results in the next subsections.
- On the right one sees the case $m = 0.2$; the initial condition is the point $(0.2, 5)$ which is located on the hyperbola $\{x_1, x_2 : x_1 x_2 = 1\}$. One sees that now the "zig-zag" tends to infinity. The system is unstable.

Comments on fig. 4 The system $\Sigma(\varepsilon, m, T)$ is considered with $\varepsilon = 0.1$ and $T = 2$.

- One sees that for $m = 3$ the system is still unstable...
- ... but for $m = 5$ is stable and "more stable" for $m = 10$.
- For large m , i.e. $m \rightarrow +\infty$, we approach the perfect mixing where $x_1 \approx x_2 \approx x$ and hence, on each patch, the solutions of the system tend (see appendix A for details) to the solutions of :

$$\frac{dx}{dt} = -\varepsilon x$$

Let us say, to conclude this paragraph that, given $\varepsilon > 0$ and $T > 0$ for small and large values of migration the system is stable, while for intermediate values it is unstable : this is *inflation*.

2.2.2 The (± 1) model in the variables (U, V) .

We make a change of variables which transforms our system of two linear, but coupled, differential equations, in a system of non linear but cascade system.

Since the solutions of $\Sigma(\varepsilon, m, T)$ remain strictly positive, it is legitimate to put :

$$U = \ln(x_1) + \ln(x_2) \quad V = \ln(x_1) - \ln(x_2)$$

In these new variables (U, V) the system is ² :

$$S(\varepsilon, m, T) \quad \begin{cases} \frac{dU}{dt} = 2(m \cosh(V) - m - \varepsilon) \\ \frac{dV}{dt} = 2(u(t) - m \sinh(V)) \end{cases} \quad (7)$$

²We recall the notations $\sinh(x) = \frac{e^x - e^{-x}}{2}$ $\cosh(x) = \frac{e^x + e^{-x}}{2}$

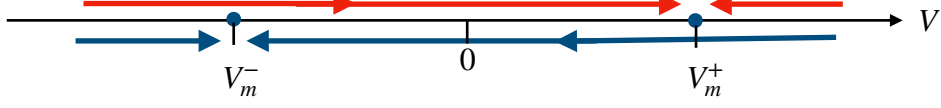


Figure 5: The switched system $F(m, T)$: in red F_m^+ , in blue F_m^- , defined by (10) and (11) respectively

One observes that the variable V is decoupled from the variable U and its equation does not depend on ε . We denote by $F(m, T)$ this system :

$$F(m, T) \quad \frac{dV}{dt} = 2(u(t) - m \sinh(V)) \quad (8)$$

Once the solution $V(t)$ is known, the solution $U(t)$ is obtained by the simple quadrature :

$$U(t) = U_0 + \int_0^t 2(m \cosh(V(s)) - m - \varepsilon) ds \quad (9)$$

The switched system $F(m, T)$ The non autonomous system $F(m, T)$ is a one dimensional switched system between the two equations :

$$F_m^+ \quad \frac{dV}{dt} = 2(+1 - m \sinh(V)) \quad (10)$$

and

$$F_m^- \quad \frac{dV}{dt} = 2(-1 - m \sinh(V)). \quad (11)$$

The two differential equations (10) and (11) have respectively the points :

$$V_m^+ = \sinh^{-1}(+1/m) = \ln \left(1/m + \sqrt{1 + (1/m)^2} \right)$$

and

$$V_m^- = \sinh^{-1}(-1/m) = -\ln \left(1/m + \sqrt{1 + (1/m)^2} \right)$$

as globally asymptotically stable equilibria. From Figure 5 it is evident that the solutions are trapped in the interval $[V_m^-, V_m^+]$. The following proposition is easy to prove with elementary calculus means. It is done in Appendix B :

Proposition 2.1 *The switched system $F(m, T)$ has a unique periodic solution, denoted by $P_{m, T}(t)$, globally asymptotically stable, which oscillates between two values $P_{m, T}^-$ and $P_{m, T}^+$ contained in the interval $[V_m^-, V_m^+]$; $P_{m, T}^- = -P_{m, T}^+$ and the function $T \mapsto P_{m, T}^+$ is an increasing function of T which tends to V_m^+ when T tends to infinity.*

This proposition is illustrated on Figure 6: on the left, one sees the periodic solution in the case $m = 0.01$, for $T = 2$; when V is not too large $2(1 - m \sinh(V)) \approx 2$ and $2(-1 - m \sinh(V)) \approx -2$ and during one period $V(t)$ increases and decreases of approximately $2T = 4$; on the right the half period is $T = 10$; this duration is large enough for the solution to approach the equilibria V_m^- and V_m^+ .

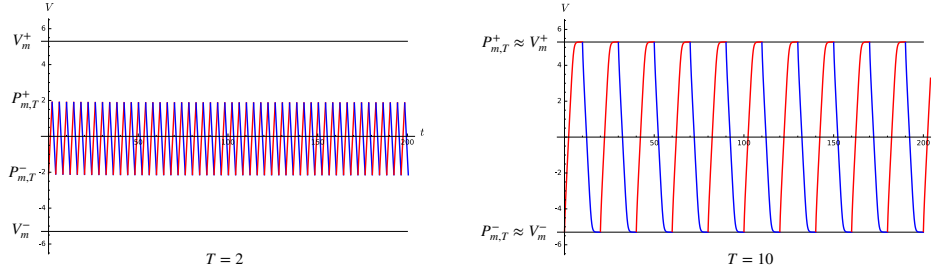


Figure 6: The switched system $F(m, T)$: $m = 0.01$, $T = 2$ (left), $T = 10$, (right)

The switched system $S(\varepsilon, m, T)$ The switched system $S(\varepsilon, m, T)$ consists in a switching each duration T between the two differential systems :

$$S^+(\varepsilon, m) \begin{cases} \frac{dU}{dt} = 2(m \cosh(V) - m - \varepsilon) \\ \frac{dV}{dt} = 2(1 - m \sinh(V)) \end{cases} \quad S^-(\varepsilon, m) \begin{cases} \frac{dU}{dt} = 2(m \cosh(V) - m - \varepsilon) \\ \frac{dV}{dt} = 2(-1 - m \sinh(V)) \end{cases} \quad (12)$$

Recall that $P_m(t)$ is the unique periodic solution of $F(m, T)$ and let

$$\Delta(\varepsilon, m, T) = \frac{1}{2T} \int_0^{2T} 2(m \cosh(P_{m,T}(s)) - m - \varepsilon) ds \quad (13)$$

From formula (9) and Proposition 2.1, we can easily prove that the mean asymptotic velocity of U on a period is $\Delta(\varepsilon, m, T)$. More precisely, we show (see Proposition 2.2) that

$$\lim_{t \rightarrow \infty} \frac{U(t)}{t} = \Delta(\varepsilon, m, T). \quad (14)$$

Hence, $U(t)$ tends to $\pm\infty$ according to the sign of $\Delta(\varepsilon, m, T)$. The function $V \mapsto 2(m \cosh(V) - m - \varepsilon)$ is even and it is easily seen that trajectories of $S^+(\varepsilon, m)$ and $S^-(\varepsilon, m)$ are symmetric with respect to the horizontal axe, thus :

$$\Delta(\varepsilon, m, T) = \frac{1}{T} \int_0^T 2(m \cosh(P_{m,T}(s)) - m - \varepsilon) ds = \frac{1}{T} \int_T^{2T} 2(m \cosh(P_{m,T}(s)) - m - \varepsilon) ds$$

We concentrate on the system :

$$S^+(\varepsilon, m) \begin{cases} \frac{dU}{dt} = 2(m \cosh(V) - m - \varepsilon) \\ \frac{dV}{dt} = 2(1 - m \sinh(V)) \end{cases} \quad (15)$$

It has the solution :

$$t \mapsto \begin{pmatrix} U(t) = 2(m \cosh(V_m^+) - m - \varepsilon) \\ V(t) = V_m^+ \end{pmatrix} \quad (16)$$

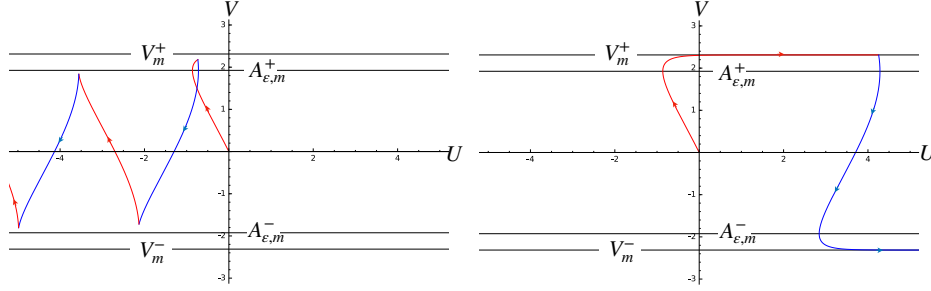


Figure 7: The switched system $S(\varepsilon, m, T)$: $\varepsilon = 0.5$ $m = 0.2$, $T = 2$ (left), $T = 10$, (right)

The function $g : V \mapsto 2(m \cosh(V) - m - \varepsilon)$ is decreasing for $V \leq 0$. Let

$$A_{\varepsilon, m}^+ = \cosh^{-1} \left(1 + \frac{\varepsilon}{m} \right),$$

then $g(V)$ is negative if and only if $V \in (-A_{\varepsilon, m}^+, A_{\varepsilon, m}^+)$. An elementary calculus shows that for $m = \frac{1-\varepsilon^2}{2\varepsilon}$ one has $A_{\varepsilon, m}^+ = V_m^+$. Thus :

- If $m > \frac{1-\varepsilon^2}{2\varepsilon}$ then $V_m^+ < A_{\varepsilon, m}^+$. Since the periodic solution $P_{m, T}(s)$ in (13) oscillate in the interval $[V_m^-, V_m^+] \subset (-A_{\varepsilon, m}^+, A_{\varepsilon, m}^+)$ whatever the value of T , the integrand is strictly negative and by the way $\Delta(\varepsilon, m, T)$ is strictly negative.
- If $m < \frac{1-\varepsilon^2}{2\varepsilon}$ then $V_m^+ > A_{\varepsilon, m}^+$. We must look to the minimum, $P_{m, T}^-$, and maximum, $P_{m, T}^+$ values of $P_{m, T}(s)$. For small values of T they are close to 0 and included in the interval $[-A_{\varepsilon, m}^+, A_{\varepsilon, m}^+]$ and the integrand being always negative $\Delta(\varepsilon, m, T)$ is negative, but, for large values of T , $P_{m, T}^+$ is close to V_m^+ , the solution $P_{m, T}(s)$ remains for a long time to a value where the integrand is strictly positive and the balance is in favor of positiveness : $\Delta(\varepsilon, m, T)$ is positive. This is shown on the Figure 7 with simulations for a small and a large value of T .

A more precise description of the behaviour of $\Delta(\varepsilon, m, T)$ is given by the following proposition which details of the proof are given in Appendix C.

Proposition 2.2 *Properties of $\Delta(\varepsilon, m, T)$*

1. For all initial conditions $(V(0), U(0))$, one has

$$\lim_{t \rightarrow \infty} \frac{U(t)}{t} = \Delta(\varepsilon, m, T).$$

2. For fixed $T > 0$, for small m , $\Delta(\varepsilon, m, T) < 0$ and thus $U(t)$ tends to $-\infty$
3. For fixed $T > 0$, for large m , $\Delta(\varepsilon, m, T) < 0$ and thus $U(t)$ tends to $-\infty$
4. For fixed $\varepsilon > 0$ and $m < \frac{1-\varepsilon^2}{2\varepsilon}$, there exists a threshold $T^*(\varepsilon, m)$ such that for $T < T^*(\varepsilon, m)$, $\Delta(\varepsilon, m, T) < 0$ and $U(t)$ tends to $-\infty$ while $\Delta(\varepsilon, m, T) > 0$ and $U(t)$ tends to $+\infty$ for $T > T^*(\varepsilon, m)$

5. For every $\varepsilon > 0$, the minimum of $T^*(\varepsilon, m)$ over m is strictly positive. In other words there exists a threshold $T^{**} > 0$ such that for $T < T^{**}$, for all values of m , $\Delta(\varepsilon, m, T) < 0$: there is no inflation.

Remark 1 Consider the first integral in (13). Between, 0 and T , $V(t) = P_{m,T}(t)$ is strictly increasing from $P_{m,T}^-$ to $P_{m,T}^+$ and we can take it as the integration variable ; since $dV = 2(1 - m \sinh(V))dt$ one has :

$$\Delta(\varepsilon, m, T) = \int_{P_{m,T}^-}^{P_{m,T}^+} \frac{2(m(\cosh(V) - 1) - \varepsilon)}{2T(1 - m \sinh(V))} dV$$

This formula can be understood in the following manner : the function $\rho_m : V \mapsto \frac{1}{2T(1 - m \sinh(V))}$ is the density of a probability measure (see Equation (56) in Appendix **) μ_m on $[V_m^-, V_m^+]$ and :

$$\Delta(\varepsilon, m, T) = \int_{P_{m,T}^-}^{P_{m,T}^+} 2(m(\cosh(V) - 1) - \varepsilon) \rho_m(V) dV = \int_{P_{m,T}^-}^{P_{m,T}^+} 2(m(\cosh(V) - 1) - \varepsilon) d\mu_m(V)$$

To the unique periodic solution of the switched system $F(m, T)$ one associate a measure on the space of the variable V and the sign of $\Delta(\varepsilon, m, T)$ is decided by the integration of the function $(m \cosh(V) - m - \varepsilon)$ with respect to this measure. It will be the same in the stochastic case where the random process V converge in law to a random variable $V_{m,T}$ with law $\Pi_{m,T}$, and the behaviour of U will be given by the sign of the integral of the function $(m \cosh(V) - m - \varepsilon)$ with respect to $\Pi_{m,T}$

2.2.3 An explicit formula for $\Delta(\varepsilon, m, T)$

From elementary calculus one can prove (see appendix D) the following explicit formula for $\Delta(\varepsilon, m, T)$:

Proposition 2.3 Let us denote :

$$b = e^T \sqrt{1+m^2} \quad C = m^2 b^4 + 2m^2 b^2 + 4b^2 + m^2$$

Then one has :

$$\Delta(\varepsilon, m, T) = \frac{1}{T} \ln \frac{m^2 b^4 + 2b^2 + m^2 + m(b^2 - 1)\sqrt{C}}{2(1+m^2)b^2} - 2(m + \varepsilon) \quad (17)$$

This formula is used to draw the picture (using the software Maple) of the graph of $\Delta(\varepsilon, m, T)$ with respect to the variables (m, T) .

On Figure 8 is plotted the graph of $(m, T) \mapsto \Delta(0.5, m, T)$

Small and large values of m or T . One sees that $\Delta(0.5, 0, T) = -1 = -2\varepsilon$, which is easily understandable : for $m = 0$ one has $\frac{dx_1}{dt} = (u(t) - \varepsilon)x_1$, $\frac{dx_2}{dt} = (-u(t) - \varepsilon)x_2$ taking the logarithm and adding the two gives $\frac{U}{dt} = -2\varepsilon$. For $T = 0$, one sees that $\Delta(0.5, m, 0)$ is equal to $-1 = -2\varepsilon$ which is explained by the general fact (see e.g. [12]) that if we consider a switched system at a rate witch tends to infinity (i.e. $T \rightarrow 0$) then the solutions tend

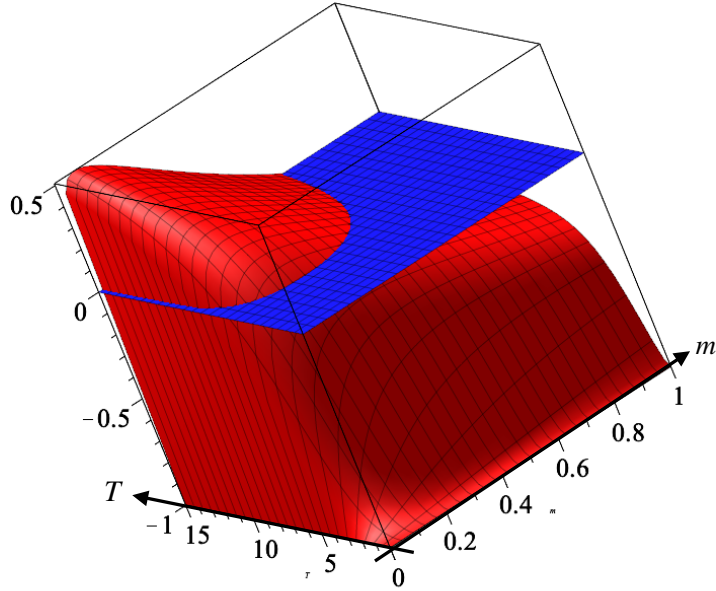


Figure 8: Graph of $\Delta(0.5, m, T)$

to solutions of the system which is the mean of the two systems ; in our case the mean of the two systems is :

$$\begin{aligned} \frac{dU}{dt} &= 2(m \cosh(V) - m - \varepsilon) \\ \frac{dV}{dt} &= \frac{2(u(t) - m \sinh(V)) + 2(-u(t) - m \sinh(V))}{2} = -2m \sinh(V) \end{aligned} \quad (18)$$

which, after a transient, are just $\frac{dU}{dt} = -2\varepsilon$.

The asymptotic behaviors for small and large values of m or T can also be derived by basic development on the explicit formula (17):

Proposition 2.4 *For fixed value of m , one has*

$$\lim_{T \rightarrow \infty} \Delta(\varepsilon, m, T) = 2 \left(\sqrt{1 + m^2} - (m + \varepsilon) \right)$$

while

$$\lim_{T \rightarrow 0} \Delta(\varepsilon, m, T) = -2\varepsilon.$$

For fixed value of $T > 0$,

$$\lim_{m \rightarrow 0} \Delta(\varepsilon, m, T) = \lim_{m \rightarrow +\infty} \Delta(\varepsilon, m, T) = -2\varepsilon.$$

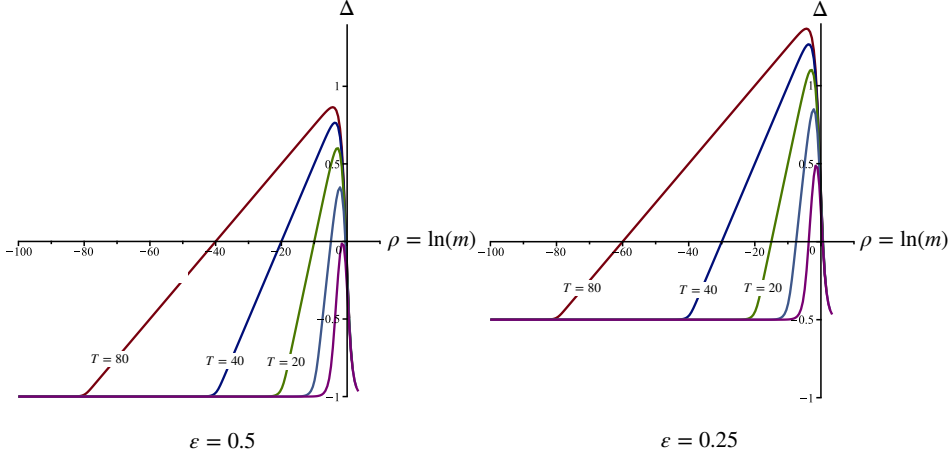


Figure 9: Graphs of $\Delta(\varepsilon, e^{\rho T}, T) : T = 80, 40, 20, 10, 5$

Threshold value of m for large T . On figure 8 one sees that, for large values of T the dependence with respect to m is very sharp close to 0 ; in order to have a better understanding of what is going on around 0 we ask to Maple to draw the graph of $\rho \mapsto \Delta(\varepsilon, e^{\rho T}, T)$ for negative values of ρ and $T = 80, 40, 20, 10, 5$. The result is shown on figure 9 with $\varepsilon = 0.5$ and $\varepsilon = 0.25$; from the picture we guess the following property, which is confirmed by the derivation of appendix E:

Proposition 2.5 *When T is large ($T \rightarrow +\infty$) the threshold value at which $m \mapsto \Delta(\varepsilon, m, T)$ becomes positive is the exponentially small value :*

$$m^*(\varepsilon, T) \sim e^{-(1-\varepsilon)T}$$

Remark 2 *This proposition gives an affirmative answer to **Conjecture 3** of Katriel's paper [18] in the particular case of piecewise constant model which takes advantage of explicit formulas for the solutions. In a forthcoming paper we shall prove this conjecture in the general case.*

2.2.4 Back to the variables x_1, x_2

One has $\exp(U(t)) = x_1(t)x_2(t)$ and we know that for large values of t one has $-V_m^+ < V(t) < +V_m^+$ which means $\frac{1}{r} < \frac{x_2}{x_1} < r$, with $r = \exp(V_m^+)$. From this we deduce that :

$$\Sigma(\varepsilon, m, T) \text{ is stable} \iff \Delta(\varepsilon, m, T) < 0 \quad (19)$$

On the other hand let us consider the "period mapping" of $\Sigma(\varepsilon, m, T)$, that is to say the linear mapping which, to an initial condition $(x_1(0), x_2(0))$ at time 0, assigns the solution of $\Delta(\varepsilon, m, T) < 0$ at time $2T$ and let us denote it by :

$$\begin{pmatrix} x_1(2T) \\ x_2(2T) \end{pmatrix} = M(\varepsilon, m, T) \begin{pmatrix} x_1(0) \\ x_2(0) \end{pmatrix} \quad (20)$$

The stability of our system $\Sigma(\varepsilon, m, T)$ is equivalent to the stability of the linear discrete system of \mathbb{R}^2 :

$$X_{n+1} = M(\varepsilon, m, T)X_n \quad (21)$$

For $u = -1, 1$, let us denote by $M_{\varepsilon, m}^u$ the matrix :

$$M_{\varepsilon, m}^u = \begin{pmatrix} u - m - \varepsilon & +m \\ +m & -u - m - \varepsilon \end{pmatrix} \quad (22)$$

With this notation the matrix $M(\varepsilon, m, T)$ is given by :

$$M(\varepsilon, m, T) = e^{TM_{\varepsilon, m}^{-1}} e^{TM_{\varepsilon, m}^{+1}} \quad (23)$$

The stability of the discrete system $X_{n+1} = M(\varepsilon, m, T)X_n$ is decided by the spectral radius :

$$\sigma(\varepsilon, m, T) = \max |\lambda_i(\varepsilon, m, T)| \quad i = 1, 2$$

where $\lambda_i(\varepsilon, m, T)$ are the two real eigenvalues of $M(\varepsilon, m, T)$ (note that since $M_{\varepsilon, m}^{+1}$ and $M_{\varepsilon, m}^{-1}$ are symmetric, so is $M(\varepsilon, m, T)$ and its eigenvalues are real). Thus :

$$\Sigma(\varepsilon, m, T) \text{ is stable} \iff \sigma(\varepsilon, m, T) < 1 \quad (24)$$

In view of (19) and (24) there must be a connection between $\Delta(\varepsilon, m, T)$ and $\sigma(\varepsilon, m, T)$. The connection is given by the proposition :

Proposition 2.6

$$\Delta(\varepsilon, m, T) = \frac{1}{T} \ln(\sigma(\varepsilon, m, T)) \quad (25)$$

2.3 The (± 1) model in stochastic environment

Since a strictly periodic environment is certainly non realistic it is important to explore the robustness of the inflation effect to the introduction of some kind of randomness in the switching times. We consider again the system (3) but we do not suppose that $t \mapsto u(t)$ is a $2T$ -periodic function but any measurable function, which we denote by $t \mapsto \mathbf{u}(t)$, with values in the set $\{-1, +1\}$. Such a function is called an *environment*.

2.3.1 The Piecewise Deterministic Markov Processes (PDMP)

In this section, we consider the case where the switching between the states 1 and -1 occur at random time, exponentially distributed. More precisely, we study the system :

$$\Sigma(\varepsilon, m, T) \quad \begin{cases} \frac{dx_1}{dt} & = (+\mathbf{u}(t) - \varepsilon)x_1 + m(x_2 - x_1) \\ \frac{dx_2}{dt} & = (-\mathbf{u}(t) - \varepsilon)x_2 + m(x_1 - x_2) \end{cases} \quad (26)$$

where $(\mathbf{u}(t))_{t \geq 0}$ is a continuous time Markov chain on the space $\{-1, +1\}$ with switching rate $\sigma := 1/T$. In other words, $\mathbf{u}(t)$ is a continuous time process such that :

1. At time 0, \mathbf{u} is in some state $h \in \{\pm 1\}$.
2. It remains equal to h for a random time τ_1 exponentially distributed with parameter σ , viz.

$$\mathbb{P}(\tau_1 > t) = e^{-\sigma t}.$$

3. At time τ_1 , the value of \mathbf{u} is switched from h to $-h$, and \mathbf{u} keeps this value for a time τ_2 , exponentially distributed with parameter σ and independent of τ_1
4. and so on.

In particular, the mean time spent by \mathbf{u} in an environment h before to switch is $\frac{1}{\sigma} = T$. As in the case of periodic environment, we perform the change of variable $V = \ln(x_1) - \ln(x_2)$ and $U = \ln(x_1) + \ln(x_2)$ to get

$$\mathbf{S}(\varepsilon, m, T) \quad \begin{cases} \frac{dU}{dt} &= 2(m \cosh(V) - m - \varepsilon) \\ \frac{dV}{dt} &= \frac{1 + \mathbf{u}(t)}{2} F_m^+(V) + \frac{1 - \mathbf{u}(t)}{2} F_m^-(V), \end{cases} \quad (27)$$

where $F_m^+(V) = 2(1 - m \sinh(V))$ and $F_m^-(V) = 2(-1 - m \sinh(V))$. The system $\mathbf{S}(\varepsilon, m, T)$ is composed of the one-dimensional system

$$\mathbf{F}(m, T) \quad \frac{dV}{dt} = \frac{1 + \mathbf{u}(t)}{2} F_m^+(V) + \frac{1 - \mathbf{u}(t)}{2} F_m^-(V) \quad (28)$$

which then gives the solution of U :

$$U(t) = U_0 + \int_0^t 2(m \cosh(V(s)) - m - \varepsilon) ds \quad (29)$$

The processes $(\mathbf{V}_t)_{t \geq 0} = (V(t), \mathbf{u}(t))_{t \geq 0}$ and $(V(t), U(t), \mathbf{u}(t))_{t \geq 0}$ are *Piecewise Deterministic Markov Processes* (PDMP).

Remark 3 *Even though we are only interested in V and U , it is mathematically more convenient to consider the processes (V, \mathbf{u}) and (V, U, \mathbf{u}) since they are Markov, whereas the processes V and (V, U) are not Markov.*

The following property can be seen as a stochastic counterpart of Proposition 2.1. It is a consequence of classical results on PDMP and is proved in Appendix F.

Proposition 2.7 *There exists a unique probability measure $\Pi_{m,T}$ on $[V_m^-, V_m^+]$ such that, for all measurable set A , all bounded measurable function $f : \mathbb{R} \rightarrow \mathbb{R}$, all $(V(0), \mathbf{u}(0))$, one has*

$$\lim_{t \rightarrow \infty} \mathbb{P}(V(t) \in A) \rightarrow \Pi_{m,T}(A)$$

and, almost surely,

$$\lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t f(V(s)) ds = \int f(v) \Pi_{m,T}(v).$$

Moreover, $\Pi_{m,T}(dv) = \rho_{m,T}(v) dv$, for some measurable function $\rho_{m,T}$, explicitly computable and positive on (V_m^-, V_m^+) .

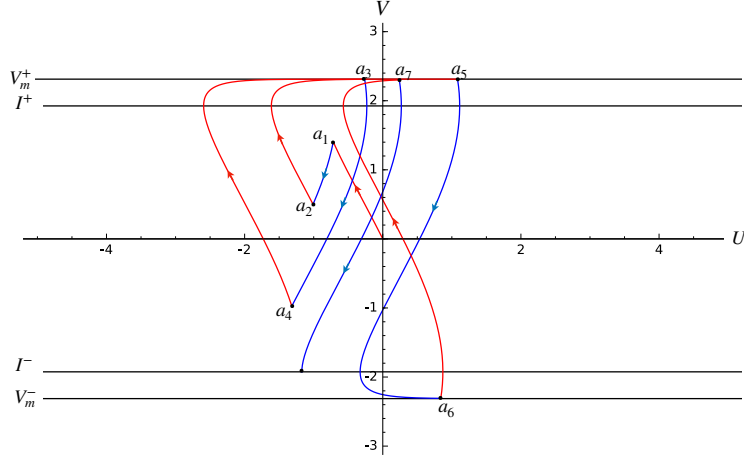


Figure 10: A trajectory of the process (V_t, U_t) : $\varepsilon = 0.5$ $m = 0.2$ $\sigma = 0.4$

Remark 4 From the explicit expression (73) of $\rho_{m,T}$ given in Appendix F, it is possible to prove that, for fixed m and T , there exists constants $C_-(m, T), C_+(m, T)$ such that, as $v \rightarrow V_m^+$,

$$\rho_{m,T}(v) \sim C_+(m, T)(e^{V_m^+} - e^v)^{\frac{1}{2T\sqrt{1+m^2}} - 1},$$

while as $v \rightarrow V_m^-$,

$$\rho_{m,T}(v) \sim C_-(m, T)(e^v - e^{V_m^-})^{\frac{1}{2T\sqrt{1+m^2}} - 1}.$$

In particular, $\rho_{m,T}$ is bounded in neighbourhoods of V_m^+ and V_m^- if and only if $1 \geq 2T\sqrt{m^2 + 1}$. This condition is consistent with the following heuristic: if T is large, the environment does not switch often, and the process V follows the vector fields F_m^+ and F_m^- for a long time, and thus spend a large amount of time close to the equilibria V_m^+ and V_m^- . Hence, for large T , one expects that the distribution $\Pi_{m,T}$ give a lot of mass near V_m^+ and V_m^- . On the contrary, if T is small, the environment switches frequently, and the process V spend most of time in the middle of the interval $[V_m^-, V_m^+]$, and therefore one expects the distribution $\Pi_{m,T}$ to vanish at the extremity of the interval.

From Proposition 2.7 and Equation (29); we have that, almost surely,

$$\lim_{t \rightarrow \infty} \frac{U(t)}{t} = \int_{V_m^-}^{V_m^+} 2(m \cosh(v) - m - \varepsilon) \rho_{m,T}(v) dv := \Delta(\varepsilon, m, T).$$

The following result is proved in Appendix G and is to be compared with Proposition 2.2 in the periodic case.

Proposition 2.8 We have the following limits:

1. For all $m > 0$,

$$\lim_{T \rightarrow 0} \Delta(\varepsilon, m, T) = -2\varepsilon < 0.$$

2. For all $m > 0$,

$$\lim_{T \rightarrow \infty} \Delta(\varepsilon, m, T) = 2 \left(\sqrt{m^2 + 1} - m - \varepsilon \right).$$

In particular,

$$\lim_{T \rightarrow \infty} \Delta(\varepsilon, m, T) > 0 \quad \Leftrightarrow \quad m < \frac{1 - \varepsilon^2}{2\varepsilon}.$$

3. For all $T > 0$,

$$\lim_{m \rightarrow 0} \Delta(\varepsilon, m, T) = \lim_{m \rightarrow \infty} \Delta(\varepsilon, m, T) = -2\varepsilon.$$

From this, we deduce that for $m < \frac{1 - \varepsilon^2}{2\varepsilon}$, there exists $T_*(m) \leq T^*(m)$ such that $T \leq T_*$ implies that $\Delta(\varepsilon, m, T) < 0$ while $T \geq T^*$ implies that $\Delta(\varepsilon, m, T) > 0$. Numerical simulations suggest that the map $T \mapsto \Delta(\varepsilon, m, T)$ is strictly increasing, which would mean that $T_*(m) = T^*(m)$.

We note that inflation occurs for intermediate values of m (nor too small, neither too large), thus is not a phenomena of mixing or non-mixing. This remind the work of Lawley, Mattingly and Reed [23], where an intermediate switching rate between two stable matrices can lead the system to inflation, while small and large rates lead to a stable system.

Comments on Figures 10 and 11 . We illustrate proposition 2.8 with these two figures. First we consider the process (V_t, U_t) when $\varepsilon = 0.5$, $m = 0.2$ and $\sigma = 0.4$. We start from $(0, 0)$, draw in red the trajectories corresponding to F_m^+ , in blue those corresponding to F_m^- . On Figure 10 we have drawn the lines $V = V_m^+$ and $V = V_m^-$. The domain $[V_m^-, V_m^+] \times \mathbb{R}$ is invariant. We have draw the lines : $I^+ \cup I^- = \{V : m \cosh(V) - m - \varepsilon = 0\}$ and we know that inside the strip $[I^-, I^+] \times \mathbb{R}$ one has $\frac{dU}{dt} < 0$ and outside $\frac{dU}{dt} > 0$.

- From $(0, 0)$ to a_1 the trajectory is inside $[I^-, I^+] \times \mathbb{R}$, it goes to the left.
- From a_1 to a_2 the trajectory is still inside $[I^-, I^+] \times \mathbb{R}$, it goes to the left.
- From a_2 to a_3 the trajectory crosses I^+ and stays some time outside of the strip $[I^-, I^+] \times \mathbb{R}$ where it is asymptotic to V_m^+ .
- From a_3 to a_4 the trajectory the major part of the time is spent in the strip : the motion is on the left.
- From a_4 to a_5 the time elapsed is rather long end te time elapsed out of the strip is long which means a significant move to the right.
- etc.

One sees that the long durations between two commutations favor the growth and conversely the short durations the decrease. For the choice that we have made $\sigma = 0.4$ it is difficult to imagine the value of $\Delta(0.5, 0.2, 2.5)$: see Figure 11 (above) where we can see 8 realizations of the process with these parameters.

But, on the same Figure 11 (below) there is no ambiguity : as predicted by Proposition 2.8, for high rate of switching ($\sigma = 5$ left), Δ is negative and for low rate of switching ($\sigma = 0.2$ right), Δ is positive.

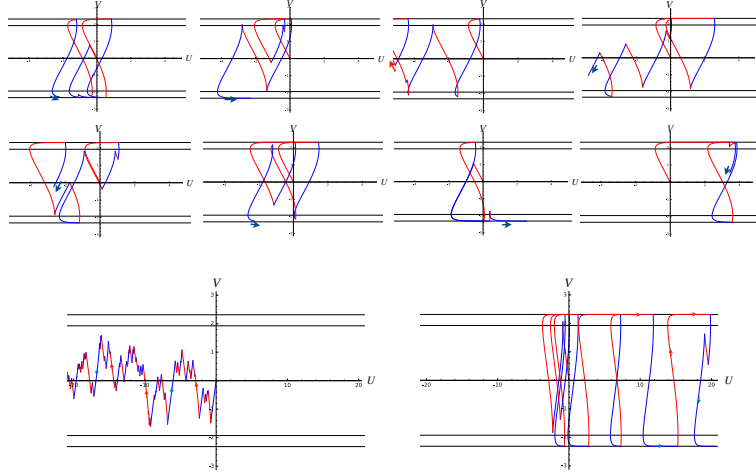


Figure 11: Above : Eight realizations of (Z_t) with : $\varepsilon = 0.5$, $m = 0.2$ and $\sigma = 0.4$. Below : Large and small rate of switching have opposite effect on the growth of $U(t)$: left $\sigma = 5$, right $\sigma = 0.2$

2.3.2 Link with the top Lyapunov exponent

Let $X_t = (x_1(t), x_2(t))$ the solution to $\Sigma(m, \varepsilon, T)$. With the notation of Section 2.2.4, one can rewrite $\Sigma(m, \varepsilon, T)$ as

$$\frac{dX_t}{dt} = M_{\varepsilon, m}^{u(t)} X_t. \quad (30)$$

The stability of the above equation is given by the sign of the following limit

$$\lim_{t \rightarrow \infty} \frac{1}{t} \ln \|X_t\|.$$

Here $\|\cdot\|$ stands for the euclidian norm on \mathbb{R}^2 . The classical Oselede't's Multiplicative ergodic theorem implies that the above limit exists, and can take at most two different values, called *Lyapunov exponent* (see e.g Chapter 1.4 in [26]). Since the matrices $M_{\varepsilon, m}^h$ are irreducible and *Metzler*, ie have non-negative off-diagonal coefficients, a random version of Perron - Frobenius Theorem (see e.g. Proposition 2.13 in [6]) implies that the top Lyapunov exponent, denoted here $\Lambda(\varepsilon, m, T)$, is such that, for all $X_0 \in \mathbb{R}_+^2 \setminus \{0\}$, almost surely,

$$\lim_{t \rightarrow \infty} \frac{1}{t} \ln \|X_t\| = \Lambda(\varepsilon, m, T).$$

Obviously, $\Lambda(\varepsilon, m, T)$ and $\Delta(\varepsilon, m, T)$ are linked. Indeed, note that the compact set $[V_m^-, V_m^+]$ is positively invariant for $V = \ln(x_1) - \ln(x_2)$ and attracts all trajectories. Hence, for all initial condition $(x_1(0), x_2(0))$, there exists a time t_0 such that, for all $t \geq t_0$, $V(t) \in [V_m^-, V_m^+]$. In particular, for $t \geq t_0$;

$$e^{V_m^-} \leq \frac{x_1(t)}{x_2(t)} \leq e^{V_m^+}$$

This yields

$$\left(e^{V_m^-} + e^{-V_m^+}\right) x_1(t)x_2(t) \leq x_1(t)^2 + x_2(t)^2 \leq \left(e^{-V_m^-} + e^{V_m^+}\right) x_1(t)x_2(t)$$

Taking the logarithm and sending t to infinity proves the following:

Proposition 2.9 *One has*

$$\Delta(\varepsilon, m, T) = 2\Lambda(\varepsilon, m, T).$$

2.3.3 A general stochastic (± 1) model

The choice of the exponential distribution in the previous section is made in order to get a Markov process and to get explicit expression for the invariant probability measure $\Pi_{m,T}$. However, in some situation, it would be more natural to consider that the sojourn time of the environment in each state has general distribution on \mathbb{R}_+ . That is, let μ_- and μ_+ be two probability measures on \mathbb{R}_+ , and let $(T_k^+)_{k \geq 1}$ and $(T_k^-)_{k \geq 1}$ be two independent sequences of independent random variables, distributed as μ_- and μ_+ , respectively. Then, the k -th sojourn times of u in state -1 and $+1$, respectively, are T_k^- and T_k^+ . This defines a continuous time stochastic process u which realizations are piecewise constant mappings $t \mapsto \mathbf{u}_t$ from \mathbb{R}^+ on $\{-1, +1\}$. Given an initial condition and a realization \mathbf{u} , we can integrate (3) and obtain the solution that we call V_t . This we call the stochastic (± 1) model. The deterministic (± 1) model that we studied so far can be considered as the particular stochastic model obtained with $\mu_- = \mu_+ = \delta_T$.

For mathematical convenience we build a Markov process from (V_t, \mathbf{u}_t) by adding the variable $\boldsymbol{\tau}_t$, equals to the time elapsed since the last jump of \mathbf{u} . We then get a strong Markov process $Z = (V, \mathbf{u}, \boldsymbol{\tau})$ on $[V_m^-, V_m^+] \times \{1, +1\} \times \mathbb{R}_+$. We shall make the following assumption on μ_- and μ_+ :

Hypothese 2.10 :

1. μ_- and μ_+ admit densities f_- and f_+ with respect to the Lebesgue measure on \mathbb{R}_+ ;
2. There exists $t_- > 0$ and $t_+ > 0$ and $\eta > 0$ such that $\inf_{|t-t_-| \leq \eta} f_-(t) > 0$ and $\inf_{|t-t_+| \leq \eta} f_+(t) > 0$;
3. There exists $C, \beta > 0$ such that for $h \in \{\pm 1\}$, $\int_t^{+\infty} f_h(t) dt \leq Ce^{-\beta t}$.

Thanks to results in a forthcoming paper [15], we can prove some kind of analogue of the existence of the stable periodic solution of the system $F(m, T)$ (Proposition 2.1) :

Proposition 2.11 *There exists a unique probability measure Π on $[V_m^-, V_m^+]$ such that, for all measurable set A , all bounded measurable function $f : \mathbb{R} \rightarrow \mathbb{R}$, all $(V(0), \mathbf{u}(0))$, one has*

$$\lim_{t \rightarrow \infty} \mathbb{P}(V(t) \in A) \rightarrow \Pi(A)$$

and, almost surely,

$$\lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t f(V(s)) ds = \int f(v) \Pi(v).$$

The proof of this result is out of the scope of the present paper.

Since $U(t)$ is just obtained by integrating $V(\cdot)$ we deduce :

Proposition 2.12

$$\lim_{t \rightarrow \infty} \frac{U(t)}{t} = \int_{(V_m^-, V_m^+)} 2(m \cosh(v) - m - \varepsilon) \Pi(dv) := \mathbf{\Delta}(\varepsilon, m, \mu_+, \mu_-).$$

The question of inflation is thus reduced to the "computation" of Π from the "data" μ_- and μ_+ which might be difficult, if not impossible. The previous section has provided an example where Π is explicitly computable. For the general case, let us show that if μ_- and μ_+ are close to δ_T , then $\mathbf{\Delta}(\varepsilon, m, \mu_+, \mu_-)$ is close to $\mathbf{\Delta}(\varepsilon, m, T)$.

Definition 2.13 We say that (μ_-, μ_+) is a (η, T) - Stochastic Approximatively Periodic Environment (SAPE) if $\mu^-([T - \eta, T + \eta]) = \mu^+([T - \eta, T + \eta]) = 1$.

Example 1 If μ_- and μ_+ are uniform laws on $[T - \eta, T + \eta]$, then (μ_-, μ_+) is a (η, T) - SAPE.

In other words, if (μ_-, μ_+) is a (η, T) - SAPE, the sojourn time of u in each environment ± 1 is between $T - \eta$ and $T + \eta$. The intuition is thus that, when η goes to 0, the signal u becomes closer and closer from a periodic signal, and trajectories of the random process should converge to the trajectories of the corresponding periodic system. This intuition is made precise in the following Lemma, proven in Appendix H.

Lemma 2.14 Let $T > 0$, and a sequence $(\mu_-^n, \mu_+^n)_{n \geq 0}$ of (η_n, T) - SAPE, for some sequence $(\eta_n)_{n \geq 0}$. Let $(V_t^n)_{t \geq 0}$ the trajectory associated to the environment (μ_-^n, μ_+^n) and $(V_t)_{t \geq 0}$ the solution of system $F(m, T)$. Assume that $\lim \eta_n = 0$. Then, for all $S > 0$, there exist n_0 and a constant $C(S, m, T)$ such that, for all $n \geq n_0$,

$$\sup_{t \in [0, S]} |V_t^n - V_t| \leq C(S, m, T) \eta_n.$$

The demonstration of Lemma 2.14 enables us to prove (see Appendix H) the following announced result:

Proposition 2.15 Let $T > 0$, and a sequence $(\mu_-^n, \mu_+^n)_{n \geq 0}$ of (η_n, T) - SAPE, for some sequence $(\eta_n)_{n \geq 0}$. Then, if $\lim \eta_n = 0$, we have

$$\lim_{n \rightarrow \infty} \mathbf{\Delta}(\varepsilon, m, \mu_+^n, \mu_-^n) = \mathbf{\Delta}(\varepsilon, m, T).$$

This proposition is illustrated by the two simulations of figure 12.

Remark 5 It is possible to weaken the definition of SAPE by only requiring that the mean sojourn times $M_- = \int t d\mu_-(t)$ and $M_+ = \int t d\mu_+(t)$ and the associated variances Var_-, Var_+ satisfy $M_-, M_+ \in [T - \eta, T + \eta]$ and $Var_-, Var_+ \leq \eta$. With such a definition, we would obtain a stochastic version of Lemma 2.14, which would be sufficient to prove Proposition 2.15. This is however out of the scope of this paper.

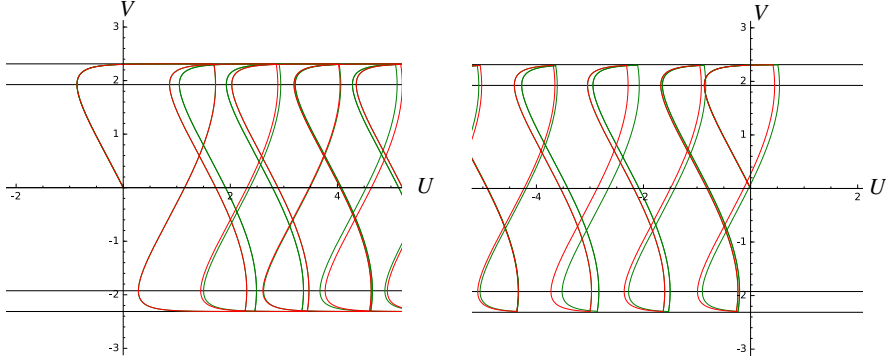


Figure 12: Stochastic Approximately Periodic Environment : μ_- and μ_+ uniform on $[T - \eta, T + \eta]$. In red solution corresponding to the T -periodic environment, in green solution corresponding to the stochastic environment ; $\varepsilon = 0.5$ $m = 0.2$; $T = 6$ $\eta = 0.6$ (left); $T = 4$ $\eta = 0.4$ (right).

3 Some extensions to more complex situations.

3.1 Migration between different patches

Our approach extends to the more general model

$$\begin{cases} \frac{dx_1}{dt} = \alpha_1(t)x_1 + m(x_2 - x_1) \\ \frac{dx_2}{dt} = \alpha_2(t)x_2 + m(x_1 - x_2) \end{cases} \quad (31)$$

where α_i are periodic functions of period $2T$. The change of variables

$$U = \ln(x_1) + \ln(x_2), \quad V = \ln(x_1) - \ln(x_2)$$

transforms (31) in

$$\begin{cases} \frac{dU}{dt} = \alpha_1(t) + \alpha_2(t) + 2m(\cosh(V) - 1) \\ \frac{dV}{dt} = \alpha_1(t) - \alpha_2(t) - 2m \sinh(V) \end{cases} \quad (32)$$

One observes that the variable V is decoupled from the variable U . Once the solution $V(t)$ of the second equation in (32) is known, the solution $U(t)$ is obtained by the simple quadrature :

$$U(t) = u(0) + \int_0^t (\alpha_1(s) + \alpha_2(s) + 2m(\cosh(V(s)) - 1)) ds$$

One can prove that the equation in V has a $2T$ -periodic solution $P(t)$, which is globally stable. Therefore, the asymptotic behaviour of (31) is reduced to the study of :

$$\Delta(m, T) = \frac{1}{2T} \int_0^{2T} (\alpha_1(t) + \alpha_2(t) + 2m(\cosh(V(t)) - 1)) dt \quad (33)$$

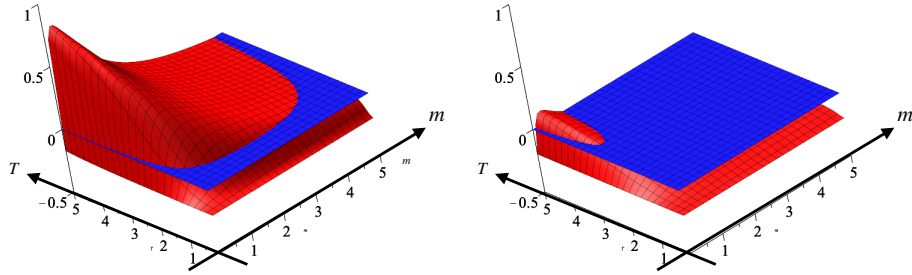


Figure 13: Graphs of $(m, T) \mapsto \frac{1}{T} \ln(\lambda_1(r_1, d_1, r_2, d_2, m, T))$ for two values of (r_1, d_1, r_2, d_2)

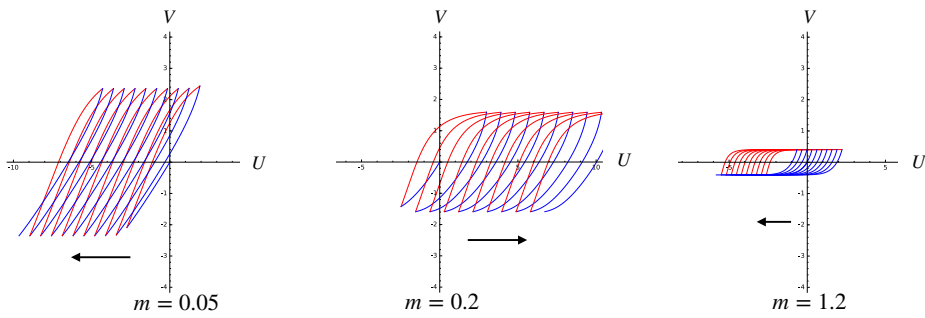


Figure 14: Trajectories of (32) $r_1 = 0.9, d_1 = 1.1, r_2 = -0.1, d_2 = 0.1, T = 5$

Remark 6 The model (31) with $\alpha_i(t)$ continuous is the model considered by Katriel in [18]. He considers the same changes of variables as us but our methods used to study the system in the (U, V) variables are different from those of [18].

Comments on figure 13. Consider the case where

$$\alpha_1(t) = \begin{cases} r_1 & \text{if } t \in [0, T] \\ -d_1 & \text{if } t \in [T, 2T] \end{cases}, \quad \alpha_2(t) = \begin{cases} -d_2 & \text{if } t \in [0, T] \\ r_2 & \text{if } t \in [T, 2T] \end{cases} \quad (34)$$

where r_1, r_2, d_1 and d_2 are real parameters. The system $\Sigma(\varepsilon, m, T)$, defined by (3) corresponds to the case where $r_1 = r_2 = 1 - \varepsilon$ and $d_1 = d_2 = 1 + \varepsilon$. We look to $\ln(\lambda_1(r_1, d_1, r_2, d_2, m, T))$ in two different cases. On the left we consider the case :

$r_1 = 0.9$	$d_1 = 1.1$	(35)
$r_2 = 0.9$	$d_2 = 1.1$	

which is the case of the (± 1) model for $\varepsilon = 0.1$ which we already considered. We compare this case to the case :

$r_1 = 0.9$	$d_1 = 1.1$	(36)
$r_2 = -0.1$	$d_2 = 0.1$	

In this case the patch n° 1 is unchanged and the patch n° 2 represent some place without seasonality. In this case the global productivity is smaller but the inflation phenomenon is still observable.

3.2 The case of non symmetric dispersal

The symmetric rate of dispersal between the two patches is a very special (and unlikely) situation. A non symmetric dispersal like in the model :

$$\begin{cases} \frac{dx_1}{dt} = \alpha_1(t)x_1 + m(\beta x_2 - (1 - \beta)x_1) \\ \frac{dx_2}{dt} = \alpha_2(t)x_2 + m((1 - \beta)x_1 - \beta x_2) \end{cases} \quad (37)$$

with $0 < \beta \leq 0.5$ is certainly more realistic. Using now

$$U = \ln(x_1) + \ln(x_2) \quad V = \ln(x_1) - \ln(x_2) - \ln(\sqrt{\beta(1 - \beta)})$$

one obtains :

$$\begin{cases} \frac{dU}{dt} = \alpha_1(t) + \alpha_2(t) + m(\sqrt{\beta(1 - \beta)} - 1) + 2m\sqrt{\beta(1 - \beta)}(\cosh(V) - 1) \\ \frac{dV}{dt} = \alpha_1(t) - \alpha_2(t) - m(1 - 2\beta) - 2m\sqrt{\beta(1 - \beta)}\sinh(V) \end{cases} \quad (38)$$

which is very similar to (32) and the treatment of this case will follow the same lines. In particular we find that, once $\beta > 0$ is fixed the asymptotics for $\Delta(m, T)$ are the same.

3.3 The case of partial phase shift

In the preceding section we considered the case where the two patches were always in opposite conditions during the whole period $2T$. A more realistic situation is when the two patches are ruled by the same periodic environment $r(t)$ shifted of φT with $\varphi \in (0, 1)$. In that case our (± 1) model could be extended in the following direction. We consider the four dynamical systems : As previously we have the two systems :

$$\Sigma^{+-}(\varepsilon, m, T, \varphi) \quad \begin{cases} \frac{dx_1}{dt} = (+1 - \varepsilon)x_1 + m(x_2 - x_1) \\ \frac{dx_2}{dt} = (-1 - \varepsilon)x_2 + m(x_1 - x_2) \end{cases} \quad (39)$$

and :

$$\Sigma^{-+}(\varepsilon, m, T, \varphi) \quad \begin{cases} \frac{dx_1}{dt} = (-1 - \varepsilon)x_1 + m(x_2 - x_1) \\ \frac{dx_2}{dt} = (+1 - \varepsilon)x_2 + m(x_1 - x_2) \end{cases} \quad (40)$$

to which we add :

$$\Sigma^{++}(\varepsilon, m, T, \varphi) \quad \begin{cases} \frac{dx_1}{dt} = (+1 - \varepsilon)x_1 + m(x_2 - x_1) \\ \frac{dx_2}{dt} = (+1 - \varepsilon)x_2 + m(x_1 - x_2) \end{cases} \quad (41)$$

and :

$$\Sigma^{--}(\varepsilon, m, T, \varphi) \quad \begin{cases} \frac{dx_1}{dt} = (-1 - \varepsilon)x_1 + m(x_2 - x_1) \\ \frac{dx_2}{dt} = (-1 - \varepsilon)x_2 + m(x_1 - x_2) \end{cases} \quad (42)$$

We switch from one system to the other according to the following scheme :

$t \in$	$[0, \varphi T[$	$[\varphi T, T[$	$[T, T(1 + \varphi), [$	$[T(1 + \varphi), 2T[$
Σ	$+-$	$++$	$-+$	$--$

(43)

Using the similar notations than those that we used in subsection 2.2.4, define :

$$M_{\varepsilon, m}^{+-} = \begin{bmatrix} 1 - m - \varepsilon & +m \\ +m & -1 - m - \varepsilon \end{bmatrix} \quad M_{\varepsilon, m}^{-+} = \begin{bmatrix} -1 - m - \varepsilon & +m \\ +m & 1 - m - \varepsilon \end{bmatrix}$$

$$M_{\varepsilon, m}^{++} = \begin{bmatrix} 1 - m - \varepsilon & +m \\ +m & +1 - m - \varepsilon \end{bmatrix} \quad M_{\varepsilon, m}^{--} = \begin{bmatrix} -1 - m - \varepsilon & +m \\ +m & -1 - m - \varepsilon \end{bmatrix}$$

The spectral radius of the matrix :

$$M(\varepsilon, m, T, \varphi) = e^{T(1-\varphi)M_{\varepsilon, m}^{--}} e^{\varphi T M_{\varepsilon, m}^{-+}} e^{T(1-\varphi)M_{\varepsilon, m}^{++}} e^{\varphi T M_{\varepsilon, m}^{+-}}$$

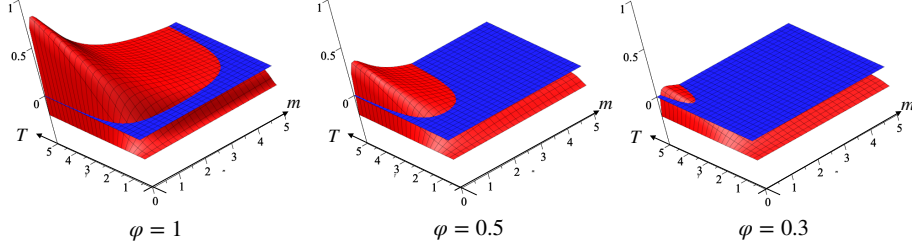


Figure 15: Graphs of $(m, T) \mapsto \frac{1}{T} \ln(\lambda_1(0.1, m, T, \varphi))$ for three values of φ

decides of the stability of the switched system associated to these four systems, T and φ . Once again, we ask to Maple to compute the eigenvalues of $M(\varepsilon, m, T, \varphi)$, we select the largest one $\lambda_1(\varepsilon, m, T, \varphi)$ and look for the mapping $(m, T) \mapsto 1/T \ln(\lambda_1(\varepsilon, m, T, \varphi))$ for $\varepsilon = 0.1$ and various values. When the shift φT is not equal to T our intuition is that the inflation effect will be proportional to the shift and will be maximum when $\varphi = 1$. This is confirmed by Figure 15.

3.4 Density dependent models

In [1, 2] a complete description of the asymptotic behavior of the model :

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \beta \left(\frac{x_2}{\gamma_2} - \frac{x_1}{\gamma_1}\right) \\ \frac{dx_2}{dt} &= r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \beta \left(\frac{x_1}{\gamma_1} - \frac{x_2}{\gamma_2}\right) \end{aligned} \quad (44)$$

is given in the space of the six independent parameters $\{r_i, K_i, (i = 1, 2), \beta/\gamma_2, \gamma_1/\gamma_2\}$, the focus being on the comparison between the total equilibrium population with the sum $K_1 + K_2$ of the two carrying capacities. Here we complement this study by considering the question of persistence when r_1 and r_2 vary in time for specific values of the parameters. Namely, we consider the system :

$$D(\varepsilon, \alpha, m, T) \quad \begin{cases} \frac{dx_1}{dt} = (+u(t) - \varepsilon)x_1 - \alpha x_1^2 + m(x_2 - x_1) \\ \frac{dx_2}{dt} = (-u(t) - \varepsilon)x_2 - \alpha x_2^2 + m(x_1 - x_2) \end{cases} \quad (45)$$

where $0 \leq \varepsilon \leq 1$, $\alpha \geq 0$, $m \geq 0$, $T \geq 0$ and the function $t \mapsto u(t)$ is periodic of period $2T$, with :

$$t \in [0, T] \Rightarrow u(t) = 1 \quad t \in [T, 2T] \Rightarrow u(t) = -1$$

We are interested in the *persistence* of (45). Recall that the system $D(\varepsilon, \alpha, m, T)$ is *uniformly persistent* (see for instance [8]) if there exist strictly positive constants $a < b$ such that every solutions $(x_1(t), x_2(t))$ of $D(\varepsilon, \alpha, m, T)$ is asymptotically bounded from below by a and from above by b (i.e. $a \leq x_i(t) \leq b$ for t sufficiently large).

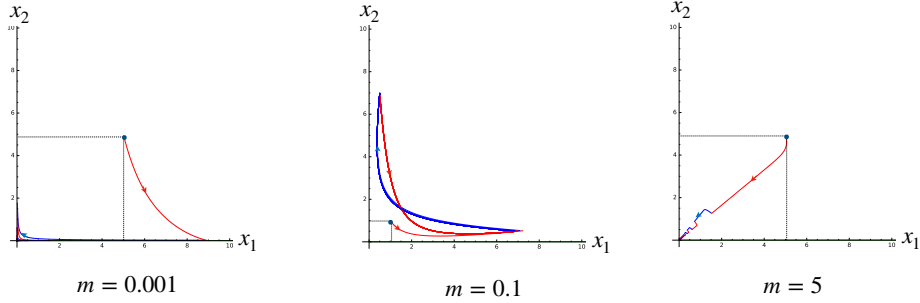


Figure 16: Simulations of $D(0.1, 0.1, m, 5)$ showing persistence for intermediate values of m .

When $\alpha = 0$ the system $D(\varepsilon, 0, m, T)$ is just the (± 1) model $\Sigma(\varepsilon, m, T)$. When α is not 0, but $m = 0$, on each patch the dynamic is :

$$\frac{dx_i}{dt} = (u(t) - \varepsilon)x_i - \alpha x_i^2 \quad i = 1, 2 \quad (46)$$

with $u(t) = \pm 1$. In both cases one has a logistic equation with a globally stable equilibrium equal to $\frac{1-\varepsilon}{\alpha}$ or 0. One sees easily that in the space $(\mathbb{R}^+)^2$ the square $S = [0, \frac{1-\varepsilon}{\alpha}] \times [0, \frac{1-\varepsilon}{\alpha}]$ is an invariant global attractor ; this implies that every trajectories of (45) are bounded from above.

Regarding boundedness from below we can say intuitively that the system $D(\varepsilon, \alpha, m, T)$ behaves around the origin like its linear approximation, namely the system $\Sigma(\varepsilon, m, T)$ and thus is persistent if and only if $\Sigma(\varepsilon, m, T)$ is unstable. Actually the following proposition can be proved (see appendix I)

Proposition 3.1 *If the parameters (ε, m, T) are such that the system $D(\varepsilon, 0, m, T) = \Sigma(\varepsilon, m, T)$ is :*

- *stable, then the solutions of $D(\varepsilon, \alpha, m, T)$ tend to 0 (extinction),*
- *unstable, then $D(\varepsilon, \alpha, m, T)$ is persistent.*

Thus we have, for T large enough, the sequence : small m : extinction – intermediate m : persistence – large m : extinction/ This is illustrated by the simulations of Figure 16.

3.4.1 A density dependent stochastic model

In this short section, we show that the Proposition 3.1 is still true under a random signal u . More precisely, we consider the system

$$\mathbf{D}(\varepsilon, \alpha, m, T) \quad \begin{cases} \frac{dx_1}{dt} = (+u(t) - \varepsilon)x_1 - \alpha x_1^2 + m(x_2 - x_1) \\ \frac{dx_2}{dt} = (-u(t) - \varepsilon)x_2 - \alpha x_2^2 + m(x_1 - x_2) \end{cases} \quad (47)$$

where u switches from 1 to -1 and conversely at random exponential time, as described in Section 2.3. Like in the periodic case described above, when $\alpha = 0$, $\mathbf{D}(\varepsilon, \alpha, m, T)$ is just the stochastic (± 1) model $\mathbf{\Sigma}(\varepsilon, m, T)$. Using a terminology borrowed to Schreiber and Chesson, we say that the system $D(\varepsilon, \alpha, m, T)$ is *stochastically persistent* if for all $\eta > 0$, there exists a compact set $K_\eta \subset \mathbb{R}_{++}^2$ such that, almost surely,

$$\liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t \mathbb{1}_{(x_1(s), x_2(s)) \in K_\eta} ds \geq 1 - \eta.$$

We now give the stochastic counterpart of Proposition 3.1:

Proposition 3.2 *We have the following dichotomy:*

- If $\Delta(\varepsilon, m, T) \leq 0$, then system $D(\varepsilon, \alpha, m, T)$ goes to extinction;
- If $\Delta(\varepsilon, m, T) > 0$, then system $D(\varepsilon, \alpha, m, T)$ is stochastically persistent, and the process (x_1, x_2, u) admits a unique stationary distribution ν such that $\nu(\mathbb{R}_{++}^2 \times \{\pm 1\}) = 1$.

3.5 The epidemic model of Holt and al.

In [19] Holt and his colleagues consider the classical S.I.R. model for a population living in two patches connected by migration. The model is the following system :

$$\begin{aligned} \frac{dS_1}{dt} &= -\beta(t)S_1I_1 + m(S_2 - S_1) \\ \frac{dI_1}{dt} &= +\beta(t)S_1I_1 - (\gamma(t) + \mu)I_1 + m(I_2 - I_1) \\ \frac{dS_2}{dt} &= -\beta(t - \varphi)S_2I_2 + m(S_1 - S_2) \\ \frac{dI_2}{dt} &= +\beta(t - \varphi)S_2I_2 - (\gamma(t - \varphi) + \mu)I_2 + m(I_1 - I_2) \end{aligned} \tag{48}$$

where $S_i(t)$ represents the number of "susceptible to be infected" at time t on each patch, $I_i(t)$ represents the number of "infected" on each patch. The parameters $\beta(\cdot)$ and $\gamma(\cdot)$ are piecewise constant function of period $2T$ varying according to the presence or absence of social distancing measures ; we examine the messages of this paper in light of our previous study of inflation phenomenon³.

The first remark of the authors of [19] is to consider that we are essentially interested by the beginning of the contamination when, as a first approximation, we can consider that $S(t)$ is almost equal to the initial total population N . Then the approximate model is :

$$\begin{aligned} \frac{dI_1}{dt} &= (\beta(t)N - (\gamma(t) + \mu))I_1 + m(I_2 - I_1) \\ \frac{dI_2}{dt} &= (\beta(t - \varphi)N - (\gamma(t - \varphi) + \mu))I_2 + m(I_1 - I_2) \end{aligned} \tag{49}$$

³The authors of [19] publish the same message in P.N.A.S. [20] but using less realistic $\beta(\cdot)$ and $\gamma(\cdot)$ like continuous sinusoidal functions. We prefer to refer to the initial paper.

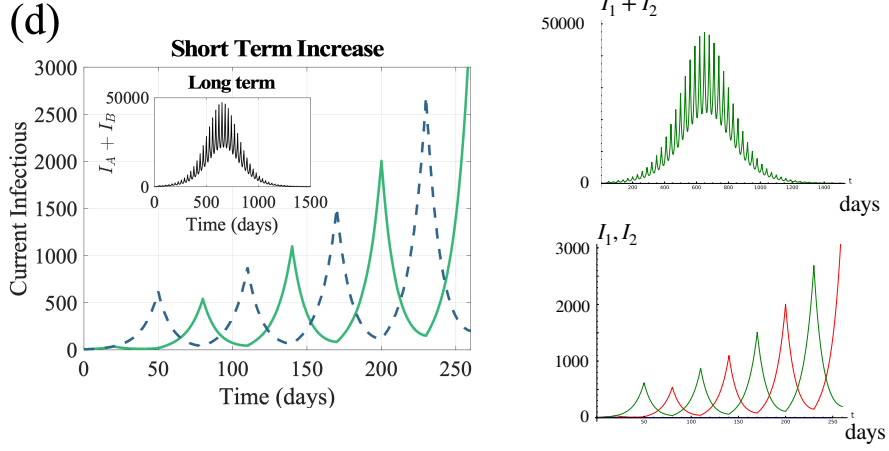


Figure 17: Simulation from [19] (left) ; our simulation (right)

They denote respectively by the subscripts n and s the values of parameters in "normal" periods and periods when the "social distancing" is in effect. They adopt, according to the current literature, the following realistic values .

$\beta_n N = 0.1988$	$\gamma_n = 0.098$	$\mu_n = 0.002$
$\beta_s N = 0.0288$	$\gamma_s = 0.128$	$\mu_s = 0.002$

$\beta_n N - (\gamma_n + \mu_n) = 0.0988$
$\beta_s N - (\gamma_s + \mu_s) = -0.1012$

and they discuss the case $T = 30$. We have done a simulation with these parameters, with $2T = 60$ and $m = 0.005$ and obtained the same picture than [19] (see figure 17) which confirms that we are actually running the same model but our objective is not to reproduce [19] results but to complete them. For this purpose we consider the effect of migration, in the case of a small phase shift in the application of social distancing. We assume that $\varphi = 4$ days.

In the absence of migration the linear model is :

$$\frac{dI_i}{dt} = 0.0988 I_i \quad (\text{normal}) \quad \frac{dI_i}{dt} = -0.1012 I_i \quad (\text{social distancing}) \quad (50)$$

If we multiply the dynamic of I_i by the factor 10 (which means a change unit for the time) we have :

$$\frac{dI_i}{dt} = 0.988 I_i \quad (\text{normal}) \quad \frac{dI_i}{dt} = -1.012 I_i \quad (\text{social distancing}) \quad (51)$$

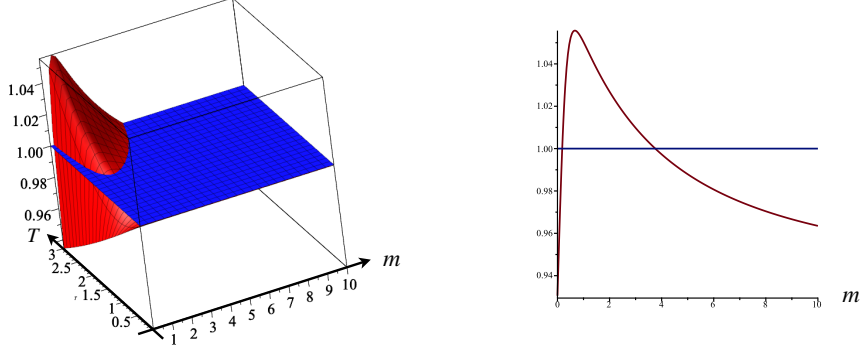


Figure 18: Graphs of $(m, T) \mapsto \lambda_1(0.012, m, T, 0.133)$ (left) and $m \mapsto \lambda_1(0.012, m, 3, 0.133)$

which we read as the “ (± 1) model”:

$$\frac{dx_i}{dt} = (1 - \varepsilon)x_i \quad (\text{normal}) \quad \frac{dx_i}{dt} = -(1 + \varepsilon)x_i \quad (\text{social distancing}) \quad (52)$$

with $\varepsilon = 0.012$. To $T = 30$ and a phase shift of 4 days in the model (48) correspond $T = 3$ a shift of 0.133 in (52). For these values one sees on the graphs of λ_1 that there is no longer instability for $m > 2$ which means $m > 0.2$ in the original system (48). This must be reflected on the epidemic. If one looks to the cumulative number of cases for a duration of 1500 days the simulation of the model gives the figure 19. We can see that no migration at all is the best, when migration grows from 0 to approximately 0.1 the number of cases is multiplied by 4 but and after that decreases. *Very low migration can increase dramatically the number of cases, while, if migration is unavoidable, comparatively large one has better effect.*

In their paper published in the P.N.A.S. the authors [20] say : "These findings highlight a need for integrated, holistic policy: Intensify mitigation locally, coordinate tactics among locations, and reduce movement."

We think, in view of our work, that the last recommendation must be qualified : reducing movement to 0 is certainly beneficial, but if it is not possible, in case of small asynchronicity, encourage movement could be better. This does not invalidate but reinforces the conclusion of their paper with which we fully agree. "It is increasingly recognized that monitoring and controlling movement is essential for effective pandemic control. The impact of such actions is, however, contextual, because their dynamical effects are intertwined with the magnitude of asynchrony in local transmission across space. More-realistic, spatially structured epidemiological models including movement and asynchronous transmission – at scales from local to international – are essential to control this and future pandemics in the coupled metapopulations of humans and their pathogens."

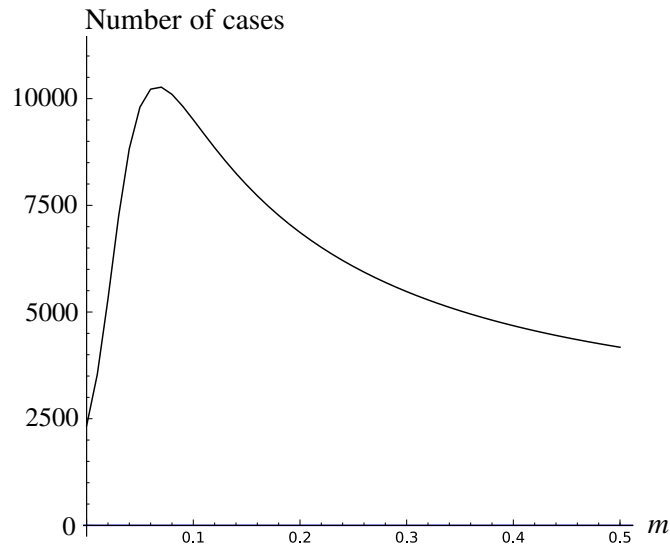


Figure 19: Cumulative number of cases up to 1500 days as a function of migration.

4 Conclusion

Inflation is a spectacular phenomenon exhibited by the system that we called the “ (± 1) model” (see section 2.2). It is a spectacular phenomenon in two respects.

- Two patches that each provide unfavorable habitat leading to extinction can become an overall favorable environment if there is migration between the two sites.
- The phenomenon can be extremely abrupt, with a very small increase in migration leading to a considerable increase in growth.

The simplicity of the “ (± 1) model” allowed us to understand the fundamental role of exponential growth and to make explicit computations (possibly using a formal calculator) which quantify the roles of the period and the rate of migration.

Insofar as our “ (± 1) model” is totally unrealistic, it is linear, strictly periodic and the two sites are exactly out of phase, it was important to verify that the phenomenon of inflation is not a specific mathematical curiosity of a very particular model, but one that is likely to arise each time the following ingredients are combined : several sites, environments that vary over time, migration between sites. We did this by considering the case of non symmetric dispersal (see subsection 3.2), the case of partial phase shifts (see subsection 3.3) and of density dependent growth models (see subsection 3.4). In all these extensions, inflation is present.

Moreover we showed that the phenomenon is not specific of deterministic systems ; we showed existence of inflation in various stochastic models like

those of subsections 2.3,2.3.1, 2.3.3, 3.4.1. For this random extension, we use the theory of Piecewise Deterministic Markov Process (PDMP), which enables us to prove the existence of a unique growth rate, and to investigate the variation of this growth rate according to the parameters. On several aspects, our study can be related to former papers, where random switching between two ODEs with the same asymptotic behaviour can completely reverse the trend. For example, in [5], switching between two competitive two-species Lotka - Volterra equations favorable to the same species may lead to the extinction of this favored species. Similarly, in [6], random switching between two epidemiological models with extinction of the disease may lead to persistence of the disease. We also briefly discussed the case of nonexponential switching time, which is far more complicate to investigate, but produces similar behaviour and which might be consider as more realistic in many situations.

In a stimulating essay, *Ecological orbits, how planets move and populations grow*, Lev Ginzburg and M. Colyvan [16] defend the idea that exponential growth is, for population dynamics, the equivalent of the principle of inertia in classical mechanics : a population whose growth rate is unconstrained grows exponentially, just as a material body subjected to no force keeps the same speed. We know how the theory of the periodically forced harmonic oscillator plays a central role in many fields of physics. From the perspective of *Ecological orbits* the ” (± 1)model” with its inflation phenomenon could be compared to the forced harmonic oscillator with the resonance phenomenon.

A The system $\Sigma(\varepsilon, m, T)$ for large m

Consider the system :

$$\begin{aligned}\frac{dx_1}{dt} &= (+u(t) - \varepsilon)x_1 + m(x_2 - x_1) \\ \frac{dx_2}{dt} &= (-u(t) - \varepsilon)x_2 + m(x_1 - x_2)\end{aligned}$$

and put :

$$S = x_1 + x_2 \quad D = x_1 - x_2$$

One has :

$$\begin{aligned}\frac{dS}{dt} &= (+u(t) - \varepsilon)x_1 + m(x_2 - x_1) + (-u(t) - \varepsilon)x_2 + m(x_1 - x_2) = u(t)D - \varepsilon S \\ \frac{dD}{dt} &= u(t) - 2(m + \varepsilon)D = -2(m + \varepsilon) \left(D - \frac{u(t)}{2(m + \varepsilon)} \right)\end{aligned}$$

From Tychonov theorem ([27, 22]), when $2(m + \varepsilon) \rightarrow \infty$ the solution to this system (called a slow-fast system), after a short transient, tends to :

$$S(t) = S(0)e^{-\varepsilon t} \quad D(t) = 0$$

Thus, in the variables (x_1, x_2) one has :

$$x_1(t) \approx x_2(t) \approx \frac{x_1(0) + x_2(0)}{2} e^{-\varepsilon t}$$

This is also called by physicists, the method of the *quasi stationary state*.

B The switched system $F(m, T)$ has a single globally stable periodic orbit

We consider the one dimensional switched system :

$$F(m, T) \quad \frac{dV}{dt} = \frac{1 + u(t)}{2} F_m^+(V) + \frac{1 - u(t)}{2} F_m^-(V) \quad (53)$$

with :

$$F_m^+(V) = 2(1 - m \sinh(V)) \quad F_m^-(V) = 2(-1 - m \sinh(V))$$

and :

$$V_m^+ = \sinh^{-1}(+1/m) \quad V_m^- = \sinh^{-1}(-1/m)$$

Since $F_m^+(V)$ is continuous, differentiable and such that $(V - V_m^+)F_m^+(V) < 0$ except for $V = V_m^+$, from the elementary theory of differential equations we know that, if we denote by $V^+(t, V)$ the unique solution of :

$$\frac{dV}{dt} = F_m^+(V) \quad V(0) = V$$

then $V^+(t, V)$ is defined for every positive t and the mapping $V \mapsto V^+(t, V)$ is continuous and differentiable.

Lemma B.1 *Let $T > 0$. The mapping $V \mapsto V^+(T, V)$ is a continuous mapping, strictly increasing, from $[V_m^-, V_m^+]$ into $[V_m^-, V_m^+]$; moreover its derivative is strictly smaller than 1.*

Proof Assume that $V \mapsto V^+(T, V)$ is not strictly increasing. Then it exists $V_1 < V_2$ such that $V^+(T, V_2) \leq V^+(T, V_1)$; and, by the way, some $t \leq T$ for which $(V^+(t), V_1) = V^+(t), V_2)$ and, thus, two solutions starting from different initial conditions meet at some point. This contradicts the uniqueness of solutions. The derivative of $V \mapsto V^+(T, V)$ at the point V_o is obtained by integrating the linearized equation along the trajectory $t \mapsto V^+(t, V_o)$ up to time T , that is to say :

$$\frac{d\delta V^+}{dt} = DF_m^+(V^+(t, V_o))\delta V^+ \quad \delta V^+(0) = 1$$

where $DF_m^+(V)$ is the derivative of $F_m^+(V)$ at point V .

$$\delta V^+(T) = \exp\left(\int_0^T DF_m^+(V^+(t, V_o))dt\right)\delta V^+(0)$$

One has :

$$\int_0^T DF_m^+(V^+(t, V_o))dt = \int_{V_o}^{V^+(T, V_o)} \frac{DF_m^+(V)}{F_m^+(V)} dV = \ln(F_m^+(V^+(T, V_o))) - \ln(F_m^+(V_o))$$

Since the function $F_m^+(V)$ is decreasing and $V^+(T, V_o) > V_o$ the integral is negative and thus $\delta V^+(T) < 1$.

□

For the same reasons we have the following : We denote by $V^-(t, V)$ the unique solution of :

$$\frac{dV}{dt} = F_m^-(V) \quad V(0) = V$$

then $V^-(t, V)$ is defined for every positive t and the mapping $V \mapsto V^-(t, V)$ is continuous and differentiable.

Lemma B.2 *Let $T > 0$. The mapping $V \mapsto V^-(T, V)$ is a continuous mapping, strictly increasing, from $[V_m^-, V_m^+]$ into $[V_m^-, V_m^+]$; moreover its derivative is strictly smaller than 1.*

Now consider "period-map", that is the composite mapping $V \mapsto \Phi(V) = V^-(T, V^+(T, V))$ from $[V_m^-, V_m^+]$ into $[V_m^-, V_m^+]$ (see figure 20, left); from the preceding lemmas it turns out that it is strictly increasing, with $\Phi'(V) < 1$ such that $V_m^- < \Phi(V_m^-)$ and $\Phi(V_m^+) < V_m^+$. From elementary calculus the discrete dynamical system defined by :

$$V(n+1, V_o) = \Phi(V(n, V_o)), \quad V(0, V_o) = V_o$$

has a unique equilibrium V_e , i.e. the unique solution of $\Phi(V) = V$, this equilibrium is globally asymptotically stable (see figure 20, right). Since $\Phi(V(n, V_o)) = V(n2T, V_o)$, where $V(n2T, V_o)$ is the solution of the switched system (53) we have proved :

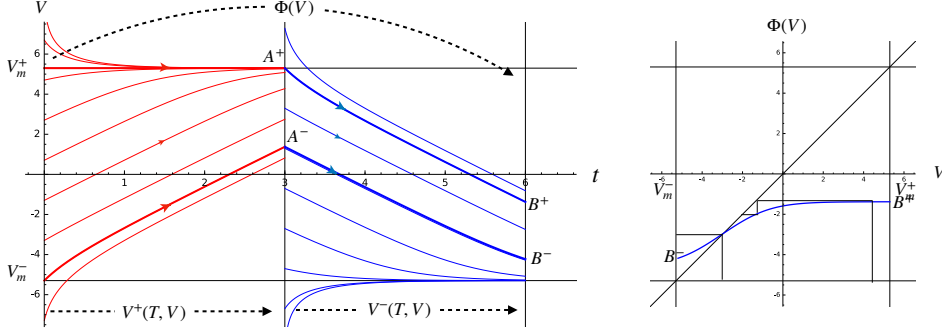


Figure 20: The switched system $F(m, T)$: $m = 0.01$; $T = 3$. The segment $[A^-, A^+]$ is the image of $[V_m^-, V_m^+]$ by the mapping $V \mapsto V^+(T, V)$, and $[B^-, B^+]$ is the image of $[A_m^-, A_m^+]$ by the mapping $V \mapsto V^-(T, V)$

Proposition B.3 *The switched system $F(m, T)$ has a unique periodic solution, denoted $P_{m, T}(t)$, globally asymptotically stable which oscillates between two values $P_{m, T}^-$, and $P_{m, T}^+$ contained in the interval $[V_m^-, V_m^+]$; $P_{m, T}^- = -P_{m, T}^+$ and the function $T \mapsto P_{m, T}^+$ is an increasing function of T which tends to V_m^+ when T tends to infinity.*

The solutions of (53) are explicitly computable as we show now.

On $[0, T]$ one has :

$$\frac{dV}{dt} = 2(1 - m \sinh(V)) \quad V(0) = V_0 \quad (54)$$

and by the way :

$$t = \int_{V_0}^{V(t)} \frac{dV}{2(1 - m \sinh(V))} \quad (55)$$

Since the function that we have to integrate is a rational fraction with respect to e^V we can integrate it explicitly (by hand or with the help of some formal software) and the result is :

$$\int \frac{dV}{2(1 - m \sinh(V))} = \frac{1}{A} \tanh^{-1} \left(\frac{\tanh(V/2) + m}{A} \right)$$

where

$$A = \sqrt{1 + m^2}$$

The periodic solution oscillate between $-P_{m, T}^+$ and $+P_{m, T}^+$ solutions of the equation :

$$T = \int_{-P_{m, T}^+}^{P_{m, T}^+} \frac{dV}{2(1 - m \sinh(V))} \quad (56)$$

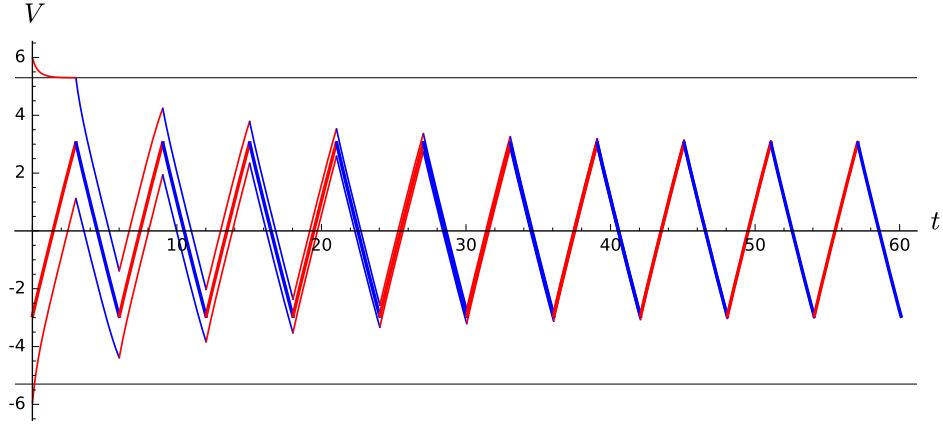


Figure 21: The switched system $F(m, T)$: $m = 0.01$; $T = 3$. Solutions converge to a unique periodic orbit.

and thus $P_{m,T}^+$ is a solution of the equation :

$$\tanh^{-1}\left(\frac{\tanh(P_{m,T}^+/2) + m}{A}\right) - \tanh^{-1}\left(\frac{\tanh(-P_{m,T}^+/2) + m}{A}\right) = TA$$

Thus, if we put $x = \tanh(P_{m,T}^+/2)$, we are searching for the solutions of the equation :

$$\tanh^{-1}\left(\frac{x+m}{A}\right) + \tanh^{-1}\left(\frac{x-m}{A}\right) = TA$$

From the formula $\tanh^{-1}(a) + \tanh^{-1}(b) = \tanh^{-1}\left(\frac{a+b}{1+ab}\right)$, one obtains the equation :

$$\tanh^{-1}\left(\frac{2Ax}{1+x^2}\right) = TA$$

and :

$$x^2 \tanh(TA) - 2Ax + \tanh(TA) = 0$$

This equation admits two solutions :

$$x = \frac{A - \sqrt{A^2 - \tanh^2(TA)}}{\tanh(TA)}, \quad x = \frac{A + \sqrt{A^2 - \tanh^2(TA)}}{\tanh(TA)}.$$

The second solution is not acceptable since it is greater than 1. We have :

$$\tanh(P_{m,T}^+/2) = \frac{A - \sqrt{A^2 - B^2}}{B}, \quad \text{with } B = \tanh(TA) \quad (57)$$

Thus we have proved the :

Proposition B.4 The maximum $P_{m,T}^+$ (respectively the minimum $P_{m,T}^- = -P_{m,T}^+$) of the periodic solution of (53) is given by :

$$P_{m,T}^+ = 2 \tanh^{-1} \left(\frac{A - \sqrt{A^2 - B^2}}{B} \right) \text{ with } A = \sqrt{1 + m^2} \text{ and } B = \tanh(TA) \quad (58)$$

C Qualitative properties of $S(\varepsilon, m, T)$

We prove :

Proposition C.1 *Qualitative properties of $S(\varepsilon, m, T)$*

1. For small m , $\Delta(\varepsilon, m, T) < 0$
2. For large m , $\Delta(\varepsilon, m, T) > 0$
3. For fixed $\varepsilon > 0$ and $m < \frac{1-\varepsilon^2}{2\varepsilon}$ there exists a threshold $T^*(\varepsilon, m)$ such that for $T < T^*(\varepsilon, m)$, $\Delta(\varepsilon, m, T) < 0$ and $\Delta(\varepsilon, m, T) > 0$ for $T > T^*(\varepsilon, m)$
4. For every $\varepsilon > 0$, the minimum of $T^*(\varepsilon, m)$ over m is strictly positive. In other words there exists a threshold $T^{**} > 0$ such that for $T < T^{**}$, for all values of m , $\Delta(\varepsilon, m, T) < 0$: there is no inflation.

Proof of 1) Since in the interval $[V_m^-, V_m^+]$, where the periodic solution lives, one has $|\frac{dV}{dt}| < 1$ we know that $P_m^+ < T$. Since $\lim_{m \rightarrow 0} A_{\varepsilon, m}^+ = \lim_{m \rightarrow 0} \cosh^{-1} \left(1 + \frac{\varepsilon}{m} \right) = +\infty$, for small enough m , the periodic solution $P_{m,T}(t)$ lives in the interval $]A_{\varepsilon, m}^-, A_{\varepsilon, m}^+[$ where the function φ is strictly negative and hence so is $\Delta(m, T)$.

Proof of 2) Given $\varepsilon > 0$ the relative positions of $V_m^+ = \sinh^{-1}(\frac{1}{m})$ and $A_{\varepsilon, m}^+ = \cosh^{-1} \left(1 + \frac{\varepsilon}{m} \right)$ depends on m . One easily compute that :

$$A_{\varepsilon, m}^+ < V_m^+ \iff m < \frac{1 - \varepsilon^2}{2\varepsilon} \quad (59)$$

hence, if $m > \frac{1-\varepsilon^2}{2\varepsilon}$ one has $[V_m^-, V_m^+] \subset [A_{\varepsilon, m}^-, A_{\varepsilon, m}^+]$ and $\varphi(P_m(t))$ is always negative.

Proof of 3) On the one hand the function $T \mapsto P_{m,T}^+$ is a strictly increasing function of T , from 0 to V_m^+ and, on the other hand, $\int_{A_{\varepsilon, m}^+}^{V_m^+} \varphi(V) dV = +\infty$. It follows that the function :

$$T \mapsto \Delta(\varepsilon, m, T) = 2 \int_{P_{m,T}^-}^{P_{m,T}^+} \varphi(V) dV$$

starts from 0, decreases to a minimum attained when $P_{m,T}^+ = A_{\varepsilon, m}^+$, then is strictly increasing and tends to $+\infty$ and is 0 for a unique value $T^*(\varepsilon, m)$ (see figure ??).

Proof of 4) Let $\varepsilon > 0$ given, consider $m_o = \frac{1-\varepsilon^2}{2\varepsilon}$ and set $T_o = A_{\varepsilon, m_o}^+ = V_{m_o}^+$. Let $T < T_o$. For $m > m_o$ we already know that $\Delta(\varepsilon, m, T) < 0$. If $m < m_o$ one

has $A_{\varepsilon,m}^+ > T_o > T$ and, by the way, $\varphi(P_{m,T}(t))$ is always negative. Thus for $T < \sinh^{-1}\left(\frac{2\varepsilon}{1-\varepsilon^2}\right)$, whatever the value of m , one has $\Delta(\varepsilon, m, T) < 0$ which proves 4).

D Explicit formula for $\Delta(\varepsilon, m, T)$

We consider the periodic solution $P_{m,T}(t)$ to $F(m, T)$. We are interested by the sign of :

$$\Delta(\varepsilon, m, T) = \frac{1}{T} \int_{P_{m,T}^-}^{P_{m,T}^+} \frac{m(\cosh(V) - 1) - \varepsilon}{1 - m \sinh(V)} dV \quad (60)$$

From the formula (60) and proposition B.4 we can deduce an explicit formula for $\Delta(\varepsilon, m, T)$. First, if we use formula (56) in the definition of $\Delta(\varepsilon, m, T)$ we get :

$$\Delta(\varepsilon, m, T) = \frac{1}{T} \int_{-P_{m,T}^+}^{P_{m,T}^+} \frac{m \cosh(V) dV}{1 - m \sinh(V)} - 2(m + \varepsilon) \quad (61)$$

Since $\frac{d}{dV} \sinh(V) = \cosh(V)$, one can explicitly compute the integral to get :

$$\int \frac{m \cosh(V) dV}{1 - m \sinh(V)} = -\ln(1 - m \sinh(V)) \quad (62)$$

and, by the way :

$$\Delta(\varepsilon, m, T) = \frac{1}{T} \ln \frac{1 + m \sinh(P_{m,T}^+)}{1 - m \sinh(P_{m,T}^+)} - 2(m + \varepsilon) \quad (63)$$

Using the formula $\sinh(a) = \frac{2 \tanh(a/2)}{1 - \tanh^2(a/2)}$, from (57) one gets :

$$\sinh(P_{m,T}^+) = \frac{A - \sqrt{A^2 - B^2} B}{B^2 - A^2 + A \sqrt{A^2 - B^2}}$$

If we replace in (63) we have :

$$\Delta(\varepsilon, m, T) = \frac{1}{T} \ln \frac{B^2 - A^2 + A \sqrt{A^2 - B^2} + m(A - \sqrt{A^2 - B^2} B)}{B^2 - A^2 + A \sqrt{A^2 - B^2} - m(A - \sqrt{A^2 - B^2} B)} - 2(m + \varepsilon)$$

and, after a multiplication by the conjugate quantity of the denominator one have the more simple expression :

$$\Delta(\varepsilon, m, T) = \frac{1}{T} \ln \frac{A^2 - B^2 + m^2 B^2 + 2mB \sqrt{A^2 - B^2}}{A^2 - B^2 - m^2 B^2} - 2(m + \varepsilon)$$

Using $A^2 = 1 + m^2$ and $B = \tanh(TA) = \frac{e^{2TA} - 1}{e^{2TA} + 1}$, one gets :

$$\Delta(\varepsilon, m, T) = \frac{1}{T} \ln \frac{m^2 b^4 + 2b^2 + m^2 + m(b^2 - 1)\sqrt{C}}{2(1 + m^2)b^2} - 2(m + \varepsilon) \quad (64)$$

with $b = e^T \sqrt{1 + m^2}$ and $C = m^2 b^4 + 2m^2 b^2 + 4b^2 + m^2$.

E Asymptotics of $\Delta(\varepsilon, m, T)$ for large T

We are looking for solutions of $m \mapsto (\Delta(\varepsilon, m, T) = 0$ which are exponentially small with respect to T , that is to say for x solutions of :

$$\Delta(\varepsilon, e^{xT}, T) = 0 \quad x < 0 \quad (65)$$

We use Landau notation o for any quantity that tends to 0 when t tends to ∞ . From (64),

$\Delta(\varepsilon, m, T) = 0$ is equivalent to :

$$\frac{m^2 b^4 + 2b^2 + m^2 + m(b^2 - 1)\sqrt{C}}{2(1 + m^2)b^2} = e^{2(m+\varepsilon)T} \quad (66)$$

with

$$b = e^{T\sqrt{1+m^2}}, \quad C = m^2 b^4 + 2m^2 b^2 + 4b^2 + m^2, \quad m = e^{xT} \quad (67)$$

From (67) one have :

$$mb = e^{Tx} e^{T\sqrt{1+e^{2Tx}}} = e^{T(1+x+\frac{1}{2}e^{2Tx}(1+o))} \quad (68)$$

since for $x < 0$ we have $T e^{2Tx} = o$ we deduce $mb = e^{T(1+x+o)}$ which tends to ∞ as long as $x > -1$. from which we deduce that as long as $x > -1$:

$$m^2 b^4 + 2b^2 + m^2 = m^2 b^4 (1 + o(1)) \quad m(b^2 - 1)\sqrt{C} = m^2 b^4 (1 + o(1)) \quad (69)$$

which introduced in (66) gives :

$$m^2 b^2 (1 + o(1)) = e^{2T(1+x)(1+o(1))} = e^{2T(\varepsilon+o(1))} \quad (70)$$

from which we deduce :

$$2T(1+x)(1+o(1)) = 2T(\varepsilon+o(1)) \implies x = -(1-\varepsilon) + o(1) \quad (71)$$

which is the evaluation of proposition 2.5.

F The randomly switched system $F(m, T)$ admits a unique stationary distribution

Proposition 2.7 is a consequence of the following property of the process \mathbf{V} :

Proposition F.1 *The process $(\mathbf{V}_t)_{t \geq 0}$ admits a unique stationary distribution $\mathbf{\Pi}_{m,T}$. The support of $\mathbf{\Pi}_{m,T}$ is the set $[V_m^-, V_m^+] \times \{-1, +1\}$, and if we denote $\mathbf{\Pi}_{m,T}^h(\cdot) = \mathbf{\Pi}_{m,T}(\cdot \times \{h\})$ for $h \in \{-1, +1\}$, then $\mathbf{\Pi}_{m,T}^h$ has a density $\rho_{m,T}^h$ with respect to the Lebesgue measure on \mathbb{R} . Furthermore, $\mathbf{\Pi}_{m,T}$ is ergodic and globally asymptotically stable for the law of \mathbf{V} in the sense that, for all initial condition $\mathbf{V}_0 \in [V_m^-, V_m^+] \times \{-1, +1\}$,*

$$\sup_{(A,h) \in \mathcal{B}([V_m^-, V_m^+] \times \{-1, +1\})} |\mathbb{P}(\mathbf{V}_t \in A \times \{h\}) - \mathbf{\Pi}_{m,T}(A \times \{h\})| \leq C e^{-\eta t},$$

and, for all bounded measurable function f , almost surely,

$$\lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t f(\mathbf{V}_s) ds = \int f(V, u) \mathbf{\Pi}_{m,T}(dV, du).$$

Proof

It is easily seen that the compact set $[V_m^-, V_m^+]$ is positively invariant by the flows generated by F_m^- and F_m^+ , hence it is also invariant for V solution to $F(m, T)$. Moreover, every point in $v \in (V_m^-, V_m^+)$ is accessible for Z in the sense of [4, Definition 3.6] and satisfy $F_m^+(v) - F_m^-(v) = 4 > 0$. Hence, the strong bracket condition is satisfied at some accessible point, and [4, Theorem 4.6] yields the result.

In addition, the density functions $\rho_{m,T}^-$ and $\rho_{m,T}^+$ are explicitly computable, and are given by (see e.g [11, Proposition 3.12] for the general formula)

$$\rho_{m,T}^h(v) = \frac{C(m)}{|F_m^h(v)|} \left(\frac{e^{V_m^+} - e^v}{e^v + e^{V_m^-}} \frac{e^v - e^{V_m^-}}{e^v + e^{V_m^+}} \right)^{\frac{1}{2T\sqrt{m^2+1}}}; \quad (72)$$

where $C(m)$ is a normalisation constant such that

$$\int_{V_m^-}^{V_m^+} \rho_{m,T}^+(v) + \rho_{m,T}^-(v) dv = 1.$$

Proposition 2.7 follows by setting $\Pi_{m,T} = \sum_h \mathbf{\Pi}_{m,T}^h$ and

$$\rho_{m,T} = \sum_h \rho_{m,T}^h = \rho_{m,T}^- + \rho_{m,T}^+, \quad (73)$$

where $\rho_{m,T}^-$ and $\rho_{m,T}^+$ are given by (72). \square

Remark 4 is a consequence of (72) and the fact that

$$F_m^+(v) = me^{-v}(e^{V_m^+} - e^v)(e^v + e^{V_m^-}).$$

G Asymptotic of $\Delta(\varepsilon, m, T)$

We now prove the statements in Proposition 2.8.

The limit as $T \rightarrow 0$ By Lemma 2.14 in [6], as $T \rightarrow 0$, $\Pi_{m,T}$ converges weakly to $\mu \otimes p$, where μ is an invariant probability measure of the flow φ generated by the average vector field

$$F_m(v) = \frac{1}{2}F_m^+(v) + \frac{1}{2}F_m^-(v) = -2ms \sinh(v)$$

and

$$p = \frac{1}{2}\delta_{+1} + \frac{1}{2}\delta_{-1}.$$

The point 0 is a globally asymptotically stable equilibrium of F_m , hence $\mu = \delta_0$. This entails

$$\lim_{T \rightarrow 0} \Delta(\varepsilon, m, T) = \int 2(m \cosh(v) - m - \varepsilon) d\mu \otimes p = 2(m \cosh(0) - m - \varepsilon) = -2\varepsilon.$$

The limit as $T \rightarrow \infty$ From Equation (72), it is possible to prove that $\mathbf{\Pi}_{m,T}^+$ and $\mathbf{\Pi}_{m,T}^-$ converge respectively to $\frac{1}{2}\delta_{V_m^+}$ and $\frac{1}{2}\delta_{V_m^-}$ as $\sigma \rightarrow 0$. From that and the fact that $\cosh(V_m^+) = \cosh(V_m^-) = \sqrt{1 + \frac{1}{m^2}}$, we deduce the result to be proven.

The limit as $m \rightarrow \infty$ Set $\delta = \frac{1}{m}$ and consider $X_t^\delta = V_{\delta t}$ and $u_t^\delta = u_{\delta t}$. Note that for fixed $m > 0$, (X^δ, u^δ) and (V, u) have the same invariant probability measures, which reduces here to $\mathbf{\Pi}_{m,T}$. From Equation (28), one has

$$\frac{dX_t^\delta}{dt} = 2\left(\delta u_t^\delta - \sinh(X_t^\delta)\right).$$

Let also $(x_t)_{t \geq 0}$ be the solution of

$$\frac{dx_t}{dt} = -2 \sinh(x_t). \quad (74)$$

Hence, X_t^δ is a perturbation of x_t when δ goes to 0, and Grönwall Lemma implies that for all $m \geq 1$, all $S > 0$,

$$\sup_{x \in [V_m^-, V_m^+]} \sup_{t \in [0, S]} |X_t^\delta - x_t| \leq \delta S e^{\sqrt{2}S}, \quad (75)$$

where $\sqrt{2}$ comes from the fact that $\max_{y \in [V_m^-, V_m^+]} \sinh'(y) = \sqrt{1 + \frac{1}{m^2}} \leq \sqrt{2}$. From (75), one can easily prove (see e.g. [6, Lemma A.5]) that $\mathbf{\Pi}_{m,T}^+ + \mathbf{\Pi}_{m,T}^-$ converges to the unique invariant probability measure of the system (74), that is the Dirac mass at 0. This entails the expected result.

The limit as $m \rightarrow 0$ For this limit, it is more convenient to use the system in the polar coordinate. For $(x_1(0), x_2(0)) \neq (0, 0)$, we set $\rho_t = \|(x_1(t), x_2(t))\|$ and $\theta(t) = \frac{x_1(t)}{\rho_t}$. Then (ρ_t, θ_t) is solution to

$$\begin{cases} \frac{d\rho}{dt} = \rho(\mathbf{u}(2\theta - 1) - \varepsilon) \\ \frac{d\theta}{dt} = 2\mathbf{u}\theta(1 - \theta) + m(1 - 2\theta). \end{cases} \quad (76)$$

It is easily seen that θ does not depend on ρ and that

$$\frac{1}{t} \ln(\rho_t) = \frac{1}{t} \ln(\rho_0) + \frac{1}{t} \int_0^t (\mathbf{u}(s)(2\theta_s - 1) - \varepsilon) ds$$

Moreover, the point $1/2$ is accessible for θ and satisfies the strong bracket condition. Hence, (θ, \mathbf{u}) admits a unique stationary distribution μ_m on $(0, 1) \times \{-1, +1\}$ by Theorem 4.6 in [4], and

$$\lim_{t \rightarrow \infty} \frac{1}{t} \ln(\rho_t) = \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t (\mathbf{u}(s)(2\theta_s - 1) - \varepsilon) ds = \int (u(2\theta - 1)\mu_m(d\theta, du) - \varepsilon).$$

On the other hand, by Proposition 2.9,

$$\lim_{t \rightarrow \infty} \frac{1}{t} \ln(\rho_t) = \mathbf{\Lambda}(\varepsilon, m, T) = \frac{1}{2} \mathbf{\Delta}(\varepsilon, m, T)$$

and thus

$$\Delta(\varepsilon, m, T) = 2 \int (u(2\theta - 1)\mu_m(d\theta, du) - 2\varepsilon).$$

To conclude, we prove that the integral term in the right hand side of the above equation goes to 0 as m goes to 0. As for the case $m \rightarrow \infty$, if for $m \geq 0$, we denote θ^m the solution to

$$\frac{d\theta^m}{dt} = 2\mathbf{u}\theta^m(1 - \theta^m) + m(1 - 2\theta^m),$$

then θ^m is a perturbation of θ^0 and we can prove that θ_t^m converges to θ_t^0 uniformly on finite time horizon and on the initial condition in $[0, 1]$. Therefore, weak limit points of $(\mu_m)_{m>0}$ for $m \rightarrow 0$ are invariant probability measure of (θ^0, \mathbf{u}) . Since

$$\frac{d\theta^0}{dt} = 2\mathbf{u}\theta^0(1 - \theta^0),$$

the process (θ^0, \mathbf{u}) has two trivial ergodic probability measures : $\delta_0 \otimes \pi$ and $\delta_1 \otimes \pi$, where $\pi = (1/2, 1/2)$ is the stationary distribution of \mathbf{u} . We claim that there is no other ergodic measures for (θ^0, \mathbf{u}) . Let us first show how this claim proves the result. For $m > 0$, let $a_m = 2 \int (u(2\theta - 1)\mu_m(d\theta, du))$ and let a be a limit point of $(a_m)_{m>0}$: for some sequence $(m_k)_{k \in \mathbb{N}}$ converging to 0,

$$a = \lim_{k \rightarrow \infty} a_{m_k} = \lim_{k \rightarrow \infty} 2 \int (u(2\theta - 1)\mu_{m_k}(d\theta, du))$$

Since $(\mu_{m_k})_{k \in \mathbb{N}}$ is a sequence of probability measures on the compact set $[0, 1] \times \{-1, +1\}$, it is tight, and thus we have a subsequence m_{n_k} such that $\mu_{m_{n_k}}$ converge to some μ which is an invariant probability measure of (θ^0, \mathbf{u}) . Since $\delta_0 \otimes \pi$ and $\delta_1 \otimes \pi$ are the only two ergodic probability measures, there exists $s \in [0, 1]$ such that $\mu = s\delta_1 \otimes \pi + (1 - s)\delta_0 \otimes \pi$. Now,

$$\int (u(2\theta - 1)\delta_1 \otimes \pi(d\theta, du)) = \frac{1}{2}1 \times 1 + \frac{1}{2}(-1) \times 1 = 0,$$

and similarly for $\int (u(2\theta - 1)\delta_0 \otimes \pi(d\theta, du))$. Therefore, $\int (u(2\theta - 1)\mu(d\theta, du)) = 0$, hence

$$a = \lim_{k \rightarrow \infty} a_{m_{n_k}} = \lim_{k \rightarrow \infty} 2 \int (u(2\theta - 1)\mu_{m_{n_k}}(d\theta, du)) = 2 \int (u(2\theta - 1)\mu(d\theta, du)) = 0$$

In other words, every limit point of (a_m) is equal to 0. Since a_m lives in the compact set $[-6, 6]$, this proves that a_m converges, as $m \rightarrow 0$, to 0 and thus that $\Delta(\varepsilon, m, T)$ converges to 0.

It remains to prove the claim. Note that $(0, 1) \times \{-1, 1\}$ is invariant for the process (θ^0, \mathbf{u}) . Moreover, every point in $(0, 1)$ is accessible from $(0, 1)$ and satisfy the strong bracket condition, hence Theorem 1 in [3] implies that if (θ^0, \mathbf{u}) has an invariant measure ν on $(0, 1) \times \{-1, 1\}$, then ν is unique and absolutely invariant with respect to the Lebesgue measure. Moreover, the density functions ρ^+ and ρ^- , should be equal to

$$\begin{aligned} \rho^+(\theta) = \rho^-(\theta) &= \frac{C}{2\theta(1-\theta)} \exp\left(-\frac{1}{T} \int \frac{1}{2\theta'(1-\theta')} + \frac{1}{-2\theta'(1-\theta')} d\theta'\right) \\ &= \frac{C}{2\theta(1-\theta)}. \end{aligned}$$

Here C would be a normalization constant such that $\int_0^1 \rho^+ + \rho^- = 1$. However, ρ^+ and ρ^- are clearly not integrable on $(0, 1)$, hence can not be normalized to a probability measure. Hence, the process (θ^0, \mathbf{u}) does not admit any invariant probability measure on $(0, 1) \times \{-1, 1\}$ and the set of its ergodic probability measures on $[0, 1] \times \{-1, 1\}$ reduces to $\delta_0 \otimes \pi$ and $\delta_1 \otimes \pi$. This shows the claim and concludes the proof.

H Stochastic Approximatively Periodic Environment

This section is devoted to the proof of Proposition 2.15. Let (μ_-^n, μ_+^n) be a (η_n, T) - SAPE for some sequence η_n converging to 0. We denote by $(V^n, \tau^n u^n)$ the associated process, and (V, τ, u) the process in the periodic environment $\mu_-^\infty = \mu_+^\infty = \delta_T$.

We begin by an approximation Lemma.

Lemma H.1 *For all $S > 0$, there exists $C(S, T, m)$ such that for n large enough,*

$$\int_0^S \|(V_t^n, u_t^n, \tau_t^n) - (V_t, u_t, \tau_t)\| dt \leq C(S, T, m) \eta_n.$$

Moreover,

$$\sup_{t \in [0, T]} |V_t^n - V_t| \leq C(S, T, m) \eta_n.$$

Proof First, let us prove that for n large enough,

$$\int_0^S |u_t^n - u_t| dt \leq 2 \left(\left\lfloor \frac{S}{T} \right\rfloor + 1 \right)^2 \eta_n.$$

Since $u^n, u \in \{\pm 1\}$, one has $|u_t^n - u_t| = 2 \mathbb{1}_{u_t^n \neq u_t}$. Let $k = \lfloor \frac{S}{T} \rfloor + 1$. Then, $S \leq kT$, and if $\eta_n \leq 1$, both processes u^n and u switches values at most k times on the interval $[0, S]$. Now, assume that $\eta_n \leq \frac{T}{2k+1}$. Then, all the intervals $[j(T - \eta_n), j(T + \eta_n)]$, for $j = 1, \dots, n$ are disjoint. Moreover, u_t^n and u_t can only be different if t belongs to one of this interval. Since the j -interval is of size $2j\eta_n$, we conclude that

$$\int_0^S |u_t^n - u_t| dt \leq 2 \left(\sum_{j=1}^k 2j \right) \eta_n \leq 2k^2 \eta_n.$$

Now, since

$$V_t^n - V_t = \int_0^t 2(u_s^n - u_s + m \sinh(V_s) - m \sinh(V_s^n)) ds,$$

Gronwall Lemma implies that, for all $t \in [0, S]$, for some constant $C(S, m)$;

$$|V_t^n - V_t| \leq C(S, m) \int_0^S |u_s^n - u_s| ds \leq 2C(S, m) k^2 \eta_n.$$

Finally, using that fact that, at some time $t \leq S$, the difference between the number of jumps of u^n and those of u before time t is at most one, one can prove that for some constant $C(T)$,

$$\int_0^S |\tau_t^n - \tau_t| dt \leq C(T) \eta_n.$$

□

For a starting point $(v, h, t_0) \in \mathbb{R} \times \{\pm 1\} \times [0, T)$, let $\phi_s(v, h, t_0) = (V_s, u_s, \tau_s)$ where (V_s, u_s, τ_s) is the process in periodic environment at time s , starting from (v, h, t_0) . We define the measure Π^P on $\mathbb{R} \times \{\pm 1\} \times [0, T)$ by

$$\Pi^P(\cdot) = \frac{1}{2T} \int_0^{2T} \mathbb{1}_{\phi_s(V_e, 1, 0) \in \cdot} ds,$$

where V_e is the unique equilibrium of the map $\Phi = V_T^- \circ V_T^+$ (see Appendix B). Elementary computations prove that Π^P is the unique stationary distribution of (V, u, τ) which furthermore satisfy that for all bounded continuous function g , for all starting point (v, h, t_0) ,

$$\lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t g(\phi_s(v, h, t_0)) ds = \Pi^P g. \quad (77)$$

Moreover, for $g(v, h, t) = 2(m \cosh(v) - m - \varepsilon)$, one has by definition $\Pi^P g = \Delta(\varepsilon, m, T)$. Hence, Proposition 2.15 is a consequence of the following lemma.

Lemma H.2 *Let Π^n the unique stationary distribution of (V^n, u^n, τ^n) granted by Proposition 2.11. Then, Π^n converges weakly to Π^P , ie for all bounded continuous functions f , $\lim \Pi^n f = \Pi^P f$.*

Proof The sequence $(\Pi^n)_{n \geq 0}$ is tight since for all n , Π^n is a probability distribution on $[V_m^-, V_m^+] \times \{\pm 1\} \times [0, T + \eta_n) \subset [V_m^-, V_m^+] \times \{\pm 1\} \times [0, K]$ for some K large enough. Let ν be a weak - limit point of $(\Pi^n)_{n \geq 0}$, ie for some sequence $(n_k)_{k \geq 0}$, Π^{n_k} converges weakly to ν . Without loss of generality, we assume that Π^n converges to ν . The proof of the lemma is complete if we can prove that $\nu = \Pi^P$. We claim that, for all $S > 0$, for all bounded Lipschitz function f

$$\frac{1}{S} \int_0^S \nu(f \circ \phi_s) ds = \nu f.$$

Combining this with (77) and dominated convergence yields $\Pi^P f = \nu f$ for all bounded Lipschitz function f , which implies that $\nu = \Pi^P$. It only remains to prove the claim. Let $S > 0$ and f bounded Lipschitz with Lipschitz constant equal to C . For all $n \geq 0$,

$$\begin{aligned} \left| \nu \left(\frac{1}{S} \int_0^S f \circ \phi_s ds \right) - \nu f \right| &\leq \left| \nu \left(\frac{1}{S} \int_0^S f \circ \phi_s ds \right) - \Pi^n \left(\frac{1}{S} \int_0^S f \circ \phi_s ds \right) \right| \\ &\quad + \left| \Pi^n \left(\frac{1}{S} \int_0^S f \circ \phi_s ds \right) - \Pi^n \left(\frac{1}{S} \int_0^S P_s^n f ds \right) \right| + |\Pi^n f - \nu f| \end{aligned}$$

where $P_s^n f(v, u, t) = \mathbb{E}_{(v, u, t)} [f(V_s^n, u_s^n, \tau_s^n)]$ and where we have used the invariance of Π^n with respect to P_s^n , ie $\Pi^n P_s^n = \Pi^n$. It is easily checked that the

function $\int_0^S f \circ \phi_s ds$ is continuous and bounded. Hence, by definition of v , the first and the third terms of the above right hand side goes to 0 as n goes to infinity. Using Lemma H.1, the second term is bounded, for n large enough, by

$$\begin{aligned} \left| \Pi^n \left(\frac{1}{S} \int_0^S f \circ \phi_s ds \right) - \Pi^n \left(\frac{1}{S} \int_0^S P_s^n f ds \right) \right| &\leq \frac{1}{S} C \sup_{(v,u,t)} \mathbb{E}_{(v,u,t)} \left[\int_0^S \| (V_s, u_s, \tau_s) - (V_s^n, u_s^n, \tau_s^n) \| \right] \\ &\leq \frac{C(S, T, m)C}{S} \eta_n \end{aligned}$$

Hence, the second term also goes to 0, and the proof is over. \square

I Density dependent model

The deterministic case

Proposition I.1 *If the parameters (ε, m, T) are such that the system $D(\varepsilon, 0, m, T) = \Sigma(\varepsilon, m, T)$ is stable, then the solutions of $D(\varepsilon, \alpha, m, T)$ tend to 0.*

Proof. We denote by $(x_1(t, x_{10}, x_{20}), x_2(t, x_{10}, x_{20}))$ the solutions of $D(\varepsilon, \alpha, m, T)$ and by $(\xi_1(t, \xi_{10}, \xi_{20}), \xi_2(t, \xi_{10}, \xi_{20}))$ the solutions of $\Sigma(\varepsilon, m, T)$. Let (x_{10}, x_{20}) be any initial condition for D and choose (ξ_{10}, ξ_{20}) such that:

$$x_{i0} < \xi_{i0} \quad i = 1, 2$$

then, for every t one has :

$$x_i(t, x_{10}, x_{20}) < \xi_i(t, \xi_{10}, \xi_{20}) \quad i = 1, 2$$

Assume this is not the case ; let t^* be the first time for which one has $x_i^* = x_i(t, x_{10}, x_{20}) = \xi_i(t, \xi_{10}, \xi_{20})$ for at least one of the two indices ; assume for the sake of definitiveness that this index is 1 ; one has:

$$\frac{dx_1(t^*)}{dt} = (\pm 1 - \varepsilon - m)x_1^* - \alpha x_1^{*2} + mx_2(t^*) < (\pm 1 - \varepsilon - m)x_1^* + m\xi_2(t^*) = \frac{d\xi_1(t^*)}{dt}$$

The inequality $\frac{dx_1(t^*)}{dt} < \frac{d\xi_1(t^*)}{dt}$ contradicts the fact that t^* is the first time for which $x_1(t, x_{10}, x_{20}) = \xi_1(t, \xi_{10}, \xi_{20})$. Since $\Sigma(\varepsilon, m, T)$ is stable $\xi_i(t, \xi_{10}, \xi_{20}) (i = 1, 2)$ tends to 0 and also $x_i(t, x_{10}, x_{20}) (i = 1, 2)$.

\square

Proposition I.2 *If the parameters (ε, m, T) are such that the system $D(\varepsilon, 0, m, T) = \Sigma(\varepsilon, m, T)$ is unstable, then the system $D(\varepsilon, \alpha, m, T)$ is uniformly persistent.*

In order to prove proposition I.2 we need two lemmas. Let :

$$U = \ln(x_1 x_2) \quad V = \ln(x_1 / x_2)$$

In the (U, V) variables the system D is :

$$D(\varepsilon, \alpha, m, T) \quad \begin{cases} \frac{dU}{dt} &= 2(m \cosh(V) - m - \varepsilon) - 2\alpha e^{U/2} \cosh(V/2) \\ \frac{dV}{dt} &= 2(u(t) - m \sinh(V)) - 2\alpha e^{U/2} \sinh(V/2) \end{cases} \quad (78)$$

which is the system $S(\varepsilon, m, T)$ perturbed by the term :

$$-2\alpha e^{U/2} \begin{pmatrix} \cosh(V) \\ \sinh(V) \end{pmatrix} \quad (79)$$

It is easily seen that the solutions of the system D enters in finite time the strip $\mathbb{R} \times [V_m^-, V_m^+]$ and thus persistence of D is equivalent to the fact that for any solution $\liminf_{t \rightarrow +\infty} U(t) > -\infty$.

Denote by :

$$(U(t, U_0, V_0, t_0, S), F(t, U_0, V_0, t_0), S) \quad (\text{resp. } (U(t, U_0, V_0, t_0, D), F(t, U_0, V_0, t_0), D))$$

the solution of S (resp. D) with initial condition (U_0, V_0) at time t_0 and simply by $(U(t, D), V(t, D))$ (resp. $(U(t, S), V(t, S))$) the solution of D (resp. S) when the reference to the initial condition is not needed.

Lemma I.3 *Assume that $S(\varepsilon, m, T)$ is unstable. Let $a > 0$. Then there is $\theta > 0$ such that :*

$$\forall V_0 \in [V_m^-, V_m^+], \forall U_0, \forall t_0 : \quad U(t_0 + \theta, U_0, V_0, t_0, S) \geq U_0 + a$$

Proof: Fix some $a > 0$. Since S is unstable, for each U_0, V_0, t_0 such a θ exists ; it follows from the compactness of $[V_m^-, V_m^+]$, the periodicity of S and the property $U(t, U_0, V_0, t_0) = U_0 + U(t, 0, V_0, t_0)$ that a universal θ does exist. \square

Lemma I.4 *For any $\delta > 0$ there exists \bar{U} such that :*

$$\left\{ \max_{t \leq t^*} U(t + t_0, U_0, V_0, t_0, D) \leq \bar{U} \right\} \implies \dots \quad (80)$$

$$\dots |U(t^* + t_0, U_0, V_0, t_0, D) - U(t^* + t_0, U_0, V_0, t_0, S)| \leq t^* \delta$$

Proof. Since the perturbation (79) tends to 0 when U tends to $-\infty$ uniformly with respect to $V \in [V_m^-, V_m^+]$ this is easily deduced from Gronwall inequality.

Proof of the proposition I.2 Fix some $a > 0$ and let θ be given by lemma I.3 and \bar{U} given by lemma I.4 such that $\delta = \frac{a}{2\theta}$. The proof goes by contradiction. Assume that:

$$\liminf_{t \rightarrow +\infty} U(t, D) = -\infty$$

then there exist (see fig. 22) t_1 and t_2 such that :

$$\bar{U} > U(t_1, D) + a > U(t_1, D) > U(t_1, D) - \frac{\theta}{\pi} = U(t_2, D) \quad (81)$$

where

$$-\pi = \min_{U \leq \bar{U}, V \in [V_m^-, V_m^+]} 2(m \cosh(V) - m - \varepsilon) - 2\alpha e^{U/2} \cosh(V/2) < -2\varepsilon$$

Since $U(t, D)$ is continuous, from the intermediate value theorem there is some $\tau > t_1$ such that :

$$t \in [\tau, t_2] \implies U(t, D) \leq U(t_1) \quad (82)$$

and since π is the minimum of the velocity of $U(t, D)$ it takes a duration $t_2 - \tau$ greater than $\theta = \pi \frac{\theta}{\pi}$ to cover the distance from $U(\tau, D)$ to $U(t_2)$.

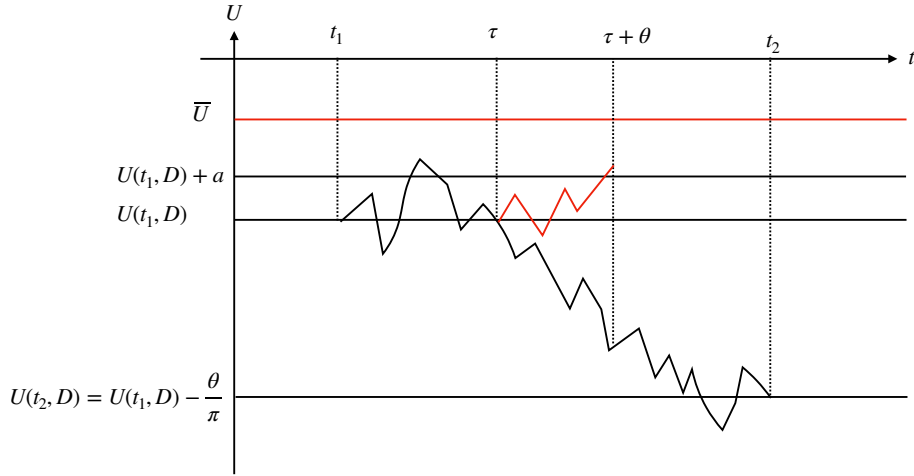


Figure 22: Illustration of the proof of proposition I.2

- From lemma I.3 :

$$U(\tau + \theta, U(t_1, D), V(\tau, D), \tau, S) > U(t_1, D) + a$$

(red curve of fig 22).

- From lemma I.4:

$$|U(\tau + \theta, U(t_1, D), V(\tau, D), \tau, S) - U(\tau + \theta, U(t_1, D), V(\tau, D), \tau, D)| < \frac{a}{2}$$

These points imply $U(\tau + \theta, U(t_1, D), V(\tau, D), \tau, D) \geq U(t_1) + \frac{a}{2}$ which is a contradiction with (82). \square

The stochastic case

We now prove Proposition 3.2 thanks to results in [6]. Note that the vector fields in the right hand side of $\mathbf{D}(\varepsilon, \alpha, m, \sigma_-, \sigma_+)$ satisfy conditions E1, E2, E3, E4 and E5 in [6, Section 4] and admit a positively invariant compact set K containing 0. Thus, Proposition 2.9, [6, Theorem 4.3] (for the case $\Lambda(\varepsilon, m, T) < 0$) and [6, Theorem 4.12] (for the case $\Lambda(\varepsilon, m, T) > 0$) and [24, Theorem 3.8] (for the case $\Lambda(\varepsilon, m, T) = 0$) conclude the proof of proposition 3.2.

J Connection between $\Delta(\varepsilon, m, T)$ and $\sigma(\varepsilon, m, T)$.

Let $(x_1(t), x_2(t))$ be any solution of $\Sigma(\varepsilon, m, T)$; let $U(t) = \ln(x_1(t)) + \ln(x_2(t)) = \ln(x_1(t)x_2(t))$ and $V(t) = \ln(x_1(t)) - \ln(x_2(t)) = \ln(x_1(t)/x_2(t))$. Then $V(t)$ is a solution of $F(m, T)$ and since the periodic solution of $F(m, T)$ is globally

asymptotically stable $V(t)$ converges to $P_{m,T}(t)$, thus :

$$\begin{aligned} \lim_{n \rightarrow +\infty} U((n+1)2T) - U(n2T) &= \dots \\ \lim_{n \rightarrow +\infty} \int_{n2T}^{(n+1)2T} 2(m \cosh(V(s)) - m - \varepsilon) ds &= \dots \\ \int_0^{2T} 2(m \cosh(P_{m,T}(s)) - m - \varepsilon) ds &= 2T \Delta(\varepsilon, m, T) \end{aligned} \quad (83)$$

and hence :

$$\Delta(\varepsilon, m, T) = \frac{1}{2T} \lim_{n \rightarrow +\infty} \ln \left(\frac{x_1((n+1)2T)x_2((n+1)2T)}{x_1(n2T)x_2(n2T)} \right) \quad (84)$$

Now, choose $(x_1(0), x_2(0)) = Z_1$ where Z_1 is the positive eigenvector of $M(\varepsilon, m, T)$ associated with λ_1 (note that $M(\varepsilon, m, T)$ has positive entries). Then, for all $n \geq 0$, $x_1((n+1)2T) = \lambda_1 x_1(n2T)$ and $x_2((n+1)2T) = \lambda_1 x_2(n2T)$, thus

$$\frac{x_1((n+1)2T)x_2((n+1)2T)}{x_1(n2T)x_2(n2T)} = \lambda_1^2$$

and thus $\Delta(\varepsilon, m, T) = \frac{1}{T} \ln(\lambda_1)$, which we wanted to prove.

We can also prove this equality directly from the explicit formulas of Δ and λ_1 . The value of λ_1 given by Maple is :

$$\lambda_1 = \frac{e^{-2(m+\varepsilon)T}}{2A^2b^2} \left(m^2b^4 + 2b^2 + m^2 + \sqrt{C_1} \right)$$

with

$$\begin{aligned} C_1 &= b^8m^4 + 4b^6m^2 - 2b^4m^4 - 8b^4m^2 + 4b^2m^2 + m^4 \\ \ln(\lambda_1) &= \ln \frac{m^2b^4 + 2b^2 + m^2 + \sqrt{C_1}}{2A^2b^2} - 2(m + \varepsilon)T \end{aligned}$$

which is the value of Δ given by the proposition (2.3) since one has :

$$C_1 = m^2(b^2 - 1)^2(m^2b^4 + 2m^2b^2 + 4b^2 + m^2)$$

Remark 7 *On figure 23 one sees on the left the graphs of $\Delta(\varepsilon, m, T)$ (in blue) and $2 \ln(\lambda_1(\varepsilon, m, T))$ (in red plotted) in slightly translated axes and, on the right, in the same axes. The perfect superposition is not surprising since we just proved the equality of $\Delta(\varepsilon, m, T)$ with $2 \ln(\lambda_1(\varepsilon, m, T))$. Nevertheless it is interesting to notice that the graphs of $\Delta(\varepsilon, m, T)$ and $2 \ln(\lambda_1(\varepsilon, m, T))$ are obtained using completely different means of simulation. The first is obtained by simulation of a differential equation using a discrete approximation scheme (we integrate from some initial condition, wait until the periodic regime is attained and, then, compute Δ) and the second using a calculus software able to compute formally the eigenvalues of a matrix depending on parameters. This indicates that our simulations of trajectories have a satisfactory precision.*

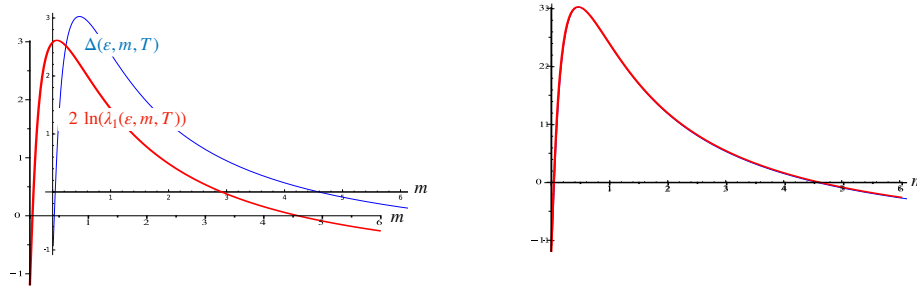


Figure 23: Comparison between $m \mapsto \Delta(\varepsilon, m, T)$ and $m \mapsto \lambda_1(\varepsilon, m, T)$. $\varepsilon = 0.1$, $T = 3$.

References

- [1] Arditi, R., Lobry, C., & Sari, T. *Is dispersal always beneficial to carrying capacity? New insights from the multi-patch logistic equation*. Theoretical population biology, 106, 45-59.(2015)
- [2] Arditi, R., Lobry, C., & Sari, T. *Asymmetric dispersal in the multi-patch logistic equation* Theoretical population biology, 120, 11-15. (2018)
- [3] Bakhtin, Y. and Hurth, T. *Invariant densities for dynamical systems with random switching*, Nonlinearity, 25(10), 2937–2952, (2012)
- [4] Benaïm, M. and Le Borgne, S. and Malrieu, F. and Zitt, P.- A. *Qualitative properties of certain piecewise deterministic Markov processes* JOURNAL = Ann. Inst. Henri Poincaré Probab. Stat. Annales de l’Institut Henri Poincaré, Probabilités et Statistiques, (2015)
- [5] Benaïm, M., & Lobry, C. *Lotka–Volterra with randomly fluctuating environments or “How switching between beneficial environments can make survival harder”*. The Annals of Applied Probability, 26(6), 3754-3785. (2016)
- [6] Benaïm, M. and Strickler, E. *Random Switching between Vector Fields Having a Common Zero* Ann. Appl. Probab., 29(1), 326-375 (2019)
- [7] Brunovsky, P. and Lobry, C. *Controlabilité Bang Bang, controlabilité différentiable, et perturbation des systemes non linéaires* Annali di Matematica Pura ed Applicata, vol 105, pp. 93-119, (1975)
- [8] Butler, G., Freedman, and Waltman P. *Uniformly persistent systems*. Proceedings of the American Mathematical Society p. 425-430 (1986)
- [9] Davis, M. H. *Piecewise deterministic Markov processes: a general class of non diffusion stochastic models*. Journal of the Royal Statistical Society: Series B (Methodological), 46(3), 353-376.(1984)
- [10] Gonzalez A, Holt RD *The inflationary effects of environmental fluctuations in source-sink systems*. Proc Natl Acad Sci U S A 99:14872–14877

- [11] Faggionato, Alessandra and Gabrielli, Davide and Crivellari, M Ribezzi *Non-equilibrium thermodynamics of piecewise deterministic Markov processes* J. Stat. Phys., 137(2), 259 - 304 (2009)
- [12] Freidlin, and Wentzell, *Random perturbations. In : Random perturbations of dynamical systems.* Springer, New York, NY, 1998. p. 15-43.
- [13] Hanski, I. *Metapopulation ecology.* Oxford University Press. (1999)
- [14] Hening, Alexandru and Strickler, Edouard *On a predator-prey system with random switching that never converges to its equilibrium* SIAM Journal on Mathematical Analysis 51(5), 3625–3640 (2019)
- [15] Hurth, Tobias and Strickler, Edouard *Randomly Switched ODES with nonexponential switching times.* Preprint, 2021
- [16] Ginzburg lev and Mark Colyvan. *Ecological orbits.* Oxford University Press. (2004)
- [17] Jurdjevic, V. *Geometric control theory* Cambridge university press. (1997)
- [18] Katriel, Guy. *Dispersal-induced growth in a time-periodic environment.* arXiv preprint arXiv:2104.01589 (2021).
- [19] Nicholas Kortessisa, Margaret W. Simon, Michael Barfield, Gregory Glass, Burton H. Singer, Robert D. Holt. *Regional COVID19 spread despite expected declines: how mitigation is hindered by spatio-temporal variation in local control measures.* medRxiv preprint doi: <https://doi.org/10.1101/2020.07.17.20155762>.
- [20] Nicholas Kortessisa, Margaret W. Simon, Michael Barfield, Gregory Glass, Burton H. Singer, Robert D. Holt. *The interplay of movement and spatiotemporal variation in transmission degrades pandemic control.* Proceedings of the National Academy of Sciences 117.48 (2020): 30104-30106.
- [21] Klausmeier, C. A. *Floquet theory: a useful tool for understanding nonequilibrium dynamics.* Theoretical Ecology, 1(3), 153-161.
- [22] Lobry C., T. Sari, S. Touhami *On Tykhonov's theorem for convergence of solutions of slow and fast systems* Electronic Journal of Differential Equations, Vol., No. 19, pp. 1–22.(1998)
- [23] Lawley, S. D. and Mattingly, J. C. and Reed, M. C. *Sensitivity to switching rates in stochastically switched ODEs* Commun Math Sci., 2014, 12 (7), pp 1343-1352
- [24] Nguyen, D. H., and Strickler, E. A method to deal with the critical case in stochastic population dynamics. SIAM Journal on Applied Mathematics, 2020, 80(3), 1567-1589.
- [25] Pakdaman, K. and Thieullen, M. and Wainrib, G *Intrinsic variability of latency to first-spike.* Biol. Cybernet., 103(1), 43 - 56 (2010)
- [26] Strickler, E. *Persistence de Processus de Markov DÈterministes par Morceaux.* ThÈse de doctorat. UniversitÈ de Neuch,tel. (2019)
- [27] Tykhonov A.N, *Systems of differential equations containing small parameters multiplying the derivatives* Mat. Sborn. 31:575-586, 1952.