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## On the persistence regime for Lotka-Volterra in randomly fluctuating environments

Florent Malrieu, Pierre-André Zitt

January 29, 2016

#### Abstract

In this note, we study the long time behavior of Lotka-Volterra systems whose coefficients vary randomly. Benaïm and Lobry (2015) recently established that randomly switching between two environments that are both favorable to the same species may lead to different regimes: extinction of one species or the other, or persistence of both species. Our purpose here is to describe more accurately the range of parameters leading to these regimes, and the support of the invariant probability measure in case of persistence.

## 1 Introduction

The aim of the present paper is to study the ergodicity of a piecewise deterministic Markov process (PDMP) linked to Lotka-Volterra type dynamics. These lines can be seen as a companion paper to [2] since we go one step further in the description of the different regimes and the support of the invariant measures.

For a given set of positive parameters  $\mathcal{E} = (a, b, c, d, \alpha, \beta)$ , consider the Lotka-Volterra differential system in  $\mathbb{R}^2_+$ , given by

$$\begin{cases} \dot{x} = \alpha x (1 - ax - by) \\ \dot{y} = \beta y (1 - cx - dy) \\ (x_0, y_0) \in \mathbb{R}^2_+. \end{cases}$$
(1)

This system modelizes the evolution of the populations of two species (x of type x and y of type y) that grow logistically and compete with each other. We denote by  $F_{\mathcal{E}}$  the associated vector field:  $(\dot{x}, \dot{y}) = F_{\mathcal{E}}(x, y)$ . In the sequel, the variable z stands for (x, y) and we will sometimes write  $F_{\mathcal{E}}(z)$  instead of  $F_{\mathcal{E}}(x, y)$ . This ODE system, taken alone, is easy to analyze; for completeness we provide a detailed description below (Section 2). Let us note already that when a < c and b < d, the point (1/a, 0) attracts any path starting in  $(0, +\infty)^2$ . We say that the environmement is favorable to species  $\mathbf{x}$ ; it leads to the extinction of species  $\mathbf{y}$ .

Consider two such systems, labeled 0 and 1, with environments  $\mathcal{E}_i = (a_i, b_i, c_i, d_i, \alpha_i, \beta_i)_{i=0,1}$ , and suppose that each of them is favorable to the first species  $(a_i < c_i, b_i < d_i)$ : in particular, taken alone, each system leads to the extinction of the second species, that is,  $y_t$  converges to 0 and lim sup  $x_t > 0$  as soon as  $x_0 > 0$ .

Finally, introduce the random process obtained by switching between these two deterministic dynamics, at rates  $(\lambda_i)_{i=0,1}$ . More precisely, we consider the process (Z, I) on  $\mathbb{R}^2 \times \{0, 1\}$  driven by the infinitesimal generator

$$Lf(z,i) = F_{\mathcal{E}_i}(z) \cdot \nabla_z f(z,i) + \lambda_i (f(z,1-i) - f(z,i)).$$

In other words, I jumps from i to 1-i after a random time with an exponential law of parameter  $\lambda_i$  and when  $I_t = i$ ,  $\dot{Z}_t = F_{\mathcal{E}_i}(Z_t)$ . The coordinates of  $Z_t$  are denoted by  $X_t$  and  $Y_t$ . We refer to [2] for a detailed biological motivation.

In [2], it is shown there are four possible regimes for the stochastic process (Z, I):

- extinction of species  $\mathbf{x}$ :  $X_t \to 0$  and  $\limsup Y_t > 0$ ,
- extinction of species  $\mathbf{y}: Y_t \to 0$  and  $\limsup X_t > 0$ ,
- extinction of one of the two species randomly chosen,
- persistence: the empirical occupation measure (and, in many cases, the distribution) of  $(X_t, Y_t)_{t\geq 0}$  converges to a probability measure on  $(0, +\infty)^2$  that is absolutely continuous with respect to the Lebesgue measure.

Moreover, one or more of these regimes may occur when the jump rates  $(\lambda_0, \lambda_1)$  vary, the environments  $(\mathcal{E}_0, \mathcal{E}_1)$  being fixed. Similar surprising behaviors for switched processes have been studied for linear ODEs in [1, 3].

Before stating our results, let us first recall some notation from [2]. By considering a particular mean growth rate of species  $\mathbf{x}$  when it is almost extinct, one can define an *invasion rate*  $\Lambda_{\mathbf{x}}$  and a similar quantity for  $\mathbf{y}$  (see Section 3 below for the precise definition).

The long time behavior of the Markov process  $(Z_t, I_t)$  is characterized by the sign of these invasion rates, as summed up in the following table (see Theorems 3.1, 3.3, 3.4 and 4.1 of [2] for precise statements).

	$\Lambda_{\mathbf{y}} > 0$	$\Lambda_{\mathbf{y}} < 0$
$\Lambda_{\mathbf{x}} > 0$	persistence of the two species	extinction of species $\mathbf{x}$
$\Lambda_{\mathbf{x}} < 0$	extinction of species $\mathbf{x}$	random extinction of one of the two species

The invasion rates depend on the jump rates  $(\lambda_0, \lambda_1) \in (0, +\infty)^2$  for which two natural parametrizations will be considered in the sequel:

- 1.  $(s,t) \in [0,1] \times (0,+\infty)$  given by  $s = \lambda_0/(\lambda_0 + \lambda_1)$  and  $t = \lambda_0 + \lambda_1$ ;
- 2.  $(u,v) \in [0,1] \times (0,+\infty)$  given by  $u = \gamma_0/(\gamma_0 + \gamma_1)$  and  $v = \gamma_0 + \gamma_1$ , where  $\gamma_i = \lambda_i/\alpha_i$ .

The change of parameters  $(u, v) = \xi(s, t)$  is triangular in the sense that u only depends on s:

$$(u,v) = \xi(s,t) = \left(\frac{s\alpha_1}{(1-s)\alpha_0 + s\alpha_1}, \frac{t}{\alpha_0\alpha_1}((1-s)\alpha_0 + s\alpha_1)\right).$$

Let us denote the invasion rates in the (u, v) coordinates by

$$\tilde{\Lambda}_{\mathbf{x}}(u,v) = \Lambda_{\mathbf{x}}(\xi^{-1}(u,v)) \quad \text{and} \quad \tilde{\Lambda}_{\mathbf{y}}(u,v) = \Lambda_{\mathbf{y}}(\xi^{-1}(u,v)).$$

As noticed in [2], for any  $s \in [0, 1]$ , the vector field  $(1 - s)F_{\mathcal{E}_0} + sF_{\mathcal{E}_1}$  is the Lotka-Volterra system associated to the environment  $\mathcal{E}_s = (a_s, b_s, c_s, d_s, \alpha_s, \beta_s)$  with

$$\begin{aligned} \alpha_s &= (1-s)\alpha_0 + s\alpha_1, \qquad a_s = \frac{(1-s)\alpha_0 a_0 + s\alpha_1 a_1}{\alpha_s}, \qquad b_s = \frac{(1-s)\alpha_0 b_0 + s\alpha_1 b_1}{\alpha_s}, \\ \beta_s &= (1-s)\beta_0 + s\beta_1, \qquad c_s = \frac{(1-s)\beta_0 c_0 + s\beta_1 c_1}{\beta_s}, \qquad d_s = \frac{(1-s)\beta_0 d_0 + s\beta_1 d_1}{\beta_s}. \end{aligned}$$

Two critical (possibly empty) parameter regions are defined in [2] by:

$$I = (s_1, s_2) = \{ s \in [0, 1], a_s > c_s \} \text{ and } J = (s_1, s_2) = \{ s \in [0, 1], d_s > b_s \}.$$
 (2)

A nice interpretation of these regions in terms of the phase portrait of the Lotka-Volterra system in environment  $\mathcal{E}_s$  can be found below in Section 2.

Let us denote by  $\tilde{I}$  the image of I for the other parametrization:  $\tilde{I} = (u_1, u_2)$ .

**Remark 1.1.** The parameter u is already implicitly considered in [2], where it appears in the computations leading to the explicit conditions for the non-emptyness of I (which are equivalent to the positivity of a second degree polynomial).

Our first result is an explicit formula for  $\tilde{\Lambda}_{\mathbf{y}}$ , suited both to fast numerical computations and theoretical study.

**Lemma 1.2** (Expression of  $\tilde{\Lambda}_2$ ). Assume (w.l.o.g.) that  $a_0 < a_1$ . Let  $u = \gamma_0/(\gamma_0 + \gamma_1)$  and  $v = \gamma_0 + \gamma_1$ . The quantity  $\tilde{\Lambda}_y$  can be rewritten as:

$$\tilde{\Lambda}_{\boldsymbol{y}}(\boldsymbol{u},\boldsymbol{v}) = \frac{1}{(a_1 - a_0) \left(\frac{1}{\alpha_0}(1 - \boldsymbol{u}) + \frac{1}{\alpha_1}\boldsymbol{u}\right)} \mathbb{E}\left[\phi(U_{\boldsymbol{u},\boldsymbol{v}})\right],$$

where  $\phi : [0,1] \to \mathbb{R}$  is defined by

$$\phi(y) = \frac{1}{a_0 + (a_1 - a_0)y} P(a_0 + (a_1 - a_0)y)$$

for some explicit second degree polynomial P, and  $U_{u,v}$  is a Beta distributed Beta(uv, (1-u)v) random variable.

Moreover,  $\phi$  has the following properties:

- If  $I = \emptyset$  then  $\phi$  is nonpositive;
- If  $I \neq \emptyset$  then  $\phi$  is concave, negative on  $(0, u_1) \cup (u_2, 1)$  and positive on  $\tilde{I} = (u_1, u_2)$ .

Recall that a function f is called quasi convex on (a, b) if its level sets  $\{f \leq t\}$  are convex, that is, f decreases on (a, c) and increases on (c, b) for some  $c \in [a, b]$ .

Our main result describes more precisely the region of positivity for  $\Lambda_{\mathbf{x}}$  and  $\Lambda_{\mathbf{y}}$ .

**Theorem 1.3** (Shape of the regions). There exists a function  $u \mapsto v_{\mathbf{y}}(u)$  from  $(0,1) \to [0,\infty]$ , with domain  $\tilde{I}$ , such that  $\tilde{\Lambda}_{\mathbf{y}}(u,v) < 0$  when  $v < v_{\mathbf{y}}(u)$  and  $\tilde{\Lambda}_{\mathbf{y}}(u,v) > 0$  when  $v > v_{\mathbf{y}}(u)$ .

Moreover  $v_y$  is quasi-convex, continuous on its domain  $\tilde{I}$ , and tends to  $+\infty$  on the endpoints of  $\tilde{I}$ .

Similarly, there exists a function  $s \mapsto t_y(s) \in [0, \infty]$ , with domain I, going to infinity at the endpoints of I, such that:

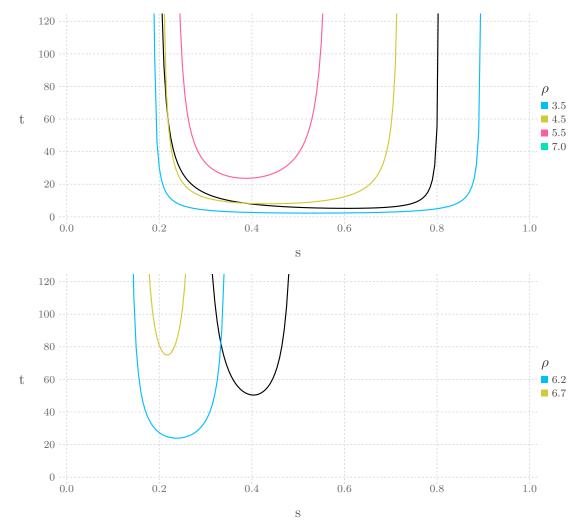
- $\Lambda_{\mathbf{y}}(s,t) < 0$  if  $t < t_{\mathbf{y}}(s)$ ,
- $\Lambda_{\mathbf{y}}(s,t) = 0$  if  $t = t_{\mathbf{y}}(s)$ ,
- $\Lambda_{\mathbf{y}}(s,t) > 0$  if  $t > t_{\mathbf{y}}(s)$ .

The same statement holds in the parameters (s,t) for the function  $(-\Lambda_{\mathbf{x}})$  with I replaced by J and with a critical function  $t_{\mathbf{x}}(s)$ .

**Remark 1.4.** This result is cited in [2] as Proposition 2.5, and answers a conjecture in a previous version of that paper. The numerical computations suggest that both  $v_y$  and  $t_y$  are in fact smooth and convex on  $\tilde{I}$  and I respectively.

For an illustration of this result, see Figure 1.

The remainder of the paper is organized as follows. In Section 2 we describe the various phase portraits for Lotka-Volterra vector fields, and narrow down the choices of  $\mathcal{E}_0$ ,  $\mathcal{E}_1$  that lead to interesting behaviour. In Section 3 we prove Lemma 1.2; the main result is proved in Section 4. The final section is dedicated to the study of the support of invariant measures in the persistence regime.



These plots represent the "critical" functions  $t_{\mathbf{y}}$  and  $t_{\mathbf{x}}$  for different choices of the environments. Denoting environments by the couple  $\begin{pmatrix} \alpha \\ \beta \end{pmatrix}$ ;  $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$ , the functions are plotted with

$$\mathcal{E}_0 = \begin{pmatrix} 1\\5 \end{pmatrix}; \begin{pmatrix} 1&1\\2&2 \end{pmatrix} \text{ (top plot)}; \qquad \mathcal{E}_0 = \begin{pmatrix} 1\\2 \end{pmatrix}; \begin{pmatrix} 1&2/3\\2&4/3 \end{pmatrix} \text{ (bottom plot)}; \qquad \mathcal{E}_1 = \begin{pmatrix} 5\\1 \end{pmatrix}; \begin{pmatrix} 3&3\\4&\rho \end{pmatrix}$$

for various values of  $\rho$ . The black curve in both plots is  $t_{\mathbf{y}}$ , and does not depend on the value of  $\rho$ . The colored curves are  $t_{\mathbf{x}}$ . The respective domains of these curves are the intervals I and J. All configurations are possible:  $I \cap J$  may be empty (bottom plot,  $\rho = 6.8$ ), a strict subset of I and J (bottom plot,  $\rho = 6.2$ ) or may be I or J itself (top plot).

Thanks to the results of [2] summarized in the table page 2, these plots describe exactly what regimes are possible when the jump rates (parametrized by s and t) vary, for a given choice of the environments.

For example the top plot for  $\rho = 5.5$  has three regimes: extinction of **x** (above the red curve), persistence (between the red and the black curves) and extinction of **y** (below the black curve). For  $\rho = 4.5$  there is an additonal zone (above the yellow curve and below the black one) of extinction of a random species. In particular, the knowledge of the relative positions of I and J is not enough to determine the possible regimes.

All these plots are computed by finding, for a fixed s, the zero of the function  $t \mapsto \Lambda(s, t)$ ; this is done by a simple root finding algorithm, using the explicit formula given in Lemma 1.2 to evaluate  $\Lambda(s, t)$ .

Figure 1: Shape of positivity regions for  $\Lambda_{\mathbf{x}}$  and  $\Lambda_{\mathbf{y}}$ 

## 2 Deterministic picture

## 2.1 Phase portraits of Lotka-Volterra vector field

We consider here the ODE (1) in an environment  $\mathcal{E} = (a, b, c, d, \alpha, \beta)$  and describe its possible qualitative behaviours. Much of this description can be found in [2], we give it here for the sake of clarity.

Barring limit cases that we will not consider, there are essentially four different phase portraits for the system, that are depicted in Figure 2. These four regimes are obtained as follows.

Notice first that the vector  $F_{\mathcal{E}}(x, y)$  is horizontal if y = 0 or cx + dy = 1: we call the line cx + dy = 1 the horizontal isocline. Similarly  $F_{\mathcal{E}}(x, y)$  is vertical if x = 0 or if (x, y) is on the vertical isocline ax + by = 1. These isoclines are the bold straight lines in Figure 2.

The three points (0,0), (0,1/d) and (1/a,0) are stationary for  $F_{\mathcal{E}}$ . The origin is always a source. The nature of the other points and the existence of a fourth stationary point depend on the parameters; this gives rise to the four types announced above.

Type 1. If a < c and b < d, species y gets extinct.

- The point (1/a, 0) is the unique global attractor: any solution of the ODE starting from a point which is not an equilibrium converges to (1/a, 0).
- The point (0, 1/d) is a hyperbolic saddle point. Its stable manifold is the vertical axis. We denote by  $\Sigma$  the intersection of its unstable manifold with the positive quadrant:  $\Sigma$  is the curve made of points  $(x_0, y_0)$  such that the solution  $(x_t, y_t)$  starting at  $(x_0, y_0)$  satisfies

$$(x_t, y_t) \xrightarrow[t \to -\infty]{} (0, 1/d).$$

We may compute explicitly some characteristics of  $\Sigma$ : in particular, it leaves (0, 1/d) with a slope  $-\frac{\alpha(d-b)+\beta d}{\beta c}$  and ends in (1/a, 0) with a possibly degenerate slope min  $\left(0, -\frac{\beta(a-c)+\alpha a}{\alpha b}\right)$ . Moreover,  $\Sigma$  lies in between the horizontal and vertical isoclines.

Type 2. If a > c and b > d, species **x** gets extinct. (0, 1/d) is the unique sink and (1/a, 0) is a saddle point. This is the same as Type 1 except that the two species **x** and **y** are swapped.

Type 3. If a > c and b > d, both species survive. The points (1/a, 0) and (0, 1/d) are saddle points. The isoclines meet at the sink  $(\bar{x}, \bar{y}) = (ad - bc)^{-1}(a - c, b - d)$ , which is the unique global attractor.

Type 4. If a > c and b < d, one of the two species gets extinct depending on the starting point. The meeting point of the isoclines  $(\bar{x}, \bar{y}) = (ad - bc)^{-1}(a - c, d - b)$  is now a saddle point, and (non trivial) trajectories converge to one of the two sinks on the axes, (1/a, 0) and (0, 1/d).

### 2.2 Relative positions of the two environments

Recall that the vector fields  $F_{\mathcal{E}_0}$  and  $F_{\mathcal{E}_1}$  are assumed favorable to species  $\mathbf{x}$ :  $a_i < c_i$  and  $b_i < d_i$  for i = 0, 1. Without loss of generality, we suppose that  $a_0 < a_1$ . The switched system may present a surprising behavior if the interval I defined in Equation (2) is not empty. This requires that  $c_0 < a_1$ . As a consequence, we impose in the sequel that

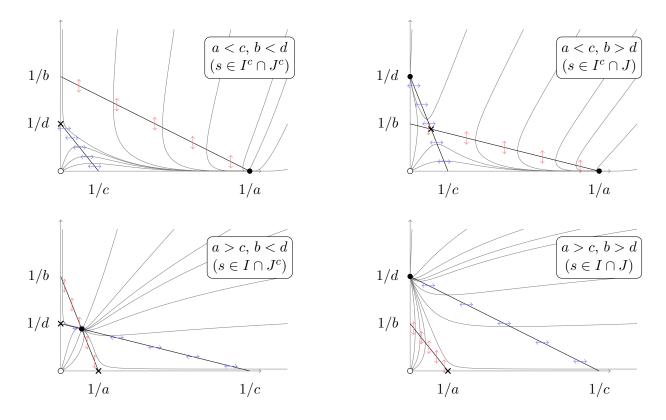
$$a_0 < c_0 < a_1 < c_1$$
,  $b_0 < d_0$  and  $b_1 < d_1$ .

**Lemma 2.1.** If the set J is not empty then  $d_1 < b_0$  or  $d_0 < b_1$ . Moreover, if  $I \cap J$  is non empty then

$$a_0 < c_0 < a_1 < c_1 \quad and \quad b_0 < d_0 < d_1 < b_1.$$
 (3)

*Proof.* The first point is clear from the definition of J. As a consequence, two configurations are compatible with I and J non empty: (3) and

$$a_0 < c_0 < a_1 < c_1$$
 and  $b_1 < d_1 < b_0 < d_0$ 



In each picture the bold lines are the horizontal and vertical isoclines, the gray lines are trajectories of the ODE. Sources, sinks and saddle points are pictured respectively by white circles, black circles and crosses.

Type 1 environments correspond to the upper left picture, Type 2 to the bottom right one. In Type 3 environments (bottom left), the intersection of the isoclines attracts the whole quadrant. In Type 4 environments (upper right) one species or the other gets extinct depending on the starting point.

For fixed environments  $\mathcal{E}_0$ ,  $\mathcal{E}_1$  of Type 1, the mixed environment  $\mathcal{E}_s$  may be of any of the four types, depending on whether s belongs to the intervals I and J.

Figure 2: The four possible deterministic regimes for a given environment.

Suppose, to derive a contradiction, that we are in the latter configuration. Define the points  $C_i = (1/c_i, 0)$  and  $D_i = (0, 1/d_i)$  for i = 0, 1. If  $M = (\tilde{x}, \tilde{y})$  is the intersection of the lines  $(C_0 D_0)$  and  $(C_1 D_1)$  then the set  $[\tilde{x}, +\infty) \times [0, \tilde{y}]$  is strongly positively invariant under the action by  $F_0$  and  $F_1$ . Furthermore, if  $I \cap J$  is not empty, this means that there exists  $s_0 \in (0, 1)$  such that  $F_{\mathcal{E}_{s_0}}$  is of Type 2. In particular, the point  $(0, 1/d_s)$  is accessible. This is incompatible with the previous remark. As a consequence,  $I \cap J$  is empty for this configuration.

## 3 Expression of the invasion rate

Let us first recall the expression of  $\Lambda_{\mathbf{y}}$  derived in [2]. Letting  $p_i = 1/a_i$ ,  $\Lambda_{\mathbf{y}}$  is given by

$$\Lambda_{\mathbf{y}} = p_0 p_1 C \int_{p_0}^{p_1} P(x) \theta(x) \, dx$$

where

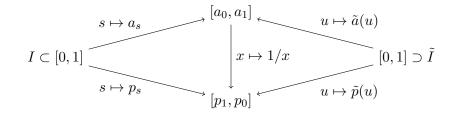
$$\begin{split} C^{-1} &= \frac{p_1}{\alpha_1} \int_{\min(p_0,p_1)}^{\max(p_0,p_1)} \frac{|x - p_0|^{\gamma_0} |p_1 - x|^{\gamma_1 - 1}}{x^{\gamma_0 + \gamma_1 + 1}} \, dx + \frac{p_0}{\alpha_0} \int_{\min(p_0,p_1)}^{\max(p_0,p_1)} \frac{|x - p_0|^{\gamma_0 - 1} |p_1 - x|^{\gamma_1}}{x^{\gamma_0 + \gamma_1 + 1}} \, dx, \\ \theta(x) &= \frac{|x - p_0|^{\gamma_0 - 1} |p_1 - x|^{\gamma_1 - 1}}{x^{\gamma_0 + \gamma_1 + 1}}, \\ P(x) &= \left[\frac{\beta_1}{\alpha_1} (1 - c_1 x) (1 - a_0 x) - \frac{\beta_0}{\alpha_0} (1 - c_0 x) (1 - a_1 x)\right] \frac{a_1 - a_0}{|a_1 - a_0|}. \end{split}$$

This quantity is obtained by averaging a growth rate of the second species with respect to the invariant measure of the one-dimensional PDMP (X, I) on  $[0, \infty) \times \{0, 1\}$  driven by

$$Lf(x,i) = \alpha_i x (1 - a_i x) \partial_x f(x,i) + \lambda_i (f(x,1-i) - f(x,i)),$$

which corresponds to the dynamics of species  $\mathbf{x}$  when species  $\mathbf{y}$  is gone. In the sequel, we assume that  $a_0 < a_1$  and set  $\delta = a_1 - a_0$ . It is obvious that the recurrent set of (X, I) is  $[p_1, p_0] \times \{0, 1\}$ .

In [2], the continuous part  $[p_1, p_0]$  of the state space is parametrized by a mapping  $[0, 1] \ni s \mapsto p_s$ given by  $p_s = 1/a_s$ , where  $a_s = (s\alpha_1 a_1 + (1-s)\alpha_0 a_0)/(s\alpha_1 + (1-s)\alpha_0)$ . It is interesting to look at another parametrization  $[0, 1] \ni u \mapsto \tilde{p}(u)$ , where  $\tilde{p}(u) = \tilde{a}(u)^{-1} = \frac{1}{a_0 + \delta u}$ . These parametrizations are summed up in the following diagram:



This parameter u is the one given in the introduction and corresponds to a ratio of the  $\gamma$ , when s corresponds to a ratio of  $\lambda$ , in the sense that:

$$\tilde{p}\left(\frac{\gamma_0}{\gamma_0 + \gamma_1}\right) = p\left(\frac{\lambda_0}{\lambda_0 + \lambda_1}\right).$$

**Remark 3.1.** As already mentioned above, the parameter u and the interval  $\tilde{I}$  are used implicitly in [2]: u appears in Remark 1, and the map S defined at the beginning of Section 4 is given in our notation by  $S(u) = p^{-1}(\tilde{p}(u))$ .

Let us study the integral  $\int_{p_1}^{p_0} P(x)\theta(x)dx$ . Set  $y = \tilde{p}^{-1}(x)$ , so that:

$$x = \tilde{p}(y) = \frac{1}{\tilde{a}(y)} = \frac{1}{a_0 + \delta y}, \qquad dx = -\delta \tilde{p}(y)^2 dy$$
$$p_0 - x = \delta p_0 y \tilde{p}(y), \qquad x - p_1 = \delta p_1 (1 - y) \tilde{p}(y).$$

Changing variables in the integral yields:

$$\begin{split} \int_{p_1}^{p_0} P(x)\theta(x)dx &= \int_0^1 P(\tilde{p}(y))(\delta p_0 y \tilde{p}(y))^{\gamma_0 - 1} (\delta p_1 (1 - y) \tilde{p}(y))^{\gamma_1 - 1} \tilde{p}(y)^{-\gamma_0 - \gamma_1 - 1} \delta \tilde{p}(y)^2 dy \\ &= \delta^{\gamma_0 + \gamma_1 - 1} p_0^{\gamma_0 - 1} p_1^{\gamma_1 - 1} \int_0^1 P(\tilde{p}(y)) \frac{1}{\tilde{p}(y)} y^{\gamma_0 - 1} (1 - y)^{\gamma_1 - 1} dy \\ &= \delta^{\gamma_0 + \gamma_1 - 1} p_0^{\gamma_0 - 1} p_1^{\gamma_1 - 1} \int_0^1 \phi(y) y^{\gamma_0 - 1} (1 - y)^{\gamma_1 - 1} dy \\ &= \delta^{\gamma_0 + \gamma_1 - 1} p_0^{\gamma_0 - 1} p_1^{\gamma_1 - 1} B(uv, (1 - u)v) \mathbb{E} \left[\phi(U_{u,v})\right]. \end{split}$$

since  $\phi(y) = \frac{1}{\tilde{p}(y)} P(\tilde{p}(y))$ . A similar computation gives the exact formula

$$C^{-1} = \left(\delta^{\gamma_0 + \gamma_1 - 1} p_0^{\gamma_0 - 1} p_1^{\gamma_1 - 1} B(uv, (1 - u)v)\right) p_0 p_1 \delta\left(\frac{1}{\alpha_0}(1 - u) + \frac{1}{\alpha_1}u\right)$$

for the normalization constant C. Therefore

$$\Lambda_{\mathbf{y}}(\gamma_0,\gamma_1) = \frac{1}{\delta\left(\frac{1}{\alpha_0}(1-u) + \frac{1}{\alpha_1}u\right)} \mathbb{E}\left[\phi(U_{u,v})\right].$$

Let us study  $\phi$  more precisely. Since P is a second-degree polynomial, let us write it down as  $P(x) = ax^2 + bx + c$ . Then

$$\phi(y) = \frac{a}{a_0 + \delta y} + b + c(a_0 + \delta y).$$

The second derivative is

$$\phi''(y) = \frac{2a\delta^2}{(a_0 + \delta y)^3},$$

which has the sign of a on [0,1], so  $\phi$  is either strictly convex or strictly concave. However, the proof of the first item of Proposition 2.2 in [2] shows that (still in the case  $a_0 < a_1$ )  $P(p_s) = \frac{\beta_s}{\alpha_1 s}(1 - a_0/a_s)(1 - c_s/a_s)$  has the same sign as  $a_s - c_s$ , that is,  $P(p_s)$  is positive iff  $s \in I$ . If I is empty, so is  $\tilde{I}$ , and  $\phi$  is negative on ]0,1[. If I is not empty, so is  $\tilde{I}$ , and  $\phi$  is positive on  $\tilde{I}$  (and nonpositive outside  $\tilde{I}$ ), therefore  $\phi$  must be concave.

## 4 Shape of the positivity region

We begin with a lemma, which is proved in the next two sections. The existence and properties of  $v_c$  and  $t_c$  stated in Theorem 1.3 are deduced from this lemma in Section 4.3.

**Lemma 4.1.** If I is non empty, the map  $(u, v) \mapsto \mathbb{E}[\phi(U_{u,v})]$  is (strictly) increasing in v and concave in u.

#### 4.1 Monotonicity in v

We wish to compare  $\mathbb{E}[\phi(U_{u,v})]$  for different values of v. Since the function  $\psi = (-\phi)$  is convex, a natural idea is to compare the distributions of  $U_{u,v}$  for various v in the *convex order*. Let us first recall the definition of this order.

**Definition 4.2** (Convex order). Let X and Y be two random variables. If the inequality

$$\mathbb{E}\left[\psi(X)\right] \leqslant \mathbb{E}\left[\psi(Y)\right]$$

holds for all convex functions  $\psi$  such that the expectations exist, X is said to be smaller than Y in the convex order. We denote by  $X \leq_{\text{cvx}} Y$  this relation.

The convex order admits the following characterization in terms of cumulative distribution functions ([5, Theorem 3.A.1]).

**Theorem 4.3** (Convex order and distribution functions). The variables X and Y satisfy  $X \leq_{\text{cvx}} Y$  if and only if  $\mathbb{E}[X] = \mathbb{E}[Y]$  and, for all x,

$$\int_{-\infty}^{x} F_X(t)dt \leqslant \int_{-\infty}^{x} F_Y(t)dt < \infty,$$
(4)

where  $F_X$  and  $F_Y$  are the cumulative distribution functions of X and Y.

**Remark 4.4** (Terminology). The convex order is one possible way of formalizing the idea that Y is "more variable/more spread out" than X. Note in particular if  $X \leq_{\text{cvx}} Y$  then  $\text{Var}(X) \leq \text{Var}(Y)$ . For details on the convex order, a survey of other formalizations of variability and many other notions of stochastic order we refer to [5].

Let us also note that, when (4) holds (without assuming  $\mathbb{E}[X] = \mathbb{E}[Y]$ ), X is said to secondorder stochastically dominate Y; this is equivalent to asking the inequality  $\mathbb{E}[\psi(X)] \leq \mathbb{E}[\psi(Y)]$ for any non-increasing convex function  $\psi$ . We refer to [4, Appendix B.19] for a proof, additional discussion, and references to the literature.

We will need the following easy fact.

**Theorem 4.5.** If  $X \leq_{\text{cvx}} Y$  and  $\mathbb{E}[\psi(X)] = \mathbb{E}[\psi(Y)]$  for some strongly convex  $\psi$ , then X and Y have the same distribution.

*Proof.* Suppose that X and Y satisfy the hypotheses. By a classical characterization of the convex order ([5, Theorem 3.A.4]) there exists a couple (X, Z) such that  $\mathbb{E}[Z|X] = 0$  and X + Z has the same distribution as Y. Since  $\psi$  is strongly convex, there exists an m > 0 such that for all  $t \in [0, 1]$ ,

$$\psi(X+tZ) = \psi((1-t)X + t(X+Z)) \leq (1-t)\psi(X) + t\psi(X+Z) - \frac{mt(1-t)}{2}Z^2.$$

Taking expectations we get

$$\mathbb{E}\left[\psi(X)\right] \leqslant \mathbb{E}\left[\psi(X+tZ)\right] \leqslant (1-t)\mathbb{E}\left[\psi(X)\right] + t\mathbb{E}\left[\psi(Y)\right] - \frac{mt(1-t)}{2}\mathbb{E}\left[Z^2\right]$$

where the first inequality comes from Jensen's inequality and  $\mathbb{E}[Z|X] = 0$ . Since  $\mathbb{E}[\psi(Y)] = \mathbb{E}[\psi(X)]$ , Z must be zero almost surely, so X and Y have the same distribution.

**Theorem 4.6** (Orderings between Beta r.v.). Let  $X \sim \text{Beta}(\alpha, \beta)$  and  $X' \sim \text{Beta}(\alpha', \beta')$ . If  $\alpha < \alpha', \beta < \beta'$  and  $\alpha/(\alpha + \beta) = \alpha'/(\alpha' + \beta')$ , then  $X' \leq_{\text{cvx}} X$ .

*Proof.* Call  $f_{\alpha,\beta}$ ,  $f_{\alpha',\beta'}$  the densities of the distributions. Compute their ratio:

$$\frac{f_{\alpha',\beta'}(x)}{f_{\alpha,\beta}(x)} = C_{\alpha,\beta,\alpha',\beta'} x^{\alpha'-\alpha} (1-x)^{\beta'-\beta}.$$

In the first case, this ratio starts and ends in zero, is strictly increasing on  $[0, x_0]$  and strictly decreasing on  $[x_0, 1]$ . Since the two functions are densities, the ratio must cross 1 exactly twice, say in  $x_1, x_2$ . Therefore

$$d(x) = f_{\alpha',\beta'} - f_{\alpha,\beta}$$

is positive on  $(x_1, x_2)$  and negative on  $(0, x_1)$  and  $(x_2, 1)$ . Therefore

$$D(x) = F_{X'}(x) - F_X(x)$$

starts at zero, decreases on  $[0, x_1]$ , increases on  $[x_1, x_2]$  and decreases on  $[x_2, 1]$ , so D(x) is negative on  $[0, x_3]$  and positive on  $[x_3, 1]$  (since it ends at zero). Integrating once more,

$$\int_0^x D(t)dt$$

starts and ends at zero (since  $\mathbb{E}[X] = \mathbb{E}[X']$ ) and is decreasing-increasing, therefore it is non-positive. Thanks to Theorem 4.3, this implies  $X' \leq_{\text{cvx}} X$ .

Proof of the monotonicity in v. Suppose v < v' and put  $\alpha = uv$ ,  $\alpha' = uv'$ ,  $\beta = (1 - u)v$ ,  $\beta' = (1 - u)v'$ . The theorem shows that  $U_{u,v'} \leq_{cvx} U_{u,v}$ . Since  $\psi = (-\phi)$  is strongly convex, this implies

$$\mathbb{E}\left[\phi(U_{u,v})\right] < \mathbb{E}\left[\phi(U_{u,v'})\right],$$

by Theorem 4.5, so  $v \mapsto \mathbb{E}[\phi(V_{u,v})]$  is (strictly) increasing.

## 4.2 Concavity in u

Even though  $\phi$  is concave and the r.v.  $U_{u,v}$ ,  $U_{u',v}$  are stochastically comparable (for the usual stochastic order), this is not enough to show the concavity of  $u \mapsto \mathbb{E}[\phi(U_{u,v})]$ . We prove it by elementary means. First, recalling the explicit expression of  $\phi$  we write:

$$\mathbb{E}\left[\phi(U_{u,v})\right] = a\mathbb{E}\left[\frac{1}{a_0 + \delta U_{u,v}}\right] + b + c\mathbb{E}\left[a_0 + \delta U_{u,v}\right]$$
$$= a\mathbb{E}\left[\frac{1}{a_0 + \delta U_{u,v}}\right] + b + c(a_0 + \delta u).$$

Since a is negative (see the proof of Lemma 1.2) and the last term is linear, it is enough to show that

$$g: u \mapsto \mathbb{E}\left[\frac{1}{a_0 + \delta U_{u,v}}\right]$$

is convex. It is a bit easier to use the symmetry of Beta random variables  $(U_{u,v} \text{ and } 1 - U_{1-u,v})$  have the same distribution) and look at

$$h: u \mapsto \mathbb{E}\left[\frac{1}{a_1 - \delta U_{u,v}}\right].$$

Since g(u) = h(1 - u), g will be convex if h is convex. Now, recalling that  $\delta = (a_1 - a_0) < a_1$ , we write the series development:

$$h(u) = \frac{1}{a_1} \mathbb{E}\left[\sum_{k=0}^{\infty} \left(\frac{\delta}{a_1}\right)^k U_{u,v}^k\right] = \frac{1}{a_1} \sum_{k=0}^{\infty} \left(\frac{\delta}{a_1}\right)^k \mathbb{E}\left[U_{u,v}^k\right]$$

so h is a mixture of the functions  $h_k$  given by:

$$h_k(u) = \mathbb{E}\left[U_{u,v}^k\right] = \prod_{r=0}^{k-1} \frac{uv+r}{v+r} = \frac{1}{\prod_{r=0}^{k-1} (v+r)} (uv)(uv+1)\cdots(uv+k-1).$$

This is a polynomial function of u with positive coefficients, therefore it is convex on [0, 1]. This concludes the proof.

#### 4.3 **Properties of the frontier**

We have just shown that  $v \mapsto \tilde{\Lambda}_{\mathbf{y}}(u, v)$  is increasing. From [2, Proposition 2.2] and the fact that in the change of variables  $(s, t) \leftrightarrow (u, v)$ , u only depends on s, and for fixed u, v is an increasing function of t, we know additionally that it admits:

- negative limits at 0 and  $\infty$  if  $u \notin \tilde{I}$ ,
- a negative limit at 0 and a positive limit at  $\infty$  if  $u \in \tilde{I}$ .

Since  $\Lambda_{\mathbf{y}}$  has the same sign as  $\mathbb{E}[\phi(U_{u,v})]$ , this justifies the existence of  $v_c$ , and we have

$$\tilde{\Lambda}_{\mathbf{v}}(u,v) = 0 \iff u \in \tilde{I}, v = v_c(u).$$

Let us prove that  $v_c$  is quasi-convex. Let a < b < c be three points in (0, 1). If a or c are not in  $\tilde{I}, v_c(b)$  is less than  $\max(v_c(a), v_c(c)) = \infty$ . If a and c are in  $\tilde{I}$ , let  $M > \max(v_c(a), v_c(c))$ . Since  $\tilde{\Lambda}_{\mathbf{y}}(u, \cdot)$  is increasing,  $\tilde{\Lambda}_2(a, M)$  and  $\tilde{\Lambda}_{\mathbf{y}}(c, M)$  are positive. Since  $\tilde{\Lambda}_{\mathbf{y}}(\cdot, M)$  is concave,  $\tilde{\Lambda}_{\mathbf{y}}(b, M)$  is positive. Therefore  $v_c(c) \leq M$ . Sending M to  $\max(v_c(a), v_c(b))$  yields the quasi-convexity of  $v_c$ .

Let us now show the regularity properties. Let  $u_n$  be an increasing sequence in I, converging to some  $u \in (0,1)$ . Since  $v_c$  is quasi-convex,  $v_n = v_c(u_n)$  is eventually monotone, so it converges to some  $v \in [0,\infty]$ . If v is finite, since the zero set of  $\Lambda_{\mathbf{y}}$  is closed, by continuity,  $v = v_c(u)$ , so umust be in  $\tilde{I}$ . Conversely, if  $u \in \tilde{I}$ ,  $v_c$  is bounded on a neighborhood of u by quasi-convexity, so vis finite. This shows that  $v_c$  is continuous on  $\tilde{I}$  and converges to  $\infty$  at the endpoints.

The properties of the change of variables  $(s,t) \leftrightarrow (u,v)$  show that  $v_c$  is well-defined and continuous with the correct limits.

## 5 Support of the invariant measure

Note that there are always two invariant probability measures, supported on the coordinate axes. In the persistence regime, we are interested in the third invariant measure, whose support  $\Gamma \times \{0, 1\}$  is such that  $\Gamma$  has non empty interior. Several properties of  $\Gamma$  are established in [2] (see below). In this section, we aim at provide a full description of  $\Gamma$ . Its shape essentially depends on the fact that  $I \cap J$  is empty or not.

#### 5.1 Persistence with "full support"

In this subsection, we assume that  $I \cap J$  is not empty. According to Lemma 2.1, the vector fields  $F_{\mathcal{E}_0}$  and  $F_{\mathcal{E}_1}$  are such that (3) holds. Let us denote by  $\Sigma_i$  the intersection of  $[0,\infty)^2$  and the unstable manifold of  $(0,1/d_i)$  and  $\Gamma'$  the bounded subset of  $[0,+\infty)^2$  with border

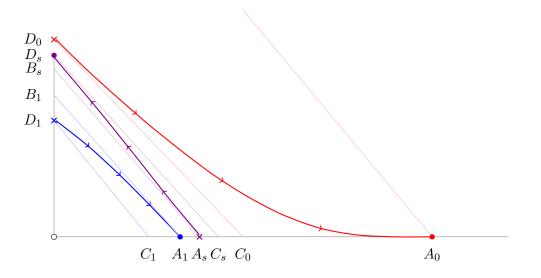
$$\Sigma_1 \cup \{(x,0) : 1/a_1 \leq x \leq 1/a_0\} \cup \Sigma_0 \cup \{(0,y) : 1/d_1 \leq x \leq 1/d_0\}.$$

**Theorem 5.1.** Suppose that  $I \cap J \neq \emptyset$ . Then, for any  $(s,t) \in [0,1] \times (0,\infty)$  such that  $\Lambda_{\mathbf{x}}(s,t) > 0$ and  $\Lambda_{\mathbf{y}}(s,t) > 0$ , then  $\Gamma' = \Gamma$ .

*Proof.* Firstly, notice that the set  $\Gamma'$  is positively invariant for each flow since both vector fields  $F_{\mathcal{E}_0}$  and  $F_{\mathcal{E}_1}$  point inside  $\Gamma'$ .

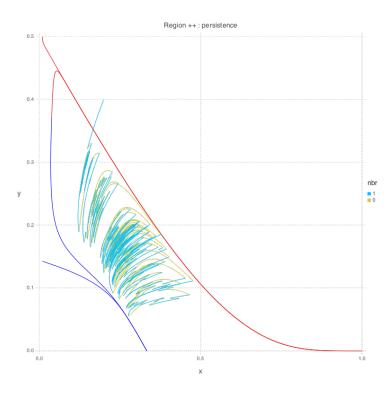
Pick an  $s \in I \cap J$ . The isoclines and the unstable manifold of the saddle point for the three environments  $\mathcal{E}_0$ ,  $\mathcal{E}_1$  and  $\mathcal{E}_s$  are necessarily in the position depicted in Figure 3. Denote by  $\Sigma_s$  the intersection of the unstable manifold of  $(1/a_s, 0)$  with the upper right quadrant.

First step: the set  $\Sigma_s$  is contained in the support. Indeed, pick a point (x, y) in the interior of the support (such a point exists by [2, Remark 6]). The loop formed by the trajectories starting from (x, y) with both flows (converging to  $A_1 : (1/a_1, 0)$  and  $A_0 : (1/a_0, 0)$  and the line segment  $[A_0, A_1]$  is included in the support (by positive invariance). As a consequence, the support must contain a closed half ball centered on  $A_s$  — let us call it  $\mathcal{B}$ . Now pick a point  $(x, y) \in \Sigma_s$ : by



The isoclines (straight lines) and unstable manifolds (curved lines) for the three environments  $\mathcal{E}_0$  (bottom left, in blue),  $\mathcal{E}_s$  (middle, in purple) and  $\mathcal{E}_1$  (upper right, in red). Note how the isoclines are "swapped" for  $\mathcal{E}_s$ , a Type 2 environment.





The outer curves are  $\Sigma_0$  and  $\Sigma_1$ . The region between these curves is positively invariant. The inner curves are the two trajectories coming from the unique point  $z \in T$ : they form the boundary of the support. The sample trajectory shows that the invariant measure is in practice often concentrated on a smaller subset.

Figure 4: Support away from the y axis

definition its  $\mathcal{E}_s$  flow converges for  $t \to -\infty$  to  $1/a_s$ . By continuity there exists a point in the past of (x, y) which is in  $\mathcal{B}$ . Running the time forward again, the point (x, y) must be in the support.

Second step: any point (strictly) between  $\Sigma_1$  and  $\Sigma_s$  is in  $\Gamma$ . Starting from such a point (x, y), run the  $\mathcal{E}_1$  flow in reverse time. The trajectory must cross  $\Sigma_s$ . So (x, y) is in the future of a point in  $\Sigma_s \subset \Gamma$ , and  $(x, y) \in \Gamma$  by positive invariance.

Third step: any point between  $\Sigma_0$  and  $\Sigma_s$  is in  $\Gamma$ . This step is similar to the previous one and is omitted.

Similarly, any point between  $\Sigma_1$  and  $\Sigma_s$  is in  $\Gamma$ .

#### 5.2 Support away from the y axis

We suppose in the sequel that  $I \cap J$  is empty. Let us introduce the set where the two vector fields  $F_0$  and  $F_1$  are collinear:

$$C = \{ z \in \mathbb{R}^2_+ : \det(F_0(z), F_1(z)) = 0 \}.$$

This set is the union of  $\{(0, y) : y \ge 0\}$ ,  $\{(x, 0) : x \ge 0\}$ , and

$$\tilde{C} = \{(x, y) \in \mathbb{R}^2_+ : G(x, y) = 0\}$$

where G is a polynomial of degree 2. As a consequence, the set  $\tilde{C}$  is a subset of a conic. It is easy to see that  $\tilde{C}$  is also the set of non-degenerate equilibrium points for the vector field  $F_{\mathcal{E}_s}$ , as s varies from 0 to 1. When  $s \in I$ ,  $\mathcal{E}_s$  is of type 3 so the equilibrium point is stable and globally attractive. Therefore the part of  $\tilde{C}$  that corresponds to  $s \in I$  must be included in  $\Gamma$ , as well as all trajectories (for both flows) starting from it.

Numerical experiments suggest that there is a unique "extremal point" on this part of  $\hat{C}$ , such that the trajectories starting from this point form the boundary of  $\Gamma$ .

To describe it more precisely, consider the subset of  $\tilde{C}$  made of the points where  $F_0$  (or  $F_1$ ) is tangent to the curve  $\tilde{C}$ . This set is given by

$$T = \{ (x, y) \in \mathbb{R}^2_+ : G(x, y) = 0 \text{ and } (F_0 \cdot \nabla G)(x, y) = 0 \}.$$

Since G and  $F_0 \cdot \nabla G$  are polynomials with respective degrees 2 and 3, T is made of at most six points according to Bezout's Theorem.

For any  $z \in T$  let us define C(z) the bounded region enclosed by the Jordan curve

$$\left\{\varphi_z^0(t) : t \in [0,\infty)\right\} \cup \left\{\varphi_z^1(t) : t \in [0,\infty)\right\} \cup [1/a_1, 1/a_0] \times \{0\}.$$

**Conjecture 5.2.** The set T is a singleton  $\{z_0\}$  and the support of the invariant measure which is absolutely continuous is  $C(z_0) \times \{0, 1\}$ .

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