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

Florent Malrieu, Pierre-André Zitt

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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

1.1 The model

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 different regimes of the process and the support of the invariant measures. Let us first provide an overview of the main results in [2] before stating our contribution.

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

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

This system modelizes the evolution of the populations of two species (x of type $\mathbf{x}$ and y of type $\mathbf{y}$). The populations grow logistically — as encoded by the $\alpha x(1 - ax)$ and $\beta y(1 - dy)$ terms — and compete with each other, which gives rise to the cross terms αbxy and βcxy. 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. In particular it has only a finite number of equilibrium points, towards which the dynamics converges. These equilibria may be on the coordinate axes — meaning that one of the species gets extinct — or inside the positive quadrant. The position and nature of the equilibria turn out to depend only on the signs of $c - a$ and $d - b$. A complete picture will be given in 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 in this case that the environnement is *favorable to species* $\boldsymbol{x}$; it leads to the extinction of species $\mathbf{y}$.

Consider now two such systems, labeled 0 and 1, with environments $\mathcal{E}_i = (a_i, b_i, c_i, d_i, \alpha_i, \beta_i)_{i=0,1}$. We make the following standing assumption:

Assumption 1.1. *The environments $\mathcal{E}_0$ and $\mathcal{E}_1$ are both favorable to $\boldsymbol{x}$: $a_i < c_i$ and $b_i < d_i$ for $i = 0, 1$. In particular, taken alone, each system leads to the extinction of the second species, that is, y_t converges to 0 and $\limsup x_t > 0$ 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 distribution of parameter λ_i, and while I_t is equal to i, Z evolves deterministically by $\dot{Z}_t = F_{\mathcal{E}_i}(Z_t)$. The coordinates of Z_t are denoted by X_t and Y_t. We refer to [2] for a detailed biological motivation.

It is shown in [2] that, depending on the environments $\mathcal{E}_0$, $\mathcal{E}_1$ and the jump rates λ_0, λ_1, one of the following four things occur almost surely:

- extinction of species **x**: $X_t \to 0$ and $\limsup Y_t > 0$,
- extinction of species **y**: $Y_t \to 0$ and $\limsup X_t > 0$,
- extinction of one of the two species, chosen randomly,
- persistence: the empirical occupation measure (and, in many cases, the distribution) of $(X_t, Y_t)_{t \geqslant 0}$ 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 (λ_0, λ_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].

1.2 The frequent jumps asymptotics and the averaged vector field

Recall that λ_0, λ_1 are the jump rates from one environment to the other. Note that the index process $(I_t)_{t \geqslant 0}$ is Markov by itself, and its invariant measure is a Bernoulli distribution with parameter $\lambda_0/(\lambda_0 + \lambda_1)$. As a consequence, it will be convenient to choose the alternative parametrization

$$(s, t) \in [0, 1] \times (0, +\infty) \mapsto (st, (1 - s)t) \tag{2}$$

for the jump rates, that is, let t be the sum $\lambda_0 + \lambda_1$ and s be the ratio $\lambda_0/(\lambda_0 + \lambda_1)$.

Remark 1.2 (Length of interjump times I)**.** *Notice that the expectations of the interjump times are given by $(st)^{-1}$ and $((1 - s)t)^{-1}$. If t is small, the jumps are rare and the jump times are large in average; as t grows the jumps become more frequent and the jump times shorter on average.*

As the parameter t goes to infinity — the frequent jumps asymptotics — it can be shown that the stochastic process $(Z_t)_{t \geqslant 0}$ converges to the solution of

$$\dot{z}_t = F_s(z_t) \quad \text{where} \quad F_s = (1 - s)F_{\mathcal{E}_0} + sF_{\mathcal{E}_1}.$$

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

$$\alpha_s = (1 - s)\alpha_0 + s\alpha_1, \qquad a_s = \frac{(1 - s)\alpha_0 a_0 + s\alpha_1 a_1}{\alpha_s}, \qquad b_s = \frac{(1 - s)\alpha_0 b_0 + s\alpha_1 b_1}{\alpha_s}, \tag{3}$$

$$\beta_s = (1 - s)\beta_0 + s\beta_1, \qquad c_s = \frac{(1 - s)\beta_0 c_0 + s\beta_1 c_1}{\beta_s}, \qquad d_s = \frac{(1 - s)\beta_0 d_0 + s\beta_1 d_1}{\beta_s}. \tag{4}$$

Recall that by our standing assumption, $a_i < c_i$ and $b_i < d_i$ for $i = 0, 1$. The key point is that *these inequalities may be reversed* for the averaged environment $\mathcal{E}_s$; in some situations $\mathcal{E}_s$ may even be *unfavorable to species* $\boldsymbol{x}$*!*

Definition 1.3 (Critical parameter regions)**.** *Two critical (possibly empty) parameter regions are defined in [2] by:*

$$I = (s_1, s_2) = \{s \in [0,1], a_s > c_s\} \quad \textit{and} \quad J = (s_3, s_4) = \{s \in [0,1], b_s > d_s\}. \tag{5}$$

The fact that I and J are indeed intervals is obvious from the definition of a_s, b_s, c_s and d_s by (3) and (4). As we have seen, the relevance of these intervals stems from the fact that they correspond to different types for the averaged environment $\mathcal{E}_s$. For example, the vector field F_s always has two stationary points on the coordinate axes, but their nature vary:

- the stationary point $(1/a_s, 0)$ is a well if $s \notin I$ and a saddle point if $s \in I$,
- the stationary point $(0, 1/d_s)$ is a saddle point if $s \notin J$ and a well if $s \in J$.

Remark 1.4. *Notice that if $a_0 = a_1$ then the interval I is empty. In the sequel we will focus on the case when $a_0 \neq a_1$ and without loss of generality we will assume that $a_0 < a_1$.*

More details and a complete description of the phase portrait of the Lotka-Volterra system will be given below (see Section 2).

1.3 Invasion rates

It is shown in [2] that the regime of the process (Z, I) is determined by the the signs of two quantities, called *invasion rates*, $\Lambda_{\mathbf{x}}$ and $\Lambda_{\mathbf{y}}$. These quantities are obtained by considering the system where one of the species, say $\mathbf{y}$, is almost extinct: $y \ll 1$. In this case, remark two things:

- if the current environment is i, the growth rate $\frac{\dot{y}}{y}$ of species $\mathbf{y}$ is approximately $\beta_i(1 - c_i x)$, by (1);
- while y stays negligible, the evolution of (X, I) looks like the dynamics of the Markov process on $[0, \infty) \times \{0, 1\}$ driven by the generator

  $$L_{\mathbf{x}} f(x, i) = \alpha_i x(1 - a_i x)\partial_x f(x, i) + \lambda_i(f(x, 1 - i) - f(x, i)),$$

  which turns out to be ergodic with an invariant measure $\mu_{\mathbf{x}}$ on $[0, \infty) \times \{0, 1\}$ that depends on the jump rates $(\lambda_0, \lambda_1) = (st, (1 - s)t)$.

Over a long period of time, the growth rate of $\mathbf{y}$ is therefore obtained by averaging $\beta_i(1 - c_i x)$ with respect to the invariant measure $\mu_{\mathbf{x}}$: this leads to the definition of the *invasion rate* $\Lambda_{\mathbf{y}}$ by

$$\Lambda_{\mathbf{y}}(s, t) = \int_{[0,\infty)\times\{0,1\}} \beta_i(1 - c_i x)\mu_{\mathbf{x}}(dx, di).$$

When $\Lambda_{\mathbf{y}}$ is positive (respectively negative) species $\mathbf{y}$ tends to increase (respectively decrease) from low density. Similarly, one can define

$$\Lambda_{\mathbf{x}}(s, t) = \int_{[0,\infty)\times\{0,1\}} \alpha_i(1 - b_i y)\mu_{\mathbf{y}}(dy, di).$$

where $\mu_{\mathbf{y}}$ is the invariant probability measure of the stochastic process on $\mathbb{R} \times \{0, 1\}$ with generator

$$L_{\mathbf{y}} f(y, i) = \beta_i y(1 - d_i y)\partial_y f(y, i) + \lambda_i(f(y, 1 - i) - f(y, i)),$$

The main result in [2] ensures that 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 $\mathbf{y}$
$\Lambda_{\mathbf{x}} < 0$	extinction of species $\mathbf{x}$	random extinction of one of the two species

1.4 Our contribution

In view of the previous result, the study of the model is reduced to finding the sign of the invasion rates, depending on the parameters of the environment and on the jump rates. To state our results, we need to introduce a second parametrization for the jump rates $(\lambda_0, \lambda_1) \in (0, +\infty)^2$ slightly different from (2):

$$(u, v) \in [0, 1] \times (0, +\infty) \mapsto (\alpha_0 uv, \alpha_1(1 - u)v)$$

in such a way that

$$u = \gamma_0/(\gamma_0 + \gamma_1) \quad \text{and} \quad v = \gamma_0 + \gamma_1 \quad \text{where } \gamma_i = \lambda_i/\alpha_i \quad \text{for } i = 0, 1. \tag{6}$$

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

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

Remark 1.5 (Length of interjump times II)**.** *Notice that the new parameter v is proportional to t when u (or s) is fixed. As a consequence, as in Remark 1.2, the interjump times are short when v is large and large when v is small.*

Definition 1.6 (Reparametrized invasion rates)**.** *The invasion rates in the (u, v) coordinates are denoted by*

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

Similarly, $\tilde{I}$ (resp. $\tilde{J}$) is the image of I (resp. J) for the other parametrization.

Note that $\tilde{I}$ and $\tilde{J}$ still are (possibly empty) intervals.

Remark 1.7. *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 1.8 (Expression of $\tilde{\Lambda}_{\mathbf{y}}$)**.** *Assume that $a_0 < a_1$ (see Remark 1.4). Let (u, v) given by* (6)*. The quantity $\tilde{\Lambda}_{\mathbf{y}}$ can be rewritten as:*

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

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 $\mathrm{Beta}(uv, (1 - u)v)$ *random variable.*

Moreover, ϕ has the following properties:

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

Recall that a function f is called quasi convex on (a,b) if its level sets $\{f \leqslant t\}$ 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 1.9 (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 $v_{\mathbf{y}}$ is quasi-convex, continuous on its domain $\tilde{I}$, and tends to $+\infty$ on the endpoints of $\tilde{I}$.

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

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

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 1.10. *Numerical computations suggest that both $v_{\mathbf{y}}$ and $t_{\mathbf{y}}$ are in fact smooth and convex on $\tilde{I}$ and I respectively.*

Remark 1.11. *This result is cited in [2, Proposition 2.5], since it answers a conjecture that appeared in a preprint version of [2].*

For an illustration of Theorem 1.9 and Remark 1.10, see Figure 1.

Finally, our last results are dedicated to the support of the non-trivial invariant probability measure in the persistence regime. In [2], it is shown that this measure has a density with respect to the Lebesgue measure on the quadrant. Theorem 5.1 provides a full description of its support when the set $I \cap J$ is not empty. Since a precise statement requires several notations introduced in Section 2, we postpone it to the last section of the document.

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 1.8; the main result is proved in Section 4. The final section is dedicated to the description of the support of invariant measures in the persistence regime.

2 Deterministic picture

2.1 Phase portraits of Lotka-Volterra vector field

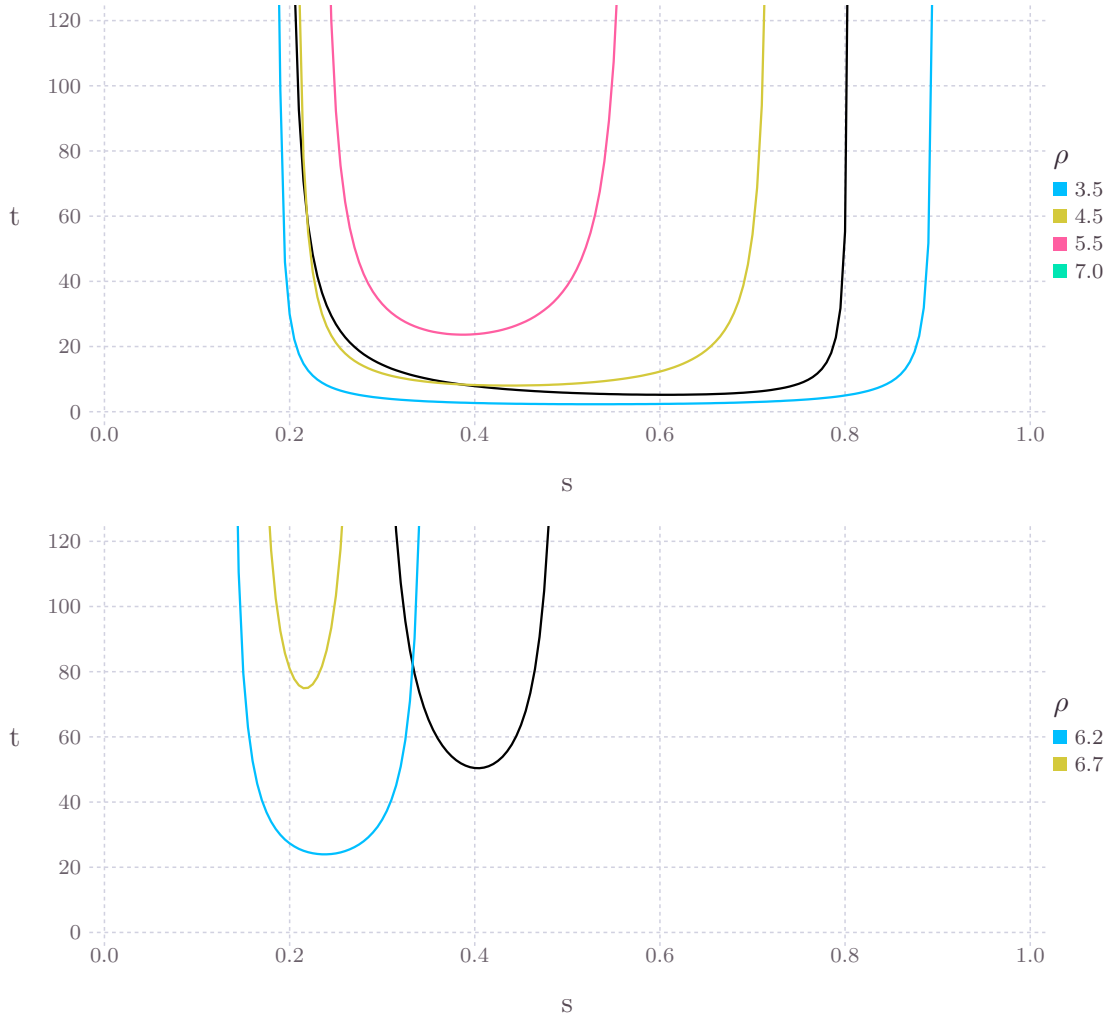
We consider here the ODE (1) in an environment $\mathcal{E} = (a,b,c,d,\alpha,\beta)$ and describe its possible qualitative behaviours. Much of this description can be found in [2], we give it here for the sake of clarity.

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.

Each axis is invariant that why in the sequel we are only interested in initial conditions with positive coordinates. 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 depends on the parameters; this gives rise to the four types announced above.

Type 1. If $a < c$ and $b < d$, species $\mathbf{y}$ gets extinct.



These plots represent the "critical" functions $t_{\mathbf{y}}$ and $t_{\mathbf{x}}$ for different choices of the environments. Denoting environments by the couple $\left(\begin{smallmatrix}\alpha\\ \beta\end{smallmatrix}\right)$; $\left(\begin{smallmatrix}a & b\\ c & d\end{smallmatrix}\right)$, 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 the parameter ρ appearing in the definition of the environment $\mathcal{E}_1$. The black curve in both plots is $t_{\mathbf{y}}$, and does not depend on the value of ρ. 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 3, 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 $\mathbf{x}$ (above the red curve), persistence (between the red and the black curves) and extinction of $\mathbf{y}$ (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 1.8 to evaluate $\Lambda(s,t)$.

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

- The point $(1/a, 0)$ is the unique global attractor: any solution of the ODE starting from a point with positive coordinates 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 Σ the intersection of its unstable manifold with the positive quadrant: Σ 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 explicitely some characteristics of Σ: 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, Σ lies in between the horizontal and vertical isoclines.

Type 2. If $a > c$ and $b > d$, species $\mathbf{x}$ 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 $\mathbf{x}$ and $\mathbf{y}$ 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 (5) is not empty. This requires that $c_0 < a_1$. As a consequence, we impose in the sequel that

$$a_0 < c_0 < a_1 < c_1, \quad b_0 < d_0 \quad \text{and} \quad b_1 < d_1.$$

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*

$$a_0 < c_0 < a_1 < c_1 \quad \textit{and} \quad b_0 < d_0 < b_1 < d_1. \tag{7}$$

Proof. The first point is clear from the definition of J. As a consequence, two configurations are compatible with I and J non empty: (7) and

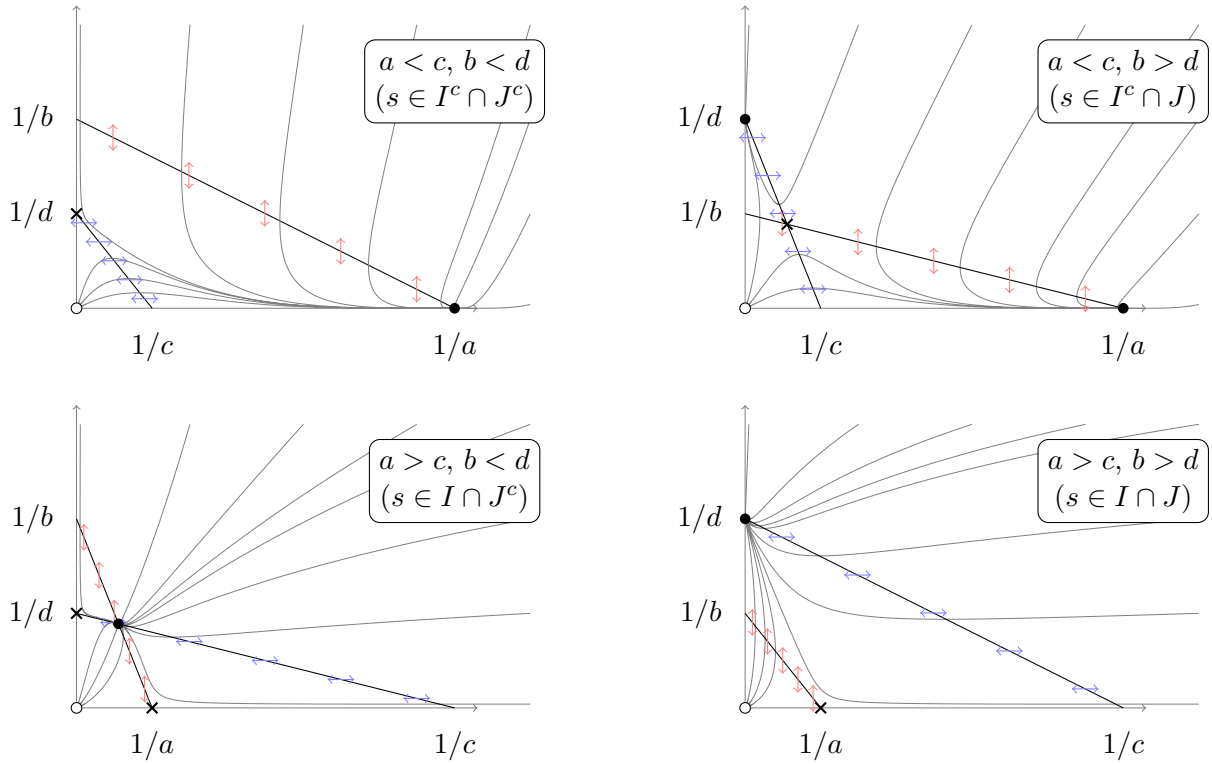
$$a_0 < c_0 < a_1 < c_1 \quad \text{and} \quad b_1 < d_1 < b_0 < d_0.$$

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_0D_0) and (C_1D_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

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



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.

where

$$C^{-1} = \frac{p_1}{\alpha_1}\int_{\min(p_0,p_1)}^{\max(p_0,p_1)} \frac{|x-p_0|^{\gamma_0}|p_1-x|^{\gamma_1-1}}{x^{\gamma_0+\gamma_1+1}}\,dx + \frac{p_0}{\alpha_0}\int_{\min(p_0,p_1)}^{\max(p_0,p_1)} \frac{|x-p_0|^{\gamma_0-1}|p_1-x|^{\gamma_1}}{x^{\gamma_0+\gamma_1+1}}\,dx,$$

$$\theta(x) = \frac{|x-p_0|^{\gamma_0-1}|p_1-x|^{\gamma_1-1}}{x^{\gamma_0+\gamma_1+1}},$$

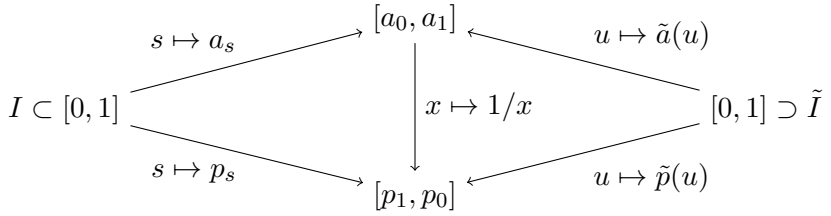
$$P(x) = \left[\frac{\beta_1}{\alpha_1}(1-c_1x)(1-a_0x) - \frac{\beta_0}{\alpha_0}(1-c_0x)(1-a_1x)\right]\frac{a_1-a_0}{|a_1-a_0|}.$$

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 **x** when species **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 γ, when s corresponds to a ratio of λ, 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:

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

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

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

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 ϕ more precisely. Since P is a second-degree polynomial, let us write it down as $P(x) = A_2 x^2 + A_1 x + A_0$. Then

$$\phi(y) = \frac{A_2}{a_0 + \delta y} + A_1 + A_0(a_0 + \delta y).$$

The second derivative is

$$\phi''(y) = \frac{2A_2\delta^2}{(a_0 + \delta y)^3},$$

which has the sign of A_2 on $[0,1]$, so ϕ 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 ϕ is negative on $]0,1[$. If I is not empty, so is $\tilde{I}$, and ϕ is positive on $\tilde{I}$ (and nonpositive outside $\tilde{I}$), therefore ϕ 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 1.9 are deduced from this lemma in Section 4.3.

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

4.1 Monotonicity in v

We wish to compare $\mathbb{E}\left[\phi(U_{u,v})\right]$ 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 ψ such that the expectations exist, X is said to be smaller than Y in the convex order*. We denote by $X \leqslant_{\text{cvx}} Y$ 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 $X \leqslant_{\text{cvx}} Y$ if and only if $\mathbb{E}[X] = \mathbb{E}[Y]$ and, for all x,*

$$\int_{-\infty}^{x} F_X(t)dt \leqslant \int_{-\infty}^{x} F_Y(t)dt < \infty, \tag{8}$$

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 $X \leqslant_{\text{cvx}} Y$ then* $\text{Var}(X) \leqslant \text{Var}(Y)$*. 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 (8) *holds (without assuming $\mathbb{E}[X] = \mathbb{E}[Y]$), X is said to* second-order stochastically dominate *Y; this is equivalent to asking the inequality $\mathbb{E}[\psi(X)] \leqslant \mathbb{E}[\psi(Y)]$ for any* non-increasing *convex function ψ. 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 $X \leqslant_{\text{cvx}} Y$ and $\mathbb{E}[\psi(X)] = \mathbb{E}[\psi(Y)]$ for some strongly convex ψ, 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 ψ is strongly convex, there exists an $m > 0$ such that for all $t \in [0, 1]$,

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

Taking expectations we get

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

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 $X' \leqslant_{\text{cvx}} X$.

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 $X' \leqslant_{\text{cvx}} X$. □

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 $U_{u,v'} \leqslant_{\text{cvx}} U_{u,v}$. Since $\psi = (-\phi)$ is strongly convex, this implies

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

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

4.2 Concavity in u

Even though ϕ 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 ϕ we write:

$$\begin{aligned}\mathbb{E}[\phi(U_{u,v})] &= A\mathbb{E}\left[\frac{1}{a_0+\delta U_{u,v}}\right] + B + C\mathbb{E}[a_0+\delta U_{u,v}] \\ &= A\mathbb{E}\left[\frac{1}{a_0+\delta U_{u,v}}\right] + B + C(a_0+\delta u).\end{aligned}$$

Since A is negative (see the proof of Lemma 1.8) 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 ($U_{u,v}$ 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

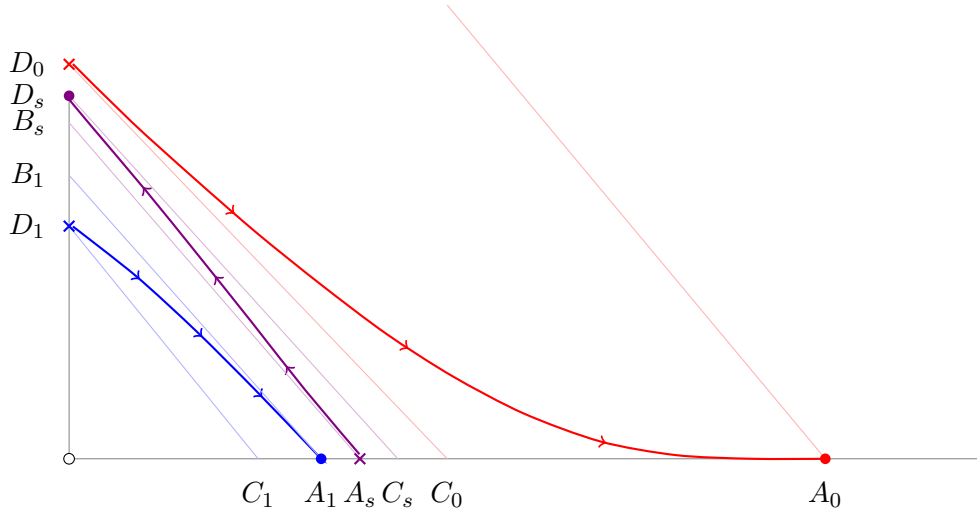
We have just shown that $v \mapsto \tilde{\Lambda}_{\mathbf{y}}(u,v)$ is increasing. From [2, Proposition 2.2] and the fact that in the change of variables $(s,t) \leftrightarrow (u,v)$, u only depends on s, and for fixed u, v is an increasing function of t, we know additionally that it admits:

- negative limits at 0 and ∞ if u does not belong to the closure of $\tilde{I}$,
- a negative limit at 0 and a positive limit at ∞ if $u \in \tilde{I}$.

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

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

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, $\tilde{\Lambda}_{\mathbf{y}}(a,M)$ and $\tilde{\Lambda}_{\mathbf{y}}(c,M)$ are positive. Since $u \mapsto \mathbb{E}\phi(U_{u,v})$ is concave, $\tilde{\Lambda}_{\mathbf{y}}(b,M)$ is positive. Therefore $v_c(c) \leqslant M$. Sending M to $\max(v_c(a), v_c(b))$ yields the quasi-convexity of v_c.



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.

Figure 3: Full support case: isoclines and unstable manifolds

Let us now show the regularity properties. Let u_n be an increasing sequence in $\tilde{I}$, 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 u must be in $\tilde{I}$. Conversely, if $u \in \tilde{I}$, v_c is bounded on a neighborhood of u by quasi-convexity, so v is finite. This shows that v_c is continuous on $\tilde{I}$ and converges to ∞ 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 the stochastic Lotka-Volterra process has at least 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 Γ has non empty interior. Several properties of Γ are established in [2] (see below). In this section, we aim at providing a full description of Γ. Its shape essentially depends on the fact that $I \cap J$ is empty or not.

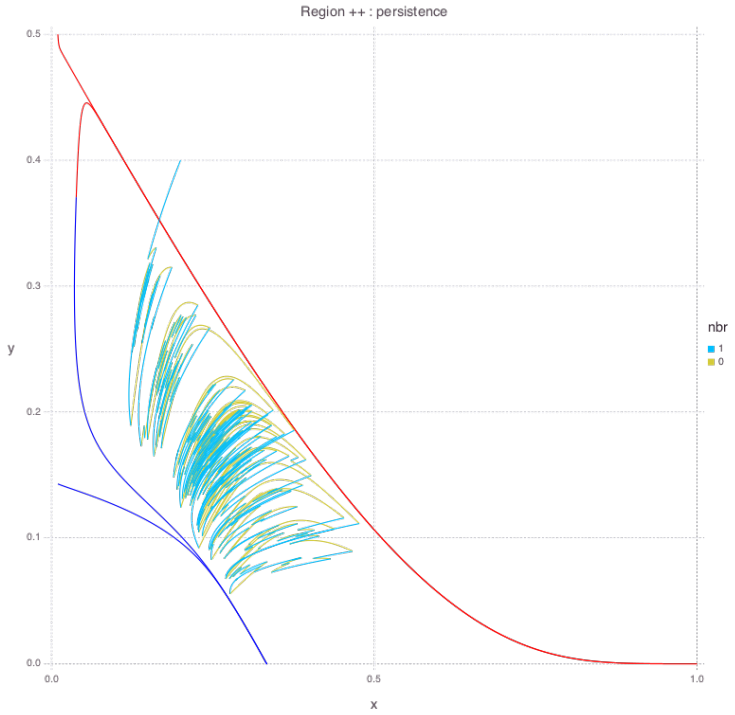
5.1 Persistence with "full support"

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 (7) holds. Let us denote by Σ_i the intersection of $[0,\infty)^2$ and the unstable manifold of $(0, 1/d_i)$ and Γ' the bounded subset of $[0,+\infty)^2$ with border

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

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 Γ' is positively invariant for each flow since both vector fields $F_{\mathcal{E}_0}$ and $F_{\mathcal{E}_1}$ point inside Γ'.



The outer curves are Σ_0 and Σ_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

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 Σ_s the intersection of the unstable manifold of $(1/a_s, 0)$ with the upper right quadrant.

First step: the set Σ_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 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 Σ_1 and Σ_s is in Γ. Starting from such a point (x, y), run the $\mathcal{E}_1$ flow in reverse time. The trajectory must cross Σ_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 Σ_0 and Σ_s is in Γ. This step is similar to the previous one and is omitted.

Similarly, any point between Σ_1 and Σ_s is in Γ. □

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:

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

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

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

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 Γ, 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 $\tilde{C}$, such that the trajectories starting from this point form the boundary of Γ. See Figure 4.

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

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

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

$$\big\{ \varphi^0_z(t) \,:\, t \in [0, \infty) \big\} \cup \big\{ \varphi^1_z(t) \,:\, t \in [0, \infty) \big\} \cup [1/a_1, 1/a_0] \times \{0\},$$

where $t \mapsto \varphi^i_z(t)$ is the flow associated to the vector field F_i for $i = 0, 1$.

Conjecture 5.2. *The set T is a singleton $\{z_0\}$ and the support of the invariant measure which is not supported by one of the two axes is $C(z_0) \times \{0, 1\}$.*

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Florent Malrieu, e-mail: `florent.malrieu(AT)univ-tours.fr`

Laboratoire de Mathématiques et Physique Théorique (UMR CNRS 7350), Fédération Denis Poisson (FR CNRS 2964), Université François-Rabelais, Parc de Grandmont, 37200 Tours, France.

Pierre-André Zitt, e-mail: `pierre-andre.zitt(AT)u-pem.fr`

Laboratoire d'Analyse et Mathématiques Appliquées (UMR CNRS 8050), Université-Paris-Est-Marne-La-Vallée, 5, boulevard Descartes, Cité Descartes, Champs-sur-Marne, 77454 Marne-la-Vallée Cedex 2, France.