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LOTKA–VOLTERRA WITH RANDOMLY FLUCTUATING ENVIRONMENTS OR "HOW SWITCHING BETWEEN BENEFICIAL ENVIRONMENTS CAN MAKE SURVIVAL HARDER"[1]

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We consider two-dimensional Lotka–Volterra systems in a fluctuating environment. Relying on recent results on stochastic persistence and piecewise deterministic Markov processes, we show that random switching between two environments that are both favorable to the same species can lead to the extinction of this species or coexistence of the two competing species.

1. Introduction. In ecology, the principle of *competitive exclusion* formulated by Gause [17] in 1932 and later popularized by Hardin [19], asserts that when two species compete with each other for the same resource, the "better" competitor will eventually exclude the other. While there are numerous evidences (based on laboratory experiences and natural observations) supporting this principle, the observed diversity of certain communities is in apparent contradiction with Gause's law. A striking example is given by the phytoplankton which demonstrate that a number of competing species can coexist despite very limited resources. As a solution to this paradox, Hutchinson [24] suggested that sufficiently frequent variations of the environment can keep species abundances away from the equilibria predicted by competitive exclusion. Since then, the idea that temporal fluctuations of the environment can reverse the trend of competitive exclusion has been widely explored in the ecology literature (see, e.g., [1, 12] and [10] for an overview and much further references).

Our goal here is to investigate rigorously this phenomenon for a two-species Lotka–Volterra model of competition under the assumption that the environment (defined by the parameters of the model) fluctuates randomly between two environments that are *both* favorable to the same species. We will precisely describe—in terms of the parameters—the range of possible behaviors and explain why counterintuitive behaviors—including coexistence of the two species, or extinction of the species favored by the environments—can occur.

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Throughout, we let $\mathbb{R}$ (resp., $\mathbb{R}_+, \mathbb{R}_+^*$) denote the set of real (resp., nonnegative, positive) numbers.

An *environment* is a pair $\mathcal{E} = (A, B)$ defined by two matrices:

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}, \qquad B = \begin{pmatrix} \alpha \\ \beta \end{pmatrix}, \tag{1}$$

where $a, b, c, d, \alpha, \beta$ are positive numbers.

The *two-species competitive Lotka–Volterra vector field* associated to $\mathcal{E}$ is the map $F_{\mathcal{E}} : \mathbb{R}^2 \mapsto \mathbb{R}^2$ defined by

$$F_{\mathcal{E}}(x, y) = \begin{cases} \alpha x(1 - ax - by), \\ \beta y(1 - cx - dy). \end{cases} \tag{2}$$

Vector field $F_{\mathcal{E}}$ induces a dynamical system on $\mathbb{R}_+^2$ given by the autonomous differential equation

$$(\dot{x}, \dot{y}) = F_{\mathcal{E}}(x, y). \tag{3}$$

Here, x and y represent the abundances of two species (denoted the **x**-species and **y**-species for notational convenience) and (3) describes their interaction in environment $\mathcal{E}$.

Environment $\mathcal{E}$ is said to be *favorable* to species **x** if

$$a < c \quad \text{and} \quad b < d.$$

In other words, the *intraspecific competition* within species **x** (measured by the parameter a) is smaller than the *interspecific competition* effect of species **x** on species **y** (measured by c) and the interspecific competition effect of species **y** on species **x** is smaller that the intraspecific competition within species **y**.

From now on, we let $\mathsf{Env}_{\mathbf{x}}$ denote the set of environments favorable to species **x**. The following result easily follows from an isocline analysis (see, e.g., [23], Chapter 3.3). It can be viewed as a mathematical formulation of the competitive exclusion principle.

PROPOSITION 1.1. *Suppose*[2] $\mathcal{E} = (A, B) \in \mathsf{Env}_{\mathbf{x}}$. *Then, for every* $(x, y) \in \mathbb{R}_+^* \times \mathbb{R}_+$ *the solution to* (3) *with initial condition* (x, y) *converges to* $(\frac{1}{a}, 0)$ *as* $t \to \infty$.

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[2] The case $\mathcal{E} \in \mathsf{Env}_{\mathbf{y}}$ is similar with $(0, \frac{1}{d})$ in place of $(\frac{1}{a}, 0)$. If now $c - a$ and $d - b$ have opposite signs, then there is a unique equilibrium $S \in \mathbb{R}_+^* \times \mathbb{R}_+^*$. If $c - a < 0$, S is a sink whose basin of attraction is $\mathbb{R}_+^* \times \mathbb{R}_+^*$. If $c - a > 0$, S is a saddle whose stable manifold $W^s(S)$ is the graph of a smooth bijective increasing function $\mathbb{R}_+^* \to \mathbb{R}_+^*$. Orbits below $W^s(S)$ converge to $(\frac{1}{a}, 0)$ and orbit above converge to $(0, \frac{1}{d})$.

If one now wants to take into account temporal variations of the environment, the autonomous system (3) should be replaced by the nonautonomous one

$$(4)\qquad (\dot{x}, \dot{y}) = F_{\mathcal{E}(t)}(x, y),$$

where, for each $t \geq 0$, $\mathcal{E}(t)$ is the environment at time t. The investigation of such dynamics began in the mid 1970s with the analysis of systems living in a periodic environment (typically justified by the seasonal or daily fluctuation of certain abiotic factors such as temperature or sunlight). In 1974, Koch [25], formalizing Hutchinson's ideas, described a plausible mechanism—sustained by numerical simulations—explaining how two species which could not coexist in a constant environment can coexist when subjected to an additional periodic kill rate (like seasonal harvesting or seasonal reduction of the population). More precisely, this means that $F_{\mathcal{E}(t)}(x, y)$ is of the form

$$F_{\mathcal{E}(t)}(x, y) = F_{\mathcal{E}}(x, y) - \bigl(p(t)x, q(t)y\bigr),$$

where $\mathcal{E} \in \mathsf{Env}_{\mathbf{x}}$ and $p(t), q(t)$ are periodic positive rates. In 1980, Cushing [13] proves rigorously that, under suitable conditions on $\mathcal{E}$, p and q, such a system may have a locally attracting periodic orbit contained in the positive quadrant $\mathbb{R}_+^* \times \mathbb{R}_+^*$.

At the same time and independently, de Mottoni and Schiaffino [14] prove the remarkable result that, when $t \to \mathcal{E}(t)$ is T-periodic, every solution to (4) is asymptotic to a T-periodic orbit and construct an explicit example having a locally attracting positive periodic orbit, while the averaged system [the autonomous system (3) obtained from (4) by temporal averaging] is favorable to the **x**-species. Papers [13] and [14] are complementary. The first one relies on bifurcations theory. The second makes a crucial use of the monotonicity properties of the Poincaré map $((x, y) \mapsto (x(T), y(T)))$ and has inspired a large amount of work on competitive dynamics (see, e.g., the discussion and the references following Corollary 5.30 in [20]).

Completely different is the approach proposed by Lobry, Sciandra and Nival in [27]. Based on classical ideas in system theory, this paper considers the question from the point of view of what is now called a *switched system* and focuses on the situation where $t \to \mathcal{E}(t)$ is piecewise constant and assumes two possible values $\mathcal{E}_0, \mathcal{E}_1 \in \mathsf{Env}_{\mathbf{x}}$. For instance, Figure 1 pictures two phase portraits (resp., colored in red and blue) associated to the environments

$$(5)\qquad \mathcal{E}_0 = \left(\begin{pmatrix} 1 & 1 \\ 2 & 2 \end{pmatrix}, \begin{pmatrix} 10 \\ 1 \end{pmatrix}\right) \quad \text{and} \quad \mathcal{E}_1 = \left(\begin{pmatrix} 0.5 & 0.5 \\ 0.65 & 0.65 \end{pmatrix}, \begin{pmatrix} 1 \\ 10 \end{pmatrix}\right)$$

both favorable to species **x**. In accordance with Proposition 1.1, we see that all the red (resp., blue) trajectories converge to the x-axis while a switched trajectory like the one shown on the picture moves away from the x-axis toward the upper left direction. This was exploited in [27] to shed light on some paradoxical effect that had not been previously discussed in the literature: Even when $\mathcal{E}(t) \in \mathsf{Env}_{\mathbf{x}}$

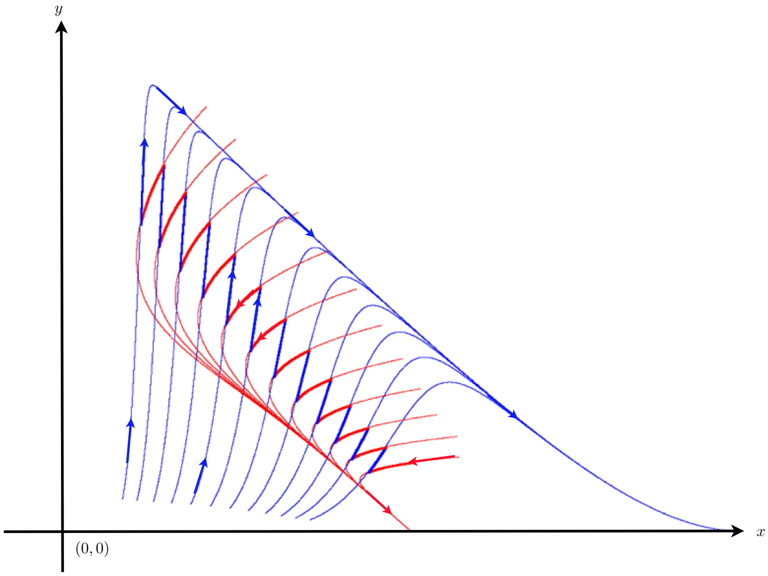

FIG. 1. *An example of a switched trajectory between* $F_{\mathcal{E}_0}$ (*red curves*) *and* $F_{\mathcal{E}_1}$ (*blue curves*) *with* $\mathcal{E}_0, \mathcal{E}_1$ *given by* (5).

for all $t \geq 0$ (which is different from the assumption that the average vector field is induced by some $\mathcal{E} \in \mathsf{Env}_{\mathbf{x}}$) not only coexistence of species but also extinction of species **x** can occur.

In the present paper, we will pursue this line of research and investigate thoroughly the behavior of the system obtained when the environment is no longer periodic but switches randomly between $\mathcal{E}_0$ and $\mathcal{E}_1$ at jump times of a continuous time Markov chain. Our motivation is twofold: First, realistic models of environment variability should undoubtedly incorporate stochastic fluctuations. Furthermore, the mathematical techniques involved for analyzing such a process are totally different from the deterministic ones mentioned above and will allow to fully characterize the long term behavior of the process in terms of quantities which can be explicitly computed.

1.1. *Model, notation and presentation of main results.*

From now on, we assume given two environments $\mathcal{E}_0, \mathcal{E}_1 \in \mathsf{Env}_{\mathbf{x}}$. For $i = 0, 1$, environment $\mathcal{E}_i$ is defined by (1) with $(a_i, b_i, \dots)$ instead of $(a, b, \dots)$. We consider the process $\{(X_t, Y_t)\}$ defined by the differential equation

$$(\dot{X}, \dot{Y}) = F_{\mathcal{E}_{I_t}}(X, Y), \tag{6}$$

where $I_t \in \{0, 1\}$ is a continuous time jump process with jump rates $\lambda_0, \lambda_1 > 0$. That is,

$$\mathbb{P}(I_{t+s} = 1 - i | I_t = i, \mathcal{F}_t) = \lambda_i s + o(s),$$

where $\mathcal{F}_t$ is the sigma field generated by $\{I_u, u \leq t\}$.

In other words, assuming that $I_0 = i$ and $(X_0, Y_0) = (x, y)$, the process $\{(X_t, Y_t)\}$ follows the solution trajectory to $F_{\mathcal{E}_i}$ with initial condition (x, y) for an exponentially distributed random time, with intensity λ_i. Then $\{(X_t, Y_t)\}$ follows the solution trajectory to $F_{\mathcal{E}_{1-i}}$ for another exponentially distributed random time, with intensity λ_{1-i} and so on.

For $\eta > 0$ small enough, the set

$$K_\eta = \{(x, y) \in \mathbb{R}_+^2 : \eta \leq x + y \leq 1/\eta\}$$

is positively invariant under the dynamics induced by $F_{\mathcal{E}_0}$ and $F_{\mathcal{E}_1}$. It then attracts every solution to (6) with initial condition $(x, y) \in \mathbb{R}_+^2 \setminus \{0, 0\}$. Fix such $\eta > 0$ and let

$$M = K_\eta \times \{0, 1\}.$$

Set $Z_t = (X_t, Y_t, I_t)$. Since Z_t eventually lies in M [whenever $(X_0, Y_0) \neq (0, 0)$], we may assume without loss of generality that $Z_0 \in M$ and we let M be the *state space* of the process $\{Z_t\}_{t\geq 0}$.

The *extinction set of species* $\mathbf{y}$ is the set

$$M_0^{\mathbf{y}} = \{(x, y, i) \in M : y = 0\}.$$

Extinction set of species $\mathbf{x}$, denoted $M_0^{\mathbf{x}}$, is defined similarly (with $x = 0$ instead of $y = 0$) and the *extinction set* is defined as

$$M_0 = M_0^{\mathbf{x}} \cup M_0^{\mathbf{y}}.$$

The process $\{Z_t\}$ defines a homogeneous Markov process on M leaving invariant the extinction sets $M_0^{\mathbf{x}}$, $M_0^{\mathbf{y}}$ and the *interior set* $M \setminus M_0$.

It is easily seen that $\{Z_t\}$ restricted to one of the sets $M_0^{\mathbf{y}}$ or $M_0^{\mathbf{x}}$ is positively recurrent. In order to describe its behavior on $M \setminus M_0$, we introduce the *invasion rates* of species $\mathbf{y}$ and $\mathbf{x}$ as

$$\Lambda_{\mathbf{y}} = \int \beta_0(1 - c_0 x)\mu(dx, 0) + \int \beta_1(1 - c_1 x)\mu(dx, 1), \tag{7}$$

and

$$\Lambda_{\mathbf{x}} = \int \alpha_0(1 - b_0 y)\hat{\mu}(dy, 0) + \int \alpha_1(1 - b_1 y)\hat{\mu}(dy, 1), \tag{8}$$

where μ (resp., $\hat{\mu}$) denotes the invariant probability measure[3] of $\{Z_t\}$ on $M_0^{\mathbf{y}}$ (resp., $M_0^{\mathbf{x}}$).

Note that the quantity $\beta_i(1 - c_i x)$ is the (per-capita) growth rate of species $\mathbf{y}$ in environment $\mathcal{E}_i$ in the limit $y \to 0$. Hence, $\Lambda_{\mathbf{y}}$ measures the long term effect of

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[3] Here, $M_0^{\mathbf{y}}$ and $M_0^{\mathbf{x}}$ are identified with $[\eta, 1/\eta] \times \{0, 1\}$ so that μ and $\hat{\mu}$ are measures on $\mathbb{R}_+^* \times \{0, 1\}$.

species $\mathbf{x}$ on the growth rate of species $\mathbf{y}$ when this later has low density. When $\Lambda_{\mathbf{y}}$ is positive (resp., negative) species $\mathbf{y}$ tends to increase (resp., decrease) from low density. Coexistence criteria based on the positivity of average growth rates go back to Turelli [33] and have been used for a variety of deterministic [16, 21, 29] and stochastic [5, 10, 11, 15] models. However, these criteria are seldom expressible in terms of the parameters of the model (average growth rates are hard to compute) and typically provide only local information on the behavior of the process near the boundary. Here surprisingly, $\Lambda_{\mathbf{x}}$ and $\Lambda_{\mathbf{y}}$ can be computed and their signs fully characterize the behavior of the process.

Our main results can be briefly summarized as follows:

(i) The invariant measures μ, $\hat{\mu}$ and the invasion rates $\Lambda_{\mathbf{y}}$ and $\Lambda_{\mathbf{x}}$ can be explicitly computed in terms of the parameters $\mathcal{E}_i, \lambda_i, i = 0, 1$ (see Section 2).

(ii) For all $u, v \in \{+, -\}$ there are environments $\mathcal{E}_0, \mathcal{E}_1 \in \mathsf{Env}_{\mathbf{x}}$ and rates λ_0, λ_1 such that $\mathrm{Sign}(\Lambda_{\mathbf{x}}) = u$ and $\mathrm{Sign}(\Lambda_{\mathbf{y}}) = v$. Thus, in view of assertion (iii) below, *the assumption that both environments are favorable to species* $\mathbf{x}$ *is not sufficient to determine the outcome of the competition.*

(iii) Let $(u, v) = (\mathrm{Sign}(\Lambda_{\mathbf{x}}), \mathrm{Sign}(\Lambda_{\mathbf{y}}))$. Assume $X_0 > 0$ and $Y_0 > 0$. Then (u, v) determines the long term behavior of $\{Z_t\}$ as follows:

  (a) $(u, v) = (+, -) \Rightarrow$ extinction of species $\mathbf{y}$:

  With probability one $Y_t \to 0$ and the empirical occupation measure of $\{Z_t\}$ converges to μ (see Theorem 3.1).

  (b) $(u, v) = (-, +) \Rightarrow$ extinction of species $\mathbf{x}$:

  With probability one $X_t \to 0$ and the empirical occupation measure of $\{Z_t\}$ converges to $\hat{\mu}$ (see Theorem 3.3).

  (c) $(u, v) = (-, -) \Rightarrow$ extinction of one species:

  With probability one either $X_t \to 0$ or $Y_t \to 0$. The event $\{Y_t \to 0\}$ has positive probability. Furthermore, if the initial condition X_0 is sufficiently small or $(-, +)$ is feasible[4] for $\mathcal{E}_0, \mathcal{E}_1$, then the event $\{X_t \to 0\}$ has positive probability (see Theorem 3.4).

  (d) $(u, v) = (+, +) \Rightarrow$ persistence:

  There exists a unique invariant (for $\{Z_t\}$) probability measure Π on $M \setminus M_0$ which is absolutely continuous with respect to the Lebesgue measure $dx\,dy \otimes (\delta_0 + \delta_1)$; and the empirical occupation measure of $\{Z_t\}$ converges almost surely to Π. Furthermore, for generic parameters, the law of the process converge exponentially fast to Π in total variation. (see Theorem 4.1).

  The density of Π cannot be explicitly computed, still its tail behavior [Theorem 4.1(ii)] and the topological properties of its support are well understood (see Theorem 4.5).

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[4] By this, we mean that there are jump rates λ'_0, λ'_1 such that the associated invasion rates verify $\mathrm{Sign}(\Lambda'_{\mathbf{x}}) = -$ and $\mathrm{Sign}(\Lambda'_{\mathbf{y}}) = +$.

The proofs rely on recent results on stochastic persistence given in [4] built upon previous results obtained for deterministic systems in [16, 21, 22, 29] (see also [32] for a comprehensive introduction to the deterministic theory), stochastic differential equations with a small diffusion term in [5], stochastic differential equations and random difference equations in [30, 31]. We also make a crucial use of some recent results on piecewise deterministic Markov processes obtained in [2, 3] and [7].

The paper is organized as follows. In Section 2, we compute $\Lambda_{\mathbf{x}}$ and $\Lambda_{\mathbf{y}}$ and derive some of their main properties. Section 3 is devoted to the situation where one invasion rate is negative and contains the results corresponding to the cases (iii), (a), (b), (c) above. Section 4 is devoted to the situation where both invasion rates are positive and contains the results corresponding to (iii), (d). Section 5 presents some illustrations obtained by numerical simulation and Section 6 contains the proofs of some propositions stated in Section 2.

2. Invasion rates.

As previously explained, the signs of the invasion rates are crucial to characterize the long term behavior of $\{Z_t\}$. In this section we compute these rates and investigate some useful properties of the maps

$$(\lambda_0, \lambda_1) \mapsto \Lambda_x(\lambda_0, \lambda_1), \Lambda_y(\lambda_0, \lambda_1)$$

and their zero sets.

Set $p_i = \frac{1}{a_i}$ and $\gamma_i = \frac{\lambda_i}{\alpha_i}$. Here, for notational convenience, $[p_0, p_1]$ (resp., $]p_0, p_1[$) stands for the closed (resp., open) interval with boundary points p_0, p_1 even when $p_1 < p_0$, and $M_0^{\mathbf{y}}$ is seen as a subset of $\mathbb{R}_+^* \times \{0, 1\}$.

The following proposition characterizes the behavior of the process on the extinction set $M_0^{\mathbf{y}}$. The proof (given in Section 6) heavily relies on the fact that the process restricted to $M_0^{\mathbf{y}}$, reduces to a one-dimensional ODE with two possible regimes for which explicit computations are possible. It is similar to some results previously obtained in [8] for linear systems.

PROPOSITION 2.1. *The process $\{Z_t = (X_t, Y_t, I_t)\}$ restricted to $M_0^{\mathbf{y}}$ has a unique invariant probability measure μ satisfying*:

(i) *If $p_0 = p_1 = p$*

$$\mu = \delta_p \otimes \nu,$$

where $\nu = \frac{\lambda_0}{\lambda_1+\lambda_0}\delta_1 + \frac{\lambda_1}{\lambda_1+\lambda_0}\delta_0$.

(ii) *If $p_0 \neq p_1$*

$$\mu(dx, 1) = h_1(x)\mathbf{1}_{[p_0,p_1]}(x)\,dx,$$

$$\mu(dx, 0) = h_0(x)\mathbf{1}_{[p_0,p_1]}(x)\,dx,$$

where

$$h_1(x) = C \frac{p_1 |x - p_1|^{\gamma_1 - 1} |p_0 - x|^{\gamma_0}}{\alpha_1 x^{1+\gamma_0+\gamma_1}},$$

$$h_0(x) = C \frac{p_0 |x - p_1|^{\gamma_1} |p_0 - x|^{\gamma_0 - 1}}{\alpha_0 x^{1+\gamma_0+\gamma_1}}$$

and C (*depending on* $p_1, p_0, \gamma_1, \gamma_0$) *is defined by the normalization condition*

$$\int_{]p_0, p_1[} \bigl(h_1(x) + h_0(x)\bigr)\, dx = 1.$$

For all $x \in]p_0, p_1[$ define

$$\theta(x) = \frac{|x - p_0|^{\gamma_0 - 1} |p_1 - x|^{\gamma_1 - 1}}{x^{1+\gamma_0+\gamma_1}} \tag{9}$$

and

$$P(x) = \left[\frac{\beta_1}{\alpha_1}(1 - c_1 x)(1 - a_0 x) - \frac{\beta_0}{\alpha_0}(1 - c_0 x)(1 - a_1 x)\right] \frac{a_1 - a_0}{|a_1 - a_0|}. \tag{10}$$

Recall that the *invasion rate* of species $\mathbf{y}$ is defined [see equation (7)] as the growth rate of species $\mathbf{y}$ averaged over μ. It then follows from Proposition 2.1 the following.

COROLLARY 2.2.

$$\Lambda_{\mathbf{y}} = \begin{cases} \dfrac{1}{\lambda_0 + \lambda_1}\bigl(\lambda_1 \beta_0 (1 - c_0 p) + \lambda_0 \beta_1 (1 - c_1 p)\bigr), & \textit{if } p_0 = p_1 = p, \\ p_0 p_1 C \displaystyle\int_{]p_0, p_1[} P(x)\theta(x)\, dx, & \textit{if } p_0 \neq p_1. \end{cases} \tag{11}$$

The expression for $\Lambda_{\mathbf{x}}$ *is similar. It suffices in equation* (11) *to permute* α_i *and* β_i, *and to replace* (a_i, c_i) *by* (d_i, b_i).

2.1. *Jointly favorable environments.* For all $0 \leq s \leq 1$, we let $\mathcal{E}_s = (A_s, B_s)$ be the environment defined by

$$s F_{\mathcal{E}_1} + (1 - s) F_{\mathcal{E}_0} = F_{\mathcal{E}_s}. \tag{12}$$

Then, with the notation of Section 1.1,

$$B_s = \begin{pmatrix} \alpha_s \\ \beta_s \end{pmatrix} = \begin{pmatrix} s\alpha_1 + (1 - s)\alpha_0 \\ s\beta_1 + (1 - s)\beta_0 \end{pmatrix}$$

and

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

Environment $\mathcal{E}_s$ can be understood as the environment whose dynamics (i.e., the dynamics induced by $F_{\mathcal{E}_s}$) is the same as the one that would result from high frequency switching giving weight s to $\mathcal{E}_1$ and weight $(1-s)$ to $\mathcal{E}_0$.[5]

Set

$$I = \{0 < s < 1 : a_s > c_s\} \tag{13}$$

and

$$J = \{0 < s < 1 : b_s > d_s\}. \tag{14}$$

It is easily checked that I (resp., J) is either empty or is an open interval which closure is contained in $]0, 1[$.

To get a better understanding of what I and J represent, observe that:

- If $s \in I^c \cap J^c$, then $\mathcal{E}_s$ is favorable to species x.
- If $s \in I \cap J$, then $\mathcal{E}_s$ is favorable to species y.
- If $s \in I \cap J^c$, then $F_{\mathcal{E}_s}$ has a positive sink whose basin of attraction contains the positive quadrant (stable coexistence regime).
- If $s \in I^c \cap J$, then $F_{\mathcal{E}_s}$ has a positive saddle whose stable manifold separates the basins of attractions of $(1/a_s, 0)$ and $(0, 1/d_s)$ (bi-stable regime).

We shall say that $\mathcal{E}_0$ and $\mathcal{E}_1$ are *jointly favorable* to species **x** if for all $s \in [0, 1]$ environment $\mathcal{E}_s$ is favorable to species x; or, equivalently, $I = J = \varnothing$. We let $\mathsf{Env}_{\mathbf{x}}^{\otimes 2} \subset \mathsf{Env}_{\mathbf{x}} \times \mathsf{Env}_{\mathbf{x}}$ denote the set of jointly favorable environments to species x.

REMARK 1. Set $R = \frac{\beta_0\alpha_1}{\alpha_0\beta_1}$ and $u = \frac{s\alpha_1}{\alpha_s}$. Then a direct computation shows that $\frac{s\beta_1}{\beta_s} = \frac{u}{u(1-R)+R}$. Thus,

$$\begin{aligned} c_s - a_s &= u\left(c_1 \frac{1}{u(1-R)+R} - a_1\right) + (1-u)\left(c_0 \frac{R}{u(1-R)+R} - a_0\right) \\ &= \frac{Au^2 + Bu + C}{u(1-R)+R} \end{aligned}$$

with

$$\begin{aligned} A &= (a_1 - a_0)(R-1), \\ B &= (2a_0 - c_0 - a_1)R + (c_1 - a_0), \end{aligned}$$

and

$$C = (c_0 - a_0)R.$$

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[5] More precisely, standard averaging or mean field approximation implies that the process $\{(X_u, Y_u)\}$ with initial condition (x, y) and switching rates $\lambda_0 = st, \lambda_1 = (1-s)t$ converges in distribution, as $t \to \infty$, to the deterministic solution of the ODE induced by $F_{\mathcal{E}_s}$ and initial condition (x, y).

Then

$$I \neq \varnothing \Leftrightarrow \begin{cases} A \neq 0, \\ \Delta = B^2 - 4AC > 0, \\ 0 < \dfrac{-B - \sqrt{\Delta}}{2A} < 1. \end{cases} \tag{15}$$

The condition for $J \neq \varnothing$ is obtained by replacing a_i by b_i and c_i by d_i in the definitions of A, B, C above, R being unchanged.

REMARK 2. The characterization given in Remark 1 shows that $\mathsf{Env}_{\mathbf{x}}^{\otimes 2}$ is a semi algebraic subset of $\mathsf{Env}_{\mathbf{x}} \times \mathsf{Env}_{\mathbf{x}}$.

The following proposition is proved in Section 6. It provides a simple expression for $\Lambda_{\mathbf{y}}$ in the limits of high and low frequency switching.

PROPOSITION 2.3. *The map*

$$\Lambda_{\mathbf{y}} : \mathbb{R}_+^* \times \mathbb{R}_+^* \mapsto \mathbb{R},$$

$$\lambda_0, \lambda_1 \mapsto \Lambda_{\mathbf{y}}(\lambda_0, \lambda_1)$$

[*as defined by formulae* (11)] *satisfies the following properties*:

(i) *If $I = \varnothing$, then for all λ_0, λ_1*

$$\Lambda_{\mathbf{y}}(\lambda_0, \lambda_1) < 0.$$

(ii) *For all $s \in]0, 1[$*

$$\lim_{t\to\infty} \Lambda_{\mathbf{y}}\big(ts, t(1-s)\big) = \beta_s\left(1 - \frac{c_s}{a_s}\right) \begin{cases} > 0, & \textit{if } s \in I, \\ = 0, & \textit{if } s \in \partial I, \\ < 0, & \textit{if } s \in]0, 1[\setminus \overline{I}, \end{cases}$$

$$\lim_{t\to 0} \Lambda_{\mathbf{y}}\big(ts, t(1-s)\big) = (1-s)\beta_0\left(1 - \frac{c_0}{a_0}\right) + s\beta_1\left(1 - \frac{c_1}{a_1}\right) < 0;$$

REMARK 3. Similarly:

(i) If $J = \varnothing$, then for all $\lambda_0, \lambda_1 \Lambda_{\mathbf{x}}(\lambda_0, \lambda_1) > 0$.

(ii) For all $s \in]0, 1[$

$$\lim_{t\to\infty} \Lambda_{\mathbf{x}}\big(ts, t(1-s)\big) = \alpha_s\left(1 - \frac{b_s}{d_s}\right) \begin{cases} < 0, & \text{if } s \in J, \\ = 0, & \text{if } s \in \partial J, \\ > 0, & \text{if } s \in]0, 1[\setminus \overline{J}, \end{cases}$$

$$\lim_{t\to 0} \Lambda_{\mathbf{x}}\big(ts, t(1-s)\big) = (1-s)\alpha_0\left(1 - \frac{b_0}{d_0}\right) + s\alpha_1\left(1 - \frac{b_1}{d_1}\right) > 0.$$

The next result follows directly from Proposition 2.3 and Remark 3.

COROLLARY 2.4. *For* $u, v \in \{+, -\}$, *let*

$$\mathcal{R}_{u,v} = \{\lambda_0 > 0, \lambda_1 > 0 : \mathrm{Sign}(\Lambda_{\mathbf{x}}(\lambda_0, \lambda_1)) = u, \mathrm{Sign}(\Lambda_{\mathbf{y}}(\lambda_0, \lambda_1)) = v\}.$$

Then:

(i) $\mathcal{R}_{+-} \neq \varnothing$,
(ii) $I \cap J^c \neq \varnothing \Rightarrow \mathcal{R}_{+,+} \neq \varnothing$,
(iii) $J \cap I^c \neq \varnothing \Rightarrow \mathcal{R}_{-,-} \neq \varnothing$,
(iv) $I \cap J \neq \varnothing \Rightarrow \mathcal{R}_{-,+} \neq \varnothing$.

By using Proposition 2.3 combined with a beautiful argument based on second-order stochastic dominance Malrieu and Zitt [28] recently proved the next result. It answers a question raised in the first version of the present paper.

PROPOSITION 2.5 (Malrieu and Zitt [28]). *If* $I =]s_0, s_1[\neq \varnothing$ *the set*

$$\{(s, t) \in]0, 1[\times \mathbb{R}_+^* : \Lambda_{\mathbf{y}}(ts, t(1-s)) = 0\}$$

is the graph of a continuous function

$$I \mapsto \mathbb{R}_+^*, \qquad s \mapsto t(s)$$

with $\lim_{s \to s_0} t(s) = \lim_{s \to s_1} t(s) = \infty$. *In particular, implication* (iv) *in Corollary* 2.4 *is an equivalence*.

Figure 2 below represents the zero set of $s, t \mapsto \Lambda_{\mathbf{y}}(ts, (1-t)s)$ for the environments given in Section 5 for $\rho = 3$.

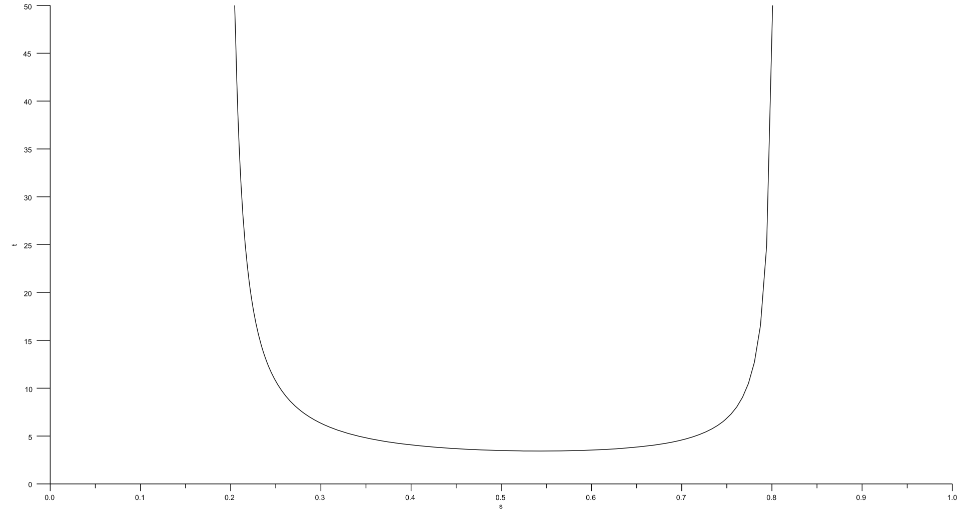

FIG. 2. *Zero set of* $\Lambda_{\mathbf{y}}(ts, (1-t)s)$ *for the environments given in Section* 5 *and* $\rho = 3$.

3. Extinction.

In this section, we focus on the situation where at least one invasion rate is negative and the other nonzero. If invasion rates have different signs, the species which rate is negative goes extinct and the other survives. If both are negative, one goes extinct and the other survives.

The *empirical occupation* measure of the process $\{Z_t\} = \{X_t, Y_t, I_t\}$ is the (random) measure given by

$$\Pi_t = \frac{1}{t}\int_0^t \delta_{Z_s}\, ds.$$

Hence, for every Borel set $A \subset M$, $\Pi_t(A)$ is the proportion of time spent by $\{Z_s\}$ in A up to time t.

Recall that a sequence of probability measures $\{\mu_n\}$ on a metric space E (such as M, M_0^i or $\mathbb{R}_+^2$) is said to *converge weakly* to μ (another probability measure on E) if $\int f\, d\mu_n \to \int f\, d\mu$ for every bounded continuous function $f : E \mapsto \mathbb{R}$.

Recall that $p_i = \frac{1}{a_i}$.

THEOREM 3.1 (Extinction of species $\mathbf{y}$). *Assume that* $\Lambda_{\mathbf{y}} < 0$, $\Lambda_{\mathbf{x}} > 0$ *and* $Z_0 = z \in M \setminus M_0$. *Then the following properties hold with probability one*:

(a) $\limsup_{t\to\infty} \frac{\log(Y_t)}{t} \le \Lambda_{\mathbf{y}}$.

(b) *The limit set of* $\{X_t, Y_t\}$ *equals* $[p_0, p_1] \times \{0\}$.

(c) $\{\Pi_t\}$ *converges weakly to* μ, *where* μ *is the probability measure on* $M_0^{\mathbf{y}}$ *defined in Proposition* 2.1.

REMARK 4. It follows from Theorem 3.1 that the marginal empirical occupation measure of $\{X_t, Y_t\}$ converges to the marginal

$$\mu(dx, 0) + \mu(dx, 1) = \begin{cases} \delta_p, & \text{if } p_0 = p_1 = p, \\ C\theta(x)\left[\dfrac{p_1}{\alpha_1}|x - p_0| + \dfrac{p_0}{\alpha_0}|p_1 - x|\right] dx, & \text{if } p_0 \neq p_1 \end{cases}$$

with θ given by (9) and C is a normalization constant.

COROLLARY 3.2. *Suppose that* $\mathcal{E}_0$ *and* $\mathcal{E}_1$ *are jointly favorable to species* $\mathbf{x}$. *Then conclusions of Theorem* 3.1 *hold for all positive jump rates* λ_0, λ_1.

PROOF. The proof follows from Theorem 3.1, Proposition 2.3(i) and Remark 3(i). ☐

If $\mathcal{E}_0$ and $\mathcal{E}_1$ are not jointly favorable to species $\mathbf{x}$, then (by Proposition 2.3 and Remark 3) there are jump rates such that $\Lambda_{\mathbf{x}} < 0$ or $\Lambda_{\mathbf{y}} > 0$. The following theorems tackle the situation where $\Lambda_{\mathbf{x}} < 0$. It show that, despite the fact that environments are favorable to the same species, this species can be the one who loses the competition.

THEOREM 3.3 (Extinction of species $\mathbf{x}$). *Assume that* $\Lambda_{\mathbf{x}} < 0$, $\Lambda_{\mathbf{y}} > 0$ *and* $Z_0 = z \in M \setminus M_0$. *Then the following properties hold with probability one*:

(a) $\limsup_{t\to\infty} \frac{\log(X_t)}{t} \leq \Lambda_{\mathbf{x}}$.

(b) *The limit set of* $\{X_t, Y_t\}$ *equals* $\{0\} \times [\hat{p}_0, \hat{p}_1]$.

(c) $\{\Pi_t\}$ *converges weakly to* $\hat{\mu}$, *where* $\hat{p}_i = \frac{1}{d_i}$ *and* $\hat{\mu}$ *is the probability measure on* $M_0^{\mathbf{x}}$ *defined analogously to* μ [*by permuting* α_i *and* β_i, *and replacing* (a_i, c_i) *by* (d_i, b_i)].

THEOREM 3.4 (Extinction of some species). *Assume that* $\Lambda_{\mathbf{x}} < 0$, $\Lambda_{\mathbf{y}} < 0$ *and* $Z_0 = z \in M \setminus M_0$. *Let* $\mathsf{Extinct}_{\mathbf{y}}$ (*resp*., $\mathsf{Extinct}_{\mathbf{x}}$) *be the event defined by assertions* (a), (b) *and* (c) *in Theorem* 3.1 (*resp*., *Theorem* 3.3). *Then*

$$\mathbb{P}(\mathsf{Extinct}_{\mathbf{y}}) + \mathbb{P}(\mathsf{Extinct}_{\mathbf{x}}) = 1 \quad \textit{and} \quad \mathbb{P}(\mathsf{Extinct}_{\mathbf{y}}) > 0.$$

If furthermore z *is sufficiently close to* $M_0^{\mathbf{x}}$ *or* $I \cap J \neq \varnothing$ *then*

$$\mathbb{P}(\mathsf{Extinct}_{\mathbf{x}}) > 0.$$

3.1. *Proofs of Theorems* 3.1, 3.3 *and* 3.4.

Proof of Theorem 3.1. The strategy of the proof is the following. Assumption $\Lambda_{\mathbf{x}} > 0$ is used to show that the process eventually enter a compact set disjoint from $M_0^{\mathbf{x}}$. Once in this compact set, it has a positive probability (independently on the starting point) to follow one of the dynamics $F_{\mathcal{E}_i}$ until it enters an arbitrary small neighborhood of $M_0^{\mathbf{y}}$. Assumption $\Lambda_{\mathbf{y}} < 0$ is then used to prove that, starting from this latter neighborhood, the process converges exponentially fast to $M_0^{\mathbf{y}}$ with positive probability. Finally, positive probability is transformed into probability one, by application of the Markov property.

Recall that $Z_t = (X_t, Y_t, I_t)$. For all $z \in M$ we let $\mathbb{P}_z$ denote the law of $\{Z_t\}_{t\geq 0}$ given that $Z_0 = z$ and we let $\mathbb{E}_z$ denote the corresponding expectation.

If E is one of the sets $M, M \setminus M_0, M \setminus M_0^{\mathbf{x}}$ or $M \setminus M_0^{\mathbf{y}}$, and $h : E \mapsto \mathbb{R}$ is a measurable function which is either bounded from below or above, we let, for all $t \geq 0$ and $z \in E$,

$$P_t h(z) = \mathbb{E}_z\big(h(Z_t)\big). \tag{16}$$

For $1 > \varepsilon > 0$ sufficiently small, we let

$$M_{0,\varepsilon}^{\mathbf{x}} = \big\{z = (x, y, i) \in M : x < \varepsilon\big\}$$

and

$$M_{0,\varepsilon}^{\mathbf{y}} = \big\{z = (x, y, i) \in M : y < \varepsilon\big\}$$

denote the ε neighborhoods of the extinction sets.

Let $V^{\mathbf{x}} : M \setminus M_0^{\mathbf{x}} \mapsto \mathbb{R}$ and $V^{\mathbf{y}} : M \setminus M_0^{\mathbf{y}} \mapsto \mathbb{R}$ be the maps defined by

$$V^{\mathbf{x}}\big((x, y, i)\big) = -\log(x) \quad \text{and} \quad V^{\mathbf{y}}\big((x, y, i)\big) = \log(y).$$

The assumptions $\Lambda_{\mathbf{x}} > 0$, $\Lambda_{\mathbf{y}} < 0$ and compactness of M_0 imply the following lemma.

LEMMA 3.5. *Let* $\Lambda_{\mathbf{x}} > \alpha_{\mathbf{x}} > 0$ *and* $-\Lambda_{\mathbf{y}} > \alpha_{\mathbf{y}} > 0$. *Then there exist* $T > 0, \theta > 0, \varepsilon > 0$ *and* $0 \le \rho < 1$ *such that for all* $z \in M_{0,\varepsilon}^{\mathbf{h}} \setminus M_0^{\mathbf{h}}, \mathbf{h} \in \{\mathbf{x}, \mathbf{y}\}$:

(i) $\frac{P_T V^{\mathbf{h}}(z) - V^{\mathbf{h}}(z)}{T} \le -\alpha_h$,

(ii) $P_T(e^{\theta V^{\mathbf{h}}})(z) \le \rho e^{\theta V^{\mathbf{h}}}(z)$.

PROOF. The proof can be deduced from Propositions 6.1 and 6.2 proved in a more general context in [4]; but for convenience and completeness we provide a simple direct proof. We suppose $\mathbf{h} = \mathbf{y}$. The proof for $\mathbf{h} = \mathbf{x}$ is identical.

(i) For all $Z_0 = z \notin M_0^{\mathbf{y}}$

$$V^{\mathbf{y}}(Z_t) - V^{\mathbf{y}}(z) = \int_0^t H(Z_s)\, ds, \tag{17}$$

where

$$H(x, y, i) = \beta_i(1 - c_i x - d_i y).$$

Thus, by taking the expectation,

$$\frac{P_T V^{\mathbf{y}}(z) - V^{\mathbf{y}}(z)}{T} = \frac{1}{T} \int_0^T P_s H(z)\, ds = \int H\, d\mu_T^z,$$

where

$$\mu_T^z(\cdot) = \frac{1}{T} \int_0^T P_s(z, \cdot).$$

We claim that for some $T > 0$ and $\varepsilon > 0$ $\int H\, d\mu_T^z < -\alpha_{\mathbf{y}}$ whenever $z \in M_{0,\varepsilon}^{\mathbf{y}}$. By continuity (in z), it suffices to show that such a bound holds true for all $z \in M_0^{\mathbf{y}}$. By Feller continuity, compactness and uniqueness of the invariant probability measure μ on $M_0^{\mathbf{y}}$, every limit point of $\{\mu_T^z : T > 0, z \in M_0^{\mathbf{y}}\}$ equals μ. Thus, $\lim_{T \to \infty} \int H \mu_T^z = \int H\, d\mu = \Lambda_y < -\alpha_y$ uniformly in $z \in M_0^{\mathbf{y}}$. This proves the claim and (i).

(ii) Composing equality (17) with the map $v \mapsto e^{\theta v}$ and taking the expectation leads to

$$P_T\big(e^{\theta V^{\mathbf{y}}}\big)(z) = e^{\theta V^{\mathbf{y}}(z)} e^{l(\theta, z)},$$

where

$$l(\theta, z) = \log\big(\mathbb{E}_z\big(e^{\theta \int_0^T H(Z_s)\, ds}\big)\big).$$

By standard properties of the log-laplace transform, the map $\theta \mapsto l(\theta, z)$ is smooth, convex and verifies

$$l(0,z) = 0,$$
$$\frac{\partial l}{\partial \theta}(0,z) = \mathbb{E}_z\left(\int_0^T H(Z_s)\,ds\right) = P_T V^{\mathbf{y}}(z) - V^{\mathbf{y}}(z)$$

and

$$0 \le \frac{\partial^2 l}{\partial \theta^2}(\theta, z) \le \left(T\|H\|_\infty\right)^2,$$

where $\|H\|_\infty = \sup_{z\in M}|H(z)|$. Thus, for all $z \in M_{0,\varepsilon}^{\mathbf{y}} \setminus M_0^{\mathbf{y}}$

$$l(\theta, z) \le T\theta\left(-\alpha_{\mathbf{y}} + \|H\|_\infty^2 T\theta/2\right).$$

This proves (ii), say for $\theta = \frac{\alpha_{\mathbf{y}}}{\|H\|_\infty^2 T}$ and $\rho = e^{-\frac{\alpha_{\mathbf{y}}^2}{2\|H\|_\infty^2}}$. $\square$

Define, for $\mathbf{h} = \mathbf{x}, \mathbf{y}$, the stopping times

$$\tau_\varepsilon^{\mathbf{h},\mathrm{Out}} = \min\{k \in \mathbb{N} : Z_{kT} \in M \setminus M_{0,\varepsilon}^{\mathbf{h}}\}$$

and

$$\tau_\varepsilon^{\mathbf{h},\mathrm{In}} = \min\{k \in \mathbb{N} : Z_{kT} \in M_{0,\varepsilon}^{\mathbf{h}}\}.$$

Step 1. We first prove that there exists some constant $c > 0$ such that for all $z \in M \setminus M_0^{\mathbf{x}}$

$$\mathbb{P}_z\left(\tau_{\varepsilon/2}^{\mathbf{y},\mathrm{In}} < \infty\right) \ge c. \tag{18}$$

Set $V_k = V^{\mathbf{x}}(Z_{kT}) + k\alpha_{\mathbf{x}}T$, $k \in \mathbb{N}$. It follows from Lemma 3.5(i) that $\{V_{k\wedge\tau_\varepsilon^{\mathbf{x},\mathrm{Out}}}\}$ is a nonnegative supermartingale. Thus, for all $z \in M_{0,\varepsilon}^{\mathbf{x}} \setminus M_0^{\mathbf{x}}$

$$\alpha_{\mathbf{x}}T\mathbb{E}_z\left(k \wedge \tau_\varepsilon^{\mathbf{x},\mathrm{Out}}\right) \le \mathbb{E}_z\left(V_{k\wedge\tau_\varepsilon^{\mathbf{x},\mathrm{Out}}}\right) \le V_0 = V^{\mathbf{x}}(z).$$

That is,

$$\mathbb{E}_z\left(\tau_\varepsilon^{\mathbf{x},\mathrm{Out}}\right) \le \frac{V^{\mathbf{x}}(z)}{\alpha_{\mathbf{x}}T} < \infty. \tag{19}$$

Now, $(1/a_i, 0)$ is a linearly stable equilibrium for $F_{\mathcal{E}_i}$ whose basin of attraction contains $\mathbb{R}_+^* \times \mathbb{R}_+$ (see Proposition 1.1). Therefore, there exists $k_0 \in \mathbb{N}$ such that for all $z = (x, y, i) \in M \setminus M_{0,\varepsilon}^{\mathbf{x}}$ and $k \ge k_0$

$$\Phi_{kT}^{\mathcal{E}_i}(x, y) \in \left\{(u, v) \in \mathbb{R}_+ \times \mathbb{R}_+ : v < \varepsilon/2\right\}.$$

Here, $\Phi^{\mathcal{E}_i}$ stands for the flow induced by $F_{\mathcal{E}_i}$. Thus, for all $z = (x, y, i) \in M \setminus M_{0,\varepsilon}^{\mathbf{x}}$

$$\mathbb{P}_z\left(Z_{k_0T} \in M_{0,\varepsilon/2}^{\mathbf{y}}\right) \ge \mathbb{P}(I_t = i \text{ for all } t \le k_0T \mid I_0 = i) = e^{-\lambda_i k_0 T} \ge c, \tag{20}$$

where $c = e^{-(\max(\lambda_0,\lambda_1)k_0T)}$. Combining (19) and (20) completes the proof of the first step.

Step 2. Let $\mathcal{A}$ be the event defined as

$$\mathcal{A} = \left\{\limsup_{t\to\infty} \frac{V^{\mathbf{y}}(Z_t)}{t} \le -\alpha_{\mathbf{y}}\right\}.$$

We claim that there exists $c_1 > 0$ such that for all $z \in M^{\mathbf{y}}_{0,\varepsilon/2}$

$$\mathbb{P}_z(\mathcal{A}) \ge c_1. \tag{21}$$

Set $W_k = e^{\theta V^{\mathbf{y}}(Z_{kT})}$. By Lemma 3.5(ii), $\{W_{k\wedge\tau_\varepsilon^{\mathbf{y},\mathrm{Out}}}\}$ is a nonnegative supermartingale. Thus, for all $z \in M^{\mathbf{y}}_{0,\varepsilon/2}$

$$\mathbb{E}_z(W_{k\wedge\tau_\varepsilon^{\mathbf{y},\mathrm{Out}}}\mathbf{1}_{\tau_\varepsilon^{\mathbf{y},\mathrm{Out}}<\infty}) \le W_0 = e^{\theta V^{\mathbf{y}}(z)} \le \left(\frac{\varepsilon}{2}\right)^\theta.$$

Hence, letting $k \to \infty$ and using dominated convergence, leads to

$$\varepsilon^\theta \mathbb{P}_z\big(\tau_\varepsilon^{\mathbf{y},\mathrm{Out}} < \infty\big) \le \mathbb{E}_z(W_{\tau_\varepsilon^{\mathbf{y},\mathrm{Out}}}\mathbf{1}_{\tau_\varepsilon^{\mathbf{y},\mathrm{Out}}<\infty}) \le W_0 \le \left(\frac{\varepsilon}{2}\right)^\theta.$$

Thus,

$$\mathbb{P}_z\big(\tau_\varepsilon^{\mathbf{y},\mathrm{Out}} = \infty\big) \ge 1 - \frac{1}{2^\theta} = c_1 > 0. \tag{22}$$

Let $M_n = \sum_{k=1}^n (V^{\mathbf{y}}(Z_{kT}) - P_T V^{\mathbf{y}}(Z_{(k-1)T}))$. By the strong law of large numbers for martingales applied to $\{M_k\}$ and Lemma 3.5(i), it follows that

$$\limsup_{k\to\infty} \frac{V^{\mathbf{y}}(Z_{kT})}{kT} \le -\alpha_{\mathbf{y}}$$

on the event $\{\tau_\varepsilon^{\mathbf{y},\mathrm{Out}} = \infty\}$. Let $C = \sup\{\beta_i|1 - c_i x - d_i y| : (x, y, i) \in M\}$. It is easy to check that $V^{\mathbf{y}}(Z_{kT+t}) - V^{\mathbf{y}}(Z_{kT}) \le Ct$. Thus,

$$\limsup_{t\to\infty} \frac{V^{\mathbf{y}}(Z_t)}{t} \le -\alpha_{\mathbf{y}}$$

almost surely on the event $\{\tau_\varepsilon^{\mathbf{y},\mathrm{Out}} = \infty\}$. This later inequality, together with (22) concludes the proof of step 2.

Step 3. From (18) and (21), we deduce that

$$\mathbb{P}_z(\mathcal{A}) \ge cc_1 \tag{23}$$

for all $z \in M \setminus M^{\mathbf{x}}_0$. Thus, for all $z \in M \setminus M^{\mathbf{x}}_0$,

$$\mathbf{1}_{\mathcal{A}} = \lim_{t\to\infty} \mathbb{P}_z(\mathcal{A}|\mathcal{F}_t) = \lim_{t\to\infty} \mathbb{P}_{Z_t}(\mathcal{A}) \ge cc_1,$$

where the first equality follows from Doob's martingale convergence theorem, and the second from the Markov property. This completes the proof.

Proof of Theorem 3.3. By permuting the roles of species $\mathbf{x}$ and $\mathbf{y}$, the proof amounts to (re)proving Theorem 3.1 under the assumption that $\mathcal{E}_0$ and $\mathcal{E}_1$ are now *favorable to species* $\mathbf{y}$. All the arguments given in the proof of Theorem 3.1 go through but for the proof of (20) (where we have explicitly used the fact that $\mathcal{E}_0$ and $\mathcal{E}_1$ are both favorable to species $\mathbf{x}$). In order to prove inequality (20) when $\mathcal{E}_0, \mathcal{E}_1 \in \mathsf{Env}_{\mathbf{y}}$, we proceed as follows.

By Proposition 2.5 (applied after permutation of x and y) the assumptions $\mathcal{E}_0, \mathcal{E}_1 \in \mathsf{Env}_{\mathbf{y}}$, $\Lambda_{\mathbf{y}} < 0$ and $\Lambda_{\mathbf{x}} > 0$ imply that there exists $0 < s < 1$ such that $\mathcal{E}_s \in \mathsf{Env}_{\mathbf{x}}$. Thus, there exists $k_0 \in \mathbb{N}$ such that for all $z = (x, y, i) \in M \setminus M^{\mathbf{x}}_{0,\varepsilon}$ and $k \geq k_0$

$$\Phi^{\mathcal{E}_s}_{kT}(x, y) \in \{(u, v) \in \mathbb{R}_+ \times \mathbb{R}_+ : v < \varepsilon/2\}, \tag{24}$$

where $\Phi^{\mathcal{E}_s}$ stands for the flow induced by $F_{\mathcal{E}_s}$. We claim that there exists $c > 0$ such that

$$\mathbb{P}_z(Z_{k_0T} \in M^{\mathbf{y}}_{0,\varepsilon/2}) \geq c \tag{25}$$

for all $z \in M \setminus M^{\mathbf{x}}_{0,\varepsilon}$. Suppose to the contrary that for some sequence $z_n \in M \setminus M^{\mathbf{x}}_{0,\varepsilon}$

$$\lim_{n\to\infty} \mathbb{P}_{z_n}(Z_{k_0T} \in M^{\mathbf{y}}_{0,\varepsilon/2}) = 0.$$

By compactness of $M \setminus M^{\mathbf{x}}_{0,\varepsilon}$, we may assume that $z_n \to z^* = (x^*, y^*, i^*) \in M^{\mathbf{x}}_{0,\varepsilon}$. Thus, by Feller continuity (Proposition 2.1 in [7]) and Portmanteau's theorem, it comes that

$$\mathbb{P}_{z^*}(Z_{k_0T} \in M^{\mathbf{y}}_{0,\varepsilon/2}) = 0. \tag{26}$$

Now, by the support theorem (Theorem 3.4 in [7]), the deterministic orbit $\{\Phi^{\mathcal{E}_s}_t(x^*, y^*) : t \geq 0\}$ lies in the topological support of the law of $\{X_t, Y_t\}$. This shows that (26) is in contradiction with (24).

Proof of Theorem 3.4. The proof is similar to the proof of Theorem 3.1, so we only give a sketch of it. Reasoning like in Theorem 3.1, we show that there exists $c, c_1 > 0$ such that for all $z \in M^{\mathbf{h}}_{0,\varepsilon}$, $\mathbf{P}_z(\mathsf{Extinct}_{\mathbf{h}}) \geq c_1$ and for all $z \in M \setminus M^{\mathbf{x}}_{0,\varepsilon}$ $\mathbb{P}_z(\{Z_t\} \text{ enters } M^{\mathbf{y}}_{0,\varepsilon/2}) \geq c$.

Thus, for all $z \in M \setminus M_0$, $\mathbb{P}_z(\mathsf{Extinct}_{\mathbf{y}}) + \mathbb{P}_z(\mathsf{Extinct}_{\mathbf{x}}) \geq c_1 + cc_1$. Hence, by the martingale argument used in the last step of the proof of Theorem 3.1, we get that $\mathbb{P}_z(\mathsf{Extinct}_{\mathbf{y}}) + \mathbb{P}_z(\mathsf{Extinct}_{\mathbf{x}}) = 1$. Since $(1/a_i, 0)$ is a linearly stable equilibrium for $F_{\mathcal{E}_i}$ whose basin contains $\mathbb{R}^*_+ \times \mathbb{R}^*_+$, $\mathbb{P}_z(\{Z_t\} \text{ enters } M^{\mathbf{y}}_{0,\varepsilon/2}) > 0$ for all $z \in M \setminus M_0$ and, consequently, $\mathbb{P}_z(\mathsf{Extinct}_{\mathbf{y}}) > 0$. If furthermore there is some $s \in I \cap J$ $(0, 1/d_s)$ is a linearly stable equilibrium for $F_{\mathcal{E}_s}$ whose basin contains $\mathbb{R}^*_+ \times \mathbb{R}^*_+$ and, by the same argument, $\mathbb{P}_z(\mathsf{Extinct}_{\mathbf{y}}) > 0$.

4. Persistence.

Here, we assume that the invasion rates are positive and show that this implies a form of "stochastic coexistence".

THEOREM 4.1. *Suppose that* $\Lambda_{\mathbf{x}} > 0$, $\Lambda_{\mathbf{y}} > 0$ *Then there exists a unique invariant probability measure* (*for the process* $\{Z_t\}$) Π *on* $M \setminus M_0$, *that is*, $\Pi(M \setminus M_0) = 1$. *Furthermore*:

(i) Π *is absolutely continuous with respect to the Lebesgue measure* $dx\,dy \otimes (\delta_0 + \delta_1)$.

(ii) *There exists* $\theta > 0$ *such that*

$$\int \left(\frac{1}{x^\theta} + \frac{1}{y^\theta}\right) d\Pi < \infty.$$

(iii) *For every initial condition* $z = (x, y, i) \in M \setminus M_0$

$$\lim_{t\to\infty} \Pi_t = \Pi$$

weakly, with probability one.

(iv) *Suppose that* $\frac{\beta_0\alpha_1}{\alpha_0\beta_1} \neq \frac{a_0c_1}{a_1c_0}$ *or* $\frac{\beta_0\alpha_1}{\alpha_0\beta_1} \neq \frac{b_0d_1}{b_1d_0}$. *Then there exist constants* $C, \lambda > 0$ *such that for every Borel set* $A \subset M \setminus M_0$ *and every* $z = (x, y, i) \in M \setminus M_0$

$$\left|\mathbb{P}(Z_t \in A | Z_0 = z) - \Pi(A)\right| \le C\left(1 + \frac{1}{x^\theta} + \frac{1}{y^\theta}\right)e^{-\lambda t}.$$

Theorem 4.1 has several consequences which express that, whenever the invasion rates are positive, species abundances tend to stay away from the extinction set. Recall that the ε-boundary of the extinction set is the set

$$M_{0,\varepsilon} = \{z = (x, y, i) \in M : \min(x, y) \le \varepsilon\}.$$

Using the terminology introduced in Chesson [9], the process is called *persistent in probability* if, in the long run, densities are very likely to remain bounded away from zero. That is,

$$\lim_{\varepsilon\to 0} \limsup_{t\to\infty} \mathbb{P}(Z_t \in M_{0,\varepsilon} | Z_0 = z) = 0$$

for all $z \in M \setminus M_0$. Similarly, it is called *persistent almost surely* (Schreiber [30]) if the fraction of time a typical population trajectory spends near the extinction set is very small. That is,

$$\lim_{\varepsilon\to 0} \limsup_{t\to\infty} \Pi_t(M_{0,\varepsilon}) = 0$$

for all $z \in M \setminus M_0$.

By assertion (ii) of Theorem 4.1 and Markov's inequality,

$$\Pi(M_{0,\varepsilon}) = O(\varepsilon^\theta).$$

Thus, assertion (iii) implies almost sure persistence and assertion (iv) persistence in probability.

4.1. *Proof of Theorem* 4.1.

Proof of assertions (i), (ii), (iii). By Feller continuity of $\{Z_t\}$ and compactness of M, the sequence $\{\Pi_t\}$ is relatively compact (for the weak convergence) and every limit point of $\{\Pi_t\}$ is an invariant probability measure (see, e.g., [7], Proposition 2.4 and Lemma 2.5).

Now, the assumption that $\Lambda_{\mathbf{x}}$ and $\Lambda_{\mathbf{y}}$ are positive, ensure that the persistence condition given in ([4] Sections 5 and 5.2) is satisfied. Then by the persistence Theorem 5.1 in [4] (generalizing previous results in [5] and [31]), every limit point of $\{\Pi_t\}$ is a probability over $M \setminus M_0$ provided $Z_0 = z \in M \setminus M_0$. By Lemma 3.5(ii), every such limit point satisfies the integrability condition (ii).

To conclude, it then suffices to show that $\{Z_t\}$ has a unique invariant probability measure **on** $M \setminus M_0$, Π and that Π is absolutely continuous with respect to $dx\,dy \otimes (\delta_0 + \delta_1)$.

We rely on Theorem 1 in [2] (see also [7], Theorem 4.4 and the discussion following Theorem 4.5). According to this theorem, a sufficient condition ensuring both uniqueness and absolute continuity of Π is that:

(i) There exists an *accessible* point $m \in \mathbb{R}_+^* \times \mathbb{R}_+^*$.
(ii) The Lie algebra generated by $(F_{\mathcal{E}_0}, F_{\mathcal{E}_1})$ has full rank at point m.

There are several equivalent formulations of accessibility (called D-approachability in [2]). One of them (see Section 3 in [7]) is that for every neighborhood U of m and every $(x, y) \in \mathbb{R}_+^* \times \mathbb{R}_+^*$ there is a solution η to the differential inclusion

$$\dot{\eta} \in \operatorname{conv}(F_{\mathcal{E}_0}, F_{\mathcal{E}_1})(\eta),$$
$$\eta(0) = (x, y)$$

which meet U (i.e., $\eta(t) \in U$ for some $t > 0$). Here, $\operatorname{conv}(F_{\mathcal{E}_0}, F_{\mathcal{E}_1})$ stands for the convex hull of $F_{\mathcal{E}_0}$ and $F_{\mathcal{E}_1}$.

REMARK 5. Note that here, accessible points are defined as points which are accessible from every point $(x, y) \in \mathbb{R}_+^* \times \mathbb{R}_+^*$. By invariance of the boundaries, there is no point in $\mathbb{R}_+^* \times \mathbb{R}_+^*$ which is accessible from a boundary point.

For any environment $\mathcal{E}$, let $(\Phi_t^{\mathcal{E}})$ denote the flow induced by $F_{\mathcal{E}}$ and let

$$\gamma_{\mathcal{E}}^{+}(m) = \{\Phi_t^{\mathcal{E}}(m) : t \geq 0\}, \qquad \gamma_{\mathcal{E}}^{-}(m) = \{\Phi_t^{\mathcal{E}}(m) : t \leq 0\}.$$

Since $\Lambda_{\mathbf{y}} > 0$, $I \neq \varnothing$ by Proposition 2.3. Choose $s \in I$. Then, point $m_s = (1/a_s, 0)$ is a hyperbolic saddle equilibrium for $F_{\mathcal{E}_s}$ [as defined by equation (12)] which stable manifold is the x-axis and which unstable manifold, denoted $W_{m_s}^u(F_{\mathcal{E}_s})$, is transverse to the x-axis at m_s.

Now, choose an arbitrary point $m \in W^u_{m_s}(F_{\mathcal{E}_s}) \cap \mathbb{R}^*_+ \times \mathbb{R}^*_+$. We claim that m is accessible. A standard Poincaré section argument shows that there exists an arc L transverse to $W^u_{m_s}(F_{\mathcal{E}_s})$ at m and a continuous maps $P :]p_0 - \eta_0, p_0 + \eta_0[\times]0, \eta_0[\mapsto L$ such that for all $(x, y) \in]p_0 - \eta_0, p_0 + \eta_0[\times]0, \eta_0[$

$$\gamma^+_{\mathcal{E}_s}(x, y) \cap L = \{P(x, y)\}$$

and $\lim_{y \to 0} P(x, y) = m^*$. On the other hand, for all $x > 0$, $y > 0$,

$$\gamma^+_{\mathcal{E}_0}(x, y) \cap]p_0 - \eta_0, p_0 + \eta_0[\times]0, \eta_0[\neq \varnothing$$

because $\mathcal{E}_0 \in \mathsf{Env}_{\mathbf{x}}$. This proves the claim. Now there must be some $m \in W^u_{m_s}(F_{\mathcal{E}_s}) \setminus \{m_s\}$ at which $F_{\mathcal{E}_0}(m)$ and $F_{\mathcal{E}_1}(m)$ span $\mathbb{R}^2$. For otherwise $W^u_{m_s}(F_{\mathcal{E}_s}) \setminus \{m_s\}$ would be an invariant curve for the flows $\Phi^{\mathcal{E}_0}$ and $\Phi^{\mathcal{E}_1}$ implying that $m_s = m_0 = m_1$, hence $a_0 = a_1$ and $I = \varnothing$.

REMARK 6. The proof above shows that the set of accessible points has nonempty interior. This will be used later in the proofs of Theorem 4.1(iv) and 4.5.

Proof of assertion (iii). The cornerstone of the proof is the following lemma which shows that the process satisfies a certain Doeblin's condition. We call a point $z_0 \in M$ a *Doeblin point* provided there exist a neighborhood U_0 of z_0, positive numbers t_0, r_0, c_0 and a probability measure ν_0 on M such that for all $z \in U_0$ and $t \in [t_0, t_0 + r_0]$

$$P_t(z, \cdot) \geq c_0 \nu_0(\cdot). \tag{27}$$

LEMMA 4.2. (i) *There exists an accessible point* $m_0 = (x_0, y_0) \in \mathbb{R}^*_+ \times \mathbb{R}^*_+$, *such that* $z_0 = (m_0, 0)$ [*or* $(m_0, 1)$] *is a Doeblin point.*

(ii) *Let* ν_0 *be the measure associated to* z_0 *given by* (27). *Let* $K \subset M \setminus M_0$ *be a compact set. There exist positive numbers* t_K, r_K, c_K *such that for all* $z \in K$ *and* $t \in [t_K, t_K + r_K]$

$$P_t(z, \cdot) \geq c_K \nu_0(\cdot).$$

PROOF. Let $\{\mathcal{G}_k, k \in \mathbb{N}\}$ be the family of vector fields defined recursively by $\mathcal{G}_0 = \{F_{\mathcal{E}_1} - F_{\mathcal{E}_0}\}$ and

$$\mathcal{G}_{k+1} = \mathcal{G}_k \cup \{[G, F_{\mathcal{E}_0}], [G, F_{\mathcal{E}_1}] : G \in \mathcal{G}_k\}.$$

For $m \in \mathbb{R}_+ \times \mathbb{R}_+$, let $\mathcal{G}_k(m) = \{G(m) : G \in \mathcal{G}_k\}$.

By Theorem 4.4 in [7], a sufficient condition ensuring that a point $z = (x, y, i) \in M$ is a Doeblin point is that $\mathcal{G}_k(m)$ spans $\mathbb{R}^2$ for some k. Since $\mathcal{G}_1 = \{(F_{\mathcal{E}_1} - F_{\mathcal{E}_0}), [F_{\mathcal{E}_1}, F_{\mathcal{E}_0}]\}$, it then suffices to find an accessible point m_0 at which

$(F_{\mathcal{E}_1} - F_{\mathcal{E}_0})(m_0)$ and $[F_{\mathcal{E}_1}, F_{\mathcal{E}_0}](m_0)$ are independent. Let

$$\begin{aligned} P(x, y) &= \mathsf{Det}\big((F_{\mathcal{E}_1} - F_{\mathcal{E}_0})(x, y), [F_{\mathcal{E}_1}, F_{\mathcal{E}_0}](x, y)\big) \\ &= \sum_{\{i,j \geq 1, 3 \leq i+j \leq 5\}} c_{ij} x^i y^j. \end{aligned}$$

Since the set Γ of accessible points has nonempty interior (see Remark 6), either $P(m_0) \neq 0$ for some $m_0 \in \Gamma$ or all the c_{ij} are identically 0. A direct computation (performed with the formal calculus program Macaulay2) leads to

$$\begin{array}{ll}
c_{41} & -BFH + B^2L \\
c_{32} & -2CFH - F^2I + BFK + 2BCL - BEL + CFL \\
c_{23} & -CEH + BEI - CFI - 2EFI + 2CFK + C^2L \\
c_{14} & -E^2I + CEK \\
c_{31} & -2AFH + 2ABL \\
c_{22} & BEG - CFG - CDH - AEH + BDI - AFI - 2DFI - BEJ + \\
 & CFJ + BDK + AFK + 2ACL + CDL - AEL \\
c_{13} & -2DEI + 2CDK \\
c_{21} & BDG - AFG - ADH + A^2L \\
c_{12} & -D^2I + CDJ - AEJ + ADK
\end{array}$$

where

$$\begin{gathered}
A = \alpha_1 - \alpha_0, \qquad B = \alpha_0 a_0 - \alpha_1 a_1, \qquad C = \alpha_0 b_0 - \alpha_1 b_1, \\
D = \beta_1 - \beta_0, \qquad E = \beta_0 d_0 - \beta_1 d_1, \\
F = \beta_0 c_0 - \beta_1 c_1, \qquad G = \alpha_0, \qquad H = -\alpha_0 a_0, \qquad I = -\alpha_0 b_0, \\
J = \beta_0, \qquad K = -\beta_0 d_0, \qquad L = -\beta_0 c_0.
\end{gathered}$$

Under the assumption of Theorem 4.1 $a_0 \neq a_1$ so that A and B cannot be simultaneously null. Thus, $c_{41} = c_{31} = 0$ if and only if $FH = BL$. That is,

$$\frac{\beta_0 \alpha_1}{\alpha_0 \beta_1} = \frac{a_0 c_1}{a_1 c_0}.$$

Similarly, $c_{14} = c_{13} = 0$ if and only if

$$\frac{\beta_0 \alpha_1}{\alpha_0 \beta_1} = \frac{b_0 d_1}{b_1 d_0}.$$

This proves that the conclusion of Lemma (i) holds as long as one of these two latter equalities is not satisfied.

We now prove the second assertion. Let $z_0 = (m_0, 0)$ be the Doeblin point given by (i), and let $U_0, t_0, r_0, c_0, \nu_0$ be as in the definition of such a point. Choose p

in the support of ν_0. Without loss of generality, we can assume that $p \in K$ (for otherwise it suffices to enlarge K). For all $t \geq 0$ and $\delta > 0$ let

$$O(t, \delta) = \{z \in M : P_t(z, U_0) > \delta\}.$$

By Feller continuity and Portmanteau theorem, $O(t, \delta)$ is open. Because m_0 is accessible, it follows from the support theorem (Theorem 3.4 in [7]) that

$$M \setminus M_0 = \bigcup_{t \geq 0, \delta > 0} O(t, \delta).$$

Thus, by compactness, there exist $\delta > 0$ and $0 \leq t_1 \leq \cdots \leq t_m$ such that

$$K \subset \bigcup_{i=1}^{m} V_i,$$

where $V_i = O(t_i, \delta)$. Let $l \in \{1, \dots, m\}$ be such that $p \in V_l$. Choose an integer $N > \frac{t_m - t_1}{r_0}$ and set $r_i = \frac{t_i - t_1}{N}$. Then $\tau = t_i + N(t_0 + r_i) + N t_l$ is independent of i and for all $z \in V_i$ and $t_0 \leq t \leq t_0 + r_0$

$$\begin{aligned} P_{\tau+t}(z, \cdot) &\geq \int_{U_0} P_{t_i}(z, dz_1) \int_{V_l} P_{t_0+r_i}(z_1, dz_1') \int_{U_0} P_{t_l}(z_1', dz_2) \cdots \\ &\quad \times \int_{V_l} P_{t_0+r_i}(z_N, dz_N') \int_{U_0} P_{t_l}(z_N', dz_{N+1}) P_t(z_{N+1}, \cdot) \\ &\geq \delta (c_0 \nu_0(V_l) \delta)^N c_0 \nu_0(\cdot). \end{aligned}$$

□

LEMMA 4.3. *There exist positive numbers* $\theta, T, \tilde{C}$ *and* $0 < \rho < 1$ *such that the map* $W : M \setminus M_0 \mapsto \mathbb{R}_+$ *defined by*

$$W(x, y, i) = \frac{1}{x^\theta} + \frac{1}{y^\theta}$$

verifies

$$P_{nT} W \leq \rho^n W + \tilde{C}$$

for all $n \geq 1$.

PROOF. By Lemma 3.5(ii), there exist $0 < \rho < 1$ and $\theta, T > 0$ such that

$$P_T W \leq \rho W + \tilde{C}, \tag{28}$$

where

$$\tilde{C} = \sup_{z \in M \setminus M_{0,\varepsilon}} P_T(W) - W$$

is finite by continuity of W on $M \setminus M_0$ and compactness of $M \setminus M_{0,\varepsilon}$. So that by iterating,

$$P_{nT} W \leq \rho^n W + \tilde{C} \sum_{k=1}^{n-1} \rho^k \leq \rho^n W + \frac{\rho}{1-\rho} \tilde{C}.$$

Replacing $\tilde{C}$ by $\frac{\rho}{1-\rho}\tilde{C}$ proves the result. □

To conclude the proof of assertion (iii), we then use from the classical Harris's ergodic theorem. Here, we rely on the following version given (an proved) in [18].

THEOREM 4.4 (Harris's theorem). *Let $\mathcal{P}$ be a Markov kernel on a measurable space E assume that*:

(i) *There exists a map $W : E \mapsto [0, \infty[$ and constants $0 < \gamma < 1$, $\tilde{K}$ such that $\mathcal{P} W \leq \gamma W + \tilde{C}$.*

(ii) *For some $R > \frac{2\tilde{C}}{1-\gamma}$, there exists a probability measure ν and a constant c such that $\mathcal{P}(x, \cdot) \geq c\nu(\cdot)$ whenever $W(x) \leq R$.*

Then there exists a unique invariant probability π for $\mathcal{P}$ and constants $C \geq 0$, $0 \leq \tilde{\gamma} < 1$ such that for every bounded measurable map $f : E \mapsto \mathbb{R}$ and all $x \in E$

$$\left|\mathcal{P}^n f(x) - \pi f\right| \leq C \tilde{\gamma}^n \left(1 + W(x)\right) \|f\|_\infty.$$

To apply this result, set $E = M \setminus M_0$, $W(x, y, i) = \frac{1}{x^\theta} + \frac{1}{y^\theta}$, $\mathcal{P} = P_{nT}$, and $\gamma = \rho^n$, where θ and T are given by Lemma 4.3 and $n \in \mathbb{N}^*$ remains to be chosen. Choose $R > \frac{2\tilde{C}}{1-\rho}$ and set $K = \{z \in M \setminus M_0 : W(z) \leq R\}$. By Lemma 4.2, $P_{mt}(z, \cdot) \geq c_K^m \nu_0$ for all $t \in [t_K, t_K + r_K]$ and $z \in K$. Choose $t \in [t_K, t_K + r_K]$ such that t/T is rational, and positive integers m, n such that $m/n = t/T$. Thus, $P_{nT} = P_{mt} = \mathcal{P}$ verifies conditions (i), (ii) above of Harris's theorem.

Let π be the invariant probability of $\mathcal{P}$. For all $t \geq 0$ $\pi P_t \mathcal{P} = \pi \mathcal{P} P_t = \pi P_t$ showing that πP_t is invariant for $\mathcal{P}$. Thus, $\pi = \pi P_t$ so that $\pi = \Pi$. Now for all $t > nT$ $t = k(nT) + r$ with $k \in \mathbb{N}$ and $0 \leq r < nT$. Thus,

$$\left|P_t f(x) - \Pi f\right| = \left|\mathcal{P}^k P_r f - \Pi(P_r f)\right| \leq C \tilde{\gamma}^k \|f - \Pi f\|_\infty \left(1 + W(x)\right).$$

This completes the proof.

4.2. *The support of the invariant measure.* We conclude this section with a theorem describing certain properties of the topological support of Π. Consider again the differential inclusion induced by $F_{\mathcal{E}_0}, F_{\mathcal{E}_1}$:

$$\dot{\eta}(t) \in \operatorname{conv}(F_{\mathcal{E}_0}, F_{\mathcal{E}_1})\left(\eta(t)\right). \tag{29}$$

A *solution* to (29) with initial condition (x, y) is an absolutely continuous function $\eta : \mathbb{R} \mapsto \mathbb{R}^2$ such that $\eta(0) = (x, y)$ and (29) holds for almost every $t \in \mathbb{R}$.

Differential inclusion (29) induces a *set valued dynamical system* $\Psi = \{\Psi_t\}$ defined by

$$\Psi_t(x, y) = \{\eta(t) : \eta \text{ is solution to (29) with initial condition } \eta(0) = (x, y)\}.$$

A set $A \subset \mathbb{R}^2$ is called *strongly positively invariant* under (29) if $\Psi_t(A) \subset A$ for all $t \geq 0$. It is called *invariant* if for every point $(x, y) \in A$ there exists a solution η to (29) with initial condition (x, y) such that $\eta(\mathbb{R}) \subset A$.

The omega limit set of (x, y) under Ψ is the set

$$\omega_\Psi(x, y) = \bigcap_{t \geq 0} \overline{\Psi_{[t,\infty[}(x, y)}.$$

As shown in ([7], Lemma 3.9) $\omega_\Psi(x, y)$ is compact, connected, invariant and strongly positively invariant under Ψ.

THEOREM 4.5. *Under the assumptions of Theorem 4.1, the topological support of* Π *writes* $\mathrm{supp}(\Pi) = \Gamma \times \{0, 1\}$ *where*:

(i) $\Gamma = \omega_\Psi(x, y)$ *for all* $(x, y) \in \mathbb{R}_+^* \times \mathbb{R}_+^*$. *In particular,* Γ *is compact connected strongly positively invariant and invariant under* Ψ;

(ii) Γ *equates the closure of its interior*;

(iii) $\Gamma \cap \mathbb{R}_+ \times \{0\} = [p_0, p_1] \times \{0\}$;

(iv) *If* $I \cap J \neq \varnothing$ *then* $\Gamma \cap \{0\} \times \mathbb{R}_+ = \{0\} \times [\hat{p}_0, \hat{p}_1]$;

(v) $\Gamma \setminus \{0\} \times [\hat{p}_0, \hat{p}_1]$ *is contractible* (*hence simply connected*).

PROOF. (i) Let $(m, i) \in \mathrm{supp}(\Pi)$. By Theorem 4.1, for every neighborhood U of m and every initial condition $z = (x, y, i) \in M \setminus M_0$ $\liminf_{t\to\infty} \Pi_t(U) > 0$. This implies that $m \in \omega_\Psi(x, y)$ (compare to Proposition 3.17(iii) in [7]). Conversely, let $m \in \omega_\Psi(x, y)$ for some $(x, y) \in \mathbb{R}_+^* \times \mathbb{R}_+^*$ and let U be a neighborhood of m. Then

$$\Pi(U \times \{i\}) = \int \mathbb{P}_z(Z_z \in U \times \{i\})\Pi(dz) = \int \mathbb{Q}_z(U \times \{i\})\Pi(dz),$$

where $\mathbb{Q}_z(\cdot) = \int_0^\infty \mathbb{P}_z(Z_t \in \cdot)e^{-t}\, dt$. Suppose $\Pi(U \times \{i\}) = 0$. Then for some $z_0 \in \mathrm{supp}(\Pi) \setminus M_0$ (recall that $\Pi(M_0) = 0$) $\mathbb{Q}_{z_0}(U \times \{i\}) = 0$. Thus $\mathbb{P}_{z_0}(Z_t \in U \times \{i\}) = 0$ for almost all $t \geq 0$. On the other hand, because $z_0 \in \mathrm{supp}(\Pi) \subset \omega_\Psi(x, y)$ there exists a solution η to (29) with initial condition (x, y) and some nonempty interval $]t_1, t_2[$ such that for all $t \in]t_1, t_2[$ $\eta(t) \in U$. This later property combined with the support theorem (Theorem 3.4 and Lemma 3.2 in [7]) implies that $\mathbb{P}_{z_0}(Z_t \in U \times \{i\}) > 0$ for all $t \in]t_1, t_2[$, a contradiction.

(ii) By Proposition 3.11 in [7] (or more precisely the proof of this proposition), either Γ has empty interior or it equates the closure of its interior. In the proof of Theorem 4.1, we have shown that there exists a point m in the interior of Γ.

(iii) Point $(p_i, 0)$ lies in Γ as a linearly stable equilibrium of $F_{\mathcal{E}_i}$. By strong invariance, $[p_0, p_1] \times \{0\} \subset \Gamma$. On the other hand, by invariance, $\Gamma \cap \mathbb{R}_+ \times \{0\}$ is compact and invariant but every compact invariant set for Ψ contained in $\mathbb{R}_+ \times \{0\}$

either equals $[p_0, p_1] \times \{0\}$ or contains the origin $(0, 0)$. Since the origin is an hyperbolic linearly unstable equilibrium for $F_{\mathcal{E}_0}$ and $F_{\mathcal{E}_1}$, it cannot belong to Γ.

(iv) If $I \cap J \neq \varnothing$, then for any $s \in I \cap J$ $F_{\mathcal{E}_s}$ has a linearly stable equilibrium $m_s \in \{0\} \times [\hat{p}_0, \hat{p}_1]$ which basin of attraction contains $\mathbb{R}_+^* \times \mathbb{R}_+^*$. Thus, $m_s \in \Gamma$ proving that $\Gamma \cap \{0\} \times \mathbb{R}_+$ is nonempty. The proof that $\Gamma \cap \{0\} \times \mathbb{R}_+ = \{0\} \times [\hat{p}_0, \hat{p}_1]$ is similar to the proof of assertion (iii).

(v) Since Γ is positively invariant under $\Phi^{\mathcal{E}_0}$ and $(p_0, 0)$ is a linearly stable equilibrium which basin contains $\mathbb{R}_+^* \times \mathbb{R}_+$, $\Gamma \setminus (\{0\} \times \mathbb{R}_+)$ is contractible to $(p_0, 0)$. ☐

5. Illustrations. We present some numerical simulations illustrating the results of the preceding sections. We consider the environments

$$A_0 = \begin{pmatrix} 1 & 1 \\ 2 & 2 \end{pmatrix}, \qquad B_0 = \begin{pmatrix} 1 \\ 5 \end{pmatrix}, \tag{30}$$

and

$$A_1 = \begin{pmatrix} 3 & 3 \\ 4 & 4+\rho \end{pmatrix}, \qquad B_1 = \begin{pmatrix} 5 \\ 1 \end{pmatrix}. \tag{31}$$

The simulations below are obtained with

$$\lambda_0 = st, \qquad \lambda_1 = (1-s)t$$

for different values of $s \in]0, 1[$, $t > 0$ and $\rho \in \{0, 1, 3\}$. Let $S(u) = \frac{u}{5(1-u)+u}$. Using Remark 1, it is easy to check that:

(a) $I = S(]\frac{3}{4} - \frac{1}{2\sqrt{6}}, \frac{3}{4} + \frac{1}{2\sqrt{6}}[)$,
(b) $J = I$ for $\rho = 0$,
(c) $J = S(]\frac{71}{96} - \frac{\sqrt{241}}{96}, \frac{71}{96} + \frac{\sqrt{241}}{96}[\subset I$ for $\rho = 1$,
(d) $J = \varnothing$ for $\rho = 3$.

The phase portraits of $F_{\mathcal{E}_0}$ and $F_{\mathcal{E}_1}$ are given in Figure 3 with $\rho = 3$.

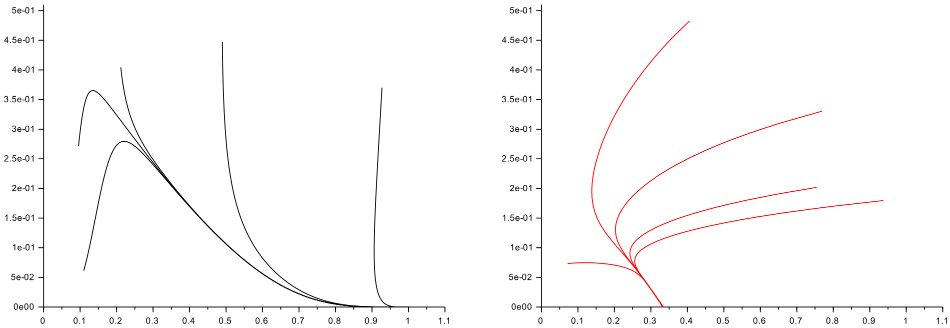

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FIG. 3. *Phase portraits of $F_{\mathcal{E}_0}$ and $F_{\mathcal{E}_1}$.*

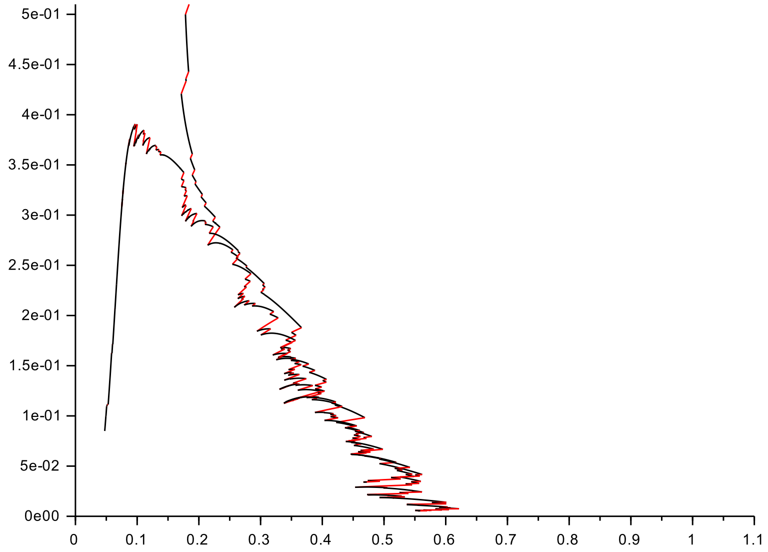

FIG. 4. $\rho = 3, u = 0.4, t = 100$ (*extinction of species* $\mathbf{y}$).

Figure 4 and 5 are obtained with $\rho = 3$ (so that $J = \varnothing$). Figure 4 with $s \notin I$ and t "large" illustrates Theorems 3.1 (extinction of species $\mathbf{y}$). Figure 5 with $s \in I$ illustrates Theorems 4.1 and 4.5 (persistence).

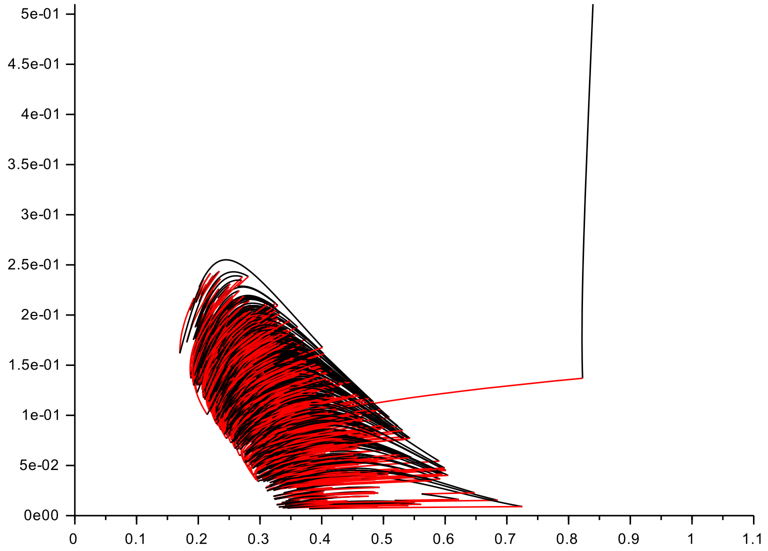

FIG. 5. $\rho = 3, u = 0.75, t = 12$ (*persistence*).

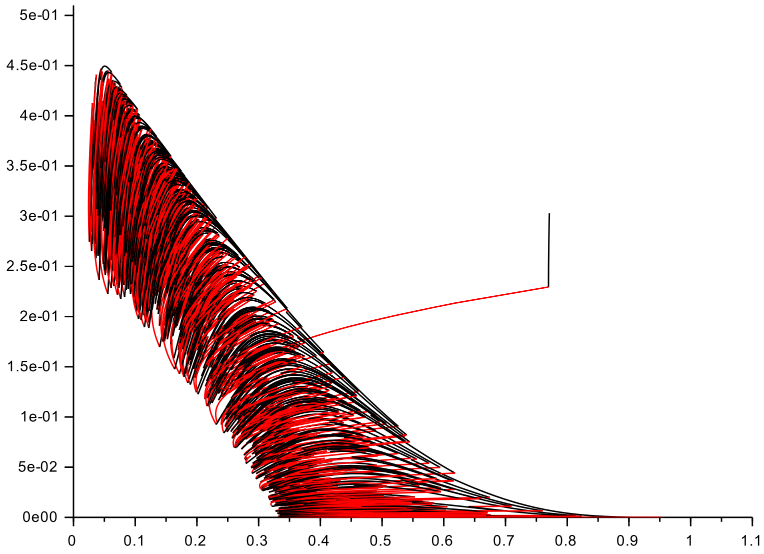

FIG. 6. $\rho = 1, u = 0.75, t = 10$ (*persistence*).

Figures 6 and 7 are obtained with $\rho = 1$. Figure 6 with $s \in I \cap J, t = 10$ illustrates Theorems 4.1 and 4.5 (persistence) in case $I \cap J \neq \varnothing$. Figure 7 with $s \in I \cap J$ and "large" t illustrates Theorem 3.3.

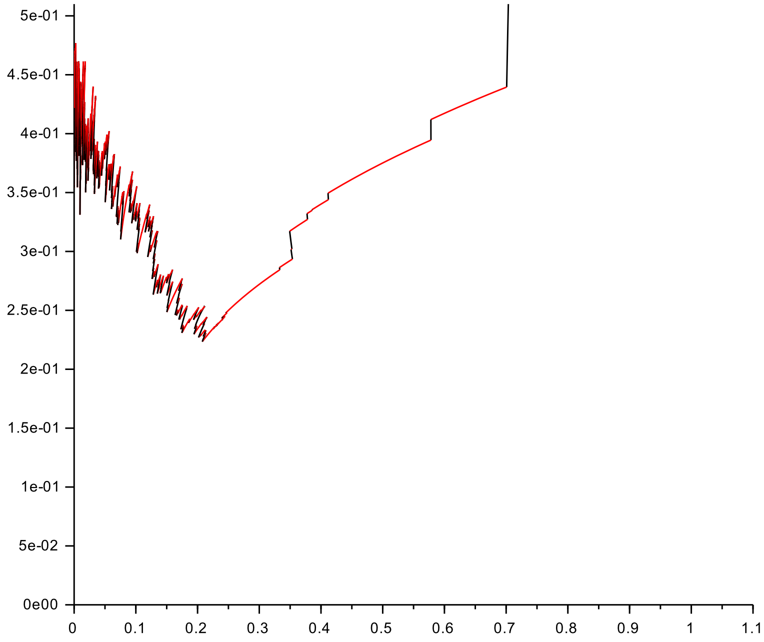

FIG. 7. $\rho = 1, u = 0.75, t = 100$ (*extinction of species* $\mathbf{x}$).

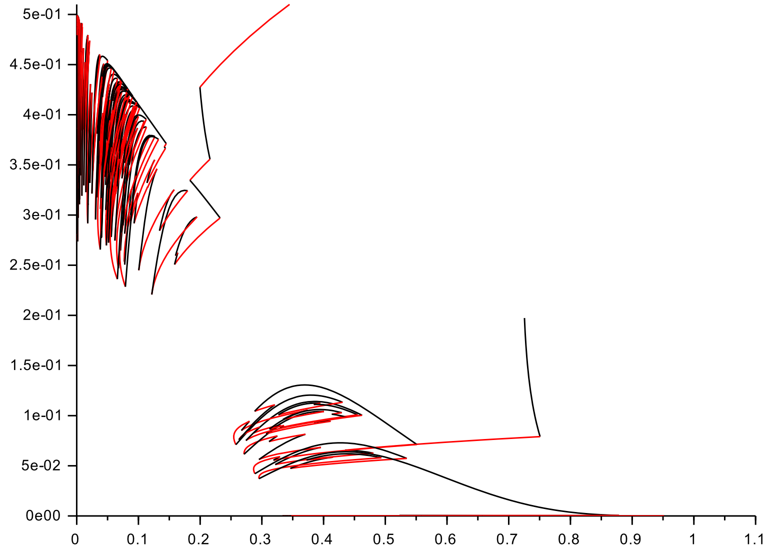

FIG. 8. $\rho = 0, u = 0.75, t = 1/0.15$ (*extinction of species* $\mathbf{x}$ *or* y).

Figures 8 is obtained with $\rho = 0$ $s \in I \cap J$ and t conveniently chosen. It illustrates Theorem 3.4.

REMARK 7. The transitions from extinction of species $\mathbf{y}$ to extinction of species $\mathbf{x}$ when the jump rate parameter t increases is reminiscent of the transition occurring with linear systems analyzed in [6] and [26].

6. Proofs of Propositions 2.1 and 2.3.

6.1. *Proof of Proposition* 2.1. The process $\{X_t, Y_t, I_t\}$ restricted to $M_0^{\mathbf{y}}$ is defined by $Y_t = 0$ and the one dimensional dynamics

$$\dot{X} = \alpha_{I_t} X(1 - a_{I_t} X). \tag{32}$$

The invariant probability measure of the chain (I_t) is given by

$$\nu = \frac{\lambda_0}{\lambda_1 + \lambda_0}\delta_1 + \frac{\lambda_1}{\lambda_1 + \lambda_0}\delta_0.$$

If $a_0 = a_1 = a$, $X_t \to 1/a = p$. Thus, (X_t, I_t) converges weakly to $\delta_p \otimes \nu$ and the result is proved.

Suppose now that $0 < a_0 < a_1$.

By Proposition 3.17 in [7] and Theorem 1 in [2] (or Theorem 4.4 in [7]), there exists a unique invariant probability measure μ on $\mathbb{R}_+^* \times \{0, 1\}$ for (X_t, I_t) which furthermore is supported by $[p_1, p_0]$. A recent result by [3] also proves that such a measure has a smooth density (in the x-variable) on $]p_1, p_0[$.

Let $\Psi : \mathbb{R} \times \{0,1\} \mapsto \mathbb{R}$, $(x,i) \mapsto \Psi(x,i)$ be smooth in the x variable. Set $\Psi'(x,i) = \frac{\partial \Psi(x,i)}{\partial x}$, and $f_i(x) = \alpha_i x(1 - \frac{x}{p_i})$. The infinitesimal generator of $(x(t), I_t)$ acts on Ψ as follows:

$$\mathcal{L}\Psi(x,1) = \langle f_1(x), \Psi'(x,1)\rangle + \lambda_1\bigl(\Psi(x,0) - \Psi(x,1)\bigr),$$
$$\mathcal{L}\Psi(x,0) = \langle f_0(x), \Psi'(x,0)\rangle + \lambda_0\bigl(\Psi(x,1) - \Psi(x,0)\bigr).$$

Write $\mu(dx,1) = h_1(x)\,dx$ and $\mu(dx,0) = h_0(x)\,dx$. Then

$$\sum_{i=0,1} \int \mathcal{L}\Psi(x,i) h_i(x)\,dx = 0.$$

Choose $\Psi(x,i) = g(x) + c$ and $\Psi(x,1-i) = 0$ where g is an arbitrary compactly supported smooth function and c an arbitrary constant. Then an easy integration by part leads to the differential equation

$$\begin{cases} \lambda_0 h_0(x) - \lambda_1 h_1(x) = -(f_0 h_0)'(x), \\ \lambda_0 h_0(x) - \lambda_1 h_1(x) = (f_1 h_1)'(x) \end{cases} \tag{33}$$

and the condition

$$\int_{p_1}^{p_0} \lambda_0 h_0(x) - \lambda_1 h_1(x)\,dx = 0. \tag{34}$$

The maps

$$h_1(x) = C\frac{p_1(x-p_1)^{\gamma_1 - 1}(p_0 - x)^{\gamma_0}}{\alpha_1 x^{1+\gamma_1+\gamma_0}}, \tag{35}$$

$$h_0(x) = C\frac{p_0(x-p_1)^{\gamma_1}(p_0 - x)^{\gamma_0 - 1}}{\alpha_0 x^{1+\gamma_1+\gamma_0}} \tag{36}$$

are solutions, where C is a normalization constant given by

$$\int_{p_1}^{p_0} h_0(x) + h_1(x)\,dx = 1.$$

Note that h_1 and h_0 satisfy the equalities

$$\int_{p_1}^{p_0} h_0(x)\,dx = \frac{\lambda_1}{\lambda_0 + \lambda_1},$$
$$\int_{p_1}^{p_0} h_1(x)\,dx = \frac{\lambda_0}{\lambda_0 + \lambda_1}.$$

This completes the proof of Proposition 2.1.

6.2. *Proof of Proposition* 2.3. (i) We assume that $I = \varnothing$. If $p_0 = p_1$ then $\Lambda_{\mathbf{y}} < 0$. Suppose that $a_0 < a_1$ (i.e., $p_0 > p_1$) (the proof is similar for $p_0 < p_1$). Let $p_s = \frac{1}{a_s}$ with a_s being given in the definition of A_s. The function $s \mapsto p_s$ maps $]0, 1[$ homeomorphically onto $]p_0, p_1[$ and by definition of $\mathcal{E}_s$

$$s\alpha_1(1 - a_1 p_s) + (1 - s)\alpha_0(1 - a_0 p_s) = 0.$$

Thus, $(1 - a_1 p_s) = -\frac{(1-s)\alpha_0}{s\alpha_1}(1 - a_0 p_s)$. Hence,

$$P(p_s) = \frac{(1 - a_0 p_s)}{\alpha_1 s}\beta_s(1 - c_s p_s) = \frac{\beta_s}{\alpha_1 s}(1 - a_0/a_s)(1 - c_s/a_s).$$

This proves that $P(x) \leq 0$ for all $x \in]p_0, p_1[$. Since P is a nonzero polynomial of degree 2, $P(x) < 0$ for all, but possibly one, points in $]p_0, p_1[$. Thus, $\Lambda_{\mathbf{y}} < 0$.

(ii) If $a_0 = a_1$ the result is obvious. Thus, we can assume (without loss of generality) that $a_0 < a_1$. Fix $s \in]0, 1[$ and let for all $t > 0$ ν_1^t (resp., y ν_0^t) be the probability measure defined as $\nu_1^t(dx) = \frac{1}{s}h_1^t(x)\mathbf{1}_{]p_1,p_0[}(x)\,dx$ ($\nu_0^t(dx) = \frac{1}{1-s}h_0^t(x)\mathbf{1}_{]p_1,p_0[}(x)\,dx$) where h_1^t (resp., h_0^t) is the map defined by equation (35) [resp., (36)] with $\lambda_0 = st$ and $\lambda_1 = (1 - s)t$. We shall prove that

$$\nu_i^t \Rightarrow \delta_{p_s} \qquad \text{as } t \to \infty \tag{37}$$

and

$$\nu_i^t \Rightarrow \delta_{p_i} \qquad \text{as } t \to 0, \tag{38}$$

where $\Rightarrow$ denotes the weak convergence. The result to be proved follows.

Let us prove (37). For all $x \in]p_0, p_1[$, $\nu_i^t(dx) = C_i^t e^{tW(x)}[x|x - p_i|]^{-1} \times \mathbf{1}_{]p_1,p_0[}(x)\,dx$ where C_i^t is a normalization constant and

$$W(x) = \frac{s}{\alpha_0}\log(p_0 - x) + \frac{1 - s}{\alpha_1}\log(x - p_1) - \frac{\alpha_s}{\alpha_0\alpha_1}\log(x).$$

We claim that

$$\operatorname*{argmax}_{]p_0,p_1[} W = p_s = \frac{1}{a_s}. \tag{39}$$

Indeed, set $Q(x) = W'(x)(\alpha_0\alpha_1 x(x - p_0)(p_1 - x))$. It is easy to verify that

$$Q(x) = s\alpha_1(p_1 - x)x - (1 - s)\alpha_0(x - p_0)x - \alpha_s(p_0 - x)(x - p_1).$$

Thus, $Q(p_0) < 0$, $Q(p_1) > 0$ and since Q is a second degree polynomial, it suffices to show that $Q(p_s) = 0$ to conclude that p_s is the global minimum of W. By definition of p_s,

$$s\alpha_1(1 - a_1 p_s) + (1 - s)\alpha_0(1 - a_0 p_s) = 0.$$

Thus,

$$(1 - s)\alpha_0(p_s - p_0) = \frac{s\alpha_1 a_1}{a_0}(p_1 - p_s).$$

Plugging this equality in the expression of $Q(p_s)$ leads to $Q(p_s) = 0$. This proves the claim. Now, from equation (39) and the Laplace principle we deduce (37).

We now turn to the proof of (38). It suffices to show that ν_i^t converges in probability to p_i, meaning that $\nu_i^t\{x : |x - p_i| \geq \varepsilon\} \to 0$ as $t \to 0$. This easily follows from the shape of h_i^t and elementary estimates.

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