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RANDOM SWITCHING IN AN ECOSYSTEM WITH TWO PREY AND ONE PREDATOR*

ALEXANDRU HENING†, DANG H. NGUYEN‡, NHU NGUYEN§, AND HARRISON WATTS‡

Abstract. In this paper, we study the long-term dynamics of two prey species and one predator species. In the deterministic setting, if we assume the interactions are of Lotka–Volterra type (competition or predation), the long-term behavior of this system is well known. However, nature is usually not deterministic. All ecosystems experience some type of random environmental fluctuations. We incorporate these into a natural framework as follows. Suppose the environment has two possible states. In each of the two environmental states the dynamics is governed by a system of Lotka–Volterra ODEs. The randomness comes from spending an exponential amount of time in each environmental state and then switching to the other one. We show how this random switching can create very interesting phenomena. In some cases the randomness can facilitate the coexistence of the three species even though coexistence is impossible in each of the two environmental states. In other cases, even though there is coexistence in each of the two environmental states, switching can lead to the loss of one or more species. We look into how predators and environmental fluctuations can mediate coexistence among competing species.

Key words. population dynamics, predator-prey, fluctuating environment, stochasticity, coexistence, extinction

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1. Introduction.

An important question in ecology is the relationship between complexity and stability. In particular, ecologists have been interested in whether predators can help facilitate coexistence or whether they are always detrimental to species diversity. Since the important work by Paine (1966) it has been clear that predators play a fundamental role in species diversity. There are experimental studies which show that the removal of predators can lead to the extinctions of various species. Other studies have shown the opposite effect, namely, that introducing a predator does not help mediate coexistence or that the addition of the predator leads to fewer species coexisting. In this paper we are interested in exploring these phenomena in the setting of Lotka–Volterra (LV) dynamics. The dynamics of two competing species is well known in this setting; it can lead to coexistence, where both species persist; to competitive exclusion, where one species is dominant and drives the other one extinct; or to bistability, where, depending on the initial conditions, one species persists and one goes extinct. There have been numerous studies which looked at how

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†Department of Mathematics, Texas A&M University, College Station, TX 77843 USA (ahening@tamu.edu).
‡Department of Mathematics, University of Alabama, Tuscaloosa, AL 35487 USA (dangnh.maths@gmail.com, hrwatts@crimson.ua.edu).
§Department of Mathematics and Applied Mathematical Sciences, University of Rhode Island, Kingston, RI 02881 USA (nhu.nguyen@uri.edu).

the introduction of a predator changes the long-term outcome of two competitors; see work by Hutson and Vickers (1983), Takeuchi and Adachi (1983), and Schreiber (1997).

Every natural system experiences unpredictable environmental fluctuations. In the ecological setting, these environmental fluctuations will change the way species grow, die, and interact with each other. It is therefore key to include environmental fluctuations in the mathematical framework when trying to determine species richness. Sometimes the deterministic dynamics can predict certain species going extinct. However, if one adds the effects of a random environment extinction might be reversed into coexistence. In other cases deterministic systems that coexist become extinct once one takes into account the random environmental fluctuations. One way of introducing the environmental fluctuations has been by modeling the populations as discrete or continuous time Markov processes and analyzing the long-term behavior of these processes (Chesson, 1982; Chesson and Ellner, 1989; Chesson, 2000; Evans et al., 2013; Evans, Hening, and Schreiber, 2015; Lande, Engen, and Saether, 2003; Schreiber and Lloyd-Smith, 2009; Schreiber, Benaïm, and Atchadé, 2011; Benaïm and Schreiber, 2009; Benaïm, Hofbauer, and Sandholm, 2008; Benaïm, 2018; Hening, Nguyen, and Chesson, 2021).

There are many ways in which one can model the environmental fluctuations that affect an ecological system. One way is by going from ordinary differential equations (ODEs) to stochastic differential equations (SDEs). This amounts to saying that the various birth, death, and interaction rates in an ecosystem are not constant but fluctuate around their average values according to some white noise. There is now a well-established general theory of coexistence and extinction for these systems (Schreiber, Benaïm, and Atchadé, 2011; Hening and Nguyen, 2018; Hening, Nguyen, and Chesson, 2021). However, this way of modeling environmental fluctuations can sometimes seem artificial in an ecological setting. In certain ecosystems, it makes more sense to assume that, when the environment changes, the dynamics also changes significantly. In a deterministic setting this can be modeled by periodic vector fields which can be interpreted to mimic seasonal fluctuations. In the random setting, these types of fluctations are captured by piecewise deterministic Markov processes (PDMPs); see the work by Davis (1984) for an introduction to these stochastic processes. In a PDMP, the environment switches between a fixed finite number of states to each of which we associate an ODE. In each state the dynamics is given by the flow of its associated ODE. After a random time, the environment switches to a different state, and the dynamics is governed by the ODE from that state.

Recently there have been some important results for two-species ecosystems that showcased how the switching behavior of PDMPs can create novel ecological phenomena. The first set of results is for a two-species competitive LV model. In Benaïm and Lobry (2016) and Hening and Nguyen (2020) the authors show that the random switching between two environments that are both favorable to the same species, e.g., the favored species is dominant and persists and the unfavored species goes extinct, can lead to the extinction of this favored species and the persistence of the unfavored species, to the coexistence of the two competing species or to bistability. This is extremely interesting as it relates to the competitive exclusion principle (Volterra, 1928; Hardin, 1960; Levin, 1970), a fundamental principle of ecology, which says in its simplest form that, when multiple species compete with each other for the same resource, one competitor will win and drive all the others to extinction. Nevertheless, it has been observed in nature that multiple species can coexist despite limited resources. Hutchinson (1961) gave a possible explanation by arguing that variations of the environment can keep species away from the deterministic equilibria that are forecasted by the competitive exclusion principle. The PDMP example from Benaïm and Lobry (2016) and Hening and Nguyen (2020) shows how the switching can save species from extinction, even though, in each fixed environment, the same species is dominant. The second result looks at the classical predator-prey LV model. In Hening and Strickler (2019) the authors study a system that switches randomly between two deterministic classical VL predator-prey systems. Even though for each deterministic predator-prey system the predator and the prey densities form closed periodic orbits, it is shown in Hening and Strickler (2019) that the switching makes the system leave any compact set. Moreover, in the switched system, the predator and prey densities oscillate between 0 and ∞. These two sets of results show that random switching can radically change the dynamics of the system and create new, possibly unexpected, long-term results.

For three-species LV systems, the classification of the dynamics is incomplete in the deterministic setting. In the setting of SDE an almost complete classification appears in Hening, Nguyen, and Shreiber (2021). Not much is known for the dynamics of three-species systems in the PDMP setting. We hope that this paper will provide valuable results both phenomenologically, by showcasing some counterintuitive results, and mathematically, by developing new tools for the analysis of the ergodic properties of PDMPs.

The deterministic dynamics are given by

$$\begin{aligned} \frac{dX_1}{dt}(t) &= X_1(t)[r - X_1(t) - b_1X_2(t) - c_1X_3(t)], \\ \frac{dX_2}{dt}(t) &= X_2(t)[r - X_2(t) - b_2X_1(t) - c_2X_3(t)], \\ \frac{dX_3}{dt}(t) &= X_3(t)[e_1X_1(t) + e_2X_2(t) - d]. \end{aligned} \tag{1.1}$$

Here $X_1(t), X_2(t)$ are the densities of the two prey species at time $t \geq 0$, while $X_3(t)$ is the density of the generalist predator at time $t \geq 0$. For simplicity we assume that the per capita growth rates of both prey species are equal and given by $r > 0$ and that the per capita intraspecies competitions are both equal to 1. The per capita interspecies competition rate of species j on species i is given by $b_i > 0$, where $i, j \in \{1, 2\}$. The predator dies, when there is no prey, at the per capita rate $d > 0$; the predation rates on species 1 and 2 are given by $c_1, c_2 > 0$; and the quantities $e_1, e_2 > 0$ measure how efficient the predator is at using up the predated species. We will sometimes write (1.1) in the more compact form

$$\frac{dX_i}{dt}(t) = X_i(t)f_i(\mathbf{X}(t)), i = 1, 2, 3, \tag{1.2}$$

where $\mathbf{X} := (X_1, X_2, X_3), f_1(\mathbf{x}) := r - x_1 - b_1x_2 - c_1x_3, f_2(\mathbf{x}) = r - x_2 - b_2x_1 - c_2x_3, f_3(\mathbf{x}) = e_1x_1 + e_2x_2 - d$. In the absence of the predator ($X_3 = 0$) if we have

$$b_1 < 1, b_2 < 1, \tag{1.3}$$

then the coexistence of (X_1, X_2) is impossible (except for a stable manifold of dimension 1); one species will go extinct (Takeuchi and Adachi, 1983; Schreiber, 1997). However, if one assumes additionally that

$$\begin{aligned}
&e_1 r > d,\\
&e_2 r > d,\\
&r - \frac{d}{e_1}b_2 - \left(r - \frac{d}{e_1}\right)\frac{c_2}{c_1} > 0,\\
&r - \frac{d}{e_2}b_1 - \left(r - \frac{d}{e_2}\right)\frac{c_1}{c_2} > 0,
\end{aligned} \tag{1.4}$$

then the three species will coexist (Takeuchi and Adachi, 1983; Schreiber, 1997). This shows that it is possible for the predator to mediate coexistence in this setting.

We next explain how the switching is introduced. We assume there are two environmental states $\mathcal{S} := \{1, 2\}$. We note that our theoretical analysis works for any finite number of environmental states. The environmental state at time $t \geq 0$ will be given by $\xi(t) \in \mathcal{S}$. We suppose that the coefficients c_1, c_2, e_1, e_2, which capture the interaction between the predator and the two prey species, are different in the two environmental states. As a result we will have coefficients $c_1(j), c_2(j), e_1(j), e_2(j)$ if the environment is in state j.

The dynamics becomes

$$\frac{dX_i}{dt}(t) = X_i(t) f_i(\mathbf{X}(t), \xi(t)), i = 1, 2, 3, \tag{1.5}$$

where $f_1(\mathbf{x}, j) := r - x_1 - b_1 x_2 - c_1(j)x_3, f_2(\mathbf{x}, j) = r - x_2 - b_2 x_1 - c_2(j)x_3, f_3(\mathbf{x}, j) = e_1(j)x_1 + e_2(j)x_2 - d$. We assume that $\xi(t)$ is an irreducible continuous time Markov chain that switches from state 1 to 2 at rate q_{12} and from state 2 to 1 at rate q_{21}:

$$\mathbb{P}\{\xi(t + \Delta) = j | \xi(t) = i, \xi(s), s \leq t\} = q_{ij}\Delta + o(\Delta) \text{ if } i \neq j. \tag{1.6}$$

In this setting, the process spends an exponential random time, whose rate can be determined as a function of q_{12}, q_{21}, in one environment, after which it switches to the other environment, spends an exponential time there, then switches, and so on. Since $\xi(t)$ is an irreducible Markov chain, it will have a unique invariant distribution on $\mathcal{S}$ given by

$$\pi = (\pi_1, \pi_2) = \left(\frac{q_{21}}{q_{12} + q_{21}}, \frac{q_{12}}{q_{12} + q_{21}}\right).$$

1.1. Mathematical setup. It is well known that a process $(\mathbf{X}(t), \xi(t))$ satisfying (1.5) and (1.6) is a Markov process with generator acting on functions $G : \mathbb{R}^3_+ \times \mathcal{S} \mapsto \mathbb{R}^3_+$ that are continuously differentiable in $\mathbf{x}$ for each $k \in \mathcal{S}$ as

$$\mathcal{L}G(\mathbf{x}, k) = \sum_{i=1}^{3} x_i f_i(\mathbf{x}, k) \frac{\partial G}{\partial x_i}(\mathbf{x}, k) + \sum_{l \in \mathcal{S}} q_{kl} G(\mathbf{x}, l). \tag{1.7}$$

We use the norm $\|\mathbf{x}\| = \sum_{i=1}^3 |x_i|$ in $\mathbb{R}^3$. For $a, b \in \mathbb{R}$, let $a \wedge b := \min\{a, b\}$ and $a \vee b := \max\{a, b\}$. Similarly we let $\bigwedge_{i=1}^3 u_i := \min_i u_i$ and $\bigvee_{i=1}^3 u_i := \max_i u_i$.

The quantity $\mathbb{P}_{\mathbf{x},k}(A)$ will denote the probability of event A if $(\mathbf{X}(0), \xi(0)) = (\mathbf{x}, k)$. Call μ an invariant measure for the process $\mathbf{X}$ if $\mu(\cdot, \cdot)$ is a measure such that for any $k \in \mathcal{S}$ one has that $\mu(\cdot, k)$ is a Borel measure on $\mathbb{R}^3_+$ and that, if one starts the process with initial conditions distributed according to $\mu(\cdot, \cdot)$, then for any time $t \geq 0$ the distribution of $(\mathbf{X}(t), \xi(t))$ is given by $\mu(\cdot, \cdot)$.

Let Conv$\mathcal{M}$ denote the set of invariant measures of $(\mathbf{X}(t), \xi(t))$ whose support is contained in $\partial\mathbb{R}^3_+ \times \mathcal{S}$. The set of extreme points of Conv$\mathcal{M}$, denoted by $\mathcal{M}$, is the set of ergodic invariant measures with support on the boundary $\partial\mathbb{R}^3_+ \times \mathcal{S}$.

We next define what we mean by persistence in our setting.

Definition 1. *The process* $\mathbf{X}$ *is strongly stochastically persistent if it has a unique invariant probability measure* π^* *on* $\mathbb{R}^{3,\circ}_+ \times \mathcal{S}$ *and*

$$\lim_{t\to\infty} \|P_{\mathbf{X}}(t, \mathbf{x}, k, \cdot) - \pi^*(\cdot)\|_{\mathrm{TV}} = 0,\ \mathbf{x} \in \mathbb{R}^{3,\circ}_+, k \in \mathcal{S}, \tag{1.8}$$

where $\|\cdot,\cdot\|_{\mathrm{TV}}$ *is the total variation norm and* $P_{\mathbf{X}}(t, \mathbf{x}, k, \cdot)$ *is the transition probability of* $(\mathbf{X}(t), \xi(t))$.

If $\mu \in$ Conv$\mathcal{M}$ is an invariant measure and $\mathbf{X}$ spends a lot of time close to its support, supp(μ), then it will get attracted or repelled in the ith direction according to the *Lyapunov exponent*, or invasion rate,

$$\lambda_i(\mu) = \sum_{k\in\mathcal{S}} \int_{\partial\mathbb{R}^3_+} f_i(\mathbf{x}, k)\mu(d\mathbf{x}, k). \tag{1.9}$$

The intuition comes from noting that $\frac{\ln X_i(t)}{t} = \frac{\ln X_i(0)}{t} + \frac{\int_0^t f_i(\mathbf{X}(s),\xi(s))\,ds}{t}$ is approximated well by $\lambda_i(\mu)$ if t is large and $\mathbf{X}$ stays close to the support of μ.

PDMPs can be quite degenerate, and proving that there exist unique invariant probability measures in certain subspaces is far from trivial; see Benaïm (2018).

2. Well-posedness and solutions on the boundary.

In this section, we prove some preliminary results which will be useful later on.

Theorem 1. *For any* $(\mathbf{x}_0, j_0) \in \mathbb{R}^3_+ \times \mathcal{S}$ *there exists a unique solution* $(\mathbf{X}_t, \xi_t)_{t\geq 0}$ *to* (1.5) *with initial value* $(\mathbf{X}(0), \xi(0)) = (\mathbf{x}_0, j_0)$. *There exists a compact set* $\mathcal{K} \subset \mathbb{R}^3_+$ *such that every nonnegative solution of* (1.5) *eventually enters* $\mathcal{K}$ *and then remains there forever. Moreover, if* $\mathbf{X}(0) = \mathbf{x}_0 \in \mathbb{R}^{3,\circ}_+$, *then with probability one* $\mathbf{X}(t) \in \mathbb{R}^{3,\circ}_+$ *for all* $t \geq 0$.

Proof. Because the coefficients of (1.5) are locally Lipschitz for each initial value, there exists uniquely a local solution to (1.5) (up to a possible explosion time). If the initial value is positive, it is clear that the solution will remain positive up to the explosion time because we can write

$$\begin{aligned} X_1(t) &= e^{\int_0^t (r - X_1(s) - b_1 X_2(s) - c_1(\xi_s) X_3(s)) ds}, \\ X_2(t) &= e^{\int_0^t (r - X_2(s) - b_2 X_1(s) - c_2(\xi_s) X_3(s)) ds}, \\ X_3(t) &= e^{\int_0^t (e_1(\xi_s) X_1(s) + e_2(\xi_s) X_2(s) - d) ds}. \end{aligned} \tag{2.1}$$

On the other hand, it is clear that any solution with nonnegative initial value cannot blow up in a finite time. Since

$$\frac{dX_1}{dt}(t) \leq X_1(t)(r - X_1(s)),$$

it is clear that if $X_1(0) \geq 0$, then $X_1(t)$ is finite for any t. Moreover, eventually, we have $X_1(t) \leq r$. The same conclusion holds true for $X_2(t)$.

Note that

$$\frac{dX_3}{dt}(t) = X_3(t)[e_1(\xi_t)X_1(t) + e_2(\xi_t)X_2(t) - d].$$

Since we already have shown that $X_1(t), X_2(t)$ are bounded, it is clear from the above that $X_3(t)$ is finite for all t.

Finally, take $\widehat{\varepsilon} > 0$ be sufficiently small such that for all $i \in \mathcal{S}$ we have

$$\begin{aligned} c_1(i) - e_1(i)\widehat{\varepsilon} &\geq 0, \\ c_2(i) - e_2(i)\widehat{\varepsilon} &\geq 0. \end{aligned}$$

From (1.5), we have for $W_t := X_1(t) + X_2(t) + \widehat{\varepsilon} X_3(t)$ that

$$\begin{aligned} \frac{dW_t}{dt} &\leq r(X_1(t) + X_2(t)) - X_1(t)^2 - X_2(t)^2 - d\widehat{\varepsilon} X_3(t) \\ &\leq (r + d\widehat{\varepsilon})(X_1(t) + X_2(t)) - (X_1(t)^2 + X_2(t)^2) - d\widehat{\varepsilon} W_t \\ &\leq \widehat{R} - d\widehat{\varepsilon} W_t \end{aligned}$$

for some $\widehat{R} > 0$. From this equation, it is easy to show that, eventually, we have $W_t \leq \frac{\widehat{R}}{d\widehat{\varepsilon}}$, and if $W_0 \leq \frac{\widehat{R}}{d\widehat{\varepsilon}}$, then $W_t \leq \frac{\widehat{R}}{d\widehat{\varepsilon}}, t \geq 0$. As a result

$$\left\{ (x_1, x_2, x_3) \in \mathbb{R}^3_+ : x_1 + x_2 + \widehat{\varepsilon} x_3 \leq \frac{\widehat{R}}{d\widehat{\varepsilon}} \right\}$$

is an attractive invariant set for (1.5). ∎

The next assumption is enforced throughout the paper.

Assumption 2.1. The following conditions hold:

(1) $b_1 < 1, b_2 < 1$.
(2) $r \sum_{j \in \mathcal{S}} e_i(j)\pi_j > d; i = 1, 2$.
(3) $c_1(i)e_1(j) - c_1(j)e_1(i) \neq 0$ for some $i, j \in \mathcal{S}$.
(4) $c_2(i)e_2(j) - c_2(j)e_2(i) \neq 0$ for some $i, j \in \mathcal{S}$.

Let $\mu_1 = \boldsymbol{\delta}_{(r,0,0)} \times \pi$ and $\mu_2 = \boldsymbol{\delta}_{(0,r,0)} \times \pi$, where $\boldsymbol{\delta}_{\mathbf{x}}$ is the Dirac measure with mass at $\mathbf{x}$. It is noted that $(r, 0, 0)$ and $(0, r, 0)$ are equilibria on the axes Ox_1 and Ox_2, respectively. Assumption 2.1(2) implies that

$$\lambda_3(\mu_i) = r \sum_{j \in \mathcal{S}} e_i(j)\pi_j - d > 0; i = 1, 2.$$

Then in view of Benaïm (2018) or Du and Dang (2014), there exist an invariant measure μ_{13} on $\mathbb{R}^{13,\circ}_+ \times \mathcal{S}$, where $\mathbb{R}^{13,\circ}_+ := \{x_1 > 0, x_3 > 0, x_2 = 0\}$ (species X_2 is extinct in this subspace), and an invariant measure μ_{23} on $\mathbb{R}^{23,\circ}_+ \times \mathcal{S}$, where $\mathbb{R}^{23,\circ}_+ := \{x_2 > 0, x_3 > 0, x_1 = 0\}$ (species X_1 is extinct in this subspace).

On $\mathbb{R}^{12,\circ}_+ \times \mathcal{S}$, because $b_1 < 1, b_2 < 1$, the point $(x_-, y_-) := (\frac{r(1-b_1)}{1-b_1 b_2}, \frac{r(1-b_2)}{1-b_1 b_2})$ will be a saddle equilibrium for the deterministic system

$$\begin{aligned} \frac{dX_1}{dt}(t) &= X_1(t)[r - X_1(t) - b_1 X_2(t)], \\ \frac{dX_2}{dt}(t) &= X_2(t)[r - X_2(t) - b_2 X_1(t)]. \end{aligned} \tag{2.2}$$

Since the coefficients r, b_1, b_2 are not influenced by the random switching, the process $\mathbf{X}$ is fully degenerate and deterministic on $\mathbb{R}^{12,\circ}_+$. As a result, if we let $\boldsymbol{\delta}_{x_-,y_-}$ be the Dirac measure at (x_-, y_-), then

$$\mu_{12} := \boldsymbol{\delta}_{x_-,y_-} \times \pi \tag{2.3}$$

is the unique invariant probability measure of the process $(\mathbf{X}, \xi)$ from (1.5) on $\mathbb{R}_+^{12,\circ} \times \mathcal{S}$.

THEOREM 2. *There exist unique invariant measures μ_{13} and μ_{23} on $\mathbb{R}_+^{13,\circ}$ and $\mathbb{R}_+^{23,\circ}$, respectively.*

Proof. Consider the system

$$(dX_1(t), dX_3(t))^\top = F_{\xi_t}(X_1(t), X_3(t))dt \tag{2.4}$$

on $\mathbb{R}_+^{2,\circ}$, where $F_j(x_1, x_3) = [x_1(r - x_1 - c_1(j)x_3), x_3(e_1(j)x_1 - d)]^\top$, $j = 1, 2$. The dynamics of (2.4) switches between two ODEs:

$$(dX_1(t), dX_3(t))^\top = F_1(X_1(t), X_3(t))dt \tag{2.5}$$

and

$$(dX_1(t), dX_3(t))^\top = F_2(X_1(t), X_3(t))dt. \tag{2.6}$$

Let $\phi_t^1(x_1, x_3), \phi_t^2(x_1, x_3)$ be the solutions to (2.5) and (2.6) with initial condition (x_1, x_3), respectively.

We define

$$\gamma^+(x_1, x_3) = \left\{\phi_{t_n}^{k_n} \circ \cdots \circ \phi_{t_1}^{k_1}(x_1, x_3) : n \in \mathbb{Z}_+, t_l \geq 0, k_l \in \mathcal{S} : l = 1, \ldots, n\right\}$$

and for the invariant set $\mathcal{K} \subset \mathbb{R}_+^{2,\circ}$ let

$$\Gamma(\mathcal{K}) = \bigcap_{\mathbf{x} \in \mathcal{K}} \overline{\gamma^+(\mathbf{x})}$$

be the possibly empty, compact subset which is accessible for the process $(\mathbf{X}(t), \xi(t))$ from any point in $\mathcal{K}$.

To complete the proof, we need to show that $(X_1(t), X_3(t), \xi_t)$, which satisfies (2.4), has a unique invariant probability measure on $\mathbb{R}_+^{2,\circ} \times \mathcal{S}$. To that end, we will check the strong bracket condition, a concept introduced in Benaïm et al. (2015). To be precise, we will show the existence of a point $(x_1^*, x_3^*) \in \Gamma(\mathbb{R}_+^{2,\circ})$ at which $G_0 = c[F_1, F_2]$ and $G_1 = [G_0, F_1]$ will span $\mathbb{R}^2$. Here c is a to-be-specified constant, and $[\cdot, \cdot]$ is the Lie bracket of two vector fields.

Because $r \sum_{j \in \mathcal{S}} e_1(j)\pi_j > d$, there is at least one j such that $re_1(j) > d$. Without loss of generality, we can assume that $re_1(1) > d$. It is well known that, if $re_1(1) > d$, $(x_1^\diamond, x_3^\diamond) := (\frac{d}{e_1(1)}, \frac{1}{c_1(1)}(r - \frac{d}{e_1(1)}))$ is the globally asymptotically stable equilibrium of the classical VL system (2.5) on $\mathbb{R}_+^{2,\circ}$. Thus, $(x_1^\diamond, x_3^\diamond) \in \Gamma(\mathbb{R}_+^{2,\circ})$. Moreover, under the condition (3) of Assumption 2.1, $(x_1^\diamond, x_3^\diamond)$ cannot be an equilibrium of (2.6). As a result $\{\phi_t^2((x_1^\diamond, x_3^\diamond)), 0 < t < t_0\} \subset \Gamma(\mathbb{R}^{2,\circ})$. Thus, there exists $t_0 > 0$ such that $H_{t_0} := \{\phi_t^2((x_1^\diamond, x_3^\diamond)), 0 < t < t_0\}$ is an one-dimensional curve on $\mathbb{R}_+^{2,\circ}$. It is easy to check that any open segment of any line $\{ax_1 + bx_3 + c = 0, a^2 + b^2 > 0\}$ cannot be the solution to (2.6). Thus, we have a claim (C1) that, for a, b, c such that $a^2 + b^2 > 0$ and $0 < t_1 < t_2 < t_0$, we can find $t_3 \in (t_1, t_2)$ such that $\phi_{t_3}^2(x_1^\diamond, x_3^\diamond)$ does not lie on $ax_1 + bx_3 = c$.

First, consider the case $c_1(1) = c_1(2)$. Then

$$F_1(x_1, x_3) - F_2(x_1, x_3) = [0, (e_1(1) - e_1(2))(x_1x_3)]^\top,$$

$$G_0(x_1,x_3) := \frac{1}{(e_1(1)-e_1(2))}[F_1(x_1,x_3)-F_2(x_1,x_3)] = [0, x_1x_3]^\top,$$

and computing the Lie bracket $[G_0, F_1]$ we have

$$G_1(x_1,x_3) := [G_0,F_1](x_1,x_3) = [-c_1(1)x_1^2x_3, f_3(x_1,x_3)]^\top$$

for some function $f_3(x_1,x_3)$. It is clear that G_0 and G_1 span $\mathbb{R}^2$ for any $(x_1,x_3)\in\mathbb{R}_+^{2,\circ}$.

Now, we consider the case $c_1(1)-c_1(2)\neq 0$. With $p=\frac{e_1(1)-e_1(2)}{c_1(1)-c_1(2)}$, we make the following transformation: $X(t):=X_1(t)$ and $Y(t)=pX_1(t)+X_3(t)$. Then (2.4) becomes

$$\Big\{(dX(t),dY(t))^\top = \widetilde{F}_{\xi_t}(X(t),Y(t))dt, \tag{2.7}$$

where

$$\widetilde{F}_j(x,y) = \Big[x\big(r-x-c_1(j)(y-px)\big); px\big(r-x-c_1(j)(y-px)\big) + (y-px)(e_1(j)x-d)\Big]^\top,\ j=1,2.$$

Let

$$\widetilde{G}_0(x,y) := \frac{1}{-(c_1(1)-c_1(2))}[\widetilde{F}_1(x,y)-\widetilde{F}_2(x,y)] = [x(y-px),0]^\top.$$

As a result,

$$\begin{aligned}\widetilde{G}_1(x,y) :=&[\widetilde{G}_0,\widetilde{F}_1](x,y)\\ =&\Big[\widetilde{f}_3(x,y), x(y-px)\big(p(r+d)+2px(-1+pc_1(1)-e_1(1))+y(e_1(1)\\ &-pc_1(1))\big)\Big]^\top\end{aligned}$$

for some function $\widetilde{f}_3(x,y)$. The couple of vector fields $\widetilde{G}_0,\widetilde{G}_1$ span $\mathbb{R}^2$ for any $(x,y)\in\{x>0, y-px>0\}$ outside the set $\{p(r+d)+2px(-1+pc_1(1)-e_1(1))+y(e_1(1)-pc_1(1))=0\}$. This set is empty if $e_1(1)-pc_1(1)=-1+pc_1(1)-e_1(1)=0$, while it is a line otherwise. Let $\widetilde{H}_{t_0}$ be the image of H_{t_0} through the linear map $(x_1,x_3)\to(x,y)=(x_1,px_1+x_3)$. Because of the linear transformation, any open segment of any line in $\{(x,y)\in\mathbb{R}^2 : x>0, y-px>0\}$ cannot be the solution to (2.7) due to claim (C1). As a result, we can find $t_3>0$ such that $\widetilde{\phi}_{t_3}^2(x^*,y^*)$ does not lie on $p(r+d)+2px(-1+pc_1(1)-e_1(1))+y(e_1(1)-pc_1(1))=0$ (if it is a line), where $\widetilde{\phi}_t^2(x,y)$ is the solution with initial value (x,y) to (2.7) with ξ_t replaced by 2 and $x^*=x_1^\diamond, y^*=px_1^\diamond+x_3^\diamond$. Thus, $\widetilde{\phi}_{t_3}^2(x^*,y^*)$ satisfies the strong bracket condition for the vector fields $\widetilde{F}_1,\widetilde{F}_2$. Equivalently, $\phi_{t_3}^2(x_1^\diamond,x_3^\diamond)\in\Gamma(\mathbb{R}_+^{2,\circ})$ satisfies the strong bracket condition for the vector fields F_1,F_2.

Now, in view of Benaïm et al. (2015, Theorems 4.4 and 4.6), the probability measure $\mathbb{P}_{(x_1,x_3,j_0)}[(X_1(t),X_3(t),\xi_t)\in\cdot\times\{j_0\}]$ is absolutely continuous with respect to Lebesgue measure on $\mathbb{R}_+^{13,\circ}$, and there exists a unique invariant probability measure μ_{13} on $\mathbb{R}_+^{2,\circ}\times\mathcal{S}$. In addition there are constants $c>1$ and $\alpha>0$ such that for any $t\geq 0, \mathbf{x}\in\mathbb{R}_+^{13,\circ}, j\in\mathcal{S}$ we have $\|\mathbb{P}_{(x_1,x_3,j)}[(X_1(t),X_3(t),\xi_t)\in\cdot]-\mu_{13}\|_{TV}\leq ce^{-\alpha t}$; that is, the convergence is exponential. ∎

Now we present some auxiliary lemmas needed to obtain the main results.

LEMMA 2.1.

$$\int_{\mathbb{R}^3_+} \sum_{j\in\mathcal{S}} \frac{x_1 f_1(\mathbf{x},j) + x_2 f_2(\mathbf{x},j)}{x_1+x_2} \nu(d\mathbf{x},j) = 0, \nu \in \{\mu_1,\mu_2,\mu_{13},\mu_{23}\}.$$

Remark 1. Note that even though $\frac{1}{x_1+x_2}$ is undefined on the set $E_0 := \{(x_1,x_2,x_3) \in \mathbb{R}^3_+ | x_1+x_2=0\}$ this does not matter since none of the measures $\{\mu_1,\mu_2,\mu_{13},\mu_{23}\}$ put any mass on the set E_0.

Proof. To prove the lemma, one can use a contradiction argument similar to Hening and Nguyen (2018, Lemmas 3.3 and 5.1). □

For each $\nu \in \mathcal{M}$, denote by I_ν the subset of $\{1,2,3\}$ such that $\operatorname{supp}(\nu) = \{(x_1,x_2,x_3) \in \mathbb{R}^3_+ : x_i = 0 \text{ if } i \notin I_\nu\}$.

LEMMA 2.2. *For any ergodic measure $\nu \in \mathcal{M}$ we have that $\lambda_i(\nu)$ is well defined and finite. Furthermore,*

$$\lambda_i(\nu) = 0, i \in I_\nu.$$

Proof. The proof is the same as the proof of Hening and Nguyen (2018, Lemma 5.1). □

Define the normalized occupation measures $\Pi_t^{\mathbf{x},j}$ by

$$\Pi_t^{\mathbf{x},j}(d\mathbf{y},i) := \frac{1}{t}\int_0^t \mathbb{P}_{\mathbf{x},j}\{\mathbf{X}(s) \in d\mathbf{y}, \xi(s)=i\}\, ds \tag{2.8}$$

and the random normalized occupation measures by

$$\widetilde{\Pi}_t(d\mathbf{y},i) := \frac{1}{t}\int_0^t \mathbf{1}_{\{\mathbf{X}(s)\in d\mathbf{y},\xi(s)=i\}}\, ds. \tag{2.9}$$

LEMMA 2.3. *Suppose the following:*

The sequences $\{(\mathbf{x}_k,j_k)\}_{k\in\mathbb{Z}_+} \subset \mathcal{K}\times\mathcal{S}, (T_k)_{k\in\mathbb{Z}_+} \subset \mathbb{R}_+$ are such that $T_k > 1$ for all $k \in \mathbb{Z}_+$ and $\lim_{k\to\infty} T_k = \infty$.

The sequence $(\Pi_{T_k}^{\mathbf{x}_k,j_k})_{k\in\mathbb{Z}_+}$ converges weakly to an invariant probability measure π.

Then for any function $h(\mathbf{x},i) : \mathcal{K}\times\mathcal{S} \to \mathbb{R}$ that is upper semicontinuous (in $\mathbf{x}$ for each fixed i), one has

$$\lim_{k\to\infty} \int_{\mathbb{R}^3_+} \sum_{j\in\mathcal{S}} h(\mathbf{x},j)\Pi_{T_k}^{\mathbf{x}_k,j_k}(d\mathbf{x},j) \le \int_{\mathbb{R}^3_+} \sum_{j\in\mathcal{S}} h(\mathbf{x},j)\pi(d\mathbf{x},j). \tag{2.10}$$

Proof. Since $\mathcal{K}$ is a compact set, (2.10) can be obtained directly from the Portmanteau theorem. The details are left to the readers. □

3. Persistence. For $\nu \in \mathcal{M}$ remember that the invasion rate of species i with respect to $\nu \in \mathcal{M}$ is defined by

$$\lambda_i(\nu) = \sum_{j\in\mathcal{S}} \int_{\partial\mathbb{R}^3_+} f_i(\mathbf{x},j)\nu(d\mathbf{x},j).$$

We assume that

$$\lambda_2(\mu_{13}) > 0 \text{ and } \lambda_1(\mu_{23}) > 0, \tag{3.1}$$

where μ_{13}, μ_{23} are in Theorem 2. Using (2.3) we have

$$\lambda_3(\mu_{12}) = \sum_{j\in\mathcal{S}}(e_1(j)x_- + e_2(j)y_- - d)\pi_j = \overline{e}_1\frac{r(1-b_1)}{1-b_1b_2} + \overline{e}_2\frac{r(1-b_2)}{1-b_1b_2} - d.$$

Since $\overline{e}_1 r > d; \overline{e}_2 r > d$ and $\frac{1-b_1}{1-b_1b_2} + \frac{1-b_2}{1-b_1b_2} > 1$ (which can be easily checked using $b_1 < 1, b_2 < 1$), we have

$$\lambda_3(\mu_{12}) > 0. \tag{3.2}$$

By the minimax principle, (3.1) and (3.2) are equivalent to the existence of $p_1, p_2, p_3 > 0$ satisfying

$$\sum_{i=1}^{3} p_i\lambda_i(\nu) > 0, \nu \in \{\mu_1, \mu_2, \mu_{13}, \mu_{23}, \mu_{12}\}. \tag{3.3}$$

Let p_0 be sufficiently large (compared to p_1, p_2, p_3) such that

$$p_0 \min\{\lambda_1(\boldsymbol{\delta}^* \times \pi), \lambda_2(\boldsymbol{\delta}^* \times \pi)\} + \sum_{i=1}^{3} p_i\lambda_i(\boldsymbol{\delta}^* \times \pi) > 0. \tag{3.4}$$

Define

$$\begin{aligned} 2\rho^* := \min\Bigg\{ & p_0 \min\{\lambda_1(\boldsymbol{\delta}^* \times \pi), \lambda_2(\boldsymbol{\delta}^* \times \pi)\} + \sum_{i=1}^{3} p_i\lambda_i(\boldsymbol{\delta}^* \times \pi), \\ & \sum_{i=1}^{3} p_i\lambda_i(\nu), \nu \in \{\mu_1, \mu_2, \mu_{13}, \mu_{23}, \mu_{12}\}\Bigg\} > 0. \end{aligned} \tag{3.5}$$

Let $\mathcal{K}$ be the attractive compact set mentioned in Theorem 1 and $\mathcal{K}^\circ = \mathbb{R}_+^{3,\circ} \cap \mathcal{K}$. Define $\Phi : \{\mathbb{R}_+^3 \setminus \{(x_1, x_2, x_3) \in \mathbb{R}_+^3 | x_1 + x_2 = 0\}\} \times \mathcal{S} \mapsto \mathbb{R}$ by

$$\begin{aligned} \Phi(\mathbf{x}, j) = & - p_1 f_1(\mathbf{x}, j) - p_2 f_2(\mathbf{x}, j) - p_3 f_3(\mathbf{x}, j) \\ & - p_0 \frac{x_1 f_1(\mathbf{x}, j) + x_2 f_2(\mathbf{x}, j)}{x_1 + x_2}. \end{aligned}$$

Let $\widehat{\Phi} : \mathbb{R}_+^3 \times \mathcal{S} \mapsto \mathbb{R}$ be the function

$$\begin{aligned} \widehat{\Phi}(\mathbf{x}, j) = & - p_1 f_1(\mathbf{x}, j) - p_2 f_2(\mathbf{x}, j) - p_3 f_3(\mathbf{x}, j) \\ & - p_0 \min\{f_1(\mathbf{x}, j), f_2(\mathbf{x}, j)\}. \end{aligned} \tag{3.6}$$

Define $\widetilde{\Phi} : \mathbb{R}_+^3 \times \mathcal{S} \mapsto \mathbb{R}$ by

$$\widetilde{\Phi}(\mathbf{x}, j) = \begin{cases} \widehat{\Phi}(\mathbf{x}, j) \text{ if } x_1 + x_2 = 0, \\ \Phi(\mathbf{x}, j) \text{ if } x_1 + x_2 \neq 0. \end{cases}$$

It is readily seen that

$$\frac{x_1 f_1(\mathbf{x}) + x_2 f_2(\mathbf{x})}{x_1 + x_2} \geq \min\{f_1(\mathbf{x}), f_2(\mathbf{x})\}. \tag{3.7}$$

In view of (3.7), for each $j \in \mathcal{S}$, $\widetilde{\Phi}(\mathbf{x}, j)$ is an upper semicontinuous function.

LEMMA 3.1. *Suppose that* (3.1) *holds. Let* $\mathbf{p}$ *and* ρ^* *be as in* (3.5). *There exists a* $T > 0$ *such that for any* $\mathbf{x} \in \partial\mathbb{R}^3_+ \cap \mathcal{K}, j \in \mathcal{S}$ *one has*

$$\frac{1}{T}\int_0^T \mathbb{E}_{\mathbf{x},j}\widetilde{\Phi}(\mathbf{X}(t), \xi(t))dt \le -\rho^*. \tag{3.8}$$

As a corollary, there is a $\tilde{\delta} > 0$ *such that*

$$\frac{1}{T}\int_0^T \mathbb{E}_{\mathbf{x},j}\Phi(\mathbf{X}(t), \xi(t))dt \le -\frac{3}{4}\rho^* \tag{3.9}$$

for any $(\mathbf{x}, j) \in \mathcal{K}^\circ \times \mathcal{S}$ *satisfying dist*$(\mathbf{x}, \partial\mathbb{R}^3_+) < \tilde{\delta}$.

Proof. We argue by contradiction to obtain (3.8). Suppose that the conclusion of this lemma is not true. Then, we can find $(\mathbf{x}_k, j_k) \in \partial\mathbb{R}^3_+ \times \mathcal{S}, \|\mathbf{x}_k\| \le M$ and $T_k > 0$, $\lim_{k\to\infty} T_k = \infty$ such that

$$\frac{1}{T_k}\int_0^{T_k} \mathbb{E}_{\mathbf{x}_k,j_k}\widetilde{\Phi}(\mathbf{X}(t), \xi(t))dt > -\rho^*\,,\ k \in \mathbb{Z}_+. \tag{3.10}$$

Remember that the normalized occupation measures are defined by

$$\Pi^{\mathbf{x},j}_t(d\mathbf{y}, i) := \frac{1}{t}\int_0^t \mathbb{P}_{\mathbf{x},j}\{\mathbf{X}(s) \in d\mathbf{y}, \xi(s) = i\}\, ds.$$

It follows from Hening and Nguyen (2018, Lemma 4.1) that $(\Pi^{\mathbf{x}_k,j_k}_{T_k})_{k\in\mathbb{Z}_+}$ is tight. As a result $(\Pi^{\mathbf{x}_k,j_k}_{T_k})_{k\in\mathbb{Z}_+}$ has a convergent subsequence in the weak*-topology. Without loss of generality, we can suppose that $(\Pi^{\mathbf{x}_k,j_k}_{T_k})_{k\in\mathbb{Z}_+}$ is a convergent sequence in the weak*-topology. It can be shown (see Lemma 4.1 from Hening and Nguyen, 2018 or Theorem 9.9 from Ethier and Kurtz, 2009) that its limit is an invariant probability measure μ of $(\mathbf{X}, \xi)$. Since $(\mathbf{x}_k, j_k) \in \partial\mathbb{R}^3_+ \times \mathcal{S}$, the support of μ lies in $\partial\mathbb{R}^3_+ \times \mathcal{S}$. As a consequence of Lemma 2.3

$$\lim_{k\to\infty}\frac{1}{T_k}\int_0^{T_k} \mathbb{E}_{\mathbf{x}_k,j_k}\widetilde{\Phi}(\mathbf{X}(t), \xi(t))dt \le \int_{\mathbb{R}^3_+}\sum_{j\in\mathcal{S}}\widetilde{\Phi}(\mathbf{x}, j)\mu(d\mathbf{x}, j).$$

Using Lemmas 2.1 and 2.2 together with (3.5) we get that

$$\lim_{k\to\infty}\frac{1}{T_k}\int_0^{T_k} \mathbb{E}_{\mathbf{x}_k,j_k}\widetilde{\Phi}(\mathbf{X}(t), \xi(t))dt \le -2\rho^*.$$

This contradicts (3.10), which means (3.8) is proved.

With $\widehat{\Phi}$ defined in (3.6), we have $\widehat{\Phi}(\mathbf{x}, j) \ge \Phi(\mathbf{x}, j)$ for $x_1 + x_2 \ne 0$ and $\widehat{\Phi}(\mathbf{x}, j) = \widetilde{\Phi}(\mathbf{x}, j)$ if $x_1 + x_2 = 0$. As a result of (3.5)

$$\widehat{\Phi}(\mathbf{0}) = \widetilde{\Phi}(\mathbf{0}) = -\sum(p_i f_i(\mathbf{0})) - p_0 \min\{f_1(\mathbf{0}), f_2(\mathbf{0})\} \le -2\rho^*.$$

Thus

$$\begin{aligned}&\frac{1}{T}\int_0^T \mathbb{E}_{(0,0,x_3),j}\widehat{\Phi}(\mathbf{X}(t), \xi(t))dt \\ &\quad= \frac{1}{T}\int_0^T \mathbb{E}_{(0,0,x_3),j}\widetilde{\Phi}(\mathbf{X}(t), \xi(t))dt \le -\rho^*, (0,0,x_3) \in \mathcal{K}.\end{aligned} \tag{3.11}$$

Due to the Feller property of $(\mathbf{X}(t), \xi(t))$ on $\mathbb{R}^3_+ \times \mathcal{S}$ and the continuity of $\widehat{\Phi}$ on $\mathbb{R}^3_+$, there is an $\widehat{\varepsilon} > 0$ such that

$$\frac{1}{T}\int_0^T \mathbb{E}_{\mathbf{x},j}\widehat{\Phi}(\mathbf{X}(t), \xi(t))dt \leq -\frac{3}{4}\rho^* \text{ if } x_1 + x_2 \leq \widehat{\varepsilon}, (\mathbf{x}, j) \in \mathcal{K} \times \mathcal{S}.$$

Together with $\Phi(\mathbf{x}, j) \leq \widehat{\Phi}(\mathbf{x}, j), x_1 + x_2 \neq 0$, this implies

$$\frac{1}{T}\int_0^T \mathbb{E}_{\mathbf{x},j}\Phi(\mathbf{X}(t), \xi(t))dt \leq -\frac{3}{4}\rho^*,\ (\mathbf{x}, j) \in \mathcal{K}^\circ \times \mathcal{S}, x_1 + x_2 \leq \widehat{\varepsilon}. \tag{3.12}$$

If $x_1 + x_2 \neq 0$, then

$$\mathbb{P}_{\mathbf{x},j}\left\{\widetilde{\Phi}(\mathbf{X}(t), \xi(t)) = \Phi(\mathbf{X}(t), \xi(t)), t \geq 0\right\} = 1.$$

Using the Feller property of $(\mathbf{X}(t))$ on $\{(x_1, x_2, x_3) \in \mathbb{R}^3_+ | x_1 + x_2 \neq 0\}$, (3.8), and the continuity of $\Phi(\cdot, t) = \widetilde{\Phi}(\cdot, t)$ on $\{(x_1, x_2, x_3) \in \mathbb{R}^3_+ | x_1 + x_2 \neq 0\}$ one can see that there exists $\tilde{\delta} \in (0, \widehat{\varepsilon})$ for which

$$\begin{aligned}&\frac{1}{T}\int_0^T \mathbb{E}_{\mathbf{x},j}\Phi(\mathbf{X}(t), \xi(t))dt \leq -\frac{3}{4}\rho^*,\\ &(\mathbf{x}, j) \in \mathcal{K}^\circ \times \mathcal{S}, x_1 + x_2 \geq \widehat{\varepsilon}, \operatorname{dist}(\mathbf{x}, \partial\mathbb{R}^3_+) < \tilde{\delta}.\end{aligned} \tag{3.13}$$

Combining (3.12) and (3.13) yields (3.9). □

LEMMA 3.2. *Let Y be a random variable and $\theta_0 > 0$ be a constant, and suppose*

$$\mathbb{E}\exp(\theta_0 Y) + \mathbb{E}\exp(-\theta_0 Y) \leq K_1.$$

Then the log-Laplace transform $\phi(\theta) = \ln \mathbb{E}\exp(\theta Y)$ is twice differentiable on $[0, \frac{\theta_0}{2})$ and

$$\frac{d\phi}{d\theta}(0) = \mathbb{E}Y,$$

$$0 \leq \frac{d^2\phi}{d\theta^2}(\theta) \leq K_2\,, \theta \in \left[0, \frac{\theta_0}{2}\right),$$

for some $K_2 > 0$ depending only on K_1.

Proof. See Lemma 3.5 in Hening and Nguyen (2018). □

Let $\mathbf{p} = (p_0, \ldots, p_3)$ satisfy (3.5), and consider the function

$$V(\mathbf{x}) := V_{\mathbf{p}}(\mathbf{x}) = \frac{1}{(x_1 + x_2)^{p_0}\prod_{i=1}^3 x_i^{p_i}}. \tag{3.14}$$

PROPOSITION 3.1. *Let V be defined by* (3.14) *with $\mathbf{p}$ and ρ^* satisfying* (3.5) *and $T > 0$ satisfying the assumptions of Lemma* 3.1. *There are $\theta \in (0, 1)$, $K_\theta > 0$ such that, for $\mathbf{x} \in \mathcal{K}^\circ, j \in \mathcal{N}$,*

$$\mathbb{E}_{\mathbf{x},j}V^\theta(\mathbf{X}(T)) \leq \exp(-0.5\theta\rho^* T)V^\theta(\mathbf{x}) + K_\theta. \tag{3.15}$$

Proof. We have

$$\ln V(\mathbf{X}(T)) = \ln V(\mathbf{X}(0)) + \int_0^T \Phi(\mathbf{X}(t), \xi(t))dt. \tag{3.16}$$

Since Φ is bounded on $\mathcal{K} \times \mathcal{S}$, we can easily have that

$$\exp\{-HT\} \leq \frac{V(\mathbf{X}(T))}{V(\mathbf{x})} \leq \exp\{HT\}, \mathbf{x} \in \mathcal{K}, \tag{3.17}$$

for some nonrandom constant H. Because of (3.17) and the fact that $\int_0^T \Phi(\mathbf{X}(t), \xi(t)) dt = \ln(\frac{V(\mathbf{X}(T))}{V(\mathbf{x})})$ (due to (3.16)), the assumptions of Lemma 3.2 hold for the random variable $\int_0^T \Phi(\mathbf{X}(t), \xi(t))dt$. Therefore, there is $\tilde{K}_2 \geq 0$ such that

$$\begin{aligned} 0 \leq \frac{d^2\tilde{\phi}_{\mathbf{x},j,T}}{d\theta^2}(\theta) \leq \tilde{K}_2 \text{ for all } \theta \in [0,1), \\ (\mathbf{x}, j) \in \mathbb{R}^{3,\circ}_+ \times \mathcal{S}, \|\mathbf{x}\| \leq M, T \in [T^*, n^*T^*], \end{aligned} \tag{3.18}$$

where

$$\tilde{\phi}_{\mathbf{x},j,T}(\theta) = \ln \mathbb{E}_{\mathbf{x},j} \exp\left(\theta \int_0^T \Phi(\mathbf{X}(t), \xi(t))dt\right).$$

An application of Lemma 3.1 and (3.16) yields

$$\frac{d\tilde{\phi}_{\mathbf{x},j,T}}{d\theta}(0) = \mathbb{E}_{\mathbf{x},j} \int_0^T \Phi(\mathbf{X}(t), \xi(t))dt \leq -\frac{3}{4}\rho^* T \tag{3.19}$$

for all $(\mathbf{x}, j) \in \mathcal{K}^\circ$ satisfying $\text{dist}(\mathbf{x}, \partial\mathbb{R}^3_+) < \tilde{\delta}$. By a Taylor expansion around $\theta = 0$, for $\mathbf{x} \in \mathcal{K}^\circ$, $\text{dist}(\mathbf{x}, \partial\mathbb{R}^n_+) < \tilde{\delta}$, and $\theta \in [0, 1)$ and using (3.18)–(3.19) we have

$$\tilde{\phi}_{\mathbf{x},j,T}(\theta) = \tilde{\phi}_{\mathbf{x},j,T}(0) + \frac{d\tilde{\phi}_{\mathbf{x},j,T}}{d\theta}(0)\theta + \frac{1}{2}\frac{d^2\tilde{\phi}_{\mathbf{x},j,T}}{d\theta^2}(\theta')(\theta - \theta')^2 \leq -\frac{3}{4}\rho^* T\theta + \theta^2\tilde{K}_2.$$

If we choose any $\theta \in (0, 1)$ satisfying $\theta < \frac{\rho^* T^*}{4\tilde{K}_2}$, we obtain that

$$\begin{aligned} \tilde{\phi}_{\mathbf{x},j,T}(\theta) \leq -\frac{1}{2}\rho^* T\theta \text{ for all } (\mathbf{x}, j) \in \mathbb{R}^{3,\circ} \times \mathcal{S}, \|\mathbf{x}\| \leq M, \text{dist}(\mathbf{x}, \partial\mathbb{R}^n_+) \\ < \tilde{\delta}, T \in [T^*, n^*T^*], \end{aligned} \tag{3.20}$$

which leads to

$$\frac{\mathbb{E}_{\mathbf{x},j} V^\theta(\mathbf{X}(T))}{V^\theta(\mathbf{x})} = \exp \tilde{\phi}_{\mathbf{x},j,T}(\theta) \leq \exp(-0.5\rho^* T\theta). \tag{3.21}$$

In view of (3.17), we have for $(\mathbf{x}, j) \in \mathcal{K}^\circ \times \mathcal{S}$ satisfying $\text{dist}(\mathbf{x}, \partial\mathbb{R}^3_+) \geq \tilde{\delta}$ that

$$\mathbb{E}_{\mathbf{x},j} V^\theta(\mathbf{X}(T)) \leq \exp(\theta TH) \sup_{\mathbf{x} \in \mathcal{K}, \text{dist}(\mathbf{x}, \partial\mathbb{R}^n_+) \geq \tilde{\delta}} \{V(\mathbf{x})\} =: K_\theta < \infty. \tag{3.22}$$

The proof can be finished by combining (3.21) and (3.22). □

THEOREM 3. *Suppose*

$$\lambda_2(\mu_{13}) = \int_{\mathbb{R}^{13,\circ}_+} \sum_{j \in \mathcal{S}} (r - b_2x_1 - c_2(j)x_3)\mu_{13}(dx_1, dx_3, j) > 0$$

and

$$\lambda_1(\mu_{23}) = \int_{\mathbb{R}_+^{23,\circ}} \sum_{j\in\mathcal{S}} (r - b_1x_2 - c_1(j)x_3)\mu_{23}(dx_2, dx_3, j) > 0,$$

where μ_{13} *is the (unique) invariant measure on* $\mathbb{R}_+^{13,\circ} \times \mathcal{S}$ *and* μ_{23} *is the (unique) invariant measure on* $\mathbb{R}_+^{23,\circ} \times \mathcal{S}$. *Then for each* $\varepsilon > 0$, *there exists* $\delta > 0$ *such that for all* $(\mathbf{x}, j) \in \mathbb{R}_+^{3,\circ} \times \mathcal{S}$

$$\liminf_{t\to\infty} \mathbb{P}_{\mathbf{x},j}\{X_i(t) \geq \delta, i = 1, 2, 3\} \geq 1 - \varepsilon.$$

Moreover, let $\Phi_t^j(\mathbf{x})$ *be the solution to* $\frac{dX_i}{dt}(t) = X_i(t)f_i(\mathbf{X}(t), j), i = 1, 2, 3,$ *for* $j \in \mathcal{S}$ *and*

$$\Gamma(\mathbb{R}_+^{3,\circ}) = \bigcap_{\mathbf{x}\in\mathbb{R}_+^{3,\circ}} \left\{\phi_{t_n}^{k_n} \circ \cdots \circ \Phi_{t_1}^{k_1}(\mathbf{x}) : n \in \mathbb{Z}_+, t_l \geq 0, k_l \in \mathcal{S} : l = 1, \dots, n\right\}.$$

If the strong bracket condition is satisfied for some $\mathbf{x}^* \in \Gamma(\mathbb{R}_+^{3,\circ})$, *then it follows from Benaïm et al. (*2015, *Theorem* 4.6*) that the system is strongly stochastically persistent.*

Proof. In Proposition 3.1, we have constructed a Lyapunov function V satisfying (3.15). It follows from (3.15) that

$$\mathbb{E}_{\mathbf{x},j}V^\theta(\mathbf{X}(2T)) \leq \kappa^2 V^{\theta x} + K_\theta(1 + \kappa), \kappa := \exp(-0.5\theta\rho^* 2T).$$

Continuing this process, we have

$$\mathbb{E}_{\mathbf{x},j}V^\theta(\mathbf{X}(nT)) \leq \kappa^n V^{\theta x} + K_\theta(1 + \kappa + \cdots + \kappa^{n-1}) \leq \kappa^n V^{\theta x} + \frac{1}{1-\kappa}.$$

This inequality and (3.17) show that

$$\limsup_{t\to\infty} \mathbb{E}_{\mathbf{x}}V^\theta(\mathbf{X}(t)) \leq K_0 := \frac{e^{HT}}{1-\kappa}.$$

As a result, because $\lim_{x_1\wedge x_2\wedge x_3\to 0} V(\mathbf{x}) = \infty$, for each $\varepsilon > 0$, there exists $\delta > 0$ such that for all $(\mathbf{x}, j) \in \mathbb{R}_+^{3,\circ} \times \mathcal{S}$

$$\liminf_{t\to\infty} \mathbb{P}_{\mathbf{x},j}\{X_i(t) \geq \delta, i = 1, 2, 3\} \geq 1 - \varepsilon. \qquad \square$$

4. Extinction. PDMPs can be quite degenerate, and one has to do some additional work in order to see which parts of the state space are visited by the process.

THEOREM 4. *We have the following extinction results:*

(1) *If* $\lambda_2(\mu_{13}) < 0$, *then for any compact set* $\mathcal{K}_{13} \subset \mathbb{R}^{13,\circ}$ *and for any* $\varepsilon > 0$, *there exists* $\delta > 0$ *such that for all* $(x_1, x_3) \in \mathcal{K}_{13}, 0 < x_2 < \delta$ *we have*

$$\mathbb{P}_{\mathbf{x},i}\left\{\lim_{t\to\infty}\frac{\ln X_2(t)}{t}=\lambda_2(\mu_{13})<0\right\}\geq 1-\varepsilon.$$

(2) *If* $\lambda_1(\mu_{23})<0$, *then for any compact set* $\mathcal{K}_{23}\subset\mathbb{R}^{23,\circ}$ *and for any* $\varepsilon>0$, *there exists* $\delta>0$ *such that for all* $(x_2,x_3)\in\mathcal{K}_{23}, 0<x_1<\delta$ *we have*

$$\mathbb{P}_{\mathbf{x},i}\left\{\lim_{t\to\infty}\frac{\ln X_1(t)}{t}=\lambda_1(\mu_{23})<0\right\}\geq 1-\varepsilon.$$

(3) *If* $\lambda_2(\mu_{13})<0,\lambda_1(\mu_{23})>0$ *and* $\mathbb{R}_+^{13,\circ}$ *is accessible from any* $\mathbf{x}\in\mathbb{R}_+^{3,\circ}$, *that is,* $\mathbb{R}_+^{13,\circ}\cap\Gamma(\mathcal{K})\neq\emptyset$, *then*

$$\mathbb{P}_{\mathbf{x},i}\left\{\lim_{t\to\infty}\frac{\ln X_2(t)}{t}=\lambda_2(\mu_{13})<0\right\}=1.$$

(4) *If* $\lambda_1(\mu_{23})<0,\lambda_2(\mu_{13})>0$ *and* $\mathbb{R}_+^{23,\circ}$ *is accessible from any* $\mathbf{x}\in\mathbb{R}_+^{3,\circ}$, *then*

$$\mathbb{P}_{\mathbf{x},i}\left\{\lim_{t\to\infty}\frac{\ln X_1(t)}{t}=\lambda_1(\mu_{23})<0\right\}=1.$$

(5) *If* $\lambda_1(\mu_{23})<0,\lambda_2(\mu_{13})<0$ *and* $\mathbb{R}^{13,\circ}$ *and* $\mathbb{R}_+^{23,\circ}$ *are accessible from any* $\mathbf{x}\in\mathbb{R}_+^{3,\circ}$, *then*

$$\mathbb{P}_{\mathbf{x},i}\left\{\lim_{t\to\infty}\frac{\ln X_1(t)}{t}=\lambda_1(\mu_{23})<0\right\}+\mathbb{P}_{\mathbf{x},i}\left\{\lim_{t\to\infty}\frac{\ln X_2(t)}{t}=\lambda_2(\mu_{13})<0\right\}=1.$$

Proof. We assume $\lambda_2(\mu_{13})<0$ and prove part (1) first. Let $\overline{p}_1,\overline{p}_2,\overline{p}_3>0$ such that

$$\overline{p}_1\lambda_1(\mu)-\overline{p}_2\lambda_2(\mu)+\overline{p}_3\lambda_3(\mu)>0, \text{for any } \mu\in\{\boldsymbol{\delta}^*\times\pi,\mu_1,\mu_{13}\}. \tag{4.1}$$

Define

$$\overline{V}(\mathbf{x})=\frac{x_2^{\overline{p}_2}}{x_1^{\overline{p}_1}x_3^{\overline{p}_2}}.$$

As in the proof of Lemma 3.1, we can show that, for any $\mathbf{x}\in\mathbb{R}^{13,+}$ and $\|\mathbf{x}\|\leq M$, we have

$$\frac{1}{\overline{T}}\int_0^{\overline{T}}\mathbb{E}_{\mathbf{x},j}\left(-\overline{p}_1f_1(\mathbf{X}(t),\xi(t))-\overline{p}_3f_3(\mathbf{X}(t),\xi(t))+\overline{p}_2f_2(\mathbf{X}(t),\xi(t))\right)dt<-\overline{\rho}<0$$

for some $\overline{\rho}>0$, $\overline{T}>0$. Next, we can show as in Proposition 3.1 that

$$\mathbb{E}_{\mathbf{x},j}\overline{V}(\mathbf{X}(\overline{T}))\leq\overline{\kappa}\overline{V}(\mathbf{x}) \text{ for all } \mathbf{x}\in\mathbb{R}_+^{3,\circ}:x_2<\overline{\delta},\|\mathbf{x}\|\leq M \tag{4.2}$$

for some $\overline{\kappa}\in(0,1),\overline{\delta}>0$. Note that if $\overline{V}(\mathbf{x})<\overline{v}_M:=\frac{\overline{\delta}^{\overline{p}_2}}{M^{\overline{p}_1+\overline{p}_2}}$, then $x_2<\overline{\delta}$ given that $\|\mathbf{x}\|\leq M$. Pick $\overline{\theta}\in(\overline{\kappa},1)$, and define

$$\varsigma:=\inf\{k\geq 0:\overline{V}(X(k\overline{T}))>\overline{v}_M\overline{\theta}^{k-1}\}.$$

From (4.2), we have

$$\mathbb{P}_{\mathbf{x},j}\{\overline{V}(\mathbf{X}(\overline{T}))>\varsigma\}\leq\frac{\mathbb{E}_{\mathbf{x},j}\overline{V}(\mathbf{X}(\overline{T}))}{\varsigma}\leq\frac{\overline{\kappa}}{\varsigma}\overline{V}(\mathbf{x}). \tag{4.3}$$

In particular, we have

$$\mathbb{P}_{\mathbf{x},j}\{\eta = 1\} \le \frac{\overline{\kappa}}{\overline{v}_M\overline{\theta}}\overline{V}(\mathbf{x}).$$

Similarly, using the Markov property of $(\mathbf{X}(t), \xi(t))$ and (4.3), we have

$$\begin{aligned}\mathbb{P}_{\mathbf{x},j}\{\eta = 2\} &= \mathbb{E}_{\mathbf{x},j}\left[\mathbf{1}_{\{\eta>1\}}\mathbb{P}_{\mathbf{X}(\overline{T}),\xi(\overline{T})}\{\eta = 2\}\right]\\ &\le \mathbb{E}_{\mathbf{x},j}\left[\mathbf{1}_{\{\eta>1\}}\frac{\overline{\kappa}}{\overline{v}_M\overline{\theta}^2}\overline{V}(\mathbf{X}(\overline{T}))\right]\\ &\le \frac{\overline{\kappa}^2}{\overline{v}_M\overline{\theta}^2}\overline{V}(\mathbf{x}).\end{aligned}$$

Continuing this way, we can show that

$$\mathbb{P}_{\mathbf{x},j}\{\eta < \infty\} = \sum_{k=1}^{\infty}\mathbb{P}_{\mathbf{x},j}\{\eta = k\} \le \frac{\overline{V}(\mathbf{x})}{\overline{v}_M}\sum_{k=1}^{\infty}\frac{\overline{\kappa}^k}{\overline{\theta}^k} \le \frac{\overline{V}(\mathbf{x})}{\overline{v}_M}\frac{\overline{\theta}}{\overline{\theta}-\overline{\kappa}}.$$

This easily implies that if $\overline{V}(\mathbf{x})$ is sufficiently small, then

$$\mathbb{P}_{\mathbf{x},i}\left\{\lim_{k\to\infty} X_2(k\overline{T}) = 0\right\} > 1 - \varepsilon. \tag{4.4}$$

On the other hand, since $\mathbf{X}(t)$ lives in a compact space and the coefficients of (1.5) are locally Lipschitz, there exists $\overline{K} > 0$ such that $X_2(t) \le \overline{K}X_2(k\overline{T})$ for any $k \ge 1$, $t \in (k\overline{T}, (k+1)\overline{T})$. As a result,

$$\mathbb{P}_{\mathbf{x},i}\left\{\lim_{t\to\infty} X_2(t) = 0\right\} > 1 - \varepsilon.$$

Finally, to obtain the exact convergence rate, we use the fact that any weak limit of the random occupation measure $\widetilde{\Pi}_t := \frac{1}{t}\int_0^t \mathbf{1}_{\{(\mathbf{X}(s),\xi(s))\in\cdot\}}ds$ must be almost surely an invariant measure of $(\mathbf{X}(t), \xi(t))$. If $X_2(t)$ converges to 0, then the weak limit must be an invariant measure on $\mathbb{R}_+^{13} \times \mathcal{S}$. Suppose, with a positive probability, there exists a random sequence $\{t_k\}$ such that the limit of $\widetilde{\Pi}_{t_k}$ is of the form $a_1\boldsymbol{\delta}^* \times \pi + a_2\mu_1 + a_3\mu_{13}$ with $a_1 > 0$ or $a_2 > 0$; then we show this leads to a contradiction as follows. We have from the weak convergence that

$$\lim_{k\to\infty}\frac{\ln X_1(t_k)}{t_k} = \lim_{k\to\infty}\lambda_1(\widetilde{\Pi}_{t_k}) = \lambda_1(a_1\boldsymbol{\delta}^* \times \pi + a_2\mu_1 + a_3\mu_{13}) = a_1\lambda_1(\boldsymbol{\delta}^* \times \pi)$$

because $\lambda_1(\mu_1) = 0, \lambda_1(\mu_{13}) = 0$. Since $\lambda_1(\boldsymbol{\delta}^* \times \pi) > 0$, we must have $a_1 = 0$; otherwise $\lim_{k\to\infty} \ln X_1(t_k) = \infty$, which contradicts the fact that the solution is bounded.

Once we prove that $a_1 = 0$, we have

$$\lim_{k\to\infty}\frac{\ln X_3(t_k)}{t_k} = \lim_{k\to\infty}\lambda_3(\widetilde{\Pi}_{t_k}) = \lambda_3(a_2\mu_1 + a_3\mu_{13}) = a_2\lambda_3(\mu_1)$$

since $\lambda_3(\mu_{13}) = 0$. The fact that $X_3(t)$ is bounded implies that $a_2 = 0$ as well.

As a result, we proved that the only weak limit of $\widetilde{\Pi}_t$, if $X_2(t)$ converges to 0 is μ_{13}. Because of this uniqueness, we have

$$\lim_{t\to\infty} \frac{\ln X_2(t)}{t} = \lim_{t\to\infty} \lambda_2(\widetilde{\Pi}_t) = \lambda_2(\mu_{13})$$

for almost all trajectories satisfying $\lim_{t\to\infty} X_2(t) = 0$.

Combining this conclusion and (4.4) completes our proof for part (1). Part (2) is similar.

For parts (3), (4), and (5), we combine the result from part (1), the accessibility of the boundary, and Benaïm et al. (2015, Lemma 3.1) to obtain that

$$\mathbb{P}_{(\mathbf{x}_0,i)}\left(\lim_{t\to\infty} \operatorname{dist}(\mathbf{X}(t), \partial\mathbb{R}^3_+) = 0\right) > 0.$$

This implies that there is no invariant measure on $\mathbb{R}^{3,\circ}_+ \times \mathcal{S}$. As a result, any weak limit of $\widetilde{\Pi}_t(\cdot) := \frac{1}{t}\int_0^t \mathbf{1}_{\{(\mathbf{X}(s),\xi(s))\in\cdot\}} ds$ is an invariant measure on the boundary $\partial\mathbb{R}^{3,\circ}_+ \times \mathcal{S}$. This can be used in conjunction with a standard contradiction argument (Hening and Nguyen, 2018, Lemma 5.8) to obtain the claims in parts (3), (4), and (5). ∎

5. Examples. In this section, we showcase our theoretical results in two specific illuminating examples. For the deterministic system, without switching, corresponding to fixing $\xi(t) = j \in \mathcal{S}, t \geq 0$, if $b_1, b_2 < 1$, coexistence for the prey ecosystem (X_1, X_2) is impossible in the absence of the predator. However, if $e_1(j)r > d$ and $e_2(j)r > d$ and

$$\lambda_2(\delta_{13}, j) = r - \frac{d}{e_1(j)} b_2 - \left(r - \frac{d}{e_1(j)}\right)\frac{c_2(j)}{c_1(j)} > 0,$$

$$\lambda_1(\delta_{23}, j) = r - \frac{d}{e_2(j)} b_1 - \left(r - \frac{d}{e_2(j)}\right)\frac{c_1(j)}{c_2(j)} > 0,$$

where (δ_{13}, j) is the point mass at the unique equilibrium of (X_1, X_3) in environment j on $R^{13,\circ}_+$, then the three-species ecosystem (X_1, X_2, X_3) exhibits coexistence.

We will study how the random switching can change the long-term behavior of such ecosystems.

Example 5.1. Consider the parameters

$$\begin{cases} r = 1, \quad d = 0.1, \\ b_1 = 0.55, \quad b_2 = 0.95, \\ c_1(1) = 0.15, \quad c_1(2) = 0.4, \\ c_2(1) = 0.178, \quad c_2(2) = 0.45, \\ e_1(1) = 0.6, \quad e_1(2) = 0.85, \\ e_2(1) = 0.45, \quad e_2(2) = 0.15. \end{cases}$$

Then

$$\begin{cases}\lambda_2(\delta_{13},1)\approx -0.0667,\\ \lambda_2(\delta_{13},2)\approx -0.05,\\ \lambda_2(\delta_{23},1)\approx 0.185,\\ \lambda_2(\delta_{23},2)\approx 0.3111,\end{cases}$$

and

$$\begin{cases} r-\frac{d}{\overline{e_1}}b_2-\left(r-\frac{d}{\overline{e_1}}\right)\frac{\overline{c_2}}{\overline{c_1}}\approx 0.0022,\\ r-\frac{d}{\overline{e_2}}b_1-\left(r-\frac{d}{\overline{e_2}}\right)\frac{\overline{c_1}}{\overline{c_2}}\approx 0.1742,\end{cases}$$

where we set $\overline{g}=(g(1)+g(2))/2$ for $g=c_1,c_2,e_1,e_2$. When the switching between the two environments is fast with equal rates $1\to 2$ and $2\to 1$, standard averaging arguments show that $\lambda_2(\mu_{13})\approx r-\frac{d}{\overline{e_1}}b_2-(r-\frac{d}{\overline{e_1}})\frac{\overline{c_2}}{\overline{c_1}}$ and $\lambda_1(\mu_{23})\approx r-\frac{d}{\overline{e_2}}b_1-(r-\frac{d}{\overline{e_2}})\frac{\overline{c_1}}{\overline{c_2}}$.

As a result, the equilibrium point on the boundary $\mathbb{R}_+^{13,\circ}$ is asymptotically stable for both deterministic systems corresponding to state 1 and state 2. This shows that in the deterministic systems prey 2 goes extinct. However, with switching we have $\lambda_2(\mu_{13})>0$ and $\lambda_1(\mu_{23})>0$. By Theorem 3 the three species coexist and converge to the unique invariant measure π^* on $\mathbb{R}_+^{3,\circ}$ (see Figure 1).

Example 5.2. Consider the parameters

$$\begin{cases} r=1, \quad d=0.1,\\ b_1=0.9, \quad b_2=0.5,\\ c_1(1)=0.15, \quad c_1(2)=0.4,\\ c_2(1)=0.28, \quad c_2(2)=0.4,\\ e_1(1)=0.15, \quad e_1(2)=0.85,\\ e_2(1)=0.15, \quad e_2(2)=0.4.\end{cases}$$

Then

$$\begin{cases}\lambda_1(\delta_{13},1)\approx 0.1333,\\ \lambda_1(\delta_{13},2)\approx 0.0667,\\ \lambda_1(\delta_{23},1)\approx 0.6643,\\ \lambda_1(\delta_{23},2)\approx 0.0333,\end{cases}$$

and

$$\begin{cases} r-\frac{d}{\overline{e_1}}b_2-(r-\frac{d}{\overline{e_1}})\frac{\overline{c_2}}{\overline{c_1}}\approx -0.1114,\\ r-\frac{d}{\overline{e_2}}b_1-(r-\frac{d}{\overline{e_2}})\frac{\overline{c_1}}{\overline{c_2}}\approx 0.2483.\end{cases}$$

This shows that the equilibrium point in the interior $\mathbb{R}_+^{3,\circ}$ is asymptotically stable for both deterministic systems corresponding to state 1 and state 2. The three species coexist in both environments if there is no randomness. However, when the switching is fast, one has $\lambda_2(\mu_{13})\approx r-\frac{d}{\overline{e_1}}b_2-(r-\frac{d}{\overline{e_1}})\frac{\overline{c_2}}{\overline{c_1}}<0$ and $\lambda_1(\mu_{23})\approx r-\frac{d}{\overline{e_2}}b_1-(r-\frac{d}{\overline{e_2}})\frac{\overline{c_1}}{\overline{c_2}}>0$. Using Theorem 4 we see that, in the random system, prey 1 and the predator persist, while prey 2 can go extinct with a large probability when it starts at a small initial density (see Figures 1 and 2).

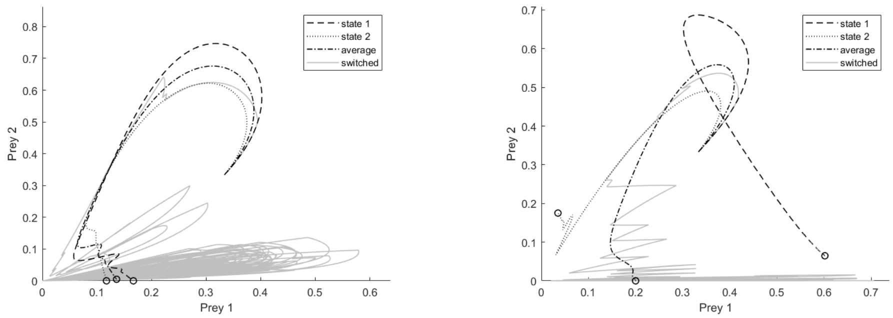
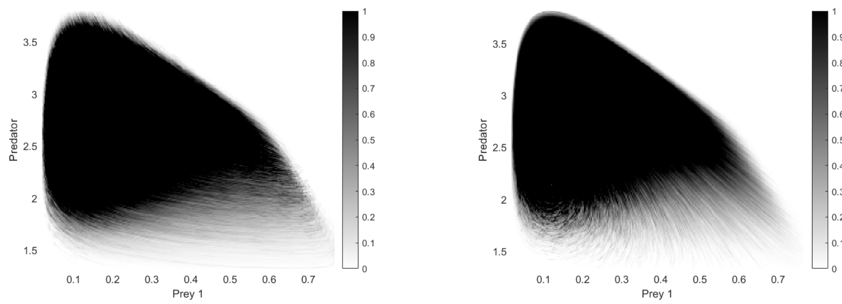


FIG. 1. *Trajectories in prey 1–prey 2 phase space. All simulations in a given panel have the same initial conditions. Small circles denote the fixed points for the various vector fields. Left panel: (Example* 5.1*) In each fixed environmental state prey* 2 *goes extinct. Switching makes all three species coexist. Right panel: (Example* 5.2*) In each fixed environmental state the three species coexist. Prey* 2 *goes extinct in the switched system.*



(a) State 1 (b) State 2

FIG. 2. *(Example* 5.2*) The joint density of $X_1 =$ Prey 1 and $X_3 =$ Predator in state* 1 *and state* 2 *was simulated* 100 *times on the time interval* $[0, 10000]$ *for a solution* (X_1, X_2, X_3) *with initial values* $(2/3, 2/3, 3/2)$*. The occupation measure for the switched system converges exponentially fast to the absolutely continuous invariant measure on* $\mathbb{R}_+^{13,\circ}$.

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