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ROBUST UNIFORM PERSISTENCE IN DISCRETE AND CONTINUOUS DYNAMICAL SYSTEMS USING LYAPUNOV EXPONENTS

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Abstract. This paper extends the work of Salceanu and Smith [12, 13] where Lyapunov exponents were used to obtain conditions for uniform persistence in a class of dissipative discrete-time dynamical systems on the positive orthant of $\mathbb{R}^m$, generated by maps. Here a unified approach is taken, for both discrete and continuous time, and the dissipativity assumption is relaxed. Sufficient conditions are given for compact subsets of an invariant part of the boundary of $\mathbb{R}^m_+$ to be robust uniform weak repellers. These conditions require Lyapunov exponents be positive on such sets. It is shown how this leads to robust uniform persistence. The results apply to the investigation of robust uniform persistence of the disease in host populations, as shown in an application.

1. **Introduction.** Even though the concept of persistence is more general (see, for example [5, 18, 21], to mention just a few sources), roughly speaking it means that the solutions of a certain deterministic difference or differential system of equations stay some positive distance away from a subset of the boundary of the positive cone $\mathbb{R}^m_+$, the natural state space for these models (here *boundary* refers to points in $\mathbb{R}^m_+$ that are not situated in $(\mathbb{R}^m_+)^0$, the *interior* of $\mathbb{R}^m_+$). Usually this subset is closed, invariant (*i.e.*, solutions that start in there stay in there for all times) and, in order to generate persistence, also a repeller for the complementary dynamics (*i.e.*, for the dynamics in $(\mathbb{R}^m_+)^0$). Among the mathematical tools that have been used in persistence theory we mention average Lyapunov functions (Garay and Hofbauer [4]), normal or external Lyapunov exponents (Ashwin, Buescu and Stewart [2]; Garay and Hofbauer [4]; Schreiber [14]), invariant probability measures (Hirsch, Smith and Zhao [6]; Garay and Hofbauer [4]; Schreiber [14]), or chain recurrence, used in combination with Morse decompositions or acyclicity theory (Hirsch, Smith and Zhao [6]; Smith and Zhao [19]; Thieme [20]). Hofbauer and Schreiber [7] use both Lyapunov exponents and invariant probability measures to obtain robust persistence results for interacting structured populations modeled by differential equations. Most of this theory requires a fair amount of knowledge about the dynamics on the boundary and in order to apply it, one needs to characterize the attracting sets for the boundary dynamics as *uniform weak repellers* (see [12, 13, 20]) for the complementary dynamics.

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As mathematical models used to help answer biological questions may be sensitive to changes in parameter values (such as birth and death rates, disease transmission rates etc.) an important question is whether or not the conclusions inferred from the model still remain valid after small changes in parameter values have been made. We are particularly interested in the form of persistence that is uniform with respect to small changes in parameters, that is, *robust uniform persistence*. Our main goal is to provide sufficient conditions for compact sets on the boundary to be *robust uniform weak repellers* (see (18) below) and we do this by using Lyapunov exponents. By choosing an appropriate positively invariant subset Z of the positive cone $\mathbb{R}_+^{p+q} = \{(x, y) \mid x \in \mathbb{R}_+^p,\ y \in \mathbb{R}_+^q\}$ as our state space, we consider a class of dynamical systems generated by autonomous difference or differential equations (of the form (4) and (5)) for which the boundary subset $X = \{z = (x, y) \in Z \mid y = 0\}$ and $Z \setminus X$ are positively invariant. This setup is motivated by certain biological applications where the vector y represents the disease, or infection, in a given population, in which case it is customary to assume X to be (positively) invariant. Thus the main application of our results would be to mathematical models of biological populations in which one wants to know under what circumstances the disease can persist in the host population. A common assumption in the literature is that the system is dissipative (*i.e.*, there is a compact set that attracts all trajectories). We relax this assumption and replace it by the existence of a closed set B that "absorbs" every trajectory of all (small) perturbations of the system, and $\{z = (x, y) \in B \mid |y| \le \delta\}$ is bounded, for some $\delta > 0$. We show that if $M = B \cap X$ is compact, positively invariant and all Lyapunov exponents $\lambda(z, \eta)$, corresponding to positive unit vectors η, are positive for all z in the union of the omega limit sets of points of M, then M is a robust uniform weak repeller, which we use then as our "key ingredient" to obtain robust uniform persistence. Besides not requiring the systems to be dissipative, we mention another important advantage of our approach, namely that it avoids dealing explicitly with the acyclic covering of M, or with M being isolated, when regarded as a subset of the boundary, both of these being common assumptions in the literature (see, for example, Theorem 1.3.2 in [21]).

We apply these results to a model of Jones et al. [8] for horizontally and vertically transmitted parasites (HTP and VTP, respectively) in a host population. In [8] the authors are primarily interested in VTP persistence in the host population, due to its interaction with HTP (*i.e.*, VTP provides the host with a certain level of protection against HTP). However, this persistence is limited to the existence of a locally stable interior equilibrium. We show that the VTP can robustly persist in the host population in the more general sense described above and also obtain other various forms of persistence in the model.

The paper is organized as follows: in Section 2 we present our framework, together with notation and some basic results. Section 3 contains our main results regarding robust uniform persistence for the type of models described in Section 2. In Section 4 we introduce the Lyapunov exponents and use them to formulate equivalent conditions for uniform persistence. We also determine when Lyapunov exponents $\lambda(z, \eta)$ are independent of η and, in the particular case when boundary attractors consist of union of periodic orbits, show how Lyapunov exponents are related to spectral radii. In Section 5 we give a summary of our results. Section 6 contains an application where we give sufficient conditions for a vertically transmitted parasite to persist in a host population. Some of the results in the present paper have been obtained by employing ideas from the author's PhD dissertation [11].

2. **Preliminaries.** Let $F : \mathbb{R}^p \times \mathbb{R}^q \to \mathbb{R}^p \times \mathbb{R}^q$ be a continuous map and consider the following discrete and continuous equations:

$$z_{n+1} = F(z_n),\ z_0 \in \mathbb{R}^p_+ \times \mathbb{R}^q_+, \tag{1}$$

and

$$z'(t) = F(z(t)),\ z(0) \in \mathbb{R}^p_+ \times \mathbb{R}^q_+,\ t \in \mathbb{R}_+. \tag{2}$$

When referring to (2), we are tacitly assuming existence and uniqueness of solutions for all t.

We consider particular forms of such systems, namely when the set

$$X = \{z = (x, y) \in \mathbb{R}^p_+ \times \mathbb{R}^q_+ \mid y = 0\} \tag{3}$$

is positively invariant (solutions that start in X at $t = 0$ remain in X for all $t > 0$). In doing so, we are primarily motivated by (but not limited to) biological models where the "subvector" y represents the disease (in which case it is customary that X is considered to be positively invariant). Thus, let $f : \mathbb{R}^p_+ \times \mathbb{R}^q_+ \to \mathbb{R}^p$ and $g : \mathbb{R}^p_+ \times \mathbb{R}^q_+ \to \mathbb{R}^q$ such that $F(z) = (f(z), g(z))$, $\forall\, z \in \mathbb{R}^p_+ \times \mathbb{R}^q_+$. We further assume that (1) and (2) can be written as

$$\begin{cases} x_{n+1} &= f(z_n) \\ y_{n+1} &= A(z_n)y_n \end{cases} \tag{4}$$

and, respectively, as

$$\begin{cases} x' &= f(z) \\ y' &= A(z)y \end{cases} \tag{5}$$

where the matrix function $A(z)$ is continuous.

Note that we do not assume either $F(0) = 0$ or that $\{z \in \mathbb{R}^{p+q}_+ \mid x = 0\}$ is positively invariant, although both often hold in applications.

Let $\mathbb{T}$ denote either the set of nonnegative integers $\mathbb{Z}_+$, or the set of nonnegative real numbers $\mathbb{R}_+$. Let $\phi(t, z)$, $t \in \mathbb{T}$, $z \in \mathbb{R}^{p+q}_+$, $\phi(0, z) = z$, be the solution generated by (4) (for $t \in \mathbb{Z}_+$) or by (5) (for $t \in \mathbb{R}_+$). ϕ, which is usually referred to as *the (solution) semiflow*, generates a dynamical system. Hereafter, when we consider $t \in \mathbb{Z}_+$, we refer to (4), while when we consider $t \in \mathbb{R}_+$ we refer to (5). Writing $t \in \mathbb{T}$ means that we consider both discrete and continuous cases. We denote by $\phi^{(2)}(t, z)$ the vector consisting of the last q components of $\phi(t, z)$ (*i.e.*, $\phi^{(2)}(t, z)$ is the projection of $\phi(t, z)$ onto $\mathbb{R}^q$). We work with the vector norm $|x| = \sum_{i=1}^m |x^{(i)}|$, where $x = (x^{(1)}, ..., x^{(m)})$, and with the matrix norm $||A|| = ||A||_1 = \max_j |A^{(j)}|$, where $A^{(j)}$ is the jth column of A. $\overline{S}$ denotes the closure of set S. A *neighborhood* of $S \subseteq \mathbb{R}^{p+q}_+$ is an open set in $\mathbb{R}^{p+q}_+$ that contains S. We define the distance between two points in the usual way: $d(x, y) = |x - y|$, while the distance between a point x and a set $S \neq \emptyset$ is $d(x, S) = \inf_{y \in S} d(x, y)$. We call a matrix A *non-negative* (*strictly positive*), and write, $A \geq 0$ ($A \gg 0$) if each entry of A is a non-negative (positive) number. We call A *positive*, and write $A > 0$, if $A \geq 0$, but A is not the zero matrix. Assume analogous definitions (and notation) for vectors.

Definition 2.1. The system (or semiflow, or dynamical system generated by) (1) or (2) is called uniformly (strongly) persistent if

$$\exists\, \varepsilon > 0,\ \liminf_{t\to\infty} |\phi(t, z)^{(2)}| > \varepsilon,\ \forall\, z = (x, y) \in \mathbb{R}^{p+q}_+,\ |y| > 0. \tag{6}$$

Usually one omits the word "strongly" and just says "uniformly persistent".

Lemma 2.2. *The following hold:*

a) *If* $\mathbb{R}_+^{p+q}$ *is positively invariant for (4), then* $A(z) \geq 0,\ \forall\, z \in X$.

b) $\mathbb{R}_+^{p+q}$ *is positively invariant for (5)* $\Leftrightarrow F_i(z) \geq 0$, *whenever* $z \in \mathbb{R}_+^{p+q}$ *satisfies* $z^{(i)} = 0 \Rightarrow A(z)$ *is quasipositive on* X, *i.e.,* $a_{ij}(z) \geq 0,\ \forall\, z \in X,\ \forall\, i \neq j$.

Proof. *a)* Using the positive invariance of X, we have:

$$\begin{aligned} g(x,y) &= g(x,y) - g(x,0) = \int_0^1 \frac{d}{ds} g(x,sy)\,ds = \int_0^1 \frac{\partial g}{\partial y}(x,sy) y\,ds \\ &= (\int_0^1 \frac{\partial g}{\partial y}(x,sy)\,ds) y. \end{aligned}$$

Hence $A(z) = \int_0^1 \frac{\partial g}{\partial y}(x,sy)\,ds$. Thus $A(x,0) = \frac{\partial g}{\partial y}(x,0)$. On the other hand,

$$\begin{aligned} \frac{\partial g_i}{\partial y^{(j)}}(x,0) &= \lim_{h\to 0^+} \frac{g_i(x^{(1)},...,x^{(p)},0,...,y^{(j)}=h,...,0) - g_i(x,0)}{h} \\ &= \lim_{h\to 0^+} \frac{g_i(x^{(1)},...,x^{(p)},0,...,y^{(j)}=h,...,0)}{h} \geq 0. \end{aligned} \tag{7}$$

b) For the equivalence relation, see [17, Proposition B.7.] and the comments which follow it.

Now we show the last implication. Let $z = (x,0) \in X$ and $i,j \in \{1,...,q\}$, $i \neq j$. Then the hypothesis $F_i(z) \geq 0$, whenever $z \in \mathbb{R}_+^{p+q}$ satisfies $z^{(i)} = 0$, implies that $g_i(x^{(1)},...,x^{(p)},0,...,y^{(j)}=h,...,0) \geq 0$, for all $h \geq 0$. Hence, $a_{ij}(z) \geq 0$ (see proof of part *a)*). □

Hereafter we assume that $\mathbb{R}_+^{p+q}$ is positively invariant for both (4) and (5). Let I denote the identity matrix. Let $P(n,z)$ and $P(t,z)$ denote the fundamental matrices of solutions, respectively for

$$u_{n+1} = A(\phi(n,z))u_n \tag{8}$$

and

$$v'(t) = A(\phi(t,z))v(t). \tag{9}$$

In other words, $P(t,z)$, $t \in \mathbb{T}$ has the form:

$$P(n,z) = \begin{cases} A(\phi(n-1,z))A(\phi(n-2,z))...A(z), & if\ n \geq 1 \\ I, & if\ n = 0 \end{cases} \tag{10}$$

for discrete time and

$$P(t,z) = I + \int_0^t A(\phi(s,z))P(s,z)ds \tag{11}$$

for continuous time.

Remark 1. $P(t,z) \geq 0, \forall\, z \in X,\ \forall\, t \in \mathbb{T}$.

Proof. The discrete case follows directly from Lemma 2.2 and the fact that X is positively invariant. For the continuous case, we have that $a_{ij}(z) \geq 0,\ \forall\, z \in X,\ \forall\, i \neq j$ (see again Lemma 2.2). Then, from [16, Remark 1.3, p. 34], we have that any solution $v(t)$ to (9) with $v(0) \geq 0$ satisfies $v(t) \geq 0,\ \forall\, t \geq 0$. Hence $P(t,z) \geq 0, \forall\, z \in X,\ \forall\, t \geq 0$. □

Notice that $P(t,z)$ is continuous in z for $t \in \mathbb{Z}_+$, and $P(t,z)$ is continuous in (t,z) for $t \in \mathbb{R}_+$. We can say that $P(t,z)$ represents the matrix cocycle (see [1, p. 5 or p. 63]) generated by (8) or by (9). A key property possessed by P is:

$$P(t_2, \phi(t_1,z))P(t_1,z) = P(t_1+t_2,z),\ \forall\, z \in \mathbb{R}^{p+q},\ \forall\, t_1,t_2 \in \mathbb{T}. \tag{12}$$

In order to avoid "problematic" dynamics, we restrict our state space to a subset Z of the positive cone $\mathbb{R}_+^{p+q}$, having the following property:

(H1) Both Z and $Z \setminus X$ are non-empty and positively invariant.

We assume that hereafter (H1) holds true.

3. **Robust uniform persistence.**

Throughout this section we assume that F as in (1) or (2) depends continuously on a parameter $\xi \in \mathbb{R}^l$, for some $l \in \mathbb{Z}_+$. Then $\phi(t,z,\xi)$, $P(t,z,\xi)$ denote the semiflow, respectively the fundamental solution matrix for (8) or (9), corresponding to ξ. To simplify notation, whenever we consider a fixed parameter ξ_0, we often write $\phi(t,z)$, $P(t,z)$ etc., in short, for $\phi(t,z,\xi_0)$, $P(t,z,\xi_0)$. If ξ_0 is a parameter and (6) holds with $\phi(t,z)$ replaced by $\phi(t,z,\xi)$, for all $\xi \in \Delta$, where Δ is some neighborhood of ξ_0, then we say that the system (or semiflow, or dynamical system generated by) (1) or (2) is *robust uniformly persistent.*

Before we present our main persistence result we need the following lemma, which gives a characterization of compact subsets of X as having certain repelling properties, in the robust sense. Denote the set of unit vectors in $\mathbb{R}_+^q$ by U.

Lemma 3.1. *Let $K \subset X$ be compact and $\xi_0 \in \mathbb{R}^l$ a fixed parameter. Assume that*

$$\forall\,(z,\eta) \in K \times U,\ \exists\, \tau = \tau(z,\eta) \in \mathbb{T}\setminus\{0\} \text{ such that } |P(\tau,z,\xi_0)\eta| > 1. \tag{13}$$

Then there exist bounded neighborhoods V and Δ of K and ξ_0 respectively, and $c > 1$, τ_{min}, $\tau_{max} > 0$ such that for all $z \in V$ and $\xi \in \Delta$ having the property that $\phi(t,z,\xi) \in V$, $\forall\, t \in [0,t_0]$, for some $t_0 > 0$, there exist numbers $0 = \nu_0, \nu_1, \ldots, \nu_n$, for some $n \in \mathbb{Z}_+$, satisfying:

(*i*) $\tau_{min} \le \nu_i - \nu_{i-1} \le \tau_{max}$, $\forall\, i \in \{1,...,n\}$,
(*ii*) $\nu_{n-1} \le t_0 < \nu_n$ *and*
(*iii*) $|P(\nu_i,z,\xi)\eta| \ge c^i, \forall \eta \in U, i \in \{1,...,n\}$, *if* $z \in K$, *or* $|P(\nu_i,z,\xi)y| \ge c^i|y|, \forall i \in \{1,...,n\}$, *if* $z = (x,y) \in V \setminus X$.

In particular, all trajectories corresponding to solutions $\phi(t,z,\xi)$, with $z \in V\setminus X$ and $\xi \in \Delta$, leave V.

Proof. Let $W = K \times U \times \{\xi_0\}$ and $\hat{w} = (\hat{z},\hat{\eta},\xi_0) \in W$. From (13) we have that there exists $\hat{\tau} = \hat{\tau}(\hat{z},\hat{\eta}) \in \mathbb{T}\setminus\{0\}$ such that $|P(\hat{\tau},\hat{z},\xi_0)\hat{\eta}| > 1$. The function $(z,\eta,\xi_0) \mapsto |P(\hat{\tau},z,\xi_0)\eta|$ being continuous, there exist $\delta_{\hat{w}} > 0$, $c_{\hat{w}} > 1$ such that

$$|P(\hat{\tau},z,\xi)\eta| > c_{\hat{w}},\ \forall\, w = (z,\eta,\xi) \in B_{\delta_{\hat{w}}}(\hat{w}), \tag{14}$$

where $B_{\delta_{\hat{w}}}(\hat{w}) := \{w \in Z \times U \times \mathbb{R}^l \mid |w - \hat{w}| < \delta_{\hat{w}}\}$ (*i.e.*, $B_{\delta_{\hat{w}}}(\hat{w})$ is the ball in W centered at $\hat{w}$ and having radius $\delta_{\hat{w}}$). Since W is compact and contained in $\cup_{w\in W} B_{\delta_w}(w)$, there exists a finite set $\{w^1,...,w^k\} \subseteq W$ such that $W \subset C := \cup_{i=1}^k B_{\delta_{w^i}}(w^i)$, where for every $i = 1,...,k$, δ_{w^i} is the quantity corresponding to w^i, coming from (14) (*i.e.*, for every $i = 1,...,k$, (14) is satisfied with $\hat{w}$ replaced by w^i). To simplify notation, let $\tau_i := \tau(w^i)$, $\delta_i := \delta_{w^i}$, $i = 1,...,k$. Also, let $c := \min_i c_{w^i}$ (hence $c > 1$), $\tau_{min} = \min_i \tau_i$ and $\tau_{max} = \max_i \tau_i$. Thus, from (14) we have that

$$|P(\tau_i,z,\xi)\eta| > c,\ \forall\, w = (z,\eta,\xi) \in B_{\delta_i}(w^i),\ \forall\, i = 1,...,k. \tag{15}$$

There exist $V \subset Z$ and $\Delta \subset \mathbb{R}^l$ bounded neighborhoods of K and ξ_0 respectively, such that $V \times U \times \Delta \subseteq C$.

Now let $z \in V$, $\xi \in \Delta$ and assume that $\phi(t, z, \xi) \in V$, $\forall t \in [0, t_0]$, for some $t_0 > 0$. First suppose $z \in K$. Let $\eta \in U$. There exists $i \in \{1, ..., k\}$ such that $(z, \eta, \xi) \in B_{\delta_i}(w^i)$. Then, from (15) we have $|P(\nu_1, z, \xi)\eta| > c$, where $\nu_1 = \tau_i$. If $\nu_1 > t_0$ we stop here, since $(i)-(iii)$ hold with $n = 1$. Otherwise, assuming that we have already obtained $\nu_0, ..., \nu_r$ ($\nu_r \leq t_0$), satisfying (i) and (iii) (with n replaced by r), we define ν_{r+1} in a similar manner as ν_1. Thus, define $\alpha_r = P(\nu_r, z, \xi)\eta / |P(\nu_r, z, \xi)\eta|$. Note that α_r is well defined. Also, $P(\nu_r, z, \xi)\eta \geq 0$ (see Remark 1), hence $\alpha_r \in U$. There exists $j \in \{1, ..., k\}$ such that $(\phi(\nu_r, z, \xi), \alpha_r, \xi) \in B_{\delta_j}(w^j)$. Then again, from (15), we have

$$|P(\tau_j, \phi(\nu_j, z, \xi), \xi)\alpha_r| > c. \tag{16}$$

Define $\nu_{r+1} = \tau_j + \nu_r$. Then (16) implies, using (12), that

$$|P(\nu_{r+1}, z, \xi)\eta| > c^{r+1}. \tag{17}$$

Now take $n - 1 = \max\{i \mid \nu_i \leq t_0\}$.

For the case when $z = (x, y) \in V \setminus K$ the proof is completely similar, with η replaced by $y/|y|$. The reason α_r's are well defined and belong to U is now that $Z \setminus X$ is positively invariant and $P(t, z, \xi)y = \phi^{(2)}(t, z, \xi)$.

The fact that any solution $\phi(t, z, \xi)$ with $z \in V \setminus X$ and $\xi \in \Delta$ eventually leaves V follows directly from (iii). $\square$

The main feature of Lemma 3.1 is that it tells us (through condition (13)) when K is a *robust uniform weak repeller* (see also [12, 13, 20]), which means that, for some fixed $\varepsilon > 0$, there is a neighborhood Δ of ξ_0, such that

$$\limsup_{t \to \infty} d(\phi(t, z, \xi), K) > \varepsilon, \ \forall\, z \in Z \setminus X, \ \xi \in \Delta. \tag{18}$$

Boundary attractors (that is, attractors for the dynamics on the boundary) that are (robust) uniform weak repellers for the complementary dynamics play an important role in persistence theory, and can be used in combination with other powerful and well established results, such as "acyclicity" type theorems (see, for example [19, Theorem 3], or [19, Theorem 5]) to obtain (robust) persistence. However, this requires that $W^S(K)$, the stable manifold of K (*i.e.*, $\{z \mid d(\phi(t, z), K) \to 0, \text{ as } t \to \infty\}$), be contained in X, and also that K be invariant and isolated in $\mathbb{R}_+^{p+q}$. As K may happen to be a "complicated" set, checking such requirements in applications can be quite a task. However, once we know that K is an invariant uniform weak repeller, not necessarily robust (that is, if (18) holds with $\xi = \xi_0$), it easily follows that $W^S(K) \subseteq X$ and that K is isolated in $\mathbb{R}_+^{p+q} \setminus X$, which facilitates the use of "acyclicity" theorems. Later we will give a different result (Theorem 3.2) that has the advantage of not being "concerned" either with the acyclic covering or with the asymptotical stability of K in X (the latter implying that K is isolated in $\mathbb{R}_+^{p+q}$, once we know it is invariant and isolated in $\mathbb{R}_+^{p+q} \setminus X$). In Section 4 we will give equivalent formulations of (13) in terms of Lyapunov exponents. Another "default" assumption in "acyclicity" theorems is that the semiflow is *point dissipative*, *i.e.*, there exists a fixed "box" that absorbs all initial conditions. This prevents the use of these results to, for example, systems of difference or differential equations that model the dynamics of a certain biological population (consisting of a single or multiple species) and where a certain subpopulation grows unbounded. Intuitively, this should not rule out the possibility that the subpopulation that grows unbounded can persist uniformly, idea that is also exploited in [20]. Next, we will address this matter.

Assume that, for every fixed parameter $\xi_0 \in \mathbb{R}^l$, there exists a closed set $B \subseteq Z$ that "absorbs" every solution ($i.e.$, $\forall z \in Z, \exists t(z) \in \mathbb{T}$ such that $\phi(t, z, \xi_0) \in B, \forall t \geq t(z)$) and $M = B \cap X$ is compact. For persistence of the discrete semiflow, we need the following assumption:

(H2) For every $\delta > 0$, there exists V_0 a neighborhood of B and Δ a neighborhood of ξ_0 such that

$$\inf_{z \in V_0^\delta, \xi \in \Delta} d(F(z, \xi), X) > 0, \tag{19}$$

where $V_0^\delta = \{z = (x, y) \in V_0 \mid |y| \geq \delta\}$.

In addition, in both discrete and continuous time, we assume the following.

(H3) There exists a $\rho > 0$ such that the set $\{z \in B \mid |y| \leq \rho\}$ is bounded (hence compact).

Since we are not assuming dissipativity, the two assumptions above give us some "control" over what happens outside the repelling neighborhood V of M, given by Lemma 3.1. Thus, as will be seen in the proof of Theorem 3.2 below, (H2) prevents points from outside V (but close to B) to be mapped inside V, arbitrarily close to the extinction set, in one iteration of the map F. Assumption (H3) does not allow orbits to get too far from M, while still being close to X.

As we are mainly interested in persistence (hence, in particular, in the asymptotic behavior of solutions), without loss of generality we can assume that B is positively invariant (hence M is also positively invariant). We give now the main result of this section, which says when (4) and (5) are robustly uniformly persistent.

Theorem 3.2. *Assume that (13) holds with $K = M$, (H3) holds, and that for every V_0 a neighborhood of B there exists Δ a bounded neighborhood of ξ_0 such that*

$$\forall z \in Z,\ \xi \in \Delta,\ \exists\, t(z, \xi) \in \mathbb{T} \text{ such that } \phi(t, z, \xi) \in V_0,\ \forall\, t \geq t(z, \xi). \tag{20}$$

Then there exists $\varepsilon > 0$ such that

$$\liminf_{t \to \infty} d(\phi(t, z, \xi), X) > \varepsilon,\ \forall\, z \in Z \setminus X,\ \xi \in \Delta, \tag{21}$$

where ϕ is the continuous solution semiflow corresponding to (5). If, in addition, we assume (H2) then (21) holds also for the discrete solution semiflow ϕ corresponding to (4).

Proof. Since (13) holds, let V be a neighborhood of M, $\tilde{\Delta}$ a neighborhood of ξ_0, $c > 1$ and $\tau_{max} > 0$ given by Lemma 3.1, with $K = M$. We claim first that there exists $\widetilde{V}_0$ a neighborhood of B such that

$$\delta := \inf_{z \in \widetilde{V}_0 \setminus V} |y| > 0. \tag{22}$$

If (22) does not hold then we can find a sequence $(z^n)_n \subset Z \setminus V$ $(*)$ satisfying $|y^n| \to 0$ and $d(z^n, B) \to 0$. But then from (H3) we have that $(z^n)_n$ is bounded, thus it has a convergent subsequence $z^{n_k} \to z$. Hence $z \in X$. On the other hand, there exists a sequence $(b_n)_n \subset B$ such that $d(z^n, b_n) \to 0$. Then, since

$$d(z, b_{n_k}) \leq d(z, z^{n_k}) + d(z^{n_k}, b_{n_k}),$$

we have that $d(z, b_{n_k}) \to 0$. This implies that $z \in B$ (because B is closed), hence $z \in M$. But, on the other hand, $z \notin V$ (see $(*)$), and so we have a contradiction to

$M = B \cap X$. Thus the claim holds. Accordingly, fix such $\widetilde{V}_0$ (for which (22) holds). Now, using (H2), we have that there exist $V_0 \subseteq \widetilde{V}_0$ a neighborhood of B and $\Delta \subseteq \tilde{\Delta}$ a bounded neighborhood of ξ_0 for which both (19) and (20) hold.

Let $\hat{z} \in Z \setminus X$ and $\hat{\xi} \in \Delta$. From (20) and Lemma 3.1 we can assume that $\hat{z} \in V_0 \setminus V$. Then there exist $\tilde{t} \geq 0$ and $\tilde{\varepsilon} \in (0, \delta)$, $\tilde{\varepsilon}$ independent of $\hat{z}$ and $\hat{\xi}$, such that $\phi(\tilde{t}, \hat{z}, \hat{\xi}) \in V$ and $|\phi(t, \hat{z}, \hat{\xi})^{(2)}| \geq \tilde{\varepsilon}$ for all $t \in [0, \tilde{t}]$. This is obvious in the continuous case, while in the discrete case it follows from (19). Thus, it suffices to prove (21) only for $z \in V_{\tilde{\varepsilon}} = \{z = (x, y) \in V \mid |y| \geq \tilde{\varepsilon}\}$ and $\xi \in \Delta$. So assume that the $\hat{z}$ that we fixed above is in $V_{\tilde{\varepsilon}}$. Let $k \in \mathbb{Z}_+$ be such that

$$c^{k-1}\tilde{\varepsilon} > \sup_{z \in V} |y|. \tag{23}$$

Let $t_0 = k\tau_{max}$. Note that t_0 is also independent of $\hat{z}$ and $\hat{\xi}$. We make another claim, namely that there exists $t \in (0, t_0]$ such that $\phi(t, \hat{z}, \hat{\xi}) \notin V$. To show this, we argue by contradiction: suppose $\phi(t, \hat{z}, \hat{\xi}) \in V$, for all $t \in [0, t_0]$ $(**)$. Then let ν_1, ν_2, ..., ν_n be as in Lemma 3.1. Thus, we have

$$|\phi^{(2)}(\nu_{n-1}, \hat{z}, \hat{\xi})| = |P(\nu_{n-1}, \hat{z}, \hat{\xi})\hat{y}| \geq c^{n-1}|\hat{y}| \geq c^{n-1}\tilde{\varepsilon}.$$

From (i) and (ii) in Lemma 3.1 it follows that $t_0 < \nu_n \leq n\tau_{max}$, which implies $n > k$. Hence $|\phi^{(2)}(\nu_{n-1}, \hat{z}, \hat{\xi})| > c^{k-1}\tilde{\varepsilon}$. This inequality implies, according to (23), that $\phi(\nu_{n-1}, \hat{z}, \hat{\xi}) \notin V$. But $\nu_{n-1} \leq t_0$ (see (ii) in Lemma 3.1), hence we have a contradiction to $(**)$. So the claim holds.

On the other hand, since $Z \setminus X$ is positively invariant (see (H1)), there exists $\varepsilon > 0$ such that $d(\phi(t, z, \xi), X) > \varepsilon$, for all (t, z, ξ) in $[0, t_0] \times \overline{V_{\tilde{\varepsilon}}} \times \overline{\Delta}$ (which is a compact set). This, together with our second claim, completes our proof. □

Even though condition (20) does not necessarily mean that the system is dissipative (because B may not be bounded), dissipativity implies (20), as the next result shows (an explanation of the technical terms used in the next proposition and its proof can be found, for example, in [18], Chapter 2).

Proposition 3.3. *Assume that B is compact. Then there exists a compact global attractor of compact sets $\mathcal{K}$ corresponding to $\phi(t, z, \xi_0)$, and (20) holds.*

Proof. Let V_B be a bounded neighborhood of B. Since B absorbs all solutions in Z, we have that, for every $z \in \overline{V_B}$, there is a $t_z \in \mathbb{T}$ such that $\phi(t_z, z) \in V_B$. By the continuity of $\phi(t, z)$ in z, there exists a $\delta_z > 0$ such that $\phi(t_z, \tilde{z}) \in V_B$ for all $\tilde{z} \in B_{\delta_z}(z)$. We have that $\overline{V_B} \subseteq \cup_{z \in \overline{V_B}} B_{\delta_z}(z)$. Then, since $\overline{V_B}$ is compact, there exist $\{z^1, ..., z^k\} \subset \overline{V_B}$ such that $\overline{V_B} \subseteq \cup_{i=1}^k B_{\delta_{z^i}}(z^i)$. Now let $z \in V_B$. Then z must belong to some $B_{\delta_{z^i}}(z^i)$ for some $i \in \{1, ..., k\}$. Hence $\phi(t_{z^i}, z) \in V_B$. Let $T = \max_i t_{z^i}$. Again by the continuity of ϕ, there exists $p > 0$ such that $|\phi(t, z)| \leq p$, $\forall\, (t, z) \in [0, T] \times \overline{V_B}$. This proves that ϕ is asymptotically compact on V_B. Then, from [18, Theorem 2.31], $\mathcal{K} := \omega(V_B) \subseteq B$ (where $\omega(V_B)$ represents the omega limit set of V_B) is the compact attractor of compact sets for ϕ (the semiflow corresponding to ξ_0), and it contains all compact invariant sets in Z (see [18, Theorem 2.19]).

Now, for any V_0 a neighborhood of B, there exists $\delta_0 > 0$ such that the compact attractor of compact sets $\mathcal{K}_\xi$ corresponding to the semiflow $\phi(t, z, \xi)$, with $|\xi - \xi_0| < \delta_0$, is contained in V_0 (see [3, A. Lemma, p.65], or [10, Proposition 1.5.]). Hence (20) holds. □

Theorem 3.2 provides no guarantee that some of the y components of the trajectories will not get arbitrarily close (or even equal to) zero. However, if it is possible to use Theorem 3.2 via Proposition 3.3, then we get a compact set in $Z \setminus X$ that attracts all orbits starting in $Z \setminus X$. Then, in the discrete case, we can improve the persistence given by (21), where we recall that $F = (f, g)$.

Proposition 3.4. *Assume that B is compact and $g(z, \xi_0) \gg 0$ for all $z \in B$. Then there exists Δ a neighborhood of ξ_0 and $\varepsilon > 0$ such that*

$$\liminf_{n\to\infty} \min_i \{y_n(\xi)^{(i)}\} > \varepsilon, \ \forall\, \xi \in \Delta, \ z_0(\xi) \in Z \setminus X.$$

Proof. Write $g = (g_1, ..., g_q)$. Each g_i being continuous and B compact, it follows that there exist neighborhoods $\widetilde{V_0}$ and $\widetilde{\Delta}$ of B and ξ_0 respectively, and $\varepsilon > 0$, such that $g_i(z, \xi) > 2\varepsilon$, for all $i = 1, ..., q$, $z \in \widetilde{V_0}$ and $\xi \in \widetilde{\Delta}$. By Proposition 3.3, there exist $V_0 \subseteq \widetilde{V_0}$ a neighborhood of B and $\Delta \subseteq \widetilde{\Delta}$ a neighborhood of ξ_0 for which (20) holds. Now let $z_0(\xi) \in Z \setminus X$, where $\xi \in \Delta$. Then there exists $N \in \mathbb{Z}_+$ such that $z_n(\xi) \in V_0$, $\forall\, n \geq N$. Thus $y_{n+1}(\xi)^{(i)} = g_i(z_n(\xi), \xi) > 2\varepsilon$, for all $i = 1, ..., q$, $n \geq N$, hence $\liminf_{n\to\infty} \min_i y_n(\xi)^{(i)} > \varepsilon$. ☐

4. Lyapunov exponents.

Following [1, 2, 9], for any $z \in \mathbb{R}^p_+ \times \mathbb{R}^q_+$ and $\eta \in \mathbb{R}^q$ we define the Lyapunov exponent $\lambda(z, \eta)$ as

$$\lambda(z, \eta) = \limsup_{t\to\infty} \frac{1}{t} \ln |P(t, z)\eta|, \ t \in \mathbb{T}. \tag{24}$$

We also define $\ln 0 := -\infty$. Note that $\lambda(z, \eta) = \lambda(z, a\eta)$, $\forall\, a \in \mathbb{R} \setminus \{0\}$. Let $\Omega(S)$ denote the union of the omega limit sets of points in S (*i.e.*, $\Omega(S) = \cup_{z\in S}\omega(z)$). Also, since $\lambda(z, \eta)$ is independent of the magnitude of η, we assume throughout this section that $\eta \in U$ (where recall that U denotes the set of unit vectors in $\mathbb{R}^q_+$).

The next result gives equivalent formulations of (13), in terms of Lyapunov exponents.

Proposition 4.1. *Let $K \subset X$ be compact and positively invariant. The following assertions are equivalent:*

a) $\forall\, (z, \eta) \in K \times U$, $\exists\, \tau = \tau(z, \eta) \in \mathbb{T} \setminus \{0\}$ such that $|P(\tau, z)\eta| > 1$;

b) $\lambda(z, \eta) > 0$, $\forall\, (z, \eta) \in K \times U$.

If, in addition,

$$\forall\, (z, \eta) \in K \times U, \forall\, t \in \mathbb{T}, \ P(t, z)\eta \neq 0 \tag{25}$$

then a) (hence b)) is equivalent to

c) $\lambda(z, \eta) > 0$, $\forall\, (z, \eta) \in \Omega(K) \times U$.

Proof. First we prove that *a*) ⇔ *b*). By the definition of $\lambda(z, \eta)$, it should be clear that *b*) ⇒ *a*). For the converse, let $(z, \eta) \in K \times U$. Then $\phi(t, z) \in K$, $\forall t \geq 0$. From Lemma 3.1, there exists a sequence $\nu_n \to \infty$ as $n \to \infty$ and $c > 1$, $\tau_{max} > 0$ such that $|P(\nu_n, z)\eta| \geq c^n$ and $\nu_n \leq n\tau_{max}$, for all $n \in \mathbb{Z}_+$. Thus, we have

$$|P(\nu_n, z)\eta|^{1/\nu_n} > c^{n/\nu_n} \geq c^{1/\tau_{max}} \Rightarrow \frac{1}{\nu_n} \ln |P(\nu_n, z)\eta| > \frac{1}{\tau_{max}} \ln c, \ \forall\, n \geq 1.$$

Hence

$$\lambda(z, \eta) = \limsup_{t\to\infty} \frac{1}{t} \ln(|P(t, z)\eta|) \geq \frac{1}{\tau_{max}} \ln c > 0.$$

Now assume that (25) holds. Obviously *b*) ⇒ *c*). We show that *c*) ⇒ *a*). Let $(z, \eta) \in K \times U$. Using that $\omega(z) \subset X$ is compact and invariant and that *b*) ⇒ *a*), we can again apply Lemma 3.1, now with $K = \omega(z)$. So let V_z be a neighborhood of $\omega(z)$ and $c > 1$ as in the above mentioned lemma. Since $\phi(t,z) \to \omega(z)$ as $t \to \infty$, there exists $\tau \in \mathbb{T}$ such that $\phi(t,z) \in V_z$, $\forall\, t \geq \tau$. Let $\tilde{z} = \phi(\tau, z)$ and $\tilde{\eta} = P(\tau,z)\eta/|P(\tau,z)\eta|$. Note that $\tilde{\eta}$ is well defined (due to (25)), and that $\tilde{\eta} \in U$. Then $\phi(t,\tilde{z}) \in V_z$, $\forall\, t \geq 0$ and so again, from Lemma 3.1, there exists $\nu_n \to \infty$ such that $|P(\nu_n,\tilde{z})\tilde{\eta}| > c^n$, $\forall\, n \geq 1$. This implies, using (12), that

$$|P(\nu_n + \tau, z)\eta| > c^n |P(\tau,z)\eta|, \ \forall\, n \geq 1.$$

We can find an n large enough so that $c^n|P(\tau,z)\eta| > 1$. Thus $a)$ holds and with this our proof is complete. □

Remark 2. Note that (25) is automatically satisfied in the continuous case. In the discrete case, it is equivalent to

$$A(z)\eta \neq 0, \ \forall\, z \in M, \ \forall\, \eta \in U. \tag{26}$$

Hereafter we will just assume that (25) holds.

Lemma 4.2. *Let e_i be the vector in $\mathbb{R}^q$ having the i^{th} component equal to one and all the other components equal to zero. Then*

$$\min_i \lambda(z,e_i) \leq \lambda(z,\eta) \leq \max_i \{\lambda(z,e_i) \mid \eta^{(i)} > 0\}, \ \forall\, z \in M, \ \eta \in U. \tag{27}$$

Proof.

$$\lambda(z,\eta) \;=\; \lambda(z, \sum_{i=1}^{q} \eta^{(i)} e_i) \leq \max_i \lambda(z, \eta^{(i)} e_i) = \max_i \{\lambda(z,e_i) \mid \eta^{(i)} > 0\},$$

where we used the following two properties of Lyapunov exponents (see [1, p. 114]):

1) $\lambda(z, \eta_1 + \eta_2) \leq \max\{\lambda(z,\eta_1), \lambda(z,\eta_2)\}$, and
2) $\lambda(z, a\eta) = \lambda(z,\eta)$, $\forall\, a \in \mathbb{R} \setminus \{0\}$.

On the other hand we have

$$\begin{aligned} \lambda(z,\eta) &= \limsup_{t\to\infty} \frac{1}{t} \ln |P(t,z)\eta| = \limsup_{t\to\infty} \frac{1}{t} \ln |\sum_{i=1}^{q} \eta^{(i)} P(t,z) e_i| \\ &\geq \limsup_{t\to\infty} \frac{1}{t} \sum_{i=1}^{q} \eta^{(i)} \ln |P(t,z)e_i| = \sum_{i=1}^{q} \eta^{(i)} \lambda(z,e_i) \qquad (28) \\ &\geq \min_i \lambda(z,e_i) \sum_{i=1}^{q} \eta^{(i)} = \min_i \lambda(z,e_i). \qquad (29) \end{aligned}$$

□

As it will be seen below, when the matrix $A(z)$ is of a special form, Lyapunov exponents are independent of the unit vector η. Recall that the *incidence* matrix of a matrix $A = (a_{ij})_{i,j}$ is a matrix whose entry on the position (i,j), for all i and j, equals one if $a_{ij} \neq 0$ and it equals zero if $a_{ij} = 0$. Also, a non-negative matrix is called *primitive* if one of its powers has all entries positive.

Proposition 4.3. *Let $z \in M$. Assume that $\exists\, (t_k)_{k \in \mathbb{Z}_+} \subseteq \mathbb{T}$ satisfying:*

i) $\exists\, 0 < a \leq b$ *such that* $a \leq t_{k+1} - t_k \leq b$, $\forall\, k \in \mathbb{Z}_+$,
ii) $P(t,\hat{z})$ *has the same primitive incidence matrix for all* $t \in [a,b]$ *and* $\hat{z} \in \overline{\{\phi(t_k,z) \mid k \in \mathbb{Z}_+\}}$.

Then

$$\lambda(z,\eta) = \limsup_{t\to\infty} \frac{1}{t} \ln ||P(t,z)||, \ \forall\, \eta \in U. \tag{30}$$

Proof. Let $B_k := P(t_{k+1}-t_k, \phi(t_k,z)), \forall k \in \mathbb{Z}_+$. Since z is fixed, let $P(t) := P(t,z)$. Note that $i)$ implies $t_k \to \infty$. Thus, for all $t \in \mathbb{T}$, there exists a $k \in \mathbb{Z}_+$, such that $t \in [t_k, t_{k+1}]$. Let

$$\tilde{P}(k) := \begin{cases} P(t_k) = B_{k-1}\cdot \ldots \cdot B_0, \ \text{if } k \geq 1 \\ I, \ \text{if } k = 0 \end{cases} \tag{31}$$

Then $P(t) = P(t-t_k, \phi(t_k,z))\tilde{P}(k)$. First, we want to apply [15, Theorem 3.4.] for the sequence of matrices $(B_k)_{k\geq 0}$. First notice that $ii)$ implies that there exists $N \in \mathbb{Z}_+$ such that $\tilde{P}(n) \gg 0, \forall\, n \geq N$. Because each entry in $P(t,\hat{z})$ is continuous in $(t,\hat{z})$, if $\mathbb{T} = \mathbb{R}$ (respectively continuous in $\hat{z}$, if $\mathbb{T} = \mathbb{Z}_+$), it follows from $i)$ and $ii)$, that there are constants c, $d > 0$ such that

$$c \leq ||P(t,z)|| \leq d, \ \forall\, t \in [0, b-a], \ z \in M. \tag{32}$$

Note that if $(B_s)_{ij}$, the entry on the position (i,j) in matrix B_s, is positive for some s, then $\liminf_{k\to\infty}(B_k)_{ij} > 0$. Otherwise we could find sequences $(t_l)_l \subset [a,b]$, $t_l \to p \in [a,b]$, and $(z_l)_l \subset M$, $z_l \to a \in M$ such that $(P(t_l, z_l))_{ij} \to 0$ as $l \to \infty$, which implies $(P(p,a))_{ij} = 0$. But $(P(t_{s+1}-t_s, \phi(t_s,z)))_{ij} = (B_s)_{ij} > 0$, hence we would have a contradiction to $ii)$.

Thus, the following hold:

$a)$ $\min^+_{i,j}(B_k)_{ij} \geq \delta > 0, \ \forall\, k \geq 0,$

$b)$ $\max_{i,j}(B_k)_{ij} \leq \gamma < \infty,$

where $\min^+_{i,j}$ above means the minimum over all positive entries. Thus, hypotheses of [15, Theorem 3.4] hold and, according to [15, Exercise 3.6], we have that

$$\frac{\tilde{P}(k)_{li}}{\tilde{P}(k)_{lj}} \to c_{ij} > 0 \text{ as } k \to \infty, \tag{33}$$

for some c_{ij} independent of l. Then (33) implies that

$$\lim_{k\to\infty} \frac{|\tilde{P}(k)^{(i)}|}{|\tilde{P}(k)^{(j)}|} = c_{ij}, \tag{34}$$

where recall that $\tilde{P}(k)^{(i)}$ denotes the ith column of $\tilde{P}(k)$.

$$\begin{aligned} \lambda(z,\eta) &= \limsup_{t\to\infty} \frac{1}{t} \ln |P(t-t_k, \phi(t_k,z))\tilde{P}(k)\eta| \\ &\leq \limsup_{t\to\infty} \frac{1}{t} (\ln ||P(t-t_k, \phi(t_k,z))|| + \ln |\tilde{P}(k)\eta|) \\ &= \limsup_{k\to\infty} \frac{1}{t_k} \ln |\tilde{P}(k)\eta|, \end{aligned} \tag{35}$$

where we used that $\limsup_{t\to\infty} \frac{1}{t} \ln ||P(t-t_k, \phi(t_k,z))|| = 0$. This follows from (32) using that $0 \leq t - t_k \leq b - a$, $\forall\, k \geq 0$ and $\phi(t,z) \in M$, $\forall\, t \geq 0$.

On the other hand,

$$\lambda(z,\eta) \geq \limsup_{k\to\infty} \frac{1}{t_k} \ln |P(t_k)\eta| = \limsup_{k\to\infty} \frac{1}{t_k} \ln |\tilde{P}(k)\eta|. \tag{36}$$

Thus, from (35) and (36) we have that

$$\lambda(z,\eta) = \limsup_{k\to\infty} \frac{1}{t_k} \ln|\tilde{P}(k)\eta|,\ \forall\, \eta \in U. \tag{37}$$

Let $e_i \in U$ be the unit vector whose ith component equals one, and the other components are zero. Then, using (34), we get, for any $i,\ j \in \{1, ..., q\}$, that

$$\begin{aligned} \limsup_{k\to\infty} \frac{1}{t_k} \ln|\tilde{P}(k)^{(i)}| &= \limsup_{k\to\infty} \frac{1}{t_k} \ln\left(\frac{|\tilde{P}(k)^{(i)}|}{|\tilde{P}(k)^{(j)}|}|\tilde{P}(k)^{(j)}|\right) \\ &= \limsup_{k\to\infty} \left(\frac{1}{t_k} \ln\frac{|\tilde{P}(k)^{(i)}|}{|\tilde{P}(k)^{(j)}|} + \frac{1}{t_k}\ln|\tilde{P}(k)^{(j)}|\right) \\ &= \limsup_{k\to\infty} \frac{1}{t_k} \ln|\tilde{P}(k)^{(j)}|. \end{aligned} \tag{38}$$

Thus, taking into account (37) and (38), we obtain

$$\lambda(z, e_i) = \limsup_{k\to\infty} \frac{1}{t_k} \ln||\tilde{P}(k)||,\ \forall\, i = 1, ..., q. \tag{39}$$

Analogous to the way we derived (37), we can find that

$$\limsup_{t\to\infty} \frac{1}{t} \ln||P(t)|| = \limsup_{k\to\infty} \frac{1}{t_k} \ln||\tilde{P}(k)||. \tag{40}$$

Now (30) is obtained from Lemma 4.2 and using (39) and (40). □

Let $\mathcal{O}^+(z) := \{\phi(t, z) \mid t \in \mathbb{T}\}$ (which is known as *the positive orbit through* z).

Corollary 4.4. *Let $z \in M$. Equation (30) holds in any of the following cases:*

a) $t \in \mathbb{Z}_+$ and $A(\hat{z})$ has the same primitive incidence matrix for all $\hat{z} \in \overline{\mathcal{O}^+(z)}$;
b) $t \in \mathbb{R}_+$ and $A(\hat{z})$ is irreducible for all $\hat{z} \in \overline{\mathcal{O}^+(z)}$.

Proof. a) The hypothesis implies that there exists $s \geq 1$ such that $A(z^1) \cdot \ldots \cdot A(z^s) \gg 0, \forall z^1, ..., z^s \in \mathcal{O}^+(z)$. We can take the sequence $(t_k)_k$ as in Proposition 4.3 to be the sequence $0,\ s,\ 2s, ...$ Then it is trivial to check that conditions i) and ii) in the proposition are satisfied (where $a = b = s$), hence (30) holds.

b) The hypothesis implies that $P(t, z) \gg 0,\ \forall\, t > 0$ [16, Theorem 1.1.]. We can take, for example, $(t_k)_k = \mathbb{Z}_+$ and then again, conditions i) and ii) in Proposition 4.3 are satisfied (where $a = b = 1$), hence (30) holds. □

Thus, if the hypotheses of Corollary 4.4 hold for all $z \in M$ and if there exists a constant matrix C, where C is non-negative in the discrete case, respectively quasipositive in the continuous case, and such that $A(z) \geq C,\ \forall\, z \in M$, then we have the following:

1) In the discrete case, $P(n, z) \geq C^n$ for all n and z, hence

$$\lambda(z,\eta) \geq \limsup_{n\to\infty} \frac{1}{n} \ln||C^n|| = \limsup_{n\to\infty} \ln||C^n||^{\frac{1}{n}} = \ln r(C),$$

where we used that, for any matrix A, its spectral radius $r(A)$ satisfies

$$r(A) = \lim_{n\to\infty} ||A^n||^{\frac{1}{n}}. \tag{41}$$

2) In the continuous case, using [17, Theorem B.1.], we have that $P(t,z) \geq e^{tC}$ for all t and z. Hence

$$\lambda(z,\eta) \geq \limsup_{n\to\infty} \frac{1}{t} \ln ||e^{tC}|| = \limsup_{t\to\infty} \frac{1}{[t]} \ln ||e^{[t]C}|| = \ln[r(e^{C})] = s(C), \tag{42}$$

where $[\cdot]$ denotes the least integer function, while $s(C)$ is the spectral bound of C (*i.e.*, the largest of the real parts of eigenvalues of C).

Thus, if $r(C) > 1$ in the discrete case, respectively $s(C) > 0$ in the continuous case, then $\lambda(z,\eta) > 0$ for all $z \in M$, $\eta \in U$.

For the remainder of this section we address the special case when $\Omega(M)$ consists of periodic orbits, in which case the Lyapunov exponents $\lambda(z,\eta)$, whenever they are independent of η (more exactly, when they are given by (30)) and z belongs to such a periodic orbit of period T, can be expressed in terms of the spectral radius of $P(T,z)$.

Lemma 4.5. *Let $\mathcal{P} \subseteq M$ be a periodic orbit of (4) or (5) with period $T > 0$. Then $r(P(T,z))$ has the same value for all z in $\mathcal{P}$.*

Proof. The discrete case follows immediately from $r(AB) = r(BA)$ for any matrices A and B. This is trivial if $A = 0$ or $B = 0$. Thus, assume that $A \neq 0$ and $B \neq 0$, hence $||A||$, $||B|| > 0$. Using formula (41) we have that

$$\begin{aligned} r(AB) &= \lim_{n\to\infty} ||(AB)^n||^{\frac{1}{n}} = \lim_{n\to\infty} ||A(BA)^{n-1}B||^{\frac{1}{n}} \\ &\leq \lim_{n\to\infty} ||A||^{\frac{1}{n}} \{||(BA)^{n-1}||^{\frac{1}{n-1}}\}^{\frac{n-1}{n}} ||B||^{\frac{1}{n}} = r(BA). \end{aligned}$$

The opposite inequality follows by symmetry.

Now let's consider the continuous case. Let z, $\tilde{z} \in \mathcal{P}$. There exists $0 \leq \tilde{t} \leq T$ such that $\tilde{z} = \phi(\tilde{t}, z)$. Then

$$P(T,\tilde{z}) = P(T,\phi(\tilde{t},z)) = P(T+\tilde{t},z)[P(\tilde{t},z)]^{-1}. \tag{43}$$

Since $P(t,z)$ is the fundamental matrix of solutions for (9), there exist a T-periodic matrix $B(t,z)$ (*i.e.*, $B(t,z) = B(t+T,z)$, $\forall\, t \geq 0$) and a matrix $R = R(z)$ such that

$$P(t,z) = B(t,z)e^{tR(z)}. \tag{44}$$

Then, substituting in (43), we get:

$$P(T,\tilde{z}) = B(T+\tilde{t},z)e^{(T+\tilde{t})R(z)}e^{-\tilde{t}R(z)}[B(\tilde{t},z)]^{-1} = B(\tilde{t},z)e^{TR(z)}[B(\tilde{t},z)]^{-1}.$$

On the other hand, from (44) we have that $B(0,z) = I$ and because $B(t,z)$ is T-periodic, $P(T,z) = B(T,z)e^{TR(z)} = e^{TR(z)}$. Hence $P(T,z)$ and $P(T,\tilde{z})$ have the same eigenvalues, hence $r(P(T,z)) = r(P(T,\tilde{z}))$. ☐

Thus, for a periodic orbit $\mathcal{P} \subseteq M$ of period T, let $r(\mathcal{P}) := r(P(T,z))$, $\forall\, z \in \mathcal{P}$. Then, we have the following result.

Proposition 4.6. *Let $\mathcal{P} \subseteq M$ be a periodic orbit of (4) or (5), of period $T > 0$. Then*

a) $\lambda(z,\eta) \leq \dfrac{\ln r(\mathcal{P})}{T}$, $\forall\, (z,\eta) \in \mathcal{P} \times U$.

b) If (30) holds then

$$\lambda(z,\eta) = \frac{\ln r(\mathcal{P})}{T}, \ \forall\, (z,\eta) \in \mathcal{P} \times U. \tag{45}$$

Moreover, if for some $z \in \mathcal{P}$, $\lambda(z,\eta) = (\ln r(\mathcal{P}))/T$, $\forall\, \eta \in U$, then (45) holds.

Proof. *a*) Let $(z,\eta)\in\mathcal{P}\times U$. Then

$$\lambda(z,\eta)\le\limsup_{t\to\infty}\frac{1}{t}\ln||P(t,z)||=\limsup_{t\to\infty}\ln||P(t,z)||^{\frac{1}{t}}. \tag{46}$$

We have that $\forall\, t,\ \exists!\, m_t\in\mathbb{Z}_+,\ j_t\in[0,T)$ such that $t=m_tT+j_t$. So,

$$\begin{aligned} ||P(t,z)||^{\frac{1}{t}} &= ||P(j_t,z)(P(T,z))^{m_t}||^{\frac{1}{m_tT+j_t}} \\ &\le ||P(j_t,z)||^{\frac{1}{t}}||(P(T,z))^{m_t}||^{\frac{1}{m_tT+j_t}}. \end{aligned} \tag{47}$$

Since $m_t\to\infty$ as $t\to\infty$, we have that

$$||(P(T,z))^{m_t}||^{\frac{1}{m_tT+j_t}}\to[r(P(T,z))]^{\frac{1}{T}}\text{ as } n\to\infty, \tag{48}$$

where we used again (41). If $r(P(T,z))=r(\mathcal{P})=0$, then from (47) and (48) we have that $\limsup_{t\to\infty}||P(T,z)||^{\frac{1}{t}}=0$. Then (46) implies $\lambda(z,\eta)=-\infty$. So, with our convention that $\ln 0=-\infty$, we are done.

If $r(\mathcal{P})>0$, notice that $P(j_t,z)\neq 0,\ \forall\, t$, hence there exist constants $a,\ b>0$, independent of t, such that $a\le||P(j_t,z)||\le b<\infty$. So, $||P(j_t,z)||^{\frac{1}{t}}\to 1$, as $t\to\infty$. Now, from (46), (47) and (48) we obtain that

$$\lambda(z,\eta)\le\limsup_{t\to\infty}\ln||P(t,z)||^{\frac{1}{t}}\le\ln[r(P(T,z))]^{\frac{1}{T}}=\frac{\ln r(\mathcal{P})}{T}.$$

b) Let $(z,\eta)\in\mathcal{P}\times U$ and assume that (30) holds. Then

$$\lambda(z,\eta)\ge\limsup_{n\to\infty}\frac{1}{nT}\ln||P(nT,z)||=\frac{1}{T}\limsup_{n\to\infty}\ln||(P(T,z))^n||^{\frac{1}{n}}=\frac{\ln r(\mathcal{P})}{T}.$$

By using part *a*) we are done.

Now suppose that $\lambda(z,\eta)=(\ln r(\mathcal{P}))/T,\forall\eta\in U$ holds for some $z\in\mathcal{P}$. Let $\tilde{z}\in\mathcal{P}$. There exists $\tilde{t}\in\mathbb{T}$ such that $z=\phi(\tilde{t},\tilde{z})$. Then, for any $\eta\in U$, let $\alpha:=P(\tilde{t},\tilde{z})\eta>0$ and $\tilde{\alpha}=\alpha/|\alpha|\in U$. Since (25) holds (see Remark 2), $\tilde{\alpha}$ is well defined. Using (12) we have

$$\begin{aligned} \lambda(\tilde{z},\eta) &= \limsup_{t\to\infty}\frac{1}{t}\ln|P(t,\tilde{z})\eta|=\limsup_{t\to\infty}\frac{1}{t}\ln|P(t-\tilde{t},z)\alpha| \\ &= \limsup_{t\to\infty}\frac{1}{t}\ln|P(t-\tilde{t},z)\tilde{\alpha}| \\ &= \limsup_{t\to\infty}\frac{1}{t}\ln|P(t,z)\tilde{\alpha}|=\lambda(z,\tilde{\alpha})=(\ln r(\mathcal{P}))/T. \end{aligned}$$

□

Corollary 4.7. *Assume that* $\Omega(M)$ *is a union of periodic orbits and the following hold:*

1) $\forall\,\mathcal{P}\subseteq\Omega(M)$ *a periodic orbit of period* T, $\exists\, z\in\mathcal{P}$ *such that* $P(T,z)$ *is primitive;*

2) $r(P)>1$, *for each periodic orbit* $\mathcal{P}\subseteq\Omega(M)$.

Then $\lambda(z,\eta)>0,\ \forall\,(z,\eta)\in M\times U$.

Proof. We can apply Proposition 4.3 with $(t_k)_{k\ge0}=(kT)_{k\ge0}$ and $a=b=T$ to conclude that (30) holds. Now the rest follows immediately from Proposition 4.6, part *b*). □

5. **Summary of results.** In this paper, using a dynamical systems approach, we have addressed the question of robust uniform persistence in systems of difference and differential equations on $\mathbb{R}^m_+$ that possess a positively invariant boundary hyperplane X and such that $\mathbb{R}^m_+ \setminus X$ is also positively invariant. The motivation has been the investigation of disease (infection) persistence in host populations. Under the hypotheses that there exists a closed set B, whose restriction to a neighborhood of the extinction states X is compact, B has an absorbing neighborhood that absorbs all trajectories corresponding to small perturbations around a fixed parameter ξ_0, and $M = B \cap X$ is a robust uniform weak repeller, then robust uniform persistence occurs in the sense that trajectories originating in $\mathbb{R}^m_+ \setminus X$ eventually stay ε distance away from X (and ε is independent of ξ, for ξ close to ξ_0). Theorem 3.2, which gives this result, does not explicitly deal with the acyclic covering of M, nor it requires M be isolated in X, thus it is different from other well established results in the persistence theory, such as [19, Theorem 5] or [21, Theorem 1.3.2]. We have given sufficient conditions for when M is a robust uniform weak repeller (Lemma 3.1), by requiring all Lyapunov exponents $\lambda(z, \eta)$ corresponding to z in $\Omega(M)$ (the union of omega limit sets of points in M) be positive. We have further provided conditions for Lyapunov exponents $\lambda(z, \eta)$ to be independent of η, in which case they can be expressed in terms of spectral radii, given that z belongs to a periodic orbit.

6. **An application.** Here we consider the model of Jones, White and Boots [8], where a host population X is infected with two parasites: one that is horizontally transmitted, denoted by Y and referred to, in short, as HTP, and the other, that is vertically transmitted, denoted by V and referred to, in short, as VTP. HTP takes also the form of a free-living stage (W). The model in [8] is:

$$\begin{cases} X' &= (r - q(X+Y+V))X + (1-p)(af - q(X+Y+V))V - \beta XW \\ V' &= p(af - q(X+Y+V))V - (\alpha_V + b)V - \delta\beta VW \\ Y' &= (X + \delta V)\beta W - (\alpha_Y + b)Y \\ W' &= \lambda Y - \mu W \end{cases} \tag{49}$$

Following [8], we give a brief description of parameters (all assumed to be nonnegative). Thus, $r = a - b > 0$, where a and b are, respectively, the birth rate and natural death rate of the host. The hosts infected with the vertically transmitted parasite (VTP) have birth rate reduced by a factor of $1 - f$, while $p \in [0, 1]$ is the fraction of the offspring of these hosts born infected with VTP. Parameter $\delta \in [0, 1]$ measures the level of protection of hosts with VTP from HTP: $\delta = 0$ means total protection, while $\delta = 1$ means no protection. α_Y and α_V are the death rates of the host due to infection with HTP and VTP, respectively. Also, μ and λ are the death rate, respectively the birth rate, of the HTP. β and $\beta\delta$ are (per number of contacts) infection rates with free-living HTP, of susceptible and VTP-infected hosts, respectively. q is a certain crowding parameter.

The primary motivation of this model is, as explained in [8], to see that HTP can "help" VTP persist in the host population, while, as previously reported, survival just of VTP by itself would not be possible. The authors give conditions for both parasitoid strains to coexist with the host, but the only form of coexistence that they discuss is at the interior equilibrium point (*i.e.*, they provide conditions for an unique interior equilibrium (X^*, V^*, Y^*, W^*) to exist and be locally asymptotically stable). Numerical simulations to suggest host-HTP or host-HTP-VTP persistence are also provided.

However, the positive cone $\mathbb{R}^4_+$ is not positively invariant for (49), because a solution with initial condition (X_0, V_0, Y_0, W_0) with $X_0 = 0$, $V_0 > 0$ and $V_0 + Y_0 > af/q$ becomes negative for positive time (because $X'(0) = (1-p)(af - q(V_0 + Y_0))V_0 < 0$). Thus, we restrict our state space to $S := \{(X, V, Y, W) \in \mathbb{R}^4_+ \mid X + V + Y \le af/q\}$. Also, in order to make S positively invariant, we further assume that $af > r$. Thus, if $X(t) + V(t) + Y(t) = af/q$, then

$$(X + V + Y)'(t) = (r - af)X(t) - (\alpha_Y + b)Y(t) - (\alpha_V + b)V(t) < 0. \tag{50}$$

Hence $\tilde{t} \mapsto (X(\tilde{t}) + V(\tilde{t}) + Y(\tilde{t}))$ is decreasing in a neighborhood of t. Also, for any $(X_0, V_0, Y_0, W_0) \in S$, a solution $(X(t), V(t), Y(t), W(t))$ starting at (X_0, V_0, Y_0, W_0) (at $t = 0$) and having $U_0 = 0$, satisfies $U'(0) \ge 0$, where U can be X, V, Y or W. This shows that S is positively invariant. Now for any solution starting in S, we have $W' \le \lambda af/q - \mu W$, which implies that $\limsup_{t\to\infty} W(t) \le \lambda af/(q\mu)$. Hence

$$\limsup_{t\to\infty} |X(t) + V(t) + Y(t) + W(t)| \le \frac{af}{q}(1 + \lambda/\mu). \tag{51}$$

Inequality (51) and Proposition 3.3 imply that (20) holds. By applying the results in Section 3 we give various forms of persistence for model (49), in the general sense given by Definition 2.1. The conditions that we require for this are, in fact, as in Proposition 4.1 part c) (*i.e.*, the Lyapunov exponents be positive on the boundary attractors). Thus, all the persistence results that we obtain below can be regarded as robust (according to Theorem 3.2), even though, for simplicity, we formulate them for a fixed set of parameters.

We begin by considering the following inequalities:

$$\frac{paf}{\alpha_V + b} > 1 \tag{52}$$

$$\frac{\lambda r \beta}{\mu q(\alpha_Y + b)} > 1 \tag{53}$$

Proposition 6.1. *The following forms of persistence can occur in regard to (49):*

a) If (52) holds then

$$\exists\, \varepsilon > 0,\ \liminf_{t\to\infty} (X(t) + V(t)) > \varepsilon, \quad \textit{whenever } X(0) + V(0) > 0; \tag{54}$$

b) If both (52) and (53) hold then

$$\exists\, \varepsilon > 0,\ \liminf_{t\to\infty} (Y(t) + W(t)) > \varepsilon, \quad \textit{whenever } Y(0) + W(0) > 0 \textit{ and } X(0) + V(0) > 0. \tag{55}$$

Proof. a) Let $X_1 = \{(X, V, Y, W) \in S \mid X = V = 0\}$. The role of the set B from Section 3 will be played first by

$$B_1 = \{(X, V, Y, W) \in S \mid X + V + Y \le af/q,\ W \le 2\lambda af/(q\mu)\} \tag{56}$$

which, based on the arguments above, is positively invariant. Putting (49) in the form (5), we have

$$A_1(0,0,Y,W) = \begin{pmatrix} r - qY - \beta W & (1-p)(af - qY) \\ 0 & p(af - qY) - (\alpha_V + b) - \delta\beta W \end{pmatrix} \tag{57}$$

It can be easily seen that $\Omega(X_1) = \{0\}$. Thus,

$$\lambda(0, \eta) = \limsup_{t\to\infty} \frac{1}{t} \ln |e^{tA_1}\eta|, \tag{58}$$

where

$$A_1 := A_1(0,0,0,0) = \begin{pmatrix} r & (1-p)af \\ 0 & paf - (\alpha_V + b) \end{pmatrix} \tag{59}$$

Hence

$$e^{tA_1} = \begin{pmatrix} e^{tr} & * \\ 0 & e^{t(paf-(\alpha_V+b))} \end{pmatrix} \tag{60}$$

Now, using Lemma 4.2, we obtain that $\lambda(0,\eta) \geq \min\{r, paf - (\alpha_V + b)\}$, which is greater than zero (see (52)). Then from Theorem 3.2 we obtain (54).

b) Let $X_2 = \{(X,V,Y,W) \in S \mid Y = W = 0\}$. Choose an ε_1 that works for (54). Without loss of generality assume that $S_2 := \{(X,V,Y,W) \in S \mid X + V \geq \varepsilon_1\}$ is positively invariant, and let $B_2 = S_2 \cap B_1$. Also let $M_2 = B_2 \cap X_2$. Using that $b = a - r$ and the other assumptions on the parameters, we have that

$$p(af - r) - (\alpha_V + b) < 0, \tag{61}$$

from which it follows that the only equilibria in X_2 are $E_0 := (0,0,0,0)$ and $E_X := (r/q, 0, 0, 0)$. For the dynamics restricted to the X-V subspace, the extinction equilibrium E_0 is an unstable node, while E_X is asymptotically stable (again, by (61)). Hence, from the Poincaré-Bendixson theorem, we have that E_X attracts all solutions in $X_2 \setminus \{E_0\}$. So $\Omega(M_2) = \{E_X\}$. We can write

$$\begin{pmatrix} Y' \\ W' \end{pmatrix} = \begin{pmatrix} -(\alpha_Y + b) & \beta(X + \delta V) \\ \lambda & -\mu \end{pmatrix} \begin{pmatrix} Y \\ W \end{pmatrix} \tag{62}$$

Denote the 2×2 matrix above by $A_2(X,V,Y,W)$ and let $A_2 := A_2(E_X)$. Then

$$A_2 = \begin{pmatrix} -(\alpha_Y + b) & \beta r/q \\ \lambda & -\mu \end{pmatrix}. \tag{63}$$

Because (53) holds, we have $det(A_2) < 0$, hence $s(A_2) > 0$. Then (see comments following Corollary 4.4), $\lambda(E_X, \eta) > 0$, for all η in U. Thus, from Theorem 3.2, (55) holds. □

Biologically, condition (52) just says that, in what regards the VTP class, births exceed losses due both to natural and VTP-caused deaths, in which case, Proposition 6.1 *a*) says that we have host-VTP persistence. Also, condition (52) says that the HTP can invade the host-VTP population at the nontrivial HTP-free equilibrium.

Using the previous forms of persistence we now obtain persistence of the VTP. Let $X_V = \{(X,V,Y,W) \in S \mid V = 0\}$. By combining the results in *a*) and *b*), there exists an $\tilde{\varepsilon} > 0$ such that the set $\tilde{B} := \{(X,V,Y,W) \in S \mid X + V \geq \tilde{\varepsilon}$ and $Y + W \geq \tilde{\varepsilon}\}$ attracts all solutions starting with $X(0) + V(0) > 0$ and $Y(0) + W(0) > 0$. Again, without loss of generality, we can assume $\tilde{B}$ to be positively invariant. Let $M = \tilde{B} \cap X_V$.

Proposition 6.2. *If, in addition to (52) and (53), there holds*

$$\limsup_{t\to\infty} \frac{1}{t} \int_0^t p(af - q(X(s) + Y(s))) - (\alpha_V + b) - \delta\beta W(s)\; ds > 0, \tag{64}$$

for all solution of (49) that start in $\Omega(M)$, *then*

$$\exists\, \varepsilon > 0,\ \liminf_{t\to\infty} V(t) > \varepsilon, \quad \textit{whenever } Y(0) + W(0) > 0 \textit{ and } V(0) > 0. \tag{65}$$

Proof. Equation (9) is one dimensional now, with $v(t)$ being $V(t)$ and $A(\phi(t,z))$ being $p(af - q(X(t)+V(t)+Y(t))) - (\alpha_V + b) - \delta\beta W(t)$. Thus, (64) just says that $\lambda(z,\eta) > 0$ for all z in $\Omega(M)$ (note that $U = \{1\}$ in this case). Hence (65) follows from Theorem 3.2. □

As mentioned in the beginning of this section, the main interest here has been persistence of the VTP (result provided in Proposition 6.2). The reason we have shown the other forms of persistence, as in Proposition 6.1, was because (64) cannot hold at E_X (see (61)).

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