

LYAPUNOV EXPONENTS AND PERSISTENCE IN DISCRETE DYNAMICAL SYSTEMS

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ABSTRACT. The theory of Lyapunov exponents and methods from ergodic theory have been employed by several authors in order to study persistence properties of dynamical systems generated by ODEs or by maps. Here we derive sufficient conditions for uniform persistence, formulated in the language of Lyapunov exponents, for a large class of dissipative discrete-time dynamical systems on the positive orthant of \mathbb{R}^m , having the property that a nontrivial compact invariant set exists on a bounding hyperplane. We require that all so-called normal Lyapunov exponents be positive on such invariant sets. We apply the results to a plant-herbivore model, showing that both plant and herbivore persist, and to a model of a fungal disease in a stage-structured host, showing that the host persists and the disease is endemic.

1. Introduction. Persistence properties of dynamical systems have been studied by the means of various techniques, such as average Lyapunov functions [5], *normal* or *external* Lyapunov exponents [5, 18] and invariant probability measures [5, 6, 18], Morse decompositions [6] and acyclicity theory [6, 20]. Many authors, among which we mention Garay and Hofbauer [5], Schreiber [18], or Hirsch, Smith and Zhao [6] have used Lyapunov exponents and/or invariant probability measures together with the notions of *unsaturated* sets and measures for Kolmogorov-type systems, to establish persistence or robust persistence results.

The use of Lyapunov exponents in the study of biological models was pioneered by Metz [13], Metz et. al. [12], who proposed that the dominant Lyapunov exponent gives the best measure of invasion fitness, and by Rand et. al. [15] who used it to characterize the invasion *speed* of a rare species. Ashwin et al. use *normal* Lyapunov exponents and invariant measures to answer the following question: if $f : M \rightarrow M$ is a smooth map on a smooth finite dimensional manifold, N is a lower dimensional submanifold for which $f(N) \subseteq N$, and $A \subseteq N$ is an attractor for $f|_N$, is A an attractor for f , or it is an unstable saddle? Roughly, they show that if all exponents are negative then A is an attractor, if some exponents are positive, it is an unstable saddle and if all are positive then it is normally repelling. Schreiber appears to be the first to apply ergodic theory to establish robust persistence results in the ground-breaking paper [18]. He measures the ability of a potential colonizing organism to invade an invariant set determined by *resident* species by the integral

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of its per-capita growth rate with respect to one of the invariant ergodic measures on the resident invariant set, obtaining an average growth rate for the invader. Roughly, if this is positive for every such ergodic measure then the outsider can invade the resident community. He shows that if the boundary dynamics of a dissipative Kolmogorov system of interacting species has a Morse decomposition with the property that each invariant set of the decomposition can be invaded by at least one outsider, then the system is uniformly persistent as is every sufficiently small C^r perturbation of it. The proof relies on the multiplicative ergodic theorem. Hirsch, Smith, and Zhao strengthened Schreiber's result by weakening the topology of perturbations from C^r to C^0 . Mierczynski et. al. [14] use Lyapunov exponents in their study of uniform persistence for nonautonomous and random parabolic Kolmogorov systems. Hofbauer and Garay, following Schreiber, use the multiplicative ergodic theorem to relate Schreiber's notion of an unsaturated boundary invariant set to the existence of a *good* average Lyapunov function and establish robust persistence results (persistence that is uniform with respect to small changes in the vector field or map). A full treatment of the theory of Lyapunov exponents can be found in [1, 2, 9].

Motivated by the work of Schreiber and of Garay and Hofbauer, we use Lyapunov exponents to characterize weak boundary repellers of discrete dynamical systems generated by a map F on the positive cone, without the use of ergodic theory. Our arguments are elementary in character. Choosing our state space to be an appropriate positively invariant subset Z of the positive cone $\mathbb{R}_+^{p+q} := \{z = (x, y) \in \mathbb{R}^p \times \mathbb{R}^q \mid x \geq 0, y \geq 0\}$, we consider a large class of (discrete) dynamical systems for which the boundary $X = \{z \in Z \mid y = 0\}$ and $Z \setminus X$ are positively invariant. The positive invariance of X and smoothness of F ensure that the y -component of the dynamics can be expressed as

$$y_{n+1} = A(F^n(z_0))y_n = A(F^n(z_0))A(F^{n-1}(z_0)) \dots A(z_0)y_0, \quad n = 0, 1, 2, \dots$$

where $y_n = \pi \circ F^n(z_0)$ and $\pi(x, y) = y$, for some continuous non-negative matrix function $A(z)$. If M is a compact positively invariant subset of X , we call it a *uniformly weak repeller* (relative to Z) if it has a neighborhood with the property that every trajectory starting in $Z \setminus X$ has omega limit points outside the neighborhood. We give conditions for M to be a weak repeller, formulated in the language of Lyapunov exponents for the cocycle defined above. We show that M is a uniformly weak repeller if all Lyapunov exponents corresponding to positive vectors y_0 are positive. In fact, it suffices for this to hold on the union of the omega limit sets of points of M provided a simple non-degeneracy condition holds. In case all such limit sets are periodic orbits, the condition for M to be a uniformly weak repeller reduces to the familiar one that the matrix given by some permutation of the product $A(z_0)A(z_1) \dots A(z_{k-1})$ is primitive and its spectral radius exceeds unity, for each such periodic orbit $\{z_0, \dots, z_{k-1}\}$ in M . Having characterized uniformly weak repellers on X , it is natural to show uniform persistence of y , that is, to show that there exists $\varepsilon > 0$ such that $\liminf_{n \rightarrow \infty} |y_n| > \varepsilon$ or the stronger $\liminf_{n \rightarrow \infty} (\min_{1 \leq i \leq q} y_n^{(i)}) > \varepsilon$. This we do under mild compactness assumptions provided that the largest compact invariant subset M in X is a uniformly weak repeller.

Finally, we apply the results obtained to two biological models: a plant-herbivore model [8] and a stage structured (juvenile and adult) fungal disease model [3, 17]. For both models we provide sufficient conditions for uniform persistence.

We denote the m -dimensional Euclidean space by \mathbb{R}^m , on which we consider the norm $|u| = |u^{(1)}| + \dots + |u^{(m)}|$, for any $u = (u^{(1)}, \dots, u^{(m)}) \in \mathbb{R}^m$, where $|u^{(i)}|$ represents the absolute value of $u^{(i)}$. Let $d : \mathbb{R}^m \times \mathbb{R}^m \rightarrow \mathbb{R}_+$ be the distance induced by the norm $|\cdot|$. In this metric, \overline{B} denotes the closure of the set $B \subset \mathbb{R}^m$. We will also work with the matrix norm $\|A\| = \sup_{|\xi|=1} |A\xi|$. The positive cone in \mathbb{R}^m is denoted by $\mathbb{R}_+^m = \{x \in \mathbb{R}^m | x^{(i)} \geq 0, \forall i = 1, \dots, m\}$ and the interior of this by $(\mathbb{R}_+^m)^0 = \{x \in \mathbb{R}^m | x^{(i)} > 0, \forall i = 1, \dots, m\}$. For a vector valued function f , we denote by f_i the i^{th} component of f . For a vector or matrix v , we write $v \geq 0$ if its entries are non-negative and $v > 0$ ($v \gg 0$) if some (all) of its entries are positive. \mathbb{N} denotes the set of non-negative integers.

2. Main Results. Let $F : \mathbb{R}_+^p \times \mathbb{R}_+^q \rightarrow \mathbb{R}_+^p \times \mathbb{R}_+^q$ be a continuous map. Let $f : \mathbb{R}_+^p \times \mathbb{R}_+^q \rightarrow \mathbb{R}_+^p, g : \mathbb{R}_+^p \times \mathbb{R}_+^q \rightarrow \mathbb{R}_+^q$ such that $F(z) = (f(z), g(z)), \forall z \in \mathbb{R}_+^p \times \mathbb{R}_+^q$, and consider the following discrete dynamical system:

$$z_{n+1} = F(z_n), z_0 \in \mathbb{R}_+^p \times \mathbb{R}_+^q. \tag{1}$$

Given $z \in \mathbb{R}_+^p \times \mathbb{R}_+^q$, the orbit of z is defined as $\{z_n | n \geq 0, z_0 = z\}$. Whenever z_n appears in our notation below, it signifies the $n + 1$ 'st term in such an orbit. Let

$$X = \{z = (x, y) \in \mathbb{R}_+^p \times \mathbb{R}_+^q | y = 0\}. \tag{2}$$

We assume X to be positively invariant and that (1) can be written as

$$\begin{cases} x_{n+1} &= f(z_n) \\ y_{n+1} &= A(z_n)y_n \end{cases} \tag{3}$$

where $A(z)$ is a continuous matrix function satisfying $0 \leq A(x, 0)$. This would follow directly from the positive invariance of X if g is C^1 in $y^{(1)}, \dots, y^{(q)}$, in which case, $A(x, 0) = (\partial g_i / \partial y^{(j)}(x, 0))_{1 \leq i, j \leq q}$.

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

2.1. Lyapunov Exponents and Weak Repeller. Following [1, 2, 9], for any $z \in \mathbb{R}_+^p \times \mathbb{R}_+^q$ and $\eta \in \mathbb{R}^q$ we define the *normal* Lyapunov exponent $\lambda(z, \eta)$ as

$$\lambda(z, \eta) = \limsup_{n \rightarrow \infty} \frac{1}{n} \ln \left| \left(\prod_{s=n-1}^0 A(z_s) \right) \eta \right|, \tag{4}$$

where $z_0 = z$ and $\prod_{s=n}^0 A(z_s) = A(z_n)A(z_{n-1}) \dots A(z_0)$, for any $n \in \mathbb{N}$. Also, we define

$\ln 0 := -\infty$. Hereafter, whenever we write $\lambda(z, \eta)$ we assume that $z_0 = z$ in the right hand side of (4), without further notice. Note that $\lambda(z, \eta) = \lambda(z, a\eta), \forall a \in \mathbb{R} \setminus \{0\}$. Thus, since our state space consists of non-negative vectors, most of the time we consider η to be a unit vector in \mathbb{R}_+^q . Denote the set of unit vectors in \mathbb{R}_+^q by U_+ .

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:

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

In what follows we consider $M \subseteq Z \cap X$ to be a non-empty, compact and positively invariant set (with respect to (1)), unless otherwise specified.

Definition 2.1. We call the set M a *uniformly weak repeller* if there exists $\varepsilon > 0$ such that $\limsup_{n \rightarrow \infty} d(z_n, M) > \varepsilon, \forall z_0 \in Z \setminus X$.

We stress that in the above definition M is a uniformly weak repeller relative to the dynamics on $Z \setminus X$, while it may be an attractor relative to the dynamics restricted to X .

Let

$$\Omega(M) = \cup_{z \in M} \omega(z), \quad (5)$$

where $\omega(z)$ represents the omega limit set of z . In the next result we establish sufficient conditions for M to be a uniformly weak repeller.

Proposition 1. *M is a uniformly weak repeller if*

$$\lambda(z, \eta) > 0, \forall (z, \eta) \in M \times U_+. \quad (6)$$

If:

- 1) $A(z)\eta \neq 0, \forall (z, \eta) \in M \times U_+$, and
- 2) $\lambda(z, \eta) > 0, \forall (z, \eta) \in \Omega(M) \times U_+$,

then (6) holds.

As it will be seen below, when the matrix $A(z)$ is of a special form, then the Lyapunov exponents are independent of the unit vector η .

Definition 2.2. The *incidence matrix* of a matrix $A = (a_{ij})_{i,j}$ is a matrix whose entry on the position (i, j) equals one if $a_{ij} \neq 0$ and it equals zero if $a_{ij} = 0$, for all i and j .

A non-negative matrix is called *primitive* if one of its powers has all entries positive.

Proposition 2. *Let $\hat{z} \in M$. Assume that $A(z)$ has the same primitive incidence matrix for all z in the closure of the orbit of \hat{z} . Then*

$$\lambda(\hat{z}, \eta) = \limsup_{n \rightarrow \infty} \frac{1}{n} \ln \left\| \prod_{s=n-1}^0 A(z_s) \right\|, \forall \eta \in U_+. \quad (7)$$

Remark 1. If $A(z)$ has the same primitive incidence matrix for all z in M , then condition 1) of Proposition 1 is satisfied. Also, since M is compact, there exists a primitive constant matrix C such that $A(z) \geq C, \forall z \in M$. Then $\lambda(z, \eta) \geq \limsup_{n \rightarrow \infty} \frac{1}{n} \ln \|C^n\| = \ln(\limsup_{n \rightarrow \infty} \|C^n\|^{\frac{1}{n}}) = \ln r(C), \forall (z, \eta) \in M \times U_+$, where we used that, for any matrix A , its spectral radius, denoted by $r(A)$, satisfies

$$r(A) = \lim_{n \rightarrow \infty} \|A^n\|^{\frac{1}{n}}. \quad (8)$$

So, $r(C) > 1$ would imply that M is a uniformly weak repeller.

When dealing with periodic orbits, Lyapunov exponents are closely related to spectral radii. Thus, if $\mathcal{P} = \{E_0, \dots, E_{k-1}\} \subseteq M$ is a periodic orbit ($E_0 \rightarrow E_1 \rightarrow \dots \rightarrow E_{k-1} \rightarrow E_0$), let

$$A_i(\mathcal{P}) = \begin{cases} A(E_{i-1}) \dots A(E_0) A(E_{k-1}) \dots A(E_i), & \text{if } i \in \{1, \dots, k-1\} \\ A(E_{k-1}) \dots A(E_0), & \text{if } i = 0. \end{cases} \quad (9)$$

The spectral radius of $A_i(\mathcal{P})$ has the same value for each $i = 0, \dots, k-1$ and denote this common value by $r(\mathcal{P})$.

Proposition 3. *The following hold:*

- a) $\lambda(E_i, \eta) \leq \frac{\ln r(\mathcal{P})}{k}, \forall (E_i, \eta) \in \mathcal{P} \times U_+.$
- b) *If $A_i(\mathcal{P})$ is primitive then*

$$\lambda(E_i, \eta) = \frac{\ln r(\mathcal{P})}{k}, \forall \eta \in U_+. \quad (10)$$

If (10) holds for some E_i in \mathcal{P} and $A(E_j)\eta \neq 0, \forall j = 0, \dots, k-1, \forall \eta \in U_+$, then (10) holds for all E_i 's in \mathcal{P} .

The next corollary (whose proof we omit) follows directly from Proposition 3 and Proposition 1.

Corollary 1. *Assume that $\Omega(M)$ is a union of periodic orbits and the following hold:*

- (i) $\forall \mathcal{P} = \{E_0, \dots, E_{k-1}\} \subseteq \Omega(M)$ a periodic orbit, $\exists i$ such that $A_i(\mathcal{P})$ is primitive,
- (ii) $r(\mathcal{P}) > 1$, for each periodic orbit $\mathcal{P} \subseteq \Omega(M)$,
- (iii) $A(z)\eta \neq 0, \forall (z, \eta) \in M \times U_+.$

Then (6) holds, so M is a uniformly weak repeller.

According to the Multiplicative Ergodic Theorem of Oseledec (see [1, 9]), for any μ - an invariant Borel probability measure for F with support in M , there exists a positively invariant set $S \in \mathcal{B}$ (where \mathcal{B} is the σ -algebra generated by the Borel subsets of M) with $\mu(S) = 1$, having the property that for any $z \in S$ there is a “filtration” of \mathbb{R}^q : $\{0\} = V_{k(z)}(z) \subset \dots \subset V_1(z) = \mathbb{R}^q$ (where the inclusions are strict) and numbers $-\infty \leq \lambda_{k(z)-1}(z) < \dots < \lambda_1(z)$, such that for and each $1 \leq i \leq k(z)-1$,

$$\lambda(z, \eta) = \lambda_i(z) = \lim_{n \rightarrow \infty} \frac{1}{n} \ln \left| \left(\prod_{s=n-1}^0 A(z_s) \right) \eta \right|, \forall \eta \in V_i(z) \setminus V_{i+1}(z).$$

If, in addition, μ is ergodic, then $k(z) = k$ and $\lambda_i(z), i \in \{1, \dots, k-1\}$, are constant on S , which means that, for all $z \in S$ and for all $\eta \in \mathbb{R}^q$, $\lambda(z, \eta)$ can take only one of the values $\lambda_{k-1} < \dots < \lambda_1$. λ_1 is called the *top Lyapunov exponent* (see [1], page 115) or *normal stability index* (see [2]) as it determines the Lyapunov stability of M (see, for example, [2] for more details).

2.2. Persistence Results. In this section we formulate our main result (Theorem 2.3) which will be used later, together with Proposition 4, for establishing persistence properties of the two models in the next section.

Assume that there exists a compact set $\mathcal{A} \subseteq Z$ such that $z_n \rightarrow \mathcal{A}, \forall z_0 \in Z$ (i.e., \mathcal{A} attracts all initial data in Z). Without loss of generality, we can assume that \mathcal{A} is positively invariant since we could replace it by $\Omega(Z)$.

Let

$$M = \mathcal{A} \cap X. \quad (11)$$

Then, when not empty, M is compact and positively invariant. Now we state our main result:

Theorem 2.3. *Assume that M (given in (11)) is either empty or a uniformly weak repeller. Then*

$$\exists \varepsilon > 0 \text{ such that } \liminf_{n \rightarrow \infty} |y_n| > \varepsilon, \forall z_0 \in Z \setminus X.$$

The above theorem gives conditions for the compact set $\{z \in \mathcal{A} \mid |y| \geq \varepsilon\}$ to attract all trajectories in $Z \setminus X$, but there is no guarantee that some of the y components of these trajectories will not get arbitrarily close (or even equal to) zero. Next we give sufficient conditions to avoid this situation, where we recall that $F = (f, g)$.

Proposition 4. *Assume that there exists a compact set B that attracts all initial data in $Z \setminus X$ and that $g(z) \gg 0, \forall z \in B$. Then*

$$\exists \varepsilon > 0 \text{ such that } \liminf_{n \rightarrow \infty} \min_i \{y_n^{(i)}\} > \varepsilon, \forall z_0 \in Z \setminus X.$$

3. Applications. In this section we apply the previously established results to study the persistence properties of two models: a plant-herbivore model and a fungal disease model. For the former model, the one dimensional dynamics restricted to the set X are given by the Ricker growth function (see [4]), about which a great deal is known. This allows us to give somewhat sharper sufficient conditions for uniform persistence, which we define below.

Let $\rho : Z \rightarrow \mathbb{R}_+$ be continuous and not identically zero.

Definition 3.1. (1) is called *uniformly (uniformly weakly) ρ persistent* if there exists $\varepsilon > 0$ such that $\liminf_{n \rightarrow \infty} \rho(z_n) > \varepsilon$ ($\limsup_{n \rightarrow \infty} \rho(z_n) > \varepsilon$), $\forall z_0$ satisfying $\rho(z_0) > 0$.

3.1. A Plant-Herbivore Model. Consider the following model (see[8]):

$$\begin{cases} x_{n+1} &= x_n e^{r(1-x_n)-ay_n} \\ y_{n+1} &= x_n e^{r(1-x_n)}(1 - e^{-ay_n}) \end{cases} \quad (12)$$

with $r, a > 0$. Variables x and y represent plants and herbivores, respectively. We see that this model is of the form (3), with $f(x, y) = x e^{r(1-x)-ay}$, and

$$A(x, y) = \begin{cases} x e^{r(1-x)}(1 - e^{-ay})/y, & \text{if } y > 0 \\ ax e^{r(1-x)}, & \text{if } y = 0 \end{cases} \quad (13)$$

The ‘‘plant dynamics’’ on $X = \{z = (x, y) \mid y = 0\}$ is given by the classical Ricker equation:

$$x_{n+1} = x_n e^{r(1-x_n)}. \quad (14)$$

It is shown in [8] that (12) is point dissipative and uniformly ρ persistent with $\rho(z) = x$. Since the right hand side in (12) defines a continuous map on \mathbb{R}_+^2 (hence a compact map), using [22, Theorem 1.1.3.] we have that there exists a global attractor (see [22, Section 1.1.] for a definition of this) in \mathbb{R}_+^2 that attracts each bounded set in \mathbb{R}_+^2 . Then, applying [11, Theorem 3.7.] (where, in the notation of that theorem, we take $M_0 = \{z = (x, y) \in \mathbb{R}_+^2 \mid x > 0\}$), we can conclude that there exists a compact and invariant set \mathcal{A} in $Z := \{z \in \mathbb{R}_+^2 \mid x > 0\}$ that attracts points of Z . Note that (H) is satisfied with this choice of Z . Denote the intersection of \mathcal{A} with X by M . Then M is non-empty, compact, bounded away from zero and attracts every initial data in $X \setminus \{0\}$. Since $Z \setminus X$ is positively invariant, it follows that M is also invariant. In the next result we show that $M = \{(1, 0)\}$ if $r \leq 2$ and that $M \subseteq [f_R^2(1/r), f_R(1/r)] \times \{0\}$ if $r > 2$, where f_R is the Ricker map $f_R(x) = x e^{r(1-x)}$.

Proposition 5. *If*

$$\limsup_{n \rightarrow \infty} \left(\prod_{s=0}^{n-1} x_s \right)^{\frac{1}{n}} > \frac{1}{a}, \forall z_0 = (x_0, 0) \in \Omega(M), \quad (15)$$

then

$$\exists \varepsilon > 0 \text{ s.t. } \liminf_{n \rightarrow \infty} \min\{x_n, y_n\} > \varepsilon, \forall (x_0, y_0) \in (R_+^2)^0. \quad (16)$$

In particular, (15) holds in any of the following cases:

- a) $\Omega(M)$ is a union of periodic orbits and for each such periodic orbit $\{(\bar{x}_0, 0), \dots, (\bar{x}_{k-1}, 0)\}$, we have $(\bar{x}_0 \bar{x}_1 \dots \bar{x}_{k-1})^{1/k} > 1/a$.
- b) $r \leq 2$ and $a > 1$.
- c) $r > 2$ and $(1/r) \exp(2r - 1 - e^{r-1}) > 1/a$.

Kon and Takeuchi ([10]) obtain similar results for a slightly different model. Their uniform persistence condition, obtained by using a theorem of Hutson [7], is equivalent (via Lemma 4.1) to (15).

3.2. A Juvenile-Adult SI Model. Here we consider the model (1) in [17], in which the Juvenile J , and Adult A stages of a host population are labeled with subscripts S and I indicating their status as susceptible or infected. F denotes density of fungus in the environment. All parameters in the model are assumed to be positive, except for c_{JS}, c_{JI} (see below), which are assumed to be non-negative (we allow them to be zero). For this model we use superscripts to indicate iterations:

$$\begin{cases} J_S^{n+1} &= p_{JS} J_S^n e^{-\beta_J w \cdot I^n} + q_{LS} b_S \phi(T^n) A_S^n + (1-f) q_{LI} b_I \phi(T^n) A_I^n \\ A_S^{n+1} &= q_{JS} J_S^n + p_{AS} A_S^n e^{-\beta_A w \cdot I^n} \\ J_I^{n+1} &= p_{JS} J_S^n (1 - e^{-\beta_J w \cdot I^n}) + p_{JI} J_I^n + f q_{LI} b_I \phi(T^n) A_I^n \\ A_I^{n+1} &= q_{JI} J_I^n + p_{AS} A_S^n (1 - e^{-\beta_A w \cdot I^n}) + p_{AI} A_I^n \\ F^{n+1} &= b_F (v_J J_I^n + v_A A_I^n) + p_F F^n \end{cases} \quad (17)$$

with

$$T = c_{JS} J_S + c_{JI} J_I + c_{AS} A_S + c_{AI} A_I \text{ and } w \cdot I = w_J J_I + w_A A_I + w_F F.$$

Parameters $p_{JS}, p_{JI}, p_{AS}, p_{AI}, q_{LS}, q_{JS}, q_{LI}$ and q_{JI} are all in $(0, 1)$, as they represent different probabilities. Subscript L stands for larvae which are not modeled in (17). Parameter “ f ” is also in $(0, 1)$, as it gives the fraction of the infected juvenile population that comes from the infected adult population. For a more detailed description of parameters involved in the model see [3, 17].

Let $x = (J_S, A_S)$ and $y = (J_I, A_I, F)$. The set $X = \{z = (x, y) | y = 0\}$ represents the positively invariant disease-free subspace, on which the dynamics are given by:

$$\begin{cases} J_S^{n+1} &= p_{JS} J_S^n + q_{LS} b_S \phi(T_S^n) A_S^n \\ A_S^{n+1} &= q_{JS} J_S^n + p_{AS} A_S^n \end{cases} \quad (18)$$

where $T_S = c_{JS} J_S + c_{AS} A_S$. Thus, as noted in the beginning of section 1, (17) can be put in the form (3), with

$$A(x, 0) = \begin{pmatrix} p_{JI} + p_{JS} \beta_J w_J J_S & p_{JS} \beta_J w_A J_S + f q_{LI} b_I \phi(T_S) & p_{JS} \beta_J w_F J_S \\ q_{JI} + p_{AS} \beta_A w_J A_S & p_{AI} + p_{AS} \beta_A w_A A_S & p_{AS} \beta_A w_F A_S \\ b_F v_J & b_F v_A & p_F \end{pmatrix}.$$

Let

$$\Delta_S = \frac{q_{LS} q_{JS} b_S}{(1 - p_{JS})(1 - p_{AS})} \quad (19)$$

If $\Delta_S > 1$ then, as shown in [17, Theorem 2.6], we have that:

$$\exists \varepsilon > 0, \forall z_0 \in \{z \in \mathbb{R}_+^5 | J_S + A_S + J_I + A_I > 0\}, \liminf_{n \rightarrow \infty} \min\{J_S^n, A_S^n\} > \varepsilon. \quad (20)$$

Also, (17) has a global attractor of bounded sets (see [17, Proposition 2.1]).

TABLE 1. A set of parameters for the JA-SI model

Susceptible	Infected	Contact	Fungus
$p_{JS} = 0.04$	$p_{JI} = 0.03$	$w_J = 0.4$	$p_F = 0.5$
$p_{AS} = 0.05$	$p_{AI} = 0.04$	$w_A = 0.4$	$v_L = 1$
$q_{LS} = 0.2$	$q_{LI} = 0.1$	$w_F = 0.4$	$v_J = 1$
$q_{JS} = 0.3$	$q_{JI} = 0.1$		$v_A = 1$
$b_S = 23$	$b_I = 9$		$b_F = 10$
$c_{JS} = 1$	$c_{JI} = 1$		
$c_{AS} = 1$	$c_{AI} = 1$		
	$f = 0.9$		

Hence, if $\Delta_S > 1$, then again, from [11, Theorem 3.7.] (where, in the context of that theorem, we take $M_0 = \{z \in \mathbb{R}_+^5 | J_S + A_S + J_I + A_I > 0\}$), we have that there exists a compact invariant set \mathcal{A} in $Z := \{z \in \mathbb{R}_+^5 | J_S + A_S + J_I + A_I > 0\}$ which attracts points of Z . Note that again, (H) is satisfied with this Z . As in the plant-herbivore model, we define $M := \mathcal{A} \cap X$, from which it follows that M is non-empty, compact, invariant, bounded away from zero and attracts all non-zero points of X . The matrix $A(z)$ is strictly positive on M (see (20)) and therefore satisfies the hypotheses of Proposition 2.

Our goal is to establish persistence of all the components of (17). As noted above, if $\Delta_S > 1$ then the first two components persist, so it suffices to consider only the last three components that make up the vector y . For this, we can use Theorem 2.3 in connection with Proposition 4 to obtain the following result.

Proposition 6. *Assume that $\Delta_S > 1$. If*

$$\limsup_{n \rightarrow \infty} \frac{1}{n} \ln \left\| \prod_{s=n-1}^0 A(z_s) \right\| > 0, \quad \forall z_0 \in \Omega(M), \quad (21)$$

then

$$\exists \varepsilon > 0 \text{ such that } \liminf_{n \rightarrow \infty} \min_i z_n^{(i)} > \varepsilon, \quad \forall z_0 \in Z \setminus X \quad (22)$$

and there exists a fixed point in $(\mathbb{R}_+^5)^0$. In particular, if $\Omega(M)$ is a union of periodic orbits, and $r(\mathcal{P}) > 1$ for each such periodic orbit \mathcal{P} , then (21) holds.

We mention that Proposition 6 applies as well to the LJA-SI model considered in [3, 16] and sufficient conditions for the corresponding uniform ρ persistence and existence of the global attractor are provided in [16, Theorem 3.3] and [16, Proposition 2.1] respectively.

In applications it is difficult to determine $\Omega(M)$, let alone to show that it consists only of periodic orbits. In [17, Theorem 2.3] we give sufficient conditions for M to consist of a unique fixed point and, in that special case, we obtain the persistence result (22) (see [17, Theorem 2.6]). Thus, Proposition 6 generalizes the corresponding result in [17, Theorem 2.6]. Here, we rely on numerical simulations (for the disease-free model (18)) shown in Figure 1, to suggest that, for parameter values given in Table 1 (which are taken from Table I in [3], except for “f”), $\Omega(M)$ consists of an unstable fixed point $E = (3.4216, 1.0805)$ and an attracting two-cycle, $\mathcal{P} = \{E_1, E_2\}$, where $E_1 = (1.5571, 1.9118)$ and $E_2 = (6.2788, 0.5627)$. Assuming the validity of our description of $\Omega(M)$, all hypotheses of Proposition 6 hold, in particular $\Delta_S = 1.5131$, $r(\mathcal{P}) = 1.6506$, and $r(A(E)) = 3.1479$. Hence each component of the population persists (*i.e.*, (22) holds) and (17) has a fixed point in $(\mathbb{R}_+^5)^0$.

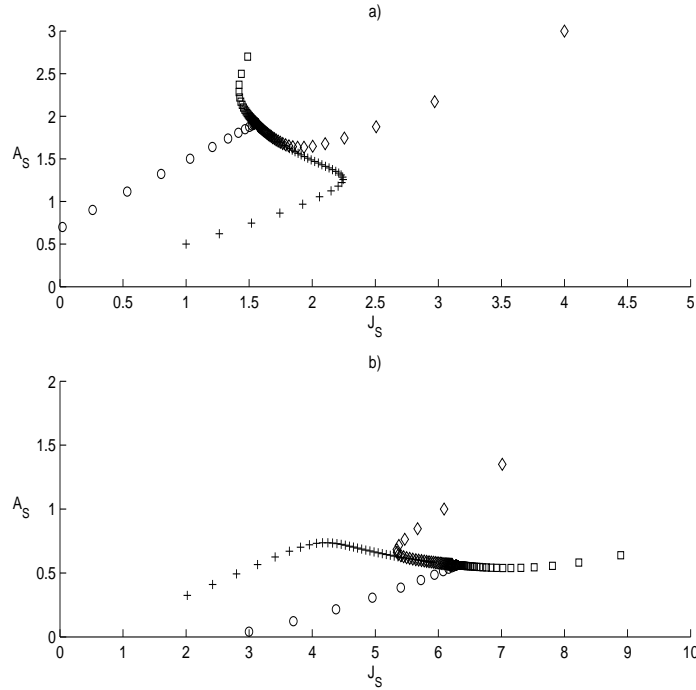


FIGURE 1. Four trajectories corresponding to the disease-free model (18), approaching the period-two globally attracting orbit. Figures a) and b) contain respectively the odd and the even iterates of these trajectories.

4. **Proofs.** We define

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

where $\phi(n, z)$ denotes the semiflow generated by (3), i.e. $\phi(n, z) = (x_n, y_n) = F^n(z)$, $n \geq 0$, where $(x_0, y_0) = z$. I denotes the $q \times q$ identity matrix. If $z \in X$ and $\eta \in U_+$ then $P(n, z)\eta \geq 0$ because X is positively invariant by (H) and $A(z) \geq 0$, $\forall z \in X$. If $z = (x_0, y_0) \in Z \setminus X$ then $y_n = P(n, z)y_0 > 0$ because $Z \setminus X$ is positively invariant, again by (H).

It is trivial to check that $P(n, z)$ has the following ‘‘cocycle’’ property (see [1], page 5):

$$P(n_2, \phi(n_1, z))P(n_1, z) = P(n_1 + n_2, z), \quad \forall n_1, n_2 \in \mathbb{N}. \quad (23)$$

First, we give a lemma that will be used in several proofs of this section. It contains an alternative formulation for the ‘‘positivity’’ of Lyapunov exponents, that will be more convenient to work with.

Lemma 4.1. *Let $K \subset X$ be compact. Assume that*

$$\forall (z, \eta) \in K \times U_+, \exists N = N(z, \eta) \geq 1 \text{ such that } |P(N, z)\eta| > 1. \quad (24)$$

Then $\exists c > 1$, $\exists V$ a bounded neighborhood of K in Z , such that if $L \subseteq V$ is a positively invariant set, then $L \subset X$ and

$$\forall (z, \eta) \in L \times U_+, \exists (n_p)_p \subseteq \mathbb{N}, n_p \rightarrow \infty, \text{ such that } |P(n_p, z)\eta| > c^p, \quad \forall p \geq 1. \quad (25)$$

If, in addition, K is positively invariant, then (24) is equivalent to

$$\lambda(z, \eta) > 0, \forall (z, \eta) \in K \times U_+. \quad (26)$$

Proof. Let $W = K \times U_+$ (so W is compact) and $\hat{w} = (\hat{z}, \hat{\eta}) \in K \times U_+$. From (24) we have that there exists $\hat{N} = \hat{N}(\hat{z}, \hat{\eta}) \geq 1$ such that $|P(\hat{N}, \hat{z})\hat{\eta}| > 1$. The function $(z, \eta) \mapsto |P(\hat{N}, z)\eta|$ being continuous, there exist $\delta_{\hat{w}} > 0$, $c_{\hat{w}} > 1$ such that

$$|P(\hat{N}, z)\eta| > c_{\hat{w}}, \forall w = (z, \eta) \in B_{\delta_{\hat{w}}}(\hat{w}) := \{\tilde{w} \in Z \times U_+ \mid |\tilde{w} - \hat{w}| < \delta_{\hat{w}}\}. \quad (27)$$

Since W is compact, there exists a finite set $\{w^1, \dots, w^k\} \subseteq W$ such that $W \subset C := \cup_{i=1}^k B_{\delta_{w^i}}(w^i)$, where for every $i = 1, \dots, k$, δ_{w^i} is the quantity corresponding to w^i , coming from (27) (i.e., for every $i = 1, \dots, k$, (27) is satisfied with \hat{w} replaced by w^i). To simplify notation, let $N_i := N(w^i)$, $\delta_i := \delta_{w^i}$, $i = 1, \dots, k$. Also, let $c := \min_i c_{w^i}$ (hence $c > 1$) and $N = \max_i N_i$. Thus, from (27) we have that

$$|P(N_i, z)\eta| > c, \forall w = (z, \eta) \in B_{\delta_i}(w^i), \forall i = 1, \dots, k. \quad (28)$$

Now let $V \subset Z$ be a bounded neighborhood of K such that $V \times U_+ \subseteq C$ and let $L \subseteq V$ be positively invariant. We prove that $L \subset X$ arguing by contradiction: suppose $L \setminus X \neq \emptyset$. Let $z_0 = (x_0, y_0) \in L \setminus X$. Since $|y_0| > 0$, we can define $\alpha := y_0/|y_0|$. Note that $\alpha \in U_+$. We will show that

$$\exists (n_p)_p \subset \mathbb{N}, n_p \rightarrow \infty, \text{ such that } |P(n_p, z_0)\alpha| > c^p, \forall p \geq 1. \quad (29)$$

by inductively constructing the sequence $(n_p)_p$. Thus, there exists $i \in \{1, \dots, k\}$ such that $(z_0, \alpha) \in B_{\delta_i}(w^i)$. Then, from (28) we have $|P(n_1, z_0)\alpha| > c$, where $n_1 = N_i$. Now suppose $|P(n_p, z_0)\alpha| > c^p$ for some $p \geq 1$. Let $\tilde{\alpha} = P(n_p, z_0)\alpha/|P(n_p, z_0)\alpha|$. Since $L \setminus X$ is positively invariant, $\phi(n_p, z_0) \in L \setminus X$, hence $y_{n_p} > 0$. So

$$P(n_p, z_0)\alpha = \frac{1}{|y_0|} P(n_p, z_0)y_0 = \frac{1}{|y_0|} y_{n_p} > 0.$$

Thus, $\tilde{\alpha} \in U_+$. There exists $j \in \{1, \dots, k\}$ such that $(\phi(n_p, z_0), \tilde{\alpha}) \in B_{\delta_j}(w^j)$. Then again, from (28) we have

$$|P(N_j, \phi(n_p, z_0))\tilde{\alpha}| > c, \text{ which implies } |P(N_j, \phi(n_p, z_0))P(n_p, z_0)\alpha| > c^{p+1}.$$

This means, using (23), that $|P(n_{p+1}, z_0)\alpha| > c^{p+1}$, where we define $n_{p+1} = n_p + N_j$. Note that, by construction, $n_p \rightarrow \infty$ as $p \rightarrow \infty$. Hence (29) holds. Then, we have that

$$|y_{n_p}| = |P(n_p, z_0)y_0| > c^p |y_0|, \forall p \geq 1,$$

which implies that $|y_{n_p}| \rightarrow \infty$ as $p \rightarrow \infty$. But this is a contradiction to L being bounded. Hence, $L \subset X$.

Now (25) can be proved identically as for (29), using that $L \subset X$ is positively invariant and that $P(n, z) \geq 0, \forall z \in X, \forall n \geq 0$.

Now assume that K is also positively invariant. The implication (26) \Rightarrow (24) is trivial. For the converse, using (25) and the fact that $n_p \leq pN, \forall p \geq 1$, we have, for all $(z, \eta) \in K \times U_+$, that

$$|P(n_p, z)\eta|^{1/n_p} > c^{p/n_p} \geq c^{1/N} \Rightarrow \frac{1}{n_p} \ln |P(n_p, z)\eta| > \frac{1}{N} \ln c, \forall p \geq 1.$$

Hence

$$\lambda(z, \eta) = \limsup_{n \rightarrow \infty} \frac{1}{n} \ln(|P(n, z)\eta|) \geq \frac{1}{N} \ln c > 0.$$

□

4.1. Proofs of results in Section 2.

Proof. (of Proposition 1)

First we show that (6) implies that M is a uniformly weak repeller. For this, we argue by contradiction: suppose M is not a uniformly weak repeller. So, there exists a sequence $(\tilde{z}^m)_m \subseteq Z \setminus X$ such that

$$\limsup_{n \rightarrow \infty} d(\phi(n, \tilde{z}^m), M) < 1/m, \forall m \geq 1.$$

Hence there exists a sequence $(s_m)_m$ such that, for each $m \geq 1$, we have

$$d(\phi(n, \tilde{z}^m), M) < 1/m, \forall n \geq s_m. \quad (30)$$

Let $z^m = (x^m, y^m) = \phi(s_m, \tilde{z}^m)$. Using the positive invariance of $Z \setminus X$, we have that

$$y^m > 0, \forall m \geq 1. \quad (31)$$

From the semiflow property of ϕ and from (30) we get

$$d(\phi(n, z^m), M) < 1/m, \forall n \geq 0, \forall m \geq 1. \quad (32)$$

Using (6), we obtain from Lemma 4.1 (applied with $K = M$) that there exists V a bounded neighborhood of M in Z , having the property that any positively invariant set contained in V is a subset of X . Then there exists $m \in \mathbb{N}$ such that $B_m := \{z \in Z | d(z, M) \leq 1/m\}$ is contained in V . The set $L = \{\phi(n, z^m) | n \geq 0\}$ is positively invariant and, according to (32), it is contained in B_m . Also (see (31)) $L \setminus X \neq \emptyset$. But this is a contradiction, according to Lemma 4.1. Hence, M is a uniformly weak repeller.

Now we prove the final assertion. First, notice that 1) is equivalent to

$$\forall (z, \eta) \in M \times U_+, \forall n \geq 0, P(n, z)\eta > 0. \quad (33)$$

Let $(a, \alpha) \in M \times U_+$. Using 2) and the fact that $\omega(a) \subset X$ is compact and invariant, we can again apply Lemma 4.1, now with $K = \omega(a)$. So let V_a be a neighborhood of $K = \omega(a)$ and $c > 1$ as in the above mentioned lemma. Since $\phi(n, a) \rightarrow \omega(a)$ as $n \rightarrow \infty$, there exists $N_a \in \mathbb{N}$ such that $\phi(n, a) \in V_a, \forall n \geq N_a$. Let $L = \{\phi(n, a) | n \geq N_a\}$. Then L is a positively invariant set contained in V_a . Let $\tilde{\alpha} = P(N_a, a)\alpha / |P(N_a, a)\alpha|$. Note that $\tilde{\alpha}$ is well defined, due to (33), and that $\tilde{\alpha} \in U_+$. So, from (25), there exists a sequence $n_p \rightarrow \infty$ such that $|P(n_p, \phi(N_a, a))\tilde{\alpha}| > c^p, \forall p \geq 1$. Thus, using (23) we get

$$|P(n_p + N_a, a)\alpha| > c^p |P(N_a, a)\alpha|, \forall p \geq 1.$$

We can find a p large enough such that to have $c^p |P(N_a, a)\alpha| > 1$. So, we proved that

$$\forall (z, \eta) \in M \times U_+, \exists N \geq 1 \text{ such that } |P(N, z)\eta| > 1,$$

which is equivalent to (6), by Lemma 4.1. □

Proof. (of Proposition 2) Let $P(n) := P(n, \hat{z})$. First, we want to apply Theorem 3.4. in [19] for the sequence of non-negative matrices $(A(z_s))_{s \geq 0}; z_0 = \hat{z}$. Denote by $\mathcal{O}(\hat{z})$ the orbit of \hat{z} . The fact that $A(z)$ has the same primitive incidence matrix for all z in $\overline{\mathcal{O}(\hat{z})}$ implies that $\exists N \in \mathbb{N}$ s.t. $P(n) \gg 0, \forall n \geq N$. For the same reason, for any i and j in $\{1, \dots, q\}$, we either have that $a_{ij}(z) = 0, \forall z \in \overline{\mathcal{O}(\hat{z})}$, or that $a_{ij}(z) > 0, \forall z \in \overline{\mathcal{O}(\hat{z})}$. Thus, let $\emptyset \neq S \subseteq \{1, \dots, q\} \times \{1, \dots, q\}$ such that

$a_{ij}(z) > 0, \forall z \in \overline{\mathcal{O}(\hat{z})}, \forall (i, j) \in S$. Let $\delta = \min_{(i,j) \in S} (\min_{z \in \overline{\mathcal{O}(\hat{z})}} a_{ij}(z))$. Since $\overline{\mathcal{O}(\hat{z})}$ is compact, we have that $\delta > 0$. So, the following hold:

- a) $\min_{i,j}^+ a_{ij}(z_s) \geq \delta > 0$,
- b) $\max_{i,j} a_{ij}(z_s) \leq \max_{i,j} (\max_{z \in \overline{\mathcal{O}(\hat{z})}} a_{ij}(z)) < \infty$,

where \min^+ refers to the minimum among all *positive* entries. Thus, hypotheses of [19, Theorem 3.4.] hold (see also the comments on page 76 in [19]), and from the above mentioned theorem (see exercise 3.6 in [19]) we have that

$$\frac{P(n)_{ki}}{P(n)_{kj}} \rightarrow c_{ij} > 0 \text{ as } n \rightarrow \infty, \quad (34)$$

for some c_{ij} independent of k , where $P(n)_{ij}$ represents the entry on the row i and column j of matrix $P(n)$. Denote by $P(n)^i$ the i^{th} column of $P(n)$. Then (34) implies that

$$\lim_{n \rightarrow \infty} \frac{|P(n)^i|}{|P(n)^j|} = c_{ij}. \quad (35)$$

Let $e_i \in U_+$ be the unit vector whose i^{th} component equals one, and the other components are zero. Then, using (35), we get, for any $i \in \{1, \dots, q\}$, that

$$\begin{aligned} \lambda(\hat{z}, e_i) &= \limsup_{n \rightarrow \infty} \frac{1}{n} \ln |P(n)e_i| = \limsup_{n \rightarrow \infty} \frac{1}{n} \ln |P(n)^i| \\ &= \limsup_{n \rightarrow \infty} \frac{1}{n} \ln \left(\frac{|P(n)^i|}{|P(n)^1|} |P(n)^1| \right) = \limsup_{n \rightarrow \infty} \left(\frac{1}{n} \ln \frac{|P(n)^i|}{|P(n)^1|} + \frac{1}{n} \ln |P(n)^1| \right) \\ &= \limsup_{n \rightarrow \infty} \frac{1}{n} \ln |P(n)^1| = \lambda(\hat{z}, e_1). \end{aligned}$$

Thus, let $c = \lambda(\hat{z}, e_i), \forall i = 1, \dots, q$. Let $\hat{\eta} \in U_+$. There exist $p_1, \dots, p_q \in [0, 1]$ such that $\hat{\eta} = \sum_{i=1}^q p_i e_i$. Then

$$\begin{aligned} \lambda(\hat{z}, \hat{\eta}) &= \limsup_{n \rightarrow \infty} \frac{1}{n} \ln |P(n)\hat{\eta}| = \limsup_{n \rightarrow \infty} \frac{1}{n} \ln \left| \sum_{i=1}^q p_i P(n)e_i \right| \\ &= \limsup_{n \rightarrow \infty} \frac{1}{n} \ln \left(\sum_{i=1}^q p_i |P(n)^i| \right) \geq \limsup_{n \rightarrow \infty} \frac{1}{n} \sum_{i=1}^q p_i \ln |P(n)^i| \\ &= \limsup_{n \rightarrow \infty} \frac{1}{n} \sum_{i=1}^q p_i \ln \left(\frac{|P(n)^i|}{|P(n)^1|} |P(n)^1| \right) \\ &= \limsup_{n \rightarrow \infty} \frac{1}{n} \left[\sum_{i=1}^q p_i \ln \left(\frac{|P(n)^i|}{|P(n)^1|} \right) + \sum_{i=1}^q p_i \ln |P(n)^1| \right] \\ &= \limsup_{n \rightarrow \infty} \frac{1}{n} \left[\sum_{i=1}^q p_i \ln |P(n)^1| \right] = \limsup_{n \rightarrow \infty} \frac{1}{n} \ln |P(n)^1| = c, \end{aligned} \quad (36)$$

where we used (following from (35)) that $\lim_{n \rightarrow \infty} \frac{1}{n} p_i \ln \left(\frac{|P(n)^i|}{|P(n)^1|} \right) = 0$, $\forall i \in \{1, \dots, q\}$ and that $1 = |\hat{\eta}| = p_1 + \dots + p_q$. On the other hand, we have

$$\lambda(\hat{z}, \hat{\eta}) = \lambda\left(\hat{z}, \sum_{i=1}^q p_i e_i\right) \leq \max_{i=1, \dots, q} \lambda(\hat{z}, e_i) = c, \quad (37)$$

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

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

From (36) and (37) we obtain $\lambda(\hat{z}, \hat{\eta}) = c$. It is clear that

$$c = \lambda(\hat{z}, \hat{\eta}) \leq \limsup_{n \rightarrow \infty} \frac{1}{n} \ln \|P(n)\|. \quad (38)$$

Now, we want to show the opposite inequality. Because all norms on a finite dimensional metric space are equivalent, there exist constants $a, b > 0$ such that $a\|P(n)\|_1 \leq \|P(n)\| \leq b\|P(n)\|_1$, where $\|P(n)\|_1 = \max_i |P(n)^i|$. Then

$$\begin{aligned} \limsup_{n \rightarrow \infty} \frac{1}{n} \ln \|P(n)\| &\leq \limsup_{n \rightarrow \infty} \frac{1}{n} \ln (b\|P(n)\|_1) \\ &= \limsup_{n \rightarrow \infty} \frac{1}{n} \ln \|P(n)\|_1 \\ &= \lim_{k \rightarrow \infty} \frac{1}{n_k} \ln \|P(n_k)\|_1, \end{aligned} \quad (39)$$

for some sequence $(n_k)_k \subseteq \mathbb{N}$, $n_k \rightarrow \infty$ as $k \rightarrow \infty$. There exists $j \in \{1, \dots, q\}$ such that $\|P(n_k)\|_1 = |P(n_k)^j|$ for infinitely many k 's, hence there exists a subsequence $(\tilde{n}_k)_k$ of $(n_k)_k$ such that $\|P(\tilde{n}_k)\|_1 = |P(\tilde{n}_k)^j|$, $\forall k$. Then, from (39) we have that

$$\limsup_{n \rightarrow \infty} \frac{1}{n} \ln \|P(n)\| \leq \lim_{k \rightarrow \infty} \frac{1}{\tilde{n}_k} \ln |P(\tilde{n}_k)^j| \leq \limsup_{n \rightarrow \infty} \frac{1}{n} \ln |P(n)^j| = c. \quad (40)$$

Now, (38) and (40) imply $\lambda(\hat{z}, \hat{\eta}) = \limsup_{n \rightarrow \infty} \frac{1}{n} \ln \|P(n)\|$. Since $\hat{\eta} \in U_+$ was arbitrarily chosen, the proof is complete. \square

Proof. (of Proposition 3) Note that $A_i(\mathcal{P}) = P(k, E_i)$.

a) Let $(E_i, \eta) \in \mathcal{P} \times U_+$. Then

$$\lambda(E_i, \eta) \leq \limsup_{n \rightarrow \infty} \frac{1}{n} \ln \|P(n, E_i)\| = \limsup_{n \rightarrow \infty} \ln \|P(n, E_i)\|^{\frac{1}{n}}. \quad (41)$$

We have that $\forall n, \exists! m_n, j_n$ such that $n = m_n k + j_n$, $j_n \in \{0, \dots, k-1\}$. So,

$$\begin{aligned} \|P(n, E_i)\|^{\frac{1}{n}} &= \|P(j_n, E_i)(P(k, E_i))^{m_n}\|^{\frac{1}{m_n k + j_n}} \\ &\leq \|P(j_n, E_i)\|^{\frac{1}{n}} \|P(k, E_i)\|^{m_n} \|^{\frac{1}{m_n k + j_n}}. \end{aligned} \quad (42)$$

Since $m_n \rightarrow \infty$ as $n \rightarrow \infty$, we have that

$$\|P(k, E_i)\|^{m_n} \|^{\frac{1}{m_n k + j_n}} \rightarrow [r(P(k, E_i))]^{\frac{1}{k}} \text{ as } n \rightarrow \infty, \quad (43)$$

where we used (8). If $r(P(k, E_i)) = r(\mathcal{P}) = 0$, then from (42) we have that $\limsup_{n \rightarrow \infty} \|P(n, E_i)\|^{\frac{1}{n}} = 0$. Then (41) implies $\lambda(E_i, \eta) = -\infty$. So, with our convention that $\ln 0 = -\infty$, we are done.

If $r(\mathcal{P}) > 0$, notice that $P(j_n, E_i) \neq 0, \forall n$, hence there exist constants $a, b > 0$, independent of n , such that $a \leq \|P(j_n, E_i)\| \leq b < \infty$. So, $\|P(j_n, E_i)\|^{\frac{1}{n}} \rightarrow 1$, as $n \rightarrow \infty$. Now, from (41), (42) and (43) we obtain that

$$\lambda(E_i, \eta) \leq \limsup_{n \rightarrow \infty} \ln \|P(n, E_i)\|^{\frac{1}{n}} \leq \ln[r(P(k, E_i))]^{\frac{1}{k}} = \frac{\ln r(\mathcal{P})}{k}.$$

b) Now assume that $P(k, E_i)$ is primitive (hence $r(\mathcal{P}) > 0$). There exist eigenvectors $v, v^* \gg 0$ of $P(k, E_i)$ and $P(k, E_i)^T$ respectively corresponding to $r(\mathcal{P}) = r(P(k, E_i))$. Here $P(k, E_i)^T$ represents the transpose of $P(k, E_i)$. Then (see [21, Theorem A.49.]) we have:

$$\frac{1}{(r(\mathcal{P}))^n} P(k, E_i)^n \eta \rightarrow \frac{\eta \cdot v^*}{v \cdot v^*} v, \forall \eta \in U_+.$$

Thus,

$$\frac{1}{n} \ln \frac{1}{(r(\mathcal{P}))^n} |P(k, E_i)^n \eta| \rightarrow 0, \text{ or } \frac{1}{n} \ln |P(k, E_i)^n \eta| \rightarrow \ln r(\mathcal{P}).$$

Hence, we have

$$\lim_{n \rightarrow \infty} \frac{1}{nk} \ln |P(nk, E_i) \eta| = \frac{\ln r(\mathcal{P})}{k} \Rightarrow \lambda(E_i, \eta) \geq \frac{\ln r(\mathcal{P})}{k}, \forall \eta \in U_+.$$

By using part a) we are done.

Now, assume that $A(E_j) \eta \neq 0, \forall j = 0, \dots, k-1, \forall \eta \in U_+$. Also, without a loss of generality assume (10) holds with $i = 0$. Then, for any $j \in \{0, \dots, k-1\}$ and $\eta \in U_+, \alpha := P(k-j, E_j) \eta > 0$. Using (23) we have

$$\begin{aligned} \lambda(E_j, \eta) &= \limsup_{n \rightarrow \infty} \frac{1}{n} \ln |P(n, E_j) \eta| = \limsup_{n \rightarrow \infty} \frac{1}{n} \ln |P(n-k+j, E_0) \alpha| \\ &= \limsup_{n \rightarrow \infty} \frac{1}{n} \ln |P(n-k+j, E_0) \tilde{\alpha}| = \limsup_{n \rightarrow \infty} \frac{1}{n} \ln |P(n, E_0) \tilde{\alpha}| \\ &= \lambda(E_0, \tilde{\alpha}) = (\ln r(\mathcal{P}))/k, \forall E_j \in \mathcal{P}, \forall \eta \in U_+, \end{aligned}$$

where $\tilde{\alpha} = \alpha/|\alpha| \in U_+$. □

Proof. (of Theorem 2.3) First assume $M = \emptyset$ (note that $Z \cap X$ must be empty in this case). Then, since \mathcal{A} is compact, there exists a bounded neighborhood V of $\mathcal{A}, \bar{V} \cap X = \emptyset$, that attracts all points in Z , i.e. $\forall z_0 \in Z, \exists N \in \mathbb{N}$ such that $z_n \in V, \forall n \geq N$. Note that for all $z = (x, y) \in \mathbb{R}_+^{p+q}, |y| = d(z, X)$. \bar{V} being compact, we have that there exists $\varepsilon > 0$ such that $d(z, X) > 2\varepsilon, \forall z \in \bar{V}$. Then $\liminf_{n \rightarrow \infty} |y_n| = \liminf_{n \rightarrow \infty} d(z_n, X) > \varepsilon, \forall z_0 \in Z$.

Now assume M is a uniformly weak repeller. Recall that $\phi(n, z)$ denotes the semiflow generated by (3). First we show that

$$\exists \varepsilon > 0 \text{ such that } \limsup_{n \rightarrow \infty} |y_n| > \varepsilon, \forall z_0 \in Z \setminus X, \quad (44)$$

i.e., (1) is uniformly weakly ρ persistent, with $\rho(z) = |y|$. For this, we argue by contradiction: suppose (44) does not hold. Then, there exists a sequence $(\tilde{z}^m)_{m \geq 1} \subset Z \setminus X$ such that

$$\limsup_{n \rightarrow \infty} d(\phi(n, \tilde{z}^m), X) < 1/m, \forall m \geq 1. \quad (45)$$

Since M is a uniformly weak repeller, there exists $\varepsilon > 0$ such that

$$\limsup_{n \rightarrow \infty} d(\phi(n, \tilde{z}^m), M) > \varepsilon, \forall m \geq 1. \quad (46)$$

Thus, combining (45) and (46) and using that \mathcal{A} attracts every point in Z , we obtain that $\forall m \geq 1, \exists s_m \in \mathbb{N}$ such that:

$$\begin{aligned} d(\phi(s_m, \tilde{z}^m), X) &< 1/m, \\ d(\phi(s_m, \tilde{z}^m), M) &> \varepsilon, \\ d(\phi(s_m, \tilde{z}^m), \mathcal{A}) &< \varepsilon/(2m). \end{aligned} \quad (47)$$

Let $z^m := \phi(s_m, \tilde{z}^m)$, $\forall m \geq 1$. Since \mathcal{A} is compact, for each $m \geq 1$ there exists $\hat{z}^m \in \mathcal{A}$ such that $d(z^m, \mathcal{A}) = d(z^m, \hat{z}^m)$. Thus, using (47), we have that, for all $m \geq 1$,

$$d(\hat{z}^m, M) \geq d(z^m, M) - d(z^m, \hat{z}^m) \geq \varepsilon - \varepsilon/2 = \varepsilon/2, \quad (48)$$

$$d(\hat{z}^m, X) \leq d(\hat{z}^m, z^m) + d(z^m, X) < \varepsilon/(2m) + 1/m.$$

Hence $d(\hat{z}^m, X) \rightarrow 0$ as $m \rightarrow \infty$. Using again the compactness of \mathcal{A} , there exists a subsequence $(\hat{z}^{m_k})_k$ of $(\hat{z}^m)_m$ such that $\hat{z}^{m_k} \rightarrow \hat{z} \in \mathcal{A}$ as $k \rightarrow \infty$. So $d(\hat{z}^{m_k}, X) \rightarrow 0$ as $k \rightarrow \infty$, which implies $\hat{z} \in X$. But $\hat{z} \notin M$ (see (48)), so we have a contradiction to (11). Thus, (44) holds. Then, due to the existence of the compact attracting set \mathcal{A} , by applying [11, Proposition 3.2], we can replace ‘‘lim sup’’ by ‘‘lim inf’’ in (44) (i.e., (1) is uniformly ρ persistent), and the theorem is proved. \square

Proof. (of Proposition 4) g_i being continuous and B compact, it follows that there exists V an open neighborhood of B and $\varepsilon > 0$ such that $g_i(z) > 2\varepsilon$, $\forall i = 1, \dots, q, \forall z \in V$. Let $z_0 \in Z \setminus X$. Since $z_n \rightarrow B$, there exists $N \geq 0$ such that $z_n \in V$, $\forall n \geq N$. Thus $y_{n+1}^{(i)} = g_i(z_n) > 2\varepsilon$, $\forall i = 1, \dots, q, \forall n \geq N$, hence $\liminf_{n \rightarrow \infty} \min_i y_n^{(i)} > \varepsilon$. \square

4.2. Proof of results in Section 4.

Proof. (of Proposition 5) Recall that $Z = \{z \in \mathbb{R}_+^2 \mid x > 0\}$ and that Z satisfies (H). Note that $U_+ = \{1\}$ and $\lambda(z, 1) = \lambda(z)$. Let $z \in \Omega(M)$. Then, using (13) and (14), we have

$$\begin{aligned} \lambda(z) &= \limsup_{n \rightarrow \infty} \frac{1}{n} \ln \left(\prod_{s=0}^{n-1} a x_s e^{r(1-x_s)} \right) = \limsup_{n \rightarrow \infty} \ln \left(\prod_{s=1}^n a x_s \right)^{1/n} > 0 \Leftrightarrow \\ &\Leftrightarrow \limsup_{n \rightarrow \infty} \left(\prod_{s=1}^n x_s \right)^{\frac{1}{n}} > \frac{1}{a} \Leftrightarrow \limsup_{n \rightarrow \infty} \left(\prod_{s=0}^{n-1} x_s \right)^{\frac{1}{n}} > \frac{1}{a} \end{aligned}$$

and the last inequality holds by hypothesis. Thus $\lambda(z) > 0$, $\forall z \in \Omega(M)$. Also note that, since $(0, 0) \notin M$, condition 1) in Proposition 1 is satisfied hence, from Proposition 1, M is a uniformly weak repeller. Now, by applying Theorem 2.3 we obtain that

$$\exists \varepsilon_1 > 0 \text{ s.t. } \liminf_{n \rightarrow \infty} y_n > \varepsilon_1, \forall (x_0, y_0) \in Z \setminus X = (\mathbb{R}_+^2)^0.$$

Combining this with the fact that (12) is uniformly ρ persistent with $\rho(z) = x$ (see [8]) we get

$$\exists \varepsilon > 0 \text{ s.t. } \liminf_{n \rightarrow \infty} \min\{x_n, y_n\} > \varepsilon, \forall (x_0, y_0) \in (\mathbb{R}_+^2)^0.$$

a)

$$\begin{aligned} \limsup_{n \rightarrow \infty} \left(\prod_{s=0}^{n-1} x_s \right)^{\frac{1}{n}} &\geq \limsup_{m \rightarrow \infty} \left(\prod_{s=0}^{mk-1} x_s \right)^{\frac{1}{mk}} = \limsup_{m \rightarrow \infty} [(x_0 \dots x_{k-1})^m]^{\frac{1}{mk}} = \\ &= (x_0 \dots x_{k-1})^{\frac{1}{k}} > \frac{1}{a}. \end{aligned}$$

In what follows, by abusing notation, we regard M as the attractor for (14).

b) In this case, $x = 1$ is asymptotically stable and attracts all non-zero solutions of (14) (see [4]). Again, $\phi(n, z)$ will denote the semiflow generated by (12). Suppose there exists $x_0 \in M \setminus \{1\}$. Then, since M is invariant, there exists a total trajectory φ through x_0 , $\varphi(0) = x_0$, whose closure is contained in M ($\varphi : \mathbb{Z} \rightarrow \mathbb{R}_+^{p+q}$, $\varphi(t+s) = \phi(t, \varphi(s))$, $\forall t \in \mathbb{N}$, $\forall s \in \mathbb{Z}$, where \mathbb{Z} denotes the set of integers). Thus, $\alpha(\varphi)$ is contained in M and it is non-empty, compact and invariant. Let $\tilde{x}_0 \in \alpha(\varphi)$. Since $0 \notin M$, we have that $\tilde{x}_n \rightarrow 1$, which implies that $1 \in \alpha(\varphi)$. Let $\varepsilon > 0$ such that $x_0 \notin B_\varepsilon(1) := (1 - \varepsilon, 1 + \varepsilon)$. Since 1 is (asymptotically) stable, there exists $\delta > 0$ such that any solution starting in $B_\delta(1) := (1 - \delta, 1 + \delta)$ stays in $B_\varepsilon(1)$ for future times. Since $1 \in \alpha(\varphi)$, there exists $s > 0$ such that $\varphi(-s) \in B_\delta(1)$. Then $x_0 = \varphi(-s + s) = \phi(s, \varphi(-s)) \in B_\varepsilon(1)$, contradiction. Hence $M = \{1\}$, and now one can easily check that (15) is equivalent to $a > 1$.

c) It can be easily checked that $f_R^2(1/r) < 1/r < 1 < f_R(1/r)$ (recall that $f_R(x) = xe^{r(1-x)}$). Also, f_R is increasing on $[0, 1/r]$ and decreasing on $[1/r, \infty)$. Thus, $f_R(x) \leq f_R(1/r)$, $\forall x \geq 0$. This implies that there is no total trajectory containing points greater than $f_R(1/r)$. Let $x_0 = \min_{x \in M} x$ and let φ be a total trajectory through x_0 , $\varphi(0) = x_0$ (which must be contained in M). So $M \subseteq [x_0, f_R(1/r)]$. Since $0 \notin M$, we have $x_0 > 0$. Suppose $x_0 < f_R^2(1/r)$. There are two possibilities:

- (1) $\varphi(-1) < 1$. Then $x_0 = \varphi(0) = \phi(1, \varphi(-1)) = \varphi(-1)e^{r(1-\varphi(-1))} > \varphi(-1)$, contradiction.
- (2) $\varphi(-1) \geq 1$. Then, using that f_R is decreasing on $[1, f_R(1/r)]$, we have $f_R(\varphi(-1)) \geq f_R(f_R(1/r)) \Rightarrow x_0 \geq f_R^2(1/r)$, contradiction.

Hence $x_0 \geq f_R^2(1/r)$, which implies $M \subseteq [f_R^2(1/r), f_R(1/r)]$. Then, for any $x_0 \in M$:

$$\limsup_{n \rightarrow \infty} \left(\prod_{s=0}^{n-1} x_s \right)^{1/n} \geq \limsup_{n \rightarrow \infty} [(f_R^2(\frac{1}{r}))^n]^{1/n} = f_R^2(\frac{1}{r}) = \frac{1}{r} \exp(2r - 1 - e^{r-1}) > \frac{1}{a}.$$

□

Proof. (of Proposition 6) Recall that $Z = \{z \in \mathbb{R}_+^5 \mid J_S + A_S + J_I + A_I > 0\}$ and that Z satisfies (H). Since $A(z) \gg 0$, $\forall z \in M$, we can apply Proposition 2 to conclude that (21) is equivalent to $\lambda(z, \eta) > 0$, $\forall (z, \eta) \in \Omega(M) \times U_+$. Then, from Proposition 1 we have that $\lambda(z, \eta) > 0$, $\forall (z, \eta) \in M \times U_+$ (so M is a uniformly weak repeller). Applying Theorem 2.3 and using (20) we obtain that

$$\exists \varepsilon_1 > 0, \liminf_{n \rightarrow \infty} \min\{J_S^n, A_S^n, |y_n|\} > \varepsilon_1, \forall z_0 \in Z \setminus X. \quad (49)$$

Let $B = \{z \in Z \mid J_S, A_S, |y| \geq \varepsilon_1\} \cap \mathcal{A}$. Note that B is a compact set which attracts all initial data in $Z \setminus X$. Also note that $g(z) \gg 0$, $\forall z \in B$. Thus, from Proposition 4 and (49) we obtain that there exists $0 < \varepsilon \leq \varepsilon_1$ such that

$$\liminf_{n \rightarrow \infty} \min\{z_n^{(i)}\} > \varepsilon, \forall z_0 \in Z \setminus X.$$

Now the existence of a fixed point in $(\mathbb{R}_+^5)^0$ follows directly from [22, Theorem 1.3.6].

The final assertion follows immediately from Proposition 3 part c), using again that $A(z) \gg 0, \forall z \in M$. □

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