GLOBAL STABILITY AND REPULSION IN AUTONOMOUS KOLMOGOROV SYSTEMS

Abstract. Criteria are established for the global attraction, or global repulsion on a compact invariant set, of interior and boundary fixed points of Kolmogorov systems. In particular, the notions of diagonal stability and Split Lyapunov stability that have found wide success for Lotka-Volterra systems are extended for Kolmogorov systems. Several examples from theoretical ecology and evolutionary game theory are discussed to illustrate the results.

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1. Summary

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For global stability of fixed points in autonomous systems, there are many results for autonomous Lotka-Volterra systems [23, 25, 11, 1], but similar results for more general Kolmogorov systems beyond those with special features such as monotonicity [7, 20, 19], are less common [13, 5, 4]. Here we extend to Kolmogorov systems two Lyapunov function approaches that have found considerable success for Lotka-Volterra systems. We will illustrate and compare the relative merits of our methods with several example systems which arise as models for population dynamics.

2. Introduction

Ecological models for a community of N species x_i often take a the general form:

$$\dot{x}_i = x_i F_i(x), \quad i = 1, \ldots, N. \tag{1}$$

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These ecologically-motivated equations have become known as the Kolmogorov equations, or Kolmogorov systems. Since such systems typically model populations of species, genes, molecules, and so on, the phase space for the study of (1) is an invariant subset of first orthant, the latter which we denote by $\mathbb{R}^N_+$. The best known examples are the quadratic Lotka-Volterra equations and the cubic Replicator equations (which are actually equivalent under transformation [8]). Kolmogorov systems are not confined to theoretical ecology, but also appear in the Maxwell-Bloch equations of laser physics [3], models from economics [2], and coagulation-annihilation systems from polymer chemistry and astrophysics [17] . In addition, many nonlinear systems of differential equations can be recast in Kolmogorov form, and even Lotka-Volterra form in which the functions F_i in (1) are affine. For example, the class of S-systems sometimes used in reaction kinetics can be recast in Lotka-Volterra form [24]. In fact given a system of differential equations $\dot{x}_i = f_i(x)$ for which the first orthant is forward invariant, suppose that $f_i(x) = x_iF_i(x)$ for $i \in I \subset I_N = \{1, \dots, N\}$ but $f_j(x)$ is not identically zero for $x_j = 0$, $j \in J = I_N \setminus I$, we may set $y_i = x_i$ for $i \in I$ and $y_j = e^{x_j}$ for $j \in J$ to obtain the (formal) Kolmogorov form $\dot{y}_k = y_kF_k(y)$ for suitable F_k, $k \in I_N$. For this to be a practical transformation, we need, for each $k \in I_N$, that $y_kF_k(y) \to 0$ as $y_k \to 0$ for all $y_j \geq 0$, $j \neq k$.

Notation. For conciseness we write (1) in the more compact form

$$\dot{x} = D(x)F(x), \quad x \in \mathbb{R}^N_+, \tag{2}$$

where $\mathbb{R}^N_+$ is the set of column vectors $x \in \mathbb{R}^N$ with nonnegative components x_i, $F : \mathbb{R}^N_+ \to \mathbb{R}^N$ is at least C^1 in a neighbourhood of $\mathbb{R}^N_+$, and $D(x) = \mathrm{diag}[x_1, \dots, x_N]$ is the diagonal matrix with diagonal entries x_i. We denote the interior of $\mathbb{R}^N_+$ by $\mathrm{int}\mathbb{R}^N_+$ and the boundary of $\mathbb{R}^N_+$ by $\partial\mathbb{R}^N_+$. Let π_i be the ith coordinate plane restricted to $\partial\mathbb{R}^N_+$, i.e.

$$\pi_i = \{x \in \mathbb{R}^N_+ : x_i = 0\}, \quad i \in I_N, \tag{3}$$

where $I_k = \{1, \dots, k\}$ for any positive integer k. Then each of π_i, $\partial\mathbb{R}^N_+$ and $\mathrm{int}\mathbb{R}^N_+$ is an invariant set of (2). For any subset $I \subset I_N$, let

$$C^0_I = \{x \in \mathbb{R}^N_+ : \forall i \in I, x_i = 0, \forall j \in I_N \setminus I, x_j > 0\}, \tag{4}$$

$$\mathbb{R}_I = \{x \in \mathbb{R}^N_+ : \forall j \in I_N \setminus I, x_j > 0\}. \tag{5}$$

Then C^0_I is a proper subset of $\mathbb{R}_I$ if $I \neq \emptyset$ but $C^0_I = \mathbb{R}_I = \mathrm{int}\mathbb{R}^N_+$ if $I = \emptyset$. For each $x_0 \in \mathbb{R}^N_+$ we denote by $x(t, x_0)$ the solution to (2) on its maximal interval of existence. When this maximal interval of existence contains $\mathbb{R}_+$, so that (2) defines a semiflow, we will denote by $O^+(x_0) = \{x(t, x_0) : t \geq 0\}$ the forward orbit through x_0. Similarly, we denote by $O^-(x_0) = \{x(t, x_0) : t \leq 0\}$ the backward orbit through x_0 if $x(t, x_0)$ has definition for all $t \leq 0$. The omega limit set of x_0 is the set $\omega(x_0) = \{p : x(t_k, x_0) \to p, \text{ for some } t_k \to \infty, k \to \infty\}$, and the alpha limit set $\alpha(x_0) = \{p : x(t_k, x_0) \to p, \text{ for some } t_k \to -\infty, k \to \infty\}$. Finally we denote by E_{fix} the set of fixed points of (2), i.e. $E_{\text{fix}} = \{x \in \mathbb{R}^N_+ : D(x)F(x) = 0\}$.

We are concerned with the global dynamics of (2) on $\mathbb{R}^N_+$, and in particular when interior or boundary fixed points are pointwise globally attracting or repelling. Suppose $p \in E_{\text{fix}} \setminus \{0\}$

is a non-trivial fixed point of (2) with $p_i = 0$ if and only if $i \in I \subset I_N$ and p is the unique fixed point in $\mathbb{R}_I$. Then p is said to be *pointwise globally attracting (in forward time)* if $\lim_{t\to+\infty} x(t, x_0) = p$ (i.e. $\omega(x_0) = \{p\}$) for all $x_0 \in \mathbb{R}_I$. In addition, if p is locally stable with respect to $\mathbb{R}_I$, then p is called *globally asymptotically stable (in forward time).* (Alternatively, we say that (2) is globally asymptotically stable at p, or in short, globally stable.) When p is not stable, we impose the assumptions (A1) and (A2) on (2) given below so that there exists a compact invariant set $K \subset \mathbb{R}^N_+ \setminus \{0\}$ that contains p and $\omega(x_0)$ for every $x_0 \in \mathbb{R}^N_+ \setminus \{0\}$. Then p is said to be *pointwise globally repelling*, or *pointwise globally attracting in backward time*, if $\lim_{t\to-\infty} x(t, x_0) = p$ (i.e. $\alpha(x_0) = \{p\}$) for all $x_0 \in \mathbb{R}_I \cap K$. In addition, if p is also stable in backward time with respect to $\mathbb{R}_I \cap K$, then p is called *globally asymptotically stable in backward time* on $\mathbb{R}_I \cap K$. The intention here of adding the word "pointwise" to our concepts of attaction (repulsion) is to distinguish these from the often used notions of attracting (repelling) bounded sets. From now on we shall use the initials P. G. for "pointwise global" or "pointwise globally".

Assumption 1.

(A1) *System (2) is dissipative: there is a compact invariant set $\mathcal{A} \subset \mathbb{R}^N_+$ such that for any $\varepsilon > 0$ and each bounded set $U \subset \mathbb{R}^N_+$, $x(t, U)$ is within ε of $\mathcal{A}$ for sufficiently large t.*

(A2) $F(0) \in \mathrm{int}\mathbb{R}^N_+$.

Under the assumptions (A1) and (A2), we make the following observations:

(i) By (A1), $\mathcal{A}$ is a global attractor of the flow generated by (2) on $\mathbb{R}^N_+$. As $\mathcal{A}$ contains all fixed points, we have $0 \in \mathcal{A}$.

(ii) By (A2), $\{0\}$ is a repellor (i.e. the attraction in backward time is uniform for points in some neighbourhood of 0). In particular, some relative neighbourhood of 0 in $\mathbb{R}^N_+$ is contained in $\mathcal{A}$.

(iii) Applying the theory of attractor-repellor pairs for flows on compact metric spaces (see, e.g. III 3.1 in [21]), we see that there is a compact invariant set $K \subset \mathcal{A}$ that is an attractor in $\mathcal{A}$ dual to the repellor $\{0\}$.

(iv) From (i)–(iii) we see that K can be viewed as a global attractor of the flow restricted to $\mathbb{R}^N_+ \setminus \{0\}$.

(v) If (2) is totally competitive (i.e. $\frac{\partial F_i}{\partial x_j} < 0$ for all $i, j \in I_N$) and assumptions (A1) and (A2) hold, then K is identical to the carrying simplex $\Sigma = \overline{B(0)} \setminus B(0)$ (see [26], [25] or [6]), where $B(0)$ is the repulsion basin of $\{0\}$ in $\mathbb{R}^N_+$.

3. Conditions for dissipativity

The assumption (A2) is easily verifiable. For assumption (A1), at least the class of totally competitive Lotka-Volterra systems satisfy it. In general, it is known that a finite dimensional dynamical system is dissipative if it is *point dissipative*, that is, there exists a bounded set such that any positive orbit enters that set in finite time and stays there. Then the following result is a simple sufficient condition for (2) to meet assumption (A1).

Theorem 3.1. *Assume that, under a permutation $(1, \ldots, N) \to (i_1, \ldots, i_N)$, there are N positive numbers $M_1, \ldots, M_N$ such that*

$$\forall M \geq M_1, \sup\{F_{i_1}(x) : x \in \mathbb{R}^N_+, M_1 \leq x_{i_1} \leq M\} < 0;\ \forall j \in \{2, \ldots, N\},$$

$$\forall M \geq M_j, \sup\{F_{i_j}(x) : x \in \mathbb{R}^N_+, x_{i_k} \leq M_k \text{ for } k < j, M_j \leq x_{i_j} \leq M\} < 0.$$

Then every solution of (2) enters into the set $S_1 = \{x : 0 \leq x_{i_j} \leq M_j, j \in I_N\}$ in finite time and remains there.

Proof. For each $x^0 \in \mathbb{R}^N_+$, if $x^0_{i_1} > M_1$, the condition guarantees the existence of $t_1 > 0$ such that the solution $x(t, x^0)$ on its existing interval satisfies $x_{i_1}(t, x^0) \leq M_1$ for $t \geq t_1$. If $x_{i_2}(t_1, x^0) > M_2$, then there is a $t_2 > t_1$ such that $x_{i_2}(t, x^0) \leq M_2$ for all $t \geq t_2$ on the existing interval of $x(t, x^0)$. Repeating the above procedure N times we see the existence of $x(t, x^0)$ on $[0, +\infty)$ satisfying $x_{i_j}(t, x^0) \leq M_j$ for all $j \in I_N$ and all large t. □

4. P. G. attraction

The following theorem is fundamental to our method. The version that we state is based on lemma 8.2 of Saperstone [22]. For any function $f : \mathbb{R}^N \to \mathbb{R}$, we view $\nabla f(x) = (\frac{\partial f}{\partial x_1}, \ldots, \frac{\partial f}{\partial x_n})$ as a row vector.

Theorem 4.1 (LaSalle's Invariance Principle)**.** *Let Ω be a subset of $\mathbb{R}^N$ and $x(t, \cdot)$ denote a semiflow on Ω generated by a C^1 vector field $f : \Omega \to \mathbb{R}^N$. Let $x_0 \in \Omega$ be given and suppose that there is a C^1 real-valued function V on $\overline{\Omega}$ for which $\dot{V}(x(t, x_0)) \geq 0$ for all $t \geq 0$, where $\dot{V} : \Omega \to \mathbb{R}$ is defined by $\dot{V}(x) = \nabla V(x) f(x)$. Denote by M the largest invariant subset of Ω. If the forward orbit $O^+(x_0)$ has compact closure (inside Ω) then $\omega(x_0) \subset M \cap \dot{V}^{-1}(0)$.*

Remark 1. We observe that the conclusion of theorem 4.1 is still true if the requirement $\dot{V}(x(t, x_0)) \geq 0$ is replaced by $V(x(t, x_0))$ being monotone for large enough t. Indeed, by the boundedness of $O^+(x_0)$ and $\overline{O^+(x_0)} \subset \Omega$, $V(x(t, x_0))$ is bounded so there is a constant c such that $V(\omega(x_0)) = c$. Then, $\forall y \in \omega(x_0)$, $V(x(t, y)) \equiv c$ for $t \in \mathbb{R}$ so $\dot{V}(x(t, y)) = 0$. This shows that $\omega(x_0) \subset \dot{V}^{-1}(0)$. Since $\overline{O^+(x_0)} \subset \Omega$ implies $\omega(x_0) \subset M$, we must have $\omega(x_0) \subset M \cap \dot{V}^{-1}(0)$.

Our general approach for Kolmogorov systems is as follows: Define a function $\Phi : \mathrm{int}\mathbb{R}^N_+ \to \mathbb{R}_+$ by $\Phi(x) = \phi(x)V(x)$, where $V(x) = \prod_{i=1}^N x_i^{\theta_i}$ for a given $\theta = (\theta_1, \ldots, \theta_N)^T \in \mathbb{R}^N$ and $\phi : \mathbb{R}^N_+ \to (0, +\infty)$ is a C^1 positive function. Let

$$I = \{i \in I_N : \theta_i = 0\}, I_+ = \{i \in I_N : \theta_i > 0\} \text{ and } I_- = \{j \in I_N : \theta_j < 0\}. \tag{6}$$

Then Φ can be continuously extended to $\mathbb{R}_{I_N \setminus I_-}$ and, if $I_- = \emptyset$, to $\mathbb{R}^N_+$. For a bounded forward solution $x = x(t, x_0)$ of (2) starting at $x_0 \in \mathbb{R}_I$ we may compute

$$\dot{\Phi}(x) = \rho(x)\Phi(x),$$

where

$$\rho(x) := \frac{1}{\phi(x)} \nabla\phi(x)D(x)F(x) + \theta^T F(x). \tag{7}$$

Remark 2. We could instead use $\Phi = \log(\phi V) = \log\phi + \sum_{i=1}^N \theta_i \log x_i$ which would give instead $\dot{\Phi} = \rho$, but we find $\Phi = \phi V$ a more convenient choice.

For θ, I, I_+ and I_- given in (6), suppose there is a fixed point $p \in C_I^0$. Our task in this section is to establish a criterion for p to be P. G. attracting. For this purpose, we first observe that the following necessary conditions hold simultaneously for p to be P. G. attracting:

(N1) $\forall x_0 \in \mathbb{R}_I, x(t, x_0)$ is bounded for $t \geq 0$ and $0 \notin \omega(x_0)$;

(N2) $\forall x_0 \in \mathbb{R}_I, \forall j \in I_+ \cup I_-, \omega(x_0) \cap \pi_j = \emptyset$;

(N3) $\forall x_0 \in \mathbb{R}_I, \exists \ell > 0$ such that $\omega(x_0) \subset \rho^{-1}(0) \cap \Phi^{-1}(\ell) \cap \mathbb{R}_I$.

These give us a clear indication that any criterion for P. G. attraction of p must include conditions that guarantee (N1)–(N3). Moreover, to ensure that $\omega(x_0) = \{p\}$ for all $x_0 \in \mathbb{R}_I$, we need some property on $(\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$ such that

$$y_0 \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I \Longrightarrow \forall \text{ small } t \neq 0, x(t, y_0) \notin (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I. \tag{8}$$

For if $\omega(x_0) \neq \{p\}$ then $(\omega(x_0) \setminus \{p\}) \subset (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$. It then follows from the invariance of $\omega(x_0) \setminus \{p\}$ and (8) that $(\omega(x_0) \setminus \{p\}) \not\subset (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$, a contradiction. We now see that property (8) holds under the following condition:

(N4) $g(x) = \nabla\rho(x)D(x)F(x)(= \dot{\rho}(x))$ on $(\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$ does not change sign and has no zeros (or has isolated zeros that are not isolated points of $(\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$).

Indeed, condition (N4) together with the three necessary conditions (N1)–(N3) suffices for the P. G. attraction of p. However, (N1)–(N3) are actual requirements on solutions of (2) rather than conditions on the system. So we need to find checkable conditions on system (2) for (N1)–(N4) to hold. Requirement (N1) can be checked easily from the system (2) so we may view it as a condition on the system. Condition (N4) is for no sign change of g on $(\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$ and it includes four distinct cases (see condition 4 (a)–(d) of theorem 4.4 below). Note that, as a by-product, condition (N4) also ensures that $\rho(x(t, x_0))$ for each fixed $x_0 \in \mathbb{R}_I$ eventually has no sign changes. Requirement (N2) actually requires that every solution in $\mathbb{R}_I$ keeps a finite distance away from $\bigcup_{j \in I_+ \cup I_-} \pi_j$, a part of the boundary $\partial\mathbb{R}^N_+$. From lemma 4.3 below we see that each of the conditions (i)–(iv) together with the above by-product of (N4) will imply (N2) and (N3). Then theorem 4.4 is formed as a summary of the above analysis.

The following definition is needed to control behaviour of orbits near the boundary $\partial\mathbb{R}^N_+$ and hence the boundedness of V when θ has some negative components.

Definition 4.2. For a nonempty subset $J \subset I_N$, (2) is said to be J-permanent if there are $M_2 > M_1 > 0$ such that every solution of (2) in $\mathbb{R}_{I_N \setminus J}$ satisfies

$$\forall j \in J, M_1 \leq \liminf_{t \to +\infty} x_j(t) \leq \limsup_{t \to +\infty} x_j(t) \leq M_2.$$

Lemma 4.3. *Let $\theta \in \mathbb{R}^N$ and I, I_+, I_- be given as in (6). For $x_0 \in \mathbb{R}_I$, suppose that the solution $x(t, x_0)$ of (2) is bounded for $t \geq 0$ and set $\rho(x) := \dot{\Phi}(x)/\Phi(x)$. Assume that one of the following conditions is met:*

(i) *(2) is I_--permanent if $I_- \neq \emptyset$ and has no invariant set in $\{x \in (\bigcup_{j \in I_+} \pi_j) \setminus \{0\} : \rho(x) \leq 0\}$.*

(ii) *(2) is I_+-permanent if $I_+ \neq \emptyset$ and has no invariant set in $\{x \in (\bigcup_{j \in I_-} \pi_j) \setminus \{0\} : \rho(x) \geq 0\}$.*

(iii) *(2) is $(I_+ \cup I_-)$-permanent.*

(iv) *(2) has no invariant set in either $\{x \in (\bigcup_{j \in I_+} \pi_j) \setminus \{0\} : \rho(x) \leq 0\}$ or $\{x \in (\bigcup_{j \in I_-} \pi_j) \setminus \{0\} : \rho(x) \geq 0\}$.*

Then if there exists a $t_0 \geq 0$ such that $\rho(x(t, x_0)) \geq 0$ for all $t \geq t_0$ or $\rho(x(t, x_0)) \leq 0$ for all $t \geq t_0$, it follows that $\omega(x_0) \subset \rho^{-1}(0) \cap \Phi^{-1}(\ell) \cap \mathbb{R}_I$ for some $\ell > 0$.

Proof. Suppose we have $\rho(x(t, x_0)) \geq 0$ for all $t \geq t_0$. As $\Phi(x_0)$ is positive for $x_0 \in \mathbb{R}_I$, we have

$$\Phi(x(t, x_0)) = \Phi(x_0) \exp\left(\int_0^t \rho(x(\tau, x_0))\, d\tau\right) \geq \Phi(x_0) \exp\left(\int_0^{t_0} \rho(x(\tau, x_0))\, d\tau\right) > 0$$

for all $t \geq t_0$.

If $\theta \in \mathbb{R}^N_+$ then $I_- = \emptyset$ so Φ is defined on $\mathbb{R}^N_+$ with $\Phi(x) = 0$ for $x \in \cup_{j \in I_N \setminus I} \pi_j$ and $\Phi(x) > 0$ for $x \in \mathbb{R}_I = \mathbb{R}^N_+ \setminus (\cup_{j \in I_N \setminus I} \pi_j)$. Since $x(t, x_0)$ is bounded, the above inequality shows that Φ has a positive minimum on $\overline{O^+(x_0)}$. Thus, $\overline{O^+(x_0)} \subset \mathbb{R}_I$. Then, if we take $M = \Omega = \mathbb{R}_I$, by LaSalle's principle, $\omega(x_0) \subseteq \mathbb{R}_I \cap (\rho^{-1}(0) \cup \Phi^{-1}(0))$. As $\Phi(x) > 0$ for all $x \in \mathbb{R}_I$, we have $\omega(x_0) \subset \rho^{-1}(0) \cap \mathbb{R}_I$. Moreover it is easy to see that $\Phi(x) = \ell$ for some $\ell > 0$ and all $x \in \omega(x_0)$ and so $\omega(x_0) \subset \rho^{-1}(0) \cap \Phi^{-1}(\ell) \cap \mathbb{R}_I$. Note that no condition of (i)–(iv) is used in this case.

If $\theta \notin \mathbb{R}_+^N$ then $I_- \neq \emptyset$ so Φ is defined on $(\cup_{j\in I_+}\pi_j)\cup\mathbb{R}_I$ with $\Phi(x) = 0$ for $x \in \cup_{j\in I_+}\pi_j$ and $\Phi(x) > 0$ for $x \in \mathbb{R}_I$. The part in any one of the conditions (i)–(iv) relating to I_- ensures that $\liminf_{t\to+\infty} x_j(t, x_0) > 0$ for all $x_0 \in \mathbb{R}_I$ and $j \in I_-$. Thus, $\overline{O^+(x_0)} \cap (\cup_{j\in I_-}\pi_j) = \emptyset$ and $\overline{O^+(x_0)} \subset (\cup_{j\in I_+}\pi_j) \cup \mathbb{R}_I$. From the above inequality $\Phi(x(t, x_0)) \geq \Phi(x(t_0, x_0)) > 0$ for $t \geq t_0$ we know that Φ has a positive minimum on $\overline{O^+(x_0)}$. This shows that $\overline{O^+(x_0)} \cap (\cup_{j\in I_+}\pi_j) = \emptyset$ so $\overline{O^+(x_0)} \subset \mathbb{R}_I$. Then, by taking $M = \Omega = \mathbb{R}_I$, the conclusion follows from LaSalle's principle.

Suppose we have $\rho(x(t, x_0)) \leq 0$ for all $t \geq t_0$. Then $\Phi(x(t, x_0))$ is positive and nonincreasing for $t \geq t_0$. If $\theta_i \leq 0$ for all $i \in I_N$ then $I_+ = \emptyset$. Then the boundedness of $x(t, x_0)$ guarantees the existence of $\ell > 0$ such that $\Phi(\omega(x_0)) = \ell$ and $\omega(x_0) \subset \mathbb{R}_I$. Hence, by LaSalle's principle, $\omega(x_0) \subset \rho^{-1}(0) \cap \Phi^{-1}(\ell) \cap \mathbb{R}_I$.

If $I_+ \neq \emptyset$, the part in any one of the conditions (i)–(iv) relating to I_+ implies that $\liminf_{t\to+\infty} x_i(t, x_0) > 0$ for all $i \in I_+$ and $x_0 \in \mathbb{R}_I$ so $\omega(x_0) \subset \mathbb{R}_I$ and the conclusion follows. □

From lemma 4.3 we see that a global analysis of an orbit of (2) through $x_0 \in \mathbb{R}_+^N$ becomes an investigation of the sign of the function $t \mapsto \rho(x(t, x_0))$. Thus we now turn to establishing sufficient conditions for which

(9) $\exists t_0 \geq 0$ such that either $\rho(x(t, x_0)) \geq 0\ \forall t \geq t_0$ or $\rho(x(t, x_0)) \leq 0\ \forall t \geq t_0$.

For this purpose, we define $g : \mathbb{R}_+^N \to \mathbb{R}$ via

$$g(x) = -\lambda\rho(x) + \nabla\rho(x)D(x)F(x)$$

for any constant $\lambda \in \mathbb{R}$, so that along a solution $x(t, x_0)$ we have $\dot{\rho}(x(t, x_0)) = \lambda\rho(x(t, x_0))+ g(x(t, x_0))$. Note that in the set $\rho^{-1}(0)$, the term $-\lambda\rho(x)$ vanishes so it does not affect the value of g.

We are now in the position to state sufficient conditions for P. G. attraction of a boundary or interior fixed point in terms of g:

Theorem 4.4 (P. G. attraction of a fixed point)**.** *With θ, I, I_+ and I_- given in (6), suppose that the system (2) satisfies the following conditions:*

(1) *There is a fixed point $p \in C_I^0$.*

(2) *For each $x_0 \in \mathbb{R}_I$, the solution $x(t, x_0)$ is bounded for $t \geq 0$ and $0 \notin \omega(x_0)$.*

(3) *One of the following conditions is met:*

   (i) *(2) has no invariant set in $\{x \in (\bigcup_{j\in I_+}\pi_j) \setminus \{0\} : \rho(x) \leq 0\}$ and, if $I_- \neq \emptyset$, is I_--permanent.*

   (ii) *(2) has no invariant set in $\{x \in (\bigcup_{j\in I_-}\pi_j) \setminus \{0\} : \rho(x) \geq 0\}$ and, if $I_+ \neq \emptyset$, is I_+-permanent.*

   (iii) *(2) is $(I_+ \cup I_-)$-permanent.*

(iv) *(2) has no invariant set in either* $\{x \in (\bigcup_{j\in I_+} \pi_j) \setminus \{0\} : \rho(x) \le 0\}$ *or* $\{x \in (\bigcup_{j\in I_-} \pi_j) \setminus \{0\} : \rho(x) \ge 0\}$.

(4) *The function g satisfies one of the following conditions:*

(a) $g(x) > 0$ *for all* $x \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$.

(b) *p is the unique fixed point of (2) in* $\mathbb{R}_I$, $g(x) \ge 0$ *for all* $x \in \rho^{-1}(0) \cap \mathbb{R}_I$ *and each zero* x_0 *of g in* $(\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$ *is an isolated zero of g in this set but is not an isolated point of this set.*

(c) $g(x) < 0$ *for all* $x \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$.

(d) *p is the unique fixed point of (2) in* $\mathbb{R}_I$, $g(x) \le 0$ *for all* $x \in \rho^{-1}(0) \cap \mathbb{R}_I$ *and each zero* x_0 *of g in* $(\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$ *is an isolated zero of g in this set but is not an isolated point of this set.*

Then p is P. G. attracting.

Remark 3. The statement of theorem 4.4 looks lengthy. But essentially this is the most economical way of presenting 16 different combinations of (i)–(iv) in condition 3 and (a)–(d) in condition 4 in one statement rather than in 16 separate shorter statements.

Remark 4. In theorem 4.4, the choice of $\theta \in \mathbb{R}^N$ depends on the fixed point p: if p is an interior fixed point (i.e. $p \in \text{int}\mathbb{R}^N_+$) then $I = \emptyset$ so $\theta_i \ne 0$ for all $i \in I_N$; if p is a boundary fixed point (i.e. $p \in \partial\mathbb{R}^N_+$) then $I \ne \emptyset$ and $\theta_i \ne 0$ if and only if $i \in I_N \setminus I$. Although we have not yet specified how to choose θ and ϕ, we shall see various examples of θ and ϕ in the next few sections. In most cases, especially for the global stability theorems in section 7, we choose $\phi = 1$ and $\theta = D(v)p$ where v^T is a left eigenvector of $J(p)$ corresponding to one of the negative eigenvalues.

Remark 5. Each of the conditions (i)–(iv) is a required property of solutions rather than a direct condition on the system. So it is not straightforward to check their validity. However, for systems with $N = 2$ or $N = 3$, $\partial\mathbb{R}^N_+$ is at most two-dimensional so the phrase "no invariant set" in (i), (ii) and (iv) is equivalent to "no fixed points". Thus, (iv) can be simplified to the following easily checkable condition:

(iv)* (2) has no fixed points in the set

$$\{x \in (\cup_{j\in I_+}\pi_j) \setminus \{0\} : \rho(x) \le 0\} \cup \{x \in (\cup_{j\in I_-}\pi_j) \setminus \{0\} : \rho(x) \ge 0\}.$$

When $N = 2$, J-permanence can be easily determined by sketching a phase portrait so any of (i)–(iv) can be easily checked. For a particular system with $N \ge 4$, since J-permanence is another specialised active research area, we need to search the literature for available J-permanence results (e.g. [10]) or analyse the location of the global attractor of the system restricted to $\bigcup_{j\in I_+} \pi_j$ and $\bigcup_{j\in I_-} \pi_j$.

Remark 6. To check condition (a) or (c), it is helpful to check that $g(x)$ and $\rho(x)$ have no common zeros in $\mathbb{R}_I \setminus \{p\}$. If $g(x) = \frac{A(x)}{\alpha(x)}$ and $\rho(x) = \frac{B(x)}{\beta(x)}$, where $\alpha(x) > 0$ and

$\beta(x) > 0$ and both $A(x)$ and $B(x)$ are polynomials, for each $n \in I_N$ we may compute the resultant $\mathrm{Res}(A(x), B(x), x_n)$ (see in the Appendix for an explanation of this notation). Since $\mathrm{Res}(A(x), B(x), x_n) = 0$ if and only if A and B have a common zero, if $\mathrm{Res}(A(x), B(x), x_n) \neq 0$ for $x \in \mathbb{R}_I \setminus \{p\}$ then $g(x) \neq 0$ for $x \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$ so (a) or (b) can be checked (see examples 1 and 2 below). Another way of verifying (a) or (c) is to convert these conditions to verifying the positive or negative definite property of a variable matrix (see sections 7.2, 7.3 and the example in section 9).

Remark 7. Although theorem 4.4 is for system (2) defined on $\mathbb{R}^N_+$, from its proof we can see that this theorem is still valid for system (2) defined on an invariant subset Ω of $\mathbb{R}^N_+$, where C^0_I, $\mathbb{R}_I$ and π_j are replaced by $C^0_I \cap \Omega$, $\mathbb{R}_I \cap \Omega$ and $\pi_j \cap \overline{\Omega}$ (see example 1 below).

We split the proof of Theorem 4.4 into a series of lemmas, some of which will be reused later.

Denote the open ball centred at $a \in \mathbb{R}^N$ with a radius $r > 0$ by $\mathcal{B}_r(a)$.

Lemma 4.5. *For any $x_0 \in \rho^{-1}(0) \cap \mathbb{R}_I$, if x_0 is not a fixed point and $g(x_0) > 0$ (< 0) then there is a $\delta > 0$ such that $\rho(x(t, x_0))$ is strictly increasing (decreasing) for $|t| \leq \delta$, so $t\rho(x(t, x_0)) > 0$ (< 0) for $0 < |t| \leq \delta$.*

Proof. Since $\dot{\rho}(x_0) = \lambda\rho(x_0) + g(x_0) = g(x_0) > 0$ (< 0) at $t = 0$, by continuity in t, there exists a $\delta > 0$ such that $\dot{\rho}(x(t, x_0)) = \lambda\rho(x(t, x_0)) + g(x(t, x_0)) > 0$ (< 0) for $|t| \leq \delta$. Thus, for any $x_0 \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$, if $g(x_0) > 0$ (< 0) then there is a $\delta > 0$ such that $\rho(x(t, x_0))$ is strictly increasing (decreasing) for $t \in [-\delta, \delta]$ so that $t\rho(x(t, x_0)) > 0$ (< 0) for $0 < |t| \leq \delta$. □

Lemma 4.6. *Assume that $p \in C^0_I$ is a fixed point of (2) and that*

$$\forall x \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I, g(x) > 0 \ (< 0).$$

Then p is the unique fixed point of (2) in $\mathbb{R}_I$ and

$$\forall x_0 \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I, \forall t > 0,\ \rho(x(t, x_0)) > 0 \ (< 0).$$

Proof. For any $x_0 \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$, since $g(x_0) > 0$ (< 0), by lemma 4.5, $\rho(x(t, x_0)) > 0$ (< 0) holds for sufficiently small $t > 0$. If $\rho(x(t, x_0))$ has a zero for some $t > 0$ then there is a $t_1 > 0$ such that $\rho(x(t_1, x_0)) = 0$ and $\rho(x(t, x_0)) > 0$ (< 0) for $0 < t < t_1$. But since $x(t_1, x_0) \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$, by lemma 4.5 again, $\rho(x(t, x_0))$ is strictly increasing (decreasing) for t in the vicinity of t_1 so $\rho(x(t, x_0)) = \rho(x(t - t_1, x(t_1, x_0))) < 0$ (> 0) for $t < t_1$ with $|t - t_1|$ small enough. This contradiction to $\rho(x(t, x_0)) > 0$ (< 0) for $t \in (0, t_1)$ shows that $\rho(x(t, x_0)) > 0$ (< 0) for all $t > 0$. From the definition of ρ we see that p is the unique fixed point of (2) in $\mathbb{R}_I$. □

Lemma 4.7. *Assume that p is the unique fixed point of (2) in $\mathbb{R}_I$. Assume also that*

$$\forall x \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I, g(x) \geq 0 \ (\leq 0).$$

Moreover, if each zero of g in $(\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$ is not an isolated point of $\rho^{-1}(0) \cap \mathbb{R}_I$ but an isolated zero of g in this set, then

$$\forall x_0 \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I, \forall t \geq 0,\ \rho(x(t, x_0)) \geq 0\ (\leq 0).$$

Further, each zero of $\rho(x(\cdot, x_0))$ is isolated in $\mathbb{R}_+$.

Proof. We first assume $g(x_0) \geq 0$ for any $x_0 \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$. Suppose $g(x_0) = 0$ and there is a $t_1 > 0$ such that $\rho(x(t, x_0)) < 0$ for $t \in (0, t_1]$. As x_0 is not an isolated point of $\rho^{-1}(0) \cap \mathbb{R}_I$ and x_0 is an isolated zero of g in this set, there is a $\delta > 0$ such that $g(x) > 0$ for all x in the nonempty set $(\rho^{-1}(0) \setminus \{x_0\}) \cap \mathcal{B}_\delta(x_0) \cap \mathbb{R}_I$. So, for each $y_0 \in (\rho^{-1}(0) \setminus \{x_0\}) \cap \mathcal{B}_\delta(x_0) \cap \mathbb{R}_I$, by lemma 4.5, $\rho(x(t, y_0)) > 0$ for sufficiently small $t > 0$. On the other hand, as

$$\lim_{y_0 \to x_0} \sup_{0 \leq t \leq t_1} \|x(t, y_0) - x(t, x_0)\| = 0$$

and ρ is continuous, for y_0 close enough to x_0, we have $\rho(x(t_1, y_0)) < 0$ so there is a $t_2 \in (0, t_1)$ such that $x(t_2, y_0) \in (\rho^{-1}(0) \setminus \{x_0\}) \cap \mathcal{B}_\delta(x_0) \cap \mathbb{R}_I$ and $\rho(x(t, y_0)) < 0$ for $t \in (t_2, t_1]$. This contradicts $\rho(x(t, y_0)) = \rho(x(t - t_2, x(t_2, y_0))) > 0$ for sufficiently small $t - t_2 > 0$. Therefore, for each $x_0 \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$ with $g(x_0) = 0$, we must have $\rho(x(t, x_0)) \geq 0$ for all $t \geq 0$.

To show the second part of the conclusion, suppose for some $x_0 \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$, there are $t_0 \geq 0$ and a sequence $\{t_k\} \subset (0, +\infty)$ such that $\lim_{k \to \infty} t_k = t_0$ and $\rho(x(t_k, x_0)) = 0$ for all $k = 0, 1, 2, \ldots$.

If $g(x(t_0, x_0)) > 0$, by lemma 4.5 there is a $\delta > 0$ such that $(t - t_0)\rho(x(t, x_0)) > 0$ if $0 < |t - t_0| < \delta$. Then, for large enough k with $0 < |t_k - t_0| < \delta$, we have $(t_k - t_0)\rho(x(t_k, x_0)) > 0$, a contradiction to $\rho(x(t_k, x_0)) = 0$.

If $g(x(t_0, x_0)) = 0$, then $x(t_0, x_0)$ is an isolated zero of g in $\rho^{-1}(0) \cap \mathbb{R}_I$ so there is a $\delta > 0$ such that $g(x) > 0$ for all $x \in (\rho^{-1}(0) \setminus \{x(t_0, x_0)\}) \cap \mathcal{B}_\delta(x(t_0, x_0)) \cap \mathbb{R}_I$. By the uniqueness of p as a fixed point in $\mathbb{R}_I$, $x(t_0, x_0)$ cannot be a fixed point. So there is a $k_0 > 0$ such that $x(t_k, x_0) \in (\rho^{-1}(0) \setminus \{x(t_0, x_0)\}) \cap \mathcal{B}_\delta(x(t_0, x_0)) \cap \mathbb{R}_I$ so that $g(x(t_k, x_0)) > 0$ for all $k \geq k_0$. Then, for each $k \geq k_0$, by lemma 4.5 we have $\rho(x(t, x_0)) < 0$ for $t < t_k$ with $|t - t_k|$ sufficiently small, a contradiction to $\rho(x(t, x_0)) \geq 0$ for all $t \geq 0$. These contradictions show that each zero of $\rho(x(t, x_0))$ is isolated in $[0, +\infty)$.

We conclude that for each $x_0 \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$, $\rho(x(t, x_0)) \geq 0$ holds for all $t \in [0, +\infty)$ and each zero of $\rho(x(t, x_0))$ is isolated in $[0, +\infty)$.

If $g(x) \leq 0$ for all $x \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$, the corresponding conclusion follows from the above reasoning by simply reversing the direction of the relevant inequalities. □

Lemma 4.8. *Assume that $p \in C_I^0$ is a fixed point of (2) and that g satisfies one of the conditions (a)–(d) given in theorem 4.4. If $\omega(x_0) \subset \rho^{-1}(0) \cap \mathbb{R}_I$ for some $x_0 \in \mathbb{R}_I$ then $\omega(x_0) = \{p\}$.*

Proof. As $\omega(x_0)$ is nonempty, connected and compact, if $\omega(x_0) \neq \{p\}$ then, by invariance of $\omega(x_0)$, $\exists y \in \omega(x_0) \setminus \{p\}$ such that $x(t,y) \in \omega(x_0) \setminus \{p\} \subset (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I$ for all $t \in \mathbb{R}$. By lemmas 4.6 and 4.7 $\exists t_1 > 0$ such that $\rho(x(t_1,y)) \neq 0$, which contradicts $x(t_1,y) \in \omega(x_0) \subset \rho^{-1}(0)$. Therefore, $\omega(x_0) = \{p\}$. □

Putting the lemmas 4.3, 4.6–4.8 together we may establish theorem 4.4:

Proof of theorem 4.4. Suppose either condition 4 (a) or (b) is met. Let $x_0 \in \mathbb{R}_I \setminus \{p\}$ be such that $\rho(x_0) \geq 0$. Then by lemmas 4.6 and 4.7 we have that $\rho(x(t,x_0)) \geq 0$ for all $t \geq 0$ and each zero of $\rho(x(\cdot,x_0))$ is isolated on $\mathbb{R}_+$. Then, by conditions 1–3 and lemma 4.3, $\omega(x_0) \subseteq \rho^{-1}(0) \cap \mathbb{R}_I$.

On the other hand, suppose that $x_0 \in \mathbb{R}_I$ is such that $\rho(x_0) < 0$. If $\exists t_1 > 0$ such that $x(t_1,x_0) \in \rho^{-1}(0)$ then from the previous paragraph we have $\omega(x_0) \subset \rho^{-1}(0) \cap \mathbb{R}_I$. Otherwise, there is no such t_1 so $\rho(x(t,x_0)) < 0$ for all $t \in \mathbb{R}_+$. Hence $\dot{\Phi} = \rho\Phi < 0$, so $\Phi(x(t,x_0))$ is strictly decreasing, for all $t \in \mathbb{R}_+$. Since each one of the conditions (i)–(iv) relating to I_+ implies that $\liminf_{t\to+\infty} x_j(t,x_0) > 0$ for $j \in I_+$ and $O^+(x_0)$ is bounded, there is a $c > 0$ such that $\lim_{t\to+\infty} \Phi(x(t,x_0)) = \Phi(\omega(x_0)) = c$. This shows that $\omega(x_0) \cap (\cup_{j\in I_+} \pi_j) = \emptyset$. If $\omega(x_0) \cap (\cup_{j\in I_-} \pi_j) \neq \emptyset$, then there exist $j \in I_-$ and a sequence $\{t_k\}$, $t_k \to +\infty$ as $k \to \infty$, such that $x_j(t_k,x_0) \to 0$, and consequently $x_j^{\theta_j} \to +\infty$ and $\Phi(x(t_k,x_0)) \to +\infty$, as $k \to \infty$. This contradiction to $\lim_{t\to+\infty} \Phi(x(t,x_0)) = c$ shows that $\omega(x_0) \cap (\cup_{j\in I_-} \pi_j) = \emptyset$. Therefore, $\omega(x_0) \subset \mathbb{R}_I$. Now taking $M = \Omega = \mathbb{R}_I$, by remark 1 we have $\omega(x_0) \subset M \cap \dot{\Phi}^{-1}(0) = \mathbb{R}_I \cap \rho^{-1}(0)$.

Now suppose either condition 4 (c) or (d) is fulfilled. Parallel to the first paragraph we see that $\rho(x_0) \leq 0$ for $x_0 \in \mathbb{R}_I \setminus \{p\}$ implies $\omega(x_0) \subseteq \rho^{-1}(0) \cap \mathbb{R}_I$; parallel to the second paragraph we also obtain that $\rho(x_0) > 0$ implies $\omega(x_0) \subseteq \rho^{-1}(0) \cap \mathbb{R}_I$.

In all cases, the conclusion follows from lemma 4.8. □

Example 1. The following example of (2) with

$$\begin{aligned} F_1(x) &= \left(1 - x_1 - \frac{x_2}{A + x_1}\right), \\ F_2(x) &= r\left(1 - \frac{hx_2}{x_1}\right) \end{aligned}$$

was considered by Hsu et al [14]. Take $r = 5, h = 1, A = \frac{1}{2}$. There is a unique interior fixed point at $p = (\frac{1}{2}, \frac{1}{2})^T$. The Jacobian matrix is

$$J = \begin{pmatrix} \frac{-8x_1^3 - 4x_1^2 + 2x_1 - 2x_2 + 1}{(2x_1+1)^2} & \frac{1}{2x_1+1} - 1 \\ \frac{5x_2^2}{x_1^2} & 5 - \frac{10x_2}{x_1} \end{pmatrix}, \quad J(p) = \begin{pmatrix} -\frac{1}{4} & -\frac{1}{2} \\ 5 & -5 \end{pmatrix}.$$

$J(p)$ has two negative eigenvalues $\frac{1}{8}(-21 \pm \sqrt{201})$ so p is asymptotically stable. To show its global stability, we show by theorem 4.4 that it is globally attracting. Since $\alpha^T = \left(\frac{1}{4}(19-\sqrt{201}), -1\right)$ is a left eigenvector of $J(p)$ corresponding to $-\frac{1}{8}(21+\sqrt{201})$, by taking $\Phi(x) = x_1^{\alpha_1 p_1} x_2^{\alpha_2 p_2}$, we have

$$
\begin{aligned}
\rho &= \frac{1}{8}\left(19-\sqrt{201}\right)\left(-\frac{x_2}{x_1+\frac{1}{2}} - x_1 + 1\right) - \frac{5}{2}\left(1-\frac{x_2}{x_1}\right) = \frac{P(x)}{x_1(x_1+\frac{1}{2})},\\
\dot{\rho} &= x_1\left(-\frac{x_2}{x_1+\frac{1}{2}} - x_1 + 1\right)\left(\frac{1}{8}\left(19-\sqrt{201}\right)\left(\frac{x_2}{\left(x_1+\frac{1}{2}\right)^2} - 1\right) - \frac{5x_2}{2x_1^2}\right)\\
&\quad +5\left(\frac{5}{2x_1} - \frac{19-\sqrt{201}}{8\left(x_1+\frac{1}{2}\right)}\right)x_2\left(1-\frac{x_2}{x_1}\right) = \frac{G(x)}{x_1^2(x_1+\frac{1}{2})^3},
\end{aligned}
$$

so that P, G are polynomials in $x^T = (x_1, x_2)$. The resultant of P and G with respect to x_1 (see Appendix) is

$$
\begin{aligned}
\operatorname{Res}(P, G, x_1) &= c x_2^4 (x_2+1)(2x_2-1)^2 \Big((58384900\sqrt{201} - 827625100)x_2^2\\
&\quad -(119899574\sqrt{201} - 1700013026)x_2\\
&\quad -10890067\sqrt{201} + 154438233\Big),
\end{aligned}
$$

where $c \neq 0$. Then $\operatorname{Res}(P, G, x_1)$ vanishes on $\mathbb{R}_+$ if and only if $x_2 = 1/2$. Since $P^{-1}(0)$ can be written as

$$
x_2 = \frac{x_1(2x_1+1)[(19-\sqrt{201})x_1 + (1+\sqrt{201})]}{2(1+\sqrt{201})x_1 + 20},
$$

x_2 is an increasing function of x_1 for $x_1 \geq 0$. Thus, $G(x) \neq 0$ for $x \in P^{-1}(0)\setminus\{p\}$ in $\mathbb{R}^2_+$. As $P^{-1}(0)\setminus\{p\}$ in $\mathbb{R}^2_+$ has two connected components, $x^0 = (0.4, 0.313896)^T$ in one component and $x^1 = (0.6, 0.624231)^T$ in the other, and $\dot{\rho}(x^0) \approx 0.00975659$ and $\dot{\rho}(x^1) \approx 0.00882231$, this shows that $\dot{\rho} > 0$ for $x \in (\rho^{-1}(0) \setminus \{p\}) \cap \operatorname{int}\mathbb{R}^2_+$ (condition 4 (a) of theorem 4.4). A simple sketch of the phase portrait shows that the system is permanent (condition 3 (iii) of theorem 4.4). By theorem 4.4 and remark 7, p is P. G. attracting. Then the global stability follows from the local stability of p.

Example 2. Two predator, one prey system We consider the system (2) with

$$F_1(x) = \left(1 - \frac{2x_1}{7}\right) - \frac{x_2}{x_1+1} - \frac{x_3}{x_1+1}, \tag{10}$$

$$F_2(x) = \frac{x_1}{x_1+1} - x_2 - \frac{1}{2}, \tag{11}$$

$$F_3(x) = \frac{x_1}{x_1+1} - x_3 - \frac{3}{7}. \tag{12}$$

The unique interior fixed point is given by $p = (3, \frac{1}{4}, \frac{9}{28})^T$. At p the Jacobian matrix

$$J = \begin{pmatrix} -\frac{3}{4} & -\frac{3}{4} & -\frac{3}{4} \\ \frac{1}{64} & -\frac{1}{4} & 0 \\ \frac{9}{448} & 0 & -\frac{9}{28} \end{pmatrix}$$

has three negative eigenvalues $-\frac{1}{112}(53+\sqrt{541})$, $-\frac{3}{8}$ and $-\frac{1}{112}(53-\sqrt{541})$ so p is asymptotically stable. We show by theorem 4.4 that p is also P. G. attracting so it is globally stable. Note that J has a left eigenvector $\alpha^T = (\frac{1}{14}, \frac{3}{7}, 1)$ corresponding to $-\frac{3}{8}$ and so we take $\Phi(x) = \prod_{i=1}^3 x_i^{\theta_i}$ with $\theta^T = \left(\frac{3}{14}, \frac{3}{28}, \frac{9}{28}\right)$. Here we have $\rho = (x_1+1)^{-1}P(x)$ where

$$\begin{aligned} P(x) \;&=\; \theta_2\left(x_1 - (x_1+1)\left(\frac{1}{2}+x_2\right)\right) + \theta_3\left(x_1 - (x_1+1)\left(\frac{3}{7}+x_3\right)\right) \\ &\quad + \theta_1\left((x_1+1)\left(1-\frac{2x_1}{7}\right) - x_2 - x_3\right). \end{aligned}$$

Similarly we find that $\dot\rho = (98(1+x_1)^3)^{-1}G(x)$ where

$$\begin{aligned} G(x) &= 49\,(x_1+1)\,x_2\,(-x_1+2\,(x_1+1)\,x_2+1)\,(\theta_1+\theta_2\,(x_1+1)) \\ &\quad +14\,(x_1+1)\,x_3\,(-4x_1+7\,(x_1+1)\,x_3+3)\,(\theta_1+\theta_3\,(x_1+1)) \\ &\quad +2x_1\,(x_1\,(2x_1-5)+7\,(x_2+x_3-1)) \\ &\quad \times(\theta_1\,(2x_1\,(x_1+2)-7x_2-7x_3+2)-7\,(\theta_2+\theta_3))\,. \end{aligned}$$

We now insert the numerical values of θ and take the resultant $\mathrm{Res}(P, G, x_3)$. The resultant is quadratic in x_2: $\mathrm{Res}(P, Q, x_3) = R_0(x_1) + R_1(x_1)x_2 + R_2(x_1)x_2^2$. This polynomial $\mathrm{Res}(P, Q, x_3)$ has real roots (x_1, x_2) only if $\delta := R_1(x_1)^2 - 4R_0(x_1)R_2(x_1) \geq 0$. We find that

$$\begin{aligned} \delta = &-\frac{729}{9834496}\,(x_1-3)^2\,(x_1+1)^2(3x_1+5)^2\big(2304x_1^6+21600x_1^5 \\ &+71975x_1^4+122908x_1^3+124866x_1^2+56476x_1+1055\big). \end{aligned}$$

Then, for $x_1 \geq 0$, $\delta = 0$ if and only if $x_1 = 3 = p_1$. Hence if $0 \leq x_1 \neq 3 = p_1$ we see that the resultant $\mathrm{Res}(P, G, x_3)$ cannot vanish. When $x_1 = 3$ we find that $\mathrm{Res}(P, G, x_3) = 0$ if and only if $x_2 = 1/4 = p_2$. The conclusion is that P, G vanish simultaneously only at the interior fixed point p. Since $P^{-1}(0)$ has the equation

$$x_3 = \frac{-8x_1^2 - 14x_2x_1 + 51x_1 - 42x_2 + 3}{14(3x_1+5)},$$

the surface $\rho^{-1}(0)\setminus\{p\}$ is connected in $\mathbb{R}^3_+$ and intersects the x_3-axis at $(0, 0, \frac{3}{70})^T$. At this point $\dot\rho = \frac{297}{27440} > 0$. Hence $\dot\rho > 0$ on $\rho^{-1}(0)\setminus\{p\}$ and condition 4 (a) of theorem 4.4 is met. At the boundary fixed point $q = (\frac{7}{2}, 0, 0)^T$, $P(q) = \frac{5}{4}\theta_2 + \frac{11}{7}\theta_3 > 0$ so $\rho(q) > 0$. At the fixed point s in the interior of π_3, from sketches of $F_1(x) = 0$ and $F_2(x) = 0$ we know that $s_1 > 1$ so $P(s) = (\frac{4}{7}s_1 - \frac{3}{7})\theta_3 > 0$ and $\rho(s) > 0$. At the fixed point u in the interior of π_2, from sketches of $F_1(x) = 0$ and $F_3(x) = 0$ we also know that $u_1 > 1$ so $P(u) = \frac{1}{2}(u_1 - 1)\theta_2 > 0$

and $\rho(u) > 0$. Therefore, from remark 5, condition 3 (iv) of theorem 4.4 holds. From theorem 4.4 we conclude that p is globally stable.

5. P. G. repulsion

Now under the assumptions (A1) and (A2) given in section 2 we consider the P. G. repulsion of p on $K \cap \mathbb{R}_I$. Parallel to all the lemmas and theorem given in the last section, we may obtain similar results about limit set $\alpha(x_0)$ when $t \to -\infty$ and the P. G. repulsion of p on $K \cap \mathbb{R}_I$. However, instead of writing out all the detailed analogues, we take a shortcut to reach to the following result. By reversing the time, system (2) becomes $\dot{x} = -D(x)F(x)$. Then the P. G. repulsion of p on $K \cap \mathbb{R}_I$ for system (2) is converted to P. G. attraction of p on $K \cap \mathbb{R}_I$ for the reversed time system. Then, from remark 7, by applying theorem 4.4 to this reversed time system on $K \cap \mathbb{R}_I$, we derive the following theorem.

Theorem 5.1 (P. G. repulsion of a fixed point)**.** *In addition to the assumptions (A1) and (A2) given in section 2, assume that $p \in C_I^0$ is a fixed point with I, I_+ and I_- given as in lemma 4.3. Assume also that one of the following conditions is met:*

- (i) *(2) is I_--permanent on K in backward time if $I_- \neq \emptyset$ and has no invariant set in $K \cap \{x \in (\bigcup_{j \in I_+} \pi_j) \setminus \{0\} : \rho(x) \geq 0\}$.*
- (ii) *(2) is I_+-permanent on K in backward time if $I_+ \neq \emptyset$ and has no invariant set in $K \cap \{x \in (\bigcup_{j \in I_-} \pi_j) \setminus \{0\} : \rho(x) \leq 0\}$.*
- (iii) *(2) is $(I_+ \cup I_-)$-permanent on K in backward time.*
- (iv) *(2) has no invariant set in either $K \cap \{x \in (\bigcup_{j \in I_+} \pi_j) \setminus \{0\} : \rho(x) \geq 0\}$ or $K \cap \{x \in (\bigcup_{j \in I_-} \pi_j) \setminus \{0\} : \rho(x) \leq 0\}$.*

Assume also that the function g satisfies one of the following conditions:

- (a) *$g(x) > 0$ for all $x \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I \cap K$.*
- (b) *p is the unique fixed point of (2) in $K \cap \mathbb{R}_I$, $g(x) \geq 0$ for all $x \in \rho^{-1}(0) \cap \mathbb{R}_I \cap K$ and each zero x_0 of g in $(\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I \cap K$ is an isolated zero of g in this set but is not an isolated point of this set.*
- (c) *$g(x) < 0$ for all $x \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I \cap K$.*
- (d) *p is the unique fixed point of (2) in $K \cap \mathbb{R}_I$, $g(x) \leq 0$ for all $x \in \rho^{-1}(0) \cap \mathbb{R}_I \cap K$ and each zero x_0 of g in $(\rho^{-1}(0) \setminus \{p\}) \cap \mathbb{R}_I \cap K$ is an isolated zero of g in this set but is not an isolated point of this set.*

Then p is P. G. repelling on $\mathbb{R}_I \cap K$.

From the examples given in section 4 we see that theorem 4.4 can be used to study the global stability of a fixed point provided we know its local stability properties, and in particular we utilise a suitable eigenvector of the Jacobian evaluated at the fixed point.

If local stability information is unknown then the power of theorem 4.4 is lost for global stability. As a supplement, we are going to demonstrate two ways of combining local stability with P. G. attraction to obtain global stability in one criterion. One way is to use the Lyapunov direct method as shown in the next result. It is an easy extension of the theorem of diagonal stability of Lotka-Volterra systems as proved for interior and boundary fixed points [23] and extended in [4] for the study of MacArthur-Style consumer-resource models met in ecology. Another way is to use the split Lyapunov function method shown in the results given in section 7.

6. Diagonal stability at a boundary or interior fixed point in forward time

In the proof of next result, we choose $\phi(x) = e^{-v^T x}$ and $\theta = D(p)v$ for some $v \gg 0$ (meaning $v_i > 0$ for all $i \in I_N$), which is interchangable with $v \in \mathrm{int}\mathbb{R}^N_+$.

Theorem 6.1. *Suppose that there exists a $v \gg 0$ and an invariant set $\Omega \subseteq \mathbb{R}_I$ for (2) containing a fixed point $p \in C^0_I$ such that $(x-p)^T D(v)(F(x)-F(p)) < 0$ for all $x \in \overline{\Omega} \setminus \{p\}$ and that $F_i(p) \leq 0$ for all $i \in I$. Then p is globally asymptotically stable on Ω.*

Proof. This result essentially follows from the proof of Theorem 3.2.1 given in [23]. But in the context of the current framework, we take $\Phi(x) = e^{-v^T x} \prod_{i \in I_+} x_i^{v_i p_i}$ with $I_+ = I_N \setminus I$. Then $\rho(x) = -(x-p)^T D(v)(F(x)-F(p)) - \sum_{i \in I} v_i x_i F_i(p) \geq 0$ with equality if and only if $x = p$. Thus, we have $\rho(y) > 0$ for all $y \in \overline{\Omega} \cap (\cup_{i \in I_+} \pi_i)$ so condition (i) of lemma 4.3 is met. Then the P. G. attraction of p on Ω follows from lemma 4.3. If we take $H(x) = \Phi(p) - \Phi(x)$, we claim that $H(x) \geq 0$ for $x \in \mathbb{R}_I$ with equality if and only if $x = p$. Indeed, $\forall x \in \mathbb{R}_I$,

$$\begin{aligned} \ln \frac{\Phi(x)}{\Phi(p)} &= -\sum_{i \in I_N} v_i x_i + \sum_{j \in I_+} v_j p_j \ln x_j + \sum_{i \in I_N} v_i p_i - \sum_{j \in I_+} v_j p_j \ln p_j \\ &= -\sum_{i \in I} v_i x_i - \sum_{i \in I_+} v_i x_i + \sum_{j \in I_+} v_j p_j \ln x_j + \sum_{i \in I_+} v_i p_i - \sum_{j \in I_+} v_j p_j \ln p_j \\ &= -\sum_{i \in I} v_i x_i + \sum_{j \in I_+} v_j p_j \left(\ln \frac{x_j}{p_j} - \frac{x_j}{p_j} + 1 \right). \end{aligned}$$

(Here we used that $I_N = I \cup I_+$ and $p_i = 0$ for all $i \in I$.) As $\ln \xi - \xi + 1 \leq 0$ for $\xi \in (0, +\infty)$ and the equality holds if and only if $\xi = 1$, and also that $\sum_{i \in I} v_i x_i \geq 0$ with equality if and only if $x = p$, we have $\ln \frac{\Phi(x)}{\Phi(p)} \leq 0$ for $x \in \mathbb{R}_I$ with equality if and only if $x = p$. This shows our claim. From $\dot{H}(x) = -\dot{\Phi}(x) = -\rho(x)\Phi(x)$, we see that $\dot{H}(x) \leq 0$ for $x \in \Omega$ with equality if and only if $x = p$. Then the local stability of p with respect to Ω follows from a standard Lyapunov theorem. Therefore, p is globally asymptotically stable on Ω. □

For any square matrix U, let $U^S = U + U^T$. Then U^S is symmetric. When Ω is convex, sufficient conditions for fulfillment of the condition of the above theorem are that there is some $v \gg 0$ such that $M(x)^S$ or $(D(v)\nabla F(x))^S$ is negative definite for all $x \in \Omega \setminus \{p\}$, where $M(x) = D(v)\int_0^1 \nabla F(sx + (1-s)p)\, ds$.

Corollary 1. *Suppose that there exists a $v \gg 0$ and an invariant convex set $\Omega \subseteq \mathbb{R}_I$ containing a fixed point $p \in C_I^0$ such that $M(x)^S$ or $(D(v)\nabla F(x))^S$ is negative definite for all $x \in \overline{\Omega} \setminus \{p\}$ and that $F_i(p) \leq 0$ for all $i \in I$. Then p is globally asymptotically stable on Ω.*

Example 3. Population Games Let $G : \mathbb{R}_+^N \to \mathbb{R}^N$ be Lipschitz continuous and consider

$$F_i(x) = G_i(x) - x^T G(x), \quad i \in I_N. \tag{13}$$

The system (2) with (13) then models a population game on the unit probability simplex $\triangle = \{x \in \mathbb{R}_+^N : \sum_{i=1}^N x_i = 1\}$. Let $p \in C_I^0$ be a fixed point (interior or boundary) of the system. Since $\triangle$ is compact and invariant, the solution $x(t, x_0)$ exists for all $t \in \mathbb{R}$ and $\Omega = \triangle \cap \mathbb{R}_I$ is invariant. Assume that $F_i(p) \leq 0$ for each $i \in I$ and $-G$ is strictly monotone: $(x-y)^T((-G)(x) - (-G)(y)) > 0$ for $x \neq y$. Then, taking $v = (1, \ldots, 1)^T$, we have

$$\begin{aligned}
&(x-p)^T D(v)(F(x) - F(p)) \\
&= \quad (x-p)^T(G(x) - G(p)) + \sum_{i=1}^N (p_i - x_i)(x^T G(x) - p^T G(p)) \\
&= \quad (x-p)^T(G(x) - G(p)) < 0
\end{aligned}$$

for $x \in \triangle \setminus \{p\}$. By theorem 6.1, p is globally stable. Hofbauer and Sandholm [9] named such population games as stable games. They showed that $(x-y)^T((-G)(x)-(-G)(y)) > 0$ for $x \neq y$ is equivalent to $z^T \nabla G(x) z < 0$ for all $x \in \triangle \setminus \{p\}$ and all $z \in T\triangle = \{z \in \mathbb{R}^N : \sum_{i=1}^N z_i = 0\}$.

Example 4. [12] Consider the system (2) with

$$\begin{aligned}
F_1(x) &= 1 - x_1 - \beta\frac{x_2}{1+x_3} - \alpha x_3, \\
F_2(x) &= 1 - \alpha x_1 - x_2 - \beta\frac{x_3}{1+x_1}, \\
F_3(x) &= 1 - \beta\frac{x_1}{1+x_2} - \alpha x_2 - x_3,
\end{aligned} \tag{14}$$

where $\alpha, \beta > 0$. It is clear that $\Omega = (0,1)^3$ is forward invariant for this system and, if $\alpha + \beta < 1$, $\omega(x_0) \subset \Omega$ for every $x_0 \in \mathrm{int}\mathbb{R}_+^3$. Since

$$\nabla F(x) = \begin{pmatrix} -1 & -\frac{\beta}{x_3+1} & \frac{\beta x_2}{(x_3+1)^2} - \alpha \\ \frac{\beta x_3}{(x_1+1)^2} - \alpha & -1 & -\frac{\beta}{x_1+1} \\ -\frac{\beta}{x_2+1} & \frac{\beta x_1}{(x_2+1)^2} - \alpha & -1 \end{pmatrix},$$

we have, choosing $v = (1,1,1)^T$, that

$$\nabla F^S(x) = \begin{pmatrix} -2 & \frac{\beta x_3}{(x_1+1)^2} - \alpha - \frac{\beta}{x_3+1} & \frac{\beta x_2}{(x_3+1)^2} - \alpha - \frac{\beta}{x_2+1} \\ \frac{\beta x_3}{(x_1+1)^2} - \alpha - \frac{\beta}{x_3+1} & -2 & \frac{\beta x_1}{(x_2+1)^2} - \alpha - \frac{\beta}{x_1+1} \\ \frac{\beta x_2}{(x_3+1)^2} - \alpha - \frac{\beta}{x_2+1} & \frac{\beta x_1}{(x_2+1)^2} - \alpha - \frac{\beta}{x_1+1} & -2 \end{pmatrix}.$$

Thus, for $x \in \Omega$ and $\alpha > \beta$, for the first row of $M(x) = \nabla F^S(x)$,

$$\begin{aligned} & M_{11} - |M_{12}| - |M_{13}| \\ = \; & -2 + \left| \frac{\beta x_3}{(x_1+1)^2} - \alpha - \frac{\beta}{x_3+1} \right| + \left| \frac{\beta x_2}{(x_3+1)^2} - \alpha - \frac{\beta}{x_2+1} \right| \\ = \; & -2 + 2\alpha - \frac{\beta x_3}{(x_1+1)^2} + \frac{\beta}{x_3+1} - \frac{\beta x_2}{(x_3+1)^2} + \frac{\beta}{x_2+1} \\ < \; & -2 + 2\alpha + 2\beta < 0 \text{ if } \alpha + \beta < 1. \end{aligned}$$

Similar expressions hold for the other two rows of ∇F^S, so that ∇F^S is negative definite if $\alpha > \beta$ and $\alpha + \beta < 1$. Hence from corollary 1 we find that the (necessarily unique) interior fixed point of (14) is globally asymptotically stable.

Example 5. We consider the two predator, one prey system modelled by (2) with

$$F_1(x) = r\left(1 - \frac{x_1}{K}\right) - \frac{x_2}{x_1+1} - \frac{x_3}{x_1+1}, \tag{15}$$

$$F_2(x) = \frac{x_1}{x_1+1} - x_2 - d_2, \tag{16}$$

$$F_3(x) = \frac{x_1}{x_1+1} - x_3 - d_3 \tag{17}$$

for $x \in \mathbb{R}^3_+$. Here x_1 is the prey and x_2, x_3 are predators. We assume that the constants r, K, d_2, d_3 are positive satisfying

$$d_2 < 1,\ d_3 < 1,\ K > 1,\ r + d_2 + d_3 \geq 2,\ r \geq \frac{K}{32} + \frac{2 - d_2 - d_3}{K}. \tag{18}$$

Notice that for $i = 2, 3$, $\dot{x}_i < 0$ for $x_1 = 0$ or for $x_1 > 0$ and $x_i \geq 1 - d_i$. Also for $x_i < 1 - d_i$ and $x_1 > 0$ we have

$$\begin{aligned} \dot{x}_1 &= x_1 \left(r\left(1 - \frac{x_1}{K}\right) - \frac{x_2}{x_1+1} - \frac{x_3}{x_1+1} \right) \\ &> x_1 \left(r\left(1 - \frac{x_1}{K}\right) - \frac{(2 - d_2 - d_3)}{1 + x_1} \right). \end{aligned}$$

The above expression is positive, so $\dot{x}_1 > 0$, if

$$0 < x_1 < \frac{K-1}{2} + \frac{1}{2}\sqrt{(K+1)^2 + \frac{4K(d_2 + d_3 - 2)}{r}}.$$

Hence $\dot{x}_1 > 0$ for $x_1 = K - 1$. Clearly, $\dot{x}_1 \leq -\frac{r}{K} x_1$ for $x_1 \geq K + 1$ so every solution satisfies $x_1(t) < K + 1$ for all large enough t. Then we come to the conclusion that all orbits eventually lie in the set $B = [K-1, K+1) \times [0, 1-d_2) \times [0, 1-d_3)$. The matrix $(D(v)\nabla F)^S$ is given by

$$(D(v)\nabla F(x))^S = -\begin{pmatrix} 2v_1\left(\frac{r}{K} - \frac{x_2+x_3}{(1+x_1)^2}\right) & \frac{-v_2+v_1(x_1+1)}{(x_1+1)^2} & \frac{-v_3+v_1(x_1+1)}{(x_1+1)^2} \\ \frac{-v_2+v_1(x_1+1)}{(x_1+1)^2} & 2v_2 & 0 \\ \frac{-v_3+v_1(x_1+1)}{(x_1+1)^2} & 0 & 2v_3 \end{pmatrix}.$$

Now choose $v = (1,1,1)^T$ so that

$$(D(v)\nabla F(x))^S = \nabla F^S = -\begin{pmatrix} \frac{2r}{K} - \frac{2(x_2+x_3)}{(1+x_1)^2} & \frac{x_1}{(x_1+1)^2} & \frac{x_1}{(x_1+1)^2} \\ \frac{x_1}{(x_1+1)^2} & 2 & 0 \\ \frac{x_1}{(x_1+1)^2} & 0 & 2 \end{pmatrix}.$$

Since ∇F^S is symmetric, $-\nabla F^S$ is positive definite in B if and only if for all $x \in B$ the following leading principal minors are positive, i.e.,

$$\begin{aligned} L_1 &= 2\left(\frac{r}{K} - \frac{x_2+x_3}{(1+x_1)^2}\right) > 0, \\ L_2 &= 4\left(\frac{r}{K} - \frac{x_1^2}{4\,(x_1+1)^{\,4}} - \frac{(x_2+x_3)}{(x_1+1)^{\,2}}\right) > 0, \\ L_3 &= 8\left(\frac{r}{K} - \frac{x_1^2}{2\,(x_1+1)^{\,4}} - \frac{(x_2+x_3)}{(x_1+1)^{\,2}}\right) > 0. \end{aligned}$$

Clearly, if $L_3 > 0$ then $L_1 > 0$ and $L_2 > 0$. Since $x \in B$ implies $x_2 + x_3 < 2 - d_2 - d_3$, we have

$$L_3 \;>\; 8\left(\frac{r}{K} - \frac{x_1^2}{2\,(x_1+1)^{\,4}} - \frac{(2-d_2-d_3)}{(x_1+1)^{\,2}}\right) \geq 8\left(\frac{r}{K} - \frac{1}{32} - \frac{(2-d_2-d_3)}{(x_1+1)^{\,2}}\right)$$

as $\frac{x_1^2}{(x_1+1)^4}$ has maximum $\frac{1}{16}$ at $x_1 = 1$. By (18) the last expression is nonnegative so $L_3 > 0$. Hence ∇F^S is negative definite in B.

Consider now fixed points. We observe that the set $\overline{B} = [K-1, K+1] \times [0, 1-d_2] \times [0, 1-d_3]$ is forward invariant, so it must contain a non-trivial fixed point. If p is an interior fixed point it must satisfy $p_2 = \frac{p_1}{p_1+1} - d_2$ and $p_3 = \frac{p_1}{p_1+1} - d_3$ and hence that $p_1 > d_0 = \max_{i=2,3} \frac{d_i}{1-d_i}$. Substituting $x = p$ into $F_1 = 0$ yields

$$C(p_1) = K(r + d_2 + d_3) + (K(d_2 + d_3 - 2) + r(2K-1))p_1 + r(K-2)p_1^2 - rp_1^3 = 0.$$

It is clear that there is at least one solution $p_1 > 0$. Since (18) implies $r \geq 2 - d_2 - d_3 > \frac{K(2-d_2-d_3)}{2K-1}$, so that $C'(0) > 0$, the cubic $C(p_1)$ has just one sign change so $C(p_1) = 0$ has then exactly one positive root p_1. Thus, $C(p_1) = 0$, $C(x_1) > 0$ for $0 \leq x_1 < p_1$ and $C(x_1) < 0$ for $x_1 > p_1$. Hence, if $C(d_0) > 0$ then p is a globally asymptotically stable interior fixed point.

However, if $C(d_0) \le 0$, which implies $p_1 \le d_0 = \max_{i=2,3} \frac{d_i}{1-d_i}$, we shall see that a boundary fixed point is globally asymptotically stable. There are three possible cases: (i) $d_2 = d_3$, (ii) $d_2 > d_3$, (iii) $d_2 < d_3$. In case (i), we have $\frac{p_1}{1+p_1} - d_j \le 0$, so $p_j = 0$, for $j = 2, 3$ and $p = (K, 0, 0)^T$ is the unique fixed point in $\overline{B}$, and it is globally asymptotically stable. In case (ii), $\frac{d_3}{1-d_3} < \frac{d_2}{1-d_2} = d_0$. If $\frac{d_3}{1-d_3} < p_1 \le \frac{d_2}{1-d_2}$ then $\frac{p_1}{1+p_1} - d_2 \le 0$ so $p_2 = 0$ but $p_3 = \frac{p_1}{1+p_1} - d_3 > 0$. Substituting $p = (p_1, 0, p_3)^T$ into $F_1(p) = 0$, we have

$$C_1(p_1) = -rp_1^3 + r(K-2)p_1^2 + [(r + d_3 - 1)K + r(K-1)]p_1 + K(r + d_3) = 0.$$

By the same reason as that for $C(x_1)$, we know that $C_1(x_1) > 0$ for $0 \le x_1 < p_1$ and $C_1(x_1) < 0$ for $x_1 > p_1$. Thus, if $C_1(\frac{d_3}{1-d_3}) > 0$ then $p = (p_1, 0, p_3)^T$ is globally asymptotically stable; if $C_1(\frac{d_3}{1-d_3}) \le 0$ then $p_1 \le \frac{d_3}{1-d_3} < \frac{d_2}{1-d_2} = d_0$ so $p_2 = p_3 = 0$ and $p = (K, 0, 0)^T$ is globally asymptotically stable. Similarly, in case (iii), $p_3 = 0$. If $p_2 = \frac{p_1}{1+p_1} - d_2 > 0$, then p_1 satisfies

$$C_2(p_1) = -rp_1^3 + r(K-2)p_1^2 + [(r + d_2 - 1)K + r(K-1)]p_1 + K(r + d_2) = 0.$$

Thus, if $C_2(\frac{d_2}{1-d_2}) > 0$ then $p = (p_1, p_2, 0)^T$ is gobally asymptotically stable; if $C_2(\frac{d_2}{1-d_2}) \le 0$ then $p_2 = 0$ so $p = (K, 0, 0)^T$ is globally asymptotically stable.

7. Split Lyapunov stability at a fixed point in forward time

7.1. **Global stability at an interior fixed point in forward time.** In this section, we consider the case where $\phi(x) = 1$ and $\theta = D(p)\alpha$, so that $\Phi(x) = V(x) = \prod_{i=1}^N x_i^{\alpha_i p_i}$. In the first instance we consider an interior fixed point $p \in \mathrm{int}\mathbb{R}_+^N$ and establish criteria for (2) to be globally asymptotically stable at p in forward time. The approach is guided by that of the Split Lyapunov method [25, 11, 1] which has been successfully applied to Lotka-Volterra systems for which each F_i is affine.

Let $J(x) = \nabla(D(x)F(x))$ and $A = -\nabla F(p)$. Then $J(p) = D(p)\nabla F = -D(p)A$. Assume that $D(p)A$ has a positive eigenvalue λ with a corresponding left eigenvector α^T: $\alpha \in \mathbb{R}^N$ with $\alpha_i \ne 0$ for all $i \in I_N$, i.e. $-\lambda$ is an eigenvalue of $J(p)$ with α^T as a left eigenvector. Then $\alpha^T D(p)A = \lambda\alpha^T$. We also set $\theta = D(p)\alpha$ and $\rho(x) = \theta^T F(x)$. Then, as

$$V(x) = \prod_{i=1}^N x_i^{\theta_i} = \prod_{i=1}^N x_i^{\alpha_i p_i}, \quad \rho(x) = \theta^T F(x) = \alpha^T D(p) F(x), \tag{19}$$

we have

$$\begin{aligned} \dot{V}(x) &= \nabla V(x)D(x)F(x) = \rho(x)V(x), \\ \dot{\rho}(x) &= \nabla\rho(x)D(x)F(x) \\ &= \alpha^T D(p)\nabla F(x)D(x)F(x) \\ &= \alpha^T J(p)D(x)F(x) + \theta^T\big[\nabla F(x) - \nabla F(p)\big]D(x)F(x) \\ &= -\lambda\alpha^T D(x)F(x) + \theta^T\big[\nabla F(x) - \nabla F(p)\big]D(x)F(x). \end{aligned} \tag{20}$$

With

$$g(x) = -\lambda\alpha^T D(x-p)F(x) + \theta^T\big[\nabla F(x) - \nabla F(p)\big]D(x)F(x), \tag{21}$$

we have

$$\dot{\rho} = -\lambda\rho(x) + g(x). \tag{22}$$

The function g can be rewritten slightly as

$$\begin{aligned} g(x) &= -\lambda\alpha^T D(x-p)F(x) + \theta^T\big[\nabla F(x) - \nabla F(p)\big]D(x)F(x) \\ &= -\lambda\alpha^T D(x-p)(F(x)-F(p)) - \lambda\alpha^T D(x-p)F(p) \\ &\quad +\theta^T\big[\nabla F(x) - \nabla F(p)\big]D(x)F(x) \\ &= -\lambda\alpha^T D(x)F(p) - \lambda\alpha^T D(x-p)(F(x)-F(p)) \\ &\quad +\theta^T\big[\nabla F(x) - \nabla F(p)\big](D(x)F(x) - D(p)F(p)). \end{aligned} \tag{23}$$

So far we have not specified whether p is an interior or boundary fixed point, i.e. equation (23) is valid in both cases. When p is interior, we have the simplification that $F(p) = 0$ and we obtain (21). When p is not interior the first term $-\lambda\alpha^T D(x)F(p)$ will be nonzero and, as we will see in section 7.3, it will play a role in determining stability of boundary fixed points.

Theorem 7.1. *Assume that the system (2) satisfies the following conditions:*

1. *There exists an interior fixed point $p \in \mathrm{int}\mathbb{R}^N_+$, and $D(p)A$ has an eigenvalue $\lambda > 0$ and a corresponding left (row) eigenvector α^T with $\alpha_i < 0$ for $i \in I_- \subset I_N$ and $\alpha_j > 0$ for $j \in I_+ = I_N \setminus I_-$.*
2. *For each $x_0 \in \mathrm{int}\mathbb{R}^N_+$, the solution $x(t, x_0)$ is bounded for $t \geq 0$ and $0 \notin \omega(x_0)$.*
3. *One of the conditions (i)–(iv) of theorem 4.4 is met.*
4. *The function g given by (21) satisfies one of the conditions (a)–(d) of theorem 4.4.*

Then p is P. G. attracting, i.e. $\lim_{t\to+\infty} x(t, x_0) = p$ for all $x_0 \in \mathrm{int}\mathbb{R}^N_+$. If, in addition,

$$\begin{aligned} &\exists r > 0, \forall x \in \mathcal{B}_r(p) \setminus \{p\} \text{ with } \rho(x) < 0\ (> 0),\ g(x) > 0\ (< 0) \\ &\text{under condition } (a) \text{ or } (b)\ ((c) \text{ or } (d)), \end{aligned} \tag{24}$$

then (2) is globally asymptotically stable at p in forward time.

Note. Remarks 3, 5–7 for theorem 4.4 also apply to theorems 7.1 and 7.2.

Proof. The P. G. attraction of p follows from theorem 4.4. To prove the global asymptotic stability of (2) at p in forward time, we need only show that

$$\forall\varepsilon > 0, \exists\delta > 0, \forall x_0 \in \mathcal{B}_\delta(p), \forall t \in [0, +\infty), x(t, x_0) \in \mathcal{B}_\varepsilon(p).$$

Suppose g satisfies (a) or (b). Let $\ell^* = V(p)$. Then $\ell^* > 0$ by (19). From lemmas 4.6 and 4.7 we know that for each $x_0 \in \mathrm{int}\mathbb{R}^N_+ \setminus \{p\}$, $\rho(x_0) \geq 0$ implies $\rho(x(t, x_0)) \geq 0$ for

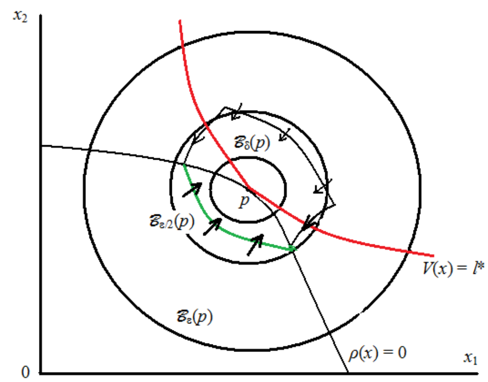

FIGURE 1. Illustration of stability at p.

all $t \geq 0$ so $V(x(t, x_0)) \uparrow \ell^*$ as $t \to +\infty$. Thus, $\rho^{-1}(0) \cap V^{-1}(\ell^*) \cap \text{int}\mathbb{R}^N_+ = \{p\}$. The surface $V^{-1}(\ell^*)$ divides $\text{int}\mathbb{R}^N_+ \setminus V^{-1}(\ell^*)$ into two parts, one on each side of $V^{-1}(\ell^*)$. For convenience, any set in the part with $V(x) > \ell^*$ is said to be above $V^{-1}(\ell^*)$ and any set in the other part is said to be below $V^{-1}(\ell^*)$. Then $\rho^{-1}(0) \setminus \{p\}$ is below $V^{-1}(\ell^*)$. From the expression for $\dot{\rho}(x)$ we see that $\nabla\rho(p) = -\lambda\alpha^T$ with nonzero components. By the implicit function theorem, in a sufficiently small neighbourhood of p, $\rho^{-1}(0)$ is an $(N-1)$-dimensional surface. Accordingly, in a small neighbourhood of p, any set in the part of $\text{int}\mathbb{R}^N_+ \setminus \rho^{-1}(0)$ containing $V^{-1}(\ell^*) \setminus \{p\}$ is above $\rho^{-1}(0)$ and any set in the other part is below $\rho^{-1}(0)$. Then from Fig. 1 we see that $\rho(x) < 0$ for x above $\rho^{-1}(0)$ and $\rho(x) > 0$ for x below $\rho^{-1}(0)$.

By condition (a) or (b) and (24), there is an $\varepsilon_0 > 0$ such that $g(x) \geq 0$ for all $x \in \mathcal{B}_{\varepsilon_0}(p)\setminus\{p\}$ with $\rho(x) \leq 0$ and each zero $x_0 \neq p$ of g is isolated in $\rho^{-1}(0) \setminus \{p\}$. Thus, for each $x_0 \in \mathcal{B}_{\varepsilon_0}(p) \setminus \{p\}$ with $\rho(x_0) \leq 0$, by (22) $\rho(x(t, x_0))$ is increasing for $t \geq 0$ as long as $x(t, x_0) \in \mathcal{B}_{\varepsilon_0}(p) \setminus \{p\}$ and $\rho(x(t, x_0)) \leq 0$.

For any $\varepsilon \in (0, \varepsilon_0]$, there exists $\ell_0 \in (0, \ell^*)$ such that the bounded closed set, with the boundary consisting of the part of $V^{-1}(\ell_0)$ below $\rho^{-1}(0)$, the part of $\rho^{-1}(0)$ above $V^{-1}(\ell_0)$ and $V^{-1}(\ell_0)\cap\rho^{-1}(0)$, is contained in $\mathcal{B}_{\varepsilon/2}(p)$. As each zero of g in $\rho^{-1}(0)\setminus\{p\}$ is isolated, by adjusting the value of ℓ_0 if necessary, we may assume that $g(x) > 0$ for all $x \in V^{-1}(\ell_0) \cap \rho^{-1}(0)$. Then, for each $x_0 \in V^{-1}(\ell_0) \cap \rho^{-1}(0)$, there exist a $\mu = \mu(x_0) > 0$ and $t_1 = t_1(x_0) < 0$ such that $\rho(x(t, x_1)) < 0$ and $x(t, x_1) \in \mathcal{B}_\varepsilon(p)$ for all $x_1 \in \mathcal{B}_\mu(x_0) \cap \rho^{-1}(0)$ and $t \in [t_1, 0)$. Since $\{\mathcal{B}_\mu(x_0) : x_0 \in \rho^{-1}(0) \cap V^{-1}(\ell_0)\}$ is an open covering of the compact set $\rho^{-1}(0) \cap V^{-1}(\ell_0)$, by selecting a finite open covering we can choose a $t_2 < 0$ such that $\rho(x(t, x_0)) < 0$ and $x(t, x_0) \in \mathcal{B}_\varepsilon(p)$ for all $x_0 \in \rho^{-1}(0) \cap V^{-1}(\ell_0)$ and $t \in [t_2, 0)$. These segments of trajectories of (2) form an $(N-1)$-dimensional surface S_0.

Let $m^* = \max\{\rho(x(t_2, x_0)) : x_0 \in \rho^{-1}(0) \cap V^{-1}(\ell_0)\}$. Then, for $m \in (m^*, 0)$ with $|m|$ small enough, every trajectory in S_0 transverses the surface $\rho^{-1}(m)$ at some $t \in [t_2, 0)$ and the bounded open set U below $\rho^{-1}(m)$, above $V^{-1}(\ell_0)$ and surrounded by S_0 is contained in $\mathcal{B}_\varepsilon(p)$ and forward invariant. As $p \in U$, there is a $\delta > 0$ such that $\mathcal{B}_\delta(p) \subset U$. Then $x_0 \in \mathcal{B}_\delta(p)$ implies $x(t, x_0) \in U \subset \mathcal{B}_\varepsilon(p)$ for all $t \geq 0$. Therefore, (2) is stable at p in forward time.

If condition (c) or (d) holds, then $\rho(x_0) \leq 0$ implies $\rho(x(t, x_0)) \leq 0$ for all $t \geq 0$ so $V(x(t, x_0)) \downarrow \ell^*$ as $t \to +\infty$. The above reasoning is still valid with obvious adjustment. □

7.2. **An alternative positive (negative) definite matrix condition.** In the rest of section 7 we assume that F is at least C^2. Note that each of (a)–(d) in condition 4 of theorem 7.1 as well as (24) looks simple but is not easily checked in practice (see remark 6). Recall that the condition $g(x) > 0$ for $x \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathrm{int}\mathbb{R}^N_+$ for Lotka-Volterra systems in [25], [11] and [1] can be converted into the positive definite property of a *constant* $(N-1) \times (N-1)$ symmetric matrix which is easily checked. The nonlinearity of F, and hence also ρ, means an easily applicable criterion for global stability of a fixed point for general system (2) may not exist. However, applying the idea used in [25, 11, 1] to the general system (2), we can convert condition (d) to positive, semi-positive, negative or semi-negative definite property of a $(N-1) \times (N-1)$ symmetric matrix that is a function of $x \in (\rho^{-1}(0) \setminus \{p\}) \cap \mathrm{int}\mathbb{R}^N_+$. This property of the variable symmetric matrix may be still difficult to check. Nevertheless, by employing the techniques of finding minima or maxima of real functions, the positive or semi-positive definiteness of a variable matrix is actually verifiable. This will be demonstrated in section 9 by a detailed analysis of an example.

For this purpose, let the $N \times N$ matrix

$$W = (W^c_1, \ldots, W^c_N)$$

be defined through its columns

$$W^c_1 = (1, 0, \ldots, 0)^T, W^c_2 = (-1, 1, 0, \ldots, 0)^T, \ldots, W^c_N = (0, \ldots, 0, -1, 1)^T. \tag{25}$$

Then

$$\alpha^T D(\alpha)^{-1} W = (1, 0, \ldots, 0). \tag{26}$$

We define new coordinates $z = (z_1, \ldots, z_N)^T$ on $\mathbb{R}^N$ by

$$z = W^{-1} D(\alpha) D(p) F(x), \quad \tilde{z} = (z_2, \ldots, z_N)^T \in \mathbb{R}^{N-1}. \tag{27}$$

From (25)–(27) we have

$$\begin{aligned} \rho(x) &= \alpha^T D(p) F(x) = \alpha^T D(\alpha)^{-1} W z = z_1, \\ F(x) &= D(p)^{-1} D(\alpha)^{-1} W z. \end{aligned}$$

Since $F(p) = 0$, $F(x) - F(p) = \int_0^1 \frac{d}{ds} F((1-s)p + sx)ds = \int_0^1 \nabla F(\bar{x})ds(x-p)$, there is an $N \times N$ matrix $M_0(x) = \int_0^1 \nabla F(\bar{x})ds$ such that

$$F(x) = F(x) - F(p) = M_0(x)(x-p). \tag{28}$$

To make the new coordinates z interchangable with $x - p$, we require invertibility of the matrix $M_0(x)$ for each $x \in \rho^{-1}(0)$. Then

$$x - p = M_0(x)^{-1}F(x) = M_0(x)^{-1}D(p)^{-1}D(\alpha)^{-1}Wz. \tag{29}$$

There are N matrices $M_i(x) = \int_0^1 \nabla(\nabla F_i(\bar{x})^T)ds$ $(i \in I_N)$ such that

$$\nabla F_i(x) - \nabla F_i(p) = (x-p)^T M_i(x), \quad i \in I_N. \tag{30}$$

Then, from (21), and using that $\theta_i = p_i\alpha_i$,

$$\begin{aligned} g(x) &= (x-p)^T\left[-\lambda D(\alpha) + \sum_{i=1}^N \alpha_i p_i M_i(x)D(x)\right]F(x) \\ &= F(x)^T M_0(x)^{-T}\left[-\lambda D(\alpha) + \sum_{i=1}^N \alpha_i p_i M_i(x)D(x)\right]F(x) \\ &= z^T W^T D(\alpha)^{-1}D(p)^{-1}M_0^{-T}(x) \\ &\quad \times\left[-\lambda D(\alpha) + \sum_{i=1}^N \alpha_i p_i M_i(x)D(x)\right]D(p)^{-1}D(\alpha)^{-1}Wz \\ &= (Wz)^T\tilde{M}(Wz), \end{aligned}$$

where

$$\tilde{M} = D(\theta)^{-1}\left\{M_0(x)^{-T}\left[-\lambda D(\alpha) + \sum_{i=1}^N \alpha_i M_i(x)D(x)\right]\right\}D(\theta)^{-1}. \tag{31}$$

Let $\tilde{W}$ be the $N \times (N-1)$ matrix obtained from W by deleting its first column. Then $Wz = W_1^c z_1 + \tilde{W}\tilde{z}$ so

$$\begin{aligned} g(x) &= [(W_1^c)^T z_1 + \tilde{z}^T\tilde{W}^T]\tilde{M}[W_1^c z_1 + \tilde{W}\tilde{z}] \\ &= g_1(x)z_1 + \tilde{z}^T\tilde{W}^T\tilde{M}\tilde{W}\tilde{z}, \end{aligned}$$

where $g_1(x) = (W_1^c)^T\tilde{M}Wz + \tilde{z}^T\tilde{W}^T\tilde{M}W_1^c$. Then, from (27) we have $z \to 0$, so $g_1(x) \to 0$, as $x \to p$. Since $x \in \rho^{-1}(0)$ if and only if $z_1 = 0$, the corollary below immediately follows from Theorem 7.1 and its proof.

Corollary 2. *The statement of Theorem 7.1 regarding global asymptotic stability is true if condition 4 and (24) are replaced by one of the following:*

(a1) *The matrix $\tilde{W}^T\tilde{M}^S\tilde{W}$ is positive definite for all $x \in \text{int}\mathbb{R}_+^N \setminus \{p\}$ with either $\rho(x) = 0$ or $\|x - p\|$ sufficiently small and $\rho(x) < 0$.*

(a2) *p is the unique fixed point of (2) in* $\mathrm{int}\mathbb{R}^N_+$*; for each* $x \in \mathrm{int}\mathbb{R}^N_+ \setminus \{p\}$ *with* $\|x-p\|$ *sufficiently small and* $\rho(x) < 0$*, the matrix* $\tilde{W}^T\tilde{M}^S\tilde{W}$ *is positive definite; for* $x \in (\mathrm{int}\mathbb{R}^N_+ \setminus \{p\}) \cap \rho^{-1}(0)$*,* $\tilde{W}^T\tilde{M}^S\tilde{W}$ *is either positive definite or semi-positive definite but the semi-positive definite points are isolated in* $\rho^{-1}(0) \cap \mathrm{int}\mathbb{R}^N_+$*.*

(a3) *The matrix* $\tilde{W}^T\tilde{M}^S\tilde{W}$ *is negative definite for all* $x \in \mathrm{int}\mathbb{R}^N_+ \setminus \{p\}$ *with either* $\rho(x) = 0$ *or* $\|x-p\|$ *sufficiently small and* $\rho(x) > 0$*.*

(a4) *p is the unique fixed point of (2) in* $\mathrm{int}\mathbb{R}^N_+$*; for each* $x \in \mathrm{int}\mathbb{R}^N_+ \setminus \{p\}$ *with* $\|x-p\|$ *sufficiently small and* $\rho(x) > 0$*, the matrix* $\tilde{W}^T\tilde{M}^S\tilde{W}$ *is negative definite; for* $x \in (\mathrm{int}\mathbb{R}^N_+ \setminus \{p\}) \cap \rho^{-1}(0)$*,* $\tilde{W}^T\tilde{M}^S\tilde{W}$ *is either negative definite or semi-negative definite but the semi-negative definite points are isolated in* $\rho^{-1}(0) \cap \mathrm{int}\mathbb{R}^N_+$*.*

Remark 8. For the Lotka-Volterra system where $F(x) = b + Bx$, $\nabla F(x) = B$, $M_i(x) = 0$ and $M_0(x) = B$, so that for a unique interior fixed point p, $B = M_0(x)$ is invertible and

$$\begin{aligned}\tilde{W}^T\tilde{M}\tilde{W} &= -\lambda\tilde{W}^T D(\theta)^{-1}B^{-T}D(\alpha)D(\theta)^{-1}\tilde{W}\\ &= -\lambda\tilde{W}^T D(\theta)^{-1}B^{-T}(D(\alpha)B)B^{-1}D(\theta)^{-1}\tilde{W}\\ &= -\lambda(B^{-1}D(\theta)^{-1}\tilde{W})^T(D(\alpha)B)B^{-1}D(\theta)^{-1}\tilde{W}.\end{aligned}$$

The $N-1$ column vectors of $B^{-1}D(\theta)^{-1}\tilde{W}$ are linearly independent, so the span of them can be described by the hyperplane $v^T(x-p) = 0$, where $v^T = \theta^T B$ as $v^T B^{-1}D(\theta)^{-1}\tilde{W} = 0$. Thus, $\tilde{W}^T\tilde{M}^S\tilde{W}$ is negative definite if and only if $(x-p)^T D(\alpha)B(x-p) > 0$ for all x satisfying $v^T(x-p) = 0$ and $x \neq p$. This is consistent with [25, 11, 1].

7.3. **Global stability at a boundary fixed point in forward time.** In this section, we consider the case of a boundary fixed point $p \in \partial\mathbb{R}^N_+$. Precisely, $p \in C^0_I$ for a proper subset $I \subset I_N$. For p to be P. G. attracting in $\mathbb{R}_I$ in forward time, it is necessary that the Jacobian matrix at p has no positive eigenvalues. For each $i \in I$, since $p_i = 0$, we can easily check that $F_i(p)$ is an eigenvalue of the Jacobian so we require $F_i(p) \leq 0$. Then p is said to be *saturated in forward (backward) time* if

$$\forall i \in I_N, p_i = 0 \Longrightarrow F_i(p) \leq 0 \ (\geq 0). \tag{32}$$

For $p \in C^0_I$ with $I \subset I_N$, from (19) we have

$$\rho(x) = \alpha^T D(p)F(x) = \sum_{j\in I_N\setminus I}\alpha_j p_j F_j(x), \quad V(x) = \prod_{j\in I_N\setminus I} x_j^{\alpha_j p_j}. \tag{33}$$

Theorem 7.2. *Assume that the system (2) satisfies the following conditions:*

1. *For a proper subset* $I \subset I_N$*, (2) has a fixed point* $p \in C^0_I$ *and p is saturated in forward time. The matrix* $D(p)A$ *has an eigenvalue* $\lambda > 0$ *and a corresponding left eigenvector* α^T *with* $\alpha_i < 0$ *for* $i \in I_- \subset I_N \setminus I$ *and* $\alpha_j > 0$ *for* $j \in I_N \setminus I_- = I \cup I_+$*.*
2. *For each* $x_0 \in \mathbb{R}_I$*, the solution* $x(t, x_0)$ *is bounded for* $t \geq 0$ *and* $0 \notin \omega(x_0)$*.*
3. *One of the conditions (i)–(iv) of theorem 4.4 is met.*

4. *The function g given by (21) satisfies one of the conditions (a)–(d) of theorem 4.4.*

Then p is P. G. attracting in $\mathbb{R}_I$. If, in addition,

$$\exists r > 0, \forall x \in (\mathcal{B}_r(p) \setminus \{p\}) \cap \mathbb{R}_I \text{ with } \rho(x) < 0\ (> 0),\ g(x) > 0\ (< 0) \tag{34}$$
$$\text{under condition } (a) \text{ or } (b)\ ((c) \text{ or } (d)),$$

then (2) is globally asymptotically stable at p in forward time.

Proof. The P. G. attraction of p follows from theorem 4.4. For the stability of p in forward time with respect to $\mathbb{R}_I$, the proof of theorem 7.1 with the replacement of $\text{int}\mathbb{R}^N_+$ by $\mathbb{R}_I$ and any open ball $\mathcal{B}_r(p)$ by $\mathcal{B}_r(p) \cap \mathbb{R}_I$ is still valid. □

As an analogue of corollary 2, we next convert condition 4 and (34) into the positive, semi-positive, negative or semi-negative definite property of an $(N-1) \times (N-1)$ symmetric matrix that can be easily checked. For convenience, we may assume without loss of generality that $I = \{k+1, \ldots, N\}$ and $I_N \setminus I = \{1, \ldots, k\} = I_k$ so

$$\forall i \in I, p_i = 0, \forall j \in I_k, p_j > 0.$$

Let $1_I \in \mathbb{R}^N_+$ be defined by 0 as its first k components and 1 as its last $N-k$ components. Let

$$\tilde{p} = p + 1_I, \quad W = W_{I_k} + W_I, \tag{35}$$

where the first k columns of W_{I_k} are given by (25) and each entry in the last $N-k$ columns of W_{I_k} is 0; each of the last $N-k$ main diagonal entries of W_I is 1 and each of the rest entries of W_I is 0. Let $\tilde{W}$ be the $N \times (N-1)$ matrix consisting of the last $N-1$ columns of W. Let

$$z = W^{-1}D(\alpha)D(\tilde{p})(F(x) - F(p)), \quad \tilde{z} = (z_2, \ldots, z_N)^T \in \mathbb{R}^{N-1}. \tag{36}$$

Note that W has the block form $W = \begin{pmatrix} U_1 & 0 \\ 0 & U_2 \end{pmatrix}$, where U_1 is a $k \times k$ matrix given by (25) and U_2 is $(N-k) \times (N-k)$ identity. Then, from (33)–(36) and by writing $W, D(\alpha), D(p)$ in block form, we have

$$\begin{aligned} \rho(x) &= \alpha^T D(p) F(x) \\ &= \alpha^T D^{-1}(\alpha) W W^{-1} D(\alpha) D(p)(F(x) - F(p)) \\ &= \alpha^T D^{-1}(\alpha) W_{I_k} W^{-1} D(\alpha) D(\tilde{p})(F(x) - F(p)) \\ &= \alpha^T D^{-1}(\alpha) W_{I_k} z \\ &= (1, 0, \ldots, 0) z \\ &= z_1. \end{aligned}$$

Similar to (28), there is an $N \times N$ matrix $M_0 = M_0(x)$ such that

$$F(x) - F(p) = M_0(x)(x - p). \tag{37}$$

Substitution of this into (36) gives

$$z = W^{-1} D(\alpha) D(\tilde{p}) M_0(x)(x-p).$$

By assuming the existence of $M_0^{-1}(x)$ for all $x \in \rho^{-1}(0)$, we have

$$x - p = M_0^{-1}(x)(F(x) - F(p)) = M_0^{-1}(x) D^{-1}(\tilde{p}) D^{-1}(\alpha) W z. \tag{38}$$

Since $p_i \neq 0$ implies $F_i(p) = 0$, we have

$$D(x)F(p) = D(F(p))x = D(F(p))(x-p) = D(x-p)F(p).$$

From (30) it follows that

$$\nabla F_i(x) - \nabla F_i(p) = (x-p)^T M_i(x), \quad i \in I_N. \tag{39}$$

Then, from (21),

$$\begin{aligned} g(x) &= -\lambda \alpha^T D(x-p)F(x) + \alpha^T D(p)\big[\nabla F(x) - \nabla F(p)\big] D(x) F(x) \\ &= -\lambda \alpha^T D(x-p)F(p) + \alpha^T D(p)\big[\nabla F(x) - \nabla F(p)\big] D(x) F(p) \\ &\quad + \big[-\lambda \alpha^T D(x-p) + \alpha^T D(p)\big(\nabla F(x) - \nabla F(p)\big) D(x)\big](F(x) - F(p)) \\ &= -\lambda \sum_{i \in I} \alpha_i F_i(p) x_i + (x-p)^T \sum_{j \in I_N \setminus I} \alpha_j p_j M_j(x) D(F(p))(x-p) \\ &\quad + (x-p)^T \left[-\lambda D(\alpha) + \sum_{j \in I_N \setminus I} \alpha_j p_j M_j(x) D(x)\right] D^{-1}(\tilde{p}) D^{-1}(\alpha) W z. \end{aligned}$$

Substitution of (38) into the above gives

$$g(x) = -\lambda \alpha^T D(F(p))x + (Wz)^T \tilde{M}(Wz), \tag{40}$$

where

$$\tilde{M} = D^{-1}(\alpha) D^{-1}(\tilde{p}) (M_0^{-1})^T M^0 D^{-1}(\tilde{p}) D^{-1}(\alpha), \tag{41}$$

$$M^0 = -\lambda D(\alpha) + \sum_{j \in I_N \setminus I} \alpha_j p_j M_j(x)(D(x) + D(F(p)) M_0^{-1}(x)). \tag{42}$$

By the same lines as those before corollary 2, we have

$$(Wz)^T \tilde{M}(Wz) = g_1(x) z_1 + \tilde{z}^T \tilde{W}^T \tilde{M} \tilde{W} \tilde{z},$$

where $g_1(x) \to 0$ as $x \to p$. Then, from (40) and (22) we obtain

$$\dot{z}_1|_{(2)} = -(\lambda - g_1(x)) z_1 - \lambda \alpha^T D(F(p))x + \tilde{z}^T \tilde{W}^T \tilde{M} \tilde{W} \tilde{z}. \tag{43}$$

By condition 1 of Theorem 7.2, $-\lambda \alpha^T D(F(p))x \geq 0$ for all $x \in \mathbb{R}_+^N$. Since $x \in \rho^{-1}(0)$ if and only if $z_1 = 0$, with a slightly stronger condition than condition 4 and (34) of Theorem 7.2, we obtain the following corollary.

Corollary 3. *The statement of Theorem 7.2 regarding global asymptotic stability is true if condition 4 and (34) are replaced by one of the following:*

(a1) *The matrix* $\tilde{W}^T\tilde{M}^S\tilde{W}$ *given by (41) is positive definite for all* $x \in \mathbb{R}_I \setminus \{p\}$ *with either* $\rho(x) = 0$ *or* $\|x - p\|$ *sufficiently small and* $\rho(x) < 0$.

(a2) p *is the unique fixed point of (2) in* $\mathbb{R}_I$*; for each* $x \in \mathbb{R}_I \setminus \{p\}$ *with* $\|x-p\|$ *sufficiently small and* $\rho(x) < 0$*, the matrix* $\tilde{W}^T\tilde{M}^S\tilde{W}$ *is positive definite; for* $x \in (\mathbb{R}_I \setminus \{p\}) \cap \rho^{-1}(0)$, $\tilde{W}^T\tilde{M}^S\tilde{W}$ *is either positive definite or semi-positive definite but the semi-positive definite points are isolated in* $\rho^{-1}(0) \cap \mathbb{R}_I$.

8. Global stability of a fixed point on K in backward time

In this section, we consider (2) under the assumptions (A1) and (A2) given in section 2 and explore conditions for a fixed point $p \in K$ to be globally asymptotically stable in backward time with respect to $\text{int}K$ or $K \cap \mathbb{R}_I$. If p is an interior fixed point and is globally asymptotically stable in backward time on $\text{int}K$, then $\{p\}$ repels any compact set in $\text{int}K \setminus \{p\}$ to ∂K in forward time. By remark 7, application of theorem 7.1 to system (2) on K in backward time results in the following.

Theorem 8.1. *Under the assumptions (A1) and (A2), we also assume that (2) satisfies the following conditions:*

1. *For* $p \in \text{int}K$, $D(p)A$ *has an eigenvalue* $\lambda > 0$ *and a corresponding left eigenvector* α^T *with* $\alpha_i < 0$ *for* $i \in I_- \subset I_N$ *and* $\alpha_j > 0$ *for* $j \in I_+ = I_N \setminus I_-$.
2. *One of the conditions (i)–(iv) of theorem 5.1 is met.*
3. *The function* g *satisfies one of the conditions (a)–(d) of theorem 5.1.*

Then p *is P. G. repelling on* K*. If, in addition,*

$$\begin{aligned}&\exists r > 0, \forall x \in \mathcal{B}_r(p) \cap \text{int}K \text{ with } \rho(x) < 0\ (> 0)\\ &\text{under condition } (a) \text{ or } (b)\ ((c) \text{ or } (d)),\ g(x) > 0\ (< 0),\end{aligned} \tag{44}$$

then (2) is globally asymptotically stable at p *in backward time with respect to* $\text{int}K$*. Hence, for the flow on* K, $\{p\}$ *is a repellor with* $\text{int}K \setminus \{p\}$ *as its repulsion basin and* ∂K *its dual attractor.*

Now recall the definition of the matrix $\tilde{M}$ given by (31), (28) and (30). As an analogue of corollary 2 in backward time, we have the corollary below.

Corollary 4. *The statement of Theorem 8.1 regarding global asymptotic stability in backward time and repellor is true if condition 3 and (44) are replaced by one of the following:*

(a1) *The matrix* $\tilde{W}^T\tilde{M}^S\tilde{W}$ *defined by (31), (25), (28) and (30) is negative definite for all* $x \in \text{int}K \setminus \{p\}$ *with either* $\rho(x) = 0$ *or* $\|x - p\|$ *sufficiently small and* $\rho(x) > 0$.

(a2) p *is the unique fixed point of (2) in* $\text{int}K$*; for each* $x \in \text{int}K \setminus \{p\}$ *with* $\|x - p\|$ *sufficiently small and* $\rho(x) > 0$*, the matrix* $\tilde{W}^T\tilde{M}^S\tilde{W}$ *is negative definite; for* $x \in$

$(\mathrm{int}K \setminus \{p\}) \cap \rho^{-1}(0)$, $\tilde{W}^T \tilde{M}^S \tilde{W}$ is either negative definite or semi-negative definite but the semi-negative definite points are isolated in $\rho^{-1}(0) \cap \mathrm{int}K$.

(a3) *The matrix $\tilde{W}^T \tilde{M}^S \tilde{W}$ is positive definite for all $x \in \mathrm{int}K \setminus \{p\}$ with either $\rho(x) = 0$ or $\|x - p\|$ sufficiently small and $\rho(x) < 0$.*

(a4) *p is the unique fixed point of (2) in $\mathrm{int}K$; for each $x \in \mathrm{int}K \setminus \{p\}$ with $\|x - p\|$ sufficiently small and $\rho(x) < 0$, the matrix $\tilde{W}^T \tilde{M}^S \tilde{W}$ is positive definite; for $x \in (\mathrm{int}K \setminus \{p\}) \cap \rho^{-1}(0)$, $\tilde{W}^T \tilde{M}^S \tilde{W}$ is either positive definite or semi-positive definite but the semi-negative definite points are isolated in $\rho^{-1}(0) \cap \mathrm{int}K$.*

When p is a boundary fixed point, $p \in C_I^0 \cap \partial K$ for a proper subset $I \subset I_N$. Applying theorem 7.2 and remark 7 to reversed time system we obtain the following.

Theorem 8.2. *Under the assumptions (A1) and (A2), we also assume that (2) satisfies the following conditions:*

1. *For a proper subset $I \subset I_N$, $p \in C_I^0 \cap K$ and p is saturated in backward time. The matrix $D(p)A$ has an eigenvalue $\lambda > 0$ and a corresponding left eigenvector α^T with $\alpha_i < 0$ for $i \in I_- \subset I_N \setminus I$ and $\alpha_j > 0$ for $j \in (I \cup I_+)$.*
2. *One of the conditions (i)–(iv) of theorem 5.1 holds.*
3. *The function g satisfies one of the conditions (a)–(d) of theorem 5.1.*

Then p is P. G. repelling on $\mathbb{R}_I \cap K$. If, in addition,

$$\begin{aligned} &\exists r > 0, \forall x \in \mathcal{B}_r(p) \cap \mathbb{R}_I \cap K \text{ with } \rho(x) < 0\ (> 0) \\ &\text{under condition } (a) \text{ or } (b)\ ((c) \text{ or } (d)),\ g(x) > 0\ (< 0), \end{aligned} \tag{45}$$

then (2) is globally asymptotically stable at p in backward time with respect to $\mathbb{R}_I \cap K$. Hence, for the flow on K, $\{p\}$ is a repellor with $\mathbb{R}_I \cap K \setminus \{p\}$ being its repulsion basin and $K \setminus \mathbb{R}_I$ as its dual attractor.

Corollary 5. *The statement of Theorem 8.2 regarding global asymptotic stability in backward time and repellor is true if condition 3 and (45) are replaced by one of the following:*

(a1) *The matrix $\tilde{W}^T \tilde{M}^S \tilde{W}$ defined by (35), (37) and (41) is negative definite for all $x \in \mathbb{R}_I \cap (K \setminus \{p\})$ with either $\rho(x) = 0$ or $\|x - p\|$ sufficiently small and $\rho(x) > 0$.*

(a2) *p is the unique fixed point of (2) in $\mathbb{R}_I \cap K$; for each $x \in \mathbb{R}_I \cap (K \setminus \{p\})$ with $\|x - p\|$ sufficiently small and $\rho(x) > 0$, the matrix $\tilde{W}^T \tilde{M}^S \tilde{W}$ is negative definite; for $x \in \mathbb{R}_I \cap (K \setminus \{p\}) \cap \rho^{-1}(0)$, $\tilde{W}^T \tilde{M}^S \tilde{W}$ is either negative definite or semi-negative definite but the semi-negative definite points are isolated in $\mathbb{R}_I \cap K \cap \rho^{-1}(0)$.*

9. Global dynamics of a three dimensional competitive system

In this section, we give a totally competitive example with detailed analysis on the dynamics of system (2) with $N = 3$ and

$$\begin{aligned} F_1(x) &= b_0 - x_1 - 2x_2 - x_3 - \gamma x_1^2, \\ F_2(x) &= b_0 - x_1 - x_2 - 2x_3 - \gamma x_2^2, \\ F_3(x) &= b_0 - 2x_1 - x_2 - x_3 - \gamma x_3^2, \end{aligned} \tag{46}$$

where $\gamma \geq 0$ is a parameter and $b_0 = 4 + \gamma$. This system has a carrying simplex Σ (see [6]) as its global attractor for the flow on $\mathbb{R}^3_+ \setminus \{0\}$. We note that $p = (1, 1, 1)^T$ is a fixed point, and the unique interior fixed point, of the system.

When $\gamma = 0$, (46) reduces to the Lotka-Volterra system $\dot{x} = D(x)(b + Bx)$. Using the results given in [11] we can show that p is P. G. repelling on the carrying simplex Σ. This fact is included in the more detailed description of theorem 9.1 below.

Theorem 9.1. *Let* $\gamma_2 = \frac{1}{2}(\sqrt{19} - 4) \approx 0.1795$ *and* $\gamma_3 = \sqrt{6} - 2 \approx 0.4495$. *Then there is a* $\gamma_1 \in (0.164, \gamma_2]$ *such that the following statements hold for (2) with (46).*

(i) *If* $\gamma \in [0, \gamma_1)$, *then the system has a heteroclinic cycle* $\Gamma_0 = \Sigma \cap \partial\mathbb{R}^3_+$. *For the flow on* Σ, $\{p\}$ *is a repellor with* $\Sigma \setminus (\{p\} \cup \Gamma_0)$ *being its repulsion basin and* Γ_0 *as its dual attractor. Moreover,* Γ_0 *is a globally asymptotically stable on* $\mathbb{R}^3_+ \setminus \{kp : k \geq 0\}$ *and* $\{kp : k > 0\}$ *is the stable manifold of* p *in* $\mathrm{int}\mathbb{R}^3_+$. *Further, for any* $x_0 \in \mathrm{int}\mathbb{R}^3_+ \setminus \{kp : k > 0\}$, *we have* $\omega(x_0) = \Gamma_0$, *i.e.* Γ_0 *is the limit cycle of* $x(t, x_0)$.

(ii) *If* $\gamma \in [\gamma_1, \gamma_2)$, *then* $\{p\}$ *is a repellor on* Σ *and* Γ_0 *is at least locally asymptotically stable.*

(iii) *If* $\gamma \in (\gamma_2, 1/4)$, *then both* $\{p\}$ *and* Γ_0 *are repellors on* Σ. *Therefore, the system has at least one nontrivial periodic solution on* Σ.

(iv) *If* $\gamma \in (1/4, \gamma_3]$, *then* p *is at least locally asymptotically stable and* Γ_0 *is a repellor on* Σ.

(v) *If* $\gamma \in (\gamma_3, 1/2]$, *then* p *is at least locally asymptotically stable but the system has no heteroclinic cycle on* $\partial\mathbb{R}^3_+$.

(vi) *If* $\gamma > 1/2$, *then* p *is globally asymptotically stable in* $\mathrm{int}\mathbb{R}^3_+$.

We break the proof of this theorem into several lemmas. For the interior fixed point $p = (1,1,1)^T$,

$$\begin{aligned}\nabla F(x) &= -\begin{pmatrix} 1+2\gamma x_1 & 2 & 1 \\ 1 & 1+2\gamma x_2 & 2 \\ 2 & 1 & 1+2\gamma x_3 \end{pmatrix},\\ A &= -\nabla F(p) = \begin{pmatrix} 1+2\gamma & 2 & 1 \\ 1 & 1+2\gamma & 2 \\ 2 & 1 & 1+2\gamma \end{pmatrix}.\end{aligned}$$

From the definition given in (19), $\alpha = (1,1,1)^T$ satisfies $\alpha^T D(p) A = \lambda \alpha^T$ for $\lambda = 4+2\gamma > 0$ so $\rho(x) = \sum_{i=1}^3 F_i(x) = 12 + 3\gamma - 4\sum_{i=1}^3 x_i - \gamma \sum_{i=1}^3 x_i^2$. Thus, $\rho(x) = 4(3 - \sum_{i=1}^3 x_i)$ for $\gamma = 0$ and

$$\rho(x) = \gamma\left[3 + \frac{12}{\gamma} + \frac{12}{\gamma^2} - \left(x_1 + \frac{2}{\gamma}\right)^2 - \left(x_2 + \frac{2}{\gamma}\right)^2 - \left(x_3 + \frac{2}{\gamma}\right)^2\right] \tag{47}$$

for $\gamma > 0$. In this example, $\rho^{-1}(0)$ for $\gamma > 0$ is a sphere, and so one possible approach would be to parameterise $\rho^{-1}(0)$ using spherical polar coordinates. We choose not to do this here so as to illustrate the methods we have developed.

Lemma 9.2. *The system (2) with F given by (46) has a globally asymptotically stable fixed point $p = (1,1,1)^T$ whenever $\gamma > 1/2$.*

Proof. Writing $F(x) = F(x) - F(p) = M_0(x)(x-p)$, we have

$$M_0(x) = -\begin{pmatrix} 1+\gamma(1+x_1) & 2 & 1 \\ 1 & 1+\gamma(1+x_2) & 2 \\ 2 & 1 & 1+\gamma(1+x_3) \end{pmatrix}, \tag{48}$$

which gives

$$M_0(x)^S = -\begin{pmatrix} 2(x_1+1)\gamma+2 & 3 & 3 \\ 3 & 2(x_2+1)\gamma+2 & 3 \\ 3 & 3 & 2(x_3+1)\gamma+2 \end{pmatrix}.$$

Now $M_0(0,0,0)^S$ has eigenvalues $-2(4+\gamma)$, $1-2\gamma$ (twice), so that $M_0(0,0,0)^S$ is negative definite for $\gamma > 1/2$. Since $M_0(x)^S = M_0(0,0,0)^S - 2\gamma D(x)$, $M_0(x)^S$ is a negative definite matrix for $\gamma > 1/2$. Hence using corollary 1, p is globally stable. □

For $\gamma > 0$, $x_1 + x_2 + x_3 = 3$ is the tangent plane of the sphere $\rho^{-1}(0)$ at p. Since $\rho^{-1}(0)$ for $\gamma > 0$ cuts the x_i-axis at $x_i = \delta = \sqrt{3 + \frac{12}{\gamma} + \frac{4}{\gamma^2}} - \frac{2}{\gamma}$ and δ is a decreasing function of γ satisfying $\sqrt{3} < \delta < 3$, for all $\gamma > 0$ the part of the sphere $\rho^{-1}(0) \cap \mathrm{int}\mathbb{R}^3_+$ is in the region below $x_1 + x_2 + x_3 = 3$ and above $x_1 + x_2 + x_3 = \delta$.

Lemma 9.3. *For all $x \in \rho^{-1}(0) \cap \mathbb{R}^3_+$ or $x \in \mathcal{B}_r(p)$ with sufficiently small $r > 0$,* $\det M_0(x) < 0$ *so the matrix $M_0(x)$ is invertible.*

Proof. We use homogeneous coordinates: $x_i = Ru_i$ where each $u_i \geq 0$ and $u_1+u_2+u_3 = 1$. For $x \in \rho^{-1}(0) \cap \mathbb{R}^3_+$, we have $\delta \leq R \leq 3$. Then, from (48),

$$\begin{aligned}\det M_0(x) &= -(4+\gamma)(1-\gamma+\gamma^2) - \gamma(-1+2\gamma+\gamma^2)R \\ &\quad -\gamma^2(1+\gamma)(u_1u_2+u_2u_3+u_3u_1)R^2 - \gamma^3 u_1u_2u_3R^3 \\ &< -(4+\gamma)(1-\gamma+\gamma^2) - \gamma(-1+2\gamma+\gamma^2)R.\end{aligned}$$

For $\gamma \geq \sqrt{2}-1$, $-1+2\gamma+\gamma^2 = (\gamma+1+\sqrt{2})(\gamma+1-\sqrt{2}) \geq 0$ and $1-\gamma+\gamma^2 > 0$ so $\det M_0(x) < 0$. For $\gamma \in [0, \sqrt{2}-1)$, replacing R by 3 we have $\det M_0(x) < -4\gamma^3 - 9\gamma^2 + 6\gamma - 4 < 6(\sqrt{2}-1) - 4 < 0$. □

For $i \in I_3$, let $u_i = 1 + x_i$ and

$$d_i = \frac{(1+\gamma u_1)(1+\gamma u_2)(1+\gamma u_3)}{1+\gamma u_i} - 2.$$

Then the inverse of $M_0(x)$ is given by

$$M_0^{-1} = \frac{1}{\det M_0}\begin{pmatrix} d_1 & -1-2\gamma u_3 & 3-\gamma u_2 \\ 3-\gamma u_3 & d_2 & -1-2\gamma u_1 \\ -1-2\gamma u_2 & 3-\gamma u_1 & d_3 \end{pmatrix}. \tag{49}$$

Writing $\nabla F_i(x) - \nabla F_i(p) = (x-p)^T M_i$ for $i \in I_3$, we have

$$M_1 = \begin{pmatrix} -2\gamma & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}, M_2 = \begin{pmatrix} 0 & 0 & 0 \\ 0 & -2\gamma & 0 \\ 0 & 0 & 0 \end{pmatrix}, M_3 = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & -2\gamma \end{pmatrix}. \tag{50}$$

Thus,

$$-\lambda D(\alpha) + \sum_{i=1}^{3} \alpha_i p_i M_i D(x) = -2\begin{pmatrix} 2+\gamma u_1 & 0 & 0 \\ 0 & 2+\gamma u_2 & 0 \\ 0 & 0 & 2+\gamma u_3 \end{pmatrix}. \tag{51}$$

From (31), (49) and (51), we obtain $\tilde{M} = -\frac{2}{\det M_0}\tilde{M}_1$, where, with $m_i = d_i(2+\gamma u_i)$ for $i \in I_3$,

$$\tilde{M}_1 = \begin{pmatrix} m_1 & (3-\gamma u_3)(2+\gamma u_2) & -(1+2\gamma u_2)(2+\gamma u_3) \\ -(1+2\gamma u_3)(2+\gamma u_1) & m_2 & (3-\gamma u_1)(2+\gamma u_3) \\ (3-\gamma u_2)(2+\gamma u_1) & -(1+2\gamma u_1)(2+\gamma u_2) & m_3 \end{pmatrix}. \tag{52}$$

From the definition of $\tilde{W}$ given by (25) we see that, for $i = 1, 2$, the ith column of $\tilde{M}_1\tilde{W}$ is the $(i+1)$th column of $\tilde{M}_1$ minus the ith column of $\tilde{M}_1$ and the ith row of $\tilde{W}^T\tilde{M}_1\tilde{W}$ is the $(i+1)$th row of $\tilde{M}_1\tilde{W}$ minus the ith row of $\tilde{M}_1\tilde{W}$. Then

$$C = \tilde{W}^T\tilde{M}_1\tilde{W} = \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix}, \tag{53}$$

where

$$\begin{aligned} c_{11} &= 2\gamma^3 u_1u_2u_3 + \gamma^2(2u_1u_2 + 5u_1u_3 + 4u_2u_3) + \gamma(2u_1 - 2u_2 + 10u_3) - 8, \\ c_{12} &= -\gamma^3 u_1u_2u_3 - \gamma^2(u_1u_2 + 3u_1u_3) - 4\gamma(u_1 - 2u_2) + 16, \\ c_{21} &= -\gamma^3 u_1u_2u_3 - \gamma^2(2u_1u_2 + 4u_1u_3 + u_2u_3) - \gamma(10u_1 - 2u_2 + 6u_3) - 8, \\ c_{22} &= 2\gamma^3 u_1u_2u_3 + \gamma^2(5u_1u_2 + 4u_1u_3 + 2u_2u_3) + \gamma(10u_1 + 2u_2 - 2u_3) - 8. \end{aligned}$$

Since $-\frac{2}{\det M_0} > 0$, the matrix $\tilde{W}^T\tilde{M}^S\tilde{W}$ is positive (negative) definite if and only if C^S is positive (negative) definite. Note that the algebraic equation

$$4\gamma^3 + 11\gamma^2 + 5\gamma = 2 \tag{54}$$

has a unique positive solution $\gamma_0 = 1/4$.

Lemma 9.4. *There is a $\gamma_1 \in (0.164, \gamma_0]$ such that, for each $\gamma \in [0, \gamma_1)$ and every $x \in \rho^{-1}(0) \cap \mathbb{R}^3_+$ or $x \in \mathcal{B}_r(p)$ for sufficiently small $r > 0$, the matrix C^S is negative definite, i.e.*

$$c_{11} < 0, \quad c_{22} < 0, \quad 4c_{11}c_{22} - (c_{12} + c_{21})^2 > 0.$$

Proof. For each fixed $\gamma > 0$, from $\sqrt{3} < \delta \le x_1 + x_2 + x_3 \le 3$ and $0 \le x_i \le 3$ we have $\sqrt{3} + 3 < \delta + 3 \le u_1 + u_2 + u_3 \le 6$ and $1 \le u_i \le 4$. Then

$$2u_1 - 2u_2 + 10u_3 \le 2u_1 - 2u_2 + 10(6 - u_1 - u_2) = 60 - 8u_1 - 12u_2 \le 40,$$

so

$$\begin{aligned} c_{11} \le\ & 2\gamma^3 u_1u_2(6 - u_1 - u_2) + 40\gamma - 8 \\ & + \gamma^2[2u_1u_2 + (5u_1 + 4u_2)(6 - u_1 - u_2)]. \end{aligned}$$

Since $u_1u_2(6-u_1-u_2)$ has maximum 8 at $(u_1, u_2) = (2, 2)$ and $2u_1u_2 + (5u_1 + 4u_2)(6-u_1-u_2)$ has maximum $\frac{1440}{31}$ at $(u_1, u_2) = (\frac{72}{31}, \frac{30}{31})$, we have

$$c_{11} \le 16\gamma^3 + \frac{1440}{31}\gamma^2 + 40\gamma - 8.$$

Similarly, $2u_2u_3 + (5u_2 + 4u_3)(6 - u_2 - u_3)$ has maximum $\frac{1440}{31}$ at $(u_2, u_3) = (\frac{72}{31}, \frac{30}{31})$ so

$$c_{22} \le 16\gamma^3 + \frac{1440}{31}\gamma^2 + 40\gamma - 8.$$

As the polynomial of γ on the right-hand side is increasing and has a negative value -0.06348 at $\gamma = 0.165$, we have shown that $c_{11} < 0$ and $c_{22} < 0$ for $0 \le \gamma \le 0.165$.

$$\begin{aligned}
& 4c_{11}c_{22} - (c_{12} + c_{21})^2 \\
= \; & 12\gamma^6(u_1u_2u_3)^2 + 44\gamma^5(u_1u_2u_3)(u_1u_2 + u_1u_3 + u_2u_3) \\
& +\gamma^4[31(u_1^2u_2^2 + u_1^2u_3^2 + u_2^2u_3^2) + 130u_1u_2u_3(u_1 + u_2 + u_3)] \\
& +2\gamma^3[174u_1u_2u_3 + 18(u_1^2u_2 + u_1^2u_3 + u_1u_2^2 + u_2^2u_3 + u_1u_3^2 + u_2u_3^2)] \\
& +\gamma^2[-116(u_1^2 + u_2^2 + u_3^2) + 40(u_1u_2 + u_1u_3 + u_2u_3)] \\
& -160\gamma(u_1 + u_2 + u_3) + 192 \\
= \; & 12\gamma^6(u_1u_2u_3)^2 + 44\gamma^5(u_1u_2u_3)(u_1u_2 + u_1u_3 + u_2u_3) \\
& +\gamma^4[31(u_1u_2 + u_1u_3 + u_2u_3)^2 + 68u_1u_2u_3(u_1 + u_2 + u_3)] \\
& +\gamma^3[240(u_1u_2u_3) + 36(u_1u_2 + u_1u_3 + u_2u_3)(u_1 + u_2 + u_3)] \\
& +\gamma^2[-116(u_1 + u_2 + u_3)^2 + 272(u_1u_2 + u_1u_3 + u_2u_3)] \\
& -160\gamma(u_1 + u_2 + u_3) + 192.
\end{aligned}$$

As $\delta+3 \le u_1+u_2+u_3 \le 6$ and $u_i \ge 1$ for $i \in I_3$, for any fixed $\epsilon \in [\delta+3, 6]$ with $\sum_{i=1}^3 u_i = \epsilon$, we have $u_1u_2u_3 = u_1u_2(\epsilon - u_1 - u_2)$ and $u_1u_2 + u_1u_3 + u_2u_3 = u_1u_2 + (u_1 + u_2)(\epsilon - u_1 - u_2)$ with $1 \le u_1 \le \epsilon - 2$ and $1 \le u_2 \le \epsilon - 1 - u_1$. By $\frac{\partial}{\partial u_2}$ we find that both of the above functions have minimum at $u_2 = 1$ and $u_2 = \epsilon - 1 - u_1$. Thus, $u_1u_2u_3 \ge u_1(\epsilon - 1 - u_1)$ and $u_1u_2 + u_1u_3 + u_2u_3 \ge u_1(\epsilon - 1 - u_1) + \epsilon - 1$. For $1 \le u_1 \le \epsilon - 2$, $u_1(\epsilon - 1 - u_1)$ has minimum $\epsilon - 2$ so $u_1u_2u_3 \ge \epsilon - 2 \ge \delta + 1$ and $u_1u_2 + u_1u_3 + u_2u_3 \ge 2\epsilon - 3 \ge 2\delta + 3$. Hence,

$$\begin{aligned}
4c_{11}c_{22} - (c_{12} + c_{21})^2 \ge \; & 12(1+\delta)^2\gamma^6 + 44(1+\delta)(3+2\delta)\gamma^5 \\
& +[31(3+2\delta)^2 + 68(1+\delta)(3+\delta)]\gamma^4 + [240(1+\delta) + 36(3+2\delta)(3+\delta)]\gamma^3 \\
& +[272(3+2\delta) - 116 \times 36]\gamma^2 - 960\gamma + 192.
\end{aligned} \tag{55}$$

For $0 \le \gamma \le 0.165$, since $2.8 < \delta \le 3$, we have $4c_{11}c_{22} - (c_{12} + c_{21})^2 \ge f(\gamma)$, where f is the polynomial on the right-hand side of the above inequality with $\delta = 2.8$, i.e.

$$f(\gamma) = 173.28\gamma^6 + 1437.92\gamma^5 + 3791.48\gamma^4 + 2707.68\gamma^3 - 1836.8\gamma^2 - 960\gamma + 192.$$

From this we have

$$\begin{aligned}
f'(\gamma) &= 1039.68\gamma^5 + 7189.6\gamma^4 + 15165.92\gamma^3 + 8123.04\gamma^2 - 3673.6\gamma - 960, \\
f''(\gamma) &= 5198.4\gamma^4 + 28758.4\gamma^3 + 45497.76\gamma^2 + 16246.08\gamma - 3673.6.
\end{aligned}$$

Since $f''(\gamma)$ is increasing, $f''(0) < 0$ and $f''(0.165) = 378.7191 > 0$, $f'(\gamma)$ has a minimum value less than $\min\{f'(0), f'(0.165)\}$ and

$$\max_{0 \le \gamma \le 0.165} f'(\gamma) = \max\{f'(0), f'(0.165)\} = \max\{-960, -1271.41\} < 0.$$

Therefore, f is decreasing for $\gamma \in [0, 0.165]$. As $f(0.164) \approx 0.01755 > 0$, we have shown that C^S is negative definite for $0 \le \gamma \le 0.164$. Since the entries of C are continuous functions of γ and the inequalities for negative definite property of C^S are strict, there is a $\gamma_1 > 0.164$ such that, for each $\gamma \in [0, \gamma_1)$ and every $x \in \rho^{-1}(0) \cap \mathbb{R}^3_+$, the matrix C^S is negative definite.

At $x = p$, we have

$$c_{11} = c_{22} = 4(4\gamma^3 + 11\gamma^2 + 5\gamma - 2) \le 16\gamma^3 + \frac{1440}{31}\gamma^2 + 40\gamma - 8$$

and $c_{12} + c_{21} = -c_{11}$ so $4c_{11}c_{22} - (c_{12} + c_{21})^2 = 3c_{11}^2$. Since $\gamma_0 = 0.25$ is the unique positive root of c_{11}, we see that $\gamma_1 \le \gamma_0$. For each $\gamma < \gamma_1$, C^S is obviously negative definite at $x = p$. By continuity, there is an $r > 0$ (dependent on γ) such that C^S is negative definite for all $x \in \mathcal{B}_r(p)$. □

Next we address when (2) with (46) has a heteroclinic cycle through the three axial fixed points $E_1 = (\rho_0, 0, 0)^T$, $E_2 = (0, \rho_0, 0)^T$ and $E_3 = (0, 0, \rho_0)^T$ where

$$\rho_0 = \sqrt{1 + \frac{4}{\gamma} + \frac{1}{4\gamma^2}} - \frac{1}{2\gamma} \ (\gamma > 0) \quad \text{or} \quad \rho_0 = 4 \ (\gamma = 0). \tag{56}$$

We note that $\gamma_3 = \sqrt{6} - 2$ is the unique positive root of $\gamma^3 + 8\gamma^2 + 14\gamma = 8$ and $\gamma_2 = \frac{1}{2}(\sqrt{19} - 4)$ is the unique positive solution of the equation $\gamma^3 + 8\gamma^2 + \frac{61}{4}\gamma = 3$.

Lemma 9.5. *System (2) with (46) has a heteroclinic cycle Γ_0 formed by the three axial fixed points E_1, E_2, E_3 and the three trajectories joining them if and only if $\gamma \in [0, \gamma_3]$. Further, Γ_0 is asymptotically stable if $\gamma \in [0, \gamma_2)$ and Γ_0 is unstable and repels on Σ if $\gamma \in (\gamma_2, \gamma_3]$.*

Proof. First note that there is a Lipschitz curve L_1 that connects E_1 and E_2 in π_3 which is the intersection of the carrying simplex Σ and π_3. Similarly, there are curves L_2 connecting E_2 to E_3 and L_3 connecting E_3 to E_1. Whether the curves L_i contain planar fixed points (that is, fixed points in $\partial\mathbb{R}^3_+$ but not on any axis) depends on the value of γ. Consider the two curves $\ell_1 = \{x \in \mathbb{R}^3_+ \cap \pi_3 : F_1(x) = 0\}$ and $\ell_2 = \{x \in \mathbb{R}^3_+ \cap \pi_3 : F_2(x) = 0\}$. Since ℓ_1 intersects x_1-axis at ρ_0 (E_1), ℓ_2 intersects x_1-axis at $4 + \gamma \ge \rho_0$ for $\gamma \ge 0$ (with equality if and only if $\gamma = 0$), ℓ_1 intersects x_2-axis at $2 + \gamma/2$ and ℓ_2 intersects x_2-axis at ρ_0 (E_2), ℓ_1 and ℓ_2 have at least one intersection point $Q_0 \notin \{E_1, E_2\}$ if $\rho_0 < 2 + \gamma/2$, which is equivalent to $\gamma > \gamma_3$. In this case, Q_0 is a planar fixed point on π_3 so there is no heteroclinic cycle. Indeed, $F_2(E_1) = 4 + \gamma - \rho_0 > 0$ and $F_3(E_1) = 4 + \gamma - 2\rho_0 > 0$ so the Jacobian at E_1 has two positive eigenvalues. This shows that $\{E_1\}$ is a repellor on Σ so E_1 is not possible to be in a heteroclinic cycle.

Next we show that E_1, E_2, E_3 are the only fixed points in $\partial\mathbb{R}^3_+ \setminus \{0\}$ for $\gamma \in [0, \gamma_3]$. This is obvious when $\gamma = 0$. For $\gamma \in (0, \gamma_3]$, the equations for ℓ_1 and ℓ_2 can be written

$$\ell_1 : \qquad x_1 = \sqrt{1 + \frac{4}{\gamma} + \frac{1}{4\gamma^2} - \frac{2}{\gamma}x_2} - \frac{1}{2\gamma}, 0 \le x_2 \le 2 + \frac{\gamma}{2} \le \rho_0, x_3 = 0,$$

$$\ell_2 : \qquad x_1 = 4 + \gamma - x_2 - \gamma x_2^2, 0 \le x_2 \le \rho_0, x_3 = 0.$$

Replacing x_2 by $2+\frac{\gamma}{2}-y$, we consider the function

$$f(y) = 4+\gamma-(2+\frac{\gamma}{2}-y)-\gamma(2+\frac{\gamma}{2}-y)^2-\sqrt{(2\gamma)^{-2}+2\gamma^{-1}y}+(2\gamma)^{-1}.$$

If we can show that $f(y)>0$ for $y\in(0,2+\frac{\gamma}{2}]$, then E_1 and E_2 are the only fixed points on $\partial\mathbb{R}^3_+\setminus\{0\}$ with $x_3=0$. It can be verified that $\sqrt{(2\gamma)^{-2}+2\gamma^{-1}y}-(2\gamma)^{-1}<2y$, $y>0$, so that $f(y)>4+\gamma-(2+\frac{\gamma}{2}-y)-\gamma(2+\frac{\gamma}{2}-y)^2-2y$ for $y>0$, which can be simplified to give $f(y)>\gamma(2+\frac{\gamma}{2}-y)(y+\gamma^{-1}-2-\frac{\gamma}{2})$. Note that $\gamma^{-1}-2-\frac{\gamma}{2}=\frac{1}{2}\gamma^{-1}(\sqrt{6}-2-\gamma)(\sqrt{6}+2+\gamma)$. Then $\gamma\in(0,\gamma_3]$ implies $\gamma^{-1}-2-\frac{\gamma}{2}\geq 0$. So $f(y)>0$ for $y\in(0,2+\frac{\gamma}{2}]$ with $\gamma\leq\gamma_3$. Therefore, on $\partial\mathbb{R}^3_+\setminus\{0\}$ with $x_3=0$, E_1 and E_2 are the only fixed points.

Note that system (2) with (46) is G-equivariant for the group $G=<\sigma>$ with $\sigma(x_1,x_2,x_3)^T=(x_2,x_3,x_1)^T$ for all $x\in\mathbb{R}^3$. Thus, the phase portraits on the invariant sets $x_1=0$ and $x_2=0$ are simple images of π_3 through σ^2 and σ respectively. Hence, the three axial fixed points are the only fixed points of the system in $\partial\mathbb{R}^3_+\setminus\{0\}$ for $\gamma\in[0,\gamma_3]$. There is a heteroclinic trajectory from E_1 to E_2 which is $\Sigma\cap\pi_3$. By the G-equivariance, there is a heteroclinic cycle $\Gamma_0: E_1\to E_2\to E_3\to E_1$ for $\gamma\in[0,\gamma_3]$, and this cycle can be identified with $\partial\Sigma$.

The stability of Γ_0 is determined by the characteristic matrix

$$\begin{aligned} H &= \begin{pmatrix} F_1(E_1) & F_2(E_1) & F_3(E_1) \\ F_1(E_2) & F_2(E_2) & F_3(E_2) \\ F_1(E_3) & F_2(E_3) & F_3(E_3) \end{pmatrix} \\ &= \begin{pmatrix} 0 & 4+\gamma-\rho_0 & 4+\gamma-2\rho_0 \\ 4+\gamma-2\rho_0 & 0 & 4+\gamma-\rho_0 \\ 4+\gamma-\rho_0 & 4+\gamma-2\rho_0 & 0 \end{pmatrix}. \end{aligned} \tag{57}$$

By [8, Theorem 17.5.1], if there is a vector $v\in\mathbb{R}^3$ such that $v\in\text{int}\mathbb{R}^3_+$ and $Hv\in\text{int}\mathbb{R}^3_+$ then Γ_0 repels on Σ; if there is a $v\in\mathbb{R}^3$ such that $-v\in\text{int}\mathbb{R}^3_+$ and $Hv\in\text{int}\mathbb{R}^3_+$ then Γ_0 is asymptotically stable in $\mathbb{R}^3_+$. By taking $v=(1,1,1)^T$ and $v=(-1,-1,-1)^T$ respectively, we see that Γ_0 repels on Σ if $\rho_0<\frac{2}{3}(4+\gamma)$, i.e. $\gamma\in(\gamma_2,\gamma_3]$, and Γ_0 is asymptotically stable on $\mathbb{R}^3_+$ if $\rho_0>\frac{2}{3}(4+\gamma)$, i.e. $\gamma\in[0,\gamma_2)$. □

Remark 9. Regarding the stability of Γ_0, instead of using the methods of [8] we may apply the theory of [15, 16] and obtain the same results given in Lemma 9.5.

Proof of theorem 9.1. For $\gamma>\frac{1}{2}$, conclusion (vi) follows from lemma 9.2. For $\gamma\in[0,\frac{1}{2}]$, since

$$\det(J(p)-\lambda I) = -(\lambda+2\gamma+4)(\lambda+2\gamma-\frac{1}{2}+i\frac{\sqrt{3}}{2})(\lambda+2\gamma-\frac{1}{2}-i\frac{\sqrt{3}}{2}),$$

all eigenvalues of $J(p)$ have a negative real part if $\gamma>\frac{1}{4}$ but a pair have a positive real part if $\gamma\in[0,\frac{1}{4})$. Thus, for $\gamma\in(\frac{1}{4},\frac{1}{2}]$, p is at least locally asymptotically stable; for $\gamma\in[0,\frac{1}{4})$,

$\{p\}$ is a repellor of the flow on Σ. Then, combining these with lemma 9.5 and applying the Poincaré-Bendixson theory on Σ, we obtain the conclusions (ii)–(v).

Now assuming $0 \leq \gamma < \gamma_1 (\leq \gamma_2)$, we need only prove the conclusion (i). The existence of the heteroclinic cycle Γ_0 and its local asymptotic stability follow from lemma 9.5. Next, we shall apply corollary 4 to the system on Σ for the global asymptotic stability of p in backward time. With $\alpha = (1,1,1)^T = p$, so $\theta = D(p)\alpha = p$, $I_- = I = \emptyset$ and $I_+ = I_3$, condition 1 of theorem 8.1 is met. From lemma 9.5 we know that E_1, E_2 and E_3 are the only fixed points on $\partial\mathbb{R}^3_+ \cap \Sigma$. Then, for $0 < \gamma < \gamma_1$ and $i \in I_3$, from (47) and (56) we have

$$\begin{aligned} \rho(E_i) &= \gamma\left[3 + \frac{12}{\gamma} + \frac{4}{\gamma^2} - \left(\sqrt{1 + \frac{4}{\gamma} + \frac{1}{4\gamma^2}} + \frac{3}{2\gamma}\right)^2\right] \\ &= 2\gamma + 8 + \frac{3}{2\gamma} - 3\sqrt{1 + \frac{4}{\gamma} + \frac{1}{4\gamma^2}}. \end{aligned}$$

As $\rho(E_i) < 0$ if and only if $\gamma^3 + 8\gamma^2 + \frac{61}{4}\gamma < 3$ (which holds for $\gamma < \gamma_2$), for $0 < \gamma < \gamma_1 \leq \gamma_2$ we have $\rho(E_i) < 0$. For $\gamma = 0$, $\rho(x) = 4(3 - x_1 - x_2 - x_3)$ so $\rho(E_i) = -4 < 0$. This shows that the system has no invariant set in $\Sigma \cap \{x \in \partial\mathbb{R}^3_+ : \rho(x) \geq 0\}$. Thus, condition (iv) of theorem 5.1, and subsequently condition 2 of theorem 8.1, is fulfilled. Form (53) and lemma 9.4 we know that the matrix $\tilde{W}^T\tilde{M}^S\tilde{W}$ is negative definite, so condition (a1) of corollary 4 is satisfied. Then, by corollary 4, for the flow on Σ, $\{p\}$ is a repellor with repulsion basin $\Sigma \cap (\text{int}\mathbb{R}^3_+ \setminus \{p\})$ and the dual attractor Γ_0.

Since we have $F_1(x_1, x_1, x_1) = F_2(x_1, x_1, x_1) = F_3(x_1, x_1, x_1)$, the set $\{kp : k > 0\}$ is invariant and the flow on this set is determined by $\dot{x}_1 = x_1(b_0 - 4x_1 - \gamma x_1^2)$. Since each positive solution of this equation satisfies $x_1 \to 1$ as $t \to +\infty$, we see that the stable manifold of p is $\{kp : k > 0\}$. Now for any $x_0 \in \mathbb{R}^3_+ \setminus \{kp : k \geq 0\}$, as $\omega(x_0) \subset \Sigma$ and $\{p\}$ is a repellor on Σ with the dual attractor Γ_0, we must have $\omega(x_0) \subset \Gamma_0$. This shows the global asymptotic stability of Γ_0 in $\mathbb{R}^3_+ \setminus \{kp : k \geq 0\}$.

Finally, we show that $\omega(x_0) = \Gamma_0$ for all $x_0 \in \text{int}\mathbb{R}^3_+ \setminus \{kp : k > 0\}$. Since Γ_0 is a heteroclinic cycle and $\omega(x_0) \subset \Gamma_0$, the flow direction on Γ_0 determines that $\omega(x_0)$ is either a singleton or Γ_0. At E_1, $J(E_1)$ has eigenvalues $-\rho_0(1 + 2\gamma) < 0$, $F_3(E_1) = 4 + \gamma - 2\rho_0 < 0$ and $F_2(E_1) = 4 + \gamma - \rho_0 \geq 0$. Thus, E_1 is globally asymptotically stable on $\pi_2 \setminus \pi_1$. But E_1 repels along L_1 to E_2 in π_3 so L_1 is the unstable manifold of E_1 in $\mathbb{R}^3_+ \setminus \pi_1$. Hence, $\omega(x_0) \neq \{E_1\}$ as x_0 is not in the stable manifold of E_1. Similarly, $\omega(x_0) \neq \{E_2\}$ and $\omega(x_0) \neq \{E_3\}$. Therefore, we must have $\omega(x_0) = \Gamma_0$. □

Figure 2 illustrates the various cases.

10. Discussion and Conclusion

In this work we have studied the global dynamics of autonomous Kolmogorov systems. Our results provide for the study of global attraction or repulsion (in the global attractor)

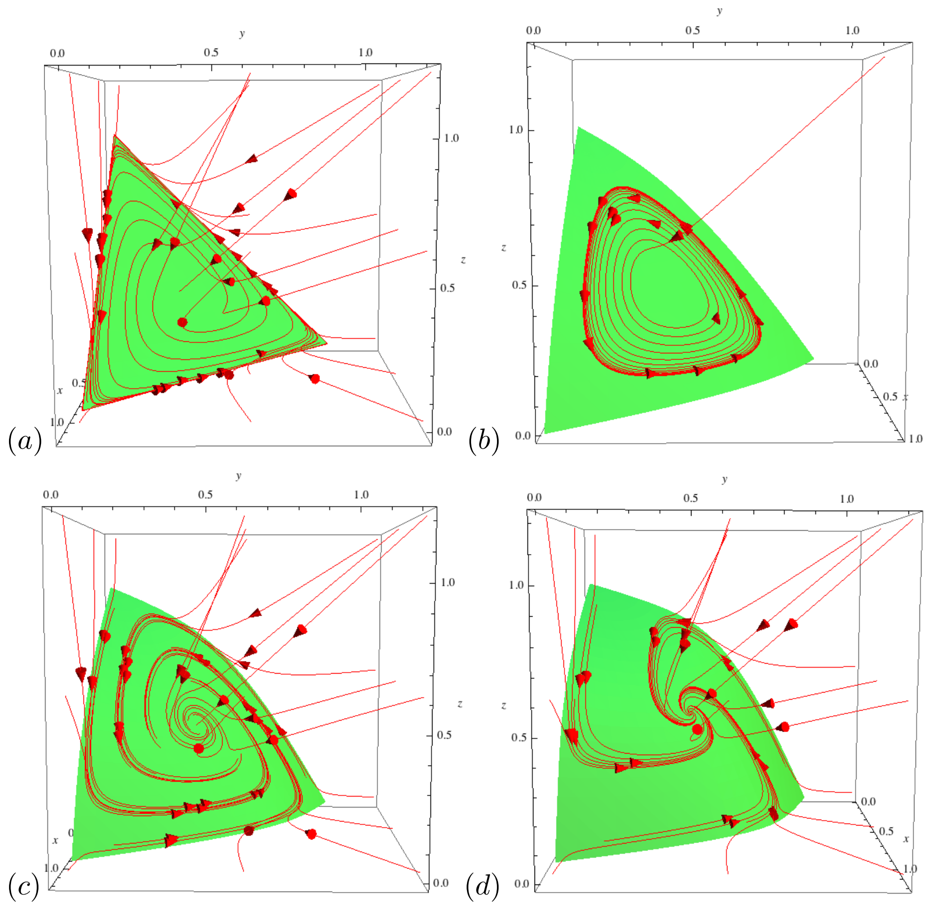

FIGURE 2. (a)-(d): Phase plots for system (50) for $\gamma = 0.1, 0.23, 0.35, 0.55$. The green surface is the carrying simplex for the system.

of both interior and boundary fixed points, and we have demonstrated the applicability of our results to a range of examples from theoretical ecology and population genetics. Our main results are generalisations, but not trivial extension, of two existing Lyapunov function methods that are well-known for Lotka-Volterra systems: diagonal stability and split Lyapunov stability. Both generalisations stem from our lemma 4.3, which is an application of LaSalle's invariance principle (in the form as described in [22]), and involve two choices of the scalar function ϕ which is used to construct the Lyapunov function Φ.

The diagonal stability in theorem 6.1 is simple to apply to a fixed point $p \in C_I^0$, but is restricted to vector fields $F : \Omega \to \mathbb{R}^N$ that satisfy $(x - y)D(v)(F(x) - F(y)) < 0$ for distinct $x, y \in \overline{\Omega}$, where $v \gg 0$; no component of v is allowed to be negative. Moreover, it only applies to asymptotic stability. The split Lyapunov method developed in theorems

7.1 to 8.2 is technically more involved, but less so for lower dimensional systems ($N \leq 3$), and it is more flexible in that it allows v to have negative components and it can be used to identify both globally attracting and globally repelling interior and boundary fixed points. Central to this second method, and perhaps the greatest challenge in its successful application, is to preclude common zeros of two functions or to establish the definiteness of a matrix function over a suitable domain. In the Lotka-Volterra case, this matrix function is a constant. Thus for the split Lyapunov method there is a trade-off between wider applicability and ease of application. It is known for the Lotka-Volterra equations [25] that either the diagonal stability or the split Lyapunov method can work when the other method fails and this extends to general Kolmogorov systems. Although both of these methods developed here have shortcomings, to the best of our knowledge, there are no other results available for global stability or repulsion of a fixed point in general autonomous Kolmogorov systems.

Our examples cover both competitive and non-competitive systems, where by competitive we mean with respect to the first orthant partial-ordering of points. For competitive systems with a unique carrying simplex, by appealing to linearisation at an interior fixed point and known results for Lotka-Volterra systems [25], the stability (instability) at that interior steady state can be linked to the convexity (concavity) of the carrying simplex near that interior fixed point (see figure 2, for example). For Kolmogorov systems, the position of the manifold $\rho^{-1}(0)$ relative to the carrying simplex can be easily used to determine stability, but our split Lyapunov method is applicable when there is no carrying simplex, or when one has not been identified. It remains an interesting open problem to determine when a fixed point of a Kolmogorov system is contained in a locally or globally attracting invariant manifold of codimension one.

Appendix: Resultant of polynomials

Let $p(x) = \sum_{i=0}^{n} a_i x^i$ and $q(x) = \sum_{i=0}^{m} b_i x^i$ be polynomials over $\mathbb{C}$ with $a_n b_m \neq 0$. We construct the $m+n$ square matrix:

$$\mathrm{Syl}(p,q,x) = \begin{pmatrix} a_0 & 0 & \cdots & 0 & b_0 & 0 & \cdots & 0 \\ a_1 & a_0 & \ddots & \vdots & b_1 & b_0 & \ddots & \vdots \\ a_2 & a_1 & \ddots & 0 & b_2 & b_1 & \ddots & 0 \\ & \vdots & & a_0 & & \vdots & & b_0 \\ a_{n-1} & & & & b_{m-1} & & & \\ a_n & a_{n-1} & & \vdots & b_m & b_{m-1} & & \vdots \\ 0 & a_n & \ddots & & 0 & b_m & \ddots & \\ \vdots & \ddots & \ddots & a_{n-1} & \vdots & \ddots & \ddots & b_{m-1} \\ 0 & \cdots & 0 & a_n & 0 & \cdots & 0 & b_m \end{pmatrix}.$$

In relation to polynomials with common roots, we recall the notion of the Resultant corresponding to remark 7 and examples 1 and 2 given in section 4. The Resultant of p, q is defined by

$$\mathrm{Res}(p, q, x) = \det \mathrm{Syl}(p, q, x).$$

The main property of the Resultant that we use is that p, q have a common zero if and only if $\mathrm{Res}(p, q, x) = 0$. If p, q are polynomials in $x = (x_1, \ldots, x_N)$ then write $p(x) = \sum_{i=0}^{n} A_i(x_1, \ldots, x_{N-1}) x_N^i$ and $q(x) = \sum_{j=0}^{n} B_j(x_1, \ldots, x_{N-1}) x_N^j$. (We may reorder the components of x to obtain this form if necessary.) By $\mathrm{Res}(p, q, x_N)$ we mean the determinant of the above matrix with each a_i replaced by $A_i(x_1, \ldots, x_{N-1})$ and each b_j replaced by $B_j(x_1, \ldots, x_{N-1})$, and this is a polynomial in $x_1, \ldots, x_{N-1}$. Accordingly then p, q have a common zero at the point $x = (x_1, \ldots, x_N)$ only if $\mathrm{Res}(p, q, x_N) = 0$. This observation is particularly useful when $N = 2$, since then $\mathrm{Res}(p, q, x_2)$ is a polynomial in x_1 and it is straightforward to test whether that polynomial can vanish on $\mathbb{R}_+$.

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