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FROM LOCAL TO GLOBAL BEHAVIOR IN COMPETITIVE LOTKA-VOLTERRA SYSTEMS

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ABSTRACT. In this paper we exploit the linear, quadratic, monotone and geometric structures of competitive Lotka-Volterra systems of arbitrary dimension to give geometric, algebraic and computational hypotheses for ruling out nontrivial recurrence. We thus deduce the global dynamics of a system from its local dynamics.

The geometric hypotheses rely on the introduction of a split Liapunov function. We show that if a system has a fixed point $p \in \operatorname{int}\mathbf{R}^n_+$ and the carrying simplex of the system lies to one side of its tangent hyperplane at p, then there is no nontrivial recurrence, and the global dynamics are known. We translate the geometric hypotheses into algebraic hypotheses in terms of the definiteness of a certain quadratic function on the tangent hyperplane. Finally, we derive a computational algorithm for checking the algebraic hypotheses, and we compare this algorithm with the classical Volterra-Liapunov stability theorem for Lotka-Volterra systems.

1. INTRODUCTION

Consider a community of n interacting species modeled by the Lotka-Volterra system

$$(1.1)\qquad \dot{x_i} = x_i(b_i - \sum_{j=1}^{n} a_{ij}x_j) = x_i(b_i - (Ax)_i) = x_i(b_i - A_i x), \qquad i = 1, \dots, n$$

where x_i is the population size of the ith species at time t, $\dot{x_i}$ denotes $\frac{dx_i}{dt}$, and A_i is the ith row of the matrix of coefficients $A = (a_{ij})$. We restrict attention to the closed positive cone $\mathbf{R}^n_+$, and we denote the open positive cone by $\operatorname{int}\mathbf{R}^n_+$.

We call system (1.1) *competitive* when $a_{ij}, b_i > 0$ for all $i, j = 1, \dots, n$. It is well known that two-dimensional competitive Lotka-Volterra systems have no periodic orbits. M. L. Zeeman proved in [21] that in dimensions three and above, competitive Lotka-Volterra systems admit Hopf bifurcations giving rise to isolated periodic orbits. Hofbauer and So [5], Xiao and Li [17] and E. C. Zeeman [18] have found examples of three-dimensional competitive Lotka-Volterra systems with at least two isolated periodic orbits.

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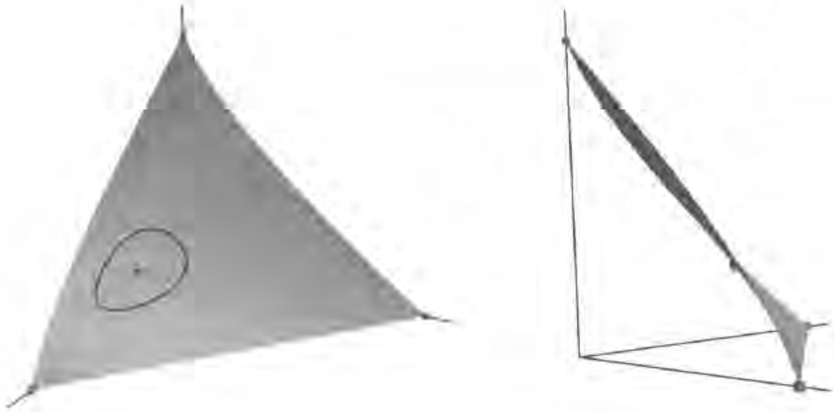

FIGURE 1. "Front" and "side" views of the carrying simplex of a three-dimensional competitive Lotka-Volterra system with an attracting periodic orbit

Hirsch proved in [3] that when system (1.1) is competitive, the growth of small populations and competition of large populations balance on a globally attracting hypersurface, which we call the *carrying simplex* and denote by Σ. See Section 2.1 and [21] for more detail. In particular, the carrying simplex of the system contains the periodic orbits.

In this paper we address the open question of how to predict whether a given competitive Lotka-Volterra system has a periodic orbit. Our approach continues the study of the relationship between the dynamics of the system and the convexity of its carrying simplex begun in [19] and [22]. This direction was inspired by numerical simulation to visualize the periodic orbits created by the Hopf bifurcations described in [21].

Figures 1 – 3 illustrate the geometric phenomenon that caught our attention: the carrying simplex is consistently more "twisted" after a Hopf bifurcation. Figure 1 shows the carrying simplex, Σ, of a system just after a Hopf bifurcation. There is an attracting periodic orbit on Σ, and the side view of Σ shows considerable negative curvature.

By contrast, Figures 2 and 3 show some orbits on the carrying simplices of two systems that are not close to a Hopf bifurcation. In Figure 2 the interior fixed point attracts on Σ, and Σ appears to be convex. In Figure 3 the interior fixed point repels on Σ, and Σ appears to be concave. See Section 4 for the definition of convex and concave in this context.

The theme of this paper is to exploit this geometric insight, and the linear, monotone and quadratic structures of system (1.1), to give hypotheses for ruling out periodic orbits and more general nontrivial recurrence in arbitrary dimension, thereby deducing the global dynamics of the system.

Liapunov functions are frequently employed to rule out recurrence from Lotka-Volterra systems with extra structure, usually involving low dimensions, or some kind of symmetry. For examples, see [4] and the references therein. To broaden the application to n-dimensional systems with no symmetry, we shift attention from

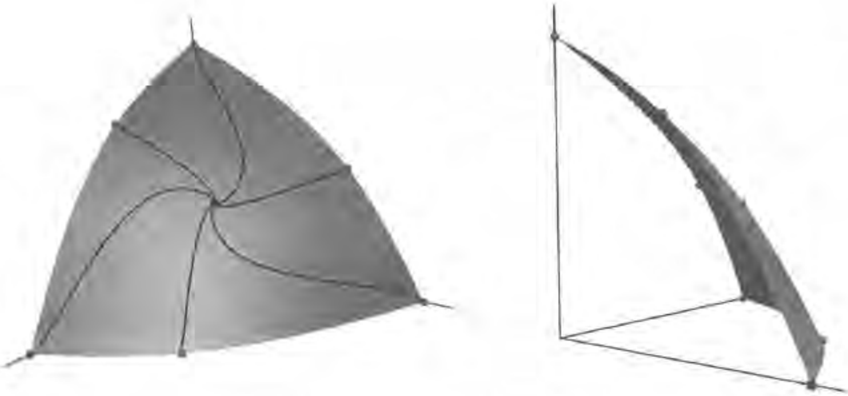

FIGURE 2. "Front" and "side" views of the carrying simplex of a three-dimensional competitive Lotka-Volterra system for which the interior fixed point attracts on Σ, and hence on the whole of $\mathbf{R}^3_+ \setminus \{0\}$

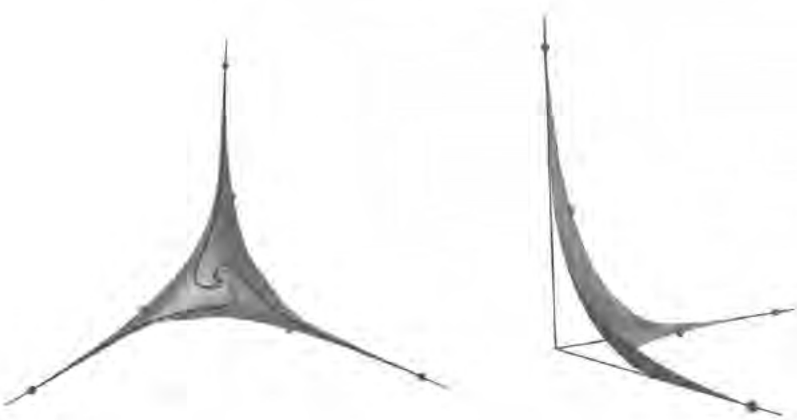

FIGURE 3. "Front" and "side" views of the carrying simplex of a three-dimensional competitive Lotka-Volterra system for which the interior fixed point repels on Σ

true Liapunov functions to the weaker concept of a *split Liapunov function* (Section 3): a function that increases along orbits in one region of space, while decreasing along orbits in another. This translates the algebraic problem of finding a true Liapunov function to the geometric problem of understanding when the limit sets of the system are contained in a region in which the split Liapunov function is monotone along orbits.

In Section 4 we use the split Liapunov function to give geometric hypotheses for ruling out recurrence in system (1.1). More precisely, we show (Theorem 4.3) that when system (1.1) is competitive and has a fixed point $p \in \operatorname{int} \mathbf{R}^n$, there is no nontrivial recurrence if the carrying simplex lies to one side of its own tangent plane at p. Thus, there is no recurrence on convex or concave carrying simplices (Corollary 4.5). So when a three-dimensional competitive Lotka-Volterra system undergoes a generic Hopf bifurcation, the carrying simplex must have negative curvature somewhere.

In Section 5 we exploit the quadratic structure of system (1.1) to give algebraic hypotheses (Theorem 5.3) from which the position of the carrying simplex relative to its tangent plane at p can be deduced, so that Theorem 4.3 can be applied. Then in Section 6 we derive a computational algorithm (Theorem 6.7) for checking the algebraic hypotheses of Theorem 5.3 from local linear information at p. The resulting computational hypotheses for ruling out recurrence in system (1.1) are reminiscent of the classical Volterra-Liapunov Stability Theorem for Lotka-Volterra systems (see [4, Theorem 15.3.1]). In Section 7 we give three examples to illustrate how the two theorems compare, and to show that neither implies the other.

2. Background

2.1. Monotone structure: the carrying simplex. It is easy to see that if system (1.1) is competitive, then 0 is a repelling fixed point, and the basin of repulsion of 0 in $\mathbf{R}^n_+$ is bounded. The carrying simplex, denoted Σ, is the boundary of that basin. To be precise, define $B(0) = \{x \in \mathbf{R}^n_+ : \alpha(x) = 0\}$, and define $\Sigma = \partial B(0)$, where $\alpha(x)$ denotes the α-limit set of the trajectory through x, and $\partial B(0)$ denotes the boundary of $B(0)$ taken in $\mathbf{R}^n_+$.

Applying a theorem of Hirsch [3], as in [21], the backwards time monotonicity structure of the competition can be exploited to show that Σ is topologically and geometrically simple, and that all the nonzero fixed points and other ω-limit sets of the system lie on Σ.

First some notation. A vector x is called *positive* if $x \in \mathbf{R}^n_+$ and *strictly* positive if $x \in \operatorname{int} \mathbf{R}^n_+$. Two points $u, v \in \mathbf{R}^n$ are *related* if either $u - v$ or $v - u$ is strictly positive, and *weakly* related if either $u - v$ or $v - u$ is positive. A set S is called *balanced* if no two distinct points of S are related, and *strongly* balanced if no two distinct points of S are weakly related.

Theorem 2.1 (Hirsch). *If system* (1.1) *is competitive, then every trajectory in* $\mathbf{R}^n_+ \setminus \{0\}$ *is asymptotic to one in* Σ; Σ *is a balanced Lipschitz submanifold homeomorphic to the closed unit simplex in* $\mathbf{R}^n_+$ *via radial projection, and* $\operatorname{int} \Sigma$ *is strongly balanced.*

Brunovský [1] and Mierczyǹski [10], [11] have given conditions under which the carrying simplex is actually C^1. Mierczyǹski [12], [13] has also proved that the carrying simplex is not necessarily C^1 at its boundary.

2.2. Linear structure: nullclines and fixed points. It is well known that the fixed points of a Lotka-Volterra system are found by exploiting the linear structure of the *per capita* growth rates. The ith component, x_i, of system (1.1) vanishes on the coordinate hyperplane $x_i = 0$, and on the ith *nullcline* N_i given by $A_i x = b_i$. The system has a fixed point in $\operatorname{int} \mathbf{R}^n_+$ if the nullclines meet in $\operatorname{int} \mathbf{R}^n_+$. More generally, there is a fixed point at $p \in \mathbf{R}^n$ if $Ap = b$, where $b = (b_i)$. If A is invertible, then $p = A^{-1}b$ is unique, and if $p \in \operatorname{int} \mathbf{R}^n_+$ we can rewrite system (1.1) as

$$\dot{x}_i = x_i(b_i - A_i x) = x_i A_i(p - x), \qquad i = 1, \ldots, n. \tag{2.1}$$

If A is not invertible, then the nullclines have either a line of intersection (at least), or no intersection. So there cannot be a unique fixed point in $\operatorname{int} \mathbf{R}^n_+$.

Similarly, if $S \subset \{1, \ldots, n\}$ and K is the coordinate subspace of $\mathbf{R}^n$ given by $x_s = 0, \forall s \in S$, then system (1.1) has a fixed point at $K \cap (\bigcap_{i \notin S} N_i)$. If the corresponding principal submatrix of A is invertible, then there is at most one fixed point in $\operatorname{int} K_+$, where $K_+ = K \cap \mathbf{R}^n_+$.

Note that when system (1.1) is competitive, each nullcline N_i is strongly balanced, since it has strictly positive normal vector A_i^T. There is a strictly positive *axial fixed point* r_i where N_i meets the x_i coordinate axis. These axial fixed points are at the vertices of the carrying simplex Σ.

3. Split Liapunov Functions

In this section we exploit the particular quadratic structure of system (1.1) to define a split Liapunov function. Note that Theorem 3.1 and Corollary 3.3 do not require the Lotka-Volterra system to be competitive.

Given system (1.1) with a unique fixed point $p \in \operatorname{int} \mathbf{R}^n_+$, let H be any hyperplane through p. If $0 \notin H$, define H_- and H_+ to be the regions of $\mathbf{R}^n_+ \setminus H$ containing and disjoint from 0 respectively. We call H_- and H_+ the regions *below* and *above* H respectively. If $0 \in H$, then label the two components of $\mathbf{R}^n_+ \setminus H$ as H_- and H_+ in either order.

Theorem 3.1. *Given system* (1.1) *with a unique fixed point* $p \in \operatorname{int} \mathbf{R}^n_+$, *let* H *be a hyperplane through* p. *Then there is a function* V *defined on* $\operatorname{int} \mathbf{R}^n_+$ *such that*

$$\begin{aligned} \dot{V} &> 0 \text{ in } \operatorname{int} H_-, \\ \dot{V} &= 0 \text{ on } H, \\ \dot{V} &< 0 \text{ in } \operatorname{int} H_+. \end{aligned}$$

We call V *the split Liapunov function corresponding to* H.

Proof. Let h be a column vector normal to H, such that

$$\begin{aligned} x \in H_- &\Leftrightarrow h^T(p - x) > 0, \\ x \in H &\Leftrightarrow h^T(p - x) = 0, \\ x \in H_+ &\Leftrightarrow h^T(p - x) < 0. \end{aligned} \tag{3.1}$$

Note that when H is strongly balanced, h is a strictly positive vector. Now A is invertible, since p is unique, and so we can define $\alpha = h^T A^{-1}$ and write

$$h^T = \alpha A = \sum_{i=1}^{n} \alpha_i A_i \tag{3.2}$$

where A_i is the ith row of A, as usual.

Now define

$$V(x) = \prod_{i=1}^{n} x_i^{\alpha_i}.$$

Then

$$\dot{V}(x) = \sum_{i=1}^{n} \frac{\partial V}{\partial x_i}\dot{x}_i = V\sum_{i=1}^{n} \alpha_i \frac{\dot{x}_i}{x_i} = V\sum_{i=1}^{n} \alpha_i A_i(p-x) = Vh^T(p-x)$$

by equations (2.1) and (3.2). But $V > 0$ on $\operatorname{int}\mathbf{R}^n_+$. Therefore, by equation (3.1),

$$\begin{aligned} \dot{V} &> 0 \text{ in } \operatorname{int} H_-, \\ \dot{V} &= 0 \text{ on } H, \\ \dot{V} &< 0 \text{ in } \operatorname{int} H_+. \end{aligned}$$

□

Remark 3.2. The split Liapunov function V can be viewed as generalizing the nullcline information in the following way. If we choose H to be a nullcline N_i, then we can choose the normal h to be A_i, so that $\alpha = e_i$, the ith standard basis vector in $\mathbf{R}^n$. Therefore,

$$V(x) = x_i, \tag{3.3}$$

and Theorem 3.1 reduces to the familiar fact that $\dot{x}_i = 0$ on N_i, $\dot{x}_i > 0$ below N_i, and $\dot{x}_i < 0$ above N_i.

Corollary 3.3. *If system* (1.1) *has a unique fixed point* $p \in \operatorname{int}\mathbf{R}^n_+$ *and a nontrivial periodic orbit* $\gamma \subset \operatorname{int}\mathbf{R}^n_+$, *then* γ *is either contained in a hyperplane through* p, *or* γ *crosses at least twice all hyperplanes through* p.

Proof. Let $\gamma \subset \operatorname{int}\mathbf{R}^n_+$ be a T-periodic orbit of system (1.1). Let H be any hyperplane through p, and suppose (for contradiction) that $\gamma \cap H = \emptyset$. Then either $\gamma \in \operatorname{int} H_-$ or $\gamma \in \operatorname{int} H_+$. In either case, by Theorem 3.1, there is a split Liapunov function V, strictly monotone on γ. But this contradicts the fact that $\gamma(t) = \gamma(t+T)$. Similarly, if $\gamma \not\subset H$, but touches H without crossing H, then V is nonconstant and monotone on γ, which also contradicts $\gamma(t) = \gamma(t+T)$. Since γ crosses H, then it must cross H again to get back to the other side. Therefore, γ crosses H at least twice. □

Remark 3.4. Since Corollary 3.3 holds for all hyperplanes H through p, we can deduce that when $n = 3$ either γ is flat ($\gamma \subset H$ for some H), or γ is shaped approximately like the seam on a tennis ball (γ crosses all H through p at least twice).

4. Geometric Hypotheses

Henceforth, we restrict attention to competitive Lotka-Volterra systems with a unique fixed point $p \in \operatorname{int}\mathbf{R}^n_+$. We exploit the split Liapunov function by choosing H to be $T_p\Sigma$, the tangent hyperplane to the carrying simplex Σ at p. In Lemma 4.1 we use the balanced structure of Σ to show that the split Liapunov function vanishes on $\partial\mathbf{R}^n_+$. In Theorem 4.3 we deduce the global dynamics of a competitive Lotka-Volterra system whose carrying simplex lies to one side of $T_p\Sigma$. We then discuss the relationship between the convexity of Σ, the edges of Σ, and the dynamics on Σ. In Section 5 we give algebraic conditions at p from which the position of Σ relative to H can be deduced, so that Theorem 4.3 can be applied. In Section 6 we give an algorithm for computing these algebraic conditions.

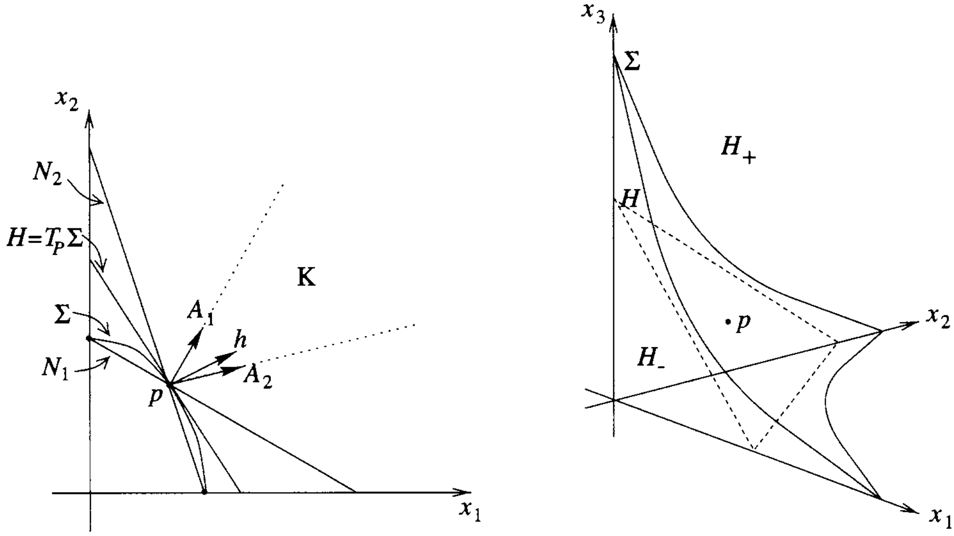

FIGURE 4. In the figure on the left, Σ and $T_p\Sigma$ lie between the nullclines, and so h lies in the convex hull K of the A_i^T. The figure on the right shows Σ and $H = T_p\Sigma$ for a three-dimensional example in which $\Sigma \setminus p$ lies in H_+.

Lemma 4.1. *Given the competitive system* (1.1) *with a unique fixed point* $p \in \operatorname{int} \mathbf{R}_+^n$, *let* $H = T_p\Sigma$ *and define the split Liapunov function* V, *corresponding to* H, *as in Theorem 3.1. Then* V *extends to* $\mathbf{R}_+^n$, *and* $V \equiv 0$ *on* $\partial\mathbf{R}_+^n$.

Proof. The interior of the carrying simplex, $\operatorname{int}\Sigma$, is invariant and strongly balanced, by Theorem 2.1. So the vector field $\dot{x}$ is neither strictly positive nor strictly negative on $\Sigma \setminus \{p\}$. Hence Σ is "trapped between" the nullclines of the system, in the sense that no point of $\Sigma \setminus \{p\}$ lies above all the nullclines (where $\dot{x}$ is negative), nor below all the nullclines (where $\dot{x}$ is positive). Therefore, the tangent hyperplane $H = T_p\Sigma$ is also trapped between the nullclines, and the normal vector h is contained in the closed convex hull K of the rays containing the normal vectors A_i^T to the nullclines N_i. See Figure 4.

Next we show that $h \notin \partial K$, the boundary of this convex hull. Suppose (for contradiction) that h lies in some face of K, say the face opposite A_1^T. In other words, h lies in the convex hull of $A_2^T, \ldots, A_n^T$. Then H contains the intersection $N_2 \cap \ldots \cap N_n$ of the corresponding nullclines, on which $\dot{x}$ is parallel to the x_1-axis.

Let R be a ray emanating from p in $N_2 \cap \ldots \cap N_n$. If $\dot{y} = By$ denotes the linear approximation of system (1.1) at p, then $By \neq 0$ for $y \neq 0$, and the direction of By is constant for all $y \in R \setminus \{p\}$. Let u denote the unit vector in this direction. Then $u \in H$, because $R \subset H$, and H is invariant under the linear approximation.

Now for each $x \in R \setminus \{p\}$, let $u(x)$ denote the unit vector in the direction of the full vector field $\dot{x}$ of system (1.1). Then, by the definition of the derivative map, $u(x) \to u$ as $x \to p$ along R. But $u(x)$ is parallel to the x_1-axis for all $x \in R \setminus \{p\}$; so the limit u is also parallel to the x_1-axis. Therefore, u is transverse to H since H is trapped between the nullclines, contradicting the fact that $u \in H$. Thus $h \notin \partial K$, and hence $h \in \operatorname{int} K$.

So

$$h = \sum_{i=1}^{n} \alpha_i A_i^T, \quad \text{where } \alpha_i > 0, \quad \forall\, i = 1, \ldots, n,$$

and thus, if $x_i = 0$ for any i,

$$V(x) = \prod_{i=1}^{n} x_i^{\alpha_i} = 0.$$

□

Definition 4.2. Given the competitive system (1.1) with a unique fixed point $p \in \operatorname{int} \mathbf{R}_+^n$, we call p a global attractor if p is an attractor with $\operatorname{int} \mathbf{R}_+^n$ as its basin of attraction. We call p a global repellor if, on Σ, p is a repellor with $\operatorname{int} \Sigma$ as its basin of repulsion. (Note that in the latter case, p is a saddle in $\mathbf{R}_+^n$, by Theorem 2.1.)

Figures 2 and 3 show examples in $\mathbf{R}_+^3$ for which p is globally attracting and globally repelling respectively. In Figure 4, on the right, we illustrate that the carrying simplex of Figure 3 lies above H, in H_+.

Theorem 4.3 (Geometric Theorem). *Given the competitive system* (1.1) *with a unique fixed point* $p \in \operatorname{int} \mathbf{R}_+^n$, *let* $H = T_p\Sigma$. *If* $\Sigma \setminus \{p\}$ *lies below* H, *then* p *is a global attractor. If* $\Sigma \setminus \{p\}$ *lies above* H, *then* p *is a global repellor.*

Proof. Let V be the split Liapunov function corresponding to H, as defined in Theorem 3.1. Then $V(p) > 0$, and $V \equiv 0$ on $\partial\Sigma$ by Lemma 4.1. If $\Sigma \setminus \{p\}$ lies below H, then V is strictly increasing along orbits on $\Sigma \setminus \{p\}$. Therefore, there is no recurrence on $\Sigma \setminus \{p\}$. Moreover, if $x \in \operatorname{int}\Sigma$, then $V(x) > 0$; so $\omega(x) \cap \partial\Sigma = \emptyset$. Thus $\omega(x)$ is a subset of the fixed points in $\operatorname{int}\Sigma$. But p is the only fixed point in $\operatorname{int}\Sigma$, and so p attracts all orbits in $\operatorname{int}\Sigma$. Hence p is globally attracting by Theorem 2.1.

Now consider the case when $\Sigma \setminus \{p\}$ lies above H. Then V is strictly decreasing along orbits on $\Sigma \setminus \{p\}$. So in backwards time, V is strictly increasing along orbits on $\Sigma \setminus \{p\}$. Thus, as in the previous case, p attracts all orbits in $\operatorname{int}\Sigma$ in backwards time. Therefore in forwards time, P is globally repelling. □

In Corollary 4.5, we ensure that $\Sigma \setminus \{p\}$ lies to one side of its own tangent plane at p by requiring that Σ is either convex or concave. We use the following definition of convexity or concavity of the carrying simplex. Let Σ_+ and Σ_- denote the two components of $\mathbf{R}_+^n \setminus \Sigma$ that lie above and below Σ respectively (so $0 \in \Sigma_-$).

Definition 4.4. We call Σ convex, flat, or concave if for all $x, y \in \Sigma$, the interior of the line segment xy lies in Σ_-, Σ, or Σ_+ respectively.

Corollary 4.5. *Given the competitive system* (1.1) *with a unique fixed point* $p \in \operatorname{int} \mathbf{R}_+^n$, *if* Σ *is convex (concave), then* p *is a global attractor (repellor).*

Proof. Consider the case when Σ is convex. Let $H = T_p\Sigma$, let $x \in \Sigma \setminus p$, and suppose that $x \in \Sigma \cap H_+$. Then the segment xp is transversal to H at p, and $\operatorname{int} xp$ meets Σ_+, contradicting the hypothesis that Σ is convex. Therefore $\Sigma \subset H \cup H_-$, so $\Sigma_- \subset H_-$, and $\operatorname{int} xp \subset \Sigma_- \subset H_-$. Thus $x \in H_-$, so $\Sigma \setminus p$ lies below H, and hence p is a global attractor by Theorem 4.3.

Similarly, when Σ is concave, p is a global repellor. □

Define an *edge* of Σ to be a one-dimensional face in the boundary of Σ. In [19] we prove that each edge of Σ is generically either convex or concave, or exceptionally flat. It is then easy to see that if there is a fixed point q in the interior of an edge σ, then σ is convex (concave) if and only if q attracts (repels) along σ.

Van den Driessche and Zeeman show in [16] that for a three-dimensional competitive Lotka-Volterra system, if every species can resist invasion at carrying capacity, then all but one of the species will be driven to extinction, while if no species can resist invasion, there will be stable coexistence of all the species. In the case when all the species can resist invasion, each axial fixed point is an attractor. So each edge of Σ contains a fixed point repelling along that edge. Thus each edge of Σ is concave (Figure 3). Similarly, when no species can resist invasion, each edge of Σ is convex (Figure 2). The following questions remain open for three-dimensional competitive Lotka-Volterra systems that have a fixed point $p \in \operatorname{int} \mathbf{R}^3_+$:

Question 4.6. If all the edges of Σ are convex (concave), is Σ convex (concave)?

Question 4.7. If all the edges of Σ are convex (concave), does Σ lie to one side of $T_p\Sigma$?

In the case that there is no fixed point in $\operatorname{int} \mathbf{R}^3_+$, the answer to Question 4.6 is negative, as shown in [20, Counterexample 6.1]. The answer to both questions is negative in dimension four, as shown by the example of Hofbauer described in [16, Addendum].

In [20] we prove that for a competitive Lotka-Volterra system of dimension greater than two, the edges of Σ generically determine Σ. In particular, if all the edges are flat, then Σ is flat. Plank proves in [15] that when Σ is flat, system (1.1) admits a Hamiltonian structure on Σ. In [14] he classifies three-dimensional Lotka-Volterra systems that admit a bi-Hamiltonian representation. As a special case of these results, in Theorem 4.8 we use the split Liapunov function to show that when the carrying simplex of a three-dimensional competitive Lotka-Volterra system is flat, it is foliated by cycles.

Theorem 4.8. *In a three-dimensional competitive Lotka-Volterra system with a unique fixed point $p \in \operatorname{int} \mathbf{R}^3_+$, if Σ is flat, then it is filled with concentric closed orbits.*

Proof. Let $H = \Sigma$, and let V be the corresponding split Liapunov function. Then $\dot{V} = 0$ on Σ and so orbits on Σ lie on the level surfaces of V. But the latter cut $H = \Sigma$ in concentric closed curves, which must therefore be the orbits (see Figure 5). Therefore, all orbits are closed except for the fixed point p and the boundary $\partial\Sigma$. $\square$

Remark 4.9. By a similar argument, if p has a neighborhood in Σ that is flat, then p has a neighborhood in Σ that is filled with concentric closed periodic orbits.

Remark 4.10. In the special case of the circulant example of May and Leonard [9],

$$A = \begin{pmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{pmatrix}, \quad b = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix},$$

when $\alpha + \beta = 2$, the edges of Σ are flat, Σ is the standard unit simplex $\{x \in \mathbf{R}^3 : x_1 + x_2 + x_3 = 1\}$, and V reduces to $V = x_1x_2x_3$. So the split Liapunov function

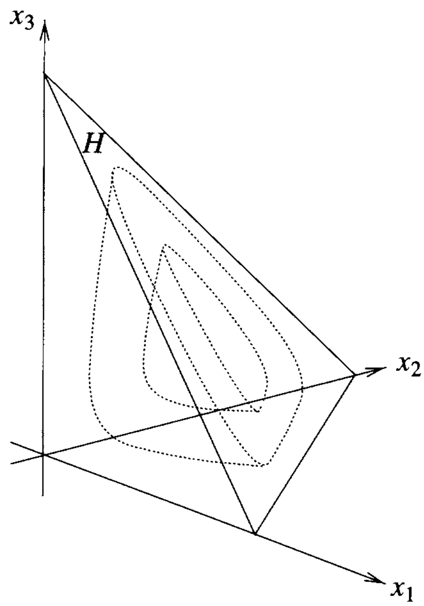

FIGURE 5. In $\mathbf{R}^3$ the level surfaces of V cut H in concentric closed curves.

can be viewed as a generalization of the method of May and Leonard. By contrast, when $\alpha + \beta \neq 2$, neither the edges of Σ nor Σ are flat. Thus the numerical results in [9] are misleading in that respect.

LaMar and Zeeman [7] have developed a program, *CSimplex*, as a module for interactive use with *Geomview* [8] to visualize the carrying simplex, nullclines, tangent plane at p, and orbits of a given three-dimensional competitive Lotka-Volterra system. Figures 1–3 and 8–10 in this paper were created using *Csimplex* and *Geomview*.

5. Algebraic Hypotheses

In this section we continue to exploit the quadratic structure of system (1.1), to give algebraic hypotheses from which the position of the carrying simplex Σ relative to $T_p\Sigma$ can be deduced, so that the Geometric Theorem can be applied.

As usual, consider the case when system (1.1) has a unique fixed point $p \in \operatorname{int} \mathbf{R}^n_+$, let H denote $T_p\Sigma$, and let h denote a strictly positive vector normal to H. Define $Q(x) = h^T\dot{x}$, which is proportional to the component of $\dot{x}$ normal to H.

Lemma 5.1. *Q is quadratic.*

The proof of Lemma 5.1 is immediate, as Q is the composition of linear maps (projection and scaling) with the quadratic map $\dot{x}$. Despite its simplicity, this lemma (originally introduced in [19]) is a powerful tool for linking algebraic and geometric properties of system (1.1). We show in Theorem 5.3 that if Q is definite on H, then $\Sigma \setminus \{p\}$ lies to one side of H, and hence the Geometric Theorem can be applied to deduce the global dynamics of system (1.1).

First we prove a technical lemma about the local implications of the definiteness of Q near p by temporarily switching to local coordinates at p. We appeal to these same local coordinates again in the proofs of Theorem 5.3 and Lemma 6.1.

Lemma 5.2. *Given the competitive system* (1.1) *with a unique fixed point* $p \in \operatorname{int}\mathbf{R}^n_+$, *let* h *be a strictly positive vector normal to* $H = T_P\Sigma$ *and let* $Q(x) = h^T\dot{x}$. *If* Q *is positive (negative) definite on* H, *then* $\exists$ *a neighborhood* N *of* p *such that if* $x \in N, x \neq p$, *and* x *lies on or below (above)* H, *then* $p \notin \alpha(x)$.

Proof. Without loss of generality, assume h is a unit vector, so that $Q(x)$ is simply the component of $\dot{x}$ normal to H. Consider the case when Q is positive definite on H. The case when Q is negative definite on H is proved similarly. A short computation shows that the linear approximation to system (1.1) at p is

$$\dot{x} = -\mathcal{P}Ax$$

where $\mathcal{P}$ is the diagonal matrix $(\operatorname{diag} p)$ with diagonal entries p_i. The matrix $\mathcal{P}A$ has strictly positive entries. So by the Perron-Frobenius theorem [6, Theorem 8.4.4], $-\mathcal{P}A$ has a simple negative eigenvalue $-\lambda$ corresponding to a strictly positive eigenvector v. The tangent space H to Σ at p is transverse to v (since H is balanced), contains all the other eigenvectors of $-\mathcal{P}A$, and is invariant under $-\mathcal{P}A$.

Now change to local coordinates $z_1, \dots, z_n$ at p, with respect to a basis $\{\beta_1, \dots, \beta_{n-1}, h\}$ of $\mathbf{R}^n$, such that $\beta_1, \dots, \beta_{n-1}$ span H. So H has equation $z_n = 0$, and v has coordinates $(v_1, \dots, v_n)$ where $v_n > 0$. The linear approximation to system (1.1) in the z coordinates is given by

$$\dot{z} = Cz,$$

for some matrix C. Note that if $z \in H$, then $Cz \in H$ by the invariance of H, and that $Cv = -\lambda v$. Hence C has the block form

$$C = \begin{pmatrix} D & u \\ 0 & -\lambda \end{pmatrix}$$

where D is $(n-1)\times(n-1)$, 0 is $1\times(n-1)$ and u is $(n-1)\times 1$. Thus the component of the linear approximation to system (1.1) in the h direction, normal to H, is

$$\dot{z_n} = -\lambda z_n. \tag{5.1}$$

The quadratic function Q is given by the component of the full Lotka-Volterra system normal to H. Thus Q is obtained by adding suitable quadratic terms to (5.1), and can be written as

$$Q(z) = \dot{z_n} = -\lambda z_n + \Lambda(z)z_n + \Pi(z)$$

where $\Lambda(z)$ is linear in $z_1, \dots, z_n$, and $\Pi(z)$ is a quadratic form in $z_1, \dots, z_{n-1}$. On H, $z_n = 0$, and so $Q(z) = \Pi(z)$. By hypothesis, Q is positive definite on H, and hence Π is positive definite.

Now choose $\mu, \epsilon > 0$ such that if $\|z\| < \epsilon$, then $|\Lambda(z)| < \lambda - \mu$, and let B be the ball in $\mathbf{R}^n$ given by $B = \{z \in \mathbf{R}^n : \|z\| < \epsilon\}$. For every $z \in B$ with $z_n \leq 0$ and $z \neq 0$, we have

$$\dot{z_n} = (-\lambda + \Lambda(z))z_n + \Pi(z) \geq -\mu z_n + \Pi(z) > 0,$$

and hence the z_n component of the backwards orbit of z decreases until the orbit crosses ∂B.

Let S be the $(n-2)$-sphere in H, center p, given by $S = \{z \in H : \|z\| = \frac{\epsilon}{2}\}$. By compactness of S, we can choose $\delta > 0$ such that for every $z \in S$, the backwards orbit of z crosses the plane $z_n = -\delta$ before it crosses ∂B. Finally, we flow S backwards to construct a neighborhood N_δ of p in $H \cup H_-$, from which all backwards orbits leave, never to return. In fact, N_δ is a tubular neighborhood of $W^{ss} \cap \{z : -\delta < z_n \leq 0\}$ in $H \cup H_-$, where W^{ss} denotes the one-dimensional strong stable manifold of p. See Figure 6.

More precisely, for each $\gamma \in [0, \delta)$ and each $z \in S$, let

$$\begin{aligned} z_\gamma &= \text{the point where the backwards orbit of } z \text{ meets the plane } z_n = -\gamma, \\ S_\gamma &= \{z_\gamma : z \in S\}, \text{ so } S_\gamma \text{ is an } (n-2)\text{-sphere in the plane } z_n = -\gamma, \\ D_\gamma &= \text{the open disc bounded by } S_\gamma \text{ in the plane } z_n = -\gamma, \\ N_\delta &= \bigcup_{\gamma \in [0,\delta)} D_\gamma. \end{aligned}$$

Now let $N = N_\delta \cup (B \cap H_+)$. Then if $x \in N$ and x lies on or below H, then $x \in N_\delta$. So the backwards orbit of x leaves N, stays in H_- since Q is positive definite on H, and hence never re-enters N. So $p \notin \alpha(x)$. □

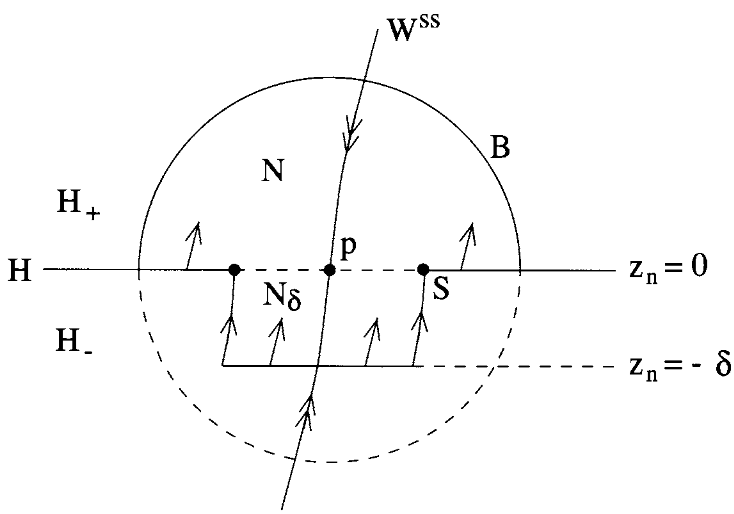

FIGURE 6. The neighborhood N of p

Theorem 5.3 (Algebraic Theorem). *Given the competitive system* (1.1) *with a unique fixed point* $p \in \operatorname{int} \mathbf{R}^n_+$, *let* h *be a strictly positive vector normal to* $H = T_P\Sigma$ *and let* $Q(x) = h^T\dot{x}$. *If* Q *is positive (negative) definite on* H, *then* p *is a global repellor (attractor).*

Proof. The positive definite and negative definite cases are proved similarly. We consider the case when Q is positive definite on H, as the need for the subtleties of Lemma 5.2 are clearer in this case (when p is, in fact, the α-limit set of orbits *on* Σ). We show by induction on the dimension of the faces of Σ, that each face lies above H. For the final induction step, we invoke Lemma 5.2 and the split Liapunov function to show that $\Sigma \setminus p$ lies above H. Thus p is globally repelling by Theorem 4.3.

First note that no fixed point in $\partial\Sigma$ can lie on H, since Q is positive on H except at p. To begin the induction, recall that the vertices r_i of Σ (the 0-dimensional faces) are the axial fixed points of system (1.1). Each r_i attracts along the positive x_i-axis, which consists of r_i together with two orbits: one running from 0 to r_i, the other running from ∞ to r_i. Thus r_i must lie above H; otherwise, Q would be negative at the point where the x_i-axis crosses H.

Now let $1 \leq k < n-1$ and assume, for induction, that every face of Σ of dimension less than k lies above H. Let $\mathbf{R}^{k+1}$ denote a $(k+1)$-dimensional coordinate subspace of $\mathbf{R}^n$; $\Sigma^k = \Sigma \cap \mathbf{R}_+^{k+1}$ the corresponding k-dimensional face of Σ; $H^k = H \cap \mathbf{R}_+^{k+1}$ the corresponding k-dimensional face of $H \cap \mathbf{R}_+^n$, and consider the restriction of system (1.1) to $\mathbf{R}^{k+1}$.

We show that if there is a fixed point $p^k \in \operatorname{int} \Sigma^k$, then p^k lies above H^k. By the Perron-Frobenius theorem and the (backwards time) monotonicity of system (1.1), p_k has a one-dimensional, totally ordered, strong stable manifold, W^{ss}, that crosses H^k exactly once. It consists of p^k together with two orbits: one running from 0 to p^k, the other running from ∞ to p^k. See Figure 7. Thus p^k must lie above H^k; otherwise, Q would be negative where W^{ss} crosses H^k. So all the fixed points in Σ^k lie above H^k.

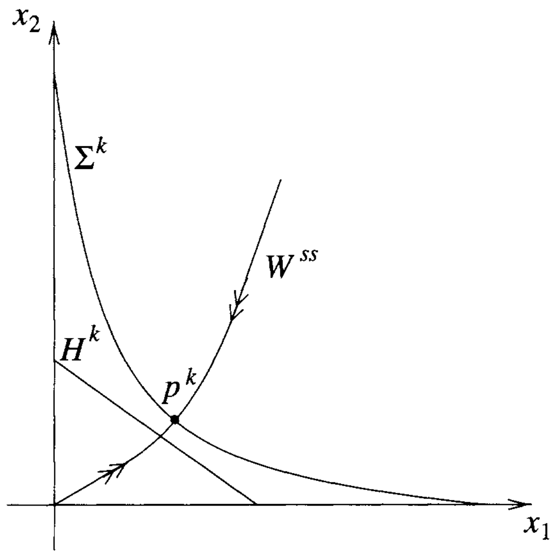

FIGURE 7. If Q is positive definite on H, then every fixed point $p^k \in \partial\mathbf{R}_+^n$ lies above H.

Now we show that Σ^k does not meet H^k, and hence lies above H^k. Suppose, for contradiction, that $\Sigma^k \cap H^k \neq \emptyset$, and let $M = \Sigma^k \cap H^k$. If $x \in M$, then the orbit through x lies in Σ^k, and is transverse to H^k since Q is positive at x. Therefore, Σ^k is transverse to H^k at all points of M, and so M is a $(k-1)$-manifold. By the induction hypothesis, $\partial\Sigma^k$ lies above H^k. So $M \cap \partial\Sigma = \emptyset$ and thus M is without boundary. Therefore M separates Σ^k into open components, at least one of which lies in H_-^k. Let C be such a component. Then $\overline{C}$ (the closure of C) is compact, and the flow on ∂C is outward from C along Σ^k, since $\partial C \subset M \subset H^k$, and Q is positive on H^k. Thus, if $x \in \overline{C}$, then $\alpha(x) \subset C$ and $\alpha(x)$ is compact and connected. We change temporarily to the local coordinates at p introduced in the proof of Lemma 5.2, where z_n represents the component of z in the positive direction normal to H. Let $z \in \alpha(x)$. Then $z_n < 0$ since $\alpha(x) \subset C \subset H_-$, and by the compactness of $\alpha(x)$,

$$\lim_{T \to -\infty} \frac{1}{T} \int_0^T z_n(t)dt < 0. \tag{5.2}$$

But the forward time average of a permanent orbit of an autonomous Lotka-Volterra system is a fixed point of the system [4, Theorem 5.2.3]. So by time reversal, and inequality (5.2), there is a fixed point of system (1.1) in H^k_-. This contradicts the fact that all the fixed points in Σ^k lie above H^k. Hence $\Sigma^k \cap H^k = \emptyset$, and every k-dimensional face of Σ lies above H.

So far we have proved that $\partial\Sigma$ lies above H. We now use Lemma 5.2 and the split Liapunov function to deduce that $\Sigma \setminus \{p\}$ lies above H. As before, we define $M = \Sigma \cap H$. This time $M \neq \emptyset$ since $p \in M$. Moreover, Σ is not transverse to H at p, since $H = T_p\Sigma$. We claim that $M = \{p\}$. Suppose, for contradiction, that $M \neq \{p\}$. For each $x \in M$, if $x \neq p$, then Σ is transverse to H at x, since Q is positive at x. Therefore, M is an $(n-2)$-manifold, except possibly at p. Let C be a component of $\Sigma \setminus M$ in H_-. Then p may be an isolated point in the interior of $\overline{C}$, or a singular point on ∂C. The flow on ∂C is outwards from C at all points of ∂C except possibly at p, where it is fixed. Thus if $x \in \overline{C} \setminus \{p\}$, then $\alpha\{x\} \subset C \cup \{p\}$. By Lemma 5.2, $p \notin \alpha\{x\}$ and so $\alpha\{x\} \subset C \setminus \{p\}$. But $C \setminus \{p\}$ contains no fixed points, because it lies in H_-. Hence $\alpha\{x\}$ contains a nontrivial recurrent orbit in H_-, contradicting the fact that V is monotone along orbits in H_-. Hence $M = \{p\}$, and $\Sigma \setminus \{p\}$ lies entirely above H.

Now we apply Theorem 4.3 to conclude that p is a global repellor. □

Remark 5.4. An ecological interpretation of Theorem 5.3 is that if Q is positive definite, so that Σ lies above H, then for almost every positive initial condition, at least one of the species is driven to extinction. If Q is negative definite, so that Σ lies below H, then any strictly positive initial condition will lead to stable coexistence of all the species at p.

Remark 5.5. Note that the time-averaging argument used in the proof of Theorem 5.3 could also have been used to prove Theorem 4.3. We chose to introduce the split Liapunov function instead, to emphasize the underlying geometry.

6. Computational Hypotheses

In this section we exploit the linear and quadratic structures of system (1.1) to develop an algorithm for checking the definiteness of $Q|_H$. In Theorem 6.7, we replace the algebraic hypotheses of Theorem 5.3 with this algorithm, so that testing the hypotheses becomes a simple matter of computation.

As usual, we assume that system (1.1) has a unique fixed point $p \in \operatorname{int} \mathbf{R}^n_+$ given by $p = A^{-1}b$, we let $H = T_p\Sigma$, and we let h be a strictly positive vector normal to H. For vectors h, p, x, y we use $\mathcal{H}, \mathcal{P}, \mathcal{X}, \mathcal{Y}$ to denote the diagonal matrices diag(h), diag(p), diag(x), diag(y) with diagonal entries h_i, p_i, x_i, y_i respectively. Then we rewrite system (1.1) as

$$\dot{x} = \mathcal{X}A(p - x). \tag{6.1}$$

Recall from the proof of Lemma 5.2, that the linear approximation to system (1.1) at p is given by $\dot{x} = -\mathcal{P}Ax$, and that by the Perron-Frobenius theorem, $-\mathcal{P}A$ has a simple negative eigenvalue $-\lambda$ with strictly positive eigenvector v. The following lemma slightly generalizes [6, Theorem 1.4.7], which states that left and right eigenvectors corresponding to distinct eigenvalues of a matrix are perpendicular.

Lemma 6.1. *h^T is a left eigenvector of $-\mathcal{P}A$ corresponding to eigenvalue $-\lambda$.*

Proof. We prove Lemma 6.1 by dipping back into the local coordinates $z_1, \ldots, z_n$ with respect to the basis $\{\beta_1, \ldots, \beta_{n-1}, h\}$ introduced in the proof of Lemma 5.2. Recall that in these coordinates, the linear approximation to system (1.1) at p is given by $\dot{z} = Cz$, where C has the block form

$$C = \begin{pmatrix} D & u \\ 0 & -\lambda \end{pmatrix}.$$

Thus

$$h^T C = (0, \ldots, 0, 1) \begin{pmatrix} D & u \\ 0 & -\lambda \end{pmatrix} = (0, \ldots, 0, -\lambda) = -\lambda h^T.$$

Therefore, h^T is a left eigenvector of C, and hence of $-\mathcal{P}A$, corresponding to eigenvalue $-\lambda$. □

Lemma 6.1 provides an algorithm for finding a positive vector h normal to H, by computing a positive left eigenvector of $-\mathcal{P}A$. Next we compute the corresponding quadratic function $Q = h^T\dot{x}$ by working in new local coordinates at p given by $y = x - p$.

In these coordinates,

$$\begin{aligned} \dot{y} &= \dot{x} \\ &= \mathcal{X}A(p - x), \text{ by equation (6.1)} \\ &= (\mathcal{P} + \mathcal{Y})A(-y) \\ &= -\mathcal{P}Ay - \mathcal{Y}Ay. \end{aligned}$$

So

$$\begin{aligned} Q(y) &= h^T\dot{y} \\ &= -h^T\mathcal{P}Ay - h^T\mathcal{Y}Ay \\ &= -\lambda h^T y - y^T\mathcal{H}Ay \end{aligned}$$

since h^T is a left eigenvector of $-\mathcal{P}A$ corresponding to eigenvalue $-\lambda$, and $h^T\mathcal{Y} = y^T\mathcal{H}$ by the diagonal structure of $\mathcal{H}$ and $\mathcal{Y}$.

Now choose $y \in H$. Then $h^T y = 0$. So on H,

$$\begin{aligned} Q(y) &= -y^T(\mathcal{H}A)y \\ &= -y^T(\mathcal{H}A)^S y \end{aligned}$$

where M^S denotes the symmetric matrix

$$M^S = \tfrac{1}{2}(M + M^T) \tag{6.2}$$

obtained from the real $n \times n$ matrix M. Therefore, Q is given by the quadratic form with matrix $-(\mathcal{H}A)^S$ on H, and we have proved:

Lemma 6.2. *Q is positive (negative) definite on H if and only if $(\mathcal{H}A)^S$ is negative (positive) definite on H.*

Lemma 6.2 provides an algorithm for computing Q on H. To test the definiteness of a quadratic form M on H, we *reduce* M as follows. Choose a basis $\{\beta_1, \dots, \beta_{n-1}\}$ for H. Let $y \in H$ and write $y = \sum_{i=1}^{n-1} y_i \beta_i$. Then

$$y^T M y = \sum_{i,j=1}^{n-1} y_i y_j (\beta_i^T M \beta_j).$$

Definition 6.3. Given an $n \times n$ matrix M and basis $\{\beta_1, \dots, \beta_{n-1}\}$ for H, let M^R denote the $(n-1)\times(n-1)$ reduced matrix given by $M^R = (m_{ij}^R) = (\beta_i^T M \beta_j)$, $i, j = 1, \dots, n-1$.

Example 6.4. If $h = (1, \dots, 1)^T$, then H is spanned by $\{\beta_1 = (1, -1, 0, \dots, 0)^T, \beta_2 = (0, 1, -1, 0, \dots, 0)^T, \dots, \beta_{n-1} = (0, \dots, 0, 1, -1)^T\}$, and a short computation shows that

$$m_{ij}^R = m_{ij} + m_{i+1,j+1} - m_{i+1,j} - m_{i,j+1} \quad \text{for all } 1 \le i, j \le n-1. \tag{6.3}$$

Thus

$$M^R = M_{nn} + M_{11} - M_{n1} - M_{1n} \tag{6.4}$$

where M_{ij} denotes the $(n-1) \times (n-1)$ submatrix of M obtained by deleting row i and column j from M.

Note that if M is symmetric, then M^R is also symmetric, and the next lemma follows immediately from a standard characterization of definite matrices. See [6, Section 7.2] for details.

Lemma 6.5. *A quadratic form with symmetric $n \times n$ matrix M is positive (negative) definite on H if and only if all the eigenvalues of M^R are positive (negative).*

The definiteness of M on H is independent of the choice of basis $\{\beta_1, \dots, \beta_{n-1}\}$ for H. In the following lemma, we fix that choice by making a diagonal change of coordinates with respect to which the basis and reduction equation (6.3) given in Example 6.4 can be used.

Lemma 6.6. *Q is positive (negative) definite on H if and only if all the eigenvalues of $(A\mathcal{H}^{-1})^{SR}$ are negative (positive), where $(A\mathcal{H}^{-1})^{SR}$ is given by equations* (6.2) *and* (6.4).

Proof. Given system (6.1), consider the change of coordinates

$$x' = Dx$$

where D is a diagonal matrix with strictly positive diagonal entries. It is easy to verify that

$$\dot{x}' = \mathcal{X}' A' (p' - x') \tag{6.5}$$

where $\mathcal{X}' = \operatorname{diag}(x')$, $A' = AD^{-1}$ and $p' = Dp$.

System (6.5) has carrying simplex Σ' with tangent hyperplane H' at p', and H' has normal vector $h' = D^{-1}h$. As in Lemma 6.1, h'^T is a left Perron-Frobenius eigenvector of $\mathcal{P}'A'$ corresponding to eigenvalue λ', and $\lambda' = \lambda$ since $\mathcal{P}'A' = D\mathcal{P}AD^{-1}$. On H' the quadratic form $h'^T\dot{x}'$ is given by

$$Q'(y') = -y'^T(\mathcal{H}'A')y'$$

where $y' = x' - p' = Dy$ and $\mathcal{H}' = \text{diag}(h')$; so $\mathcal{H}' = D^{-1}\mathcal{H}$. Therefore,

$$\begin{aligned} Q'(y') &= -(Dy)^T(D^{-1}\mathcal{H}AD^{-1})(Dy) \\ &= -y^T\mathcal{H}Ay \\ &= Q(y). \end{aligned}$$

Thus Q is invariant under the diagonal change of coordinates $x' = Dx$.

Now let $D = \mathcal{H}$ and consider the coordinate change

$$x' = \mathcal{H}x.$$

Then $A' = A\mathcal{H}^{-1}$, $h' = \mathcal{H}^{-1}h = (1, \ldots, 1)^T$, $\mathcal{H}' = I$ and

$$\begin{aligned} Q(y) &= Q'(y') \\ &= -y'^T(\mathcal{H}'A')y' \\ &= -y'^T(A\mathcal{H}^{-1})y' \\ &= -y'^T(A\mathcal{H}^{-1})^S y'. \end{aligned}$$

Thus Q is positive (negative) definite on H if and only if $(A\mathcal{H}^{-1})^S$ is negative (positive) definite on H'. But $h' = (1, \ldots, 1)^T$. So we can choose a basis $\{\beta'_1, \ldots, \beta'_{n-1}\}$ for H' as in Example 6.4 and, putting $M = (A\mathcal{H}^{-1})^S$, use the reduction equation (6.4) to compute $(A\mathcal{H}^{-1})^{SR}$. The result now follows from Lemma 6.5. □

The Computational Theorem below follows immediately from Lemma 6.6 and the Algebraic Theorem (Theorem 5.3).

Theorem 6.7 (Computational Theorem). *Given the competitive system* (1.1) *with a unique fixed point* $p = A^{-1}b \in \text{int}\,\mathbf{R}^n_+$, *let* $\mathcal{P} = \text{diag}(p)$, *let* h^T *be a strictly positive left eigenvector of* $\mathcal{P}A$ *and let* $\mathcal{H} = \text{diag}(h)$. *Define* $(A\mathcal{H}^{-1})^{SR}$ *by equations* (6.2) *and* (6.4). *If all the eigenvalues of* $(A\mathcal{H}^{-1})^{SR}$ *are negative (positive), then* p *is a global repellor (attractor).*

7. Examples

The computational hypotheses derived in Section 6 are reminiscent of the classical Volterra-Liapunov Stability Theorem stated below. See [4, Section 15.3] for more details and a proof.

Theorem 7.1 (Volterra-Liapunov Theorem). *If there exists a diagonal matrix* D *with positive diagonal entries such that* $(DA)^S$ *is positive definite, then system* (1.1) *has a globally stable fixed point.*

The two theorems are clearly different. The Volterra-Liapunov Theorem has the advantage that it does not require system (1.1) to be competitive, the result is independent of the choice of b, and the globally attracting fixed point need not be in $\text{int}\,\mathbf{R}^n_+$. The Computational Theorem has the advantage that it can also be applied to the case when p is globally repelling. In the case when system (1.1) is competitive and has an attracting fixed point $p \in \text{int}\,\mathbf{R}^n_+$, the differences are more subtle, and are illustrated by Examples 7.4 and 7.5 below. The Volterra-Liapunov

Theorem has the advantage that we are free to choose among diagonal matrices D, while the Computational Theorem has the advantage that we only need definiteness in $n-1$ dimensions. Example 7.4 satisfies the hypotheses of the Computational Theorem, but not those of the Volterra-Liapunov Theorem. By contrast, Example 7.5 satisfies the hypotheses of the Volterra-Liapunov Theorem, but not those of the Computational Theorem. Example 7.6 does not satisfy the hypotheses of either theorem, but p is locally attracting, and numerical simulations suggest that p is also globally attracting.

We will need the following lemmas:

Lemma 7.2. *For a real* 2×2 *matrix* M, $\det M^S \leq \det M$.

Proof. Let

$$M=\begin{pmatrix} a & b \\ c & d \end{pmatrix}.$$

Then

$$M^S=\begin{pmatrix} a & \frac{1}{2}(b+c) \\ \frac{1}{2}(b+c) & d \end{pmatrix}.$$

So

$$\begin{aligned} 4\det M - 4\det M^S &= 4ad-4bc-4ad+(b+c)^2 \\ &= (b-c)^2 \\ &\geq 0. \end{aligned}$$

Therefore, $\det M^S \leq \det M$. □

Lemma 7.3. *If a real* 3×3 *matrix* M *has a negative* 2×2 *principal minor, then there is no diagonal matrix* D*, with positive diagonal entries, such that* $(DM)^S$ *is positive definite.*

Proof. As usual, let M_{ij} denote the submatrix of M obtained by deleting row i and column j. To fix ideas, assume that $\det M_{33}<0$. Let

$$D=\begin{pmatrix} d_1 & 0 & 0 \\ 0 & d_2 & 0 \\ 0 & 0 & d_3 \end{pmatrix}, \quad \text{with } d_1,d_2,d_3>0.$$

Then

$$\begin{aligned} \det((DM)^S)_{33} &= \det((DM)_{33})^S \\ &\leq \det(DM)_{33}, \quad \text{by Lemma 7.2} \\ &= \det(D_{33}M_{33}) \\ &= d_1d_2\det M_{33} \\ &< 0. \end{aligned}$$

This contradicts the definiteness of $(DM)^S$. (See [6, Corollary 7.1.5] for details.) □

Example 7.4. Let

$$\dot{x}=\mathcal{X}(b-Ax)$$

where

$$b=\begin{pmatrix} 8 \\ 15 \\ 8 \end{pmatrix}, \quad A=\begin{pmatrix} 3 & 4 & 1 \\ 4 & 5 & 6 \\ 4 & 1 & 3 \end{pmatrix}, \quad \text{so } p=A^{-1}b=\begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}.$$

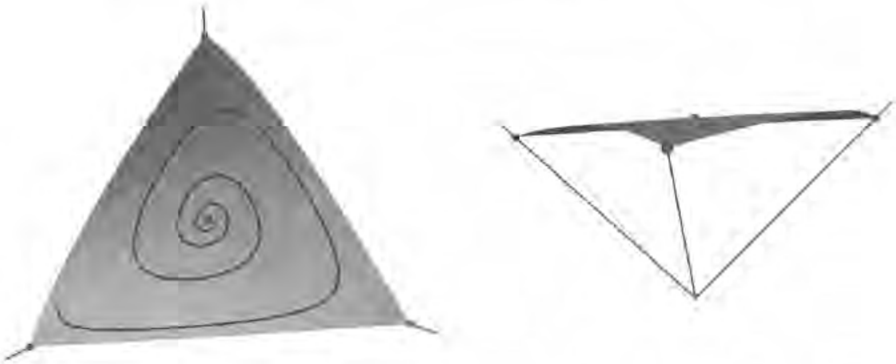

FIGURE 8. "Front" and "side" views of the Carrying Simplex of Example 7.4

Figure 8 shows a trajectory on the carrying simplex of Example 7.4, spiraling in to p. In the side view, the carrying simplex appears slightly convex; so we expect the Geometric (and hence Computational) Theorem to apply.

Example 7.4 satisfies the hypotheses of the Computational Theorem. We have $p = (1,1,1)^T$, and so $\mathcal{P} = I$ and $\mathcal{P}A = A$. Following the computational algorithm of Theorem 6.7 using Maple, we have (to two decimal places)

$$h = \begin{pmatrix} 1 \\ 0.93 \\ 0.9 \end{pmatrix}, \quad (A\mathcal{H}^{-1})^S = \begin{pmatrix} 3 & 4.16 & 2.56 \\ 4.16 & 5.4 & 3.88 \\ 2.56 & 3.88 & 3.34 \end{pmatrix},$$

and

$$(A\mathcal{H}^{-1})^{SR} = \begin{pmatrix} 0.08 & 0.08 \\ 0.08 & 0.98 \end{pmatrix}.$$

The leading principal minors of $(A\mathcal{H}^{-1})^{SR}$ are both positive. Hence $(A\mathcal{H}^{-1})^{SR}$ is positive definite (see [6, Theorem 7.2.5] for details), and p is global attracting by the Computational Theorem.

Example 7.4 does not satisfy the hypotheses of the Volterra-Liapunov Theorem. This follows immediately from Lemma 7.3, since $\det A_{33} = -1 < 0$.

Example 7.5. Let

$$\dot{x} = \mathcal{X}(b - Ax)$$

where

$$b = \begin{pmatrix} 11 \\ 9 \\ 10 \end{pmatrix}, \quad A = \begin{pmatrix} 3 & 6 & 1 \\ 1 & 3 & 3 \\ 3 & 1 & 3 \end{pmatrix}, \quad \text{so } p = A^{-1}b = \frac{1}{46}\begin{pmatrix} 63 \\ 40 \\ 77 \end{pmatrix}.$$

Figure 9 shows a trajectory on the carrying simplex of Example 7.5, spiraling in to p in the side view the carrying simplex appears to have negative curvature; so we do not expect the Geometric (or Computational) Theorem to apply.

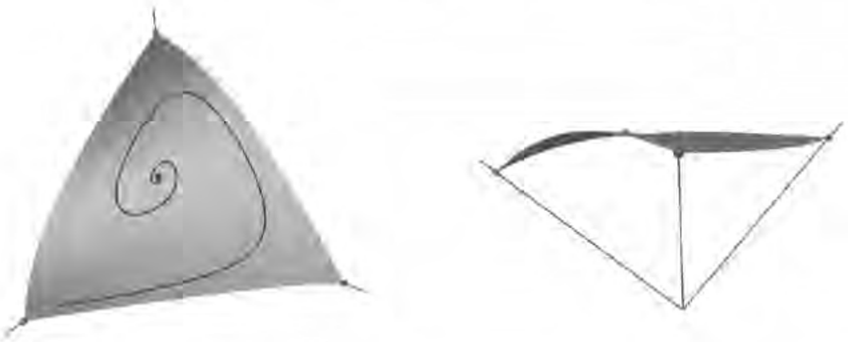

FIGURE 9. "Front" and "side" views of the Carrying Simplex of Example 7.5

Example 7.5 satisfies the hypotheses of the Volterra-Liapunov Theorem. Let

$$D = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 2 & 0 \\ 0 & 0 & 1 \end{pmatrix}, \text{ so } (DA)^S = \begin{pmatrix} 3 & 4 & 2 \\ 4 & 6 & 3.5 \\ 2 & 3.5 & 3 \end{pmatrix}.$$

The leading principal minors of $(DA)^S$ are all positive. Hence $(DA)^S$ is positive definite (by [6, Theorem 7.2.5]), and p is globally attracting by the Volterra-Liapunov Theorem.

Example 7.5 does not satisfy the hypotheses of the Computational Theorem. Following the computational algorithm using Maple, we have (to two decimal places)

$$\mathcal{P}A = \begin{pmatrix} 4.11 & 8.22 & 1.37 \\ 0.87 & 2.61 & 2.61 \\ 5.02 & 1.67 & 5.02 \end{pmatrix}, \quad h = \begin{pmatrix} 1 \\ 1.32 \\ 0.96 \end{pmatrix},$$

and

$$(A\mathcal{H}^{-1})^{SR} = \begin{pmatrix} -0.28 & 0.43 \\ 0.43 & 1.52 \end{pmatrix}.$$

Thus $\det(A\mathcal{H}^{-1})^{SR} < 0$, so $(A\mathcal{H}^{-1})^{SR}$ is not definite, and the Computational Theorem does not apply.

Example 7.6. Let

$$\dot{x} = \mathcal{X}(b - Ax)$$

where

$$b = \begin{pmatrix} 17 \\ 22 \\ 20 \end{pmatrix}, \quad A = \begin{pmatrix} 5 & 10 & 2 \\ 4 & 7 & 11 \\ 10 & 2 & 8 \end{pmatrix}, \quad \text{so } p = A^{-1}b = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}.$$

Figure 10 shows a trajectory on the carrying simplex of Example 7.6, spiraling in to p. Again, the carrying simplex appears to have negative curvature and so we do not expect the Geometric (or Computational) Theorem to apply.

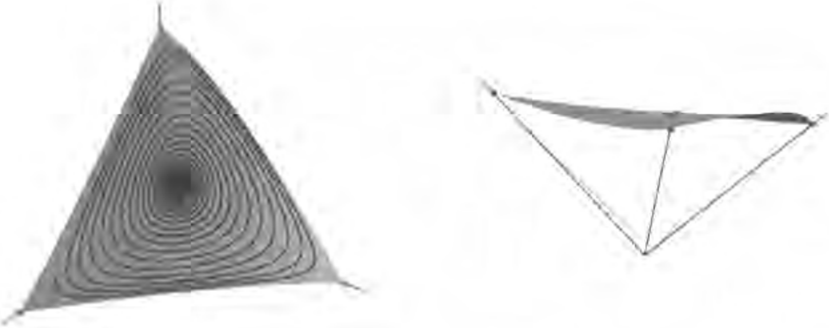

FIGURE 10. "Front" and "side" views of the Carrying Simplex of Example 7.6

Example 7.6 does not satisfy the hypotheses of the Computational Theorem. We have $p = (1,1,1)^T$, and so $\mathcal{P} = I$ and $\mathcal{P}A = A$. Using Maple, we find (to two decimal places)

$$h = \begin{pmatrix} 1.04 \\ 1 \\ 1.12 \end{pmatrix} \text{ and } (A\mathcal{H}^{-1})^{SR} = \begin{pmatrix} -2.04 & 0.12 \\ 0.12 & 2.33 \end{pmatrix}.$$

Thus $\det(A\mathcal{H}^{-1})^{SR} < 0$, so $(A\mathcal{H}^{-1})^{SR}$ has a negative eigenvalue, and the Computational Theorem does not apply.

Example 7.6 does not satisfy the hypotheses of the Volterra-Liapunov Theorem. Again, this follows from Lemma 7.3, since $\det A_{33} = -5 < 0$.

Meanwhile the eigenvalues of $-A$ are $-19.65, -0.18 \pm 6.48i$, and so p is a spiral attractor on Σ. We conjecture that in fact p is a global attractor.

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