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EXTINCTION IN COMPETITIVE LOTKA-VOLTERRA SYSTEMS

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ABSTRACT. It is well known that for the two species autonomous competitive Lotka-Volterra model with no fixed point in the open positive quadrant, one of the species is driven to extinction, whilst the other population stabilises at its own carrying capacity. In this paper we prove a generalisation of this result to arbitrary finite dimension. That is, for the n-species autonomous competitive Lotka-Volterra model, we exhibit simple algebraic criteria on the parameters which guarantee that all but one of the species is driven to extinction, whilst the one remaining population stabilises at its own carrying capacity.

1. INTRODUCTION

Consider a community of n mutually competing species modeled by the autonomous Lotka-Volterra system

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

where x_i is the population size of the ith species at time t, and $\dot{x}_i$ denotes $\frac{dx_i}{dt}$.

Each k-dimensional coordinate subspace of $\mathbb{R}^n$ is invariant under system (1) ($k \in \{1, \dots, n\}$), and we adopt the tradition of restricting attention to the closed positive cone $\mathbb{R}^n_+$. We denote the open positive cone by $\overset{\circ}{\mathbb{R}}{}^n_+$.

The mutual competition between the species dictates that $a_{ij} > 0$ for all $i \neq j$. In addition we assume throughout that, for each i, $b_i > 0$ and $a_{ii} > 0$, meaning that each species, in isolation, would exhibit logistic growth. That is, when we consider system (1) restricted to the ith coordinate axis, we have

$$\dot{x}_i = x_i(b_i - a_{ii}x_i), \qquad b_i,\ a_{ii} > 0,$$

in which the repulsion at 0 (growth of small populations) and the repulsion at ∞ (competition within large populations) balance at an attracting fixed point, R_i, at the *carrying capacity* $\frac{b_i}{a_{ii}}$. Note that the invariance of the axes ensures that R_i is also fixed by the full n-dimensional system. We call R_i the ith *axial fixed point* of (1).

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It is well known that for the two-species competitive Lotka-Volterra model with no fixed point in the open positive cone $\overset{\circ}{\mathbb{R}}{}^2_+$, one of the species is driven to extinction, whilst the other population stabilises at its own carrying capacity. In other words, one of the axial fixed points is a saddle, whilst the other is the unique global attractor for $\overset{\circ}{\mathbb{R}}{}^2_+$.

There are many directions in which to consider generalisations of this result. For example, Ahmad [2] proves an analogous result for nonautonomous two-dimensional competitive Lotka-Volterra systems. In this paper we prove a generalisation to autonomous competitive Lotka-Volterra systems of arbitrary finite dimension (Theorem 2.1). That is, we exhibit simple algebraic criteria on the parameters which guarantee that all but one of the species is driven to extinction, whilst the one remaining population stabilises at its own carrying capacity.

2. Statement of result

Theorem 2.1. *If system* (1) *satisfies the inequalities*

$$\frac{b_j}{a_{jj}} < \frac{b_i}{a_{ij}} \quad \forall i < j, \quad \text{and} \quad \frac{b_j}{a_{jj}} > \frac{b_i}{a_{ij}} \quad \forall i > j, \tag{2}$$

then the axial fixed point

$$R_1 = \left(\frac{b_1}{a_{11}}, 0, \dots, 0\right)$$

is globally attracting on $\overset{\circ}{\mathbb{R}}{}^n_+$.

In other words, for all strictly positive initial conditions, species $x_2, \dots, x_n$ are driven to extinction, whilst species x_1 stabilises at its own carrying capacity. Allowing for relabeling of the axes, we have:

Corollary 2.2. *If there is a permutation ϕ of the indices $\{1, \dots, n\}$, after which system* (1) *satisfies inequalities* (2), *then $R_{\phi^{-1}(1)}$ is globally attracting on $\overset{\circ}{\mathbb{R}}{}^n_+$ under the original system.*

3. Two dimensions

We begin by discussing the special case of two dimensions, to illuminate the ideas behind the proof of Theorem 2.1.

When $n = 2$, inequalities (2) reduce to

$$\frac{b_2}{a_{22}} < \frac{b_1}{a_{12}} \quad \text{and} \quad \frac{b_1}{a_{11}} > \frac{b_2}{a_{21}}. \tag{3}$$

It is well known that this corresponds to the case mentioned in the introduction, in which R_1 is globally attracting on $\overset{\circ}{\mathbb{R}}{}^2_+$. The classical way to see this is by a geometric analysis of the nullclines of the system: the sets on which one component of the vector field vanishes. The x_1 nullcline is given by

$$\dot{x_1} = 0 \Leftrightarrow x_1(b_1 - a_{11}x_1 - a_{12}x_2) = 0 \Leftrightarrow \begin{cases} x_1 = 0 \\ \text{or } a_{11}x_1 + a_{12}x_2 = b_1 \end{cases}$$

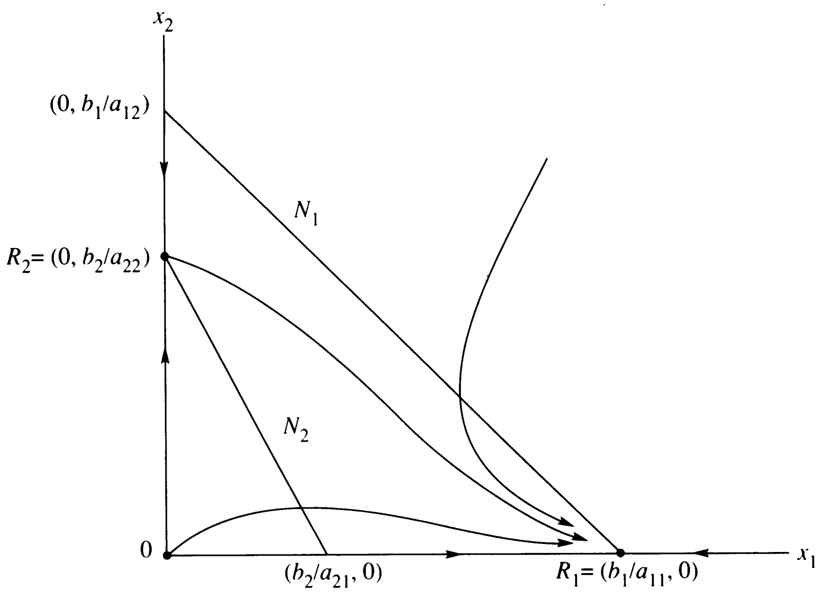

FIGURE 1. The nullclines and dynamics in two dimensions. Each fixed point is represented by a closed dot $\bullet$.

and so consists of the x_2-axis together with the line N_1 which has axial intercepts $R_1 = (\frac{b_1}{a_{11}}, 0)$ and $(0, \frac{b_1}{a_{12}})$. Similarly, the x_2 nullcline consists of the x_1-axis together with the line N_2 with axial intercepts

$$\left(\frac{b_2}{a_{21}}, 0\right) \quad \text{and} \quad R_2 = \left(0, \frac{b_2}{a_{22}}\right).$$

See Figure 1.

The fixed points of the system lie at the intersections of the two nullclines. Generically, there are four such intersections. They are at 0, R_1, R_2, and the point $N_1 \cap N_2$. Now, inequalities (3) provide information about the geometric configuration of the N_i via the axial intercepts. More precisely, the inequalities ensure that on each axis the N_2 intercept is smaller than the N_1 intercept, so that $N_1 \cap N_2 \not\subset \mathbb{R}^2_+$. See Figure 1. With this fixed point information there are plenty of elementary arguments with which to verify that R_1 is indeed globally attracting on $\overset{\circ}{\mathbb{R}}{}^2_+$. See May [7], Hofbauer and Sigmund [6], Zeeman [9], or apply the Liapunov function of Theorem 5.1.

In summary, inequalities (3) were translated into nonintersection properties of the nullclines, from which the dynamical result followed. Inequalities (2) generalise these geometric nonintersection properties to higher dimensions, and we shall adopt the same nullcline viewpoint to prove Theorem 2.1.

First some preliminaries.

4. THE CARRYING SIMPLEX

It is easy to see that 0 is a repelling fixed point of system (1), and that the basin of repulsion of 0 in $\mathbb{R}^n_+$ is bounded. We denote by Σ the boundary of that basin. To be precise, we define $B(0) = \{x \in \mathbb{R}^n_+ : \alpha(x) = 0\}$, and $\Sigma = \partial B(0) \setminus B(0)$, where $\alpha(x)$ denotes the *alpha*-limit set of the trajectory through x and $\partial B(0)$ denotes the boundary of $B(0)$ taken in $\mathbb{R}^n_+$. We remove $B(0)$ from $\partial B(0)$ to avoid topological awkwardness at the coordinate subspaces. The *unit simplex* in $\mathbb{R}^n_+$ has the standard meaning of $U \cap \mathbb{R}^n_+$, where U denotes the hyperplane with equation

$$\sum_{i=1}^{n} x_i = 1.$$

Applying a theorem of M. W. Hirsch [5, Theorem 1.7], we have:

Theorem 4.1 (Hirsch). *Given system* (1), *every trajectory in* $\mathbb{R}^n_+ \setminus \{0\}$ *is asymptotic to one in* Σ, *and* Σ *is a Lipschitz submanifold homeomorphic to the unit simplex in* $\mathbb{R}^n_+$ *by radial projection.*

Remarks. This theorem generalises the idea of the carrying capacity of the single species equation. The growth of small populations and the competition between large populations balance at the hypersurface Σ, which we call the *carrying simplex.* All the nonzero ω-limit sets of system (1) lie in Σ, and in particular Σ meets the x_j-axis precisely at the axial fixed point R_j.

It should be noted that the carrying simplex is not just Lipschitz. Recent results of Brunovski [3] and Mierczynski [8] show that under mild restrictions, it is at least C^1.

5. A Liapunov function

We shall make use of the Liapunov function given in the following theorem. For details and a proof, see Hofbauer and Sigmund [6, §9.2].

Theorem 5.1. *If system* (1) *has no fixed point in* $\overset{\circ}{\mathbb{R}}{}^n_+$, *then there is a vector* $c = (c_1, \dots, c_n) \in \mathbb{R}^n$, *such that the function*

$$V = \prod_{i=1}^{n} x_i^{c_i}$$

is a strict Liapunov function for system (1) *on* $\overset{\circ}{\mathbb{R}}{}^n_+$.

Remarks. By a *strict* Liapunov function, we mean that V is strictly monotone (increasing, in this case) along orbits of system (1) in $\overset{\circ}{\mathbb{R}}{}^n_+$. Thus the system has no limit points in $\overset{\circ}{\mathbb{R}}{}^n_+$, and all nonzero trajectories must be asymptotic to a trajectory in $\partial\Sigma$. That is, all trajectories in $\overset{\circ}{\mathbb{R}}{}^n_+$ must approach the coordinate subspaces.

Note that to simplify the differentiation, it is convenient to require that $c_i \neq -1$ for each i. This condition is easy to satisfy by a scaling of c if necessary.

Note also that V may not give dynamical information about the flow on the coordinate subspaces of $\mathbb{R}^n$. Indeed, on each coordinate subspace H, the function V could be either undefined, or constant, depending on the signs of the c_i. However, system (1) restricted to H is a competitive Lotka-Volterra system of lower dimension, to which we can reapply Theorem 5.1, and thus find a (different) Liapunov function defined on $\overset{\circ}{H}_+$.

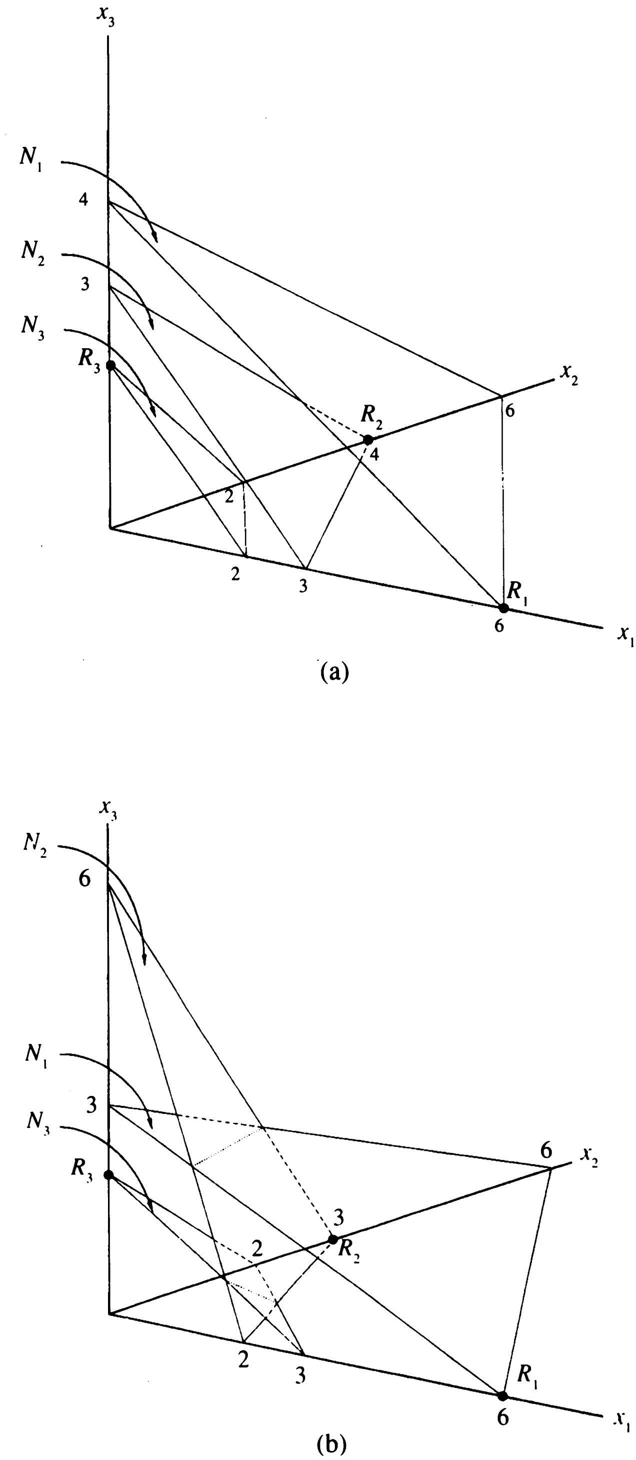

FIGURE 2. The nullclines of systems (4)(a) and (4)(b). Each fixed point is represented by a closed dot $\bullet$.

6. Three dimensions

The proof of Theorem 2.1 (below) uses geometric properties of the nullclines of system (1) in arbitrary dimensions. Figure 2 shows the nullclines of the following two examples of three-dimensional competitive Lotka-Volterra systems:

(4)

$$\text{(a)} \begin{cases} \dot{x_1} = x_1(12 - 2x_1 - 2x_2 - 3x_3) \\ \dot{x_2} = x_2(12 - 4x_1 - 3x_2 - 4x_3) \\ \dot{x_3} = x_3(12 - 6x_1 - 6x_2 - 6x_3) \end{cases} \qquad \text{(b)} \begin{cases} \dot{x_1} = x_1(6 - x_1 - x_2 - 2x_3) \\ \dot{x_2} = x_2(6 - 3x_1 - 2x_2 - x_3) \\ \dot{x_3} = x_3(6 - 2x_1 - 3x_2 - 3x_3) \end{cases}$$

It is easy to verify that both of these systems satisfy inequalities (2). Thus by Theorem 2.1, R_1 is globally attracting on $\overset{\circ}{\mathbb{R}}{}^3_+$ in both cases.

From Figure 2(a), we can see that the nullclines of system (4)(a) are disjoint, thus generalising the two-dimensional picture (Figure 2) in a simple way. By contrast, Figure 2(b) shows that the nullclines do not have to be disjoint for inequalities (2) to be satisfied.

The proof of Theorem 2.1 involves a close inspection of how particular nullclines can intersect. The combination of that analysis and these three-dimensional examples builds intuition for the potential complexity of the nullcline intersections of high-dimensional systems satisfying inequalities (2).

We return to these examples, and discuss related questions, after the proof of Theorem 2.1.

7. Proof of Theorem 2.1

To prove Theorem 2.1, we interpret inequalities (2) as geometric properties of the nullclines of the system. We then use the geometric analysis developed in [9] to determine the dynamical behaviour at the axial fixed points R_i (Lemma 7.1), and to show that the system has no other fixed points (Lemmas 7.2 and 7.3). The result then follows from successive applications of Theorem 4.1, and the appropriate Liapunov functions (Theorem 5.1).

We shall need the following notation: for $k \in \{2, \dots, n\}$, let $H_{i_1,\dots,i_k}$ denote the k-dimensional coordinate subspace of $\mathbb{R}^n$ corresponding to the coordinates $x_{i_1}, \dots, x_{i_k}$. To simplify notation and fix our ideas, let $H^k = H_{1,\dots,k}$. That is, H^k denotes the k-dimensional subspace on which $x_{k+1}, \dots, x_n$ all vanish. As usual, H^k_+ and $\overset{\circ}{H}{}^k_+$ denote respectively the closed and open positive cones in H^k.

Lemma 7.1. *If system* (1) *satisfies inequalities* (2), *then each axial fixed point* R_j *is a hyperbolic fixed point with a stable manifold of dimension* $n - j + 1$ *contained in the coordinate subspace* $H_{j,\dots,n}$, *and an unstable manifold of dimension* $j - 1$.

Proof. The x_j-axis is an eigenspace of DF_{R_j}, along which R_j attracts, since R_j is at the carrying capacity of species x_j. The invariance of the two-dimensional coordinate planes guarantees that the other $n - 1$ eigenvectors of DF_{R_j} lie one in each of the coordinate planes containing the x_j-axis. Using the geometric analysis described in [9], we can deduce the dynamical behaviour in each eigendirection as follows.

The ith nullcline of the system is the coordinate hyperplane $x_i = 0$ together with the hyperplane N_i with equation $\sum_{j=1}^{n} a_{ij}x_j = b_i$. Note that N_i meets the x_j-axis at the value $x_j = \frac{b_i}{a_{ij}}$, and that N_j meets the x_j-axis at R_j. Thus inequalities (2) tell us the position of each axial fixed point R_j amongst all the other intercepts of the nullclines N_i with the x_j-axis. For each $i < j$, $\frac{b_j}{a_{jj}} < \frac{b_i}{a_{ij}}$. Thus R_j lies in the bounded component of $\mathbb{R}^n_+ \setminus N_i$, and hence R_j repels along the eigendirection in the (i, j) coordinate plane. Similarly, for each $i > j$, $\frac{b_j}{a_{jj}} > \frac{b_i}{a_{ij}}$; so R_j lies in the unbounded component of $\mathbb{R}^n_+ \setminus N_i$, and hence attracts along the eigendirection in the (i, j) coordinate plane. Q.E.D.

Lemma 7.2. *Let $k \in \{2, \dots, n\}$. If system* (1) *satisfies inequalities* (2), *then there is no fixed point in* $\overset{\circ}{H^k_+}$.

Proof. Any fixed point of the system lies at an intersection of all n nullclines. Generically there are 2^n of these fixed points, one in each coordinate subspace of $\mathbb{R}^n$ (with the lower-dimensional coordinate subspaces removed). In particular, since $x_{k+1}, \dots, x_n$ vanish on H^k, the set of fixed points in $\overset{\circ}{H^k_+}$ is given by $N_1 \cap \dots \cap N_k \cap \overset{\circ}{H^k_+}$. We shall show that this set is empty, meaning that any fixed point in H^k either lies outside $\mathbb{R}^n_+$, or lies in a lower-dimensional subspace of H^k.

Fix $j \in \{1, \dots, k\}$. As mentioned in the proof of Lemma 7.1, inequalities (2) tell us the position of the axial fixed point R_j amongst all the other intercepts of the nullclines N_i with the x_j-axis. In particular, in the special cases of $i = 1$ (so $i \le j$) and $i = k$ (so $i \ge j$), we have

$$\frac{b_1}{a_{1j}} \ge \frac{b_j}{a_{jj}} \ge \frac{b_k}{a_{kj}}$$

where at most one equality holds (the first when $j = 1$, the second when $j = k$), and hence

$$\frac{b_1}{a_{1j}} > \frac{b_k}{a_{kj}}.$$

So on the x_j-axis, the N_1 intercept is positive and strictly greater than the N_k intercept. This holds for every coordinate axis in H_k, so the hyperplanes N_1 and N_k do not meet in $\overset{\circ}{H^k_+}$. Thus $N_1 \cap \dots \cap N_k \cap \overset{\circ}{H^k_+} = \varnothing$. Q.E.D.

Lemma 7.3. *Let $k \in \{2, \dots, n\}$, and choose distinct $i_1, \dots, i_k \in \{1, \dots, n\}$. If system* (1) *satisfies inequalities* (2), *then there is no fixed point in* $(\overset{\circ}{H}_{i_1, \dots, i_k})_+$.

Proof. This is simply a generalisation of Lemma 7.2, and is proved the same way. Without loss of generality, we may assume that $i_1 < \dots < i_k$. Fix $j \in \{i_1, \dots, i_k\}$; then in the special cases of $i = i_1$ (so $i \le j$) and $i = i_k$ (so $i \ge j$), inequalities (2) ensure that

$$\frac{b_{i_1}}{a_{i_1 j}} > \frac{b_{i_k}}{a_{i_k j}}.$$

Thus N_{i_1} and N_{i_k} do not meet in $(H_{i_1,\dots,i_k})_+$ and

$$N_1 \cap \cdots \cap N_k \cap (\overset{\circ}{H}_{i_1,\dots,i_k})_+ = \varnothing. \quad \text{Q.E.D.}$$

Combining Lemmas 7.1 and 7.3 we have:

Corollary 7.4. *If system* (1) *satisfies inequalities* (2), *then every fixed point of the system lies on an axis, and* R_1 *is the only attracting fixed point.*

Proof of Theorem 2.1. Let system (1) satisfy inequalities (2). By Lemma 7.2 (with $k = n$), there is no fixed point in $\overset{\circ}{\mathbb{R}}{}^n_+$, and hence by Theorems 4.1 and 5.1 every trajectory in $\overset{\circ}{\mathbb{R}}{}^n_+$ is asymptotic to one in $\partial\Sigma$, which is contained in the coordinate subspaces of $\mathbb{R}^n$.

Now we can inductively apply the same argument to each of the k-dimensional coordinate subspaces of $\mathbb{R}^n$, letting k decrease from $n-1$ to 2. We thus conclude that every trajectory in $\mathbb{R}^n_+$ is asymptotic to a trajectory contained in the coordinate axes. That is, every trajectory in $\mathbb{R}^n_+ \setminus \{0\}$ converges to one of the axial fixed points R_j. By Lemma 7.1 and Corollary 7.4, R_1 is therefore globally attracting on $\overset{\circ}{\mathbb{R}}{}^n_+$. Q.E.D.

8. Examples and further questions

The examples of systems (4)(a) and (4)(b) both satisfy inequalities (2), so that R_1 is globally attracting on $\overset{\circ}{\mathbb{R}}{}^3_+$ in both cases. For a more complete understanding of the global dynamics of these systems, recall from Theorem 4.1 that every trajectory in $\mathbb{R}^3_+ \setminus \{0\}$ is asymptotic to one in the carrying simplex Σ, so the dynamics on Σ dictate the global dynamics on $\mathbb{R}^3_+$. Moreover, the dynamics on Σ can be viewed as dynamics on the unit simplex (also by Theorem 4.1), which we remove from the ambient $\mathbb{R}^3_+$, and picture in Figure 3 as an equilateral triangle. The location and dynamical type of each fixed point follows from Lemmas 7.1–7.3. The fixed point notation used is described in the figure caption.

In [9] the author made a partial classification of three-dimensional competitive Lotka-Volterra systems, using techniques of nullcline analysis similar to those used in this paper. The examples described here illustrate that in the case of three-dimensions, inequalities (2) characterise nullcline class 1 of the classification in [9]. That classification also shows that the result in this paper is not sharp: nullcline classes 2, 3, 7, and 8 also consist of systems for which one of the R_i is a global attractor on $\overset{\circ}{\mathbb{R}}{}^3_+$. See Figure 4. On the other hand, nullcline classes 4, 5, 6, and 9–12 all consist of systems for which there is a globally attracting fixed point in the strictly positive cone of one of the two-dimensional coordinate planes of $\mathbb{R}^3$, thus corresponding to the survival of precisely two of the species, and extinction of the other. See Figure 4.

These facts naturally suggest the following problems:

1. Generalise inequalities (2) to include nullcline classes 2, 3, 7, and 8.
2. Find analogous algebraic criteria that characterise the survival of precisely two species; or others that characterise the extinction of precisely one species.

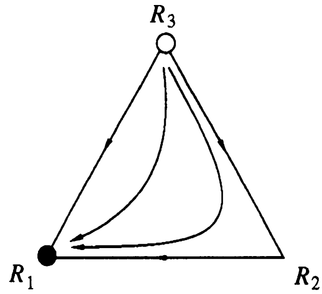

FIGURE 3. The dynamics on the carrying simplex Σ of systems (4)(a) and 4)(b). A fixed point is represented by a closed dot $\bullet$ if it attracts, by an open dot $\circ$ if it repels, and by the intersection of its hyperbolic manifolds if it is a saddle.

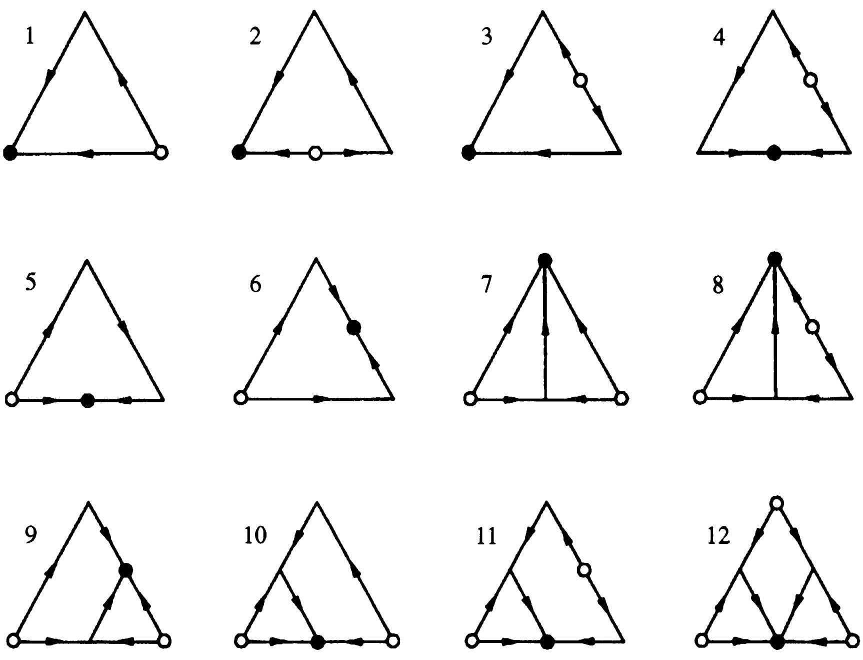

FIGURE 4. The dynamics on Σ of the nullcline classes for which a fixed point on $\partial\Sigma$ is globally attracting on $\overset{\circ}{\mathbb{R}}{}^3_+$. Fixed point notation as in Figure 3.

3. In [4], Hallam et al. use similar geometric methods to give criteria, in terms of pairwise interactions, for the persistence or extinction of species in autonomous three-dimensional competitive Lotka-Volterra systems. Generalise these ideas to arbitrary finite dimension.

4. Following the work of Ahmad [1] and [2], generalise Theorem 2.1 to nonautonomous Lotka-Volterra systems.

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