Geometry of carrying simplices of 3-species competitive Lotka-Volterra systems

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Abstract. We investigate the existence, uniqueness and Gaussian curvature of the invariant carrying simplices of 3 species autonomous totally competitive Lotka-Volterra systems. Explicit examples are given where the carrying simplex is convex or concave, but also where the curvature is not single-signed. Our method monitors the curvature of an evolving surface that converges uniformly to the carrying simplex, and generally relies on establishing that the Gaussian image of the evolving surface is confined to an invariant cone. We also discuss the relationship between the curvature of the carrying simplex near an interior fixed point and its Split Lyapunov stability. Finally we comment on extensions to general Lotka-Volterra systems that are not competitive.
1. Introduction

The Lotka-Volterra equations were introduced by Lotka and Volterra in the early 1920s to study populations of interacting species. For 3 species we will write them in the form

$$\dot{x}_i = x_i (b_i - (A x)_i) = F_i(x), \ i \in I_3,$$

where $b \in \mathbb{R}^3$, $A \in \mathbb{R}^{3 \times 3}$, and $I_n = \{1, 2, \ldots, n\}$. We restrict to the case $b_i > 0$, so that the origin $O$ is a repeller and normalize so that $a_{ii} = b_i$. This normalization means that there are axial fixed points $e_1 = (1, 0, 0)^T$, $e_2 = (0, 1, 0)^T$ and $e_3 = (0, 0, 1)^T$. The system (1) is mainly studied in the context of population dynamics, so phase space is the nonnegative cone $C = \mathbb{R}^3_+$, where $\mathbb{R}^+ = [0, \infty)$.

We will use the standard notation for ordering of vectors in $\mathbb{R}^n$: For $x, y \in \mathbb{R}^n$, $x \geq y \iff x - y \in C$, $x > y$ if $x \geq y$ and $x \neq y$, and $x \gg y \iff x - y \in C^0$, the interior of $C$. Similar orderings are defined for real $n \times m$ matrices by considering them as elements of $\mathbb{R}^{nm}$.

We will be particularly interested in the asymmetric May-Leonard system [5] which is a generalisation of the system studied by May and Leonard [18] and takes the form

$$\begin{align*}
\dot{x}_1 &= x_1 (1 - x_1 - a_{12} x_2 - a_{13} x_3) \\
\dot{x}_2 &= x_2 (1 - x_2 - a_{21} x_1 - a_{23} x_3) \\
\dot{x}_3 &= x_3 (1 - x_3 - a_{31} x_1 - a_{32} x_2)
\end{align*}$$

(2)

where each $a_{ij} > 0$. As we shall see the special form ($b_i = a_{ii} = 1$, $i \in I_3$) is particularly suitable for the methods that we develop here, and many of the examples that we present will be for May-Leonard systems of the form (2).

In the case where $A \gg 0$, so that the system (1) is totally competitive, one of the most striking observations is that $C$ contains a unique two-dimensional, compact invariant Lipschitz manifold $\Sigma$ known as the carrying simplex that contains all nontrivial limit sets of (1). As shown by Hirsch [8] this carrying simplex is a feature of all totally competitive Kolmogorov systems. More recently, Liang and Jiang [16, 17] have extended Hirsch’s results to type-K competitive systems (see below for definitions).

The purpose of this paper is to study the geometry of carrying simplices for 3-species Lotka-Volterra equations and how it relates to the stability of fixed points.

Figure 1 offers motivation for this study. It shows three examples of carrying simplices for totally competitive Lotka-Volterra systems. Here the carrying simplices are each graphs of functions defined on compact subsets of $\mathbb{R}^2_+ = \{x \in \mathbb{R}^2 : x_i \geq 0, i \in I_2\}$. Moreover, at the resolution of these figures, it appears that the Gaussian curvature of each surface does not change sign. We will show here that while in many cases the curvature does have a single sign, this is not always the case. Examples are given where the carrying simplex is convex or concave, and also where for the same carrying simplex there are regions of $\Sigma^0$, the relative interior of $\Sigma$ in $C$, where the curvature is of different sign. Computations are also presented for cases where the carrying simplex appears to be saddle-like. (See below for a definition of convex, concave and saddle-like carrying simplices). It is known that for planar Lotka-Volterra systems, the carrying simplex is either concave, convex or a straight-line [30, 2].

Also hinted at by the figures, together with simulations for many other sets of parameters, is a possible relation between curvature of $\Sigma$ and stability of the interior fixed point when it exists. When $\Sigma^0$ is $C^2$ we will show by utilising the Split Liapunov method...
Geometry of carrying simplices

Figure 1. Examples of the computed carrying simplex for competitive 3 dimensional Lotka-Volterra equations together with selected interior orbits to indicate stability of fixed points. From left to right the carrying simplex appears to be (i) concave, (ii) convex and (iii) saddle-like. Parameters \( b, A \) are: (i) \( \left( 0.5, 0.7, 0.5 \right), \left( 0.5, 1, 1.5 \right) \), (ii) \( \left( 2.5, 1.7 \right), \left( 2.5, 1, 1.5 \right), \left( 3.5, 0.7 \right), \left( 3.5, 1, 1 \right) \). Notice that the interior fixed point is globally repelling in \( \Sigma \) for (i) and globally attracting in \( C \) for (ii). In (iii) the axial fixed point \( e_1 \) is globally attracting in \( C \).

method [37, 12, 3] that a fixed point is globally repelling in \( \Sigma \) when \( \Sigma \) is locally concave at \( p \) and globally attracting in \( C \) when \( \Sigma \) is locally convex at \( p \).

Our key observation is that under the flow generated by (1) (or indeed any quadratic vector field), for small enough time, a plane is transported into a smooth surface that has Gaussian curvature of a single sign (or zero). The problem, then, is to show that the sign of curvature is preserved under the flow for all time. In [2] we showed that this was the case for planar totally competitive Lotka-Volterra systems. It turns out that a significant obstacle in showing concavity or convexity of the carrying simplex for 3 species is proving that the Gaussian image (the image of the unit normal map of the surface) of the evolving surface remains confined to a suitable convex cone.

2. Carrying simplices

Consider the Kolmogorov system on the nonnegative cone \( C = \mathbb{R}^3_+ \):

\[
\dot{x}_i = x_i f_i(x), \quad x \in C, \tag{3}
\]

where \( f \) is a smooth vector field defined on an open subset \( U \) of \( \mathbb{R}^3 \) containing \( C \). We impose \( f(0) \gg 0 \), so that the origin is a repellor, and total competitiveness, so that \( Df(x) \ll 0 \) for \( x \in C \). We also suppose that there are axial fixed points at \( e_1 = (1, 0, 0)^T, e_2 = (0, 1, 0)^T, e_3 = (0, 0, 1)^T \). The stated conditions ensure that these axial fixed points are unique.

For (1) the origin \( O \) repels trajectories and its basin of repulsion in \( C, B(O) \), is open and bounded. Moreover the boundary of \( B(O) \) in \( C \) is identical to the boundary of \( B(\infty) \), the basin of repulsion of infinity, and is known as the carrying simplex; we denote it by \( \Sigma \). The properties of \( \Sigma \) are summarized by:

**Theorem 1 (Adapted from Hirsch [8])** For system (3) with \( f(0) \gg 0, Df \ll 0 \), there is a unique Lipschitz invariant manifold \( \Sigma \) that attracts \( C \setminus \{0\} \) and every trajectory in \( C \setminus \{0\} \) is asymptotic to one in \( \Sigma \). \( \Sigma \) is a balanced submanifold.
homeomorphic to the closed unit simplex $S = \{ x \geq 0 : x_1 + x_2 + x_3 = 1 \}$ under radial projection, and its interior $\Sigma^0$ is strongly balanced.

(A set $S$ is said to be balanced if both $u \gg v$ and $v \gg u$ hold, and strongly balanced if both $u \nless v$ and $v \nless u$ hold, for any distinct $u, v \in S$.)

The geometry of $\Sigma$ has been studied by several authors. In the case of planar strongly competitive Kolmogorov systems (where only the off-diagonal terms of the Jacobian matrix need be negative), it is known that the carrying simplex joining the axial fixed points $e_1 = (1, 0)$ and $e_2 = (0, 1)$ is at least $C^1[0, 1]$ [20]. For planar totally competitive Lotka-Volterra systems, it is known that $\Sigma$ is either (i) strictly convex, (ii) strictly concave or (iii) a straight line segment [38, 30, 2]. Interestingly, the sign of a single parameter

$$\nu = p(1-a) + q(1-b)$$

where $p = b_1, q = b_2$ and $a = a_{21}/a_{11}, b = a_{12}/a_{22}$ determines which of (i) - (iii) occurs for a given set of $b_i$ and $a_{ij}$ [30]. Indeed, if $\nu > 0(<0)$ then the carrying simplex is strictly convex(concave), and if $\nu = 0$ the carrying simplex is a straight line. We explained this trichotomy in [2] by showing that $\nu$ is proportional to the rate of change of the Gaussian curvature of a straight line segment joining $e_1$ and $e_2$. In [39], the author shows examples of convex and concave planar carrying simplices that are zero sets of quadratic functions.

To study the 3-species case, Zeeman and LaMar developed CSimplex [14], a Geomview module [15], that enables computation and visualisation of $\Sigma$. Figure 1 shows examples from our own computations of carrying simplices for 3-species totally competitive Lotka-Volterra systems. The surface $\Sigma$ was obtained as the steady solution $(x_1, x_2) \mapsto u(x_1, x_2)$ (when it exists) of the quasilinear partial differential equation

$$u_t = h - f u_x_1 - g u_x_2$$

for $(x_1, x_2, t) \in (0, 1)^2 \times (0, \infty)$, and with initial conditions $u(x_1, x_2, 0) = 1 - x_1 - x_2$. Here $f_{x_1}$ denotes the partial derivative $\partial f / \partial x_1$ and similar subscript notation for partial derivatives is used elsewhere. (Since $\Sigma$ is strongly balanced on its interior, one could also work with any of $x_1, x_2$ or $x_3$ as the dependent variable.)

We will follow Zeeman and Zeeman [37], who, in the case of totally competitive systems, defined $\Sigma$ to be convex if whenever $m_1, m_2 \in \Sigma$ then $m = \lambda m_1 + (1-\lambda)m_2$ lies below $\Sigma$ for all $\lambda \in (0, 1)$. Here ‘below’ is defined as follows: Partition $C = L \cup \Sigma \cup U$, where $L \cap U = \emptyset$, and $0 \in L$. Then $x$ is strictly below(above) $\Sigma$ if and only if $x \in L(U)$. This choice of orientation means that the outward normal points into $U$, and mean curvature is positive(negative) where $\Sigma$ is convex(concave). It might help to think of convexity in terms of solid bodies. Let $\Omega = L \cap C$. Since (3) is dissipative, $\Omega$ is the global attractor. Then $\Sigma$ is convex if the solid $\Omega$ is convex in the traditional sense: If $x, y \in \Omega$ then $\lambda x + (1-\lambda)y \in \Omega$ for all $\lambda \in [0, 1]$.

To define what we mean by saddle-like surfaces that are merely Lipschitz we need to introduce the notion of cutting a crust off a surface (see, for example, page 57 in [35]). Let $M \subset \mathbb{R}^3$ be a surface defined by a continuous mapping $\psi : U \to \mathbb{R}^3$ of $U \subset \mathbb{R}^2$. A non-empty open set $E \subset U$ with compact closure $\bar{E} \subset U^0$ is called a crust if there is a hyperplane $\Pi$ such that $E$ is a component of $U \setminus \psi^{-1}(\Pi)$. If $U_1 \subset U$ is such a component then we call $\psi(U_1)$ a crust. We say that the Lipschitz surface $M$ is saddle-like if there is no plane that cuts off a crust from $M$. When $M$ is $C^2$, this definition is consistent with the definition of a saddle surface as one where the principal curvatures at each point have opposite sign.
3. Existence and Uniqueness of Carrying Simplices

In this section we will show how to obtain the carrying simplex Σ as the limit of the image of a plane mapped by the flow of (3). While existence and uniqueness of Σ follows from the work of Hirsch [8] (see also [10, 32]), we provide an adaptation of Hirsch’s method which allows us to provide an elementary proof that certain planes evolving under the competitive flow converge uniformly to Σ. This adaptation enables us to study the curvature of the evolving surface and hence the curvature of the limiting surface Σ.

Our method is based on the Graph transform method developed by Hadamard [7] and used widely in the construction of inertial manifolds (see for example, [29]) and stable manifolds. We start with a triangle $M_0$ in $\mathbb{R}^3$ that is formed from the convex hull of 3 axial points. This surface with corners is carried by the semiflow $\varphi_t$ to a new smooth surface $M_t$ with corners. By choosing $M_0$ close to (far from) the origin $O$ we may ensure that $M_t$ is an increasing (decreasing) sequence of surfaces. These surfaces converge uniformly to a unique invariant surface with corners which is the carrying simplex Σ. We prove:

**Theorem 2** Suppose that the Kolmogorov system (3) is totally competitive and generates a semiflow $\varphi_t: C \to C$ for which the origin $O$ is a repellor. Then there is a unique Lipschitz invariant surface $\Sigma$ such that if $M$ is a plane with normal $N \gg 0$ for which $M_0 = M \cap C \neq \emptyset$ then $M_t = \varphi_t(M_0)$ is a sequence of smooth surfaces (with corners) that converges uniformly to $\Sigma$.

### 3.0.1. Surface Evolution

Let $\Omega \subseteq \mathbb{R}^3$ be open, simply-connected, and $F: \Omega \to \mathbb{R}^3$ a vector field, at least $C^1$, that generates a semiflow $\varphi_t: \Omega \to \Omega$, $t \geq 0$. Let $M_0 \subseteq \Omega$ be a $C^k$ parameterized regular surface ($k \geq 1$) $u \mapsto x_0(u)$ on a simply-connected open set $U \subseteq \mathbb{R}^2$ and define $M_t = \varphi_t(M_0)$ to be the new surface obtained by transporting $M_0$ by $\varphi_t$. By smooth dependence on initial conditions for autonomous ordinary differential equations with smooth vector fields, the map $u \in U \mapsto \varphi_t(x_0(u)) \in M_t$ is smooth for each $t \geq 0$.

We wish to find, for a given point $u = (u_1, u_2) \in U$, how the outward unit normal $N(u, t)$ at the point $x(u, t) = \varphi_t(x_0(u))$ on $M_t$ evolves. In some instances we will not work with the unit normal $N$ (which is always denoted with a capital $N$), but with $n = x_{u_1} \times x_{u_2}$ which is also normal to the evolving surface at $u$ but not necessarily of unit length. The advantage of working with $n$ is that its evolution equation is linear in $n$ (and for the Lotka-Volterra equation, also linear in $x$).

We denote by $\langle \cdot, \cdot \rangle$ the standard Euclidean inner product and $|x| = \sqrt{\langle x, x \rangle}$ for the Euclidean norm. $DF$ is the Jacobian matrix with elements $(F_i)_{x_j} = \partial F_i / \partial x_j$. For a square matrix $W$, $\text{Tr}(W)$ is the sum of its diagonal elements.

**Lemma 1** Under the semiflow generated by the vector field $F: \Omega \to \mathbb{R}^3$, we have, for each $u \in U$, $n = n(u, t) = x_{u_1} \times x_{u_2}$ normal to the surface $M_t$ at $x = x(u, t) \in \Omega$,

$$\dot{n} = -DF(x)^T n + \text{Tr}(DF(x))n.$$  \hspace{1cm} (6)

**Proof.** We have $\dot{x} = F(x)$ and hence $\dot{x}_{u_1} = DF(x)x_{u_1}$ and similarly $\dot{x}_{u_2} = DF(x)x_{u_2}$. Hence $\frac{\partial}{\partial t}(x_{u_1} \times x_{u_2}) = (DF(x)x_{u_1}) \times x_{u_2} + x_{u_1} \times (DF(x)x_{u_2})$. Now let $W$ be a real $3 \times 3$ matrix and consider $w = W e_1 \times e_2 + e_1 \times W e_2$. Then

$$w = (w_{11}e_1 + w_{12}e_2 + w_{13}e_3) \times e_2 + e_1 \times (w_{21}e_1 + w_{22}e_2 + w_{23}e_3).$$
There is a (relatively) open set \( \Omega \subset \text{context} \) by a smooth surface \( M \). Similarly

\[
W e_2 \times e_3 + e_2 \times W e_3 = \text{Tr}(W) e_2 \times e_3 - w_{11} e_2 \times e_3 - w_{12} e_2 \times e_3 - w_{31} e_1 \times e_2
\]

By linearity, for \( p = \sum \rho_i e_i, q = \sum q_i e_i \) we obtain \( W p \times q + p \times W q = \text{Tr}(W)(p \times q) - W^T(p \times q) \). Now let \( p = x_{u_1}, q = x_{u_2} \) and \( W = DF(x) \).

Recall that a regular (parameterized) surface in \( \mathbb{R}^3 \) is a \( C^1 \) parameterized surface \( x : U \to \mathbb{R}^3 \) such that \( x_{u_1} \times x_{u_2} \neq 0 \) for all \( (u_1, u_2) \in U \).

**Corollary 1** If \( M_0 \) is regular then the surface \( M_t = \varphi_t(M_0) \) is regular for all \( t \geq 0 \).

After a little more work we also obtain:

**Corollary 2** For totally competitive \( F \) in (1), if for \( u \in U \) we have \( n(u, 0) \in C \) and \( x(u, 0) \in C^0 \) then \( n(u, t) \in C^0 \) for all \( t > 0 \). If \( n(u, 0) \in C^0 \) then \( n(u, t) \in C^0 \) for all \( t \geq 0 \).

A simple calculation for \( N = n/|n| \) shows

**Corollary 3** Under the flow generated by the vector field \( F : \Omega \to \mathbb{R}^3 \), we have, for \( u \in U \) and \( N(u, t) \) the unit normal to the surface \( M_t = \varphi_t(M_0) \) at \( x = x(u, t) \in M_t \),

\[
\dot{N} = -DF(x)^T N + \langle N, DF(x)N \rangle N.
\]  

We now follow the general idea of [8]. We say that a \( C^1 \) surface \( M \) given parametrically by \( x : U \to \mathbb{R}^3 \) whose Gaussian image \( S(M) = \left\{ x_{u_1} \times x_{u_2} / |x_{u_1} \times x_{u_2}| : (u_1, u_2) \in U \right\} \) is a subset of \( C \) has a nonnegative Gaussian image.

Let \( t = \frac{1}{\sqrt{3}}(1, 1, 1)^T \) and denote by \( \pi_t : \mathbb{R}^3 \to \Pi_t \) the projection given by \( \pi_t(x) = x - \langle x, t \rangle t \). We also denote by \( \pi_{e_3} : \mathbb{R}^3 \to \mathbb{R}^2 \) denote the projection defined by \( \pi_{e_3}(x_1, x_2, x_3) = (x_1, x_2) \).

Before turning to the proof of theorem 2, a comment on smoothness is in order. If \( A \subset \mathbb{R}^3 \) is a set (not necessarily open) we say that \( f : A \to \mathbb{R} \) is smooth if there is an open set \( A' \supset A \) and smooth function \( \hat{f} : A' \to \mathbb{R} \) such that \( f \) restricted to \( A \) coincides with \( \hat{f} \). If \( M \) is a plane through the origin with normal \( N \gg 0 \) such that \( M_0 = M \cap C \neq \emptyset \) then \( M_0 \) is a smooth surface (manifold) with corners. In the present context, by a smooth surface \( M \) with corners we mean that each point \( m \in M \subset \mathbb{R}^3 \) there is (relatively) open set \( \Omega \subset [0, \infty)^2 \) and a diffeomorphism \( \phi : \Omega \to \phi(\Omega) \subset M \) with \( \phi(\Omega) \) (relatively) open in \( \mathbb{R}^3 \) and \( m \in \phi(\Omega) \). If \( M_t = \varphi_t(M_0) \), where \( \varphi_t \) is the semiflow of (3), for \( t \geq 0 \) \( M_t \) is a smooth surface with corners (see [13] for a discussion of manifolds with corners in relation to carrying simplices).

**Remark** In [13] the authors find necessary and sufficient conditions for \( \Sigma \) to be a \( C^1 \) manifold with corners neatly embedded in \( C \). If \( \Delta \subset C \) is the unit probability simplex and \( \Sigma = \{ r(x) \mid x \in \Delta \} \), then \( \Sigma \) is said to be a \( C^1 \) manifold with corners neatly embedded in \( C \) if \( r \) is \( C^1 \) (on an open subset \( X \supset \Delta \) of the affine hull of \( \triangle \)), so that at no point in \( \partial \Sigma \) is the carrying simplex \( \Sigma \) tangent to \( \partial C \). Examples are given in [21] and [13] where \( \Sigma \) is not a neat embedding, and also where \( \Sigma \) is not differentiable on its boundary. In the context of the current paper, existence of a strongly balanced tangent
plane to the carrying simplex $\Sigma$ at each of the axial fixed points (or equivalently that $DF(e_i)^T$ has a positive right eigenvector for each $i \in I_3$) is necessary and sufficient for $\Sigma$ to be a $C^1$ manifold with corners (neatly embedded in $C$).

In the sequel, when we speak of a surface, unless otherwise specified we mean a surface with corners.

In the next result, we make use of the well-known fact (see, for example, [25, 9]) that a competitive flow is order-preserving backwards in time. In other words, if $\varphi_t : C \rightarrow C$ denotes the semiflow of (3) and $\varphi_t(x) \geq \varphi_t(y)$ then $\varphi_s(x) \geq \varphi_s(y)$ for all $0 \leq s \leq t$.

**Lemma 2** Let $M$ be a plane with unit normal $N \gg 0$ such that $M_0 = M \cap C \neq \emptyset$. If $M_\ell = \varphi_\ell(M_0)$, where $\varphi_\ell$ is the semiflow of (3), then $M_\ell$ is a sequence of smooth Lipschitz surfaces of rank unity with positive Gaussian images $S(M_\ell)$.

**Proof.** Let $M_0$ be the convex hull of three axial points $P_i, i \in I_3$. The boundary $\partial M_0$ is the union of the three line segments $P_1P_2, P_2P_3, P_3P_1$. The flow $\varphi_\ell : C \rightarrow C$ is a diffeomorphism that leaves, for each $i \in I_3$, the faces $F_i = x_i^{-1}(0)$ of $C$ invariant. Since $\varphi_\ell$ is a diffeomorphism, $\varphi_\ell(\partial M_0) = \partial(\varphi_\ell(M_0)) = \partial M_\ell$ and by invariance of the $F_i$, $\partial M_\ell = \varphi_\ell(P_1P_2) \cup \varphi_\ell(P_2P_3) \cup \varphi_\ell(P_3P_1) \subset \partial C$. Since $M_\ell = \varphi_\ell(M_0)$ is simply connected, $x^0 \in M_0 \Rightarrow \varphi_\ell(x^0) \in M_\ell$ is a smooth map and defines a smooth surface $M_\ell$ (with boundary belonging to $\partial C$). By corollary 2, $M_\ell$ has positive Gaussian image since $M_0$ has.

Let $\Pi_\ell$ denote the plane through $O$ with unit normal $\ell$. Following [8], suppose that there are distinct $x, x' \in M_\ell$ such that $\pi_\ell(x) = \pi_\ell(x')$. Then $x - x' = (x - x')\ell$ so that $x, x'$ are ordered. But then $\varphi_{-\ell}(x), \varphi_{-\ell}(x')$ are ordered points in $M_0$, which is a contradiction. Thus we must have $x = x'$, and so we conclude that $\pi_\ell$ restricted to $M_\ell$ is one-to-one. Choose a pair of vectors which are orthogonal to $\ell$, say $v_1 = (1, -1, 0)^T, v_2 = (0, 1, -1)^T$. Then $x = X_1v_1 + X_2v_2 + X_3\ell$ for some $X_1, i \in I_3$. Let $V_\ell = \{ (X_1, X_2) \in \mathbb{R}^2 : X_1v_1 + X_2v_2 \in \pi_\ell(M_\ell) \}$. Since $\pi_\ell$ restricted to $M_\ell$ is one-to-one, we may write $x(X_1, X_2) = X_1v_1 + X_2v_2 + \phi_\ell(X_1, X_2)\ell$, and so $M_\ell$ is the graph of a smooth function $\phi_\ell : V_\ell \rightarrow \mathbb{R}$. The vector $(\phi_\ell)_{X_1}v_1 + (\phi_\ell)_{X_2}v_2 + \ell$ is normal to $M_\ell$ at $X_1v_1 + X_2v_2$ and, since $M_\ell$ has positive Gaussian image, $(\phi_\ell)_{X_1}X_1, (\phi_\ell)_{X_2}X_2$ are constrained by the three inequalities $(\phi_\ell)_{X_1}(\ell, v_1, e_i) + (\phi_\ell)_{X_2}(v_2, e_i) + (\ell, e_i) > 0$ for $i \in I_3$. Writing $p = (\phi_\ell)_{X_1}, q = (\phi_\ell)_{X_2}$, these inequalities read $1 - q - 2p > 0, 1 - q - 2p > 0, 1 + 2p + q > 0$ which defines a triangular region in $p, q$-space that is contained in $[-1, 1]^2$. Hence $\phi_\ell : V_\ell \rightarrow \mathbb{R}$ is Lipschitz rank unity for each $t \geq 0$.

For each $t \geq 0$ let $M^-_\ell$ denote the set of points in $C$ lying below $M_\ell$ and $M^+_\ell$ denote the set of points in $C$ lying above $M_\ell$. Then we say that the sequence of surfaces $M_\ell$ is increasing(decreasing) if for each $t > s$ we have $M^+_s \subset M^-_t$ ($M^+_t \subset M^-_s$).

**Lemma 3** Let $M$ be a plane with outward unit normal $N \gg 0$ such that $M_0 = M \cap C \neq \emptyset$. Let the Kolmogorov vector field $F$ generate the semiflow $\varphi_t : C \rightarrow C$ via (3). If $\langle F, N \rangle > \langle F, N \rangle > 0$ on $M_0$ then the surfaces $M_\ell = \varphi_\ell(M_0)$ form an increasing (decreasing) sequence of smooth Lipschitz surfaces.

**Proof.** Let $M_0 = \{ m \in C : \langle m, N \rangle = 0 \}$ and write each $x \in M_\ell$ as $x = R(m)m$ where $m \in M_0$ and $R(m) > 0$. Then $\langle N, F \rangle = \langle N, x \rangle = Rd$. Since at $t = 0$ we have $\langle N, F \rangle > 0, R > 0$ at $t = 0$ for all $m \in M_0$ and $R$ is strictly increasing in some interval $t \in (0, \tau^*)$. Hence $M^-_\ell \subset M^-_\ell$ for all $\tau, \varsigma \in (0, \tau^*)$ with $\varsigma < \tau$. It then follows that
almost everywhere), and divergence theorem, since $F$ is tangent to $\Sigma$ (where $\Sigma$ is differentiable, which it is almost everywhere), and hence that $M^{-}_t$ is an increasing sequence of nested, simply-connected subsets of $C$. \hfill \Box

**Lemma 4** For the totally competitive Kolmogorov system (3) there exists an increasing(decreasing) sequence of smooth Lipschitz surfaces with positive Gaussian images that converges uniformly to a unique invariant Lipschitz surface $\Sigma$.

**Proof.** Let $M_0 = (M + \epsilon t) \cap C$. Since $O$ is an unstable node, by choosing $\epsilon > 0$ small enough we may arrange that at each point on $M_0$ we have $\langle \iota, F \rangle > 0$ at $t = 0$. By lemma 3, $M_t$ is a (bounded) increasing sequence of uniformly Lipschitz surfaces. Following the notation of lemma 2, each surface $M_t$ is the graph of a Lipschitz function $\phi_t : V_t \to \mathbb{R}$ rank unity, and $\phi_t$ can be extended to a Lipschitz function $\hat{\phi}_t : \mathbb{R}^2 \to \mathbb{R}$ of rank unity on all of $\mathbb{R}^2$ [19] and explicitly given by $\hat{\phi}_t(X) = \sup_{Y \in V_t} \{ \phi_t(Y) - |X - Y| \}$. Notice that for increasing $M_t$ we have for the Lipschitz extensions $\hat{\phi}_t(X) \geq \hat{\phi}_s(X)$ for all $X \in \mathbb{R}^2$ and $t \geq s$. To see this note that $M_t \supset M_s$ implies that $\pi_t(M_t) \subset \pi_s(M_s)$ and hence that $V_t \subset V_s$. Thus for all $X \in \mathbb{R}^2$, $\hat{\phi}_t(X) \geq \sup_{Y \in V_t} \{ \phi_t(Y) - |X - Y| \} \geq \sup_{Y \in V_s} \{ \phi_s(Y) - |X - Y| \} = \hat{\phi}_s(X)$.

If $K \subset \mathbb{R}^2$ is compact then by the Arzelà-Ascoli theorem $\hat{\phi}_t$ restricted to $K$ converges uniformly to a Lipschitz function $\phi^1 : K \to \mathbb{R}$ of rank unity. Thus by taking the set $K$ sufficiently large to contain all $V_t$ for $t \geq 0$, by monotonicity in $t$ we obtain a Lipschitz invariant surface $\Sigma^1$ as the intersection of $C$ with the graph of $\phi^1$. Similarly, taking $\epsilon > 0$ large enough we may generate a decreasing sequence that converges uniformly to an invariant surface $\Sigma_2$.

To show $\Sigma_1 = \Sigma_2 = \Sigma$, let us suppose not. We introduce, for $\epsilon > 0$ small, the function $\sigma(x) = (\langle x_1 + \epsilon |x_2 + \epsilon |x_3 + \epsilon \rangle)^{-1} > 0 \forall x \in C$. Then, writing $F_i(x) = x_i f_i(x)$,

$$\text{div}(\sigma F) = \sigma \left( \epsilon \left( \sum_{i=1}^{3} \frac{f_i}{x_i + \epsilon} \right) - \sum_{i=1}^{3} x_i (f_i x_i) \right) < 0$$

for all $x \in C \setminus \Sigma_\epsilon$, where $\Sigma_\epsilon$ is a neighbourhood of the origin of order $\epsilon$ and so can be made as small as we wish by choosing $\epsilon > 0$ small enough. If there are two distinct Lipschitz invariant surfaces $\Sigma_1, \Sigma_2$ then as the origin is an unstable node (so that $\Sigma_1, \Sigma_2$ are disjoint from a small neighbourhood of $O$), we may take $\epsilon$ sufficiently small that the volume $J$ enclosed by $\Sigma_1, \Sigma_2$ has $\text{div}(\sigma F) < 0$. Then, from the divergence theorem, since $F$ is tangent to $\Sigma$ (where $\Sigma$ is differentiable, which it is almost everywhere), and $\langle F, n \rangle = 0$ on $\partial J \cap \partial C$, we have

$$0 = \int_{\partial J} \sigma \langle F, n \rangle \, dA = \int_J \text{div}(\sigma F) \, dV < 0,$$

which is a contradiction, so that we must have $\Sigma_1 = \Sigma_2$. \hfill \Box

Combining lemmas 2, 3 and 4 gives theorem 2.

**Remark** Consequently, if $M_0 \subset C$ is any surface not containing $O$ that is the image of the unit probability simplex under a continuous map that leaves $\partial C$ invariant, we have $\varphi_t(M_0) \to \Sigma$ as $t \to \infty$. 
4. Evolution of Gaussian curvature

In this section we are interested in tracking the change in curvature of a regular surface by computing the change in its second fundamental form. As we shall see the advantage of starting with a plane is that the flow deforms it so that for small enough times its Gaussian curvature is uniformly single-signed.

Let \( u \in U \subset \mathbb{R}^2 \mapsto x(u) \in \mathbb{R}^3 \) define the surface. Pick a point \( x \in M \) and denote by \( T_xM \) the tangent space to \( M \) at \( x \). Given a vector field \( Y : M \to T_x \mathbb{R}^3 = \mathbb{R}^3 \), for \( X \in T_xM \), denote by \( D_XY \) the directional derivative of \( Y \) (in the direction of \( X \)). If \( N \) is the unit outward normal of \( M \), \( 0 = D_X|N|^2 = 2\langle D_XN, N \rangle \) so that \( D_XN \in T_xM \).

Now define the Weingarten map \( L_x : T_xM \to T_xM \) via \( L_x(X) = -D_XN \). The 2nd fundamental form at \( x \in M \) is the bilinear form \( B : T_xM \times T_xM \to \mathbb{R} \) defined by \( B(X, Y) = \langle L(X), Y \rangle \) for \( X, Y \in TM \). If the surface \( M \) is parameterized \( u \in U \mapsto x(u) \), we denote by \( \Psi \) the matrix with \( i, j \)th element \( \langle x_{ui}, x_{uj} \rangle \).

It can be shown that for tangent vectors \( x_{ui} \) at a point \( u \in U \),

\[
\Psi_{ij} = \langle x_{ui}, x_{uj}, N \rangle.
\]

In our present application \( \Psi \) is the \( 2 \times 2 \) real symmetric matrix

\[
\Psi = \begin{pmatrix}
\langle x_{u1u1}, x_{u1} \times x_{u2} \rangle \\
\langle x_{u1u2}, x_{u1} \times x_{u2} \rangle \\
\langle x_{u1u2}, x_{u1} \times x_{u2} \rangle \\
\langle x_{u2u2}, x_{u1} \times x_{u2} \rangle
\end{pmatrix}.
\]

We recall that a real symmetric matrix \( P \) is positive(negative) definite if \( \langle v, Pv \rangle > 0(< 0) \) for all \( v \neq 0 \), or equivalently that its spectrum is positive(negative). Also, if strictly inequality is replaced by inequality, we replace ‘definite’ by ‘semidefinite’. If \( \Psi \) is positive(negative) definite at \( x \in M \) then \( M \) is locally convex(concave) at \( x \), whereas if the eigenvalues of \( \Psi \) have opposite sign at \( x \in M \) then \( M \) is locally saddle-like at \( x \). The Gaussian curvature of \( M \) at \( x(u) \) is \( \kappa = \det \Psi / |x_{u1} \times x_{u2}|^2 \).

4.1. Evolution of the Second Fundamental Form

The following lemma determines how the sign of the Gaussian curvature of the evolving surface \( M_t = \varphi_t(M_0) \) evolves following a point moving with the surface. Let the outward unit normal of the surface be \( N \).

In the following \( F : \mathbb{R}^3 \to \mathbb{R}^3 \) denotes the vector field that generates the flow via \( \dot{x} = F(x) \).

Lemma 5

\[
\dot{\Psi} = \Theta + \langle N, DFN \rangle \Psi
\]

and

\[
\Psi(t) = \exp \left( \int_0^t \langle N, DFN \rangle \, d\tau \right) \Psi(0) + \int_0^t \Theta(s) \exp \left( \int_s^t \langle N, DFN \rangle \, d\tau \right) \, ds
\]

where the \( 2 \times 2 \) matrix \( \Theta \) has elements

\[
\Theta_{ij}(t) = \langle x_{ui}, \sum_{k=1}^3 N_k D^2 F_k \rangle x_{uj}.
\]
Proof. We have
\[
\dot{\Psi}_{ij} = \frac{d}{dt} \left( \langle x_{u_i}, N \rangle \right) \\
= \langle (\dot{x})_{u_i}, N \rangle + \langle x_{u_i}, \dot{N} \rangle \\
= \langle (F)_{u_i}, N \rangle + \langle x_{u_i}, (-DF^T N + \langle N, DFN \rangle N) \rangle \\
= \langle (x_i D^2 F x_j + DF_{u_i u_j}), N \rangle \\
+ \langle x_{u_i u_j}, (-DF^T N + \langle N, DFN \rangle N) \rangle \\
= \langle (x_i D^2 F x_j), N \rangle + \langle N, DFN \rangle \Psi_{ij} \\
= \Theta_{ij} + \langle N, DFN \rangle \Psi_{ij}. 
\]
This last matrix equation can be integrated explicitly to give (9).

In what follows, for a given square matrix \( M \) we denote by \( M^S \) the symmetrisation of \( M \); that is, \( M^S = M + M^T \).

Corollary 4 If \( M_0 \) is a plane with unit normal \( N \) then at \( t = 0 \) (taking a parameterisation linear in the \( u_i \))
\[
\dot{\Psi}_{ij}(t = 0) = \left\langle x_{u_i}, \left( \sum_{k=1}^{3} N_k D^2 F_k \right) x_{u_j} \right\rangle, \ i, j \in I_2. 
\]
and
\[
\Psi(t) = \int_0^t \Theta(s) \eta(t, s) \, ds \tag{10}
\]
where \( \eta(t, s) = \exp\left( \int_s^t \langle N, DFN \rangle \, d\tau \right) > 0 \). In particular, for the Lotka-Volterra equations (1) we obtain
\[
\Theta_{ij}(t) = -\left\langle x_{u_i}, V x_{u_j} \right\rangle, \ i, j \in I_2. \tag{11}
\]
where
\[
V = (\text{diag}[N] A)^S. \tag{12}
\]
Remark The matrix \( V = (\text{diag}[N] A)^S \) has been utilised by Zeeman and Zeeman in their Split Liapunov method [37]. They showed that for totally competitive Lotka-Volterra systems with a unique interior fixed point \( p \), if all (non-trivial) trajectories crossed the strongly-balanced tangent plane \( T_p \Sigma \), with outward normal \( N \gg 0 \), through \( p \) downwards, then \( p \) is a global attractor (on the interior of \( \mathbb{R}^n_+ \)). The condition that they obtained for all trajectories to cross \( T_p \Sigma \setminus \{p\} \) downwards is precisely that \( \langle v, (\text{diag}[N] A)^S \rangle v > 0 \) for \( v \in T_p \Sigma \setminus \{0\} \). In [12, 3] the Split Liapunov method was extended to deal with not-necessarily competitive Lotka-Volterra systems and also for boundary fixed points.

4.2. Useful expressions for \( \Theta \)

Let us suppose that the initial surface \( M_0 \) is planar. The second fundamental form at time \( t \geq 0 \) is given by (10) and with (12)
\[
\Theta(t) = -\left( \begin{array}{cc} \langle x_{u_1}, V x_{u_1} \rangle & \langle x_{u_1}, V x_{u_2} \rangle \\ \langle x_{u_2}, V x_{u_1} \rangle & \langle x_{u_2}, V x_{u_2} \rangle \end{array} \right),
\]
so that \( \det \Theta = \langle x_{u_1}, V_{x_{u_1}} \rangle \langle x_{u_2}, V_{x_{u_2}} \rangle - \langle x_{u_1}, V_{x_{u_2}} \rangle \langle x_{u_2}, V_{x_{u_1}} \rangle = \langle x_{u_1} \times x_{u_2}, V_{x_{u_1}} \times V_{x_{u_2}} \rangle \). Now we use the identity: For \( W \) a real 3 \times 3 matrix and \( a, b \in \mathbb{R}^3 \), \( Wa \times Wb = \text{adj}(W) (a \times b) \), where \( \text{adj}(W) \) is the transpose of the cofactor of \( W \). Then 
\[
\text{det} \Theta = \langle x_{u_1} \times x_{u_2}, V_{x_{u_1}} \times V_{x_{u_2}} \rangle = \langle x_{u_1} \times x_{u_2}, (N, \text{adj}(V))N \rangle. \]
Since \( V = (\text{diag}[N]A)^S \), \( \text{adj}(V) \) is a 3 \times 3 symmetric matrix with entries that are homogeneous in \( N \) of degree 2, and \( (N, \text{adj}(V)N) \) is a homogeneous polynomial in \( N \) of degree 4. By regularity of the surface \( \det \Theta \geq 0 \) if and only if \( (N, \text{adj}(V)N) \geq 0 \).

For convenience, set
\[
A_1 = a_{31} - a_{11}, \quad A_2 = a_{12} - a_{22}, \quad A_3 = a_{23} - a_{33}
B_1 = a_{11} - a_{21}, \quad B_2 = a_{22} - a_{32}, \quad B_3 = a_{33} - a_{13}
\]
and define the 3 \times 3 symmetric matrix
\[
L = \begin{pmatrix}
-(A_1 + B_1)^2 & A_1(A_2 - B_2) + B_1(A_2 + B_2) & A_1(A_3 - B_3) + A_3(A_1 + B_1) \\
A_1(A_2 - B_2) + B_1(A_2 + B_2) & -(A_2 + B_2)^2 & A_2(A_3 - B_3) + A_3(A_2 + B_2) \\
A_1(A_3 - B_3) + A_3(A_1 + B_1) & A_2(A_3 - B_3) + A_3(A_2 + B_2) & -(A_3 + B_3)^2
\end{pmatrix}.
\]
The matrix \( L \) satisfies \( \det L = 4(A_1A_2A_3 - B_1B_2B_3)^2 \geq 0 \) and
\[
\text{det} \Theta = |x_{u_1} \times x_{u_2}|^2(N, \text{adj}(V)N) = |x_{u_1} \times x_{u_2}|^2\Delta_L(N),
\]
where \( \Delta_L : \mathbb{R}^3 \to \mathbb{R} \) is defined by
\[
\Delta_L(p) = \langle (p_2p_3, p_1p_3, p_1p_2), L(p_2p_3, p_1p_3, p_1p_2) \rangle, \quad p = (p_1, p_2, p_3)^T \in \mathbb{R}^3.
\]
For a regular surface \( M \), \( \det \Theta = 0 \) at a point on \( M \) where the unit normal is \( N \) if and only if \( \Delta_L(N) = 0 \). The function \( \Delta_L \) is a quartic, and sometimes it is more convenient to use the quadratic function \( \delta_L : \mathbb{R}^3 \to \mathbb{R} \) defined by
\[
\delta_L(v) = \langle v, Lv \rangle, \quad v \in \mathbb{R}^3.
\]
In fact, when \( N \gg 0 \), we may set \( v_i = 1/N_i \) for each \( i \in I_3 \) so that
\[
\delta_L(v_1, v_2, v_3) = (N_1N_2N_3)^2\Delta_L(N_1, N_2, N_3).
\]
Thus \( N \in \Delta_L^{-1}(0) \cap C^0 \) if and only if \( v = (1/N_1, 1/N_2, 1/N_3) \in \delta_L^{-1}(0) \). This means that to find unit normals where \( \det \Theta = 0 \), we need only investigate zeros of quadratic.

Suppose that a plane \( \Pi \ni x \) has unit normal \( N = (N_1, N_2, N_3) \). Since \( N \gg 0 \), we may take linearly independent tangent vectors \( w_1 = (-N_2, N_1, 0) \) and \( w_2 = (0, -N_3, N_2) \) that span \( T_x \Pi \), so that \( w_1 \times w_2 = N_2(N_1, N_2, N_3) \). For given \( r_{u_1} = p_1w_1 + p_3w_2, r_{u_2} = q_1w_1 + q_2w_2 \), then \( (r_{u_1}, (\text{diag}[N]A)^Sw_{u_2}) = \sum_{i,j=1}^2 p_ip_j\langle w_i, (\text{diag}[N]A)^Sw_j \rangle = \langle p, \Upsilon p \rangle \), where \( \Upsilon_{ij} = \langle w_i, (\text{diag}[N]A)^Sw_j \rangle \). Then
\[
\Theta = -\begin{pmatrix}
\langle p, \Upsilon p \rangle & \langle p, \Upsilon q \rangle \\
\langle q, \Upsilon p \rangle & \langle q, \Upsilon q \rangle
\end{pmatrix} = -J\Upsilon J^T.
\]
where \( J = (p|q)^T \). Hence \( \Theta \) is positive(negative) definite if and only if \( \Upsilon \) is negative(positive) definite. An explicit expression for \( \Upsilon \) is
\[
\Upsilon = \frac{-1}{N_2} \begin{pmatrix}
2N_1(A_2N_1 - B_1N_2) & (B_2 - A_2)N_1N_3 \\
(B_2 - A_2)N_1N_3 & -(A_3 + B_3)N_1N_2 + (A_1 + B_1)N_2N_3
\end{pmatrix}.
\]
Geometry of carrying simplices

Since $N \gg 0$ we may set $v_i = 1/N_i$ for $i \in I_3$, so that $v_2 \mathbf{Y} = -\text{diag}[(1/v_1, 1/v_3)] \theta \text{diag}[(1/v_1, 1/v_3)]$ where $\theta$ is the $2 \times 2$ symmetric matrix

$$
\theta = \begin{pmatrix}
2(A_2v_2 - B_1v_1) & (B_2 - A_2)v_2 \\
(B_2 - A_2)v_2 & -(A_3 + B_3)v_3 + (A_1 + B_1)v_1
\end{pmatrix}.
$$

(18)

$\Theta$ is positive(negative) definite if and only if $\theta$ is negative(positive) definite.

4.2.1. $\det \Theta$ positive  This means that $\Theta$, or equivalently $\theta$, is definite.

Lemma 6 If $\Theta(\tau)$ is positive(negative) semidefinite for $0 \leq \tau < t$, and $\Psi(0)$ is positive(negative) semidefinite then $\Psi(t)$ is positive(negative) semidefinite for $0 \leq \tau < t$. If $\Theta(\tau)$ is positive(negative) semidefinite for $0 \leq \tau < t$, and actually positive(negative) definite for $t$ in a measurable subset of $[0, t]$ of positive measure, and $\Psi(0)$ is positive(negative) semidefinite, then $\Psi(t)$ is positive(negative) definite for $0 \leq \tau < t$.

Proof.  We deal with the positive definite or semidefinite case only. If $\Psi(0)$ is positive semidefinite, then so is $I_1 = \exp \left( \int_0^t \langle N, DFN \rangle \, d\tau \right) \Psi(0)$. If $\Theta(\tau)$ is positive semidefinite for $0 \leq \tau < t$ then so is the integral $I_2 = \int_0^t \Theta(s) \exp \left( \int_s^t \langle N, DFN \rangle \, d\tau \right) \, ds$. Then $\Psi(t) = I_1 + I_2$ is positive semidefinite. If $\Theta(\tau)$ is positive definite on a measurable subset of $[0, t]$ of positive measure then $I_2$ is positive definite so that then $\Psi(t) = I_1 + I_2$ is positive definite.

Theorem 3 Let $M$ be a plane with normal $N \gg 0$ such that $M_0 = M \cap C \neq \{0\}$. Let $M_t = \varphi_t(M_0)$ for $t \geq 0$ where $\varphi_t : C \to C$ is the semiflow generated by the totally competitive Lotka-Volterra system (1). Then if $\theta(t)$ defined by (18) is positive(negative) semidefinite for $0 \leq t < T$ then $M_t$ is a concave(convex) surface for $0 \leq t < T$. If $T = \infty$ then $M_t$ converges uniformly to a concave(convex) carrying simplex $\Sigma$.

Proof.  If $\theta(t)$ is positive(negative) semidefinite for $0 \leq t < T$ then $\Theta(t)$ is negative(positive) semidefinite for $0 \leq t < T$. By lemma 6, this means that $\Psi(t)$ is negative(positive) semidefinite for $0 \leq t < T$. Since $M_t$ is a graph of a function, local concavity(convexity) due to global negative(positive) definiteness of $\Psi(t)$ extends to global concavity(convexity).

First consider the case that each surface $M_t = \varphi_t(M_0)$ has negative semidefinite 2nd fundamental form $\Psi(t)$ for each $t \geq 0$. Each $M_t$ is the graph of a function $\psi_t : \pi_t(M_t) \to \mathbb{R}$ that can be extended outside $\pi_t(M_t)$ to form a continuous convex function $\hat{\psi}_t : K \to \mathbb{R}$ where $\pi_t(M_t) \subset K$ and $K$ is convex. By Theorem 10.8 of [24] the (Lipschitz) limit $\Sigma$ of the sequence of $M_t$ is the graph of a continuous convex function $\hat{\psi} = \lim_{t \to \infty} \hat{\psi}_t$ on $K$, and so $\Sigma$ is concave.

When each surface $M_t = \varphi_t(M_0)$ has positive semidefinite 2nd fundamental form $\Psi(t)$ then each $M_t$ is convex and we replace $M_t$ by $M_t = -M_t$ which yields a sequence of concave surfaces that converge to a concave $-\Sigma$ so that $\Sigma$ is convex.

Corollary 5 If each $F_i(x) = x_i f_i(x)$ is convex(concave) then $\Sigma$ is convex(concave).
Proof. If each $F_i$ is convex(concave) then each $D^2 F_i$ is positive(negative) semidefinite. If $\xi \in \mathbb{R}^2$ is any fixed vector,
\[
(\xi, \Theta(t) \xi) = \sum_{i,j=1}^{2} \xi_i \Theta_{ij}(t) \xi_j = \sum_{i,j=1}^{2} \xi_i \xi_j \langle x_{u_i}, V(t)x_{u_j} \rangle,
\]
where $V(t) = \sum_{k=1}^{3} N_k D^2 F_k$ is positive(negative) semidefinite. But
\[
\sum_{i,j=1}^{2} \xi_i \xi_j \langle x_{u_i}, V(t)x_{u_j} \rangle = \langle \xi, V(t) \xi \rangle
\]
where $\zeta = \sum_{i=1}^{2} \xi_i x_{u_i}$. Since $V(t)$ is positive(negative) semidefinite, $(\xi, \Theta(t) \xi) = \langle \xi, V(t) \xi \rangle \geq 0$ and hence $\Theta(t)$ is positive(negative) semidefinite and the result follow from theorem 3. \hfill \Box

Remark Corollary 5 does not require knowledge of how the Gaussian image $S(M_t)$ of $M_t$ evolves, but it is rather limited in its application. We will give another example, namely Example 2 in 7.2, where knowledge of the Gaussian image of $M_t$ is not needed to determine the curvature of $\Sigma$. However, in general, it is necessary to monitor the development of the normal of $M_t$ in order to ensure that $\Theta(t)$ remains definite, so that theorem 3 may be applied.

Remark If we change coordinates in (1) via $y_i = \log x_i$, $i \in I_3$, we obtain the transformed system
\[
\dot{y}_i = G_i(y) = b_i - \sum_{j=1}^{3} a_{ij} e^{y_j}, \quad i \in I_3.
\]
This is another totally competitive system, but this time on the whole of $\mathbb{R}^3$. In these new coordinates, $D^2 G_k(y) = -\text{diag}[[a_{k1} e^{y_1}, a_{k2} e^{y_2}, a_{k3} e^{y_3}]]$, so that $\sum_{k=1}^{3} N_k D^2 G_k$ is now negative definite. Thus in these new coordinates the invariant surface is always concave.

Remark For (3), $V = \text{diag}([N], A)^S$, so from the calculations in corollary 5, a sufficient condition for $\Theta$ to be positive definite at a point on $M_t$ where the unit normal is $N$ is that $\text{diag}([N], A)^S$ is positive definite.

4.2.2. det $\Theta$ negative If $\det \Theta(0) < 0$ then $\det \Psi(t) < 0$ for $t > 0$ sufficiently small, but as is well known the set of $2 \times 2$ symmetric matrices with negative determinant does not form a convex set, so using (10) does not appear to be fruitful. If, for example, $a_{31} < a_{11}$, $a_{33} > a_{13}$, $a_{32} > a_{22}$, $a_{23} > a_{33}$, then $\det \Theta(t) < 0$ for all $t > 0$, but this cannot be easily translated into $\det \Psi(t) < 0$ for $t > 0$.

5. Global geometry of $\Sigma$

5.1. Establishing bounds on the Gaussian image $S(M_t)$

As we have seen, via (17), the Gaussian image $S(M_t)$ of the surface $M_t$ has a strong bearing on its curvature. In this section the aim is to find ways to ensure that the Gaussian image $S(M_t)$ of the surface $M_t$ is confined to a suitable cone $K \subset \mathbb{R}^m$.

We recall that a set $K \subset \mathbb{R}^m$ is a cone provided that $\mu K \subset K$ for all $\mu \geq 0$. A cone is proper provided that it is closed, convex, has non-empty interior and is pointed ($K \cap (-K) = \{0\}$). Two commonly used proper cones are $K_q = \mathbb{R}^m_+$, and
the ice cream cone $K_{ice} = \{ x \in \mathbb{R}_+^m : \|x_m\| \geq \sqrt{\sum_{i=1}^{m-1} x_i^2} \}$. $K_q$ is an example of a polyhedral cone; that is, a cone formed from the intersection of a finite number of closed half spaces. The cone dual to $K$, denoted by $K^*$ is the convex cone of linear functions $\{ y \in (\mathbb{R}^m)^* : (y, k) \geq 0 \ \forall k \in K \}$. A flow $\varphi_t : U \to U$ on an open set $U \subset \mathbb{R}^m$ preserves a proper cone $K \subset U$ if $\varphi_t K \subset K$.

Our objective is to control the deviation of the surface normal from a fixed vector $t \gg 0$ by ensuring that it is confined to a suitable convex cone $K$.

Let $\varrho : \mathbb{R}^3 \to \mathbb{R}$ be a $C^1$ homogeneous function of degree $r$, i.e. $\varrho(tz) = t^r \varrho(z)$ for each $z \in \mathbb{R}^3$, $t \in \mathbb{R}$ and suppose that the cone $K_\varrho = \{ n : \varrho(n) \geq 0 \}$ has nonempty interior. Then using (6)

$$\hat{\varrho}(n) = \langle D\varrho(n), \hat{n} \rangle = \langle D\varrho(n), (-DF(x)^T n + \text{Tr}(DF(x))n) \rangle = -\langle D\varrho(n), DF(x)^T n \rangle + \text{Tr}(DF(x))\langle D\varrho(n), n \rangle = -\langle D\varrho(n), DF(x)^T n \rangle \text{ whenever } \varrho(n) = \frac{1}{r} \langle D\varrho, n \rangle = 0.$$

Thus if the cone $K_\varrho$ is to remain invariant under the dynamics (6) of the surface normal $n(t)$, we need $\langle DF(x)D\varrho(n), n \rangle \leq 0$ whenever $\varrho(n) = 0$ and $x \in C$. Since for the Lotka-Volterra system $DF(x) = \Lambda - \sum_{i=1}^3 x_i \Omega_i$ where $\Lambda = \text{diag}[(a_{11}, a_{22}, a_{33})]$ is the diagonal matrix of diagonal elements of $A$, and

$$\Omega_1 = \begin{pmatrix} 2a_{11} & a_{12} & a_{13} \\ 0 & a_{21} & 0 \\ 0 & 0 & a_{31} \end{pmatrix}, \Omega_2 = \begin{pmatrix} a_{12} & 0 & 0 \\ a_{21} & 2a_{22} & a_{23} \\ 0 & 0 & a_{32} \end{pmatrix}, \Omega_3 = \begin{pmatrix} a_{13} & 0 & 0 \\ 0 & a_{23} & 0 \\ a_{31} & a_{32} & 2a_{33} \end{pmatrix},$$

a sufficient condition for invariance is

$$-\langle \Lambda D\varrho(n), n \rangle + \sum_{i=1}^3 x_i \langle \Omega_i D\varrho(n), n \rangle \geq 0 \text{ when } \varrho(n) = \frac{1}{r} \langle D\varrho, n \rangle = 0, \forall x \in C. \quad (21)$$

**Lemma 7 (Cone invariance)** A sufficient condition for invariance of a given cone $K_\varrho = \{ n \in C : \varrho(n) \geq 0 \}$, for $\varrho$ homogeneous degree $r > 0$, under (6) is that

$$\langle D\varrho(n), \Lambda n \rangle \leq 0 \quad \text{whenever } \varrho(n) = 0,$$

(22)

together with

$$\forall i \in I_3, \langle \Omega_i D\varrho(n), n \rangle \geq 0 \quad \text{whenever } \varrho(n) = 0. \quad (23)$$

For the asymmetric May-Leonard system (2), $\Lambda$ is the identity matrix and by Euler’s theorem $\langle D\varrho(n), n \rangle = r\varrho(n)$ and the condition (22) becomes redundant.

Recall that we wish to confine the Gaussian image $S(M_t)$ of an evolving surface, so that $\Theta(t)$ remains definite for $t > 0$. In terms of $\theta(t)$ in (18), this means that $\det \theta(t) > 0$ for $t > 0$. Recall that $\delta_L(v) = \langle v, L v \rangle$ and that $\delta_L(v) = 0$ if and only if $\det L = 0$. We define $K_L = \{ n \in C : \delta_L(1/n) \geq 0 \}$ which is a cone. Our broad aim, then, is to show that there is a cone $K_\varrho$, defined via a homogeneous function $\varrho$ as above, which is invariant under the normal dynamics (6), and which is a subset of $K_L$, since this is then enough to ensure that $\Theta(t)$ is either positive or negative definite for all $t > 0$.

**Theorem 4 (Convex and concave carrying simplices)** Let $M$ be a plane with outward unit normal $N \gg 0$ such that $M_0 = M \cap C^0 \neq \emptyset$, and $\varphi_t : C \to C$ the flow generated by the totally competitive Lotka-Volterra system (1). Suppose that there
exists a cone \( K_P \subset K_L \) which is invariant under the normal dynamics (6). Then if \( \theta(0) \) is positive(negative) definite, \( M_t = \varphi_t(M_0) \) is a sequence of concave(convex) Lipschitz surfaces that converges uniformly to a concave(convex) carrying simplex \( \Sigma \).

5.2. Conditions for an invariant cone

Let \( S \) be a symmetric \( 3 \times 3 \) matrix with one positive eigenvalue \( \lambda_3 \) and two negative eigenvalues \(-\lambda_1, -\lambda_2\). Then there is an orthogonal matrix \( W \) such that \( W^T \text{diag}([-\lambda_1, -\lambda_2, \lambda_3]) W = S \). Hence \( g_S(\chi) = \langle \chi, S \chi \rangle = \langle W \chi, \text{diag}(|\lambda|) W \chi \rangle = \lambda_3(W \chi)^2 - \lambda_1(W \chi)^2 - \lambda_2(W \chi)^2 \) and

\[
\varrho_S(\chi) = 0 \iff \chi = \mu W^T \left( \sqrt{\frac{\lambda_1}{\lambda_1}} \cos s, \sqrt{\frac{\lambda_2}{\lambda_2}} \sin s, 1 \right)^T, \mu \in \mathbb{R}_+, s \in [0, 2\pi).
\]

Hence the matrix \( S \) defines an ellipsoidal cone in \( \mathbb{R}^3 \) with boundary \( \varrho_S^{-1}(0) \).

Given a unit vector \( \ell \gg 0 \), then \( K = \{ n \in \mathbb{R}^3 : \langle \ell, n \rangle \geq |\gamma| n \} \) where \( \gamma \in (0, 1) \) is a solid convex cone with nonempty interior whose boundary subtends an angle \( \cos^{-1} \gamma \) with \( \ell \). If \( \gamma > \max_{i \in I_3} \sqrt{1 - \ell_i^2} \) then \( K \setminus \{0\} \subset C^0 \). It is easy to see that \( K = K_P \) where

\[
K_P = \{ n \in \mathbb{R}^3 : \langle n, P n \rangle \geq 0, \langle n, \ell \rangle \geq 0 \}, \quad P = \Phi - \gamma^2 I, \quad \Phi = (\langle \ell, \ell \rangle).
\]

For \( K_P \) to be invariant under (6), we need \( \langle n, (PDF(x)^T + DF(x) P)n \rangle \leq 0 \) whenever \( \langle n, P n \rangle = 0 \). This is ensured if for each \( i \in I_3 \) we have

\[
\langle n, (\Omega_i P + P \Omega_i^T) n \rangle \geq 0 \quad \text{whenever} \quad \langle n, P n \rangle = 0.
\]

One way of proceeding would be to follow the methods developed in [26, 22, 1] where it is used that \( \langle n, P A n \rangle > 0 \) on \( \langle n, P n \rangle = 0 \) if and only if there exists \( \xi \) such that \( (PA)^S + \xi P \) is positive definite. In our case, however, we find it more convenient to use an explicit approach using the one-parameter parameterization of the intersection of the cone \( \langle n, P n \rangle = 0 \) with the unit sphere as now described. The real symmetric matrix \( \Phi \) has eigenvalues \( \{0, 0, 1\} \) (since the third eigenvalue is \( \ell_1^2 + \ell_2^2 + \ell_3^2 = 1 \)), which in turn means that \( P \) has eigenvalues \( \{-\gamma^2, -\gamma^2, 1 - \gamma^2\} \). Moreover, \( \ell \) is an eigenvector of \( P \) associated with the eigenvalue \( 1 - \gamma^2 \). Two linearly independent eigenvectors for the eigenvalues \(-\gamma^2\) are \((-\ell_2, \ell_1, 0)^T\) and \((-\ell_3, 0, \ell_1)^T\). From these, the Gram-Schmidt process can be used to form the orthogonal matrix

\[
E = \begin{pmatrix}
\frac{-\ell_2}{\sqrt{\ell_1^2 + \ell_2^2}} & \frac{\ell_1}{\sqrt{\ell_1^2 + \ell_2^2}} & 0 \\
\frac{-\ell_2}{\sqrt{\ell_1^2 + \ell_2^2}} & -\frac{\ell_1}{\sqrt{\ell_1^2 + \ell_2^2}} & \sqrt{\ell_1^2 + \ell_2^2} \\
\frac{\ell_1}{\ell_2} & \frac{\ell_2}{\ell_2} & \ell_3
\end{pmatrix}.
\]

We then have \( E P E^T = \text{diag}([-\gamma^2, -\gamma^2, 1-\gamma^2]) \) and so \( n = E^T (\sqrt{\frac{1-\gamma^2}{\gamma}} \cos s, \sqrt{\frac{1-\gamma^2}{\gamma}} \sin s, 1)^T \) and we may take the parameterization

\[
n(\tau) = \begin{pmatrix}
\ell_1 \left( -2r \tau \ell_3 + \tau^2 \gamma + \gamma \\ 2r \tau \left( \ell_1^2 + \ell_2^2 \right) + \gamma \ell_3 \left( \tau^2 + 1 \right) \\
\ell_2 \left( -2r \tau \ell_3 + \tau^2 \gamma + \gamma \\ 2r \tau \left( \ell_1^2 + \ell_2^2 \right) + \gamma \ell_3 \left( \tau^2 + 1 \right) \\
\ell_3 \left( -2r \tau \ell_3 + \tau^2 \gamma + \gamma \\ 2r \tau \left( \ell_1^2 + \ell_2^2 \right) + \gamma \ell_3 \left( \tau^2 + 1 \right) \\
\end{pmatrix}
\]

where \( r = \sqrt{(1-\gamma^2)/(\ell_1^2 + \ell_2^2)} \) and \( \sin s = 2\tau/(1+\tau^2), \cos s = (1-\tau^2)/(1+\tau^2) \). If \( \gamma > \max_{i \in I_3} \sqrt{1 - \ell_i^2} \) then \( n(\tau) \in C^0 \) for each \( \tau \).

Let \( q_i(\tau) = -\langle \Delta P n(\tau), n(\tau) \rangle \) and for each \( i \in I_3 \), \( q_i(\tau) = \langle n(\tau), (P \Omega_i)^S n(\tau) \rangle \).

These four functions are quartics in \( \tau \). If \( q_i(0) > 0 \) and the quartic \( q_i(\tau) = 0 \) has no real roots, then \( q_i(\tau) > 0 \) for all \( \tau \). We have thus shown:
Lemma 8 (Invariance of $K_P$) Let $\ell \gg 0$, and $\gamma \in (\max_{i \in I_3} \sqrt{1-T_i^2}, 1)$ be given and define the cone

$$K_P = \{n \in \mathbb{R}^3 : \langle n, Pn \rangle \geq 0, \langle \ell, n \rangle \geq 0\}, \quad P = ((\ell_i \ell_j)) - \gamma^2 I. \quad (26)$$

Define also $n(\tau)$ via (25), $q_0(\tau) = -\langle APn(\tau), n(\tau) \rangle$, and $q_i(\tau) = \langle n(\tau), (P\Omega_i)^S n(\tau) \rangle$ for each $i \in I_3$, with each $\Omega_i$ given by (20). Then if

$$q_i(0) > 0 \quad \forall i \in \{0, 1, 2, 3\}$$

and none of the 4 quartics $q_i(\tau)$ have a real root

then $K_P$ is an invariant cone for the normal dynamics (6).

If (1) is the asymmetric May-Leonard system (2) then we have the simplification that $q_0 \equiv 0$.

Since each $q_i$ is a quartic, we may use explicit inequalities on the coefficients of quartics (see Appendix B) to verify when all the $q_i$ have no real roots.

5.3. Conditions for $K_P \subset K_L$

We now seek a condition that the invariant cone $K_P$ lies within the cone $K_L$, since in that case $\det \Theta \geq 0$. Recall that for $n \in C^0$, by $\frac{1}{n}$ we mean the vector with components $\frac{1}{n_i}$ for $i \in I_3$ in turn. We have a means of ensuring that the surface normal is constrained to a positive cone $K_P$ defined by a matrix $P$, and we have just shown that when $v = \frac{1}{n}$ is constrained to a second positive cone $K_L$ defined by a matrix $L$ the determinant $\det \theta$ cannot change sign.

Lemma 9 (Condition that $K_P \subset K_L$) Define

$$v(\tau) = (n_2(\tau)n_3(\tau), n_1(\tau)n_3(\tau), n_1(\tau)n_2(\tau))^T,$$

where $n_i(\tau)$ are given by (25), and $r(\tau) = \langle v(\tau), L v(\tau) \rangle$. If the degree 8 polynomial $r(\tau)$ has no real roots and $r(0) > 0$ then $K_P \subset K_L$.

Lemma 9 can be applied by using the Sturm theorem for roots of polynomials (see Appendix A).

We also offer an alternative test that $K_P \subset K_L$. Recall that $g_P(n) = \langle n, Pn \rangle$ and that if $\gamma > \max_{i \in I_3} \sqrt{1-T_i^2}$ then $g_P^{-1}(0) \cap C$ is the boundary of the cone $K_P$. If $(p,q,1) \in g_P^{-1}(0) \cap C$ then $s(p,q,1) \in g_P^{-1}(0) \cap C$ for any $s > 0$. Similarly $(u,v,1) \in \delta_L^{-1}(0) \cap C$ then $s(u,v,1) \in \delta_L^{-1}(0) \cap C$ for any $s > 0$. Therefore to show $K_P \subset K_L$ we only need show that

$$\forall p,q \in \mathbb{R}_+, g_P(p,q,1) \geq 0 \Rightarrow \delta_L(q,p,pq) \geq 0. \quad (27)$$

We give an explicit calculation of this condition in Example 5 of section 7.

In Appendix B, lemma 10 gives conditions that the ellipse $g_P(p,q,1) \geq 0$ lies inside a rectangle $B$. With $\pi_K = \{(u,v,1) \in C : \delta_L(v,u,uv) \geq 0\}$ we may simply check that $B \subset \pi_K$, and this is equivalent to checking whether four quartics have no real roots.

6. Local geometry of $\Sigma$ and global stability of an interior fixed point

We now demonstrate how to determine, for a given interaction matrix $A$, whether the carrying simplex is convex, concave or saddle-like in a neighbourhood of an interior fixed point. Then we indicate how the global stability of that interior fixed point depends on the curvature of $\Sigma$. 
In the following we assume that an interior fixed point \( p \) exists and that the carrying simplex is at least \( C^2 \) in a neighbourhood of \( p \). The eigenvalue in the direction normal to the \( \Sigma \) at \( p \) is negative, so that from the Stable manifold theorem (see, for example, [23]) if \( p \) is repelling in \( \Sigma \) then the unstable manifold through \( p \) is analytic (because the Lotka-Volterra \( F \) is analytic) and of dimension 2.

**Theorem 5** Suppose that the carrying simplex \( \Sigma \) of (1) is \( C^2 \) in a neighbourhood of an interior fixed point \( p \). If \( \theta \) is the \( 2 \times 2 \) square matrix at \( p \) defined by (18) then there is a neighbourhood of \( p \) in which the surface \( \Sigma \) is

- Strictly convex if \( \theta \) at \( p \) has two positive eigenvalues
- Strictly concave if \( \theta \) at \( p \) has two negative eigenvalues
- Saddle-like if \( \theta \) at \( p \) has eigenvalues of different sign.

**Proof.** Let \( p \in \Sigma^0 \) be a fixed point of (1) with strongly-balanced tangent plane with positive normal \( N^* \). \( N^* \) is a positive left unit eigenvector of \( DF(p) \). We will use this normal to find the steady matrix representation \( \Psi^* \) of the 2nd fundamental form from (9), via the formula

\[
\Psi^* = -\frac{\Theta^*}{(N^*, DF(p)N^*)} = -\frac{1}{\lambda_0} \Theta^*,
\]

where \( \lambda_0 > 0 \) is the dominant eigenvalue of \(-DF(p)\). If \( \theta \) has two negative eigenvalues at \( p \), it also has two negative eigenvalues in a small neighbourhood of \( p \), and so \( \Theta^* \) has two positive eigenvalues in a neighbourhood of \( p \). Hence, in that case, \( \Psi^* \) has two positive eigenvalues in a neighbourhood of \( p \), so that the carrying simplex is locally convex at \( p \). The other cases are similar. \( \square \)

The method of the Split Lyapunov function as introduced by Zeeman and Zeeman [37] enables a direct link to the geometry of the surface \( \Sigma \) near an interior fixed point and the stability of the fixed point. Our matrix \( \theta \) here plays the same role as the matrix \( \mu = (AH^{-1})^SR \) appearing in section 6 of [37]. Indeed, \( \mu \) has two positive (negative) eigenvalues if and only of \( \theta \) has two positive (negative) eigenvalues. Theorem 6.7 of [37] links positive eigenvalues of \( \mu \) to global stability of an interior fixed point. In this case the flow across the tangent plane to \( \Sigma \) at the fixed point is downwards, and this results in local convexity of \( \Sigma \). Similarly if \( \theta \) has two negative eigenvalues \( \Sigma \) is locally concave and finally if \( \theta \) has eigenvalues of opposite sign it is locally saddle-like. Similarly, a \( \theta \) with two negative eigenvalues means that the flow across \( \Sigma \) is upwards and results in a concave carrying simplex. Thus we obtain:

**Corollary 6** Let \( \Sigma \) be the carrying simplex of (1). If \( \theta \) is the \( 2 \times 2 \) square matrix defined by (18) then an interior fixed point \( p \) is

- globally attracting in \( C^0 \) if \( \Sigma \) near \( p \) is convex
- globally repelling in \( \Sigma^0 \) if \( \Sigma \) near \( p \) is concave.

### 7. Example Applications

#### 7.1. Example 1: A carrying simplex with curvature that changes sign

Consider system (1) with

\[
\mathcal{A} = \begin{pmatrix} 1 & \varepsilon & \delta \\ \varepsilon & 1 & \delta \\ \delta & \delta & 1 \end{pmatrix}, \quad b = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix},
\]

(28)
where \(0 < \varepsilon < 1\) and \(0 < \delta < 1\). It is shown in [36, Counterexample 6.1] that, although all the edges of \(\Sigma\) are concave, \(\Sigma\) is not globally concave if \(\delta > 2 - \frac{4}{3+\varepsilon}\). We consider the case where \(\varepsilon = 1/4\) and \(\delta = 3/4\), so that the condition \(\delta > 2 - \frac{4}{3+\varepsilon}\) holds. There is no interior fixed point, but there are boundary fixed points at \((4/5, 4/5, 0)^T\), \((4/7, 0, 4/7)^T\) and \((0, 4/7, 4/7)^T\). The boundary fixed point \((4/5, 4/5, 0)^T\) is globally attracting on \(C^0\). With \(e_1 = (1, 0, 0)^T\), \(e_2 = (0, 1, 0)^T\) and \(e_3 = (0, 0, 1)^T\), we find that the eigenvalues of the Jacobian at the axial fixed points \(e_1, e_2, e_3\) are \(\{−1, 3/4, 1/4\}\), \(\{3/4, −1, 1/4\}\), \(\{1/4, 1/4, −1\}\) respectively. Hence each of the axial fixed points \(e_i\) has a 2-dimensional local unstable manifold \(U_i\) which is analytic because the vector field for the flow is analytic. Moreover, each \(U_i \cap C \subset \Sigma\), so that \(\Sigma\) is smooth in a sufficiently small neighbourhood of each axial fixed point. Now let us consider the sign of the curvature of \(\Sigma\) at each \(e_i\). The tangent planes at \(e_1, e_2, e_3\) have normals \((5/3, 5/21, 1)^T\), \((5/21, 5/3, 1)^T\) and \((3/5, 3/5, 1)^T\). We find that
\[
\theta(e_1) = \begin{pmatrix} -36/5 & 9/2 \\ 9/2 & -13/5 \end{pmatrix}, \theta(e_2) = \begin{pmatrix} -36/5 & 27/10 \\ 27/10 & -4/5 \end{pmatrix}, \theta(e_3) = \begin{pmatrix} -5 & 5/2 \\ 5/2 & -4/3 \end{pmatrix}
\]
with respective eigenvalues \(\frac{1}{10}(-49 \pm \sqrt{2554}) \approx -9.95, 0.154, \frac{1}{10}(-40 \pm \sqrt{1753}) \approx -8.2, 0.19\), and \(\frac{1}{6}(-19 \pm \sqrt{346}) \approx -6.27, -0.066\). Consequently \(\Psi(e_i)\) is negative definite for \(i = 3\) and has eigenvalues of opposite sign when \(i \in I_2\). By smoothness near the axial fixed points we conclude that the second fundamental form of \(\Sigma\) is negative definite sufficiently close to \(e_3\) where \(\Sigma\) is convex, but close to \(e_1, e_2\) where the second fundamental form will have eigenvalues of opposite sign, \(\Sigma\) will have negative curvature (see figure 2).

**Figure 2.** Carrying simplex for which the curvature is not single-signed. Close to \(e_1, e_2\) the curvature is negative (red, dark shading), but elsewhere it is nonnegative (green, lighter shading).

### 7.2. Example 2: A family of convex or concave carrying simplices

Consider the asymmetric May-Leonard system (2) characterised by the interaction matrix
\[
\mathcal{A} = \begin{pmatrix} 1 & \alpha & \beta \\ \varepsilon & 1 & \beta \\ \varepsilon & \alpha & 1 \end{pmatrix}.
\]
The matrix $L$ of (14) is given by

$$L = \begin{pmatrix} 0 & 2(\alpha - 1)(\varepsilon - 1) & 2(\beta - 1)(\varepsilon - 1) \\ 2(\alpha - 1)(\varepsilon - 1) & 0 & 2(\alpha - 1)(\beta - 1) \\ 2(\beta - 1)(\varepsilon - 1) & 2(\alpha - 1)(\beta - 1) & 0 \end{pmatrix}.$$ 

Thus if $(\alpha - 1)(\varepsilon - 1) \geq 0$ and $(\beta - 1)(\varepsilon - 1) \geq 0$ then $\Delta L(N) \geq 0$ for all unit vectors $N \in C$. Thus we have either a convex or concave carrying simplex. Now apply Theorem 3 using for $M_0$ the unit simplex in $C$ which has outward unit normal $\iota$. Then at $t = 0$ the matrix $\theta$ in (18) is given by

$$\theta = \begin{pmatrix} 2(\alpha + \varepsilon - 2) & 2 - 2\alpha \\ 2 - 2\alpha & 2(\alpha + \beta - 2) \end{pmatrix}.$$ 

We find $\det \theta = (\alpha - 1)(\beta - 1) + (\beta - 1)(\varepsilon - 1) + (\varepsilon - 1)(\alpha - 1)$ and $\text{Tr}(\theta) = 4\alpha + 2\beta + 2\varepsilon - 2$. If $\alpha, \beta, \varepsilon \geq 1$ then (29) is satisfied and $\text{Tr}(\theta) > 0$ and so $\theta$ is positive definite. In this case, by theorem 3 $\Sigma$ is concave. On the other hand, if $\alpha, \beta, \varepsilon \leq 1$ then (29) is satisfied and $\text{Tr}(\theta) < 0$ and so $\theta$ is negative definite and $\Sigma$ is convex.

7.2.1. Example 2: A convex carrying simplex  
We take

$$\mathcal{A} = \begin{pmatrix} 1 & 1/2 & 1/3 \\ 3/4 & 1 & 2/5 \\ 3/5 & 2/7 & 1 \end{pmatrix}.$$ 

The computed carrying simplex along with orbits converging to the unique interior fixed point $(40/61, 25/61, 48/61)^T$ are shown in in the left plot of figure 3.

**Figure 3.** Left: Example 2: Global convergence to a convex carrying simplex. Right: Example 3: Concave carrying simplex.

$$\Omega_1 = \begin{pmatrix} 2 & 1/2 & 1/3 \\ 0 & 3/4 & 0 \\ 0 & 0 & 3/5 \end{pmatrix}, \quad \Omega_2 = \begin{pmatrix} 1/2 & 0 & 0 \\ 3/4 & 2 & 2/5 \\ 0 & 0 & 2/7 \end{pmatrix}, \quad \Omega_3 = \begin{pmatrix} 1/3 & 0 & 0 \\ 0 & 2/5 & 0 \\ 3/5 & 2/7 & 2 \end{pmatrix}.$$
We now apply lemma 8 with \( \ell = \iota \) and \( \gamma = \sqrt{\frac{707}{1041}} \). Here we find

\[
q_1(\tau) = \left( \frac{11452693 + 9935\sqrt{354207}}{195062580} \right) \tau^4 + \left( \frac{25975180\sqrt{3} + 21838\sqrt{118069}}{195062580} \right) \tau^3 \\
+ \left( \frac{12161107\tau^2 + (21838\sqrt{118069} - 25975180\sqrt{3}) \tau}{195062580} \right) + \left( \frac{11452693 - 9935\sqrt{354207}}{195062580} \right)
\]

\[
q_2(\tau) = \left( \frac{6190189 - 7097\sqrt{354207}}{65020860} \right) \tau^4 + \left( \frac{83974\sqrt{118069} - 72730504\sqrt{3}}{455146020} \right) \tau^3 \\
+ \left( \frac{4672159\tau^2 + (72730504\sqrt{3} + 83974\sqrt{118069}) \tau}{455146020} \right) + \left( \frac{6190189 + 7097\sqrt{354207}}{65020860} \right)
\]

\[
q_3(\tau) = \left( \frac{5296238\tau^2 + (3093045\sqrt{3} - 4\sqrt{118069}) \tau}{341359515} \right) + \left( \frac{83974\sqrt{118069} - 72730504\sqrt{3}}{48765645} \right) \tau^7
\]

We now use the Sturm Theorem for counting roots of a polynomial (see Appendix B), implemented in Mathematica as “CountRoots” to show that none of the \( q_i, i \in I_3 \) have real roots. Since each \( q_i(0) > 0 \) we conclude via lemma 8 that the cone \( K_P \) is invariant under the normal dynamics (6). Moreover, for this interaction matrix,

\[
L = \begin{pmatrix}
-\frac{9}{100} & \frac{151}{280} & \frac{29}{100} \\
\frac{151}{280} & -\frac{9}{100} & \frac{143}{210} \\
\frac{29}{100} & \frac{143}{210} & -\frac{225}{210}
\end{pmatrix}
\]

which gives

\[
r(\tau) = \Delta_L(n(\tau)) = \\
\frac{(4804209544 + 1612281\sqrt{354207}) \tau^8}{122889425400} + \frac{(-26006502186\sqrt{3} - 566662042\sqrt{118069}) \tau^7}{860225977800}
\]

\[
+ \frac{(12966060100 + 22571934\sqrt{354207}) \tau^6}{860225977800} + \frac{(50836884123\sqrt{3} + 642367033\sqrt{118069}) \tau^5}{430112988900}
\]

\[
+ \frac{(34821800351\tau^4 + (1284734066\sqrt{118069} - 10077376624\sqrt{3}) \tau^3}{107528247225} + \frac{860225977800}{860225977800} \\
+ \frac{(12966060100 - 22571934\sqrt{354207}) \tau^2}{860225977800} + \frac{(26006502186\sqrt{3} - 566662042\sqrt{118069}) \tau}{860225977800}
\]

\[
+ \frac{33629466808 - 11285967\sqrt{354207}}{860225977800}
\]

has no real roots via the Sturm Theorem and \( r(0) = \frac{33629466808 - 11285967\sqrt{354207}}{860225977800} \approx 0.313 > 0 \), which shows that \( r(\tau) > 0 \) for all \( \tau \). Hence by lemma 9 \( \det \Theta > 0 \) for all \( t \).

Finally, at \( t = 0 \)

\[
\theta = \begin{pmatrix}
-\frac{3}{2} & \frac{419}{420} \\
\frac{419}{420} & -\frac{92}{35}
\end{pmatrix}
\]

which has negative trace and hence by theorem 4 \( \Sigma \) is convex.
7.3. Example 3: A concave carrying simplex

The interaction matrix is given by

\[ A = \begin{pmatrix}
1 & 5/4 & 3/2 \\
7/5 & 1 & 8/5 \\
11/10 & 3/2 & 1
\end{pmatrix}. \]

There is an interior fixed point at \((2/11, 21/55, 5/22)^T\). For the \(\Omega_i\) we have:

\[ \Omega_1 = \begin{pmatrix}
2 & 5/4 & 3/2 \\
0 & 7/5 & 0 \\
0 & 0 & 11/10
\end{pmatrix}, \quad \Omega_2 = \begin{pmatrix}
5/4 & 0 & 0 \\
7/5 & 2 & 8/5 \\
0 & 0 & 3
\end{pmatrix}, \quad \Omega_3 = \begin{pmatrix}
3/2 & 0 & 0 \\
0 & 8/5 & 0 \\
11/10 & 3/2 & 2
\end{pmatrix}. \]

As in the previous example we choose \(\ell = \iota\), but now \(\gamma = \frac{\sqrt{21}}{21}\). The conditions of lemma 8 are then satisfied and we have \(K_P\) as an invariant cone for the normal dynamics.

For the matrix \(L\),

\[ L = \begin{pmatrix}
-9/100 & 7/40 & 9/25 \\
7/40 & -1/16 & 9/40 \\
9/20 & 9/40 & -1/100
\end{pmatrix}, \]

we find that \(r(0) > 0\) and \(r(\tau) > 0\) for all \(\tau\), so that by lemma 9 \(K_P \subset K_L\). Finally, at \(t = 0\)

\[ \theta = \begin{pmatrix}
13/20 & -23/20 \\
-23/20 & 11/5
\end{pmatrix} \]

which has positive trace, so that by theorem 4 \(\Sigma\) is concave.

7.4. Example 4: The Symmetric May-Leonard model

Here the competition model specialises to

\[ \begin{align*}
\dot{x}_1 &= x_1(1 - x_1 - \alpha x_2 - \beta x_3) \\
\dot{x}_2 &= x_2(1 - x_2 - \beta x_1 - \alpha x_3) \\
\dot{x}_3 &= x_3(1 - x_3 - \alpha x_1 - \beta x_2)
\end{align*} \]

where \(\alpha, \beta > 0\). The steady states are \((0, 0, 0)^T, e_1, e_2, e_3\), an interior steady state \(\frac{1}{1+\alpha+\beta}(1, 1, 1)^T\), and when either \(\alpha < 1, \beta < 1 \) or \(\alpha > 1, \beta > 1\) there are three more steady states \(\frac{1}{1-\alpha\beta}(1 - \alpha, 1 - \beta, 0)^T, \frac{1}{1-\alpha\beta}(1 - \beta, 0, 1 - \alpha)^T\) and \(\frac{1}{1-\alpha\beta}(0, 1 - \alpha, 1 - \beta)^T\). Let us assume that \(\alpha, \beta < 2\) so that 1 is the dominant eigenvalue of \(-DF(e_1)\) and a corresponding (right) eigenvector of \(DF(e_1)^T\) is \((\frac{2-\alpha}{\beta}, \frac{\alpha(2-\alpha)}{\beta(2-\beta)}, 1)^T\)). Similarly for points \(e_2, e_3\) we have eigenvectors \((\frac{\beta(\beta-2)}{\alpha(\alpha-2)}, \frac{2-\beta}{\beta}, 1)^T\)) and \((\frac{\alpha}{\beta-2}, \frac{\beta}{\alpha-2}, 1)^T\)). The unit right eigenvector of \(DF^T\) for the smallest eigenvalue at the interior fixed point is \(\iota\).

We take the cone \(K_P\) to be an ellipsoidal cone subtending an angle \(\cos^{-1} \gamma\) to \(\ell\). The \(\Omega_i\) are given by

\[ \Omega_1 = \begin{pmatrix}
2 & \alpha & \beta \\
0 & \beta & 0 \\
0 & 0 & \alpha
\end{pmatrix}, \quad \Omega_2 = \begin{pmatrix}
\alpha & 0 & 0 \\
\beta & 2 & \alpha \\
0 & 0 & \beta
\end{pmatrix}, \quad \Omega_3 = \begin{pmatrix}
\beta & 0 & 0 \\
0 & \alpha & 0 \\
\alpha & \beta & 2
\end{pmatrix}. \]

By symmetry, to find an invariant cone \(K_P\) we need only apply lemma 8 for \(\Omega_1\). For a given \(\alpha, \beta\) we may use lemma 8 to find values of \(\gamma\) for which \(K_P\) invariant.
Alternatively, we may fix $\gamma$ and use lemma 8 to determine the convex region in $\alpha, \beta$-space for which there is an invariant cone. We chose to do the latter. In figure 4 we show this region for $\gamma = \frac{1}{2} \left( 1 + \sqrt{\frac{2}{3}} \right)$.

![Figure 4](image)

Figure 4. Region of $\alpha, \beta$ space, as calculated using lemma 8, for which $K_P$ is invariant when $\gamma = \frac{1}{2} \left( 1 + \sqrt{\frac{2}{3}} \right)$.

Now let us examine the regions in $C^0$ for which $\theta$ at $t = 0$ is definite. In this example $L$, as defined in (14), is given by

$$L = \begin{pmatrix} -\frac{(A + B)^2}{2} & A^2 + B^2 & \frac{A^2 + B^2}{2} \\ A^2 + B^2 & -\frac{(A + B)^2}{2} & \frac{A^2 + B^2}{2} \\ A^2 + B^2 & \frac{A^2 + B^2}{2} & -\frac{(A + B)^2}{2} \end{pmatrix},$$

and $A = \alpha - 1$, $B = 1 - \beta$. Let $\gamma > 0$ be given and consider the circle of points $N = 1/v$ of unit modulus satisfying $\langle 1, N \rangle = \langle 1, \frac{1}{v} \rangle = \frac{1}{v_1} + \frac{1}{v_2} + \frac{1}{v_3} = \sqrt{3}\gamma$. Then

$$3\gamma^2 = \left( \sum_{i=1}^{3} \frac{1}{v_i} \right)^2 = \sum_{i=1}^{3} \left( \frac{1}{v_i} \right)^2 + 2 \sum_{i<j} \frac{1}{v_i v_j} = 1 + 2 \sum_{i<j} \frac{1}{v_i v_j},$$

so that

$$\frac{3\gamma^2 - 1}{2} = \frac{v_1 + v_2 + v_3}{v_1 v_2 v_3},$$

and $\sqrt{3}\gamma v_1 v_2 v_3 = v_1 v_2 + v_2 v_3 + v_3 v_1$,

which gives $2(v_1 + v_2 + v_3) = (3\gamma^2 - 1)v_1 v_2 v_3$ and

$$v_1^2 + v_2^2 + v_3^2 = \left( \frac{3\gamma^2 - 1}{2} \right)^2 (v_1 v_2 v_3)^2 - 2(v_1 v_2 + v_2 v_3 + v_3 v_1)$$

$$= \left( \frac{3\gamma^2 - 1}{2} \right)^2 (v_1 v_2 v_3)^2 - 2\sqrt{3}v_1 v_2 v_3.$$

But

$$\delta_L(v) = -\frac{(A + B)^2(v_1^2 + v_2^2 + v_3^2) + 2(A^2 + B^2)(v_1 v_2 + v_2 v_3 + v_3 v_1)}{2}$$

$$= 2\sqrt{3}\gamma(A^2 + B^2) + 2\gamma\sqrt{3}(A + B)^2 - v_1 v_2 v_3 \frac{(A + B)^2(3\gamma^2 - 1)^2}{4}$$

$$= 2\gamma\sqrt{3}(A + B)^2 - v_1 v_2 v_3 \frac{(A + B)^2(3\gamma^2 - 1)^2}{4}$$
so that $\delta_L(v) > 0$ whenever

$$\frac{8\sqrt{3}\gamma((A^2 + B^2) + (A + B)^2)}{(A + B)^2(3\gamma^2 - 1)^2} > v_1v_2v_3 = \frac{1}{N_1N_2N_3},$$

that is, whenever

$$N_1N_2N_3 > \frac{(A + B)^2(3\gamma^2 - 1)^2}{8\sqrt{3}\gamma((A^2 + B^2) + (A + B)^2)}.$$ 

Now the set $|N| = 1$ and $N_1 + N_2 + N_3 = \sqrt{3}\gamma$ is parameterized by

$$N = \left(\frac{\sqrt{1 - \gamma^2(\sqrt{3}\sin \vartheta + 3\cos \vartheta)}}{3\sqrt{2}} + \frac{\gamma}{\sqrt{3}},
\frac{\sqrt{1 - \gamma^2(\sqrt{3}\sin \vartheta - 3\cos \vartheta)}}{3\sqrt{2}} + \frac{\gamma - \sqrt{2 - 2\gamma^2\sin \vartheta}}{\sqrt{3}}\right)^T,$$

and for such points

$$N_1N_2N_3 = 5\gamma^3 + \sqrt{2}(1 - \gamma^2)^{3/2}\sin(3\theta) - 3\gamma$$

which has the minimum value

$$\frac{5\gamma^3 - \sqrt{2}(1 - \gamma^2)^{3/2} - 3\gamma}{6\sqrt{3}} > 0 \text{ if } \gamma \in \left(\sqrt{\frac{2}{3}}, 1\right),$$

so we require $\gamma \in \left(\sqrt{\frac{2}{3}}, 1\right)$. Let us take $\gamma = \frac{1}{2} \left(1 + \sqrt{\frac{2}{3}}\right)$, for which the inequality in (31) becomes

$$29\sqrt{6} + 49 > \frac{3(6\sqrt{2} + \sqrt{3})(A + B)^2}{4(A^2 + AB + B^2)},$$

which expands to give

$$\left(196 - 18\sqrt{2} - 3\sqrt{3} + 116\sqrt{6}\right)A^2 + 2\left(98 - 18\sqrt{2} - 3\sqrt{3} + 58\sqrt{6}\right)AB
+ \left(196 - 18\sqrt{2} - 3\sqrt{3} + 116\sqrt{6}\right)B^2 \geq 0.$$ 

This last expression is actually satisfied for all $A, B \in \mathbb{R}$. Hence $K_P \subset K_L$. Finally, at $t = 0$

$$\theta = \begin{pmatrix} 2(\alpha + \beta - 2) & -\alpha - \beta + 2 \\ -\alpha - \beta + 2 & 2(\alpha + \beta - 2) \end{pmatrix}$$

which shows, via theorem 4, that, for values of $\alpha, \beta$ in the parameter region where there is an invariant cone, $\Sigma$ is concave if $\alpha + \beta < 2$, convex if $\alpha + \beta > 2$. When $\alpha + \beta = 2$, it is easy to show that $\Sigma$ is the unit simplex in $C$. 

7.5. Example 5: A two-parameter competitive interaction model

Now consider the case where
\[ A = \begin{pmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \beta & \alpha & 1 \end{pmatrix}. \]

Here we find from (20) that
\[ \Omega_1 = \begin{pmatrix} 2 & \alpha & \beta \\ 0 & \beta & 0 \\ 0 & 0 & \beta \end{pmatrix}, \quad \Omega_2 = \begin{pmatrix} \alpha & 0 & 0 \\ \beta & 1 & \alpha \\ 0 & 0 & \alpha \end{pmatrix}, \quad \Omega_3 = \begin{pmatrix} \beta & 0 & 0 \\ 0 & \alpha & 0 \\ \beta & \alpha & 2 \end{pmatrix}. \]

and \( \delta_L(v) = -(A + B)^2 v_3^2 - 4AB(v_1 v_2 + v_1 v_2 + v_1 v_2). \) If \( \alpha = \beta = 1, \) we find that \( A = B = 0 \) and \( \det \Psi = 0, \) and in fact \( \Sigma \) is the unit simplex in \( C. \) Now consider the remaining possibilities. We consider only the case \( AB < 0. \) Numerical evidence suggests that for \( AB > 0 \) the carrying simplex is saddle-like, but we have not yet been able to prove this. We take \( \ell = \iota \) and the cone \( K_P \)

![Figure 5](image)

**Figure 5.** Region of \( \alpha, \beta \) space for example 2, as calculated using lemma 8, for which there exists an invariant ellipsoidal cone for the surface normal when \( \gamma = \frac{1}{2} \left( 1 + \sqrt{\frac{2}{3}} \right). \) The region is the intersection of the interiors of each region inside the 3 curves.

to be an ellipsoidal cone subtending an angle \( \gamma \) to \( \ell. \) We find that \( \delta_L(y, x, xy) = -xy \left( x(A + B)^2 + 4AB \right) + 4AB(x + 1) \) and \( \delta_L = 0 \) on
\[ y(x) = -\frac{4AB(x + 1)}{x(A + B)^2 + 4AB}. \]

The denominator vanishes when \( AB < 0 \) at \( x^* = -4AB/(A + B)^2 > 0. \) Moreover, \( y \to x^* \) as \( x \to \infty, \) so that, by symmetry we conclude that \( \delta_L \geq 0 \) if \( (x, y) \in [0, x^*)^2. \)
Now use lemma 10 from the Appendix to see that the ellipse \( \varrho_P(x, y, 1) = 0 \) is bounded by
\[
X_\pm = Y_\pm = \frac{1 \pm \sqrt{3(1 - \gamma^2)(3\gamma^2 - 1)}}{3\gamma^2 - 2}.
\]
Hence, using (27), \( K_P \) is contained in \( K_L \) if \( 0 \leq X_- \) and \( X_+ < x^* \), that is
\[
1 + \sqrt{3(1 - \gamma^2)(3\gamma^2 - 1)} < -\frac{4AB}{(A + B)^2}.
\]
With \( \gamma = \frac{1}{2} \left( 1 + \sqrt{\frac{3}{5}} \right) \) this reads
\[
\frac{4 + \sqrt{12\sqrt{6} - 17}}{2\sqrt{6} - 3} < -\frac{4AB}{(A + B)^2}. \tag{32}
\]
For example, by inspection of figure 5, the point \( \alpha = 3/5, \beta = 4/5 \) \((A = -2/5, B = 1/5)\) has an invariant cone when \( \gamma = \frac{1}{2} \left( 1 + \sqrt{\frac{2}{3}} \right) \), and \( x^* = -\frac{4AB}{(A + B)^2} = 8 \), so that (32) holds and \( K_P \subset K_L \). Moreover at \( t = 0 \) \( \det \theta > \left( \frac{16\sqrt{3} - 3}{3\gamma^2 - 1} \right) > 0 \), and since \( \alpha, \beta < 1 \), \( \theta \) has negative trace and so by theorem 4 \( \Sigma \) is concave. On the other hand the point \( \alpha = 5/4, \beta = 3/2 \) \((A = 1/4, B = -1/2)\) we also have \( -\frac{4AB}{(A + B)^2} = 8 \), but now at \( t = 0 \) \( \det \theta > 0 \) and \( \theta \) has positive trace, so that \( \Sigma \) is concave. The results are summarised in figure 6.

8. Discussion and Outlook

In this paper we have developed methods for studying the geometry of the carrying simplex for totally competitive 3-species Lotka-Volterra systems. Our method involves following the changing curvature of the image of a strongly balanced plane under the totally competitive flow. In a limited set of cases, convexity or concavity of the carrying simplex can be established without detailed knowledge of the Gaussian images of the evolving surface, but in general our method requires being able to confine the Gaussian images inside a suitable convex cone. The method works through establishing that the rate of change of the matrix representation of the second fundamental form is either positive or negative definite. If this can be done then theorem 4 shows that
the carrying simplex is concave (convex) if the initial rate of change of the second fundamental form is (positive) negative definite.

We have also shown that the geometry of the unique carrying simplex of a totally competitive Lotka-Volterra system can be linked to the stability of an interior fixed point. There is a connection between our work and the Split Lyapunov method introduced by Zeeman and Zeeman [37]. In the Split Lyapunov Method, the method works when it can be shown that all interior orbits eventually end up in a half space defined as the region above or below the tangent plane $T_p\Sigma$ to $\Sigma$ through the interior fixed point $p$. Once in the half-space there is a Lyapunov function that shows global attraction or repulsion around $p$. If all trajectories cross $T_p\Sigma$ in one direction, then if one follows the evolution of $T_p\Sigma$ under the flow $\varphi_t$, this means that the surface $\varphi_t(T_p\Sigma)$ bends below or above $T_p\Sigma$. Since the Lotka-Volterra vector field is quadratic, the bent surface is convex, concave or saddle-like for small enough time. We have shown that the bending of planes depends on the direction of the plane’s normal, and that provided the Gaussian image $S(M_t)$ of the evolving surface is confined to a suitable subset of $C = \mathbb{R}^3$, the evolving surface remains either convex or concave for all time and hence also in the limit. If $\Sigma$ is convex (concave) near an interior fixed point, that interior fixed point must be globally repelling (attracting), but when $\Sigma$ is saddle-like there may be global repulsion or attraction, or there may exist periodic orbits. More work is needed to determine when $\Sigma$ is saddle-like and how the geometry of $\Sigma$ relates to local and global stability in the saddle case. Most of the methods outlined in the paper can be extended to work for totally competitive Lotka-Volterra systems for more than 3 species.

Our numerical simulations suggest that carrying simplices exist outside the classes of totally competitive or type-K competitive systems. In figure 7 we give 3 examples of non-competitive systems that have carrying simplices. The surfaces were computed by solving the quasilinear pde (5) in polar coordinates. The use of polar coordinates simplifies the imposition of boundary conditions and also enables the computation of surfaces that do not project in a 1-to-1 way onto the faces of the first quadrant. It is clear that in the first example the curvature must change sign since there are regions where $\Sigma$ is convex and others where $\Sigma$ is concave. In future work we will seek conditions for existence of such carrying simplices, extend methods to deal with the saddle case and also investigate smoothness of $\Sigma$ by using that it is the limit of smooth surfaces, where often strong properties of each surface’s curvature can be established.

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References

Figure 7. Numerical simulations show that there are carrying simplices outside the class of totally competitive systems (and the type-K competitive systems studied by Liang & Jiang.) Parameters $b = (1, 1, 1)^T$, and left to right: (i) $A = \begin{pmatrix} 1 & -1/2 & -1 \\ 1/2 & 1 & -0.5 \\ 1/2 & 1/2 & 1 \end{pmatrix}$, (ii) $A = \begin{pmatrix} 1 & 2 & -1/2 \\ 1/2 & 1 & -1/2 \\ 1/2 & 1/2 & 1 \end{pmatrix}$, (iii) $A = \begin{pmatrix} 1 & 0 & 1 \\ 1 & 1 & 2 \\ 3 & -1/2 & 1 \end{pmatrix}$.

[8] Hirsch, M W 1988 Systems of differential equations that are competitive or cooperative III: competing species Nonlinearity 1 51–71
[16] Liang, X & Jiang, J 2003 The dynamical behavior of Type-K competitive Kolmogorov systems and its application to 3-dimensional Type-K competitive Lotka-Volterra systems Nonlinearity 16 785–801
Appendix A. Sturm theorem for counting roots of a polynomial

Let $p$ be a polynomial of positive degree $n$ with real coefficients. Define the sturm chain of polynomials $f_i, i \in I_m$ by $f_0 = p, f_1 = p', f_2 = -\text{rem}(f_0, f_1) = f_1 q_0 - f_0, f_3 = -\text{rem}(f_1, f_2) = f_2 q_1 - f_1, \ldots, 0 = -\text{rem}(f_{m-1}, f_m) = f_m q_{m-1} - f_{m-1}$, where the degree of $f_m$ is zero if $p$ has no repeated root.

For a given sturm sequence $f_i, i \in I_m$ we denote by $V_\varepsilon$ the number of sign changes in the sequence $\{f_0(x), f_1(x), \ldots, f_m(x)\}$, where zeroes are not counted.

**Theorem 6 (Sturm)** Let $p$ be a polynomial with sturm chain $f_i, i \in I_m$. Let $[a, b] \subset \mathbb{R}$ be an interval for which neither of a nor $b$ are roots or multiple roots of $p$. Then the number of distinct real roots of $p$ in $[a, b]$ is $V_a - V_b$.

Appendix B. Necessary and sufficient condition for a quartic to have no real roots

Consider the quartic $f(x) = a_0 x^4 + 4a_1 x^3 + 6a_2 x^2 + 4a_3 x + a_4$ where $a_i \in \mathbb{R}, i \in I_5$.

Define the following:

$$G = a_0^2 a_3 - 3a_0 a_1 a_2 + 2a_1^3, \quad H = a_0 a_2 - a_1^2, \quad I = a_0 a_4 - 4a_1 a_3 + 3a_2^2$$
Lemma 10

Let \( \varrho \) the final lemma provides a box which bounds the ellipse given by

\[
\sum_{ij} y_{corners} (p_i, p_j) \in \text{corners of points } p_i \end{align}
\]

Theorem 7 If \( a_0 > 0 \) then \( f(x) = 0 \) has no real roots if and only if

(i) \( \Delta = 0, G = 0, K = 0 \) and \( H > 0 \);

OR

(ii) \( \Delta > 0 \) and

(a) \( H \geq 0 \);

OR

(b) \( H < 0 \) and \( K < 0 \).

The final lemma provides a box which bounds the ellipse given by \( g_P(x, y, xy) = 0 \).

Lemma 10 Let \( P \) be a symmetric matrix with \( i, j \)th element \( p_{ij} = \ell_i \ell_j - \delta_{ij} \gamma^2 \) where \( \sum_{i=1}^{\text{dim}} \ell_i^2 = 1 \) and \( 1 > \gamma > \max_{i < \text{dim}} \sqrt{1 - \ell_i^2} \), and suppose that \( P \) has 2 negative eigenvalues and one positive eigenvalue. Define \( P : \mathbb{R}_+^2 \rightarrow \mathbb{R} \) by \( p(x, y) = g_P(x, y, 1) \). Then \( p^{-1}(0) \) is an ellipse \( E \) and \( E \) is contained in the box \( B \) with corners \( (X_+, Y_+), (X, Y), (X_-, Y_-) \) where

\[
X_{\pm} = \frac{\ell_1 \ell_3 \pm \sqrt{(1 - \gamma^2)(\gamma^2 - \ell_1^2)}}{(\gamma^2 - \ell_1^2)},
\]

\[
Y_{\pm} = \frac{\ell_2 \ell_3 \pm \sqrt{(1 - \gamma^2)(\gamma^2 - \ell_1^2)}}{(\gamma^2 - \ell_1^2)}.
\]

Proof. It is easy to compute that \( p(x, y) = g_P(x, y, 1) = (\ell_1 x + \ell_2 y + \ell_3)^2 - \gamma^2 (x^2 + y^2 + 1) \). If \( \gamma > \max_{i < \text{dim}} \sqrt{1 - \ell_i^2} \), then \( p^{-1}(0) \) is an ellipse \( E \) and the set of points \( p^{-1}(\geq 0) \) is the interior of \( E \). The ellipse \( E \) is contained in the box \( B \) with corners \( (X_+, Y_+), (X, Y), (X_-, Y_-) \) obtained by computing where \( E \) goes vertical or horizontal. Let \( y = y(x) \) be a local description of the ellipse near where its tangent is vertical. Then

\[
(\ell_1 x + \ell_2 y(x) + \ell_3)^2 - \gamma^2 (x^2 + y(x)^2 + 1) = 0, \tag{B.1}
\]

so that

\[
2(\ell_1 + \ell_2 y'(x)) (\ell_1 x + \ell_2 y(x) + \ell_3) - \gamma^2 (2x + 2y(x)y'(x)) = 0.
\]

At points where \( y' = 0 \), we have

\[
2\ell_1 (\ell_1 x + \ell_2 y(x) + \ell_3) - 2\gamma^2 x = 0,
\]

which can be rearranged to give

\[
x = \frac{\ell_1 \ell_3 + \ell_1 \ell_2 y(x)}{(\gamma^2 - \ell_1^2)}. \tag{B.1}
\]

Substituting this last expression in (B.1) we obtain

\[
\left( \ell_1 \left( \frac{\ell_1 \ell_3 + \ell_1 \ell_2 y(x)}{(\gamma^2 - \ell_1^2)} + \ell_2 y(x) + \ell_3 \right)^2 = \gamma^2 \left( \frac{\ell_1 \ell_3 + \ell_1 \ell_2 y(x)}{(\gamma^2 - \ell_1^2)} + y(x)^2 + 1 \right) \right)
\]

Solving this last quadratic for \( y(x) \) gives the desired values of \( Y_{\pm} \) and the calculation for \( X_{\pm} \) is similar. \( \square \)