On existence and uniqueness of the carrying simplex for competitive dynamical systems†

Morris W. Hirsch*

University of California, Berkeley University of Wisconsin, Madison

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Certain dynamical models of competition are shown to have a unique invariant hypersurface \( \Sigma_1 \), having simple geometry and topology, such that every non-zero tractory is asymptotic to a trajectory in \( \Sigma_1 \).

Keywords: dynamical systems, competition, population models, carrying simplex

Introduction

Consider a system of \( n \) competing species whose states are characterized by vectors in the closed positive cone \( K = [0, \infty)^n \subset \mathbb{R}^n \). When time is discrete, the development of the system is given by a continuous map \( T : K \to K \). When time is continuous, the development is governed by a periodic system of differential equations \( \dot{x} = F(t, x) \equiv F(t + 1, x) \). In this case, \( T \) denotes the Poincaré map.

For discrete time, the trajectory of a state \( x \) is the sequence \( \{ T^k x \} \), also denoted by \( \{ x(k) \} \), where \( k \) varies over the set \( \mathbb{N} \) of non-negative integers. In the case of an autonomous differential equation (i.e., \( F \) is independent of \( t \)), the trajectory of \( x \) is the solution curve through \( x \), denoted by \( T^t x \) or \( x(t) \), where \( t \in [0, \infty) \). In both cases, the limit set \( \omega(x) \) is the set of limit points of sequences \( x(t_k) \) where \( t_k \to \infty \).

In order to exclude spontaneous generation, we assume \( T_i(x) = 0 \) when \( x_i = 0 \). Thus, there are functions \( G_i : K \to [0, \infty) \), assumed continuous, such that

\[
T_i(x) = x_i G_i(x), \quad (x \in K, \quad i = 1, \ldots, n). \tag{1}
\]

For continuous time, we assume that the differential equation is a system of having the form \( \dot{x}_i = x_i G_i(t, x) \). If \( x_i \) is interpreted as the size of species \( i \), then \( G_i(x) \) is its per capita growth rate.

†Dedicated to Professor Hal Smith on the occasion of his 60th birthday.
*Email: mwhirsch@chorus.net

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We take ‘competition’ to mean that increasing any one species does not tend to increase the \( \textit{per capita} \) growth rate of any other species, conventionally modelled by the assumption
\[
\frac{\partial G_i}{\partial x_j} \leq 0, \quad (i \neq j).
\]

A \textit{carrying simplex} for the map \( T \) is a compact invariant hypersurface \( \Sigma \subset K \) such that every trajectory except the origin is asymptotic with a trajectory in \( \Sigma \), and \( \Sigma \) is unordered for the standard vector order in \( K \). In the case of an autonomous differential equation, we require that \( \Sigma \) be invariant under the maps \( T^t \) for all \( t \geq 0 \). Some maps have no carrying simplices, others have infinitely many. Our main results give conditions guaranteeing a unique carrying simplex.

\textbf{Terminology}

A set \( Y \subset K \) is \textit{positively invariant} under a map or an autonomous differential equation if it contains the trajectories of all its points, so that \( T^tY \subset Y \) for all \( t \geq 0 \) (here, \( t \in \mathbb{N} \) or \( [0, \infty) \) as appropriate). We call \( Y \) \textit{invariant} if \( T^tY = Y \) for all \( t \geq 0 \).

If \( S \) is a differentiable map, its matrix of partial derivatives matrix at \( p \) is denoted by \( S'(p) \).

The geometry of \( K \) plays an important role. For each subset \( I \subset \{1, \ldots, n\} \), the \( I \)th facet of \( K \) is
\[
K_I = \{ x \in K : x_j = 0 \iff j \notin I \}.
\]
Thus, \( K_{\{1\}} \) is the \( i \)th positive coordinate axis. A facet is \textit{proper} if it lies in the boundary of \( K \), meaning \( I \neq \{0\} \). The intersection of facets is a facet: \( K_I \cap K_J = K_{I \cup J} \). The boundary of \( K \) in \( \mathbb{R}^n \), denoted by \( \delta K \), is the union of the proper facets. Each \( x \in K \setminus \{0\} \) belongs to the unique facet \( K_{I(x)} = \{ i : x_i > 0 \} \).

For each \( n \times n \) matrix \( A \) and non-empty \( I \subset \{1, \ldots, n\} \), we define the principal submatrix
\[
A_I := [A_{ij}]_{i,j \in I}.
\]

The \textit{vector order} in \( \mathbb{R}^n \) is the relation defined by \( x \succeq y \iff x - y \in K \). We write \( x \succ y \) if also \( x \neq y \). For each set \( I \subset \{1, \ldots, n\} \), we write \( x \succ_I y \) if \( x, y \in K_I \) and \( x \succeq y \), and \( x \succ_i y \) if also \( x_i > y_i \) for all \( i \in I \). The reverse relations are denoted by \( \preceq \), \( \prec \) and so forth.

The \textit{closed order interval} defined by \( a, b \in \mathbb{R}^n \) is
\[
[a, b] := \{ x \in \mathbb{R}^n : a \leq x \leq b \}.
\]

\textbf{Carrying simplices}

A \textit{carrying simplex} is a set \( \Sigma \subset K \setminus \{0\} \) having the following properties:

\begin{enumerate}
  \item[(CS1)] \( \Sigma \) is compact and invariant.
  \item[(CS2)] For every \( x \in K \setminus \{0\} \), the trajectory of \( x \) is asymptotic with some \( y \in \Sigma \), i.e., \( \lim_{t \to \infty} |T^t x - T^t y| = 0 \).
  \item[(CS3)] \( \Sigma \) is unordered: if \( x, y \in \Sigma \) and \( x \succeq y \), then \( x = y \).
\end{enumerate}

It follows that each line in \( K \) through the origin meets \( \Sigma \) in a unique point. Therefore, \( \Sigma \) is mapped homeomorphically onto the unit \((n-1)\)-simplex
\[
\Delta^{n-1} := \left\{ x \in K : \sum_i x_i = 1 \right\}
\]
by the radial projection \( x \mapsto x / (\sum_i x_i) \).
Long-term dynamical properties of trajectories are accurately reflected by the dynamics in $\Sigma$ by (CS1) and (CS2), and (CS3) means that $\Sigma$ has simple topology and geometry. The existence of a carrying simplex has significant implications for limit sets $\omega(x)$:

- If $x > 0$ then $\omega(x) \subset \Sigma$, a consequence of (CS2). In particular, $\Sigma$ contains all non-trivial fixed points and periodic orbits.
- If $a, b \in K$ are distinct limit points of respective states $x, y \geq 0$ (possibly the same state), then there exist $i, j$ such that $a_i > b_i, a_j < b_j$; this follows from (CS3). Thus, either $\omega(x) = \omega(y)$, or else there exist $i, j$ such that
  \[
  \limsup_{t \to \infty} x_i(t) - y_i(t) > 0, \quad \liminf_{t \to \infty} x_j(t) - y_j(t) < 0.
  \]

In many cases, $\Sigma$ is the global attractor for the dynamics in $K \setminus \{0\}$, meaning that as $t$ goes to infinity, the distance from $x(t)$ to $\Sigma$ goes to zero uniformly for $x$ in any given compact subset of $K \setminus \{0\}$. This implies [29] that there is a continuous function $V : K \setminus \{0\} \to [0, \infty)$ such that if $x \neq 0$ then

- $V(x) = 0 \iff x \in \Sigma$,
- $V(x(t)) < V(x) \iff x \notin \Sigma$,
- $\lim_{t \to \infty} V(x(t)) = 0$.

We can think of $V$ as an ‘asymptotic conservation law’. While there are many such functions for any carrying simplex, it is rarely possible to find a formula for any of them.

Before stating results we give two simple examples for $n = 1$:

**Example 1** If $T$ is the time-one map for the flow defined by the logistic differential equation

\[
\dot{x} = rx(\sigma - x), \quad r, \sigma > 0, \quad (x \geq 0),
\]

the carrying simplex is just the classical carrying capacity $\sigma$. Here, one can define $V(x) = |x - \sigma|$ for $x > 0$.

**Example 2** Consider the map

\[
T : [0, \infty) \to [0, \infty), \quad Tx = xe^{b-ax}, \quad b, a > 0, \quad x \in [0, \infty). \tag{2}
\]

Note that

\[
T'(x) = (1 - x)e^{b-ax}, \quad T'(b/a) = 1 - b.
\]

If there is a carrying simplex, it has to be the unique positive fixed point $b/a$, in which case $\lim_{k \to \infty} T^k x = b/a$ for all $x > 0$.

*If $b \leq 2$, then $b/a$ is the carrying simplex.* See P. Cull, Local and global stability for population models, Biol. Cybern. Vol. 54 (1986), pp. 141–149, Theorem 2.

*If $b > 2$, there is no carrying simplex.* For then $|T'(b/a)| > 1$, making $b/a$ a locally repelling fixed point. The only way the trajectory of $y \neq b/a$ can converge to $b/a$ is for $T^j y = b/a$ for some $j > 0$. The set of such points $y$ is nowhere dense because $T$ is a non-constant analytic function; hence, there is no carrying simplex. For sufficiently large $b$, the dynamics is chaotic.

Example 5 is an $n$-dimensional generalization of Equation (2).
We say that $T$ is strictly sublinear in a set $X \subset K$ if the following holds: $x \in X$ and $0 < \lambda < 1$ imply $\lambda x \in X$ and
\[ \lambda T(x) < T(\lambda x), \quad (x \in X \setminus 0). \] (3)

Thus, the restricted map $T|X$ exhibits what economists call ‘decreasing returns to scale.’

A state $x$ majorizes a state $y$ if $x > y$, and $x$ strictly majorizes $y$ if $x_i > 0$ implies $x_i > y_i$.

The map $T : K \to K$ is strictly retrotone in a subset $X \subset K$ if for all $x, y \in X$ we have
\[ Tx \text{ majorizes } Ty \implies x \text{ strictly majorizes } y. \]

Equivalently:
\[ x, y \in X \cap K_1 \text{ and } Tx > Ty \implies x \gg_1 y. \]

The origin is a repellor if $T^{-1}(0) = 0$ and there exists $\delta > 0$ and an open neighbourhood $W \subset K$ of the origin such that $\lim \inf_{k \to \infty} |T^k x| \geq \delta$ uniformly in compact subsets of $W \setminus \{0\}$.

If in addition there is a global attractor $\Gamma$, as will be generally assumed, then $\Gamma$ contains a global attractor $\Gamma_0$ for $T|K\setminus\{0\}$.

We will assume that $T$ given in Equation (1) has the following properties:

(C0) $T^{-1}(0) = 0$ and $G_1(0) > 1$.

The first condition means that no non-trivial population dies out in finite time. The second means that small populations increase.

(C1) There is a global attractor $\Gamma$ containing a neighbourhood of 0.

Together with condition (C0) this implies that there is a global attractor $\Gamma_0 \subset \Gamma$ for $T|K\setminus\{0\}$.

The connected component of the origin in $K\setminus\Gamma_0$ is the repellor basin $B(0)$.

(C2) $T$ is strictly sublinear in a neighbourhood of $\Gamma$.

This holds when $0 < \lambda < 1 \implies G(x) < G(\lambda x)$.

(C3) $T$ is strictly retrotone in a neighbourhood of the global attractor.

A similar property was introduced by Smith [25].

Denote the set of boundary points of $\Gamma$ in $K$ by $\partial_K \Gamma$.

**Theorem 1** When conditions (C0)–(C3) hold, the unique carrying simplex is $\Sigma = \partial_K \Gamma = \partial_K B(0)$, and $\Sigma$ is the global attractor for $T|K\setminus\{0\}$.

The proof will appear elsewhere.

The same hypotheses yield further information. It turns out that if $T|\Gamma$ is locally injective (which Smith assumed), it is a homeomorphism of $\Gamma$, and in any case the following condition holds:

(C4) The restriction of $T$ to each positive coordinate axis $K_{[1]}^0$ has a globally attracting fixed point $q_{[i]}$.

We call $q_{[i]}$ an axial fixed point. Denoting its $i$th coordinate by $q_i > 0$, we set
\[ q := (q_1, \ldots, q_n) = \sum_i q_{[i]}. \]

Smith [29] shows that conditions (C3) and (C4) imply condition (C1) with $\Gamma \subset [0, q]$. In many cases, the easiest way to establish a global attractor is to compute the axial fixed points and apply Smith’s result.

The following condition implies condition (C3) for maps $T$ having Form (1) when $G$ is $C^1$:

(C5) If $x \in K\setminus\{0\}$, the matrix $[G'(x)]_{[i]}$ has strictly negative entries.
For \( d \in \mathbb{R}^n \), we denote the diagonal matrix \( D \) with diagonal entries \( D_{ii} := d_i \) by \([d] \text{ diag}\) and also by \([d_i] \text{ diag}\). The \( n \times n \) identity matrix is denoted by \( I \).

A computation shows that

\[
T'(x) = [G(x)] \text{ diag} + [x] \text{ diag} \frac{d}{dx} G'(x).
\]

When \( x \) is such that all \( G_i(x) > 0 \), this can be written as

\[
T'(x) = [G(x)] \text{ diag} (I - M(x)),
\]

\[
M(x) := -\left[ \frac{x_i}{G_i(x)} \right] \text{ diag} \frac{d}{dx} G'(x), \tag{4}
\]

and the entries in the \( n \times n \) matrix \( M(x) \) are

\[
M_{ij}(x) := -x_i \frac{\partial G_i(x)}{G_i(x)} \frac{\partial}{\partial x_j}(x),
\]

\[
= -x_i \frac{\partial \log G_i(x)}{\partial x_j}(x). \tag{5}
\]

Note that condition (C5) implies \( M_{ij}(x) > 0 \).

The spectral radius \( \rho(M) \) of an \( n \times n \) matrix \( M \) is the maximum of the norms of its eigenvalues. It is a standard result that if \( \rho(M) < 1 \) then \( I - M \) is invertible and \( (I - M)^{-1} = \sum_{k=0}^{\infty} M^k \).

**Theorem 2** Suppose \( G \) is \( C^1 \). Assume conditions (C0), (C1), (C2), (C5), let condition (C4) hold with \( [0, q] \subset X \), and assume

\[
0 < x \leq q \implies \rho(M(x)) < 1. \tag{6}
\]

Then condition (C3) holds, whence the hypotheses and conclusions of Theorem 3 are valid.

The proof will be given elsewhere. Under the same hypotheses, the following conclusions also hold:

- \( T|\Gamma \) is a diffeomorphism.
- If \( x \in \Gamma \cap K^0 \), then the matrix \( [T'(x)]^{-1} \) has strictly positive entries.

When condition (C5) holds, either of the following conditions implies Equation (6):

\[
0 < x \leq q \implies \sum_i M_{ij}(x) < 1, \quad (j = 1, \ldots, n), \tag{7}
\]

\[
0 < x \leq q \implies \sum_j M_{ij}(x) < 1, \quad (i = 1, \ldots, n). \tag{8}
\]

Each of these conditions implies that the largest positive eigenvalue of \( M(x) \) is the spectral radius by condition (C5) and the theorem of Perron and Frobenius [2], and that this eigenvalue is bounded above by the maximal row sum and the maximal column sum by Gershgorin’s theorem [3].
Competition models

In the following illustrative examples, we calculate bounds on parameters that make row sums of $M(x)$ obey Equation (7), validating the hypotheses and conclusions of Theorems 3 and 4.

Example 3  Consider a multidimensional version of Equation (2), based on an ecological model of May and Oster [19]:

$$T: K \rightarrow K, \quad T_i(x) = x_i \exp \left( B_i - \sum_j A_{ij} x_j \right), \quad B_i, A_{ij} > 0. \quad (9)$$

This map is not locally injective. In a small neighbourhood of the origin $T$ is approximated by the discrete-time Lotka–Volterra map $\hat{T}$ defined by $(\hat{T}x)_i = (\exp B_i) x_i (1 - \sum_j A_{ij} x_j)$, but as $\hat{T}$ does not map $K$ into itself, it is not useful as a global model. $T$ has a global attractor $\Gamma$ and a source at the origin, so a carrying simplex is plausible. But the special case $n = 1$, treated in Example 2, shows that further restrictions are needed.

Condition (C5) holds with $G_i(x) = \exp (B_i - \sum_j A_{ij} x_j)$. Evidently, these functions are strictly decreasing in $x$, which implies that $T$ is strictly sublinear. Condition (C4) holds with $q_i = B_i / A_{ii}$, and it can be shown that $\Gamma \subset [0, q]$. In Equation (4), the matrix entries are

$$M_{ij}(x) = x_i A_{ij}. \quad (10)$$

Therefore, Theorem 2 shows that if

$$0 < x \leq q \implies \rho(M(x)) < 1, \quad (11)$$

then $\partial K \Gamma$ is the unique carrying simplex and $T|\Gamma$ is a diffeomorphism. From Equations (7), (8) and (10), we see that Equation (11) holds in case one of the following conditions is satisfied:

$$\frac{B_i}{A_{ii}} \sum_j A_{ij} < 1 \quad \text{for all } i, \quad (12)$$

or

$$\frac{B_i}{A_{ii}} \sum_i A_{ij} < 1 \quad \text{for all } j. \quad (13)$$

These conditions thus imply a unique carrying simplex, by Theorem 2.

To arrive at a biological interpretation of Equation (12), we rewrite it as

$$q_i \sum_j A_{ij} < 1, \quad (14)$$

where $q_i := B_i / A_{ii}$ is the axial equilibrium for species $i$, that is, its stable population in the absence of competitors. Equation (9) tells us that $A_{ij}$ is the logarithmic rate by which the growth of population $i$ inhibits the growth rate of population $j$. Thus, Equation (14) means that the average of these rates must be rather small compared to the single species equilibrium for population $i$. The plausibility of this $x_1$ is left to the reader, as is the biological meaning of Equation (13).

When $n = 1$, Equation (9) defines the map $T x = x e^{b-a x}$ of Example 2. The positive fixed point is $q = a / b$, and both Equations (12) and (13) boil down to $b < 1$, which was shown to imply a unique carrying simplex. That example also showed that there is no carrying simplex when $b > 2$.  

As Equation (9) reduces to Example 2 on each coordinate axis, we see that Equation (9) lacks a carrying simplex provided

\[ \frac{B_i}{A_{ii}} \sum_j A_{ij} > 2 \text{ for some } i, \]

or

\[ \frac{B_i}{A_{ii}} \sum_i A_{ij} > 2 \text{ for some } j. \]

**Example 4** Consider a competing population model due to Leslie and Gower [16]:

\[ T : \mathbb{K} \rightarrow \mathbb{K}, \quad T_i x = \frac{C_i x_i}{1 + \sum_j A_{ij} x_j}, \quad C_i, A_{ij} > 0. \] (15)

Note that \( T \) need not be locally injective. When \( n = 1 \) all trajectories converge to 0 if \( C \leq 1 \), and all non-constant trajectories converge to \( (C - 1)/A \) if \( C > 1 \). The case \( n = 2 \) is thoroughly analyzed by Cushing et al. [5].

Here,

\[ G_i(x) := \frac{C_i}{1 + \sum_j A_{ij} x_j} > 0; \]

hence, condition (C5) holds. We assume that \( C_i > 1 \), guaranteeing condition (C4) with \( q_i = (C_i - 1)/A_{ii} \). In Equation (5), we have

\[ M_{ij}(x) = \frac{x_i A_{ij}}{1 + \sum_l A_{il} x_l} < x_i A_{ij}. \]

So the row sums of \( M(x) \) are < 1 for all \( x \) provided \( q_i \sum_j A_{ij} < 1 \). Therefore, when

\[ 1 < C_i < 1 + \frac{A_{ii}}{\sum_j A_{ij}}, \]

Theorems 3 and 4 yield the following conclusions: there is a global attractor \( \Gamma \subset [0, q] \), the unique carrying simplex is \( \partial \mathbb{K} \cap \Gamma \) and \( T|\Gamma \) is a diffeomorphism.

**Example 5** Consider a recurrent, fully connected neural network of \( n \) cells (or ‘cell assemblies’, [11]). At discrete times \( t = 0, 1, \ldots \), cell \( i \) has activation level \( x_i(t) \geq 0 \) and the state of the system is \( x(t) := (x_1(t), \ldots, x_n(t)) \). Cell \( i \) receives an input signal \( s_i(x(t)) \), which is a weighted sum of all the activations plus a bias term. Its activation is multiplied by a positive transfer function \( \tau_i \) evaluated on \( s_i \), resulting in the new activation \( x_i(t+1) = x_i(t) \tau_i(s_i) \).

We assume that each cell’s activation tends to decrease the activations of all cells, but each cell receives a bias that tends to increase its activation. We model this with negative weights \( -A_{ij} < 0 \), positive biases \( B_i > 0 \) and positive increasing transfer functions. For simplicity, we assume that all the transfer functions are \( e^\sigma \) where \( \sigma : [0, \infty) \rightarrow [0, \infty) \) is \( C^1 \). States evolve according to
the law
\[ T: K \rightarrow K, \quad T_i(x) = x_i \exp \sigma (s_i(x)), \quad s_i(x) := B_i - \sum_j A_{ij} x_j. \]

We also assume that
\[ \sigma(0) = 0, \quad \sigma'(s) > 0, \quad \sup \sigma'(s) = \gamma < \infty, \quad (s \in \mathbb{R}). \]  
(16)

It is easy to verify that conditions (C1), (C2), (C4) and (C5) hold, with
\[ q_i := \frac{B_i}{A_{ii}}, \quad G_i(x) := \exp \left( B_i - \sum_j A_{ij} x_j \right), \quad M_{ij} = \sigma'(s_i(x)) A_{ij}, \]  
(17)

where \( M_{ij}(x) \) is defined as in Equation (5).

It turns out that for given weights and biases, the system has a unique carrying simplex provided the gain parameter \( \gamma \) in Equation (16) is not too large. It suffices to assume that
\[ \gamma < \left[ \max_i \left( \frac{B_i}{A_{ii}} \sum_j A_{ij} \right) \right]^{-1}. \]  
(18)

For then Equations (16), (17) and (18) imply Equation (8) and hence condition (C3), so Theorems 1 and 2 imply a unique carrying simplex for \( T \).

There is a vast literature on neural networks, going back to the seminal book of Hebb [10]. Network models of competition were analyzed in the pioneering works of Grossberg [6] and Cohen and Grossberg [4]. Generic convergence in certain types of competitive and cooperative networks is proved in [13]. Levine’s book [17] has mathematical treatments of several aspects of neural network dynamics.

### Competitive differential equations

Consider a periodic differential equation in \( K \):
\[ \dot{u}_i = u_i G_i(t, u_1, \ldots, u_n) \equiv u_i G_i(t + 1, u_1, \ldots, u_n), \quad t, u_i \geq 0, \quad (i = 1, \ldots, n), \]  
(19)

where the maps \( G_i: K \rightarrow \mathbb{R} \) are \( C^1 \). The solution with initial value \( u(0) = x \) is denoted by \( t \mapsto T_{i,t}x \). Solutions are assumed to be defined for all \( t \geq 0 \). Each map \( T_i \) maps \( K \) diffeomorphically onto a relatively open set in \( K \) that contains the origin. The Poincaré map is \( T := T_1 \).

We postulate the following conditions for Equation (19):

(A1) total competition: \( G_i/x_j \leq 0, \quad (i, j = 1, \ldots, n) \),

(A2) strong self-competition: \( \sum_{k \in I_i(x)} G_k/x_k(t, x) < 0 \),

(A3) decrease of large population: \( G_i(t, x) < 0 \) for \( x_i \) sufficiently large.

This implies existence of a global attractor for the Poincaré map \( T \).

(A4) increase of small populations: \( G_i(t, 0) > 0 \).

Under these assumptions, there are two obvious candidates for a carrying simplex for \( T \), namely \( \partial K B \) and \( \partial K \Gamma \), the respective boundaries in \( K \) of \( B(0) \) and \( \Gamma \). Existence of a unique carrying simplex implies \( \partial K B = \partial K \Gamma \).
THEOREM 3 Assume System (19) has properties (A1)–(A4). Then, there is a unique carrying simplex, and it is the global attractor for the dynamics in $\mathbb{K} \setminus \{0\}$.

The proof, which will be given elsewhere, uses a subtle dynamical consequence of competition discovered by Wang and Jiang [34]: if $u(t), v(t)$ are solutions to Equation (19) such that for all $i$

$$u_i(t) < v_i(t), \quad (s < t < s_1),$$

then

$$\frac{d}{dt}(u_i/v_i) > 0, \quad (s < t < s_1).$$

Example 6 A competitive, periodic Volterra–Lotka system in $\mathbb{K}$ of the form

$$\dot{u}_i = u_i \left( B_i(t) - \sum_j A_{ij}(t)u_j \right), \quad B_i, A_{ij} > 0$$

satisfies (A1)–(A4) and thus the conclusion of Theorem 8.

Example 7 Several mathematicians have investigated carrying simplex dynamics for competitive, autonomous Volterra–Lotka systems in $\mathbb{K}$ having the form

$$\dot{u}_i = u_i \left( B_i - \sum_j A_{ij}u_i \right) := u_iH_i(u_1, \ldots, u_n), \quad B_i, A_{ij} > 0. \quad (20)$$

The best results are for $n = 3$: the interesting dynamics is on a two-dimensional cell, therefore, the Poincaré–Bendixson theorem [9] precludes any kind of chaos and makes the dynamics easy to analyze. The dynamics for generic systems were classified by Zeeman [33], with computer graphics exhibited in Zeeman [34]. She proved that in many cases simple algebraic criteria on the coefficients determine the existence of limit cycles and Hopf bifurcations.

Van den Driessche and Zeeman [27] applied Zeeman’s classification to model two competing species with species 1, but not species 2, susceptible to disease. They showed that if species 1 can drive species 2 to extinction in the absence of disease, then the introduction of disease can weaken species 1 sufficiently to permit stable or oscillatory coexistence of both species.

Zeeman and Zeeman [36] showed that generically, but not in all cases, the carrying simplex is uniquely determined by the dynamics in the two-dimensional facets of $\mathbb{K}$. Systems with two and three limit cycles have been found by Hofbauer and So [15], Lu and Luo [18]), and Gyllenberg et al. [8]. No examples of Equation (20) with four limit cycles are known.

More information on the dynamics of Equation (20) can be found in [26, 30, 31, 35, 37].

Background

In an important paper on competitive maps, Smith [25] investigated $C^2$ diffeomorphisms $T$ of $\mathbb{K}$. Under assumptions similar to (C0)–(C5), he proved $T$ is strictly retrotone and established the existence of the global attractor $\Gamma$ and the repulsion basin $B(0)$. He showed that $\partial_{\mathbb{K}} B(0)$ and $\partial_{\mathbb{K}} \Gamma$ are compact unordered invariant sets homeomorphic to the unit simplex, and each of them contains all periodic orbits except the origin. His conjecture that $\partial_{\mathbb{K}} B = \partial_{\mathbb{K}} \Gamma$ remains unproved from his hypotheses. He also showed that for certain types of competitive planar maps every
bounded trajectory converges, extending earlier results of Hale and Somolinos [3] and de Mottoni and Schiaffino [24].

Using Smith’s results and those of Hess and Poláčik [11], Wang and Jiang [28] obtained unique carrying simplices for competitive $C^2$ maps.

For further results on the smoothness, geometry and dynamics of carrying simplices, see [1,20–23].

Mea culpa Uniqueness of the carrying simplex for Equation (20) was claimed in [12], but Zeeman [32] discovered an error in the proof of Proposition 2.3(d).

References


[34] ———, http://www.bowdoin.edu/faculty/m/mlzeeman/index.shtml.

