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Journal

Journal of Biological Dynamics, 2(2)

Author

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Publication Date

2008-04-01

DOI

10.1080/17513750801939236

Peer reviewed

This article was downloaded by: [Hirsch, Morris W.]

On: 9 September 2009

Access details: Access Details: [subscription number 793186637]

Publisher Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK

Journal of Biological Dynamics

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title-content=t744398444>

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Online Publication Date: 01 April 2008

To cite this Article Hirsch, Morris W.(2008)'On existence and uniqueness of the carrying simplex for competitive dynamical systems',Journal of Biological Dynamics,2:2,169 — 179

To link to this Article: DOI: 10.1080/17513750801939236

URL: <http://dx.doi.org/10.1080/17513750801939236>

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

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(Received 2 August 2007; final version received 19 January 2008)

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

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 $T : K \rightarrow K$. 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 $t_k \rightarrow \infty$.

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

$$T_i(x) = x_i G_i(x), \quad (x \in K, \quad i = 1, \dots, n). \quad (1)$$

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.

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We take ‘competition’ to mean that increasing any one species does not tend to increase the *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 *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 Σ , and Σ is unordered for the standard vector order in K . In the case of an autonomous differential equation, we require that Σ 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.

Terminology

A set $Y \subset K$ is *positively invariant* under a map or an autonomous differential equation if it contains the trajectories of all its points, so that $T^t Y \subset Y$ for all $t \geq 0$ (here, $t \in \mathbf{N}$ or $[0, \infty)$ as appropriate). We call Y *invariant* if $T^t Y = Y$ 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 $\mathbf{I} \subset \{1, \dots, n\}$, the $\mathbf{I}$ th *facet* of K is

$$K_{\mathbf{I}} = \{x \in K : x_j = 0 \iff j \notin \mathbf{I}\}.$$

Thus, $K_{\{i\}}$ is the i th positive coordinate axis. A facet is *proper* if it lies in the boundary of K , meaning $\mathbf{I} \neq \{0\}$. The intersection of facets is a facet: $K_{\mathbf{I}} \cap K_{\mathbf{J}} = K_{\mathbf{I} \cup \mathbf{J}}$. The boundary of K in $\mathbf{R}^n$, denoted by $\bar{K}$, is the union of the proper facets. Each $x \in K \setminus \{0\}$ belongs to the unique facet $K_{\mathbf{I}(x)}$ where $\mathbf{I}(x) := \{i : x_i > 0\}$.

For each $n \times n$ matrix A and non-empty $\mathbf{I} \subset \{1, \dots, n\}$, we define the principal submatrix

$$A_{\mathbf{I}} := [A_{ij}]_{i,j \in \mathbf{I}}.$$

The *vector order* in $\mathbf{R}^n$ is the relation defined by $x \geq y \iff x - y \in K$. We write $x > y$ if also $x \neq y$. For each set $\mathbf{I} \subset \{1, \dots, n\}$, we write $x >_{\mathbf{I}} y$ if $x, y \in \bar{K}_{\mathbf{I}}$ and $x > y$, and $x >_{\mathbf{I}} y$ if also $x_i > y_i$ for all $i \in \mathbf{I}$. The reverse relations are denoted by $\leq$, $<$ and so forth.

The *closed order interval* defined by $a, b \in \mathbf{R}^n$ is

$$[a, b] := \{x \in \mathbf{R}^n : a \leq x \leq b\}.$$

Carrying simplices

A *carrying simplex* is a set $\Sigma \subset K \setminus \{0\}$ having the following properties:

- (CS1) Σ is compact and invariant.
- (CS2) For every $x \in K \setminus \{0\}$, the trajectory of x is asymptotic with some $y \in \Sigma$, i.e., $\lim_{t \rightarrow \infty} |T^t x - T^t y| = 0$.
- (CS3) Σ is *unordered*: if $x, y \in \Sigma$ and $x \geq y$, then $x = y$.

It follows that each line in K through the origin meets Σ in a unique point. Therefore, Σ 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 Σ by (CS1) and (CS2), and (CS3) means that Σ 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, Σ 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

$$\limsup_{t \rightarrow \infty} x_i(t) - y_i(t) > 0, \quad \liminf_{t \rightarrow \infty} x_j(t) - y_j(t) < 0.$$

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

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

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 σ . Here, one can define $V(x) = |x - \sigma|$ for $x > 0$.

Example 2 Consider the map

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

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 $\lim_{k \rightarrow \infty} T^k x = b/a$ 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 $X \subset \mathbf{K}$ if the following holds: $x \in X$ and $0 < \lambda < 1$ imply $\lambda x \in X$ and

$$\lambda T(x) \prec T(\lambda x), \quad (x \in X \setminus \{0\}). \quad (3)$$

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

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

The map $T : \mathbf{K} \rightarrow \mathbf{K}$ is *strictly retrotone* in a subset $X \subset \mathbf{K}$ if for all $x, y \in X$ we have

$$Tx \text{ majorizes } Ty \implies x \text{ strictly majorizes } y.$$

Equivalently:

$$x, y \in X \cap \overline{\mathbf{K}_I} \text{ and } Tx \succ Ty \implies x \gg_I y.$$

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

If in addition there is a global attractor Γ , as will be generally assumed, then Γ contains a global attractor Γ_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 $G_i(0) > 1$.

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 Γ 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 *repulsion basin* $B(0)$.

(C2) *T is strictly sublinear in a neighbourhood of Γ .*

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

(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 Γ in $\mathbf{K}$ 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 Σ 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 Γ , and in any case the following condition holds:

(C4) *The restriction of T to each positive coordinate axis $\mathbf{K}_{\{i\}}^o$ 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

$$q := (q_1, \dots, q_n) = \sum_i q_{(i)}.$$

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 $[G'(x)]_{I(x)}$ has strictly negative entries.*

For $d \in \mathbf{R}^n$, 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

$$T'(x) = [G(x)]^{\text{diag}} + [x]^{\text{diag}} G'(x).$$

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

$$\begin{aligned} T'(x) &= [G(x)]^{\text{diag}} (I - M(x)), \\ M(x) &:= - \left[\frac{x_i}{G_i(x)} \right]^{\text{diag}} G'(x), \end{aligned} \quad (4)$$

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

$$\begin{aligned} M_{ij}(x) &:= \frac{-x_i}{G_i(x)} \frac{\partial G_i}{\partial x_j}(x), \\ &= -x_i \frac{\partial \log G_i}{\partial x_j}(x). \end{aligned} \quad (5)$$

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

$$0 < x \leq q \implies \rho(M(x)) < 1. \quad (6)$$

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 $x \in \Gamma \cap \mathbf{K}_{\mathbf{P}}^o$, then the matrix $[T'(x)_{\mathbf{I}}]^{-1}$ has strictly positive entries.

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

$$0 < x \leq q \implies \sum_i M_{ij}(x) < 1, \quad (j = 1, \dots, n), \quad (7)$$

$$0 < x \leq q \implies \sum_j M_{ij}(x) < 1, \quad (i = 1, \dots, n). \quad (8)$$

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]:

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

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 $\mathbf{K}$ into itself, it is not useful as a global model. T has a global attractor Γ 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 $\partial_{\mathbf{K}}\Gamma$ 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 is left to the reader, as is the biological meaning of Equation (13).

When $n = 1$, Equation (9) defines the map $Tx = xe^{b-ax}$ 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

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

or

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

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

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

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 $\partial_{\mathbb{K}} \Gamma$ 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 $t = 0, 1, \dots$, cell i has activation level $x_i(t) \geq 0$ and the state of the system is $x(t) := (x_1(t), \dots, x_n(t))$. 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 τ_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^σ where $\sigma: [0, \infty) \rightarrow [0, \infty)$ is C^1 . States evolve according to

the law

$$T: \mathbf{K} \longrightarrow \mathbf{K}, \quad T_i(x) = x_i \exp \sigma(s_i(x)), \quad s_i(x) := B_i - \sum_j A_{ij} x_j.$$

We also assume that

$$\sigma(0) = 0, \quad \sigma'(s) > 0, \quad \sup \sigma'(s) = \gamma < \infty, \quad (s \in \mathbf{R}). \quad (16)$$

It is easy to verify that conditions (C1), (C2), (C4) and (C5) hold, with

$$q_i := \frac{B_i}{A_{ii}}, \quad G_i(x) := \exp \sigma \left(B_i - \sum_j A_{ij} x_j \right), \quad M_{ij} = \sigma'(s_i(x)) A_{ij}, \quad (17)$$

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* γ in Equation (16) is not too large. It suffices to assume that

$$\gamma < \left[\max_i \left(\frac{B_i}{A_{ii}} \sum_j A_{ij} \right) \right]^{-1}. \quad (18)$$

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 $\mathbf{K}$:

$$\dot{u}_i = u_i G_i(t, u_1, \dots, u_n) \equiv u_i G_i(t+1, u_1, \dots, u_n), \quad t, u_i \geq 0, \quad (i = 1, \dots, n), \quad (19)$$

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

We postulate the following conditions for Equation (19):

- (A1) *total competition*: $G_i/x_j \leq 0$, $(i, j = 1, \dots, n)$,
- (A2) *strong self-competition*: $\sum_{k \in \mathbf{I}(x)} G_k/x_k(t, x) < 0$,
- (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 $\partial_{\mathbf{K}} B$ and $\partial_{\mathbf{K}} \Gamma$, the respective boundaries in $\mathbf{K}$ of $B(0)$ and Γ . Existence of a unique carrying simplex implies $\partial_{\mathbf{K}} B = \partial_{\mathbf{K}} \Gamma$.

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 $K \setminus \{0\}$.

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 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 K having the form

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

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 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 K . Under assumptions similar to (C0)–(C5), he proved T is strictly retrotone and established the existence of the global attractor Γ and the repulsion basin $B(0)$. He showed that $\partial_K B(0)$ and $\partial_K \Gamma$ are compact unordered invariant sets homeomorphic to the unit simplex, and each of them contains all periodic orbits except the origin. His conjecture that $\partial_K B = \partial_K \Gamma$ 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).

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