

## ON SMOOTHNESS OF CARRYING SIMPLICES

JANUSZ MIERCZYŃSKI

(Communicated by Hal L. Smith)

ABSTRACT. We consider dissipative strongly competitive systems  $\dot{x}_i = x_i f_i(x)$  of ordinary differential equations. It is known that for a wide class of such systems there exists an invariant attracting hypersurface  $\Sigma$ , called the carrying simplex. In this note we give an amenable condition for  $\Sigma$  to be a  $C^1$  submanifold-with-corners. We also provide conditions, based on a recent work of M. Benaïm (*On invariant hypersurfaces of strongly monotone maps*, J. Differential Equations **136** (1997), 302–319), guaranteeing that  $\Sigma$  is of class  $C^{k+1}$ .

### 1. INTRODUCTION

We consider systems of ordinary differential equations (ODE's) of class (at least)  $C^1$

$$(E) \quad \dot{x}_i = x_i f_i(x)$$

on the nonnegative orthant  $C := \{x \in \mathbb{R}^n : x_i \geq 0 \text{ for } 1 \leq i \leq n\}$ ,  $n \geq 3$ .

We write  $F_i(x) = x_i f_i(x)$ ,  $F = (F_1, \dots, F_n)$ . The symbol  $DF = [\partial F_i / \partial x_j]_{i,j=1}^n$  stands for the derivative matrix of the vector field  $F$ . The local flow generated by (E) on  $C$  will be denoted by  $\phi = \{\phi_t\}$ . A subset  $B \subset C$  is *invariant* [resp. *forward invariant*] if  $\phi_t x \in B$  for all  $(t, x) \in \mathbb{R} \times B$  [resp. for all  $(t, x) \in [0, \infty) \times B$ ] for which  $\phi_t x$  is defined. For  $x \in C$ ,  $B \subset C$  the symbols  $\omega(x)$ ,  $\alpha(x)$ ,  $\omega(B)$ ,  $\alpha(B)$  have their usual meanings (see e.g. Hale [3]). A point  $x \in C$  is a *rest point* if  $\phi_t x = x$  for each  $t \in \mathbb{R}$  (alternatively, if  $F(x) = 0$ ). An invariant subset  $B$  of a compact invariant set  $S$  is called an *attractor* (resp. a *repeller*) *relative to S* if there is a relative neighborhood  $U$  of  $B$  in  $S$  such that  $\omega(U) = B$  (resp.  $\alpha(U) = B$ ). For an attractor  $B$  relative to  $S$ , by the repeller *complementary to B* we understand the set  $\{x \in S : \omega(x) \cap B = \emptyset\}$ . The attractor *complementary to a repeller R* is defined in an analogous way.

System (E) is *dissipative* if there is a compact set  $B \subset C$  such that for each bounded  $D \subset C$  its  $\omega$ -limit set  $\omega(D)$  is a nonempty subset of  $B$ . By standard results on global attractors (see [3]), for a dissipative system (E) there exists a compact invariant set  $\Gamma \subset C$  (the *global attractor* for (E)) such that  $\omega(D) \subset \Gamma$  for each bounded  $D \subset C$ . Evidently,  $0 \in \Gamma$ .

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Received by the editors June 2, 1997.

1991 *Mathematics Subject Classification*. Primary 34C30, 34C35; Secondary 58F12, 92D40.

The author's research was supported by KBN grant 2 P03A 076 08 (1995–97).

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For  $I \subset \{1, \dots, n\}$  denote

$$\begin{aligned} C_I &:= \{x \in C : x_i = 0 \text{ for } i \in I\}, \\ C_I^\circ &:= \{x \in C_I : x_j > 0 \text{ for } j \notin I\}, \\ \partial C_I &:= C_I \setminus C_I^\circ. \end{aligned}$$

From the form of (E) it follows readily that any  $C_I$ , as well as  $\partial C_I$  and  $C_I^\circ$ , is invariant. We denote by  $(E)_I$  the restriction of system (E) to  $C_I$ . Instead of  $C_\emptyset^\circ$ ,  $\partial C_\emptyset$ , we write  $C^\circ$ ,  $\partial C$ .  $I'$  means  $\{1, \dots, n\} \setminus I$ .

If system (E) is dissipative, so are all of its subsystems  $(E)_I$ . For each  $I \subset \{1, \dots, n\}$ , the global attractor  $\Gamma_I$  for  $(E)_I$  equals  $\Gamma \cap C_I$ .

System (E) is called *strongly competitive* if  $(\partial f_i / \partial x_j)(x) < 0$  for each  $1 \leq i, j \leq n$ ,  $i \neq j$ ,  $x \in C$ . A strongly competitive system is called *totally competitive* if  $(\partial f_i / \partial x_i)(x) < 0$  for  $1 \leq i \leq n$ ,  $x \in C$ . Such systems describe a community of  $n$  interacting species where the growth of each species inhibits the growth of any other.

Throughout the rest of the paper the standing assumption will be:

(E) is a  $C^1$  dissipative strongly competitive system of ODE's satisfying the following:

1.  $\{0\}$  is a repeller relative to  $\Gamma$ .
2. At each rest point  $x \in C \setminus \{0\}$  one has  $(\partial f_i / \partial x_i)(x) < 0$  for  $1 \leq i \leq n$ .

The following important result was established by M. W. Hirsch ([4]).

**Proposition 1.1.** *The attractor  $\Sigma \subset \Gamma$  complementary to the repeller  $\{0\}$  is homeomorphic via radial projection to the standard  $(n-1)$ -simplex  $\Delta := \{x \in C : x_1 + \dots + x_n = 1\}$ . Moreover, the global attractor  $\Gamma$  equals the convex hull of  $\Sigma \cup \{0\}$ .*

Following M. L. Zeeman [15], the invariant compact set  $\Sigma$  is referred to as the *carrying simplex* for (E). In the ecological interpretation, the carrying simplex can be thought of as expressing the balance between the growth of small populations ( $\{0\}$  is a repeller) and the competition of large populations (dissipativity).

M. W. Hirsch in [4] asked about sufficient conditions for the carrying simplex  $\Sigma$  to be of class  $C^1$ . The time reverse flow  $\{\phi_{-t}\}_{t \geq 0}$  restricted to the invariant set  $C^\circ$  is strongly monotone and its derivative flow is strongly positive (for these terms see H. L. Smith's monograph [12]). Therefore, when (E) possesses a repeller  $R \subset \Sigma \cap C^\circ$  relative to  $\Sigma$  we can utilize a powerful recent result of I. Tereščák [13] on nonmonotone manifolds to conclude that the repulsion basin  $B(R) := \{x \in \Sigma^\circ : \alpha(x) \subset R\}$  is a  $C^1$  hypersurface. However, even in that case Tereščák's theorem does not apply to the whole of  $\Sigma$ , for the time reverse flow fails to be strongly monotone on the boundary  $\partial C$ . Moreover, if we assume that (E) is permanent (a natural assumption from the applied viewpoint) then there is an attractor  $A$  having the whole  $C^\circ$  as its attraction basin, hence its repulsion basin (relative to  $\Sigma$ ) equals  $A$ . In his paper [10] the present author gave a fairly weak condition implying the  $C^1$  smoothness of  $\Sigma$ . It was done, however, at the expense of making use (for  $n \geq 5$ ) of Pesin's theory of invariant measurable families of embedded manifolds, which compels one to assume that  $f$  has Hölder continuous derivatives.

In this note we show that a well-known, robust, and readily testable condition (see (A)) is enough to conclude that  $\Sigma$  is  $C^1$ . Because our proofs exploit Oseledets' theory of Lyapunov exponents, it suffices to assume  $f$  is  $C^1$  to get  $C^1$  smoothness

of  $\Sigma$ . Next, conditions are given, based on recent results of M. Benaïm [1], for the carrying simplex to possess higher order smoothness.

I would like to thank Michel Benaïm for sending me a preprint of [1].

2. STATEMENT OF MAIN RESULTS

For  $I \subset \{1, \dots, n\}$  put

$$\Sigma_I := C_I \cap \Sigma, \quad \Sigma_I^\circ := C_I^\circ \cap \Sigma, \quad \partial \Sigma_I := \partial C_I \cap \Sigma.$$

We will call  $\Sigma_I$  a  $k$ -dimensional face of  $\Sigma$ , where  $k = n - 1 - \text{card } I$ . Evidently all  $\Sigma_I$ , as well as  $\Sigma_I^\circ$  and  $\partial \Sigma_I$ , are invariant. For  $I \subset \{1, \dots, n\}$ , the face  $\Sigma_I$  is the carrying simplex for subsystem  $(E)_I$ . The 0-dimensional face  $\Sigma_{i'}$  consists of a single rest point  $x^{(i)} = (0, \dots, 0, x_i^{(i)}, 0, \dots, 0)$  with  $x_i^{(i)} > 0$  (called the  $i$ -th axial rest point).

Let  $V = \{v = (v_1, \dots, v_n) : v_i \in \mathbb{R}\}$  stand for the vector space of all free  $n$ -dimensional vectors (in particular, we write the tangent bundle of the orthant  $C$  as  $TC = C \times V$ ). Depending on the context,  $\|\cdot\|$  may mean the Euclidean norm of a vector, or the operator norm of a matrix, associated with the Euclidean norm. For  $I \subset \{1, \dots, n\}$ , we denote

$$V_I := \{v \in V : v_i = 0 \text{ for } i \in I\}.$$

For any two points  $x, y \in C_I$ , we write  $x \leq_I y$  if  $x_i \leq y_i$  for all  $i \in I'$ , and  $x <_I y$  if  $x \leq_I y$  and  $x \neq y$ . Moreover,  $x \ll_I y$  if  $x_i < y_i$  for all  $i \in I'$ . For  $I = \emptyset$  we write simply  $\leq, <, \ll$ . The reversed symbols are used in the obvious way. As each  $(C_I, \leq_I)$  is a lattice, we can define, for  $I \subset \{1, \dots, n\}$  with  $\text{card } I \leq n - 1$

$$x^{[I]} := \bigvee_{i \in I'} x^{(i)},$$

where it is easy to see that  $x^{[J]} <_I x^{[I]}$  for  $I \subsetneq J$ .

The following result probably belongs to the folklore in the theory of competitive systems, but I have not been able to locate its proof.

**Lemma 2.1.** *For each  $I \subset \{1, \dots, n\}$  with  $1 \leq \text{card } I \leq n - 2$  we have  $y <_I x^{[I]}$  for all  $y \in \Sigma_I$ .*

*Proof.* Suppose to the contrary that there is  $y \in \Sigma_I$  not in the  $<_I$  relation to  $x^{[I]}$ . Assume first that  $y = x^{[I]}$ , that is,  $x^{[I]} \in \Sigma_I$ . For  $i \in I', j \in I', i \neq j$ , we have  $x_j^{[I]} > x_j^{(i)} = 0$ . As  $f_i(x^{(i)}) = 0$ , it follows by strong competitiveness that  $f_i(x^{[I]}) < 0$  for  $i \in I'$ . Therefore we have  $F_i(x^{[I]}) = x_i^{[I]} f_i(x^{[I]}) < 0$  for all  $i \in I'$ . Consequently,  $\phi_t x^{[I]} \ll_I x^{[I]}$  for  $t > 0$  sufficiently small. But  $\Sigma_I$  is invariant, so  $\phi_t x^{[I]} \in \Sigma_I$  for all  $t > 0$ . We have thus obtained two points in  $\Sigma_I$  related by  $\ll_I$ , which contradicts Lemma 2.5 in Hirsch [4]. Assume that  $y \in \Sigma_I$  is not in the  $\leq_I$  relation to  $x^{[I]}$ . Take an index  $k$  for which  $y_k > x_k^{[I]}$ . Let  $J \subset \{1, \dots, n\}$  stand for the set of those indices  $j$  for which  $y_j = 0$ . Evidently  $k \in J'$  and  $I \subset J$ . We have  $y \in \Sigma_I \cap C_J^\circ = \Sigma \cap C_I \cap C_J^\circ = \Sigma \cap C_J^\circ = \Sigma_J^\circ$ . As a consequence,  $y_j > x_j^{(k)} = 0$  for  $j \in J', j \neq k$ , and  $y_k > x_k^{[I]} = x_k^{(k)}$  (since  $k \notin I$ ). But this means that  $y \gg_J x^{(k)}$ . As both these points are in  $\Sigma_J$ , this again is in contradiction to Lemma 2.5 in [4].  $\square$

We say (E) satisfies hypothesis (A) if  
 For each  $1 \leq i \leq n$  one has  $f_i(x^{[i]}) \geq 0$ .

In light of the strong competitiveness, (A) can be equivalently formulated as:

For each  $I \subset \{1, \dots, n\}$  with  $1 \leq \text{card } I \leq n - 1$  one has  $f_i(x^{[I]}) \geq 0$  for  $i \in I$ .

Hypothesis (A) is well known in the literature on mathematical ecology. Consider the Lotka–Volterra competitive system

$$(2.1) \quad \dot{x}_i = x_i(b_i - \sum_{j=1}^n a_{ij}x_j),$$

with  $b_i > 0$ ,  $a_{ij} > 0$ . For (2.1) the  $i$ -th axial rest point is given by  $x_i^{(i)} = b_i/a_{ii}$ . It is easy to see that (A) is now equivalent to

$$b_i \geq \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} \frac{b_j}{a_{jj}} \quad \text{for each } 1 \leq i \leq n.$$

We are now in a position to state our main result.

**Theorem A.** *Assume that (E) satisfies (A). Then the carrying simplex  $\Sigma$  is a  $C^1$  submanifold-with-corners neatly embedded in  $C$ .*

For submanifolds-with-corners their neat embeddings, see [10].

We now state some consequences of hypothesis (A). System  $(E)_I$  is called *permanent* if there is  $\epsilon > 0$  such that  $\liminf_{t \rightarrow \infty} \rho(\phi_t x, \partial C_I) \geq \epsilon$  for each  $x \in C_I^\circ$ , where  $\rho$  stands for the Euclidean distance between a point and a set.

**Proposition 2.2.** *If (A) is satisfied, then each of the subsystems  $(E)_I$  is permanent.*

*Proof.* In order not to encumber our presentation with too many subscripts, we prove the assertion for  $I = \emptyset$ , that is, for system (E) only. For each  $i$ ,  $1 \leq i \leq n$ , we have as a result of strong competitiveness and Lemma 2.1 that  $f_i(x) > 0$  for all  $x \in \Sigma_{i'}$ . Now take a neighborhood  $U_i$  of  $\Sigma_{i'}$  in  $C$  of the form

$$U_i = \{(x_1, \dots, x_n) : 0 \leq x_i < \epsilon_i, (x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_n) \in \tilde{U}_i\},$$

where  $\epsilon_i > 0$  and a relative neighborhood  $\tilde{U}_i$  of  $\Sigma_{i'}$  in  $C_{i'}$  are so small that  $f_i(x) > 0$  for all  $x \in U_i$ . As  $\Gamma$  is the global attractor for (E) and  $\Sigma$  is the attractor relative to  $\Gamma$  complementary to  $\{0\}$ , there exists a forward invariant neighborhood  $U$  of  $\Sigma$  in  $C$  with the property that  $\phi_t x \in U$  for  $x \in C \setminus \{0\}$  and sufficiently large  $t$ . Also,  $U$  can be taken so small that all the sets  $\{x \in U : x_i < \epsilon_i\}$  are contained in  $U_i$ . Now observe that for  $t$  so large that  $\phi_t x$  belongs to  $U$  one has

$$\frac{d(\phi_t x)_i}{dt} = F_i(\phi_t x) = x_i f_i(\phi_t x) > 0$$

as long as  $(\phi_t x)_i < \epsilon_i$ . From this it readily follows that  $\liminf_{t \rightarrow \infty} \rho(\phi_t x, \Sigma_{i'}) \geq \epsilon_i$  for any  $x \in C^\circ$ .  $\square$

In view of results on attractors contained in Hale [3] we have the following.

**Lemma 2.3.** *Under the assumptions of Proposition 2.2, for each  $I \subset \{1, \dots, n\}$  the invariant compact set  $\partial \Sigma_I$  is a repeller relative to  $\Sigma_I$ .*

For  $I \subset \{1, \dots, n\}$  denote by  $A_I$  the attractor (relative to  $\Sigma_I$ ) complementary to  $\partial \Sigma_I$ . As  $A_I$  can be viewed as the global attractor for the semiflow  $\{\phi_t\}_{t \geq 0}$  restricted to the connected metric space  $\Sigma_I^\circ$ , a result of Gobbino and Sardella (Thm. 3.1 in [2]) yields that  $A_I$  is connected.

The ecological interpretation of the property described in Proposition 2.2 is as follows. In each subcommunity none of the species goes extinct, and invasion of a proper subcommunity by others causes the populations of the previously present species to shrink due to the larger amount of competition.

Before formulating sufficient conditions for  $\Sigma$  to be of class  $C^{k+1}$  we need to introduce some notation (we follow Benaïm’s paper [1]). For  $x \in A_I$ ,  $I \subset \{1, \dots, n\}$  with  $\text{card } I \leq n - 2$ , we denote by  $\lambda(x)$  the largest eigenvalue of the symmetrization of the matrix  $(-DF^I(x))$ , where  $DF^I := [\partial F_i / \partial x_j]_{(i,j) \in I' \times I'}$ . Further,  $d(x)$  stands for the square root of

$$\min_{\substack{i \neq j \\ i, j \notin I}} \frac{\partial F_i}{\partial x_j}(x) \frac{\partial F_j}{\partial x_i}(x).$$

Put  $\lambda_I := \sup\{\lambda(x) : x \in A_I\}$  and  $d_I := \inf\{d(x) : x \in A_I\}$ .

We say that (E) satisfying (A) fulfills (C) if for each  $I$  with  $0 \leq \text{card } I \leq n - 2$  any one of the conditions (C1) or (C2) holds:

(C1)  $k \sup\{\|DF^I(x)\| : x \in A_I\} < 2(k + 1)d_I$ .

(C2)  $k\lambda_I < 2(k + 1)d_I$ .

**Theorem B.** *Assume that a  $C^{k+1}$  system (E) satisfies (A) and (C). Then the carrying simplex  $\Sigma$  is a  $C^{k+1}$  submanifold-with-corners.*

### 3. PROOF OF THEOREM A

Let  $\mathbb{S}$  be the  $(n - 1)$ -dimensional sphere  $\{v \in V : \|v\| = 1\}$ . For a vector subspace  $W$  of  $V$  and  $0 \leq k \leq \dim W$ , the symbol  $\mathbb{G}_k W$  denotes the compact metrizable space of all  $k$ -dimensional vector subspaces of  $W$ , endowed with the standard topology: for any two  $Z_1, Z_2 \in \mathbb{G}_k W$ , their distance is defined as the Hausdorff distance between  $Z_1 \cap \mathbb{S}$  and  $Z_2 \cap \mathbb{S}$ .

The linearization of (E) generates on  $TC$  a linear skew-product (local) flow  $(\phi_t x, D\phi_t(x)v)$ , where  $D\phi_{t_0}(x)v_0$  is the value at time  $t_0$  of the solution of the variational equation  $\dot{\xi} = DF(\phi_t x)\xi$  with initial condition  $\xi(0) = v_0$ .

For a linear subset  $\mathcal{C}$  of the product bundle  $B \times W$ , where  $B \subset \Sigma$  and  $W$  is a vector subspace of  $V$ , we will denote by  $\mathcal{C}_x$  the set of all those  $v \in W$  such that  $(x, v) \in \mathcal{C}$  (in other words,  $\{x\} \times \mathcal{C}_x$  is the fiber of  $\mathcal{C}$  over  $x$ ). A linear subset  $\mathcal{C}$  of  $B \times W$  is called *invariant* if for each  $(x, v) \in \mathcal{C}$  and each  $t \in \mathbb{R}$  one has  $(\phi_t x, D\phi_t(x)v) \in \mathcal{C}$ .

Denote the set of all ergodic measures supported on a compact invariant  $B \subset \Sigma$  by  $\mathbf{M}_{\text{erg}}(B)$ . The multiplicative ergodic theorem of Oseledets (see e.g. Mañé [8]) assures us that if  $B \times W$  is an invariant bundle, then for each  $m \in \mathbf{M}_{\text{erg}}(B)$  there exist an invariant  $m$ -measurable set  $B_{\text{reg}} \subset B$  (the set of *regular points*), a collection  $\mathcal{C}_1, \dots, \mathcal{C}_l$  of invariant linear subsets given by  $m$ -measurable maps  $B_{\text{reg}} \ni x \mapsto (\mathcal{C}_k)_x \in \mathbb{G}_{d_k} W$  (the *Oseledets decomposition*) and a collection  $\Lambda_1 < \dots < \Lambda_l$  of reals (*Lyapunov exponents*) such that

1.  $W = \bigoplus_{k=1}^l (\mathcal{C}_k)_x$  for  $x \in B_{\text{reg}}$ ,
- 2.

$$\lim_{t \rightarrow \pm\infty} \frac{\log \|D\phi_t(x)v\|}{t} = \Lambda_k$$

for  $1 \leq k \leq l$ ,  $x \in B_{\text{reg}}$  and  $v \in (\mathcal{C}_k)_x$ .

**Lemma 3.1.** *For each  $m \in \mathbf{M}_{\text{erg}}(\Sigma)$  there is  $I = I(m) \subsetneq \{1, \dots, n\}$  such that the support  $\text{supp } m$  of  $m$  is contained in  $A_I$ .*

*Proof.* By ergodicity of  $m$  and invariance of all  $\Sigma_I^\circ$ , there is precisely one  $I \subset \{1, \dots, n\}$  such that  $m(\Sigma_I^\circ) = 1$  and  $m(\partial\Sigma_I) = 0$ . Further, as points from  $\Sigma_I^\circ \setminus A_I$  are wandering (relative to  $\Sigma$ ), one has  $m(\Sigma_I^\circ \setminus A_I) = 0$ .  $\square$

Fix  $m \in \mathbf{M}_{\text{erg}}(\Sigma_I)$  with  $m(\Sigma_I^\circ) = 1$ , and put  $\mathcal{B} := \Sigma_I \times V_I$ ,  $\mathcal{B}^{(i)} := \Sigma_I \times V_{I \setminus i}$ ,  $i \in I$ . Evidently,  $\mathcal{B}$  is a subbundle of  $\mathcal{B}^{(i)}$  of codimension one. From the structure of system (E) it follows that the bundles  $\mathcal{B}$ ,  $\mathcal{B}^{(i)}$  are invariant. Denote by  $\Lambda_1 < \Lambda_2 \cdots < \Lambda_l$  the Lyapunov exponents on  $\mathcal{B}$  for the ergodic measure  $m$  (we will call them the *internal Lyapunov exponents* for  $m$ ). Among the Lyapunov exponents on  $\mathcal{B}^{(i)}$  there is one (denoted by  $\lambda^{(i)}(m)$ ) corresponding to the measurable linear set  $\mathcal{C}_k^{(i)} \subset \mathcal{B}^{(i)}$  such that  $(\mathcal{C}_k^{(i)})_x \subsetneq V_I$  for  $m$ -a.e.  $x \in \Sigma_I^\circ$ . We will refer to  $\lambda^{(i)}(m)$  as the  $i$ -th *external Lyapunov exponent* for  $m$  (this terminology is modeled on Hofbauer's [6]).

The following result was essentially proved in the author's paper [10] (except for terminology).

**Theorem 3.2.** *Assume that for each  $m \in \mathbf{M}_{\text{erg}}(\partial\Sigma)$  all its external Lyapunov exponents are nonnegative. Then the following hold:*

1. *The carrying simplex  $\Sigma$  is a  $C^1$  submanifold-with-corners neatly embedded in  $C$ .*
2. *There are  $\mu > 0$  and an invariant one-dimensional subbundle  $\mathcal{S}$  of  $\Sigma \times V$  such that for each  $m \in \mathbf{M}_{\text{erg}}(\Sigma)$  one has*
  - (a)  $\Sigma \times V = T\Sigma \oplus \mathcal{S}$ , where  $T\Sigma$  denotes the tangent bundle of  $\Sigma$ , and  $(\mathcal{C}_1)_x \subset \mathcal{S}$  for  $m$ -a.e.  $x \in \Sigma$ .
  - (b)  $\Lambda_1$  is internal.
  - (c)  $\Lambda_1 \leq -\mu$ .

In the present section we make use of part 1 of Theorem 3.2 only.

In view of the above result, we need to prove only the following.

**Proposition 3.3.** *Under the assumptions of Theorem A, for each  $m \in \mathbf{M}_{\text{erg}}(\partial\Sigma)$  all its external Lyapunov exponents are nonnegative.*

*Proof.* Fix a measure  $m \in \mathbf{M}_{\text{erg}}(\Sigma_I)$  with  $m(\Sigma_I^\circ) = 1$ , and an index  $i \in I$ . By Lemma 3.1,  $\text{supp } m \subset A_I$ . Take a regular point  $x \in \text{supp } m$  and a vector  $v \in (\mathcal{B}^{(i)})_x \setminus V_I$  such that its  $i$ -th coordinate  $v_i$  is positive. As  $(\partial F_i / \partial x_j)(\phi_t x) = 0$  for  $j \neq i$ , and  $(\partial F_i / \partial x_i)(\phi_t x) = f_i(\phi_t x)$ , it follows that the  $i$ -th coordinate  $(D\phi_t(x)v)_i$  is the solution of the (nonautonomous) scalar linear ODE  $\dot{\eta} = f_i(\phi_t x)\eta$  with initial condition  $\eta(0) = v_i$ . By strong competitiveness and Lemma 2.1,  $f_i$  is positive on the compact invariant set  $A_I \subset \Sigma_I$ , hence there is  $M > 0$  such that  $f_i(\phi_t x) \geq M$  for all  $(t, x) \in \mathbb{R} \times A_I$ . The standard theory of differential inequalities yields

$$\liminf_{t \rightarrow \infty} \frac{\log(D\phi_t(x)v)_i}{t} \geq M.$$

$\|\cdot\|$  is the Euclidean norm on  $\mathbb{R}^n$ , therefore for all  $t \in \mathbb{R}$  we have  $\|D\phi_t(x)v\| \geq (D\phi_t(x)v)_i$ . By regularity of  $x$  we derive

$$\lim_{t \rightarrow \infty} \frac{\log \|D\phi_t(x)v\|}{t} = \lambda^{(i)}(m) \geq M > 0.$$

$\square$

4. PROOF OF THEOREM B

We begin by stating a result which is an adaptation of a theorem of M. Benaïm.

**Theorem 4.1.** *Assume that a  $C^{k+1}$ ,  $k = 1, \dots$ , system (E) satisfies the following:*

1. *For each  $m \in \mathbf{M}_{\text{erg}}(\partial\Sigma)$  all external Lyapunov exponents are nonnegative.*
2. *There is  $\eta > 0$  such that for each  $m \in \mathbf{M}_{\text{erg}}(\Sigma)$  the inequality*

$$(4.1) \quad \Lambda_1(m) - (k + 1)\Lambda_2(m) < -\eta$$

*holds, where  $\Lambda_1(m)$  and  $\Lambda_2(m)$  denote respectively the smallest and the second smallest Lyapunov exponents (on  $\Sigma \times V$ ) for  $m$ .*

*Then the carrying simplex  $\Sigma$  is a  $C^{k+1}$  submanifold-with-corners.*

*Indication of proof.* Theorem 3.2.2 asserts that the tangent bundle  $TC$  restricted to  $\Sigma$  invariantly decomposes as the Whitney sum  $T\Sigma \oplus \mathcal{S}$ , and for each  $m \in \mathbf{M}_{\text{erg}}(\Sigma)$  the smallest Lyapunov exponent  $\Lambda_1(m) \leq -\mu < 0$  is the exponential growth rate of a vector from  $\mathcal{S}$ , while any of the remaining Lyapunov exponents is the exponential growth rate of a vector tangent to  $\Sigma$ . This, together with (4.1), gives, with the help of Prop. 3.3 in [1] (based on a result of S. Schreiber [11]), that there are  $c \geq 1$ ,  $\alpha > 0$  and  $\beta > 0$  such that

$$\|D\phi_t(x)v\| \leq ce^{-\alpha t}\|v\| \quad \text{for } t \geq 0, (x, v) \in \mathcal{S},$$

and

$$\frac{\|D\phi_t(x)v\|}{\|D\phi_t(x)w\|^{k+1}} \leq ce^{-\beta t} \quad \text{for } t \geq 0, x \in \Sigma, v \in (\mathcal{S})_x, w \in T_x\Sigma \setminus \{0\}.$$

The rest of the proof consists in applying the  $C^{k+1}$  section theorem of Hirsch, Pugh and Shub [5], as in the proof of Thm. 3.4 in [1]. □

As a consequence of the above theorem and Proposition 3.3, we will have Theorem B once we prove the following.

**Proposition 4.2.** *Assume that a  $C^{k+1}$  system (E) satisfies (A) and (C). Then there exists  $\eta > 0$  such that for each  $m \in \mathbf{M}_{\text{erg}}(\Sigma)$  the inequality (4.1) holds.*

*Proof.* Take  $m \in \mathbf{M}_{\text{erg}}(\Sigma)$ , and let  $I \subset \{1, \dots, n\}$  be such that  $m(\Sigma_I^\circ) = 1$ . From Lemma 3.1 we have  $\text{supp } m \subset A_I$ . By results contained in Sections 3 and 4 of [1], it follows that under assumption (C) there is  $\eta_I > 0$  such that

$$\Lambda_1^*(m) - (k + 1)\Lambda_2^*(m) < -\eta_I$$

for all  $m$  supported on  $A_I$ , where  $\Lambda_1^*(m)$  [resp.  $\Lambda_2^*(m)$ ] stands for the smallest [resp. second smallest] internal Lyapunov exponent for  $m$ . Theorem 3.2.2 gives  $\Lambda_1^*(m) = \Lambda_1(m)$ . Denote by  $\lambda_{\min}$  the smallest external Lyapunov exponent for  $m$ . If  $\lambda_{\min} \geq \Lambda_2^*(m)$ , then  $\Lambda_2^*(m) = \Lambda_2(m)$  and the inequality (4.1) is satisfied with  $\eta_I$ . Assume that  $\lambda_{\min} < \Lambda_2^*(m)$ . Applying Theorem 3.2.2 and Proposition 3.3, we obtain  $\Lambda_1(m) \leq -\mu < 0 \leq \lambda_{\min} = \Lambda_2(m)$ . Consequently,  $\Lambda_1(m) \leq -\mu < 0 \leq (k + 1)\Lambda_2(m)$ . It suffices to put

$$\eta := \min\{\mu, \eta_I : I \subset \{1, \dots, n\}, \text{card } I \leq n - 1\}.$$

□

## 5. DISCUSSION

*Remark 5.1.* In formulating our results, we preferred that the assumptions be easily tractable rather than the weakest possible or that they cover a wide range of applications. In fact, they can be substantially weakened, as the following example shows.

A celebrated Lotka–Volterra system due to May and Leonard [9] has the form

$$(5.1) \quad \begin{aligned} \dot{x}_1 &= x_1(1 - x_1 - \alpha x_2 - \beta x_3), \\ \dot{x}_2 &= x_2(1 - \beta x_1 - x_2 - \alpha x_3), \\ \dot{x}_3 &= x_3(1 - \alpha x_1 - \beta x_2 - x_3), \end{aligned}$$

with  $0 < \beta < 1 < \alpha$  and  $\alpha + \beta > 2$ . It is easily verified that (5.1) is dissipative, totally competitive and has five rest points on  $C$ : 0 (repelling),  $y$  with  $y_i = 1/(1 + \alpha + \beta)$  and three axial ones  $x^{(i)}$  with  $x_i^{(i)} = 1$ . Furthermore,  $\partial\Sigma$  is an attractor relative to  $\Sigma$  with  $\{y\}$  as its complementary repeller (see pp. 67–68 in the book [7] by Hofbauer and Sigmund). As a consequence,  $\mathbf{M}_{\text{erg}}(\Sigma) = \{\delta_y, \delta_{x^{(1)}}, \delta_{x^{(2)}}, \delta_{x^{(3)}}\}$ . The Lyapunov exponents for the Dirac delta on a rest point  $x$  are simply the real parts of the eigenvalues of  $DF(x)$ . At  $y$  the smallest Lyapunov exponent is negative and the remaining ones are positive (see [7]). A simple calculation shows that at an axial rest point the unique internal Lyapunov exponent equals  $-1$  and the external exponents are  $1 - \beta > 0$  and  $1 - \alpha < 0$ .

Assume now that  $\alpha < 2$ . Then for each ergodic measure on  $\Sigma$  the smallest Lyapunov exponent  $-1$  is internal. Applying ideas of the author's earlier paper [10] we prove that the carrying simplex  $\Sigma$  for (5.1) is a  $C^1$  submanifold-with-corners. Observe that if  $1 < \alpha < 1 + 1/l$  for some  $l = 2, \dots$ , then  $-1 - l(1 - \alpha)$  is negative and one can deduce along the lines of the proof of Theorem 4.1 to conclude that  $\Sigma$  is of class  $C^l$ .

*Remark 5.2.* The systems (E) satisfying (A) [resp. (A) and (C)] are robust in the sense that if we perturb  $f$  in a neighborhood of  $\Sigma$  in the  $C^1$  [resp. in the  $C^{k+1}$ ] topology, then the perturbed system possesses a carrying simplex of class  $C^1$  [resp.  $C^{k+1}$ ] (and each of its subsystems  $(E)_I$  is permanent). This can be proved by reasoning similar to that in the proof of Cor. 4.3 in [1].

*Remark 5.3.* In principle, results contained in Section 3 should carry over to the case where we allow  $f$  to depend periodically on  $t$ , although finding an analog of (A) might be tricky (for time-periodic Lotka–Volterra strongly competitive systems, compare e.g. [14]).

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INSTITUTE OF MATHEMATICS, WROCLAW UNIVERSITY OF TECHNOLOGY, WYBRZEŻE WYSPIAŃSKIEGO 27, PL-50-370 WROCLAW, POLAND

*E-mail address:* mierzyn@banach.im.pwr.wroc.pl