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ANTIBIFURCATION AND THE n-SPECIES LOTKA-VOLTERRA COMPETITION MODEL WITH DIFFUSION

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Abstract. The system

$$\begin{aligned} -\Delta u_k &= \Big(a_k - u_k - \sum_{j\neq k,\, j=1}^{n} \gamma_{kj} u_j\Big) u_k \quad \text{in } \Omega \\ u_k &= 0 \quad \text{on } \partial\Omega, \end{aligned} \tag{*}$$

$k = 1, \ldots, n$, where Ω is a bounded domain in $\mathbb{R}^n$ and a_k, γ_{kj} are positive parameters, determines the possible equilibrium configurations for a diffusive Lotka-Volterra competition model and is of interest in the study of the role of competition in structuring communities where space or resources are limited. The componentwise nonnegative solutions to $(*)$ can perhaps best be understood for fixed γ_{kj} and varying a_k as a subset of the Banach space $\mathbb{R}^n \times [C_0^1(\overline{\Omega})]^n$. The aims of this article are to enhance understanding of the structure of this set and to provide a firmer foundation for future analysis. We accomplish these aims through some new observations regarding the set of componentwise nonnegative solutions to $(*)$ which enable us to unify some preceding analyses.

1. Introduction. Systems of differential equations of the form

$$\begin{aligned} -d_k \Delta u_k &= a_k(x) u_k + g_k(x, u_1, \ldots, u_n) u_k \quad && \text{in } \Omega \\ B_k u_k &= 0 && \text{on } \partial\Omega, \end{aligned} \tag{1.1}$$

$k = 1, \ldots, n$, where Ω is a bounded domain in $\mathbb{R}^N$ with smooth boundary $\partial\Omega$ and B_k represents a homogeneous boundary condition of Dirichlet, Neumann or Robin type, have been the focus of an enormous amount of mathematical research in recent years. One of the principal reasons for such active interest in (1.1) is that solutions to (1.1) represent steady-state or equilibrium solutions to the corresponding reaction-diffusion system

$$\begin{aligned} u_{k_t} &= d_k \Delta u_k + a_k(x) u_k + g_k(x, u_1, \ldots, u_n) u_k \quad && \text{in } \Omega \times (0, \infty) \\ B_k u_k &= 0 && \text{on } \partial\Omega \times (0, \infty). \end{aligned} \tag{1.2}$$

Systems of the form (1.2) in turn are important as mathematical formulations or models of the dynamics of a community of interacting species, particularly so when spatial

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heterogeneity is taken into account. In such models $u_k(x,t) \geq 0$ represents the population density of the k^{th} species in the community at position x in the habitat Ω and time t. Consequently, componentwise nonnegative solutions to (1.1) represent the possible equilibrium configurations of the model community. An initially zero component indicates extinction of the species in question.

Systems of the form (1.1) are flexible enough to encompass a wide variety of modeling assumptions. The local interaction terms g_i can model competition, predation, mutualism or various combinations thereof. Indeed, if the g_k terms depend explicitly on x, the type of model can depend on location within the overall habitat Ω; for instance, competition in some parts of Ω and mutualism in others. The models can be of Lotka-Volterra type (i.e., g_k is a linear combination of some or all of the u_k) or of a more general form. There may or may not be explicit x dependence in a_k and g_k.

In this article we are concerned with the special case of Lotka-Volterra competition models with no x dependence, assuming each species competes with every other species and exhibits self-regulation. We also assume that the boundary of the habitat Ω is lethal to each species. Under these assumptions, (1.1) can without loss of generality be expressed as

$$\begin{aligned} -\Delta u_k &= \Big(a_k - u_k - \sum_{j\neq k} \gamma_{kj} u_j\Big) u_k \quad \text{in } \Omega \\ u_k &= 0 \qquad\qquad\qquad\qquad\qquad \text{on } \partial\Omega, \end{aligned} \tag{1.3}$$

$k = 1, \ldots, n$, where a_k, γ_{kj} are positive constants. (That such is the case follows from a simple rescaling argument. See [6], e.g.)

Many ecologists are interested in the role of competition in structuring communities where space or resources are limited; for example, in islands. Consequently, understanding the structure of the solution set to a competition model with diffusion on a bounded domain such as (1.3) could be viewed as a first step in the development of a theory of the biogeography of islands based on the population dynamics of the species involved. (So far, treatments of this problem in the ecological literature view species as present or absent. The few spatially explicit treatments based on population dynamics (e.g. [5]) do not incorporate density-dependent competition between species.) The basic approach we take to the question of existence of *componentwise nonnegative* solutions to (1.3) is to consider the a_k's and γ_{kj}'s as parameters, and then to express the componentwise nonnegative solutions to (1.3) in terms of these parameters. It is then natural to view and analyze the solution set as a subset of the Banach space $\mathbb{R}^{n+n(n-1)} \times [C_0^1(\overline{\Omega})]^n$ or as a subset of $\mathbb{R}^n \times [C_0^1(\overline{\Omega})]^n$ (if the interaction parameters γ_{kj} are fixed). This topological-functional analytic approach has served numerous investigators (e.g. [6], [11]) well in the case when $n = 2$ (about which we shall say more shortly). In the case of general n, with its implications for community structure, we believe that this approach is likely even more valuable. There have been comparatively fewer articles in the general case. Among them we note the contributions of Ali and Cosner ([2]), Cantrell ([3]), Korman and Leung ([16]), Lopez-Gomez and Pardo ([17]), and McKenna and Walter ([18]). Of these, [3] and [17] partake mostly closely of the viewpoint we advocate. However, these papers emphasize different aspects of the structure of the solution set to (1.3), viewed as a subset of $\mathbb{R}^n \times [C_0^1(\overline{\Omega})]^n$, and there is a need to unify them in order to provide a better foundation for future investigation into the problem. This is the principal aim of this paper. In order to carry out our objective, we will require new information of independent interest regarding the solution set to (1.3). Presenting this information is the secondary aim of this article.

At this point, some observations are in order concerning the cases when $n = 1$ and $n = 2$. First of all, the case when $n = 1$, namely

$$\begin{aligned} -\Delta u &= (a-u)u \quad \text{in } \Omega \\ u &= 0 \qquad\qquad\;\; \text{on } \partial\Omega, \end{aligned} \tag{1.4}$$

is completely understood and a very satisfactory analysis of the set of positive solutions to (1.4) when a is allowed to range over the real numbers can be based on the celebrated Rabinowitz Global Bifurcation Theorem ([19]). Indeed, for every $a > \lambda^1(0)$, where $\lambda^1(0)$ denotes the principal positive eigenvalue for

$$\begin{aligned} -\Delta z &= \lambda z \quad \text{in } \Omega \\ z &= 0 \qquad \text{on } \partial\Omega, \end{aligned} \tag{1.5}$$

there is a unique positive solution to (1.4), which we denote by θ_a. In fact, $\{(a, \theta_a) : a > \lambda^1(0)\}$ forms a smooth arc in the space $\mathbb{R} \times C_0^{1+\alpha}(\overline{\Omega})$ and $\lim_{a\to\lambda^1(0)^+}\theta_a = 0$ in $C_0^{1+\alpha}(\overline{\Omega})$. Moreover, when considered as a steady-state to

$$\begin{aligned} u_t &= \Delta u + (a-u)u \quad \text{in } \Omega \times (0,\infty) \\ u &= 0 \qquad\qquad\qquad\;\; \text{on } \partial\Omega \times (0,\infty), \end{aligned} \tag{1.6}$$

θ_a is an attractor for solutions to (1.6) with nonnegative nontrivial initial data on Ω. (For details, see [4], where a far more general class of problems is treated.) However, once $n \geq 2$, the structure of the set of componentwise-positive solutions to (1.3) is not nearly so well understood, basically because in general uniqueness is completely lost. Indeed, it is fair to suggest that there is a "quantum leap" in the difficulty of analysis when attention is shifted from (1.4) to the deceptively simple-looking system

$$\begin{aligned} -\Delta u &= u[a-u-cv], \quad -\Delta v = v[d-eu-v] \quad \text{in } \Omega \\ u &= 0 = v \quad \text{on } \partial\Omega \end{aligned} \tag{1.7}$$

which accounts for much of the sustained interest in (1.7) by authors too numerous to list. The article [14] demonstrates how complicated the solution set to (1.7) can be, even under the additional assumption $a = d$. Perhaps the most thorough overall analysis of (1.7) to date is that found in the recent article of Eilbeck, Furter and López-Gómez ([11]), to which the interested reader is directed not only for its content, but also for its list of references.

Let us now consider [3] and [17]. Each considers (1.3), views the competition coefficients γ_{kj}, $k \neq j$, as fixed (and small) positive numbers, and attempts to analyze the structure of the set of componentwise-positive solutions to (1.3) in terms of the growth rate parameters $(a_1, \ldots, a_n)$, which are allowed to vary over $\mathbb{R}^n$. Moreover, each relies on the Alexander-Antman Global Multiparameter Bifurcation Theorem ([1]) for its theoretical underpinning. The articles differ substantially in terms of emphasis and degree of specificity. To understand the difference, note first that for (1.3) to admit a componentwise-positive solution, it must be the case that $a_k > \lambda^1(0)$, $k = 1, \ldots, n$, where $\lambda^1(0)$ is as in (1.5). (This condition can be interpreted as saying in order for a species to survive in the presence of competitors, it must first be able to survive on their absence.) In [17], López-Gómez and Pardo employ a Lyapunov-Schmidt type argument to establish a bifurcation from the trivial solutions to (1.3) (i.e., $(a_1, \ldots, a_n, 0, \ldots, 0)$) to the set of solutions with $u_k > 0$ on Ω for $k = 1, \ldots, n$ at the point $(\lambda^1(0), \ldots, \lambda^1(0), 0, \ldots, 0)$. They then establish a change of topological degree in order to invoke the Alexander-Antman Multiparameter Bifurcation Theorem ([1]) to conclude that the bifurcation is global in the Čech cohomological sense described in [1]. In particular, they guarantee the existence of a global continuum of dimension $\geq n$ at every point of solutions $(a_1, \ldots, a_n, u_1, \ldots, u_n)$ to (1.3) with $u_k > 0$ on Ω emerging from $(\lambda^1(0), \ldots, \lambda^1(0), 0, \ldots, 0)$. The results in [3] are considerably less specific but provide substantial insight into the bifurcation processes at work. Specifically, observe for example that if $(\tilde{a}_1, \tilde{a}_2, \tilde{u}_1, \tilde{u}_2)$ solves

$$-\Delta u_1 = u_1[a_1 - u_1 - \gamma_{12}u_2], \quad -\Delta u_2 = u_2[a_2 - u_2 - \gamma_{21}u_1] \quad \text{in } \Omega$$
$$u_1 = 0 = u_2 \quad \text{on } \partial\Omega,$$

then $(\tilde{a}_1, \tilde{a}_2, a_3, \ldots, a_n, \tilde{u}_1, \tilde{u}_2, 0, \ldots, 0)$ solves (1.3) for any choice of $(a_3, \ldots, a_n) \in \mathbb{R}^{n-2}$. Consequently, it might well be expected that the continuum of solutions to (1.3) with $u_k > 0$ in Ω for all k arise via a succession of n bifurcations, starting from the trivial solutions, each bifurcation adding one more positive state component u_j until all components are positive. In [3], an abstract result that in principle applies to (1.3) is proved using the Alexander-Antman Multiparameter Bifurcation Theorem ([1]), wherein each n-dimensional bifurcating sheet is global with respect to the preceding sheet in the sense described in [1]. The limitation to using the result of [3] to analyze (1.3) is that as n becomes larger than 2, the precise character of a sheet of solutions to (1.3) with m nontrivial components, $2 \leq m \leq n$, becomes difficult to "pin down" due to the potential loss of uniqueness, as is noted in [17].

To unify the results of [3] and [17] it suffices to show that if one starts at a solution $(a_1^0, \ldots, a_n^0, u_1^0, \ldots, u_n^0)$ of (1.3) with $u_k^0 > 0$ on Ω for $k = 1, \ldots, n$ and can continue the solution set from there, then one reaches a set of solutions $(a_1, \ldots, a_n, u_1, \ldots, u_n)$ of dimension $\geq n-1$ where at least one $u_k \equiv 0$. We call such a phenomenon "antibifurcation." There are obvious limitations on being able to "antibifurcate." First of all, being able to start a continuation process at $(a_1^0, \ldots, a_n^0, u_1^0, \ldots, u_n^0)$ requires some form of nondegeneracy at $(a_1^0, \ldots, a_n^0, u_1^0, \ldots, u_n^0)$; for example, that an appropriate linearization of the map corresponding to (1.3) is nonsingular at $(a_1^0, \ldots, a_n^0, u_1^0, \ldots, u_n^0)$. Then even if continuation is possible, phenomena such as osceolas must be ruled out. (That is, it is possible that the set of solutions to (1.3) that we start at $(a_1^0, \ldots, a_n^0, u_1^0, \ldots, u_n^0)$

contains only solutions with $u_k > 0$ for all k and meets $(a_1^0, \ldots, a_n^0, \overline{u}_1, \ldots, \overline{u}_n)$ with $(\overline{u}_1, \ldots, \overline{u}_n) \neq (u_1^0, \ldots, u_n^0)$.) To get around these obstacles, we adapt to our needs the multiparameter global continuation theory of Fitzpatrick, Massabò and Pejsachowicz ([12]), which is based upon the notion of a complementing map, and formulate an abstract "antibifurcation" theorem as a corollary to the results of [12]. We then show that the hypotheses of our result are met in the case of (1.3). We choose to attack the problem in this fashion for two basic reasons. First, it enables us better to focus on what additional information regarding (1.3) we need to unify the results of [3] and [17], and secondly, we are able to obtain in a relatively concise manner a result which is likely applicable in other contexts.

The remainder of the article is structured as follows. In Section 2, we collect the information on global continuation theory from [12] which is needed in Section 3 to formulate and prove our "antibifurcation" theorem. Then in Section 4, we demonstrate that the hypotheses of the theorem are met in the case of (1.3).

2. Background on complementing maps. In this section, we collect the information on global continuation theory from [12] which we need to formulate the antibifurcation results of Section 3. The results in [12] are couched in the language of complementing maps. To understand what is meant by a complementing map, let X be a real Banach space, n a positive integer and $\mathcal{O}$ an open subset of $\mathbb{R}^n \times X$, and consider

$$f(\lambda, x) = x - F(\lambda, x),$$

where $F : \mathcal{O} \to X$ is completely continuous. Now f can be viewed as a map into $\mathbb{R}^n \times X$. In fact, when f is so viewed, it is a completely continuous perturbation of the identity, and so the Leray-Schauder degree $\deg_{LS}(f, \mathcal{O}, 0)$ may well be defined. However, since the range of f is contained in a subspace of $\mathbb{R}^n \times X$ of codimension n, such a degree is necessarily 0 any time it is defined. So we shall say that a continuous map $g : \mathcal{O} \to \mathbb{R}^n$ which maps bounded sets into bounded sets is a *complement* for $f : \mathcal{O} \to X$ provided the Leray-Schauder degree $\deg_{LS}((g, f), \mathcal{O}, 0)$ is defined and nonzero, where

$$(g, f)((\lambda, x)) = (g(\lambda, x), f(\lambda, x)).$$

(Since (g, f) is a completely continuous perturbation of the identity in $\mathbb{R}^n \times X$, the degree is defined precisely when $\{(\lambda, x) \in \mathcal{O} : (g, f)((\lambda, x)) = 0\}$ is compact.)

We shall make strong use of the following criterion for the existence of a complement for f.

Proposition 2.1 ([12]). *Let $\lambda_0 \in \mathbb{R}^n$ and let $\mathcal{O}_{\lambda_0} = \{x \in X : (\lambda_0, x) \in \mathcal{O}\}$. Define $f_{\lambda_0} : \mathcal{O}_{\lambda_0} \to X$ by $f_{\lambda_0}(x) = f(\lambda_0, x) = x - F(\lambda_0, x)$. Then $f : \mathcal{O} \to X$ is complemented by $g : \mathcal{O} \to \mathbb{R}^n$ given by*

$$g(\lambda, x) = \lambda - \lambda_0$$

if and only if $\deg_{LS}(f_{\lambda_0}, \mathcal{O}_{\lambda_0}, 0) \neq 0$.

Remark. When f is continuously Fréchet differentiable, $(\lambda_0, x_0) \in \mathcal{O} \cap f^{-1}(0)$ and $\frac{\partial f}{\partial x}(\lambda_0, x_0)$ is a bijection, the classical implicit function theorem implies that $f^{-1}(0)$ is an n-manifold in a neighborhood of (λ_0, x_0). It is natural to want to extend $f^{-1}(0)$ beyond such a neighborhood, maintaining as much topological information as possible. The following two results from [12] address just this issue and form the theoretical basis for the antibifurcation results of the next section.

Theorem 2.2 (Theorem 2.2, [12]). *Let $n, X, \mathcal{O}$ and f be as above (f need not be Fréchet differentiable). Assume that $g : \mathcal{O} \to \mathbb{R}^n$ is continuous and maps bounded sets into bounded sets. Suppose $V \subseteq \mathcal{O}$ is open and $g : V \to \mathbb{R}^n$ complements $f : V \to X$. Let $K = ((g, f)\,{:_V})^{-1}(0)$. Then there exists a closed connected subset, $\mathcal{C}$, of $f^{-1}(0)$, whose dimension at each point is at least n such that $\mathcal{C} \cap K \neq \emptyset$ and such that at least one of the following properties hold:*
(a) *$\mathcal{C}$ is unbounded.*
(b) *$\overline{\mathcal{C}} \cap \partial\mathcal{O} \neq \emptyset$.*
(c) *$\mathcal{C} \cap \{(g, f)^{-1}(0) \backslash K\} \neq \emptyset$.*

Remark. First of all, note that $\overline{\mathcal{C}}$ refers to the closure of $\mathcal{C}$ in $\overline{\mathcal{O}} = \mathcal{O} \cup \partial\mathcal{O}$. Second, when f is continuously Fréchet differentiable, $(\lambda_0, x_0) \in f^{-1}(0)$ and $\frac{\partial f}{\partial x}(\lambda_0, x_0)$ is a bijection, Theorem 2.2 may be applied to extend $f^{-1}(0)$ past a sufficiently small neighborhood V of (λ_0, x_0). That such is the case follows from Proposition 2.1 and the nondegeneracy of f at (λ_0, x_0). When F is defined on $\overline{\mathcal{O}}$, a sharper result is possible.

Theorem 2.3 (Corollary 2.1, [12]). *Let $n, X, \mathcal{O}$ and f be as before and assume additionally that F is defined on $\overline{\mathcal{O}}$. Suppose $\lambda_0 \subset \mathbb{R}^n$ is such that $0 \notin f_{\lambda_0}(\partial\mathcal{O}_{\lambda_0})$ and $\deg_{LS}(f_{\lambda_0}, \mathcal{O}_{\lambda_0}, 0) \neq 0$. Let the following a priori bound hold: if $(\lambda_n, x_n) \subseteq \overline{\mathcal{O}} \cap f^{-1}(0)$ and $\{\lambda_n\}$ is bounded, then $\{x_n\}$ is bounded. Then there exists a closed connected subset $\mathcal{C}$ of $f^{-1}(0)$, whose dimension at each point is at least n, so that $\mathcal{C} \cap \mathcal{O}_{\lambda_0} \neq \emptyset$ and so that at least one of the following two properties hold:*

(a) $\dim(\mathcal{C} \cap \partial\mathcal{O}) \geq n - 1$ *when $n > 1$, while $\mathcal{C} \cap \partial\mathcal{O}$ contains at least two points when $n = 1$.*
(b) *for each $\lambda \in \mathbb{R}^n$ there is some $x \in X$ with $(\lambda, x) \in \mathcal{C}$.*

Remarks. (i) Theorem 2.3 does not explicitly mention a complementing map. However, it is evident from Proposition 2.1 that the map $g(\lambda, x) = \lambda - \lambda_0$ is the complement to f in this case.

(ii) Theorem 2.2 and Theorem 2.3 are particular cases of the main result of [12].

(iii) In neither theorem is there a requirement that $\mathcal{O}$ be homeomorphic to $\mathbb{R}^n \times X$. This flexibility will be of enormous value to us in formulating an antibifurcation result that we can apply to system (1.3).

3. Antibifurcation results. Consider the system of equations

$$A_i u_i = \lambda_i u_i + u_i h_i(u_1, \dots, u_n), \tag{3.1}$$

$i = 1, \dots, n$, where for $i = 1, \dots, n$, $u_i \in E_i$, a real Banach algebra, $\lambda_i \in \mathbb{R}$, $A_i : D(A_i) \subseteq E_i \to E_i$ is a densely defined closed operator such that $A_i^{-1} : E_i \to E_i$ exists and is compact, and $h_i : E_1 \times \cdots \times E_n \to E_i$ is continuously differentiable and maps bounded sets into bounded sets with $h_i(0, \dots, 0) = 0$. It is evident that (3.1) is equivalent to

$$u_i = \lambda_i A_i^{-1} u_i + A_i^{-1}(u_i h_i(u_1, \dots, u_n)). \tag{3.2}$$

We assume that there exist open sets $\mathcal{O}_i \subseteq E_i$ satisfying the following:

(H1) $0 \in \partial\mathcal{O}_i$.
(H2) If $A_i u_i = \lambda_i u_i + u_i h_i(u_1, \dots, u_n)$ for some i with $u_i \in \partial\mathcal{O}_i$, $u_j \in E_j$, $j \neq i$, then $u_i = 0$.
(H3) If $\Gamma \subseteq \mathbb{R}^n$ is bounded, then the set S_Γ is bounded in $E_1 \times \cdots \times E_n$, where

$$S_\Gamma = \{(u_1, \dots, u_n) \in \overline{\mathcal{O}}_1 \times \cdots \overline{\mathcal{O}}_n : (\lambda_1, \dots, \lambda_n, u_1, \dots, u_n) \text{ satisfies (3.1)}$$
$$\text{for some } (\lambda_1, \dots, \lambda_n) \in \Gamma\}.$$

(H4) The set $\mathbb{R}^n - \{(\lambda_1, \dots, \lambda_n) \in \mathbb{R}^n :$ there is $(u_1, \dots, u_n) \in \mathcal{O}_1 \times \cdots \times \mathcal{O}_n$ such that $(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n)$ solves (3.1)$\}$ has nonempty interior.

Let

$$F_i(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n) = \lambda_i A_i^{-1} u_i + A_i^{-1}(u_i h_i(u_1, \dots, u_n))$$
$$F(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n)$$
$$= (F_1(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n), \dots, F_n(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n)).$$

Then (3.1) is equivalent to $f(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n) = 0$, where

$$f(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n) = (u_1, \dots, u_n) - F(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n).$$

Finally, let $f_E(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n) : E_1 \times \cdots \times E_n \to E_1 \times \cdots \times E_n$ denote the linearization of f with respect to its last n components at the point $(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n)$. We may now state the basic result of this section.

Theorem 3.1. *Consider* (3.1) *and assume* (H1)-(H4). *Suppose that* $(\lambda_1^0, \dots, \lambda_n^0) \in \mathbb{R}^n$ *and that* $(u_1^0, \dots, u_n^0) \in E_1 \times \cdots \times E_n$ *is such that* $\{(u_1, \dots, u_n) \in \mathcal{O}_1 \times \cdots \times \mathcal{O}_n : (\lambda_1^0, \dots, \lambda_n^0, u_1, \dots, u_n)$ *solves* (3.1)$\} = \{(u_1^0, \dots, u_n^0)\}$. *Then if* $f_E(\lambda_1^0, \dots, \lambda_n^0, u_1^0, \dots, u_n^0)$ *is a linear homeomorphism, there is a closed connected subset* C *of* $\mathbb{R}^n \times \overline{\mathcal{O}_1 \times \cdots \times \mathcal{O}_n}$ *of dimension* $\geq n$ *at every point with the following properties*:

(i) $(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n) \in C$ *implies* $(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n)$ *solves* (3.1).
(ii) $(\lambda_1^0, \dots, \lambda_n^0, u_1^0, \dots, u_n^0) \in C$.
(iii) *There is* $(\overline{\lambda}_1, \dots, \overline{\lambda}_n, \overline{u}_1, \dots, \overline{u}_n) \in C$, *where for at least one* i, $\overline{u}_i = 0$.

Remarks. (i) The theorem guarantees that $(\lambda_1^0, \dots, \lambda_n^0, u_1^0, \dots, u_n^0)$ emanates from the set of solutions to (3.1) where at least one state component vanishes, which is the "antibifurcation" phenomenon described in the Introduction.

(ii) The assumption in the statement of Theorem 3.1 that $f_E(\lambda_1^0, \dots, \lambda_n^0, u_1^0, \dots, u_n^0)$ is nonsingular can be relaxed to the assumption that

$$\deg_{LS}(f(\lambda_1^0, \dots, \lambda_n^0, \dots), B((u_1^0, \dots, u_n^0), \varepsilon), 0) \neq 0$$

for all ε sufficiently small, where $B((u_1^0, \dots, u_n^0), \varepsilon)$ is the ε ball about $(u_1^0, \dots, u_n^0)$ in $E_1 \times \cdots \times E_n$.

(iii) The proof of Theorem 3.1 is to construct a sequence $\mathcal{O}^{(k)}$ of open sets in $E_1 \times \cdots \times E_n$ to which Theorem 2.3 applies and then to pass to a limit in an appropriate sense. Theorem 2.2 is not explicitly referenced in the proof. However, we believe that having in mind the notion of a complementing map for f and the three global options for continuation of $f^{-1}(0)$ (listed in Theorem 2.2) is highly desirable (in fact, almost essential) as background in order to read and comprehend the proof of Theorem 3.1.

Proof. Since $f_E(\lambda_1^0, \dots, \lambda_n^0, u_1^0, \dots, u_n^0)$ is a linear homeomorphism, the solution set to (3.1) in a neighborhood of $(\lambda_1^0, \dots, \lambda_n^0, u_1^0, \dots, u_n^0)$ is an n-manifold. Moreover, there are $\varepsilon_0 > 0$ and $\tilde{\varepsilon}_0 > 0$ so that

(i) $B_1(u_1^0, \varepsilon_0) \times \cdots \times B_n(u_n^0, \varepsilon_0) \subseteq \mathcal{O}_1 \times \cdots \times \mathcal{O}_n$, where $B_i(u_i^0, \varepsilon_0)$ is the open ε_0 ball about u_i^0 in E_i and

(ii) for all $(\lambda_1, \dots, \lambda_n)$ with $| (\lambda_1, \dots, \lambda_n) - (\lambda_1^0, \dots, \lambda_n^0) |_{\mathbb{R}^n} < \tilde{\varepsilon}_0$, $\{(u_1, \dots, u_n) \in \partial(B_1(u_1^0, \varepsilon_0) \times \cdots \times B_n(u_n^0, \varepsilon_0)) : (\lambda_1, \dots, \lambda_n, u_1, \dots, u_n)$ solves (3.1)$\} = \emptyset$. Let $k_0 \in \mathbf{Z}_+$ be such that $1/k_0 < \tilde{\varepsilon}_0$. For $k \geq k_0$, define

$$\begin{aligned}\mathcal{O}^{(k)} &= \overline{B_{\mathbb{R}^n}((\lambda_1^0, \dots, \lambda_n^0), 1/k)} \times B_1(u_1^0, \varepsilon_0) \times \cdots \times B_n(u_n^0, \varepsilon_0)\\ &\cup [\mathbb{R}^n - \overline{(B_{\mathbb{R}^n}((\lambda_1^0, \dots, \lambda_n^0), 1/k))}] \times \mathcal{O}_1 \times \cdots \times \mathcal{O}_n.\end{aligned}$$

It is not difficult to see that $\mathcal{O}^{(k)}$ is open in $\mathbb{R}^n \times E_1 \times \cdots \times E_n$ and that

$$\begin{aligned}\partial\mathcal{O}^{(k)} = &\left[\overline{B_{\mathbb{R}^n}((\lambda_1^0, \dots, \lambda_n^0), 1/k)} \times \partial(B_1(u_1^0, \varepsilon_0) \times \cdots \times B_n(u_n^0, \varepsilon_0))\right]\\ \bigcup &\left[\partial(B_{\mathbb{R}^n}((\lambda_1^0, \dots, \lambda_n^0), 1/k)) \times [\overline{\mathcal{O}_1 \times \cdots \times \mathcal{O}_n} - \overline{(B_1(u_1^0, \varepsilon_0) \times \cdots \times B_n(u_n^0, \varepsilon_0))}]\right]\\ \bigcup &\left[[\mathbb{R}^n - B_{\mathbb{R}^n}((\lambda_1^0, \dots, \lambda_n^0), 1/k)] \times \partial(\mathcal{O}_1 \times \cdots \times \mathcal{O}_n)\right].\end{aligned}$$

Theorem 2.3 is applicable. So there is a closed connected set $\mathcal{C}_k$ of solutions to (3.1) of dimension $\geq n$ everywhere (contained in $\overline{\mathcal{O}}^{(k)} \subseteq \mathbb{R}^n \times \overline{\mathcal{O}_1 \times \cdots \times \mathcal{O}_n}$) containing the point $(\lambda_1^0, \dots, \lambda_n^0, u_1^0, \dots, u_n^0)$ and satisfying at least one of the two options of Theorem 2.3. Suppose now that $\mathcal{C}_k$ does not contain a point $(\lambda_1', \dots, \lambda_n', u_1', \dots, u_n')$ with $(u_1', \dots, u_n') \in \partial(\mathcal{O}_1 \times \cdots \times \mathcal{O}_n)$. Then $\mathcal{C}_k \subseteq \mathbb{R}^n \times (\mathcal{O}_1 \times \cdots \times \mathcal{O}_n)$. Consequently, (H4) rules out alternative (b) of Theorem 2.3. Hence $\mathcal{C}_k \cap \partial\mathcal{O}^{(k)}$ has dimension $\geq n-1$ at every point. The choice of ε_0 implies that there are no solutions to (3.1) in

$$\overline{B_{\mathbb{R}^n}((\lambda_1^0, \dots, \lambda_n^0), 1/k)} \times \partial(B_1(u_1^0, \varepsilon_0) \times \cdots \times B_n(u_n^0, \varepsilon_0)),$$

and we are assuming that there are no solutions to (3.1) in $\mathcal{C}_k \cap ([\mathbb{R}^n - B_{\mathbb{R}^n}((\lambda_1^0, \dots, \lambda_n^0), 1/k)] \times \partial(\mathcal{O}_1 \times \cdots \times \mathcal{O}_n))$. So $\mathcal{C}_k \cap \partial\mathcal{O}^{(k)} \subseteq \partial(B_{\mathbb{R}^n}((\lambda_1^0, \dots, \lambda_n^0), 1/k)) \times [\mathcal{O}_1 \times \cdots \times \mathcal{O}_n - (B_1(u_1^0, \varepsilon_0) \times \cdots \times B_n(u_n^0, \varepsilon_0))]$. Let $\mathcal{C} = \overline{\bigcup_{k \geq k_0} \mathcal{C}_k}$. Assumption (H3) and the compactness of A_i^{-1}, $i = 1, \dots, n$ imply the existence of $(\overline{u}_1, \overline{u}_2, \dots, \overline{u}_n) \neq (u_1^0, u_2^0, \dots, u_n^0)$ such that $(\lambda_1^0, \lambda_2^0, \dots, \lambda_n^0, \overline{u}_1, \overline{u}_2, \dots, \overline{u}_n) \in \mathcal{C}$. Since $\mathcal{C}_k \subseteq \mathbb{R}^n \times$

$\overline{\mathcal{O}_1 \times \cdots \times \mathcal{O}_n}$ for all k, $\mathcal{C} \subseteq \mathbb{R}^n \times \overline{\mathcal{O}_1 \times \cdots \times \mathcal{O}_n}$. Since $\{(u_1, \dots, u_n) \in \mathcal{O}_1 \times \cdots \times \mathcal{O}_n : (\lambda_1^0, \dots, \lambda_n^0, u_1, \dots, u_n)$ solves (3.1) $\} = \{(u_1^0, \dots, u_n^0)\}$, it must be the case that $(\overline{u}_1, \dots, \overline{u}_n) \in \partial(\mathcal{O}_1 \times \cdots \times \mathcal{O}_n)$. Assumption (H2) implies there is an i so that $\overline{u}_i = 0$ and the proof is complete.

If we now strengthen the assumptions of the theorem slightly, we can substantially strengthen its conclusions, as we demonstrate next.

Theorem 3.2. *Suppose in addition to the assumptions of Theorem* 3.1 *that there is an* $\varepsilon_1 > 0$ *so that if* $|(\lambda_1, \dots, \lambda_n) - (\lambda_1^0, \dots, \lambda_n^0)|_{\mathbb{R}^n} < \varepsilon_1$, *there is a unique* $(u_1, \dots, u_n) \in \mathcal{O}_1 \times \cdots \times \mathcal{O}_n$ *such that* $(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n)$ *solves* (3.1). *Then the continuum* $\mathcal{C}$ *whose existence is asserted in Theorem 3.1 has the property that* $\mathcal{C} \cap (\mathbb{R}^n \times \partial(\mathcal{O}_1 \times \cdots \times \mathcal{O}_n))$ *has dimension* $\geq n - 1$.

Proof. We need only to modify the proof of Theorem 3.1. Recall the definitions of ε_0 and $\tilde{\varepsilon}_0$. Let $k \in \mathbf{Z}^+$ be such that $1/k < \min\{\tilde{\varepsilon}_0, \varepsilon_1\}$, and let $\mathcal{O}^{(k)}$ be as in the proof of Theorem 3.1. Choose $\mathcal{C}$ relative to $\overline{\mathcal{O}}^{(k)}$ via Theorem 2.3. Since $1/k < \varepsilon_1$, the additional uniqueness hypothesis guarantees that

$$\mathcal{C} \cap [\partial(B_{\mathbb{R}^n}((\lambda_1^0, \dots, \lambda_n^0), 1/k)) \times \{\mathcal{O}_1 \times \cdots \times \mathcal{O}_n - \overline{(B_1(u_1^0, \varepsilon_0) \times \cdots \times B_n(u_n^0, \varepsilon_0))}\}] = \emptyset.$$

We conclude that either

$$\mathcal{C} \cap [\mathbb{R}^n \times \partial(\mathcal{O}_1 \times \cdots \times \mathcal{O}_n)]$$

has dimension $\geq n - 1$ or that $\{(\lambda_1, \dots, \lambda_n) :$ there is $(u_1, \dots, u_n) \in \overline{\mathcal{O}_1 \times \cdots \times \mathcal{O}_n}$ such that $(\lambda_1, \dots, \lambda_n, u_1, \dots, u_n) \in \mathcal{C}\} = \mathbb{R}^n$. By assumption (H4), the second alternative necessarily implies the first, and the proof is complete.

4. Applications to n-species diffusive competition models. We now want to apply the results of the previous section to analyze the componentwise-positive steady-state solutions to the diffusive Lotka-Volterra competition model

$$\begin{aligned} \frac{\partial u_k}{\partial t} &= \Delta u_k + \Big(a_k - u_k - \sum_{j \neq k} \gamma_{kj} u_j\Big) u_k && \text{in } \Omega \times (0, \infty) \\ u_k &= 0 && \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{4.1}$$

$k = 1, \dots, n$, where $\Omega \subseteq \mathbb{R}^N$ is a bounded domain with sufficiently smooth boundary and a_k, γ_{kj} are positive constants. As noted in the Introduction, various authors have considered this problem, among them Ali and Cosner ([2]). Ali and Cosner ([2]) show that the condition

$$a_k > \sum_{j \neq k} \gamma_{kj} a_j + \lambda^1(0) \tag{4.2}$$

for $k = 1, \dots, n$, is sufficient for the existence of a componentwise-positive steady-state to (4.1), where $\lambda^1(0)$ denotes the principal eigenvalue of $-\Delta$ on Ω subject to zero

Dirichlet boundary data. If the γ_{kj} are considered as given and fixed and $(a_1, \ldots, a_n)$ satisfies (4.2), they demonstrate (see [2, Proposition 4]) that there are functions w_k, $k = 1, \ldots, n$, positive on Ω, so that if $(u_1, \ldots, u_n)$ is a componentwise-positive steady-state for (4.1) associated with $(a_1, \ldots, a_n)$, $u_k \geq w_k$. Moreover, it is possible to make the same choice of the w_k for different choices of $(a_1, \ldots, a_n)$, so long as $(a_1, \ldots, a_n)$ is taken from a compact subset of the open set described by (4.2).

The arguments used by Ali and Cosner in [2] can be employed to obtain a more general condition than (4.2) sufficient for the existence of a componentwise-positive steady-state to (4.1). (See also [7].) Before stating this condition, it is necessary to give some notation. Suppose that m is continuous on $\overline{\Omega}$ and that $m(x_0) > 0$ for some $x_0 \in \Omega$. Then we define $\lambda_1(m)$ to be the unique positive number so that the eigenvalue problem

$$\begin{aligned} -\Delta z &= \lambda m(x) z \quad && \text{in } \Omega \\ z &= 0 && \text{on } \partial\Omega \end{aligned} \tag{4.3}$$

admits a positive eigenfunction and we define θ_m to be the unique positive solution of the problem

$$\begin{aligned} -\Delta w &= mw - w^2 \quad && \text{in } \Omega \\ w &= 0 && \text{on } \partial\Omega \end{aligned} \tag{4.4}$$

provided $\lambda_1(m) < 1$ and to be 0 if $\lambda_1(m) \geq 1$. (That (4.3) and (4.4) admit positive solutions as indicated is by now well known and we refer the interested reader to [4] for details. Note also that $\lambda_1(1) = \lambda^1(0)$.) Then (4.1) has a componentwise-positive steady-state provided

$$\lambda_1\Big(a_k - \sum_{j \neq k} \gamma_{kj}\theta_{a_j}\Big) < 1, \tag{4.5}$$

$k = 1, \ldots, n$. To see that (4.2) implies (4.5), we proceed as follows. Suppose that $\lambda_1\big(a_k - \sum_{j\neq k} \gamma_{kj}\theta_{a_j}\big) = 1$. Then

$$\begin{aligned} -\Delta w + \sum_{j \neq k} \gamma_{kj}\theta_{a_j} w &= a_k w \quad && \text{in } \Omega \\ w &= 0 && \text{on } \partial\Omega \end{aligned}$$

admits a positive solution. Hence

$$\int_\Omega |\nabla\varphi|^2 + \sum_{j\neq k} \int_\Omega \gamma_{kj}\theta_{a_j}\varphi^2 \geq a_k \int_\Omega \varphi^2$$

for all $\varphi \in H_0^1(\Omega)$. If we choose φ to be an eigenfunction corresponding to the principal eigenvalue of $-\Delta$ on Ω and use the fact that $\theta_{a_j} \leq a_j$ (which is a consequence of the maximum principle), we obtain

$$\lambda^1(0) + \sum_{j\neq k} \gamma_{kj} a_j \geq a_k.$$

Since $\lambda_1(m) < \lambda_1(m')$ if $m > m'$ (see [15]), it follows that if $a_k > \sum_{j\neq k}\gamma_{kj}a_j + \lambda^1(0)$, then $\lambda_1\big(a_k - \sum_{j\neq k}\gamma_{kj}\theta_{a_j}\big) < 1$. So (4.5) follows from (4.2).

Suppose now that $\sum_{j\neq k}\gamma_{kj} < 1$ for $k = 1, \dots, n$. Let $a_1 = a_2 = \cdots = a_n = a$. Then condition (4.2) holds provided $a > \frac{\lambda^1(0)}{1-\sum_{j\neq k}\gamma_{kj}} > \lambda^1(0)$. On the other hand, if $a > \lambda^1(0) = \lambda_1(1)$, $\lambda_1(a) < 1$. Hence $\theta_a > 0$ on Ω. It is immediate from (4.4) that $\lambda_1(a - \theta_a) = 1$. Since $\sum_{j\neq k}\gamma_{kj} < 1$, $\sum_{j\neq k}\gamma_{kj}\theta_{a_j} = \sum_{j\neq k}\gamma_{kj}\theta_a < \theta_a$ and so $\lambda_1\big(a_k - \sum_{j\neq k}\gamma_{kj}\theta_{a_j}\big) < 1$, $k = 1, \dots, n$ holds when $a_1 = a_2 = \cdots = a_n = a$ for any $a > \lambda^1(0)$. So the critical parameter value $(a_1, \dots, a_n) = (\lambda^1(0), \dots, \lambda^1(0))$ is a boundary value of the set of $(a_1, \dots, a_n)$ satisfying (4.5) but not of the set of $(a_1, \dots, a_n)$ satisfying (4.2), under the restriction $\sum_{j\neq k}\gamma_{kj} < 1$, $k = 1, \dots, n$. (We use the term "critical parameter value" since $\lambda^1(0)$ is the growth rate threshold in the model for survival of each species in the absence of competitive interaction.)

Now suppose that (4.5) holds. Let U_k denote the unique positive solution to

$$\begin{aligned} -\Delta z &= z\Big[a_k - \sum_{j\neq k}\gamma_{kj}\theta_{a_j} - z\Big] && \text{in } \Omega \\ z &= 0 && \text{on } \partial\Omega. \end{aligned} \tag{4.6}$$

Let $(u_1, \dots, u_n)$ be a componentwise-positive steady-state to (4.1). Then for $k = 1, \dots, n$

$$-\Delta u_k \le (a_k - u_k)u_k$$

on Ω, so that $u_k \le \theta_{a_k}$, and hence

$$-\Delta u_k \ge u_k\Big[a_k - \sum_{j\neq k}\gamma_{kj}\theta_{a_j} - u_k\Big].$$

So u_k is an upper solution for (4.6). Since $\lambda_1\big(a_k - \sum_{j\neq k}\gamma_{kj}\theta_{a_j}\big) < 1$, there is $\tilde a < a_k$ so that $\lambda_1\big(\tilde a - \sum_{j\neq k}\gamma_{kj}\theta_{a_j}\big) < 1$. Hence there is $y > 0$ on Ω so that

$$\begin{aligned} -\Delta y &= \Big(\tilde a - \sum_{j\neq k}\gamma_{kj}\theta_{a_j}\Big)y - y^2 && \text{in } \Omega \\ y &= 0 && \text{on } \partial\Omega. \end{aligned}$$

Now let $0 < \varepsilon < 1$. Then

$$-\Delta(\varepsilon y) = \Big(\tilde a - \sum_{j\neq k}\gamma_{kj}\theta_{a_j}\Big)(\varepsilon y) - y(\varepsilon y) \le \Big(a_k - \sum_{j\neq k}\gamma_{kj}\theta_{a_j}\Big)(\varepsilon y) - (\varepsilon y)^2,$$

and hence εy is a lower solution to (4.6). Since we have $\varepsilon y < u_k$ on Ω for $\varepsilon \in (0, 1)$ and sufficiently small, we have proved the following result.

Proposition 4.1. *Suppose that* (4.5) *holds, and for* $k = 1, \ldots, n$, *let* U_k *denote the unique positive solution to* (4.6). *Then if* $(u_1, \ldots, u_n)$ *is a componentwise-positive steady-state solution to* (4.1), $u_k \geq U_k$ *on* Ω, *for* $k = 1, \ldots, n$.

Remarks. (i) The map $(a_1, \ldots, a_n) \to U_k$ is a continuous map from the open subset of $\mathbb{R}^n$ described by (4.5) into $C_0^1(\overline{\Omega})$ ([4]). So, if K is a compact subset of the set described by (4.5), there will be continuous functions w_k, $k = 1, \ldots, n$, positive on Ω, so that $u_k \geq w_k$ for $k = 1, \ldots, n$, if $(u_1, \ldots, u_n)$ is a componentwise-positive steady-state for (4.1) associated with $(a_1, \ldots, a_n)$, $(a_1, \ldots, a_n) \in K$.

(ii) An argument along the lines of the proof of Theorem 3.5 of [8] shows that if $(a_1, \ldots, a_n) \in I$, where

$$\begin{aligned} I = \Big\{(a_1, \ldots, a_n) : (a_k - \lambda^1(0)) \geq \sum_{j \neq k} \gamma_{kj}(a_j - \lambda^1(0))|\Omega|^{\frac{1}{2}}\Big(\int_\Omega \psi^4 dx\Big)^{\frac{1}{2}},\\ k = 1, \ldots, n\Big\} - \big\{(\lambda^1(0), \ldots, \lambda^1(0))\big\}, \end{aligned}$$

then $(a_1, \ldots, a_n)$ satisfies (4.5). Here ψ denotes the positive solution of

$$\begin{aligned} -\Delta z &= \lambda^1(0) z \quad \text{in } \Omega \\ z &= 0 \quad \text{on } \partial\Omega \end{aligned}$$

so that $\int_\Omega \psi^2 dx = 1$ and $|\Omega|$ denotes the measure of Ω.

Suppose now that $(u_1, \ldots, u_n)$ is a componentwise-positive steady-state solution to (4.1). Then $(u_1, \ldots, u_n)$ satisfies

$$\begin{aligned} -\Delta u_k - \Big(a_k - u_k - \sum_{j \neq k} \gamma_{kj} u_j\Big) u_k &= 0 \quad \text{in } \Omega \\ u_k &= 0 \quad \text{on } \partial\Omega \end{aligned} \tag{4.7}$$

for $k = 1, \ldots, n$. The linearization of the left-hand side of (4.7) with respect to the state variables at $(u_1, \ldots, u_n)$ is the linear map (which can be viewed as mapping say $[C_0^{2+\alpha}(\overline{\Omega})]^n$ into $[C^\alpha(\overline{\Omega})]^n$) given by

$$\begin{pmatrix} z_1 \\ z_2 \\ \vdots \\ z_n \end{pmatrix} \to \begin{pmatrix} -\Delta z_1 \\ -\Delta z_2 \\ \vdots \\ -\Delta z_n \end{pmatrix} - \begin{pmatrix} a_1 - 2u_1 - \sum_{j \neq 1} \gamma_{1j} u_j & -\gamma_{12} u_1 \cdots - \gamma_{1n} u_1 \\ -\gamma_{n1} u_n & -\gamma_{n2} u_n \cdots a_n - \sum_{j \neq n} \gamma_{n_j} u_j - 2u_n \end{pmatrix} \begin{pmatrix} z_1 \\ z_2 \\ \vdots \\ z_n \end{pmatrix}. \tag{4.8}$$

Suppose

$$\begin{pmatrix} -\Delta z_1 \\ \vdots \\ -\Delta z_n \end{pmatrix} = \begin{pmatrix} a_1 - 2u_1 - \sum_{j \neq 1} \gamma_{1j} & u_j - \gamma_{12} u_1 \cdots - \gamma_{1n} u_1 \\ -\gamma_{n1} u_n & -\gamma_{n2} u_n \cdots a_n - \sum_{j \neq n} \gamma_{nj} u_j - 2u_n \end{pmatrix} \begin{pmatrix} z_1 \\ \vdots \\ z_n \end{pmatrix}.$$

Then for $k = 1, \ldots, n$,

$$\int_\Omega |\nabla z_k|^2 - \int_\Omega (a_k - u_k - \sum_{j\neq k} \gamma_{kj} u_j) z_k^2 + \int_\Omega u_k z_k^2 + \int_\Omega \sum_{j\neq k} \gamma_{kj} u_k z_j z_k = 0.$$

Since $-\Delta u_k = u_k(a_k - u_k - \sum_{j\neq k} \gamma_{kj} u_j)$,

$$\int_\Omega |\nabla z_k|^2 - \int_\Omega (a_k - u_k - \sum_{j\neq k} \gamma_{kj} u_j) z_k^2 \geq 0,$$

so that

$$\sum_{j\neq k} \int_\Omega \gamma_{kj} u_k z_j z_k + \int_\Omega u_k z_k^2 \leq 0$$

for $k = 1, \ldots, n$. Consequently, the map given by (4.8) is a linear homeomorphism provided that the quadratic form

$$(z_1, \ldots, z_n) \to \sum_{k=1}^{n} (\sum_{j\neq k} \int_\Omega \gamma_{kj} u_k z_j z_k + \int_\Omega u_k z_k^2) \tag{4.9}$$

is positive definite. In [2, Section 3], Ali and Cosner establish conditions on $(a_1, \ldots, a_n)$ which guarantee that (4.9) is positive definite. Their purpose was to establish the uniqueness of a componentwise-positive steady-state to (4.1) associated to $(a_1, \ldots, a_n)$. The conditions they find (Theorem 5 in [2]) describe a subset of the set given by (4.2). Consequently, we have uniqueness and nondegeneracy (in the sense described above) of componentwise-positive steady-states associated with $(a_1, \ldots, a_n)$ for $(a_1, \ldots, a_n)$ throughout this subset.

We now focus on the special case $a_1 = a_2 = \cdots = a_n = a > \lambda^1(0)$, and seek a steady-state solution to (4.1) of the form $(\alpha_1\theta_a, \ldots, \alpha_n\theta_a)$ with $\alpha_k > 0$ for $k = 1, \ldots, n$. Substituting into (4.6), we have a solution of the form $(\alpha_1\theta_a, \ldots, \alpha_n\theta_a)$ (not yet necessarily positive, however) if $\alpha_k + \sum_{j\neq k} \gamma_{kj}\alpha_j = 1$ for $k = 1, \ldots, n$; i.e., provided

$$\begin{bmatrix} 1 & \gamma_{12} & \cdots & \gamma_{1n} \\ \gamma_{21} & 1 & & \gamma_{2n} \\ & & & \\ \gamma_{n1} & \cdots & \gamma_{n,n-1} & 1 \end{bmatrix} \begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \vdots \\ \alpha_n \end{bmatrix} = \begin{bmatrix} 1 \\ 1 \\ \vdots \\ 1 \end{bmatrix}$$

can be solved for $(\alpha_1, \ldots, \alpha_n)$. The following result is now immediate.

Proposition 4.2. *Suppose that γ_{kj}, $j \neq k$, $k = 1, \ldots, n$ are such that the $k+1$ determinants*

$$\begin{vmatrix} 1 & \gamma_{12} & \cdots & \gamma_{1n} \\ \gamma_{21} & 1 & & \gamma_{2n} \\ & & & \\ \gamma_{n1} & \cdots & & 1 \end{vmatrix} \quad \text{and} \quad \begin{array}{c} \begin{array}{ccccc} & & k^{\text{th}} & & \\ & & \text{column} & & \end{array} \\ \begin{vmatrix} 1 & \cdots & 1 & \cdots & \gamma_{1n} \\ \gamma_{21} & \cdots & 1 & \cdots & \gamma_{2n} \\ & & & & \\ \gamma_{n1} & \cdots & 1 & \cdots & 1 \end{vmatrix} \end{array}$$

$k = 1, \ldots, n$, *are positive. Then* (4.1) *admits a componentwise-positive steady-state for* $(a, \ldots, a)$, $a > \lambda^1(0)$, *of the form* $(\alpha_1\theta_a, \ldots, \alpha_n\theta_a)$ *with*

$$\alpha_k = \begin{array}{c} \begin{array}{ccccc} & & k^{\text{th}} & & \\ & & \text{column} & & \end{array} \\ \left| \begin{array}{ccccc} 1 & \cdots & 1 & \cdots & \gamma_{1n} \\ \gamma_{21} & \cdots & 1 & \cdots & \gamma_{2n} \\ & & & & \\ \gamma_{n1} & \cdots & 1 & & 1 \end{array} \right| \end{array} \Bigg/ \left| \begin{array}{cccc} 1 & \gamma_{12} & \cdots & \gamma_{1n} \\ \gamma_{21} & 1 & \cdots & \gamma_{2n} \\ & & & \\ \gamma_{n1} & \cdots & \cdots & 1 \end{array} \right|. \tag{4.10}$$

Remark. As γ_{kj}, $j \neq k$, tends to 0, the numerator and denominator of α_k tend to 1. Consequently, the positivity assumptions of Proposition 4.2 are met, among other instances, if the competitive interaction is relatively weak.

Suppose now in addition that

$$\begin{bmatrix} 1 & \gamma_{12} & \cdots & \gamma_{1n} \\ \gamma_{21} & 1 & \cdots & \gamma_{2n} \\ & & & \\ \gamma_{n1} & \gamma_{n2} & \cdots & 1 \end{bmatrix}$$

is positive definite, by which we mean that the associated quadratic form is positive definite. Suppose $(\phi_1, \ldots, \phi_n)$ is a componentwise-positive steady-state to (4.1) corresponding to $(a, \ldots, a)$, $a > \lambda^1(0)$. Let $z_k = \phi_k - y_k$, where $y_k = \alpha_k\theta_a$. Then

$$-\Delta z_k = z_k\big[a - \sum_{j\neq k}\gamma_{kj}\phi_j - \phi_k\big] - y_k\big[\sum_{j\neq k}\gamma_{kj}z_j + z_k\big].$$

Hence

$$\int_\Omega |\nabla z_k|^2 = \int_\Omega z_k^2\big[a - \sum_{j\neq k}\gamma_{kj}\phi_j - \phi_k\big] - \int_\Omega y_k\big[\sum_{j\neq k}\gamma_{kj}z_j z_k + z_k^2\big],$$

or equivalently,

$$-\int_\Omega y_k\big[\sum_{j\neq k}\gamma_{kj}z_j z_k + z_k^2\big] = \int_\Omega |\nabla z_k|^2 - \int_\Omega z_k^2\big[a - \sum_{j\neq k}\gamma_{kj}\phi_j - \phi_k\big].$$

Since

$$-\Delta\phi_k - \big(a - \sum_{j\neq k}\gamma_{kj}\phi_j - \phi_k\big)\phi_k = 0,$$

the variational characterization of eigenvalues implies that

$$\int_\Omega |\nabla z_k|^2 - \int_\Omega z_k^2\big[a - \sum_{j\neq k}\gamma_{kj}\phi_j - \phi_k\big] \geq 0,$$

hence

$$\int_\Omega y_k\Big[\sum_{j\neq k}\gamma_{kj}z_j z_k + z_k^2\Big] \leq 0 \quad \text{for } k = 1, \dots, n.$$

Since $y_k = \alpha_k\theta_a$, with $\alpha_k > 0$, this last statement can be expressed

$$\int_\Omega \Big[\sum_{j\neq k}\gamma_{kj}r_j r_k + r_k^2\Big] \leq 0 \quad \text{for } k = 1, \dots, n,$$

where $r_k = \sqrt{\theta_a}z_k$. Since

$$\begin{bmatrix} 1 & \gamma_{12} & \dots & \gamma_{1n} \\ \gamma_{21} & 1 & \dots & \gamma_{2n} \\ & & & \\ \gamma_{n1} & & \dots & 1 \end{bmatrix}$$

is positive definite,

$$\sum_{k=1}^n\Big(\sum_{j\neq k}\gamma_{kj}r_j r_k + r_k^2\Big) \geq 0,$$

so that

$$\int_\Omega \sum_{k=1}^n\Big[\sum_{j\neq k}\gamma_{kj}r_j r_k + r_k^2\Big] \geq 0.$$

Consequently, it must be the case that

$$\int_\Omega \sum_{k=1}^n\Big[\sum_{j\neq k}\gamma_{kj}r_j r_k + r_k^2\Big] = 0.$$

Since

$$\sum_{k=1}^n\Big(\sum_{j\neq k}\gamma_{kj}r_j r_k + r_k^2\Big) \geq 0$$

for all x,

$$\sum_{k=1}^n\Big(\sum_{j\neq k}\gamma_{kj}r_j r_k + r_k^2\Big) \equiv 0,$$

which in turn implies $r_k \equiv 0$. So $\phi_k \equiv \alpha_k\theta_a$, and we have the following result.

Proposition 4.3. *Suppose in addition to the assumptions of Proposition* 4.2 *that*

$$\begin{bmatrix} 1 & \gamma_{12} & \dots & \gamma_{1n} \\ \gamma_{21} & 1 & \dots & \gamma_{2n} \\ & & & \\ \gamma_{n1} & & \dots & 1 \end{bmatrix}$$

is positive definite. Then $(\alpha_1\theta_a, \dots, \alpha_k\theta_a)$ *with* α_k *given by* (4.10) *is the unique componentwise-positive steady-state to* (4.1) *for* $(a_1, \dots, a_n) = (a, \dots, a), a > \lambda^1(0)$.

Remarks. (i) Proposition 4.3 extends the result on the case $n = 2$, given in [9]. The result in [9] has also been extended to the case $n = 3$ in Proposition 1 of [10].

(ii) The argument for Proposition 4.3 also shows that the linearization of the left-hand side of (4.7) at $(\alpha_1\theta_a, \dots, \alpha_n\theta_a)$ is a linear homeomorphism from $[C_0^{2+\alpha}(\overline{\Omega})]^n$ to $[C^\alpha(\overline{\Omega})]^n$.

(iii) Suppose in addition to the assumptions of Proposition 4.3 that $\sum_{j\neq k}\gamma_{kj} < 1$ for $k = 1, \dots, n$. Then for any $a > \lambda^1(0)$, there is an $\varepsilon = \varepsilon(a) > 0$ so that if $|(a_1, \dots, a_n) - (a, \dots, a)| < \varepsilon$, there is a unique componentwise-positive steady-state solution for (4.1) corresponding to $(a_1, \dots, a_n)$. To see that such is the case, recall that $(a, \dots, a)$ satisfies (4.5) (since $\sum_{j\neq k}\gamma_{kj} < 1$ for $k = 1, \dots, n$). Choose $\varepsilon_0 > 0$ so that $\overline{B((a, \dots, a), \varepsilon_0)}$ is contained in the set $\{(a_1, \dots, a_n) : (a_1, \dots, a_n)$ satisfies (4.5)$\}$. Then there are continuous functions w_k, positive on Ω, so that $u_k \geq w_k$ if $(u_1, \dots, u_n)$ is a componentwise-positive steady-state to (4.1) associated with $(a_1, \dots, a_n) \in \overline{B((a, \dots, a), \varepsilon_0)}$. The existence of such an $\varepsilon(a) > 0$ now follows from the uniqueness and nondegeneracy of $(\alpha_1\theta_a, \dots, \alpha_n\theta_a)$ and the compactness of $(-\Delta)^{-1}$.

We may now apply Theorem 3.2 to the analysis of the steady-states to (4.1) to demonstrate a synthesis of the approaches to the problem described in [3] and [17]. To this end, consider (4.7). For $k = 1, \dots, n$, take $E_k = C_0^1(\overline{\Omega})$ and $\mathcal{O}_k = \{u \in E_k : u > 0$ on Ω, $\frac{\partial u}{\partial \nu} < 0$ on $\partial\Omega\}$. Next verify (H1)–(H4). Observe first that (H1) is apparent and that (H2) is a consequence of the strong maximum principle ([13]). If $u_1, \dots, u_n$ are nonnegative and

$$-\Delta u_k = \Big(a_k - u_k - \sum_{j\neq k}\gamma_{kj}u_j\Big)u_k,$$

the maximum principle implies that $0 \leq u_k \leq a_k$. Consequently, if $\Gamma \subseteq \mathbb{R}^n$ is bounded and $(u_1, \dots, u_n)$ is a componentwise-nonnegative solution to (4.7) corresponding to $(a_1, \dots, a_n) \in \Gamma$, there is $M = M(\Gamma) > 0$ so that $\| (u_1, \dots, u_n) \|_{[C(\overline{\Omega})]^n} \leq M$. Since $(u_1, \dots, u_n)$ is a solution to (4.7), elliptic regularity theory ([13]) now implies there is a $\tilde{M} = \tilde{M}(\Gamma)$ so that $\| (u_1, \dots, u_n) \|_{[C^1(\overline{\Omega})]^n} \leq \tilde{M}$, and (H3) obtains. If $(u_1, \dots, u_n)$ satisfies (4.7) for some $(a_1, \dots, a_n)$ with $u_k > 0$ on Ω for $k = 1, \dots, n$, then

$$\lambda^1(0)\int_\Omega u_k^2 \leq \int_\Omega |\nabla u_k|^2 = \int_\Omega a_k u_k^2 - \int_\Omega u_k^2 - \int_\Omega u_k\Big(\sum_{j\neq k}\gamma_{kj}u_j\Big) < \int_\Omega a_k u_k^2.$$

So $a_k > \lambda^1(0)$ for $k = 1, \dots, n$, and (H4) holds.

All that remains is to identify $(a_1^0, \dots, a_n^0, u_1^0, \dots, u_n^0)$ that meets the uniqueness and nondegeneracy conditions of Theorem 3.2. To do so is to impose conditions on the size of the competition coefficients γ_{kj}, $j \neq k$. For instance, if γ_{kj} satisfies Proposition 4.3 and $\sum_{j\neq k}\gamma_{kj} < 1$ for $k = 1, \dots, n$, it follows from Proposition 4.3 and the remarks following it that $(a_1^0, \dots, a_n^0, u_1^0, \dots, u_n^0)$ can be chosen $(a, \dots, a, \alpha_1\theta_a, \dots, \alpha_n\theta_a)$ for any $a > \lambda^1(0)$. On the other hand, suppose $(\overline{a}_1, \dots, \overline{a}_n)$ satisfies (4.2). Then if γ_{kj} satisfies Theorem 5 of [2] and $\sum_{j\neq k}\gamma_{kj} < 1$ for $k = 1, \dots, n$, we may choose $(a_1^0, \dots, a_n^0, u_1^0, \dots, u_n^0) = (\overline{a}_1, \dots, \overline{a}_n, \overline{u}_1, \dots, \overline{u}_n)$, where $(\overline{u}_1, \dots, \overline{u}_n)$ is the unique componentwise-positive solution to (4.7) corresponding to

$(\overline{a}_1, \dots, \overline{a}_n)$. In either case, there will be a continuum $\mathcal{C}$ of dimension $\geq n$ of componentwise positive solutions to (4.7) containing $(a_1^0, \dots, a_n^0, u_1^0, \dots, u_n^0)$ meeting (in a set of dimension $\geq n-1$) the solutions to (4.7) having at least one zero component. So $(a_1^0, \dots, a_n^0, u_1^0, \dots, u_n^0)$ arises through a sequence of bifurcations as described in [3]. Moreover, $(\lambda^1(0), \dots, \lambda^1(0), 0, \dots, 0) \in \mathcal{C}$, so that $\mathcal{C}$ is also as described in [17].

As a final observation, we note that the results of this article are in a sense quantitative as well as qualitative. The lower bounds we establish in Proposition 4.1 guarantee that there can be no transition from a componentwise-positive steady-state to (4.1) to a steady-state to (4.1) with one or more trivial components in the region described by (4.5). In particular, any such transition occurs outside the region given by (4.2) and outside the region I described in the Remark following Proposition 4.1.

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