

CONDITIONS FOR PERMANENCE IN WELL-KNOWN BIOLOGICAL COMPETITION MODELS

JAN H. VAN VUUREN¹ and JOHN NORBURY²

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Abstract

Reaction-diffusion systems are widely used to model the population densities of biological species competing for natural resources in their common habitat. It is often not too difficult to establish positive uniform upper bounds on solution components of such systems, but the task of establishing *strictly positive* uniform lower bounds (when they exist) can be quite troublesome. Two previously established criteria for the permanence (non-extinction and non-explosion) of solutions of general weakly-coupled competition-diffusion systems with diagonally convex reaction terms are used here as background to develop more easily verifiable and concrete conditions for permanence in various well-known competition-diffusion models. These models include multi-component reaction-diffusion systems with (i) the by now classical Lotka-Volterra (logistic) reaction terms, (ii) higher order “logistic” interaction between the species, (iii) logistic-logarithmic reaction terms, (iv) Ayala-Gilpin-Ehrenfeld θ -interaction terms (which are used to model *Drosophila* competition), (v) logistic-exponential interaction between the species, (vi) Schoener-exploitation and (vii) modified Schoener-interference between the species. In (i) a known condition for permanence (for the ODE-system) is recovered, while in (ii)–(vii) new criteria for permanence are established.

1. Introduction

One of the most fundamental problems in the analysis of asymptotic solution behaviour of biological population dynamics models is the study of *permanence* of solution components, in other words, the non-extinction (uniform persistence) and non-explosion (uniform dissipation) of the interacting biological species under consideration. Of these two issues the former is often much more difficult to establish than the latter.

¹Department of Applied Mathematics, Stellenbosch University, Private Bag XI, 7602 Matieland, South Africa; email: vuuren@ing.sun.ac.za

²Mathematical Institute, University of Oxford, 24–29 St Giles’, OX1 3LB, United Kingdom; email: ecmigb@vax.ox.ac.uk

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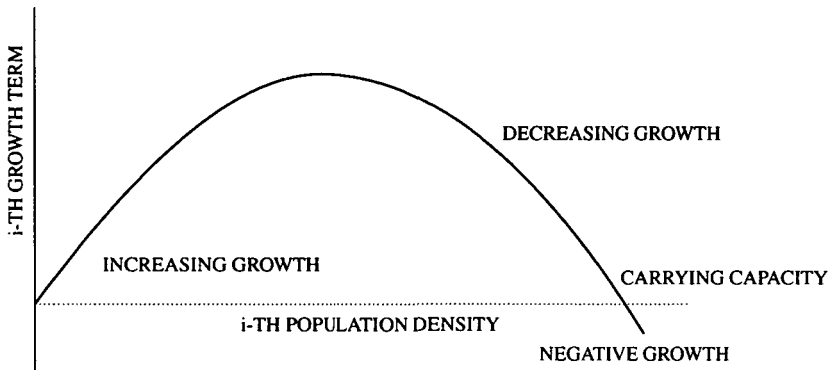


FIGURE 1. Diagonally convex reaction terms.

A number of papers discuss this topic (see for example [2, 4, 6, 8, 9, 12, 13, 15, 16, 20] and [22, 23]), but research has hitherto largely been confined to two or three component biological systems, or, in the case of multi-component models, population densities were assumed to be constant over space (resulting in ordinary differential models), or otherwise only very specific reaction terms were considered. In the above mentioned papers the conditions for permanence obtained are either very specific or else quite complex (involving, for example, definite integrals which are difficult to evaluate, *etc.*).

One exception is an easily verifiable and concrete condition on the system parameters for the uniform persistence of solution components of Lotka-Volterra ordinary differential systems proved in [6, 12] and [20], and confirmed in [23] for two-component Lotka-Volterra systems with constant diffusion and interaction coefficients. This condition, together with uniform upper boundedness, implies permanence of solutions. As far as the authors could establish there are no such concrete conditions for permanence available for models consisting of general competitive partial differential systems, or, for that matter, for models of biological competition other than that of Lotka-Volterra type. It has often been pointed out (see, for example, [3]) that Lotka-Volterra interaction is based on the logistic theory of population growth and that it is therefore subject to the same serious criticisms as the logistic theory: it does not take into account the age of organisms, their sex, or genetic differences between them. It also ignores time lags and assumes the competitive interactions, both intra and inter-specific, are linear. Ayala *et al.* [3] write “Despite these limitations, the model is widely used. It does give a fair representation of competition between protozoan species . . . and [it] has [been] argued that the model is always applicable near equilibrium populations. Yet these considerations do not explain why the Lotka-Volterra model should be almost

TABLE 1. Diagonally convex reaction terms

No	Interaction term in i -th equation
I	$\frac{r_i w_i}{k_i} \left[k_i - w_i - \sum_{j \neq i}^n \alpha_{ij} w_j \right]$
II	$\frac{r_i w_i}{k_i} \left[k_i - w_i - \sum_{j \neq i}^n \alpha_{ij} w_j - \beta_i w_i^2 \right]$
III	$\frac{r_i w_i}{k_i} \left[k_i - w_i - \sum_{j \neq i}^n \alpha_{ij} w_j - \sum_{j=1}^n \beta_j w_j^2 \right]$
IV	$\frac{r_i w_i}{k_i} \left[k_i - w_i - \sum_{j \neq i}^n \alpha_{ij} w_j - \sum_{j=1}^n \beta_{ij} w_i w_j \right]$
V	$\frac{r_i w_i}{k_i} \left[k_i - w_i - \sum_{j \neq i}^n \alpha_{ij} w_j - \sum_{j=1}^n \beta_{ij} w_i w_j - \delta_i w_i^2 \right]$
VI	$\frac{r_i w_i}{k_i} \left[k_i - w_i - \sum_{j \neq i}^n \alpha_{ij} w_j - \sum_{j=1}^n (\beta_{ij} w_i w_j + \gamma_j w_j^2) \right]$
VII	$\frac{r_i w_i}{\log k_i} \left[\log k_i - \log w_i - \sum_{j \neq i}^n \alpha_{ij} \log w_j \right], \quad k_i > 1$
VIII	$\frac{r_i w_i}{k_i} \left[k_i - w_i - \sum_{j \neq i}^n \alpha_{ij} w_j - \beta_i (1 - e^{-\gamma_i w_i}) \right], \quad \gamma_i k_i \leq 2$
IX	$\frac{r_i w_i}{k_i} \left[k_i - w_i - \sum_{j \neq i}^n \alpha_{ij} w_j - \sum_{j=1}^n \beta_j (1 - e^{-\gamma_j w_j}) \right], \quad \gamma_i k_i \leq 2$
X	$\frac{r_i w_i}{\sqrt{k_i}} \left[\sqrt{k_i} - \sqrt{w_i} - \sum_{j \neq i}^n \frac{\alpha_{ij} w_j}{\sqrt{k_i}} \right]$
XI	$\frac{r_i w_i}{k_i^{\theta_i}} \left[k_i^{\theta_i} - w_i^{\theta_i} - \sum_{j \neq i}^n \frac{\alpha_{ij} w_j}{k_i^{1-\theta_i}} \right], \quad 0 \leq \theta_i \leq 1$
XII	$\delta_i w_i \left[\frac{\alpha_i \beta_i}{\sum_{j=1}^n \beta_j w_j} - \gamma_i \right]$
XIII	$\delta_i w_i \left[\frac{\alpha_i \beta_i}{\sum_{j=1}^n \beta_j w_j^{\psi_j}} + \frac{\lambda_i}{w_i^{\psi_i}} - \sum_{j=1}^n \sigma_{ij} w_j - \gamma_i \right], \quad 0 < \psi_i < 1$

the only model of competition, when, for predation, there is a host of alternative models.”¹ Hence it is, in our opinion, clearly desirable to also establish concrete and easily verifiable conditions for permanence in non Lotka-Volterra competitive systems.

The most striking common feature of models of biological competition is often convexity of the growth rate of the i -th species with respect to its population density, which can be justified by the expectation that, due to the competitive species interaction, the growth rate of each species should be small and increasing for small population densities, while for densities close to the carrying capacity of the ecosystem, the growth rate should decrease until the population density reaches some threshold due to limited natural resources, after which the growth rate should become negative and decreasing (as shown in Figure 1). Table 1 contains thirteen sets of diagonally convex reaction terms which have been widely used to model biological competition in the past (see for example [3, 10, 11, 17–19]).

In a previous paper [21] we considered the relatively general class of non-autono-

¹See paragraph 3 on page 332 of [3].

mous, space-dependent competitive reaction-diffusion systems with diagonally convex reaction terms (for an arbitrary number of competing species in an arbitrary dimensional habitat) and found criteria for the i -th growth rate which is sufficient to ensure uniform persistence and upper boundedness of the i -th solution component. Because of the generality of the system, these conditions for persistence seemed somewhat “theoretical”, but in this paper we use them as background to develop concrete and more easily verifiable conditions for permanence in seven special classes of well-known competition-diffusion models. The aim of this paper is therefore twofold: first to generalise the result of [12] and [20] to multi-component reaction-diffusion systems of Lotka-Volterra type and secondly (and more importantly) to establish similar results for multi-component non Lotka-Volterra reaction-diffusion systems with reaction terms as in entries II–XIII of Table 1 (where the parameters are allowed to vary over space and time).

In Section 2 the general diagonally convex competition-diffusion model, together with the assumptions which will be made throughout, is given and in Section 3 the results obtained in [21] for this system are briefly stated and preliminary definitions are given. The seven special sub-classes of the model to be considered (in Sections 4–10) are:

- (1) classical Lotka-Volterra (logistic) interaction (entry I in Table 1)
- (2) higher order “logistic” interaction (entries II-VI in Table 1)
- (3) logistic-logarithmic interaction (entry VII in Table 1)
- (4) logistic-exponential interaction (entries VIII and IX in Table 1)
- (5) Ayala-Gilpin-Ehrenfeld θ -interaction (entries X and XI in Table 1)
- (6) Schoener exploitation (entry XII in Table 1)
- (7) modified Schoener interference (entry XIII in Table 1).

In each of these sections uniform upper boundedness of solution components is established and then a sufficient condition for the persistence of solution components is proved. We conclude in Section 11 by listing (in table form) the various conditions for permanence and asymptotic stability of the models in Sections 4-10.

2. The general model

The initial and Neumann boundary-value problem,

$$\frac{\partial \underline{w}}{\partial \tau} = \underline{f}(\underline{\xi}, \tau, \underline{w}) + \nabla \cdot [\underline{D}(\underline{\xi}, \tau) \nabla \underline{w}], \tag{1}$$

$$\underline{w}(\underline{\xi}, 0) = \underline{\phi}(\underline{\xi}), \quad \underline{\xi} \in \mathcal{D} \quad \text{and} \tag{2}$$

$$\frac{\partial \underline{w}}{\partial \eta}(\underline{\xi}, \tau) = \underline{0} \quad \text{for all } \underline{\xi} \text{ on the boundary } \partial \mathcal{D} \text{ of } \mathcal{D} \text{ and all } \tau \in \mathcal{T}, \tag{3}$$

has often been used to model the population densities, $w_i(\underline{\xi}, \tau)$, $i = 1, \dots, n$, of n competing biological species at time $\tau \in \mathcal{T} = [0, \infty)$ and at position $\underline{\xi} = [\xi_1, \dots, \xi_m]^T$ in a simply connected, m -dimensional spatial domain $\mathcal{D} \in \mathfrak{R}^m$ with smooth boundary $\partial\mathcal{D}$. Here $\underline{\eta}$ denotes the outward pointing unit normal to the boundary $\partial\mathcal{D}$ and the zero-flux Neumann boundary conditions represent the situation where the habitat \mathcal{D} is enclosed and species members cannot leave or enter the domain.

ASSUMPTIONS 2.1. Define $\mathcal{E} = \mathcal{D} \times \mathcal{T}$.

1. Diffusion in isotropic media: (No cross-diffusion) The (diagonal) diffusion matrix, $\underline{\mathbf{D}}(\underline{\xi}, \tau) = \text{diag}\{d_1(\underline{\xi}, \tau), \dots, d_n(\underline{\xi}, \tau)\}$, is strictly positive, uniformly bounded and analytic on \mathcal{E} .

2. Nature of interaction between the species: Let $\mathfrak{R}_+^n = \{\underline{x} \in \mathfrak{R}^n : \underline{x} > \underline{0}\}$ denote the positive cone of the n -dimensional real vector space and define $\mathcal{A} = \mathcal{E} \times \mathfrak{R}_+^n$.

(a) (Structure of reaction terms)

(i) The i -th component of $\underline{f} : \mathcal{A} \rightarrow \mathfrak{R}_+^n$ has the form

$$f_i(\underline{\xi}, \tau, \underline{w}) = w_i(\underline{\xi}, \tau)g_i(\underline{\xi}, \tau, \underline{w}),$$

where the functions $g_i : \mathcal{A} \rightarrow \mathfrak{R}$ are once continuously differentiable with respect to w_j ($j \neq i$) and twice continuously differentiable with respect to w_i , and where $\lim_{w_i \rightarrow 0} f_i(\underline{\xi}, \tau, \underline{w}) = 0$ for all $(\underline{\xi}, \tau) \in \mathcal{E}$.

(ii) For any $(\underline{\xi}, \tau) \in \mathcal{E}$ the hyper surfaces $g_i(\underline{\xi}, \tau, \underline{w}) = 0$, $i = 1, \dots, n$, intersect in exactly one point $\underline{w}^*(\underline{\xi}, \tau) > \underline{0}$; the function $\underline{w}^* : \mathcal{E} \rightarrow \mathfrak{R}_+^n$ being continuous and uniformly bounded away from zero.

(iii) The set of all points in \mathcal{A} on the hyper surface $g_i(\underline{\xi}, \tau, \underline{w}) = 0$ is uniformly bounded for all $i = 1, \dots, n$.

(b) (Competitive interaction) The off-diagonal entries of the Jacobian matrix

$$\mathbf{J}(\underline{\xi}, \tau, \underline{w}) = \left[\frac{\partial f_i}{\partial w_j} \right]_{i,j=1,\dots,n}$$

are non-positive, continuous and uniformly bounded on \mathcal{A} , while the diagonal entries are continuously differentiable and uniformly bounded on \mathcal{A} .

(c) (Diagonal convexity) The i -th component of \underline{f} is strictly convex with respect to the i -th component of \underline{w} , that is, there exist constants \bar{f}_i such that on \mathcal{A} ,

$$\frac{\partial^2 f_i}{\partial w_i^2} \leq \bar{f}_i < 0, \quad i = 1, \dots, n.$$

3. Preliminaries

Define $\mathcal{G}_i(\underline{\xi}, \tau)$ as the set of the i -th components of all points in \mathcal{A} on the hyper surface $g_i(\underline{\xi}, \tau, \underline{w}) = 0$. It then follows by Assumptions 2.1.2(a)(ii)–(iii) that $\sup_{(\underline{\xi}, \tau) \in \mathcal{D}} \{\mathcal{G}_i(\underline{\xi}, \tau)\} > 0$ exists. It was shown in [21] that Assumptions 2.1 are sufficient to guarantee the existence of a unique, continuous and strictly positive solution to the system (1)–(3), and the following uniform upper boundedness result was also established.

THEOREM 3.1 (Solution vector uniformly bounded from above). (a) *The solution vector $\underline{w}(\underline{\xi}, \tau)$ of (1)–(3) is uniformly bounded from above by the constant vector $\underline{\kappa} = [\kappa_1, \dots, \kappa_n]^T$, where*

$$\kappa_i = \max \left\{ \max_{\underline{\xi} \in \mathcal{D}} \{\phi_i(\underline{\xi})\}, \sup_{(\underline{\xi}, \tau) \in \mathcal{D}} \{\mathcal{G}_i(\underline{\xi}, \tau)\} \right\}, \quad i = 1, \dots, n.$$

(b) *There exists a non-negative constant $\bar{\tau}_i$ such that the i -th component, $w_i(\underline{\xi}, \tau)$, of the solution vector $\underline{w}(\underline{\xi}, \tau)$ of (1)–(3) is uniformly bounded from above on $\mathcal{D} \times [\bar{\tau}_i, \infty)$ by*

$$\kappa_i = \sup_{(\underline{\xi}, \tau) \in \mathcal{D}} \{\mathcal{G}_i(\underline{\xi}, \tau)\}, \quad i = 1, \dots, n.$$

A solution component of the system (1)–(3) is said to be *permanent* if there exists a compact set \mathcal{X} in the interior of $\mathfrak{R}_+ = \{x \in \mathfrak{R} : x > 0\}$ such that the solution component eventually enters \mathcal{X} after some finite time and then remains within \mathcal{X} as $\tau \rightarrow \infty$. Therefore a solution component is permanent if it does not explode (is uniformly bounded from above) and is *persistent* (uniformly bounded from below by a positive constant). A solution component of (1)–(3) is said to be *automatically permanent* if it is permanent regardless of the choice of possible system parameters, otherwise it is said to be *conditionally permanent*. The solution of (1)–(3) itself is said to be (automatically/conditionally) permanent if all its components are (automatically/conditionally) permanent. The automatic non-explosion of all solution components of (1)–(3) is a consequence of Theorem 3.1(a). In [21] the following criteria were found to be sufficient to ensure uniform persistence of the i -th solution component of (1)–(3).

THEOREM 3.2 (Permanence result I: Automatic permanence). *If, in addition to Assumptions 2.1, the function $g_i(\underline{\xi}, \tau, \underline{w})$ blows up everywhere on the hyper plane $w_i = 0$, then the i -th component, $w_i(\underline{\xi}, \tau)$, of the solution vector of (1)–(3) is (automatically) permanent.*

Note that, by Assumption 2.1.2 (a) (i), the function $g_i(\underline{\xi}, \tau, \underline{w})$ can blow up no faster than $1/w_i$ as $w_i \downarrow 0$.

THEOREM 3.3 (Permanence result II: Conditional permanence). *If the function $g_i(\underline{\xi}, \tau, \underline{w})$ is uniformly bounded from above on \mathcal{A} , and if there exists a positive constant η_i , such that*

$$\frac{\partial g_i}{\partial w_i}(\underline{\xi}, \tau, \underline{w}(\underline{\xi}, \tau)) + \eta_i < \frac{g_i(\underline{\xi}, \tau, \underline{w}(\underline{\xi}, \tau))}{w_i(\underline{\xi}, \tau)} \tag{4}$$

on \mathcal{A} , then the i -th component, $w_i(\underline{\xi}, \tau)$, of the solution vector of (1)–(3) is (conditionally) permanent.

The qualitative large-time behaviour of solutions of (1)–(3) within the upper and lower bounds of permanence does not fall within the scope of this paper. However, we quote, without proof, the following three results from [21] for the sake of completeness.

THEOREM 3.4 (Autonomous asymptotic behaviour). *If $\underline{w}(\underline{\xi}, \tau)$ is a permanent solution of (1)–(3), and if the system (1) is autonomous and spatially homogeneous, then $\lim_{\tau \rightarrow \infty} \underline{w}(\underline{\xi}, \tau) = \underline{w}^*$ uniformly for $\underline{\xi} \in \mathcal{D}$.*

THEOREM 3.5 (Non-autonomous asymptotic behaviour). *If there exist constants $\Gamma_i > 0$ such that*

$$\sum_{j \neq i}^n \frac{\partial f_i}{\partial w_j}(\underline{\xi}, \tau, \underline{w}) > \Gamma_i + \frac{\partial f_i}{\partial w_i}(\underline{\xi}, \tau, \underline{w}), \quad i = 1, \dots, n, \tag{5}$$

uniformly on $\mathcal{D} \times (t^, \infty) \times \mathbb{R}_+^n$ for some $t^* \geq 0$, then solutions of (1)–(3) are asymptotically stable with respect to perturbations of the initial conditions (2) in the sense that there exist, for any two solution vectors $\underline{w}(\underline{\xi}, \tau)$ and $\underline{v}(\underline{\xi}, \tau)$ of (1)–(3), a $\gamma > 0$ and a $\beta > 0$ such that*

$$\left\| \underline{w}(\underline{\xi}, \tau) - \underline{v}(\underline{\xi}, \tau) \right\|_{\infty} < \beta e^{\gamma \tau}$$

uniformly on \mathcal{E} .

THEOREM 3.6 (Periodic asymptotic behaviour). *If there exist constants $\Gamma_i > 0$ such that (5) holds uniformly on $\mathcal{D} \times (t^*, \infty) \times \mathbb{R}_+^n$ for some $t^* \geq 0$, and if the system functions $g_i(\underline{\xi}, \tau, \underline{w})$ and $d_i(\underline{\xi}, \tau)$ are Ω -periodic with respect to τ for all $i = 1, \dots, n$, then there exists a unique, strictly positive, uniformly bounded Ω -periodic global (exponentially) asymptotic attractor of permanent solutions of (1)–(3).*

It is known that when $n = 2$, the conditions (5) (which may be seen as conditions for resilience) may be dropped from Theorems 3.5 and 3.6 (see, for example, [1, 2, 7] and [14] for the special case of Lotka-Volterra interaction).

In the following six sections the results quoted above are applied to well-known competition models in order to obtain concrete and easily verifiable conditions for permanence of their solutions.

Well-known special cases

4. Logistic (Lotka-Volterra) interaction

Consider the classical Lotka-Volterra *competition* equations with diffusion,

$$\frac{\partial w_i}{\partial \tau} = w_i(\underline{\xi}, \tau) \left[b_i(\underline{\xi}, \tau) - \sum_{j=1}^n a_{ij}(\underline{\xi}, \tau) w_j(\underline{\xi}, \tau) \right] + \sum_{k=1}^m \frac{\partial}{\partial \xi_k} \left[d_i(\underline{\xi}, \tau) \frac{\partial w_i}{\partial \xi_k} \right], \quad (6)$$

for $i = 1, \dots, n$, where the analytic functions $a_{ij}(\underline{\xi}, \tau)$ and $b_i(\underline{\xi}, \tau)$ are assumed to be uniformly bounded from above and below on \mathcal{E} by positive constants for all $i = 1, \dots, n$, while the analytic functions $a_{ij}(\underline{\xi}, \tau)$ need only be uniformly bounded from above and non-negative on \mathcal{E} for all $i \neq j = 1, \dots, n$. Here b_i represents the birth rate proportion of the i -th species; a_{ij} ($i \neq j$) represents the death rate proportion of the i -th species due to the competitive behaviour between species i and j ; and a_{ii} represents the death rate proportion of the i -th species due to self overcrowding. To avoid degenerate cases it will also be assumed that the linear algebraic system

$$\sum_{j=1}^n a_{ij}(\underline{\xi}, \tau) w_j(\underline{\xi}, \tau) = b_i(\underline{\xi}, \tau), \quad i = 1, \dots, n, \quad (7)$$

has a unique, strictly positive solution for each $(\underline{\xi}, \tau) \in \mathcal{E}$. For the system (6),

$$\frac{\partial f_i}{\partial w_j} = -a_{ij}(\underline{\xi}, \tau) w_i(\underline{\xi}, \tau) \leq 0, \quad i \neq j$$

and

$$\frac{\partial^2 f_i}{\partial w_i^2} = -2a_{ii}(\underline{\xi}, \tau) < 0.$$

Since the functions $a_{ii}(\underline{\xi}, \tau)$ are uniformly bounded from below on \mathcal{E} by positive constants, there exist constants \bar{f}_i such that

$$\frac{\partial^2 f_i}{\partial w_i^2} \leq \bar{f}_i < 0, \quad i = 1, \dots, n,$$

so that Assumptions 2.1.2 are indeed satisfied by the system (6).

For this case the set $\mathcal{G}_i(\underline{\xi}, \tau)$ is defined as all points in \mathcal{A} on the i -th hyper plane (7), and it can easily be verified that

$$\sup_{(\underline{\xi}, \tau) \in \mathcal{G}} \{\mathcal{G}_i(\underline{\xi}, \tau)\} \leq \frac{\sup_{(\underline{\xi}, \tau) \in \mathcal{G}} \{b_i(\underline{\xi}, \tau)\}}{\inf_{(\underline{\xi}, \tau) \in \mathcal{G}} \{a_{ii}(\underline{\xi}, \tau)\}},$$

so that, by Theorem 3.1 (a), the solution vector $\underline{w}(\underline{\xi}, \tau)$ of (6) and (2)–(3) is uniformly bounded from above by the constant vector $\underline{\kappa} = [\kappa_1, \dots, \kappa_n]^T$, where

$$\kappa_i = \max \left\{ \max_{\underline{\xi} \in \mathcal{D}} \{\phi_i(\underline{\xi})\}, \frac{\sup_{(\underline{\xi}, \tau) \in \mathcal{G}} \{b_i(\underline{\xi}, \tau)\}}{\inf_{(\underline{\xi}, \tau) \in \mathcal{G}} \{a_{ii}(\underline{\xi}, \tau)\}} \right\}, \quad i = 1, \dots, n.$$

By Theorem 3.1 (b) there also exists a non-negative constant $\bar{\tau}_i$ such that the i -th component of the solution vector $\underline{w}(\underline{\xi}, \tau)$ of (6) and (2)–(3) is uniformly bounded from above on $\mathcal{D} \times [\bar{\tau}_i, \infty)$ by

$$\bar{\kappa}_i = \frac{\sup_{(\underline{\xi}, \tau) \in \mathcal{G}} \{b_i(\underline{\xi}, \tau)\}}{\inf_{(\underline{\xi}, \tau) \in \mathcal{G}} \{a_{ii}(\underline{\xi}, \tau)\}}, \quad i = 1, \dots, n.$$

Let $\bar{\tau}^* = \max_{1 \leq i \leq n} \{\bar{\tau}_i\}$ and define $\mathcal{F} = \mathcal{D} \times [\bar{\tau}^*, \infty) \subset \mathcal{G}$. It is clear that for this case all the functions

$$g_i(\underline{\xi}, \tau, \underline{w}) = b_i(\underline{\xi}, \tau) - \sum_{j=1}^n a_{ij}(\underline{\xi}, \tau) w_j(\underline{\xi}, \tau), \quad i = 1, \dots, n,$$

are uniformly bounded from above on \mathcal{A} and hence that solutions of the system will not necessarily be permanent. The condition for persistence of the i -th species,

$$\inf_{\tau \in \mathcal{F}} \{b_i(\tau)\} > \sum_{j=1, j \neq i}^n \frac{\sup_{\tau \in \mathcal{F}} \{a_{ij}(\tau)\}}{\inf_{\tau \in \mathcal{F}} \{a_{jj}(\tau)\}} \sup_{\tau \in \mathcal{F}} \{b_j(\tau)\},$$

which was proposed in [12] and [20] for the spatially independent Lotka-Volterra system,

$$\frac{dw_i}{d\tau} = w_i(\tau) \left[b_i(\tau) - \sum_{j=1}^n a_{ij}(\tau) w_j(\tau) \right], \quad i = 1, \dots, n,$$

has the obvious generalisation,

$$\inf_{(\underline{\xi}, \tau) \in \mathcal{G}} \{b_i(\underline{\xi}, \tau)\} > \sum_{j=1, j \neq i}^n \frac{\sup_{(\underline{\xi}, \tau) \in \mathcal{G}} \{a_{ij}(\underline{\xi}, \tau)\}}{\inf_{(\underline{\xi}, \tau) \in \mathcal{G}} \{a_{jj}(\underline{\xi}, \tau)\}} \sup_{(\underline{\xi}, \tau) \in \mathcal{G}} \{b_j(\underline{\xi}, \tau)\}, \quad (8)$$

to incorporate the spatial dependence of (6). The sufficiency of this condition for the permanence of the i -th solution component of (6) is proved by noting that, since $w_i(\underline{\xi}, \tau)$ is uniformly bounded from above on \mathcal{F} by $\bar{\kappa}_i$, there exists by (8) a positive constant η_i such that

$$\inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{b_i(\underline{\xi}, \tau)\} > \eta_i w_i(\underline{\xi}, \tau) + \sum_{j=1, j \neq i}^n \frac{\sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{a_{ij}(\underline{\xi}, \tau)\}}{\inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{a_{jj}(\underline{\xi}, \tau)\}} \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{b_j(\underline{\xi}, \tau)\}$$

on \mathcal{F} , since $\mathcal{F} \subset \mathcal{E}$. But now

$$\begin{aligned} b_i(\underline{\xi}, \tau) &\geq \inf_{(\underline{\xi}, \tau) \in \mathcal{E}} \{b_i(\underline{\xi}, \tau)\} \\ &> \eta_i w_i(\underline{\xi}, \tau) + \sum_{j=1, j \neq i}^n \frac{\sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{a_{ij}(\underline{\xi}, \tau)\}}{\inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{a_{jj}(\underline{\xi}, \tau)\}} \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{b_j(\underline{\xi}, \tau)\} \\ &\geq \eta_i w_i(\underline{\xi}, \tau) + \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{a_{ij}(\underline{\xi}, \tau)\} \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \left\{ \frac{b_j(\underline{\xi}, \tau)}{a_{jj}(\underline{\xi}, \tau)} \right\} \\ &\geq \eta_i w_i(\underline{\xi}, \tau) + \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{a_{ij}(\underline{\xi}, \tau)\} \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{w_j(\underline{\xi}, \tau)\} \\ &\geq \eta_i w_i(\underline{\xi}, \tau) + \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \left\{ \sum_{j=1, j \neq i}^n a_{ij}(\underline{\xi}, \tau) w_j(\underline{\xi}, \tau) \right\} \\ &\geq \eta_i w_i(\underline{\xi}, \tau) + \sum_{j=1, j \neq i}^n a_{ij}(\underline{\xi}, \tau) w_j(\underline{\xi}, \tau), \end{aligned}$$

so that

$$b_i(\underline{\xi}, \tau) - \sum_{j=1, j \neq i}^n a_{ij}(\underline{\xi}, \tau) w_j(\underline{\xi}, \tau) > \eta_i w_i(\underline{\xi}, \tau) \tag{9}$$

on \mathcal{F} . Finally,

$$\begin{aligned} \frac{g_i(\underline{\xi}, \tau, \underline{w}(\underline{\xi}, \tau))}{w_i(\underline{\xi}, \tau)} &= \frac{b_i(\underline{\xi}, \tau) - \sum_{j=1}^n a_{ij}(\underline{\xi}, \tau) w_j(\underline{\xi}, \tau)}{w_i(\underline{\xi}, \tau)} \\ &> \frac{\eta_i w_i(\underline{\xi}, \tau) - a_{ii}(\underline{\xi}, \tau) w_i(\underline{\xi}, \tau)}{w_i(\underline{\xi}, \tau)} \quad (\text{by (9)}) \\ &= \eta_i - a_{ii}(\underline{\xi}, \tau) = \eta_i + \frac{\partial g_i}{\partial w_i}(\underline{\xi}, \tau, \underline{w}(\underline{\xi}, \tau)) \end{aligned}$$

on $\mathcal{F} \times \mathfrak{R}_+^n$, so that the general condition for persistence of the i -th component, (4), is satisfied on $\mathcal{F} \times \mathfrak{R}_+^n$. Therefore, by Theorem 3.3, the i -th component of the solution

vector is uniformly bounded from below by a positive constant on \mathcal{F} , which, in this case, is given by

$$\epsilon_i = \min \left\{ \min_{\underline{\xi} \in \mathcal{D}} \{w_i(\underline{\xi}, \tau_i)\}, \zeta_i \right\},$$

where

$$\zeta_i = \frac{\inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{b_i(\underline{\xi}, \tau)\} - \sum_{j=1, j \neq i}^n \kappa_j \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{a_{ij}(\underline{\xi}, \tau)\}}{\sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{a_{ii}(\underline{\xi}, \tau)\}}.$$

This result is already known for the two-component Lotka-Volterra system with diffusion, where the system functions a_{ij} and b_i are constant over time and space (see for example [23]).

Note that when the Lotka-Volterra interaction terms in (6) are reformulated in terms of logistic theory as in entry I of Table 1, that is, if the i -th component of the reaction term is defined by

$$f_i(\underline{\xi}, \tau, \underline{w}) = \frac{r_i(\underline{\xi}, \tau)w_i}{k_i(\underline{\xi}, \tau)} \left[k_i(\underline{\xi}, \tau) - w_i - \sum_{j=1, j \neq i}^n \alpha_{ij}(\underline{\xi}, \tau)w_j \right], \quad i = 1, \dots, n,$$

where the functions $r_i(\underline{\xi}, \tau)$ and $k_i(\underline{\xi}, \tau)$ represent the linear growth rate for small population densities and the carrying capacity of the ecosystem for the i -th species respectively (here both $r_i(\underline{\xi}, \tau)$ and $k_i(\underline{\xi}, \tau)$ are assumed to be uniformly bounded from above and below by positive constants, while the functions $\alpha_{ij}(\underline{\xi}, \tau)$ need only be nonnegative and uniformly bounded from above on \mathcal{E}), then the condition for permanence of the i -th species, (8), becomes

$$\inf_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\} > \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\alpha_{ij}(\underline{\xi}, \tau)\} \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_j(\underline{\xi}, \tau)\}. \tag{10}$$

5. Higher-order “logistic” interaction

In this section the permanence of solutions of competitive reaction-diffusion systems containing M -th order “logistic” reaction terms, that is, systems of the form

$$\begin{aligned} \frac{\partial w_i}{\partial \tau} = & \frac{r_i(\underline{\xi}, \tau)w_i}{k_i(\underline{\xi}, \tau)} \left[k_i(\underline{\xi}, \tau) - w_i - \sum_{j=1, j \neq i}^n \alpha_{ij}(\underline{\xi}, \tau)w_j \right. \\ & \left. - \sum_{p=2}^M \sum_{q=1}^p \sum_{j=1}^n \beta_{ij}^{(p,q)}(\underline{\xi}, \tau)w_i^q w_j^{p-q} \right] + \sum_{k=1}^m \frac{\partial}{\partial \xi_k} \left[d_i(\underline{\xi}, \tau) \frac{\partial w_i}{\partial \xi_k} \right], \quad i = 1, \dots, n, \end{aligned} \tag{11}$$

together with initial and boundary conditions of the form (2)–(3), will be considered (see entries II–VI in Table 1). Here the analytic functions $r_i(\underline{\xi}, \tau)$ and $k_i(\underline{\xi}, \tau)$

are assumed to be uniformly bounded from above and below by positive constants, while the analytic functions $\alpha_{ij}(\underline{\xi}, \tau)$ and $\beta_{ij}^{(p,q)}(\underline{\xi}, \tau)$ need only be nonnegative and uniformly bounded from above on \mathcal{E} . To avoid degenerate cases it will also be assumed that the nonlinear algebraic system

$$w_i(\underline{\xi}, \tau) + \sum_{j=1, j \neq i}^n \alpha_{ij}(\underline{\xi}, \tau)w_j + \sum_{p=2}^M \sum_{q=1}^p \sum_{j=1}^n \beta_{ij}^{(p,q)}(\underline{\xi}, \tau)w_i^q w_j^{p-q} = k_i(\underline{\xi}, \tau), \quad (12)$$

for $i = 1, \dots, n$, has a unique, strictly positive solution for each $(\underline{\xi}, \tau) \in \mathcal{E}$. Note that, for this case,

$$\begin{aligned} \frac{\partial f_i}{\partial w_j} &= -\frac{r_i}{k_i} \left[\alpha_{ij} + \sum_{p=2}^M \sum_{q=1}^p (p - q)\beta_{ij}^{(p,q)} w_i^{q+1} w_j^{p-q-1} \right] < 0, \quad i \neq j, \\ \frac{\partial^2 f_i}{\partial w_i^2} &= -\frac{r_i}{k_i} \left[2 + \sum_{p=2}^M \sum_{q=1}^p p(p + 1)\beta_{ii}^{(p,q)} w_i^{p-1} \right. \\ &\quad \left. + \sum_{p=2}^M \sum_{q=1}^p \sum_{j \neq i}^n q(q + 1)\beta_{ij}^{(p,q)} w_i^{q-1} w_j^{p-q} \right] < 0, \end{aligned}$$

so that Assumptions 2.1.2 are indeed satisfied by the system (11). For this case the set $\mathcal{G}_i(\underline{\xi}, \tau)$ is defined by the set of all points on the hyper surface (12), so that it can easily be seen that

$$\sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\mathcal{G}_i(\underline{\xi}, \tau)\} \leq \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\},$$

and hence, by Theorem 3.1 (a), the solution vector $\underline{w}(\underline{\xi}, \tau)$ of (11) and (2)–(3) is uniformly bounded from above by the constant vector $\underline{\kappa} = [\kappa_1, \dots, \kappa_n]^T$, where

$$\kappa_i = \max \left\{ \max_{\underline{\xi} \in \mathcal{D}} \{\phi_i(\underline{\xi})\}, \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\} \right\}, \quad i = 1, \dots, n.$$

By Theorem 3.1 (b) there also exists a non-negative constant $\bar{\tau}_i$ such that the i -th component, $w_i(\underline{\xi}, \tau)$, of the solution vector of (11) and (2)–(3) is uniformly bounded from above on $\mathcal{D} \times [\bar{\tau}_i, \infty)$ by

$$\bar{\kappa}_i = \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\} \quad i = 1, \dots, n.$$

Let $\bar{\tau}^* = \max_{1 \leq i \leq n} \{\bar{\tau}_i\}$ and define the set $\mathcal{F} = \mathcal{D} \times [\bar{\tau}^*, \infty) \subset \mathcal{E}$. Persistence of solution components is considered next. It is clear that, also for this case, all the functions

$$g_i(\underline{\xi}, \tau, \underline{w}) = k_i(\underline{\xi}, \tau) - w_i - \sum_{j=1, j \neq i}^n \alpha_{ij}(\underline{\xi}, \tau)w_j - \sum_{p=2}^M \sum_{q=1}^p \sum_{j=1}^n \beta_{ij}^{(p,q)}(\underline{\xi}, \tau)w_i^q w_j^{p-q},$$

$i = 1, \dots, n$, are uniformly bounded from above on \mathcal{A} , so that solution components of the system will *not necessarily* be permanent. It is now shown that the condition for permanence, (10), obtained in Section 4, is in fact also sufficient for solution permanence in higher-order logistic systems of the form (11). To prove this, note that, since the i -th solution component of (11) is uniformly bounded from above on \mathcal{F} by $\sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{k_i(\underline{\xi}, \tau)\}$, and since the functions $r_i(\underline{\xi}, \tau)$ and $k_i(\underline{\xi}, \tau)$ are also uniformly bounded from above, with $r_i(\underline{\xi}, \tau)$ additionally bounded away from zero on \mathcal{F} , there exists by (10) a positive constant η_i such that

$$\inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{k_i(\underline{\xi}, \tau)\} > \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{\alpha_{ij}(\underline{\xi}, \tau)\} \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{k_j(\underline{\xi}, \tau)\} + \frac{\eta_i k_i(\underline{\xi}, \tau) w_i(\underline{\xi}, \tau)}{r_i(\underline{\xi}, \tau)},$$

but now

$$\begin{aligned} k_i(\underline{\xi}, \tau) &\geq \inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{k_i(\underline{\xi}, \tau)\} \\ &> \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{\alpha_{ij}(\underline{\xi}, \tau)\} \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{k_j(\underline{\xi}, \tau)\} + \frac{\eta_i k_i(\underline{\xi}, \tau) w_i(\underline{\xi}, \tau)}{r_i(\underline{\xi}, \tau)} \\ &\geq \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{\alpha_{ij}(\underline{\xi}, \tau)\} \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{w_j(\underline{\xi}, \tau)\} + \frac{\eta_i k_i(\underline{\xi}, \tau) w_i(\underline{\xi}, \tau)}{r_i(\underline{\xi}, \tau)} \\ &\geq \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{\alpha_{ij}(\underline{\xi}, \tau) w_j(\underline{\xi}, \tau)\} + \frac{\eta_i k_i(\underline{\xi}, \tau) w_i(\underline{\xi}, \tau)}{r_i(\underline{\xi}, \tau)} \\ &\geq \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \left\{ \sum_{j=1, j \neq i}^n \alpha_{ij}(\underline{\xi}, \tau) w_j(\underline{\xi}, \tau) \right\} + \frac{\eta_i k_i(\underline{\xi}, \tau) w_i(\underline{\xi}, \tau)}{r_i(\underline{\xi}, \tau)} \\ &\geq \sum_{j=1, j \neq i}^n \alpha_{ij}(\underline{\xi}, \tau) w_j(\underline{\xi}, \tau) + \frac{\eta_i k_i(\underline{\xi}, \tau) w_i(\underline{\xi}, \tau)}{r_i(\underline{\xi}, \tau)}, \end{aligned}$$

so that

$$k_i(\underline{\xi}, \tau) - \sum_{j=1, j \neq i}^n \alpha_{ij} w_j > \frac{\eta_i k_i w_i}{r_i}$$

on \mathcal{F} . Finally,

$$\begin{aligned} \frac{g_i(\underline{\xi}, \tau, \underline{w})}{w_i(\underline{\xi}, \tau)} &= \frac{r_i}{k_i w_i} \left[k_i - w_i - \sum_{j=1, j \neq i}^n \alpha_{ij} w_j - \sum_{p=2}^M \sum_{q=1}^p \sum_{j=1}^n \beta_{ij}^{(p,q)} w_i^q w_j^{p-q} \right] \\ &= \frac{r_i}{k_i w_i} \left[k_i - \sum_{j=1, j \neq i}^n \alpha_{ij} w_j \right] - \frac{r_i}{k_i w_i} \left[w_i + \sum_{p=2}^M \sum_{q=1}^p \sum_{j=1}^n \beta_{ij}^{(p,q)} w_i^q w_j^{p-q} \right] \\ &> \frac{r_i}{k_i w_i} \left[\frac{\eta_i k_i w_i}{r_i} \right] - \frac{r_i}{k_i w_i} \left[w_i + \sum_{p=2}^M \sum_{q=1}^p \sum_{j=1}^n \beta_{ij}^{(p,q)} w_i^q w_j^{p-q} \right] \end{aligned}$$

$$\begin{aligned}
 &= \eta_i - \frac{r_i}{k_i w_i} \left[w_i + \sum_{p=2}^M \sum_{q=1}^p \left\{ \beta_{ii}^{(p,q)} w_i^p + w_i^q \sum_{j=1, j \neq i}^n \beta_{ij}^{(p,q)} w_j^{p-q} \right\} \right] \\
 &\geq \eta_i - \frac{r_i}{k_i} \left[1 + \sum_{p=2}^M \sum_{q=1}^p \left\{ p \beta_{ii}^{(p,q)} w_i^{p-1} + q w_i^{q-1} \sum_{j=1, j \neq i}^n \beta_{ij}^{(p,q)} w_j^{p-q} \right\} \right] \\
 &= \eta_i + \frac{\partial g_i}{\partial w_i}(\underline{\xi}, \tau, \underline{w})
 \end{aligned}$$

on $\mathcal{F} \times \mathbb{R}_+^n$, so that the general condition for permanence, (4), is met on $\mathcal{F} \times \mathbb{R}_+^n$ and hence the permanence of the i -th solution component of the system follows by Theorem 3.3.

The condition for persistence of the i -th solution component of the system (11) and (2)–(3) is the same as that for the system with logistic reaction terms—the addition of higher-order interaction does not affect the condition for persistence. This illustrates the underlying relationship between a condition for persistence and a condition for *linear* instability of the origin and all the other unacceptable steady states (those representing the extinction of some species) as well as the simultaneous *linear* stability of the non-trivial steady state (representing the co-existence of the species with other species).

6. Logistic-logarithmic interaction

The permanence of solutions of competitive reaction-diffusion systems containing logistic-logarithmic reaction terms, that is, systems of the form

$$\begin{aligned}
 \frac{\partial w_i}{\partial \tau} &= \frac{r_i(\underline{\xi}, \tau) w_i}{\log k_i(\underline{\xi}, \tau)} \left[\log k_i(\underline{\xi}, \tau) - \log w_i - \sum_{j=1, j \neq i}^n \alpha_{ij}(\underline{\xi}, \tau) \log w_j \right] \\
 &+ \sum_{k=1}^m \frac{\partial}{\partial \xi_k} \left[d_i(\underline{\xi}, \tau) \frac{\partial w_i}{\partial \xi_k} \right], \quad i = 1, \dots, n,
 \end{aligned} \tag{13}$$

together with initial and boundary conditions of the form (2)–(3), are considered in this section (see entry VII in Table 1). Here the analytic functions $r_i(\underline{\xi}, \tau)$ are assumed be uniformly bounded from above and below by positive constants, the analytic functions $k_i(\underline{\xi}, \tau)$ are also assumed to be uniformly bounded from above, but uniformly bounded from below by constants greater than unity, while the analytic functions $\alpha_{ij}(\underline{\xi}, \tau)$ need only be nonnegative and uniformly bounded from above. Finally, to avoid degenerate cases, the algebraic system

$$\log w_i(\underline{\xi}, \tau) + \sum_{j=1, j \neq i}^n \alpha_{ij}(\underline{\xi}, \tau) \log w_j(\underline{\xi}, \tau) = \log k_i(\underline{\xi}, \tau), \quad i = 1, \dots, n, \tag{14}$$

is assumed to have a unique, strictly positive solution for each $(\underline{\xi}, \tau) \in \mathcal{E}$. Note that for this case

$$\frac{\partial f_i}{\partial w_j} = -\frac{r_i(\underline{\xi}, \tau)\alpha_{ij}(\underline{\xi}, \tau)w_i(\underline{\xi}, \tau)}{w_j(\underline{\xi}, \tau)\log k_i(\underline{\xi}, \tau)} \leq 0, \quad i \neq j$$

and

$$\frac{\partial^2 f_i}{\partial w_i^2} = -\frac{r_i(\underline{\xi}, \tau)}{w_i(\underline{\xi}, \tau)\log k_i(\underline{\xi}, \tau)} < 0.$$

Since $r_i(\underline{\xi}, \tau)$ is uniformly bounded from below on \mathcal{E} by a positive constant, and $k_i(\underline{\xi}, \tau)$ and hence $\log k_i(\underline{\xi}, \tau)$ is uniformly bounded from above on \mathcal{E} , there exist constants \bar{f}_i such that

$$\frac{\partial^2 f_i}{\partial w_i^2} \leq \bar{f}_i < 0, \quad i = 1, \dots, n,$$

provided that all solution components of the system are uniformly bounded from above. To prove this uniform upper boundedness, observe that the set $\mathcal{G}_i(\underline{\xi}, \tau)$ is defined by all points on the hyper surface (14) and hence

$$\sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\mathcal{G}_i(\underline{\xi}, \tau)\} \leq \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\},$$

so that, by Theorem 3.1 (a), the solution vector $\underline{w}(\underline{\xi}, \tau)$ of (13) and (2)–(3) is uniformly bounded from above by the constant vector $\underline{\kappa} = [\kappa_1, \dots, \kappa_n]^T$, where

$$\kappa_i = \max \left\{ \max_{\underline{\xi} \in \mathcal{D}} \{\phi_i(\underline{\xi})\}, \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\} \right\}, \quad i = 1, \dots, n.$$

Hence Assumptions 2.1.2 are indeed satisfied by the system (13). By Theorem 3.1 (b) there also exists a non-negative constant $\bar{\tau}_i$ such that the i -th component, $w_i(\underline{\xi}, \tau)$, of the solution vector of (13) and (2)–(3) is uniformly bounded from above on $\mathcal{D} \times [\bar{\tau}_i, \infty)$ by

$$\bar{\kappa}_i = \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\}, \quad i = 1, \dots, n.$$

Persistence of solution components is considered next. Let $\bar{\tau}^* = \max_{1 \leq i \leq n} \{\bar{\tau}_i\}$ and define $\mathcal{F} = \mathcal{D} \times [\bar{\tau}^*, \infty) \subset \mathcal{E}$. For this case it is clear that the function

$$g_i(\underline{\xi}, \tau, \underline{w}) = \log k_i(\underline{\xi}, \tau) - \log w_i - \sum_{j=1, j \neq i}^n \alpha_{ij}(\underline{\xi}, \tau) \log w_j$$

blows up everywhere on the hyper plane $w_i = 0$, and hence that all solution components of (13) and (2)–(3) are necessarily permanent by Theorem 3.2. It is in fact

possible to show that the solution is uniformly bounded from below by the strictly positive constant vector $\tilde{\kappa} = [\tilde{\kappa}_1, \dots, \tilde{\kappa}_n]^T$, where

$$\tilde{\kappa}_i = \min \left\{ \min_{\xi \in \mathcal{D}} \{\phi_i(\xi)\}, \frac{\inf_{\mathcal{E}} \{k_i(\xi, \tau)\}}{\prod_{j=1, j \neq i}^n \sup_{\mathcal{E}} \{k_j(\xi, \tau)\}^{\sup_{\mathcal{E}} \{\alpha_{ij}(\xi, \tau)\}}} \right\}, \quad i = 1, \dots, n.$$

We prove this by contradiction. Suppose that at some point $(\xi^*, \tau^*) \in \mathcal{E}$ we have that $w_i(\xi^*, \tau^*) < \tilde{\kappa}_i$ for an arbitrary $1 \leq i \leq n$. Then there exists by the continuity of w_i a positive constant ρ_i and a point $(\xi^{**}, \tau^{**}) \in \mathcal{D} \times [0, \tau^*)$ such that $w_i(\xi, \tau) \geq \tilde{\kappa}_i - \rho_i$ for all $(\xi, \tau) \in \mathcal{D} \times [0, \tau^{**}]$ and $w_i(\xi^{**}, \tau^{**}) = \tilde{\kappa}_i - \rho_i$. Since the function $w_i(\xi, \tau)$ attains its minimum value in $\mathcal{D} \times [0, \tau^{**}]$ at (ξ^{**}, τ^{**}) , we must have

$$\frac{\partial w_i}{\partial \tau}(\xi^{**}, \tau^{**}) \leq 0, \quad \frac{\partial w_i}{\partial \xi_k}(\xi^{**}, \tau^{**}) = 0$$

and

$$\frac{\partial^2 w_i}{\partial \xi_k^2}(\xi^{**}, \tau^{**}) \geq 0, \quad k = 1, \dots, m,$$

which, if substituted into (13), yields

$$\frac{r_i^{**} w_i^{**}}{\log k_i^{**}} \left[\log k_i^{**} - \log w_i^{**} - \sum_{j=1, j \neq i}^n \alpha_{ij}^{**} \log w_j^{**} \right] \leq 0,$$

which in turn means that

$$\log w_i^{**} \geq \log k_i^{**} - \sum_{j=1, j \neq i}^n \alpha_{ij}^{**} \log w_j^{**}, \tag{15}$$

where $r_i^{**}, k_i^{**}, \alpha_{ij}^{**}$ and w_i^{**} denote the values of $r_i(\xi^{**}, \tau^{**}), k_i(\xi^{**}, \tau^{**}), \alpha_{ij}(\xi^{**}, \tau^{**})$ and $w_i(\xi^{**}, \tau^{**})$ respectively. Since $w = \tilde{\kappa}_i - \rho_i < \tilde{\kappa}_i$ and $\mathcal{F} \subset \mathcal{E}$, we also have

$$w_i^{**} < \frac{\inf_{\mathcal{F}} \{k_i(\xi, \tau)\}}{\prod_{j=1, j \neq i}^n \sup_{\mathcal{F}} \{k_j(\xi, \tau)\}^{\sup_{\mathcal{F}} \{\alpha_{ij}(\xi, \tau)\}}}$$

and hence

$$\begin{aligned} \log w_i^{**} &< \log \inf_{\mathcal{F}} \{k_i(\xi, \tau)\} - \sum_{j=1, j \neq i}^n \sup_{\mathcal{F}} \{\alpha_{ij}(\xi, \tau)\} \log \sup_{\mathcal{F}} \{k_j(\xi, \tau)\} \\ &\leq \log \inf_{\mathcal{F}} \{k_i(\xi, \tau)\} - \sum_{j=1, j \neq i}^n \sup_{\mathcal{F}} \{\alpha_{ij}(\xi, \tau)\} \log \sup_{\mathcal{F}} \{w_j(\xi, \tau)\} \\ &\leq \log k_i^{**} - \sum_{j=1, j \neq i}^n \alpha_{ij}^{**} \log w_j^{**}, \end{aligned}$$

which contradicts (15), and establishes the above mentioned uniform lower bounds of permanence.

7. Logistic-exponential interaction

In this section the permanence of solutions of competitive reaction-diffusion systems containing logistic-exponential reaction terms, that is, systems of the form

$$\begin{aligned} \frac{\partial w_i}{\partial \tau} = & \frac{r_i(\underline{\xi}, \tau) w_i}{k_i(\underline{\xi}, \tau)} \left[k_i(\underline{\xi}, \tau) - w_i - \sum_{j=1, j \neq i}^n \alpha_{ij}(\underline{\xi}, \tau) w_j - \sum_{j=1}^n (1 - e^{-\gamma_j(\underline{\xi}, \tau) w_j}) \right] \\ & + \sum_{k=1}^m \frac{\partial}{\partial \xi_k} \left[d_i(\underline{\xi}, \tau) \frac{\partial w_i}{\partial \xi_k} \right], \quad i = 1, \dots, n, \end{aligned} \quad (16)$$

together with initial and boundary conditions of the form (2)–(3), are considered (see entries VIII and IX of Table 1). Here the analytic functions $r_i(\underline{\xi}, \tau)$ and $k_i(\underline{\xi}, \tau)$ are assumed to be uniformly bounded from above and below by positive constants, while the analytic functions $\alpha_{ij}(\underline{\xi}, \tau)$ and $\gamma_j(\underline{\xi}, \tau)$ need only be uniformly bounded from above, non-negative and satisfy

$$\gamma_i(\underline{\xi}, \tau) \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\} \leq 2, \quad i = 1, \dots, n, \quad (17)$$

on \mathcal{E} . To avoid degenerate cases it will be assumed that the algebraic system

$$w_i + \sum_{j=1, j \neq i}^n \alpha_{ij}(\underline{\xi}, \tau) w_j + \sum_{j=1}^n (1 - e^{-\gamma_j(\underline{\xi}, \tau) w_j}) = k_i(\underline{\xi}, \tau), \quad i = 1, \dots, n, \quad (18)$$

has a unique, strictly positive solution for each $(\underline{\xi}, \tau) \in \mathcal{E}$. For this case the set $\mathcal{G}_i(\underline{\xi}, \tau)$ is defined as the set of all points on the hyper surface (18), so that it can easily be verified that

$$\sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\mathcal{G}_i(\underline{\xi}, \tau)\} \leq \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\},$$

and hence, by Theorem 3.1 (a), the solution vector $\underline{w}(\underline{\xi}, \tau)$ of (16) and (2)–(3) is uniformly bounded from above by the constant vector $\underline{\kappa} = [\kappa_1, \dots, \kappa_n]^T$, where

$$\kappa_i = \left\{ \max_{\underline{\xi} \in \mathcal{D}} \{\phi_i(\underline{\xi})\}, \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\} \right\}, \quad i = 1, \dots, n.$$

By Theorem 3.1 (b) there also exists a non-negative constant $\bar{\tau}_i$ such that the i -th component, $w_i(\underline{\xi}, \tau)$, of the solution vector of (11) and (2)–(3) is uniformly bounded from above on $\mathcal{D} \times [\bar{\tau}_i, \infty)$ by

$$\bar{\kappa}_i = \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\}, \quad i = 1, \dots, n.$$

Let $\bar{\tau}^* = \max_{1 \leq i \leq n} \{\bar{\tau}_i\}$ and define $\mathcal{F} = \mathcal{D} \times [\bar{\tau}^*, \infty) \subset \mathcal{E}$. On \mathcal{F} we now have by (17) that

$$w_i(\underline{\xi}, \tau) \leq \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\} \leq \frac{2}{\gamma_i(\underline{\xi}, \tau)}$$

and hence

$$\gamma_i(\underline{\xi}, \tau)w_i(\underline{\xi}, \tau) - 2 \leq 0$$

on \mathcal{F} , so that

$$\frac{\partial f_i}{\partial w_j} = -\frac{r_i(\underline{\xi}, \tau)w_i(\underline{\xi}, \tau)}{k_i(\underline{\xi}, \tau)} \left(\alpha_{ij}(\underline{\xi}, \tau) + \gamma_j(\underline{\xi}, \tau)e^{-\gamma_j(\underline{\xi}, \tau)w_j(\underline{\xi}, \tau)} \right) \leq 0, \quad i \neq j$$

and

$$\frac{\partial^2 f_i}{\partial w_i^2} = -\frac{2r_i(\underline{\xi}, \tau)}{k_i(\underline{\xi}, \tau)} + \frac{r_i(\underline{\xi}, \tau)\gamma_i(\underline{\xi}, \tau)[\gamma_i(\underline{\xi}, \tau)w_i(\underline{\xi}, \tau) - 2]}{k_i(\underline{\xi}, \tau)} e^{-\gamma_i(\underline{\xi}, \tau)w_i(\underline{\xi}, \tau)} < 0.$$

Since $r_i(\underline{\xi}, \tau)$ and $k_i(\underline{\xi}, \tau)$ are uniformly bounded from above and below on \mathcal{F} by positive constants, there exist constants \bar{f}_i such that

$$\frac{\partial^2 f_i}{\partial w_i^2} \leq \bar{f}_i < 0, \quad i = 1, \dots, n,$$

and hence Assumptions 2.1.2 are indeed satisfied by the system (16). It is clear that the functions

$$g_i(\underline{\xi}, \tau, \underline{w}) = k_i(\underline{\xi}, \tau) - w_i - \sum_{j=1, j \neq i}^n \alpha_{ij}(\underline{\xi}, \tau)w_j - \sum_{j=1}^n (1 - e^{-\gamma_j(\underline{\xi}, \tau)w_j})$$

are uniformly bounded from above on \mathcal{A} , so that solution components of the system are *not necessarily* permanent. We now show that the condition

$$\begin{aligned} & \inf_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i\} + \inf_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\beta_i\} \left(e^{-\sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\gamma_i\} \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i\}} - 1 \right) \\ & > \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\alpha_{ij}\} \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i\} + \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\beta_j\} (1 - e^{-\sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\gamma_j\} \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i\}}) \end{aligned} \tag{19}$$

is sufficient to ensure permanence of the i -th solution component. To prove this, observe that by (19) and the uniform upper and lower boundedness of $r_i(\underline{\xi}, \tau)$ and $k_i(\underline{\xi}, \tau)$ as well as the uniform upper boundedness of $w_i(\underline{\xi}, \tau)$ on \mathcal{E} , there exists a positive constant η_i , such that

$$\inf \{k_i\} + \inf \{\beta_i\} \left(e^{-\sup \{\gamma_i\} \sup \{k_i\}} - 1 \right)$$

$$> \sum_{j=1, j \neq i}^n (\sup\{\alpha_{ij}\} \sup\{k_i\} + \sup\{\beta_j\} (1 - e^{-\sup\{\gamma_j\} \sup\{k_i\}})) + \frac{\eta_i k_i w_i}{r_i}$$

on \mathcal{F} . Now

$$\begin{aligned} & k_i + \beta_i (e^{-\gamma_i w_i} - 1) \\ & \geq \inf\{k_i\} + \inf\{\beta_i\} (e^{-\sup\{\gamma_i\} \sup\{k_i\}} - 1) \\ & > \sum_{j=1, j \neq i}^n (\sup\{\alpha_{ij}\} \sup\{k_j\} + \sup\{\beta_j\} (1 - e^{-\sup\{\gamma_j\} \sup\{k_j\}})) + \frac{\eta_i k_i w_i}{r_i} \\ & \geq \sum_{j=1, j \neq i}^n (\sup\{\alpha_{ij}\} \sup\{w_j\} + \sup\{\beta_j\} (1 - e^{-\sup\{\gamma_j\} \sup\{w_j\}})) + \frac{\eta_i k_i w_i}{r_i} \\ & \geq \sum_{j=1, j \neq i}^n (\sup\{\alpha_{ij} w_j\} + \sup\{\beta_j (1 - e^{-\gamma_j w_j})\}) + \frac{\eta_i k_i w_i}{r_i} \\ & \geq \sup \left\{ \sum_{j=1, j \neq i}^n (\alpha_{ij} w_j + \beta_j (1 - e^{-\gamma_j w_j})) \right\} + \frac{\eta_i k_i w_i}{r_i} \\ & \geq \sum_{j=1, j \neq i}^n (\alpha_{ij} w_j + \beta_j (1 - e^{-\gamma_j w_j})) + \frac{\eta_i k_i w_i}{r_i}, \end{aligned}$$

so that

$$k_i - \sum_{j=1, j \neq i}^n \alpha_{ij} w_j - \sum_{j=1}^n \beta_j (1 - e^{-\gamma_j w_j}) > \frac{\eta_i k_i w_i}{r_i}$$

on \mathcal{F} . Finally,

$$\begin{aligned} & \frac{g_i(\underline{\xi}, \tau, \underline{w}(\underline{\xi}, \tau))}{w_i(\underline{\xi}, \tau)} \\ & = \frac{r_i}{k_i w_i} \left[k_i - w_i - \sum_{j=1, j \neq i}^n \alpha_{ij} w_j - \sum_{j=1}^n \beta_j (1 - e^{-\gamma_j w_j}) \right] \\ & > \frac{r_i}{k_i w_i} \left[k_i - \sum_{j=1, j \neq i}^n \alpha_{ij} w_j - \sum_{j=1}^n \beta_j (1 - e^{-\gamma_j w_j}) \right] - \frac{r_i}{k_i} - \frac{r_i \gamma_i}{k_i} e^{-\gamma_i w_i} \\ & > \frac{r_i}{k_i w_i} \left[\frac{\eta_i k_i w_i}{r_i} \right] - \frac{r_i}{k_i} (1 + \gamma_i e^{-\gamma_i w_i}) = \eta_i + \frac{\partial g_i}{\partial w_i}(\underline{\xi}, \tau, \underline{w}(\underline{\xi}, \tau)) \end{aligned}$$

on $\mathcal{F} \times \mathbb{R}_+^n$, so that the general condition for persistence of the i -th solution component, (4), is satisfied on $\mathcal{F} \times \mathbb{R}_+^n$ and hence (conditional) permanence of the i -th solution component of (16) and (2)–(3) holds by Theorem 3.3.

8. Ayala-Gilpin-Ehrenfeld θ -interaction

In this section the permanence of solutions of competitive reaction-diffusion systems containing Ayala-Gilpin-Ehrenfeld θ -reaction terms, that is, systems of the form

$$\frac{\partial w_i}{\partial \tau} = \frac{r_i(\underline{\xi}, \tau) w_i}{k_i^{\theta_i(\underline{\xi}, \tau)}(\underline{\xi}, \tau)} \left[k_i^{\theta_i(\underline{\xi}, \tau)}(\underline{\xi}, \tau) - w_i^{\theta_i(\underline{\xi}, \tau)} - \sum_{j=1, j \neq i}^n \frac{\alpha_{ij}(\underline{\xi}, \tau) w_j}{k_i^{1-\theta_i(\underline{\xi}, \tau)}(\underline{\xi}, \tau)} \right] + \sum_{k=1}^m \frac{\partial}{\partial \xi_k} \left[d_i(\underline{\xi}, \tau) \frac{\partial w_i}{\partial \xi_k} \right], \quad i = 1, \dots, n, \tag{20}$$

together with initial and boundary conditions of the form (2)–(3), are considered (see entries X and XI of Table 1). Here the analytic functions $k_i(\underline{\xi}, \tau)$ and $r_i(\underline{\xi}, \tau)$ are assumed to be uniformly bounded from above and below by positive constants, while the analytic functions $\alpha_{ij}(\underline{\xi}, \tau)$ need only be nonnegative and uniformly bounded from above on \mathcal{E} . The analytic exponents $\theta_i(\underline{\xi}, \tau)$ are assumed to be uniformly sandwiched between positive constants less than or equal to unity. Finally, to avoid degenerate cases, the algebraic system

$$w_i^{\theta_i(\underline{\xi}, \tau)}(\underline{\xi}, \tau) + \sum_{j=1}^n \frac{\alpha_{ij}(\underline{\xi}, \tau) w_j(\underline{\xi}, \tau)}{k_i^{1-\theta_i(\underline{\xi}, \tau)}(\underline{\xi}, \tau)} = k_i^{\theta_i(\underline{\xi}, \tau)}(\underline{\xi}, \tau), \quad i = 1, \dots, n, \tag{21}$$

is assumed to have a unique, strictly positive solution for each $(\underline{\xi}, \tau) \in \mathcal{E}$. Note that, for this case,

$$\frac{\partial f_i}{\partial w_j} = - \frac{r_i(\underline{\xi}, \tau) \alpha_{ij}(\underline{\xi}, \tau) w_i(\underline{\xi}, \tau)}{k_i(\underline{\xi}, \tau)} \leq 0, \quad i \neq j$$

and

$$\frac{\partial^2 f_i}{\partial w_i^2} = - \frac{\theta_i(\underline{\xi}, \tau) [\theta_i(\underline{\xi}, \tau) + 1] r_i(\underline{\xi}, \tau) w_i^{\theta_i(\underline{\xi}, \tau)-1}(\underline{\xi}, \tau)}{k_i^{\theta_i(\underline{\xi}, \tau)}(\underline{\xi}, \tau)} < 0.$$

Since the functions $r_i(\underline{\xi}, \tau)$ are uniformly bounded from below on \mathcal{E} by positive constants, since the functions $k_i(\underline{\xi}, \tau)$ are uniformly bounded from above on \mathcal{E} , and since the exponents $\theta_i(\underline{\xi}, \tau)$ are uniformly sandwiched on \mathcal{E} between positive constants less than or equal to unity, there exist constants \bar{f}_i such that

$$\frac{\partial^2 f_i}{\partial w_i^2} \leq \bar{f}_i < 0, \quad i = 1, \dots, n,$$

and hence the system (20) indeed satisfies Assumptions 2.1.2.

Non-explosion of solution components of the above system is settled first. For this case the set $\mathcal{G}_i(\underline{\xi}, \tau)$ is defined by all points on the hyper surface (21). Hence it can easily be shown that

$$\sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\mathcal{G}_i(\underline{\xi}, \tau)\} \leq \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\},$$

and consequently, by Theorem 3.1 (a), the solution vector $\underline{w}(\underline{\xi}, \tau)$ of (20) and (2)–(3) is uniformly bounded from above by the constant vector $\underline{\kappa} = [\kappa_1, \dots, \kappa_n]^T$, where

$$\kappa_i = \max \left\{ \max_{\underline{\xi} \in \mathcal{D}} \{\phi_i(\underline{\xi})\}, \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\} \right\}, \quad i = 1, \dots, n.$$

By Theorem 3.1 (b) there also exists a non-negative constant $\bar{\tau}_i$ such that the i -th component, $w_i(\underline{\xi}, \tau)$, of the solution vector of (20) and (2)–(3) is uniformly bounded from above on $\mathcal{D} \times [\bar{\tau}_i, \infty)$ by

$$\bar{\kappa}_i = \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_i(\underline{\xi}, \tau)\}, \quad i = 1, \dots, n.$$

Persistence of solution components is considered next. Let $\bar{\tau}^* = \max_{1 \leq i \leq n} \{\bar{\tau}_i\}$ and define $\mathcal{F} = \mathcal{D} \times [\bar{\tau}^*, \infty) \subset \mathcal{E}$. It is clear that the functions

$$g_i(\underline{\xi}, \tau, \underline{w}) = k_i^{\theta_i(\underline{\xi}, \tau)}(\underline{\xi}, \tau) - w_i^{\theta_i(\underline{\xi}, \tau)} - \sum_{j=1, j \neq i}^n \frac{\alpha_{ij}(\underline{\xi}, \tau)w_j}{k_i^{1-\theta_i(\underline{\xi}, \tau)}(\underline{\xi}, \tau)}, \quad i = 1, \dots, n,$$

are uniformly bounded from above on \mathcal{A} and hence the solution components of the system are *not necessarily* permanent. We however show that the condition

$$\inf_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\theta_i(\underline{\xi}, \tau)\} \inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{k_i(\underline{\xi}, \tau)\} > \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\alpha_{ij}(\underline{\xi}, \tau)\} \sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{k_j(\underline{\xi}, \tau)\} \quad (22)$$

is sufficient to ensure the permanence of the i -th solution component. To prove this, note that since the i -th solution component of (20) is uniformly bounded from above on \mathcal{F} by $\sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{k_i(\underline{\xi}, \tau)\}$, and since the functions $r_i(\underline{\xi}, \tau)$ and $k_i(\underline{\xi}, \tau)$ are also uniformly bounded from above, with $r_i(\underline{\xi}, \tau)$ additionally bounded away from zero on \mathcal{F} , there exists by (22) a positive constant η_i such that

$$\inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{\theta_i\} \inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{k_i\} > \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{\alpha_{ij}\} \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{k_j\} + \frac{\eta_i k_i w_i}{r_i}$$

on \mathcal{F} , since $\mathcal{F} \subset \mathcal{E}$. But since $\sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{\theta_i\} \leq 1$, it follows that

$$k_i + (\theta_i - 1)k_i^{1-\theta_i} w_i^{\theta_i} \geq \inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{k_i + (\theta_i - 1)k_i^{1-\theta_i} w_i^{\theta_i}\}$$

$$\begin{aligned}
 &\geq \inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{k_i + (\theta_i - 1)k_i^{1-\theta_i}k_i^{\theta_i}\} = \inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{\theta_i k_i\} \\
 &\geq \inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{\theta_i\} \inf_{(\underline{\xi}, \tau) \in \mathcal{F}} \{k_i\} > \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{\alpha_{ij}\} \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{k_j\} + \frac{\eta_i k_i w_i}{r_i} \\
 &\geq \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{\alpha_{ij}\} \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{w_j\} + \frac{\eta_i k_i w_i}{r_i} \\
 &\geq \sum_{j=1, j \neq i}^n \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \{\alpha_{ij} w_j\} + \frac{\eta_i k_i w_i}{r_i} \\
 &\geq \sup_{(\underline{\xi}, \tau) \in \mathcal{F}} \left\{ \sum_{j=1, j \neq i}^n \alpha_{ij} w_j \right\} + \frac{\eta_i k_i w_i}{r_i} \geq \sum_{j=1, j \neq i}^n \alpha_{ij} w_j + \frac{\eta_i k_i w_i}{r_i},
 \end{aligned}$$

so that

$$k_i + (\theta_i - 1)k_i^{1-\theta_i}w_i^{\theta_i} - \sum_{j=1, j \neq i}^n \alpha_{ij} w_j > \frac{\eta_i k_i w_i}{r_i}$$

on \mathcal{F} . Now,

$$\begin{aligned}
 \frac{g_i(\underline{\xi}, \tau, \underline{w}(\underline{\xi}, \tau))}{w_i(\underline{\xi}, \tau)} &= \frac{r_i}{k_i^{\theta_i} w_i} \left[k_i^{\theta_i} - w_i^{\theta_i} - \sum_{j=1, j \neq i}^n \frac{\alpha_{ij} w_j}{k_i^{1-\theta_i}} \right] \\
 &= \frac{r_i}{k_i^{\theta_i} w_i} \left[k_i^{\theta_i} - w_i^{\theta_i} + \theta_i w_i^{\theta_i} - \sum_{j=1, j \neq i}^n \frac{\alpha_{ij} w_j}{k_i^{1-\theta_i}} \right] - \frac{r_i \theta_i w_i^{\theta_i-1}}{k_i^{\theta_i}} \\
 &= \frac{r_i}{k_i w_i} \left[k_i + (\theta_i - 1)k_i^{1-\theta_i} w_i^{\theta_i} - \sum_{j=1, j \neq i}^n \alpha_{ij} w_j \right] - \frac{r_i \theta_i w_i^{\theta_i-1}}{k_i^{\theta_i}} \\
 &> \frac{r_i}{k_i w_i} \left[\frac{\eta_i k_i w_i}{r_i} \right] - \frac{r_i \theta_i w_i^{\theta_i-1}}{k_i^{\theta_i}} = \eta_i + \frac{\partial g_i}{\partial w_i}(\underline{\xi}, \tau, \underline{w}(\underline{\xi}, \tau))
 \end{aligned}$$

on $\mathcal{F} \times \mathbb{R}_+^n$. Hence the general condition for permanence, (4), holds on $\mathcal{F} \times \mathbb{R}_+^n$, and the (conditional) permanence of the i -th solution component of (20) and (2)–(3) is a consequence of Theorem 3.3.

Note that in the special case where $\theta_i \equiv 1$, the condition for persistence of the i -th solution component, (22), reduces to (10), as expected.

9. Schoener exploitation

In this section the permanence of solutions of competitive reaction-diffusion systems containing Schoener exploitation reaction terms (see entry XII in Table 1) are

considered, that is, systems of the form

$$\begin{aligned} \frac{\partial w_i}{\partial \tau} &= \delta_i(\underline{\xi}, \tau) w_i \left[\frac{\alpha_i(\underline{\xi}, \tau) \beta_i(\underline{\xi}, \tau)}{\sum_{j=1}^n \beta_j(\underline{\xi}, \tau) w_j} - \gamma_i(\underline{\xi}, \tau) \right] \\ &+ \sum_{k=1}^m \frac{\partial}{\partial \xi_k} \left[d_i(\underline{\xi}, \tau) \frac{\partial w_i}{\partial \xi_k} \right], \quad i = 1, \dots, n. \end{aligned} \tag{23}$$

Here the analytic functions $\alpha_i(\underline{\xi}, \tau)$, $\beta_i(\underline{\xi}, \tau)$, $\gamma_i(\underline{\xi}, \tau)$ and $\delta_i(\underline{\xi}, \tau)$ are assumed to be uniformly bounded from above and below on \mathcal{E} by positive constants. To avoid degenerate cases it is also assumed that the linear algebraic system

$$\gamma_i(\underline{\xi}, \tau) \sum_{j=1}^n \beta_j(\underline{\xi}, \tau) w_j = \alpha_i(\underline{\xi}, \tau) \beta_i(\underline{\xi}, \tau), \quad i = 1, \dots, n, \tag{24}$$

has a unique, positive solution for each $(\underline{\xi}, \tau) \in \mathcal{E}$. For this case

$$\frac{\partial f_i}{\partial w_j} = - \frac{\alpha_i(\underline{\xi}, \tau) \beta_i(\underline{\xi}, \tau) \beta_j(\underline{\xi}, \tau) \delta_i(\underline{\xi}, \tau) w_i(\underline{\xi}, \tau)}{\left(\sum_{k=1}^n \beta_k(\underline{\xi}, \tau) w_k(\underline{\xi}, \tau) \right)^2} \leq 0$$

and

$$\frac{\partial^2 f_i}{\partial w_i^2} = - \frac{2\alpha_i(\underline{\xi}, \tau) \beta_i^2(\underline{\xi}, \tau) \delta_i(\underline{\xi}, \tau) \sum_{j=1, j \neq i}^n \beta_j(\underline{\xi}, \tau) w_j(\underline{\xi}, \tau)}{\left(\sum_{j=1}^n \beta_j(\underline{\xi}, \tau) w_j(\underline{\xi}, \tau) \right)^3} < 0,$$

so that the uniform boundedness of the sum $\sum_{j=1}^n \beta_j w_j$ on \mathcal{E} by positive constants from both above and below will imply the uniform upper boundedness of $\partial^2 f_i / \partial w_i^2$ by a negative constant, since the functions α_i , β_i and δ_i are uniformly bounded away from zero. We first prove the uniform upper boundedness of the sum in question.

Note that the set $\mathcal{G}_i(\underline{\xi}, \tau)$ is defined by all points on the hyper surface (24) and hence it can easily be shown that

$$\sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\mathcal{G}_i(\underline{\xi}, \tau)\} \leq \frac{\sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\alpha_i(\underline{\xi}, \tau)\}}{\inf_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\gamma_i(\underline{\xi}, \tau)\}}.$$

Consequently it follows by Theorem 3.1 (a) that the solution vector $\underline{w}(\underline{\xi}, \tau)$ of (23) and (2)–(3) is uniformly bounded from above by the constant vector $\underline{\kappa} = [\kappa_1, \dots, \kappa_n]^T$, where

$$\kappa_i = \max \left\{ \max_{\underline{\xi} \in \mathcal{D}} \{\phi_i(\underline{\xi})\}, \frac{\sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\alpha_i(\underline{\xi}, \tau)\}}{\inf_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\gamma_i(\underline{\xi}, \tau)\}} \right\}, \quad i = 1, \dots, n.$$

Moreover, there exists, by Theorem 3.1 (b), a non-negative constant $\bar{\tau}_i$, such that the i -th component, $w_i(\underline{\xi}, \tau)$, of the solution vector, $\underline{w}(\underline{\xi}, \tau)$, is uniformly bounded from above on $\mathcal{D} \times [\bar{\tau}_i, \infty)$ by

$$\bar{\kappa}_i = \frac{\sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\alpha_i(\underline{\xi}, \tau)\}}{\inf_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\gamma_i(\underline{\xi}, \tau)\}}, \quad i = 1, \dots, n.$$

The uniform upper boundedness of the sum $\sum_{j=1}^n \beta_j w_j$ therefore follows by the uniform upper boundedness of the individual functions β_j (by assumption) and w_j (by the above).

The uniform lower boundedness of the sum $\sum_{j=1}^n \beta_j w_j$ follows by a simple contradiction argument, so that Assumptions 2.1 are indeed satisfied by the system (23) and moreover the functions

$$g_i(\underline{\xi}, \tau, \underline{w}) = \frac{\alpha_i(\underline{\xi}, \tau)\beta_i(\underline{\xi}, \tau)}{\sum_{j=1}^n \beta_j(\underline{\xi}, \tau)w_j} - \gamma_i(\underline{\xi}, \tau)$$

do *not* blow up everywhere on the hyper plane $w_i = 0$ (only at the origin). Consequently it seems that solution components of the system are *not necessarily* permanent. However, the contrary can be proved by noting that since $(\sqrt{5} - 1)/2 > 0$, and since the system functions $\alpha_i(\underline{\xi}, \tau)$, $\beta_i(\underline{\xi}, \tau)$ and $\gamma_i(\underline{\xi}, \tau)$ are positive, uniformly bounded from above and uniformly bounded away from zero on \mathcal{E} , there exists a strictly positive constant Φ_i , satisfying

$$\Phi_i < \sqrt{5} \frac{\inf_{\mathcal{F}} \{\alpha_i\} \inf_{\mathcal{F}} \{\beta_i\}}{\sup_{\mathcal{F}} \{\gamma_i\}}, \tag{25}$$

such that

$$\left(\frac{\sqrt{5} - 1}{2}\right) \frac{\alpha_i \beta_i}{\gamma_i} + \sum_{j=1}^n \frac{\alpha_j \beta_j}{\gamma_j} > \Phi_i$$

on $\mathcal{F} = \mathcal{D} \times [\bar{\tau}^*, \infty) \subset \mathcal{E}$, where $\bar{\tau}^* = \max_{1 \leq i \leq n} \{\bar{\tau}_i\}$. Therefore

$$\frac{\alpha_i \beta_i}{2\gamma_i} - \sum_{j=1}^n \beta_j \frac{\sup_{\mathcal{F}} \{\alpha_j\}}{\inf_{\mathcal{F}} \{\gamma_j\}} \leq \frac{\alpha_i \beta_i}{2\gamma_i} - \sum_{j=1}^n \frac{\alpha_j \beta_j}{\gamma_j} \leq \frac{\sqrt{5}\alpha_i \beta_i}{2\gamma_i} - \Phi_i,$$

and, by squaring both sides of the above inequality, it follows that

$$\begin{aligned} \left(\frac{\alpha_i \beta_i}{2\gamma_i} - \sum_{j=1}^n \beta_j \frac{\sup_{\mathcal{F}} \{\alpha_j\}}{\inf_{\mathcal{F}} \{\gamma_j\}}\right)^2 &< \frac{5\alpha_i^2 \beta_i^2}{4\gamma_i^2} - \frac{\sqrt{5}\alpha_i \beta_i}{\gamma_i} \Phi_i + \Phi_i^2 \\ &= \frac{\alpha_i \beta_i^2}{\gamma_i} \left(\frac{\alpha_i}{\gamma_i} + \frac{\alpha_i}{4\gamma_i}\right) - \psi_i \end{aligned}$$

$$\leq \frac{\alpha_i \beta_i^2}{\gamma_i} \left(\frac{\sup_{\mathcal{F}} \{\alpha_i\}}{\inf_{\mathcal{F}} \{\gamma_i\}} + \frac{\alpha_i}{4\gamma_i} \right) - \psi_i, \tag{26}$$

where

$$\psi_i = \frac{\sqrt{5}\alpha_i\beta_i}{\gamma_i} \Phi_i - \Phi_i^2 \geq \left(\frac{\sqrt{5} \inf_{\mathcal{F}} \{\alpha_i\} \inf_{\mathcal{F}} \{\beta_i\}}{\sup_{\mathcal{F}} \{\gamma_i\}} - \Phi_i \right) \Phi_i > 0, \quad (\text{by (25)}),$$

so that, by developing the square on the left-hand side of (26), we have

$$\left(\sum_{j=1}^n \beta_j \frac{\sup_{\mathcal{F}} \{\alpha_j\}}{\inf_{\mathcal{F}} \{\gamma_j\}} \right)^2 - \frac{\alpha_i \beta_i}{\gamma_i} \sum_{j=1}^n \beta_j \frac{\sup_{\mathcal{F}} \{\alpha_j\}}{\inf_{\mathcal{F}} \{\gamma_j\}} < \frac{\alpha_i \beta_i^2 \sup_{\mathcal{F}} \{\alpha_i\}}{\gamma_i \inf_{\mathcal{F}} \{\gamma_i\}} - \psi.$$

By multiplying both sides of the above inequality by the quantity

$$\frac{-\delta_i \gamma_i \inf_{\mathcal{F}} \{\gamma_i\}}{\sup_{\mathcal{F}} \{\alpha_i\} \left(\sum_{j=1}^n \beta_j \frac{\sup_{\mathcal{F}} \{\alpha_j\}}{\inf_{\mathcal{F}} \{\gamma_j\}} \right)^2},$$

it follows that

$$\frac{\delta_i \inf_{\mathcal{F}} \{\gamma_i\}}{\sup_{\mathcal{F}} \{\alpha_i\}} \left[\frac{\alpha_i \beta_i}{\sum_{j=1}^n \beta_j \frac{\sup_{\mathcal{F}} \{\alpha_j\}}{\inf_{\mathcal{F}} \{\gamma_j\}}} - \gamma_i \right] > \frac{-\alpha_i \beta_i^2 \delta_i}{\left(\sum_{j=1}^n \beta_j \frac{\sup_{\mathcal{F}} \{\alpha_j\}}{\inf_{\mathcal{F}} \{\gamma_j\}} \right)^2} + \eta_i, \tag{27}$$

where

$$\eta_i = \inf_{(\xi, \tau) \in \mathcal{F}} \left\{ \frac{\delta_i \gamma_i \inf_{\mathcal{F}} \{\gamma_i\} \psi_i}{\sup_{\mathcal{F}} \{\alpha_i\} \left(\sum_{j=1}^n \beta_j \frac{\sup_{\mathcal{F}} \{\alpha_j\}}{\inf_{\mathcal{F}} \{\gamma_j\}} \right)^2} \right\} > 0.$$

Now,

$$\begin{aligned} \frac{g_i(\underline{\xi}, \tau, \underline{w}(\underline{\xi}, \tau))}{w_i(\underline{\xi}, \tau)} &= \frac{\delta_i}{w_i} \left[\frac{\alpha_i \beta_i}{\sum_{j=1}^n \beta_j w_j} - \gamma_i \right] \\ &\geq \frac{\delta_i \inf_{\mathcal{F}} \{\gamma_i\}}{\sup_{\mathcal{F}} \{\alpha_i\}} \left[\frac{\alpha_i \beta_i}{\sum_{j=1}^n \beta_j \frac{\sup_{\mathcal{F}} \{\alpha_j\}}{\inf_{\mathcal{F}} \{\gamma_j\}}} - \gamma_i \right] \\ &> \eta_i - \frac{\alpha_i \beta_i^2 \delta_i}{\left(\sum_{j=1}^n \beta_j \frac{\sup_{\mathcal{F}} \{\alpha_j\}}{\inf_{\mathcal{F}} \{\gamma_j\}} \right)^2} \quad (\text{by (27)}) \\ &\geq \eta_i - \frac{\alpha_i \beta_i^2 \delta_i}{\left(\sum_{j=1}^n \beta_j w_j \right)^2} = \eta_i + \frac{\partial g_i}{\partial w_i}(\underline{\xi}, \tau, \underline{w}(\underline{\xi}, \tau)) \end{aligned}$$

on $\mathcal{F} \times \mathfrak{R}_+^n$, so that the condition for permanence, (4), is satisfied on $\mathcal{F} \times \mathfrak{R}_+^n$. Automatic solution permanence of (23) and (2)–(3) is therefore a consequence of Theorem 3.3.

10. Schoener-interference

Competitive reaction-diffusion systems containing modified Schoener exclusive resource reaction terms, that is, systems of the form

$$\frac{\partial w_i}{\partial \tau} = \delta_i(\underline{\xi}, \tau) w_i \left[\frac{\alpha_i(\underline{\xi}, \tau) \beta_i(\underline{\xi}, \tau)}{\sum_{j=1}^n \beta_j(\underline{\xi}, \tau) w_j^{\psi_j(\underline{\xi}, \tau)}} + \frac{\lambda_i(\underline{\xi}, \tau)}{w_i^{\psi_i(\underline{\xi}, \tau)}} - \sum_{j=1}^n \sigma_{ij}(\underline{\xi}, \tau) w_j - \gamma_i(\underline{\xi}, \tau) \right] + \sum_{k=1}^m \frac{\partial}{\partial \xi_k} \left[d_i(\underline{\xi}, \tau) \frac{\partial w_i}{\partial \xi_k} \right], \quad i = 1, \dots, n, \tag{28}$$

together with initial and boundary conditions of the form (2)–(3) (see entry XIII in Table 1), are considered in this section. Here the analytic functions $\alpha_i(\underline{\xi}, \tau)$, $\beta_i(\underline{\xi}, \tau)$, $\gamma_i(\underline{\xi}, \tau)$, $\delta_i(\underline{\xi}, \tau)$ and $\lambda_i(\underline{\xi}, \tau)$ are assumed to be uniformly bounded from above and below by positive constants, the exponents $\psi_i(\underline{\xi}, \tau)$ are assumed to be uniformly sandwiched between strictly positive constants less than unity, while the analytic functions $\sigma_{ij}(\underline{\xi}, \tau)$ need only be non-negative and uniformly bounded from above on \mathcal{E} . To avoid degenerate cases it is also assumed that the nonlinear algebraic system

$$\frac{\alpha_i(\underline{\xi}, \tau) \beta_i(\underline{\xi}, \tau)}{\sum_{j=1}^n \beta_j(\underline{\xi}, \tau) w_j^{\psi_j(\underline{\xi}, \tau)}} + \frac{\lambda_i(\underline{\xi}, \tau)}{w_i^{\psi_i(\underline{\xi}, \tau)}} = \sum_{j=1}^n \sigma_{ij}(\underline{\xi}, \tau) w_j + \gamma_i(\underline{\xi}, \tau), \quad i = 1, \dots, n, \tag{29}$$

has a unique, strictly positive solution for each $(\underline{\xi}, \tau) \in \mathcal{E}$. Here Schoener’s reaction terms have been modified by the introduction of the exponents $\psi_i(\underline{\xi}, \tau)$ to ensure that the function $g_i(\underline{\xi}, \tau, \underline{w})$ blows up no faster than $1/w_i$ as $w_i \downarrow 0$. Note that for this case

$$\frac{\partial f_i}{\partial w_i} = -\delta_i w_i \left[\frac{\alpha_i \beta_i \beta_j \psi_j w_j^{\psi_j - 1}}{(\sum_{k=1}^m \beta_k w_k^{\psi_k})^2} + \sigma_{ij} \right] \leq 0 \quad \text{for } i \neq j$$

and

$$\frac{\partial^2 f_i}{\partial w_i^2} = -\frac{\alpha_i \beta_i^2 \delta_i \psi_i w_i^{\psi_i - 1} [\beta_i (1 - \psi_i) w_i^{\psi_i} + (1 + \psi_i) \sum_{k=1, k \neq i}^n \beta_k w_k^{\psi_k}]}{(\sum_{k=1}^m \beta_k w_k^{\psi_k})^3} - \delta_i [\lambda_i \psi_i (1 - \psi_i) w_i^{-\psi_i - 1} + 2\sigma_{ii}] < 0.$$

Now there will exist constants \bar{f}_i such that

$$\frac{\partial^2 f_i}{\partial w_i^2} \leq \bar{f}_i < 0, \quad i = 1, \dots, n,$$

and hence Assumptions 2.1.2 will be satisfied by the reaction terms (28) if *all* solution components of the system are uniformly bounded from above on \mathcal{E} . To prove this

TABLE 2. Criteria for permanence of solutions of reaction-diffusion models of the form (1)-(3) with reaction terms defined as in Table 1.

Model no in Table 1	Condition for permanence of the <i>i</i> -th component	§
I-VI	$\inf\{k_i\} > \sum_{j=1, j \neq i}^n \sup\{\alpha_{ij}\} \sup\{k_j\}$	4 & 5
VII	Automatic permanence	6
VIII	$\inf\{k_i\} + \inf\{\beta_i\} (e^{-\sup\{\gamma_i\} \sup\{k_i\}} - 1) > \sum_{j=1, j \neq i}^n \sup\{\alpha_{ij}\} \sup\{k_j\}$	7
IX	$\inf\{k_i\} + \inf\{\beta_i\} (e^{-\sup\{\gamma_i\} \sup\{k_i\}} - 1) > \sum_{j=1, j \neq i}^n [\sup\{\alpha_{ij}\} \sup\{k_j\} + \sup\{\beta_i\} (1 - e^{-\sup\{\gamma_i\} \sup\{k_i\}})]$	7
X	$\inf\{k_i\} > 2 \sum_{j=1, j \neq i}^n \sup\{\alpha_{ij}\} \sup\{k_j\}$	8
XI	$\inf\{\theta_i\} \inf\{k_i\} > \sum_{j=1, j \neq i}^n \sup\{\alpha_{ij}\} \sup\{k_j\}$	8
XII	Automatic permanence	9
XIII	Automatic permanence	10

uniform boundedness, observe that since the set $\mathcal{G}_i(\underline{\xi}, \tau)$ is defined as the set of all the *i*-th components of points in \mathcal{A} on the hyper surface (29),

$$\sup_{(\underline{\xi}, \tau) \in \mathcal{E}} \{\mathcal{G}_i(\underline{\xi}, \tau)\} \leq \left[\frac{\sup_{\mathcal{E}}\{\alpha_i\} + \sup_{\mathcal{E}}\{\lambda_i\}}{\inf_{\mathcal{E}}\{\gamma_i\}} \right]^{1/\inf_{\mathcal{E}}\{\psi_i\}}$$

Hence the solution vector of (28) and (2)–(3) is uniformly bounded from above on \mathcal{E} by the constant vector $\underline{\kappa} = [\kappa_1, \dots, \kappa_n]^T$, where

$$\kappa_i = \max \left\{ \max_{\underline{\xi} \in \mathcal{D}} \{\phi_i(\underline{\xi})\}, \left[\frac{\sup_{\mathcal{E}}\{\alpha_i\} + \sup_{\mathcal{E}}\{\lambda_i\}}{\inf_{\mathcal{E}}\{\gamma_i\}} \right]^{1/\inf_{\mathcal{E}}\{\psi_i\}} \right\}$$

for all $i = 1, \dots, n$ by Theorem 3.1 (a). For this case it is clear that the function $g_i(\underline{\xi}, \tau, \underline{w})$ blows up everywhere on the hyper plane $w_i = 0$, and hence, by Theorem 3.2, we are assured that all solution components of the system will be permanent. It is in fact possible to show that the solution vector of (28) and (2)–(3) is uniformly bounded from below on \mathcal{E} by the positive constant vector $\underline{\tilde{\kappa}} = [\tilde{\kappa}_1, \dots, \tilde{\kappa}_n]^T$, where

$$\tilde{\kappa}_i = \min \left\{ \min_{\underline{\xi} \in \mathcal{D}} \{\phi_i(\underline{\xi})\}, \left[\frac{\inf_{\mathcal{E}}\{\lambda_i\}}{\sup_{\mathcal{E}}\{\gamma_i\} + \sum_{j=1}^n \sup_{\mathcal{E}}\{\sigma_{ij}\} \frac{\sup_{\mathcal{E}}\{\alpha_j\} + \sup_{\mathcal{E}}\{\lambda_j\}}{\inf_{\mathcal{E}}\{\gamma_j\}}} \right]^{1/\sup_{\mathcal{E}}\{\psi_i\}} \right\}$$

for all $i = 1, \dots, n$.

11. Conclusions

The criteria for permanence in Theorems 3.2 and 3.3 were found to be not only of academic value; they may be used profitably to establish concrete and easily verifiable conditions for the permanence of solutions of specific competitive reaction-diffusion systems with diagonally convex reaction terms, as was done in Sections 4–10 of this paper for seven well-known classes of competition systems. We conclude by listing, again in table form, the criteria for the permanence of the i -th solution component of reaction-diffusion systems with reaction terms as given in Table 1. Here the parameters in Table 1 are of course allowed to be functions of time and space. For more details on the system parameters the reader is referred to the relevant sections of this paper (which are also listed in Table 2).

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References

- [1] S. Ahmad and A. C. Lazer, "Asymptotic behaviour of solutions of periodic competition diffusion systems", *Nonlinear Analysis TMA* **13** (1989) 263–284.
- [2] C. Alvarez and A. C. Lazer, "An application of topological degree to the periodic competing species problem", *J. Austral. Math. Soc., Ser. B* **28** (1986) 202–219.
- [3] F. J. Ayala, M. E. Gilpin and J. G. Ehrenfeld, "Competition between species: theoretical models and experimental tests", *Theoretical Population Biology* **4** (1973) 331–356.
- [4] T. A. Burton and V. Hutson, "Permanence for non-autonomous predator-prey systems", *Differential and Integral Equations* **4** (1991) 1269–1280.
- [5] N. Chen and Z. Y. Lu, "Global stability of periodic solutions to reaction-diffusion systems", *Mathematica Applicata* **4** (1991) 111–114.
- [6] C. Cosner and A. C. Lazer, "Stable coexistence states in the Lotka-Volterra competition model with diffusion", *SIAM J. Appl. Math.* **44** (1984) 1112–1132.
- [7] P. de Mottoni and A. Schiaffino, "Competition systems with periodic coefficients: a geometrical approach", *J. Math. Biology* **11** (1981) 319–335.
- [8] M. L. C. Fernands and F. Zanolin, "Repelling conditions for boundary sets using Liapunov-like functions. II: Persistence and periodic solutions", *J. Diff. Eqns* **86** (1990) 33–58.
- [9] A. Fonda, "Uniformly persistent semi-dynamical systems", *Proc. Amer. Math. Soc.* **104** (1988) 111–116.
- [10] M. E. Gilpin and F. J. Ayala, "Global models of growth and competition", *Proc. Nat. Acad. Sci. USA* **70** (1973) 3590–3593.

- [11] M. E. Gilpin and F. J. Ayala, "Schoener's models and *Drosophila* competition", *Theoretical Population Biology* **9** (1974) 12–14.
- [12] K. Gopalsamy, "Global stability in a periodic Lotka-Volterra system", *J. Austral. Math. Soc., Ser. B* **27** (1985) 66–72.
- [13] J. K. Hale and P. Waltman, "Persistence in infinite-dimensional systems", *SIAM J. Math. Analysis* **20** (1989) 388–395.
- [14] P. Hess, *Periodic-parabolic boundary value problems and positivity*, Pitman Research Notes in Math. 247 (Longman, Essex, 1991).
- [15] G. Kiriinger, "Permanence of some ecological systems with several predator and one prey species", *J. Math. Biology* **26** (1988) 217–232.
- [16] C. V. Pao, "Coexistence and stability of a competition-diffusion system in population dynamics", *J. Math. Analysis Appl.* **83** (1981) 54–76.
- [17] T. W. Schoener, "Population growth regulated by intra-specific competition for energy or time: some simple representations", *Theoretical Population Biology* **4** (1973) 56–84.
- [18] T. W. Schoener, "Competition and the form of habitat shift", *Theoretical Population Biology* **6** (1974) 265–307.
- [19] T. W. Schoener, "Alternatives to Lotka-Volterra competition: models of intermediate complexity", *Theoretical Population Biology* **10** (1976) 309–333.
- [20] A. Tineo and C. Alvarez, "A different consideration about the globally asymptotically stable solution of the periodic n -species problem", *J. Math. Analysis Appl.* **159** (1991) 44–50.
- [21] J. H. van Vuuren and J. Norbury, "Permanence and asymptotic stability in diagonally convex reaction-diffusion systems", *Proc. Royal Soc. of Edinburgh, Ser. A (Math.)*, **128 A** (1998) 147–172.
- [22] F. Zanolin, "Permanence and positive periodic solutions for Kolmogorov competing species systems", *Results in Math.* **21** (1992) 224–250.
- [23] X. Q. Zuao and B. D. Sleeman, "Permanence in Kolmogorov competition models with diffusion", *IMA J. Appl. Math.* **15** (1993) 1–11.