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Extinction and Asymptotic Behavior of Solutions to a System Arising in Biology

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Abstract. A generalization to n species of a system by Bass et al. (cf. [4]), which describes the self-organization of liver zones in a liver capillary in the case of two species, is proposed. We establish some hypotheses on the coefficient parameters of the system under which a part of the species is driven to extinction while the remaining ones are attracted by the non-trivial stationary solution.

Keywords: *Coexistence, extinction, global asymptotic stability, integro-differential system, logistic equation, Lyapunov function, persistence*

AMS subject classification: 45K05, 45M05, 34D23, 92B05

1. The model

In their paper Bass et al. (cf. [4]) derived a model which describes the self-organization of zones of enzymatic activity along a liver capillary lined with cells of two kinds which contain different enzymes and compete for sites on the wall of the capillary. This interaction between the cells arises from consumption of oxygen from blood flowing through the liver in turn influencing rates of division and of death of the two cell types. If we denote by $\rho_i = \rho_i(t,x)$ the density of the cell type i $(i = 1, 2)$ as a function of time t and position x, the process is modelled by the system of two integro-differential equations

$$\begin{aligned} \frac{\partial \varrho_i}{\partial t}(t,x) = \varrho_i(t,x)\Big\{ & k_i\big(\sigma - \rho_1(t,x) - \rho_2(t,x)\big) - \mu_i \\ & - \frac{\nu_i}{f}\int_0^x \big(k_1\rho_1(t,\xi) + k_2\rho_2(t,\xi)\big)d\xi \Big\}. \end{aligned} \tag{1.1}$$

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The x-axis is taken along the blood flow in the capillary with inlet at $x = 0$ and outlet at $x = l$. As division of cells is limited by the phenomenon of contact inhibition, the total cell density $\rho_1 + \rho_2$ cannot exceed the fixed maximum density σ of cell sites. In (1.1), $k_i\rho_i$ is the rate of consumption of oxygen by the i type cells which is transported by convection with the blood along the capillary, f is the steady rate of blood flow through the capillary and μ_i is the specific death rate of the i type cells. It is easy to see from the equations of system (1.1) that if the growth rate $k_i\sigma$ is smaller than the death rate μ_i, then $\rho_i \to 0$ as $t \to \infty$. The cells of type i go then to extinction everywhere in the capillary. This leads us to suppose $k_i\sigma \geq \mu_i$ $(i = 1, 2)$. The spatial dependence enters in our model because death rates at each position x depend on the cumulative oxygen consumption by all cells located upstream of x. This competitive interaction between cells is mediated by oxygen consumption and blood flow, and is a consequence of interplay of the unidirectional blood flow.

System (1.1) can be reduced to the simplified form (see [4, 9])

$$\left.\begin{aligned} \frac{\partial v_1}{\partial t} &= v_1 \left\{1 - v_1 - v_2 - \int_0^x (v_1 + \theta v_2)\, d\xi\right\} \\ \frac{\partial v_2}{\partial t} &= \gamma v_2 \left\{\lambda - v_1 - v_2 - \eta \int_0^x (v_1 + \theta v_2)\, d\xi\right\} \end{aligned}\right\} \begin{pmatrix} t > 0 \\ x \in (0, L) \end{pmatrix} \tag{1.2}$$

with initial data

$$v_i(x, 0) = v_{i0}(x) \qquad (x \in [0, L],\ i = 1, 2) \tag{1.3}$$

where v_1 and v_2 of system (1.2) are proportional to ρ_1 and ρ_2, respectively. The coefficients $\lambda, \gamma, \eta, \theta$ are positive constants. The initial data v_{i0} are non-negative bounded and measurable functions on $[0, L]$ such that $v_{i0}(x) \geq \delta$ for $x \in [0, L]$ and some constant $\delta > 0$. Holmåker proved in [9] that for some set of coefficient parameters one of the two species is driven to extinction while the other species stabilizes at its non-trivial stationary solution. As pointed out in [4], this principle (known as *principle of competitive exclusion*) is the mechanism by which these cells are self-organized in the liver capillary.

A generalization to n species and in the autonomous case of model (1.1) was described by the same authors at the end of their paper (see [4: p. 193]). In the present paper we propose a generalization of model (1.1) to the non-autonomous case by considering the problem (for $i = 1, ..., n$)

$$\left.\begin{aligned} \frac{\partial u_i}{\partial t} &= u_i \left\{a_i(t) - \sum_{j=1}^n b_{ij}(t) u_j - \sum_{j=1}^n c_{ij}(t) \int_0^x u_j(t, \xi)\, d\xi\right\} \\ &\qquad (t > 0, x \in [0, L]) \\ u_i(0, x) &= u_{0i}(x) \quad (x \in [0, L]) \end{aligned}\right\} \tag{1.4}$$

where $[0, L] \subset \mathbb{R}_+$.

We assume throughout this paper the following:

(i) The functions a_i, b_{ij}, c_{ij} $(1 \leq i, j \leq n)$ are non-negative, bounded and continuous on $(0, \infty)$.

(ii) The initial data u_{0i} $(1 \leq i \leq n)$ are non-negative, measurable and bounded on $[0, L]$ such that $u_{0i}(x) \geq \delta$ $(x \in [0, L])$ for some constant $\delta > 0$.

System (1.4) may be compared to similar ones such as the non-autonomous Lotka-Volterra competitive systems (see [1, 2, 11 - 16]). As is common to most multi-species systems of population dynamics, the basic questions to investigate are extinction and global asymptotic stability of species of the system. This paper provides some answers to these questions. Following the works in [3, 12, 13, 15, 17] on competing Lotka-Volterra systems, we derive some criterions which assure the balancing survival of the species. In particular, we give sufficient conditions under which a part of the species is driven to extinction everywhere in $(0, L)$, whilst the remaining ones coexist globally and stabilize at the non-trivial stationary solution of the system. This result generalizes those obtained by Holmåker in [9] for some set of coefficient parameters and extends the *principle of competitive exclusion* to the multi-species case (see Corollary 2).

System (1.4) may be used as a model for a large class of processes. For example, in the case of the distribution of certain plant species in a river with a limited resource originating upstream (cf. [4]).

The paper is organized as follows. In Section 2 we prove global existence and uniqueness of the solution. In Section 3 we establish a criterion which gives the extinction of a part of the species in the non-autonomous case. The last section, Section 4, is devoted to the autonomous case. We give, in particular, a sufficient condition on the matrix coefficients to obtain global stability of the stationary solution.

2. Existence and uniqueness

The existence and uniqueness may be proved in a standard manner. Nevertheless, for the readers convenience, we shall give below some details.

By a solution of problem (1.4) we will mean a function $u = (u_1, ..., u_n)$ defined on $I_0 \times [0, L]$, where $I_0 \subset \mathbb{R}_+$ is some time interval containing the initial time $t = 0$, u continuously differentiable in t for each fixed $x \in [0, L]$, measurable in x for each fixed t such that $\int_0^x u_i(t, \xi)\, d\xi$ $(i = 1, ..., n)$ is finite and continuous in t for each fixed x, and satisfying (1.4).

Let X be the Banach space

$$X = \Big\{ u = (u_1, ..., u_n) : u_1, ..., u_n \text{ measurable and bounded on } (0, L) \Big\}$$

equipped with the norm $\|u\|_X = \sum_{i=1}^n \sup_{x\in[0,L]} |u_i(x)|$, and let the function $f = (f_1, ..., f_n) : \mathbb{R}_+ \times X \to X$ be defined by

$$f_i(t,u) = u_i \left\{ a_i(t) - \sum_{j=1}^n b_{ij}(t)u_j - \sum_{j=1}^n c_{ij}(t) \int_0^x u_j(\xi)\, d\xi \right\}$$

for $i = 1, ..., n$. Consider now the Cauchy problem

$$\left.\begin{aligned} \frac{du}{dt}(t) = f(t,u) \quad (t > 0) \\ u(0) = u_0 \end{aligned}\right\} \tag{2.1}$$

where $u_0 = (u_{01}, ..., u_{0n}) \in X$. By a solution of this problem we mean a strong continuously differentiable function $u : I_0 \to X$ on some time interval $I_0 \subset \mathbb{R}_+$ containing the initial time $t = 0$, such that (2.1) is satisfied. We point out here that any solution of problem (1.4) is a solution of problem (2.1).

Since the function f is continuous for $(t,u) \in \mathbb{R}_+ \times X$ and locally Lipshitz with respect to u, then by the fundamental theorem on differential equations (cf. [7: Theorem 2.1]), problem (2.1) has a unique solution u defined on some time interval $I_0 \subset \mathbb{R}_+$. Define now the real-valued function

$$u(t,x) = (u(t))(x) \qquad (t \in I_0, x \in [0,L]). \tag{2.2}$$

We want to prove that $u(t,x)$ defined in (2.2) is a solution of problem (1.4).

Proposition 1. *The function $u = u(t,x)$ defined in* (2.2) *is a positive solution of problem* (1.4)*. Furthermore, this solution is unique and global in time.*

Proof. It suffices to prove that $u = u(t,x)$ is continuously differentiable in t for each fixed x and satisfies (1.4). Let x be fixed. Since the linear form $p_x : X \to \mathbb{R}^n, u \to u(x)$ is $C^\infty(X;\mathbb{R}^n)$ and

$$u(t,x) = p_x \circ u(t), \tag{2.3}$$

it follows that u is continuously differentiable in t as composition of two continuously differentiable functions $t \to u(t)$ and $u \to p_x(u)$. Furthermore, by differentiating (2.3) with respect to t we obtain

$$\frac{\partial u}{\partial t}(t,x) = \frac{dp_x}{du} \circ \frac{du}{dt}(t) = p_x \circ \frac{du}{dt}(t) = \frac{du}{dt}(t)(x).$$

Therefore u satisfies (1.4).

The uniqueness of the solution of problem (1.4) follows from that of problem (2.1). System (1.4) may be written as $\frac{\partial u_i}{\partial t} = u_i(t,x) f_i(t,x)$ $(i = 1, ..., n)$ for some continuous function f_i in t. Therefore

$$u_i(t,x) = u_{0i}(x) \exp\left(\int_0^t f_i(s,x)\,ds\right) > 0$$

since $u_{0i}(x) > 0$. We infer that $u_i(t,x) \le u_{0i}(x) \exp\left(\int_0^t a_i(s)\,ds\right)$ as long as the solution exists. Consequently, u_i is global in time ∎

3. Extinction

In this section we shall use some comparison theorems on differential equations. Namely, solutions of our problem will be compared with those of the non-autonomous logistic equation

$$\frac{dw}{dt} = w(t)\big\{a(t) - b(t)w(t)\big\} \qquad (t > 0) \tag{3.1}$$

where a and b are non-negative continuous and bounded functions on $(0, \infty)$.

To prove boundedness of solutions of system (1.4) we need the following lemma which can be found in [14] or [16].

Lemma 1. *Suppose that the coefficients a and b in (3.1) are non-negative, continuous and bounded functions such that* $\liminf_{t\to\infty} b(t) > 0$. *Then:*

(1)$_{\mathbf{a}}$ *There is a constant $M > 0$ such that, for any solution w of equation* (3.1) *with $w(0) > 0$, $0 < w(t) \le M$ for all $t > 0$.*

(1)$_{\mathbf{b}}$ *If* $\liminf_{t\to\infty} a(t) > 0$, *then there is a constant $m > 0$ such that $w(t) > m$ for all $t > 0$.*

(2) *Furthermore, if in addition* $\lim_{t\to\infty} a(t) = 0$, *then* $\lim_{t\to\infty} w(t) = 0$ *for any solution w of equation* (3.1) *such that $w(0) > 0$.*

First let us state a result giving sufficient conditions yielding boundedness and extinction of all the species.

Proposition 2. *Assume that* $\liminf_{t\to\infty} b_{ii}(t) > 0$. *Then there exist constants $M_i > 0$ such that if u_i is a solution of problem* (1.4), *then*

$$u_i(t,x) \le M_i \qquad (t > 0, x \in [0, L]).$$

Furthermore, if $\lim_{t\to\infty} a_i(t) = 0$, *then* $\lim_{t\to\infty} u_i(t,x) = 0$ *for all* $x \in [0, L]$ $(1 \le i \le n)$.

Proof. Let us note that our solution u_i satisfies $\frac{\partial u_i}{\partial t} \leq u_i\{a_i(t) - b_{ii}(t)u_i\}$. We denote by w_i $(i = 1, ..., n)$ the solution of the ordinary differential system

$$\left.\begin{aligned} &\frac{dw_i}{dt} = w_i\{a_i(t) - b_{ii}(t)w_i(t)\} \quad (t > 0) \\ &w_i(0) = \|u_{0i}\|_\infty \end{aligned}\right\}$$

where $\|u_{0i}\|_\infty = \sup_{x\in[0,L]} u_{0i}(x)$. By the monotonity property of the logistic equation (3.1) (see, for example, [14]) we have

$$u_i(t, x) \leq w_i(t) \qquad (t > 0, x \in [0, L]).$$

Since $\liminf_{t\to\infty} b_{ii}(t) > 0$, then in view of Lemma 1 there is a constant $M_i > 0$ such that $w_i(t) \leq M_i$. Hence, $u_i(t, x) \leq M_i$ for $t > 0$ and $x \in [0, L]$. The second part of the proposition follows readily from the second part of Lemma 1 ∎

By adapting and improving the techniques introduced by Montes de Oca et al. [12, 13] and by Teng et al. [15] on competing Lotka-Volterra systems we can derive the following extinction result. For this let $1 \leq r < n$ be an integer and consider the following assumption:

(H1) **(i)** $\liminf_{t\to\infty} b_{ii}(t) > 0$ for each $1 \leq i \leq n$.

(ii) For each integer $k > r$ there is an $i_k < k$ such that

$$\left.\begin{aligned} &\liminf_{t\to\infty} a_{i_k}(t) \\ &\liminf_{t\to\infty} b_{i_k j}(t) \\ &\liminf_{t\to\infty} c_{i_k j}(t) \end{aligned}\right\} > 0 \quad \text{and} \quad \begin{aligned} &\limsup_{t\to\infty} \frac{a_k(t)}{a_{i_k}(t)} < \liminf_{t\to\infty} \frac{b_{kj}(t)}{b_{i_k j}(t)} \\ &\limsup_{t\to\infty} \frac{a_k(t)}{a_{i_k}(t)} < \liminf_{t\to\infty} \frac{c_{kj}(t)}{c_{i_k j}(t)} \end{aligned}$$

for $j = 1, ..., k$.

Theorem 1. *Suppose there is an* $1 \leq r < n$ *such that hypothesis* (H1) *holds. Then*

(a) $\lim_{t\to\infty} u_i(t, x) = 0$ $\ (x \in [0, L])$

(b) $\int_0^L \int_0^\infty u_i(t, x)\, dt dx < \infty$

for $r + 1 \leq i \leq n$. *Furthermore, the convergence in assertion* (a) *is exponential in* X, *the space of bounded and measurable functions equipped with the supremum norm.*

Proof. We prove the theorem by induction on k. First, we prove that $\lim_{t\to\infty} u_n(t, x) = 0$ and $\int_0^\infty u_n(s, x)\, ds < \infty$. From hypothesis (H1) there exist real numbers $\alpha_n, \varepsilon_n, \eta_n > 0$ such that

$$\left.\begin{matrix} a_{i_n}(t) \\ b_{i_nj}(t) \\ c_{i_nj}(t) \end{matrix}\right\} > \eta_n, \quad \frac{a_n(t)}{a_{i_n}(t)} < \alpha_n - \varepsilon_n, \quad \left.\begin{matrix} \dfrac{b_{nj}(t)}{b_{i_nj}(t)} \\ \dfrac{c_{nj}(t)}{c_{i_nj}(t)} \end{matrix}\right\} > \alpha_n$$

for $j = 1, \dots, n$ and for $t \geq T_n$ where T_n is sufficiently large. This implies

$$\begin{aligned} a_n(t) - \alpha_n a_{i_n}(t) &< -\varepsilon_n \eta_n =: -\delta_n \\ \alpha_n b_{i_nj}(t) - b_{nj}(t) &< 0 \\ \alpha_n c_{i_nj}(t) - c_{nj}(t) &< 0 \end{aligned} \tag{3.2}$$

for $t \geq T_n$ and $j = 1, ..., n$. Define now the function

$$V_n(t,x) = u_n(u_{i_n})^{-\alpha_n} \qquad (t > 0, x \in [0,L]).$$

From (1.4) and assumption (ii) in Section 1 we have

$$\begin{aligned} u_{i_n}(t,x) &= u_{0i_n}(x) \exp\Bigg(\int_0^t \Bigg[a_{i_n}(s) - \sum_{j=1}^n b_{i_nj}(s) u_j \\ &\qquad - \sum_{j=1}^n c_{i_nj}(s) \int_0^x u_j(s,\xi)\, d\xi \Bigg] ds \Bigg) \\ &\geq \delta \exp\left(- \sum_{j=1}^n \|b_{i_nj}\|_\infty M_j t - \sum_{j=1}^n L \|c_{i_nj}\|_\infty M_j t \right) \\ &=: \delta'_{i_n} > 0 \end{aligned} \tag{3.3}$$

where δ'_{i_n} is independent on x. The function V_n is then well defined and differentiable with respect to t for each fixed x. Differentiation of V_n with respect to t using (1.4) yields

$$\begin{aligned} \frac{\partial V_n}{\partial t} &= -\alpha_n (u_{i_n})_t (u_{i_n})^{-\alpha_n - 1} u_n + (u_{i_n})^{-\alpha_n} (u_n)_t \\ &= V_n(t,x) \Bigg\{ (a_n - \alpha_n a_{i_n}) + \sum_{j=1}^n (\alpha_n b_{i_nj} - b_{nj}) u_j \\ &\qquad + \sum_{j=1}^n (\alpha_n c_{i_nj} - c_{nj}) \int_0^x u_j(t,\xi)\, d\xi \Bigg\}. \end{aligned}$$

In view of inequalities (3.2) we get

$$\frac{\partial V_n}{\partial t} \leq -\delta_n V_n(t,x) \qquad (t \geq T_n, x \in [0,L]).$$

Then the Gronwall lemma implies

$$V_n(t,x) \leq V_n(T_n,x)\exp(-\delta_n(t-T_n)) \qquad (t \geq T_n).$$

We entail from (3.3) that $V_n(T_n,x) \leq M_n(\delta'_{i_n})^{-\alpha_n} =: \delta_n^*$ where δ_n^* is independent on x and therefore $V_n(t,x) \leq \delta_n^* \exp(-\delta_n(t-T_n))$. Back to u_n we deduce that

$$u_n(t,x) \leq (M_{i_n})^{\alpha_n}\delta_n^* \exp(-\delta_n(t-T_n)) = R_n \exp(-\delta_n(t-T_n))$$

for $t \geq T_n$ and $x \in [0,L]$. This implies $\lim_{t\to\infty} u_n(t,x) = 0$. Finally, integrating both sides over (T_n,∞) we get $\int_{T_n}^{\infty} u_n(s,x)\,ds \leq C_n$ for any $x \in [0,L]$ where C_n is independent of x. Hence $\int_0^{\infty} u_n(s,x)\,ds < \infty$.

Suppose now that we have obtained

$$\lim_{t\to\infty} u_i(t,x) = 0 \quad \text{and} \quad \int_0^{\infty} u_i(s,x)\,ds < C \tag{3.4}$$

for all $i > k$ where k is such that $k > r$ and C is independent of x. We want to show that

$$\lim_{t\to\infty} u_k(t,x) = 0 \quad \text{and} \quad \int_0^{\infty} u_k(s,x)\,ds < \infty.$$

Using hypothesis (H1) once again there are $i_k < k, \alpha_k > 0$ and $\delta_k > 0$ such that

$$\begin{aligned} &a_k(t) - \alpha_k a_{i_k}(t) < -\delta_k \\ &\alpha_k b_{i_k j}(t) - b_{kj}(t) < 0 \\ &\alpha_k c_{i_k j}(t) - c_{kj}(t) < 0 \end{aligned} \tag{3.5}$$

for $j = 1, ..., k$ and $t > T_k$. Consider now the function

$$V_k(t,x) = u_k(u_{i_k})^{-\alpha_k} \qquad (t > 0, x \in [0,L]).$$

We have

$$\begin{aligned} \frac{\partial V_k}{\partial t} &= V_k(t,x) \times (a_k - \alpha_k a_{i_k}) + V_k(t,x)\left(\sum_{j=1}^{k}(\alpha_k b_{i_k j} - b_{kj})u_j\right) \\ &\quad + V_k(t,x)\left\{\sum_{j=1}^{k}(\alpha_k c_{i_k j} - c_{kj})\int_0^x u_j(t,\xi)\,d\xi + f_k(t,x)\right\} \end{aligned}$$

where f_k contain the residual terms

$$f_k(t,x) = \sum_{j=k+1}^{n} (\alpha_k b_{i_k j} - b_{kj})u_j + \sum_{j=k+1}^{n} (\alpha_k c_{i_k j} - c_{kj}) \int_0^x u_j(t,\xi)\, d\xi.$$

From inequalities (3.5) $\frac{\partial V_k}{\partial t} \leq V_k\{-\delta_k + f_k(t,x)\}$ follows and by the induction hypothesis (3.4)

$$\begin{aligned}\int_{T_k}^{t} |f_k(s,x)|\, ds \leq & \sum_{j=k+1}^{n} \big(\alpha_k \|b_{i_k j}\|_\infty + \|b_{kj}\|_\infty\big) \int_{T_k}^{x} u_j(t,\xi)\, d\xi \\ & + \sum_{j=k+1}^{n} \big(\alpha_k \|c_{i_k j}\|_\infty + \|c_{kj}\|_\infty\big) \int_{T_k}^{t} \int_0^x u_j\, d\xi ds \\ < & \ \beta_k\end{aligned}$$

where β_k is independent of t and x. Then

$$V_k(t,x) \leq V_k(T_k,x) \exp\big(-\delta_k(t-T_k) + \beta_k\big) \qquad (t \geq T_k).$$

We deduce that

$$u_k(t,x) \leq R_k \exp\big(-\delta_k(t-T_k) + \beta_k\big) \qquad (t \geq T_k).$$

Consequently,

$$\lim_{t\to\infty} u_k(t,x) = 0 \quad \text{and} \quad \int_0^\infty u_k(t,x)\, dt < \infty.$$

This completes the proof of Theorem 1 ∎

In the following we use the notations

$$f^l = \inf_{t\geq 0} f(t) \qquad \text{and} \qquad f^m = \sup_{t \geq 0} f(t).$$

Corollary 1. *Let r be an integer, $1 \leq r < n$, and assume that the following hypothesis holds:*

(H1)′ *If $b^l_{ii} > 0$ $(1 \leq i \leq n)$ and to each $k > r$ there corresponds $i_k < k$ such that $a^l_{i_k}, b^l_{i_k j}, c^l_{i_k j} > 0$ and*

$$\frac{a^m_k}{a^l_{i_k}} < \frac{b^l_{kj}}{b^m_{i_k j}} \qquad (j = 1, ..., k) \tag{3.6}$$

$$\frac{a^m_k}{a^l_{i_k}} < \frac{c^l_{kj}}{c^m_{i_k j}} \qquad (j = 1, ..., k), \tag{3.7}$$

then the species $u_{r+1}, ..., u_n$ go to extinction exponentially in X.

Remark 1. One can point out that the conclusion of Theorem 1 remains true if either of $b^m_{i_k j}$ or $c^m_{i_k j}$ vanishes since the inequalities in (3.5) remain true.

Remark 2. If $c_{ij} \equiv 0$, then system (1.4) reduces to the well known non-autonomous Lotka-Volterra competitive system

$$\frac{\partial u_i}{\partial t} = u_i \Big\{ a_i(t) - \sum_{j=1}^{n} b_{ij}(t) u_j \Big\}.$$

Hence, if (3.6) holds, then the species $u_{r+1}, ..., u_n$ go to extinction. This result was derived in [1 - 3, 12, 13].

4. The autonomous case

In this section we consider system (1.4) with non-negative constant coefficients

$$\frac{\partial u_i}{\partial t} = u_i \left\{ a_i - \sum_{j=1}^{n} b_{ij} u_j - \sum_{j=1}^{n} c_{ij} \int_0^x u_j \, d\xi \right\} \tag{4.1}$$
$$(1 \le i \le n, t > 0)$$

where $b_{ii} > 0$. We proved in Section 3 that if hypothesis (H1)$'$ holds, then $u_{r+1}, ..., u_n$ are driven to extinction everywhere in $[0, L]$.

The purpose of the present section is to establish sufficient conditions assuring global attractivity of the non-trivial stationary solution for the remaining species $u_1, ..., u_r$ of system (4.1), that is the solution u_i^* of the system

$$a_i - \sum_{j=1}^{r} b_{ij} u_j^* - \sum_{j=1}^{r} c_{ij} \int_0^x u_j^* d\xi = 0 \quad (x \in [0, L], 1 \le i \le r). \tag{4.2}$$

Before stating our next result on global asymptotic stability we first introduce the concept of Volterra-Lyapunov stability of matrices (cf. [8]) and precise some hypotheses on the coefficients.

Definition. We say that a matrix $A = (\alpha_{ij})_{i,j=1}^n$ is *Volterra-Lyapunov stable* if there is a positive diagonal matrix $D = \mathrm{Diag}(d_1, ..., d_n)$ (i.e. $d_1, ..., d_n > 0$) and some real numbers $\gamma_i > 0$ verifying

$$\frac{1}{2} \zeta^\top (DA + A^\top D) \zeta = \sum_{i,j=1}^{n} d_i \alpha_{ij} \zeta_i \zeta_j \ge \sum_{i=1}^{n} \gamma_i \zeta_i^2 \tag{4.3}$$

for any $\zeta = (\zeta_1, ..., \zeta_n)^\top \in \mathbb{R}^n$.

The following proposition ensures existence, uniqueness and positivity of the stationary solution u_i^*.

Proposition 3. *Assume that there is $1 \le r \le n$ such that:*

(i) *The sub-matrix $(b_{ij})_{i,j=1}^r$ is non-singular with $b_{ii} > 0 \quad (1 \le i \le r)$ and all the off-diagonal elements of the matrix $B^{-1}C$ are non-positive.*

(ii) *$a_i > \sum_{\substack{j=1 \\ j\neq i}}^r a_j \frac{b_{ij}}{b_{jj}}$ for $1 \le i \le r$.*

Then the stationary system (4.2) has a unique solution $u_i^* > 0 \quad (1 \le i \le r)$ which is positive and continuous on $[0, L]$.

Proof. It is easy to check that system (4.2) is equivalent to the system

$$\left.\begin{aligned} \sum_{j=1}^r b_{ij}(u_j^*)_x(x) + \sum_{j=1}^r c_{ij}u_j^*(x) = 0 \quad (0 < x \le L) \\ \sum_{j=1}^r b_{ij}u_j^*(0) = a_i \end{aligned}\right\}.$$

In turn, this system may take the form

$$\left.\begin{aligned} (u^*)_x + B^{-1}Cu^* = 0 \qquad (0 < x \le L) \\ u^*(0) = B^{-1}A \end{aligned}\right\} \tag{4.4}$$

because the matrix $B = (b_{ij})_{i,j=1}^r$ is non-singular. Here $u^* = (u_1^*, ...,_r^*)$, $C = (c_{ij})_{i,j=1}^r$ and $A = (a_1, ..., a_r)$. By classical results on differential systems, system (4.4) has a unique solution restricted on the interval $[0, L]$ which is continuously differentiable on $[0, L]$. This leads to the existence and uniqueness of a solution to system (4.2). Now, since $a_i > \sum_{j=1, j\neq i}^r a_j \frac{b_{ij}}{b_{jj}}$ we can prove (see [5: Lemma 4.1.1] or [6: p. 429]) that $B^{-1}A > 0$ and thereafter $u^*(0) > 0$. So, by the comparison principle for linear systems (see [5: Corollary 3.6.9]) it follows that $u^*(x) > 0$ for $x \in [0, L]$ ∎

The following lemma on the persistence of Lotka-Volterra systems can be found in [11: Theorem 3.1].

Lemma 2. *Consider the autonomous competitive Lotka-Volterra system*

$$\frac{dw_i}{dt} = w_i\left\{d_i - \sum_{j=1}^n f_{ij}w_j\right\} \qquad (t > 0) \tag{4.5}$$

where d_i and f_{ij} are non-negative constants with $d_i > 0$ and $f_{ii} > 0$. Assume the following:

(1) *The matrix $F = (f_{ij})_{i,j=1}^n$ is non-singular and for $X = (x_1, ..., x_n)^T$ the algebraic system $\sum_{j=1}^n f_{ij}x_j = d_i$ has one positive solution $(x_1^0, ..., x_n^0)^T$.*

(2) *The inverse matrix* $F^{-1} = (\tau_{ij})_{i,j=1}^{n}$ *is such that* $\tau_{ii} > 0$ *and* $\tau_{ij} \leq 0$ *for* $i \neq j$.

Then the positive solutions of system (4.5) *are persistent.*

We will use the following new hypothesis

(H2) Assume that there is r $(1 \leq r \leq n)$ such that:

- **(i)** For each integer $k > r$ there is $i_k < k$ such that $a_{i_k}, b_{i_k j}, c_{i_k j} > 0$ and $\frac{a_k}{a_{i_k}} < \frac{b_{kj}}{b_{i_k j}}$ as well as $\frac{a_k}{a_{i_k}} < \frac{c_{kj}}{c_{i_k j}}$ for $j = 1, ..., k$.
- **(ii)** $b_{ii} > 0$ for $1 \leq i \leq n$ and $a_i > \sum_{j=1, j\neq i}^{r} a_j \frac{b_{ij}}{b_{jj}}$ for $1 \leq i \leq r$.
- **(iii)** The sub-matrix $(b_{ij})_{i,j=1}^{n}$ is Volterra-Lyapunov stable and non-singular with an inverse matrix $B^{-1} = (\beta_{ij})$ such that $\beta_{ii} > 0$, $\beta_{ij} \leq 0$ for $i \neq j$ and the sub-matrix $(c_{ij})_{i,j=1}^{r}$ is diagonal.

Theorem 2. *Suppose there is* $1 \leq r \leq n$ *such that Hypothesis* (H2) *holds. Then there are constants* $\beta, \omega > 0$ *and a large time* $T > 0$ *such that if* u_i *is the solution of problem* (1.4), *then*

$$\sum_{i=1}^{r} |u_i(t,x) - u_i^*(x)| \leq \beta e^{-\omega t} \qquad (t > T, x \in [0,L]) \tag{4.6}$$

while $u_{r+1}, ..., u_n$ *go to extinction exponentially in* X (*eventually*).

Proof. The proof is based on an improvement of an idea by Holmåker [9] using the induction principle and a Lyapunov functional. Denote

$$\begin{aligned} \underline{u}_i^* &= \min_{x\in[0,L]} u_i^*(x) \\ \overline{u}_i^* &= \max_{x\in[0,L]} u_i^*(x). \end{aligned} \tag{4.7}$$

From Hypothesis (H2) and Proposition 3, $\underline{u}_i^* > 0$. Denote by M_i an upper bound of u_i (see Proposition 2). Since the algebraic system

$$\sum_{j=1}^{r} b_{ij} x_j = \sum_{j=1}^{r} b_{ij} \underline{u}_j^* \qquad (1 \leq i \leq r)$$

has one positive solution $x_i = \underline{u}_i^* > 0$, then by continuity there are $\varepsilon, \delta > 0$ sufficiently small such that the system

$$\sum_{j=1}^{r} b_{ij} x_j = \sum_{j=1}^{r} b_{ij} \underline{u}_j^* - \delta \sum_{j=1}^{r} c_{ij} M_j - \varepsilon \tag{4.8}$$

has one positive solution $(x_1^0, ..., x_r^0)^T$. Now divide the interval $[0, L]$ into N parts $[x_{k-1}, x_k]$ $(k = 1, ..., N)$ so that $x_k - x_{k-1} = \delta$ and $x_N \geq L$.

We prove Theorem 2 by induction on k. Suppose that we have found $\beta_{k-1}, \omega_{k-1}, T_{k-1} > 0$ such that

$$|u_i(t,x) - u_i^*(x)| \leq \beta_{k-1} e^{-\omega_{k-1} t} \qquad (i = 1, ..., r) \tag{4.9}$$

for $t > T_{k-1}$ and $x \in [0, x_{k-1}]$. We would like to prove that there are $\beta_k > \beta_{k-1}, \omega_k < \omega_{k-1}, T_k > T_{k-1}$ such that

$$\sum_{i=1}^{r} |u_i(t,x) - u_i^*(x)| \leq \beta_k e^{-\omega_k t} \qquad (t > T_k, x \in [0, x_k]).$$

Let $x \in [x_{k-1}, x_k]$ and write that

$$\begin{aligned}\frac{\partial u_i}{\partial t} = u_i \Big\{ a_i &- \sum_{j=1}^{r} b_{ij} u_j - \sum_{j=1}^{r} c_{ij} \int_0^{x_{k-1}} u_j(t,\xi)\, d\xi \\ &- \sum_{j=1}^{r} c_{ij} \int_{x_{k-1}}^{x} u_j(t,\xi)\, d\xi \Big\} \\ &- u_i \Big\{ \sum_{j=r+1}^{n} b_{ij} u_j + \sum_{j=r+1}^{n} c_{ij} \int_0^{x} u_j(t,\xi)\, d\xi \Big\}\end{aligned}$$

for $t > T_{k-1}$. From Hypothesis (H2)/(i) and Theorem 1 we conclude the existence of constants $C_1, \gamma > 0$ (independent of x) and of a sufficiently large time T' such that

$$\sum_{j=r+1}^{n} b_{ij} u_j + \sum_{j=r+1}^{n} c_{ij} \int_0^{x} u_j(t,\xi)\, d\xi \leq C_1 e^{-\gamma t} \tag{4.10}$$

for $t > T'$ and $x \in [0, L]$. If we put $T'_{k-1} = \max(T_{k-1}, T')$, then from (4.2), (4.9), (4.10) and the property of $\underline{u}_j^*$ we have

$$\begin{aligned}\frac{\partial u_i}{\partial t} &\geq u_i \Big\{ a_i - \sum_{j=1}^{r} b_{ij} u_j - \sum_{j=1}^{r} c_{ij} \int_0^{x_{k-1}} u_j^*(\xi)\, d\xi \\ &\quad - \sum_{j=1}^{r} c_{ij} x_{k-1} \beta_{k-1} e^{-\omega_{k-1} t} - \delta \sum_{j=1}^{r} c_{ij} M_j - C_1 e^{-\gamma t} \Big\} \\ &\geq u_i \Big\{ \sum_{j=1}^{r} b_{ij} \underline{u}_j^* - \delta \sum_{j=1}^{r} c_{ij} M_j - \sum_{j=1}^{r} c_{ij} x_{k-1} \beta_{k-1} e^{-\omega_{k-1} t} \\ &\quad - \sum_{j=1}^{r} b_{ij} u_j - C_1 e^{-\gamma t} \Big\}\end{aligned}$$

for $t > T'_{k-1}$. Choose then $T_k > T'_{k-1}$ sufficiently large so that

$$\sum_{j=1}^{r} c_{ij} x_{k-1} \beta_{k-1} e^{-\omega_{k-1} t} + C_1 e^{-\gamma t} < \varepsilon$$

for $t > T_k$, where ε is defined in (4.8). We obtain

$$\frac{\partial u_i}{\partial t} \geq u_i \left\{ \sum_{j=1}^{r} b_{ij} \underline{u}_j^* - \delta \sum_{j=1}^{r} c_{ij} M_j - \varepsilon - \sum_{j=1}^{r} b_{ij} u_j \right\} \tag{4.11}$$

for $t > T_k$ and $x \in [x_{k-1}, x_k]$. Now by (3.3) there is a constant $\delta'_i > 0$ independent of x such that $u_i(T_k, x) \geq \delta'$ for any $x \in [0, L]$. Thus by Lemma 2 and the comparison principle (see [10]) the species u_i $(1 \leq i \leq r)$ are persistent. So there are constants $\alpha'_k > 0$ (independent of x) such that

$$u_i(t, x) > \alpha'_k \qquad (1 \leq i \leq r) \tag{4.12}$$

for $t > T_k$ and $x \in [x_{k-1}, x_k]$. As in [9] let us introduce the Lyapunov functional

$$V(t) = \sum_{i=1}^{r} d_i \int_{x_{k-1}}^{x_k} \left\{ (u_i - u_i^*) - u_i^* \ln \frac{u_i}{u_i^*} \right\} dx$$

where d_i are the coefficients of the Volterra-Lyapunov stability (see Hypothesis (H2)/(iii)). Put $w_i(t, x) = u_i(t, x) - u_i^*(x)$. Since the function

$$f(v, v_0) = \frac{v - v_0 - v_0 \ln \frac{v}{v_0}}{(v - v_0)^2} \qquad (0 < v_0 \neq v)$$

is decreasing in v for fixed v_0 and decreasing in v_0 for fixed v and since $u_i > \alpha'_k$ for $t > T_k$, we have

$$0 < f(M_i, \overline{u}_i^*) \leq f(u_i, u_i^*) \leq f(\alpha'_k, \underline{u}_i^*).$$

This implies the existence of constants $c_k > 0$ depending on α'_k and of $d > 0$ such that

$$d \sum_{i=1}^{r} \gamma_i w_i^2 \leq \sum_{i=1}^{r} d_i \left\{ (u_i - u_i^*) - u_i^* \ln \frac{u_i}{u_i^*} \right\} \leq c_k \sum_{i=1}^{r} \gamma_i w_i^2 \qquad (t > T_k) \tag{4.13}$$

where γ_i is as in the definition of the Volterra-Lyapunov stability. Integrating all three sides of (4.13) over (x_{k-1}, x_k) we obtain

$$d \sum_{i=1}^{r} \gamma_i \int_{x_{k-1}}^{x_k} w_i^2 dx \leq V(t) \leq c_k \sum_{i=1}^{r} \gamma_i \int_{x_{k-1}}^{x_k} w_i^2 dx. \tag{4.14}$$

A differentiation of $V = V(t)$ with respect to t along the solution yields

$$V'(t) = \sum_{i=1}^{r} \int_{x_{k-1}}^{x_k} d_i(u_i - u_i^*)\Big\{a_i - \sum_{j=1}^{r} b_{ij}u_j - \sum_{j=1}^{r} c_{ij} \int_0^x u_j(t,\xi)\,d\xi\Big\}dx$$
$$- \sum_{i=1}^{r} \int_{x_{k-1}}^{x_k} d_i(u_i - u_i^*)\Big\{ \sum_{j=r+1}^{n} b_{ij}u_j + \sum_{j=r+1}^{n} c_{ij} \int_0^x u_j(t,\xi)\,d\xi\Big\}dx.$$

Using the definition of u_i^* and since the matrix $(c_{ij})_{i,j=1}^r$ is diagonal, we get

$$\begin{aligned} V'(t) \le &- \int_{x_{k-1}}^{x_k} \sum_{i,j=1}^{r} d_i b_{ij}(u_i - u_i^*)(u_j - u_j^*)\,dx \\ &- \sum_{i=1}^{r} d_i c_{ii} \int_{x_{k-1}}^{x_k} (u_i - u_i^*) \int_0^{x_{k-1}} (u_i - u_i^*)\,d\xi \\ &- \frac{1}{2}\sum_{i=1}^{r} d_i c_{ii}\Big(\int_{x_{k-1}}^{x_k} (u_i - u_i^*)\,d\xi\Big)^2 \\ &- \int_{x_{k-1}}^{x_k} \sum_{i=1}^{r} d_i(u_i - u_i^*)\Big(\sum_{j=r+1}^{n} b_{ij}u_j\Big)dx \\ &- \int_{x_{k-1}}^{x_k} \sum_{i=1}^{r} d_i(u_i - u_i^*)\Big(\sum_{j=r+1}^{n} c_{ij} \int_0^x u_j(\xi)\,d\xi\Big)dx. \end{aligned}$$

Now from (4.3), (4.9), (4.10) we have

$$\begin{aligned} V'(t) \le &- \sum_{i=1}^{r} \gamma_i \|u_i - u_i^*\|^2_{L^2(x_{k-1},x_k)} \\ &+ \sum_{i=1}^{r} d_i c_{ii} \delta K_i x_{k-1} \beta_{k-1} e^{-\omega_{k-1}t} + \delta \sum_{i=1}^{r} d_i K_i C_1 e^{-\gamma t} \end{aligned}$$

where the constants K_i are such that $|u_i - u_i^*| \le K_i$ for $x \in [0, L]$ and $t > T_k$. Therefore, by the right-hand side inequality in (4.14),

$$V'(t) \le -\frac{1}{c_k}V(t) + \sum_{i=1}^{r} d_i c_{ii} \delta K_i x_{k-1} \beta_{k-1} e^{-\omega_{k-1}t} + \delta \sum_{i=1}^{r} d_i K_i C_1 e^{-\gamma t}.$$

From the Gronwall lemma, after a simple integration of this relation, we obtain using the left-hand side inequality in (4.14) the existence of constants $C', \omega' > 0$ such that

$$\|u_i - u_i^*\|^2_{L^2(x_{k-1},x_k)} \le C' e^{-\omega' t} \qquad (t > T_k, 1 \le i \le r). \tag{4.15}$$

Let us next introduce the function

$$W(t,x) = \sum_{i=1}^{r} d_i \Big\{ (u_i - u_i^*) - u_i^* \ln \frac{u_i}{u_i^*} \Big\}. \tag{4.16}$$

As in the differentiation of $V(t)$ we find after use of (4.3) and (4.10)

$$\begin{aligned}\frac{\partial W}{\partial t} \leq & -\sum_{i=1}^{r} \gamma_i (u_i - u_i^*)^2 + \sum_{i=1}^{r} d_i K_i c_{ii} \int_0^{x_{k-1}} |u_i - u_i^*| \, dx \\ & + \sum_{i=1}^{r} d_i K_i c_{ii} \int_{x_{k-1}}^{x} |u_i - u_i^*| \, dx + \sum_{i=1}^{r} d_i K_i C_1 e^{-\gamma t}\end{aligned}$$

for $t > T_k$. Using the right side of (4.13), (4.9) and the Hölder inequality we find

$$\begin{aligned}\frac{\partial W}{\partial t} \leq & -\frac{1}{c_k} W(t,x) + \sum_{i=1}^{r} d_i K_i c_{ii} x_{k-1} \beta_{k-1} e^{-\omega_{k-1} t} \\ & + \sum_{i=1}^{r} d_i K_i c_{ii} \sqrt{\delta} \| u_i - u_i^* \|_{L^2(x_{k-1}, x_k)} + \sum_{i=1}^{r} d_i K_i C_1 e^{-\gamma t}.\end{aligned}$$

Now, from (4.15),

$$\begin{aligned}\frac{\partial W}{\partial t} \leq & -\frac{1}{c_k} W(t,x) + \sum_{i=1}^{r} d_i K_i c_{ii} x_{k-1} \beta_{k-1} e^{-\omega_{k-1} t} \\ & + \sum_{i=1}^{r} d_i K_i c_{ii} \sqrt{\delta C'} e^{-\frac{1}{2}\omega' t} + \sum_{i=1}^{r} d_i K_i C_1 e^{-\gamma t}.\end{aligned}$$

The Gronwall Lemma leads to

$$W(t,x) \leq C'' e^{-\omega'' t} \qquad (t > T_k, x \in [x_{k-1}, x_k]) \tag{4.17}$$

for some constants $C'', \omega'' > 0$. Combining this inequality and the very left-hand side of (4.13) we find

$$\sum_{i=1}^{r} \gamma_i w_i^2 \leq \frac{C''}{d} \, e^{-\omega'' t}.$$

Finally, one can choose $\beta_k > \beta_{k-1}$ and $\omega_k < \omega_{k-1}$ such that

$$\sum_{i=1}^{r} |w_i| \leq \beta_k e^{-\omega_k t} \qquad (t > T_k, x \in [x_{k-1}, x_k]).$$

The case $k = 1$ can be easily checked from the previous considerations and steps since u_i are persistent in $[0, x_1]$ for x_1 sufficiently small. The proof of the Theorem 2 is complete ∎

Proposition 4. *Assume that there is $1 \leq r \leq n$ such that:*

(i) *The sub-matrix $(b_{ij})_{i,j=1}^{r}$ is diagonal with $b_{ii} > 0$.*

(ii) $a_i > L \sum_{j=1}^{r} c_{ij} \frac{a_j}{b_{jj}}$ *for all $1 \leq i \leq r$.*

Then system (4.2) has a unique positive solution $u_i^*(x) > 0$ for $x \in [0, L]$ and $i = 1, ..., r$.

Proof. Since the matrix $(b_{ij})_{i,j=1}^{r}$ is diagonal, system (4.2) takes the form

$$b_{ii}u_i^* + \int_0^x \sum_{j=1}^{r} c_{ij}u_j^*(\xi)\, d\xi = a_i \qquad (1 \leq i \leq r). \tag{4.18}$$

Define the set

$$X = \left\{ z = (z_1, ..., z_r) \in C([0, L]; \mathbb{R}^r) : 0 \leq z_i(x) \leq \frac{a_i}{b_{ii}} \quad \begin{pmatrix} x \in [0, L] \\ 1 \leq i \leq r \end{pmatrix} \right\}$$

and the operator

$$Az = (A_1z, ..., A_rz) : C([0, L]; \mathbb{R}^r) \to C([0, L]; \mathbb{R}^r)$$
$$(A_iz)(x) = \frac{a_i}{b_{ii}} - \frac{1}{b_{ii}} \int_0^x \sum_{j=1}^{r} c_{ij}z_j(\xi)\, d\xi \quad (x \in [0, L]).$$

We can easily check that X is a closed, bounded and convex set and that A is bounded on $C([0, L]; \mathbb{R}^r)$. Let $z \in X$. Then $A_iz \leq \frac{a_i}{b_{ii}}$ and by assumption (ii) of Proposition 4 we have

$$A_iz \geq \frac{a_i}{b_{ii}} - \frac{1}{b_{ii}} \int_0^x \sum_{j=1}^{r} c_{ij}\frac{a_j}{b_{jj}}\, d\xi \geq \frac{a_i}{b_{ii}} - \frac{L}{b_{ii}} \sum_{j=1}^{r} c_{ij}\frac{a_j}{b_{jj}} > 0, \tag{4.19}$$

so $Az \in X$. Now, since the set AX is equicontinuous, then by the Arzela-Ascoli theorem AX has a compact closure, and by the Schauder fixed point theorem A has a fixed point $u^* \in X$ which is the solution of system (4.18). Further, by (4.19),

$$\begin{aligned} u_i^*(x) = (A_iu^*)(x) &= \frac{a_i}{b_{ii}} - \frac{1}{b_{ii}} \int_0^x \sum_{j=1}^{r} c_{ij}u_j^* d\xi \\ &\geq \frac{a_i}{b_{ii}} - \frac{L}{b_{ii}} \sum_{j=1}^{r} c_{ij}\frac{a_j}{b_{jj}} \\ &> 0 \end{aligned}$$

for any $x \in [0, L]$. By the uniqueness property of system (4.18) (see Proposition 3) u^* is the unique positive solution of system (4.18) ∎

Theorem 2 is completed by the following result.

Theorem 3. *Assume that there is* $1 \le r \le n$ *such that:*

(H2)′ (i) *For each integer* $k > r$ *there is* $i_k < k$ *such that* $a_{i_k}, b_{i_k j}, c_{i_k j} > 0$ *and* $\frac{a_k}{a_{i_k}} < \frac{b_{kj}}{b_{i_k j}}$ *as well as* $\frac{a_k}{a_{i_k}} < \frac{c_{kj}}{c_{i_k j}}$ *for* $j = 1, ..., k$.

(ii) $a_i > L \sum_{j=1}^{r} c_{ij} \frac{a_j}{b_{jj}}$ *for all* $i = 1, ..., r$.

(iii) *The sub-matrix* $(b_{ij})_{i,j=1}^{r}$ *is diagonal with* $b_{ii} > 0$ $(1 \le i \le n)$ *and the sub-matrix* $C = (c_{ij})_{i,j=1}^{r}$ *is symmetric and positive definite.*

Then there are constants $\overline{\beta}, \overline{\omega} > 0$ *and a large time* $\overline{T} > 0$ *such that*

$$\sum_{i=1}^{r} |u_i(t,x) - u_i^*(x)| \le \overline{\beta} e^{-\overline{\omega} t} \qquad (t > \overline{T}, x \in [0, L])$$

while $u_{r+1}, ..., u_n$ *are driven to extinction exponentially in* X *(eventually).*

Proof. The proof is essentially the same as that of Theorem 2 with some minor refinements. Since the matrix $(b_{ij})_{i,j=1}^{r}$ is diagonal, inequality (4.11) is reduced to an inequality closely related to the well known Logistic equation (3.1). Choosing δ and ε sufficiently small, by Lemma 1/(b) there exists an $\alpha_k'' > 0$ such that $u_i > \alpha_k''$ $(1 \le i \le r)$ for $t > T_{k-1}$ and $x \in [x_{k-1}, x_k]$. Put $T_k = \max(T_{k-1}, T')$, where T' is given in (4.10). Now using the functional

$$V(t) = \sum_{j=1}^{r} \int_{x_{k-1}}^{x_k} \Big\{ (u_i - u_i^*) - u_i^* \ln \frac{u_i}{u_i^*} \Big\} dx,$$

as in the proof of Theorem 2 with the help of inequality (4.10), the fact that

$$\begin{aligned} &\sum_{i,j=1}^{r} c_{ij} \int_{x_{k-1}}^{x_k} \Big(w_i \int_{x_{k-1}}^{x} w_j d\xi \Big) dx \\ &\quad = \frac{1}{2} \sum_{i,j=1}^{r} c_{ij} \Big(\int_{x_{k-1}}^{x_k} w_i(t,\xi)\, d\xi \Big) \Big(\int_{x_{k-1}}^{x_k} w_j(t,\xi)\, d\xi \Big) \\ &\quad \ge 0 \end{aligned}$$

and the induction hypothesis (4.9) we obtain

$$\begin{aligned} V'(t) \le &- \sum_{i=1}^{r} b_{ii} \int_{x_{k-1}}^{x_k} (u_i - u_i^*)^2 dx \\ &+ \sum_{i,j=1}^{r} c_{ij} \Big(\int_0^{x_{k-1}} |u_i - u_i^*|\, d\xi \Big) \Big(\int_0^{x_{k-1}} |u_j - u_j^*|\, d\xi \Big) \end{aligned}$$

$$
\begin{aligned}
&+\delta\sum_{i=1}^{r}K_iC_1e^{-\gamma t}\\
&\le -\sum_{i=1}^{r}b_{ii}\int_{x_{k-1}}^{x_k}(u_i-u_i^*)^2dx+\sum_{i,j=1}^{r}c_{ij}x_{k-1}^2\beta_{k-1}^2e^{-2\omega_{k-1}t} \qquad (4.20)\\
&+\delta\sum_{i=1}^{r}K_iC_1e^{-\gamma t}
\end{aligned}
$$

for $t>T_k$. By the property of the function $f(u_i,u_i^*)$ we can find constants $d',c'_k>0$ (depending on α''_k) such that

$$
d'\sum_{i=1}^{r}b_{ii}w_i^2\le\sum_{i=1}^{r}\left\{(u_i-u_i^*)-u_i^*\ln\frac{u_i}{u_i^*}\right\}\le c'_k\sum_{i=1}^{r}b_{ii}w_i^2. \tag{4.21}
$$

Integrating all sides herein over (x_{k-1},x_k) we find

$$
d'\sum_{i=1}^{r}b_{ii}\int_{x_{k-1}}^{x_k}w_i^2dx\le V(t)\le c'_k\sum_{i=1}^{r}b_{ii}\int_{x_{k-1}}^{x_k}w_i^2dx \tag{4.22}
$$

by (4.20) and the right side of (4.22) as

$$
V'(t)\le-\frac{1}{c'_k}V(t)+\sum_{i,j=1}^{r}c_{ij}x_{k-1}^2\beta_{k-1}^2e^{-2\omega_{k-1}t}+\delta\sum_{i=1}^{r}K_iC_1e^{-\gamma t}.
$$

The Gronwall Lemma and the left-side inequality in (4.22) allow us to entail that

$$
\|u_i-u_i^*\|^2_{L^2(x_{k-1},x_k)}\le C_2e^{-\omega_1 t}\qquad (t>T_k,1\le i\le r) \tag{4.23}
$$

for some constants $C_2,\omega_1>0$. Calculating the derivative $\frac{\partial W}{\partial t}$, where $W=W(t,x)$ is defined as in the proof of Theorem 2 with $d_i=1$, taking into account that the matrix $(b_{ij})_{i,j=1}^r$ is diagonal, we get after use of (4.21), of the Hölder inequality and of relations (4.23) and (4.9) that

$$
\begin{aligned}
\frac{\partial W}{\partial t}&\le-\sum_{i=1}^{r}b_{ii}(u_i-u_i^*)^2+\sum_{i,j=1}^{r}c_{ij}K_ix_{k-1}\beta_{k-1}e^{-\omega_{k-1}t}\\
&\quad+\sum_{i,j=1}^{r}c_{ij}K_i\sqrt{L}\|u_j-u_j^*\|_{L^2(x_{k-1},x_k)}+\sum_{i=1}^{r}K_iC_1e^{-\gamma t}\\
&\le-\frac{1}{c'_k}W+\sum_{i,j=1}^{r}c_{ij}K_ix_{k-1}\beta_{k-1}e^{-\omega_{k-1}t}+\sum_{i,j=1}^{r}c_{ij}K_i\sqrt{LC_2}e^{-\frac{1}{2}\omega_1 t}\\
&\quad+\sum_{i=1}^{r}K_iC_1e^{-\gamma t}.
\end{aligned}
$$

Using Gronwall's lemma once again and the left-hand side of (4.21) we infer the existence of positive constants $\beta_k > \beta_{k-1}$ and $\omega_k < \omega_{k-1}$ such that

$$\sum_{i=1}^{r} |w_i| \leq \beta_k e^{-\omega_k t} \qquad (t > T_k, x \in [x_{k-1}, x_k]).$$

This completes the proof of Theorem 3 ∎

In the particular case when $r = 1$, Theorem 2 leads to the following

Corollary 2.

(i) *Assume that* $b_{ii} > 0 \ \ (1 \leq i \leq n)$, $a_1, b_{1j}, c_{1j} > 0 \ \ (j = 1, ..., n)$ *and that*

$$\frac{a_k}{a_1} < \frac{b_{kj}}{b_{1j}}, \frac{c_{kj}}{c_{1j}} \qquad (j = 1, ..., n). \tag{4.24}$$

Then the species $u_2, ..., u_n$ *are driven to extinction exponentially in* X, *while* $u_1 \to u_1^*(x) = \frac{a_1}{b_{11}} e^{-\frac{c_{11}}{b_{11}} x}$ *in* X *as* $t \to \infty$.

(ii) *If there is a permutation* ϕ *of the indices* $\{1, ..., n\}$ *under which the coefficients* a_i, b_{ij}, c_{ij} *satisfy* (4.24), *then* $u_{\phi^{-1}(1)} \to u^*_{\phi^{-1}(1)}$, *while the remaining species are driven to extinction exponentially in* X.

The following example (see [9]) is a particular case of Corollary 2.

Example. Back to system $(1.2) - (1.3)$, we have the following assertions:

(1) If $\lambda < \min(1, \eta)$, then $\lim_{t \to \infty} v_1(t, x) = e^{-x}$ and $\lim_{t \to \infty} v_2(t, x) = 0$ for $x \in [0, L]$.

(2) If $\lambda > \max(1, \eta)$, then $\lim_{t \to \infty} v_1(t, x) = 0$ and $\lim_{t \to \infty} v_2(t, x) = \lambda e^{-\eta \theta x}$ for $x \in [0, L]$.

Indeed, since $\lambda < \min(1, \eta)$, then (4.24) holds ($n = 2$). So, by Corollary 2/(i), $\lim_{t \to \infty} v_1(t, x) = e^{-x}$ and $\lim_{t \to \infty} v_2(t, x) = 0$ for any $x \in [0, L]$. Further, assertion (2) follows from Corollary 2/(ii) by use of the permutation $\phi(1) = 2$, $\phi(2) = 1$.

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