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EXTINCTION IN NONAUTONOMOUS KOLMOGOROV SYSTEMS

Abstract. We consider nonautonomous competitive Kolmogorov systems, which are generalizations of the classical Lotka–Volterra competition model. Applying Ahmad and Lazer's definitions of lower and upper averages of a function, we give an average condition which guarantees that all but one of the species are driven to extinction.

1. Introduction. In recent years investigation of population dynamics has developed rapidly. One of the famous models for dynamics of a population is the Lotka–Volterra competition system

$$\text{(LV)} \qquad u_i'(t) = u_i(t)\Big(a_i(t) - \sum_{j=1}^{N} b_{ij}(t)u_j(t)\Big), \qquad i = 1,\dots,N.$$

where $a_i, b_{ij}\colon [0,\infty) \to (0,\infty)$. The model (LV) has been studied by many authors. They obtained a lot of results dealing with persistence and global attractivity. Gopalsamy [5], [6] and Tineo and Alvarez [9] showed that if

$$\text{(GAT)} \qquad a_{iL} > \sum_{\substack{j=1\\ j\neq i}}^{N} \frac{b_{ijM}a_{jM}}{b_{jjL}} \qquad \text{for } i = 1,\dots,N$$

where g_L (resp. g_M) denotes the infimum (resp. supremum) of the function g, then system (LV) is persistent and globally attractive. To be more precise, Gopalsamy proved that in the almost periodic case the conditions (GAT)

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together with the conditions

$$\text{(D)} \qquad b_{jjL} > \sum_{\substack{j=1\\ j\neq i}}^{N} b_{ijL} \quad \text{for } i = 1, \ldots, N$$

imply persistence and global attractivity of (LV). Then Alvarez and Tineo showed that we may drop assumption (D). Ahmad and Lazer [2] proved that persistence and global attractivity hold under the conditions

$$m[a_i] > \sum_{\substack{j=1\\ j\neq i}}^{N} \frac{b_{ijM} M[a_j]}{b_{jjL}} \quad \text{for } i = 1, \ldots, N$$

where

$$m[g] = \liminf_{t-s\to\infty} \frac{1}{t-s} \int_s^t g(\tau)\, d\tau, \qquad M[g] = \limsup_{t-s\to\infty} \frac{1}{t-s} \int_s^t g(\tau)\, d\tau.$$

In [1] and [4] a nonautonomous logistic equation

$$\text{(L)} \qquad u_0'(t) = u_0(t)(a(t) - b(t)u_0(t)), \quad t \in \mathbb{R},$$

is considered. It is well known that an autonomous logistic equation

$$u' = u(b - au)$$

with $a, b > 0$ has a global attractor on $(0, \infty)$ at the carrying capacity $x = b/a$. Ahmad [1] and Coleman [4] showed that in the nonautonomous equation (L) the role of the globally attracting carrying capacity of the autonomous equation is played by a well defined canonical solution $u_i^*(t)$ to which all other solutions converge.

LEMMA 1 (Ahmad and Coleman [1], [4]). *Assume that in* (L) *the functions $a(t)$, $b(t)$ are continuous and bounded above and below by positive constants. Then equation* (L) *has a unique solution u^* which is bounded above and below by positive reals for all t.*

We should emphasize that in Lemma 1 we assume that the solution of equation (L) is bounded and bounded away from zero on the whole of $\mathbb{R}$.

LEMMA 2 (Coleman [4]). *Suppose that in* (L) *the functions $a(t)$, $b(t)$ are continuous and bounded above and below by positive constants. If $u(t), v(t)$ are positive solutions of* (L) *then $u(t) - v(t) \to 0$ as $t \to \infty$.*

Thus $u(t), v(t) \to u^*$. At the same time Francisco Montes de Oca and Mary Lou Zeeman dealt with extinction. They considered a competing system (LV), where $a_i, b_{ij} \colon \mathbb{R} \to (0, \infty)$ are continuous functions bounded by positive reals. In [7] they gave algebraic criteria on the parameters which guarantee that all but one of the species are driven to extinction; namely, for each $k > 1$ there exists $i_k < k$ such that for any $j \le k$,

$$a_{kM} b_{i_k jM} < b_{i_k L} a_{kjL}. \tag{E}$$

They proved that under condition (E) the species $u_2, \ldots, u_N$ are driven to extinction whilst u_1 stabilizes at the unique bounded solution u_1^* of the logistic equation on the u_1 axis. Moreover, they showed convergence of trajectories to u_1^*. Further, they gave a geometric interpretation of (E). In [3], Ahmad and Montes de Oca studied the T-periodic system (LV), i.e., the coefficients of (LV) are continuous and periodic with a common period T. They obtained the same result as in [7] under the assumption that for each $k > 1$, there exists $i_k < k$ such that for any $j \le k$,

$$\bar{a}_k b_{i_k j}(t) - \bar{a}_{i_k} b_{kj}(t) < 0,$$

where

$$\bar{a}_i = \frac{1}{T} \int_0^T a_i(\tau)\, d\tau > 0, \quad i = 1, \ldots, N.$$

In this paper we extend some of the above results to the case of N-species nonautonomous competitive Kolmogorov systems. We consider a system

$$u_i' = u_i f_i(t, u) \tag{1.1}$$

on the nonnegative cone

$$C = \{u = (u_1, \ldots, u_N) : u_i \ge 0,\ 1 \le i \le N\},$$

where

(1) $f = (f_1, \ldots, f_N) : [0, \infty) \times C \to \mathbb{R}^N$ is continuous together with its first derivatives $\partial f_i / \partial u_j$,
(2) for each compact set $\tilde{C} \subset C$, $\frac{\partial f_i}{\partial u_j}(t, u)$ are bounded and uniformly continuous on $[0, \infty) \times \tilde{C}$,
(3) there exist $a_i^{(1)}, a_i^{(2)} > 0$ such that $a_i^{(1)} \le f_i(t, 0, \ldots, 0) \le a_i^{(2)}$ for all $t \ge 0$ and $1 \le i \le N$,
(4) $\frac{\partial f_i}{\partial u_j}(t, u) \le 0$ for all $t \ge 0$, $u \in C$, and $i, j = 1, \ldots, N$,
(5) there exist $b_{ii}^{(1)} > 0$ such that $\frac{\partial f_i}{\partial u_i}(t, u) \le -b_{ii}^{(1)}$ for all $t \ge 0$, $u \in C$, and $i = 1, \ldots, N$.

We give a condition (Theorem 1) which implies that all but one of the species are driven to extinction. Moreover, if $U_1^*(t)$ is the solution of the equation

$$U_1'(t) = U_1'(t) f_1(t, u_1(t), \ldots, u_N(t))$$

and $u(t) = (u_1(t), \ldots, u_N(t))$ is the positive solution of (1.1) then $u_1(t) - U_1^*(t) \to 0$ as $t \to \infty$ (Theorem 2).

2. Preliminaries. We start by proving the following

LEMMA 3. *If $u : [t_0, \tau_{\max}) \to C$, $t_0 \ge 0$, is a maximally defined solution of* (1.1) *such that $u_i(0) > 0$ for $i = 1, \dots, N$, then $u_i(t) > 0$ for $i = 1, \dots, N$ and $t \in [t_0, \tau_{\max})$,*

Proof. By (1.1),

$$u_i(t) = u_i(0) \exp\Big(\int_{t_0}^{t} f_i(s, u_1(s), \dots, u_N(s))\, ds\Big) > 0, \qquad t \in [t_0, \tau_{\max}). \ \blacksquare$$

LEMMA 4. *If $u : [t_0, \tau_{\max}) \to C$, $t_0 \ge 0$, is a maximally defined solution of* (1.1) *such that $u_i(0) > 0$ for $i = 1, \dots, N$, then*

(i) $\tau_{\max} = \infty$,
(ii) $\limsup_{t\to\infty} u_i(t) \le a_i^{(2)}/b_{ii}^{(1)}$ *for* $i = 1, \dots, N$.

Proof. (i) Note that by assumption (4),

$$u_i(t) \le u_i(t_0) \exp\Big(\int_{t_0}^{\tau_{\max}} f_i(s, 0, \dots, 0)\, ds\Big).$$

Hence we see that $\tau_{\max} = \infty$.

(ii) By assumptions (3), (4) and (5),

$$u_i' \le u_i(a_i^{(2)} - b_{ii}^{(1)} u_i(t)).$$

Let $x_i(t)$ be the solution of the logistic equation

$$x_i' = x_i(a_i^{(2)} - b_{ii}^{(1)} x_i(t)) \tag{1.2}$$

satisfying the initial condition $x_i(t_0) = u_i(t_0)$. Then by the comparison principle,

$$u_i(t) \le x_i(t) \quad \text{for } t \ge t_0,\ i = 1, \dots, N. \tag{1.3}$$

For any positive solution $x_i(t)$ of (1.2) we have $\lim_{t\to\infty} x_i(t) = a_i^{(2)}/b_{ii}^{(1)}$ for $i = 1, \dots, N$. This yields the desired result. ■

Define

$$B := [0, a_1^{(2)}/b_{11}^{(1)}] \times \dots \times [0, a_N^{(2)}/b_{NN}^{(1)}],$$

$$b_{ij}^{(2)} := -\inf\Big\{\frac{\partial f_i}{\partial u_j}(t, x) : t \ge 0,\ x \in B\Big\}. \tag{1.4}$$

Assumptions (2) and (4) guarantee that $0 \le b_{ij}^{(2)} < \infty$. Further, define

$$a^{(1)} := \min\{a_i^{(1)} : i = 1, \dots, N\}, \qquad b^{(2)} := \max\{b_{ij}^{(2)} : i, j = 1, \dots, N\}.$$

Lemma 5. *There exists $\delta > 0$ such that if $u(t) = (u_1(t), \ldots, u_N(t))$ is a positive solution of* (1.1) *then*

$$\liminf_{t\to\infty} \sum_{i=1}^{N} u_i(t) \ge \delta.$$

Proof. Let

$$V(t) := \sum_{i=1}^{N} u_i(t).$$

Then

$$\begin{aligned} V'(t) = \sum_{i=1}^{N} u_i'(t) &= \sum_{i=1}^{N} u_i(t) f_i(t, u_1(t), \ldots, u_N(t)) \\ &\ge V(t) \min\{f_i(t, u_1(t), \ldots, u_N(t)) : 1 \le i \le N\}. \end{aligned}$$

We take $0 \le \delta < a^{(1)}/b^{(2)}$ such that the set

$$P_\delta = \Big\{u \in C : \sum_{i=1}^{N} u_i \le \delta\Big\}$$

is contained in B. We claim that $V'(t) > 0$ if $u(t) = (u_1(t), \ldots, u_N(t)) \in P_\delta$. Indeed, if $u(t) \in P_\delta$ then

$$V'(t) \ge V(t)\Big[a^{(1)} - \sum_{j=1}^{N} b^{(2)} u_j(t)\Big] = V(t)[a^{(1)} - b^{(2)} V(t)] > 0.$$

We have thus proved that $V'(t) > 0$ as long as $(0 <)\ V(t) \le \delta$. Consequently, $\liminf_{t\to\infty} V(t) \ge \delta$. By the definition of V we have $\liminf_{t\to\infty} \sum_{i=1}^{N} u_i(t) \ge \delta$. ■

Define

$$\begin{aligned} B(\eta) &:= [0, a_1^{(2)}/b_{11}^{(1)} + \eta] \times \cdots \times [0, a_N^{(2)}/b_{NN}^{(1)} + \eta], \qquad \eta \ge 0, \\ \beta_{ij}(\eta) &:= -\inf\Big\{\frac{\partial f_i}{\partial u_j}(t, x) : t \ge 0,\ x \in B(\eta)\Big\}, \qquad 1 \le i, j \le N. \end{aligned}$$

By assumptions (2), (4) and (5), $0 \le \beta_{ij}(\eta) < \infty$.

Lemma 6.

$$\lim_{\eta\to 0^+} \beta_{ij}(\eta) = b_{ij}^{(2)}.$$

In the proof of Lemma 6, u, v are elements of C, and $\|\cdot\|$ denotes the Euclidean norm in $\mathbb{R}^N$.

Proof of Lemma 6. Notice that $\eta \mapsto \beta_{ij}(\eta)$ is nondecreasing. Hence the limit $\lim_{\eta\to 0^+} \beta_{ij}(\eta)$ exists, and $\lim_{\eta\to 0^+} \beta_{ij}(\eta) \ge b_{ij}^{(2)}$. Take $\varepsilon > 0$. It suffices to prove that there exists $\vartheta > 0$ such that for all $t \ge 0$ and $u \in B(\vartheta)$,

$$-\frac{\partial f_i}{\partial u_j}(t,u) - b_{ij}^{(2)} \le \varepsilon. \tag{1.5}$$

By assumption (2), there exists $\eta > 0$ such that if $\|u - v\| < \eta$ then

$$\left|\frac{\partial f_i}{\partial u_j}(t,u) - \frac{\partial f_i}{\partial u_j}(t,v)\right| < \varepsilon, \qquad u, v \in B(\eta),\ t \ge 0.$$

For each $u \in B(\eta/2)$ there is $v \in B$ such that $\|u - v\| \le \eta/2 < \eta$. Hence

$$\frac{\partial f_i}{\partial u_j}(t,u) - \frac{\partial f_i}{\partial u_j}(t,v) \ge -\varepsilon, \quad t \ge 0,\ u \in B(\eta/2). \tag{1.6}$$

Therefore

$$-\frac{\partial f_i}{\partial u_j}(t,u) + \frac{\partial f_i}{\partial u_j}(t,v) \le \varepsilon, \quad t \ge 0.$$

By (1.4), for all $t \ge 0$, $x \in B$,

$$\frac{\partial f_i}{\partial u_j}(t,x) \ge -b_{ij}^{(2)}.$$

Hence, by (1.6),

$$-\frac{\partial f_i}{\partial u_j}(t,u) \le -\frac{\partial f_i}{\partial u_j}(t,v) + \varepsilon \le b_{ij}^{(2)} + \varepsilon, \qquad t \ge 0,\ u \in B(\eta/2),$$

which proves (1.5). ∎

We now define the lower and upper averages of a function g which is continuous and bounded above and below on $[0,\infty)$. If $0 < s < t$ we set

$$A[g,t,s] := \frac{1}{t-s}\int_s^t g(\tau)\,d\tau.$$

The lower and upper averages of g are defined by

$$m[g] := \liminf_{t-s\to\infty} A[g,t,s], \qquad M[g] := \limsup_{t-s\to\infty} A[g,t,s].$$

Notice that by assumption (3),

$$a_i^{(1)} \le \frac{1}{t-s}\int_s^t f_i(\tau,0,\ldots,0)\,d\tau \le a_i^{(2)} \quad \text{ for } 1 \le i \le N,\ 0 < s < t.$$

Hence

$$a_i^{(1)} \le m[f_i(\cdot,0,\ldots,0)] \le M[f_i(\cdot,0,\ldots,0)] \le a_i^{(2)}.$$

In [8] we introduced average conditions for Kolmogorov systems

$$m[f_i(\cdot,0,\ldots,0)] > \sum_{\substack{j=1\\ j\ne i}}^{N} \frac{b_{ij}^{(2)} M[f_j(\cdot,0,\ldots,0)]}{b_{jj}^{(1)}} \quad \text{ for } i = 1,\ldots,N,$$

which guarantee that system (1.1) is permanent and globally attractive.

Define

$$(1.7)\qquad b_{ij}^{(1)} := -\sup\left\{\frac{\partial f_i}{\partial u_j}(t,x) : t \ge 0,\, x \in B\right\}.$$

3. Main theorem

THEOREM 1. *Assume that for every $k > 1$ there exists $i_k < k$ such that for all $j \le k$,*

$$(\mathrm{E}')\qquad \frac{M[f_k(\cdot,0,\ldots,0)]}{m[f_{i_k}(\cdot,0,\ldots,0)]} < \frac{b_{kj}^{(1)}}{b_{i_k j}^{(2)}}.$$

If $u = (u_1(t),\ldots,u_N(t))$ is a positive solution of (1.1) *then $u_i(t) \to 0$ as $t \to \infty$ for all $i = 2,\ldots,N$.*

The idea of the proof comes from [7].

Proof. Let $u(t) = (u_1(t),\ldots,u_N(t))$ be a positive solution of system (1.1). We argue by induction. First we show that $u_N(t) \to 0$ as $t \to \infty$. Let $i = i_N$ be given by inequality (E′). By assumptions (3)–(5) and the mean value theorem,

$$(1.8)\qquad u_N'(t) \le u_N(t)\Big(f_N(t,0,\ldots,0) - \sum_{j=1}^{N} b_{Nj}^{(1)} u_j(t)\Big).$$

Fix $\eta > 0$ such that

$$(1.9)\qquad \frac{M[f_N(t,0,\ldots,0)]}{m[f_i(t,0,\ldots,0)]} < \frac{b_{Nj}^{(1)}}{\beta_{ij}(\eta)}.$$

By Lemma 4(ii) there is $t_1 > 0$ such that $u(t) \in B(\eta)$ for $t > t_1$. Hence and by the mean value theorem,

$$(1.10)\qquad u_i'(t) \ge u_i(t)\Big(f_i(t,0,\ldots,0) - \sum_{j=1}^{N} \beta_{ij}(\eta) u_j(t)\Big) \quad \text{for } t > t_1.$$

By (1.9), we can choose $\alpha, \gamma > 0$ such that for $j \le N$,

$$(1.11)\qquad \frac{M[f_N(\cdot,0,\ldots,0)]}{m[f_i(\cdot,0,\ldots,0)]} < \frac{\alpha}{\gamma} < \frac{b_{Nj}^{(1)}}{\beta_{ij}(\eta)}.$$

Let

$$V_N := u_i^{-\alpha} u_N^{\gamma}.$$

Then

$$(1.12)\qquad \frac{dV_N}{dt} = V_N\left(-\alpha\frac{u_i'(t)}{u_i(t)} + \gamma\,\frac{u_N'(t)}{u_N(t)}\right).$$

Therefore by (1.8) and (1.10),

$$\begin{aligned}\frac{dV_N}{dt} &\le V_N\Big(-\alpha\Big(f_i(t,0,\ldots,0)-\sum_{j=1}^N \beta_{ij}(\eta)u_j(t)\Big)\\ &\qquad + \gamma\Big(f_N(t,0,\ldots,0)-\sum_{j=1}^N b_{Nj}^{(1)}u_j(t)\Big)\Big)\\ &= V_N\bigg(\gamma f_N(t,0,\ldots,0)-\alpha f_i(t,0,\ldots,0)\\ &\qquad + \sum_{j=1}^N \gamma\beta_{ij}(\eta)\bigg(\frac{\alpha}{\gamma}-\frac{b_{Nj}^{(1)}}{\beta_{ij}(\eta)}\bigg)u_j(t)\bigg) \quad \text{for } t>t_1.\end{aligned}$$

By (1.11) we can choose $\zeta>0$ such that

$$\frac{\alpha}{\gamma}-\frac{b_{Nj}^{(1)}}{\beta_{ij}(\eta)} < -\zeta \quad \text{for } j\le N.$$

Hence

$$\frac{dV_N}{dt} \le V_N\Big(\gamma f_N(t,0,\ldots,0)-\alpha f_i(t,0,\ldots,0)-\zeta\gamma\hat\beta_i(\eta)\sum_{j=1}^N u_j(t)\Big) \tag{1.13}$$

where $\hat\beta_i(\eta)=\min\{\beta_{ij}(\eta): j=1,\ldots,N\}$. By Lemma 5, there exists $t_2>t_1$ such that

$$\sum_{j=1}^N u_j(t) > \delta/2 \quad \text{for } t>t_2.$$

Hence

$$\frac{dV_N}{dt} \le V_N(\gamma f_N(t,0,\ldots,0)-\alpha f_i(t,0,\ldots,0)-\xi) \quad \text{for } t>t_2,$$

where

$$\xi=\zeta\gamma\beta_{ij}(\eta)\delta/2>0.$$

Hence

$$V_N(t)\le V_N(t_2)\exp\Big\{\int_{t_2}^t(\gamma f_N(\tau,0,\ldots,0)-\alpha f_i(\tau,0,\ldots,0)-\xi)\,d\tau\Big\} \quad \text{for } t>t_2.$$

By the definition of V_N we have

$$\begin{aligned}u_N(t) &< \bigg(u_i^\alpha(t)\,\frac{u_N^\gamma(t_2)}{u_i^\alpha(t_2)}\bigg)^{1/\gamma}\\ &\qquad \times\exp\Big\{\frac{1}{\gamma}\int_{t_2}^t(\gamma f_N(\tau,0,\ldots,0)-\alpha f_i(\tau,0,\ldots,0)-\xi)\,d\tau\Big\}\end{aligned}$$

for $t > t_2$. By Lemma 4(i) there exists $R > 0$ such that $u_j(t) < R$ for $j = 1, \ldots, N$. Therefore

$$u_N(t) < C\exp\left\{\frac{1}{\gamma}\int_{t_2}^{t}(\gamma f_N(\tau,0,\ldots,0) - \alpha f_i(\tau,0,\ldots,0) - \xi)\,d\tau\right\} \tag{1.14}$$

for $t > t_2$, where

$$C = \left(R^{\alpha}\,\frac{u_N^{\gamma}(t_2)}{u_i^{\alpha}(t_2)}\right)^{1/\gamma}.$$

Now we show that

$$\lim_{t\to\infty}\int_{t_2}^{t}(\gamma f_N(\tau,0,\ldots,0) - \alpha f_i(\tau,0,\ldots,0) - \xi)\,d\tau = -\infty.$$

By (1.11),

$$\gamma M[f_N(t,0,\ldots,0)] - \alpha m[f_i(t,0,\ldots,0)] < 0. \tag{1.15}$$

Since

$$\begin{aligned}
&\limsup_{t-t_2\to\infty}\frac{1}{t-t_2}\int_{t_2}^{t}(\gamma f_N(t,0,\ldots,0) - \alpha f_i(t,0,\ldots,0))\,d\tau\\
&\quad\le \gamma\limsup_{t-t_2\to\infty}\frac{1}{t-t_2}\int_{t_2}^{t} f_N(t,0,\ldots,0)\,d\tau - \alpha\liminf_{t-t_2\to\infty}\frac{1}{t-t_2}\int_{t_2}^{t} f_i(t,0,\ldots,0)\,d\tau\\
&\quad= \gamma M[f(t,0,\ldots,0)] - \alpha m[f(t,0,\ldots,0)] < 0 \quad \text{for } t > t_2,
\end{aligned}$$

it follows that

$$\limsup_{t-t_2\to\infty}\int_{t_2}^{t}(\gamma f_N(\tau,0,\ldots,0) - \alpha f_i(\tau,0,\ldots,0))\,d\tau = -\infty \quad \text{for } t > t_2.$$

Therefore

$$\lim_{t\to\infty}\int_{t_2}^{t}(\gamma f_N(\tau,0,\ldots,0) - \alpha f_i(\tau,0,\ldots,0) - \xi)\,d\tau = -\infty \tag{1.16}$$

for $t > t_2$. Hence and by (1.14) it follows that $u_N(t) \to 0$ as $t \to \infty$.

Now we prove that for $1 < p < N$, $u_p(t) \to 0$ as $t \to \infty$ under the assumption that for $p < j < N$, $u_j(t) \to 0$ as $t \to \infty$. Let $i = i_p$ be given by inequality (E′). Fix $\eta > 0$ such that

$$\frac{M[f_p(\cdot,0,\ldots,0)]}{m[f_i(\cdot,0,\ldots,0)]} < \frac{b_{pj}^{(1)}}{\beta_{ij}(\eta)}. \tag{1.17}$$

From assumption (4), (5) and by the mean value theorem,

$$u_p'(t) \le u_p(t)\Big(f_p(t,0,\ldots,0) - \sum_{j=1}^{N} b_{pj}^{(1)} u_j(t)\Big). \tag{1.18}$$

Lemma 4(ii) implies the existence of $t_1 > 0$ such that $u(t) \in B(\eta)$ for $t > t_1$. Hence

$$u_i'(t) \ge u_i(t)\Big(f_i(t,0,\ldots,0) - \sum_{j=1}^{N} \beta_{ij}(\eta) u_j(t)\Big) \quad \text{for } t > t_1. \tag{1.19}$$

By (1.17), we can choose $\lambda, \kappa > 0$ such that for $j \le p$,

$$\frac{M[f_p(\cdot,0,\ldots,0)]}{m[f_i(\cdot,0,\ldots,0)]} < \frac{\lambda}{\kappa} < \frac{b_{pj}^{(1)}}{\beta_{ij}(\eta)}. \tag{1.20}$$

Note that by (1.20) there exists $\varsigma > 0$ such that

$$\frac{\lambda}{\kappa} - \frac{b_{pj}^{(1)}}{\beta_{ij}(\eta)} < -\varsigma < 0 \quad \text{for } j \le p.$$

Let

$$V_p := u_i^{-\lambda} u_p^{\kappa}.$$

Similarly to (1.12)–(1.13) we get

$$\begin{aligned}\frac{dV_p}{dt} \le V_p\Big(&\kappa f_p(t,0,\ldots,0) - \lambda f_i(t,0,\ldots,0)\\ &- \rho\sum_{j=1}^{p} u_j(t) + \sum_{j=p+1}^{N} (\lambda\beta_{ij}(\eta) - \kappa b_{pj}^{(1)}) u_j(t)\Big),\end{aligned}$$

where $\rho = \kappa \min\{\beta_{ij}(\eta) : j = 1,\ldots,N\}\varsigma > 0$. Note that by Lemma 5 there exists $t_2 > 0$ such that

$$\sum_{i=1}^{p} u_i(t) + \sum_{i=p+1}^{N} u_i(t) > \delta/2 \quad \text{for } t > t_2.$$

Hence

$$\begin{aligned}\frac{dV_p}{dt} \le V_p\Big(&\kappa f_p(t,0,\ldots,0) - \lambda f_i(t,0,\ldots,0) - \rho\delta/2\\ &+ \sum_{j=p+1}^{N} (\lambda\beta_{ij}(\eta) - \kappa b_{pj}^{(1)}) u_j(t)\Big).\end{aligned}$$

Choose $\mu > 0$ such that $\mu < \rho\delta/2$. Since $\sum_{i=p+1}^{N} u_i(t) \to 0$ as $t \to \infty$, there exists $t_3 > t_2$ such that

$$\sum_{i=1}^{p} u_i(t) > \delta/3 \quad \text{for } t > t_3.$$

Hence

$$\sum_{j=p+1}^{N} (\lambda\beta_{ij}(\eta) - \kappa b_{pj}^{(1)}) u_j(t) < \mu < \rho\delta/2 \quad \text{for } t > t_3. \tag{1.21}$$

Therefore

$$\frac{dV_p}{dt} \le V_p(\kappa f_p(t,0,\ldots,0) - \lambda f_i(t,0,\ldots,0) + \sigma),$$

where $\sigma = \mu - \rho\delta/2 < 0$ for $t > t_3$. Hence

$$V_p(t) \le V_p(t_3) \exp\Big\{\int_{t_3}^{t} (\kappa f_p(t,0,\ldots,0) - \lambda f_i(t,0,\ldots,0) + \sigma)\, d\tau\Big\}.$$

By the definition of V_p we have

$$u_p(t) < \left(u_p^\lambda(t)\, \frac{u_p^\kappa(t_3)}{u_i^\lambda(t_3)}\right)^{1/\kappa} \exp\left\{\frac{1}{\kappa}\int_{t_3}^{t} (\kappa f_p(\tau,0,\ldots,0) - \lambda f_i(\tau,0,\ldots,0) - \sigma)\, d\tau\right\}$$

for $t > t_3$. By Lemma 4(i) there exists $R > 0$ such that $u_j(t) < R$. Hence

$$u_p(t) < D \exp\left\{\frac{1}{\kappa}\int_{t_3}^{t} (\kappa f_p(\tau,0,\ldots,0) - \lambda f_i(\tau,0,\ldots,0) - \sigma)\, d\tau\right\} \tag{1.22}$$

for $t > t_3$, where

$$D = \left(R^\lambda\, \frac{u_p^\kappa(t_3)}{u_i^\lambda(t_3)}\right)^{1/\kappa}$$

Similarly to (1.13)–(1.15) we show that

$$\lim_{t\to\infty} \int_{t_3}^{t} (\kappa f_p(\tau,0,\ldots,0) - \lambda f_i(\tau,0,\ldots,0) - \sigma)\, d\tau = -\infty.$$

By (1.22) it now follows that $u_p(t) \to 0$ as $t \to \infty$. ∎

Lemma 7. *Any positive solution of the equation*

$$U_1'(t) = U_1(t) f_1(t, U_1(t), 0, \ldots, 0) \tag{1.23}$$

is defined on $[0,\infty)$, *bounded above and below by positive constants, and globally attractive.*

Proof. By assumption (5) we have

$$U_1'(t) \le U_1(t)(f_1(t,0,\ldots,0) - b_{11}^{(1)} U_1(t)).$$

From assumptions (3) and (5) it follows that

$$\begin{aligned} U_1(t)(a_1^{(1)} - b_{11}^{(1)} U_1(t)) &\le U_1(t)(f_1(t,0,\ldots,0) - b_1^{(1)} U_1(t)) \\ &\le U_1(t)(a_1^{(2)} - b_{11}^{(1)} U_1(t)). \end{aligned}$$

Let c_1 and d_1 be positive numbers such that $0 \le c_1 < a_1^{(1)}/b_{11}^{(1)}$ and $d_1 > a_1^{(2)}/b_{11}^{(1)}$. The theory of differential inequalities shows that there exists $T > 0$ such that

$$c_1 \le U_1(t) \le d_1 \quad \text{for } t \ge T.$$

Now we prove attractivity of (1.23).

Suppose that $\tilde{U}_1(t)$,$\tilde{V}_1(t)$ are any two positive solutions of (1.23). Then

$$\tilde{U}_1'(t) = \tilde{U}_1(t) f_1(t, \tilde{U}_1, 0, \ldots, 0), \tag{1.24}$$

$$\tilde{V}_1'(t) = \tilde{V}_1(t) f_1(t, \tilde{V}_1, 0, \ldots, 0). \tag{1.25}$$

For simplicity, assume $\tilde{U}_1(0) > \tilde{V}_1(0)$. Consequently, $\tilde{U}_1(t) > \tilde{V}_1(t)$ for all $t \ge 0$. Let

$$\Theta(t) = \ln \frac{\tilde{U}_1(t)}{\tilde{V}_1(t)}.$$

Then

$$\Theta'(t) = \frac{\tilde{U}_1'(t)}{\tilde{U}_1(t)} - \frac{\tilde{V}_1'(t)}{\tilde{V}_1(t)}.$$

By (1.24) and (1.25),

$$\Theta'(t) = \frac{\tilde{U}_1'(t)}{\tilde{U}_1(t)} - \frac{\tilde{V}_1'(t)}{\tilde{V}_1(t)} = f_1(t, \tilde{U}_1(t), 0, \ldots, 0) - f_1(t, \tilde{V}_1(t), 0, \ldots, 0),$$

and assumptions (4) and (5) yield

$$\Theta'(t) \le -b_{11}^{(1)}(\tilde{U}_1(t) - \tilde{V}_1(t)).$$

Since $\underline{\nu} \le \tilde{U}_1(t) \le \overline{\nu}$ and $\underline{\nu} \le \tilde{V}_1(t) \le \overline{\nu}$, using the mean value theorem we find that for $t > 0$,

$$\frac{1}{\overline{\nu}}(\tilde{U}_1(t) - \tilde{V}_1(t)) \le \ln\left(\frac{\tilde{U}_1(t)}{\tilde{V}_1(t)}\right) \le \frac{1}{\underline{\nu}}(\tilde{U}_1(t) - \tilde{V}_1(t)).$$

Therefore

$$\tilde{U}_1(t) - \tilde{V}_1(t) \ge \underline{\nu} \ln\left(\frac{\tilde{U}_1(t)}{\tilde{V}_1(t)}\right).$$

Hence

$$\Theta'(t) \le -b_{11}^{(1)}(\eta)\, \underline{\nu}\, \Theta(t).$$

So

$$0 \le \Theta(t) \le e^{-b_{11}^{(1)} \underline{\nu} t} \Theta(0) \quad \text{for } t > 0. \tag{1.26}$$

By (1.26), $\Theta(t) \to 0$ as $t \to \infty$. By the definition of Θ it follows that (1.23) is globally attractive. ∎

Fix a positive solution $U_1^*(t)$ of the equation

$$U_1'(t) = U_1(t)(f_1(t, U_1(t), 0, \ldots, 0)).$$

THEOREM 2. *If* $u(t) = (u_1(t), \ldots, u_N(t))$ *is a positive solution of* (1.1) *then* $u_1(t) - U_1^*(t) \to 0$ *as* $t \to \infty$.

Proof. Let $u(t) = (u_1(t), \ldots, u_N(t))$ be a positive solution of system (1.1). Let $U_1(t)$ be the solution of the equation

$$U_1'(t) = U_1(t)(f_1(t, U_1(t), 0, \ldots, 0)) \tag{2.1}$$

satisfying the initial condition $U_1(0) = u_1(0)$. Then by the comparison principle

$$u_1(t) \le U_1(t) \quad \text{for } t \ge 0,\ i = 1, \ldots, N.$$

By assumption (5) and by the mean value theorem,

$$u_1'(t) \le u_1(t)\Big(f_1(t, u_1(t), 0, \ldots, 0) - \sum_{j=2}^{N} b_{1j}^{(1)} u_j(t)\Big). \tag{2.2}$$

Let

$$V := \ln\left(\frac{u_1(t)}{U_1(t)}\right).$$

Hence

$$\frac{d}{dt}\left(\ln \frac{u_1(t)}{U_1(t)}\right) = \frac{u_1'(t)}{u_1(t)} - \frac{U_1'(t)}{U_1(t)}.$$

Therefore by (2.1),

$$\frac{U_1'(t)}{U_1(t)} = f_1(t, U_1(t), 0, \ldots, 0).$$

By (2.2),

$$\frac{u_1'(t)}{u_1(t)} \le f_1(t, u_1(t), 0, \ldots, 0) - \sum_{j=2}^{N} b_{1j}^{(1)} u_j(t).$$

Hence

$$\frac{dV}{dt} \le f_1(t, u_1(t), 0, \ldots, 0) - f_1(t, U_1(t), 0, \ldots, 0) - \sum_{j=2}^{N} b_{1j}^{(1)} u_j(t). \tag{2.3}$$

By the Lagrange theorem and assumption (4),

$$f_1(t, U_1(t), 0, \ldots, 0) - f_1(t, u_1(t), 0, \ldots, 0) \ge -\beta_{11}(\eta)(U_1(t) - u_1(t)) \tag{2.4}$$

for $t > t_1$. Therefore

$$\frac{dV}{dt} \le \beta_{11}(\eta)(U_1(t) - u_1(t)) - \sum_{j=2}^{N} b_{1j}^{(1)} u_j(t).$$

Since $\sum_{i=1}^{N} u_i(t) \ge \delta/2$ for $t > t_2$ and $\sum_{i=2}^{N} u_i(t) \to 0$ exponentially as $t \to \infty$ it follows that

$$u_1(t) > \delta/2 \quad \text{for } t > t_2.$$

Hence and by Lemma 4(ii),

$$\delta/2 \le u_1(t) \le R \quad \text{for } t > t_2.$$

Using the mean value theorem we see that for $t > 0$,

$$\frac{1}{R}\,(u_1(t) - U_1(t)) \le \ln\biggl(\frac{u_1(t)}{U_1(t)}\biggr) \le \frac{2}{\delta}\,(u_1(t) - U_1(t)).$$

Therefore

$$U_1(t) - u_1(t) \le -R\ln(u_1(t) - U_1(t)).$$

Hence

$$\begin{aligned}\frac{dV}{dt} &\le -\beta_{11}(\eta)R\ln(u_1(t) - U_1(t)) - \sum_{j=2}^{N} b_{1j}^{(1)} u_j(t),\\ &\le -\beta_{11}(\eta)RV(t) - \sum_{j=2}^{N} b_{1j}^{(1)} u_j(t) \le -\phi V(t) + g(t)\end{aligned}$$

where

$$g(t) = -\sum_{j=2}^{N} b_{1j}^{(1)} u_j(t) \quad \text{and} \quad \phi = \beta_{11}(\eta)R.$$

Hence

$$V(t) \le e^{-\phi(t-t_2)}\Bigl(\int_t^{t_2} g(\tau)e^{\phi(\tau-t_2)}\,d\tau + V(t_2)\Bigr).$$

Since $g(t) \to 0$ as $t \to \infty$ it is easy to prove that $V(t) \to 0$ as $t \to \infty$. Hence and by the definition of V it follows that $u_1(t) - U_1(t) \to 0$. Since (1.23) is globally attractive, we conclude that $u_1(t) - U_1^*(t) \to 0$. ∎

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