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THE GLOBAL STABILITY OF A SYSTEM MODELING A COMMUNITY WITH LIMITED COMPETITION

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Abstract. In this paper the global behavior of solutions of a class of ordinary differential equations modelling a biological community of species is determined. The community consists of two competing subcommunities each of which has the property that each pair of species of the subcommunity interact in a mutually beneficial manner. Sufficient conditions are presented that the two subcommunities can coexist in a globally asymptotically stable steady state.

1. Introduction

Consider the system of n differential equations

$$(S) \qquad \dot{x}_i = x_i f_i(x_1, x_2, \cdots, x_n), \quad 1 \leq i \leq n,$$

which models an n-species ecosystem for which x_i represents the population density of ith species and $f_i(x_1, x_2, \cdots, x_n)$ represents the per capita growth rate of the ith species. We write $x = (x_1, x_2, \cdots, x_n), f = (f_1, f_2, \cdots, f_n)$ and $F(x) = (x_1 f_1(x), x_2 f_2(x), \cdots, x_n f_n(x))$ where it is assumed that f is a continuously differentiable function defined on some open set containing the nonnegative orthant $\mathbb{R}^n_+$. Assume that the species community can be devided into two groups $I = \{1, 2, \cdots, k\},\ J = \{k+1, \cdots, n\}, 0 \leq k \leq n$, in such a way that the species in group I form a mutualistic or cooperative subcommunity, the species in group J form a cooperative subcommunity and that species i and species j compete if $i \in I$ and $j \in J$. Hereafter the letters i and j will always represent elements of I and J respectively, and u, u^0 and u^1 etc. always represent vectors in k-dimensional Euclidean space $\mathbb{R}^k$ and v, v^0 and v^1 etc. always represent vectors in $(n-k)$-dimensional Euclidean space $\mathbb{R}^{n-k}$. Mathematically, we write

$$\mathbb{R}^n = \mathbb{R}^k \times \mathbb{R}^{n-k},$$

$$x = (u, v) \quad \text{ where } u = (x_1, \cdots, x_k) \text{ and } v = (x_{k+1}, \cdots, x_n),$$

$$f(x) = (f^1(u, v), f^2(u, v))$$

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where $f^1 = (f_1(x), \cdots, f_k(x))$ and $f^2 = (f_{k+1}(x), \cdots, f_n(x))$,

$$Df(x) = {}^k\begin{bmatrix} \frac{\partial f^1}{\partial u} & \frac{\partial f^1}{\partial v} \\ \frac{\partial f^2}{\partial u} & \frac{\partial f^2}{\partial v} \end{bmatrix}_{n-k} \tag{1.1}$$

where $\partial f^1/\partial u$ and $\partial f^2/\partial v$ have nonnegative off-diagonal elements and $\partial f^1/\partial v \le 0$, $\partial f^2/\partial u \le 0$. If L is a nonempty subset of $\{1, 2, \cdots, n\}$, then the set $H_L^+ = \{x \in \mathbb{R}_+^n : x_p = 0 \text{ for } p \notin L\}$ is an invariant set for (S) and moreover the dynamics on H_L^+

$$\dot{x}_l = x_l f_l(x), l \in L, x \in H_L^+, \tag{S_L}$$

inherits all the properties of (S) except (S_I) and (S_J). Smith [1] extended the ideas for cooperative systems developed by Hirsch [3, 4] to the system (S) having limited competition and presented sufficient conditions for the persistence of all species. The essential conditions given by Smith [1] are that (S_I) possesses a positive steady state u^0 which is unstable to $\mathbb{R}_+^{n-k}$ (that is, $f^2(u^0, 0) > 0$) and (S_J) possesses a positive steady state v^0 which is unstable to $\mathbb{R}_+^k$ (that is, $f^1(0, v^0) > 0$). The persistence asserted in the main results of [1, Theorems 3.6 and 3.8] is an attractor block lying in the interior of the positive orthant with steady states at two corners each of which attracts an unbounded open set of positive initial conditions. Meanwhile, he pointed out that " an interesting open problem is to give sufficient conditions for uniqueness of a positive steady state in the context of Theorems 3.6 or 3.8" (see [1, p. 869]). For the Lotka-Volterra systems in which $Df(x) \equiv \text{const}$ has the structure of (1.1), he sharpened the above-mentioned result and showed that there is a unique positive asymptotically stable steady state (see [1, Theorem 4.1]).

The main purpose of this paper is to give sufficient conditions to guarantee that (S) has a unique positive asymptotically stable steady state. Together with the assumptions of Theorem 3.6 of Smith [1] with the additional concave assumption: $Df(x) \leqq_K Df(y)$ whenever $x, y \in \mathbb{R}_+^n$ with $y \leqq_K x$, we shall prove that there is a unique positive steady state which attracts all positive initial conditions. This result is a generalization of Theorem 4.1 of [1] to the case that f is nonlinear.

2. Notation and preliminaries

In this section we agree on certain notation and state some results which will prove to be useful.

Let $\mathbb{R}_+^n = \{x \in \mathbb{R}^n : x_i \ge 0, 1 \le i \le n\}$ denote the nonnegative orthant and $\dot{\mathbb{R}}_+^n = \{x \in \mathbb{R}_+^n : x_i > 0, 1 \le i \le n\}$ denote its interior. In this work, we need two partial orderings which are generated by two cones. Recall that a cone K in $\mathbb{R}^n$ is a closed convex set with the property $K \cap (-K) = \{0\}$. The first cone is $\mathbb{R}_+^n$ and the second cone is $K = \mathbb{R}^k \times (-\mathbb{R}^{n-k}) = \{x \in \mathbb{R}^n, x_i \ge 0, 1 \le i \le k, \text{ and } x_j \le 0 \text{ for } k+1 \le j \le n\}$. We write $x \leqq y (x \leqq_K y)$ if $y - x \in \mathbb{R}_+^n(K)$; $x \lneqq y (x \lneqq_K y)$ if $x \leqq y (x \leqq_K y)$ but $\ne x$; and $x < y (x <_K y)$ if $y - x \in \dot{\mathbb{R}}_+^n(\dot{K})$. Therefore, $x \leqq y (x < y)$ if and only if $x_i \le y_i (x_i < y_i)$ for $i = 1, 2, \cdots, n$ and $x \leqq_K y (x <_K y)$ if and only if $x_i \le y_i (x_i < y_i)$ for $i = 1, 2, \cdots, k$ and $x_j \ge y_j (x_j > y_j)$ for $j = k+1, \cdots, n$. For $x, y \in \mathbb{R}^n$, we set $[x, y]_K = \{z \in \mathbb{R}^n : x \leqq_K z \leqq_K y\}$. We drop the K if the cone is $\mathbb{R}_+^n$. We say a vector $x \in \mathbb{R}^n$ is positive if $x > 0$.

We will reserve the letter n for the dimension of our Euclidean space and set $N = \{1, 2, \cdots, n\}, I = \{1, 2, \cdots, k\}$ and $J = \{k+1, \cdots, n\}$ where $1 \le k \le n$. If L

is a nonempty subset of N, let $H_L = \{x \in \mathbb{R}^n : x_l = 0 \text{ if } l \notin L\}$, $H_L^+ = H_L \cap \mathbb{R}_+^n$ and $\dot{H}_L^+ = \{x \in H_L^+ : x_l > 0, l \in L\}$. The subsystems (S_I) and (S_J) are important for this work which are written in the following if $x = (u, v)$:

$$(S_I) \qquad \dot{u} = \operatorname{diag}(u) f^1(u, 0),$$

$$(S_J) \qquad \dot{v} = \operatorname{diag}(v) f^2(0, v).$$

Let M be an $n \times n$ matrix having the following structure:

$$M = {}^k \begin{bmatrix} A & -B \\ -C & D \end{bmatrix}_{n-k} \tag{2.1}$$

where $A = (a_{lm})_{k \times k}$ satisfies $a_{lm} \geq 0$ if $l \neq m$, similarly for the $(n-k) \times (n-k)$ matrix D and all elements of B and C are nonnegative. Such a matrix M is said to have type K.

The $n \times m$ matrix A is called nonnegative if $a_{ij} \geq 0$ for all i, j. We use the symbol $A \geq 0$ to signify that A is nonnegative. For two $n \times m$ matrices A and B we write $A \geq B$ if $A - B \geq 0$. If M has the structure of (2.1) and satisfies $M(K) \subset K$, then we write $M \geqq_K 0$ which is equivalent to saying that A, B, C and D are nonnegative. If M_1 and M_2 have been written in the form of (2.1), then $M_1 \leqq_K M_2$ means $M_2 - M_1 \geqq_K 0$. It is easy to see that $M_1 \leqq_K M_2$ if and only if $A_1 \leqq A_2, B_1 \leqq B_2, C_1 \leqq C_2$ and $D_1 \leqq D_2$. If A is an $n \times n$ matrix, we write $s(A)$ for the stability modulus of A, i.e., $s(A) = \max \operatorname{Re}\lambda$ where λ runs over the eigenvalues of A. The square matrix A is called cooperative if $a_{ij} \geq 0$ for all $i \neq j$. Let $P : \mathbb{R}^n \to \mathbb{R}^n$ be the diagonal matrix with $p_{ii} = 1, 1 \leq i \leq k$, and $p_{jj} = -1, k+1 \leq j \leq n$, and M be the $n \times n$ matrix having the form of (2.1). Then $P^{-1} = P$ and

$$PMP = \begin{pmatrix} A & B \\ C & D \end{pmatrix} = M^+ \tag{2.2}$$

is an $n \times n$ cooperative matrix. Thus, the following result (see [1, Theorem 2.2]) is an immediate consequence of the Perron-Frobenius theory.

Theorem 2.1. *Let M have type K, $K = \mathbb{R}_+^k \times (-\mathbb{R}_+^{n-k})$. Then $s(M)$ is an eigenvalue of M and there exists a corresponding eigenvector in K. If $N \geqq_K M$, then $s(M) \geq s(M)$.*

The following result was proved by Smith [2].

Theorem 2.2. *Let A be an $n \times n$ cooperative matrix. Consider the equation*

$$Ax + r = 0.$$

If $r > 0$, the equation has a solution with $x > 0$ only if A is a stable matrix (i.e., $s(A) < 0$). If A is a stable matrix, then for every $r \geqq 0$ the equation has a unique solution $x \geqq 0$. If, in addition, $r > 0$, then $x > 0$.

Observing the relation between M and M^+ in (2.2), we immediately obtain the following.

Theorem 2.3. *Let M have type $K, K = \mathbb{R}_+^k \times (-\mathbb{R}_+^{n-k})$. Consider the equation*

$$Mx + r = 0.$$

If $r >_K 0$, the equation has a solution with $x >_K 0$ only if M is stable. If M is a stable matrix, then for every $r \geqq_K 0$ the equation has a unique solution $x \geqq_K 0$. If, in addition, $r >_K 0$, then $x >_K 0$.

The system (S) is said to be type K monotone if f is C^1 and $Df(x)$ has the structure of (2.1) for every $x \in \mathbb{R}^n_+$.

Let $\varphi_t(x), \varphi_t^I(u)$ and $\varphi_t^J(v)$ be the flows generated by $(S), (S_I)$ and (S_J) respectively. Then we have

Theorem 2.4. *Let f be continuously differentiable on some open set containing $\mathbb{R}^n_+$. Suppose that the system (S) is a type K monotone system. Then*

(i) $x, y \in \mathbb{R}^n_+, x \leqq_K y$ *implies* $\varphi_t(x) \leqq_K \varphi_t(y)$ *for* $t \geq 0$*;*
(ii) $u^1, u^2 \in \mathbb{R}^k_+, u^1 \leqq u^2$ *implies* $\varphi_t^I(u^1) \leqq \varphi_t^I(u^2)$ *for* $t \geq 0$*; and*
(iii) $v^1, v^2 \in \mathbb{R}^{n-k}_+, v^1 \leqq v^2$ *implies* $\varphi_t^J(v^1) \leqq \varphi_t^J(v^2)$ *for* $t \geq 0$*.*

This theorem is adapted from [1, p. 861–863].

Selgrade [5] gave a creterion for the monotonicity of every component of a solution $\varphi_t(x)$ which is stated in [1, p. 862] for the type K monotone system.

Theorem 2.5. *Let (S) be a type K monotone system and let $f(x) \geqq_K 0$ for some $x \in \mathbb{R}^n_+$. Then $[\phi_t(x)]_p$ is nondecreasing if $p \in I$ and nonincreasing if $p \in J$ for all $t \geq 0$ for which the solution exists. A similar result holds if $f(x) \leqq_K 0$.*

We want to know when the component $[\phi_t(x)]_p$ is eventually strictly increasing for $p \in I$ and when the component $[\phi_t(x)]_p$ is eventually strictly decreasing for $p \in J$ in Theorem 2.5. This plays an important role in the proof of our main result. So we improve the result of Selgrade as follows.

Theorem 2.6. *Let (S) be a type K monotone system and let $f(x) \gneqq_K 0$. Then*

(i) *if $i \in I_0 = \{i \in I : f_i(x) > 0\}$, then $[\phi_t(x)]_i$ is strictly increasing for $t \geq 0$;*
(ii) *if $j \in J_0 = \{j \in J : f_i(x) < 0\}$, then $[\phi_t(x)]_j$ is strictly decreasing for $t \geq 0$;*
(iii) *if $i \in I \backslash I_0$, then either $[\phi_t(x)]_i$ is constant for all $t \geq 0$ or $[\phi_t(x)]_i$ is eventually strictly increasing; and*
(iv) *if $j \in J \backslash J_0$, then either $[\phi_t(x)]_j$ is constant for all $t \geq 0$ or $[\phi_t(x)]_j$ is eventually strictly decreasing.*

Moreover, if every component of $\varphi_t(x)$ is eventually strictly monotone, then there is an open interval (a, b) such that $f(\varphi_t(x)) >_K 0$ for all $t \in (a, b)$.

Proof. Since the transformation $y = Px$ changes (S) into a cooperative system, we only have to suppose that $k = n$, that is, (S) is a cooperative system. The theory of differential inequalities which is nicely presented in [6, p. 27–30] will be applied in the following proof. Actually we shall go along the line of proof of Selgrade [5, p. 83–84].

From the argument of Coppel [6, p. 30], we know that if $y(t)$ is a differentiable vector function satisfying $\dot{y}(t) \leqq F(y(t))$ for $t \in [a, b]$ and if $\varphi_t(x) := x(t)$ is a solution of (S) defined on $[a, b]$ satisfying $y(a) \leqq x(a)$, then $x(b) \leqq y(b)$ and $x_i(b) = y_i(b)$ if and only if $x_i(t) \equiv y_i(t)$ for all $t \in [a, b]$. The following proof is due to Selgrade.

Suppose that $\varphi_t(x) = x(t)$ is defined on $[0, \alpha)$ and $y(t) \equiv x$ for $t \in [0, \alpha)$. Then we have for $t \geq 0$

$$\dot{y}(t) = 0 \leqq F(x) = F(y(t)).$$

Hence the differential inequality theory implies that for all $t \in [0, \alpha)$

$$x = y(t) \leqq x(t),$$

and moreover, if $i \in I_0 = \{i \in N, F_i(x) > 0\}$ then $x_i < x_i(t)$ for all $t \in (0, \alpha)$. Fixing $i \in I_0$ and $t_1, t_2 \in (0, \alpha)$ with $t_2 - t_1 > 0$, we have $x_i < x_i(t_2 - t_1)$. It follows from the theory of differential inequality stated in the last paragragh that $x(t_1) \lneqq x(t_2)$ and $x_i(t_1) < x_i(t_2)$ for all $i \in I_0$. This shows that for $i \in I_0$ the component $x_i(t)$ is strictly increasing.

Suppose that $i \in N \backslash I_0$. Then either $x_i(t) \equiv x_i$ or there exists a $t_0 \in (0, \alpha)$ such that $x_i < x_i(t_0)$.

Assume that the latter case occurs and let $t^* = \inf\{t \in (0, \alpha) : x_i(t) > x_i\}$. Then $x_i(t) \equiv x_i$ for $t \in [0, t^*]$ and $x_i(t) > x_i$ for all $t > t^*$. For $t_1, t_2 > 0$ with $t_1 < t_2$, we have $x(t^*) \lneqq x(t^* + t_2 - t_1)$ and $x_i(t^*) < x_i(t^* + t_2 - t_1)$. The theory of differential inequality implies that $x(t^* + t_1) \lneqq x(t^* + t_2)$ and $x_i(t^* + t_1) < x_i(t^* + t_2)$. This shows that $x_i(t)$ is strictly increasing on $[t^*, \alpha)$.

Finally, we assume that every component of $x(t)$ is eventually strictly increasing. More precisely, we assume that every component of $x(t)$ is strictly increasing on $[t_0, \alpha)$ with $0 < t_0 < \alpha$. Since $x_1(t)$ is strictly increasing on $[t_0, \alpha)$, $\dot{x}_1(t) \not\equiv 0$ on (t_0, α). Thus there exists an open subinterval $(a_1, b_1) \subset (t_0, \alpha)$ such that $\dot{x}_1(t) > 0$ for all $t \in (a_1, b_1)$. Similarly, $x_2(t)$ is strictly increasing on (a_1, b_1), and we can choose an open subinterval $(a_2, b_2) \subset (a_1, b_1)$ such that $\dot{x}_2(t) > 0$ for all $t \in (a_2, b_2)$. Therefore, $\dot{x}_1(t) > 0$, $\dot{x}_2(t) > 0$ for all $t \in (a_2, b_2)$. In such a manner, we can find subintervals (a_i, b_i) for $i = 1, 2, \cdots, n$ such that

$$(a_n, b_n) \subset (a_{n-1}, b_{n-1}) \subset \cdots \subset (a_2, b_2) \subset (a_1, b_1)$$

and $\dot{x}_p(t) > 0$ for all $1 \le p \le i$ and $t \in (a_i, b_i)$. Let $(a_n, b_n) = (a, b)$. Then $\dot{x}_i(t) > 0$ for all $t \in (a, b)$ and $i \in N$. Thus $F(x(t)) > 0$ for all $t \in (a, b)$. □

Before finishing this section, we give several useful definitions. $p \in \mathbb{R}^n_+$ is said to be a steady state of (S) if $F(p) = 0$. Let $u^0 = (x^0_1, \cdots, x^0_k)$ be a positive steady state of (S_I). We say that u^0 is unstable to $\mathbb{R}^{n-k}_+$ if $f^2(u^0, 0) > 0$. One has a similiar statement for $v^0 = (x^0_{k+1}, \cdots, x^0_n)$, a positive steady state of (S_J). Let $\omega(x)$ be the omega limit set of an orbit $\{\phi_t(x) : t \ge 0\}$. If $\overline{x}$ is a steady state of (S), the domain of attraction of $\overline{x}$ is the set of initial conditions x for which $\omega(x) = \{\overline{x}\}$. We say $\overline{x}$ is globally asymptotically stable with respect to a set S if $\overline{x}$ is asymptotically stable and S belongs to the domain of attraction of $\overline{x}$.

3. The main result and its proof

Throughout this section, we always assume that f is continuously differentiable on some open set containing $\mathbb{R}^n_+$ and that (S) is a type K monotone system. The main result we shall prove is the following.

Theorem 3.1. *Let u^0 be a positive steady state of (S_I) which is unstable to $\mathbb{R}^{n-k}_+$ and attracts all initial conditions in $u^0 + \mathbb{R}^k_+$ and v^0 be a positive steady state of (S_J) which is unstable to $\mathbb{R}^k_+$ and attracts all initial conditions in $v^0 + \mathbb{R}^{n-k}_+$. If the following additional conditions are satisfied:*

(1) $s(\frac{\partial f^2}{\partial v}(0, v^0)) < 0$*; and*

(2) $Df(y) \leqq_K Df(x)$ *whenever* $x, y \in [0, (u^0, v^0)]$ *with* $x \leqq_K y$,

then (S) has a unique positive steady state $\overline{x}$ such that it is globally asymptotically stable with respect to $\dot{\mathbb{R}}^n_+$.

Remark 1. Assume that $f = r + Mx$ where $x = (u, v) \in \mathbb{R}^k \times \mathbb{R}^{n-k}, r = (r_1, r_2)$ and M is of type K. Then it is easy to prove that such a $f(x)$ satisfies the concave condition (2). If (S_I) has a positive steady state u^0 which is unstable to $\mathbb{R}_+^{n-k}$ and if (S_J) has a positive steady state v^0 which is unstable to $\mathbb{R}_+^k$, then the structure of M implies that $r_1 > 0$ and $r_2 > 0$. Thus, by Theorem 2.2, $s(A) < 0$ and $s(D) < 0$. Theorem 2.1 of [2] asserted that u^0 is globally asymptotically stable in $\dot{\mathbb{R}}_+^k$ and v^0 is globally asymptotically stable in $\dot{\mathbb{R}}_+^{n-k}$. Therefore, in this case, f satisfies all assumptions of Theorem 3.1. This shows that the Lotka-Volterra system satisfying the basic assumptions of Theorem 3.1 has a unique positive steady state which is globally asymptotically stable with respect to $\dot{\mathbb{R}}_+^n$. This result was just proved by Smith in [1, Theorem 4.1]. So our Theorem 3.1 can be regarded as a generalization of [1, Theorem 4.1] to the case that f is nonlinear.

Remark 2. Under the assumptions of Theorem 3.1 without the additional assumptions (1) and (2), Smith [1] proved that there exist positive steady states x^1 and x^2 of (S) such that $\omega(x) = \{x^1\}$ for all $x > 0$ with $x \leqq_K x^1$, $\omega(x) = \{x^2\}$ for all $x > 0$ with $x \leqq_K x^2$ and $\omega(x) \subset [x^1, x^2]_K$ for all $x > 0$ (see [1, Theorem 3.6]). Therefore, our Theorem 3.1 gives sufficient conditions for uniqueness of a positive steady state in the context of Theorem 3.6. This provides an answer of the interesting open problem proposed by Smith [1, p. 869].

Remark 3. In order to show that our result is a set of conditions which is symmetric, we make the change of variables $(u, v) \to (v, u)$. Thus, the system (S) is transformed into

$$(S') \qquad \begin{aligned} \dot{u} &= diag(u) g^1(u, v) \\ \dot{v} &= diag(v) g^2(u, v) \end{aligned}$$

where $u \in \mathbb{R}_+^{n-k}$, $v \in \mathbb{R}_+^k$, $g^1(u, v) = f^2(v, u)$ and $g^2(u, v) = f^1(v, u)$. Therefore, the solution flow of (S') is monotone in the order generated by the cone $\mathbb{R}_+^{n-k} \times (-\mathbb{R}_+^k) = -K$. Applying Theorem 3.1 to (S'), we conclude that the result of Theorem 3.1 is also true if the conditions (1) and (2) are respectively replaced by

(1′) $s(\frac{\partial f^1}{\partial u}(u^0, 0)) < 0$ and
(2′) $Df(y) \leq_K Df(x)$ whenever $x, y \in [0, (u^0, v^0)]$ with $y \leq_K x$.

Before proceeding to the proof of the main result, we present several propositions.

Proposition 3.2. *Let the assumptions of Theorem 3.1 hold. Then $f(u, v^0) \gneqq_K 0$ for u sufficiently small and $f(u^0, v) \lneqq_K 0$ for v sufficiently small and there exist positive steady states x^1 and x^2 with the following properties:*

(i) $0 < x^1 \leqq (u^0, v^0), 0 < x^2 \leqq (u^0, v^0), x^1 \leqq_K x^2$;
(ii) $\omega(x) = \{x^1\}$ *for all* $x > 0$ *with* $x \leqq_K x^1$ *and* $\omega(x) = \{x^2\}$ *for all* $x > 0$ *with* $x \geqq_K x^2$;
(iii) $\omega(x) \subset [x^1, x^2]_K$ *for all* $x > 0$.

This proposition is taken from the context of Proposition 3.5 and Theorem 3.6 of Smith [1].

Proposition 3.3. *Suppose that all assumptions of Theorem 3.1 hold. Then*

(i) *If every row of the matrix $\frac{\partial f^2}{\partial u}(0, v^0)$ has at least a nonzero element (hence it is negative), then $f(u, v^0) >_K 0$ for $u > 0$ sufficiently small and $(u, v^0) <_K x^1$ for u sufficiently small.*

(ii) *If there exists a j such that every element of the jth row of the matrix $\frac{\partial f^2}{\partial u}(0, v^0)$ is zero, then for every $x \geqq_K (0, v^0)$, every element of the jth row of the matrix $\frac{\partial f^2}{\partial u}(x)$ is zero.*

Proof. Since every row of the matrix $\frac{\partial f^2}{\partial u}(0, v^0)$ is nonzero, for $u > 0$ sufficiently small, the matrix $\frac{\partial f^2}{\partial u}(u, v^0)$ has the same property. Therefore, for $u > 0$ sufficiently small,

$$\begin{aligned} f^2(u, v^0) &= f^2(0, v^0) + [\int_0^1 \frac{\partial f^2}{\partial u}(su, v^0) ds] u \\ &= [\int_0^1 \frac{\partial f^2}{\partial u}(su, v^0) ds] u < 0 \end{aligned} \tag{3.1}$$

where we have used the fact that the matrices $\frac{\partial f^2}{\partial u}(su, v^0)(0 \leq s \leq 1)$ are nonpositive every row of which is nonzero. The assumptions of Theorem 3.1 tell us that v^0 is unstable to $\mathbb{R}^k_+$. Hence, $f^1(0, v^0) > 0$ which implies that $f^1(u, v^0) > 0$ for $u > 0$ sufficiently small. Taking this fact together with (3.1), we can conclude that $f(u, v^0) >_K 0$ for $u > 0$ sufficiently small. Theorem 2.6 implies that $[\varphi_t(u, v^0)]_p$ is strictly increasing if $p \in I$ and strictly decreasing if $p \in J$ for $t \geq 0$. This shows that $(u, v^0) <_K \omega(u, v^0) = x^1$. (i) is proved.

Suppose that the jth row of the matrix $\frac{\partial f^2}{\partial u}(0, v^0)$ is zero. Then the concave condition (2) implies that

$$\frac{\partial f^2}{\partial u}(0, v^0) \leqq \frac{\partial f^2}{\partial u}(x) \leqq 0 \quad \text{for all } x \geqq_K (0, v^0).$$

This implies that the jth row of the matrix $\frac{\partial f^2}{\partial u}(x)$ is zero for all $x \geqq_K (0, v^0)$. □

Remark 4. From (3.1) we know that if the jth row of $\frac{\partial f^2}{\partial u}(0, v^0)$ is nonzero then $f_{k+j}(u, v^0) < 0$ for $u > 0$ sufficiently small.

Proof of Theorem 3.1. It follows from Proposition 3.2 that we have $f^1(u, v^0) > 0$ and $f^2(u, v^0) \leq 0$ for $u > 0$ sufficiently small. By Theorem 2.6, $[\varphi_t(u, v^0)]_p$ is strictly increasing in $t \geq 0$ and $p \in I$ and nonincreasing for $p \in J$. As an immediate consequence of (ii) of Proposition 3.2, we have $\varphi_t(u, v^0)$ tends to the positive steady state x^1 as $t \to \infty$. In the following, we fix such a u.

First, we shall prove that if there exists a $t_0 \geq 0$ such that $f(\varphi_{t_0}(u, v^0)) >_K 0$ then $s(Df(x^1)) < 0$. Hence x^1 is asymptotically stable (see [1, Theorem 2.3]). Under this assumption, we have $\varphi_{t_0}(u, v^0) <_K x^1$ and

$$0 = f(x^1) = f(\varphi_{t_0}(u, v^0)) + [\int_o^1 Df(sx^1 + (1-s)\varphi_{t_0}(u, v^0)) ds](x^1 - \varphi_{t_0}(u, v^0)).$$

If we let M be the matrix in brackets and $r = f(\varphi_{t_0}(u, v^0))$ then $r >_K 0$ and M is of type K and

$$M(x^1 - \varphi_{t_0}(u, v^0)) + r = 0.$$

By Theorem 2.3, $s(M) < 0$. Since $Df(x^1) \leqq_K M$, we have $s(Df(x^1)) \leq s(M) < 0$ by Theorem 2.1, so x^1 is asymptotically stable.

Second, we shall prove that if $s(Df(x^1)) < 0$ then x^1 is a unique positive steady state. Suppose (S) has a positive steady state $\overline{x}$ with $\overline{x} \neq x^1$. By Proposition 3.2, $x^1 \lneqq \overline{x}$. Thus

$$0 = f(\overline{x}) - f(x^1) = [\int_0^1 Df(s\overline{x} + (1-s)x^1)ds](\overline{x} - x^1).$$

Again, letting M denote the matrix in brackets above, then the concave condition (2) deduces that $Df(\overline{x}) \leqq_K M \leqq_K Df(x^1)$ and so by Theorem 2.1, $s(M) \leq s(Df(x^1)) < 0$. Hence M is invertible and we have the contradiction that $\overline{x} \neq x^1$.

By Theorem 2.6, $(u, v^0) <_K x^1$ if and only if there exists a $t_0 \geq 0$ such that $f(\varphi_{t_0}(u, v^0)) >_K 0$. In this case, we have proved the theorem. It follows from (i) of Proposition 3.3 that a sufficient condition for $(u, v^0) <_K x^1$ is that every row of the matrix $\frac{\partial f^2}{\partial u}(0, v^0)$ is nonzero.

Let $x^1 = (u^1, v^1)$. Then $u < u^1$. The remaining case to consider is that $J_0 = \{j \in J : v_j^0 = v_j^1\} \neq \phi$. From Theorem 2.6, we know that $[\varphi_t(u, v^0)]_j$ is eventually strictly decreasing for $j \in J\backslash J_0$ and $[\varphi_t(u, v^0)]_j \equiv v_j^0 = v_j^1$ for $j \in J_0$. By Remark 4, if the jth row of $\frac{\partial f^2}{\partial u}(0, v^0)$ is nonzero then $f_{k+j}(u, v^0) < 0$ for $u > 0$ sufficiently small, which implies $v_{k+j}^1 < v_{k+j}^0$. This shows that for any $j \in J_0$, $\frac{\partial f_j}{\partial u}(0, v^0) = 0$. Without loss of generality, we may assume that $J_0 = \{k+m, \cdots, n\}$ where $1 \leq m \leq n-k$. The above arguments show that $\frac{\partial f_j}{\partial u}(0, v^0) = 0$ for $k+m \leq j \leq n$. Applying (ii) of Proposition 3.3, we have $\frac{\partial f_j}{\partial u}(x) = 0$ for all $x \geqq_K (0, v^0)$ and $k+m \leq j \leq n$. Therefore, for each j with $k+m \leq j \leq n$, $f_j(x)$ is independent of the variable $u = (x_1, \cdots, x_k)$, that is,

$$f_j(x) = f_j(x_{k+1}, \cdots, x_n)$$

for $k+m \leq j \leq n$ and $x \geqq_K (0, v^0)$. Since v^0 is a positive steady state of (S_J) and $x^1 = (u^1, v^1)$ is a positive steady state of (S), we have

$$f_j(v^0) = f_j(v^1) = 0$$

for $k+m \leq j \leq n$. Since (S_J) is cooperative, for $j \in J_0$, $f_j(x)$ is nondecreasing in x_p with $k+1 \leq p \leq k+m-1$. Therefore for $v_p^1 \leq x_p \leq v_p^0$ with $k+1 \leq p \leq k+m-1$, $f_j(x_{k+1}, \cdots, x_{k+m-1}, v_{k+m}^0, \cdots, v_n^0) \equiv 0$, which implies that

$$\frac{\partial f_j}{\partial x_p}(v^1) = 0$$

for any $j \in J_0$ and $p \in \{k+1, \cdots, k+m-1\}$. So far, we have proved that in the remaining case $Df(x^1)$ has the following form

$$Df(x^1) = \begin{bmatrix} A & B \\ 0 & C \end{bmatrix} \tag{3.2}$$

where $C = (c_{jp})$ is an $(n-k-m+1) \times (n-k-m+1)$ matrix with $c_{jp} = \frac{\partial f_j}{\partial x_p}(v^1)$ for $k+m \leq j, p \leq n$. Clearly, $v^1 \leqq v^0$, and hence $(0, v^0) \leqq_K (0, v^1)$. The concave condition (2) implies that $Df(0, v^1) \leqq_K Df(0, v^0)$. Let $\overline{C} = (\overline{c}_{jp})$ with $\overline{c}_{jp} = \frac{\partial f_j}{\partial x_p}(v^0)$ for $k+m \leq j, p \leq n$. Then we have $C \leqslant \overline{C}$. Obviously, $\overline{C}$ is a principal minor of $\frac{\partial f^2}{\partial v}(0, v^0)$. By Theorem 2.1 and the additional assumption (1), $s(C) \leq s(\overline{C}) \leq s(\frac{\partial f^2}{\partial v}(0, v^0)) < 0$. By (3.2), $s(Df(x^1)) \leq \max(s(A), s(C))$. Thus, in order to prove that $s(Df(x^1)) < 0$ it suffices to prove that $s(A) < 0$.

For this goal, we denote the solution $\varphi_t(u, v^0)$ of (S) by $(x_1(t), \cdots, x_{k+m-1}(t), v^0_{k+m}, \cdots, v^0_n)$. Then $(x_1(t), \cdots, x_{k+m-1}(t))$ is a solution of the $(k+m-1)$-dimensional ordinary differential equations

$$\dot{x}_p = x_p f_p(x_1, \cdots, x_{k+m-1}, v^0_{k+m}, \cdots, v^0_n), 1 \leq p \leq k+m-1. \tag{3.3}$$

By the choice of J_0, we obtain that there exists a $t_0 > 0$ such that

$$\begin{cases} u_i < x_i(t) < u^1_i & \text{for } t > 0 \text{ and } i \in I, \\ v^0_j > x_j(t) > v^1_j & \text{for } t > t_0 \text{ and } j \in J|J_0, \\ x_j(t) \equiv v^0_j = v^1_j & \text{for } t \geq 0 \text{ and } j \in J_0. \end{cases}$$

Obviously, $(u^1_1, \cdots, u^1_k, v^1_{k+1}, \cdots, v^1_{k+m-1})$ is a positive steady state of (3.3) and (3.3) inherits all properties of (S). Applying Theorem 2.6 to the solution $(x_1(t), \cdots, x_{k+m-1}(t))$, we conclude that there exists a $t_1 \geq t_0$ with the property that

$$f_p(x_1(t_1), \cdots, x_{k+m-1}(t_1), v^0_{k+m}, \cdots, v^0_n) > 0$$

for all $p \in \{1, 2, \cdots, k\}$ and

$$f_p(x_1(t_1), \cdots, x_{k+m-1}(t_1), v^0_{k+m}, \cdots, v^0_n) < 0 \text{ for all } p \in \{k+1, \cdots, k+m-1\}.$$

Let

$$G(x_1, \cdots, x_{k+m-1}) = (f_1(x_1, \cdots, x_{k+m-1}, v^0_{k+m}, \cdots, v^0_n), \cdots, f_{k+m-1}(x_1, \cdots, x_{k+m-1}, v^0_{k+m}, \cdots, v^0_n)).$$

Then the result proved in the second paragraph shows that

$$s(DG(u^1, v^1_{k+1}, \cdots, v^1_{k+m-1})) < 0.$$

It is not difficult to see that

$$A = DG(u^1_1, \cdots, u^1_k, v^1_{k+1}, \cdots, v^1_{k+m-1}).$$

So $s(A) < 0$. This proves that $s(Df(x^1)) < 0$ in the remaining case. The fact in the third paragragh implies that x^1 is a unique positive steady state of (S). The conclusion of Theorem 3.1 follows immediately from Proposition 3.2. This completes the proof. □

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