

## TIME DELAYS IN $n$ -SPECIES COMPETITION - I: GLOBAL STABILITY IN CONSTANT ENVIRONMENTS

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Sufficient conditions which are verifiable in a finite number of arithmetical steps are derived for the existence and global asymptotic stability of a feasible steady state in an integro-differential system modelling the dynamics of  $n$  competing species in a constant environment with delayed interspecific interactions. A novel method involving a nested sequence of "asymptotic" upper and lower bounds is developed.

### 1. Introduction

The purpose of this article is to discuss the asymptotic behaviour of solutions of a class of integrodifferential equations (see (2.8) below) modelling the dynamics of  $n$  competing species ( $n \geq 2$ ) with possibly time delayed interspecific interactions. Various aspects of time delays in dynamic ecosystem models have been considered by numerous authors since the pioneering work of Volterra [14]. Most of the mathematical analyses of such systems existing in the literature have been restricted to an examination of the asymptotic (local or global) stability or instability of feasible steady states (that is, steady states in the open positive cone of the state space) assuming that such steady states exist. The method of characteristic equations (Cushing [3], Busenberg and Travis [1]) or the method of Lyapunov functions (Wörz-Busekros [15], Post and Travis [13]) have been the principal methods used in such investigations. Without making an explicit assumption on the existence of a feasible steady state,

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one can examine the "persistence" of an ecosystem in the sense that no species can ever become extinct. A number of studies on persistence of special ecosystems with no delays have been performed recently (Gard and Hallam [4], Gard [5], [6], Hallam *et al.* [10] and Harrison [11]).

It is known (Coste *et al.* [2]) that in the case of a Lotka-Volterra system of the form

$$(1.1) \quad \frac{dx_i}{dt} = x_i \left\{ r_i + \sum_{j=1}^n a_{ij} x_j \right\}, \quad i = 1, 2, \dots, n,$$

a necessary condition for persistence is that (1.1) has a feasible steady state  $x^* = (x_1^*, \dots, x_n^*)$ . Steady states of (1.1) satisfying

$$(1.2) \quad \sum_{j=1}^n a_{ij} x_j^* + r_i = 0, \quad i = 1, 2, \dots, n,$$

are said to be nontrivial steady states of (1.1). In general no conditions (necessary or sufficient) on the coefficients of (1.1) are known for its nontrivial steady states to be feasible also. It is for this reason that everyone interested in the stability analysis of (1.1) has assumed the existence of a feasible or partially feasible (that is, lying on the boundary of the positive cone of the state space) steady state and derived conditions for the stability of such a steady state. If such steady states do not exist, then the stability analysis and the conditions derived for the stability of such hypothetical steady states will be worthless. In the analysis we present below we provide sufficient conditions for the existence of feasible steady states which are globally asymptotically stable in the sense that all orbits in the state space originating in the open positive cone approach the feasible steady state as  $t \rightarrow \infty$  in the presence of delayed interspecific interactions. We will postpone further discussion to the end of the article.

## 2. Asymptotic bounds and convergence

It is an elementary fact that the solution  $u$  of the scalar initial value problem

$$(2.1) \quad \frac{du(t)}{dt} = u(t) \{r - au(t)\}, \quad t > 0, \quad u(0) = u_0,$$

is given by

$$(2.2) \quad u(t) = ru_0 [au_0 + (r-au_0)\exp(-rt)]^{-1}, \quad t \geq 0.$$

If  $u_0, a, r$  are positive constants then the solution  $u$  in (2.2) is defined for all  $t > 0$  and furthermore

$$(2.3) \quad u(t) > 0 \quad \text{and} \quad \lim_{t \rightarrow \infty} u(t) = r/a.$$

The existence of  $u$  for all  $t \geq 0$  and its asymptotic behaviour in (2.3) is usually referred to as the global asymptotic stability of the positive steady state  $(r/a)$  of the system (2.1). Equations of the form (2.1) play a fundamental role in mathematical ecology.

One of the consequences of (2.3) is that for arbitrary positive constants  $\epsilon_1 > 0, \epsilon_2 > 0$ , there exist positive numbers  $t_1^*, t_2^*$  such that

$$(2.4) \quad u(t) \leq (r/a) + \epsilon_1 \quad \text{for} \quad t \geq t_1^*$$

and

$$(2.5) \quad u(t) \geq (r/a) - \epsilon_2 \quad \text{for} \quad t \geq t_2^*.$$

Using this elementary fact repeatedly we will construct sequences of "asymptotic upper" and "asymptotic lower" bounds for solutions of a vector system modelling  $n$ -species competition with delayed interspecific interactions. In particular we establish the following:

**THEOREM.** Assume that  $r_i, a_{ij}$  ( $i, j = 1, 2, \dots, n$ ) are positive fixed constants such that

$$(2.6) \quad a_{ii} \neq 0, \quad a_{ii} > \sum_{\substack{j=1 \\ j \neq i}}^n a_{ji}, \quad r_i > \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} (r_j/a_{jj}),$$

$$i = 1, 2, \dots, n.$$

Let  $k_{ij} : [-T, 0] \rightarrow [0, \infty)$  ( $i, j = 1, 2, \dots, n$ ) denote continuous delay kernels normalised such that

$$(2.7) \quad \int_{-T}^0 k_{ij}(s) ds = 1, \quad i, j = 1, 2, \dots, n.$$

Consider the integrodifferential system

$$(2.8) \quad \frac{du_i(t)}{dt} = u_i(t) \left\{ r_i - a_{ii} u_i(t) - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} \int_{-T}^0 k_{ij}(s) u_j(t+s) ds \right\},$$

$$i = 1, 2, \dots, n,$$

$$(2.9) \quad u_i(s) = \phi_i(s) \geq 0, \quad s \in [-T, 0],$$

where  $T$  is a fixed positive constant and  $\phi_i$  ( $i = 1, 2, \dots, n$ ) are bounded integrable nonnegative functions with possible jump discontinuities at  $s = 0$  so that

$$(2.10) \quad u_i(0) = \phi_i(0) > 0, \quad i = 1, 2, \dots, n.$$

Then the system (2.8) has a feasible steady state  $x^* = (x_1^*, \dots, x_n^*)$  with  $x_i^* > 0$  ( $i = 1, 2, \dots, n$ ); also solutions of (2.8)-(2.10) exist for all  $t \geq 0$  and satisfy the following:

$$(2.11) \quad u_i(t) \geq 0 \quad \text{for } t \geq 0 \quad \text{and} \quad \lim_{t \rightarrow \infty} u_i(t) = x_i^* > 0,$$

$$i = 1, 2, \dots, n,$$

where

$$(2.12) \quad \sum_{j=1}^n a_{ij} x_j^* = r_i \quad (i = 1, 2, \dots, n).$$

Proof. We first note from the form of (2.8) and the nonnegativity of initial conditions, solutions of (2.8)-(2.10) can never become negative. The local existence of  $u_i$  for small  $t > 0$  can be established by constructing the usual Picard iterates; boundedness and global existence for all  $t \geq 0$  of  $u_1, u_2, \dots, u_n$  is a consequence of our arguments below. We shall directly proceed to examine the behaviour of  $u_i(t)$  ( $i = 1, 2, \dots, n$ ) as  $t$  increases unboundedly.

Let  $v_i^{(1)}(t)$  be the solution of

$$(2.13) \quad \frac{dx_i}{dt} = x_i (r_i - a_{ii} x_i), \quad x_i(0) = u_i(0).$$

Then since  $u_j(t+s) \geq 0$  ( $j = 1, 2, \dots, n$ ) it will follow that

$$(2.14) \quad \frac{du_i}{dt} \leq u_i(r_i - a_{ii}u_i) \quad \text{for } t > 0.$$

From (2.13)-(2.14) one derives

$$(2.15) \quad u_i(t) \leq V_i^{(1)}(t) = r_i u_i(0) [a_{ii}u_i(0) + (r_i - a_{ii}u_i(0)) \exp(-r_i t)]^{-1},$$

$t > 0.$

Choose  $\epsilon_1 > 0$  such that

$$(2.16) \quad \epsilon_1 < 1 \quad \text{and} \quad \frac{1}{a_{ii}} \left[ r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} \left( \frac{r_j}{a_{jj}} + \epsilon_1 \right) \right] > 0, \quad i = 1, 2, \dots, n,$$

Such a choice of  $\epsilon_1$  is possible by hypothesis (2.6). As remarked before, there exists a  $t_1 > 0$  such that

$$(2.17) \quad u_i(t) \leq N_i^{(1)} \equiv (r_i/a_{ii}) + \epsilon_1 \quad \text{for } t \geq t_1, \quad i = 1, 2, \dots, n.$$

Now let  $U_i^{(1)}(t)$  be the solution of

$$(2.18) \quad \frac{dx_i}{dt} = x_i \left[ r_i - a_{ii}x_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij}N_j^{(1)} \right], \quad t > t_1 + T,$$

$$x_i(t_1 + T) = u_i(t_1 + T).$$

From the choice of  $\epsilon_1$  we have

$$r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij}N_j^{(1)} > 0 \quad (i = 1, 2, \dots, n)$$

and the solution of (2.18) is given by

$$(2.19) \quad x_i(t) = \left[ \left( r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij}N_j^{(1)} \right) x_i(t_1 + T) \right] / G(t)$$

where

$$G(t) = \left[ a_{ii} x_i(t_1+T) + \left[ r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} N_j^{(1)} \right] - a_{ii} x_i(t_1+T) \right] \\ \times \exp \left[ - \left( r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} N_j^{(1)} \right) (t - t_1 - T) \right], \quad i = 1, 2, \dots, n, \quad t > t_1 + T.$$

Since

$$(2.20) \quad \frac{du_i}{dt} \geq u_i \left[ r_i - a_{ii} u_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} N_j^{(1)} \right], \quad t \geq t_1 + T,$$

it follows that

$$(2.21) \quad u_i(t) \geq U_i^{(1)}(t) \quad \text{for } t \geq t_1 + T.$$

Hence from (2.18)-(2.21) we have the following: there exists a  $t_2 > t_1 + T$  such that

$$(2.22) \quad u_i(t) \geq M_i^{(1)} \equiv \left[ r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} N_j^{(1)} \right] \frac{1}{a_{ii}} - \epsilon_2 \quad \text{for } t \geq t_2 > t_1 + T, \\ i = 1, 2, \dots, n,$$

where

$$(2.23) \quad \epsilon_2 < \min \left\{ \frac{1}{2}, \epsilon_1, \min \left( \frac{1}{2} \right) \left[ r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} N_j^{(1)} \right] \frac{1}{a_{ii}} \right\}.$$

We thus have the following first asymptotic upper  $N_i^{(1)}$  and first asymptotic lower  $M_i^{(1)}$  bounds respectively so that

$$(2.24) \quad M_i^{(1)} \leq u_i(t) \leq N_i^{(1)} \quad \text{for } t \geq t_2.$$

(The appendage "asymptotic" is used since the bounds are not valid for all  $t \geq 0$  .) Using the upper and lower bounds in (2.24) we will generate as before new upper and lower bounds valid for still larger values of  $t$  .

Let  $V_i^{(2)}(t)$  be the solution of

$$\frac{dx_i}{dt} = x_i \left\{ r_i - a_{ii}x_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij}M_j^{(2)} \right\}, \quad t > t_2 + T,$$

(2.25)

$$x_i(t_2+T) = u_i(t_2+T).$$

Now since

$$r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij}M_j^{(1)} = r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} \left[ \left\{ r_j - \sum_{\substack{k=1 \\ k \neq j}}^n a_{jk}N_k^{(1)} \right\} \frac{1}{a_{jj}} - \epsilon_2 \right]$$

$$\geq r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} \left( \frac{r_j}{a_{ij}} \right) > 0, \quad i = 1, 2, \dots, n,$$

and

$$\frac{du_i}{dt} \leq u_i \left\{ r_i - a_{ii}u_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij}M_j^{(1)} \right\}, \quad i = 1, 2, \dots, n,$$

(2.26)

there exists a  $t_3 > 0$  such that for  $t \geq t_3 > t_2+T$  we have

$$u_i(t) \leq N_i^{(2)} \equiv \left( r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij}M_j^{(1)} \right) \frac{1}{a_{ii}} + \epsilon_3, \quad i = 1, 2, \dots, n,$$

(2.27)

where

$$0 < \epsilon_3 < \min \cdot \left\{ \frac{1}{3}, \epsilon_2 \right\} \quad \text{and} \quad \left[ r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} \left( \frac{r_j}{a_{jj}} + \epsilon_3 \right) \right] > 0,$$

$i = 1, 2, \dots, n.$

Now let  $U_i^{(2)}(t)$  be the solution of

$$\frac{dx_i}{dt} = x_i \left\{ r_i - a_{ii}x_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij}N_j^{(2)} \right\}, \quad t > t_3 + T,$$

(2.29)

$$x_i(t_3+T) = U_i(t_3+T).$$

By the choice of  $\epsilon_3$ ,

$$(2.30) \quad r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} \left[ \left( r_j - \sum_{\substack{k=1 \\ k \neq j}}^n a_{jk} M_k^{(1)} \right) \frac{1}{a_{jj}} + \epsilon_3 \right] > 0 .$$

Also we have

$$(2.31) \quad \frac{du_i}{dt} \geq u_i \left\{ r_i - a_{ii} u_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} N_j^{(2)} \right\} .$$

Hence there exists a  $t_4 > 0$  such that

$$(2.32) \quad u_i(t) \geq M_i^{(2)} \equiv \left( r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} N_j^{(2)} \right) \frac{1}{a_{ii}} - \epsilon_4 \quad \text{for } t \geq t_4 > t_3 + T$$

where

$$(2.33) \quad 0 < \epsilon_4 < \min \left\{ \frac{1}{4}, \epsilon_3, \min_i \left( r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} N_j^{(2)} \right) \frac{1}{a_{ii}} \right\} .$$

Thus we have

$$(2.34) \quad M_i^{(2)} \leq u_i(t) \leq N_i^{(2)} \quad \text{for } t \geq t_4 .$$

At this stage let us compare the relative magnitudes of the respective bounds; from the definitions of these bounds we derive that

$$\begin{aligned} N_i^{(2)} - N_i^{(1)} &= \left( r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} M_j^{(1)} \right) \frac{1}{a_{ii}} + \epsilon_3 - \left( \frac{r_i}{a_{ii}} + \epsilon_1 \right) \\ &= - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} M_j^{(1)} + \epsilon_3 - \epsilon_1 \\ &< 0 \quad \text{since } \epsilon_3 < \epsilon_1 \quad \text{and } M_j^{(1)} > 0 \quad (j = 1, 2, \dots, n) . \end{aligned}$$

Thus

$$(2.35) \quad N_i^{(2)} \leq N_i^{(1)} \quad , \quad i = 1, 2, \dots, n .$$

Similarly



$$\begin{aligned}
 M_i^{(2)} - M_i^{(1)} &= \left[ r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} N_j^{(2)} \right] \frac{1}{a_{ii}} - \varepsilon_4 - \left[ r_i - \sum_{j=1}^n a_{ij} N_j^{(1)} \right] \frac{1}{a_{ii}} + \varepsilon_2 \\
 &= - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} \left( N_j^{(2)} - N_j^{(1)} \right) + \varepsilon_2 - \varepsilon_4 \\
 &\geq 0
 \end{aligned}$$

and hence

$$(2.36) \quad M_i^{(2)} \geq M_i^{(1)}, \quad i = 1, 2, \dots, n.$$

Thus we have

$$(2.37) \quad M_i^{(1)} \leq M_i^{(2)} \leq u_i(t) \leq N_i^{(2)} \leq N_i^{(1)} \quad \text{for } t \geq t_4,$$

$i = 1, 2, \dots, n.$

Repeating the above procedure we generate sequences of upper and lower bounds for larger and larger values of  $t$  so that

$$(2.38) \quad M_i^{(1)} \leq M_i^{(2)} \leq \dots \leq M_i^{(k)} \leq \dots \leq u_i(t) \leq \dots$$

$$\leq N_i^{(k)} \leq \dots \leq N_i^{(2)} \leq N_i^{(1)} \quad \text{for } t \geq t_{2k}, \quad i = 1, 2, \dots, n.$$

The sequence  $\{N_i^{(k)}, k = 1, 2, \dots\}$  is a nonincreasing sequence bounded below by  $M_i^{(1)}$  and hence

$$(2.39) \quad \lim_{k \rightarrow \infty} N_i^{(k)} \text{ exists and let } \lim_{k \rightarrow \infty} N_i^{(k)} = \beta_i^*, \quad i = 1, 2, \dots, n.$$

Similarly the sequence  $\{M_i^{(k)}, k = 1, 2, \dots\}$  is a nondecreasing sequence bounded above by  $N_i^{(1)}$  and hence

$$(2.40) \quad \lim_{k \rightarrow \infty} M_i^{(k)} \text{ exists and let } \lim_{k \rightarrow \infty} M_i^{(k)} \rightarrow \alpha_i^*, \quad i = 1, 2, \dots, n.$$

Since

$$M_i^{(1)} \geq \frac{1}{2} \left( r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} M_j^{(1)} \right) \frac{1}{a_{ii}} > 0, \quad i = 1, 2, \dots, n,$$

we note that  $\alpha_i^* > 0$  ( $i = 1, 2, \dots, n$ ) and thus we have

$$(2.41) \quad 0 < \alpha_i^* \leq \liminf_{t \rightarrow \infty} u_i(t) \leq \limsup_{t \rightarrow \infty} u_i(t) \leq \beta_i^*, \quad i = 1, 2, \dots, n.$$

From the definition of  $\beta_i^*$  we have

$$\begin{aligned} (2.42) \quad \beta_i^* &= \lim_{k \rightarrow \infty} N_i^{(k)} \\ &= \lim_{k \rightarrow \infty} \left[ \left( r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} M_j^{(k-1)} \right) \frac{1}{a_{ii}} + \epsilon_{k+1} \right] \\ &= \lim_{k \rightarrow \infty} \left[ \frac{r_i}{a_{ii}} - \frac{1}{a_{ii}} \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} \left\{ \frac{r_j}{a_{jj}} - \frac{1}{a_{jj}} \sum_{\substack{l=1 \\ l \neq j}}^n a_{jl} N_l^{(k-1)} - \epsilon_{k+2} \right\} + \epsilon_{k+1} \right] \\ (2.43) \quad &= \frac{r_i}{a_{ii}} - \frac{1}{a_{ii}} \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} \left[ \frac{r_j}{a_{jj}} - \frac{1}{a_{jj}} \sum_{\substack{l=1 \\ l \neq j}}^n a_{jl} \beta_l^* \right], \quad i = 1, 2, \dots, n, \end{aligned}$$

since  $\epsilon_k \rightarrow 0$  as  $k \rightarrow \infty$ .

By the assumption

$$a_{ii} > \sum_{\substack{j=1 \\ j \neq i}}^n a_{ji},$$

it follows that the matrix  $A = (a_{ij})$  is nonsingular and hence there exists a unique solution  $(x_1^*, \dots, x_n^*)$  of the linear system

$$(2.44) \quad \sum_{j=1}^n a_{ij} x_j = r_i, \quad i = 1, 2, \dots, n,$$

satisfying

$$x_i^* = \frac{r_i}{a_{ii}} - \frac{1}{a_{ii}} \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} x_j^*$$

so that

$$(2.45) \quad x_i^* = \frac{r_i}{a_{ii}} - \frac{1}{a_{ii}} \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} \left\{ \frac{r_j}{a_{jj}} - \frac{1}{a_{jj}} \sum_{\substack{k=1 \\ k \neq j}}^n a_{jk} x_k^* \right\}.$$

Since  $(x_1^*, \dots, x_n^*)$  satisfying (2.45) is unique by the nonsingularity of  $A$ , it follows that

$$(2.46) \quad \beta_i^* = x_i^* \quad (i = 1, 2, \dots, n).$$

Exactly in a similar way one can show that

$$(2.47) \quad \alpha_i^* = x_i^* \quad (i = 1, 2, \dots, n).$$

Thus it follows from (2.41)-(2.47) that

$$(2.48) \quad \lim_{t \rightarrow \infty} u_i(t) \text{ exists and } \lim_{t \rightarrow \infty} u_i(t) = x_i^*$$

where  $(x_1^*, \dots, x_n^*)$  is a feasible steady state of the system (2.7)-(2.8).

The positivity of  $x_i^*$  follows from that of  $\beta_i^* = \alpha_i^* = x_i^*$

$(i = 1, 2, \dots, n)$  and our proof is complete.

### 3. A discussion

Stability or instability criteria developed for mathematical analysis of model ecosystems are usually expressed in several different forms; some of these forms can be easily interpreted directly in terms of the parameters of the model systems than some other forms. The most common criterion expressed in terms of the negativity of the real parts of the eigenvalues of the "community matrix" (coefficient matrix of the linear variational system about the steady state in question) is not directly interpretable in terms of the model parameters since in general eigenvalues have no intuitive relation with the elements of the relevant matrix; the same remark applies to the Routh-Hurwitz criterion also. Furthermore criteria based on eigenvalues are not applicable when the parameters of the model are time dependent. Requiring the existence of a Lyapunov function in ecosystem analyses always presupposes the existence of a feasible (at least partially) steady state (Goh [7], Ikeda and Siljak [12]). Also finding Lyapunov functions or Lyapunov functionals for time delayed systems

is usually difficult. In view of these remarks, the method we have proposed has great potential in applications. In a future investigation we apply our technique for the analysis of a system with time varying model parameters.

The sufficient conditions we have obtained in Theorem 2.1 have the following ecological interpretations. The positivity  $a_{ii} > 0$  ( $i = 1, 2, \dots, n$ ) implies that each species has a self-regulating negative feedback. It is known that if a species fails to self-regulate or self-regulates with some time delay then a feasible steady state if exists will not be stable (Gopalsamy and Aggarwala [8, 9]). The sufficient condition

$$a_{ii} > \sum_{\substack{j=1 \\ j \neq i}}^n a_{ji} \quad (i = 1, 2, \dots, n)$$

is known as diagonal (column) dominance of the matrix  $A = (a_{ij})$  which ecologically means that the self-regulating negative feedback in each species is stronger than the interaction of that species on all others. Such a diagonal dominance guarantees mathematically that the matrix  $A = (a_{ij})$  is nonsingular. One can also consider instead of the above strict diagonal dominance the so called quasi-diagonal dominance as follows: there exist positive constants  $d_1, d_2, \dots, d_n$  such that

$$d_i a_{ii} > \sum_{\substack{j=1 \\ j \neq i}}^n d_j a_{ji} \quad (i = 1, 2, \dots, n).$$

In this case however, there is no ecologically realistic interpretation of the abstract positive numbers  $d_1, d_2, \dots, d_n$ ; in spite of this drawback numerous authors have used such a quasi-diagonal dominance condition.

The other set of conditions

$$r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} (r_j / a_{jj}) > 0 \quad (i = 1, 2, \dots, n)$$

have the following interpretation: one can consider

$$r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} (r_j / a_{jj})$$

as the growth rate of the  $i$ th species when the population of the  $i$ th species is small while that of all others are near their potential maximum (achievable in the absence of interspecific competition) sizes. In this sense if

$$r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} (r_j / a_{jj}) > 0$$

then the  $i$ th species can successfully recover when its population is low in the presence of the other  $(n-1)$  competitors; thus

$$r_i - \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} (r_j / a_{jj})$$

denotes the potential of the  $i$ th species to successfully invade and establish itself in a community consisting originally of the other  $(n-1)$  species. Thus we can translate our analytical result of Theorem 2.1 in the following form.

**AN ECOTHEOREM.** *If each species of an  $n$ -species competition community ( $n \geq 2$ ) has a sufficiently strong self-regulating negative feedback and has a positive potential to invade a community of all other competitors, then all the  $n$ -species of the competition system can not only persist in the sense that no species is ever threatened with extinction but can co-exist in the sense that the sizes of all the competing populations approach constant positive values in the long run and this happens in spite of the fact that there are various time delays in the interspecific interactions.*

We conclude with the following mathematical note; consider a system of "positive" linear nonhomogeneous equations

$$\sum_{j=1}^n a_{ij} x_j = r_i \quad (i = 1, 2, \dots, n)$$

in the unknowns  $x_1, x_2, \dots, x_n$  where  $a_{ij}, r_i$  ( $i, j = 1, 2, \dots, n$ )

are all positive constants. What is a necessary or sufficient or necessary

and sufficient set of conditions on the  $a_{ij}$ ,  $r_i$  for the above positive linear system to have a solution  $(x_1^*, \dots, x_n^*)$  with  $x_i^* > 0$  ( $i = 1, 2, \dots, n$ )? Theorem 2.1 provides an ecologically motivated sufficient condition for the existence of a positive solution of the above positive linear system. An otherwise independent answer to this algebraic problem is of interest by itself.

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