ASYMPTOTIC BEHAVIOUR FOR A CLASS OF DELAYED
COOPERATIVE MODELS WITH PATCH STRUCTURE

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Abstract. For a class of cooperative population models with patch structure and multiple discrete delays, we give conditions for the absolute global asymptotic stability of both the trivial solution and – when it exists – a positive equilibrium. The existence of positive heteroclinic solutions connecting the two equilibria is also addressed. As a by-product, we obtain a criterion for the existence of positive traveling wave solutions for an associated reaction-diffusion model with patch structure. Our results improve and generalize criteria in the recent literature.

1. Introduction. Many systems of one or multiple biological species are composed of a network of connected different patches, with migration of the populations among them. Due to several features of an heterogeneous environment, the growth of the populations often depends on the resources of each particular patch, and on the dispersal and interactions of the populations distributed over the different patches of the entire system. Patch-structured models are also used to capture the dynamics of species which go through several different life stages according to age or size, or in disease models with transitions between stages of normal and infected cells. Frequently, the past history of the species is important for their dynamics, to account for the time of the spatial dispersion of the populations from one patch to another, or to represent maturation periods, hunting delays, etc., and therefore these models should incorporate time-delays. For these reasons, in recent years population dynamics models with patch structure and delays have attracted the attention of an increasing number of mathematicians and biologists.

In this paper, we study some aspects of the long time behaviour of solutions for a class of n-dimensional cooperative delay differential equations (DDEs) of the form

$$x'_i(t) = x_i(t)\left[ a_i - b_i x_i(t) + c_i x_i(t - \sigma_i) \right] + \sum_{j=1}^{n} d_{ij} x_j(t - \tau_{ij}), \quad i = 1, \ldots, n, \quad (1.1)$$

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with \( a_i \in \mathbb{R}, b_i > 0, c_i \geq 0, d_{ij} \geq 0 \) and discrete delays \( \sigma_i \geq 0, \tau_{ij} \geq 0, i, j = 1, \ldots, n \).
Actually, we can consider more general models given by
\[
x_i'(t) = x_i(t) \left[ a_i - b_i x_i(t) + \sum_{p=1}^{m} c_i^{(p)} x_i(t - \sigma_i^{(p)}) \right] + \sum_{j=1}^{n} \sum_{p=1}^{m} d_{ij}^{(p)} x_j(t - \tau_{ij}^{(p)}), \quad i = 1, \ldots, n,
\]
where: \( a_i \in \mathbb{R}, b_i > 0, c_i^{(p)} \geq 0, d_{ij}^{(p)} \geq 0, \sigma_i^{(p)} \geq 0, \tau_{ij}^{(p)} \geq 0 \), for \( i, j = 1, \ldots, n, p = 1, \ldots, m \).
For simplicity, we shall consider (1.1) instead of (1.2), but all our results apply to (1.2) by replacing \( c_i \) with \( c_i = \sum_{p=1}^{m} c_i^{(p)} \) and \( d_{ij} \) with \( d_{ij} = \sum_{p=1}^{m} d_{ij}^{(p)} \).
The case \( c_i = 0 \) for all \( i \),
\[
x_i'(t) = x_i(t) [a_i - b_i x_i(t)] + \sum_{j=1}^{n} d_{ij} x_j(t - \tau_{ij}), \quad i = 1, \ldots, n, \tag{1.3}
\]
constitutes an important subclass of (1.1): since it satisfies the sublinearity assumption (see Section 2 for the definition), sharper results are obtained for (1.3).
An interesting application was studied by Takeuchi et al \[8, 9\], who considered the following delayed population model with patch structure:
\[
x_i'(t) = x_i(t) [a_i - b_i x_i(t)] + \sum_{j=1}^{n} \varepsilon_{ij} d_{ij} x_j(t - \tau_{ij}) - d_{ij} x_i(t), \quad i = 1, \ldots, n \tag{1.4}
\]
for \( b_i > 0, a_i \in \mathbb{R}, d_{ij} \geq 0 \) for \( i \neq j, d_{ii} = 0, \tau_{ij} \geq 0 \) and \( \varepsilon_{ij} = e^{-\gamma_{ij} \tau_{ij}} \in (0, 1] \), for \( i, j = 1, \ldots, n \). Note that in (1.4) there are no diagonal delays. System (1.4) models the growth of a single species population distributed over \( n \) different food-rich patches, where \( x_i(t) \) denotes the density of the species in patch \( i \), \( \tau_{ij} \) is the time the species takes to move from patch \( j \) to patch \( i \), \( \gamma_{ij} \) is the death rate during the dispersion, and \( a_i, b_i \) are the intrinsic rate and the regulation capacity in each patch \( i \), respectively. The natural growth in each patch is of logistic type, however without requiring \( a_i > 0 \). Another significant model, which has the form (1.2) with \( c_i = \sum_{p=1}^{m} c_i^{(p)} > 0 \), was studied by Liu \[5\] and will be later investigated in this paper.

Our purpose is to study two aspects of the global dynamics of (1.1): the global stability of equilibria, and the existence of a positive heteroclinic solution, connecting the trivial equilibrium to a positive equilibrium, when it exists.

If the matrix \( D = [d_{ij}] \) is irreducible, the theory of cooperative systems in \[6\] and the results by Zhao and Jing \[11\] can be used to obtain a sharp criterion of exchange of global attractivity between the zero solution and a positive equilibrium for the sublinear system (1.3), as the spectral bound of a certain matrix, named here as the (linear) community matrix, changes sign (cf. \[9\]). As regards the stability analysis, the novelty in this paper is not only to consider the more general system (1.1) (or (1.2)), but also to address the case of a reducible community matrix which is generally not treated in the literature. For \( b_i > c_i \) for all \( i \), we further show that the positive equilibrium of (1.1) is always a global attractor of all positive solutions whenever it exists. For stability results for non-cooperative patch-structured models, see \[1, 5\], also for further references.

If \( D \) is irreducible, we also give conditions for the linearized equation at zero to have a positive dominant eigenvalue, with a positive associated eigenfunction. We can therefore use some recent results in \[3\] on the existence of a positive heteroclinic solution for (1.1), connecting the trivial equilibrium to a positive equilibrium. In
fact, in the vicinity of $-\infty$ this heteroclinic solution was constructed in [3] as a perturbation of a positive eigenfunction. Adding a spatial variable to system (1.1) and diffusion terms, we obtain an associated reaction-diffusion model, for which the existence of positive traveling wave solutions for large wave speeds also follows from [3]. Such traveling fronts were obtained in [3] via a contraction principle argument as perturbations of the heteroclinic solution for the system without diffusion.

The paper is organized as follows. In Section 2, we set some notation and recall preliminary results from the literature. The absolute (i.e., independent of the size of the delays) local and global asymptotic stabilities of the equilibria of (1.1) are studied in Section 3. Section 4 is devoted to the existence of a positive heteroclinic solution for (1.1), as well as to positive traveling fronts for a diffusive version of (1.1). Several examples of application are given at the end of Sections 3 and 4; these include patch-structured models studied in [5, 9].

2. Notation and preliminary results. We set some standard notation. Let $	au > 0$ and define $C = C([\tau, 0]; \mathbb{R}^n)$ as the space of continuous functions from $[\tau, 0]$ to $\mathbb{R}^n$, equipped with the supremum norm for some fixed norm in $\mathbb{R}^n$, $\|\varphi\| = \max_{\theta \in [-\tau, 0]} |\varphi(\theta)|$ for $\varphi \in C$. For an abstract autonomous DDE in $C$

$$x'(t) = f(x_t),$$

(2.1)

for which uniqueness of solutions is assumed, $x(t; \varphi)$ designates the solution of (2.1) with initial condition $x_0 = \varphi$ ($\varphi \in C$). As usual, $x_t$ is the function in $C$ given by $x_t(\theta) = x(t + \theta)$. For $\tau \leq \theta \leq 0$, and $x_t(\varphi)$ denotes $x_t(\cdot; \varphi)$.

A constant function $\varphi(\theta) = v$ for $\theta \in [-\tau, 0]$ is denoted simply by $v$. If $v \in \mathbb{R}^n$ is a non-negative (respectively non-negative) vector, i.e., all its components are positive (respectively non-negative) equilibrium of (2.1). For (1.1), we take the phase space $C = C([\tau, 0]; \mathbb{R}^n)$ where $\tau$ is the maximum of the delays, $\tau = \max\{\sigma_i, \tau_{ij} : 1 \leq i, j \leq n\}$, and assume $\tau > 0$. However, the case $\tau = 0$ is included in our analysis. Due to its biological interpretation, only non-negative solutions are meaningful. For (1.1), we shall restrict the set of admissible initial conditions to either the positive cone $C^+ = \{\varphi \in C : \varphi_i(0) \geq 0 \text{ for all } \theta \in [-\tau, 0], i = 1, \ldots, n\}$, or the subset of $C^+$ of functions which are strictly positive at zero, $C_0^+ = \{\varphi \in C^+ : \varphi_i(0) > 0, i = 1, \ldots, n\}$.

A non-negative equilibrium $v$ of system (1.1) is said to be stable (in a set $S \subset C^+$) if for every $\varepsilon > 0$ there is $\delta = \delta(\varepsilon) > 0$ such that $\|x_t(\varphi) - v\| < \varepsilon$ for all $\varphi \in S$ with $\|\varphi - v\| < \delta$ and $t \geq 0$; and $v$ is said to be globally attractive (relative to $S$) if $x(t) \to v$ as $t \to \infty$, for all admissible solutions $x(t)$ of (1.1) (i.e., solutions with initial conditions $x_0 = \varphi \in S$); we say that $v$ is globally asymptotically stable if it is stable and globally attractive.

System (1.1) is written as (2.1), where $f = (f_1, \ldots, f_n)$ and

$$f_i(\varphi) = \varphi_i(0)\left[a_i - b_i\varphi_i(0) + c_i\varphi_i(-\sigma_i)\right] + \sum_{j=1}^{n} d_{ij}\varphi_j(-\tau_{ij}), \quad i = 1, \ldots, n.$$  

(2.2)

Observe that system (1.1) is cooperative, i.e., $Df_i(\varphi)(\psi) \geq 0$, for all $\varphi, \psi \in C^+$ with $\psi_i(0) = 0, i = 1, \ldots, n$. This implies that $f$ satisfies the quasi-monotonicity condition on p. 78 of [6]. Thus, solutions $x(t; \varphi)$ with initial conditions $\varphi \in C^+$ remain nonnegative for $t \geq 0$ whenever they are defined; moreover $x(t; \varphi) > 0$ for $t \geq 0$ if $\varphi \in C_0^+$. 

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Typically, in population dynamics the stability of equilibria is closely related to the algebraic properties of some kind of competition matrix of the community. Denote $A = \text{diag}(a_1, \ldots, a_n)$, $D = [d_{ij}]$. For convenience, here we shall refer to $M = A + D$ as the (linear) community matrix:

$$M = \begin{bmatrix}
    a_1 + d_{11} & d_{12} & \cdots & d_{1n} \\
    d_{21} & a_2 + d_{22} & \cdots & d_{2n} \\
    \cdots & \cdots & \cdots & \cdots \\
    d_{n1} & d_{n2} & \cdots & a_n + d_{nn}
\end{bmatrix}. \quad (2.3)$$

Since $d_{ij} \geq 0$ for $j \neq i$, the matrix $M$ is called cooperative. We have $Df_0(0) = M$ for $f_0 : \mathbb{R}^n \to \mathbb{R}^n$ given by $f_0(x) = f(x)$, with components $f_0,i(x) = x_i[a_i - (b_i - c_i)x_i] + \sum_{j=1}^n d_{ij}x_j$, $i = 1, \ldots, n$, for $x = (x_1, \ldots, x_n)$. If $D$ is irreducible, then $M$ is also irreducible; in this case, (1.1) is called an irreducible system [6] p. 88, and the semiflow $\varphi \mapsto x_t(\varphi)$ is eventually strongly monotone.

System (1.3) reads as (2.1), where now

$$f_i(\varphi) = \varphi_i(0)[a_i - b_i\varphi_i(0)] + \sum_{j=1}^n d_{ij}\varphi_j(-\tau_{ij}), \quad i = 1, \ldots, n, \quad (2.4)$$

and $f = (f_1, \ldots, f_n)$. One easily sees that in this case $f(\varphi)$ is sublinear and $f_0(x) = f(x)$ ($x \in \mathbb{R}^n$) strictly sublinear, i.e., $f(\alpha \varphi) \geq \alpha f(\varphi)$ for $\varphi \in C^+, \alpha \in (0, 1)$, and $f_0(\alpha x) > \alpha f_0(x)$ for $x \in \mathbb{R}_+^n \setminus \{0\}, \alpha \in (0, 1)$ (cf. [9]). Cooperative DDEs satisfying these sublinearity conditions have significant properties [11].

Let $\sigma(M)$ be the spectrum of $M$. As usual, we define the spectral bound of $M$ and the spectral radius of $M$ given respectively by

$$s(M) = \max \{\Re \lambda : \lambda \in \sigma(M)\} \quad \text{and} \quad r(M) = \max \{|\lambda| : \lambda \in \sigma(M)\}.$$

For (1.3), it is known that all positive solutions are defined for $t \geq 0$ and are uniformly bounded (see e.g. [10, 8]). Wang et al. [10] and Takeuchi et al. [9] studied the stability of sublinear systems in the form (1.3), as well as of their periodic versions, however with more restrictions on the sign of the coefficients in (1.3). Regarding the stability of equilibria for autonomous systems, the following result is deduced from [10].

**Theorem 2.1.** [10] Consider (1.3) with $a_i \in \mathbb{R}, b_i > 0, d_{ij} > 0$ for $j \neq i$, $d_{ii} = 0$, and $\tau_{ij} \geq 0$. If

$$\beta_i := a_i + \sum_j d_{ij} > 0 \quad \text{for} \quad i = 1, \ldots, n, \quad (2.5)$$

then there is a unique positive equilibrium of (1.3), which is globally asymptotically stable (with respect to $C^+_0$).

Since $f(\varphi)$ defined in (2.4) is cooperative and sublinear, and $f_0(x)$ is strictly sublinear with $f_0(0) = 0$, if $M = Df_0(0)$ is irreducible we can apply the theory in [11] to (1.3). From Theorem 2.1 in [9] we easily obtain the following sharp criterion:

**Theorem 2.2.** For (1.3), assume that the matrix $M$ in (2.3) is irreducible. Then:

(i) if $s(M) \leq 0$, the equilibrium 0 is globally asymptotically stable;

(ii) if $s(M) > 0$, there exists a positive equilibrium $x^*$ which is globally asymptotically stable (with respect to $C^+ \setminus \{0\}$).

**Remark 2.1.** Theorem 2.2 was stated in [9] for systems (1.4) and did not include the case $s(M) = 0$ in (i) (cf. Theorem 2.1 of [9]), however Theorem 3.2 of [11] allows...
the inclusion of this case. Moreover, the restriction of having no diagonal delays in (1.4) is not relevant for the proof.

3. Local and global stability of the equilibria. In this section, we investigate the stability and attractivity of equilibria for systems (1.1).

When $M$ is an irreducible matrix, Theorem 2.2 provides a threshold criterion for the global asymptotic behaviour of all positive solutions of (1.3), determined by the sign of $s(M)$. We show first that Theorem 2.1 can be deduced as a corollary of Theorem 2.2. In fact, on one hand the matrix $M$ in (2.3) is irreducible if the assumption $d_{ij} > 0$ $(j \neq i)$ holds; on the other hand, (2.5) is indeed more restrictive than condition $s(M) > 0$.

**Theorem 3.1.** If (2.5) holds, then $\mu_0 := s(M) > 0$.

**Proof.** Assume first that $M$ is irreducible. Since $M$ has nonnegative off-diagonal entries, then $\mu_0 \in \sigma(M)$ and there is a positive vector $v = (v_1, \ldots, v_n)$ such that $Mv = \mu_0v$ (cf. Appendix A of [7]). Without loss of generality, let $v_i = \min_j v_j = 1$.

If (2.5) holds, then $\mu_0 = a_i + \sum d_{ij}v_j \geq \beta_i > 0$.

Consider now the case of a reducible matrix $M$. After a simultaneous permutation of rows and columns, $M$ can be reduced to the form $M = \begin{bmatrix} M_{11} & 0 \\ M_{21} & M_{22} \end{bmatrix}$ with $M_{kk}$ $n_k \times n_k$ square matrices, $k = 1, 2$, and $M_{11}$ either zero or irreducible. Clearly, after reordering the conditions in (2.5) according to the above mentioned permutation, from $\beta_i > 0$ for $i = 1, \ldots, n_1$ we obtain that $M_{11}$ is irreducible and $s(M_{11}) > 0$, hence $s(M) > 0$.

For (1.1), the linearized equation at zero reads as

$$x_i'(t) = a_i x_i(t) + \sum_{j=1}^n d_{ij} x_j(t - \tau_{ij}) \quad i = 1, \ldots, n.$$  \hspace{1cm} (3.1)

To establish the local asymptotic stability about the equilibrium 0, we apply a result in [2] which uses the properties of M-matrices.

Recall that a square matrix $A = [a_{ij}]$ with non-positive off-diagonal entries is said to be an M-matrix if all the eigenvalues of $A$ have a non-negative real part, or, equivalently, if all its principal minors are non-negative; and $A$ is said to be a non-singular M-matrix if all the eigenvalues of $A$ have positive real part, or, equivalently, if all its principal minors are positive (cf. [4]).

**Theorem 3.2.** [2] Let $\alpha_i \in \mathbb{R}$ and $L_{ij} : C([-\tau, 0] : \mathbb{R}) \to \mathbb{R}$ be bounded linear operators, $i, j = 1, \ldots, n$. Define $A = \text{diag}(\alpha_1, \ldots, \alpha_n)$, $N = A + [L_{ij}(1)]$, $\bar{N} = A - [\|L_{ij}\|]$. The linear system

$$x_i'(t) = -[\alpha_i x_i(t) + \sum_j L_{ij}(x_{i, j})], \quad 1 \leq i \leq n,$$  \hspace{1cm} (3.2)

is absolutely (i.e., for all choices of delay functions) asymptotically stable if and only if $\det \bar{N} = 0$ and $\bar{N}$ is an M-matrix.

**Lemma 3.1.** If $\mu_0 := s(M) < 0$, then the linear equation (3.1) is asymptotically stable.

**Proof.** Equation (3.1) has the form (3.2) for $\alpha_i = -a_i$ and $L_{ij}(\varphi_j) = -d_{ij}\varphi_j(-\tau_{ij})$. These operators have norms $\|L_{ij}\| = d_{ij} = -L_{ij}(1)$. With the notation in Theorem 3.2, $N = \bar{N} = -M$. Next, observe that $\mu_0 < 0$ is equivalent to having $-M$ a non
satisfactory. From Theorem 3.2 we deduce that all the characteristic roots of (3.1) have negative real parts.

For solutions $x(t)$ of the sublinear DDE (1.3), we obtain the inequalities $x_i'(t) \leq a_i x_i(t) + \sum_{j=1}^{n} d_{ij} x_j(t - \tau_{ij}), 1 \leq i \leq n$. From comparison results for cooperative systems, it follows immediately that if $\mu_0 < 0$ then 0 is a global attractor of all nonnegative solutions. In fact, this result holds for the general class (1.1) with $b_i > c_i$.

**Theorem 3.3.** Suppose that $b_i > c_i$ for $i = 1, \ldots, n$. If $s(M) < 0$, then the equilibrium 0 of (1.1) is hyperbolic and globally asymptotically stable (in $C^+$).

**Proof.** For $f_0(x) = f(x), x \in \mathbb{R}^n$, where $f$ is as in (2.2) and $1 \leq i \leq n$, observe that $f_0, i(l, \ldots, l) = l \left[ a_i + \sum_{j} d_{ij} - (b_i - c_i)l \right] \leq 0$ for $l > 0$ sufficiently large. Hence, we easily conclude that all admissible solutions are bounded [6]. Since $-M$ is a non-singular M-matrix, there is $v = (v_1, \ldots, v_n) \in \mathbb{R}^n, v > 0$, such that $Mv < 0$, hence

$$a_i v_i + \sum_{j=1}^{n} d_{ij} v_j < 0, \quad i = 1, \ldots, n.$$  

(cf. Theorem 5.1 of [4]). Let $x(t) \geq 0$ be a solution of (1.1). After the changes of variables $y_i(t) = \frac{x_i(t)}{v_i}, (1.1)$ becomes

$$y_i'(t) = y_i(t) \left[ a_i - v_i(b_i y_i(t) - c_i y_i(t - \sigma_i)) \right] + \sum_{j=1}^{n} d_{ij} \frac{v_j}{v_i} y_j(t - \tau_{ij}), \quad i = 1, \ldots, n.$$  

It suffices to prove that $L_i := \limsup_{t \to \infty} y_i(t) = 0$ for $1 \leq i \leq n$. Let $L_i = \max_{1 \leq j \leq n} L_j$, and suppose that $L_i > 0$. From (3.3), we can choose $\varepsilon > 0$ such that

$$L_i \left[ a_i + \sum_{j=1}^{n} d_{ij} \frac{v_j}{v_i} - v_i(b_i - c_i)L_i \right] + \varepsilon \left[ v_i c_i + \sum_{j=1}^{n} d_{ij} \frac{v_j}{v_i} \right] =: \gamma_i < 0.$$  

Let $T > 0$ be such that $y_j(t) \leq L_i + \varepsilon$ for all $t \geq T - \tau$ and $1 \leq j \leq n$, and separate the cases of $y_i(t)$ eventually monotone and not eventually monotone. If $y_i(t)$ is eventually monotone, then $y_i(t) \to L_i$ as $t \to \infty$, and for $t \geq T$ we obtain

$$y_i'(t) \leq y_i(t) \left[ a_i - v_i b_i y_i(t) + v_i c_i (L_i + \varepsilon) \right] + (L_i + \varepsilon) \sum_{j=1}^{n} d_{ij} \frac{v_j}{v_i} \to \gamma_i$$  

as $t \to \infty$. Since $\gamma_i < 0$, this implies that $\lim_{t \to \infty} y_i(t) = -\infty$, which is not possible. If $y_i(t)$ is not eventually monotone, there is a sequence $t_n \to \infty$ such that $y_i(t_n) \to L_i$, $y'_i(t_n) = 0$. For $t_n \geq T$, we obtain (3.4) with $t$ replaced by $t_n$, again a contradiction. This proves that $L_i = 0$. \hfill $\Box$

When the trivial solution attracts all non-negative solutions, the population is driven to extinction in all the patches. An interesting open question is whether $s(M) = 0$ still implies the global attractivity of 0 if $M$ is reducible. The situation when a positive equilibrium $x^* = (x_1^*, \ldots, x_n^*)$ $(x_i^* > 0)$ of (1.3) exists is however biologically more significant. Next, we show that, if $b_i > c_i$ for all $i$, then the positive equilibrium is globally asymptotically stable whenever it exists, and give conditions for its existence.
Lemma 3.2. Suppose there is a positive equilibrium \( x^* = (x_1^*, \ldots, x_n^*) \) of (1.1), and that \( b_i > c_i \) for \( i = 1, \ldots, n \). Then \( x^* \) is hyperbolic and locally asymptotically stable.

Proof. For \( x^* \) an equilibrium of (1.1), we have

\[
a_i x_i^* + \sum d_{ij} x_j^* = (b_i - c_i)(x_i^*)^2, \quad 1 \leq i \leq n. \tag{3.5}
\]

After the change \( y(t) = x(t) - x^* \), equation (1.1) becomes

\[
y_i'(t) = y_i(t) \left[ a_i - (2b_i - c_i)x_i^* - b_i y_i(t) + c_i y_i(t - \sigma_i) \right] + c_i x_i^* y_i(t - \sigma_i) + \sum_{j=1}^n d_{ij} y_j(t - \tau_{ij}), \quad i = 1, \ldots, n, \tag{3.6}
\]

with linearization at zero given by

\[
y_i'(t) = y_i(t) [a_i - (2b_i - c_i)x_i^*] + c_i x_i^* y_i(t - \sigma_i) + \sum_{j=1}^n d_{ij} y_j(t - \tau_{ij}), \quad i = 1, \ldots, n. \tag{3.7}
\]

Equation (3.7) has the form (3.2), with \( a_i = -[a_i - (2b_i - c_i)x_i^*] \) and operators

\[
L_{ij} : C([-\tau, 0]; \mathbb{R}) \rightarrow \mathbb{R} \text{ defined by } L_{ij}(\phi_j) = -d_{ij}\phi_j(-\tau_{ij}) \text{ for } i \neq j, \quad L_{ii}(\phi_i) = -[c_i x_i^*\phi(-\sigma_i) + d_i\phi_i(-\tau_{ii})].
\]

With the notation in Theorem 3.2, the matrices \( N, \hat{N} \) are given by

\[
N = \hat{N} = -M + 2 \text{diag} ((b_i - c_i)x_i^*)_{i=1}^n.
\]

Clearly all off-diagonal entries of \( N \) are non-positive.

From (3.5), we have \( Mx^* = col ((b_1 - c_1)(x_1^*)^2, \ldots, (b_n - c_n)(x_n^*)^2) \), from which we deduce

\[
(Nx^*)_i = -(Mx^*)_i + 2(b_i - c_i)(x_i^*)^2 = (b_i - c_i)(x_i^*)^2 > 0, \quad i = 1, \ldots, n.
\]

In particular, \( x^* > 0 \) and \( Nx^* > 0 \), which implies that \( N \) is a non-singular M-matrix (cf. Theorem 5.1 of [4]). Now applying Theorem 3.2, we conclude that all characteristic roots of (3.7) have negative real parts, hence \( x^* \) is locally asymptotically stable as a solution of (1.3).

\[\Box\]

Lemma 3.3. Suppose there is a positive equilibrium \( x^* = (x_1^*, \ldots, x_n^*) \) of (1.1), and that \( b_i > c_i \) for \( i = 1, \ldots, n \). Then all solutions \( x(t; \varphi) \) of (1.1) with \( \varphi \in C_0^+ \) satisfy

\[
\liminf_{t \to \infty} x_i(t; \varphi) \geq x_i^* \quad \text{for } 1 \leq i \leq n.
\]

Proof. From (3.5), we have \( \beta_i^* := (b_i - c_i)x_i^* = a_i + \sum d_{ij} \frac{x_j^*}{x_i^*} > 0 \). After the change of variables \( \bar{x}_i(t) = \frac{x_i(t)}{x_i^*} \) in (1.1), and dropping the bars for simplicity, we get

\[
x_i'(t) = x_i(t) [a_i - b_i x_i^* x_i(t) + c_i x_i^* x_i(t - \sigma_i)] + \sum_{j=1}^n d_{ij} \frac{x_j^*}{x_i^*} x_j(t - \tau_{ij}), \quad i = 1, \ldots, n. \tag{3.8}
\]

For a solution \( x(t) = x(t; \varphi) \) of (3.8) with \( \varphi \in C_0^+ \), we first claim that \( \ell_i := \liminf_{t \to \infty} x_i(t) > 0 \) for \( 1 \leq i \leq n \). Otherwise, there are \( \delta \in (0, 1), \ t_0 > \tau \) and \( i \in \{1, \ldots, n\} \), such that \( x_i(t_0) = \min \{x_j(t) : t \in [0, t_0], 1 \leq j \leq n\} \) and \( x_i(t_0) < \delta \). Clearly,

\[
x_i'(t_0) = x_i(t_0) [a_i - b_i x_i^* x_i(t_0) + c_i x_i^* x_i(t_0 - \sigma_i)] + \sum_{j=1}^n d_{ij} \frac{x_j^*}{x_i^*} x_j(t_0 - \tau_{ij}) \\
\geq x_i(t_0) \left[ \beta_i^* - (b_i - c_i)x_i^* x_i(t_0) \right] = (b_i - c_i)x_i^* x_i(t_0)(1 - x_i(t_0)) > 0.
\]

But this is not possible, since the definition of \( t_0 \) implies \( x_i'(t_0) \leq 0 \).
Next, we prove that \( \ell_i \geq 1 \) for all \( i = 1, \ldots, n \). Choose \( i \) such that \( \ell_i = \min_{1 \leq j \leq n} \ell_j \), and suppose that \( \ell_i < 1 \). Let \( T > 0 \) and \( \varepsilon > 0 \) be chosen so that \( x_j(t) \geq \ell_i - \varepsilon \) for all \( t \geq T - \tau \) and \( 1 \leq j \leq n \), and

\[
\ell_i (b_i - c_i) x_i^*(1 - \ell_i) - \varepsilon \left( c_i x_i^* \ell_i + \sum_{j=1}^n d_{ij} \frac{x_j^*}{x_i^*} \right) =: m_i > 0.
\]

If \( x_i(t) \) is eventually monotone, then \( x_i(t) \to \ell_i \), and for \( t \geq T \) we have

\[
x_i'(t) \geq x_i(t) [a_i - b_i x_i(t) + c_i x_i^*(\ell_i - \varepsilon)] + (\ell_i - \varepsilon) \sum_{j=1}^n d_{ij} \frac{x_j^*}{x_i^*} \to m_i \quad \text{as} \quad t \to \infty,
\]

leading to \( x_i(t) \to \infty \) as \( t \to \infty \), which is a contradiction. If \( x_i(t) \) is not eventually monotone, there is a sequence \( t_n \to \infty \) with \( x_i(t_n) \to \ell_i \) and \( x_i'(t_n) = 0 \). For \( t_n \geq T \), we obtain the inequality above for \( t_n \) instead of \( t \), which yields \( 0 = x_i'(t_n) \geq m_i \), again a contradiction. This proves that \( \ell_i \geq 1 \). \( \square \)

We are ready to state the main results of this section:

**Theorem 3.4.** Consider (1.1) with \( b_i > c_i \) for \( 1 \leq i \leq n \). If there is a positive equilibrium \( x^* \) of (1.1), then \( x^* \) is hyperbolic and globally asymptotically stable (with respect to \( C_0^+ \)).

**Proof.** Let \( x^* = (x_1^*, \ldots, x_n^*) \). After the changes \( x_i(t) \mapsto \frac{x_i(t)}{x_i^*} \), consider system (3.8), with positive equilibrium \( \mathbf{1} \), where \( \mathbf{1} = (1, \ldots, 1) \in \mathbb{R}^n \). In view of Lemmas 3.2 and 3.3, we only need to prove that \( L_i := \limsup_{t \to \infty} x_i(t) \leq 1 \) for \( 1 \leq i \leq n \) and any positive solution \( x(t) \) of (3.8).

For the sake of contradiction, suppose that \( L_i = \max_j L_j > 1 \). Choose \( \varepsilon > 0 \) and \( t > \tau \), such that \( x_j(t) \leq L_i + \varepsilon \) for all \( t \geq T - \tau \) and \( 1 \leq j \leq n \), and

\[
L_i (b_i - c_i) x_i^*(1 - L_i) + \varepsilon \left( c_i x_i^* L_i + \sum_{j=1}^n d_{ij} \frac{x_j^*}{x_i^*} \right) < 0.
\]

Separating the cases of \( x_i(t) \) eventually monotone and not eventually monotone, and reasoning as in the proofs of Theorem 3.3 and Lemma 3.3, we obtain a contradiction. Details are omitted. \( \square \)

We now give sufficient conditions for the existence of a positive equilibrium of (1.1).

**Theorem 3.5.** Consider (1.1) and suppose that

\[
b_i - c_i > 0, \quad a_i + \sum_j d_{ij} > 0 \quad \text{for} \quad i = 1, \ldots, n. \tag{3.9}
\]

Then, there is a positive equilibrium of (1.1), which is globally asymptotically stable (in \( C_0^+ \)).

**Proof.** Arguing as in the proof of Lemma 3.3 with \( \beta_i = a_i + \sum_j d_{ij} \) instead of \( \beta_i^* \), if \( \beta_i > 0 \) for all \( i = 1, \ldots, n \), we easily conclude that \( \liminf_{t \to \infty} x(t; \varphi) > 0 \) for any \( \varphi \in C_0^+ \).

Next, denote \( \mathbf{1} = (1, \ldots, 1) \in C^+ \) as before. Let \( l > 0 \) be large enough so that \( f_i(\mathbf{1}) = l \left[ a_i + \sum_j d_{ij} - (b_i - c_i)l \right] \leq 0 \), for \( f_i \) as in (2.2). Since (1.1) is cooperative, then the components of the solution \( x(t) = x(t; \mathbf{1}) \) are non-increasing.
and globally asymptotically stable (with respect to $C^+$).

If there is a positive equilibrium $x^*$ which generalizes Theorem 2.1: equilibrium always exists if (2.5) holds.

$$\lim_{t \to \infty} x_i(t) = x^*_i$$

and does not imply the existence of a positive equilibrium. For instance, for $[8, 9]$, the matrix $M$ does not have a positive equilibrium. For the patch-structured model (1.4) introduced by Takeuchi et al.

Example 3.1. Consider the system:

$$x_{i}^r(t) = x_{i}(t)[a_{i} - b_{i} x_{i}(t)] + \sum_{j=1}^{n} d_{ij} [x_{j}(t - \tau_{ij}) - x_{i}(t)], \quad i = 1, \ldots, n$$

with $a_{i} > 0, b_{i} > 0, d_{ij} \geq 0$ and delays $\tau_{ij} \geq 0$. For $\beta_{i}$ as in (2.5), we have $\beta_{i} = a_{i}$, and thus system (3.11) has a positive equilibrium which is globally asymptotically stable.

Example 3.2. Consider the system:

$$x_{i}^r(t) = x_{i}(t)[a_{i} - b_{i} x_{i}(t)] - \sum_{j=1}^{n} b_{ij} x_{i}(t - \sigma_{ij}) + \sum_{j=1}^{n} a_{ij} x_{j}(t), \quad i = 1, \ldots, n$$

for $a_{i0} \in \mathbb{R}, b_{i0} > 0, b_{ik} \leq 0, a_{ij} \geq 0$ for $i \neq j$, and $\sigma_{ik} > 0, i, j = 1, \ldots, n, k = 1, \ldots, m$. System (3.12) has the form (1.2) with $a_{i} = a_{i0} + a_{ii}$, so we adapt conditions (3.9) and Theorem 3.5 (stated for (1.1)) to this situation by replacing $c_{i}$ with $- \sum_{k=1}^{m} b_{ik}$, and derive the following criterion:

Theorem 3.6. Define $b_{i} := \sum_{k=0}^{m} b_{ik}$ and $a_{i} := \sum_{j=0}^{n} a_{ij}$. If

$$b_{i} > 0 \quad \text{and} \quad a_{i} > 0, \quad i = 1, \ldots, n$$

then there exists a positive equilibrium of (3.12), which is a global attractor of all positive solutions.
Remark 3.1. Theorem 3.6 strongly improves Theorem 3.2 of Liu [5], who considered (3.12) with severe additional restrictions: in [5], it is assumed that conditions (3.13) are fulfilled, that the matrix $[a_{ij}]$ (and hence also $M$) is irreducible and that $\frac{a_{11}}{s_1} = \frac{a_{22}}{s_2} = \cdots = \frac{a_{nn}}{s_n} = K$. Under these conditions, Liu proved that the equilibrium $x^* = (K, K, \ldots, K)$ is globally attractive.

4. Positive heteroclinic solutions. In this section, we always assume that $M$ is irreducible. Under conditions that guarantee the existence of a globally attractive equilibrium $x^* > 0$, the goal is to prove that there is a positive heteroclinic solution for (1.1) connecting the two equilibria 0 and $x^*$. We first need to show that if $\mu_0 > 0$ then there is a positive eigenfunction for the linearization of (1.1) at zero.

Lemma 4.1. Assume that $M$ is an irreducible matrix, with $s(M) > 0$. Then there is a dominant characteristic eigenvalue of (3.1) (i.e., $\lambda_0$ is a characteristic eigenvalue, and $\Re \lambda < 0$ for all the other characteristic eigenvalues $\lambda \neq \lambda_0$ of (3.1)) and a positive eigenvector associated with $\lambda_0$.

Proof. The linearization of (1.1) at 0, given by (3.1), has characteristic equation

$$\det \Delta(\lambda) = 0,$$

where $\Delta(\lambda) = M(\lambda) - \lambda I$ (4.1)

and $M(\lambda)$ is defined by $M(\lambda) = A + D(\lambda)$, where

$$A = \text{diag}(a_i)_{i=1}^n, \quad D(\lambda) = \left[ d_{ij} e^{-\lambda \tau_{ij}} \right].$$

(4.2)

Observe that when $\lambda = 0$ we obtain $M(0) = M$. For $\lambda$ real and positive, clearly $M(\lambda_1) < M(\lambda_2)$ and $\Delta(\lambda_1) < \Delta(\lambda_2)$ for $\lambda_1 > \lambda_2 > 0$. The matrix $M$ is cooperative and irreducible, hence the matrices $M(\lambda)$, $\Delta(\lambda)$ are cooperative and irreducible as well, therefore

$$\mu_\lambda := s(M(\lambda)) \in \sigma(M(\lambda)), \quad s_\lambda := s(\Delta(\lambda)) = \mu_\lambda - \lambda \in \sigma(\Delta(\lambda)) \quad \text{for} \quad \lambda \geq 0.$$ 

This notation includes the case $\mu_0 = s(M)$ previously defined. The properties of cooperative irreducible matrices (see e.g. Appendix A of [7]) imply that the functions $\lambda \mapsto \mu_\lambda$ and $\lambda \mapsto s_\lambda$ are strictly decreasing on $[0, \infty)$. Since $\mu_0 = s_0 > 0$ and $s_\lambda \to -\infty$ as $\lambda \to \infty$, there is a unique positive number $\lambda_0$ satisfying

$$\lambda_0 = \mu_0.$$ (4.3)

Moreover, $\lambda_0 = \mu_\lambda_0$ is a (simple) eigenvalue of $M(\lambda_0)$, and there exists a positive vector $v$ such that

$$\lambda_0 v = M(\lambda_0) v$$

(see [7], p. 258). Thus $\Delta(\lambda_0) v = 0$, i.e., $\lambda_0$ is a root of (4.1) and $\text{Ker} \Delta(\lambda_0)$ is one dimensional, spanned by $v$. This implies that $x(t) = e^{\lambda_0 t} v$, $t \in \mathbb{R}$, is a positive solution of (3.1). Furthermore, $\lambda_0$ is given by $\lambda_0 := \max \{ \lambda > 0 : \lambda \leq \mu_\lambda \}$.

Next, we claim that $\lambda_0$ is the positive dominant root of (4.1). The proof follows along the lines of the proof of Lemma 4.3 in [1]. Let $\lambda = a + ib$ be a solution of (4.1), with $\lambda \neq \lambda_0$ and $a > 0$. Since $\lambda \in \sigma(M(\lambda))$, we get $a \leq \mu_\lambda$.

If $b = 0$, then $a \leq \mu_a$, and the definition of $\lambda_0$ yields $a < \lambda_0$. Suppose now that $b > 0$. Choose a vector $\eta = (\eta_1, \ldots, \eta_n) \neq 0$, for which

$$A + D(a + ib) - (a + ib) I \eta = 0,$$
and a constant \( c > a \) satisfying \( a_i + c - a > 0, i = 1, \ldots, n \). Then, \( [A + (c - a)I + D(a + ib)]\eta = (c + ib)\eta \). Set \( |\eta| \in \mathbb{R}^n \) as the vector \( |\eta| = (|\eta_1|, \ldots, |\eta_n|) \). For the coordinates of \( |\eta| \), we obtain
\[
|c + ib||\eta_i| \leq (a_i + c - a)|\eta_i| + \sum_j d_{ij}e^{-\sigma_{ij}|\eta_j|}, \quad i = 1, \ldots, n.
\]
If \( a \geq \lambda_0 \), then
\[
|c + ib||\eta_i| \leq (c - \lambda_0)|\eta_i| + (M(\lambda_0)|\eta|), \quad i = 1, \ldots, n,
\]
where \( (M(\lambda_0)|\eta|)_i \) is the \( i \)th-coordinate of the vector \( M(\lambda_0)|\eta| \). We have \( b > 0 \) and \( \eta_i \neq 0 \) for some \( i \), thus
\[
c|\eta| \leq [(c - \lambda_0)I + M(\lambda_0)]|\eta|
\]
with \( c|\eta| \neq [(c - \lambda_0)I + M(\lambda_0)]|\eta| \). From the properties of irreducible non-negative matrices, it follows that the spectral radius \( r = r((c - \lambda_0)I + M(\lambda_0)) \) satisfies \( r > c \) and \( r \in \sigma((c - \lambda_0)I + M(\lambda_0)) \). This implies that for some \( \xi \in \mathbb{R}^n, \xi \neq 0 \), we have
\[
[(c - \lambda_0)I + M(\lambda_0)]\xi = r\xi
\]
and we get \( M(\lambda_0)\xi = (r - c + \lambda_0)\xi \). The definition of \( \lambda_0 \) and (4.3) imply now that \( r - c + \lambda_0 \leq \mu\lambda_0 = \lambda_0 \), which contradicts the fact that \( r - c > 0 \). Hence \( a < \lambda_0 \), and the proof is complete.

We now state the existence of positive heteroclinic solutions.

**Theorem 4.1.** Assume that \( M \) is an irreducible matrix with \( s(M) > 0 \). If \( c_i > 0 \) for some \( i \), assume in addition that (3.9) holds. Then, there exists a positive heteroclinic solution \( u^*(t) \) of (1.1) with \( u^*(-\infty) = 0 \) and \( u^*(\infty) = x^* \), where \( x^* \) is the positive equilibrium of (1.1). Moreover, \( u^*(t) \) has exponential asymptotical decay at \( -\infty \) given by \( u^*(t) = ce^{\lambda_0 t} + O(e^{(\lambda_0 - \varepsilon) t}) \) for some \( \alpha > 0 \) and each fixed \( \varepsilon > 0 \), where \( \lambda_0 \) and \( \varepsilon \) are as in (4.4).

**Proof.** From the results in Section 3, the positive equilibrium \( x^* \) is hyperbolic, locally asymptotically stable, and a global attractor relative to the set of solutions with initial conditions in \( C^+_0 \). The result is now a consequence of Lemma 4.1 and Theorem 2.1 of [3] (cf. Remark 4.1 below).

The work in [3] also motivates the consideration of a diffusive version of system (1.1), given by the reaction-diffusion equation
\[
\frac{\partial u_i}{\partial t}(t,x) = \delta_i \Delta u_i(t,x) + u_i(t,x)[a_i - b_i u_i(t,x) + c_i u_i(t - \sigma_i,x)] + \sum_{j=1}^n d_{ij} u_j(t - \tau_{ij},x), \quad i = 1, \ldots, n, \tag{4.5}
\]
for \( t \in \mathbb{R}, x \in \Omega \subset \mathbb{R}^p \), with diffusion coefficients \( \delta_i > 0 \) and all other coefficients as in (1.1).

**Theorem 4.2.** Assume that \( M \) is an irreducible matrix with \( s(M) > 0 \), and that \( \text{det} \Delta'(\lambda_0) \neq 0 \), for \( \lambda_0 \) the dominant eigenvalue of (3.1). If \( c_i > 0 \) for some \( i \), assume in addition that (3.9) is satisfied. Then, for \( c > 0 \) sufficiently large, system (4.5) has a positive traveling wave solution of the form \( u(x,t) = \psi(ct + w \cdot x) \) for each unit vector \( w \in \mathbb{R}^p \), with \( \psi(-\infty) = 0 \) and \( \psi(\infty) = x^* \), where \( x^* \) is the positive equilibrium of (1.1).
Proof. To check the hypotheses in [3], it remains to show that \( \lambda_0 \) is a simple eigenvalue of (3.1). The proof of Lemma 4.1 guarantees that \( K e^T \Delta(\lambda_0) \) is one dimensional, thus \( \det \Delta'(\lambda_0) \neq 0 \) implies that \( \lambda_0 \) is a simple root of (4.1). The theorem follows now from Theorem 4.3 of [3].

Remark 4.1. Actually, the set of hypotheses in [3] requires the existence of a positive simple dominant characteristic root \( \lambda_0 \) for the linearized equation (3.1). However, in [3] the requirement of \( \lambda_0 \) being simple was only used to prove that the linearized second order DDE for the wave profiles \( \psi(t) \) has a characteristic root \( \lambda(c) \) with \( \lambda(c) \to \lambda_0 \) as \( c \to \infty \) (cf. Lemma 4.1 and Theorem 4.3 in [3]). As one can see from the proof of Theorem 2.1 in [3], establishing the existence of a positive heteroclinic solution for the model without diffusion does not require the assumption of \( \lambda_0 \) being simple.

Example 4.1. For model (1.4), if \( M \) in (3.10) is irreducible and \( s(M) > 0 \), then (1.4) has a positive heteroclinic solution. We have \( \varepsilon_{ij} = e^{-\tau_i \tau_j} \), where \( \tau_{ij} \) is the time for the species to move from patch \( j \) to \( i \), and \( \gamma_{ij} \geq 0 \) is the per capita death rate for the species during that dispersion. Since \( \Delta'(\lambda_0) = -[I + \text{diag} \left( \sum_{j=1}^m \varepsilon_{ij} d_{ij} e^{-\lambda_0 \tau_{ij}} \right) ] \) (where \( d_{ii} = 0 \)), from Gerschgorin circle theorem all the eigenvalues \( z \) of \( \Delta'(\lambda_0) \) must satisfy \( |z + 1| \leq \sum \varepsilon_{ij} d_{ij} e^{-\lambda_0 \tau_{ij}} \) for some \( i \in \{1, \ldots, n\} \). Thus, if the time-delays \( \tau_{ij} \) are sufficiently small, \( \Delta'(\lambda_0) \neq 0 \), implying that \( \lambda_0 \) is a simple root of (4.1). Hence, in this situation the diffusive version of (1.4) has positive traveling wave fronts.

Example 4.2. Consider the special case \( n = 2 \) in (1.3):

\[
x_1'(t) = x_1(t)(a_1 - b_1 x_1(t) + d_{11} x_1(t - \tau_{11}) + d_{12} x_2(t - \tau_{12})) \\
x_2'(t) = x_2(t)(a_2 - b_2 x_2(t) + d_{12} x_1(t - \tau_{12}) + d_{22} x_2(t - \tau_{22}))
\]

(4.6)

where \( a_i \in \mathbb{R}, b_i > 0, \tau_{ij} \geq 0, d_{ij} \geq 0, i, j = 1, 2 \). The community matrix is given by \( M = \begin{bmatrix} \alpha_1 & d_{12} \\ d_{21} & \alpha_2 \end{bmatrix} \) for \( \alpha_i = a_i + d_{ii} \). The eigenvalues of \( M \) are always real, and \( M \) is irreducible if and only if \( d_{12} d_{21} \neq 0 \). If det \( M > 0 \) and \( \alpha_1 + \alpha_2 < 0 \), then \( \mu_0 = s(M) \) is negative, and \( x_i(t) \to 0 \) as \( t \to -\infty \) for \( i = 1, 2 \), for any non-negative solution of (4.6). With \( d_{12} d_{21} \neq 0 \), if either det \( M < 0 \), or det \( M \geq 0 \) and \( \alpha_1 + \alpha_2 > 0 \), then \( \mu_0 > 0 \) and there is a globally attractive positive equilibrium \((x_1^*, x_2^*)\) of (4.6); moreover, (4.6) has a positive heteroclinic solution \((u_1^*(t), u_2^*(t))\), with \( \lim_{t \to -\infty} (u_1^*(t), u_2^*(t)) = (0, 0) \) and \( \lim_{t \to -\infty} (u_1^*(t), u_2^*(t)) = (x_1^*, x_2^*) \). If \( d_{12} d_{21} = 0 \) and \( \alpha_1 + d_{12} > 0, \alpha_2 + d_{21} > 0 \), then there is an equilibrium \((x_1^*, x_2^*) > 0\), which is globally asymptotically stable.

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