

Global Dynamics for Lotka-Volterra Systems with Infinite Delay and Patch Structure

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Abstract

We study some aspects of the global dynamics of an n -dimensional Lotka-Volterra system with infinite delay and patch structure, such as extinction, persistence, existence and global attractivity of a positive equilibrium. Both the cases of an irreducible and reducible linear community matrix are considered, and no restriction on the signs of the intra- and inter-specific delayed terms is imposed. Although the system is not cooperative, our approach often uses comparison results applied to an auxiliary cooperative system. Some models in recent literature are generalised, and results improved.

Keywords: Lotka-Volterra system; infinite delay; patch-structure; global attractivity; persistence; extinction.

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1. Introduction

In recent years, mathematicians and biologists have been analysing biological models given by differential equations with time-delays and patch-structure. Models with patch-structure are frequently quite realistic, to account for heterogeneous environments and other biological features, where single or multiple species are distributed over several different patches or classes, with migration among them. Time-delays are very often present in models from population dynamics, neurosciences, ecology, epidemiology, chemistry and other sciences. Moreover, infinite delays have been considered in equations used in population dynamics since the works of Volterra, to translate the cumulative effect of the past history of a system. Typically, the “memory functions” appear as integral kernels and, although defined in the entire past, the delay should be introduced in such a way that its effect diminishes when going back in time.

In this paper, the following patch-structured Lotka-Volterra system with both infinite distributed and discrete delays is considered:

$$\begin{aligned} x_i'(t) = x_i(t) & \left(b_i - \mu_i x_i(t) - \sum_{j=1}^n a_{ij} \int_0^\infty K_{ij}(s) x_j(t-s) ds \right) \\ & + \sum_{j \neq i, j=1}^n (\varepsilon_{ij} \alpha_{ij} x_j(t - \tau_{ij}) - \alpha_{ji} x_i(t)), \quad i = 1, 2, \dots, n. \end{aligned} \quad (1.1)$$

Here, $\mu_i > 0$, $b_i, a_{ij} \in \mathbb{R}$, and, for $i \neq j$, $\alpha_{ij} \geq 0, \tau_{ij} \geq 0$, $\varepsilon_{ij} \in (0, 1]$, $i, j = 1, \dots, n$; the kernels $K_{ij} : [0, \infty) \rightarrow [0, \infty)$ are L^1 functions, normalized so that

$$\int_0^\infty K_{ij}(s) ds = 1, \quad \text{for } i, j = 1, \dots, n. \quad (1.2)$$

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Moreover, we suppose that for all i the linear operators defined by $L_{ii}(\varphi) = \int_0^\infty K_{ii}(s)\varphi(-s)ds$, for $\varphi : (-\infty, 0] \rightarrow \mathbb{R}$ bounded, are non-atomic at zero, which amounts to have $K_{ii}(0) = K_{ii}(0^+)$.

System (1.1) serves as a population model for the growth of single or multiple species distributed over n patches or classes: $x_i(t)$ is the density of the population on patch i , with b_i and μ_i as its usual Malthusian growth rate and (instantaneous) self-limitation coefficient, respectively, a_{ii} and a_{ij} ($i \neq j$) are respectively the intra- and inter-specific delayed acting coefficients; α_{ij} ($i \neq j$) are the dispersal rates of populations moving from patch j to patch i , and τ_{ij} the times taken during this dispersion; the coefficients $\varepsilon_{ij} \in (0, 1]$ appear to account for some lost of the populations during migration from one patch to another. Frequently, one takes $\varepsilon_{ij} = e^{-\gamma_{ij}\tau_{ij}}$ for some $\gamma_{ij} > 0$, $i, j = 1, \dots, n$, $i \neq j$, cf. e.g. [19]. Denoting

$$d_{ij} := \varepsilon_{ij}\alpha_{ij} \text{ for } i \neq j, \quad \beta_i := b_i - \sum_{j \neq i} \alpha_{ji},$$

(1.1) is written as

$$\begin{aligned} x'_i(t) = x_i(t) & \left(\beta_i - \mu_i x_i(t) - \sum_{j=1}^n a_{ij} \int_0^\infty K_{ij}(s)x_j(t-s)ds \right) \\ & + \sum_{j \neq i, j=1}^n d_{ij} x_j(t - \tau_{ij}), \quad i = 1, 2, \dots, n, \end{aligned} \quad (1.3)$$

where $\beta_i \in \mathbb{R}$, $\mu_i > 0$, $a_{ij} \in \mathbb{R}$, $d_{ij} \geq 0$, $\tau_{ij} \geq 0$ and the kernels K_{ij} are as above.

With model (1.1) in mind, in the present paper some aspects of the asymptotic behaviour of solutions to delayed Lotka-Volterra systems (1.3) are analysed. Although not very meaningful in biological terms, actually all the techniques and results in this paper apply to systems with several bounded delays or even infinite delays in the migration terms, which leads to more general systems of the form

$$\begin{aligned} x'_i(t) = x_i(t) & \left(\beta_i - \mu_i x_i(t) - \sum_{j=1}^n a_{ij} \int_0^\infty K_{ij}(s)x_j(t-s)ds \right) \\ & + \sum_{j \neq i, j=1}^n \sum_{p=1}^m d_{ij}^{(p)} x_j(t - \tau_{ij}^{(p)}), \quad i = 1, 2, \dots, n, \end{aligned} \quad (1.4)$$

with $d_{ij}^{(p)}, \tau_{ij}^{(p)} \geq 0$, or

$$\begin{aligned} x'_i(t) = x_i(t) & \left(\beta_i - \mu_i x_i(t) - \sum_{j=1}^n a_{ij} \int_0^\infty K_{ij}(s)x_j(t-s)ds \right) \\ & + \sum_{j \neq i, j=1}^n d_{ij} \int_0^\infty G_{ij}(s)x_j(t-s)ds, \quad i = 1, 2, \dots, n, \end{aligned} \quad (1.5)$$

with the kernels $G_{ij} \geq 0$ being L^1 functions with L^1 -norm one. Moreover, our method can be easily adapted to Lotka-Volterra systems with continuous coefficients and discrete delays depending on t .

Due to the biological interpretation of the model, only positive or non-negative solutions should be considered admissible. On the other hand, there are natural constraints on admissible phase spaces for functional differential equations (FDEs) with infinite delay (cf. Section 2). To deal with such kind of equations, a careful choice of a so-called ‘fading memory space’ as phase space is in order, see e.g. [10, 11], and one must consider *bounded* initial conditions. Thus, our framework accounts only for solutions of (1.3) with initial conditions of the form

$$x_i(\theta) = \varphi_i(\theta), \quad \theta \in (-\infty, 0], \quad \varphi_i(0) > 0, \quad i = 1, \dots, n, \quad (1.6)$$

where φ_i are non-negative and bounded continuous functions on $(-\infty, 0]$.

There is an immense literature on FDEs of Lotka-Volterra type, and it is impossible to mention all the relevant contributions. The present investigation was motivated by several papers, among them those of Takeuchi et al. [18, 19], Liu [14], and Faria [3, 4]. For other related papers, we refer to [2, 5, 15, 20], also for further references.

In [14], Liu considered a cooperative model for a species following a delayed logistic law, with the population structured in several classes and no delays in the migration terms, of the form

$$x'_i(t) = x_i(t) \left[b_i - \mu_i x_i(t) + \sum_{p=1}^m c_i^{(p)} x_i(t - \sigma_i^{(p)}) \right] + \sum_{j=1}^n d_{ij} x_j(t), \quad i = 1, \dots, n, \quad (1.7)$$

where $\mu_i > 0, b_i > 0$ and $c_i^{(p)}, d_{ij}, \sigma_i^{(p)} \geq 0$ for $i, j = 1, \dots, n, p = 1, \dots, m$. Moreover, in [14] only the case $D = [d_{ij}]$ an irreducible matrix was studied, and the further quite restrictive conditions $(b_i + \sum_{j=1}^n d_{ij}) / (\mu_i - \sum_{p=1}^m c_i^{(p)}) = k$ for $1 \leq i \leq n$ (k a positive constant) were imposed. On the other hand, Takeuchi et al. [19] studied the system

$$x'_i(t) = x_i(t) (b_i - \mu_i x_i(t)) + \sum_{j \neq i, j=1}^n (e^{-\gamma_{ij} \tau_{ij}} \alpha_{ij} x_j(t - \tau_{ij}) - \alpha_{ji} x_i(t)), \quad i = 1, \dots, n, \quad (1.8)$$

where $\mu_i > 0, b_i \in \mathbb{R}$ and $\alpha_{ij}, \tau_{ij}, \gamma_{ij} \geq 0$ for $i, j = 1, \dots, n, j \neq i$. Note that (1.1) is a natural generalization of (1.8), obtained by the addition of interacting terms with infinite delay. Again, only the case of an irreducible matrix $D = [d_{ij}]$, where now $d_{ij} = e^{-\gamma_{ij} \tau_{ij}} \alpha_{ij}$, was studied in [19].

In [4], the author analyses several aspects of the asymptotic behaviour of solutions to the more general cooperative system

$$x'_i(t) = x_i(t) \left[b_i - \mu_i x_i(t) + \sum_{p=1}^m c_i^{(p)} x_i(t - \sigma_i^{(p)}) \right] + \sum_{j=1}^n \sum_{p=1}^m d_{ij}^{(p)} x_j(t - \tau_{ij}^{(p)}), \quad i = 1, \dots, n, \quad (1.9)$$

where: $b_i \in \mathbb{R}, \mu_i > 0$ and $c_i^{(p)}, d_{ij}^{(p)}, \sigma_i^{(p)}, \tau_{ij}^{(p)} \geq 0$, for $i, j = 1, \dots, n, p = 1, \dots, m$. The situations of $D = [d_{ij}]$ an irreducible or a reducible matrix were both addressed. Note that models (1.7) and (1.8) are particular cases of (1.9).

For the patch structured Lotka-Volterra models (1.3), (1.4) or (1.5), for simplicity we write $A = [a_{ij}]$ and $D = [d_{ij}]$, with $d_{ii} := 0$, and where $d_{ij} := \sum_{p=1}^m d_{ij}^{(p)}$ for (1.4). The matrix $M(0) = \text{diag}(\beta_1, \dots, \beta_n) - D$, i.e.,

$$M(0) = \begin{bmatrix} \beta_1 & d_{12} & \cdots & d_{1n} \\ d_{21} & \beta_2 & \cdots & d_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ d_{n1} & d_{n2} & \cdots & \beta_n \end{bmatrix}, \quad (1.10)$$

may be interpreted as the *linear community matrix*. For coefficients $a_{ij} \in \mathbb{R}$, we shall use the standard notation

$$a_{ij}^- = \max(0, -a_{ij}), \quad a_{ij}^+ = \max(0, a_{ij}).$$

Throughout the paper, together with $M(0)$ we shall consider the matrix

$$N_0 = \text{diag}(\mu_1, \dots, \mu_n) - [a_{ij}^-]. \quad (1.11)$$

The algebraic properties of $M(0)$ and N_0 will play a crucial role in the global dynamics of the system.

For simplicity, this paper deals with system (1.3), rather than (1.4) or (1.5), and addresses its global asymptotic behaviour, in what concerns its dissipativity and persistence, extinction of the populations, and the existence and global attractivity of a positive equilibrium. As in the cited papers

[14, 19], most papers dealing with patch structured models only analyse the situation of an irreducible linear community matrix. Here, both the cases of $M(0)$ irreducible and reducible are considered. Of course, if $M(0)$ is irreducible, sharper criteria can be obtained, namely a threshold criterion of exchanging of global attractivity between the trivial solution and a positive equilibrium. Rather than Lyapunov functional techniques, the approach exploited here is based on comparison results and monotone techniques (see [16]) applied to an auxiliary cooperative system, coupled with theory of M-matrices.

The contents of the paper are now briefly described. Section 2 is a preliminary section, where an abstract formulation to deal with (1.3) is set, and some notation and auxiliary results are given, including some known properties from matrix theory; also we prove some important estimates used throughout the paper. Section 3 provides criteria for the local stability and global attractivity of the trivial equilibrium – in biological terms, the latter translates as the extinction of the populations in all patches. In Section 4, we consider the particular case of (1.3) with all coefficients $a_{ij} \leq 0$, thus a cooperative Lotka-Volterra system, and investigate its persistence and global asymptotic convergence to an equilibrium. Finally, Section 5 is devoted to the study of the persistence, the existence and the global attractivity of a positive equilibrium for the general model (1.3).

2. Preliminaries: abstract framework, notation and auxiliary results

In this preliminary section, we first set an abstract framework to deal with system (1.3). In view of the unbounded delays, the problem must be carefully formulated by defining an appropriate Banach phase space where the problem is well-posed.

Let g be a function satisfying the following properties:

- (g1) $g : (-\infty, 0] \rightarrow [1, \infty)$ is a non-increasing continuous function, $g(0) = 1$;
- (g2) $\lim_{u \rightarrow 0^-} \frac{g(s+u)}{g(s)} = 1$ uniformly on $(-\infty, 0]$;
- (g3) $g(s) \rightarrow \infty$ as $s \rightarrow -\infty$.

For $n \in \mathbf{N}$, define the Banach space $UC_g = UC_g(\mathbb{R}^n) := \{\phi \in C((-\infty, 0]; \mathbb{R}^n) : \sup_{s \leq 0} \frac{|\phi(s)|}{g(s)} < \infty, \frac{\phi(s)}{g(s)} \text{ is uniformly continuous on } (-\infty, 0]\}$, with the norm

$$\|\phi\|_g = \sup_{s \leq 0} \frac{|\phi(s)|}{g(s)},$$

where $|\cdot|$ is a chosen norm in $\mathbb{R}^n$. Consider also the space $BC = BC(\mathbb{R}^n)$ of bounded continuous functions $\phi : (-\infty, 0] \rightarrow \mathbb{R}^n$. It is clear that $BC \subset UC_g$.

The space UC_g is an admissible phase space for n -dimensional FDEs with infinite delay (cf. [10, 11]) written in the abstract form

$$\dot{x}(t) = f(t, x_t), \tag{2.1}$$

where $f : D \subset \mathbb{R} \times UC_g \rightarrow \mathbb{R}^n$ is continuous and, as usual, segments of solutions in the phase space UC_g are denoted by x_t , $x_t(s) = x(t+s)$, $s \leq 0$. When f is regular enough and the initial conditions are *bounded*, it is known that the initial value problem is well-posed, in the sense that there exists a unique solution $x(t)$ of the problem $\dot{x}(t) = f(t, x_t)$, $x_\sigma = \varphi \in BC$, denoted by $x(t; \sigma, \varphi)$ in $\mathbb{R}^n$ or $x_t(\sigma, \varphi)$ in UC_g ; for autonomous systems $\dot{x}(t) = f(x_t)$ and $\varphi \in BC$, the solution of $\dot{x}(t) = f(x_t)$, $x_0 = \varphi$ is simply denoted by $x(t; \varphi) \in \mathbb{R}^n$ and $x_t(\varphi) \in UC_g$. Moreover, bounded positive orbits of (2.1) are precompact in UC_g [10, 11].

An appropriate formulation for problem (1.3)-(1.6) is set as follows. From Lemma 4.1 in [7], for any $\delta > 0$ there is a continuous function g satisfying (g1)–(g3) and such that

$$\int_0^\infty g(-s)K_{ij}(s) ds < 1 + \delta, \quad i, j = 1, \dots, n. \tag{2.2}$$

Whenever it is necessary, one fixes a positive δ and inserts the problem into the phase space UC_g , where g is any function satisfying the above conditions (g1)-(g3) and (2.2). Of course, if one considers the more general system (1.5), one should demand that g also satisfies the conditions $\int_0^\infty g(-s)K_{ij}(s)ds < 1 + \delta$, $i, j = 1, \dots, n$.

In the space UC_g , a vector c is identified with the constant function $\psi(s) = c$ for $s \leq 0$. A vector c in $\mathbb{R}^n$ is said to be *positive* (respectively *non-negative*) if all its components are positive (respectively non-negative). We use the notation $\mathbb{R}_+^n = \{x \in \mathbb{R}^n : x \geq 0\}$, and $BC^+ = BC^+(\mathbb{R}^n) = \{(\varphi, \psi) \in BC : \varphi(s), \psi(s) \geq 0 \text{ for all } s \leq 0\}$. In view of the biological meaning of (1.3), the framework is restricted to positive or non-negative initial conditions. As a set of admissible initial conditions for (1.3), we take the subset BC_0^+ of BC^+ , $BC_0^+ = \{(\varphi, \psi) \in BC^+ : \varphi(0) > 0, \psi(0) > 0\}$. It is easy to see that all the coordinates of solutions with initial conditions in BC^+ , respectively BC_0^+ , remain non-negative, respectively positive, for all $t \geq 0$ whenever they are defined (see e.g. [16]).

A system (2.1) is said to be *cooperative* if it satisfies the quasi-monotonicity condition in p. 78 of Smith's monograph [16]: whenever $\varphi, \psi \in BC^+$, $\varphi \leq \psi$ and $\varphi_i(0) = \psi_i(0)$ holds, then $f_i(\varphi) \leq f_i(\psi)$, for $1 \leq i \leq n$. Hence, system (1.3) is cooperative if and only if $a_{ij} \leq 0$ for all $i, j = 1, \dots, n$.

The following crucial estimates will be used throughout the paper. For similar arguments, cf. [5].

Lemma 2.1 *Let $x : \mathbb{R} \rightarrow \mathbb{R}^n$ be a continuous function with $x_0 = \varphi \in BC$. For each $j \in \{1, \dots, n\}$, suppose that there are constants $M \in \mathbb{R}$ and $t_0 > 0$ such that $x_j(t) \leq M$, respectively $x_j(t) \geq M$, for $t \geq t_0$. Then, for any $\varepsilon > 0$ there exists $T_0 \geq t_0$ such that*

$$\int_0^\infty K_{ij}(s)x_j(t-s)ds \leq M + \varepsilon, \quad t \geq T_0, 1 \leq i \leq n,$$

respectively

$$\int_0^\infty K_{ij}(s)x_j(t-s)ds \geq M - \varepsilon, \quad t \geq T_0, 1 \leq i \leq n.$$

Proof. Suppose that $x_j(t) \leq M$ for $t \geq t_0$. Fix $\varepsilon > 0$, and take g satisfying conditions (g1)-(g3) and (2.2) with $0 < \delta(1 + \delta) \leq \varepsilon$. Since $x_j(t)$ is bounded from above on $(-\infty, \infty)$, take $K > 0$ such that $\sup_{t \in \mathbb{R}} x_j(t) \leq K$, and choose $T > 0$ such that $K/g(-T) < \delta$. For $t \geq T_0 := T + t_0$, from (1.2) and (2.2) we have

$$\begin{aligned} \int_0^\infty K_{ij}(s)x_j(t-s)ds &= \int_0^T K_{ij}(s)x_j(t-s)ds + \int_T^\infty K_{ij}(s)x_j(t-s)ds \\ &\leq M \int_0^T K_{ij}(s)ds + \int_T^\infty g(-s)K_{ij}(s)\frac{K}{g(-s)}ds \\ &\leq M \int_0^T K_{ij}(s)ds + \int_T^\infty g(-s)K_{ij}(s)\frac{K}{g(-T)}ds \\ &\leq M \int_0^T K_{ij}(s)ds + \delta \int_T^\infty g(-s)K_{ij}(s)ds \\ &\leq M + \delta(1 + \delta) \leq M + \varepsilon. \end{aligned}$$

The other inequality is proven in a similar way.

We now recall some notation and results from matrix theory. An $n \times n$ matrix $M = [m_{ij}]$ is said to be *cooperative* if all its off-diagonal entries are nonnegative: $m_{ij} \geq 0$ for $i \neq j$.

Let $\sigma(M)$ be the spectrum of M . The *spectral bound* $s(M)$ of M is defined as

$$s(M) = \max\{\operatorname{Re} \lambda : \lambda \in \sigma(M)\}.$$

It is well-known that if M is cooperative and irreducible, then $s(M) \in \sigma(M)$ and there is a positive eigenvector associated with $s(M)$ (see e.g. [1, 8]).

A square matrix M is said to be an *M-matrix* (respectively *non-singular M-matrix*) if all its off-diagonal entries are non-positive and all its eigenvalues have a non-negative (respectively positive) real part.

Lemma 2.2 For a square matrix $M = [m_{ij}]$ with $m_{ij} \leq 0$ for $i \neq j$, the following conditions are equivalent:

- (i) M is a non-singular M-matrix;
- (ii) M is an M-matrix and is non-singular;
- (iii) all principal minors of M are positive;
- (iv) there is a positive vector v such that $Mv > 0$;
- (v) M is non-singular and $M^{-1} \geq 0$.

There are many other equivalent ways of defining non-singular M-matrices, as well as M-matrices, see [1, 8] for a proof of Lemma 2.2 and further properties of these matrices. In [8], non-singular M-matrices and M-matrices are also designated by *matrices of classes K* and K_0 , respectively. The notation is far from being uniform, and many authors call *M-matrices* the matrices defined here as *non-singular M-matrices*.

From these definitions, it is apparent that for a cooperative matrix M , $s(M) \leq 0$ (respectively $s(M) < 0$) if and only if $-M$ is an M-matrix (respectively a non-singular M-matrix).

For (1.3), the matrix $M(0)$ defined in (1.10) is cooperative. If $D = [d_{ij}]$ is irreducible, then $M(0)$ is irreducible as well. For cooperative and irreducible matrices, the following lemma is useful.

Lemma 2.3 If $M = [m_{ij}]$ is a cooperative and irreducible matrix, then $s(M) > 0$ if and only if there exists a positive vector v such that $Mv > 0$.

Proof. Let $M = [m_{ij}]$ be cooperative and irreducible. Then $s(M)$ is an eigenvalue of M with a positive associated eigenvalue v , thus $s(M) > 0$ implies that $Mv = s(M)v > 0$ for some positive vector v (cf. [1]).

Conversely, let v be a positive vector such that $Mv > 0$, and for the sake of contradiction suppose that $s(M) \leq 0$. Then $-M$ is an M-matrix, or, in other words, for any $\delta > 0$ the matrix $\delta I - M$ is a non-singular M-matrix [8]; this implies that $(\delta I - M)^{-1} \geq 0$. Choose $\delta > 0$ small so that $Mv > \delta v$. Then we have $v = (\delta I - M)^{-1}(\delta I - M)v \leq 0$, a contradiction.

3. Stability of the trivial equilibrium

The standard notions of stability and attractivity used here are always defined in the context of the set BC_0^+ of admissible initial conditions, as recalled below.

Definition 3.1. An equilibrium $x^* \geq 0$ of (1.3) is said to be *stable* if for any $\varepsilon > 0$ there is $\delta = \delta(\varepsilon) > 0$ such that $\|x_t(\varphi) - x^*\|_g < \varepsilon$ for all $\varphi \in BC_0^+$ with $\|\varphi - x^*\|_g < \delta$ and $t \geq 0$; x^* is said to be *globally attractive* if $x(t) \rightarrow x^*$ as $t \rightarrow \infty$, for all solutions $x(t)$ of (1.3) with initial conditions $x_0 = \varphi \in BC_0^+$; and x^* is *globally asymptotically stable (GAS)* if it is stable and globally attractive.

In this section, we address the stability and attractivity of the trivial equilibrium. When (1.3) refers to a population model, the global attractivity of 0 means the extinction of the populations in all patches.

Theorem 3.1 For system (1.3), (i) if $s(M(0)) < 0$, then the equilibrium 0 is hyperbolic and locally asymptotically stable; (ii) if $s(M(0)) > 0$, then 0 is unstable.

Proof. We have already observed that $s(M(0)) < 0$ if and only if $-M(0)$ is a non-singular M-matrix.

(i) Assume that $s(M(0)) < 0$. The linearization of (1.3) at zero is given by

$$x'_i(t) = \beta_i x_i(t) + \sum_{j \neq i} d_{ij} x_j(t - \tau_{ij}), \quad i = 1, 2, \dots, n. \quad (3.1)$$

Denote $B = \text{diag}(\beta_1, \dots, \beta_n)$. The characteristic equation for (3.1) is

$$\det \Delta(\lambda) = 0, \quad \text{where } \Delta(\lambda) = M(\lambda) - \lambda I \quad (3.2)$$

and

$$M(\lambda) = \begin{bmatrix} \beta_1 & d_{12}e^{-\lambda\tau_{12}} & \cdots & d_{1n}e^{-\lambda\tau_{1n}} \\ d_{21}e^{-\lambda\tau_{21}} & \beta_2 & \cdots & d_{2n}e^{-\lambda\tau_{2n}} \\ \vdots & \vdots & \ddots & \vdots \\ d_{n1}e^{-\lambda\tau_{n1}} & d_{n2}e^{-\lambda\tau_{n2}} & \cdots & \beta_n \end{bmatrix} =: B + D(\lambda).$$

Since $-M(0)$ is a non-singular M-matrix, from a result in [6] (which can be generalised to linear FDEs with infinite delay) $x = 0$ is asymptotically stable as a solution of (3.1), for all values of the delays.

(ii) Assume now that $s(M(0)) > 0$.

First consider the case of $D = D(0)$ an irreducible matrix. Observe that $\Delta(0) = M(0)$ and $\Delta(\lambda_1) > \Delta(\lambda_2)$ for $0 \leq \lambda_1 < \lambda_2$. Since the matrices $\Delta(\lambda)$, $0 \leq \lambda < \infty$, are irreducible and cooperative, then $s(\Delta(\lambda)) \in \sigma(\Delta(\lambda))$, and $\lambda \mapsto s(\Delta(\lambda))$ is continuous and strictly decreasing on $[0, \infty)$. Clearly, $s(\Delta(\lambda)) \rightarrow -\infty$ as $\lambda \rightarrow \infty$; together with the condition $s(\Delta(0)) > 0$, this implies the existence of a unique $\lambda^* > 0$ such that $s(\Delta(\lambda^*)) = 0$. But $s(\Delta(\lambda^*)) \in \sigma(\Delta(\lambda^*))$, or, in other words, λ^* is a characteristic root for (3.1). This proves that (3.1) is unstable, hence 0 is unstable as a solution of (1.3).

Next, consider the case of D reducible. After a simultaneous permutation of rows and columns, for each $\lambda \geq 0$ the matrix $D(\lambda)$ is written in a triangular form as

$$D(\lambda) = \begin{bmatrix} D_{11}(\lambda) & \cdots & D_{1\ell}(\lambda) \\ & \ddots & \\ 0 & \cdots & D_{\ell\ell}(\lambda) \end{bmatrix},$$

where $D_{lm}(\lambda)$ are $n_l \times n_m$ matrices, with $D_{ll}(\lambda)$ irreducible blocks and $\sum_{l=1}^{\ell} n_l = n$. Only to prove the result for $\ell = 2$ is needed, since the general case will follow by induction.

For $\lambda \geq 0$, let $D(\lambda) = \begin{bmatrix} D_{11}(\lambda) & D_{12}(\lambda) \\ 0 & D_{22}(\lambda) \end{bmatrix}$, where $D_{11}(\lambda), D_{22}(\lambda)$ are irreducible, and write $M(\lambda), \Delta(\lambda)$ in the form

$$\begin{aligned} M(\alpha) &= B + D(\lambda) = \begin{bmatrix} M_{11}(\lambda) & M_{12}(\lambda) \\ 0 & M_{22}(\lambda) \end{bmatrix}, \\ \Delta(\lambda) &= M(\lambda) - \lambda I_n = \begin{bmatrix} M_{11}(\lambda) - \lambda I_{n_1} & M_{12}(\lambda) \\ 0 & M_{22}(\lambda) - \lambda I_{n_2} \end{bmatrix}. \end{aligned}$$

We have $\sigma(M(0)) = \sigma(M_{11}(0)) \cup \sigma(M_{22}(0))$ and $\sigma(\Delta(\lambda)) = \sigma(M_{11}(\lambda) - \lambda I_{n_1}) \cup \sigma(M_{22}(\lambda) - \lambda I_{n_2})$. Hence, $s(M_{ii}(0)) > 0$ either for $i = 1$ or $i = 2$, and by the irreducible case we deduce that there exists $\lambda^* > 0$ such that $0 \in \sigma(M_{ii}(\lambda^*) - \lambda^* I_{n_i})$. This shows that $\lambda^* > 0$ is a solution of the characteristic equation (3.2), and thus 0 is unstable.

In the case of cooperative systems, we shall prove that if $M(0)$ is irreducible, then $s(M(0)) > 0$ is a sharp criterion for persistence, conf. Theorem 4.1. For the moment, a result for the extinction of all populations is given.

Theorem 3.2 *Consider (1.3), and assume that N_0 is a non-singular M-matrix. Then, all positive solutions of (1.3) are bounded. Moreover, if there exists a positive vector $q = (q_1, \dots, q_n)$ which satisfies the conditions*

$$\begin{aligned} \mu_i q_i - \sum_{j=1}^n c_{ij} q_j &> 0, \\ \beta_i q_i + \sum_{j \neq i} d_{ij} q_j &\leq 0, \quad i = 1, \dots, n, \end{aligned} \tag{3.3}$$

then all the populations go extinct in every patch, i.e., all positive solutions $x(t)$ of (1.3) satisfy $x(t) \rightarrow 0$ as $t \rightarrow \infty$.

Proof. Consider the following auxiliary cooperative system:

$$\begin{aligned} x'_i(t) = & x_i(t) \left(\beta_i - \mu_i x_i(t) + \sum_{j=1}^n a_{ij}^- \int_0^{+\infty} K_{ij}(s) x_j(t-s) ds \right), \\ & + \sum_{j \neq i} d_{ij} x_j(t - \tau_{ij}) =: f_i(x_t), \quad i = 1, 2, \dots, n, \end{aligned} \quad (3.4)$$

where as before $a_{ij}^- = \max(0, -a_{ij})$, and observe that the solutions of (1.3) satisfy

$$\begin{aligned} x'_i(t) \leq & x_i(t) \left(\beta_i - \mu_i x_i(t) + \sum_{j=1}^n a_{ij}^- \int_0^{\infty} K_{ij}(s) x_j(t-s) ds \right), \\ & + \sum_{j \neq i} d_{ij} x_j(t - \tau_{ij}), \quad i = 1, 2, \dots, n. \end{aligned}$$

By Theorem 5.1.1 of [16], the solution $x(t)$ of each initial value problem (1.3)-(1.6) satisfies $x(t) \leq X(t)$, $t \geq 0$, where $X(t)$ is the solution of (3.4)-(1.6). Therefore, it is enough to prove the statements of the theorem for (3.4).

Since N_0 is a non-singular M-matrix, there is $q = (q_1, \dots, q_n) > 0$ such that $N_0 q > 0$, i.e., $\mu_i q_i - \sum_{j=1}^n a_{ij}^- q_j > 0$, $i = 1, \dots, n$ (cf. Lemma 2.2). For $L > 0$ sufficiently large, we have

$$f_i(Lq) = Lq_i \left[\beta_i - L(\mu_i q_i - \sum_{j=1}^n a_{ij}^- q_j) \right] + L \sum_{j \neq i} d_{ij} q_j < 0, \quad i = 1, \dots, n. \quad (3.5)$$

Consider solutions $x(t) = x(t; \varphi)$ of (3.4)-(1.6). From Smith's results (cf. Corollary 5.2.2 in [16]), and since bounded positive orbits in UC_g are precompact, this implies that

$$x(t; \varphi) \leq x(t; Lq) \searrow x^* \quad \text{for } \varphi \leq Lq,$$

where $x^* = (x_1^*, \dots, x_n^*)$ is necessarily an equilibrium of (3.4) (recall that ω -limit sets are invariant sets). In particular, this proves that all positive solutions of (3.4) are bounded.

Next, we assume (3.3) and prove that $L_i := \limsup_{t \rightarrow \infty} \frac{x_i(t)}{q_i} = 0$ for all i .

Let $L_i = \max_j L_j$. If $L_i > 0$, by the fluctuation lemma there is a sequence $(t_k), t_k \rightarrow \infty$, with $x_i(t_k) \rightarrow L_i q_i, x'_i(t_k) \rightarrow 0$. For $\varepsilon > 0$ small and k large, the application of Lemma 2.1 yields

$$x'_i(t_k) \leq x_i(t_k) [\beta_i - \mu_i x_i(t_k) + \sum_j a_{ij}^- q_j (L_i + \varepsilon)] + (L_i + \varepsilon) \sum_{j \neq i} d_{ij} q_j. \quad (3.6)$$

By letting $k \rightarrow \infty, \varepsilon \rightarrow 0^+$, the above formula and (3.3) lead to

$$\begin{aligned} 0 & \leq L_i q_i \left[\beta_i - L_i (\mu_i q_i - \sum_{j=1}^n a_{ij}^- q_j) \right] + L_i \sum_{j \neq i} d_{ij} q_j \\ & = L_i \left[\beta_i q_i + \sum_{j \neq i} d_{ij} q_j - L_i q_i (\mu_i q_i - \sum_{j=1}^n a_{ij}^- q_j) \right] < 0. \end{aligned} \quad (3.7)$$

This is a contradiction, and the proof is complete.

Remark 3.1 Condition (3.3) reads as

$$M(0)q \leq 0 \quad \text{and} \quad N_0 q > 0, \quad (3.8)$$

where $M(0)$ and N_0 are given by (1.10) and (1.11); this is equivalent to saying that N_0 is a non-singular M-matrix and

$$M(0)N_0^{-1}v \leq 0$$

for some positive vector v . Clearly, (3.8) also implies that $-M(0)$ is an M-matrix [8]; this condition also translates as $s(M(0)) \leq 0$. Note however that the converse is not true: in fact, even if $M(0)$ is an irreducible matrix with $s(M(0)) \leq 0$ and N_0 is a non-singular M-matrix, then there exist positive vectors v and q such that $M(0)v \leq 0$ and $N_0 q > 0$, but one cannot conclude that there is one positive vector q satisfying simultaneously $M(0)q \leq 0$ and $N_0 q > 0$, and the extinction of the populations cannot be derived. This is illustrated below by a counter-example.

Example 3.1 Consider the system (1.3) with $n = 2$, $\beta_1 = \beta_2 = -2$, $d_{12} = 1$, $d_{21} = \frac{7}{2}$ and $\mu_1 = -a_{12} = 1$, $\mu_2 = \frac{13}{45}$, $a_{21} = -\frac{1}{10}$, $a_{11} = a_{22} = 0$:

$$\begin{aligned} x'_1(t) &= x_1(t) \left(-2 - x_1(t) + \int_0^\infty K_{12}(s)x_2(t-s) ds \right) + x_2(t - \tau_1) \\ x'_2(t) &= x_2(t) \left(-2 - \frac{13}{45}x_2(t) + \frac{1}{10} \int_0^\infty K_{21}(s)x_1(t-s) ds \right) + \frac{7}{2}x_1(t - \tau_2). \end{aligned} \quad (3.9)$$

with delays $\tau_1, \tau_2 \geq 0$ and positive kernels K_{12}, K_{21} satisfying (1.2). With the previous notation,

$$M(0) = \begin{bmatrix} -2 & 1 \\ \frac{7}{2} & -2 \end{bmatrix}, \quad N_0 = \begin{bmatrix} 1 & -1 \\ -\frac{1}{10} & \frac{13}{45} \end{bmatrix}.$$

Clearly N_0 is a non-singular M-matrix and $s(M(0)) < 0$. The positive vectors $v = (1, v_2)$ satisfying $M(0)v \leq 0$ are the ones for which $\frac{7}{4} \leq v_2 \leq 2$; a positive vector $q = (1, q_2)$ satisfies $N_0 q > 0$ if and only if $\frac{9}{26} < q_2 < 1$. Hence there is no vector $q > 0$ satisfying both conditions (3.8). In this example, the trivial equilibrium is not a global attractor, since $(1, \frac{3}{2})$ is a positive equilibrium of (3.9).

The next result follows clearly from the the proof of Theorem 3.1.

Theorem 3.3 *If there exists a positive vector $q = (q_1, \dots, q_n)$ satisfying $M(0)q < 0$ and $N_0 q \geq 0$, then the equilibrium 0 of (1.3) is GAS.*

The case of no patch structure, has been studied by the author in [3] (see also Faria and Oliveira [6]), where the local stability and attractivity of a positive equilibrium was investigated, but not the extinction, for which sufficient conditions are given below.

Corollary 3.1 *Consider (1.1) with $\alpha_{ij} = 0$ for $1 \leq i, j \leq n$ (no patch structure):*

$$x'_i(t) = x_i(t) \left(b_i - \mu_i x_i(t) - \sum_{j=1}^n a_{ij} \int_0^\infty K_{ij}(s)x_j(t-s) ds \right), \quad i = 1, \dots, n,$$

where all the coefficients and kernels are as in (1.1). As in (1.11), denote $N_0 = \text{diag}(\mu_1, \dots, \mu_n) - [a_{ij}^-]$. If either (i) N_0 is a non-singular M-matrix and $b_i \leq 0$, $1 \leq i \leq n$, or (ii) $N_0 q \geq 0$ for some positive vector q , and $b_i < 0$, $1 \leq i \leq n$, then all positive solutions satisfy $x(t) \rightarrow 0$ as $t \rightarrow \infty$.

In the case of competitive systems, the next corollary generalises and improves Theorem 3.3 in [4].

Corollary 3.2 *Consider (1.3), with $\mu_i > a_{ii}^-$ and $a_{ij} \geq 0$ for $j \neq i$, $i, j = 1, \dots, n$. If there is a positive vector q such that $M(0)q \leq 0$, then the equilibrium 0 is globally attractive. In particular, this holds if either $s(M(0)) < 0$, or $s(M(0)) = 0$ and $M(0)$ is irreducible.*

Proof. In this situation, N_0 reads as $N_0 = \text{diag}(\mu_1 - a_{11}^-, \dots, \mu_n - a_{nn}^-)$. The first assertion follows immediately from Theorem 3.2. If $s(M(0)) < 0$, then there is a vector $q > 0$ such that $M(0)q < 0$. Moreover, if $M(0)$ is irreducible, since it is also cooperative, then $s(M(0)) = 0$ implies the existence of a positive vector q such that $M(0)q = 0$ [8].

4. Persistence and stability for the cooperative Lotka-Volterra system

In this section, attention is devoted to the cooperative case of (1.3), written here as

$$\begin{aligned} x'_i(t) = & x_i(t) \left(\beta_i - \mu_i x_i(t) + \sum_{j=1}^n c_{ij} \int_0^\infty K_{ij}(s) x_j(t-s) ds \right) \\ & + \sum_{j \neq i, j=1}^n d_{ij} x_j(t - \tau_{ij}), \quad i = 1, 2, \dots, n, \end{aligned} \quad (4.1)$$

where $c_{ij} = -a_{ij} \geq 0$ for $i, j = 1, \dots, n$. For (4.1), the matrix N_0 given in (1.11) is rewritten as $N_0 = \text{diag}(\mu_1, \dots, \mu_n) - [c_{ij}]$.

For the definitions of persistence and dissipativity used below, see e.g. [13, 17].

Definition 4.1. A system $x'(t) = f(x_t)$ with $S \subset BC$ as set of admissible initial conditions is said to be *persistent* if any solution $x(t; \varphi)$ with initial condition $\varphi \in S$ is bounded away from zero, i.e.,

$$\liminf_{t \rightarrow \infty} x_i(t; \varphi) > 0, \quad 1 \leq i \leq n,$$

for any $\varphi \in S$; and the system is said to be *dissipative* if there is a positive constant K such that, given any $\varphi \in S$, there exists $t_0 = t_0(\varphi)$ such that

$$|x_i(t, \varphi)| \leq K, \quad \text{for } 1 \leq i \leq n, t \geq t_0.$$

Clearly, $S = BC_0^+$ for (1.3).

Theorem 4.1 *If there is a positive vector v such that $M(0)v > 0$, then (4.1) is persistent; moreover, there is a positive equilibrium. In particular, this is the case if $s(M(0)) > 0$ and $M(0)$ is irreducible.*

Proof. Write (4.1) in the form

$$x'_i(t) = f_i(x_t), \quad i = 1, \dots, n.$$

For $v = (v_1, \dots, v_n) > 0$ such that $M(0)v > 0$ and $l > 0$ small, we obtain

$$f_i(lv) = l \left(\beta_i v_i + \sum_{j \neq i} d_{ij} v_j \right) - l^2 v_i \left(\mu v_i - \sum_{j=1}^n c_{ij} v_j \right) > 0, \quad i = 1, \dots, n.$$

Hence, there exists a positive equilibrium x^* with $x(t; lv) \nearrow x^*$; moreover, since the system (4.1) is cooperative, $x(t; \varphi) \geq x(t; lv)$ if $l > 0$ is sufficiently small so that $\varphi \geq lv$ [16]. This shows the persistence of (4.1). The last assertion of the theorem follows from Lemma 2.3.

A criterion for the global attractivity of a positive equilibrium for (4.1) is now established.

Theorem 4.2 *Assume there is a vector $v > 0$ such that $M(0)v > 0$ and $N_0 = \text{diag}(\mu_1, \dots, \mu_n) - [c_{ij}]$ is a non-singular M -matrix. If x^* is a positive equilibrium (whose existence is given by Theorem 4.1) and $M(0)x^* > 0$, then x^* is the unique positive equilibrium of system (4.1) and is globally attractive.*

Proof. Consider vectors $q > 0, v > 0$ such that $N_0 q > 0, M(0)v > 0$. Using the above notation, for $L \gg 1$ and $0 < l \ll 1$, we have $f_i(Lq) < 0$ and $f_i(lv) > 0, 1 \leq i \leq n$. Thus there exist positive equilibria x^*, y^* , with

$$x(t; lv) \nearrow x^*, \quad x(t; Lq) \searrow y^*, \quad \text{for } 0 < l \ll 1 \ll L,$$

and

$$x(t; lv) \leq x(t; \varphi) \leq x(t; Lq), \quad \text{for } lv \leq \varphi \leq Lq.$$

In particular, all positive solutions of (4.1) are bounded and bounded away from zero. To show the uniqueness and global attractivity of a positive equilibrium, it is sufficient to prove the following:

Claim: if $x^* = (x_1^*, \dots, x_n^*)$ is a positive equilibrium of (4.1), then any positive solution $x(t) = (x_1(t), \dots, x_n(t))$ of (4.1) satisfies

$$\liminf_{t \rightarrow \infty} x_i(t) \geq x_i^*, \quad i = 1, \dots, n.$$

First observe that a positive equilibrium x^* of (4.1) satisfies

$$x_i^* \left[\beta_i - \mu_i x_i^* + \sum_j c_{ij} x_j^* \right] + \sum_{j \neq i} d_{ij} x_j^* = 0, \quad 1 \leq i \leq n, \quad (4.2)$$

or, in other words,

$$M(0)x^* = x^* \otimes N_0 x^*, \quad (4.3)$$

where we use the notation $u \otimes v = (u_1 v_1, \dots, u_n v_n)$ for $u = (u_1, \dots, u_n), v = (v_1, \dots, v_n) \in \mathbb{R}^n$. By assumption $M(0)x^* > 0$, or equivalently $N_0 x^* > 0$.

To prove the claim, effect the changes of variables $\bar{x}_i(t) = x_i(t)/x_i^*$ in (4.1), and define $\ell_i := \liminf_{t \rightarrow \infty} \bar{x}_i(t) > 0$.

Choose i such that $\ell_i = \min_j \ell_j$. We now drop the bars for simplicity, and consider a sequence $t_k \rightarrow \infty$ with $x'_i(t_k) \rightarrow 0$ and $x_i(t_k) \rightarrow \ell_i$. For any $\varepsilon \in (0, \ell_i)$ and k sufficiently large, from Lemma 2.1 we get

$$x'_i(t_k) \geq x_i(t_k) \left[\beta_i - \left(\mu_i x_i^* x_i(t_k) - (\ell_i - \varepsilon) \sum c_{ij} x_j^* \right) \right] + (\ell_i - \varepsilon) \frac{1}{x_i^*} \sum_{j \neq i} d_{ij} x_j^*.$$

By taking limits $k \rightarrow \infty, \varepsilon \rightarrow 0^+$, we obtain

$$0 \geq \ell_i(1 - \ell_i) \left(\beta_i + \frac{1}{x_i^*} \sum_{j \neq i} d_{ij} x_j^* \right) = \ell_i(1 - \ell_i)(N_0 x^*)_i.$$

This yields $\ell_i \geq 1$, which proves the claim.

Corollary 4.1 *Assume that $N_0 = \text{diag}(\mu_1, \dots, \mu_n) - [c_{ij}]$ is a non-singular M -matrix and $\beta_i > 0$ for $1 \leq i \leq n$. Then, there is a positive equilibrium of system (4.1), which is a global attractor.*

Proof. If $\beta_i > 0$ for $1 \leq i \leq n$, then $M(0)v > 0$ for $v = (1, \dots, 1)$. Moreover, if x^* is a positive equilibrium of (4.1), then by (4.3) we have $N_0 x^* > 0$. The result follows from Theorem 4.2.

We now treat the generalisation of model (1.9) obtained by introducing infinite delay.

Corollary 4.2 *Consider*

$$x'_i(t) = x_i(t) \left(\beta_i - \mu_i x_i(t) + c_i \int_0^\infty K_i(s) x_i(t-s) ds \right) + \sum_{j \neq i} \sum_{p=1}^m d_{ij}^{(p)} x_j(t - \tau_{ij}^{(p)}), \quad i = 1, \dots, n, \quad (4.4)$$

where: $\beta_i \in \mathbb{R}, \mu_i > 0$ and $c_i, d_{ij}^{(p)}, \tau_{ij}^{(p)} \geq 0$; $K_i : [0, \infty) \rightarrow [0, \infty)$ are in L^1 with L^1 -norm equal to 1, $1 \leq i, j \leq n$. Consider $M(0)$ given by (1.10), where $d_{ij} = \sum_{p=1}^m d_{ij}^{(p)}$. If $\mu_i > c_i$ for $1 \leq i \leq n$, then:

(i) if there is a positive vector q such that $M(0)q \leq 0$, the equilibrium 0 is a global attractor; (ii) if there is a positive vector q such that $M(0)q > 0$, there exists a positive equilibrium x^* which is a global attractor.

When $M(0)$ is irreducible, a threshold criterion for (4.4) is as follows:

Corollary 4.3 Consider (4.4) with $M(0)$ irreducible and $\mu_i > c_i$ for $1 \leq i \leq n$. Then: (i) if $s(M(0)) \leq 0$, the equilibrium 0 is a global attractor; (ii) if $s(M(0)) > 0$, there exists a positive equilibrium x^* which is a global attractor.

Remark 4.1 System (4.4) generalizes both (1.7) and (1.9). Not only the model is more general, but also Corollaries 4.2 and 4.3 provide stronger criteria than the ones in [4, 14]. In fact, for (1.7), Liu [14] assumed that $[d_{ij}]$ is irreducible, $\mu_i, b_i > 0$, all the other coefficients are non-negative with $\mu_i > \sum_{p=1}^m c_i^{(p)}$, and proved that if the constants $\alpha_i^* := (b_i + \sum_{j=1}^n d_{ij}) / (\mu_i - \sum_{p=1}^m c_i^{(p)})$, $1 \leq i \leq n$, are all equal to some constant k , then the equilibrium $x^* = (k, \dots, k)$ is a global attractor of all positive solutions; while in Faria [4] the existence and global attractivity of a positive equilibrium was proven simply under the assumptions of $\mu_i > \sum_{p=1}^m c_i^{(p)}$ and $b_i + \sum_{j=1}^n d_{ij} > 0$, $1 \leq i \leq n$.

5. Persistence and stability for the general Lotka-Volterra system

We now return to the general case of the Lotka-Volterra model (1.3) with no prescribed signs for the interaction coefficients a_{ij} , whose extinction was already studied in Section 2. Sufficient conditions for dissipativeness, persistence, and global attractivity of a positive equilibrium will be given.

In what follows, $M(0)$ and N_0 are as in (1.10) and (1.11). For the case of $M(0)$ irreducible, first observe that there are no non-trivial equilibria on the boundary of the non-negative cone $\mathbb{R}_+^n$; moreover, if the system is dissipative and 0 is unstable, this implies the existence of a positive equilibrium. A more exact result is stated in the lemma below.

Lemma 5.1 If $s(M(0)) > 0$ and (1.3) is dissipative, then (1.3) has a non-trivial equilibrium $x^* \geq 0$. If in addition $M(0)$ is an irreducible matrix, (1.3) has a positive equilibrium x^* .

Proof. Consider the ODE system associated with (1.3), given by

$$x_i'(t) = x_i(t) \left(\beta_i - \mu_i x_i(t) - \sum_{j=1}^n a_{ij} x_j(t) \right) + \sum_{j \neq i} d_{ij} x_j(t), \quad i = 1, \dots, n. \quad (5.1)$$

Clearly, (1.3) and (5.1) share the same equilibria. By assumption, (5.1) is dissipative. Since the non-negative cone $\mathbb{R}_+^n$ is forward invariant for (5.1), by [12] (5.1) has at least a saturated equilibrium $x^* \geq 0$. The linearization of (5.1) at 0 is given by

$$x_i'(t) = \beta_i x_i(t) + \sum_{j \neq i} d_{ij} x_j(t), \quad i = 1, 2, \dots, n.$$

With $s(M(0)) > 0$, this linear system is unstable (cf. Theorem 3.1), and therefore the equilibrium 0 is not saturated, hence $x^* \neq 0$. If in addition $M(0)$ is irreducible, 0 is the only equilibrium of (5.1) on the boundary of $\mathbb{R}_+^n$: otherwise (after a permutation of variables) there is an equilibrium of the form $x^* = (0, \dots, 0, x_{k+1}^*, \dots, x_n^*)$ for some $k \in \{1, \dots, n-1\}$, then $\sum_{j=k+1}^n d_{ij} x_j^* = 0$ for $1 \leq i \leq k$, hence $d_{ij} = 0$ for $1 \leq i \leq k, k+1 \leq j \leq n$, and $[d_{ij}]$ is not irreducible. Therefore, we conclude that there is an equilibrium of (5.1) in the interior of $\mathbb{R}_+^n$.

Remark 5.1 Through the remainder of this section, for the matrix $M(0)$ in (1.10) we shall assume that there is some positive vector v such that $M(0)v > 0$. In the case of $M(0)$ an irreducible matrix, this condition can be simply replaced by the assumption $s(M(0)) > 0$ (cf. Lemma 2.3).

By comparison with the cooperative system (3.4), clearly Theorem 4.2 provides an immediate criterion for dissipativeness.

Theorem 5.1 Suppose that $M(0)v > 0$ for some positive vector v , and let $X^* = (X_1^*, \dots, X_n^*)$ be a positive equilibrium for (3.4), whose existence is given by Theorem 4.1. Assume that N_0 is a non-singular M -matrix, and that $M(0)X^* > 0$. Then, system (1.3) is dissipative; to be more precise, all positive solutions $x(t)$ of (1.3) satisfy

$$\limsup_{t \rightarrow \infty} x_i(t) \leq X_i^*, \quad i = 1, \dots, n. \quad (5.2)$$

If in addition $M(0)$ is irreducible, system (2.1) has a positive equilibrium x^* .

Next, we study the persistence of (1.3). The notion of persistence in Section 3 means that the population persists on each patch. We start with the discussion of persistence of the total population, therefore we refer to the more general concept of ρ -persistence as in the monograph of Smith and Thieme [17]. Namely, with $\rho(\varphi) = \sum_{i=1}^n \varphi_i(0)$, ρ -persistence means persistence of the total population.

Theorem 5.2 Assume that (1.3) is dissipative. If $M(0)v > 0$ for some positive vector v , then the total population is (weakly) persistent, i.e.,

$$\limsup_{t \rightarrow \infty} \sum_{i=1}^n x_i(t) > 0$$

for all positive solutions $x(t)$ of (1.3). Furthermore, if $\beta_i > 0$ for $i = 1, \dots, n$, then the total population is (strongly) uniformly persistent; i.e., there exists $\theta > 0$ such that

$$\liminf_{t \rightarrow \infty} \sum_{i=1}^n x_i(t) > \theta$$

for all positive solutions $x(t)$ of (1.3).

Proof. Let $x(t)$ be a solution of (1.3). Since the system is dissipative,

$$\bar{x}_i := \limsup_{t \rightarrow \infty} x_i(t) < \infty, \quad i = 1, \dots, n.$$

Choose $i \in \{1, \dots, n\}$ such that $\bar{x}_i = \max_{1 \leq j \leq n} \bar{x}_j$. We first claim that $\bar{x}_i > 0$.

If $\bar{x}_i = 0$, then $x_j(t) \rightarrow 0$ as $t \rightarrow \infty$ for all components j . Take a positive vector v such that $M(0)v > 0$, and choose $\varepsilon > 0$ small enough so that $(M(0) - \varepsilon I)v > 0$. From Lemma 2.1, if t is sufficiently large we have

$$x'_i(t) \geq x_i(t)[\beta_i - \varepsilon - \mu_i x_i(t)] + \sum_{j \neq i} d_{ij} x_j(t - \tau_{ij}), \quad i = 1, \dots, n.$$

From Theorem 4.2, the cooperative system

$$u'_i(t) = u_i(t)[\beta_i - \varepsilon - \mu_i u_i(t)] + \sum_{j \neq i} d_{ij} u_j(t - \tau_{ij}), \quad i = 1, \dots, n,$$

has a globally asymptotically stable equilibrium $u^* > 0$. By comparison results [16], we now obtain $\liminf_{t \rightarrow \infty} x_i(t) \geq u_i^* > 0$, which is not possible. Therefore, $\bar{x}_i > 0$.

Now, suppose that $\beta_i > 0$ for all i . By the fluctuation lemma there exists a sequence (t_k) with $t_k \rightarrow \infty$, $x_i(t_k) \rightarrow \bar{x}_i$ and $x'_i(t_k) \rightarrow 0$. Again from Lemma 2.1, for any $\varepsilon > 0$, if k is sufficiently large we obtain

$$x'_i(t_k) \geq x_i(t_k)[\beta_i - \mu_i x_i(t_k) - (\bar{x}_i + \varepsilon) \sum a_{ij}^+],$$

By letting $k \rightarrow \infty$ and $\varepsilon \rightarrow 0^+$, we obtain $\bar{x}_i \geq \frac{\beta_i}{\mu_i + \sum a_{ij}^+} > 0$. These arguments also show that

$$\limsup_{t \rightarrow \infty} \sum_{j=1}^n x_j(t) \geq \min_{1 \leq i \leq n} \frac{\beta_i}{\mu_i + \sum a_{ij}^+} =: \theta_1 > 0.$$

Note that the lower bound θ_1 does not depend on the particular solution $x(t)$. This means that the total population $\sum_{j=1}^n x_j(t)$ is *uniformly weakly persistent* (see [17] for a definition). On the other hand, since (1.3) is dissipative, it has a compact global attractor [9], and the hypotheses of Theorem 4.5 of [17] are satisfied. This allows to conclude the strong uniform persistence of the total population.

Corollary 5.1 *Assume that $\beta_i > 0$ for all i , and that N_0 is a non-singular M -matrix. Then (1.3) is dissipative, the total population uniformly persists, and there exists a non-trivial equilibrium $x^* \geq 0$.*

Conditions for the persistence of the population on each patch are given below. To simplify the notation, denote

$$\hat{N} = \text{diag}(\mu_1, \dots, \mu_n) - [a_{ij}].$$

Theorem 5.3 *Assume that $M(0)v > 0$ for some positive vector v and that N_0 is a non-singular M -matrix. If in addition $\hat{N}X^* > 0$, where X^* is the positive equilibrium of (3.4), then (1.3) is persistent and there is a positive equilibrium.*

Proof. The existence of X^* , the unique positive equilibrium of (3.4), is guaranteed by Theorem 4.1. Condition $\hat{N}X^* > 0$ translates as

$$\mu_i X_i^* - \sum_j |a_{ij}| X_j^* > 0, \quad i = 1, \dots, n, \quad (5.3)$$

and in particular implies that $M(0)X^* = X^* \otimes N_0 X^* > 0$, i.e.,

$$\mu_i X_i^* - \sum_j a_{ij}^- X_j^* > 0, \quad i = 1, \dots, n.$$

Theorem 5.1 provides the upper bounds $\bar{x}_i := \limsup_{t \rightarrow \infty} x_i(t) \leq X_i^*$, for all i and all solutions $x(t)$ of (1.3). Now, define the matrix

$$\widetilde{M}(0) = \text{diag}(\gamma_1, \dots, \gamma_n) + [d_{ij}],$$

where $\gamma_i = \beta_i - \sum_j a_{ij}^+ X_j^*$, $1 \leq i \leq n$. From (5.3),

$$\begin{aligned} (\widetilde{M}(0)X^*)_i &= X_i^* \left[\beta_i - \sum_j a_{ij}^+ X_j^* \right] + \sum_{j \neq i} d_{ij} X_j^* \\ &= X_i^* \left[\mu_i X_i^* - \sum_j |a_{ij}| X_j^* \right] > 0, \quad 1 \leq i \leq n. \end{aligned} \quad (5.4)$$

From Lemma 2.1, for each $\varepsilon > 0$ there exists $t_0 > 0$ such that $\int_0^\infty K_{ij}(s)x_j(t-s)ds \leq (1+\varepsilon)X_j^*$ for any $i, j = 1, \dots, n$ and $t \geq t_0$. Thus, for $t \geq t_0$,

$$\begin{aligned} x_i'(t) &\geq x_i(t) \left(\beta_i - (1+\varepsilon) \sum_j a_{ij}^+ X_j^* - \mu_i x_i(t) + \sum_j a_{ij}^- \int_0^\infty K_{ij}(s)x_j(t-s)ds \right) \\ &\quad + \sum_{j \neq i} d_{ij} x_j(t - \tau_{ij}), \quad i = 1, 2, \dots, n. \end{aligned}$$

In virtue of (5.4), we can choose $\varepsilon > 0$ small enough so that $\widetilde{M}_\varepsilon(0)X^* > 0$, where

$$\widetilde{M}^\varepsilon(0) = \text{diag}(\gamma_1^\varepsilon, \dots, \gamma_n^\varepsilon) + [d_{ij}], \quad \text{for } \gamma_i^\varepsilon = \beta_i - (1+\varepsilon) \sum_j a_{ij}^+ X_j^*.$$

From Theorem 4.1, observe that the cooperative system

$$u'_i(t) = u_i(t) \left(\gamma_i^\varepsilon - \mu_i u_i(t) + \sum_j a_{ij}^- \int_0^\infty K_{ij}(s) u_j(t-s) ds \right) + \sum_{j \neq i} d_{ij} u_j(t - \tau_{ij}), \quad i = 1, 2, \dots, n, \quad (5.5)$$

is persistent. Comparing the solutions of (1.3) with the solutions of (5.5), we deduce that (1.3) is persistent as well. Now, from the persistence and Theorem 5.1, there is a positive equilibrium.

We finally present a criterion for the global asymptotic stability of a positive equilibrium for (1.3).

Theorem 5.4 *Assume that (1.3) is dissipative, persistent and has an equilibrium $x^* > 0$. If in addition $\widehat{N}x^* > 0$, then x^* is globally attractive.*

Proof. By the change of variables $y(t) = x(t) - x^*$, (1.3) becomes

$$\begin{aligned} y'_i(t) = & -(y_i(t) + x_i^*) \left(\mu_i y_i(t) + \sum_j a_{ij} \int_0^\infty K_{ij}(s) y_j(t-s) ds \right) \\ & - y_i(t) \frac{1}{x_i^*} \sum_{j \neq i} d_{ij} x_j^* + \sum_{j \neq i} d_{ij} y_j(t - \tau_{ij}), \quad i = 1, 2, \dots, n. \end{aligned} \quad (5.6)$$

Define $u_j = \limsup_{t \rightarrow \infty} y_j(t)$, $-v_j = \liminf_{t \rightarrow \infty} y_j(t)$, and

$$U = \max_j \frac{u_j}{x_j^*}, \quad V = \max_j \frac{v_j}{x_j^*}, \quad L = \max(U, V).$$

Clearly $L \geq 0$. Moreover, from the persistence $v_j < x_j^*$ for all components j , and therefore $V < 1$.

It suffices to show that $L = 0$. We argue by contradiction, so assume $L > 0$.

Consider first the case of $L = U$, and choose i such that $U = \frac{u_i}{x_i^*}$. Take a sequence $t_k \rightarrow \infty$ such that $y_i(t_k) \rightarrow u_i$ and $y'_i(t_k) \rightarrow 0$. Applying Lemma 2.1 to (5.6), for any $\varepsilon > 0$, if k is sufficiently large we obtain

$$\begin{aligned} y'_i(t_k) \leq & -(y_i(t_k) + x_i^*) \left(\mu_i y_i(t_k) - (1 + \varepsilon) L \sum_j |a_{ij}| x_j^* \right) - y_i(t_k) \frac{1}{x_i^*} \sum_{j \neq i} d_{ij} x_j^* \\ & + (1 + \varepsilon) L \sum_{j \neq i} d_{ij} x_j^*. \end{aligned}$$

By letting $k \rightarrow \infty$ and $\varepsilon \rightarrow 0^+$, we get

$$0 \leq -(L + 1) x_i^* \left(\mu_i x_i^* - \sum_{j=1}^n |a_{ij}| x_j^* \right) L < 0, \quad (5.7)$$

a contradiction. Now, consider the case $L = V = \frac{v_i}{x_i^*}$ for some i . Then, there is a sequence $t_k \rightarrow \infty$ with $y_i(t_k) \rightarrow -v_i = -L x_i^* > -x_i^*$ and $y'_i(t_k) \rightarrow 0$. We proceed as in the above case and instead of (5.7) obtain

$$0 \geq (-L + 1) x_i^* \left(\mu_i x_i^* - \sum_{j=1}^n |a_{ij}| x_j^* \right) L > 0, \quad (5.8)$$

which is again a contradiction. The proof is complete.

By Theorems 5.1, 5.3 and 5.4, we immediately get:

Corollary 5.2 *Assume that $M(0)v > 0$ for some positive vector v , N_0 is a non-singular M -matrix, and $\widehat{N}X^* > 0$, where X^* is the positive equilibrium of (3.4). Then there exists an equilibrium $x^* > 0$ of (1.3). If in addition $\widehat{N}x^* > 0$, then x^* is globally attractive.*

If $M(0)$ is a positive matrix, the assumption $\widehat{N}X^* > 0$ can be dropped in the above criterion, since one can use the persistence of the total population, rather than the persistence on each patch.

Theorem 5.5 *Assume that N_0 is a non-singular M -matrix, and $\beta_i, d_{ij} > 0$ for all $i, j = 1, \dots, n$. If the equilibrium $x^* > 0$ of (1.3) (whose existence is given in Theorem 5.1) satisfies $\widehat{N}x^* > 0$, then x^* is globally attractive.*

Proof. Under the assumption $\beta_i, d_{ij} > 0$ for all i, j , by Theorems 5.1 and 5.2, system (1.3) is dissipative, the total population is uniformly persistent, and there is an equilibrium $x^* > 0$.

We now use the same notation and proceed as in the proof of Theorem 5.4, noting however that $V \leq 1$, but the situation $V = 1$ is possible. In fact, $v_j \leq x_j^*$ for all j , and $v_j < x_j^*$ for at least one component j , because of the persistence of the total population. By repeating that proof, we only have to further assure that the case of $L = V = 1$ is not possible.

Let $L = V = \frac{v_i}{x_i^*} = 1$ for some i . Consider a sequence $t_k \rightarrow \infty$ with $y_i(t_k) \rightarrow -v_i = -x_i^*$ and $y_i'(t_k) \rightarrow 0$. Applying Lemma 2.1 to (5.6), for any $\varepsilon > 0$, if k is sufficiently large we obtain

$$\begin{aligned} y_i'(t_k) \geq & -(y_i(t_k) + x_i^*) \left(\mu_i y_i(t_k) + (1 + \varepsilon) \sum_j |a_{ij}| x_j^* \right) \\ & - y_i(t_k) \frac{1}{x_i^*} \sum_{j \neq i} d_{ij} x_j^* + (1 + \varepsilon) \sum_{j \neq i} d_{ij} v_j. \end{aligned}$$

By letting $k \rightarrow \infty$ and $\varepsilon \rightarrow 0^+$, we obtain a contradiction, since $0 \geq -\sum_{j \neq i} d_{ij} x_j^* + \sum_{j \neq i} d_{ij} v_j > 0$.

Example 5.1 Consider the following system of the form (1.3) with $n = 2$:

$$\begin{aligned} x_1'(t) = & x_1(t) \left(\beta_1 - \mu_1 x_1(t) - a_{11} \int_0^\infty K_{11}(s) x_1(t-s) ds \right. \\ & \left. - a_{12} \int_0^\infty K_{12}(s) x_2(t-s) ds \right) + d_1 x_2(t - \tau_1) \\ x_2'(t) = & x_2(t) \left(\beta_2 - \mu_2 x_2(t) - a_{21} \int_0^\infty K_{21}(s) x_1(t-s) ds \right. \\ & \left. - a_{22} \int_0^\infty K_{22}(s) x_2(t-s) ds \right) + d_2 x_1(t - \tau_2). \end{aligned} \tag{5.9}$$

with delays $\tau_1, \tau_2 \geq 0$ and coefficients $d_i > 0, a_{ij} \geq 0$ and $\beta_i \in \mathbb{R}, i, j = 1, 2$. For this system, and with the previous notation,

$$M(0) = \begin{bmatrix} \beta_1 & d_1 \\ d_2 & \beta_2 \end{bmatrix}, \quad N_0 = \begin{bmatrix} \mu_1 & 0 \\ 0 & \mu_2 \end{bmatrix}.$$

Note that $M(0)$ is irreducible. We have $s(M(0)) \leq 0$ if and only if $\beta_1 \leq 0, \beta_2 \leq 0$ and $\beta_1 \beta_2 \geq d_1 d_2$, in which case the trivial equilibrium is a global attractor of all positive solutions (cf. Theorem 3.2); otherwise, Theorem 5.1 assures that there exists a positive equilibrium.

As an illustration, now take (5.9) subject to the constraints

$$\begin{aligned} \mu_1 &> a_{11} + a_{12}, \quad \mu_2 > a_{12} + a_{22}, \\ \frac{\beta_1 + d_1}{\mu_1 + a_{11} + a_{12}} &= \frac{\beta_2 + d_2}{\mu_2 + a_{12} + a_{22}} =: c > 0. \end{aligned} \tag{5.10}$$

Under these conditions, one easily verifies that $s(M(0)) > 0$, and that $x^* = (c, c)$ is an equilibria of (5.9). The matrix $\widehat{N}$ reads as $\widehat{N} = \begin{bmatrix} \mu_1 - a_{11} & -a_{12} \\ -a_{21} & \mu_2 - a_{22} \end{bmatrix}$, so $\widehat{N}x^* > 0$. Hence, if $\beta_1 > 0, \beta_2 > 0$, Theorem 5.5 implies that $x^* = (c, c)$ is a global attractor of all positive solutions of (5.9).

For the situation $\beta_1 \leq 0$ or $\beta_2 \leq 0$, together with (5.10) if we now assume

$$\frac{\beta_1 + d_1}{\mu_1} = \frac{\beta_2 + d_2}{\mu_2} =: \gamma,$$

then $X^* = (\gamma, \gamma)$ is a globally attractive equilibrium for the cooperative system associated with (5.9):

$$\begin{aligned} x_1'(t) &= x_1(t)(\beta_1 - \mu_1 x_1(t)) + d_1 x_2(t - \tau_1) \\ x_2'(t) &= x_2(t)(\beta_2 - \mu_2 x_2(t)) + d_2 x_1(t - \tau_2). \end{aligned} \quad (5.11)$$

Since $\widehat{N}X^* > 0$, from Corollary 5.2 then $x^* = (c, c)$ globally attracts the positive solutions of (5.9).

Remark 5.2 The requirements $\widehat{N}X^* > 0$ and $\widehat{N}x^* > 0$ in Theorems 5.3, 5.4 and 5.5 are expressed in terms of the positive equilibria X^* of (3.4) and x^* of (1.3). It would be therefore relevant to improve the above criteria, in the sense of achieving sufficient conditions for the uniform persistence of (1.3) and the global attractivity of x^* involving only the coefficients of the system. The theorem below is a first attempt to establish such type of criteria.

Theorem 5.6 Suppose that, for all $i, j = 1, \dots, n$,

$$\begin{aligned} \mu_i &> \sum_j a_{ij}^-, \\ \beta_i &\geq Ma_{ii}^+, \quad d_{ij} \geq Ma_{ij}^+, \quad i \neq j \end{aligned} \quad (5.12)$$

with $\beta_i + \sum_{j \neq i} d_{ij} > M \sum_j a_{ij}^+$, where

$$M = \max_{1 \leq i \leq n} \frac{\beta_i + \sum_{j \neq i} d_{ij}}{\mu_i - \sum_j a_{ij}^-}. \quad (5.13)$$

Then (1.3) is dissipative and persistent. If, for all $i, j = 1, \dots, n$,

$$\begin{aligned} \mu_i &> \sum_j a_{ij}^-, \\ \beta_i &\geq 2Ma_{ii}^+, \quad d_{ij} \geq 2Ma_{ij}^+, \quad i \neq j \end{aligned} \quad (5.14)$$

with $\beta_i + \sum_{j \neq i} d_{ij} > 2M \sum_j a_{ij}^+$, then (1.3) has an equilibrium $x^* > 0$ which is globally attractive.

Proof. If (5.12) holds, we have $M(0)q > 0$ and $N_0q > 0$, for $q = (1, \dots, 1)$. From Theorem 4.2, we derive that there exists a positive equilibrium $X^* = (X_1^*, \dots, X_n^*)$ of (3.4), with $M(0)X^* > 0$. For $X_i^* = \max_{1 \leq j \leq n} X_j^*$, one easily checks that $X_i^* \leq \frac{\beta_i + \sum_{j \neq i} d_{ij}}{\mu_i - \sum_j a_{ij}^-}$, and hence the estimates $X_j^* \leq M$ for M defined in (5.13). To conclude the persistence of (1.3), from Theorem 5.3 it is sufficient to show that $\widehat{N}X^* > 0$. From the identities

$$\beta_i X_i^* + \sum_{j \neq i} d_{ij} X_j^* = X_i^* (\mu_i X_i^* - \sum_j a_{ij}^- X_j^*), \quad i = 1, \dots, n,$$

we deduce that

$$\begin{aligned} X_i^* (\widehat{N}X_i^*)_i &= X_i^* \left(\mu_i X_i^* - \sum_j |a_{ij}| X_j^* \right) \\ &= X_i^* \left(\mu_i X_i^* - \sum_j a_{ij}^- X_j^* - \sum_j a_{ij}^+ X_j^* \right) \\ &= (\beta_i - a_{ii}^+ X_i^*) X_i^* + \sum_{j \neq i} (d_{ij} - a_{ij}^+ X_i^*) X_j^* \\ &\geq (\beta_i - Ma_{ii}^+) X_i^* + \left(\min_{1 \leq j \leq n} X_j^* \right) \sum_{j \neq i} (d_{ij} - Ma_{ij}^+) > 0. \end{aligned}$$

Next, suppose that the stronger conditions (5.14) hold. The components of the positive equilibrium $x^* = (x_1^*, \dots, x_n^*)$ of (1.3) also satisfy the estimates $x_i^* \leq M, i = 1, \dots, n$, for M as in (5.13). Proceeding as above, $\widehat{N}x^* > 0$, hence the conclusion follows from Theorem 5.5. Details are omitted.

Example 5.2 Consider again the system (5.9), with all coefficients being positive. If $\mu_1 \geq \beta_1 + d_1, \mu_2 \geq \beta_2 + d_2, \beta_1 > 2a_{11}, \beta_2 > 2a_{22}, d_1 \geq 2a_{12}, d_2 \geq 2a_{21}$, then $M \leq 1$ for M as in (5.13) and the constraints (5.14) are fulfilled, hence there is a positive equilibrium which is a global attractor.

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