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Persistence, Permanence and Global Stability for an *n*-Dimensional Nicholson System

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Abstract For a Nicholson's blowflies system with patch structure and multiple discrete delays, we analyze several features of the global asymptotic behavior of its solutions. It is shown that if the spectral bound of the community matrix is non-positive, then the population becomes extinct on each patch, whereas the total population uniformly persists if the spectral bound is positive. Explicit uniform lower and upper bounds for the asymptotic behavior of solutions are also given. When the population uniformly persists, the existence of a unique positive equilibrium is established, as well as a sharp criterion for its absolute global asymptotic stability, improving results in the recent literature. While our system is not cooperative, several sharp threshold-type results about its dynamics are proven, even when the community matrix is reducible, a case usually not treated in the literature.

Keywords Nicholson's blowflies equation · Delays · Persistence · Permanence · Global asymptotic stability

Mathematics Subject Classification (2010) 34K20 · 34K25 · 34K12 · 92D25

1 Introduction

In recent years, population dynamics models with patch structure and delays have attracted the attention of an increasing number of mathematicians and biologists. The heterogeneity of the environment is inherently captured by patchy models, in which the spatial distribution of the population is governed by both the migration between patches and the growth of the local populations, which depends on the resources of each particular patch. Patch-structured

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systems of differential equations are also used as disease models with transitions between stages of normal and infected cells. Delay differential equations (DDEs) frequently provide quite realistic models in population dynamics, epidemiology and mathematical biology in general, since the incorporation of delays appears naturally to express the maturation period of biological species, the maturation time of blood cells, the incubation period in disease models, and several other features. Understanding the interplay of spatial dispersal and time delays is therefore a key point for many models.

In the present paper, we study some aspects of the asymptotic behavior of solutions for the following Nicholson's blowflies system with patch structure and multiple discrete delays:

$$x_i'(t) = -d_i x_i(t) + \sum_{j=1}^{n} a_{ij} x_j(t) + \sum_{k=1}^{m} \beta_{ik} x_i(t-\tau_{ik}) e^{-x_i(t-\tau_{ik})}, \quad i = 1, \ldots, n, \tag{1.1}$$

where $d_i > 0$, $a_{ij} \geq 0$, $\tau_{ik} > 0$, $\beta_{ik} \geq 0$ and

$$\beta_i := \sum_{k=1}^{m} \beta_{ik} > 0 \tag{1.2}$$

for $i, j = 1, \ldots, n$, $k = 1, \ldots, m$. By condition (1.2), there is at least one delayed nonlinearity on each patch i. To simplify the notation and without loss of generality, in what follows we shall always assume that $a_{ii} = 0$ for all $1 \leq i \leq n$.

Among other applications, system (1.1) fits as a population model for the growth of single or multiple biological species divided into n patches or classes, with migration of the populations among them. On each patch i, $x_i(t)$ denotes the density of the population, d_i is its decreasing rate, the birth function is of Nicholson-type $\sum_{k=1}^{m} \beta_{ik} x_i(t-\tau_{ik}) e^{-x_i(t-\tau_{ik})}$, and the coefficients a_{ij} are the migration rates of populations moving from patch j to patch i. In view of this biological meaning, it is natural to take

$$d_i = m_i + \sum_{j=1}^{n} a_{ji}, \quad m_i > 0, \tag{1.3}$$

where m_i is the mortality rate on patch i. Therefore, together with conditions $a_{ii} = 0$ and (1.2), unless otherwise stated, in what follows we assume (1.3).

Model (1.1) was motivated by the celebrated scalar Nicholson's blowflies equation

$$x'(t) = -dx(t) + \beta x(t-\tau) e^{-ax(t-\tau)},$$

where $d, \beta, a, \tau > 0$, introduced by Gurney et al. [6] in 1980 as a model for the Australian sheep-blowfly population, as it agreed with the Nicholson's experimental data published in [13]. Since then, Nicholson's equation has been generalized, modified, and extensively studied by many mathematicians, in what concerns stability, persistence, existence and attractivity of periodic or almost periodic solutions, occurrence of bifurcations, and other dynamical aspects. In contrast, the literature on Nicholson's systems is quite recent and scarce. We refer to the works of Liu [10,11], Berezansky et al. [1], Faria [3], Liu and Meng [12], and Wang [18].

Throughout the paper, we designate A, B, D as the matrices

$$A = [a_{ij}], \quad D = \mathrm{diag}(d_1, \ldots, d_n), \quad B = \mathrm{diag}(\beta_1, \ldots, \beta_n), \tag{1.4}$$

and refer to

$$M := A + B - D$$

as the **community matrix**. The algebraic properties of the community matrix will play an important role in the study of either the persistence or the extinction of the species in all patches, as well as in the existence of a positive equilibrium—whereas the stability of the positive equilibrium depends heavily on the shape of the non-linear terms in (1.1). While most papers dealing with multiple dimensional DDEs used in population dynamics only consider the situation of an *irreducible* community matrix, in the present paper we also treat the case a *reducible* matrix.

The present paper is as an extension of the research in [3], where sufficient conditions for the global attractivity of both the trivial equilibrium and the positive equilibrium, when it exists, were established. Here, we pursue a deeper analysis of system (1.1), improving the criteria established in [3] and addressing new aspects of its dynamics. The paper provides answers for current important open problems. Namely, it gives a threshold condition for the extinction of the populations in all patches versus the uniform persistence of the total population—which applies even for the particular case of a *reducible* community matrix—, shows the existence of a positive equilibrium under very general assumptions, and establishes a (sharp) criterion for its absolute global asymptotic stability. Some of our results naturally hold for delayed systems with a more general class of nonlinearities, however the criteria for the global asymptotic stability of the positive equilibrium, as well as some explicit upper and lower bounds for the asymptotic behavior of solutions are very specific to the Ricker-type nonlinearity in (1.1).

Some of main techniques used here rely on M-matrix theory and on properties of cooperative systems of DDEs. We refer the reader to the monograph of Fiedler [5] for properties of M-matrices, the monograph of Smith on monotone systems [15] for cooperative behavior of DDEs, and the recent book of Smith and Thieme [16] for terminology and results on population persistence. Also, the method developed by Faria and Oliveira [4] to study the stability of linear n-dimensional DDEs was used to address the local asymptotic stability of the equilibria of system (1.1), an aspect previously exploited in [3]. Another major source of inspiration for our work was the paper of Hofbauer [8], where the concept of *saturated equilibrium* for autonomous systems of ordinary differential equations (ODEs) which are positively invariant in the positive cone $\mathbb{R}^n_+$ was introduced, and powerful results on the existence of a saturated equilibrium for dissipative systems were established. Hofbauer's results were a key point in our research, to provide a very general criterion for the existence of a unique positive fixed point of (1.1).

We now introduce some notation and set some terminology. For the DDE (1.1), we choose the usual phase space $C := C([-\tau, 0]; \mathbb{R}^n)$ of continuous functions from $[-\tau, 0]$ to $\mathbb{R}^n$ with the supremum norm $\|\varphi\| = \max_{\theta\in[-\tau,0]} |\varphi(\theta)|$, where $\tau = \max_{1\le i\le n, 1\le k\le m} \tau_{ik} > 0$ and $|\cdot|$ is any chosen norm in $\mathbb{R}^n$. In Sect. 2, when dealing with the concept of *ρ-uniform persistence*, for practical reasons it will be convenient to choose the norm $|x| = \sum_{i=1}^n |x_i|$, for the calculations in the persistence proof. For similar reasons, in Sect. 5 we choose the maximum norm in $\mathbb{R}^n$, to address the global asymptotic stability of the positive equilibrium. Due to the biological interpretation of model (1.1), we shall restrict our attention to non-negative solutions, and consider as set of admissible initial conditions either the positive cone $C^+ = \{\varphi \in C : \varphi_i(\theta) \ge 0 \text{ for all } \theta \in [-\tau, 0], i = 1, \ldots, n\}$ or the subset C_0^+ of C^+ of functions which are strictly positive at zero, $C_0^+ = \{\varphi \in C^+ : \varphi_i(0) > 0, i = 1, \ldots, n\}$. One can use the method of steps to verify that both sets C^+ and C_0^+ are positively invariant under (1.1). Moreover, for each $\varphi \in C^+$ system (1.1) has a unique solution $x(t) = x(t; \varphi)$ defined on $[0, \infty)$, with $x_i(t)$ positive on $[0, \infty)$ provided that $x_i(0) = \varphi_i(0) > 0$. As usual, segments

of solutions in the phase space C are denoted by x_t, $x_t(\theta) = x(t+\theta), \theta \in [-\tau, 0]$, with components $x_{t,i}$. When analyzing (1.1), our concept of stability always refers to the setting of *admissible solutions*, i.e., solutions $x(t;\varphi)$ with φ in the set of admissible initial conditions. In particular, the trivial equilibrium of (1.1) is *globally asymptotically stable* (GAS) if it is stable and attracts all solutions $x(t) = x(t;\varphi)$ of (1.1) with initial conditions $\varphi \in C^+$, i.e., $\lim_{t\to\infty} x(t) = 0$; if $x^* > 0$ is an equilibrium of (1.1), x^* is said to be GAS if it is stable and attracts all solutions $x(t) = x(t;\varphi)$ of (1.1) with initial conditions $\varphi \in C_0^+$.

For a vector $c \in \mathbb{R}^n$, we also use c to denote the constant function $\varphi(\theta) = c$ for $\theta \in [-\tau, 0]$ in C. A vector c is said to be *positive*, or *non-negative*, if all its components are positive, or non-negative, respectively. We define in a similar way *positive* and *non-negative functions* in C, and *positive* and *non-negative matrices*.

We recall below some concepts from matrix theory, included here for convenience of the reader, since they will be often referred to in the next sections.

Definition 1.1 Let $N = [n_{ij}]$ be an $n \times n$ matrix. We say that N is **cooperative** if its off-diagonal entries are non-negative: $n_{ij} \geq 0$ for $j \neq i$. The matrix N is a **reducible matrix** if there is a simultaneous permutation of rows and columns that brings N to the form

$$\begin{bmatrix} N_{11} & 0 \\ N_{21} & N_{22} \end{bmatrix}$$

with N_{11} and N_{22} square matrices; N is an **irreducible matrix** if it is not reducible. The **spectrum** of N is denoted by $\sigma(N)$. The **spectral bound** of N is defined as

$$s(N) = \max\{Re\,\lambda : \lambda \in \sigma(N)\}.$$

The matrix N is said to be an **M-matrix** if $a_{ij} \leq 0$ for $i \neq j$ and all its eigenvalues have non-negative real parts. If N is an M-matrix and $\det N \neq 0$, then we say that N is a **non-singular M-matrix**.

It is well-known that there are several equivalent ways of defining M-matrices and non-singular M-matrices, see e.g. [5,17] for further properties of these matrices. However we emphasize that many authors use the term *M-matrix* with the above meaning of the term *non-singular M-matrix*. We also recall that if a square matrix N is cooperative and irreducible, then its spectral bound $s(N)$ is always a simple, dominant eigenvalue, with a positive associated eigenvector [17].

The remainder of the paper consists of four sections. The persistence and permanence of the Nicholson-type system (1.1), two crucial aspects in population dynamics (see e.g. [16]), are studied in Sect. 2. When $s(M) > 0$, a further analysis is carried out to obtain strong uniform persistence of the population at least on one patch, and for all the patches in the case of an irreducible community matrix. Explicit lower and upper uniform bounds for the positive solutions of (1.1) given in terms of the coefficients in (1.1) are also included. In Sect. 3, we prove the global attractivity of the equilibrium 0 when $s(M) \leq 0$, which means the extinction of the populations in all patches. Therefore, a threshold criterion for extinction versus persistence is provided; moreover, this persistence is uniform in the special case of an irreducible community matrix. Clearly, from the point of view of applications, it is most relevant to study the existence, stability and attractivity of a positive equilibrium. The last sections are dedicated to these aspects. In Sect. 4, we study the undelayed ODE version of (1.1), obtained by taking all the delays equal to zero, and prove the existence of a unique positive equilibrium for (1.1) if $Mc > 0$ for some positive vector c. Finally, in Sect. 5 we give a sharp criterion for the absolute global asymptotic stability of such equilibrium, which significantly improves recent results in the literature, see e.g. [1,3,10,11].

2 Boundedness of Solutions, Persistence, Permanence

In this section, we analyze the permanence and persistence of (1.1).

We first observe that condition (1.3) implies that the matrix $D-A^T$ is diagonally dominant, therefore from Theorems 5.14 and 5.1 in [5] it follows that $D-A^T$ is always a non-singular M-matrix, and thus $D-A$ as well. As an immediate consequence of $D-A$ being a non-singular M-matrix, we get the boundedness of all admissible solutions of (1.1).

Theorem 2.1 *System (1.1) is dissipative on C^+, i.e., the components of all solutions of (1.1) with initial conditions in C^+ are uniformly bounded. To be more precise, all the solutions $x(t)=x(t,\varphi)$ of (1.1) with initial conditions $x_0=\varphi\in C^+$ satisfy*

$$d_i u_i - \sum_{j=1}^{n} a_{ij}\, u_j \le \beta_i e^{-1}, \quad i=1,\dots,n, \tag{2.1}$$

or, in other words,

$$\begin{bmatrix} u_1 \\ \vdots \\ u_n \end{bmatrix} \le (D-A)^{-1} \begin{bmatrix} \beta_1 \\ \vdots \\ \beta_n \end{bmatrix} e^{-1}, \tag{2.2}$$

where $u_i=\limsup_{t\to\infty} x_i(t),\ i=1,\dots,n$.

Proof Fix $s>0$. For any $\varphi\in C^+$, consider the solution $x(t)=x(t,\varphi)$ of (1.1), and define $\bar u_i=\sup_{t\in[0,s]} x_i(t),\ i=1,\dots,n$. Since $h(x):=xe^{-x}\le e^{-1}, x\ge 0$, then $x_i'(t)\le -d_i x_i(t)+\sum_{j=1}^n a_{ij}\bar u_j+\beta_i e^{-1}$, implying that $e^{d_i t}x_i(t)\le x_{0i}+(e^{d_i t}-1)\bar\eta_i/d_i$, $0\le t\le s$, where $\varphi(0)=(x_{01},\dots,x_{0n})\in\mathbb{R}^n_+$, and $\bar\eta_i=\sum_{j=1}^n a_{ij}\bar u_j+\beta_i e^{-1}$. Hence we obtain

$$x_i(t)\le x_{0i}e^{-d_i t}+d_i^{-1}\bar\eta_i(1-e^{-d_i t}), \quad i=1,\dots,n, \tag{2.3}$$

from which we deduce $d_i\bar u_i\le d_i x_{0i}+\beta_i e^{-1}+\sum_{j=1}^n a_{ij}\bar u_j,\ i=1,\dots,n$; in other words, for $\bar u=(\bar u_1,\dots,\bar u_n)$, we have

$$(D-A)\bar u\le c, \quad \text{with} \quad c=\begin{bmatrix} d_1x_{01} \\ \vdots \\ d_nx_{0n}\end{bmatrix}+\begin{bmatrix}\beta_1\\ \vdots\\ \beta_n\end{bmatrix}e^{-1}. \tag{2.4}$$

Since $D-A$ is a non-singular M-matrix, then its inverse is a non-negative matrix [5, Theorem 5.1], and from (2.4) we get $\bar u\le (D-A)^{-1}c$. This estimate does not depend on $s>0$, thus we derive

$$u\le (D-A)^{-1}c, \tag{2.5}$$

for $u=(u_1,\dots,u_n)$ and $u_i=\limsup_{t\to\infty}x_i(t),\ i=1,\dots,n$, implying that all positive solutions are bounded. Next, we prove that the uniform estimate (2.2) holds.

Let $\varepsilon>0$. For $t>0$ large, we have $x_i(t)\le u_i+\varepsilon$, thus the estimate (2.3) is obtained with $\bar\eta_i$ replaced by $\eta_i=\sum_{j=1}^n a_{ij}\,(u_j+\varepsilon)+\beta_i e^{-1}$, for $i=1,\dots,n$. By letting $\varepsilon\to 0^+$ and $t\to\infty$, it follows that $d_iu_i\le\beta_i e^{-1}+\sum_{j=1}^n a_{ij}\,u_j$, for all i, which proves (2.1), and therefore $(D-A)u\le[\beta_1\ \cdots\ \beta_n]^T e^{-1}$. □

For the definitions of persistence and permanence given below, see e.g. [9].

Definition 2.1 System (1.1) is said to be **persistent** (in C_0^+) if any solution $x(t;\varphi)$ with initial condition $\varphi \in C_0^+$ is bounded away from zero, i.e., $\liminf_{t\to\infty} x_i(t;\varphi) > 0$, $1 \le i \le n$, for any any $\varphi \in C_0^+$; and **uniformly persistent** (in C_0^+) if there is $\eta > 0$ such that $\liminf_{t\to\infty} x_i(t;\varphi) \ge \eta$, $1 \le i \le n$, for any any $\varphi \in C_0^+$. System (1.1) is said to be **permanent** (in C_0^+) if there are positive constants m_0, M_0, with $m_0 < M_0$, such that, given any $\varphi \in C_0^+$, there exists $t_0 = t_0(\varphi)$ such that $m_0 \le x_i(t,\varphi) \le M_0$ for $1 \le i \le n$ and $t \ge t_0$.

The notion of persistence in Definition 2.1 means that the population persists on each patch. In the following, we shall discuss population persistence on a particular patch, on a given subset of patches, or the persistence of the total population. In order to perform such analysis, we also use the more general terminology of ρ-persistence as it has been presented in the monograph of Smith and Thieme [16].

Definition 2.2 Let X be a nonempty set of a Banach space and $\rho : X \to \mathbb{R}_+$. A semiflow $\Phi : \mathbb{R}_+ \times X \to X$ is called **uniformly weakly ρ-persistent**, if there exists some $\varepsilon > 0$ such that

$$\limsup_{t\to\infty} \rho(\Phi(t,x)) > \varepsilon \qquad \forall x \in X,\ \rho(x) > 0.$$

Φ is called **uniformly (strongly) ρ-persistent** if there exists some $\varepsilon > 0$ such that

$$\liminf_{t\to\infty} \rho(\Phi(t,x)) > \varepsilon \qquad \forall x \in X,\ \rho(x) > 0.$$

System (1.1) generates a semiflow on C^+. To discuss the persistence on a given patch j, we may choose $\rho_j(\phi) := \phi_j(0)$. Then the uniform ρ_j-persistence of (1.1) for all j coincides with the concept of uniform persistence of (1.1) in the sense of Definition 2.1. Choosing $\rho(\phi) := |\phi(0)| = \sum_{i=1}^n \phi_i(0)$, we can talk about the persistence of the total population of (1.1).

Next, we prove the persistence of system (1.1).

Theorem 2.2 *Consider (1.1) and assume that there is a vector $c = (c_1, \ldots, c_n) > 0$ such that*

$$\beta_i c_i > d_i c_i - \sum_{j=1}^n a_{ij} c_j, \quad i = 1, \ldots, n. \tag{2.6}$$

Then, $\liminf_{t\to\infty} x_i(t;\varphi) > 0$, $1 \le i \le n$, *for any solution $x(t;\varphi)$ with initial condition $\varphi \in C_0^+$.*

Proof The statement was proved in [3, Lemma 2.5], with (2.6) replaced by the condition $\beta_i > d_i - \sum_{j=1}^n a_{ij}$ for all i. The proof of this theorem is similar after the changes of variables $x_i \mapsto c_i^{-1} x_i$, $1 \le i \le n$, so it is omitted. □

Clearly the matrix M is cooperative. Note that condition (2.6) is equivalent to saying that $Mc > 0$, for some positive vector c. If the matrix A is irreducible, the matrix M is irreducible as well, thus the spectral bound of M, $s(M) = \max\{Re\,\lambda : \lambda \in \sigma(M)\}$, is an eigenvalue of M with a positive associated eigenvector, and (2.6) holds if $s(M) > 0$. Actually, for irreducible matrices one can use algebraic arguments—or, in alternative, the results in Sect. 3 (cf. Theorem 3.3)—to show that the converse is also true. Hence, for irreducible matrices, $s(M) > 0$ is a criterion for the persistence of (1.1) in C_0^+, which will be shown to be sharp. For the reducible case, however, $s(M) > 0$ is not a sufficient condition for persistence, as shown by the following counter-example.

Example 2.1 Consider the 2-patch system

$$\begin{aligned} x_1'(t) &= -d_1 x_1(t) + \beta_1 e^{-x_1(t-\tau_1)} x_1(t-\tau_1) \\ x_2'(t) &= -d_2 x_2(t) + \beta_2 e^{-x_1(t-\tau_2)} x_2(t-\tau_2) + a_{21} x_1(t) \end{aligned} \tag{2.7}$$

with $\beta_1, \beta_2, d_1, d_2, a_{21} > 0$, $\tau_1, \tau_2 \geq 0$, and $\beta_1 < d_1$, $\beta_2 > d_2$. Then we have

$$A = \begin{bmatrix} 0 & 0 \\ a_{21} & 0 \end{bmatrix}, \quad M = \begin{bmatrix} \beta_1 - d_1 & 0 \\ a_{21} & \beta_2 - d_2 \end{bmatrix},$$

so $s(M) = \beta_2 - d_2 > 0$. On the other hand the first equation of (2.7) decouples, and since $\beta_1 < d_1$, we can apply Proposition 3.1 of [14] to the scalar equation of $x_1(t)$ to see that $x_1(t) \to 0$ as $t \to \infty$ for all values of the delay τ_1, so (2.7) is not persistent.

To study the permanence of (1.1), we start with an auxiliary lemma.

Lemma 2.1 *Consider the system*

$$x_i'(t) = -d_i x_i(t) + \sum_{j=1}^{n} a_{ij} x_j(t) + \sum_{k=1}^{m} \beta_{ik} x_i(t-\tau_{ik}) e^{-c_i x_i(t-\tau_{ik})}, \quad i = 1, \ldots, n, \tag{2.8}$$

where $c_1, \ldots, c_n > 0$, all the other coefficients are as in (1.1), and conditions (1.2) and (1.3) hold. Assume in addition that

$$\textbf{(A1)} \quad \gamma_i := \frac{\beta_i}{d_i - \sum_{j=1}^{n} a_{ij}} > 1, \quad i = 1, \ldots, n. \tag{2.9}$$

Let $t_* \geq 0$, $L > 1$, and $x(t)$ be a positive solution of (2.8) satisfying $x_i(t) \leq L$ for $t \geq t_*$ and $i = 1, \ldots, n$. Choose $m > 0$ such that

$$c_i m < 1, \quad h_i(m) \leq h_i(L) \quad \text{and} \quad e^{c_i m} \leq \gamma_i, \quad i = 1, \ldots, n, \tag{2.10}$$

where $h_i(x) = x e^{-c_i x}$, $x \geq 0$, for $1 \leq i \leq n$. Then $\liminf_{t\to\infty} x_i(t) \geq m$ for all $1 \leq i \leq n$.

Proof The proof was inspired by an idea in [2]. Let $x(t)$ be a solution of (2.8), and fix m satisfying (2.10). Note that each function h_i is strictly increasing on $[0, c_i^{-1}]$ and strictly decreasing on $[c_i^{-1}, \infty)$. First, we prove:

Claim 1 If $\min_{1\leq j\leq n, t\in[T,T+\tau]} x_j(t) \geq m$ for some $T \geq t_*$, then $x_j(t) \geq m$ for all $t \geq T$ and $j = 1, \ldots, n$.

Without loss of generality take $t_* = T = 0$, and assume that $x_j(t) \geq m$ for $t \in [0, \tau]$ and $j = 1, \ldots, n$. Let $t_0 \in [\tau, 2\tau]$ and $i \in \{1, \ldots, n\}$ such that $x_i(t_0) = \min_{1\leq j\leq n, t\in[\tau,2\tau]} x_j(t)$.

If $x_i(t_0) < m$, we have

$$0 \geq x_i'(t_0) = -d_i x_i(t_0) + \sum_{j=1}^{n} a_{ij} x_j(t_0) + \sum_{k=1}^{m} \beta_{ik} h_i(x_i(t_0 - \tau_{ik})). \tag{2.11}$$

Note that $x_i(t_0 - \tau_{ik}) \in [m, L]$ if $t_0 - \tau_{ik} \in [0, \tau]$, and $x_i(t_0 - \tau_{ik}) \geq x_i(t_0)$ if $t_0 - \tau_{ik} \in [\tau, t_0]$, hence $h_i(x_i(t_0 - \tau_{ik})) \geq \min\{h_i(x_i(t_0)), h_i(m)\} = h_i(x_i(t_0))$, and from $e^{c_i m} \leq \gamma_i$ we obtain

$$0 \geq \left(-d_i + \sum_{j=1}^{n} a_{ij} + \beta_i e^{-c_i x_i(t_0)}\right) x_i(t_0) > \left(-d_i + \sum_{j=1}^{n} a_{ij} + \beta_i e^{-c_i m}\right) x_i(t_0) \geq 0,$$

and a contradiction. Thus, $x_i(t_0) \geq m$. By the method of steps, this proves Claim 1.

Next, denote $s_0 := \min_j \min_{t\in[0,\tau]} x_j(t) > 0$.

If $s_0 \geq m$, the result follows from Claim 1.

If $s_0 < m$, define

$$s_1 := \min\Big\{m, \min_j \Big(\gamma_j h_j(s_0)\Big)\Big\}.$$

Note that $h_j(s_0)\gamma_j \geq e^{c_j(m-s_0)}s_0 > s_0$ for all j, thus $s_1 > s_0$. In this setting, we prove:

Claim 2 $\min_j \min_{t\in[\tau,2\tau]} x_j(t) \geq s_1$.

Otherwise, there are $t_1 \in [\tau, 2\tau]$ and $i \in \{1,\dots,n\}$ such that $x_i(t_1) < s_1$ and $x_j(t) \geq x_i(t_1)$ for all $t \in [\tau, t_1]$ and $j \in \{1,\dots,n\}$, so (2.11) holds with t_0 replaced by t_1. Since $x_i(t_1 - \tau_{ik}) \geq \min\{s_0, x_i(t_1)\}$, we have $h_i(x_i(t_1 - \tau_{ik})) \geq \min\{h_i(x_i(t_1)), h_i(s_0)\}$. We now consider two cases separately.

If $h_i(s_0) \geq h_i(x_i(t_1))$, then $s_0 \geq x_i(t_1)$ and we get

$$0 \geq \left(-d_i + \sum_{j=1}^n a_{ij}\right) x_i(t_1) + \beta_i h_i(x_i(t_1)) = \left(-d_i + \sum_{j=1}^n a_{ij} + \beta_i e^{-c_i x_i(t_1)}\right) x_i(t_1)$$
$$> \left(-d_i + \sum_{j=1}^n a_{ij} + \beta_i e^{-c_i m}\right) x_i(t_1) \geq 0,$$

with is not possible.

If $h_i(s_0) < h_i(x_i(t_1))$, then $s_0 < x_i(t_1)$. Since $x_i(t_1) < s_1 \leq \gamma_i h_i(s_0)$, we derive

$$0 \geq \big(-d_i + \sum_{j=1}^n a_{ij}\big)x_i(t_1) + \beta_i h_i(s_0) > \big(-d_i + \sum_{j=1}^n a_{ij}\big)\gamma_i h_i(s_0) + \beta_i h_i(s_0) > 0,$$

which is again a contradiction, ending the proof of Claim 2.

Next, we define by recurrence the sequence

$$s_{k+1} = \min\Big\{m, \min_j \Big(\gamma_j h_j(s_k)\Big)\Big\}.$$

If $s_k = m$ for some $k \geq 0$, then $\gamma_j h_j(s_k) = \gamma_j e^{-c_j m} m \geq m$, hence $s_p = m$ for all $p > k$. In this case, the result follows from Claim 1. Otherwise,

$$s_{k+1} = \min_j \Big(\gamma_j h_j(s_k)\Big) \geq \min_j e^{c_j(m-s_k)} s_k > s_k, \tag{2.12}$$

and (s_k) is strictly increasing. For $s^* = \lim s_k$, from (2.12) we have

$$0 < s^* \leq m \quad \text{and} \quad s^* \geq \min_j e^{c_j(m-s^*)} s^* \geq s^*,$$

and therefore $s^* = m$. On the other hand, Claim 2 and an inductive argument imply that $\min_j \min_{t\in[k\tau,(k+1)\tau]} x_j(t) \geq s_k$, $k \geq 0$, and we get $\liminf_{t\to\infty} x_j(t) \geq s^* = m$ for $1 \leq j \leq n$. □

The permanence of (1.1) is now an immediate consequence of the lemma above.

Theorem 2.3 *If* **(A1')** $\exists\, c = (c_1,\dots,c_n) > 0 : \dfrac{\beta_i c_i}{d_i c_i - \sum_{j=1}^n a_{ij} c_j} > 1, \quad i = 1,\dots,n,$ *holds, then system (1.1) is uniformly persistent, and thus permanent.*

Proof The changes of variables $x_i \mapsto c_i^{-1}x_i = \bar{x}_i$, $1 \le i \le n$, transform (1.1) into

$$\bar{x}_i'(t) = -d_i\bar{x}_i(t) + \sum_{j=1}^{n} \bar{a}_{ij}\bar{x}_j(t) + \sum_{k=1}^{m} \beta_{ik}\bar{x}_i(t-\tau_{ik})e^{-c_i\bar{x}_i(t-\tau_{ik})}, \quad i = 1, \dots, n,$$

where $\bar{a}_{ij} = \frac{c_j}{c_i}a_{ij}$. After dropping the bars, we may consider system (2.8), for which condition **(A1)** is satisfied.

Condition **(A1)** is equivalent to $\beta_i > d_i - \sum_{j=1}^{n} a_{ij} > 0$ for $i = 1, \dots, n$. Choose $L > \max_i(c_i^{-1})$ with $L \ge (\max_i \gamma_i)e^{-1}$ and $m \in (0, c_i^{-1})$ with $m \le \min_i(c_i^{-1}\log\gamma_i)$. For $\varepsilon > 0$ fixed, let $L_\varepsilon = L + \varepsilon$ and $m_\varepsilon \in (0, m)$ such that $h_i(m_\varepsilon) \le h_i(L_\varepsilon)$. For any positive solution $x(t)$ of (2.8), let $u_i = \limsup_{t\to\infty} x_i(t)$ and $v_i = \liminf_{t\to\infty} x_i(t)$. Note that $\max_{x\ge 0} h_i(x) = e^{-1}$ for $1 \le i \le n$. As in the proof of Theorem 2.1, from (2.1) we deduce that $\max_i u_i \le \gamma_i e^{-1} < L_\varepsilon$. From Lemma 2.1, we now have $\min_i v_i > m_\varepsilon$. By letting $\varepsilon \to 0^+$, we obtain

$$m \le \liminf_{t\to\infty} x_i(t;\varphi) \le \limsup_{t\to\infty} x_i(t;\varphi) \le L, \quad 1 \le i \le n,$$

for all solutions $x(t;\varphi)$ of (2.8) with initial condition $\varphi \in C_0^+$. For positive solutions of (1.1), we therefore obtain

$$c_i m \le \liminf_{t\to\infty} x_i(t;\varphi) \le \limsup_{t\to\infty} x_i(t;\varphi) \le c_i L, \quad 1 \le i \le n. \tag{2.13}$$

□

Remark 2.1 Consider a general system (1.1) with coefficients d_i positive, but not given by (1.3). Clearly, Theorem 2.1 remains true under the additional condition of $D - A$ being a non-singular M-matrix; and Theorem 2.3 is valid without further assumptions, since **(A1')** implies in particular that $D - A$ is a non-singular M-matrix, because $(D - A)c > 0$ for some vector $c > 0$ [5].

Rather than the estimates (2.13), one can actually give explicit uniform lower and upper bounds for solutions of (1.1), if lower and upper bounds for the coefficients γ_i as defined in (2.9) are known.

Theorem 2.4 *Assume $e^\alpha \le \gamma_i \le e^\beta$, $i = 1, \dots, n$, with $0 < \alpha < \beta$, $\beta > 1$. Then any positive solution $x(t) = (x_1(t), \dots, x_n(t))$ of (1.1) satisfies*

$$\min\{\alpha, \exp\left(\alpha + \beta - 1 - e^{\beta-1}\right)\} \le \liminf_{t\to\infty} x_i(t) \le \limsup_{t\to\infty} x_i(t) \le e^{\beta-1}, \quad i = 1, \dots, n.$$

Proof As before, we define $h(x) = xe^{-x}$ for $x \ge 0$. If $\max_j u_j = u_i$ for some i, from Theorem 2.1 we obtain $(d_i - \sum_{j=1}^{n} a_{ij})u_i \le d_i u_i - \sum_{j=1}^{n} a_{ij}u_j \le \beta_i e^{-1}$, which yields $u_i \le \gamma_i e^{-1} \le e^{\beta-1}$. Since $e^{\beta-1} > 1$, from Lemma 2.1 with $c_1 = \cdots = c_n = 1$, we have $v_i \ge m$, $1 \le i \le n$, where $m \in (0, 1)$ and is such that $m \le \alpha$ and $h(m) \le h(e^{\beta-1})$.

We now argue as in the proof of Theorem 2.1. Fix a small $\varepsilon > 0$, and $T \ge 0$ such that $m - \varepsilon \le v_i - \varepsilon \le x_i(t) \le e^{\beta-1} + \varepsilon$ for $t \ge T$ and $1 \le i \le n$. Without loss of generality, take $T = 0$. For an arbitrary $t > 0$, $x_i'(t) \ge -d_i x_i(t) + \sum_{j=1}^{n} a_{ij}(v_j - \varepsilon) + \beta_i \min\{h(m-\varepsilon), h(e^{\beta-1}+\varepsilon)\}$, implying that $e^{d_i t}x_i(t) \ge x_i(0) + (e^{d_i t} - 1)\eta_i(\varepsilon)/d_i$, $t \ge 0$, where $\eta_i(\varepsilon) = \sum_{j=1}^{n} a_{ij}(v_j - \varepsilon) + \beta_i \min\{h(m-\varepsilon), h(e^{\beta-1}+\varepsilon)\}$. Hence we obtain

$$x_i(t) \ge x_i(0)e^{-d_i t} + d_i^{-1}\eta_i(\varepsilon)(1 - e^{-d_i t}), \quad i = 1, \dots, n.$$

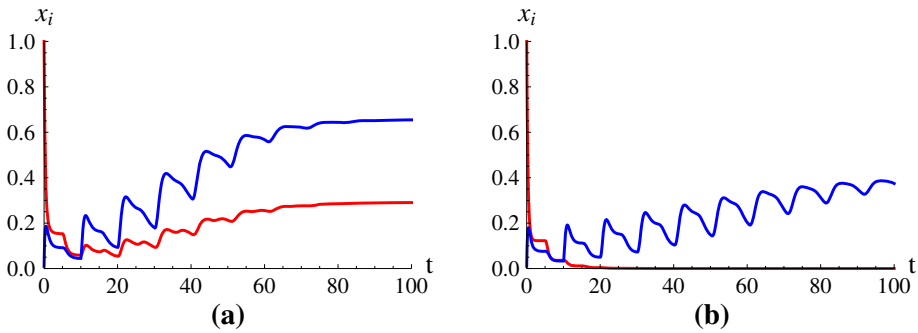

Fig. 1 In **a**, Example 2.2 is depicted with $\tau_1 = 5$ and $\tau_2 = 10$. (A1) is not satisfied, but (A1') is, and also $s(M) > 0$, hence the population persists on both patches. Furthermore, one can check that the conditions of Theorem 5.2 hold and the positive equilibrium is globally asymptotically stable. In **b**, we set $a_{12} = 0$, other parameters are the same. Then $s(M) = 1 > 0$, but we are in the reducible case of Example 2.1, and the population becomes extinct on the first patch

By letting $\varepsilon \to 0^+$ and $t \to \infty$, this leads to $v_i \geq d_i^{-1}\left(\sum_{j=1}^n a_{ij}v_j + \beta_i h(m)\right)$, for $i = 1, \ldots, n$. For $v_k = \min_i v_i$, this inequality yields

$$v_k \geq \gamma_k h(m) \geq e^{\alpha} h(m) = e^{\alpha} \min\{h(\alpha), h(e^{\beta-1})\} = \min\{\alpha, \exp\left(\alpha + \beta - 1 - e^{\beta-1}\right)\}.$$

□

In spite of the explicit estimates provided by Theorem 2.4, clearly the criterion for the uniform persistence in Theorem 2.3 is more general.

Example 2.2 In (1.1), let $n = 2, m = 1, \beta_1 = 1, \beta_2 = 3, a_{12} = a_{21} = 1, d_1 = 3, d_2 = 2$. Then $M = \begin{pmatrix} -2 & 1 \\ 1 & 1 \end{pmatrix}$ and $\gamma_1 < 1$, hence **(A1)** is not satisfied, so Theorem 2.4 does not apply directly. However, it is easy to check that hypothesis **(A1')** is satisfied with any $c_1, c_2 > 0$ such that $2c_1 < c_2 < 3c_1$, and therefore we are able to conclude that system (1.1) is permanent (Fig. 1).

Next result establishes that $s(M) > 0$ is a criterion for the uniform persistence of the total population, i.e., the uniform ρ-persistence of (1.1) in the sense of Smith and Thieme's nomenclature [16] with $\rho(\phi) = \sum_{i=1}^n \phi_i(0)$; moreover, in the case of an irreducible matrix A, the persistence is uniform in all patches. It will be shown in the next section that this criterion is sharp. In the theorem below, we use the norm $|x| = \sum_{i=1}^n |x_i|$ in $\mathbb{R}^n$, so $\rho(\phi) = |\phi(0)|$ for all $\phi \in C_0^+$.

Theorem 2.5 *Assume $s(M) > 0$. Then for system (1.1) the total population strongly uniformly persists. If M is irreducible, then the population strongly uniformly persist on each patch. If M is reducible, there exists at least one patch, where the population strongly uniformly persists.*

Proof The proof is organized in three steps.

(i) Finding an irreducible block with positive spectral bound

If M is reducible, then (after a permutation of the variables), it can be written in the diagonal form

$$M = \begin{pmatrix} M_{11} & \dots & M_{1\ell} \\ & \ddots & \\ 0 & \dots & M_{\ell\ell} \end{pmatrix},$$

where M_{lm} are $n_l \times n_m$ matrices, with M_{ll} irreducible $n_l \times n_l$ blocks, $\sum_{l=1}^{\ell} n_l = n$. Then $s(M) = \max\{s(M_{\ell\ell}) : i = 1, \dots, \ell\}$, and there exists an index $\kappa \le \ell$ such that $s(M_{\kappa\kappa}) > 0$. Let $\underline{\kappa} := \sum_{l=1}^{\kappa-1} n_l + 1$ and $\overline{\kappa} := \sum_{l=1}^{\kappa} n_l$. Define the index set $\Omega := \{i \in \mathbb{N} : \underline{\kappa} \le i \le \overline{\kappa}\}$, then $|\Omega| = n_\kappa > 0$. Now consider the following subsystem of (1.1), which corresponds to the κth block:

$$x_i'(t) = -d_i x_i(t) + \sum_{j\in\Omega} a_{ij} x_j(t) + \sum_{j\notin\Omega} a_{ij} x_j(t) + \sum_{k=1}^{m} \beta_{ik} x_i(t-\tau_{ik}) e^{-x_i(t-\tau_{ik})}, \quad i \in \Omega. \tag{2.14}$$

In the sequel we let $p_i(t) := \sum_{j\notin\Omega} a_{ij} x_j(t) \ge 0$ for all $i \in \Omega$, and let $\rho^\kappa(\phi) := \sum_{j\in\Omega} \phi_j(0)$. We use the notation $M_{\kappa\kappa} = A_{\kappa\kappa} + B_{\kappa\kappa} - D_{\kappa\kappa}$, where $A_{\kappa\kappa}, B_{\kappa\kappa}, D_{\kappa\kappa}$ are $n_\kappa \times n_\kappa$ matrices, corresponding to the κth block in A, B, D. If M is irreducible, we have only one block $M_{11} = M$, and in this case $|\Omega| = n$ and $p_i(t) = 0$ for all $i = 1, \dots, n$.

(ii) Uniform weak persistence of the total population of an irreducible block with positive spectral bound

Consider (2.14). For any $0 < \varepsilon < 1$, we define the auxiliary system

$$w_i' = -d_i w_i(t) + \sum_{k=1}^{m} \beta_{ik}(1-\varepsilon) w_i(t-\tau_{ik}) + \sum_{j\in\Omega} a_{ij} w_j(t), \quad i \in \Omega, \tag{2.15}$$

and the auxiliary matrix $M_{\kappa\kappa}(\varepsilon) = A_{\kappa\kappa} + B_{\kappa\kappa}(\varepsilon) - D_{\kappa\kappa}$, where

$$B_{\kappa\kappa}(\varepsilon) = \mathrm{diag}(\beta_{\underline{\kappa}}(1-\varepsilon), \beta_{\underline{\kappa}+1}(1-\varepsilon), \dots, \beta_{\overline{\kappa}-1}(1-\varepsilon), \beta_{\overline{\kappa}}(1-\varepsilon)).$$

If $s(M_{\kappa\kappa}) > 0$, then also $s(M_{\kappa\kappa}(\varepsilon)) > 0$ for sufficiently small ε. Fix such an ε. Since $M_{\kappa\kappa}(\varepsilon)$ (and thus also $M_{\kappa\kappa}(\varepsilon)^T$) is a cooperative irreducible matrix, $s(M_{\kappa\kappa}(\varepsilon))$ is a simple dominant eigenvalue with a positive eigenvector. Let q be the positive vector that corresponds to the transpose of $M_{\kappa\kappa}(\varepsilon)$, i.e. $M_{\kappa\kappa}(\varepsilon)^T q = s(M_{\kappa\kappa}(\varepsilon))q$.

Define for any positive solution segment w_t of system (2.15) the vector $y(t)$ by

$$y_i(t) = \left(w_i(t) + \sum_{k=1}^{m} \beta_{ik}\,(1-\varepsilon) \int_{t-\tau_{ik}}^{t} w_i(u)du \right).$$

We construct the Lyapunov functional $V := \langle y(t), q\rangle$ (here $\langle\cdot,\cdot\rangle$ denotes the Euclidean scalar product). Then it is easily seen that $y(t)$ satisfies the relation

$$y'(t) = M_{\kappa\kappa}(\varepsilon) w(t)$$

and we have

$$\frac{dV(t)}{dt} = \langle y'(t), q\rangle = \langle M_{\kappa\kappa}(\varepsilon)w(t), q\rangle = \langle w(t), M_{\kappa\kappa}(\varepsilon)^T q\rangle = \langle w(t), s(M_{\kappa\kappa}(\varepsilon))q\rangle > 0, \tag{2.16}$$

because in the last scalar product all terms are positive. Hence V is increasing and $V > 0$ except at zero, so either $\lim_{t\to\infty} V(t) = \infty$ or $\lim_{t\to\infty} V(t) = V_* < \infty$ with $V_* > 0$. We claim that the latter case is not possible. Suppose the contrary: then by the fluctuation lemma there is a sequence $t_l \to \infty$ as $l \to \infty$ such that $V(t_l) \to V_*$ and $V'(t_l) \to 0$. Then from (2.16) it follows that $w(t_l) \to 0$. Given that $w_i'(t) \geq -d_i w_i(t)$, we have that $w_i(s) \leq e^{d_i\tau} w_i(t)$ for any $s \in [t-\tau, t]$, consequently $y_i(t) \leq w_i(t)(1+\beta_i(1-\varepsilon)\tau e^{d_i\tau})$. As $w(t_l) \to 0$, necessarily $y(t_l) \to 0$ and thus $V(t_l) \to 0$ which is a contradiction. Thus, only $\lim_{t\to\infty} V(t) = \infty$ is possible.

Now consider a positive solution $x(t)$ of (1.1), and let $\tilde{x}(t) = (x_{\underline{\kappa}}(t), \ldots, x_{\overline{\kappa}}(t))^T$. There is a $\delta_0 = \delta_0(\varepsilon) > 0$ such that $e^{-\xi} > (1-\varepsilon)$ for $\xi \in [0, \delta_0]$. Then $\beta_{ik}\xi e^{-\xi} \geq \beta_{ik}\xi\,(1-\varepsilon)$ for all $i = 1, ...n,\ k = 1, \ldots, m$ and $\xi \in [0, \delta_0]$. Define the set U_ε by

$$U_\varepsilon = \{\psi \in C^+([\tau, 0], \mathbb{R}^{|\Omega|}) : ||\psi_i|| \leq \delta_0 \text{ for all } i \in \Omega\}.$$

Suppose that there is a t_0 such that $\tilde{x}_t \in U_\varepsilon$ for all $t \geq t_0$. Then we can consider a solution $w(t)$ of (2.15) for $t \geq t_0$ with $w_{t_0} = \tilde{x}_{t_0}$, and by a standard comparison principle (using $p_i(t) \geq 0$ and $\beta_{ik}\xi e^{-\xi} \geq \beta_{ik}\xi\,(1-\varepsilon)$) we obtain $\tilde{x}(t) \geq w(t)$ for all $t \geq t_0$, and $\tilde{x}_t \in U_\varepsilon$ implies $w_t \in U_\varepsilon$ for all $t \geq t_0$, which contradicts $V(t) \to \infty$.

Therefore, there is a sequence $t_l \to \infty$ as $l \to \infty$ such that $\tilde{x}_{t_l} \notin U_\varepsilon$. Then for each t_l there is a $j(l) \in \Omega$ such that $||(\tilde{x}_{t_l})_{j(l)}|| > \delta_0$, thus there is a $t_l^* \in [t_l - \tau, t_l]$ such that $\tilde{x}_{j(l)}(t_l^*) > \delta_0$. By $\tilde{x}_{j(l)}'(t) \geq -d_{j(l)}\tilde{x}_{j(l)}(t)$ we have $\tilde{x}_{j(l)}(t_l) \geq \tilde{x}_{j(l)}(t_l^*)e^{-d_{j(l)}(t_l - t_l^*)} \geq e^{-d_{j(l)}\tau}\delta_0$, thus

$$|\tilde{x}(t_l)| \geq \delta := \min_{i=1,\ldots,n}\{e^{-\tau d_i}\delta_0\},$$

and we obtain that $\limsup_{t\to\infty} |\tilde{x}(t)| \geq \delta$, hence we obtain the uniform weak persistence of the total population on the patches of the κth block.

We conclude that system (1.1) is uniformly weakly ρ^κ-persistent with $\rho^\kappa(\phi) = \sum_{i\in\Omega}\phi_i(0)$, which represents the persistence of the total population of the patches of the κth block.

(iii) Uniform strong persistence on each patch of an irreducible block with positive spectral bound

To show the uniform strong ρ^κ-persistence (i.e. there is a $\theta > 0$ such that $\liminf_{t\to\infty} \rho^\kappa(x_t) > \theta$), we can apply Theorem 4.5 of [16, Chapter 4.1]. By the dissipativity (Theorem 2.1), there exists a compact global attractor of system (1.1) (by [7], Theorem 3.4.8), and the conditions of Theorem 4.5 of [16] hold, which guarantees the uniform strong ρ^κ-persistence. Next we show the persistence of the population in each patch of the κth block. We shall use the persistence functions $\rho_i(x_t) = x_i(t)$, which express the actual population on patch i. Let $\epsilon \in (0, \theta)$, where θ corresponds to ρ^κ-persistence, i.e. $\liminf_{t\to\infty} \rho^\kappa(x_t) > \theta$. Then for any solution x_t there is a sequence $t_l \to \infty$ as $l \to \infty$ such that $\sum_{i\in\Omega} x_i(t_l) > \theta - \epsilon$ for all l. Then there must be an index $j \in \Omega$ such that $x_j(t_l) > \frac{\theta-\epsilon}{n}$ holds for infinitely many t_l. We may assume $j = \underline{\kappa}$. Thus, $\limsup_{t\to\infty} x_{\underline{\kappa}}(t) \geq \frac{\theta-\epsilon}{n}$, and the system is uniformly weakly $\rho_{\underline{\kappa}}$-persistent. We can apply again Theorem 4.5 of [16] to conclude the uniform strong $\rho_{\underline{\kappa}}$-persistence, thus there is an $\eta_{\underline{\kappa}} > 0$ such that $\liminf_{t\to\infty} x_{\underline{\kappa}}(t) > \eta_{\underline{\kappa}}$ and the population persists on patch $\underline{\kappa}$. By the irreducibility of $M_{\kappa\kappa}$, there is an index $j \in \Omega$, such that $a_{j\underline{\kappa}} > 0$. We may assume $j = \underline{\kappa} + 1$, then $x_{\underline{\kappa}+1}'(t) \geq -d_{\underline{\kappa}+1}x_{\underline{\kappa}+1}(t) + a_{\underline{\kappa}+1,1}x_{\underline{\kappa}}(t)$, thus $\liminf_{t\to\infty} x_{\underline{\kappa}+1}(t) > \eta_{\underline{\kappa}+1}$, where we can choose $\eta_{\underline{\kappa}+1} = \eta_{\underline{\kappa}}a_{\underline{\kappa}+1,\underline{\kappa}}/d_{\underline{\kappa}+1}$. By the irreducibility of this block, we can reach all patches inductively and by choosing $\eta = \min_{i\in\Omega}\{\eta_i\}$ we have proved the statement of the theorem, and the population strongly uniformly persists on each single patch $i \in \Omega$.

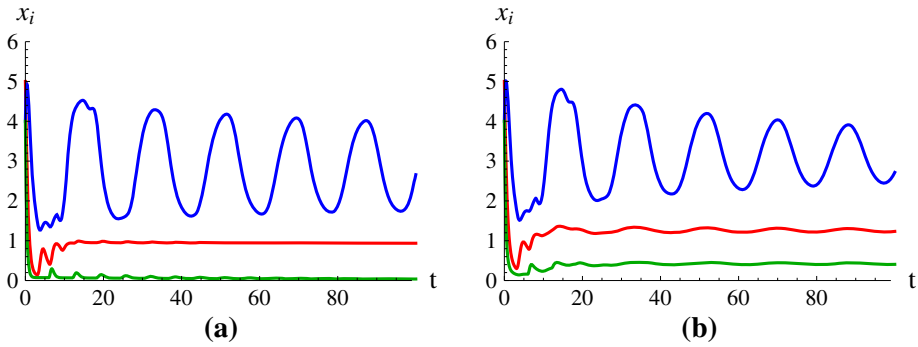

Fig. 2 Illustration of a system with three patches. In **a**, parameters are set to $n = 3, m = 1, \beta_1 = 5, \beta_2 = 10, \beta_3 = 3, d_1 = 2, d_2 = 1, d_3 = 3, a_{12} = a_{31} = a_{32} = 0, a_{13} = a_{21} = a_{23} = 1, \tau_1 = 3, \tau_2 = 8, \tau_3 = 6$. Then M is reducible but $s(M) = 9 > 0$. We can observe different behavior on the patches: oscillation, convergence to a positive value, extinction. In **b**, parameters are the same, except that $a_{12} = a_{31} = a_{32} = 0.1$, thus M is irreducible and the system is persistent

In the irreducible case, Ω contains all indices $i = 1, \ldots, n$ and the population strongly uniformly persists on each patch (Fig. 2). □

3 Extinction

In this section, a sharp criterion for the global asymptotic stability of the trivial equilibrium of (1.1) is established. In biological terms, this means the extinction of the population in all patches.

Theorem 3.1 *Suppose that $s(M) \leq 0$. Then the equilibrium 0 of (1.1) is GAS (in C^+).*

Proof If $s(M) < 0$, or if $s(M) = 0$ and $A = [a_{ij}]$ is an irreducible matrix, the global asymptotic stability of $x = 0$ follows from Theorems 2.1 and 3.1 in [3], respectively; for the latter case, the framework in [19] was used.

Now, suppose that A is reducible and $s(M) = 0$. After a permutation of the variables in (1.1), we may suppose that A has the form

$$A = \begin{pmatrix} A_{11} & \ldots & A_{1\ell} \\ & \ddots & \\ 0 & \ldots & A_{\ell\ell} \end{pmatrix},$$

where A_{km} are $n_k \times n_m$ matrices, with A_{kk} irreducible $n_k \times n_k$ blocks, $\sum_{k=1}^{\ell} n_k = n$. (According to our definition, here a square matrix of size one is always irreducible; cf. e.g. Appendix A of [17].)

We prove the result for $\ell = 2$; the general case follows by induction. Suppose that $n_1 + n_2 = n$ and $a_{ij} = 0$ for $n_1 + 1 \leq i \leq n$, $1 \leq j \leq n_1$, so that

$$A = \begin{pmatrix} A_{11} & A_{12} \\ 0 & A_{22} \end{pmatrix}, \quad M = \begin{pmatrix} M_{11} & M_{12} \\ 0 & M_{22} \end{pmatrix}, \tag{3.1}$$

where A_{ij}, M_{ij} are $n_i \times n_j$ blocks and M_{ii} are irreducible matrices. Since $\sigma(M) = \sigma(M_{11}) \cup \sigma(M_{22})$, we have $s(M_{ii}) \leq 0$, $i = 1, 2$.

Write a solution $x(t) = x(t;\varphi)$ (for $\varphi \in C^+$) of (1.1) as $x(t) = (y(t), z(t)) \in \mathbb{R}^{n_1} \times \mathbb{R}^{n_2}$ according to the decomposition of M in (3.1). The result for the irreducible case implies that 0 is the unique equilibrium of (1.1), and that $z(t) \to 0$ as $t \to \infty$. If suffices to show that $y(t) \to 0$ as $t \to \infty$.

Since $s(M_{11}) \le 0$, then $-M_{11}$ is an M-matrix; moreover, $-M_{11}$ is an irreducible matrix, therefore that there exists a positive vector $c = (c_1, \ldots, c_{n_1})$ such that $M_{11}c \le 0$ [5], i.e.,

$$\beta_i - d_i + \sum_{j=1}^{n_1} \frac{c_j}{c_i} a_{ij} \le 0, \quad i = 1, \ldots, n_1. \tag{3.2}$$

Rewrite system (1.1) with the change of variables $\bar{y}_i = c_i^{-1} y_i$, $i = 1, \ldots, n_1$. Dropping the bars for the sake of simplification, we get

$$\begin{aligned} y_i'(t) &= d_i y_i(t) + \sum_{j=1}^{n_1} \frac{c_j}{c_i} a_{ij} y_j(t) + \sum_{k=1}^{m} \beta_{ik} y_i(t-\tau_{ik}) e^{-c_i y_i(t-\tau_{ik})} + g_i(t), \quad i = 1, \ldots, n_1 \\ z_p'(t) &= -d_p z_p(t) + \sum_{j=n_1+1}^{n} a_{pj} z_p(t) + \sum_{k=1}^{m} \beta_{pk} z_p(t-\tau_{pk}) e^{-z_p(t-\tau_{pk})}, \quad p = 1, \ldots, n_2, \end{aligned} \tag{3.3}$$

where $g_i(t) := \sum_{k=1}^{n_2} a_{i(n_1+k)} z_k(t) \to 0$ as $t \to \infty$. Next, define

$$u_j = \limsup_{t\to\infty} y_j(t), \tag{3.4}$$

where y_j, z_p satisfy (3.3). We need to prove that $u := \max_{1\le j\le n_1} u_j = 0$.

Suppose that $u > 0$. For each $i \in \{1, \ldots, n_1\}$ such that $u_i = u$, by the fluctuation lemma there is a sequence (t_k), with $t_k \to \infty$, $y_i(t_k) \to u_i$, $y_i'(t_k) \to 0$. Choose $\varepsilon \in (0, u_i)$. For t and k large, we have $y_i(t_k) \ge u_i - \varepsilon$, $y_j(t) \le u_j + \varepsilon$, $j = 1, \ldots, n_1$, and $0 \le g_i(t) \le \varepsilon$, leading to

$$y_i'(t_k) \le -d_i(u_i - \varepsilon) + \sum_{j=1}^{n_1} \frac{c_j}{c_i} a_{ij}(u_j + \varepsilon) + \beta_i(u_i + \varepsilon) + \varepsilon.$$

By letting $\varepsilon \to 0^+$ and $k \to \infty$, from (3.2) we get

$$0 \le (\beta_i - d_i)u_i + \sum_{j=1}^{n_1} \frac{c_j}{c_i} a_{ij} u_j \le \Big(\beta_i - d_i + \sum_{j=1}^{n_1} \frac{c_j}{c_i} a_{ij}\Big) u_i \le 0.$$

This leads to

$$\beta_i - d_i + \sum_{j=1}^{n_1} \frac{c_j}{c_i} a_{ij} = 0, \quad \sum_{j=1}^{n_1} \frac{c_j}{c_i} a_{ij}(u_j - u_i) = 0, \quad \text{if} \quad u_i = u. \tag{3.5}$$

On the other hand, reasoning as in the proof of Theorem 2.1, and since $\lim_{t\to\infty} z_p(t) = 0$ for $1 \le p \le n_2$, (3.2) and (3.5) yield the estimate

$$\beta_i u = d_i u - \sum_{j=1}^{n_1} \frac{c_j}{c_i} a_{ij} u \le \beta_i (c_i e)^{-1},$$

implying that $u \le (c_i e)^{-1}$. In particular, for any $\varepsilon > 0$ and i such that $u_i = u$, the bounds $0 \le y_i(t) < (u + \varepsilon) < 1/c_i$ hold for $t > 0$ large.

Next, for i such that $u_i = u$ consider again a sequence (t_k) as above. For $\varepsilon > 0$ small and k large,

$$y_i'(t_k) \le -d_i(u-\varepsilon) + \sum_{j=1}^{n_1} \frac{c_j}{c_i} a_{ij}(u+\varepsilon) + \sum_{q=1}^{m} \beta_{iq} h_i(y_i(t_k - \tau_{iq})) + \varepsilon,$$

where $h_i(x) = xe^{-c_i x}$. The functions h_i are strictly increasing for $0 \le x \le 1/c_i$, hence $h_i(y_i(t_k - \tau_{iq})) \le h_i(u+\varepsilon)$ for k large. From (3.5), and letting $\varepsilon \to 0^+$ and $k \to \infty$, we thus obtain

$$0 \le \beta_i u\,(e^{-c_i u} - 1) < 0,$$

which is not possible. This shows that $u = 0$, and the proof is complete. □

In view of Theorems 2.2, 2.5 and 3.1, we therefore have a sharp threshold criterion for *extinction* versus *uniform persistence* of the *total population* in the general case; and in the case of an irreducible matrix A, we have a sharp threshold criterion for extinction versus uniform persistence of the population in *all patches*. Such consequences are formulated in the following two theorems.

Theorem 3.2 *If $s(M) \le 0$, the equilibrium 0 of (1.1) is GAS; while if $s(M) > 0$, the total population is uniformly persistent.*

Theorem 3.3 *Suppose that the matrix A is irreducible. Then: (i) if $s(M) \le 0$, the equilibrium 0 of (1.1) is GAS; (ii) if $s(M) > 0$, system (1.1) is uniformly persistent, i.e., the population uniformly persists on each patch. Moreover, $s(M) > 0$ if and only if there is a positive vector $c \in \mathbb{R}^n$ such that $Mc > 0$.*

As observed, $s(M) > 0$ is a sharp condition for the uniform persistence of (1.1) in the irreducible case, whereas this criterion fails in the case of reducible community matrices. In the latter case, while the total population uniformly persists if $s(M) > 0$, the population can become extinct on some of the patches (see Example 2.1). However, by Theorem 2.3 the uniform persistence follows under the stronger hypothesis **(A1')**.

Two final notes in this section open the present framework to possible generalizations.

Remark 3.1 Theorem 3.1 is also valid for a system (1.1) without condition (1.3). In fact, since $s(M) \le 0$ is equivalent to saying that $-M = D - A - B$ is an M-matrix, and $\underline{\beta} = \min_i \beta_i$ is strictly positive, then $s(M) \le 0$ implies that $D - A \ge M + \underline{\beta} I$ is a non-singular M-matrix [5, Theorem 5.3]. In view of this, by Theorem 2.1 and Remark 2.1, all solutions of (1.1) with initial conditions in C^+ are bounded, and in this way the limits in (3.4) are well-defined.

Remark 3.2 Some results in Sects. 2 and 3 can be extended in a natural way to a more general class of delayed systems with patch structure of the form $x_i'(t) = -d_i x_i(t) + \sum_{j=1}^n a_{ij} x_j(t) + b_i(x_{t,i})$, $1 \le i \le n$, where the birth functions $b_i : C([-\tau, 0]; \mathbb{R}) \to \mathbb{R}_+$ are C^1-smooth, bounded, with $b_i(0) = 0$, $Db_i(0)(1) = \beta_i$, and satisfy some additional conditions. Nevertheless, we emphasize that the uniform estimates provided by Theorems 2.3 and 2.4 are valid for the specific Ricker-type non-linearity only. Also, the main result on the global asymptotic stability of the positive equilibrium, which will be presented in Sect. 5, depends heavily on the shape of the non-linearity $h(x) = xe^{-x}$, and cannot be extrapolated for a more general class of population models.

4 Existence of a Positive Equilibrium

Together with (1.1), we consider the ODE model in the positive cone $\mathbb{R}^n_+$:

$$x_i' = -d_i x_i + \sum_{j=1}^{n} a_{ij} x_j + \beta_i x_i e^{-x_i} =: f_i(x), \quad i = 1, \ldots, n. \tag{4.1}$$

For all $i \in \{1, \ldots, n\}$ and $x \in \mathbb{R}^n_+$ with $x_i = 0$, we have $f_i(x) \geq 0$, thus the positive cone $\mathbb{R}^n_+$ is positively invariant for (4.1).

The ODE (4.1) may be seen as the particular case of (1.1) with $\tau = 0$. Clearly, systems (1.1) and (4.1) share the same equilibria. In this section, we look for equilibria of (4.1).

In the following, we adopt some definitions and notation of Hofbauer [8], namely the definition of a saturated equilibrium (or saturated fixed point). For an ODE system $x' = f(x)$ for which $\mathbb{R}^n_+$ is positively invariant, if an equilibrium point x^* lies on the frontier of $\mathbb{R}^n_+$, say $x^* = (0, \ldots, 0, x^*_{p+1}, \ldots, x^*_n)$, then necessarily the Jacobian matrix $Df(x^*)$ has the form (cf. [8])

$$Df(x^*) = \begin{bmatrix} C & 0 \\ D & E \end{bmatrix},$$

where C is a $p \times p$ matrix, called the *external part* of $Df(x^*)$.

Definition 4.1 For an ODE system $x' = f(x)$, positively invariant in $\mathbb{R}^n_+$, an equilibrium $x^* \geq 0$ is said to be a **saturated equilibrium** if x^* is an equilibrium and: (i) either $x^* \in \operatorname{int}(\mathbb{R}^n_+)$ and $Df(x^*)$ is stable, i.e., $s\big(Df(x^*)\big) \leq 0$; (ii) or $x^* \in fr(\mathbb{R}^n_+)$, $x^* = (0, \ldots, 0, x^*_{p+1}, \ldots, x^*_n)$, and $Df(x^*) = \begin{bmatrix} C & 0 \\ D & E \end{bmatrix}$, where the $p \times p$ matrix C is stable, i.e., $s(C) \leq 0$.

An equilibrium $x^* \geq 0$ of (4.1) is said to be **regular** if $\det Df(x^*) \neq 0$; in this case, the **index** of x^* is defined as the sign of $\det(-Df(x^*))$.

With these definitions, note that an asymptotically stable equilibrium has index $+1$, in any dimension n.

The following theorem plays an important role in this section.

Theorem 4.1 *[8] Any system $x' = f(x)$ for $x \in \mathbb{R}^n_+$, where f is a C^1 vector field, which is dissipative and forward invariant on $\mathbb{R}^n_+$ has at least one saturated equilibrium; moreover, if all saturated equilibria are regular, the sum of their indices equals $+1$.*

For system (4.1), the ODE version of Theorem 2.1 shows that (4.1) dissipative. Consequently, from Hofbauer's theorem we deduce that there is at least a saturated fixed point of (4.1) in the cone $\mathbb{R}^n_+$.

Next, we give sufficient conditions for the existence and stability of a positive equilibrium of (4.1), both for the irreducible and reducible case. A sharp criterion is obtained when A is irreducible.

Theorem 4.2 *Assume A is irreducible. If $s(M) > 0$, there is a unique positive equilibrium x^* of (4.1), which is GAS in $\mathbb{R}^n_+ \setminus \{0\}$; if $s(M) \leq 0$, zero is a global attractor in $\mathbb{R}^n_+$.*

Proof The last assertion follows from Theorem 3.1. Now, suppose that $s(M) > 0$. From Theorem 4.1, there is a saturated equilibrium of (4.1). Since A is irreducible, the Jacobian

matrix at an equilibrium u^*, $Df(u^*) = A - D + \mathrm{diag}\left(\beta_i e^{-u_i^*}(1-u_i^*)\right)_{i=1}^n$, is also irreducible, thus the only possible saturated equilibrium on the boundary of $\mathbb{R}_+^n$ is zero, for which the external part of $Df(0)$ coincides with the full matrix. However, condition $s(M) > 0$ implies that the linearized equation at 0, $\dot{x} = Mx$, has an eigenvalue with positive real part, hence zero is an unstable fixed point of (4.1). Consequently, there is a positive saturated equilibrium x^*. But any other possible positive equilibrium of (4.1) is saturated. In fact, if $u^* > 0$ is an equilibrium of (4.1), we have

$$-Df(u^*)u^* = \mathrm{col}\left(\beta_i e^{-u_i^*}(u_i^*)^2\right)_{i=1}^n > 0.$$

This implies that $-Df(u^*)$ is a non-singular M-matrix (see [5]), which is equivalent to saying that $s(Df(u^*)) < 0$. Therefore u^* is regular with index +1. Again by Theorem 4.1 we conclude that the positive equilibrium x^* of (4.1) is unique, and locally asymptotically stable. Since (4.1) is an irreducible and cooperative system, by Theorem 6 of [8] (see also the proof of Lemma 4.2 below) x^* is a global attractor of all positive solutions $x(t)$. On the other hand, any solution $x(t) = x(t; x_0)$ of (4.1) with initial condition in $x_0 \in \mathbb{R}_+^n \setminus \{0\}$ is strictly positive for $t > 0$ (cf. e.g. [15]). □

Theorem 4.3 *Assume (2.6) for some $c = (c_1, \ldots, c_n) > 0$. Then, there is a unique positive equilibrium x^* of (4.1), which is GAS in* $\mathrm{int}(\mathbb{R}_+^n)$.

Proof If A is irreducible, (2.6) is equivalent to $s(M) > 0$ (cf. Theorem 3.3). If A is a reducible matrix, the existence of a globally asymptotically stable positive equilibrium of (4.1) is an immediate consequence of the next two lemmas. □

Lemma 4.1 *If (2.6) holds, then there is a unique positive equilibrium of (4.1).*

Proof As before, write the ODE (4.1) as $x' = f(x)$, for $f = (f_1, \ldots, f_n)$ and $f_i(x) = (\beta_i e^{-x_i} - d_i)x_i + \sum a_{ij}x_j$, and designate by $x(t, x_0)$ the solution of (4.1) with initial condition $x(0) = x_0 \in \mathbb{R}_+^n$. For a vector c as in (2.6) , we have $f_i(\varepsilon c) = \varepsilon[-(c_i d_i - \sum c_j a_{ij}) + c_i \beta_i e^{-\varepsilon c_i}]$, hence $f_i(\varepsilon c) > 0$ for $\varepsilon > 0$ small and $1 \le i \le n$. Since (4.1) is cooperative and dissipative, from Corollary 5.2.2 of [15, p. 82], $x(t, \varepsilon c) \to x^*$ as $t \to \infty$ for some $x^* > 0$. Clearly x^* is an equilibrium of (4.1). It suffices to show that x^* is the unique positive fixed point.

The case of A irreducible has already been addressed. Now, suppose that A is reducible, with

$$A = \begin{pmatrix} A_{11} & A_{12} \\ 0 & A_{22} \end{pmatrix},$$

where the $n_i \times n_i$ matrices A_{ii} are irreducible , $i = 1, 2,\ n_1 + n_2 = n$. (Recall that this includes the case of some of the A_{ii} equal to zero if $n_i = 1$.) The general case where A can be written in a triangular form with ℓ irreducible diagonal blocks A_{ii} follows by induction. We write accordingly

$$M = \begin{pmatrix} M_{11} & M_{12} \\ 0 & M_{22} \end{pmatrix}, \quad c = \begin{pmatrix} c^{(1)} \\ c^{(2)} \end{pmatrix},$$

with $n_i \times n_i$ matrices M_{ii} and $c^{(i)} \in \mathbb{R}^{n_i}$, $i = 1, 2$. Since $Mc > 0$, then $M_{22}c^{(2)} > 0$, and Theorem 3.2 yields $s(M_{22}) > 0$.

For $x(t) = (y(t), z(t)) \in \mathbb{R}^{n_1} \times \mathbb{R}^{n_2}$, system (4.1) becomes

$$y_i' = (\beta_i e^{-y_i} - d_i)y_i + \sum_{j=1}^{n_1} a_{ij} y_j + \sum_{k=1}^{n_2} a_{i(n_1+k)} z_k, \quad i = 1, \ldots, n_1 \tag{4.2a}$$

$$z_p' = (\beta_p e^{-z_p} - d_p)z_p + \sum_{k=1}^{n_2} a_{p(n_1+k)} z_k, \quad p = 1, \ldots, n_2. \tag{4.2b}$$

Write $x^* = (y^*, z^*) \in \mathbb{R}^{n_1} \times \mathbb{R}^{n_2}$. From the irreducible case, z^* is the unique positive equilibrium of (4.2_b), which is GAS. If $A_{12} = 0$, then clearly y^* is the unique positive equilibrium of (4.2_a). Otherwise, define $l := A_{12}z^*$ and note that $l = (l_1, \ldots, l_{n_1}) \geq 0, l \neq 0$. Consider the system

$$y_i' = (\beta_i e^{-y_i} - d_i)y_i + \sum_{j=1}^{n_1} a_{ij} y_j + l_i =: g_i(y), \quad i = 1, \ldots, n_1. \tag{4.3}$$

Obviously 0 is not a fixed point of (4.3). The positive cone $\mathbb{R}_+^{n_1}$ is positively invariant for (4.3). For $u^* = (u_1^*, \ldots, u_{n_1}^*)$ an equilibrium of (4.3), $Dg(u^*) = \operatorname{diag}\Big(\beta_i h'(u_i^*) - d_i\Big) + A_{11}$ is irreducible, thus there are no saturated equilibria on the boundary of $\mathbb{R}_+^{n_1}$. Also, $Dg(u^*)u^* = -\operatorname{col}\Big((u_i^*)^2 e^{-u_i^*} + l_i\Big)_{i=1}^{n_1} < 0$, and therefore we conclude that $-Dg(u^*)$ is a non-singular M-matrix, which implies that u^* is regular with index +1. From Theorem 4.1, we deduce that (4.3) has a unique saturated equilibrium, which is y^*. This ends the proof. □

Lemma 4.2 *If there exists a unique positive equilibrium x^* of (4.1), then x^* is GAS in* $\operatorname{int}(\mathbb{R}_+^n)$.

Proof Let $x_0 \in \operatorname{int}(\mathbb{R}_+^n)$. Choose l, L, $0 < l < 1 < L$, such that $lx^* \leq x_0 \leq Lx^*$. With the same notations as above, we have that $f_i(lx^*) > lf_i(x^*) = 0$ and $f_i(Lx^*) < Lf_i(x^*) = 0$. This implies that the components $x_i(t, lx^*)$ are non-decreasing and $x_i(t, Lx^*)$ are non-increasing, for $t \geq 0$ [15, Corollary 5.2.2], . Reasoning as above, let K_1, K_2 be such that $x(t, lx^*) \to K_1$ and $x(t, Lx^*) \to K_2$ as $t \to \infty$. Clearly K_1, K_2 are positive equilibria, hence $K_1 = K_2 = x^*$. Since (4.1) is cooperative, $x(t, lx^*) \leq x(t, x_0) \leq x(t, Lx^*)$, hence $x(t, x_0) \to x^*$ as $t \to \infty$. □

The results in Sects. 2, 3 and 4 yield some interesting algebraic consequences, which may be useful in applications.

Theorem 4.4 *(i) For a cooperative matrix M, if $Mc > 0$ for some positive vector c, then $s(M) > 0$; the converse is true if M is irreducible. (ii) If $M = B - D + A$ for A, B, D as in (1.4), with either (1.3) or $D - A$ a non-singular M-matrix, then* **(A1')** *holds if and only if $Mc > 0$ for some positive vector c.*

Proof (i) From Theorems 2.2 and 3.1, condition (2.6) implies $s(M) > 0$. (ii) Obviously, **(A1')** implies (2.6). If $Mc > 0$ for some positive vector c, from Theorem 4.3 there is a unique positive equilibrium $x^* > 0$ of (4.1) (and (1.1)) (note that the dissipativity of (4.1) follows from $D - A$ being a non-singular M-matrix, in case (1.3) is not satisfied). Consequently, $Bx^* > \operatorname{diag}(\beta_i x_i^* e^{-x_i^*}) = (D - A)x^* > 0$, thus **(A1')** is satisfied with $c = x^*$. □

5 Global Asymptotic Stability of the Positive Equilibrium

In this section, we give a criterion for the (absolute) global attractivity of the positive equilibrium. We shall use an auxiliary result established in [3].

Lemma 5.1 *[3] The function $h(x) = xe^{-x}$ satisfies*

$$|h(y) - h(x)| < e^{-x}|y - x| \quad \text{for all } x \in (0, 2] \text{ and } y > 0,\ y \neq x.$$

We now prove the main result of this section.

Theorem 5.1 *Assume* **(A2)** $1 < \gamma_i \leq e^2,\ \ i = 1, \ldots, n$, *where* $\gamma_i := \dfrac{\beta_i}{d_i - \sum_{j=1}^n a_{ij}}$. *Then the positive equilibrium x^* for (1.1) is GAS (in C_0^+).*

Proof Theorems 2.1 and 4.3 guarantee that all positive solutions of (1.1) are bounded and that there is a unique positive equilibrium $x^* = (x_1^*, \ldots, x_n^*)$ of (1.1). For $x_i^* = \max_j x_j^*$, we obtain

$$e^{x_i^*} \leq \gamma_i \leq e^2,$$

hence $0 < x_j^* \leq x_i^* \leq 2,\ 1 \leq j \leq n$. Thus, x^* is locally asymptotically stable (cf. Theorem 2.2 and [3, Remark 2.1]).

As before, let $h(x) = xe^{-x}$ for $x \geq 0$, and effect the changes

$$z_i(t) = \frac{x_i(t)}{x_i^*} - 1, \quad 1 \leq i \leq n. \tag{5.1}$$

System (1.1) becomes

$$z_i'(t) = \frac{1}{x_i^*}\left[-d_i x_i^* z_i(t) + \sum_{j=1}^n a_{ij} x_j^* z_j(t) + \sum_{k=1}^m \beta_{ik}\Big(h(x_i^* + x_i^* z_i(t-\tau_{ik})) - h(x_i^*)\Big)\right],\ i = 1, \ldots, n. \tag{5.2}$$

Consider any solution $z(t) = z(t; \phi)$ of (5.2) with initial condition $\phi \in S$, where $S := \{\phi = (\phi_1, \ldots, \phi_n) \in C([-\tau, 0]; \mathbb{R}^n) : \phi_i(\theta) \geq -1$ for $-\tau \leq \theta < 0$ and $\phi_i(0) > -1,\ i = 1, \ldots, n\}$. Then, there are constants m, M, $0 < m < M$, with $m - 1 < z_i(t) < M$ for all i and $t > 0$ sufficiently large. To prove that $z(t) \to 0$ as $t \to \infty$, we now follow closely some arguments in [3].

Fix the maximum norm in $\mathbb{R}^n$, $|x| = \max_{1 \leq i \leq n} |x_i|$ for $x = (x_1, \ldots, x_n)$. If $\phi = 0$, then $z(t) \equiv 0$. For $\phi \neq 0$, we claim that

$$|z(t)| < \|\phi\| \text{ for } t \geq \tau. \tag{5.3}$$

For the sake of contradiction, suppose that (5.3) fails. Then, there exists $T \geq \tau$ such that $|z(T)| \geq \|\phi\| > 0$ and $|z(T)| \geq |z(t)|$ for $-\tau \leq t \leq T$.

Let $i \in \{1, \ldots, n\}$ be such that $|z(T)| = |z_i(T)|$, and consider the case $z_i(T) > 0$ (the case $z_i(T) < 0$ is similar). From the definition of T, we have $z_i'(T) \geq 0$. On the other hand, we obtain

$$z_i'(T) = \frac{1}{x_i^*}\left[-d_i x_i^* z_i(T) + \sum_{j=1}^n a_{ij} x_j^* z_j(T) + \sum_{k=1}^m \beta_{ik}\Big(h(x_i^* + x_i^* z_i(T-\tau_{ik})) - h(x_i^*)\Big)\right]. \tag{5.4}$$

Note $T-\tau_{ik} \geq 0$, hence $x_i^*+x_i^* z_i(T-\tau_{ik})$ is strictly positive. By Lemma 5.1, if $z_i(T-\tau_{ik}) \neq 0$, then

$$|h(x_i^* + x_i^* z_i(T - \tau_{ik})) - h(x_i^*)| < e^{-x_i^*} x_i^* |z_i(T - \tau_{ik})| \leq e^{-x_i^*} x_i^* z_i(T);$$

and $h(x_i^* + x_i^* z_i(T - \tau_{ik})) - h(x_i^*) = 0$ if $z_i(T - \tau_{ik}) = 0$. Since $\beta_i = \sum_k \beta_{ik} > 0$, then $\beta_{ik} > 0$ for some k, and clearly we obtain $\sum_{k=1}^m \beta_{ik}\Big(h(x_i^* + x_i^* z_i(T - \tau_{ik})) - h(x_i^*)\Big) < \beta_i e^{-x_i^*} x_i^* z_i(T)$. Also, $|z_j(T)| \leq z_i(T)$ for all j, and consequently (5.4) yields

$$z_i'(T) < \frac{1}{x_i^*}\left[\left(-d_i x_i^* + \sum_{j=1}^n a_{ij} x_j^*\right) + \beta_i e^{-x_i^*} x_i^*\right] z_i(T) = 0,$$

which contradicts the fact $z_i'(T) \geq 0$. This proves (5.3).

Define $\Phi_\phi(t) := \|z_t(\phi)\|$. Since (5.2) is an autonomous system, then $\Phi_\phi(t_2) = \Phi_{z_{t_1}(\phi)}(t_2 - t_1)$ for $t_2 > t_1 > 0$, and the above estimate proves that $\Phi_\phi(t_2) < \Phi_\phi(t_1)$ if $t_2 > t_1 + \tau$. The same arguments yield that $t \mapsto \|z_t(\phi)\|$ is non-increasing for $t \geq 0$, so $\Phi_\phi(t) \searrow \alpha$ as $t \to \infty$, for some $\alpha \geq 0$.

Next, consider the ω-limit set $\omega(\phi)$, which is non-empty. The invariance of $\omega(\phi)$ under (5.2) implies that $\omega(\phi) \subset \{\psi \in \bar{S} : \|\psi\| = \alpha\}$, where $\bar{S}$ denotes the closure of S in C. But the components $z_i(t)$ are bounded away from -1 (cf. Theorem 2.2), and therefore $\omega(\phi) \subset S$.

If $\alpha > 0$, let $\psi \in \omega(\phi)$. We have $\psi \in S$ and $\|\psi\| = \alpha$. However this is not possible, since $z_t(\psi) \in \omega(\phi)$ and from (5.3) we get $\|z_t(\psi)\| < \|\psi\| = \alpha$ for $t \geq \tau$. This shows that $\alpha = 0$, and the theorem is proved. □

Remark 5.1 In [3], the global asymptotic stability (with respect to C_0^+) of x^* was proved under the stronger hypothesis $1 < \gamma_i \leq \min\{e^2, e^{x_i^*}\}$, $i = 1, \ldots, n$, which turned out to be very restrictive, since for i such that $x_i^* = \max_{1 \leq j \leq n} x_j^*$ we necessarily have $\gamma_i \geq e^{x_i^*}$, and where the equality holds if and only if either $a_{ij} = 0$ or $x_j^* = x_i^*$ for all $j \neq i$. Furthermore, criteria for the existence of such a positive equilibrium were not established in [3].

In the above proof, observe that hypothesis **(A2)** was not directly applied to system (5.2), obtained as a consequence of the change of variables (5.1). Actually, **(A2)** was used only to guarantee the existence of a positive equilibrium with all its components in the interval $(0, 2]$, which is crucial for two reasons: on one hand, its local stability is deduced regardless of the size of the positive delays, and, on the other hand, Lemma 5.1 can be applied. Note that the estimate in Lemma 5.1 is no longer valid for $x > 2$. This observation permits to state the global attractivity of the positive equilibrium under weaker assumptions, as follows.

Theorem 5.2 *Assume (2.6) for some positive vector $c = (c_1, \ldots, c_n)$. Then, the unique positive equilibrium $x^* = (x_1^*, \ldots, x_n^*)$ (whose existence is given by Theorem 4.2) is GAS if $x_i^* \leq 2$ for $i = 1, \ldots, 2$.*

Remark 5.2 For the scalar Nicholson's blowflies equation, it is well-known that if $\gamma_1 = \beta_1/d_1 > e^2$, large delays can lead to the existence of periodic solutions appearing from a Hopf bifurcation. Also for $n > 1$, we can show that hypothesis **(A2)** is a sharp condition for the *absolute* global asymptotic stability (i.e., for the global asymptotic stability independently of the size of positive delays τ_{ik}) of x^*; if $\gamma_i > e^2$ for some i, in general large delays bring instability, as illustrated in the example below.

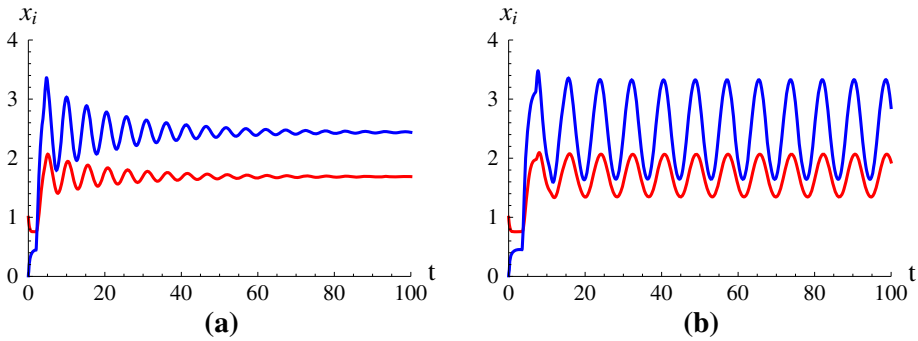

Fig. 3 Illustration of Example 5.1. Parameters are $a_{12} = a_{21} = 1$, $d_1 = d_2 = 2$, $\beta_1 = 3$, $\beta_2 = 15$, $\tau_1 = 1$. Then $\gamma_1 = \beta_1 < e^2$ and $\gamma_2 = \beta_2 > e^2$. In **a**, we set $\tau_2 = 2$, and we observe the convergence of solutions to an equilibrium. Increasing the delay to $\tau_2 = 3.5$, the equilibrium becomes unstable and we can see a periodic oscillation in **b**

Example 5.1 Consider (1.1) with $n = 2$, $m = 1$:

$$\begin{aligned} x_1'(t) &= -d_1 x_1(t) + a_{12} x_2(t) + \beta_1 x_1(t-\tau_1) e^{-x_1(t-\tau_1)} \\ x_2'(t) &= -d_2 x_2(t) + a_{21} x_1(t) + \beta_2 x_2(t-\tau_2) e^{-x_2(t-\tau_2)} \end{aligned} \tag{5.5}$$

and $a_{12} \geq 0, a_{21}, d_i, \beta_i, \tau_i > 0, i = 1, 2$, with $1 < \gamma_1 = \beta_1/(d_1 - a_{12}) \leq e^2$ and $\gamma_2 = \beta_2/(d_2 - a_{21}) > e^2$, so that **(A2)** fails. Under some further conditions on the coefficients in (5.5), we show that the positive equilibrium $x^* = (x_1^*, x_2^*)$ is not asymptotically stable if the size of the delay τ_2 is large.

Let $a_{21} > 0$ be sufficiently small so that $\beta_2/d_2 > e^2$. The linearization about $x^* = (x_1^*, x_2^*)$ is given by

$$y_i(t) = -[d_i y_i(t) + L_{i1}(y_t) + L_{i2}(y_t)], \quad i = 1, 2,$$

where the linear operators L_{ij} are defined by

$$\begin{aligned} &L_{11}(\varphi) = -\beta_1 h'(x_1^*)\varphi_1(-\tau_1), \ L_{12}(\varphi) = 0 \\ &L_{21}(\varphi) = -a_{21}\varphi_1(0), \ L_{22}(\varphi) = -\beta_2 h'(x_2^*)\varphi_2(-\tau_2), \quad \varphi = (\varphi_1, \varphi_2) \in C. \end{aligned}$$

Define now

$$\hat{N} = D - \left[\|L_{ij}\|\right] = \begin{pmatrix} d_1 - \beta_1|h'(x_1^*)| & 0 \\ -a_{21} & d_2 - \beta_2|h'(x_2^*)| \end{pmatrix},$$

with eigenvalues $\lambda_1 = d_1 - \beta_1|h'(x_1^*)|$ and $\lambda_2 = d_2 - \beta_2|h'(x_2^*)|$. We claim that it is possible to have $\lambda_2 < 0$. If this is the case, from Theorem 2.3 in [4] we conclude that there is $\tau_2 > 0$ for which the equilibrium $x^* = (x_1^*, x_2^*)$ of (5.5) is unstable (Fig. 3).

For $\alpha := a_{21}x_1^*$, we have $e^{x_2^*} = \frac{\beta x_2^*}{d_2 x_2^* - \alpha} \to \beta_2/d_2 > e^2$ as $\alpha \to 0^+$. This implies $x_2^* = x_2^*(\alpha) > 2$, for either a_{21} or x_1^* small (for instance, with $a_{12} = 0$, we have that $x_1^* = \log(\beta_1/d_1) \to 0^+$ if $\beta_1/d_1 \to 1^+$). Thus, $\lambda_2 = d_2 + \beta_2(1 - x_2^*)e^{-x_2^*}$ and for $x_2^*(0) := \log(\beta_2/d_2)$ we obtain

$$\lambda_2 = \lambda_2(\alpha) = \frac{1}{x_2^*}[-d_2(x_2^*)^2 + (2d_2 + \alpha)x_2^* - \alpha] \to d_2(2 - x_2^*(0)) < 0 \quad \text{as} \quad \alpha \to 0^+.$$

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