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Attractors in almost periodic Nicholson systems and some numerical simulations ☆

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The existence of a global attractor is proved for the skew-product semiflow induced by almost periodic Nicholson systems and new conditions are given for the existence of a unique almost periodic positive solution which exponentially attracts every other positive solution. Besides, some numerical simulations are included to illustrate our results in some concrete Nicholson systems.

1. Introduction

After Gurney et al. [10] came up with a scalar delay equation called Nicholson's blowflies equation, there has been an increasing interest in the dynamical behaviour of the solutions of this equation, as well as of its generalisations, such as Nicholson systems or their non-autonomous versions, often periodic or almost periodic. Firstly, the interest is in the extinction versus the persistence of the population, or of the population within some patch, when dealing with a compartmental model. In the case of persistence, the goal is to describe the picture of the population's evolution, depending on the initial situation. These models lie within the field of delayed functional differential equations (FDEs for short). A relevant reference for the theory of FDEs is Hale and Verduyn Lunel [11].

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Although there is extensive literature on Nicholson models, we mention some publications which are closer to our approach, namely, the works by Faria [5–7], Faria et al. [8], Faria and Röst [9], and Obaya and Sanz [19,20]. The reader can find many other references therein. In many papers dealing with the almost periodic model, the idea is to impose conditions forcing an invariant zone where a unique almost periodic solution is found by means of fixed-point theorems. New alternative methods can be found in Zhang et al. [24]. Very recently, almost periodic Nicholson systems have been considered by Novo et al. [17], as models in biology where the use of the exponential ordering can lead to new conditions that force the existence of a unique attracting almost periodic solution. This turns out to be the case for persistent systems provided that the delays are small enough.

In this paper, we apply methods of the theory of skew-product semiflows to analyse the long-term dynamics of almost periodic Nicholson systems. The monograph by Shen and Yi [22] can be a useful reference for this theory. Due to the time dependence of the system, solutions do not define a semiflow in a direct way. The almost periodic time variation in the model permits adding a compact base flow component Ω by means of the so-called hull construction, so that solutions induce a dynamical system on a product space of the form $\Omega \times X$. In the scalar case, X is the space of continuous functions on an interval $[-r, 0]$, where r is the delay in the equation and, in the m-dimensional case, X is the product of m such spaces. Then, dynamical techniques are applied in order to prove the existence of a global attractor in the standard positive cone $\Omega \times X_+$, which is the appropriate set from the biological point of view. This is a basic result which guarantees the existence of a subset approached by the trajectories in $\Omega \times X_+$ as time evolves. When persistence is assumed, then there also exists a global attractor in the interior of the positive cone $\Omega \times \operatorname{Int} X_+$.

Describing the structure of an attractor is a difficult task in general. Here, we focus on finding new conditions which imply that the latter attractor is as simple as it can be. If one thinks of an autonomous equation, that means a globally attracting equilibrium point. The counterpart of this simple situation in the non-autonomous setting is a unique attracting invariant set $K \subset \Omega \times \operatorname{Int} X_+$ which is a copy of the base flow Ω, that is, $K = \{(\omega, b(\omega)) \mid \omega \in \Omega\}$ for a continuous map $b : \Omega \to \operatorname{Int} X_+$. For the initial Nicholson model, this implies the existence of a unique attracting positive almost periodic solution, so that the behaviour of any other positive solution is asymptotically almost periodic.

It is important to mention that, although the Nicholson systems are not cooperative, they induce a local monotone and concave skew-product semiflow τ in a neighbourhood of $\Omega \times \{0\}$. This allows us to apply standard methods of comparison of solutions for the usual order in X_+, as well as the general theory for monotone and concave skew-product semiflows by Núñez et al. [18].

The conditions in this work guaranteeing the existence of a unique attracting positive almost periodic solution are complementary to those in the literature. This fact extends the scope of applicability of our results and allows us to illustrate the structure of the global attractor with the aid of numerical techniques in these new cases. Moreover, the behaviour of the global attractors when the migration and mortality rates of the Nicholson system vary is investigated numerically.

We briefly describe the structure of the paper. In Section 2, we include some preliminaries to make the paper reasonably self-contained. In Section 3, the theoretical results on the existence of attractors for Nicholson systems are presented and, under the hypothesis of uniform persistence, precise inequalities are given which imply that the attractor in the interior of the positive cone is an exponentially stable copy of the base. Results of this type have also been obtained by Faria [6,7]. Finally, in Section 4, some numerical simulations illustrate the applicability of our results and compare them with other results given in the previous literature.

2. Some preliminaries

We include some basic concepts of the theory of non-autonomous dynamical systems relevant in this work. In Section 3, we will provide a detailed explanation of the process to address the study of Nicholson systems in this context, by means of the hull construction.

Let (Ω, d) be a compact metric space. A real *continuous flow* $(\Omega, \sigma, \mathbb{R})$ is defined by a continuous map $\sigma : \mathbb{R} \times \Omega \to \Omega$, $(t, \omega) \mapsto \sigma(t, \omega) = \sigma_t(\omega) = \omega{\cdot}t$ satisfying (i) $\sigma_0 = \mathrm{Id}$, and (ii) $\sigma_{t+s} = \sigma_t \circ \sigma_s$ for all s, $t \in \mathbb{R}$. The set $\{\omega{\cdot}t \mid t \in \mathbb{R}\}$ is called the *orbit* of the point ω. We say that a subset $\Omega_1 \subset \Omega$ is *σ-invariant* if $\sigma_t(\Omega_1) = \Omega_1$ for every $t \in \mathbb{R}$. The flow $(\Omega, \sigma, \mathbb{R})$ is called *minimal* if it does not contain properly any other compact σ-invariant set, or equivalently, if every orbit is dense.

Given a continuous flow $(\Omega, \sigma, \mathbb{R})$ on a compact metric space Ω and a complete metric space (X, d), a continuous *skew-product semiflow* $(\Omega \times X, \tau, \mathbb{R}_+)$ on the product space $\Omega \times X$ is determined by a continuous map

$$\begin{array}{rccl} \tau: & \mathbb{R}_+ \times \Omega \times X & \longrightarrow & \Omega \times X \\ & (t, \omega, x) & \mapsto & (\omega{\cdot}t, u(t, \omega, x)) \end{array}$$

which preserves the flow on Ω, called the *base flow*. The semiflow property means (i) $\tau_0 = \mathrm{Id}$, and (ii) $\tau_{t+s} = \tau_t \circ \tau_s$ for $t, s \geq 0$, where $\tau_t(\omega, x) = \tau(t, \omega, x)$ for each $(\omega, x) \in \Omega \times X$ and $t \in \mathbb{R}_+$. This leads to the so-called (nonlinear) semicocycle property,

$$u(t + s, \omega, x) = u(t, \omega{\cdot}s, u(s, \omega, x)) \quad \text{for } t, s \geq 0 \text{ and } (\omega, x) \in \Omega \times X. \tag{2.1}$$

The set $\{\tau(t, \omega, x) \mid t \geq 0\}$ is the *semiorbit* of the point (ω, x). A subset K of $\Omega \times X$ is *positively invariant* if $\tau_t(K) \subset K$ for all $t \geq 0$ and it is *τ-invariant* if $\tau_t(K) = K$ for all $t \geq 0$. A compact τ-invariant set K for the semiflow is *minimal* if it does not contain any nonempty compact τ-invariant set other than itself.

Some relevant references for global attractors and pullback attractors in non-autonomous dynamical systems are Carvalho et al. [3] and Kloeden and Rasmussen [13]. For a skew-product semiflow over a compact base flow Ω, the *global attractor* $\mathbb{A} \subset \Omega \times X$, when it exists, is an invariant compact set attracting a certain class $\mathcal{D}(X)$ of subsets of $\Omega \times X$ forwards in time; namely,

$$\lim_{t\to\infty} \mathrm{dist}(\tau_t(\Omega \times X_1), \mathbb{A}) = 0 \quad \text{for each } X_1 \in \mathcal{D}(X)\,,$$

for the Hausdorff semidistance. The standard choices for $\mathcal{D}(X)$ are either the class $\mathcal{D}_b(X)$ of bounded subsets of X or the class $\mathcal{D}_c(X)$ of compact subsets of X (see Cheban et al. [4]).

Since Ω is compact, the non-autonomous set $\{A(\omega)\}_{\omega\in\Omega}$, formed by the ω-sections of $\mathbb{A}$ defined by $A(\omega) = \{x \in X \mid (\omega, x) \in \mathbb{A}\}$ for each $\omega \in \Omega$, is a *pullback attractor*, that is, $\{A(\omega)\}_{\omega\in\Omega}$ is compact, invariant, and it pullback attracts all the sets $X_1 \in \mathcal{D}(X)$:

$$\lim_{t\to\infty} \mathrm{dist}(u(t, \omega{\cdot}(-t), X_1), A(\omega)) = 0 \quad \text{for all } \omega \in \Omega\,. \tag{2.2}$$

Note that the notion of pullback attractor is well-defined within the context of semiflows because the time variable in (2.2) is positive.

3. Attractors in Nicholson systems

In this section, we apply the theory of non-autonomous dynamical systems to get some useful information about the so-called Nicholson systems, regarding the existence of attractors. We also determine new conditions to ensure a simple structure of the global attractor, meaning the existence of a unique almost periodic attracting solution of the Nicholson system. For completeness, recall that a continuous function $h : \mathbb{R} \to \mathbb{R}$ is almost periodic if, for every $\varepsilon > 0$, the set of the so-called *ε-periods* of h, $\{s \in \mathbb{R} \mid |h(t+s) - h(t)| < \varepsilon \text{ for all } t \in \mathbb{R}\}$, is relatively dense.

Since the model has been explained in detail in many publications (e.g., see [6], [7], [17], and [19]), we do not include here the details of its history or the biological meaning of the imposed conditions. We consider an m-dimensional system of delay FDEs with patch structure (m patches) and a nonlinear term of Nicholson type, where the environment exhibits an almost periodic time variation:

$$y_i'(t) = -\widetilde{d}_i(t)\, y_i(t) + \sum_{j=1}^{m} \widetilde{a}_{ij}(t)\, y_j(t) + \widetilde{\beta}_i(t)\, y_i(t - r_i)\, e^{-\widetilde{c}_i(t)\, y_i(t-r_i)}\,, \quad t \geq 0 \tag{3.1}$$

for $i = 1, \ldots, m$. Here, $y_i(t)$ denotes the density of the population on patch i at time $t \geq 0$ and $r_i > 0$ is the maturation time on that patch. The coefficient $\widetilde{a}_{ij}(t)$ stands for the migration rate of the population moving from patch j to patch i at time $t \geq 0$. Finally, the nonlinear term is the delay Nicholson term. We make the following assumptions on the coefficient functions:

(a1) $\widetilde{d}_i(t)$, $\widetilde{a}_{ij}(t)$, $\widetilde{c}_i(t)$ and $\widetilde{\beta}_i(t)$ are almost periodic functions on $\mathbb{R}$;
(a2) $\widetilde{d}_i(t) \geq d_0 > 0$ for each $t \in \mathbb{R}$ and $i \in \{1, \ldots, m\}$;
(a3) $\widetilde{a}_{ij}(t)$ are all nonnegative functions and $\widetilde{a}_{ii}$ is identically null;
(a4) $\widetilde{\beta}_i(t) > 0$ for each $t \in \mathbb{R}$ and $i \in \{1, \ldots, m\}$;
(a5) $\widetilde{c}_i(t) \geq c_0 > 0$ for each $t \in \mathbb{R}$ and $i \in \{1, \ldots, m\}$;
(a6) $\widetilde{d}_i(t) - \sum_{j=1}^{m} \widetilde{a}_{ji}(t) > 0$ for each $t \in \mathbb{R}$ and $i \in \{1, \ldots, m\}$.

Although the procedure to build the *hull* of the Nicholson system has recently been explained in detail in [17], we include it here for the sake of completeness. Take $X = C([-r_1, 0]) \times \ldots \times C([-r_m, 0])$ with the usual cone of positive elements, denoted by X_+, and the supremum norm. Namely, $X_+ = \{\phi \in X \mid \phi_i(s) \geq 0 \text{ for } s \in [-r_i, 0],\ 1 \leq i \leq m\}$ with interior $\operatorname{Int} X_+ = \{\phi \in X \mid \phi_i(s) > 0 \text{ for } s \in [-r_i, 0],\ 1 \leq i \leq m\}$. Then, X is a strongly ordered Banach space. Note that, for $y \in \mathbb{R}^m$, $y \geq 0$ means that all components are nonnegative and $y \gg 0$ means that all components are positive. The induced partial order relation on X is then given by:

$$\begin{aligned} \phi \leq \psi \quad &\iff \quad \psi - \phi \in X_+\,; \\ \phi \ll \psi \quad &\iff \quad \psi - \phi \in \operatorname{Int} X_+\,. \end{aligned}$$

The usual notation is that, given a continuous map $y : [-r, \infty) \to \mathbb{R}^m$ for $r := \max(r_1, \ldots, r_m)$ and a time $t \geq 0$, y_t denotes the map in X defined by $(y_t)_i(s) = y_i(t+s)$, $s \in [-r_i, 0]$, for each component $i = 1, \ldots, m$. Let us write (3.1) as $y_i'(t) = f_i(t, y_t)$, $1 \leq i \leq m$, for the maps $f_i : \mathbb{R} \times X \to \mathbb{R}$,

$$f_i(t, \phi) = -\widetilde{d}_i(t)\, \phi_i(0) + \sum_{j=1}^{m} \widetilde{a}_{ij}(t)\, \phi_j(0) + \widetilde{\beta}_i(t)\, \phi_i(-r_i)\, e^{-\widetilde{c}_i(t)\, \phi_i(-r_i)}\,.$$

Consider the map $l : \mathbb{R} \to \mathbb{R}^N$ given by all the almost periodic coefficients $l(t) = (\widetilde{d}_i(t), \widetilde{a}_{ij}(t), \widetilde{\beta}_i(t), \widetilde{c}_i(t))$ and let Ω be its hull, that is, the closure of the time-translates of l for the compact-open topology. Then, Ω is a compact metric space thanks to the boundedness and uniform continuity of almost periodic maps. Besides, the shift map $\sigma : \mathbb{R} \times \Omega \to \Omega$, $(t, \omega) \mapsto \omega{\cdot}t$, with $(\omega{\cdot}t)(s) = \omega(t+s)$, $s \in \mathbb{R}$, defines an almost periodic and minimal flow. By considering the continuous nonnegative maps d_i, a_{ij}, β_i, $c_i : \Omega \to \mathbb{R}$ such that $(d_i(\omega), a_{ij}(\omega), \beta_i(\omega), c_i(\omega)) = \omega(0)$, the initial system is included in the family of systems over the hull, which can be written for each $\omega \in \Omega$ as

$$y_i'(t) = -d_i(\omega{\cdot}t)\, y_i(t) + \sum_{j=1}^{m} a_{ij}(\omega{\cdot}t)\, y_j(t) + \beta_i(\omega{\cdot}t)\, y_i(t-r_i)\, e^{-c_i(\omega\cdot t)\, y_i(t-r_i)} \tag{3.2}$$

for $i = 1, \ldots, m$. For each $\omega \in \Omega$ and $\varphi \in X$, the solution of (3.2) with initial value φ is denoted by $y(t, \omega, \varphi)$. The solutions induce a skew-product semiflow $\tau : \mathbb{R}_+ \times \Omega \times X \to \Omega \times X$, $(t, \omega, \varphi) \mapsto (\omega{\cdot}t, y_t(\omega, \varphi))$ (in principle only locally defined). This semiflow has a trivial minimal set $\Omega \times \{0\}$, as the null map is a solution of all the systems over the hull.

Note that this family of systems does not satisfy the standard *cooperative* or *quasimonotone condition*, which for a single system of delay FDEs $y'(t) = g(t, y_t)$ given by a map $g : \mathbb{R}_+ \times X \to \mathbb{R}^m$ reads as: whenever $\phi \le \psi$ and $\phi_i(0) = \psi_i(0)$ for some i, then $g_i(t, \phi) \le g_i(t, \psi)$ for all $t \ge 0$. This condition implies that ordered initial data $\phi \le \psi$ lead to ordered solutions, as far as defined (e.g., see Smith [23]). In any case, the set $\Omega \times X_+$ is invariant for the dynamics, that is, the solutions of (3.2) starting inside the positive cone remain inside the positive cone while defined (see [23, Theorem 5.2.1]). Also, if $\varphi \ge 0$ with $\varphi(0) \gg 0$, then $y(t, \omega, \varphi) \gg 0$ for all $t \ge 0$. Besides, the induced semiflow is globally defined on $\Omega \times X_+$, since all the solutions of (3.2) are bounded (see [20, Theorem 3.3]).

The advantage when a global attractor exists for the induced semiflow is that there is a dynamical object approached by the trajectories in the product space $\Omega \times X_+$ in a forward sense. In our first result, we prove that the induced semiflow always has a global attractor. To the best of our knowledge, this general result has not been stated before. Recall that $\mathcal{D}_b(X_+)$ stands for the class of bounded sets in X_+. Also, given a constant $\rho > 0$, we denote by $\bar{\rho}$ either the vector in $\mathbb{R}^m$ or the map in X which takes the constant value ρ in all components.

Theorem 3.1. *Assume that the Nicholson system* (3.1) *satisfies* (a1)–(a6)*. Then, there is a global attractor* $\mathbb{A} \subset \Omega \times X_+$ *with respect to the class* $\mathcal{D}_b(X_+)$ *for the induced skew-product semiflow* $\tau : \mathbb{R}_+ \times \Omega \times X_+ \to \Omega \times X_+$.

Proof. To get the existence of a global attractor, it suffices to find an absorbing compact set (e.g., see [13, Theorem 1.36]). Under the regularity conditions satisfied by the Nicholson systems, for $r := \max(r_1, \ldots, r_m)$, the map $y_r : \Omega \times X \to X$ is compact, meaning that it takes bounded sets into relatively compact sets. Then, given a constant $\rho > 0$, the set

$$H = \operatorname{cls}\left\{ y_r(\omega, \varphi) \mid \omega \in \Omega\,,\ 0 \le \varphi \le \bar{\rho} \right\} \subset X_+ \tag{3.3}$$

is compact. Now we search for the appropriate $\rho > 0$ so that $\Omega \times H$ is absorbing, that is, for every bounded subset $X_1 \subset X_+$ there exists $t_1 = t_1(X_1)$ such that $\tau_t(\Omega \times X_1) \subset \Omega \times H$ for all $t \ge t_1$.

For the constants c_0 given in condition (a5) and $\beta_i^+ := \sup_{t\in\mathbb{R}} \widetilde{\beta}_i(t)$, $1 \le i \le m$, let us consider the family of ODEs given by

$$z_i'(t) = -d_i(\omega{\cdot}t)\, z_i(t) + \sum_{j=1}^{m} a_{ij}(\omega{\cdot}t)\, z_j(t) + \frac{\beta_i^+}{e\, c_0}\,, \quad 1 \le i \le m\,,\ \omega \in \Omega\,. \tag{3.4}$$

This family is cooperative by (a3) and it is easy to check that it is a majorant family of the Nicholson family (3.2), considering the extrema of the maps $h_i(y) = y\, e^{-c_i(\omega)\, y}$ for $y \ge 0$, $1 \le i \le m$, and condition (a5). Let $z(t, \omega, z_0)$ denote the solution of the previous system of ODEs for $\omega \in \Omega$ with initial value $z_0 \in \mathbb{R}^m$.

It can be deduced from condition (a6) that the homogeneous part of the family of ODEs (3.4) admits an exponential dichotomy with full stable subspace. From this, it follows that the solutions of (3.4) are ultimately bounded, uniformly for $\omega \in \Omega$, that is, there exists $\rho > 0$ such that, given an initial condition $z_0 \in \mathbb{R}^m$, there is a $t_0 = t_0(z_0)$ such that $z(t, \omega, z_0) \le \bar{\rho}$ for all $\omega \in \Omega$ and $t \ge t_0$. We refer the reader to the proof of [19, Theorem 6.1] for all the details.

To finish, let us see that this value of ρ serves our purposes. Given a bounded subset $X_1 \subset X_+$, we can take $\varphi_0 \in X_+$ which satisfies $\varphi \leq \varphi_0$ for all $\varphi \in X_1$. For $z_0 = \varphi_0(0)$, we take the corresponding t_0 as in the previous paragraph. Then, by comparing the solutions (see [23, Theorem 5.1.1]), $y(t,\omega,\varphi) \leq z(t,\omega,\varphi(0)) \leq z(t,\omega,\varphi_0(0)) \leq \bar{\rho}$ for all $(\omega,\varphi) \in \Omega \times X_1$ and $t \geq t_0$. That is, $0 \leq y_t(\omega,\varphi) \leq \bar{\rho}$ for all $t \geq t_0 + r$. Now, it suffices to apply the semicocycle property (2.1) to conclude that, if $t \geq t_1 := t_0 + 2r$, then $y_t(\omega,\varphi) = y_r(\omega{\cdot}(t-r), y_{t-r}(\omega,\varphi)) \in H$ for all $(\omega,\varphi) \in \Omega \times X_1$, as wanted. We are done with the proof. □

In some situations, we can give a description of the global attractor. Often the interest is in the extinction *versus* the persistence of the species. Regarding the extinction at an exponential rate, Novo et al. [15] have proved that the uniform exponential stability of the null solution is equivalent to the uniform exponential stability of the null solution of the linearised systems along the null solution,

$$z_i'(t) = -d_i(\omega{\cdot}t)\, z_i(t) + \sum_{j=1}^{m} a_{ij}(\omega{\cdot}t)\, z_j(t) + \beta_i(\omega{\cdot}t)\, z_i(t-r_i)\,, \quad t \geq 0\,, \tag{3.5}$$

for $i = 1, \ldots, m$, for each $\omega \in \Omega$. In [15, Proposition 3.4] one can find a series of equivalent conditions for this behaviour. In particular, it is enough that the null solution of (3.5) is uniformly asymptotically stable. In this situation, the global attractor in the positive cone is the trivial set $\mathbb{A} = \Omega \times \{0\}$.

Hereafter, we focus on situations in which the population persists. First of all, we give the definition of persistence for the initial system (3.1), meaning that, if there are some individuals on every patch at the initial time $t = 0$, the population will surpass a positive lower bound on all the patches in the long run. We use the terminology introduced in [20].

Definition 3.2. The Nicholson system (3.1) is *uniformly persistent at* 0 if there exists $M > 0$ such that for every initial map $\varphi \geq 0$ with $\varphi(0) \gg 0$ there exists a time $t_0 = t_0(\varphi)$ such that

$$y_i(t,\varphi) \geq M \quad \text{for all } \; t \geq t_0 \; \text{ and } \; i = 1, \ldots, m\,.$$

As shown in [20, Theorem 3.4], this dynamical property for the system implies the uniform persistence of the whole family (3.2), according to the next definition. Because of this, we say that Nicholson systems are well-behaved, as this implication is not to be expected in general (see [20] for more details).

Definition 3.3. The skew-product semiflow induced by the family of systems (3.2) is *uniformly persistent* in the interior of the positive cone $\operatorname{Int} X_+$ if there is a map $\psi \gg 0$ such that, for every $\omega \in \Omega$ and every initial map $\varphi \gg 0$, there exists a time $t_0 = t_0(\omega,\varphi)$ such that $y_t(\omega,\varphi) \geq \psi$ for all $t \geq t_0$.

When the Nicholson system is uniformly persistent at 0, the induced semiflow has an attractor in the interior of the positive cone.

Theorem 3.4. *Assume that the Nicholson system* (3.1) *satisfies conditions* (a1)–(a6) *and it is uniformly persistent at* 0*. Then, there exists a global attractor for* τ *in* $\Omega \times \operatorname{Int} X_+$ *with respect to the class of compact subsets of* $\operatorname{Int} X_+$*.*

Proof. As in the proof of Theorem 3.1, we search for a compact absorbing set in $\Omega \times \operatorname{Int} X_+$. First of all, let H be the compact set defined in (3.3), and consider $H' := H \cap \{\varphi \mid \varphi \geq \psi\}$ for a certain $\psi \gg 0$. Note that H' is compact and it lies within the interior of the positive cone. It remains to prove that, making the appropriate choice of ψ, for each compact subset $X_1 \subset \operatorname{Int} X_+$, the set $\Omega \times H'$ absorbs the set $\Omega \times X_1$, that is, there exists $t_0 = t_0(X_1)$ such that $\tau_t(\Omega \times X_1) \subset \Omega \times H'$ for $t \geq t_0$. We already know by the aforementioned theorem that, given such a subset X_1, there is a $t_1 = t_1(X_1)$ such that $\tau_t(\Omega \times X_1) \subset \Omega \times H$ for $t \geq t_1$.

Clearly, the fact that trajectories starting in X_1 will eventually surpass a certain ψ is related to the uniform persistence property.

Since Nicholson systems are not cooperative, it is necessary to build an auxiliary family of cooperative systems, so that some results that enable a comparison of solutions can be applied. (Note that we have already used this technique in the proof of Theorem 3.1.) The idea is not new, so we refer the reader to the proof of [19, Theorem 6.2] for all the details. A family of delay systems is built with the following properties: it is cooperative, concave, of class C^1 with respect to the functional variable, it shares the linearised family along the null solution (3.5), and it is a minorant family of (3.2) in the long run. We denote by $z(t, \omega, \varphi)$ the solutions of this family for each $\omega \in \Omega$ and $\varphi \in X_+$. Then, this cooperative family inherits the property of uniform persistence from the linearised family, and this happens uniformly for $\omega \in \Omega$, that is, there exists $\psi \gg 0$ such that given $\varphi_0 \gg 0$ there is a time $t_2 = t_2(\varphi_0)$ such that $z_t(\omega, \varphi_0) \geq \psi$ for all $t \geq t_2$ and all $\omega \in \Omega$. The uniformity in ω can be justified because the uniform persistence forces the auxiliary family into the dynamical situation described in Case A1 in Theorem 3.8 in [18].

At this point, since $X_1 \subset \operatorname{Int} X_+$, we can find a $\varphi_0 \gg 0$ such that $\varphi_0 \leq \varphi$ for all $\varphi \in X_1$, and take the corresponding $t_2 = t_2(\varphi_0)$. Then, for all $\omega \in \Omega$ and $\varphi \in X_1$, $\psi \leq z_t(\omega, \varphi_0) \leq z_t(\omega, \varphi)$ for $t \geq t_2$, by monotonicity. Since we can compare these solutions with those of the Nicholson systems from one time on (see [23, Theorem 5.1.1]), uniformly for $\omega \in \Omega$, we find a time $t_3 \geq t_2$ such that $\psi \leq y_t(\omega, \varphi)$ for all $\omega \in \Omega$, $\varphi \in X_1$ and $t \geq t_3$. By taking $t_0 := \max(t_1, t_3)$, the proof is finished. □

For Nicholson systems, the compartmental structure and the relations among the different compartments have a strong influence on the property of uniform persistence. One crucial fact for the nonlinear and noncooperative Nicholson systems (among other systems, e.g., see the Mackey and Glass model for hematopoiesis [14]) is that its uniform persistence turns out to be equivalent to the uniform persistence of the linearised systems along the null solution (3.5). Since these linear equations are cooperative, the general methods in Novo et al. [16] (see also [19]) to study the uniform persistence of cooperative recurrent non-autonomous delay FDEs apply, giving a complete spectral characterisation of this dynamical property.

The next statement is part of [20, Theorem 3.5] and is included here for completeness and because it will be useful in Section 4. It offers a characterisation of the uniform persistence of an almost periodic Nicholson system (3.1) in terms of a few Lyapunov exponents, which can be numerically calculated.

Theorem 3.5. *Assume that the Nicholson system* (3.1) *satisfies conditions* (a1)–(a6), *and assume without loss of generality that the constant matrix* $\bar{A} = [a_{ij}^+]$ *with entries* $a_{ij}^+ := \sup_{t\in\mathbb{R}} \widetilde{a}_{ij}(t)$ *has a block lower triangular structure*

$$\begin{bmatrix} \bar{A}_{11} & 0 & \dots & 0 \\ \bar{A}_{21} & \bar{A}_{22} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ \bar{A}_{k1} & \bar{A}_{k2} & \dots & \bar{A}_{kk} \end{bmatrix}$$

with irreducible diagonal blocks $\bar{A}_{jj}$ *of dimension* n_j *for* $j = 1, \dots, k$ $(n_1 + \cdots + n_k = m)$. *Arrange the set of delays as* $\{r_1, \dots, r_m\} = \{r_1^1, \dots, r_{n_1}^1, \dots, r_1^k, \dots, r_{n_k}^k\}$ *and write* $X = X^{(1)} \times \dots \times X^{(k)}$ *for*

$$X^{(j)} = C([-r_1^j, 0]) \times \dots \times C([-r_{n_j}^j, 0]), \quad j = 1, \dots, k.$$

For each $j = 1, \dots, k$, *consider the* n_j*-dimensional almost periodic linear delay system*

$$z_i'(t) = -\widetilde{d}_i(t)\, z_i(t) + \sum_{l\in I_j} \widetilde{a}_{il}(t)\, z_l(t) + \widetilde{\beta}_i(t)\, z_i(t-r_i)\,, \quad t\geq 0\,,$$

for $i\in I_j$, the set of indices corresponding to the rows of the block $\bar{A}_{jj}$, and let $z^j(t,\bar{1})$ be the solution with initial map $\bar{1}$, the map with all components identically equal to 1 in the space $X^{(j)}$. Then, let $\widetilde{\lambda}_j$ be defined as

$$\widetilde{\lambda}_j = \lim_{t\to\infty} \frac{\log \|z_t^j(\bar{1})\|_\infty}{t}\,.$$

Finally, consider the set of indices I associated to the structure of the linear part of the system as follows: if $k=1$, i.e., if the matrix $\bar{A}$ is irreducible, let $I=\{1\}$; else, let

$$I = \{j\in\{1,\dots,k\} \mid \bar{A}_{ji} = 0 \text{ for all } i\neq j\},$$

that is, I is composed by the indices j such that all off-diagonal blocks in the row of $\bar{A}_{jj}$ are null. Then, the almost periodic Nicholson system (3.1) is uniformly persistent at 0 if and only if $\widetilde{\lambda}_j>0$ for all $j\in I$.

Assuming the uniform persistence of the Nicholson system, we give a new result on the existence of a unique positive almost periodic solution which attracts every other positive solution as $t\to\infty$. In these cases, the attractor in the interior of the positive cone is as simple as it can be, i.e., a copy of the base which reproduces the almost periodic dynamics on the base Ω. Briefly, whenever the attractor lies within the region of monotonicity of τ for the usual ordering, it is a copy of the base. This is a nontrivial generalisation to the almost periodic case of the same result in the autonomous case: see [5, Theorem 3.1]. Some other related results are [6, Theorem 4.1] for a class of periodic Nicholson systems and [7, Theorem 3.4].

We want to note that in the mentioned related results, and in many others in the literature, there are conditions which imply the uniform persistence of the system, given in terms of the spectral bound of an associated matrix in the autonomous case, or by introducing a positive lower bound in expressions of the type (3.6). However, we have chosen to directly assume the fact that the system is persistent, and whenever a particular system is given, calculate the Lyapunov exponents and check the persistence using the sufficient, but also necessary, conditions given in Theorem 3.5.

Theorem 3.6. *Assume that the Nicholson system (3.1) satisfies conditions (a1)–(a6) and it is uniformly persistent at 0. If, for every $t\in\mathbb{R}$,*

$$0 < \frac{\widetilde{\beta}_i(t)}{\widetilde{d}_i(t) - \sum_{j\neq i} \widetilde{a}_{ij}(t)\, \frac{c_i^+}{c_j^+}} \leq e^{c_i^-/c_i^+} \quad \text{for each } i=1,\dots,m\,, \tag{3.6}$$

for the positive constants $c_i^- := \inf_{t\in\mathbb{R}} \widetilde{c}_i(t)$ and $c_i^+ := \sup_{t\in\mathbb{R}} \widetilde{c}_i(t)$, then there exists a unique positive almost periodic solution of (3.1) which attracts every other positive solution at an exponential rate; more precisely, it attracts every other solution $y(t,\varphi)$ with initial value $\varphi\geq 0$ such that $\varphi(0)\gg 0$.

Proof. The proof relies on the application of the general theory for monotone and concave skew-product semiflows developed in [18]. Thus, we consider the family of systems over the hull (3.2) and the induced skew-product semiflow τ. From condition (3.6), it follows that for every $\omega\in\Omega$ and every $i=1,\dots,m$,

$$-d_i(\omega) + \sum_{j=1}^m a_{ij}(\omega)\, \frac{c_i^+}{c_j^+} + \beta_i(\omega)\, e^{-c_i^-/c_i^+} \leq 0\,.$$

Then, it is easy to check that for the constant map $\bar{\varphi}$ in X with value the vector

$$\left(\frac{1}{c_1^+},\ldots,\frac{1}{c_m^+}\right)\in\mathbb{R}^m\,,$$

the region $\Omega\times[\bar{0},\bar{\varphi}]$ is positively invariant: just apply the criterion given in [23, Remark 5.2.1] for non-quasimonotone delay FDEs, bearing in mind the Nicholson nonlinear term. Actually, it is easy to check that the restriction of the semiflow to this positively invariant region is monotone, concave, and of class C^1 with respect to φ. Besides, recall that the persistence property of the initial system implies the uniform persistence of the semiflow in the interior of the positive cone. Then, if we fix $\omega_0\in\Omega$ and $0\ll\phi_0\le\bar{\varphi}$, the omega-limit set of the pair (ω_0,ϕ_0) is a strongly positive compact and positively invariant set, which thus contains a minimal set K such that $0\ll K$ and $\phi\le\bar{\varphi}$ for all $(\omega,\phi)\in K$. Due to the uniform persistence, [18, Theorem 3.8] implies that K is the only strongly positive minimal set for $\tau\,|_{\Omega\times[\bar{0},\bar{\varphi}]}$, it is a copy of the base, namely, $K=\{(\omega,b(\omega))\mid\omega\in\ \Omega\}$ for a continuous map $b:\Omega\to\operatorname{Int}X_+$, and it exponentially attracts every other semiorbit for $\omega\in\Omega$ and $0\ll\varphi\le\bar{\varphi}$, that is, $\lim_{t\to\infty}\|y_t(\omega,\varphi)-b(\omega{\cdot}t)\|_\infty=0$ exponentially fast.

Let us now prove that the semiorbit $\tau(t,\omega,\varphi)$ of each $\omega\in\Omega$ and $\varphi\gg0$ is attracted by K too. In order to check it, we introduce a majorant family of systems which satisfy the quasimonotone condition, are concave, and of class C^1 with respect to φ. More precisely, for each $1\le i\le m$, we consider the map $h_i:\Omega\times[0,\infty)\to[0,\infty)$ defined by

$$h_i(\omega,y)=\begin{cases} y\,e^{-c_i(\omega)\,y} & \text{if }\ 0\le y\le\frac{1}{c_i(\omega)}\,,\\ \frac{1}{c_i(\omega)\,e} & \text{if }\ y\ge\frac{1}{c_i(\omega)}\,,\end{cases}$$

together with the family of delayed nonlinear systems given for each $\omega\in\Omega$ by

$$y_i'(t)=-d_i(\omega{\cdot}t)\,y_i(t)+\sum_{j=1}^m a_{ij}(\omega{\cdot}t)\,y_j(t)+\beta_i(\omega{\cdot}t)\,h_i(\omega{\cdot}t,y_i(t-r_i))\,,\tag{3.7}$$

for $i=1,\ldots,m$, where the coefficients are just those of (3.2). Let $\widetilde{\tau}:\mathbb{R}^+\times\Omega\times X_+\to\Omega\times X_+$, $(t,\omega,\varphi)\mapsto(\omega{\cdot}t,z_t(\omega,\varphi))$ denote the induced skew-product semiflow, where $z(t,\omega,\varphi)$ is the solution of system (3.7) with initial value $\varphi\in X_+$. This semiflow turns out to be monotone, concave, and of class C^1 in φ. Besides, $K\gg0$ is also a minimal set for $\widetilde{\tau}$, because the systems coincide when restricted to $\Omega\times[\bar{0},\bar{\varphi}]$. Then, in particular $\widetilde{\tau}$ is globally defined (see [18, Proposition 3.6]). Also, the fact that K attracts all the semiorbits starting below it implies that K is the only minimal set for $\widetilde{\tau}$, and thus attracts all the solutions in the interior of the positive cone (see [18, Theorem 3.8]), that is, for each $\omega\in\Omega$ and $\varphi\gg0$, $\|z_t(\omega,\varphi)-b(\omega{\cdot}t)\|_\infty\to0$ as $t\to\infty$ exponentially fast. In other words, there is a global attractor for $\widetilde{\tau}$ in the interior of the positive cone given by the set $K\subset[\bar{0},\bar{\varphi}]$. Now, as systems (3.7) satisfy the quasimonotone condition, we can apply a standard argument of comparison of solutions (see [23, Theorem 5.1.1]) to get that $0\le y_i(t,\omega,\varphi)\le z_i(t,\omega,\varphi)$ for all $\omega\in\Omega$, $\varphi\in X_+$ and $t\ge0$. Hence, it is easy to deduce that also the attractor in $\Omega\times\operatorname{Int}X_+$ for the Nicholson systems is in $[\bar{0},\bar{\varphi}]$, and thus it must be K, as desired.

Finally, when we take ω_1 as the element in the hull giving the initial system (3.1), we get the positive almost periodic solution $b(\omega_1{\cdot}t)$ attracting every other solution $y_t(\omega_1,\varphi)$ with $\varphi\gg0$. Moreover, if $\varphi\ge0$ with $\varphi(0)\gg0$, then $y(t,\omega_1,\varphi)\gg0$ for all $t\ge0$, so that we just need to move forwards in time and apply the semicocycle property to obtain the attraction result for these initial data. The proof is finished. □

Remark 3.7. Some other systems in the literature with a similar structure can also be treated in the same fashion. For instance, similar results can be stated for useful almost periodic population models which are written as

$$y_i'(t) = -\widetilde{d}_i(t)\, y_i(t) + \sum_{j=1}^{m} \widetilde{a}_{ij}(t)\, y_j(t) + \widetilde{\beta}_i(t)\, h_i(t, y_i(t - r_i))\,,$$

for $i = 1, \dots, m$, with assumption (a6) on the linear part of the systems, and where the nonlinearities are of the form

$$h_i(t, y) = \frac{y}{1 + \widetilde{c}_i(t)\, y^\alpha} \quad (\alpha \geq 1)\,, \quad t \in \mathbb{R}\,,\, y \in \mathbb{R}_+.$$

See [20] for more details on the structure of these systems from an analytical point of view. For example, the scalar model for the process of hematopoiesis for a population of mature circulating cells in [14] falls within this class.

4. Numerical simulations

The aim of this section is twofold. First, we will illustrate the results presented in Section 3 and compare their applicability with those in the literature. We will then explore the behaviour of the omega-limit sets of Nicholson equations when their coefficients undergo certain variations.

Let $\mathbb{T}^2 = (\mathbb{R}/[0, 2\pi])^2$ be the two-dimensional torus endowed with the Kronecker flow $\sigma : \mathbb{R} \times \mathbb{T}^2 \to \mathbb{T}^2$, $(t, \theta_1, \theta_2) \mapsto \sigma_t(\theta_1, \theta_2) = (\theta_1 + t, \theta_2 + \sqrt{2}\, t)$ (mod 2π). As in the previous sections, we simply write $\sigma_t(\theta) = \theta{\cdot}t$ for each $\theta = (\theta_1, \theta_2) \in \mathbb{T}^2$. This flow is minimal because 1 and $\sqrt{2}$ are linearly independent over $\mathbb{Q}$.

Let us consider the family of two-dimensional quasi-periodic Nicholson systems given for each $\theta = (\theta_1, \theta_1) \in \mathbb{T}^2$ by

$$\begin{aligned} y_1'(t) &= -\, d_1(\theta{\cdot}t)\, y_1(t) + a_{12}(\theta{\cdot}t)\, y_2(t) + \beta_1(\theta{\cdot}t)\, y_1(t-1)\, e^{-c_1(\theta\cdot t)\, y_1(t-1)}\,, \\ y_2'(t) &= -\, d_2(\theta{\cdot}t)\, y_2(t) + a_{21}(\theta{\cdot}t)\, y_1(t) + \beta_2(\theta{\cdot}t)\, y_2(t-2)\, e^{-c_2(\theta\cdot t)\, y_2(t-2)}\,, \end{aligned} \tag{4.1}$$

for $t \geq 0$, determined by the continuous coefficients defined for each $t \in \mathbb{R}$ by

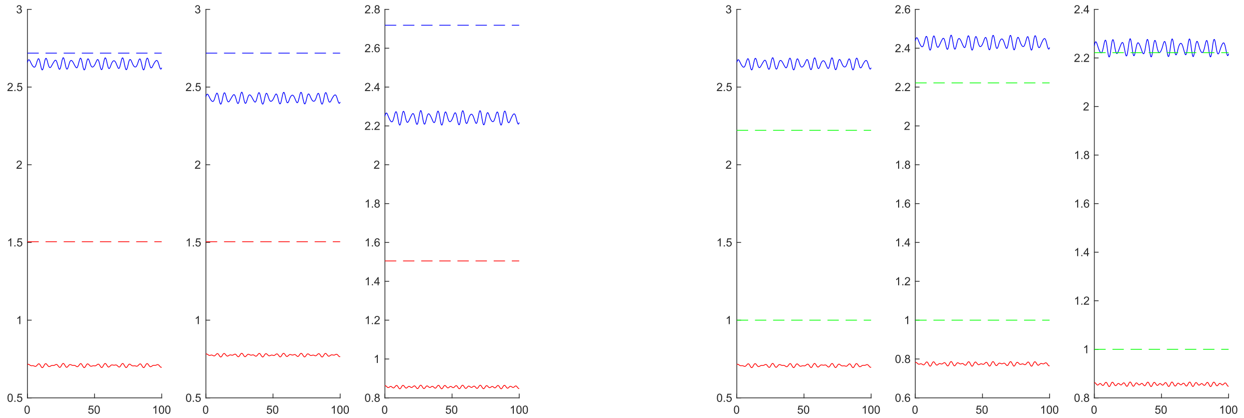
$$\begin{aligned} c_1(\theta{\cdot}t) &= 1, \quad c_2(\theta{\cdot}t) = 0.5 + 0.2\, p(\theta_1 + t) + 0.01\, q(\theta_2 + \sqrt{2}\, t), \\ a_{12}(\theta{\cdot}t) &= \alpha_{12}\, (0.1 + 0.03\, p(\theta_1 + t) + 0.01\, q(\theta_2 + \sqrt{2}\, t)), \\ a_{21}(\theta{\cdot}t) &= \alpha_{21}\, (1 + 0.03\, p(\theta_1 + t) + 0.01\, q(\theta_2 + \sqrt{2}\, t)), \\ m_1(\theta{\cdot}t) &= 1.2, \quad d_1(\theta{\cdot}t) = m_1(\theta{\cdot}t) + a_{21}(\theta{\cdot}t), \\ m_2(\theta{\cdot}t) &= \mu\, (1.9 + 0.02\, p(\theta_1 + t)), \quad d_2(\theta{\cdot}t) = m_2(\theta{\cdot}t) + a_{12}(\theta{\cdot}t), \\ \beta_1(\theta{\cdot}t) &= 5 + 0.03\, p(\theta_1 + t) + 0.01\, q(\theta_2 + \sqrt{2}\, t), \\ \beta_2(\theta{\cdot}t) &= 1 + 0.03\, p(\theta_1 + t) + 0.01\, q(\theta_2 + \sqrt{2}\, t), \end{aligned}$$

where μ, α_{12}, and α_{21} are positive real numbers, and $p, q \in C(\mathbb{R}, \mathbb{R})$ are 2π-periodic functions (or, equivalently, continuous maps on the torus $\mathbb{T}$). Recall that quasi-periodic maps are a relevant class within the set of almost periodic maps. For each $\theta \in \mathbb{T}^2$, system (4.1) may be seen as a quasi-periodic perturbation of an autonomous Nicholson system. Notice that m_1 and m_2 represent the mortality rates.

Fix $p(t) = \sin(t)$ and $q(t) = \cos(t)$, $t \in \mathbb{R}$. It is straightforward to check that conditions (a1)–(a6) are satisfied for the system for $\theta = (0, 0)$, which can be considered as the initial Nicholson system (3.1). Moreover, it can be checked that condition (3.6) holds as well for $\mu = 1$ and $\alpha_{12} = \alpha_{21} \in \{0.8, 1, 1.2\}$. The bound given in [7, Theorem 3.4] fails for the vector with positive components $(1/c_1^+, 1/c_2^+)$ used in the proof of Theorem 3.6 (see Fig. 1). We also performed a parameter sweep over the grid

$$\{0.01\,k \mid k = 0, 1, \ldots, 10000\} \times \{0.01\,k \mid k = 0, 1, \ldots, 10000\}$$

which seems to indicate that the bound given in [7, Theorem 3.4] fails for all the vectors with positive components.



(a) Upper bound (dashed) and middle expression (continuous) of (3.6).

(b) Upper and lower bounds (dashed) and middle expression (continuous) of (3.10) in [7] for $v = (1/c_1^+, 1/c_2^+)$.

Fig. 1. In both cases, $\mu = 1$, $p(t) = \sin(t)$, $q(t) = \cos(t)$, and $\alpha_{12} = \alpha_{21} = 0.8, 1, 1.2$, resp. The first component is blue and the second one is red. (For interpretation of the colours in the figures, the reader is referred to the web version of this article.)

In order to apply Theorem 3.6, it remains to check that the quasi-periodic Nicholson system (4.1) for $\theta = (0, 0)$ is uniformly persistent at 0. Assuming the notation of Theorem 3.5, we have $\bar{A} = [\bar{A}_{11}]$, that is, an irreducible matrix of dimension 2. As a result, it suffices to check that the Lyapunov exponent $\widetilde{\lambda}_1 > 0$.

We are in a position to apply an adaptation of the techniques introduced in Calzada et al. [2] to compute $\widetilde{\lambda}_1$. Specifically, we will use some appropriate methods to perform the numerical integration of the delay linear system

$$\begin{aligned} y_1'(t) &= -\,d_1(\theta{\cdot}t)\,y_1(t) + a_{12}(\theta{\cdot}t)\,y_2(t) + \beta_1(\theta{\cdot}t)\,y_1(t-1)\,, \\ y_2'(t) &= -\,d_2(\theta{\cdot}t)\,y_2(t) + a_{21}(\theta{\cdot}t)\,y_1(t) + \beta_2(\theta{\cdot}t)\,y_2(t-2) \end{aligned} \tag{4.2}$$

for $\theta = (0, 0)$. Note that the appropriate state space for this problem is $X = C([-1, 0]) \times C([-2, 0])$. As suggested by Theorem 3.5, we take $\bar{1}$ as the initial map, the map in X with both components identically equal to 1.

A first approach is given by Matlab's code *dde23* (see Shampine and Thompson [21]), which relies on an explicit Runge-Kutta (2,3) pair of Bogacki and Shampine [1]. The results of that integration present an evident numerical instability, as seen on the left-hand side of Fig. 2. In order to circumvent this issue, the Gauss-Legendre method of order four for delay equations was considered. Its implementation was validated against both the symbolic solution and the numerical approximation given by Matlab's *dde23* of the unperturbed system (4.2) with parameters $\mu = \alpha_{12} = \alpha_{21} = 1$, $p = q \equiv 0$. The Gauss-Legendre method is an implicit Runge-Kutta method with two stages and Butcher tableau

$$\begin{array}{c|cc} \frac{1}{2} - \frac{1}{6}\sqrt{3} & \frac{1}{4} & \frac{1}{4} - \frac{1}{6}\sqrt{3} \\ \frac{1}{2} + \frac{1}{6}\sqrt{3} & \frac{1}{4} + \frac{1}{6}\sqrt{3} & \frac{1}{4} \\ \hline & \frac{1}{2} & \frac{1}{2} \end{array}$$

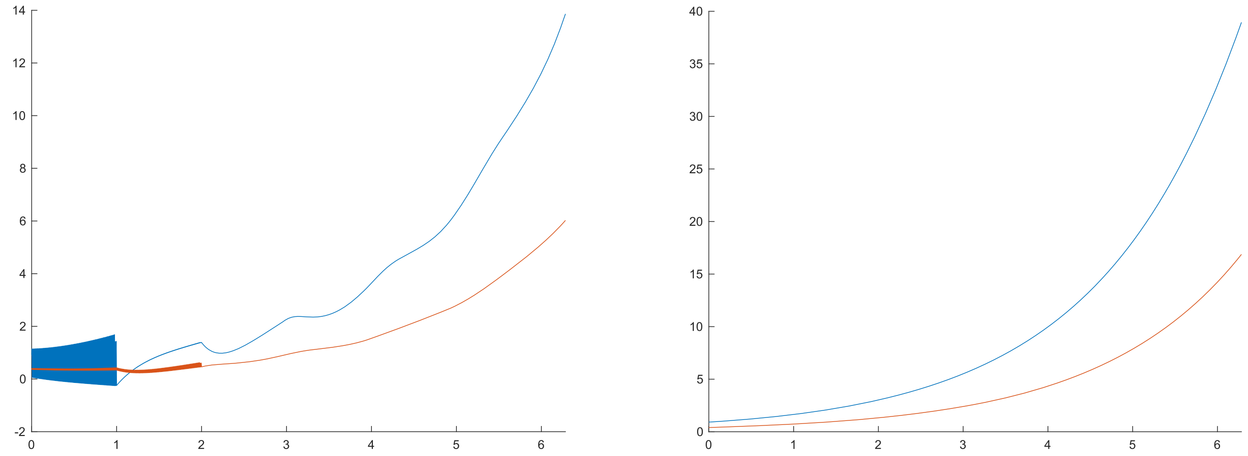


Fig. 2. Results of the numerical integration of system (4.2) on $[-20, 2\pi]$ with Matlab's *dde23* (left) and with the implicit Gauss-Legendre method with two stages for delay equations (right). The first component is blue and the second one is red.

It is noteworthy that this method has order four and is A-stable as a consequence of the Wanner-Hairer-Nørsett Theorem (see, e.g., Iserles [12]). The results of the integration of system (4.2) leading to the computation of the required Lyapunov exponent by the Gauss-Legendre method show no instabilities, as seen on the right-hand side of Fig. 2. Therefore, the techniques in [2] can be applied to conclude that the approximate value of $\widetilde{\lambda}_1$ is 0.597, which is positive. Finally, an application of Theorem 3.5 yields the uniform persistence at 0 of system (4.1) for $\theta = (0, 0)$, as desired.

As a consequence, Theorem 3.4 implies that the skew-product semiflow τ defined by the family (4.1), $\theta \in \mathbb{T}^2$ has a global attractor K in $\mathbb{T}^2 \times \operatorname{Int} X_+$. Furthermore, by Theorem 3.6 (see also its proof), the global attractor K is a copy of the base, that is, there exists a continuous map $b : \mathbb{T}^2 \to \operatorname{Int} X_+$ such that $K = \{(\theta_1, \theta_2, b(\theta_1, \theta_2)) \mid (\theta_1, \theta_2) \in \mathbb{T}^2\}$. The implication in terms of solutions is that for each $\theta \in \mathbb{T}^2$ there exists a unique positive quasi-periodic solution of (4.1) which attracts every other positive solution at an exponential rate. This allows us to compute the global attractor K, having in mind that $\{K(\theta)\}_{\theta\in\mathbb{T}^2} = \{b(\theta)\}_{\theta\in\mathbb{T}^2}$ is the pullback attractor of the semiflow (see (2.2)).

Note that the graphs of the components of the map $\mathbb{T}^2 \to \mathbb{R}^2$, $(\theta_1, \theta_2) \mapsto b(\theta_1, \theta_2)(0)$ determine two copies of $\mathbb{T}^2$. Fix $(\theta_1, \theta_2) \in \mathbb{T}^2$. Then $b(\theta_1, \theta_2)(0) = \lim_{t\to\infty} y(t, \sigma_{-t}(\theta_1, \theta_2), \bar{1})$ and the limit converges exponentially fast. As a result, we can divide the 2-torus $\mathbb{T}^2$ into a uniform grid $\{(\theta_1^i, \theta_2^j) \mid i, j = 1, \ldots, 16\}$ and fix a tolerance 10^{-6}. Therefore, we compute $y^{ij} = y(T, \sigma_{-T}(\theta_1^i, \theta_2^j), \bar{1})$, for each $i, j = 1, \ldots, 16$, where $T > 0$ is such that the distance between y^{ij} and $y(T - 10, \sigma_{-(T-10)}(\theta_1^i, \theta_2^j), \bar{1})$ is under the tolerance. This procedure yields an approximation of both copies of $\mathbb{T}^2$, as shown in Fig. 3.

By repeating the procedure above for the parameters $\mu = 1$, $p(t) = \sin(t)$, $q(t) = \cos(t)$, and $\alpha_{12} = \alpha_{21} = 0.8, 1, 1.2$, we can see that both components of the global pullback attractor vary monotonically, either increasingly or decreasingly, when both migration rates undergo similar variations (see Fig. 4).

If, on the other hand, only one of the migration rates is modified, the components of the global pullback attractor still vary monotonically, but their increasing and decreasing characters are reversed (see Fig. 4 again). Notice that, in this case, we are considering the parameters $\mu = 1$, $p(t) = \sin(t)$, $q(t) = \cos(t)$, $\alpha_{21} = 1$, and $\alpha_{12} = 0.01, 0.5, 1$, for which it is easy to check that hypotheses (a1)–(a6) and condition (3.6) hold.

Finally, let us investigate how the global pullback attractor is modified when the mortality rate in the second patch is increased or decreased. In either case, both components of the global pullback attractor vary monotonically according to the value of the parameter μ (see Fig. 5). We are considering the parameters $\mu = 0.7, 0.85, 1, 3, 9, 27$, $p(t) = \sin(t)$, $q(t) = \cos(t)$, $\alpha_{21} = \alpha_{12} = 1$, for which hypotheses (a1)–(a6) and condition (3.6) hold.

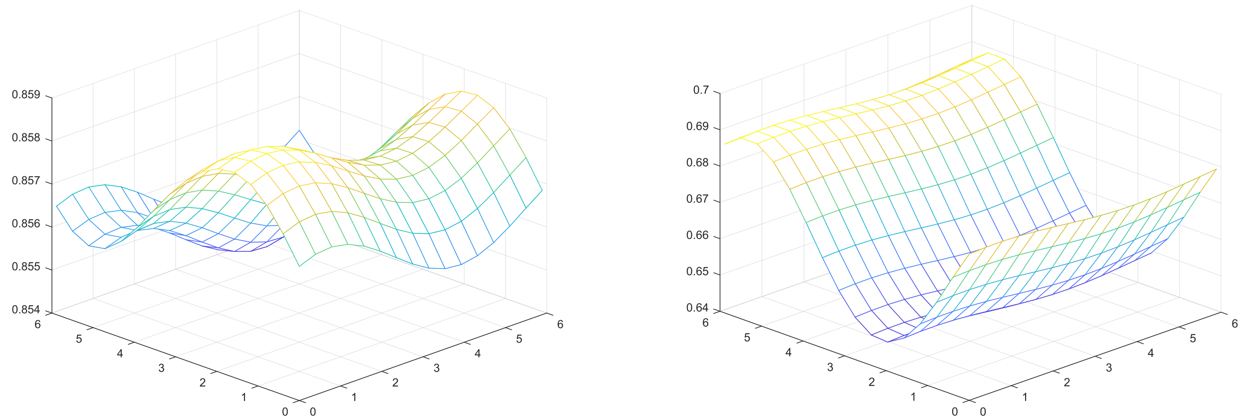
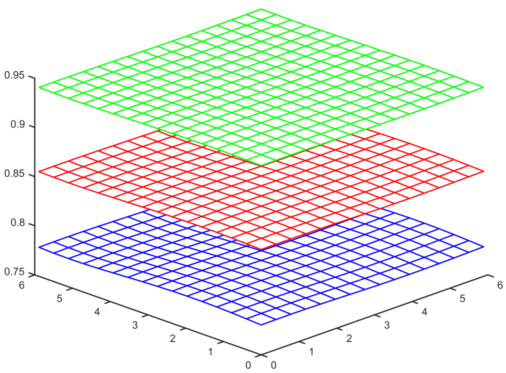
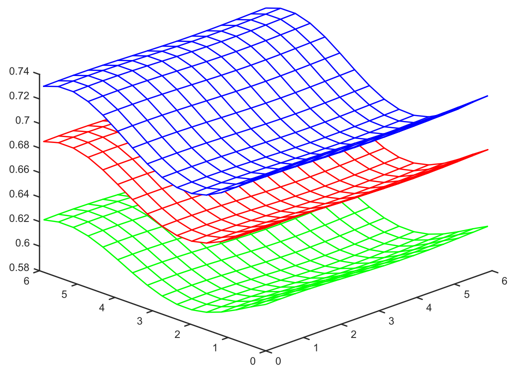


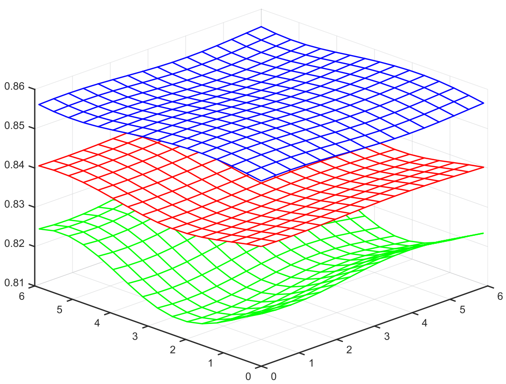
Fig. 3. Mesh of points $(\theta_1^i, \theta_2^j, y_1^{ij})$ on the left and $(\theta_1^i, \theta_2^j, y_2^{ij})$ on the right, $i, j = 1, \ldots, 16$, for the parameters $\mu = 1$, $p(t) = \sin(t)$, $q(t) = \cos(t)$, and $\alpha_{12} = \alpha_{21} = 1$.



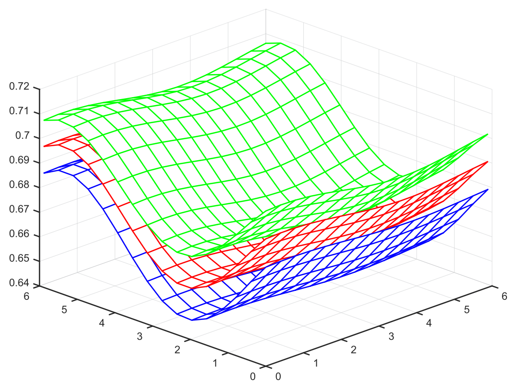
(a) 1st component.



(b) 2nd component.

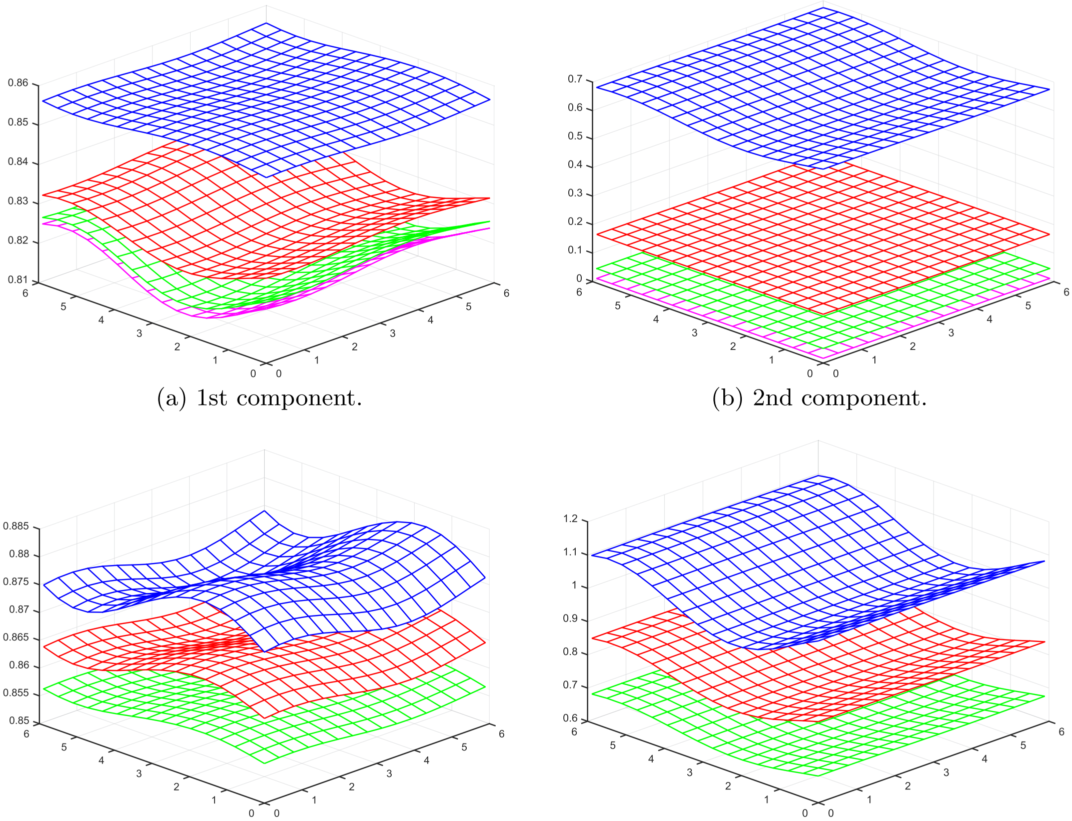


(c) 1st component.



(d) 2nd component.

Fig. 4. Variation of the attractor for the parameters $\mu = 1$, $p(t) = \sin(t)$, $q(t) = \cos(t)$. Plots 4a and 4b: $\alpha_{12} = \alpha_{21} = 0.8$ (green), 1 (red), 1.2 (blue). Plots 4c and 4d: $\alpha_{12} = 0.01$ (green), 0.5 (red), 1 (blue).



(a) 1st component. (b) 2nd component.

(c) 1st component. (d) 2nd component.

Fig. 5. Variation of the attractor for the parameters $p(t) = \sin(t)$, $q(t) = \cos(t)$, $\alpha_{21} = \alpha_{12} = 1$. Plots 5a and 5b: $\mu = 27$ (magenta), 9 (green), 3 (red), 1 (blue). Plots 5c and 5d: $\mu = 1$ (green), 0.85 (red), 0.7 (blue).

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