IS UNIFORM PERSISTENCE A ROBUST PROPERTY IN ALMOST PERIODIC MODELS? A WELL-BEHAVED FAMILY: ALMOST PERIODIC NICHOLSON SYSTEMS

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ABSTRACT. Using techniques of non-autonomous dynamical systems, we completely characterize the persistence properties of an almost periodic Nicholson system in terms of some numerically computable exponents. Although similar results hold for a class of cooperative and sublinear models, in the general non-autonomous setting one has to consider persistence as a collective property of the family of systems over the hull: the reason is that uniform persistence is not a robust property in models given by almost periodic differential equations.

1. INTRODUCTION

In the field of non-autonomous differential equations with a certain recurrent variation in time (such as almost periodicity) it is a common approach to consider a system not just as a system on its own, but as a member of a whole family of systems: the one obtained through the so-called *hull construction* (for instance, see Johnson [14], or Section 2). The reason it that then the theory of non-autonomous dynamical systems or skew-product semiflows applies. In this context the study of the robustness of some dynamical properties has been a common issue. For instance, for linear differential systems the existence of an exponential dichotomy is a robust property, meaning that if a given system has an exponential dichotomy, then the family of systems over the hull also has an exponential dichotomy (see Sacker and Sell [29] in the finite-dimensional case). In this paper we focus on the property of uniform persistence. The question whether persistence is robust in autonomous equations has long been considered (for instance see Hofbauer and Schreiber [13]).

Persistence is a dynamical property which has a great interest in mathematical modelling, in areas such as biological population dynamics, epidemiology, ecology or neural networks. In the field of dynamical systems, different notions of persistence have been introduced, with the general meaning that in the long run the trajectories of the system place themselves above a prescribed region of the phase space. In many applications this region is determined by the null solution, so that, roughly speaking, uniform persistence means that solutions eventually become uniformly strongly positive.

This paper is heavily motivated by the recent papers by Novo et al. [22] and Obaya and Sanz [26], where the authors determine sufficient conditions for the uniform and strict persistence, respectively, of families of non-autonomous cooperative

systems of ordinary differential equations (ODEs for short) and delay functional differential equations (FDEs for short) over a minimal base flow. The concepts of persistence are given as a collective property of the whole family. In the linear case the conditions given are not only sufficient but also necessary. Moreover, as a nontrivial application of the results, in [26] a spectral characterization of the persistence properties of families of almost periodic Nicholson systems has been given. We refer the reader unfamiliar with Nicholson systems to Section 3 and we just cite some very recent related works such as Berezansky et al. [2], Liu and Meng [15], Faria [8], Wang [35], Faria and Röst [10] and Faria et al. [9].

At this point it is natural to wonder whether a characterization of the persistence properties, similar to that in [26], can be given when one considers not a whole family, but only an individual almost periodic Nicholson system. In other words, if we can decide on the persistence properties of a given Nicholson system in terms of some computable items coming out of the system. In this case, the answer is in the affirmative, as it is stated in Theorem 3.5. But, as the reader might expect, the answer comes after a nice transfer of the property of persistence from the individual system to the whole family of systems over the hull, to which the characterization given in [26] applies, so that it only remains to check that the exponents involved can in fact be computed just out of the individual system. This is clearly the most desirable situation, but, is it the general situation?

The last question demands to solve the underlying problem on the robustness of uniform persistence. We show that this dynamical property is not robust in almost periodic ODEs or delay FDEs, meaning that in general it is not transferred from an individual almost periodic system to the family of systems over the hull. Besides, when the transfer fails to happen in models given by almost periodic cooperative and linear or sublinear ODEs or delay FDEs, the set of systems which do not gain the property is big, both from a topological and from a measure theory point of view. This means that in the non-robust situation it is highly improbable that we can experimentally or numerically detect uniform persistence.

The previous fact naturally raises a discussion on the proper definition of uniform persistence in the non-autonomous field, which in the general case results in the convenience of adopting the collective formulation given in [22]. Notwithstanding, still uniform persistence is a robust property in some other models of real life processes, as those given by cooperative and sublinear ODEs or delay FDEs with some strongly positive bounded solution. In this case the consideration of an individual system is enough in what refers to the study of its persistence properties, and we can characterize persistence through a set of numerically computable objects.

To emphasize the importance of the latter fact from the point of view of applications, recall that there is a long tradition in the study of monotone and sublinear, concave or convex semiflows generated by families of differential equations, clearly motivated by their frequent appearence in mathematical modelling, apart from the theoretical interest itself. The works by Shen and Yi [30, 31], Zhao [36, 37], Mierczyński and Shen [17], Novo et al. [20] and Núñez et al. [23, 24, 25] contain some significant examples of the application of dynamical arguments to analyze non-autonomous differential equations modelling processes in engineering, biology and ecology, among other branches of science.

We finally briefly describe the organization and main results of the paper. Section 2 contains some necessary preliminaries in order to make the paper reasonably

self-contained. In particular, the definitions of skew-product semiflow and of a continuous separation for linear monotone skew-product semiflows are included, as they are important tools in our results.

Section 3 is devoted to the persistence properties of an almost periodic Nicholson system. We prove that a persistence property of a particular Nicholson system is transferred to the family of systems over the hull. As a consequence, taking advantage of the results in [26] for such a family, we characterize the persistence properties of an almost periodic Nicholson system by means of some numerically computable exponents. The same results hold for other models considered in the literature, as the one for hematopoiesis given in Mackey and Glass [16].

Finally, in Section 4, being aware of the dynamical complexity that scalar almost periodic linear differential equations can exhibit (see Poincaré [27] or Johnson [14]) in contrast with the cases of autonomous or periodic equations, we offer a concrete example of an almost periodic linear scalar equation for which uniform persistence is not a robust property, that is, it is not transferred to the family of systems over the hull. This phenomenon can also appear in higher dimensional linear and nonlinear systems. Despite this fact, still we can determine a wide class of almost periodic cooperative and sublinear ODEs and delay FDEs systems for which things go nicely in what refers to persistence, i.e., as in the Nicholson's case. The additional condition needed is the existence of a strongly positive bounded solution.

2. Some preliminaries

In this section we include some preliminaries of topological dynamics for non-autonomous dynamical systems, as well as some classes of almost periodic systems of ODEs and finite-delay FDEs which will be considered.

Let (Ω, d) be a compact metric space. A real *continuous flow* $(\Omega, \sigma, \mathbb{R})$ is defined by a continuous map $\sigma : \mathbb{R} \times \Omega \to \Omega, \ (t, \omega) \mapsto \sigma(t, \omega)$ satisfying

   (i) $\sigma_0 = \mathrm{Id}$,
   (ii) $\sigma_{t+s} = \sigma_t \circ \sigma_s$ for each $s, t \in \mathbb{R}$,

where $\sigma_t(\omega) = \sigma(t, \omega)$ for all $\omega \in \Omega$ and $t \in \mathbb{R}$. The set $\{\sigma_t(\omega) \mid t \in \mathbb{R}\}$ 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 $t \in \mathbb{R}$. A subset $\Omega_1 \subset \Omega$ is called *minimal* if it is compact, σ-invariant and it does not contain properly any other compact σ-invariant set. Based on Zorn's lemma, every compact and σ-invariant set contains a minimal subset. Furthermore, a compact σ-invariant subset is minimal if and only if every orbit is dense. We say that the continuous flow $(\Omega, \sigma, \mathbb{R})$ is *recurrent* or *minimal* if Ω is minimal. The flow $(\Omega, \sigma, \mathbb{R})$ is *almost periodic* if the family of maps $\{\sigma_t\}_{t \in \mathbb{R}} : \Omega \to \Omega$ is uniformly equicontinuous on Ω, that is, for every $\varepsilon > 0$ there is a $\delta > 0$ such that, if ω_1, $\omega_2 \in \Omega$ with $d(\omega_1, \omega_2) < \delta$, then $d(\sigma(t, \omega_1), \sigma(t, \omega_2)) < \varepsilon$ for every $t \in \mathbb{R}$.

A finite regular measure defined on the Borel sets of Ω is called a Borel measure on Ω. Given μ a normalized Borel measure on Ω, it is σ-*invariant* (or *invariant under* σ) if $\mu(\sigma_t(\Omega_1)) = \mu(\Omega_1)$ for every Borel subset $\Omega_1 \subset \Omega$ and every $t \in \mathbb{R}$. It is *ergodic* if, in addition, $\mu(\Omega_1) = 0$ or $\mu(\Omega_1) = 1$ for every σ-invariant subset $\Omega_1 \subset \Omega$. We denote by $\mathcal{M}_{\mathrm{inv}}(\Omega, \sigma, \mathbb{R})$ the set of all positive and normalized σ-invariant measures on Ω. The Krylov-Bogoliubov theorem asserts that $\mathcal{M}_{\mathrm{inv}}(\Omega, \sigma, \mathbb{R})$ is nonempty when Ω is a compact metric space. The extremal points of the convex and weakly compact set $\mathcal{M}_{\mathrm{inv}}(\Omega, \sigma, \mathbb{R})$ are the ergodic measures, and thus the set of ergodic measures $\mathcal{M}_{\mathrm{erg}}(\Omega, \sigma, \mathbb{R})$ is nonempty. We say that $(\Omega, \sigma, \mathbb{R})$ is *uniquely ergodic* if

it has a unique normalized invariant measure, which is then necessarily ergodic. A minimal and almost periodic flow $(\Omega, \sigma, \mathbb{R})$ is uniquely ergodic.

Let $\mathbb{R}_+ = \{t \in \mathbb{R} \,|\, t \geq 0\}$. Given a continuous compact flow $(\Omega, \sigma, \mathbb{R})$ 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

$$
\begin{array}{cccc}
\tau: & \mathbb{R}_+ \times \Omega \times X & \longrightarrow & \Omega \times X \\
& (t, \omega, x) & \mapsto & (\omega{\cdot}t, u(t, \omega, x))
\end{array}
\tag{2.1}
$$

which preserves the flow on Ω, denoted by $\omega{\cdot}t = \sigma(t, \omega)$ and referred to as the *base flow*. The semiflow property means that

  (i) $\tau_0 = \mathrm{Id}$,
  (ii) $\tau_{t+s} = \tau_t \circ \tau_s$ for all $t, s \geq 0$,

where again $\tau_t(\omega, x) = \tau(t, \omega, x)$ for each $(\omega, x) \in \Omega \times X$ and $t \in \mathbb{R}_+$. This leads to the so-called semicocycle property,

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

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*, or τ-*invariant*, if $\tau_t(K) \subseteq K$ 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. The restricted semiflow over a compact and τ-invariant set K admits a *flow extension* if there exists a continuous flow $(K, \widetilde{\tau}, \mathbb{R})$ such that $\widetilde{\tau}(t, \omega, x) = \tau(t, \omega, x)$ for all $(\omega, x) \in K$ and $t \in \mathbb{R}_+$.

Whenever a semiorbit $\{\tau(t, \omega_0, x_0) \mid t \geq 0\}$ is relatively compact, one can consider the *omega-limit set* of (ω_0, x_0), denoted by $\mathcal{O}(\omega_0, x_0)$ and formed by the limit points of the semiorbit as $t \to \infty$, that is, the pairs $(\omega, x) = \lim_{n \to \infty} \tau(t_n, \omega_0, x_0)$ for some sequence $t_n \uparrow \infty$. The set $\mathcal{O}(\omega_0, x_0)$ is then a nonempty compact connected and τ-invariant set.

The reader can find in Ellis [7], Sacker and Sell [29], Shen and Yi [31] and references therein, a more in-depth survey on topological dynamics.

In this paper we will sometimes work under differentiability assumptions. When X is a Banach space, the semiflow (2.1) is said to be of class $\mathcal{C}^1$ when u is assumed to be of class $\mathcal{C}^1$ in x, meaning that $u_x(t, \omega, x)$ exists for any $t > 0$ and any $(\omega, x) \in \Omega \times X$ and for each fixed $t > 0$, the map $(\omega, x) \mapsto u_x(t, \omega, x) \in \mathcal{L}(X)$ is continuous in a neighborhood of any compact set $K \subset \Omega \times X$; moreover, for any $z \in X$, $\lim_{t \to 0^+} u_x(t, \omega, x)\, z = z$ uniformly for (ω, x) in compact sets of $\Omega \times X$.

In that case, whenever $K \subset \Omega \times X$ is a compact positively invariant set, we can define a continuous linear skew-product semiflow called the *linearized skew-product semiflow* of (2.1) over K,

$$
\begin{array}{cccc}
L: & \mathbb{R}_+ \times K \times X & \longrightarrow & K \times X \\
& (t, (\omega, x), z) & \mapsto & (\tau(t, \omega, x), u_x(t, \omega, x)\, z) \,.
\end{array}
$$

We note that u_x satisfies the linear semicocycle property

$$
u_x(t + s, \omega, x) = u_x(t, \tau(s, \omega, x))\, u_x(s, \omega, x)\,, \quad s, t \in \mathbb{R}_+\,, \ (\omega, x) \in K.
$$

We now introduce Lyapunov exponents. For $(\omega, x) \in K$ we denote by $\lambda(\omega, x)$ the *Lyapunov exponent* defined as

$$
\lambda(\omega, x) = \limsup_{t \to \infty} \frac{\log \|u_x(t, \omega, x)\|}{t} \,.
$$

The number $\lambda_K = \sup_{(\omega, x) \in K} \lambda(\omega, x)$ is called the *upper Lyapunov exponent* of K.

Also, reference will be made to monotone, and to monotone and concave or monotone and sublinear skew-product semiflows. When the state space X is a strongly ordered Banach space, that is, there is a closed convex solid cone of nonnegative vectors X_+ with a nonempty interior, then, a (partial) *strong order relation* on X is defined by

$$x \leq y \iff y - x \in X_+ \,;$$
$$x < y \iff y - x \in X_+ \text{ and } x \neq y \,;$$
$$x \ll y \iff y - x \in \operatorname{Int} X_+ \,.$$

The positive cone is usually assumed to be *normal* (see Amann [1] for more details). In this situation, the skew-product semiflow (2.1) is *monotone* if

$$u(t, \omega, x) \leq u(t, \omega, y) \quad \text{for } t \geq 0, \, \omega \in \Omega \text{ and } x, y \in X \text{ with } x \leq y \,.$$

A monotone skew-product semiflow is said to be *concave* if for any $t \geq 0$, $\omega \in \Omega$, $x \leq y$ and $\lambda \in [0, 1]$,

$$u(t, \omega, \lambda y + (1 - \lambda) x) \geq \lambda \, u(t, \omega, y) + (1 - \lambda) \, u(t, \omega, x) \,,$$

and a skew-product semiflow with the positivity property (that is, $\Omega \times X_+$ is τ-invariant) is *sublinear* if

$$u(t, \omega, \lambda x) \geq \lambda \, u(t, \omega, x) \quad \text{for any } t \geq 0, \, \omega \in \Omega, \, x \in X_+ \text{ and } \lambda \in [0, 1] \,.$$

The dynamical description of monotone and sublinear and of monotone and concave skew-product semiflows found respectively in Núñez et al. [23] and [25] will be useful in this work.

We now include the definitions of a continuous separation in the classical terms of Poláčik and Tereščák [28] in the discrete case, generalized by Shen and Yi [31] to the continuous case, and of a continuous separation of type II in the terms introduced by Novo et al. [21]. A continuous linear and monotone skew-product semiflow over a minimal base flow $(\Omega, \cdot, \mathbb{R})$ and a strongly ordered Banach space X,

$$
\begin{aligned}
L: \quad & \mathbb{R}_+ \times \Omega \times X && \longrightarrow && \Omega \times X \\
& (t, \omega, v) && \mapsto && (\omega \cdot t, \Phi(t, \omega) \, v) \,,
\end{aligned}
$$

which satisfies that for each $t > 0$ the map $\Omega \to \mathcal{L}(X)$, $\omega \mapsto \Phi(t, \omega)$ is continuous, is said to admit a *continuous separation* if there are families of subspaces $\{X_1(\omega)\}_{\omega \in \Omega}$ and $\{X_2(\omega)\}_{\omega \in \Omega} \subset X$ satisfying the following properties:

(S1) $X = X_1(\omega) \oplus X_2(\omega)$ and $X_1(\omega)$, $X_2(\omega)$ vary continuously in Ω;

(S2) $X_1(\omega) = \operatorname{span}\{v(\omega)\}$, with $v(\omega) \gg 0$ and $\|v(\omega)\| = 1$ for any $\omega \in \Omega$;

(S3) $X_2(\omega) \cap X_+ = \{0\}$ for any $\omega \in \Omega$;

(S4) for any $t > 0$, $\omega \in \Omega$,

$$\Phi(t, \omega) X_1(\omega) = X_1(\omega \cdot t) \,,$$
$$\Phi(t, \omega) X_2(\omega) \subset X_2(\omega \cdot t) \,;$$

(S5) there are $M > 0$, $\delta > 0$ such that for any $\omega \in \Omega$, $z \in X_2(\omega)$ with $\|z\| = 1$ and $t > 0$,

$$\|\Phi(t, \omega) \, z\| \leq M \, e^{-\delta t} \|\Phi(t, \omega) \, v(\omega)\| \,.$$

When property (S3) does not hold, but still it is replaced by (S3)' below, then the continuous separation is said to be of type II.

(S3)' there exists a $T > 0$ such that if for some $\omega \in \Omega$ there is a $z \in X_2(\omega)$ with $z > 0$, then $\Phi(t, \omega) \, z = 0$ for any $t \geq T$.

To finish this section, we include a general class of almost periodic ODEs and delay FDEs whose solutions can be immersed into a skew-product semiflow by using the so-called hull construction. In order to build the hull, admissibility is the key property. A function $f \in C(\mathbb{R} \times \mathbb{R}^m, \mathbb{R}^n)$ is said to be *admissible* if for any compact set $K \subset \mathbb{R}^m$, f is bounded and uniformly continuous on $\mathbb{R} \times K$. Recall that a continuous function $f : \mathbb{R} \to \mathbb{R}$ is *almost periodic* if for any $\varepsilon > 0$ the ε-translate set of f, $T_\varepsilon(f) = \{r \in \mathbb{R} \mid |f(t+r) - f(t)| < \varepsilon \text{ for any } t \in \mathbb{R}\}$ is a relatively dense set in $\mathbb{R}$, that is, there exists an $l > 0$ such that any interval of length l has a nonempty intersection with the set $T_\varepsilon(f)$.

We consider n-dimensional systems of ODEs given by a uniformly almost periodic function $f \colon \mathbb{R} \times \mathbb{R}^n \to \mathbb{R}^n$ (that is, f is admissible and $f(t, y)$ is almost periodic in t for any $y \in \mathbb{R}^n$), of class $\mathcal{C}^1$ with respect to y and such that its first order derivatives $\partial f / \partial y_i$, $i = 1, \ldots, n$ are admissible,

$$y'(t) = f(t, y(t)), \quad t \in \mathbb{R}; \tag{2.2}$$

and n-dimensional systems of finite-delay differential equations with a fixed delay, which we take to be 1, given by a uniformly almost periodic function $f : \mathbb{R} \times \mathbb{R}^n \times \mathbb{R}^n \to \mathbb{R}^n$, with the same regularity and admissibility conditions as before,

$$y'(t) = f(t, y(t), y(t-1)), \quad t > 0. \tag{2.3}$$

In both of the previous situations, let Ω be the *hull* of f, that is, the closure for the topology of uniform convergence on compacta of the set of t-translates of f, $\{f_t \mid t \in \mathbb{R}\}$ with $f_t(s, z) = f(t+s, z)$ for $s \in \mathbb{R}$ and $z \in \mathbb{R}^n$ or $\mathbb{R}^{2n}$, adequate to each case. The translation map $\mathbb{R} \times \Omega \to \Omega$, $(t, \omega) \mapsto \omega \cdot t$ given by $\omega \cdot t(s, z) = \omega(s + t, z)$ ($s \in \mathbb{R}$ and $z \in \mathbb{R}^n$ or $\mathbb{R}^{2n}$) defines a continuous flow σ on the compact metric space Ω, which is minimal and almost periodic, and thus uniquely ergodic. Each function $\omega \in \Omega$ has the same regularity and admissibility properties as those of f, and $F \colon \Omega \times \mathbb{R}^p \to \mathbb{R}^n$, $(\omega, z) \mapsto \omega(0, z)$ (with $p = n$ or $p = 2n$) can be looked at as the unique continuous extension of f to its hull. Thus, in each case we can consider the family of n-dimensional systems over the hull, which we write for short as:

$$y'(t) = F(\omega \cdot t, y(t)), \quad \omega \in \Omega \tag{2.4}$$

for the ODEs case; and

$$y'(t) = F(\omega \cdot t, y(t), y(t-1)), \quad \omega \in \Omega \tag{2.5}$$

in the delay case, whose solutions induce a forward dynamical system of skew-product type (2.1) (in principle only locally-defined) on the product $\Omega \times X$. Namely, in the ODEs case we take $X = \mathbb{R}^n$ endowed with the norm $\|x\| = |x_1| + \cdots + |x_n|$ for $x \in \mathbb{R}^n$, with the normal positive cone $\mathbb{R}^n_+ = \{y \in \mathbb{R}^n \mid y_i \geq 0 \text{ for } i = 1, \ldots, n\}$ which induces a (partial) strong ordering on $\mathbb{R}^n$ defined componentwise, and $u(t, \omega, x)$ is the value of the solution of system (2.4) for ω at time t with initial condition $x \in X$. In the delay case we take $X = C([-1, 0], \mathbb{R}^n)$ with the norm $\|\varphi\| = \|\varphi_1\|_\infty + \ldots + \|\varphi_n\|_\infty$ for $\varphi \in X$, and the positive cone $X_+ = \{\varphi \in X \mid \varphi(s) \geq 0 \text{ for all } s \in [-1, 0]\}$ which is normal and has nonempty interior $\operatorname{Int} X_+ = \{\varphi \in X \mid \varphi(s) \gg 0 \text{ for all } s \in [-1, 0]\}$. In this case $u(t, \omega, x) = y_t(\omega, x)$, which is defined as $y_t(\omega, x)(s) = y(t + s, \omega, x)$ for $s \in [-1, 0]$ for the solution $y(t, \omega, x)$ of system (2.5) for ω at time t with initial condition $x \in X$. In both cases, a bounded solution gives rise to a relatively compact semiorbit, so that the omega-limit set is well-defined. (For the standard theory of delay FDEs see Hale and Verduyn Lunel [12].)

In order that the skew-product semiflow be monotone, f is required to be *cooperative*. Under the former regularity assumptions, the cooperative condition for system (2.2) is written as

$$\frac{\partial f_i}{\partial y_j}(t, y) \geq 0 \quad \text{for } i \neq j, \quad \text{for any } (t, y) \in \mathbb{R} \times \mathbb{R}^n \,;$$

and for system (2.3) it is written as

$$\frac{\partial f_i}{\partial y_j}(t, y, w) \geq 0 \quad \text{for } i \neq j \quad \text{and} \quad \frac{\partial f_i}{\partial w_j}(t, y, w) \geq 0 \quad \text{for any } i, j \,,$$

for any $(t, y, w) \in \mathbb{R} \times \mathbb{R}^n \times \mathbb{R}^n$. If the initial system is cooperative, then so are all the systems over the hull. By standard arguments of comparison of solutions (for instance, see Smith [33]), this condition implies that the induced semiflow is monotone (on its domain of definition).

Finally, system (2.2) (resp. system (2.3)) is (order) *concave* if

$$f(t, \lambda y + (1 - \lambda) x) \geq \lambda f(t, y) + (1 - \lambda) f(t, x)$$

for any $t \in \mathbb{R}$, $\lambda \in [0, 1]$ and $x, y \in \mathbb{R}^n$ (resp. $x, y \in \mathbb{R}^{2n}$) with $x \leq y$; and it is *sublinear* if

$$f(t, \lambda y) \geq \lambda f(t, y)$$

for any $t \in \mathbb{R}$, $\lambda \in [0, 1]$ and $y \in \mathbb{R}_+^n$ (resp. $y \in \mathbb{R}_+^{2n}$). Note that, under the assumption that 0 is a solution, the concave condition actually implies the sublinear condition. Once more, by standard arguments of comparison of solutions (see Smith [33]), if the system is cooperative and concave/sublinear, the induced semiflow is monotone and concave/sublinear (on its domain of definition).

3. Persistence properties of almost periodic Nicholson systems

For the reader unfamiliar with Nicholson systems, the most remarkable facts are the following. In 1954 Nicholson [18] published experimental data on the behaviour of the population of the Australian sheep-blowfly. Then, Gurney et al. [11] studied the scalar delay equation

$$x'(t) = -\mu x(t) + p x(t - \tau) e^{-\gamma x(t - \tau)} \,,$$

which was called the Nicholson's blowflies equation, as it suited the experimental data reasonably well. Here, μ, p, γ and τ are positive constants with a biological interpretation. In particular the delay τ stands for the maturation time of the species. The interest of Nicholson himself was in the existence of oscillatory solutions for the behaviour of the adult population. Later on, many authors have determined different relations of the coefficients so as to have global asymptotic stability of the nontrivial positive steady state solution, though the general problem is still not closed (see Smith [33] and Berezansky et al. [2]). Concerned with stability, persistence or existence of certain kind of solutions, among other dynamical issues, some generalizations and modifications of the Nicholson equation have also been considered.

More recently, Nicholson systems have been introduced, as they fit models for one single species in an environment with a patchy structure or for multiple biological species. Taking time-dependent coefficients and adding a patch-structure helps to model the seasonal variation of the environment as well as the presence of a heterogeneous environment, so that there are n patches in which the individuals

can live, each of them determined by different climate, different food resources, and so on. In this way, the distribution of the population is influenced by the growth and death rates of the populations in each patch and migrations among patches. Also the maturation time is assumed to be possibly different in each patch.

In this section we consider an almost periodic noncooperative system with delay which is among the family of Nicholson systems. Namely, we consider an n-dimensional system of delay FDEs with a patch-structure (n patches) and a nonlinear term of Nicholson type, which is able to reflect an almost periodic temporal variation in the environment,

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

for $i = 1, \ldots, n$. Here $y_i(t)$ denotes the density of the population in patch i at time $t \geq 0$, and $\tau_i > 0$ is the maturation time in that patch. We consider the delay system together with an initial condition, which is given by a map $\varphi = (\varphi_1, \ldots, \varphi_n) \in C([-\tau_1, 0]) \times \ldots \times C([-\tau_n, 0])$, which is assumed to be nonnegative in all components, due to the implicit biological meaning. Let us denote by $y(t, \varphi)$ the solution of this problem, whenever defined.

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 maps on $\mathbb{R}$;

(a2) $\widetilde{d}_i(t) \geq d_0 > 0$ for any $t \in \mathbb{R}$, for any i;

(a3) $\widetilde{a}_{ij}(t)$ are all nonnegative maps and $\widetilde{a}_{ii}$ is taken to be identically null;

(a4) $\widetilde{\beta}_i(t) > 0$ for any $t \geq 0$, for any i;

(a5) $\widetilde{c}_i(t) \geq c_0 > 0$ for any $t \geq 0$, for any i;

(a6) $\widetilde{d}_i(t) - \sum_{j=1}^{n} \widetilde{a}_{ji}(t) > 0$ for any $t \geq 0$, for any i.

To get a biological meaning of the imposed conditions, the coefficient $\widetilde{a}_{ij}(t)$ stands for the migration rate of the population moving from patch j to patch i at time $t \geq 0$. As for the birth function in each patch, it is given by the delay nonlinear Nicholson term. Finally, the decreasing rate in patch i, given by $\widetilde{d}_i(t)$, includes the mortality rate as well as the migrations coming out of patch i, so that condition (a6) makes sense, saying that the mortality rate is positive at any time.

From an analytical point of view, condition (a5) is imposed so as to guarantee the uniform boundedness of the terms $y\, e^{-\widetilde{c}_i(t)\, y}$ for $y \geq 0$ and $t \in \mathbb{R}$, and condition (a6) is a weak column dominance condition for the matrix of coefficients of the ODEs linear part of system (3.1). This last condition is enough, in this almost periodic setting, to deduce that the null solution of the ODEs linear system is globally exponentially stable. Therefore, a direct application of the variation of constants formula permits to check that system (3.1) is dissipative or, in other words, solutions are ultimately bounded (see Faria et al. [9] for more details), and in particular they are defined for all $t \geq 0$.

Note also that the Nicholson system (3.1) does not satisfy the *quasimonotone condition* given in Smith [33], here just called cooperative condition for simplicity (see Section 2), but still solutions starting with a nonnegative initial map, remain nonnegative forever, just by applying the invariance criterion given in Theorem 5.2.1 in [33]. Alternatively, one can note that $y_i'(t) \geq -\widetilde{d}_i(t)\, y_i(t)$ for $i = 1, \ldots, n$, so that by a standard comparison of solutions argument (once more, see [33]), we can affirm

that $\varphi \geq 0$ implies $y(t, \varphi) \geq 0$ for any $t \geq 0$ and besides, $\varphi \geq 0$ with $\varphi(0) \gg 0$ implies $y(t, \varphi) \gg 0$ for any $t \geq 0$.

Considering the previous properties of the solutions of the population model (3.1), at least two natural approaches to the concept of persistence arise. On the one hand, if at time $t = 0$ there are some individuals in every patch, one wonders whether the population will eventually persist in all the patches, namely, whether in the long run the population will overpass a positive lower bound in all patches. On the other hand, if at time $t = 0$ there are some individuals at least in one patch, one wants to know whether the population will persist in some patch (possibly a different one). We refer to these situations as uniform persistence at 0 and strict persistence at 0, respectively, and the precise definitions are the following.

Definition 3.1. (i) The Nicholson system (3.1) is *uniformly persistent at* 0 (u_0-*persistent* for short) if there exists an $m > 0$ such that for any initial map $\varphi \geq 0$ with $\varphi(0) \gg 0$ there exists a time $t_0 = t_0(\varphi)$ such that

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

(ii) The Nicholson system (3.1) is *strictly persistent at* 0 (s_0-*persistent* for short) if there exists an $m > 0$ such that for any initial map $\varphi \geq 0$ with $\varphi(0) > 0$ there exists a time $t_0 = t_0(\varphi)$ such that at least for one component i,

$$y_i(t, \varphi) \geq m \quad \text{for any} \ \ t \geq t_0.$$

Note that both definitions agree with the concept of uniform (strong) ρ-persistence in the terms of Smith and Thieme [34] for an adequate choice of the map $\rho : X \to \mathbb{R}_+$ (see also Faria and Röst [10] and Faria et al. [9]). Our main purpose is to have a characterization of these two properties in terms of some computable objects related to the system.

Recently, in [26] the authors have characterized the properties of uniform persistence and strict persistence at 0 for families of almost periodic Nicholson systems. If we want to take advantage of their approach, the first thing that we have to do is to include the initial non-autonomous system (3.1) into the family of systems over the hull of the vector-valued map determined by all the almost periodic coefficients. Note that we need coefficients of (3.1) to be defined on $\mathbb{R}$ to easily build the hull Ω of the system, and define the continuous translation flow $\mathbb{R} \times \Omega \to \Omega$, just denoted by $(t, \omega) \mapsto \omega \cdot t$. Then, for each $\omega \in \Omega$ the corresponding system in the family can be written as

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

$i = 1, \ldots, n$, for certain continuous nonnegative maps d_i, a_{ij}, β_i, c_i defined on Ω.

We take $X = C([-\tau_1, 0]) \times \ldots \times C([-\tau_n, 0])$ with the usual cone of positive elements, denoted by X_+, and the sup-norm. Then, solutions $y(t, \omega, \varphi)$ of systems (3.2) for $\omega \in \Omega$ with initial values $\varphi \in X_+$ induce a globally defined (see Theorem 3.3 (i)) skew-product semiflow (2.1), $\mathbb{R}_+ \times \Omega \times X_+ \to \Omega \times X_+$, $(t, \omega, \varphi) \mapsto (\omega \cdot t, y_t(\omega, \varphi))$, with the usual notation in delay equations, $y_t(\omega, \varphi)_i(s) = y_i(t + s, \omega, \varphi)$ for any $s \in [-\tau_i, 0]$, for each $i = 1, \ldots, n$. The fact that the set $\Omega \times X_+$ is invariant for the dynamics follows once more from the criterion given in Theorem 5.2.1 in [33]. Besides, this semiflow has a trivial minimal set $K = \Omega \times \{0\}$, as the null map is a solution of any of the systems over the hull.

In this situation, the properties of uniform persistence and strict persistence at 0 for the family of systems (3.2) have the following collective formulation, directly adapted from Definitions 3.1 and 5.2 in [26], respectively.

Definition 3.2. (i) The family of Nicholson systems (3.2) is *uniformly persistent* (*u-persistent* for short) if there exists a map $\psi \gg 0$ such that for any $\omega \in \Omega$ and any initial map $\varphi \gg 0$ there exists a time $t_0 = t_0(\omega, \varphi)$ such that $y_t(\omega, \varphi) \geq \psi$ for any $t \geq t_0$.

(ii) The family of Nicholson systems (3.2) is *strictly persistent at* 0 (s_0-*persistent* for short) if there exists a collection of maps $e_1, \ldots, e_p \in X$, with $e_k > 0$ for $k = 1, \ldots, p$, such that for any $\omega \in \Omega$ and any initial map $\varphi \geq 0$ with $\varphi(0) > 0$ there exists a time $t_0 = t_0(\omega, \varphi)$ such that $y_t(\omega, \varphi) \geq e_k$ for any $t \geq t_0$, for some $k \in \{1, \ldots, p\}$.

More precisely, Section 6 in [26] is devoted to the study of these persistence properties for the family of almost periodic Nicholson systems (3.2), where the coefficients $\widetilde{c}_i(t)$ in the initial system (3.1) have been taken to be identically equal to 1 just for simplicity. It is straightforward to check that, under hypothesis (a5), all the results in Section 6 in [26] still apply. For the sake of completeness we include here the following result, whose items are respectively Theorem 6.1 and Theorem 6.2 in [26].

Theorem 3.3. *Let us consider the Nicholson system* (3.1) *under assumptions* (a1)-(a6). *Then:*

(i) *Solutions of the family* (3.2) *with initial condition in* X_+ *are ultimately bounded, in the sense that there exists a constant* $r > 0$ *such that for any* $\omega \in \Omega$ *and any* $\varphi \in X_+$, *any component of the vectorial solution satisfies* $0 \leq y_i(t, \omega, \varphi) \leq r$ *from some time on. In particular the induced semiflow is globally defined on* $\Omega \times X_+$.

(ii) *The family of Nicholson systems* (3.2) *is uniformly persistent (resp. strictly persistent at* 0*) if and only if the linearized family of systems along the null solution, which is given by*

$$z_i'(t) = -d_i(\omega{\cdot}t)\, z_i(t) + \sum_{j=1}^{n} a_{ij}(\omega{\cdot}t)\, z_j(t) + \beta_i(\omega{\cdot}t)\, z_i(t - \tau_i)\,, \qquad (3.3)$$

for $i = 1, \ldots, n$, *for each* $\omega \in \Omega$, *is uniformly persistent (resp. strictly persistent at* 0*) in the sense of Definition* 3.2.

The importance of the first approximation result to check persistence stated in (ii) lies on the fact that Nicholson systems are not cooperative, as for cooperative systems the result for uniform persistence has already been proved in [22]. Note that the linearized systems along the null solution (3.3) are independent of the coefficients $c_i(\omega)$ and they are cooperative thanks to conditions (a3) and (a4), so that the spectral characterization of uniform persistence and strict persistence at 0 given in [26] for general cooperative delay linear families directly applies to them. The precise spectral characterization of the persistence properties for the almost periodic Nicholson family (3.2) is stated in Theorem 6.3 in [26].

At this point it is natural to pose some questions:

(Q1) What is the relation between the definitions of persistence for the initial system (3.1) given in Definition 3.1, and the definitions stated in Definition 3.2 in a collective way for the family of systems (3.2)?

(Q2) Can we give a precise characterization of the persistence properties of system (3.1) in terms of some computable items of the system?

The purpose of this section is to give an answer to these two questions. In short, we are going to see that things go smoothly for the almost periodic Nicholson systems. We will also determine another class of systems for which things go exactly as in the Nicholson systems. However, as it will be shown in the next section, the transfer of the property of persistence from one particular non-autonomous almost periodic system to the family of systems over the hull, as it occurs in the Nicholson systems, is not to be expected in general: it fails even for one-dimensional linear almost periodic equations. This supports the convenience of considering a collective formulation of the properties of persistence on the family of systems over the hull, as otherwise, the property may hold for some systems of the family and may not hold for others, which is not desirable in applications to real world models.

Theorem 3.4. *Let us consider the almost periodic Nicholson system* (3.1) *under assumptions* (a1)-(a6) *and the family of systems over the hull* (3.2)*. Then, system* (3.1) *is uniformly persistent at* 0 *(resp. strictly persistent at* 0*) if and only if the family of systems* (3.2) *is uniformly persistent (resp. strictly persistent at* 0*).*

Proof. In both cases, the easy implication is the one transferring the persistence property from the family to the initial system. In the case of u-persistence, for the map $\psi \gg 0$ given in Definition 3.2 (i), define $m = \min\{\psi_1(0), \ldots, \psi_n(0)\} > 0$. Now, in order to check the u_0-persistence of the initial system, recall that it is one of the systems in the family over the hull: let it be the system for $\omega_0 \in \Omega$, and let us keep this notation throughout the whole proof. Now, fixed any initial map $\varphi \geq 0$ with $\varphi(0) \gg 0$, note that the solution $y(t, \varphi) = y(t, \omega_0, \varphi) \gg 0$ for any $t \geq 0$, so that for $\tau_0 = \max\{\tau_1, \ldots, \tau_n\}$ it holds that $y_{\tau_0}(\omega_0, \varphi) \gg 0$. Therefore, by the u-persistence of the family, for $\omega_0 \cdot \tau_0$ and $y_{\tau_0}(\omega_0, \varphi) \gg 0$ there exists a time $t_0 = t_0(\omega_0, \tau_0, \varphi)$ such that $y_t(\omega_0 \cdot \tau_0, y_{\tau_0}(\omega_0, \varphi)) \geq \psi$ for any $t \geq t_0$. By the cocycle property, this means that $y_{t+\tau_0}(\omega_0, \varphi) \geq \psi$ for any $t \geq t_0$, and therefore, $y_i(t, \varphi) \geq m$ for any $t \geq t_0 + \tau_0$ and any $i = 1, \ldots, n$, and we are done.

As for the case of s_0-persistence, for each of the maps $e_k > 0$ given in Definition 3.2 (ii), there is at least one component $i = i(k)$ such that $(e_k)_i > 0$, so that there exists at least a $s_k \in [-\tau_i, 0]$ with $(e_k)_i(s_k) > 0$. Now, define $m = \min\{(e_1)_{i(1)}(s_1), \ldots, (e_p)_{i(p)}(s_p)\} > 0$. Then, given $\varphi \geq 0$ with $\varphi(0) > 0$, by the s_0-persistence of the family there exists a time $t_0 = t_0(\omega_0, \varphi)$ such that $y_t(\omega_0, \varphi) \geq e_k$ for $t \geq t_0$, for some $k \in \{1, \ldots, p\}$. In particular, for the component $i = i(k)$ previously defined, $y_t(\omega_0, \varphi)_i(s_k) = y_i(t + s_k, \varphi) \geq (e_k)_i(s_k) \geq m$ for any $t \geq t_0$, so that $y_i(t, \varphi) \geq m$ for any $t \geq t_0$, as we wanted.

For the converse implication in the case of u-persistence the arguments are more subtle, and we make use of the general theory of monotone and concave $\mathcal{C}^1$ skew-product semiflows developed by Núñez et al. in [25]. To begin with, taking condition (a5) into consideration we note that for any $y \geq 0$, $\omega \in \Omega$ and $i = 1, \ldots, n$, $y\, e^{-c_i(\omega)\, y} \leq y\, e^{-c_0\, y}$. Then, we define the nondecreasing, bounded and concave map $h : [0, \infty) \to [0, \infty)$ of class $\mathcal{C}^1$,

$$h(y) = \begin{cases} y\, e^{-c_0\, y} & \text{if } y \in [0, 1/c_0], \\ \frac{1}{c_0}\, e^{-1} & \text{if } y \in [1/c_0, \infty), \end{cases}$$

we look at the family of cooperative and concave delay nonlinear systems given for each $\omega \in \Omega$ by

$$z_i'(t) = -d_i(\omega{\cdot}t)\, z_i(t) + \sum_{j=1}^{n} a_{ij}(\omega{\cdot}t)\, z_j(t) + \beta_i(\omega{\cdot}t)\, h(z_i(t - \tau_i)) \,, \qquad (3.4)$$

for $i = 1, \ldots, n$, where the coefficients are just those of (3.2), and consider the induced skew-product semiflow $\bar{\tau} : \mathbb{R}^+ \times \Omega \times X_+ \to \Omega \times X_+$, $(t, \omega, \varphi) \mapsto (\omega{\cdot}t, z_t(\omega, \varphi))$, where $z(t, \omega, \varphi)$ is the solution of system (3.4) with initial value φ. As the nonlinear terms are uniformly bounded, the same argument as that in the proof of Theorem 6.1 in [26] implies that solutions of (3.4) are ultimately bounded and in particular $\bar{\tau}$ is globally defined. Besides, since the systems are cooperative and concave, the semiflow is monotone and concave, and it is also $\mathcal{C}^1$.

Now, assuming that the property of u_0-persistence in Definition 3.1 (i) holds for system (3.1), take an initial map $\varphi_0 \geq 0$ with $\varphi_0(0) \gg 0$ and take $t_0 = t_0(\varphi_0)$ such that $y_i(t, \varphi_0) = y_i(t, \omega_0, \varphi_0) \geq m$ for any $t \geq t_0$ and any $i = 1, \ldots, n$. Then, as systems (3.4) are cooperative, we can apply a standard argument of comparison of solutions to state that for $t \geq t_0$, $m \leq y_i(t, \omega_0, \varphi_0) \leq z_i(t, \omega_0, \varphi_0)$.

At this point, we can build the omega-limit set $\mathcal{O}(\omega_0, \varphi_0)$ of the pair (ω_0, φ_0) for the semiflow $\bar{\tau}$, which contains a minimal set K which necessarily lies on the zone $\Omega \times \{\varphi \in X_+ \mid \varphi \geq \bar{m}\}$, for the map $\bar{m} \in X$ whose components are identically equal to m. In other words, there is a strongly positive minimal set for $\bar{\tau}$. Then, Theorem 3.8 in [25] applied to the $\mathcal{C}^1$ monotone and concave skew-product semiflow $\bar{\tau}$ asserts that the dynamics suits one the following cases: the so-called case A1 when K is the unique minimal set strongly above 0, or case A2 when there are infinitely many minimal sets strongly above 0.

If we can discard case A2, we are done, as in case A1 the unique minimal set is a hyperbolic copy of the base, that is, $K = \{(\omega, c(\omega)) \mid \omega \in \Omega\}$ for certain continuous map $c : \Omega \to X_+$, which exponentially attracts any trajectory starting inside the interior of the positive cone. Therefore, it is immediate that the semiflow $\bar{\tau}$ is u-persistent in the interior of the positive cone according to Definition 3.1 in [26] or, in other words, the family (3.4) is u-persistent. Now, for $\bar{\tau}$ regular monotone and concave, with 0 being a trajectory, it holds that

$$z_t(\omega, \varphi) \leq D_\varphi z_t(\omega, 0)\, \varphi \,, \quad \text{for any } \omega \in \Omega, \ \varphi \geq 0 \text{ and } t \geq 0 \,, \qquad (3.5)$$

and it is well-known that $z(t) = (D_\varphi z_t(\omega, 0)\, \varphi)(0)$ provide the solutions of the linearized family along 0 of the family (3.4), which by construction coincides with (3.3), the family of linearized Nicholson systems along 0, which then turn out to be u-persistent. In this case, to finish, we can apply Theorem 3.3 (ii) to conclude the u-persistence for the Nicholson family (3.2).

Finally, we discard case A2. Argue for contradiction and assume that case A2 holds for $\bar{\tau}$. Then, according to the proof of Theorem 3.8 in [25] we can consider the family of strongly positive minimal sets $K_s = \mathcal{O}(\omega_0, s\,\bar{\varphi})$ for $s \in (0, 1]$ for a fixed $\bar{\varphi} \gg 0$ with $(\omega_0, \bar{\varphi}) \in K$, which must satisfy property (vi) in the statement of case A2: if $(\omega, \psi) \in \Omega \times X_+$ is such that for any $s \in (0, 1]$ there exists $(\omega, \varphi_s) \in K_s$ with $\psi \leq \varphi_s$, then $\psi \gg 0$. Nevertheless, by the u_0-persistence, as done before, we have that $K_s \subset \Omega \times \{\varphi \in X_+ \mid \varphi \geq \bar{m}\}$ for any $s \in (0, 1]$, and we get a contradiction just by taking $\psi = \bar{m}/2 \gg 0$. We are finished.

It remains to deal with the s_0-persistence property of the family, assuming the s_0-persistence property of the initial system. Once more this is quite delicate and the proof follows the line of ideas used in [26], in what refers to a rearrangement of the family of systems in view of the linearized family. Recall here that a square matrix $A = [a_{ij}]$ is *reducible* if there is a simultaneous permutation of rows and columns that brings A to the form

$$\left[\begin{array}{cc} A_{11} & 0 \\ A_{21} & A_{22} \end{array}\right],$$

with A_{11} and A_{22} square matrices; and it is *irreducible* if it is not reducible. Equivalently, for $n > 1$, A is irreducible if for any nonempty proper subset $I \subset \{1, \ldots, n\}$ there are $i \in I$ and $j \in \{1, \ldots, n\} \setminus I$ such that $a_{ij} \neq 0$.

More precisely, as stated in Theorem 6.3 in [26], for each $\omega \in \Omega$ we can look at the linearized system along the null solution (3.3) and assume without loss of generality that the constant matrix $\bar{A} = [\bar{a}_{ij}]$ defined as

$$\bar{a}_{ij} = \sup_{\omega \in \Omega} a_{ij}(\omega) \text{ for } i \neq j, \quad \text{and } \bar{a}_{ii} = 0 \tag{3.6}$$

has a block lower triangular structure

$$\left[\begin{array}{cccc} \bar{A}_{11} & 0 & \ldots & 0 \\ \bar{A}_{21} & \bar{A}_{22} & \ldots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ \bar{A}_{k1} & \bar{A}_{k2} & \ldots & \bar{A}_{kk} \end{array}\right], \tag{3.7}$$

with irreducible diagonal blocks $\bar{A}_{jj}$ of dimension n_j for $j = 1, \ldots, k$ ($n_1 + \cdots + n_k = n$). To simplify the notation, we arrange the set of delays by blocks by denoting $\{\tau_1, \ldots, \tau_n\} = \{\tau_1^1, \ldots, \tau_{n_1}^1, \ldots, \tau_1^k, \ldots, \tau_{n_k}^k\}$ and we write $X = X^{(1)} \times \ldots \times X^{(k)}$ for

$$X^{(j)} = C([-\tau_1^j, 0]) \times \ldots \times C([-\tau_{n_j}^j, 0]), \quad j = 1, \ldots, k. \tag{3.8}$$

For each $j = 1, \ldots, k$ let L_j be the linear skew-product semiflow induced on the product space $\Omega \times X^{(j)}$ by the solutions of the n_j-dimensional delay linear systems corresponding to the jth diagonal block in (3.3),

$$z_i'(t) = -d_i(\omega \cdot t) z_i(t) + \sum_{l \in I_j} a_{il}(\omega \cdot t) z_l(t) + \beta_i(\omega \cdot t) z_i(t - \tau_i), \quad t \geq 0, \tag{3.9}$$

for $i \in I_j$, for each $\omega \in \Omega$, where I_j is the set formed by the n_j indexes corresponding to the rows of the block $\bar{A}_{jj}$. Then, L_j admits a continuous separation (of type II) and its principal spectrum is just given by the upper Lyapunov exponent λ_j of the minimal set $K^j = \Omega \times \{0\} \subset \Omega \times X^{(j)}$. Besides, Theorem 6.3 in [26] gives a precise characterization of the properties of u-persistence and s_0-persistence for the Nicholson family (3.2) in terms of the positivity of a certain set of these exponents λ_j in each case. Now we distinguish two cases.

(C1): $k = 1$, that is, the matrix $\bar{A}$ is irreducible. In this case, starting with a positive component of the solution, we are going to raise the other ones, so as to actually obtain u_0-persistence for system (3.1). We remark that a similar argument has been used in the proof of Theorem 5.4 in [22]. More precisely, given $\varphi \geq 0$ with $\varphi(0) > 0$ there exists a $t_0 = t_0(\varphi)$ and there exists a component i_1 such that $y_{i_1}(t, \varphi) = y_{i_1}(t, \omega_0, \varphi) \geq m$ for any $t \geq t_0$, for the constant $m > 0$ given in Definition 3.1 (ii). Now, as $\bar{A}$ is irreducible, there exists an index $i_2 \in \{1, \ldots, n\} \setminus$

$\{i_1\}$ such that $\bar{a}_{i_2 i_1} > 0$. As $y'_{i_2}(t, \omega_0, \varphi) \geq -d_{i_2}(\omega_0 \cdot t)\, y_{i_2}(t, \omega_0, \varphi) + a_{i_2 i_1}(\omega_0 \cdot t)\, m$ for $t \geq t_0$, we consider the scalar family of ODEs for $\omega \in \Omega$,

$$h'(t) = -d_{i_2}(\omega \cdot t)\, h(t) + a_{i_2 i_1}(\omega \cdot t)\, m \,, \qquad (3.10)$$

written for short as $h'(t) = F(\omega \cdot t, h(t))$, for which the null map is a lower solution because $F(\omega, 0) \geq 0$ for any $\omega \in \Omega$. Besides, since $\bar{a}_{i_2 i_1} > 0$, there exists an $\omega^* \in \Omega$ such that $F(\omega^*, 0) = a_{i_2 i_1}(\omega^*)\, m > 0$. In this situation 0 is a strong sub-equilibrium (see Lemma 3.15 in [19], which applies to ODEs). As a consequence, there exist $t_{i_2} > 0$ and $m_{i_2} > 0$ such that, if $h(t, \omega, 0)$ is the solution of (3.10) with initial value 0, then $h(t, \omega, 0) > m_{i_2}$ for any $t \geq t_{i_2}$ and any $\omega \in \Omega$. Therefore, a standard argument of comparison of solutions leads to the fact that, for any $t \geq t_0 + t_{i_2}$,

$$y_{i_2}(t, \omega_0, \varphi) \geq h(t - t_0, \omega_0 \cdot t_0, y_{i_2}(t_0, \omega_0, \varphi)) \geq h(t - t_0, \omega_0 \cdot t_0, 0) > m_{i_2} \,.$$

Now, if there are any more components, the process is just the same. We just give a sketch for the next step. By the irreducible character of $\bar{A}$, there exist indexes $i_3 \in \{1, \ldots, n\} \setminus \{i_1, i_2\}$ and $i \in \{i_1, i_2\}$ such that $\bar{a}_{i_3 i} > 0$, and then note that $y'_{i_3}(t, \omega_0, \varphi) \geq -d_{i_3}(\omega_0 \cdot t)\, y_{i_3}(t, \omega_0, \varphi) + a_{i_3 i}(\omega_0 \cdot t)\, m_i$ for $t \geq t_0 + t_{i_2}$, for the constant m_i given by m if $i = i_1$ and by m_{i_2} if $i = i_2$. The same argument as before leads to the existence of some $t_{i_3} > 0$ and $m_{i_3} > 0$ such that $y_{i_3}(t, \omega_0, \varphi) \geq m_{i_3}$ for any $t \geq t_0 + t_{i_2} + t_{i_3}$. Iterating the process we finally obtain that, taking $m_0 = \min\{m, m_{i_2}, \ldots, m_{i_n}\}$, $y_i(t, \omega_0, \varphi) \geq m_0$ for any $t \geq t_0 + t_{i_2} + \ldots + t_{i_n}$ and any $i = 1, \ldots, n$.

Note that the constant m_0 just defined depends on the component $i_1 = i_1(\varphi)$ we started with. As there are just n different components with which the process can start, depending on the initial map φ, and the process in each case exclusively depends on the irreducible structure of the constant matrix $\bar{A}$, we can conclude that system (3.1) is u_0-persistent. As we already know, this property extends as u-persistence to the whole family (3.2), $\omega \in \Omega$, and we can apply Theorem 6.3 in [26], which in the case $k = 1$ says that the upper Lyapunov exponent $\lambda > 0$, and the family is also s_0-persistent. We are done with this case.

(C2): $k > 1$, that is, the matrix $\bar{A}$ is reducible and it has the block lower triangular structure (3.7). In this case Theorem 6.3 in [26] asserts that the Nicholson family (3.2) is s_0-persistent if and only if $\lambda_j > 0$ for any $j \in J$ for the set of indexes

$$J = \{j \in \{1, \ldots, k\} \mid \bar{A}_{ij} = 0 \text{ for any } i \neq j\}.$$

Thus, we fix $j \in J$ and we consider the n_j-dimensional Nicholson-type system

$$y'_i(t) = -\widetilde{d}_i(t)\, y_i(t) + \sum_{l \in I_j} \widetilde{a}_{il}(t)\, y_l(t) + \widetilde{\beta}_i(t)\, y_i(t - \tau_i)\, e^{-\widetilde{c}_i(t)\, y_i(t - \tau_i)} \,, \qquad (3.11)$$

for $i \in I_j$, which is included for $\omega = \omega_0$ in the family of systems for $\omega \in \Omega$,

$$y'_i(t) = -d_i(\omega \cdot t)\, y_i(t) + \sum_{l \in I_j} a_{il}(\omega \cdot t)\, y_l(t) + \beta_i(\omega \cdot t)\, y_i(t - \tau_i)\, e^{-c_i(\omega \cdot t)\, y_i(t - \tau_i)} \,,$$

for $i \in I_j$, with linearized family along 0 given by (3.9) and associated constant matrix $\bar{A}_{jj}$, which is irreducible. If system (3.11) is s_0-persistent, we can apply to it the result in case (C1) to get that the upper Lyapunov exponent $\lambda_j > 0$.

So, to finish, let us check that for each $j \in J$ system (3.11) is s_0-persistent. For that, take $\bar{\varphi}^j \in X_+^{(j)}$ with $\bar{\varphi}^j(0) > 0$, and build a map $\varphi \in X_+ = X_+^{(1)} \times \ldots \times X_+^{(k)}$, $\varphi = (\varphi^1, \ldots, \varphi^k)$ such that $\varphi^j = \bar{\varphi}^j$ and $\varphi^i = 0$ for $i \neq j$, which satisfies $\varphi \geq 0$

and $\varphi(0) > 0$. The s_0-persistence of the initial system (3.1) says that there exists a $t_0 = t_0(\varphi)$ such that for some component i_0, $y_{i_0}(t, \varphi) \geq m$ for $t \geq t_0$. Now, by the structure of the system noting that $j \in J$, and the structure of the initial map φ, it is easy to check that, writing the solution by blocks $y(t, \varphi) = (y^1(t, \varphi), \ldots, y^k(t, \varphi))$, it is $y^i(t, \varphi) = 0$ for $i \neq j$, whereas $y^j(t, \varphi)$ coincides with the solution of system (3.11) with initial condition $\varphi^j = \bar{\varphi}^j$. Therefore, necessarily $i_0 \in I_j$ and we are done. The proof is finished. $\qquad\square$

Once we have given a satisfactory answer to question (Q1), we now present an answer to question (Q2).

Theorem 3.5. *Let us consider the almost periodic Nicholson system (3.1) under assumptions* (a1)-(a6)*, and let us assume without loss of generality that the constant matrix $\bar{A} = [\bar{a}_{ij}]$ defined as*

$$\bar{a}_{ij} = \sup_{t \in \mathbb{R}} \widetilde{a}_{ij}(t) \;\; \text{for } i \neq j \,, \quad \text{and } \bar{a}_{ii} = 0$$

has a block lower triangular structure as in (3.7) with irreducible diagonal blocks $\bar{A}_{jj}$ of dimension n_j for $j = 1, \ldots, k$ $(n_1 + \cdots + n_k = n)$. For each $j = 1, \ldots, k$ let us consider the n_j-dimensional almost periodic linear delay system

$$z_i'(t) = -\widetilde{d}_i(t)\, z_i(t) + \sum_{l \in I_j} \widetilde{a}_{il}(t)\, z_l(t) + \widetilde{\beta}_i(t)\, z_i(t - \tau_i)\,, \quad t \geq 0\,, \qquad (3.12)$$

for $i \in I_j$, the set of indexes 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 $X^{(j)}$ defined in (3.8). Then, let $\widetilde{\lambda}_j$ be defined as

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

Finally, let us consider two sets of indexes associated to the structure of the linear part of the system: if $k = 1$, i.e., if the matrix $\bar{A}$ is irreducible, let $I = J = \{1\}$; else, let

$$I = \{j \in \{1, \ldots, k\} \mid \bar{A}_{ji} = 0 \text{ for any } i \neq j\},$$
$$J = \{j \in \{1, \ldots, k\} \mid \bar{A}_{ij} = 0 \text{ for any } i \neq j\},$$

that is, I is composed by the indexes j such that any off-diagonal block in the row of $\bar{A}_{jj}$ is null, whereas J contains those indexes j such that any off-diagonal block in the column of $\bar{A}_{jj}$ is null. Then:

   (i) *The almost periodic Nicholson system (3.1) is uniformly persistent at 0 if and only if $\widetilde{\lambda}_j > 0$ for any $j \in I$.*
   (ii) *The almost periodic Nicholson system (3.1) is strictly persistent at 0 if and only if $\widetilde{\lambda}_j > 0$ for any $j \in J$.*

Proof. First of all, recall that if the matrix $\bar{A}$ does not have the required structure, we just need to permute the variables in order to obtain it. Also, note that when the Nicholson system is included in the family of systems (3.2) over the hull Ω, the matrix $\bar{A}$ defined under the same name in (3.6) coincides with the matrix $\bar{A}$ here defined, because of the hull construction.

Now, as stated in Theorem 3.4, the properties of u_0-persistence and s_0-persistence of system (3.1) are equivalent respectively to the properties of u-persistence and s_0-persistence for the family of systems (3.2), and the last properties are completely

characterized in Theorem 6.3 in [26], which is a parallel result to the above one just given in terms of the upper Lyapunov exponents λ_j of the trivial minimal set $K^j = \Omega \times \{0\}$ for the linear skew-product semiflow L_j induced on $\Omega \times X^{(j)}$ (see (3.8)) by the solutions of the n_j-dimensional linear delay family (3.9), for each $j = 1, \ldots, k$.

At this point, it remains to check that the number $\widetilde{\lambda}_j$ coincides with λ_j for each $j = 1, \ldots, k$. The thing is that, as already commented before, thanks to the irreducible character of the diagonal block $\bar{A}_{jj}$, the linear skew-product semiflow $L_j(t, \omega, \varphi) = (\omega{\cdot}t, \Phi_j(t, \omega)\,\varphi)$ admits a continuous separation (of type II), which roughly speaking means that there is an invariant one-dimensional subbundle dominating the dynamics of L_j in the long run. More precisely, if $X^{(j)} = X_1^{(j)}(\omega) \oplus X_2^{(j)}(\omega)$ for $\omega \in \Omega$ is the decomposition given by the continuous separation of L_j, with $X_1^{(j)}(\omega) = \mathrm{span}\{v^j(\omega)\}$, for a continuous map $v^j : \Omega \to X^{(j)}$ such that $v^j(\omega) \gg 0$ and $\|v^j(\omega)\| = 1$ for any $\omega \in \Omega$, then $\Phi_j(t, \omega)\,v^j(\omega) = c_j(t, \omega)\,v^j(\omega{\cdot}t)$, and the positive coefficients $c_j(t, \omega)$, which can be defined for all $t \in \mathbb{R}$ and $\omega \in \Omega$, satisfy the linear cocycle property $c_j(t + s, \omega) = c_j(t, \omega{\cdot}s)\,c_j(s, \omega)$ for any $t, s \in \mathbb{R}$ and any $\omega \in \Omega$ (the reader is referred to [22] or [26] for more details). That is, the one-dimensional linear skew-product flow given by the scalar cocycle $c_j(t, \omega)$ can be seen as a flow extension of the restriction of the linear semiflow L_j to the leading one-dimensional subbundle, turning the problem into the setting of the spectral theory for one-dimensional linear skew-product flows, which has been studied in Sacker and Sell [29].

Note also that the almost periodicity of the coefficients implies that the flow in Ω is uniquely ergodic, so that the Sacker-Sell spectrum of the previous one-dimensional linear skew-product flow (which is called the principal spectrum by definition) reduces to a singleton, namely, $\{\lambda_j\}$, for the upper Lyapunov exponent $\lambda_j = \sup_{\omega \in \Omega} \lambda_j(\omega)$, where the Lyapunov exponent for each $\omega \in \Omega$ is defined as

$$\lambda_j(\omega) = \limsup_{t \to \infty} \frac{\log \|\Phi_j(t, \omega)\|}{t} \,.$$

Now, Remark 2 in [29] says that the result given in Theorem 7 for almost periodic linear ODEs does extend to the case of differentiable linear skew-product flows on vector bundles, provided that the base flow is minimal and uniquely ergodic. Therefore, we can apply Theorem 7 in [29] to the one-dimensional invariant subbundle determined by the continuous separation, so that the upper Lyapunov exponent λ_j can be calculated along the trajectories in the one-dimensional subbundle. More precisely, for all $\omega \in \Omega$ there exists the limit

$$\lambda_j = \lim_{t \to \infty} \frac{\log \|\Phi_j(t, \omega)\,v^j(\omega)\|}{t} = \lim_{t \to \infty} \frac{\log \|c_j(t, \omega)\,v^j(\omega{\cdot}t)\|}{t} = \lim_{t \to \infty} \frac{\log c_j(t, \omega)}{t},$$

and the last limit has been shown in [22] to give the value $\lambda_j(\omega)$, so that the value of the upper Lyapunov exponent λ_j is attained at any $\omega \in \Omega$.

In particular, for ω_0 giving the initial system (3.1), one can calculate $\lambda_j = \lambda_j(\omega_0)$. To finish, it is well-known that for any fixed $\varphi_0 \in X^{(j)}$ with $\varphi_0 \gg 0$, the norm of the differential operators $\|\Phi_j(t, \omega)\|$ can be controlled by $\|\Phi_j(t, \omega)\,\varphi_0\|$, namely, there exists an $l = l(\varphi_0) > 0$ such that $\|\Phi_j(t, \omega)\| \le l\,\|\Phi_j(t, \omega)\,\varphi_0\|$ for any $t > 0$ and $\omega \in \Omega$. From here, taking $\varphi_0 = \bar{1}$ just for the sake of simplicity, and noting that $\Phi_j(t, \omega_0)\,\bar{1} = z_t^j(\bar{1})$, we conclude that $\lambda_j = \widetilde{\lambda}_j$, as we wanted. The proof is finished. $\qquad\square$

Remark 3.6. The existence of a continuous separation for the linear semiflows L_j is crucial to reduce the problem to the setting of 1-dimensional dynamics. Also the fact that the flow on Ω is minimal and uniquely ergodic is crucial in two respects: first, to guarantee that the principal spectral intervals reduce to singletons, and second, to permit the calculus of the upper Lyapunov exponent as the Lyapunov exponent of any point $\omega \in \Omega$.

The advantage of the previous result is that, given a concrete Nicholson system, one can easily compute the matrix $\bar{A}$ and permute the variables so as to get the required block triangular structure. After that, to estimate the numbers $\bar{\lambda}_j$, one has to numerically solve the linear delay systems (3.12), corresponding to each of the diagonal blocks in $\bar{A}$, starting with a strongly positive map, which in the statement has been taken to be $\bar{1}$, but it might be any other. This can be done in many different ways. The reader is referred to Breda and Van Vleck [3] for a general approach and to Calzada et al. [4] for a recent approach in the quasi-periodic case, taking advantage of the presence of a continuous separation for the linear skew-product semiflows L_j defined in the previous proof.

To finish this section, we remark that for systems with a similar structure things regarding persistence go as in the almost periodic Nicholson systems. For instance, the same results can be stated for useful almost periodic population models which are written as

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

for $i = 1, \ldots, n$, with similar hypotheses on the linear part to the ones imposed in the Nicholson systems, and where the nonlinearities are of the form

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

For instance, see the scalar model for the process of hematopoiesis for a population of mature circulating cells studied in Mackey and Glass [16].

Here we collect some analytical features of all these systems which make things go nicely in what refers to questions (Q1) and (Q2).

(1) The almost periodicity of the coefficients, which produces a minimal and uniquely ergodic hull.
(2) The ODE linear part of the system is cooperative. It is also uniformly asymptotically stable and the nonlinearities are bounded, which makes the system dissipative.
(3) The nonlinear terms $h_i(y)$ are, apart from bounded, sublinear maps, and they are increasing in a right neighborhood of 0, so that the induced skew-product semiflow is monotone and sublinear in a region of the phase space.
(4) Thanks to (2) and (3), the persistence properties of the family of systems over the hull can be studied through the linearized family along the null solution.

Note that for $\alpha = 1$, the map in the family of nonlinearities is just given by $h_i(y) = \frac{y}{1 + \widetilde{c}_i(t)\, y}$ which is always increasing and concave, so that the system is in this case dissipative, cooperative and concave, and Theorem 4.4 in Section 4 applies to it. This kind of nonlinearities have been used in epidemic models with positive feedback; for instance, see Capasso [5] and Zhao [36].

4. Uniform persistence in cooperative linear/sublinear models: an individual or a collective property?

In this section, we first provide a precise example in which the property of uniform persistence is not transferred from one particular non-autonomous almost periodic equation to the family of equations over the hull. In other words, we can affirm that uniform persistence is not a robust property in almost periodic equations. Note that neither is robust the property of strict persistence, since uniform and strict persistence are equivalent properties in the general case of linear monotone skew-product semiflows with a continuous separation of classical type (see [26]). Besides, in the cooperative linear or sublinear setting, if the property of uniform persistence is not inherited by the family, it happens in a strong way, meaning that there might be just a few systems in the family which are uniformly persistent. Thinking of applications, in models of real world processes given by cooperative and linear/sublinear systems of ODEs or delay FDEs, it is highly improbable that we can experimentally or numerically detect uniform persistence under these circumstances.

As a consequence, there is a general need for definitions of persistence given globally for the family of systems over the hull of a particular non-autonomous system with a recurrent behaviour in time. This is the collective approach that has been taken in [22] and [26]. This supports the coherence of the results in the previous section, as what happens in Nicholson systems regarding persistence cannot at all be given for granted. In connection with this, another general class of systems inside the class of globally cooperative and sublinear systems is determined, for which the individual uniform persistence implies the collective uniform persistence.

Following this outline, first of all we characterize the property of uniform persistence in the case of a scalar linear ODE.

Proposition 4.1. *Given a continuous function $a : \mathbb{R} \to \mathbb{R}$, let us consider the scalar linear equation*

$$y'(t) = a(t)\, y(t)\,, \quad t \in \mathbb{R}\,,$$

and for each $y_0 \in \mathbb{R}$ let us denote by $y(t, y_0)$ the solution such that $y(0, y_0) = y_0$. Then, the following conditions are equivalent:

(i) *The equation is uniformly persistent, in the sense that there exists an $m > 0$ such that for any $y_0 > 0$ there exists a $t_0 = t_0(y_0)$ such that $y(t, y_0) \geq m$ for any $t \geq t_0$.*

(ii) $\displaystyle \lim_{t \to \infty} \int_0^t a(s)\, ds = \infty.$

Proof. (i)$\Rightarrow$(ii) To see that the limit is infinity, take any $M > 0$. Then, we can take $y_0 > 0$ small enough so that $\log(m/y_0) > M$. Now, associated to y_0 there exists a $t_0 = t_0(y_0)$ such that $y(t, y_0) \geq m$ for any $t \geq t_0$. Now, as in this scalar linear case

$$y(t, y_0) = y_0\, e^{\int_0^t a(s)\, ds}\,, \quad t \in \mathbb{R}\,,$$

it follows immediately that $\int_0^t a(s)\, ds \geq M$ for any $t \geq t_0$, and we are done.

(ii)$\Rightarrow$(i) In this situation, all solutions with positive initial data go to ∞ as $t \to \infty$, so that the definition of uniform persistence holds for any value of $m > 0$. $\square$

We now provide the announced example. It is based on a previous example given by Conley and Miller [6], although examples of the same nature date back to the end of the nineteenth century in the work by Poincaré: for instance, see [27].

Example 4.2. Let $f(t)$ be the map constructed in Conley and Miller [6] with the following properties:

  i) $f : \mathbb{R} \to \mathbb{R}$ is almost periodic;

  ii) $\displaystyle \lim_{t \to \infty} \int_0^t f(s)\,ds = \infty$;

  iii) f has zero mean value, that is, $\displaystyle \lim_{t \to \infty} \frac{1}{t} \int_0^t f(s)\,ds = 0.$

In this situation, on the one hand one looks at the equation $y'(t) = f(t)\,y(t)$, which satisfies condition (ii) in Proposition 4.1, so that it is uniformly persistent; and, on the other hand, we consider the family of linear scalar almost periodic equations over the hull Ω of f, that is,

$$y'(t) = g(t)\,y(t), \quad t \in \mathbb{R}, \quad \text{for each } g \in \Omega, \tag{4.1}$$

which is often written as $y'(t) = F(\omega{\cdot}t)\,y(t)$, $t \in \mathbb{R}$, for each $\omega \in \Omega$, for the continuous map F on Ω given by $F(\omega) = \omega(0)$.

Now, once more according to Definition 3.1 in [26], we say that the family of equations over the hull (4.1) is *uniformly persistent* if there exists an $m > 0$ such that for any $g \in \Omega$ and any $y_0 > 0$ there exists a time $t_0 = t_0(g, y_0)$ such that $y(t, g, y_0) \geq m$ for any $t \geq t_0$, where $y(t, g, y_0)$ is the solution of the equation given by g with initial value y_0 at time $t = 0$.

Thus, the condition of uniform persistence for the family of equations on the hull needs condition (ii) in Proposition 4.1 to be satisfied for any $g \in \Omega$. However, this is not the case in this concrete example. On the one hand, the set of maps g in Ω for which the corresponding equation is not uniformly persistent is of full measure. This is a corollary of Theorem 1 in Shneiberg [32]: under the zero mean value assumption on f, for almost every g in Ω there exists a sequence $t_n \to \infty$ such that $\int_0^{t_n} g(s)\,ds = 0$ for every $n \geq 1$. Note that these g are among the set of so-called (Poincaré) *recurrent* points at ∞, meaning that there exists a sequence $t_n \to \infty$ such that $\lim_{n \to \infty} \int_0^{t_n} g(s)\,ds = 0$. An application of Fubini's theorem permits to see that for almost every recurrent point g, its orbit is made of recurrent points too. Then, the set

$$\Omega_1 = \{ g \in \Omega \mid g(t + \cdot) \text{ is recurrent at } \infty \text{ for every } t \in \mathbb{R} \}, \tag{4.2}$$

which is invariant, has full measure. On the other hand, to the almost periodic function $f(t)$ with mean value zero and unbounded integral we can apply Theorem 3.7 in Johnson [14] which affirms that the set $\Omega_2 \subset \Omega$ made up by those g for which the integral has a strong oscillatory behaviour, namely:

$$\liminf_{t \to \infty} \int_0^t g(s)\,ds = -\infty, \quad \limsup_{t \to \infty} \int_0^t g(s)\,ds = \infty,$$

$$\liminf_{t \to -\infty} \int_0^t g(s)\,ds = -\infty, \quad \limsup_{t \to -\infty} \int_0^t g(s)\,ds = \infty,$$

is a residual set, that is, a topologically big set. Since clearly $\Omega_2 \subset \Omega_1$, Ω_1 is also a residual set.

Connecting with this linear scalar example, it is clear that whenever the former equation is included as a decoupled 1-dimensional subsystem of any n-dimensional ($n \geq 2$) linear or nonlinear system of almost periodic ODEs or delay FDEs which is uniformly persistent, the family over the hull cannot be uniformly persistent.

Having noticed that the non-robust phenomenon can well appear in higher dimensions, in the following results we describe what is behind this situation, in the monotone and linear/sublinear settings: the thing is that the uniform persistence of the individual almost periodic system is not a representative quality, as there are just a few systems in the hull with the persistence property, from both a topological and a measure theory points of view.

Although the results are stated in the case of delay FDEs, they can just be rephrased for ODEs. In that case the proofs follow the same lines with some simpler arguments because of the finite-dimensional scenario. Also, the linear case is formulated in a more general context than that of the hull, because it is going to be used as a basis for the sublinear setting.

Theorem 4.3. *Let $(\Omega, \cdot, \mathbb{R})$ be a minimal and uniquely ergodic flow and let us consider a family of linear cooperative delay systems over Ω,*

$$y'(t) = A(\omega{\cdot}t)\,y(t) + B(\omega{\cdot}t)\,y(t-1)\,, \quad \omega \in \Omega\,, \tag{4.3}$$

for certain continuous maps A, $B : \Omega \to M_n(\mathbb{R})$ taking values in the set of $n \times n$-real matrices. Let us assume that for a certain $\omega_0 \in \Omega$ the corresponding system (4.3) is uniformly persistent, that is, there exists an $m > 0$ such that for any initial map $\varphi \in C([-1,0], \mathbb{R}^n)$, $\varphi \gg 0$ there exists a time $t_0 = t_0(\omega_0, \varphi)$ such that

$$y_i(t, \omega_0, \varphi) \geq m \quad \text{for any } t \geq t_0 \text{ and any } i = 1, \ldots, n\,, \tag{4.4}$$

whereas the whole family of systems over Ω is not uniformly persistent, in the sense of Definition 3.2 (i). Then, there exists an invariant, residual set $\Omega_1 \subset \Omega$ of full measure such that for any $\omega \in \Omega_1$, system (4.3) is not uniformly persistent.

Proof. First of all, systems (4.3) are assumed to be cooperative, that is, all the off-diagonal entries of $A(\omega) = [a_{ij}(\omega)]$ and all the entries of $B(\omega) = [b_{ij}(\omega)]$ are nonnegative maps on Ω. Then, the solutions of the family (4.3) generate a linear monotone skew-product semiflow $L : \mathbb{R}_+ \times \Omega \times C([-1,0], \mathbb{R}^n) \to \Omega \times C([-1,0], \mathbb{R}^n)$. Note that Definition 3.2 (i) of u-persistence can be naturally applied to the cooperative linear family (4.3).

Now, once more following the procedure introduced in [22], after a permutation of the variables, if necessary, we can assume that the matrix $\bar{A} + \bar{B} = [\bar{a}_{ij} + \bar{b}_{ij}]$ defined as

$$\bar{a}_{ij} = \sup_{\omega \in \Omega} a_{ij}(\omega) \quad \text{for } i \neq j\,, \quad \text{and } \bar{a}_{ii} = 0\,,$$

$$\bar{b}_{ij} = \sup_{\omega \in \Omega} b_{ij}(\omega) \quad \text{for } i \neq j\,, \quad \text{and } \bar{b}_{ii} = 0\,,$$

has the form

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

and the diagonal blocks, denoted by $\bar{A}_{11} + \bar{B}_{11}, \ldots, \bar{A}_{kk} + \bar{B}_{kk}$, of size $n_1, \ldots, n_k$ respectively ($n_1 + \cdots + n_k = n$), are irreducible. For each $j = 1, \ldots, k$, let L_j be

the linear skew-product semiflow induced on $\Omega \times C([-1,0],\mathbb{R}^{n_j})$ by the solutions of the linear systems for $\omega \in \Omega$ given by the corresponding diagonal block of (4.3),

$$y'(t) = A_{jj}(\omega{\cdot}t)\, y(t) + B_{jj}(\omega{\cdot}t)\, y(t-1)\,, \quad t > 0\,. \tag{4.5}$$

Then, L_j admits a continuous separation (of type II) and its principal spectrum reduces to the upper Lyapunov exponent of the trivial minimal set $K^j = \Omega \times \{0\} \subset \Omega \times C([-1,0],\mathbb{R}^{n_j})$, let us call it λ_j, because Ω is minimal and uniquely ergodic. As stated in Theorems 5.3 and 5.4 in [26], which apply in this situation, the linear cooperative family (4.3) is u-persistent if and only if $\lambda_j > 0$ for any $j \in I$, for the set of indexes I defined as $I = \{1\}$ if the matrix $\bar{A} + \bar{B}$ is irreducible (i.e., if $k = 1$), and

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

if the matrix $\bar{A} + \bar{B}$ is reducible (i.e., if $k > 1$); that is, $j \in I$ if and only if any off-diagonal block in the row of $\bar{A}_{jj} + \bar{B}_{jj}$ is null, and consequently the corresponding system (4.5) is a decoupled subsystem of the total system for each $\omega \in \Omega$. In particular this means that, as system (4.3) for ω_0 is u-persistent, for any $j \in I$ system (4.5) for ω_0 is u-persistent as well.

At this point, since by hypothesis the whole family is not u-persistent, at least for some $j \in I$ we have that $\lambda_j \leq 0$. It cannot be $\lambda_j < 0$, as in that case all solutions of the whole family (4.5) would tend to 0 as $t \to \infty$, contradicting the u-persistence for ω_0. Therefore it must be $\lambda_j = 0$ for some $j \in I$.

So, let us fix such a $j \in I$ with $\lambda_j = 0$, and let $C([-1,0],\mathbb{R}^{n_j}) = X_1(\omega) \oplus X_2(\omega)$ for $\omega \in \Omega$ be the continuous splitting given by the continuous separation of the linear semiflow $L_j(t,\omega,\varphi) = (\omega{\cdot}t, \Phi_j(t,\omega)\,\varphi)$, $(t,\omega,\varphi) \in \mathbb{R}_+ \times \Omega \times C([-1,0],\mathbb{R}^{n_j})$. Recall that $X_1(\omega) = \mathrm{span}\{v(\omega)\}$ determines a one-dimensional invariant subbundle, with $v : \Omega \to C([-1,0],\mathbb{R}^{n_j})$ continuous and such that $v(\omega) \gg 0$ and $\|v(\omega)\| = 1$ for any $\omega \in \Omega$. In particular, $0 < v_i(\omega)(s) \leq 1$ for any $\omega \in \Omega$, any component $i = 1,\dots,n_j$ and any $s \in [-1,0]$.

Now, we follow the arguments used in Proposition 5.1 (iii) in Calzada et al. [4] in a quasi-periodic setting, which remain valid here. All the details are explained in that paper. For the norm $\|\varphi\|_2 = \left(\|\varphi(0)\|^2 + \int_{-1}^0 \|\varphi(s)\|^2\, ds\right)^{1/2}$ in the space $Y = L^2([-1,0],\mathbb{R}^{n_j},\mu_0)$ for the measure $\mu_0 = \delta_0 + l$, where δ_0 is the Dirac measure concentrated at 0 and l is the Lebesgue measure on $[-1,0]$, we consider the normalized functions $\widetilde{v}(\omega) = v(\omega)/\|v(\omega)\|_2$ and we recall that there is a $\delta > 0$ such that $\delta \leq \|v(\omega)\|_2$ for any $\omega \in \Omega$. Then, we consider the map $\widetilde{c}(t,\omega)$ satisfying $\Phi_j(t,\omega)\,\widetilde{v}(\omega) = \widetilde{c}(t,\omega)\,\widetilde{v}(\omega{\cdot}t)$ for any $t \geq 0$ and $\omega \in \Omega$, which can be extended to the whole line fulfilling the linear cocycle identity $\widetilde{c}(t+s,\omega) = \widetilde{c}(t,\omega{\cdot}s)\,\widetilde{c}(s,\omega)$ for any $t,s \in \mathbb{R}$ and any $\omega \in \Omega$. Besides, the expression $\widetilde{a}(\omega) = \frac{d}{dt}\log\widetilde{c}(t,\omega)\big|_{t=0}$ defines a continuous map on Ω. We remark that the L^2-norm has been taken in order to have nice differentiability properties on the scalar map $\log\widetilde{c}(t,\omega)$ associated with the continuous separation. Moreover, as shown in [4], the Lyapunov exponent of each $\omega \in \Omega$ can be calculated as

$$\lambda_j(\omega) = \limsup_{t \to \infty} \frac{\log\widetilde{c}(t,\omega)}{t}\,,$$

and arguing as in the proof of Theorem 3.5, in what refers to the application of the theory by Sacker and Sell [29], we can conclude that for any $\omega \in \Omega$, the upper

Lyapunov exponent $\lambda_j = \lambda_j(\omega)$, and so

$$\lambda_j = \lim_{t\to\infty} \frac{\log \widetilde{c}(t,\omega)}{t} = \lim_{t\to\infty} \frac{1}{t} \int_0^t (\log \widetilde{c}(s,\omega))' ds = \lim_{t\to\infty} \frac{1}{t} \int_0^t \widetilde{a}(\omega{\cdot}s)\, ds = \int_\Omega \widetilde{a}\, d\mu\,,$$

where μ is the unique ergodic measure on Ω and Birkhoff ergodic theorem has been applied to the map $\widetilde{a} \in C(\Omega)$ in the last equality.

As a consequence, since $\lambda_j = 0$, then $\widetilde{a} \in C(\Omega)$ has zero mean value and $\widetilde{c}(t,\omega)$ is the scalar linear cocycle giving the solutions $h(t,\omega,y_0) = y_0\,\widetilde{c}(t,\omega)$ ($y_0 \in \mathbb{R}$) of the family of recurrent scalar linear equations for $\omega \in \Omega$,

$$h'(t) = \widetilde{a}(\omega{\cdot}t)\, h(t)\,, \quad t \in \mathbb{R}\,. \tag{4.6}$$

Then, arguing as in Example 4.2, after the zero mean value of $\widetilde{a}$ we can deduce that there is an invariant set $\Omega_1 \subset \Omega$ of full measure formed by recurrent points at ∞. In particular, for any $\omega \in \Omega_1$, $\lim_{n\to\infty} \int_0^{t_n} \widetilde{a}(\omega{\cdot}s)\, ds = 0$ for a sequence $t_n \to \infty$. Since $\Phi_j(t,\omega)\,\widetilde{v}(\omega) = \widetilde{c}(t,\omega)\,\widetilde{v}(\omega{\cdot}t)$ for any $t \geq 0$ and $\omega \in \Omega$, we get that for each $\omega \in \Omega_1$, $\Phi_j(t_n,\omega)\,\alpha\,\widetilde{v}(\omega) = \widetilde{c}(t_n,\omega)\,\alpha\,\widetilde{v}(\omega{\cdot}t_n) \to \alpha\,\widetilde{v}(\omega{\cdot}t_n)$, as $n \to \infty$ for a sequence $t_n = t_n(\omega) \to \infty$ and for any $\alpha > 0$, which precludes the property of u-persistence for system (4.5), and consequently also for system (4.3) whenever $\omega \in \Omega_1$.

Besides, the set Ω_1 is also residual. To see it, note that the u-persistence of system (4.3) for ω_0 implies for the decoupled subsystem (4.5) that, for each $y_0 > 0$, given the initial map $y_0\,\widetilde{v}(\omega_0) \gg 0$, there is a $t_0 = t_0(y_0\,\widetilde{v}(\omega_0))$ such that $\Phi_j(t,\omega_0)\,y_0\,\widetilde{v}(\omega_0) = \widetilde{c}(t,\omega_0)\,y_0\,\widetilde{v}(\omega_0{\cdot}t) \geq \bar{m}$ for any $t \geq t_0$, for the map $\bar{m} \in C([-1,0],\mathbb{R}^{n_j})$ with all components identically equal to m. Therefore, for $\delta > 0$ such that $\delta \leq \|v(\omega)\|_2$ for any $\omega \in \Omega$, it holds that for any $t \geq t_0$,

$$\frac{1}{\delta}\, y_0\,\widetilde{c}(t,\omega_0) \geq y_0\,\widetilde{c}(t,\omega_0)\, \frac{v_i(\omega_0{\cdot}t)}{\|v(\omega_0{\cdot}t)\|_2} \geq m\,,$$

where any component of $v(\omega_0{\cdot}t)$ can been chosen. That is, $y_0\,\widetilde{c}(t,\omega_0) \geq m\,\delta$ for any $t \geq t_0$, and this is exactly u-persistence for the scalar linear equation (4.6) for ω_0, with eventual positive lower bound $m\,\delta$. Proposition 4.1 then asserts that $\lim_{t\to\infty} \int_0^t \widetilde{a}(\omega_0{\cdot}s)\, ds = \infty$, and in particular this means unbounded integral of $\widetilde{a}$ along the orbit of ω_0. This, together with the zero mean value of $\widetilde{a}$, permits to apply once more Theorem 3.7 in [14] to conclude that the set $\Omega_2 \subset \Omega$ composed by those ω for which the integral $\int_0^t \widetilde{a}(\omega{\cdot}s)\, ds$ has a strong oscillatory behaviour, in the precise terms explained in Example 4.2, is a residual set. To finish, since clearly $\Omega_2 \subset \Omega_1$, we conclude that Ω_1 is also a residual set. $\qquad\square$

Finally, we consider cooperative and sublinear systems. Since we are especially interested in systems which are modelling real world biological processes, it is quite natural to assume that 0 is a solution and that solutions starting with nonnegative initial data keep being nonnegative while defined. This is so if $f(t,0) = 0$ for any $t \in \mathbb{R}$ in the ODEs case and $f(t,0,0) = 0$ for any $t \in \mathbb{R}$ in the delay case, together with the cooperative condition. In this situation, uniform persistence is considered in the sense of (4.4) for an individual delay system, and in the sense of Definition 3.2 (i) for the induced families over the hull.

More precisely, we are assuming the following hypotheses either for system (2.2) $y'(t) = f(t,y(t))$ or for the delay system (2.3) $y'(t) = f(t,y(t),y(t-1))$.

(H1) The function f defining the system is uniformly almost periodic, it satisfies the regularity and admissibility conditions stated in Section 2, and the identically null map is a solution.

(H2) The system is cooperative and sublinear.

Recall that, under the assumption that 0 is a solution, if the system is cooperative and concave, it is also sublinear, so that this case is also included. Once more, we only write the result for delay equations.

Theorem 4.4. *Let us consider a finite-delay FDEs nonlinear system* (2.3) *under assumptions* (H1) *and* (H2) *and let τ be the monotone and sublinear skew-product semiflow of class $\mathcal{C}^1$ defined on $\Omega \times C_+([-1,0], \mathbb{R}^n)$ by the solutions $y(t, \omega, \varphi)$ of the family of systems over the hull* (2.5) $y'(t) = F(\omega \cdot t, y(t), y(t-1))$, $\omega \in \Omega$. *Then:*

(i) *The family of systems* (2.5) *is uniformly persistent if and only if the family of linearized systems along the null solution is uniformly persistent.*

(ii) *If system* (2.3) *is uniformly persistent, whereas the family of systems over the hull* (2.5) *is not uniformly persistent, then there exists an invariant, residual set $\Omega_1 \subset \Omega$ of full measure such that for any $\omega \in \Omega_1$, system* (2.5) *is not uniformly persistent.*

If we assume further that there exists a map $\varphi_0 \gg 0$ such that the solution $y(t, \varphi_0)$ of system (2.3) *with initial value φ_0 is bounded, then:*

(iii) *System* (2.3) *is uniformly persistent if and only if the family of systems* (2.5) *is uniformly persistent.*

(iv) *The uniform persistence of system* (2.3) *can be characterized by a set of computable Lyapunov exponents determined by the structure of its linearized system along* 0.

Proof. First of all, the same proof as that of Proposition 2.3 in [24] for 2-dimensional systems permits to conclude that the induced semiflow is globally defined.

(i) The transfer of the u-persistence from the linearized family to the nonlinear family is a direct consequence of Theorem 5.4 in [26] for general recurrent and cooperative systems. Conversely, one just applies a comparison of solutions argument having in mind the inequality (3.5) which also holds in the sublinear setting. More precisely, let us write down the family of linearized systems along the null solution, which is of the form (4.3) for the matrix-valued continuous maps on Ω defined by $A(\omega) = D_y F(\omega, 0, 0)$ and $B(\omega) = D_w F(\omega, 0, 0)$, where we have written $F = F(\omega, y, w)$. Then, $y_t(\omega, \varphi) \leq D_\varphi y_t(\omega, 0) \varphi$, for any $\omega \in \Omega$, $\varphi \geq 0$ and $t \geq 0$, and the functions $z(t, \omega, \varphi) = (D_\varphi y_t(\omega, 0) \varphi)(0)$ ($t \geq 0$) are precisely the solutions of the linearized family. Therefore, the u-persistence of the sublinear family below forces the u-persistence of the linearized family above.

(ii) As just mentioned, since the family over the hull (2.5) is not u-persistent, neither is u-persistent the associated family (4.3) of linearized systems along 0, described in (i). On the other hand, calling $\omega_0 = f \in \Omega$ the element providing the initial system (2.3), the u-persistence of system (2.3) implies that of the linearized system (4.3) for ω_0. Then, we can apply Theorem 4.3 to assert that there exists an invariant, residual set $\Omega_1 \subset \Omega$ of full measure such that for any $\omega \in \Omega_1$, system (4.3) is not u-persistent. Once more by the inequality in (i), this implies that neither is system (2.5) u-persistent for $\omega \in \Omega_1$, and we are done.

(iii) First of all, note that the existence of a bounded solution under the assumption of u-persistence of system (2.3) completely precludes the linear case. Now, as

it could not be otherwise, it is immediate that the u-persistence goes nicely from the family to a particular system.

Conversely, if system (2.3) is u-persistent we apply to τ the dynamical description developed in Núñez et al. [23] for general monotone and sublinear skew-product semiflows. Arguing as in the proof of Theorem 3.4 for Nicholson systems, for $\omega_0 = f$ we consider the orbit of (ω_0, φ_0) which is bounded. Then, one can consider its omega-limit set, which contains a minimal set K necessarily lying on the zone $\Omega \times \{\varphi \in C_+([-1, 0], \mathbb{R}^n) \mid \varphi \geq \bar{m}\}$, for the map $\bar{m}$ whose components are identically equal to m, the constant involved with the property of u-persistence of system (2.3). In other words, there is a strongly positive minimal set for τ. Thus, Theorem 3.8 in [23] asserts that the dynamics suits one the following three cases: the so-called case A1 when K is the unique minimal set strongly above 0; case A2 when there are infinitely many minimal sets strongly above 0 and, among them, there exists one K^- which is the lowest one; or case A3 when there are infinitely many minimal sets strongly above 0 but there is not a lowest one.

Exactly as in the proof of Theorem 3.4, case A3 is discarded thanks to the u-persistence of system (2.3), and in both cases A1 and A2 the family (2.5) turns out to be u-persistent, due to the attracting properties enjoyed by the minimal sets K and K^- respectively (see [23] for more details).

(iv) The statement of this item has not been written more precisely in order not to make the paper too long, but the reader is referred to Theorem 3.5 for a very detailed statement in the same line in the case of almost periodic Nicholson systems.

The key is in (i) and (iii) together, saying that the property of u-persistence for system (2.3) is equivalent to that of the family of systems (2.5) and also to that of the family of linearized systems along 0. Besides, for the associated linear family (4.3) described in (i), which is cooperative, the property of u-persistence has been characterized in terms of a precise set of upper Lyapunov exponents $\{\lambda_j \mid j \in I\}$, as it has been explained in detail in the proof of Theorem 4.3.

Once more, the theory by Sacker and Sell [29] applies to the 1-dimensional linear skew-product semiflow associated with the dynamics in the 1-dimensional invariant subbundle given by the continuous separation of L_j for each $j \in I$ (for L_j defined in the proof of Theorem 4.3). As a consequence, for each $j \in I$ the exponent $\lambda_j = \lambda_j(\omega)$ for any $\omega \in \Omega$, and in particular $\lambda_j = \lambda_j(\omega_0)$ for $\omega_0 = f$, the element providing the initial system (2.3). So that, in the end, the property of u-persistence is characterized in terms of a set of Lyapunov exponents of some lower-dimensional linear systems chosen from the structure of the linearized system along 0. $\square$

To end the paper, we make a couple of remarks. First, a more general recurrent time variation rather than almost periodicity may be admitted in the statement of Theorem 4.4 (i) and (iii), as we just need Ω to be minimal (for instance, see [22]). However, the unique ergodicity of Ω is also needed in both (ii) and (iv). Second and last, the fact that there exists a bounded solution is sometimes implicitly required in the literature by assuming the existence of an upper-solution (for instance, see Zhao [36] and Mierczyński and Shen [17]) or by asking the system to be dissipative.

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