

UNIFORM AND STRICT PERSISTENCE IN MONOTONE SKEW-PRODUCT SEMIFLOWS WITH APPLICATIONS TO NON-AUTONOMOUS NICHOLSON SYSTEMS

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ABSTRACT. We determine sufficient conditions for uniform and strict persistence in the case of skew-product semiflows generated by solutions of non-autonomous families of cooperative systems of ODEs or delay FDEs in terms of the principal spectrums of some associated linear skew-product semiflows which admit a continuous separation. Our conditions are also necessary in the linear case. We apply our results to a noncooperative almost periodic Nicholson system with a patch structure, whose persistence turns out to be equivalent to the persistence of the linearized system along the null solution.

1. INTRODUCTION

Different notions of persistence have been introduced and investigated in the mathematical theory of dynamical systems. Basically all of them mean that in the long run the trajectories of the system place themselves above a prescribed region of the phase space. In many practical applications this region is determined by a constant or null value of the state variables. In this last case persistence means that the solutions eventually become uniformly strongly positive. The dynamical theory of persistence has been extensively used in biological population dynamics, ecology, epidemiology, chemical reactions, game theory, neural networks and other important areas of applied sciences and engineering. The references Anderson [2], Bonneuil [3], Butler and Wolkowicz [4], Calzada *et al.* [5], Cantrell and Cosner [6], Craciun *et al.* [7], Hale and Waltman [19], Hofbauer and Sigmund [22], Johnston *et al.* [25], Smith and Thieme [49] and Takeuchi [50] illustrate some of the classical and also more recent applications of the mentioned theory in these fields.

The presence and consequences of persistence in dynamical systems have been broadly investigated in the literature using topological methods, Lypunov functions, comparison methods, Morse decompositions, invariant splitting, Lyapunov exponents and computational methods, among other techniques. The papers by Faria and Röst [12], Freedman and Ruan [15], Garay and Hofbauer [16], Hetzer and Shen [20], Hirsch *et al.* [21], Langa *et al.* [26], Magal and Zhao [28], Mierczyński and Shen [30], Mierczyński *et al.* [31], Novo *et al.* [36], Salceanu and Smith [43], Schreiber [44, 45], Thieme [51, 52], Wang and Zhao [54], and references therein, provide a long but not complete list of works on this topic.

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The objective of this paper is to continue the study of the dynamical theory of persistence in monotone skew-product semiflows generated by non-autonomous differential equations, initiated in Novo *et al.* [36], as well as to show the applicability of this theory in the description of some mathematical models widely investigated in the literature, which are locally cooperative in small regions of the phase space. In particular we give a complete characterization of persistence for non-autonomous n -dimensional Nicholson systems with a patchy structure, which are able to model the temporal changes of the environment.

We investigate relevant properties of non-autonomous dynamical systems by using the skew-product formalism. The phase space is a product space $\Omega \times X$, where the base Ω is a compact metric space under the action of a continuous flow $\sigma : \mathbb{R} \times \Omega \rightarrow \Omega$, $(t, \omega) \mapsto \omega \cdot t$, and the state space X is a strongly ordered Banach space with a normal positive cone. The skew-product semiflow is defined by $\tau : \mathbb{R}_+ \times \Omega \times X \rightarrow \Omega \times X$, $(t, \omega, x) \mapsto (\omega \cdot t, u(t, \omega, x))$, where the map u satisfies the usual semicycle identity, it is monotone on some region of the phase space and smooth with respect to the state component x . We frequently assume that the base flow is minimal, *i.e.*, that all the trajectories on Ω are dense. In particular, this formalism permits to carry out a dynamical study of solutions of non-autonomous differential equations in which the temporal variation of the vector field is almost periodic, almost automorphic, or more in general, recurrent. The papers by Chow and Leiva [8, 9], Johnson *et al.* [23], Johnson *et al.* [24], Sacker and Sell [41, 42], Novo and Obaya [34], Novo *et al.* [35], Poláčik and Tereščák [39], Shen and Yi [47] and Yi [55] contain the main mathematical ingredients required to follow the contents of this work.

We introduce natural definitions of uniform and strict persistence which become relevant in applications. Both definitions agree with the concept of uniform (strong) ρ -persistence in the terms of Smith and Thieme [49] for an adequate choice of the map $\rho : X \rightarrow \mathbb{R}_+$. We develop part of the methods mentioned above to investigate the presence of persistence in non-autonomous and (globally or locally) cooperative families of ordinary differential equations (ODEs for short) and delay functional differential equations (FDEs for short) with finite delay. The study and applications of this theory to non-autonomous families of parabolic partial differential equations (PDEs for short) will be included in a forthcoming publication.

The concept of continuous separation plays a fundamental role in the main conclusions of this theory. The classical notion of continuous separation, which we also call continuous separation of type I, was introduced by Poláčik and Tereščák [39] and Shen and Yi [47] in a context valid for cooperative families of linear ODEs and parabolic PDEs. Recently, Novo *et al.* in [35] came up with the more general concept of a continuous separation of type II, which also applies in a context of cooperative families of linear delay FDEs with finite delay. In this paper, whenever we say that there is a continuous separation, we mean that there is a continuous separation either of type I or of type II. In any of the cases, to the continuous separation one associates the principal spectrum, which is the Sacker-Sell spectrum or dynamical spectrum of the one-dimensional dominant subbundle.

In [36] Novo *et al.* investigate the presence of uniform persistence in the areas situated strongly above (or below) a minimal set K of the phase space of a non-autonomous family of cooperative differential equations. It is proved that after a convenient permutation of the variables, the coefficient matrix (or matrices in the

delay case) of the linearized semiflow over K has a block lower triangular structure such that the linear semiflows generated by the lower-dimensional diagonal blocks admit a continuous separation. In this situation, a sufficient condition for the property of uniform persistence is given in terms of the principal spectrums of an adequate subset of such systems. In the present work we complete important aspects of the theory of persistence in monotone skew-product semiflows. We show that the given condition for uniform persistence is actually also a necessary condition in the linear case, so that the property of uniform persistence is completely characterized in this case. When we introduce the notion of strict persistence in the region situated above (or below) a minimal set K , the same strategy as before leads to an efficient characterization of the presence of this type of persistence in terms of the principal spectrums of a second subset of the family of linear semiflows generated by the lower-dimensional diagonal blocks of the linearized equations over K . It is important to mention that although the results obtained for uniform and strict persistence share a common organization, the arguments required for the proofs of the main results are quite different.

Let us finally explain the structure of the paper. After including some preliminaries in Section 2, Section 3 is dedicated to the general abstract setting of a monotone skew-product semiflow under the main assumption of the existence of a continuous separation for the semiflow itself in the linear case, or for the linearized semiflow over a minimal set K in the nonlinear case. Uniform persistence and strict persistence are characterized in the linear case in terms of the principal spectrum. Besides, these two properties are seen to be equivalent if the continuous separation is of type I. In the nonlinear case we offer a first approximation result for uniform and strict persistence above a minimal set K .

In Section 4 we consider monotone skew-product semiflows generated by cooperative families of ODEs. By rearranging the linearized systems over a minimal set K so that the associated block diagonal lower-dimensional subsystems have a continuous separation, we prove the afore-mentioned sufficient condition for strict persistence above the minimal set K and we check that it is also a necessary condition in the linear case. Again, a first approximation result is given, so that persistence in the nonlinear case can be studied through linearization. The same outline fits Section 5, which deals with finite delay FDEs. Nevertheless, there is an important issue in this context, as continuous separations are of type II. Because of that, the notion of strict persistence, still keeping its dynamical meaning, needs to be technically modified into what we have called strict persistence at 0.

To finish, in Section 6 we want to emphasize the applicability of our theory to systems modelling real processes. We have focused on Nicholson systems for a species on an heterogeneous environment giving rise to patches in the model. In this case we prove that uniform or strict persistence at 0 for the nonlinear noncooperative model turns out to be equivalent to uniform or strict persistence at 0, respectively, for the linearized system along the null solution. The good thing is that the linear equations are cooperative, so that our methods can be applied, giving a complete spectral characterization of the dynamical properties of persistence.

2. SOME PRELIMINARIES

In this section we include some preliminaries of topological dynamics. Let (Ω, d) be a compact metric space. A real *continuous flow* $(\Omega, \sigma, \mathbb{R})$ is defined by a continuous map $\sigma : \mathbb{R} \times \Omega \rightarrow \Omega$, $(t, \omega) \mapsto \sigma(t, \omega)$ satisfying

- (i) $\sigma_0 = \text{Id}$,
- (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.

Let $\mathbb{R}_+ = \{t \in \mathbb{R} \mid t \geq 0\}$. 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

$$\begin{aligned} \tau : \mathbb{R}_+ \times \Omega \times X &\longrightarrow \Omega \times X \\ (t, \omega, x) &\longmapsto (\omega \cdot t, u(t, \omega, x)) \end{aligned} \quad (2.1)$$

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) $\tau_0 = \text{Id}$,
- (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 semicycle property,

$$u(t+s, \omega, x) = u(t, \omega \cdot s, u(s, \omega, x)) \quad \text{for } s, t \geq 0 \text{ and } (\omega, x) \in \Omega \times X. \quad (2.2)$$

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 $(K, \tilde{\tau}, \mathbb{R})$ such that $\tilde{\tau}(t, \omega, x) = \tau(t, \omega, x)$ for all $(\omega, x) \in K$ and $t \in \mathbb{R}_+$.

The reader can find in Ellis [10], Sacker and Sell [41], Shen and Yi [47] and references therein, a more in-depth survey on topological dynamics.

In this work we will work under some differentiability assumptions. More precisely, 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 $z \in X$, $\lim_{t \rightarrow 0^+} u_x(t, \omega, x)z = z$ 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 ,

$$\begin{aligned} L : \mathbb{R}_+ \times K \times X &\longrightarrow K \times X \\ (t, (\omega, x), z) &\longmapsto (\tau(t, \omega, x), u_x(t, \omega, x)z). \end{aligned} \quad (2.3)$$

We note that u_x satisfies the linear semicycle property

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

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

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

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

3. UNIFORM AND STRICT PERSISTENCE IN ABSTRACT MONOTONE SKEW-PRODUCT SEMIFLOWS WITH A CONTINUOUS SEPARATION

In this section, we analyze the notions of uniform and strict persistence in a very general context of monotone skew-product semiflows, but under the main assumption that there is a continuous separation. Although this may seem rather restrictive at first sight, it turns out to be really enough when aiming at characterizing persistence in the broad context of skew-product semiflows generated by non-autonomous differential equations with a recurrent behavior in time, as we will see in the next sections.

So, let us consider a continuous skew-product semiflow τ (2.1) which is defined over a minimal base flow $(\Omega, \sigma, \mathbb{R})$ and a Banach space X , and it is of class \mathcal{C}^1 in x . We also assume that X is a strongly ordered Banach space, that is, there is a closed convex solid cone (*i.e.*, a nonempty closed subset $X_+ \subset X$ satisfying $X_+ + X_+ \subset X_+$, $\mathbb{R}_+ X_+ \subset X_+$ and $X_+ \cap (-X_+) = \{0\}$) with nonempty interior. Then, a (partial) *strong order relation* on X is defined by

$$\begin{aligned} x \leq y &\iff y - x \in X_+; \\ x < y &\iff y - x \in X_+ \text{ and } x \neq y; \\ x \ll y &\iff y - x \in \text{Int } X_+. \end{aligned}$$

Besides, the positive cone is assumed to be *normal* or, equivalently, the norm of the Banach space X is *semimonotone*, *i.e.*, there is a positive constant $l > 0$ such that $\|x\| \leq l \|y\|$ whenever $0 \leq x \leq y$. A norm on X is *monotone* if $l = 1$. One can assume without loss of generality that the norm is monotone, as with a normal cone there is always an equivalent norm which is monotone (see Amann [1] for more details).

The order structure in the state space X permits to introduce the concept of monotone semiflow: the skew-product semiflow (2.1) is *monotone* if

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

Note that, if the semiflow τ is monotone and it is also \mathcal{C}^1 in x , then the differential operators $u_x(t, \omega, x)$ turn out to be *positive*, in the sense that given $t \geq 0$ and $(\omega, x) \in \Omega \times X$, $u_x(t, \omega, x)z \geq 0$ whenever $z \geq 0$. Besides, strongly ordered initial states give rise to strongly ordered semiorbits, that is, if $\omega \in \Omega$ and $x \ll y$, then $u(t, \omega, x) \ll u(t, \omega, y)$ for any $t \geq 0$ (see Proposition 3.4 in Núñez *et al.* [38]). The operator $u_x(t, \omega, x)$ is said to be *strongly positive* if $u_x(t, \omega, x)z \gg 0$ whenever $z > 0$.

We now recall the notion of uniform persistence for a monotone skew-product semiflow based on the properties of the order, in the region situated strongly above a compact τ -invariant set K , as already defined in Novo *et al.* [36], and then introduce

the concept of strict persistence. When $K = \Omega \times \{0\}$ our definition of uniform persistence agrees with Definition 3.1 of uniform persistence given in Mierczyński *et al.* [31] or with Definition 3.1 of uniform (strong) ρ -persistence in Smith and Thieme [49] for an adequate ρ depending on the space X . Also our notion of strict persistence can be seen as uniform (strong) ρ -persistence for a precise ρ on each case. Although here we give the definitions and results for the region situated above a compact τ -invariant set, the parallel definitions and results can be easily stated for the region situated below that set.

Definition 3.1. Let τ be a continuous monotone skew-product semiflow defined on $\Omega \times X$, and let $K \subset \Omega \times X$ be a compact τ -invariant set. The semiflow τ is said to be *uniformly persistent* (*u-persistent* for short) in the region situated *strongly above* K if there exists a $z_0 \gg 0$ such that for any $(\omega, x) \in K$ and any $y \gg x$ there exists a time $t_0 = t_0(\omega, x, y)$ such that $u(t, \omega, y) \geq u(t, \omega, x) + z_0$ for any $t \geq t_0$.

Again for monotone skew-product semiflows, here we have the definition of strict persistence in the area situated above K .

Definition 3.2. Let τ be a continuous monotone skew-product semiflow defined on $\Omega \times X$, and let $K \subset \Omega \times X$ be a compact τ -invariant set. The semiflow τ is said to be *strictly persistent* (*s-persistent* for short) in the region situated above K if there exists a collection of strictly positive vectors $e_1, \dots, e_m \in X$, $e_i > 0$ for every i , such that for any $(\omega, x) \in K$ and any $y > x$ there exists a time $t_0 = t_0(\omega, x, y)$ such that $u(t, \omega, y) \geq u(t, \omega, x) + e_i$ for any $t \geq t_0$ for one of the vectors e_1, \dots, e_m .

Note that the two concepts of uniform and strict persistence are not directly related to one another: on the one hand the set of starting vectors for which a determined forward behavior is to be expected is different, as we look at vectors situated strongly above K in the uniform case, whereas we consider the whole area above K in the strict case; on the other hand the expected forward behavior is also different in each case.

The first result we give is stated for a general continuous linear monotone skew-product semiflow over a minimal base flow (K, \cdot, \mathbb{R}) and a strongly ordered Banach space X ,

$$\begin{aligned} L : \mathbb{R}_+ \times K \times X &\longrightarrow K \times X \\ (t, \theta, v) &\longmapsto (\theta \cdot t, \Phi(t, \theta) v), \end{aligned} \quad (3.1)$$

which satisfies that for each $t > 0$ the map $K \rightarrow \mathcal{L}(X)$, $\theta \mapsto \Phi(t, \theta)$ is continuous. In this situation $\Phi(t, \theta)$ is a linear semicyclole, that is,

$$\Phi(t + s, \theta) = \Phi(t, \theta \cdot s) \Phi(s, \theta), \quad s, t \in \mathbb{R}_+, \theta \in K.$$

We need to recall the definitions of a continuous separation in the classical terms of Poláčik and Tereščák [39] in the discrete case, generalized by Shen and Yi [47] to the continuous case, and of a continuous separation of type II in the terms introduced by Novo *et al.* [35]. In the literature one can sometimes find names such as dominant splitting or exponential separation referring to this concept too.

Definition 3.3. (i) The linear monotone skew-product semiflow (3.1) is said to admit a *continuous separation* if there are families of subspaces $\{X_1(\theta)\}_{\theta \in K}$ and $\{X_2(\theta)\}_{\theta \in K} \subset X$ satisfying the following properties:

- (S1) $X = X_1(\theta) \oplus X_2(\theta)$ and $X_1(\theta)$, $X_2(\theta)$ vary continuously in K ;
- (S2) $X_1(\theta) = \text{span}\{v(\theta)\}$, with $v(\theta) \gg 0$ and $\|v(\theta)\| = 1$ for any $\theta \in K$;

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

(S4) for any $t > 0$, $\theta \in K$,

$$\Phi(t, \theta)X_1(\theta) = X_1(\theta \cdot t),$$

$$\Phi(t, \theta)X_2(\theta) \subset X_2(\theta \cdot t);$$

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

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

(ii) 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 $\theta \in K$ there is a $z \in X_2(\theta)$ with $z > 0$, then $\Phi(t, \theta)z = 0$ for any $t \geq T$.

(iii) Given a monotone semiflow (2.1) of class \mathcal{C}^1 for which there exists a compact positively invariant set K , we say that K admits a continuous separation if L , the linearized skew-product semiflow over K (2.3), does.

In this paper, whenever we say that there is a continuous separation, we mean that there is a continuous separation either of the classical type or of type II. The continuous variation of the subspaces $X_1(\theta)$ and $X_2(\theta)$ for $\theta \in K$ stated in (S1) means precisely the following: the continuity of the map $K \rightarrow X_+$, $\theta \mapsto v(\theta)$, for the vectors $v(\theta)$ given in (S2); and the fact that for each $\theta \in K$, $X_2(\theta) = \ker(l_\theta)$ for certain $l_\theta \in X_+^*$, the cone of positive functionals in the dual space of X , with $\|l_\theta\| = 1$ and such that the map $K \rightarrow X_+^*$, $\theta \mapsto l_\theta$ is continuous (see [39], [47] for the case of a classical continuous separation, and [35] for the case of a continuous separation of type II). Besides, in any of the cases, because of properties (S2) and (S4) we can write

$$\Phi(t, \theta)v(\theta) = c(t, \theta)v(\theta \cdot t) \quad (3.2)$$

for a certain real coefficient $c(t, \theta)$ for each $t > 0$ and $\theta \in K$, which is well-known to be positive. Note also that, by taking $c(0, \theta) = 1$ and $c(-t, \theta) = 1/c(t, \theta \cdot (-t))$ for any $t > 0$ and $\theta \in K$, we actually have a linear skew-product flow over the one-dimensional invariant subbundle

$$\bigcup_{\theta \in K} \{\theta\} \times X_1(\theta), \quad (3.3)$$

that is, c satisfies the linear cocycle relation $c(t + s, \theta) = c(t, \theta \cdot s)c(s, \theta)$ for any $t, s \in \mathbb{R}$ and any $\theta \in K$, and this linear skew-product flow can be seen as a flow extension of the restriction of the linear semiflow L to the previous one-dimensional subbundle. Besides, the Lyapunov exponents $\lambda(\theta)$ of the points $\theta \in K$ are just given by

$$\lambda(\theta) = \limsup_{t \rightarrow \infty} \frac{\log c(t, \theta)}{t}.$$

Following Mierczyński and Shen [29], whenever a linear semiflow admits a continuous separation, its *principal spectrum* Σ_p is defined as the dynamical spectrum (Sacker-Sell spectrum or dichotomy spectrum, see [41, 42]) of the restriction of L to the one-dimensional invariant subbundle (3.3), and is thus a compact interval of the real line which might well reduce to a point. The reader is referred to [36] for further details. We are now in a position to state the main result in this section.

Theorem 3.4. *Let us consider a continuous linear monotone skew-product semiflow L (3.1) over a minimal flow (K, \cdot) which admits a continuous separation. Then:*

- (i) *The linear semiflow is uniformly persistent in the region situated strongly above $K \times \{0\}$ if and only if the principal spectrum is contained in the positive real semi-axes, that is, $\Sigma_p \subset (0, \infty)$.*
- (ii) *If the linear semiflow is strictly persistent in the region above $K \times \{0\}$, then $\Sigma_p \subset (0, \infty)$. In this case, the converse implication is true provided that the continuous separation is of classical type.*

Proof. First of all, let us consider the scalar linear flow given by the restriction of L to the one-dimensional invariant subbundle (3.3) given by the continuous separation, $\pi : \mathbb{R} \times K \times \mathbb{R} \rightarrow K \times \mathbb{R}$, $(t, \theta, r) \mapsto (\theta \cdot t, c(t, \theta) r)$ where c is the map in (3.2) determined by the continuous separation. In any of the two cases, the property of persistence of L is inherited by π as u-persistence in the region situated strongly above $K \times \{0\} \subset K \times \mathbb{R}$. To see it, assume that we are in the case of u-persistence and just take the vector $z_0 \gg 0$ given in Definition 3.1 and consider $\varepsilon_0 = \|z_0\| > 0$. Then, given any $\theta \in K$ and any $r > 0$, associated to the vector $r v(\theta) \gg 0$ there is a t_0 such that $\Phi(t, \theta) r v(\theta) = r c(t, \theta) v(\theta \cdot t) \geq z_0$ for any $t \geq t_0$. By the monotonicity of the norm, then $c(t, \theta) r \geq \varepsilon_0$ for any $t \geq t_0$ and there is u-persistence. In the case of s-persistence of L just argue in a similar way and take $\varepsilon_0 = \min\{\|e_1\|, \dots, \|e_m\|\} > 0$ for the vectors given in Definition 3.2.

Now, note that this precludes the existence of a bounded nontrivial trajectory for the scalar flow π : if there was one, let it be the orbit of (θ_0, r_0) for certain $\theta_0 \in K$ and $r_0 > 0$, and take $m = \sup_{t \geq 0} c(t, \theta_0) r_0$. In this situation the second component of the semiorbit of $(\theta_0, \varepsilon_0 r_0 / 2m)$ would never overpass ε_0 as t goes to ∞ , in contradiction with the u-persistence proved in the previous paragraph. According to a result by Selgrade [46] (see also [40]), then the linear flow π admits an exponential dichotomy and then, by the definition of the Sacker-Sell spectrum, $0 \notin \Sigma_p$.

Finally, since Σ_p is a compact interval of the real line, it can only be contained in $(0, \infty)$, as negative Lyapunov exponents lead to contradiction with the u-persistence of π , as before. With this we have proved the first implication in both items.

To conclude the proof of (i), note that the fact that $\Sigma_p \subset (0, \infty)$ implies that the linear semiflow is u-persistent in the region situated strongly above $K \times \{0\}$ is a consequence of Theorem 4.5 in [36] applied to the linear semiflow itself.

As for (ii), if $\Sigma_p \subset (0, \infty)$, by (i) there is u-persistence in the area strongly above $K \times \{0\}$. Let us see that the vector $z_0 \gg 0$ given in Definition 3.1 gives the property of s-persistence too. So, take $\theta \in K$ and $x > 0$. According to Remark 3.6 in [35], when the continuous separation is of classical type, there exists a $T = T(\theta, x) > 0$ such that $\Phi(T, \theta) x \gg 0$. Then, by the u-persistence there exists a time $t_0 > 0$ such that $\Phi(t, \theta \cdot T) \Phi(T, \theta) x = \Phi(t + T, \theta) x \geq z_0$ for any $t \geq t_0$, that is, $\Phi(t, \theta) x \geq z_0$ for any $t \geq T + t_0$, and s-persistence holds. The proof is finished. \square

After this first result, we want to emphasize two facts. First, that when the linear semiflow has a classical continuous separation, the notions of uniform persistence in the area strongly above $K \times \{0\}$ and strict persistence in the area above $K \times \{0\}$ turn out to be equivalent. Second, that when there is a continuous separation of type II, property (S3)' precludes the strict persistence of the semiflow in the region

above $K \times \{0\}$, as for some $\theta \in K$ and some $z > 0$, $\Phi(t, \theta)z = 0$ from some time on.

Now, for a general monotone \mathcal{C}^1 skew-product semiflow for which there is a minimal set with a continuous separation, we have the following result.

Theorem 3.5. *Let us assume that $K \subset \Omega \times X$ is a minimal set with a flow extension for the monotone \mathcal{C}^1 skew-product semiflow τ on $\Omega \times X$ and assume further that K admits a continuous separation.*

Then, if the linearized semiflow over K is uniformly persistent in the area situated strongly above $K \times \{0\}$:

- (i) τ is uniformly persistent in the area situated strongly above K .
- (ii) Provided that the continuous separation is of classical type, τ is strictly persistent in the area situated above K .

Proof. Let Σ_p be the principal spectrum of K . To see (i), first apply Theorem 3.4 (i) to obtain that $\Sigma_p \subset (0, \infty)$ and then apply Theorem 4.5 in [36].

As for (ii), the key is to see that, if $(\omega, x) \in K$ and $y > x$, then for some $T > 0$, $u(T, \omega, y) \gg u(T, \omega, x)$, as then the u-persistence and the cocycle property (2.2) solve the problem, in such a way that the vector $z_0 \gg 0$ given in Definition 3.1 gives the property of s-persistence too. So, take $(\omega, x) \in K$ and $y > x$. Recall that because of monotonicity the differential operators are all positive. If the continuous separation is classical, Remark 3.6 in [35] says that there exists a $T > 0$ such that $u_x(T, \omega, x)(y - x) \gg 0$. Now, by continuity, for some $\varepsilon > 0$ we have that $u_x(T, \omega, sy + (1 - s)x)(y - x) \gg 0$ for any $s \in [0, \varepsilon]$, and as a consequence,

$$u(T, \omega, y) - u(T, \omega, x) = \int_0^1 u_x(T, \omega, sy + (1 - s)x)(y - x) ds \gg 0,$$

as we wanted to see. The proof is finished. \square

4. UNIFORM AND STRICT PERSISTENCE IN COOPERATIVE RECURRENT NON-AUTONOMOUS ODES

Even if the results in the previous section are not applicable when there is not a continuous separation, yet they turn out to be really useful in any case provided that the semiflow is induced by solutions of non-autonomous cooperative systems of differential equations with a recurrent variation in time. In this context, the key point lies on the fact that one can restructure the linearized semiflow by means of a block lower triangular form where there is a continuous separation for the lower-dimensional systems given by the diagonal blocks. It is for this reason, together with the applications to real problems, that the study of the properties of persistence for skew-product semiflows induced by solutions of non-autonomous differential equations is specially rich and important.

In this section we concentrate on non-autonomous ODEs, whereas Section 5 will deal with delay FDEs. In the ODEs context we give a spectral characterization of strict persistence in the linear case, which results in sufficient conditions for the nonlinear case. In the delay context, the same will be done but with a slight technical modification: the definition of strict persistence at 0 and the necessity of this will be explained in detail in the next section.

Though the general systems we study are already stated in [36], we include them here for the sake of completeness. The concept of admissibility plays a fundamental

role in the description of the systems of equations we work with. 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 $\mathbb{R} \times K$.

We consider n -dimensional systems of ODEs given by a function $f: \mathbb{R} \times \mathbb{R}^n \rightarrow \mathbb{R}^n$ of class C^1 with respect to y , such that f and its first order derivatives $\partial f / \partial y_i$, $i = 1, \dots, n$ are admissible,

$$y'(t) = f(t, y(t)), \quad t \in \mathbb{R}. \quad (4.1)$$

To fall into the field of non-autonomous dynamical systems, we build Ω , the *hull* of f , that is, the closure in the compact-open topology of the set of mappings $\{f_t \mid t \in \mathbb{R}\}$ with $f_t(s, y) = f(t + s, y)$ for $s \in \mathbb{R}$ and $y \in \mathbb{R}^n$. The translation map $\mathbb{R} \times \Omega \rightarrow \Omega$, $(t, \omega) \mapsto \omega \cdot t$ given by $\omega \cdot t(s, y) = \omega(s + t, y)$ defines a continuous flow σ on the compact metric space Ω . We assume f to be *recurrent*, meaning that the flow on Ω is minimal. This happens for instance whenever f is periodic or almost periodic in t . Each function $\omega \in \Omega$ has the same regularity and admissibility properties as those of f , and $F: \Omega \times \mathbb{R}^n \rightarrow \mathbb{R}^n$, $(\omega, y) \mapsto \omega(0, y)$ can be looked at as the unique continuous extension of f to its hull. Thus, we can consider the family of n -dimensional systems over the hull, which we write for short as:

$$y'(t) = F(\omega \cdot t, y(t)), \quad \omega \in \Omega. \quad (4.2)$$

This family includes the initial system for $\omega = f$. Note that if we are given a family of equations such as (4.2) for a continuous function $F: \Omega \times \mathbb{R}^n \rightarrow \mathbb{R}^n$, F is said to be admissible if for each fixed $\omega \in \Omega$ the map F evaluated along the orbit of ω is admissible.

The solutions of the former family induce a dynamical system of skew-product type (2.1) (in principle only locally-defined) on the product $\Omega \times X$ where X is taken to be \mathbb{R}^n endowed with the norm $\|x\| = |x_1| + \dots + |x_n|$ for $x \in \mathbb{R}^n$. The strong partial order in \mathbb{R}^n is defined componentwise:

$$\begin{aligned} x \leq y &\iff x_i \leq y_i \quad \text{for } i = 1, \dots, n, \\ x < y &\iff x \leq y \quad \text{and} \quad x_j < y_j \quad \text{for some } j \in \{1, \dots, n\}, \\ x \ll y &\iff x_i < y_i \quad \text{for } i = 1, \dots, n. \end{aligned}$$

The positive cone X_+ is given by those $x \geq 0$, it is normal and its (nonempty) interior is the set of strongly positive vectors $x \gg 0$.

To get into the framework of monotone dynamical systems, we impose a cooperative condition on the initial systems, which, under the imposed regularity assumptions, is the following.

Definition 4.1. System (4.1) is *cooperative* if at any $(t, y) \in \mathbb{R} \times \mathbb{R}^n$,

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

From now on we will work with non-autonomous cooperative families of ODEs which generate a monotone skew-product flow and for which there exists a minimal set K . This happens, for instance, when there exists a bounded solution of the initial system, for then one can build the corresponding ω -limit set, which necessarily contains a minimal set. Although we will assume, without any further mention, that the semiflow is globally defined in the area situated above K , keep in mind that this detail is to be checked whenever a concrete model is considered.

In the next results we will need to restructure the linearized systems over a minimal set by means of a block lower triangular form with associated irreducible diagonal blocks, as already done in [36]. For that, let us recall that it is well-known (for instance, see Fiedler [13]) that after an adequate simultaneous permutation of rows and columns any square $n \times n$ -matrix A can be transformed into a block lower triangular matrix whose diagonal blocks, $\bar{A}_{11}, \dots, \bar{A}_{kk}$ of size n_1, \dots, n_k respectively ($n_1 + \dots + n_k = n$), are irreducible:

$$PAP^T = \begin{bmatrix} \bar{A}_{11} & 0 & 0 & \dots & 0 \\ \bar{A}_{21} & \bar{A}_{22} & 0 & \dots & 0 \\ \bar{A}_{31} & \bar{A}_{32} & \bar{A}_{33} & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \bar{A}_{k1} & \bar{A}_{k2} & \bar{A}_{k3} & \dots & \bar{A}_{kk} \end{bmatrix}, \quad (4.3)$$

where P is the row-permutation matrix. The case in which the matrix is irreducible is included when $k = 1$. Recall that a real $n \times n$ -matrix $A = [a_{ij}]$ is *irreducible* if for any nonempty proper subset $I \subset \{1, \dots, n\}$ there are $i \in I$ and $j \in \{1, \dots, n\} \setminus I$ such that $a_{ij} \neq 0$.

In Theorem 5.4 in [36] conditions for the property of uniform persistence in the ODEs case are given. In this paper we now study the case of strict persistence, which requires a new criterion to be determined and new techniques to write the proof. We now state and prove the result giving a condition for strict persistence in terms of the principal spectrums of some associated linear systems of lower dimension which have a continuous separation. We include the result on uniform persistence proved in Theorem 5.4 in [36] for the sake of completeness.

Theorem 4.2. *Consider a cooperative system (4.1) of ODEs with $f(t, y)$ recurrent, of class \mathcal{C}^1 in y and such that f and $\partial f / \partial y_i$, $i = 1, \dots, n$ are all admissible, and assume that $K \subset \Omega \times \mathbb{R}^n$ is a minimal set for the flow τ defined on $\Omega \times \mathbb{R}^n$ generated by the solutions of the associated family (4.2). For each $(\omega, x) \in K$ consider the linearized system of (4.2) along the orbit of (ω, x) ,*

$$z'(t) = D_y F(\omega \cdot t, u(t, \omega, x)) z(t) = [a_{ij}(\tau(t, \omega, x))] z(t), \quad (4.4)$$

and assume, without loss of generality, that the matrix $\bar{A} = [\bar{a}_{ij}]$ defined as

$$\bar{a}_{ij} = \sup_{(\omega, x) \in K} a_{ij}(\omega, x), \quad \text{for } i \neq j, \quad (4.5)$$

and $\bar{a}_{ii} = 0$, has the block lower triangular form (4.3). For each $j = 1, \dots, k$, let L_j be the linear skew-product flow on $K \times \mathbb{R}^{n_j}$ induced by the solutions of the linear systems given by the corresponding diagonal block of (4.4),

$$z'(t) = A_{jj}(\tau(t, \omega, x)) z(t), \quad (\omega, x) \in K, \quad (4.6)$$

which admits a continuous separation (of classical type), and let Σ_p^j be its principal spectrum.

If $k = 1$, i.e., if the matrix \bar{A} is irreducible, let $I = J = \{1\}$. Else, let

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

that is, I is composed by the indexes j such that any other block in the row of \bar{A}_{jj} is null, whereas J contains those indexes j such that any other block in the column of \bar{A}_{jj} is null. The conditions for uniform and strict persistence are the following:

- (i) If $\Sigma_p^j \subset (0, \infty)$ for any $j \in I$, then τ is uniformly persistent in the area situated strongly above K .
- (ii) If $\Sigma_p^j \subset (0, \infty)$ for any $j \in J$, then τ is strictly persistent in the area situated above K .

Proof. First of all, note that if the matrix \bar{A} was not in the form given in (4.3), a change of variables in the system $\tilde{z} = Pz$, which just permutes the variables, would take it to the required structure. Note also that $\bar{a}_{ij} \geq 0$ by the cooperative condition.

As already commented before, (i) is part of Theorem 5.4 in [36].

To make the proof of (ii) simpler, let us distinguish some cases.

(C1): $k = 1$, that is, \bar{A} is an irreducible matrix. In this case, Theorem 4.4 in [35] says that K admits a continuous separation of classical type. Then, a combination of Theorem 3.4 and Theorem 3.5 implies that there hold both u-persistence and s-persistence. Besides, as commented in the proof of the second result, the vector $z_0 \gg 0$ given in Definition 3.1 gives the property of s-persistence too.

Before we distinguish any further cases, let us carry out some general preliminary arguments which we will use when $k > 1$. Then, we have a general decomposition (4.3) for the matrix \bar{A} with k irreducible diagonal blocks of size n_1, \dots, n_k , respectively. As in case (C1), it is precisely the irreducible character of the diagonal blocks which implies that each linear semiflow L_j admits a continuous separation of classical type. For any vector or map v , let us denote $v^j = (v_i)_{i \in I_j}$, where I_j is the set formed by the n_j indexes corresponding to the rows of the block \bar{A}_{jj} , that is, $I_j = \{n_1 + \dots + n_{j-1} + 1, \dots, n_1 + \dots + n_j\}$.

Now, let us fix $j \in J$. As the following first argument is exactly the same in all the cases, let us assume for the sake of simplicity of writing that $1 < j < k$ and let us consider the family of n_j -dimensional systems of ODEs over the base flow K , given for each $(\omega, x) \in K$ by

$$(y^j)'(t) = F^j(\omega \cdot t, u^1(t, \omega, x), \dots, y^j(t), \dots, u^k(t, \omega, x)),$$

whose solutions generate a skew-product flow on $K \times \mathbb{R}^{n_j}$, which we write as $\tilde{\tau}(t, \omega, x, v) = (\tau(t, \omega, x), \tilde{u}(t, \omega, x, v))$. There exists a trivial minimal set for this flow, which is

$$K_1 = \text{cls}\{(\omega_0 \cdot t, u(t, \omega_0, x_0), u^j(t, \omega_0, x_0)) \mid t \geq 0\},$$

for a certain fixed $(\omega_0, x_0) \in K$. Besides, when we calculate the linearized equations along the orbit of (ω, x, x^j) , for $(\omega, x) \in K$, the system we obtain is exactly (4.6), which has irreducible associated matrix \bar{A}_{jj} , so that the induced linear semiflow L_j has a continuous separation, and by hypothesis the principal spectrum $\Sigma_p^j \subset (0, \infty)$. In this situation we can apply to $\tilde{\tau}$ the result proved in case (C1), so that there exists a $z_0^j \in \mathbb{R}^{n_j}$ with $z_0^j \gg 0$ such that in particular for any $(\omega, x) \in K$ and any $v \in \mathbb{R}^{n_j}$ with $v > x^j$ there exists a $t_0 = t_0(\omega, x, v)$ such that $\tilde{u}(t, \omega, x, v) \geq \tilde{u}(t, \omega, x, x^j) + z_0^j = u^j(t, \omega, x) + z_0^j$ for any $t \geq t_0$.

Finally, a second preliminary argument. As done in the proof of Theorem 4.4 in [35], associated to the minimal set K there exists a $T_0 > 0$ such that for any $(\omega, x) \in K$ and any i, j with $\bar{a}_{ij} > 0$ there is a $t_0 \in (0, T_0)$ such that $a_{ij}(\tau(t_0, \omega, x)) > 0$.

Now, for $k > 1$ we distinguish two situations that may occur when we want to check s-persistence and we take $(\omega, x) \in K$ and $\tilde{x} \in \mathbb{R}^n$ with $\tilde{x} > x$.

(C2): $k > 1$ and there is a component i with $\tilde{x}_i > x_i$ such that $i \in I_j$ for some $j \in J$. In this case, applying the first preliminary argument above, there exists a t_0 such that $\tilde{u}(t, \omega, x, \tilde{x}^j) \geq \tilde{u}(t, \omega, x, x^j) + z_0^j = u^j(t, \omega, x) + z_0^j$ for any $t \geq t_0$. Now, by the cooperative condition on F and the fact that $u(t, \omega, \tilde{x}) \geq u(t, \omega, x)$ for any $t \geq 0$, we can write

$$\begin{aligned} \frac{d}{dt} u^j(t, \omega, \tilde{x}) &= F^j(\omega \cdot t, u(t, \omega, \tilde{x})) \\ &\geq F^j(\omega \cdot t, u^1(t, \omega, x), \dots, u^j(t, \omega, \tilde{x}), \dots, u^k(t, \omega, x)), \end{aligned}$$

and then a standard argument of comparison of solutions says that $u^j(t, \omega, \tilde{x}) \geq \tilde{u}(t, \omega, x, \tilde{x}^j)$ for any $t \geq 0$. Combining this with the previous inequality, $u^j(t, \omega, \tilde{x}) \geq u^j(t, \omega, x) + z_0^j$ for any $t \geq t_0$, and therefore, $u(t, \omega, \tilde{x}) \geq u(t, \omega, x) + e_j$ for any $t \geq t_0$, for the vector $e_j \in \mathbb{R}^n$ defined by $e_j^j = z_0^j$ and 0 otherwise, which satisfies $e_j > 0$. In this case, we are done.

(C3): $k > 1$ and whenever $\tilde{x}_i > x_i$ for some component, $i \in I_j$ and $j \notin J$ (in other words, $\tilde{x}^j = x^j$ for any $j \in J$). In this situation, look at a precise component i such that $\tilde{x}_i > x_i$ with $i \in I_j$. As $j \notin J$, by the block lower triangular structure of \bar{A} , necessarily for some integer $m \geq 1$, $\bar{A}_{j+m, j} \neq 0$, and it might happen that $j + m \in J$ or not. So, again let us distinguish two different situations:

(C3.i) Assume that there exists an $m \geq 1$ such that $\bar{A}_{j+m, j} \neq 0$ and $j + m \in J$. Then, we just need to find a time $\tilde{t} > 0$ such that $u^{j+m}(\tilde{t}, \omega, \tilde{x}) > u^{j+m}(\tilde{t}, \omega, x)$, for then we can apply case (C2) to $(\omega \cdot \tilde{t}, u(\tilde{t}, \omega, x)) \in K$ and $u(\tilde{t}, \omega, \tilde{x}) > u(\tilde{t}, \omega, x)$, and the s-persistence follows straightforward thanks to the cocycle property (2.2).

For this purpose, let us consider the map $h(t) = u(t, \omega, \tilde{x}) - u(t, \omega, x)$, for $t \geq 0$. Because of the monotonicity of the flow, $h(t) \geq 0$ for any $t \geq 0$. Besides, h satisfies a linear system $h'(t) = B(t)h(t)$ for the cooperative matrix $B(t) = [b_{ij}(t)]$ given by

$$B(t) = \int_0^1 D_y F(\omega \cdot t, s u(t, \omega, \tilde{x}) + (1-s) u(t, \omega, x)) ds, \quad t \in \mathbb{R}.$$

Now, we proceed in two steps.

Step 1: For j such that $i \in I_j$ and $\tilde{x}_i > x_i$, we find a time $t_j \geq 0$ such that $h^j(t_j) \gg 0$, that is, such that $u^j(t_j, \omega, \tilde{x}) \gg u^j(t_j, \omega, x)$. To do that, first of all recall that in a cooperative linear system of ODEs, whenever a component of a solution is positive at one time, it stays on positive. In other words, if a component is null at one time, it has always been null before. Therefore, as $\tilde{x}_i > x_i$, we already know that $h_i(t) > 0$ for any $t \geq 0$. If \bar{A}_{jj} is just the 1×1 null matrix, we are done with this step, as we already have $h^j(0) \gg 0$. If that is not the case, since \bar{A}_{jj} is irreducible, there is a $j_1 \in I_j \setminus \{i\}$ such that $\bar{a}_{j_1 i} > 0$. As stated just before case (C2), we can take a $t_1 \in (0, T_0)$ such that $a_{j_1 i}(\tau(t_1, \omega, x)) > 0$. Then, in a neighborhood of $\tau(t_1, \omega, x)$ the map $a_{j_1 i}$ is still positive, that is, there is an $\varepsilon > 0$ such that for any $s \in [0, \varepsilon]$, $a_{j_1 i}(\omega \cdot t_1, s u(t_1, \omega, \tilde{x}) + (1-s) u(t_1, \omega, x)) > 0$ and consequently also $b_{j_1 i}(t_1) > 0$. It cannot be $h_{j_1}(t_1) = 0$, as in that case we would have $h'_{j_1}(t_1) \geq b_{j_1 i}(t_1) h_i(t_1) > 0$, a contradiction. Therefore $h_{j_1}(t_1) > 0$ and consequently $h_{j_1}(t) > 0$ for any $t \geq t_1$ and in particular for any $t \geq T_0$.

If $n_j > 2$, once more since \bar{A}_{jj} is irreducible, we find $l \in \{i, j_1\}$ and $j_2 \in I_j \setminus \{i, j_1\}$ such that $\bar{a}_{j_2 l} > 0$. For $\tau(T_0, \omega, x) \in K$ we find $t_2 \in (0, T_0)$ such that $a_{j_2 l}(\tau(t_2, \tau(T_0, \omega, x))) = a_{j_2 l}(\tau(T_0 + t_2, \omega, x)) > 0$, and just as done before, then also $b_{j_2 l}(T_0 + t_2) > 0$. Now, arguing with $h_{j_2}(T_0 + t_2)$ as before, we deduce that

$h_{j_2}(t) > 0$ for any $t \geq 2T_0$. Iterating the process we conclude that $h^j(t) \gg 0$ for any $t \geq (n_j - 1)T_0$, and in particular $u^j(t_j, \omega, \tilde{x}) \gg u^j(t_j, \omega, x)$ for $t_j = (n_j - 1)T_0$.

Step 2: Roughly speaking, we establish a link between the set of indexes I_j and I_{j+m} , by means of the block $\bar{A}_{j+m,j} \neq 0$, in order to get separation of the trajectories for one component in I_{j+m} in a future time. More precisely, since $\bar{A}_{j+m,j} \neq 0$, there exist indexes $j_1 \in I_{j+m}$, $j_2 \in I_j$ such that $\bar{a}_{j_1 j_2} > 0$. Then, arguing as in Step 1, associated with $\tau(t_j, \omega, x) \in K$ there is a $t_m \in (0, T_0)$ such that $b_{j_1 j_2}(t_j + t_m) > 0$. As $j_2 \in I_j$ and $t_j + t_m > t_j$, $h_{j_2}(t_j + t_m) > 0$ as seen in Step 1. Now, looking at the equation for $h_{j_1}(t)$, if it were $h_{j_1}(t_j + t_m) = 0$, we could write $h'_{j_1}(t_j + t_m) \geq b_{j_1 j_2}(t_j + t_m) h_{j_2}(t_j + t_m) > 0$ by the cooperative character, but that cannot happen. Therefore, necessarily $h_{j_1}(t_j + t_m) > 0$, that is, $u_{j_1}(t_j + t_m, \omega, \tilde{x}) > u_{j_1}(t_j + t_m, \omega, x)$. In all, we have found a time $\tilde{t} = t_j + t_m > 0$ such that $u^{j+m}(\tilde{t}, \omega, \tilde{x}) > u^{j+m}(\tilde{t}, \omega, x)$, as we wanted.

(C3.ii) Assume that for any $m \geq 1$ such that $\bar{A}_{j+m,j} \neq 0$, it happens that $j+m \notin J$. In this situation we take the greatest $m \geq 1$ such that $\bar{A}_{j+m,j} \neq 0$ and, as before, we first apply Step 1 to obtain a time t_j such that $h^j(t_j) \gg 0$ and then apply Step 2 to find another $t_m > 0$ such that $h^{j+m}(t_j + t_m) > 0$. At this point, as $j+m \notin J$ again there exists an $l \geq 1$ such that $\bar{A}_{j+m+l,j+m} \neq 0$. If for some such $l \geq 1$, $j+m+l \in J$ then we fall again in case (C3.i) and we are done. If not, we repeat the previous steps 1 and 2 once more. Clearly, since $k \in J$, in a finite number of steps we get at the situation in (C3.i).

Summing up, for each $j \in J$ we have found a vector $e_j \in \mathbb{R}^n$ such that $e_j^j \gg 0$ and $e_j^l = 0$ for $l \neq j$. This collection of vectors is the one giving the property of s -persistence of τ above K . The proof is finished. \square

The condition of the previous result is often a condition on Lyapunov exponents. For instance, recall that in the almost periodic case, unique ergodicity makes the principal spectrum reduce to a singleton, given precisely by the upper Lyapunov exponent (for instance, see [41]).

Besides, as it turns out, the sufficient conditions for both uniform and strict persistence stated in the previous theorem are actually necessary conditions in the linear case. Although we prove this result for the linearized semiflow over K , it is clearly applicable to any non-autonomous recurrent cooperative linear system of ODEs. The conclusion is that, in our context of work, uniform persistence and strict persistence of the linearized systems imply the same property in the nonlinear systems.

Theorem 4.3. *Consider a non-autonomous cooperative and recurrent system of ODEs (4.1) under the same assumptions as in Theorem 4.2 and let us keep to the notation there used. Assuming the existence of a minimal set K , let L be the linearized semiflow over K (2.3). Then:*

- (i) *If L is uniformly persistent in the interior of the positive cone, then $\Sigma_p^j \subset (0, \infty)$ for any $j \in I$, and τ is uniformly persistent in the area situated strongly above K .*
- (ii) *If L is strictly persistent in the positive cone, then $\Sigma_p^j \subset (0, \infty)$ for any $j \in J$, and τ is strictly persistent in the area situated above K .*

Proof. Keeping to the notation used in Theorem 4.2, again permute the variables in the system if necessary so as to have that the matrix $\bar{A} = [\bar{a}_{ij}]$ defined in (4.5) has the block lower triangular form (4.3).

(i) For each $j \in I$, the linear skew-product semiflow L_j generated by the solutions of the family of linear systems (4.6) inherits the property of u-persistence in the area situated strongly above the minimal set $K^j = K \times \{0\} \subset K \times \mathbb{R}^{n_j}$. The reason is that, as $j \in I$, system (4.6) is in this case an independent subsystem of the linearized system (4.4), whose solutions are u-persistent by hypothesis. In this situation Theorem 3.4 applies and says that the principal spectrum $\Sigma_p^j \subset (0, \infty)$. Then, Theorem 4.2 (i) permits to conclude the proof.

(ii) This time, let us check that for each $j \in J$, L_j is s-persistent in the area situated above the minimal set $K^j = K \times \{0\} \subset K \times \mathbb{R}^{n_j}$. Fixed any $z^j \in \mathbb{R}^{n_j}$ with $z^j > 0$, consider $z \in \mathbb{R}^n$ such that $z_i = z_i^j$ for $i \in I_j$ and else $z_i = 0$. To this $z > 0$, we apply the s-persistence of L , and so there is a time t_0 such that for any $t \geq t_0$, $u_x(t, \omega, x) z \geq e$ for e one of the vectors e_1, \dots, e_m given in Definition 3.2. Now, it is not difficult to realize that, when we solve system (4.4), because $j \in J$, what happens to the components of the solution in I_j does not interfere with the other components. This, together with the structure of z , means that the components of $u_x(t, \omega, x) z$, other than the ones in I_j , are null, whereas $(\tau(t, \omega, x), (u_x(t, \omega, x) z)^j) = L_j(t, \omega, x, z^j)$. Therefore, in $u_x(t, \omega, x) z \geq e > 0$ it is necessarily $e^j > 0$ and the property of s-persistence holds for L_j . Once more, in this situation Theorem 3.4 applies and says that the principal spectrum $\Sigma_p^j \subset (0, \infty)$. Finally, by Theorem 4.2 (ii) the proof is complete. \square

5. UNIFORM PERSISTENCE AND STRICT PERSISTENCE AT 0 IN COOPERATIVE RECURRENT NON-AUTONOMOUS DELAY FDES

Here we consider n -dimensional systems of finite-delay differential equations with a fixed delay, which we take to be 1, given by a function $f : \mathbb{R} \times \mathbb{R}^n \times \mathbb{R}^n \rightarrow \mathbb{R}^n$, such that $f(t, y, w)$ is of class \mathcal{C}^1 with respect to (y, w) and f as well as all its first order derivatives $\partial f / \partial y_i, \partial f / \partial w_i, i = 1, \dots, n$ are admissible,

$$y'(t) = f(t, y(t), y(t-1)), \quad t > 0. \quad (5.1)$$

Besides, we assume f to be recurrent in time, so that the translation flow on the hull Ω is minimal. Now we look at the family of systems over the hull,

$$y'(t) = F(\omega \cdot t, y(t), y(t-1)), \quad \omega \in \Omega, \quad (5.2)$$

whose solutions induce a forward dynamical system of skew-product type (2.1) (in principle only locally-defined) on the product $\Omega \times X$, where we take $X = C([-1, 0], \mathbb{R}^n)$, the space of vector-valued continuous functions on $[-1, 0]$ with the norm $\|x\| = \|x_1\|_\infty + \dots + \|x_n\|_\infty$ for $x \in X$ (see Hale and Verduyn Lunel [18] for more details). The space X is strongly ordered when we consider the positive cone $X_+ = \{x \in X \mid x(s) \geq 0 \text{ for all } s \in [-1, 0]\}$ which is normal and has a nonempty interior $\text{Int } X_+ = \{x \in X \mid x(s) \gg 0 \text{ for all } s \in [-1, 0]\}$.

To get into the framework of monotone skew-product semiflows, we need to impose the so-called *quasimonotone condition* on the initial system, which, under the imposed regularity assumptions, can be written as follows. To keep terms simple, we will call these systems cooperative, just as in the ODEs case.

Definition 5.1. System (5.1) is *cooperative* if at any $(t, y, w) \in \mathbb{R} \times \mathbb{R}^n \times \mathbb{R}^n$,

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

As in the previous section, if the initial system has a bounded solution, one can prove that there exists a minimal set for the induced skew-product semiflow. The reader is referred to [36] for any further details. Finally keep in mind that although we will be assuming that the semiflow is globally defined in the area situated above a minimal set, this cannot be taken for granted in the general case.

Theorem 5.8 in [36] gives conditions for the property of uniform persistence in the delay case. When we look at the property of strict persistence, one realizes that we cannot give the parallel result of Theorem 4.2 (ii) in the case of delay equations, as in the general case the irreducibility of the associated constant matrices does not imply the eventual strong positivity of the linearized solution operators, but only a dichotomy-type result which says that there might be positive initial vectors $z_0 > 0$ such that the corresponding solutions go to 0 after some time, and the continuous separation is of type II (see Theorem 4.6 and Proposition 5.7 in [35] for the precise results). This completely precludes the property of strict persistence. For this reason, when dealing with delay equations we need to introduce a slight modification in the property of strict persistence, still maintaining the same meaning about the behaviour of solutions. We will call this property strict persistence at 0 or just s_0 -persistence, and the definition is the following.

Definition 5.2. Consider a cooperative and recurrent system of delay FDEs (5.1) with the regularity conditions stated before and let τ be the induced skew-product semiflow (2.1). Let $K \subset \Omega \times C([-1, 0], \mathbb{R}^n)$ be a compact τ -invariant set. The semiflow τ is said to be *strictly persistent at 0* (s_0 -persistent for short) in the region situated above K if there exists a collection of strictly positive maps $e_1, \dots, e_m \in C([-1, 0], \mathbb{R}^n)$, $e_i > 0$ for every i , such that for any $(\omega, x) \in K$ and any $y \geq x$ with $y(0) > x(0)$ there exists a time $t_0 = t_0(\omega, x, y)$ such that $u(t, \omega, y) \geq u(t, \omega, x) + e_i$ for any $t \geq t_0$ for one of the maps e_1, \dots, e_m .

Here we have the main result for delay FDEs, which includes the already known result on uniform persistence for the sake of completeness.

Theorem 5.3. Consider a cooperative system (5.1) of finite-delay equations with $f(t, y, w)$ recurrent, of class C^1 in y and w and such that f , $\partial f / \partial y_i$ and $\partial f / \partial w_i$ are all admissible for $i = 1, \dots, n$. Assume that there exists a minimal set $K \subset \Omega \times C([-1, 0], \mathbb{R}^n)$ for the semiflow τ generated by the solutions of the associated family (5.2) which admits a flow extension. For each $(\omega, x) \in K$ consider the linearized system of (5.2) along the semitrajectory of (ω, x) ,

$$z'(t) = \tilde{A}(\tau(t, \omega, x)) z(t) + \tilde{B}(\tau(t, \omega, x)) z(t-1), \quad t > 0, \quad (5.3)$$

where we have denoted, for the matrices $A(\omega, y, w) = D_y F(\omega, y, w)$ and $B(\omega, y, w) = D_w F(\omega, y, w)$,

$$\begin{aligned} \tilde{A}(\tau(t, \omega, x)) &= A(\omega \cdot t, y(t, \omega, x), y(t-1, \omega, x)), \\ \tilde{B}(\tau(t, \omega, x)) &= B(\omega \cdot t, y(t, \omega, x), y(t-1, \omega, x)), \end{aligned}$$

where, as usual, $y(t, \omega, x)$ is the solution of system (5.2) with initial map x . Without loss of generality, assume that the matrix $\bar{A} + \bar{B} = [\bar{a}_{ij} + \bar{b}_{ij}]$ defined as

$$\begin{aligned}\bar{a}_{ij} &= \sup_{(\omega, x) \in K} a_{ij}(\omega, x(0), x(-1)) \quad \text{for } i \neq j, \quad \text{and } \bar{a}_{ii} = 0, \\ \bar{b}_{ij} &= \sup_{(\omega, x) \in K} b_{ij}(\omega, x(0), x(-1)) \quad \text{for } i \neq j, \quad \text{and } \bar{b}_{ii} = 0,\end{aligned}$$

has the form

$$\begin{bmatrix} \bar{A}_{11} + \bar{B}_{11} & 0 & \dots & 0 \\ \bar{A}_{21} + \bar{B}_{21} & \bar{A}_{22} + \bar{B}_{22} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ \bar{A}_{k1} + \bar{B}_{k1} & \bar{A}_{k2} + \bar{B}_{k2} & \dots & \bar{A}_{kk} + \bar{B}_{kk} \end{bmatrix} \quad (5.4)$$

whose diagonal blocks, denoted by $\bar{A}_{11} + \bar{B}_{11}, \dots, \bar{A}_{kk} + \bar{B}_{kk}$, of size n_1, \dots, n_k respectively ($n_1 + \dots + n_k = n$), are irreducible. For each $j = 1, \dots, k$, let L_j be the linear skew-product semiflow induced on $K \times C([-1, 0], \mathbb{R}^{n_j})$ by the solutions of the linear systems for $(\omega, x) \in K$ given by the corresponding diagonal block of (5.3),

$$z'(t) = \tilde{A}_{jj}(\tau(t, \omega, x)) z(t) + \tilde{B}_{jj}(\tau(t, \omega, x)) z(t-1), \quad t > 0. \quad (5.5)$$

Then, $K^j = K \times \{0\} \subset K \times C([-1, 0], \mathbb{R}^{n_j})$ is a minimal set for L_j which admits a continuous separation (of type II). Let Σ_p^j be its principal spectrum.

If $k = 1$, i.e., if the matrix $\bar{A} + \bar{B}$ is irreducible, let $I = J = \{1\}$. Else, let

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

that is, I is composed by the indexes j such that any other block in the row of $\bar{A}_{jj} + \bar{B}_{jj}$ is null, whereas J contains those indexes j such that any other block in the column of $\bar{A}_{jj} + \bar{B}_{jj}$ is null. The conditions for uniform and strict persistence at 0 are the following:

- (i) If $\Sigma_p^j \subset (0, \infty)$ for any $j \in I$, then τ is uniformly persistent in the area situated strongly above K .
- (ii) If $\Sigma_p^j \subset (0, \infty)$ for any $j \in J$, then τ is strictly persistent at 0 in the area situated above K .

Proof. As usual, a permutation of the variables, if needed, takes the matrix $\bar{A} + \bar{B}$ into the form (5.4). Note that $\bar{a}_{ij}, \bar{b}_{ij} \geq 0$ by the cooperative condition.

This time (i) is part of Theorem 5.8 in [36].

As for (ii), we distinguish the parallel cases to those in the proof of Theorem 4.2. Although the arguments follow the line of the ones there used, due to the delay some technical changes are needed.

(C1): $k = 1$, that is, $\bar{A} + \bar{B}$ is an irreducible matrix. In this case, Proposition 5.7 in [35] says that K admits a continuous separation of type II. More precisely, the following dichotomy property holds for the linearized operators: there exists a $T > 0$ such that, for any $(\omega, x) \in K$ and any initial map $v > 0$, either $u_x(T, \omega, x)v = 0$ or $u_x(T, \omega, x)v \gg 0$. Now, by (i) we already know that τ is u-persistent in the area situated strongly above K ; so let $z_0 \gg 0$ be the vector given in Definition 3.1 and let us see that it is the appropriate vector to check s_0 -persistence.

So, take $(\omega, x) \in K$ and $y \in C([-1, 0], \mathbb{R}^n)$ with $y \geq x$ and $y(0) > x(0)$, and look at the map $z(t) = (u_x(t, \omega, x)(y - x))(0)$, $t \geq 0$, which is the solution of the

linearized system (5.3) of delay equations with initial condition map $y - x$. Take $i \in \{1, \dots, n\}$ such that $y_i(0) > x_i(0)$, that is, $z_i(0) > 0$. Then Lemma 5.1.3 in [48] says that $z_i(t) > 0$ for any $t \geq 0$. In particular for $y - x > 0$ this precludes the case $u_x(T, \omega, x)(y - x) = 0$, so that it must be $u_x(T, \omega, x)(y - x) \gg 0$. At this point, argue as in the proof of Theorem 3.5 to see that then $u(T, \omega, y) \gg u(T, \omega, x)$. To finish, just apply u-persistence in the area situated strongly above K and the cocycle property (2.2).

Before we distinguish any further cases, once more we carry out some general preliminary arguments for the case $k > 1$. In this case we have a general decomposition (5.4) for the matrix $\bar{A} + \bar{B}$ with k irreducible diagonal blocks of size n_1, \dots, n_k , respectively. As in case (C1), it is precisely the irreducible character of the diagonal blocks which implies that each linear semiflow L_j admits a continuous separation of type II. Also here for any vector or map v , let us denote $v^j = (v_i)_{i \in I_j}$, where I_j is the set formed by the n_j indexes corresponding to the rows of the block $\bar{A}_{jj} + \bar{B}_{jj}$.

Now, let us fix $j \in J$. As the following first argument is exactly the same in all the cases, let us assume for the sake of simplicity of writing that $1 < j < k$. Let us consider the family of n_j -dimensional systems of delay FDEs over the base flow K , given for each $(\omega, x) \in K$ by

$$(y^j)'(t) = F^j(\omega \cdot t, \bar{y}^1(t), \dots, y^j(t), \dots, \bar{y}^k(t), \bar{y}^1(t-1), \dots, y^j(t-1), \dots, \bar{y}^k(t-1)),$$

where we have denoted by $\bar{y}(t) = y(t, \omega, x)$ the solution of system (5.2) with initial map x . Their solutions generate a skew-product semiflow on $K \times C([-1, 0], \mathbb{R}^{n_j})$ which we write as $\tilde{\tau}(t, \omega, x, v) = (\tau(t, \omega, x), \tilde{u}(t, \omega, x, v))$ and there exists a trivial minimal set for this semiflow, which is

$$K_1 = \text{cls}\{(\omega \cdot t, u(t, \omega_0, x_0), u^j(t, \omega_0, x_0)) \mid t \geq 0\},$$

for a certain fixed $(\omega_0, x_0) \in K$. Besides, when we calculate the linearized equations along the orbit of (ω, x, x^j) , for $(\omega, x) \in K$, the system we obtain is exactly (5.5), the induced linear semiflow L_j has a continuous separation of type II, and by hypothesis the principal spectrum $\Sigma_p^j \subset (0, \infty)$. In this situation we can apply to $\tilde{\tau}$ the result proved in case (C1), so that there exists a $z_0^j \in C([-1, 0], \mathbb{R}^{n_j})$ with $z_0^j \gg 0$ such that in particular for any $(\omega, x) \in K$ and any $v \in C([-1, 0], \mathbb{R}^{n_j})$ with $v \geq x^j$ and $v(0) > x^j(0)$ there exists a $t_0 = t_0(\omega, x, v)$ such that $\tilde{u}(t, \omega, x, v) \geq \tilde{u}(t, \omega, x, x^j) + z_0^j = u^j(t, \omega, x) + z_0^j$ for any $t \geq t_0$.

Finally, a second preliminary result. Arguing as in the proof of Theorem 4.6 in [35], associated to the minimal set K there exists a $T_0 > 2$ such that for any $(\omega, x) \in K$ and any i, j with $\bar{a}_{ij} + \bar{b}_{ij} > 0$,

$$\text{if } \bar{a}_{ij} > 0, \exists t_0 \in (2, T_0) \text{ such that } a_{ij}(\omega \cdot t_0, y(t_0, \omega, x), y(t_0 - 1, \omega, x)) > 0,$$

$$\text{if } \bar{b}_{ij} > 0, \exists t_0 \in (2, T_0) \text{ such that } b_{ij}(\omega \cdot t_0, y(t_0, \omega, x), y(t_0 - 1, \omega, x)) > 0.$$

Now, for $k > 1$ we distinguish two situations that may occur when we want to check s_0 -persistence and we take $(\omega, x) \in K$ and $\tilde{x} \in C([-1, 0], \mathbb{R}^n)$ such that $\tilde{x} \geq x$ and $\tilde{x}(0) > x(0)$.

(C2): $k > 1$ and there is a component i with $\tilde{x}_i(0) > x_i(0)$ such that $i \in I_j$ for some $j \in J$. In this case, applying the first preliminary argument above, there exists a t_0 such that $\tilde{u}(t, \omega, x, \tilde{x}^j) \geq \tilde{u}(t, \omega, x, x^j) + z_0^j = u^j(t, \omega, x) + z_0^j$ for any $t \geq t_0$. Now, by the cooperative condition on F and the fact that $u(t, \omega, \tilde{x}) \geq u(t, \omega, x)$ for any

$t \geq 0$, we can write

$$\begin{aligned} \frac{d}{dt} y^j(t, \omega, \tilde{x}) &= F^j(\omega \cdot t, y(t, \omega, \tilde{x}), y(t-1, \omega, \tilde{x})) \\ &\geq F^j(\omega \cdot t, \bar{y}^1(t), \dots, y^j(t, \omega, \tilde{x}), \dots, \bar{y}^k(t), \bar{y}^1(t-1), \dots, y^j(t-1, \omega, \tilde{x}), \dots, \bar{y}^k(t-1)), \end{aligned}$$

and then a standard argument of comparison of solutions says that $u^j(t, \omega, \tilde{x}) \geq \tilde{u}(t, \omega, x, \tilde{x}^j)$ for any $t \geq 0$ (for instance, see [48]). Combining this with the previous inequality, $u^j(t, \omega, \tilde{x}) \geq u^j(t, \omega, x) + z_0^j$ for any $t \geq t_0$, and therefore, $u(t, \omega, \tilde{x}) \geq u(t, \omega, x) + e_j$ for any $t \geq t_0$, for the map $e_j \in C([-1, 0], \mathbb{R}^n)$ defined by $e_j^j = z_0^j$ and 0 otherwise, which satisfies $e_j > 0$. In this case, we are done.

(C3): $k > 1$ and whenever $\tilde{x}_i(0) > x_i(0)$ for some component, $i \in I_j$ and $j \notin J$ (in other words, $\tilde{x}^j(0) = x^j(0)$ for any $j \in J$). In this situation, look at a precise component i such that $\tilde{x}_i(0) > x_i(0)$ with $i \in I_j$. As $j \notin J$, by the block lower triangular structure of $\bar{A} + \bar{B}$, necessarily $\bar{A}_{j+m, j} + \bar{B}_{j+m, j} \neq 0$ for some integer $m \geq 1$, and it might happen that $j+m \in J$ or not. So, again let us distinguish two different situations:

(C3.i) Assume that there exists an $m \geq 1$ such that $\bar{A}_{j+m, j} + \bar{B}_{j+m, j} \neq 0$ and $j+m \in J$. Then, we just need to find a time $\tilde{t} > 0$ such that $y^{j+m}(\tilde{t}, \omega, \tilde{x}) > y^{j+m}(\tilde{t}, \omega, x)$, for then we can apply case (C2) to $(\omega \cdot \tilde{t}, u(\tilde{t}, \omega, \tilde{x})) \in K$ with $u(\tilde{t}, \omega, \tilde{x}) \geq u(\tilde{t}, \omega, x)$ and $u(\tilde{t}, \omega, \tilde{x})(0) > u(\tilde{t}, \omega, x)(0)$, and the s_0 -persistence follows straightforward thanks to the cocycle property (2.2).

For this purpose, let us consider the map $h(t) = y(t, \omega, \tilde{x}) - y(t, \omega, x)$, for $t \geq 0$. Because of the monotonicity of the semiflow, $h(t) \geq 0$ for any $t \geq 0$. Due to the delay, the treatment of $h(t)$ is more delicate this time, and we need to look at it as the solution of two different delay linear systems. More precisely, on the one hand h satisfies the linear cooperative delay system

$$h'(t) = C(t)h(t) + D(t)h(t-1), \quad t \geq 0, \quad (5.6)$$

for the matrices $C(t) = [c_{ij}(t)]$, $D(t) = [d_{ij}(t)]$ given by

$$\begin{aligned} C(t) &= \int_0^1 D_y F(\omega \cdot t, s y(t, \omega, \tilde{x}) + (1-s)y(t, \omega, x), y(t-1, \omega, \tilde{x})) ds, \quad t \geq 0, \\ D(t) &= \int_0^1 D_w F(\omega \cdot t, y(t, \omega, x), s y(t-1, \omega, \tilde{x}) + (1-s)y(t-1, \omega, x)) ds, \quad t \geq 0, \end{aligned}$$

and on the other hand, it is a solution of the second linear cooperative delay system

$$h'(t) = E(t)h(t) + G(t)h(t-1), \quad t \geq 0, \quad (5.7)$$

for the matrices $E(t) = [e_{ij}(t)]$, $G(t) = [g_{ij}(t)]$ given by

$$\begin{aligned} E(t) &= \int_0^1 D_y F(\omega \cdot t, s y(t, \omega, \tilde{x}) + (1-s)y(t, \omega, x), y(t-1, \omega, x)) ds, \quad t \geq 0, \\ G(t) &= \int_0^1 D_w F(\omega \cdot t, y(t, \omega, \tilde{x}), s y(t-1, \omega, \tilde{x}) + (1-s)y(t-1, \omega, x)) ds, \quad t \geq 0. \end{aligned}$$

Now, we proceed in two steps.

Step 1: For j such that $i \in I_j$ and $\tilde{x}_i(0) > x_i(0)$, we find a time $t_j \geq 0$ such that $h^j(t_j) \gg 0$, that is, such that $y^j(t_j, \omega, \tilde{x}) \gg y^j(t_j, \omega, x)$. To do that, first, as $\tilde{x}_i(0) > x_i(0)$, in a cooperative linear system of delay FDEs we already know that $h_i(t) > 0$ for any $t \geq 0$ (once more, see Lemma 5.1.3 in [48]). If $\bar{A}_{jj} + \bar{B}_{jj}$ is just

the 1×1 null matrix, we are done with this step, as we already have $h^j(0) \gg 0$. If that is not the case, since $\bar{A}_{jj} + \bar{B}_{jj}$ is irreducible, there is a $j_1 \in I_j \setminus \{i\}$ such that $\bar{a}_{j_1 i} + \bar{b}_{j_1 i} > 0$. As stated just before case (C2), either $\bar{a}_{j_1 i} > 0$ and we can take a $t_1 \in (2, T_0)$ such that $a_{j_1 i}(\omega \cdot t_1, y(t_1, \omega, x), y(t_1 - 1, \omega, x)) > 0$, or $\bar{b}_{j_1 i} > 0$ and then we can take a $t_1 \in (2, T_0)$ (call it the same just to keep the notation easy) such that $b_{j_1 i}(\omega \cdot t_1, y(t_1, \omega, x), y(t_1 - 1, \omega, x)) > 0$. In the first case, in a neighborhood of $(\omega \cdot t_1, y(t_1, \omega, x), y(t_1 - 1, \omega, x))$ the map $a_{j_1 i}$ is still positive, whereas in the second case the same happens for the map $b_{j_1 i}$. This implies in the first case that $e_{j_1 i}(t_1) > 0$, whereas in the second case it is $d_{j_1 i}(t_1) > 0$.

Then, let us see why in any of the two cases it cannot be $h_{j_1}(t_1) = 0$. In the case $\bar{a}_{j_1 i} > 0$, if it were $h_{j_1}(t_1) = 0$, then looking at the cooperative system (5.7) we would have $h'_{j_1}(t_1) \geq e_{j_1 i}(t_1) h_i(t_1) > 0$, leading to a contradiction. As for the case $\bar{b}_{j_1 i} > 0$, if it were $h_{j_1}(t_1) = 0$, then we would look at the cooperative system (5.6) to get $h'_{j_1}(t_1) \geq d_{j_1 i}(t_1) h_i(t_1 - 1) > 0$, again a contradiction. Therefore $h_{j_1}(t_1) > 0$ and consequently $h_{j_1}(t) > 0$ for any $t \geq t_1$.

As in the ODEs case, also here we iterate this procedure using that $\bar{A}_{jj} + \bar{B}_{jj}$ is irreducible until we finally get that $h^j(t) \gg 0$ for any $t \geq (n_j - 1)T_0$, and in particular $y^j(t_j, \omega, \tilde{x}) \gg y^j(t_j, \omega, x)$ for $t_j = (n_j - 1)T_0$.

Step 2: Roughly speaking, we establish a link between the set of indexes I_j and I_{j+m} , by means of the block $\bar{A}_{j+m, j} + \bar{B}_{j+m, j} \neq 0$, in order to get separation of the solutions for one component in I_{j+m} in a future time. More precisely, since $\bar{A}_{j+m, j} + \bar{B}_{j+m, j} \neq 0$, there exist indexes $j_1 \in I_{j+m}$, $j_2 \in I_j$ such that $\bar{a}_{j_1 j_2} + \bar{b}_{j_1 j_2} > 0$. Then, arguing as in Step 1, associated with $\tau(t_j, \omega, x) \in K$, either there is a $t_m \in (2, T_0)$ such that $e_{j_1 j_2}(t_j + t_m) > 0$ if it is $\bar{a}_{j_1 j_2} > 0$, or there is a $t_m \in (2, T_0)$ such that $d_{j_1 j_2}(t_j + t_m) > 0$ if it is $\bar{b}_{j_1 j_2} > 0$. In the first situation, as $j_2 \in I_j$ and $t_j + t_m > t_j$, $h_{j_2}(t_j + t_m) > 0$ by Step 1, and looking at the equation for $h_{j_1}(t)$ in system (5.7), if it were $h_{j_1}(t_j + t_m) = 0$, we would have $h'_{j_1}(t_j + t_m) \geq e_{j_1 j_2}(t_j + t_m) h_{j_2}(t_j + t_m) > 0$, a contradiction. In the second situation, as $j_2 \in I_j$ and $t_j + t_m - 1 > t_j$, $h_{j_2}(t_j + t_m - 1) > 0$ again by Step 1, and this time looking at the equation for $h_{j_1}(t)$ in system (5.6), if it were $h_{j_1}(t_j + t_m) = 0$, we would have $h'_{j_1}(t_j + t_m) \geq d_{j_1 j_2}(t_j + t_m) h_{j_2}(t_j + t_m - 1) > 0$, a contradiction. Therefore, necessarily $h_{j_1}(t_j + t_m) > 0$, that is, $y_{j_1}(t_j + t_m, \omega, \tilde{x}) > y_{j_1}(t_j + t_m, \omega, x)$. In all, we have found a time $\tilde{t} = t_j + t_m > 0$ such that $y^{j+m}(\tilde{t}, \omega, \tilde{x}) > y^{j+m}(\tilde{t}, \omega, x)$, as we wanted.

(C3.ii) Assume that for any $m \geq 1$ such that $\bar{A}_{j+m, j} + \bar{B}_{j+m, j} \neq 0$, it happens that $j+m \notin J$. In this situation we take the greatest $m \geq 1$ such that $\bar{A}_{j+m, j} + \bar{B}_{j+m, j} \neq 0$ and, as before, we first apply Step 1 to obtain a time t_j such that $h^j(t_j) \gg 0$ and then apply Step 2 to find another $t_m > 0$ such that $h^{j+m}(t_j + t_m) > 0$. At this point, as $j+m \notin J$ again there exists an $l \geq 1$ such that $\bar{A}_{j+m+l, j+m} + \bar{B}_{j+m+l, j+m} \neq 0$. If for some such $l \geq 1$, $j+m+l \in J$ then we fall again in case (C3.i) and we are done. If not, we repeat the previous steps 1 and 2 once more. Clearly, since $k \in J$, in a finite number of steps we get at the situation in (C3.i).

Summing up, for each $j \in J$ we have found a map $e_j \in C([-1, 0], \mathbb{R}^n)$ such that $e_j^j \gg 0$ and $e_j^l = 0$ for $l \neq j$. This collection of maps is the one giving the property of s_0 -persistence of τ above K . The proof is finished. \square

We finish this section with the following result, which essentially says that in the linear case the spectral conditions given for persistence are not only sufficient

but also necessary, and besides, persistence in the nonlinear case can be studied through persistence in the linearized systems.

Theorem 5.4. *Consider a non-autonomous cooperative and recurrent system of delay FDEs (5.1) with the regularity conditions stated in Theorem 5.3, and keep to the notation there used. Assuming the existence of a minimal set K with a flow extension, consider L the linearized skew-product semiflow over K (2.3). Then:*

- (i) *If L is uniformly persistent in the interior of the positive cone, then $\Sigma_p^j \subset (0, \infty)$ for any $j \in I$, and τ is uniformly persistent in the area situated strongly above K .*
- (ii) *If L is strictly persistent at 0 in the positive cone, then $\Sigma_p^j \subset (0, \infty)$ for any $j \in J$, and τ is strictly persistent at 0 in the area situated above K .*

Proof. Once more, by doing a permutation in the variables if needed, we can assume that the matrix $\bar{A} + \bar{B}$ defined in Theorem 5.3 has the structure (5.4).

The proof of (i) just follows the lines of the proof of the corresponding result in the ODEs case, Theorem 4.3 (i), so that we omit it.

As for (ii), first of all, it is easy to check that if a delay linear skew-product semiflow with a continuous separation (of type II) is s_0 -persistent in the positive cone, then its principal spectrum $\Sigma_p \subset (0, \infty)$: just follow the arguments in the proof of Theorem 3.4. Secondly, to check that the property of s_0 -persistence of L is inherited by the linear semiflows L_j for $j \in J$, once more we just adapt the proof of Theorem 4.3 (ii) to the delay context, with no difficulty. Therefore, we obtain that $\Sigma_p^j \subset (0, \infty)$ for any $j \in J$, and by Theorem 5.3 (ii), τ is s_0 -persistent in the area situated above K . The proof is finished. \square

6. NONLINEAR NICHOLSON SYSTEMS

In this section we consider a non-autonomous noncooperative system with delay which is among the family of so-called Nicholson systems. In 1954 Nicholson [32] published experimental data on the behaviour of the population of the Australian sheep-blowfly. Then, Gurney *et al.* [17] 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. In this equation, 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. Many authors have studied generalizations and modifications of the Nicholson equation, concerned with stability, persistence or existence of certain kind of solutions, among other dynamical issues. More recently Nicholson systems have also been considered, as they fit models for one single species in an environment with a patchy structure or for multiple biological species. To keep the list short, we just cite some recent related works such as Faria [11], Faria and Röst [12], Liu and Meng [27], Wang [53] and Wang and Zhao [54].

Here we consider a generalization of this model by taking time-dependent coefficients and adding a patch structure. This helps to model the temporal variation of the environment as well as the presence of a heterogeneous environment, so that the distribution of the population is influenced by migrations among patches and the growth of the populations on each patch, which depends on the local resources

among other conditions. Also the maturation time is assumed to be possibly different on each patch. One important remark is that, to apply our methods, the temporal variation of the coefficients has to be at least recurrent. To keep things easy, in this section we assume the temporal variation to be almost periodic.

More precisely, we consider an n -dimensional system of delay FDEs with patch structure (n patches) and a nonlinear term of Nicholson type, which is able to reflect an almost periodic temporal variation in the environment,

$$y_i'(t) = -\tilde{d}_i(t) y_i(t) + \sum_{j=1}^n \tilde{a}_{ij}(t) y_j(t) + \tilde{\beta}_i(t) y_i(t - \tau_i) e^{-y_i(t - \tau_i)}, \quad t \geq 0, \quad (6.1)$$

for $i = 1, \dots, n$. Here $y_i(t)$ denotes the density of the population on patch i at time $t \geq 0$ and $\tau_i > 0$ is the maturation time on that patch. We make the following assumptions on the coefficient functions:

- (a1) $\tilde{d}_i(t)$, $\tilde{a}_{ij}(t)$, and $\tilde{\beta}_i(t)$ are almost periodic maps on \mathbb{R} ;
- (a2) $\tilde{d}_i(t) \geq d_0 > 0$ for every $t \in \mathbb{R}$ and $i \in \{1, \dots, n\}$;
- (a3) $\tilde{a}_{ij}(t)$ are all nonnegative maps and \tilde{a}_{ii} is taken to be identically null;
- (a4) $\tilde{\beta}_i(t) > 0$ for any $t \geq 0$, for any i ;
- (a5) $\tilde{d}_i(t) - \sum_{j=1}^n \tilde{a}_{ji}(t) > 0$ for any $t \geq 0$, for any i .

To get a meaning of the imposed conditions, note that we need coefficients defined on \mathbb{R} to easily build the hull of the system. The coefficient $\tilde{a}_{ij}(t)$ 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, it is given by the delay Nicholson term. Finally, the decreasing rate on patch i , given by $\tilde{d}_i(t)$, includes the mortality rate as well as the migrations coming out of patch i , so that condition (a5) makes sense, saying that the mortality rate is positive at any time. Note that this system does not satisfy the cooperative condition given in Definition 5.1.

By the construction of the hull Ω , the previous system is included in a family of systems over the hull. For each $\omega \in \Omega$ the corresponding system can be written as

$$y_i'(\omega \cdot t) = -d_i(\omega \cdot t) y_i(\omega \cdot t) + \sum_{j=1}^n a_{ij}(\omega \cdot t) y_j(\omega \cdot t) + \beta_i(\omega \cdot t) y_i(\omega \cdot t - \tau_i) e^{-y_i(\omega \cdot t - \tau_i)}, \quad (6.2)$$

for $i = 1, \dots, n$, for certain continuous nonnegative maps d_i , a_{ij} , β_i defined on Ω . We take $X = C([- \tau_1, 0]) \times \dots \times C([- \tau_n, 0])$ with the usual cone of positive elements, denoted by X_+ , and the sup-norm. Then, solutions of (6.2) induce a skew-product semiflow (2.1) defined on $\mathbb{R}_+ \times \Omega \times X$ (in principle only locally-defined) which has a trivial minimal set $K = \Omega \times \{0\}$, as the null map is a solution of any of the equations over the hull. Furthermore, the set $\Omega \times X_+$ is invariant for the dynamics, that is, solutions of (6.2) starting inside the positive cone remain inside the positive cone while defined: just apply the criterion given in Theorem 5.2.1 in [48].

Now, first of all let us check that all solutions of (6.2) are bounded, so that the induced semiflow is globally defined on $\Omega \times X_+$.

Theorem 6.1. *Let us consider the nonlinear system with delay (6.1) under assumptions (a1)-(a5). Then, all solutions of (6.2) with initial condition in X_+ are bounded, and therefore the induced semiflow is globally defined on $\Omega \times X_+$. Actually, the solutions are ultimately bounded, in the sense that there exists a constant $r > 0$ such that for any $\omega \in \Omega$ and any initial condition $x \in X_+$, any component of the vectorial solution satisfies $0 \leq y_i(t, \omega, x) \leq r$ from some time on.*

Proof. By the fact that $\sup_{y \geq 0} y e^{-y} = e^{-1} < 1$ and the continuity of the maps β_i on Ω , for each $i = 1, \dots, n$ we can take $M_i = \sup_{\omega \in \Omega} \beta_i(\omega)$ and then consider the family of nonhomogeneous linear systems

$$y'_i(t) = -d_i(\omega \cdot t) y_i(t) + \sum_{j=1}^n a_{ij}(\omega \cdot t) y_j(t) + M_i, \quad \omega \in \Omega, \quad (6.3)$$

for $i = 1, \dots, n$, which is cooperative and besides it is a majorant of the family of systems (6.2) on the positive cone. Therefore, if we prove the result for this last family of systems, by a standard argument of comparison of solutions (once more, see Theorem 5.1.1. in [48]) we are done.

More precisely, for the family of nonhomogeneous almost periodic linear systems (6.3) we are going to prove that the homogeneous part, $y'(t) = A(\omega \cdot t) y(t)$ for short, admits an exponential dichotomy with full stable subspace. In that case, for the nonhomogeneous term (M_1, \dots, M_n) there exists a unique solution $y_b(t, \omega)$ of (6.3) which is bounded (actually almost periodic, for instance, see Theorem 7.7 in Fink [14]), and $y_b(t, \omega)$ are uniformly bounded for $\omega \in \Omega$. Therefore, any solution can be written as $y(t, \omega) = y_b(t, \omega) + y_0(t, \omega)$ for the appropriate solution $y_0(t, \omega)$ of the linear homogeneous part, which tends to 0 as $t \rightarrow \infty$. From this, the property of ultimately bounded solutions for (6.3) easily follows.

Now, note that if we had a positive inferior bound for the mortality rate on each patch for the initial system, that is, if $\tilde{d}_i(t) - \sum_{j=1}^n \tilde{a}_{ji}(t) \geq \delta$ for any $t \in \mathbb{R}$ and $i = 1, \dots, n$ for a certain $\delta > 0$, then we could directly apply Lemma 7.17 in [14] which affirms that in a column dominant family of linear almost periodic systems, the null solution is exponentially stable as $t \rightarrow \infty$. However, our requirement in hypothesis (a5) is not so restrictive, and we have to follow another argument, based on the existence of a so-called strong super-equilibrium (see Novo *et al.* [33] for the introduction of this concept in the field of non-autonomous FDEs).

Since condition (a5) makes reference to columns of $y'(t) = A(\omega \cdot t) y(t)$, we consider the adjoint system, given by $y'(t) = -A(\omega \cdot t)^T y(t)$, where A^T denotes the transpose matrix. Let us reverse time, *i.e.*, let us make the change of variables $s = -t$ which takes the adjoint system into $z'(s) = A(\omega \cdot s)^T z(s)$, and let us first prove that the null solution is uniformly asymptotically stable as $s \rightarrow \infty$. Let us denote by $\bar{1}$ the vector in \mathbb{R}^n with all components equal to 1. From condition (a5) we know that $A(\omega)^T \bar{1} \leq 0$ and there exists an $\omega_0 \in \Omega$ such that $A(\omega_0)^T \bar{1} \ll 0$: just consider ω_0 determining the initial system. In this situation, the map $a : \Omega \rightarrow \mathbb{R}^n$ defined by $a \equiv \bar{1}$ is a strong super-equilibrium for the family $z'(s) = A(\omega \cdot s)^T z(s)$, $\omega \in \Omega$ (see Lemma 2.11 in [37], which is valid for n -dimensional ODEs). And the same happens, by linearity, with any of the constant maps given by $\lambda \bar{1}$ for any $\lambda > 0$, so that we have a family of strong super-equilibria approaching 0. In this situation, we can apply Theorem 5.3 in [33] also in this linear context of cooperative ODEs to conclude that the null solution of $z'(s) = A(\omega \cdot s)^T z(s)$ determines a unique attractor as $s \rightarrow \infty$, which is uniformly asymptotically stable.

Secondly, according to [46] (once more, see also [40]), if the systems $z'(s) = A(\omega \cdot s)^T z(s)$ have no nontrivial bounded solutions, then there is an exponential dichotomy, in this case with full stable subspace. So, assume that there is a bounded solution $z(s, \omega_0, z_0)$ and let us see that it is necessarily identically null. The trick is to build the α -limit set of the pair (ω_0, z_0) , which must contain a minimal set, which as seen before must be the trivial one $\Omega \times \{0\}$. Then, by the uniform asymptotic

stability, given any $\varepsilon > 0$ there exists a $\delta > 0$ such that whenever $\|z_1\| \leq \delta$, $\|z(t, \omega, z_1)\| \leq \varepsilon$ for any $t \geq 0$ and any $\omega \in \Omega$. For this $\delta > 0$, by the definition of the α -limit set, there exists a sufficiently large s_0 such that $\|z(-s_0, \omega_0, z_0)\| \leq \delta$, and therefore $\|z(s_0, \omega_0 \cdot (-s_0), z(-s_0, \omega_0, z_0))\| = \|z_0\| \leq \varepsilon$. As this happens for any $\varepsilon > 0$, it must be $z_0 = 0$ and the bounded solution is the trivial one.

Finally, reversing time back, the adjoint systems $y'(t) = -A(\omega \cdot t)^T y(t)$ have an exponential dichotomy with null stable subspace. By Proposition 1.71 in [23] this implies that the initial systems $y'(t) = A(\omega \cdot t) y(t)$ have an exponential dichotomy with full stable subspace, as we wanted to see. \square

In the next result we prove that, even if the initial nonlinear system is not cooperative, persistence for the nonlinear systems (6.2) is equivalent to persistence of the linearized systems along the null solution,

$$z'_i(t) = -d_i(\omega \cdot t) z_i(t) + \sum_{j=1}^n a_{ij}(\omega \cdot t) z_j(t) + \beta_i(\omega \cdot t) z_i(t - \tau_i), \quad t \geq 0, \quad (6.4)$$

for $i = 1, \dots, n$, for each $\omega \in \Omega$. Note that these linearized systems are cooperative thanks to conditions (a3) and (a4). Although the Banach space X here is the product space $C([- \tau_1, 0]) \times \dots \times C([- \tau_n, 0])$, after going through the proofs we can affirm that the results on uniform persistence and strict persistence at 0 stated in the last section for cooperative systems are still valid. The reader is referred once more to [48] for the results of comparison of solutions used in this delay equations setting.

Theorem 6.2. *Let us consider a nonlinear Nicholson system with delay (6.1) with assumptions (a1)-(a5). The following statements are equivalent:*

- (i) *The induced nonlinear semiflow is uniformly persistent in the interior of the positive cone (resp. strictly persistent at 0 in the positive cone).*
- (ii) *The linearized semiflow along 0 is uniformly persistent in the interior of the positive cone (resp. strictly persistent at 0 in the positive cone).*

Proof. To see (i) \Rightarrow (ii) just note that in the positive cone, the nonlinear term in system (6.2) is bounded above by the corresponding linearized term at 0, and systems (6.4), for $\omega \in \Omega$, are cooperative. Then, by a standard comparison argument, a persistence property in the nonlinear case forces the same kind of persistence behaviour in the linear case.

For the converse (ii) \Rightarrow (i), let us assume that the linearized semiflow along 0 has a persistence property. In this case the idea is to build a new family of nonlinear systems which are cooperative, for which the null map is a solution and the linearized systems along the null map are just given by (6.4), and besides, the solutions of the new family keep below the solutions of (6.2) from some time on, so that a comparison can be made.

More precisely, take the constant $r > 0$ given in Theorem 6.1 and assume without loss of generality that $r > 1$. It is easy to check that there exists a unique $0 < \rho < 1$ such that $\rho e^{-\rho} = r e^{-r}$. Then, take $\varepsilon > 0$ such that $\rho - \varepsilon > 0$ and build a map $\varphi : [0, \infty) \rightarrow [0, \infty)$ of class \mathcal{C}^1 , nondecreasing and such that:

$$\varphi(y) = \begin{cases} y e^{-y} & \text{if } y \in [0, \rho - \varepsilon], \\ r e^{-r} & \text{if } y \in [\rho + \varepsilon, \infty), \end{cases}$$

and besides, $\varphi(y) \leq y e^{-y}$ for $y \in [\rho - \varepsilon, \rho + \varepsilon]$. At this point, consider the family of cooperative systems given for each $\omega \in \Omega$ by

$$y'_i(t) = -d_i(\omega \cdot t) y_i(t) + \sum_{j=1}^n a_{ij}(\omega \cdot t) y_j(t) + \beta_i(\omega \cdot t) \varphi(y_i(t - \tau_i)), \quad (6.5)$$

for $i = 1, \dots, n$, where the coefficients are just those of (6.2). The solutions of this family generate a monotone skew-product semiflow on $\Omega \times X$ and once more $K = \Omega \times \{0\}$ is a trivial minimal set. Besides, the linearized equations along the null solution are still (6.4). Therefore, Theorem 5.4 says that this semiflow inherits the same persistence property as the one assumed in (ii) for the linearized semiflow.

To finish, for each $\omega \in \Omega$ and each initial map $x \geq 0$, by Theorem 6.1 there exists a time $t_1 = t_1(\omega, x) > 0$ such that the vectorial solution $y(t, \omega, x)$ of (6.2) satisfies $0 \leq y_i(t, \omega, x) \leq r$ for any $t \geq t_1$ and any $i = 1, \dots, n$. Consequently, taking $\tau_0 = \max\{\tau_1, \dots, \tau_n\}$, we can solve systems (6.2) and (6.5) for $\omega \cdot (t_1 + \tau_0)$ with initial map $u(t_1 + \tau_0, \omega, x)$ and once more a standard argument of comparison of solutions says that the solution of the cooperative system (6.5) lies below the solution $y(t, \omega \cdot (t_1 + \tau_0), u(t_1 + \tau_0, \omega, x)) = y(t + t_1 + \tau_0, \omega, x)$ of (6.2) for any $t \geq 0$. Therefore, the persistent behaviour of the solution of system (6.5) forces the same persistent behaviour in the solution of the Nicholson nonlinear and noncooperative system. The proof is finished. \square

A combination of Theorems 5.3 and 5.4 and the previous result leads to the following theorem, which can be stated without proof. We just remark three facts. First, recall that in the almost periodic case the principal spectrum of a precise linear system with a continuous separation is just given by the corresponding upper Lyapunov exponent. Second, that in this case the matrix $\bar{A} + \bar{B}$ defined in Theorem 5.3 reduces to \bar{A} , as the delays only appear in the diagonal terms of the linearized systems (6.4). Finally, note that the upper Lyapunov exponents do depend on the delays.

Theorem 6.3. *Let us consider the Nicholson system with delay (6.1) under assumptions (a1)-(a5), and consider the semiflow τ induced on $\Omega \times C_+([- \tau_1, 0]) \times \dots \times C_+([- \tau_n, 0])$ by the solutions of the family of equations over the hull (6.2) for which $K = \Omega \times \{0\}$ is a minimal set with a trivial flow extension. For each $\omega \in \Omega$ consider the linearized system along the null solution (6.4) and assume without loss of generality that the matrix $\bar{A} = [\bar{a}_{ij}]$ defined as*

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

has the block lower triangular structure (4.3) with irreducible diagonal blocks \bar{A}_{j_j} of dimension n_j for $j = 1, \dots, k$ ($n_1 + \dots + n_k = n$). To simplify the notation, arrange the set of delays by blocks by denoting $\{\tau_1, \dots, \tau_n\} = \{\tau_1^1, \dots, \tau_{n_1}^1, \dots, \tau_1^k, \dots, \tau_{n_k}^k\}$. For each $j = 1, \dots, k$ let L_j be the linear skew-product semiflow induced on the product space $\Omega \times C([- \tau_1^j, 0]) \times \dots \times C([- \tau_{n_j}^j, 0])$ by the solutions of the n_j -dimensional systems corresponding to the j th diagonal block of (6.4),

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

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}_{j_j} . 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 $K^j = \Omega \times \{0\} \subset \Omega \times C([- \tau_1^j, 0]) \times \dots \times C([- \tau_{n_j}^j, 0])$.

If $k = 1$, i.e., if the matrix \bar{A} is irreducible, let $I = J = \{1\}$. Else, let

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

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

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

- (i) τ is uniformly persistent in the interior of the positive cone if and only if $\lambda_j > 0$ for any $j \in I$.
- (ii) τ is strictly persistent at 0 in the positive cone if and only if $\lambda_j > 0$ for any $j \in J$.

Under some additional conditions on the coefficients of the initial system (6.1), one can talk of strict persistence instead of strict persistence at 0, in this delay setting. We just need to strengthen condition (a4) into (a4)' as follows:

$$(a4)' \quad \tilde{\beta}_i(t) \geq \beta_0 > 0 \text{ for any } t \in \mathbb{R} \text{ and any } i.$$

The result is the following.

Proposition 6.4. *Let us consider the nonlinear system with delay (6.1) under assumptions (a1)-(a3), (a4)' and (a5). Then, the properties of strict persistence at 0 and strict persistence in the positive cone are equivalent.*

Proof. Obviously, s-persistence always implies s_0 -persistence. Conversely, assume that s_0 -persistence holds, and let us take $\omega_0 \in \Omega$ and $x > 0$ with $x(0) = 0$. This means that there is a component i such that $x_i > 0$ and, in turn, this means that necessarily for some $s_1 \in (-\tau_i, 0)$, $x_i(s_1) > 0$. At this point, it suffices to find a positive $t_1 > 0$ such that the solution $y(t, \omega_0, x)$ of (6.2) for ω_0 satisfies $y_i(t_1, \omega_0, x) > 0$, as then we can apply s_0 -persistence to $(\omega_0 \cdot t_1, u(t_1, \omega_0, x))$ with $u(t_1, \omega_0, x)(0) = y(t_1, \omega_0, x) > 0$, and combine it with the cocycle property (2.2) to obtain s-persistence in the trajectory of (ω_0, x) .

Recall that by (a4)', $\beta_i(\omega) \geq \beta_0 > 0$ for any $\omega \in \Omega$. If $y_i(t_1, \omega_0, x) > 0$ for some $t_1 \in (0, s_1 + \tau_i]$, we are done. If not, that is, if $y_i(t, \omega_0, x) = 0$ for every $t \in (0, s_1 + \tau_i]$, then $y_i'(s_1 + \tau_i, \omega_0, x) \geq \beta_{i1}(\omega_0 \cdot (s_1 + \tau_i)) x_i(s_1) e^{-x_i(s_1)} > 0$, and therefore there exists a $t_1 > s_1 + \tau_i$ such that $y_i(t_1, \omega_0, x) > 0$, as wanted. The proof is finished. \square

REFERENCES

- [1] H. AMANN, Fixed point equations and nonlinear eigenvalue problems in ordered Banach spaces, *SIAM Rev.* **18** (1976), 620–709.
- [2] D.F. ANDERSON, Global asymptotic stability for a class of nonlinear chemical equations, *SIAM J. Appl. Math.* **68** (5) (2008), 1464–1476.
- [3] N. BONNEUIL, The mathematics of maintenance and acquisition, *Ecosystem Ecology Research Trends*, 153–175, Nova Science Publisher, New York, 2008.
- [4] G.J. BUTLER AND G.S.K. WOLKOWICZ, A mathematical model of the chemostat with a general class of functions describing nutrient uptake, *SIAM J. Appl. Math.* **45** (1) (1985), 138–151.
- [5] J.A. CALZADA, R. OBAYA, A.M. SANZ, Continuous separation for monotone skew-product semiflows: From theoretical to numerical results, *Discrete Contin. Dyn. Syst. Series B* **20** (3) (2015), 915–944.

- [6] R.S. CANTRELL, C. COSNER, *Spatial Ecology via Reaction-Diffusion Equations*, Wiley, 2003.
- [7] G. CRACIUN, F. NAZAROV, C. PANTEA, Persistence and permanence of mass-action and power-law dynamical systems, *SIAM J. Appl. Math.* **73** (1) (2013), 305–329.
- [8] S.N. CHOW, H. LEIVA, Dynamical spectrum for time dependent linear systems in Banach spaces, *Japan J. Indust. Appl. Math.* **11** (1994), 379–415.
- [9] S.N. CHOW, H. LEIVA, Existence and roughness of the exponential dichotomy for skew-product semiflow in Banach spaces, *J. Differential Equations* **120** (1995), 429–477.
- [10] R. ELLIS, *Lectures on Topological Dynamics*, Benjamin, New York, 1969.
- [11] T. FARIA, Asymptotic behaviour for a class of delayed cooperative models with patch structure, *Discrete Contin. Dyn. Syst. Series B* **18** (6) (2013), 1567–1579.
- [12] T. FARIA, G. RÖST, Persistence, permanence and global stability for an n-dimensional Nicholson system, *J. Dynamics Differential Equations* **26** (2014), 723–744.
- [13] M. FIEDLER, *Special Matrices and Their Applications in Numerical Mathematics*, Dover Publications, Inc., Mineola, New York, 2008.
- [14] A.M. FINK, *Almost Periodic Differential Equations*, Lecture Notes in Math. **377**, Springer-Verlag, Berlin, 1974.
- [15] H.I. FREEDMAN, S. RUAN, Uniform persistence in functional differential equations, *J. Differential Equations* **115** (1995), 173–192.
- [16] B.M. GARAY, J. HOFBAUER, Robust permanence for ecological differential equations, min-max, and discretizations, *SIAM J. Math. Anal.* **34** (5) (2003), 1007–1039.
- [17] W.S.C. GURNEY, S.P. BLYTHE, R.M. NISBET, Nicholson’s blowflies revisited, *Nature* **287** (1980), 17–21.
- [18] J.K. HALE, S.M. VERDUYN LUNEL, *Introduction to Functional Differential Equations*, Applied Mathematical Sciences **99**, Springer-Verlag, Berlin, Heidelberg, New York, 1993.
- [19] J.K. HALE AND P. WALTMAN, Persistence in infinite-dimensional systems, *SIAM J. Math. Anal.* **20** (2) (1989), 388–395.
- [20] G. HETZER, W. SHEN, Uniform persistence, coexistence, and extinction in almost periodic/nonautonomous competition diffusion systems, *SIAM J. Math. Anal.* **34** (1) (2002), 204–227.
- [21] W.M. HIRSCH, H.L. SMITH, X.-Q. ZHAO, Chain transitivity, attractivity, and strong repellers for semidynamical systems, *J. Dynamics Differential Equations* **13** (1) (2001), 107–131.
- [22] J. HOFBAUER, K. SIGMUND, *Evolutionary Games and Population Dynamics*, Cambridge University Press, 1998.
- [23] R. JOHNSON, R. OBAYA, S. NOVO, C. NÚÑEZ, R. FABBRI, *Nonautonomous Linear Hamiltonian Systems: Oscillation, Spectral Theory and Control*, Development in Mathematics, Springer-Verlag, 2016.
- [24] R. JOHNSON, K.J. PALMER, G.R. SELL, Ergodic properties of linear dynamical systems, *SIAM J. Math. Anal.* **13** (1987), 1–33.
- [25] M.D. JOHNSTON, C. PANTEA, P. DONNELL, A computational approach to persistence, permanence, and endotacticity of biochemical reaction systems, *J. Math. Biol.* **72** (2016), 467–498.
- [26] J.A. LANGA, J.C. ROBINSON, A. RODRÍGUEZ-BERNAL, A. SUÁREZ, Permanence and asymptotically stable complete trajectories for nonautonomous Lotka-Volterra models with diffusion, *SIAM J. Math. Anal.* **40** (2009), no. 6, 2179–2216.
- [27] X. LIU, J. MENG, The positive almost periodic solution for Nicholson-type delay systems with linear harvesting term, *Appl. Math. Model.* **36** (2012), 3289–3298.
- [28] P. MAGAL, X.-Q. ZHAO, Global attractors and steady states for uniformly persistent dynamical systems, *SIAM J. Math. Anal.* **37** (1) (2005), 251–275.
- [29] J. MIERCZYŃSKI, W. SHEN, Lyapunov exponents and asymptotic dynamics in random Kolmogorov models, *J. Evol. Equ.* **4** (2004), 371–390.
- [30] J. MIERCZYŃSKI, W. SHEN, Persistence in forward nonautonomous competitive systems of parabolic equations, *J. Dynamics Differential Equations* **23** (2011), no. 3, 551–571.
- [31] J. MIERCZYŃSKI, W. SHEN, X.-Q. ZHAO, Uniform persistence for nonautonomous and random parabolic Kolmogorov systems, *J. Differential Equations* **204** (2004), 471–510.
- [32] A.J. NICHOLSON, An outline of the dynamics of animal populations, *Austral. J. Zool.* **2** (1954), 9–65.
- [33] S. NOVO, C. NÚÑEZ, R. OBAYA, Almost automorphic and almost periodic dynamics for quasimonotone non-autonomous functional differential equations, *J. Dynamics Differential Equations* **17** (3) (2005), 589–619.

- [34] S. NOVO, R. OBAYA, Non-autonomous functional differential equations and applications. *Stability and Bifurcation for non-autonomous differential equations*, 185–264, Lecture Notes in Math. **2065**, Springer-Verlag, Berlin, Heidelberg, 2013.
- [35] S. NOVO, R. OBAYA, A.M. SANZ, Topological dynamics for monotone skew-product semiflows with applications, *J. Dynamics Differential Equations* **25** (4) (2013), 1201–1231.
- [36] S. NOVO, R. OBAYA, A.M. SANZ, Uniform persistence and upper Lyapunov exponents for monotone skew-product semiflows, *Nonlinearity* **26** (2013), 1–32.
- [37] C. NÚÑEZ, R. OBAYA, A.M. SANZ, Minimal sets in monotone and sublinear skew-product semiflows II: Two-dimensional systems of differential equations, *J. Differential Equations* **248** (2010), 1899–1925.
- [38] C. NÚÑEZ, R. OBAYA, A.M. SANZ, Minimal sets in monotone and concave skew-product semiflows I: A general theory, *J. Differential Equations* **252** (10) (2012), 5492–5517.
- [39] P. POLÁČIK, I. TEREŠČÁK, Exponential separation and invariant bundles for maps in ordered Banach spaces with applications to parabolic equations, *J. Dynamics Differential Equations* **5** No. 2 (1993), 279–303.
- [40] R.J. SACKER, G.R. SELL, Existence of dichotomies and invariant splittings for linear differential systems I, *J. Differential Equations* **15** (1974), 429–458.
- [41] R.J. SACKER, G.R. SELL, A spectral theory for linear differential systems, *J. Differential Equations* **27** (1978), 320–358.
- [42] R.J. SACKER, G.R. SELL, Dichotomies for linear evolutionary equations in Banach spaces, *J. Differential Equations* **113** (1994), 17–67.
- [43] P.L. SALCEANU, H.L. SMITH, Lyapunov exponents and persistence in discrete dynamical systems, *Discrete Contin. Dyn. Syst.* **12** No. 1 (2009), 187–203.
- [44] S.J. SCHREIBER, Criteria for C^r robust permanence, *J. Differential Equations* **162** (2000), 400–426.
- [45] S.J. SCHREIBER, Permanence of weakly coupled vector fields, *SIAM J. Math. Anal.* **33** (5) (2002), 1048–1057.
- [46] J. SELGRADE, Isolated invariant sets for flows on vector bundles, *Trans. Amer. Math. Soc.* **203** (1975), 359–390.
- [47] W. SHEN, Y. YI, Almost Automorphic and Almost Periodic Dynamics in Skew-Product Semiflows, *Mem. Amer. Math. Soc.* **647**, Amer. Math. Soc., Providence 1998.
- [48] H.L. SMITH, *Monotone Dynamical Systems. An Introduction to the Theory of Competitive and Cooperative Systems*, Amer. Math. Soc., Providence, 1995.
- [49] H.L. SMITH, H.R. THIEME, *Dynamical Systems and Population Persistence*, Graduate Studies in Mathematics, **118**. Amer. Math. Soc., Providence, 2011.
- [50] Y. TAKEUCHI, *Global Dynamical Properties of Lotka-Volterra Systems*, World Scientific, 1996.
- [51] H.R. THIEME, Uniform weak implies uniform strong persistence for non-autonomous semiflows, *Proc. Amer. Math. Soc.* **127** (1999), 2395–2403.
- [52] H.R. THIEME, Uniform persistence and permanence for non-autonomous semiflows in population biology, *Math. Biosci.* **166** (2000), 173–201.
- [53] L. WANG, Almost periodic solution for Nicholson’s blowflies model with patch structure and linear harvesting terms, *Appl. Math. Model.* **37** (2013), 2153–2165.
- [54] W. WANG, X.-Q. ZHAO, An age-structured epidemic model in a patchy environment, *SIAM J. Appl. Math.* **65** (5) (2005), 1597–1614.
- [55] Y. YI, On almost automorphic oscillations, *Difference and Differential Equations. Proceedings of the 7th ICDEA*, Fields Institute Communications **42**, 75–99. Amer. Math. Soc., Providence, 2004.

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